

Density, Demography,
& Mating Success
of
Kirtland's Warblers
in Managed & Natural
Habitats

DENSITY, DEMOGRAPHY, AND MATING SUCCESS

OF KIRTLAND'S WARBLERS IN
MANAGED AND NATURAL HABITATS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of the Ohio State University

By

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* * * * *

The Ohio State University

1994

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ACKNOWLEDGEMENTS

I would like to thank my adviser, Jonathan Bart, for his guidance and support. He has a way of teaching that reassures me, promoting my strengths and never making me feel inferior for my weaknesses. Thanks for reminding me that I was here to learn! I am also grateful for the excellent advice from committee members, Theodore Bookhout, Thomas Grubb, and Patricia Parker. Special thanks to Patty for listening to me and understanding more than simply my academic experience at graduate school. John Harder and Brian Smith provided valuable comments during the final exam and on the draft document. I would also like to thank Diane Rano for her expert administrative assistance and friendship.

I would like to thank the fine, hard-working, assistants that joined me in the field: Mark Korducki, Michael Quinn, Laurel Moore, Lori Munro, Susan Patlyek, Robb Deihl, and Katy Weakland. In addition, Duncan Evered, David Cimprich, Rebecca Fitzmaurice, Mark Roemer, Jason Murphy, and Robert Curtis joined me as short term assistants. Thanks to all for a job well done! Special thanks to Lori and Susie who have become great friends and respected colleagues.

I am indebted to Corinna Theiss for her instruction on the field techniques for ecosystem typing. Many of the techniques were incorporated into the habitat analysis. I am grateful to Brad Andres who provided useful feedback on my experimental design for vegetation sampling. I thank Pam Frost for her helpful instruction on the use of the digitizer and GIS system, and Matthias Hofschien for his assistance and independent work on the GIS portion of the female distribution data. I am grateful to John Probst who graciously shared his habitat management data. Mike Fligner provided valuable insight to the statistical analysis of the habitat management data. I also thank Randy Dettmers for his advice on manuscripts, abstracts, computer software, and life. Thanks to all my fellow graduate student "commiserates" (just kidding!) for years of fruitful academic discussions and social fun!

I would like to thank the Kirtland's Warbler Recovery Team for their strong support of my research project and their belief in me as a scientist. Cameron Kepler, Paul Sykes, and John Probst were wonderful collaborators as we all cooperated to investigate our own piece of the warbler's puzzle. I was very fortunate to work closely with Cam and Paul, and they both remain great friends and role models to me. Special thanks to Sylvia Taylor and Jerry Weinrich who continue to be valuable sources of information and endless encouragement.

I am forever grateful for the love and support of my family and friends. They have always been my refuge from doubt, where the theme was "you can make it happen." My father plays a special role in my commitment to education, and I want to thank him for a lifetime of encouragement. Most of all, I wish to express a special thanks to Dean, who has patiently waited, constantly encouraged, and tenderly loved me through this project. I am deeply grateful for his partnership.

This project was funded by U. S. Fish and Wildlife Service, National Biological Survey, U.S. Forest Service, and Michigan Department of Natural Resources. The Michigan Department of Natural Resources provided facilities during the summer field seasons. The Ohio State University and the Ohio Cooperative Fish and Wildlife Research Unit provided facilities and support for the duration of the study.

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FIELDS OF STUDY

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TABLE OF CONTENTS

	PAGE
ACKNOWLEDGEMENTS	iii
VITA	vi
LIST OF TABLES	x
LIST OF FIGURES	xiv
INTRODUCTION	1
Purpose	8
Organization	9
Literature Cited	9
 CHAPTER	
I. DENSITY OF KIRTLAND'S WARBLER MALES IN MANAGED AND NATURAL HABITATS	11
Methods	14
Results	19
Discussion	25
Literature Cited	27
II. PHYSICAL DESCRIPTION OF BREEDING HABITAT OCCUPIED BY KIRTLAND'S WARBLERS	29
Methods	31
Results	36
Discussion	56
Literature Cited	67
III. MATING SUCCESS AND REPRODUCTIVE SUCCESS OF MALE KIRTLAND'S WARBLERS	69
Methods	73
Results	80
Discussion	94
Literature Cited	97

IV. DISTRIBUTION OF NEST SITES	100
Methods	106
Results	110
Discussion	114
Literature Cited	117
CONCLUSIONS	120
Summary of Major Findings	120
Management Recommendations	123
Suggestions For Future Research	124
LIST OF REFERENCES	128
APPENDICES	133
A. List of plant species found during habitat analysis	134
B. Abbreviations for male identification and study site identification	137

LIST OF TABLES

TABLE

PAGE

1.	Analysis of variance for mean density deviation (an index of male Kirtland's warbler density) as calculated from a general linear model investigating the influence of habitat type (C2), stand size (C3), complex size (C4), distance to the center of the range (C5), distance to nearest occupied stand (C6), and distance to nearest source stand (C7)	22
2.	Adjusted means for mean density deviation from general linear model	23
3.	Characteristics of trees around randomly selected points in 10 plantations and 11 wildfire sites	37
4.	Characteristics of openings around randomly selected points in 10 plantations and 11 wildfire sites	38
5.	Mean proportion of randomly selected points that were in each topographic position in 10 plantations and 11 wildfire sites	41
6.	Physiographic characteristics of randomly selected points in 10 plantations and 11 wildfire sites	42
7.	Mean number of plant species and mean index of cover (range = 0 - 5) for woody debris, bare ground, and plant species in 1-m X 1-m plots centered at randomly selected points in 10 plantations and 11 wildfire sites ...	43
8.	Relative frequency of plants in 1-m X 1-m plots centered at randomly selected points in 10 plantations and 11 wildfire sites ...	44
9.	Relative frequency of soil characteristics at randomly selected points in 10 plantations and 11 wildfire sites	46

10.	Mean soil characteristics at randomly selected points in 10 plantations and 11 wildfire sites	47
11.	Characteristics of trees around randomly selected points and nests in 20 sites	48
12.	Characteristics of openings around randomly selected points and nests in 20 sites	49
13.	Mean proportion of randomly selected points and nests that were in each topographic position in 20 sites	52
14.	Physiographic characteristics of randomly selected points and nests in 20 sites	53
15.	Mean number of plant species and mean index of cover (range = 0 -5) for woody debris, bare ground and plant species in 1-m X 1-m plots centered at randomly selected points and nests in 20 sites	54
16.	Relative frequency of plants in 1-m X 1-m plots centered at randomly selected points and nests from 20 sites	55
17.	Relative frequency of soil characteristics at randomly selected points and nests in 20 sites	57
18.	Mean soil characteristics at randomly selected points and nests in 20 sites	58
19.	Preliminary data on the proportion of territorial males in two wildfire areas and one plantation that are unmated (U), monogamous (M), and polygynous (P)	81
20.	Proportion of territorial males in 11 wildfire areas and nine plantations that are unmated (U), monogamous (M), and polygynous (P)	82
21.	Number of polyterritorial males / number of males in each mating status (unmated, monogamous, and polygynous) in each habitat category (wildfire and plantation)	83

22.	Number of sites studied each year and mean proportion of males that were unmated or polygynous in both habitat categories (wildfire = W and plantation = P) each year, as habitat became less limiting	83
23.	Mating status of males seen in more than one year (unmated = U, monogamous = M, polygynous = P)	84
24.	Mean clutch size (number of eggs per nest) for each site and the grand means for each habitat category	86
25.	Mean number of young fledged per nest attempt for each site and the grand means for each habitat category	87
26.	Number of nests and core areas and the proportion depredated (a failed nest was assumed to be due to predation), for each site and the grand means for each habitat category	89
27.	Density of Kirtland's warblers per 40 acres per year over the life of a stand in each habitat type	90
28.	Density of young per 40 acres per year over the life of a plantation that must be produced to maintain the population from year to year, showing the effect of variation in adult and juvenile survivorship	92
29.	Density of young per 40 acres per year over the life of a wildfire stand that must be produced to maintain the population from year to year, showing the effect of variation in adult and juvenile survivorship	93
30.	Observed standard deviation of nearest neighbor distances (v_i), the expected standard deviation of nearest neighbor distances under the null hypothesis of random nest placement (\bar{n}_i), and the "observed - expected" difference (s_i), for $i = 1$ to 15 Kirtland's warbler study sites..	113

31.	Complete list of plant species found in 1-m X 1-m plots during a study of the characteristics of Kirtland's warbler habitat	135
32.	Abbreviations for colored bands placed on Kirtland's warblers for unique identification	138
33.	Abbreviations, counties, and legal descriptions (T = township, R = range, S = section) for wildfire sites	139
34.	Abbreviations, counties, and legal descriptions (T = township, R = range, S = section) for plantations	140

LIST OF FIGURES

FIGURE		PAGE
1.	Former nesting range of the Kirtland's warbler in Michigan (Byelich et al. 1976)...	2
2.	Population trend of Kirtland's warblers in Michigan from annual census of singing males (Weinrich pers. comm.)	3
3.	Nesting range of the Kirtland's warbler in Michigan during 1975 (Byelich et al. 1976)	5
4.	Predicted density of male Kirtland's warblers per 40 acres over the life of a stand for all stands (curve from 4 th -order polynomial regression)	17
5.	Proportion of habitat available and proportion of habitat occupied by Kirtland's warblers in each habitat type during 1984...	20
6.	Proportion of habitat available and proportion of habitat occupied by Kirtland's warblers in each habitat type during 1989...	21
7.	Predicted density of male Kirtland's warblers per 40 acres over the life of a stand for each habitat type (curves from 4 th -order polynomial regression)	24
8.	Distribution of sizes of openings in plantations (above) and in wildfire sites (below)	39
9.	Distribution of sizes of openings around nests (above) and random points (below)....	50
10.	Distribution of study sites in Michigan....	75

11. Frequency of nests in five zones defined by distance from the edge of territories (see text) and expected frequency under the hypothesis that nests are placed randomly within territories 111

INTRODUCTION

The Kirtland's warbler (Dendroica kirtlandii) is an endangered species that breeds in the jack pine (Pinus banksiana)/ Grayling sand communities in the north central part of the Lower Peninsula of Michigan (Figure 1). The warbler winters in the Bahama Island Archipelago where the habitat does not appear to be limiting (Kepler and Sykes, unpub. data). The specific habitat requirements of this species on the breeding grounds may contribute to its endangered status (Mayfield 1983). It breeds only in large tracts (>32 ha) of young jack pine, 5-24 years old, which are 1.5-6.0 m in height (Byelich et al. 1976). Historically, these pine barrens were maintained in early succession by large wildfires that occurred approximately every 40 years (Mayfield 1993). Due to modern fire suppression techniques and land use changes, wildfires became smaller and less frequent, and Kirtland's warbler habitat was lost. In addition, the invasion of the brown-headed cowbird (Molothrus ater) contributed significantly to the decline of this species, especially between 1961 and 1971 (Mayfield 1972), as shown in Figure 2. Walkinshaw (1983) reported that the average number of fledglings per

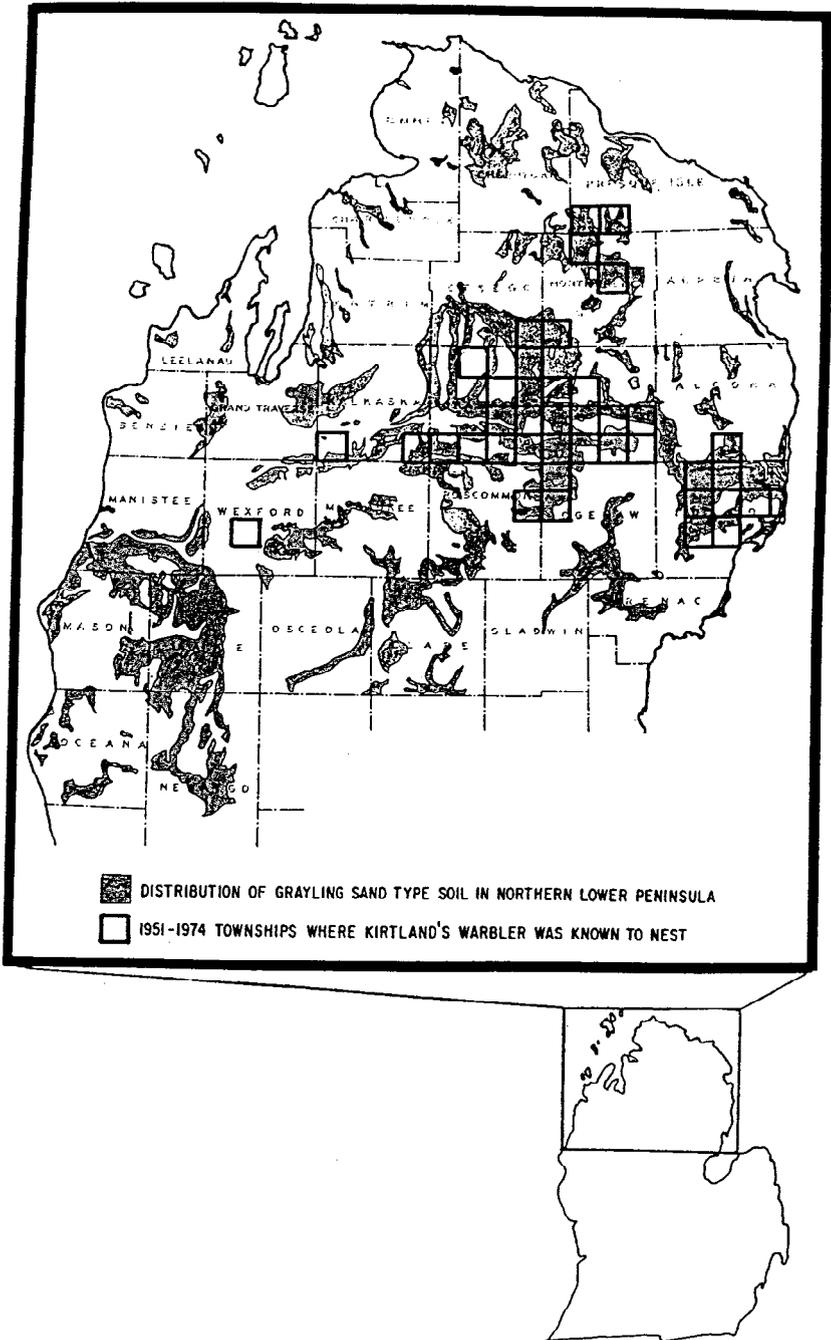


Figure 1. Former nesting range of the Kirtland's warbler in Michigan (Byelich et al. 1976).

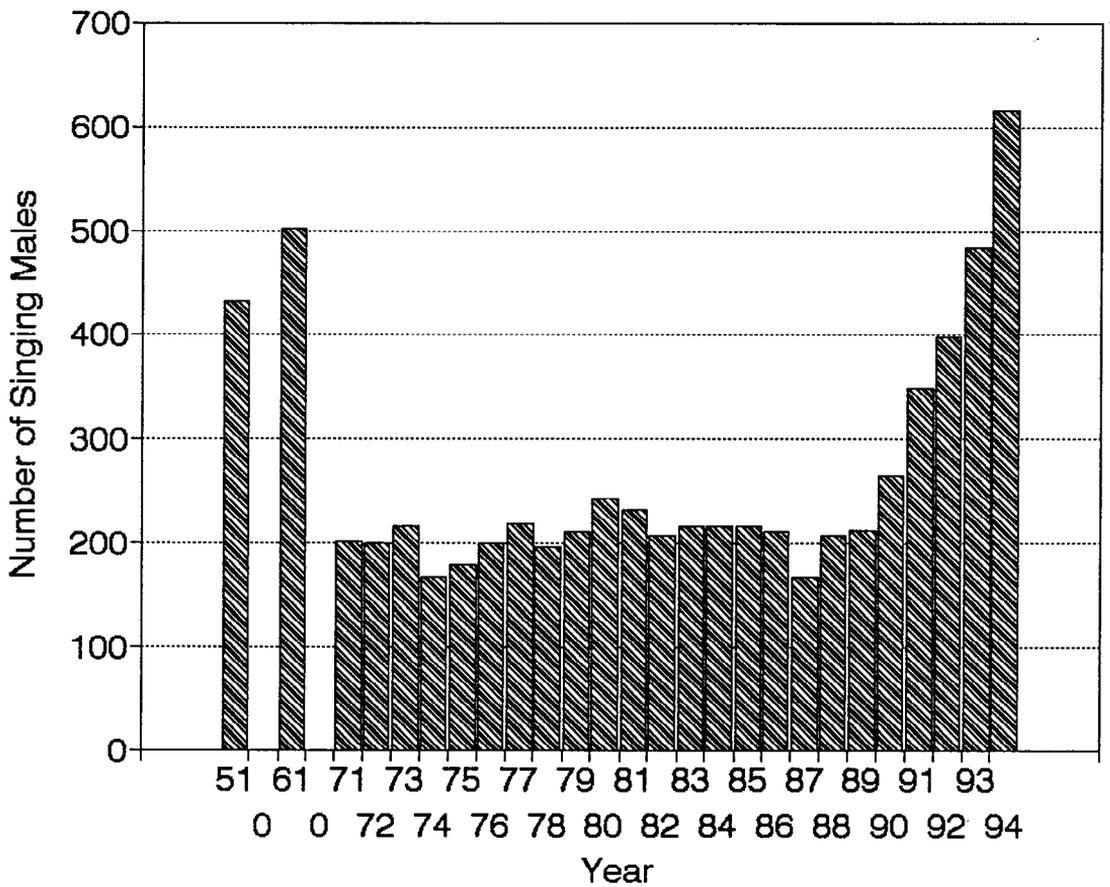


Figure 2. Population trend of Kirtland's warbler in Michigan from annual census of singing males (Weinrich pers. comm.).

pair was less than one during the years of cowbird parasitism.

In response, land managers committed tracts of public land to early-succession jack pine management (Mayfield 1963, Radtke and Byelich 1963), and cowbirds were trapped and removed (Shake and Mattsson 1975). The warbler population stabilized (Figure 2). In the initial years of cowbird control (1972-1977), Walkinshaw (1983) showed that the average number of fledglings per pair rebounded to more than two. Since 1971 the population has fluctuated closely around 200 singing males (Weinrich 1989), until 1990 when the population increased in response to increased availability of suitable habitat (Probst and Weinrich 1993). The current breeding range of this ground-nesting warbler is limited to approximately 7 counties (Figure 3). During the 1993 census of the Kirtland's warbler, 485 singing males were counted (Weinrich pers. comm.).

The Kirtland's Warbler Recovery Plan recommended the management of jack pine plantations to provide suitable habitat for the endangered species (Byelich et al. 1976). The habitat management plan was designed to replicate the natural wildfire habitat, and provide approximately 12,150 ha of suitably-aged habitat each year. Approximately 54,650 ha of land has been designated as critical habitat, to be managed on a 50-year rotation. The warbler plantations are planted with greater tree density than forestry plantations

and the rows of trees are planted in a sine-wave pattern that is reversed every 10 to 15 rows to create openings and thickets at the union of the inverted rows. Each stand is allowed to grow for 50 years to reach a harvestable size for the pulp industry. Implementation of the plan began in 1977, but plantation management did not become well-established until the early 1980's.

Evaluation of the plantations as suitable habitat is critical to the success of the Recovery Plan. The future of the species will depend on managed lands. Wildfires may always occur in the jack pine, but the size and frequency of fires are likely too low to predictably sustain the endangered species. Managed lands must provide an adequate substitute for the natural pine barren ecosystem for Kirtland's warblers, as well as the other plants and animals that co-evolved in that system.

As plantations reach suitable age (5-24 years), they are included in the annual census of singing males. The census provides an initial evaluation of habitat use (Weinrich 1989), but Van Horne (1983) showed that density was not a reliable indicator of habitat quality. He showed that a positive correlation of density with habitat quality cannot always be assumed, and suggested that demographic data was a better indicator of habitat quality. The census does not address the mating status of the males counted. Birds may be present but not mated. Probst and Hayes (1987)

7

studied mating success of Kirtland's warbler males in different habitats, but compared only the number of mated males to unmated males. They assumed polygyny was minimal, and did not report any cases of more than one female per male. At the time it was thought that the species was almost exclusively monogamous (Mayfield 1960, Walkinshaw 1983), with only very rare instances of polygyny (Radabaugh 1972, Walkinshaw 1983). Since polygynous males have more than one female, the extent of occupancy of a site is unclear unless the frequency of polygyny is known. Data on the mated status of males in different habitats in combination with census data provides an accurate evaluation of plantation use by adult warblers compared to use of natural areas.

To extrapolate the quality of managed and natural lands, managers must know the productivity in each habitat type. Pulliam (1988) warned that in regions with more than one habitat type, the population growth in each habitat type should be calculated, because the immigration of surplus individuals from a source habitat type will mask the low productivity of a population in a sink habitat type. The reproductive success of Kirtland's warblers in managed and natural lands must be known to calculate population growth in each habitat type and determine if plantations are sources or sinks.

Purpose

The primary goal of the study was to determine whether plantations were providing suitable habitat for the Kirtland's warbler. Plantations must serve as habitat sources and not habitat sinks. The study was designed as an exploratory, comparative investigation of male density, mating success and reproductive success of Kirtland's warblers in plantations and naturally regenerated areas that resulted from wildfires. Wildfire sites historically provided habitat for the species and served as the guideline for evaluating the plantations. The project was timely because the Mack Lake burn of 1980 (approximately 4,000 ha in Oscoda County, MI) provided a large area of wildfire habitat for the warblers, and the management efforts in the early 1980's provided a large area of plantation habitat that was suitably-aged.

In addition to the important applied issue of plantation evaluation, the project addressed an interesting theoretical issue: the distribution of nest placement by female Kirtland's warblers. Nest distributions, within territories and between territories, were investigated to determine if the patterns were non-random. Males establish territories, and then females choose nest sites. Determining the patterns of nest dispersion was a first step in understanding the potentially conflicting reproductive goals of males and females.

Organization

The study is divided into 3 major parts: I) a landscape scale evaluation of the density of singing, male Kirtland's warblers in all habitat types; II) a local scale evaluation of habitat characteristics, mating success of male warblers, and demography of the species in plantations and wildfire areas; and III) an investigation of the patterns of nest placement by female Kirtland's warblers within and between the territories established by male warblers. Parts I and II address the applied issue of plantation evaluation, using laboratory and field techniques, respectively. Part III is a basic research question that is answered with a combination of laboratory and field data.

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DENSITY OF KIRTLAND'S WARBLER MALES
IN MANAGED AND NATURAL HABITATS

The Kirtland's warbler (Dendroica kirtlandii) breeds in north central Lower Michigan. This endangered species requires large tracts (>32 ha) of jack pine (Pinus banksiana) barrens which occur on Grayling sand soils. The warblers use the jack pine barrens during the early-succession stage, when the pines are approximately five to 24 years old, or 1.5 to 6.0 m tall (Byelich et al. 1976).

Historically, the pine barrens were maintained in early succession by large, frequent wildfires (Mayfield 1993). Due to modern fire suppression technology and land-use changes during the 1950's and 1960's, the size and frequency of wildfires declined, and Kirtland's warbler habitat was lost (Byelich et al. 1976). The population index of warblers declined from 502 singing males in 1961 to 201 singing males in 1971 (Mayfield 1972), and by 1975 the distribution of the species had collapsed to the center of the breeding range (Byelich et al. 1976).

The Kirtland's Warbler Recovery Team identified approximately 54,600 ha of critical habitat, selecting sites

throughout the former range of the species with Grayling sand and low site indices that were dominated by jack pine. They recommended the management of jack pine plantations on a 50-year rotation to provide habitat for the species (Byelich et al. 1976). The initial implementation of the Recovery Plan included clear-cuts to place stands in rotation, but not all harvested areas were planted. Some stands were left to naturally regenerate while others were planted. Habitat creation was usually accomplished in management complexes, where new stands were placed near recently established stands. In addition, habitat was created by several wildfires during the mid-1970's.

As a result of management efforts and natural fires, three distinct habitat types developed within the Kirtland's warbler breeding range. Wildfire stands are naturally burned and naturally regenerated. Harvested stands are cut (without burning) and naturally regenerated. Plantations are cut and anthropogenically regenerated.

The Recovery Plan also recommends that management efforts be evaluated to determine if they are providing suitable habitat (Byelich et al. 1976). The annual singing male census provides data regarding the abundance and distribution of warblers throughout the breeding range (Weinrich 1989). In combination with the historical data regarding management efforts, the census data provide a landscape-scale, preliminary evaluation of management

efforts. Probst and Weinrich (1993) used this approach to determine the relative area, and density of warblers, in each habitat type. They inferred the relative suitability of each habitat type in the past, and predicted the carrying capacity of each habitat type in the future. They found that harvested sites were under-utilized, and wildfire sites were used at greater than random utilization. Utilization of plantations was not different than random.

The occupancy and density of warblers in any stand may be influenced by stand size and biogeography (Fritz 1979, Probst 1988), and so these variables must be evaluated simultaneously with habitat type to determine their relative importance. Mayfield (1960) and Walkinshaw (1983) suggested that stands must be at least 32 ha to attract warblers, and stands that were at least 81 ha were more likely to attract the endangered species. Mayfield (1993) recognized that the combined area of all early-succession stands within a management complex was important, suggesting that the vast openness of the management complex replicated the large areas of historical wildfires. In addition to the size of stands or complexes, biogeography may be very important. Because the distribution of warblers collapsed to the center of the range, the distance to the center of the range may influence the occupancy of a stand. Also, the distance to another occupied stand or the distance to a source stand (as defined by Pulliam 1988) may influence the occupancy of a

stand. The metapopulation dynamics of the endangered species are poorly understood, and so predictions regarding the influence of biogeographic variables are difficult.

The objectives of this investigation were 1) to compare the area of suitably-aged habitat to the area of occupied habitat in each habitat type during 1984 when habitat was extremely limited and during 1989 when habitat was not limited, 2) to estimate the density of Kirtland's warblers in each habitat type, and 3) to explore the influence of habitat type, stand size, complex size, distance to the center of the range, distance to the nearest occupied stand, and distance to the nearest source stand on the warbler density of a stand. The density of male warblers will be used to determine the relative suitability of habitat types, and thus provide a preliminary evaluation of the habitat management for the endangered species. The density of male warblers in plantations and wildfire sites will also be used in Chapter 4 (in combination with mating success and demography) as the basis for comparison of population growth potential among the habitat types to determine if plantations are habitat sources or sinks.

Methods

The results of the annual singing male census were available at the Houghton Lake Heights Wildlife Research Station (Michigan Department of Natural Resources), and

habitat management data were collected from the files of land managers at the Michigan Department of Natural Resources and the U. S. Forest Service. The wildfire data were collected from burn reports at the same agencies, and most of the data for harvested stands were contributed by J. Probst. A stand was defined as a parcel of land at least 20 ha in size with a given harvest method and a given regeneration method that was initiated in a given year. A complex was defined as a group of stands that were spatially adjacent with tree ages that were separated by no more than 20 years. The locations of singing males were then compared to the boundaries of each stand to determine the number of birds in a stand for each year from 1980 to 1992. The size of the stand and the size of the complex to which the stand belonged were recorded, as were X and Y coordinates for the legal section of each stand.

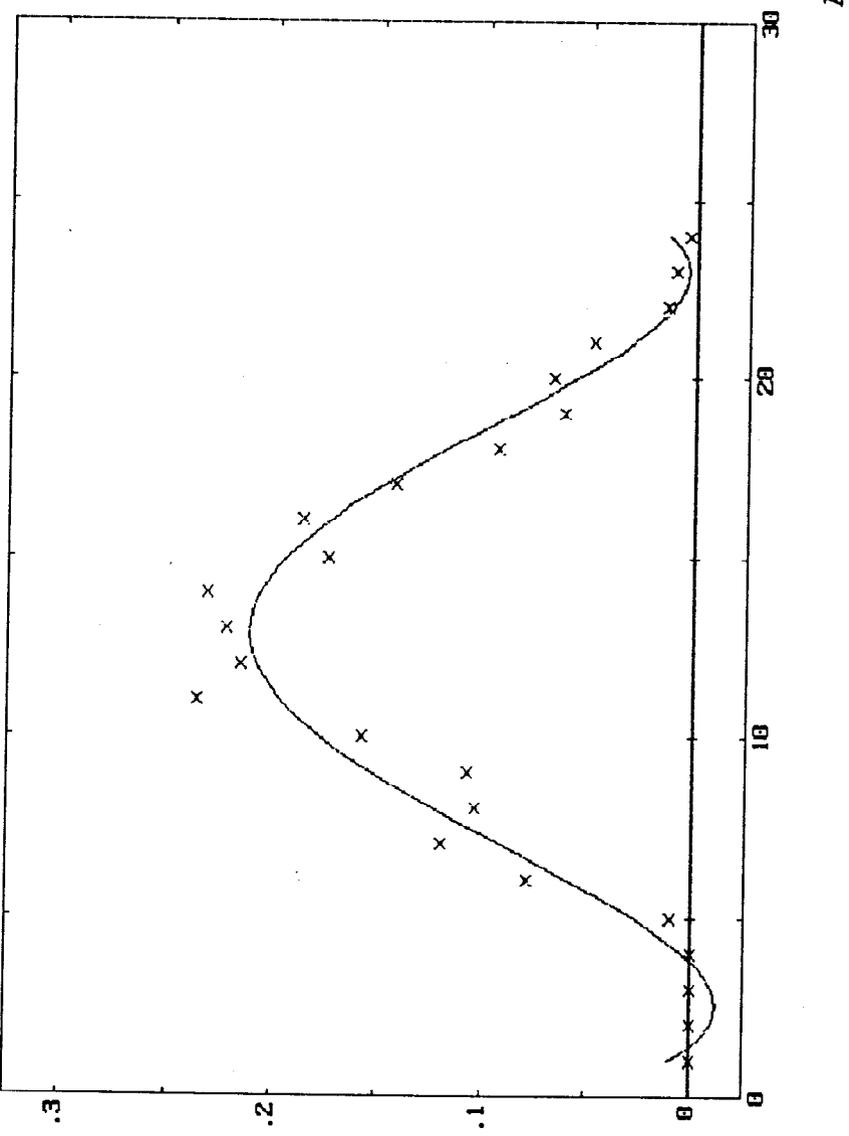
All analyses were conducted on 265 stands that were at least 20 ha in size and ranged from five to 24 years old. Forty-two stands were categorized as wildfire, and 120 stands were plantations, and 103 stands were harvested.

For 1984 and 1989, the total area of suitably-aged habitat was summed, and the proportion in each habitat type was calculated. The same was done for occupied habitat. For each year, the proportion of suitably-aged area in each habitat type was compared to the proportion of occupied area in each habitat type with Chi-square tests.

The density of male warblers was calculated for the life of a stand. The age of a stand was determined by subtracting the regeneration year from the census year. Most stands were censused at more than one age during the period from 1980 to 1992. At each age, i , let the density per 40 acres of the j^{th} stand, y_{ij} , = the number of singing males counted on the census/the number of acres of the stand * 40. The mean density per 40 acres of all stands at age i is \bar{y}_i , and $\bar{y}_i = \sum y_{ij} / n$ where $j = 1$ to n , and $n_1 \neq n_2 \dots \neq n_i$. A scatterplot of \bar{y}_i 's against age (abscissa) is then constructed, and a curve is fitted to the data by fourth-order polynomial regression (Figure 4). The value of the curve at age i , \hat{Y}_i , is the predicted density of male warblers per 40 acres of a stand at age i . The area under the curve is the predicted density of males per 40 acres over the life of the stand, $\sum \hat{Y}_i$, and the predicted density of birds per 40 acres per year over the life of the stand = $\sum \hat{Y}_i / m$ where $i = 1$ to m , and m is oldest age of any stand occupied by warblers.

The same procedure was used to independently generate curves for each habitat type. The predicted density of birds per 40 acres per year over the life of the stand was calculated for each habitat type as a description of singing male density in each habitat type.

Density of males per 40 acres



X = ALL STANDS

Figure 4. Predicted density of male Kirtland's warblers per 40 acres over the life of a stand for all stands (curve from 4th-order polynomial regression)

A general linear model was constructed to determine the influence of habitat type, area, and biogeography on the density of singing males. The model required a single description of density for each stand as the dependent variable. Because most stands had male density values for more than one age, and the density of warblers was expected to change as the age of a stand changed (Probst 1988), a single description of male density for each stand was developed with the effect of age removed. This was accomplished by calculating the mean density deviation for each stand from the curve of predicted densities (for all stands) described above. Recall that \hat{Y}_i = the predicted density of male warblers per 40 acres at age i , and for each stand let y_i = the observed male density per 40 acres at age i . For each stand, the mean density deviation is: $\sum y_i - \hat{Y}_i / m$ where $i = 1$ to m , and m is the number of ages that a stand was censused.

A general linear model was constructed with the mean density deviation for each stand as the dependent variable, habitat type as a categorical predictor variable, and five other continuous predictor variables as follows: size of the stand, size of the complex to which the stand belonged, distance from the stand to the center of the range, distance from the stand to the nearest occupied stand, and distance from the stand to the nearest source stand, such that:

$$y_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + \beta_4 x_{4i} + \beta_5 x_{5i} + \beta_6 x_{6i}$$

The assumptions of the model were tested and were not violated.

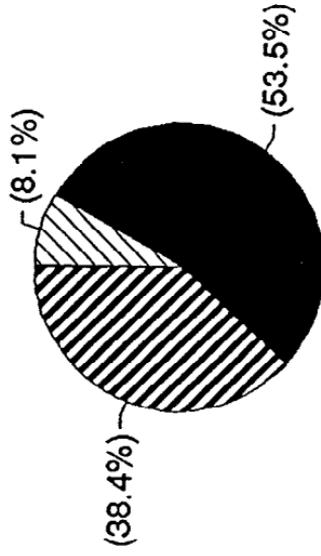
Results

In 1984, the proportion of area occupied by the warblers in each habitat type (Figure 5) was significantly different than expected if the warblers were distributed at random in the suitably-aged area ($\chi^2 = 4155$, $p < 0.001$). Harvested stands were used less than expected, and wildfire stands were used more than expected. In 1989, the proportion of area occupied by the warblers in each habitat type (Figure 6) was significantly different than expected if the warblers were randomly distributed in the suitably-aged area ($\chi^2 = 5108$, $p < 0.001$). The same trends were observed in 1989 as described for 1984. Harvested stands were not occupied at all in 1989 when habitat was increasingly available.

The general linear model explained 17.6% (R^2) of the variation in mean density deviation (Table 1). Habitat type significantly influenced the mean density deviation ($F = 12.28$, $p < 0.0009$), as did distance to the center of the range ($F = 3.91$, $p = 0.049$). The size of the complex had a nearly significant influence on mean density deviation ($F = 2.69$, $p = 0.102$). Habitat type (H) influenced the mean density deviation independently from the distance to the center of the range (D) and complex size (C) (coefficients of interaction terms, H*D and H*C, are not significantly

1984

AVAILABLE ACREAGE



PLANTATION



WILDFIRE



HARVESTED

1984

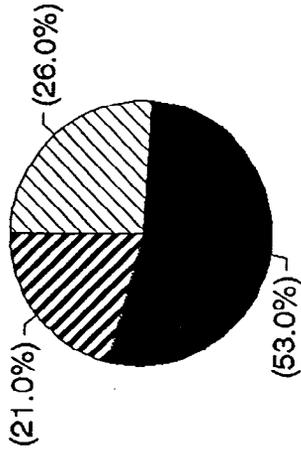
OCCUPIED ACREAGE



Figure 5. Proportion of habitat available and proportion of habitat occupied by Kirtland's warblers in each habitat type during 1984.

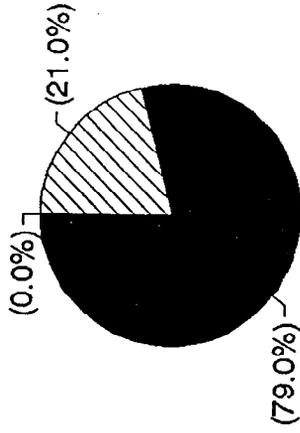
1989

AVAILABLE ACREAGE



1989

OCCUPIED ACREAGE



PLANTATION



WILDFIRE



HARVESTED

Figure 6. Proportion of habitat available and proportion of habitat occupied by Kirtland's warblers in each habitat type during 1989.

Table 1. Analysis of variance for mean density deviation (an index of male Kirtland's warbler density) as calculated from a general linear model investigating the influence of habitat type (C2), stand size (C3), complex size (C4), distance from a stand to the center of the range (C5), distance from a stand to the nearest occupied stand (C6), and distance from a stand to the nearest source stand (C7).

Source	DF	Seq SS	Adj SS	Adj MS	F	P
C2	2	1.30517	1.21296	0.60648	12.28	0.000
C3	1	0.06489	0.00554	0.00554	0.11	0.738
C4	1	0.25664	0.13271	0.13271	2.69	0.102
C5	1	0.57967	0.19323	0.19323	3.91	0.049
C6	1	0.00513	0.00039	0.00039	0.01	0.930
C7	1	0.02960	0.02960	0.02960	0.60	0.440
Error	257	12.69123	12.69123	0.04938		
Total	264	14.93233				

Term	Coeff	SD	t-value	P
Constant	0.09134	0.03296	2.77	0.006
C3	0.000008	0.000022	0.34	0.738
C4	0.000010	0.000006	1.64	0.102
C5	-0.003289	0.001663	-1.98	0.049
C6	0.000570	0.006438	0.09	0.930
C7	-0.002842	0.003671	-0.77	0.440

different from 0, $p = 0.15$ and $p = 0.43$, respectively).

Habitat type has the strongest influence on the mean density deviation. The adjusted means of the mean density deviations for each habitat type (Table 2) are significantly different from each other (Bonferroni t-tests, $p < 0.001$ for all three comparisons).

The predicted density of male Kirtland's warblers per 40 acres over the life of a stand for each habitat type (Figure 7) shows that plantations and wildfire stands have much higher densities than harvested stands from ages 5 to 24. The predicted density of male warblers per 40 acres per year over the life of a stand is 0.21 in plantations, 0.19 in wildfire stands, and 0.02 in harvested stands.

Table 2. Adjusted means for the mean density deviation from the general linear model.

Habitat Type	Mean	SD
Plantation	0.05225	0.02115
Wildfire	0.09385	0.03707
Harvested	-0.07905	0.02249

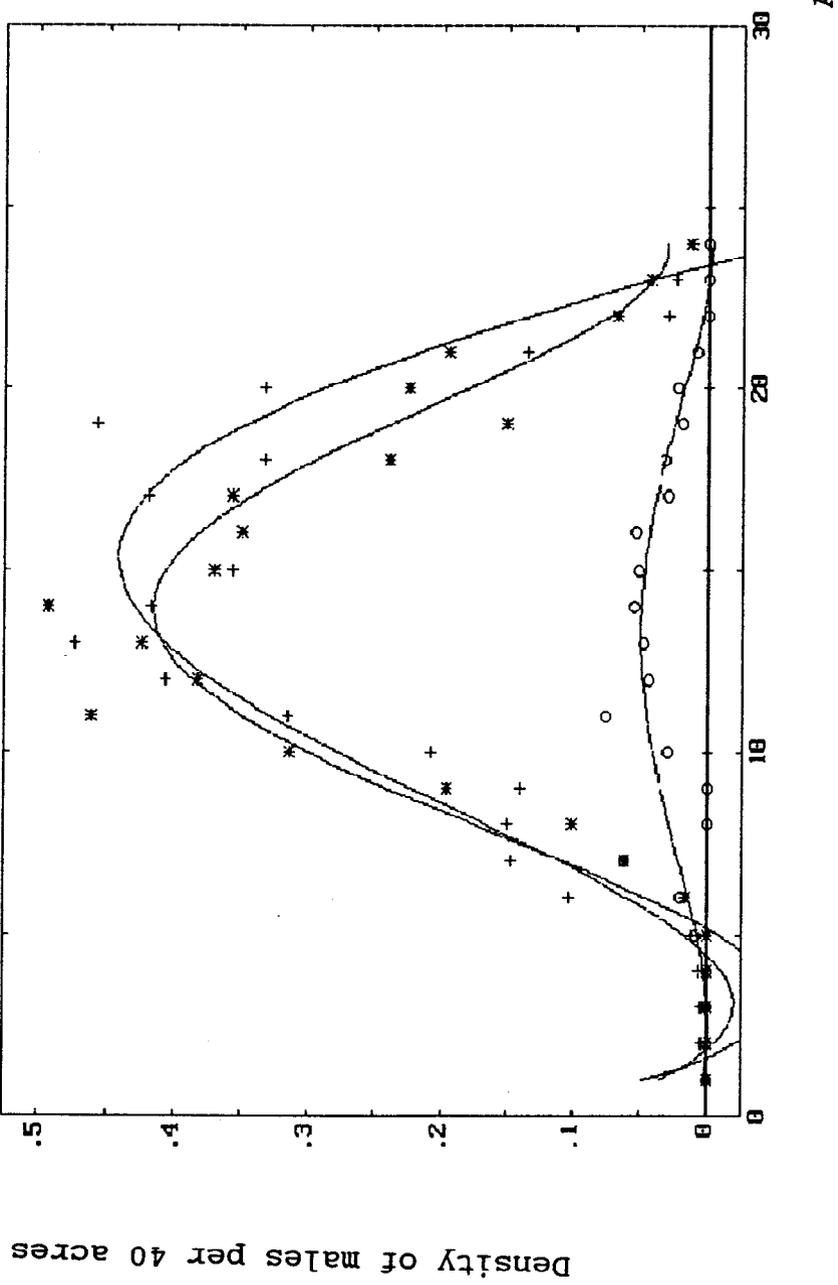


Figure 7. Predicted density of male Kirtland's warblers per 40 acres over the life of a stand for each habitat type (curves from 4th-order polynomial regression)

Discussion

The relative suitability of habitat types was revealed by the comparison of the proportion of suitably-aged area in each habitat type and the proportion of occupied area in each habitat type. If warblers settled in the habitat according to an ideal-free distribution (Fretwell and Lucas 1969), then wildfire stands were the most suitable and harvested stands were the least suitable. These findings support the conclusions of Probst and Weinrich (1993). Because harvested stands were not occupied at all in 1989 when habitat was available, it appears that harvested stands were marginal habitat and were used in 1984 due to severe habitat limitation.

According to the general linear model, habitat type is the most influential predictor of mean density deviation. The adjusted means for each habitat type corroborate the conclusions of the above analysis. Wildfire stands have the largest, positive mean density deviation, and plantations also have a positive mean density deviation. Harvested stands, on average, had mean densities that fell below the predicted density of warblers per 40 acres over the life of a stand.

The general linear model also showed that the distance from a stand to the center of the range was a significant predictor of mean density deviation. As that distance increased, the mean density deviation became negative.

Stands on the periphery of the range had mean densities that were, on average, below the predicted densities. Critical habitat was selected by the Kirtland's Warbler Recovery Team from throughout the former range of the species, but the range of the species had collapsed to its center by the time management efforts were established. The data suggest that the average distance to stands in the periphery of the range is farther than the average dispersal distance of the species.

The general linear model also showed that complex size was a nearly significant predictor of mean density deviation. As complex size increased, the mean density deviation was more positive. This trend concurs with Mayfield's (1993) postulation that large complexes of managed areas attract warblers. He supposed that large complexes replicate the vast habitat areas of historical wildfires.

The predicted density per 40 acres per year over the life of a stand provided a preliminary description of habitat use in each habitat type, and thus provided a measure of the success of management efforts for the endangered species. Plantations provided suitable habitat, but harvested stands did not. Wildfire stands were the natural habitat and, as expected, provided suitable habitat. Density of warblers per 40 acres per year over the life of a stand was only a preliminary measure of habitat suitability,

because it can be a misleading indicator of habitat quality. Van Horne (1983) showed that density was not always positively correlated with survival and productivity. The density data will be combined with mating success and demography data in Chapter 4 to provide a complete evaluation of habitat quality. By investigating density, mating success, and demography in each habitat type, the population growth potential of the endangered species can be estimated for each habitat type. For a species that occupied multiple habitat types in a region, Pulliam (1988) warned that the population dynamics in each habitat type must be understood because some habitats may be sources while others are sinks.

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PHYSICAL DESCRIPTION OF BREEDING HABITAT
OCCUPIED BY KIRTLAND'S WARBLERS

Kirtland's warblers (Dendroica kirtlandii) historically bred in large tracts (> 32 ha) of young jack pine (Pinus banksiana) from five to 24 years old, maintained in early succession by wildfires (Byelich et al. 1976). Wildfires were common in the pine barren ecosystem that stretched across central Michigan in association with Grayling sand (Mayfield 1993). However, as land use changes modified the landscape and fire suppression technology improved, the frequency and size of wildfires decreased, and Kirtland's warbler habitat was lost. To compensate for the loss of habitat, land managers designed jack pine plantations in an attempt to replicate naturally regenerated wildfire sites. The pines were planted more densely than for timber production in sine-wave rows that were inverted every 10-15 rows, creating openings and dense patches of pines (Byelich et al. 1976). According to the Kirtland's Warbler Recovery Plan (Byelich et al. 1976), 1,133 ha of jack pine plantation should be planted every year to provide habitat for this

endangered species. Plantation management became well-established by 1980, providing suitably-aged habitat by the late 1980's. Some plantations were not occupied, and others were occupied at lower densities than wildfire sites (Probst and Weinrich 1993, Chapter 2). The reasons for lower plantation success were unknown. Were plantations providing habitat physically similar to the natural wildfire habitat? What were the habitat characteristics used by the warblers that should be provided by plantations?

Several studies of the Kirtland's warbler described habitat characteristics of occupied stands (Mayfield 1960, Smith 1979, Walkinshaw 1983), but they did not compare habitat characteristics between habitat types, nor did they compare habitat characteristics used by warblers to those available. Anderson and Storer (1976) related habitat characteristics to reproductive success, concentrating their analysis on the effects of habitat variables on cowbird (Molothrus ater) parasitism. They provided an evaluation of a wildfire site, and described the habitat characteristics of nests. Probst and Weinrich (1993) compared habitat types on a landscape scale, and thus did not compare local habitat features between habitat types or habitat characteristics used by warblers versus those available. Zou et al. (1992) compared habitat characteristics of nest sites and randomly selected sites at both landscape and local scales, by

defining ecosystem types at sample points. Their analysis was restricted to one wildfire site.

By comparing the habitat characteristics of plantations and wildfire sites, land managers could evaluate how well plantations replicated the physical features of wildfire sites. By comparing the habitat characteristics used by warblers to the characteristics available to warblers, land managers could better understand the habitat requirements of the species. The habitat characteristics that were important to the warblers should be provided by plantations. The objectives of this study were 1) to describe and compare the vegetation, soil, and physiographic characteristics of plantations and wildfire sites to determine which wildfire features were adequately replicated in plantations, and 2) to describe and compare the vegetation, soil, and physiographic characteristics of nests and randomly selected points throughout each stand to determine which habitat features were used by Kirtland's warblers.

Methods

The data were collected and analyzed under a multiple stage sampling design. Sites were randomly selected in each habitat category and treated as the primary sampling unit. Points and nests were randomly selected within sites as the secondary sampling units. Randomly selected points

represent available habitat characteristics of a site, and nest sites represent the characteristics used by warblers in the site. Measurements of all response variables were taken at randomly selected points and nests, and means were calculated for each site.

For the comparison of habitat characteristics between habitat types, let \bar{s}_i = the mean of some habitat characteristic at the i^{th} wildfire site, and \bar{t}_j is the mean of that habitat characteristic at the j^{th} plantation site. Point estimates were made for habitat characteristics by calculating the grand means from the site means for each habitat category, \bar{s} and \bar{t} , and the standard errors of the grand means were calculated at the primary sampling unit to make inferences about the habitat categories. Comparisons between habitat categories were made with unequal variance t-tests with Satterthwaite's approximation for degrees of freedom, at $\alpha = 0.05$.

For the comparison of habitat characteristics used by warblers to those available to warblers, let \bar{t}_i = the mean of territory points and \bar{n}_i = the mean of randomly selected points at the i^{th} site. Comparisons of habitat characteristics between nests and randomly selected points were made with paired t-tests at $\alpha = 0.05$, such that $d_i = \bar{n}_i - \bar{t}_i$ for each site, and under the null hypothesis of no difference between habitat characteristics of nests and randomly selected points, the expected value of $\bar{d} = 0$.

Many comparisons for each assemblage of habitat characteristics, such as vegetation, soils, or physiography, were made with univariate statistics. The multiple comparison issue was minimized by first combining wildfire and plantation data to evaluate the difference between nests and randomly selected points for all sites, and then for significant differences only, searching for conflicting trends between the habitat categories. This reduced the number of comparisons for each assemblage of habitat characteristics. The significance level was used in combination with the percent difference (actual paired difference/random (or wildfire) value * 100) between point categories to determine statistical and biological significance.

Data were collected during July and August of 1990-1992 from 10 plantations and 11 wildfire sites distributed throughout the breeding range. Within each site, 50 points were randomly selected, except in one wildfire site that was more than twice as large as any other site where 100 sample points were randomly selected. The number of nests that were studied varied from two to 14 in different sites.

At each point and nest, the nearest tree in each cardinal direction was selected, and the following variables were measured: height of the tree, height of the first live branch, diameter of the tree at 10 cm, distance to the tree, and the tree species. The tree species was used to

calculate the proportion of trees that were deciduous. Statistical inferences for these response variables are restricted to the population of trees around points in a site, rather than trees in a site.

Distance from the point to the tree was used to calculate two derived variables, the area of open space around all points and the proportion of points situated in an opening, as defined by a rule that was tested against an independent, subjective assessment of openings on the aerial photos. As a subsample of the random points (10 points from each site), each point was observed on aerial photographs and categorized as an opening or non-opening based on the estimated, minimum size of an opening for nest placement. Various rules regarding the four point-to-tree distances were tested, using computer programming to determine the number of points correctly identified as in an opening. The most reliable criterion for designation of a point in an opening was that the point-to-tree distance was at least 300 cm in at least 2 directions. This rule was 85% reliable for the 210 random points that were compared to the aerial photos.

Of the points that landed in openings, the relative frequency of various opening sizes was calculated and graphed for each habitat category and for each point type. The distributions were compared with Kolmogorov-Smirnov tests at $\alpha = 0.05$.

Physiographic characteristics were also described at each sample point. Each point was assigned to a topographic position category: plateau (flat terrain), upper slope, midslope, footslope, knoll, or depression. Also, the aspect and slope were recorded. The slope was defined as the angle between horizontal and the surface of the land, and was estimated at each point. The aspect was defined as the azimuth of the slope, and was later categorized into 6 aspect categories: none (i.e. no slope), all (slopes in all directions as for knolls or depressions), north, east, south, and west.

A 1-m X 1-m plot was established at all the nests and 20% (randomly chosen) of the randomly selected points with the point or nest as the center. The relative frequency and percent cover of ground vegetation were measured in each plot. The percent covers of bare ground and woody debris were also measured. Percent cover was recorded as an index that ranged from 0 to 5 (0 = absent, 1 = 1-10%, 2 = 11-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-100%). The relative frequency of plant species was also calculated. A mean relative frequency was then determined for each habitat category.

A soil core was collected to a minimum depth of 150 cm at the center of each plot. Soil features below this depth have minimal effect on the surface ecosystem (Barnes, pers. comm.). Soil features measured included: soil textures and

depths; depth of organic layer; presence and depth of clay bands, clay mottling, gravel, and cobble; and the cumulative width of clay bands, clay mottling, and gravel. Means were calculated only from cores that had the soil feature. In addition, the relative frequency of the soil characteristics was calculated by dividing the number of cores with the characteristic by the total number of cores.

Tree density was sampled at 15 new, randomly selected points (30 at the large wildfire site). The density of tree stems for seven plantations was measured from aerial photographs, in 35-m diameter circular plots with the point as the center. For three plantations and all wildfire sites, individual trees were not distinguishable on the photos, and trees were counted on the ground in 15-m diameter circular plots.

Results

Comparison of plantations and wildfire sites

Density of jack pines is the only tree characteristic that differed significantly between habitat types (Table 3). Jack pine density is much greater in wildfire sites than in plantations.

The data suggest that plantations have fewer open spaces, but the differences are not significant (Table 4). Of the points that land in an opening, the distribution of sizes of openings is shown in Figure 8, and the curves

Table 3. Characteristics of trees around randomly selected points in 10 plantations and 11 wildfire sites.

VARIABLE	WILDFIRE			PLANTATION			DIFFERENCE		
	MEAN	SE		MEAN	SE		ACTUAL	P-VALUE	% ^a
Tree height ^b (cm)	272.6	11.6		250.1	12.3		22.5	0.20	8.4
Height of lowest live branch (cm) ^b	35.1	7.1		22.0	2.5		13.1	0.11	37.0
Tree diameter ^b (cm)	6.3	0.4		7.1	0.5		-0.8	0.23	12.8
% deciduous trees in sample ^b	6.9	0.1		8.6	0.3		-1.7	0.61	24.8
Density of jack pine per ha ^c (X1000)	7.0	1.1		2.0	0.1		5.0	0.001	71.3

^a % = actual difference/wildfire value * 100.

^b Data collected from nearest trees in the four cardinal directions from randomly selected points.

^c Data collected from plots with center at randomly selected points.

Table 4. Characteristics of openings around randomly selected points in 10 plantations and 11 wildfire sites.

VARIABLE	WILDFIRE		PLANTATION			DIFFERENCE	
	MEAN	SE	MEAN	SE	ACTUAL	P-VALUE	% ^a
Prop. of points in opening ^b	0.38	0.06	0.25	0.04	0.13	0.075	34.2
Distance from pt. to tree (cm)	391.8	53.9	300.0	31.3	91.8	0.16	23.4
Area around all points (m ²)	223.3	83.4	21.8	6.8	201.5	0.07	90.2

^a % = actual difference/wildfire value * 100.

^b A point is in an opening if ≥ 2 distances from the point to the nearest tree in four cardinal directions is 300 cm or more.

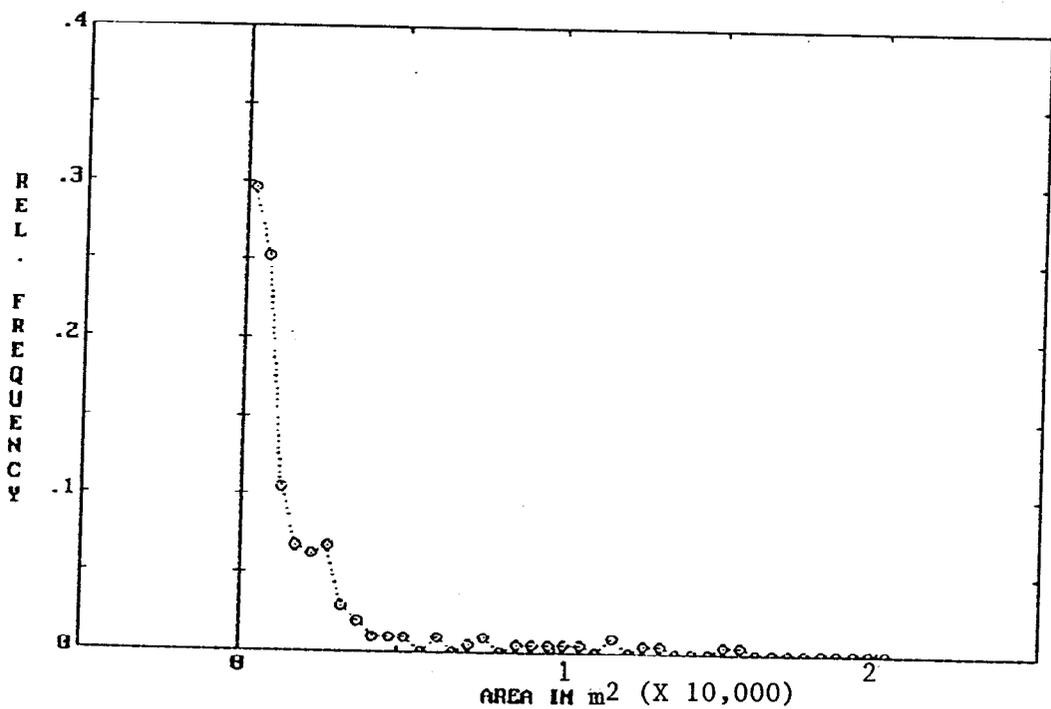
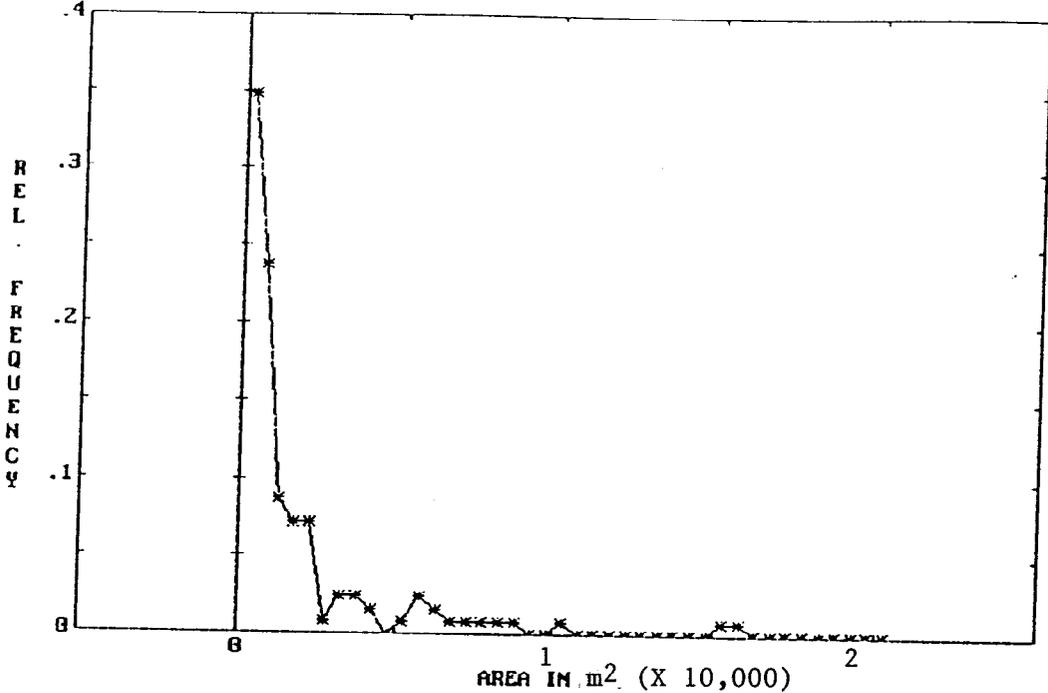


Figure 8. Distribution of sizes of openings in plantations (above) and in wildfire sites (below). Kolmogorov-Smirnov test shows $d = 0.135$, $P = 0.114$ so from the same population.

appear to be from the same population (Kolmogorov-Smirnov test, $p=0.114$).

Measures of topography are not significantly different between plantations and wildfire sites (Table 5). In both habitat categories, the most common topographic category is plateau, indicating an overall flat landscape.

The physiography of plantations is similar to wildfire sites (Table 6). The slope is relatively small in both habitat categories, averaging less than five degrees above or below horizontal. The most common aspect in each habitat category is none, which corresponds to the plateau topography category. Of the points with a slope, the proportion of points in each aspect category is similar.

The percent cover of woody debris is significantly less in plantations than in wildfire sites (Table 7). The 52 plant species found in the jack pine plains are listed in Appendix A. Only nine species were at least nearly significantly different, and only three were strongly significantly different. Jack pine and bearberry (Arctostaphylos Uva-ursi) have smaller indices of cover in plantations than in wildfire sites, and the sedge, Carex pennsylvanica, has a greater index of cover in plantations than in wildfire sites (Table 7). The relative frequencies of jack pine and bearberry are significantly smaller in plantations than in wildfire sites (Table 8). The greater relative frequency and percent cover of jack pine in 1-m X

Table 5. Mean proportion of randomly selected points that were in each topographic position in 10 plantations and 11 wildfire sites.

TOPOGRAPHIC POSITION	WILDFIRE		PLANTATION		DIFFERENCE		
	MEAN	SE	MEAN	SE	ACTUAL	P-VALUE	% ^a
Plateau	0.53	0.11	0.69	0.10	-0.16	0.301	30.2
Upper Slope	0.12	0.05	0.08	0.04	0.04	0.475	33.3
Mid-slope	0.25	0.05	0.14	0.06	0.11	0.175	44.0
Foot Slope	0.02	0.01	0.05	0.03	-0.03	0.361	150.0
Depression	0.04	0.02	0.03	0.03	0.01	0.764	25.0
Knoll	0.03	0.02	0.00	0.00	0.03	---	100.0

^a % = actual difference/wildfire value * 100.

Table 6. Physiographic characteristics of randomly selected points in 10 plantations and 11 wildfire sites. Slope is reported in degrees of the angle above or below horizontal, and aspect is reported as the proportion of points in each aspect category.

VARIABLE	WILDFIRE			PLANTATION			DIFFERENCE		
	MEAN	SE		MEAN	SE		ACTUAL	P-VALUE	% ^a
Slope	4.3	3.4		3.5	2.1		0.8	0.534	18.6
Aspect									
None	0.47	0.08		0.69	0.09		-0.22	0.069	46.8
All	0.02	0.01		0.01	0.01		0.01	0.365	50.0
North	0.14	0.03		0.08	0.03		0.06	0.171	42.8
East	0.10	0.03		0.04	0.02		0.06	0.082	60.0
South	0.14	0.02		0.12	0.03		0.02	0.579	14.3
West	0.13	0.03		0.06	0.02		0.07	0.052	53.8

^a % = actual difference/wildfire value * 100.

Table 7. Mean number of plant species and mean index of cover (range = 0 - 5) for woody debris, bare ground and plant species in 1-m X 1-m plots centered at randomly selected points in 10 plantations and 11 wildfire sites.

VARIABLE	WILDFIRE			PLANTATION			DIFFERENCE		
	MEAN	SE		MEAN	SE		ACTUAL	P-VALUE	% ^a
No. Species	7.94	0.35		6.86	0.43		1.08	0.067	13.6
Woody Debris	1.86	0.06		1.13	0.06		0.73	0.0000	39.2
Bare Ground	1.35	0.04		1.48	0.16		-0.13	0.442	9.6
<u>Pinus banksiana</u>	1.21	0.22		0.31	0.07		0.90	0.002	74.4
<u>Amelanchier sanguinea</u>	0.30	0.10		0.10	0.04		0.20	0.074	66.7
<u>Antennaria neglecta</u>	0.06	0.02		0.02	0.01		0.04	0.092	66.7
<u>Arctostaphylos Uva-ursi</u>	0.48	0.10		0.11	0.05		0.37	0.006	77.1
<u>Melampyrum lineare</u>	0.11	0.03		0.01	0.01		0.10	0.013	90.9
<u>Rubus</u> sp.	0.08	0.03		0.26	0.09		-0.18	0.078	225.0
<u>Vaccinium angustifolium</u>	2.15	0.22		2.01	0.31		0.14	0.018	6.5
<u>Carex pensylvanica</u>	2.19	0.12		2.90	0.09		-0.71	0.0001	32.4
<u>Deschampsia flexuosa</u>	0.47	0.16		0.06	0.02		0.41	0.026	87.2

^a % = actual difference/wildfire value * 100.

Table 8. Relative frequency of plants in 1-m X 1-m plots centered at randomly selected points in 10 plantations and 11 wildfire sites.

PLANT SPECIES	WILDFIRE			PLANTATION			DIFFERENCE	
	MEAN	SE		MEAN	SE	ACTUAL	P-VALUE	% ^a
<u>Pinus banksiana</u>	0.34	0.07		0.15	0.03	0.19	0.006	55.9
<u>Arctostaphylos Uva-ursi</u>	0.32	0.06		0.08	0.03	0.24	0.002	75.0
<u>Melampyrum lineare</u>	0.11	0.03		0.01	0.01	0.10	0.013	90.9
<u>Rubus</u> sp.	0.07	0.03		0.22	0.07	-0.15	0.084	214.3
<u>Amelanchier sanguinea</u>	0.22	0.05		0.10	0.04	0.12	0.090	54.5
<u>Antennaria neglecta</u>	0.06	0.02		0.02	0.01	0.04	0.092	66.7
<u>Deschampsia flexuosa</u>	0.25	0.08		0.05	0.02	0.20	0.037	80.0

^a % = actual difference/wildfire value * 100.

1-m plots in wildfire sites corroborates the greater density of jack pine in 15-m-diameter plots in wildfire sites.

There were no significant differences in soil characteristics between plantations and wildfire sites (Tables 9 and 10). The most common soil texture is medium sand, and gravel is found in the majority of cores, indicating a well-drained soil condition. The low relative frequency of cores with clay banding and the deep average depth of clay banding and mottling are also indicative of dry soil conditions at the surface.

Comparison of nests and randomly selected points

The tree diameter and height of the first live branch are significantly smaller at trees around nests than trees around randomly selected points, but the differences are not very large (Table 11). Density of jack pine is significantly greater at nests than at randomly selected points (Table 11).

The distance from the sample point to a tree and the area of open space around all points is significantly smaller at nests than at randomly selected points (Table 12). Fewer nest sites land in openings (as defined by the rule) than randomly selected points (Table 12). Of points that do land in openings, the distribution of opening sizes is shown in Figure 9. The curves appear to be from the same population (Kolmogorov-Smirnov test, $p=0.227$).

Table 9. Relative frequency of soil characteristics at randomly selected points in 10 plantations and 11 wildfire sites (rel. freq. = # cores with characteristic/ all cores).

SOIL CHARA.	WILDFIRE			PLANTATION			DIFFERENCE		
	MEAN	SE		MEAN	SE		ACTUAL	P-VALUE	% ^a
Clay mottling	0.40	0.07		0.60	0.12		-0.20	0.157	50.0
Clay banding	0.13	0.03		0.12	0.04		0.01	0.851	7.7
Fine sand	0.22	0.07		0.27	0.09		-0.05	0.664	22.7
Coarse sand	0.25	0.05		0.19	0.04		0.06	0.350	24.0
Gravel	0.70	0.06		0.64	0.09		0.06	0.613	8.6
Cobble	0.40	0.08		0.36	0.06		0.04	0.689	10.0
Dominant texture = coarse sand	0.04	0.03		0.00	0.00		0.04	0.408	100.0
Dominant texture = fine sand	0.04	0.03		0.11	0.06		-0.07	0.276	175.0
Dominant texture = medium sand	0.92	0.04		0.88	0.05		0.04	0.500	0.0

^a % = actual difference/wildfire value * 100.

Table 10. Measurements (in cm) of soil characteristics at randomly selected points in 10 plantations and 11 wildfire sites.

SOIL CHARA.	WILDFIRE			PLANTATION			DIFFERENCE	
	MEAN	SE		MEAN	SE	ACTUAL	P-VALUE	% ^a
Depth to AO	8.2	0.6		6.9	0.7	1.3	0.180	15.8
Depth to clay mottling	117.4	4.2		117.0	3.1	0.4	0.937	0.3
Cumulative clay mottling	44.8	3.2		46.5	4.2	-1.7	0.745	3.8
Depth to clay banding	95.4	11.7		111.5	13.4	-16.1	0.387	16.9
Cumulative clay banding	39.1	12.0		14.9	4.7	24.2	0.094	61.9
Depth to fine sand	106.9	10.4		87.4	13.4	19.5	0.277	18.2
Depth to coarse sand	101.9	9.6		124.1	11.2	-22.2	0.155	21.8
Depth to gravel	52.0	4.9		67.4	8.8	-15.4	0.148	29.6
Cumulative gravel	54.8	4.8		45.9	6.4	8.9	0.282	16.2
Depth to cobble	85.3	12.2		95.1	10.1	-9.8	0.546	11.5

^a % = actual difference/wildfire value * 100.

Table 11. Characteristics of trees around randomly selected points and nests in 20 sites

VARIABLE	RANDOM		NEST		PAIRED DIFFERENCE		
	MEAN	SE	MEAN	SE	ACTUAL	SE	P-VALUE % ^a
Tree height ^b (cm)	260.1	8.8	250.0	8.7	10.1	9.4	0.30
Height of lowest live branch (cm) ^b	28.3	4.2	24.6	3.2	3.8	1.7	0.04
Diameter ^b (cm)	6.7	0.3	5.6	0.3	1.1	0.3	0.001
% deciduous trees in sample ^b	6.4	5.6	4.9	4.9	2.2	1.8	0.22
Density of jack pine per ha ^c (X1000)	4.8	0.8	5.8	0.8	-1.0	0.4	0.02

^a % = actual paired difference/random value * 100.

^b Data collected from nearest trees in the four cardinal directions from randomly selected points or nests.

^c Data collected from plots with center at randomly selected points or nests.

Table 12. Characteristics of openings around randomly selected points and nests in 20 sites.

VARIABLE	RANDOM		NEST		PAIRED DIFFERENCE		
	MEAN	SE	MEAN	SE	ACTUAL	SE	P-VALUE % ^a
Prop. of points in opening ^b	0.33	0.04	0.20	0.05	0.13	0.04	0.005 38.4
Distance from pt. to tree (cm)	354.5	33.8	233.0	26.00	121.5	38.8	0.005 34.3
Area around all points (m ²)	149.1	48.3	35.3	79.5	113.8	49.5	0.03 76.3

^a % = actual paired difference/random value * 100.

^b A point is in an opening if ≥ 2 distances from the point to nearest tree in four cardinal directions is 300 cm or more.

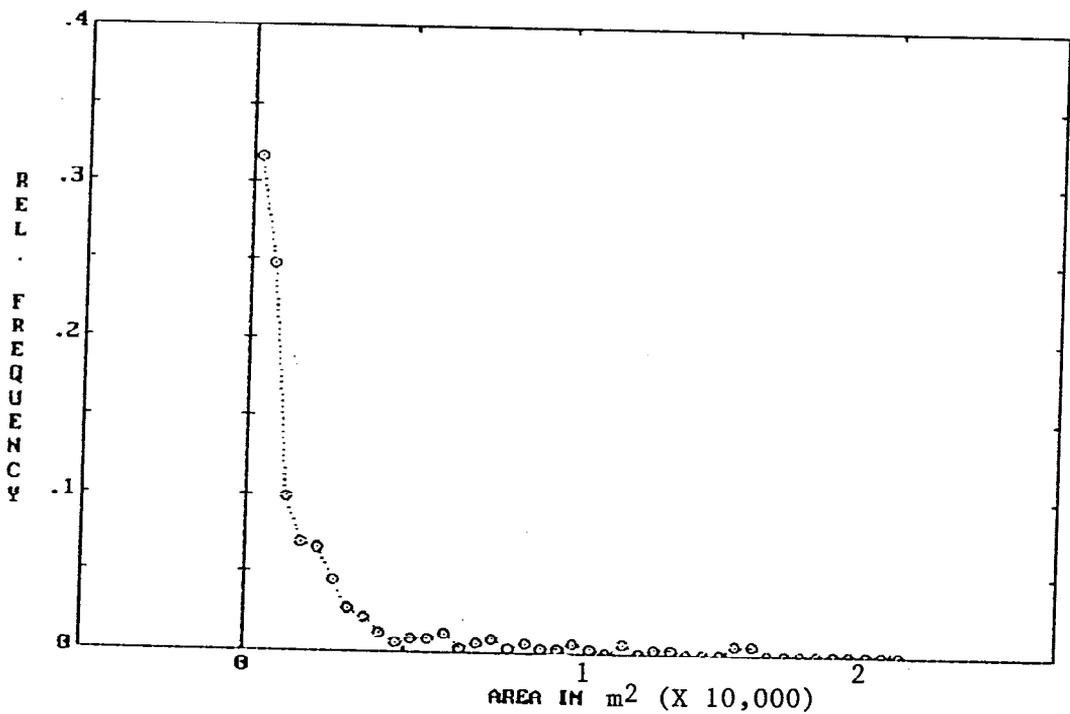
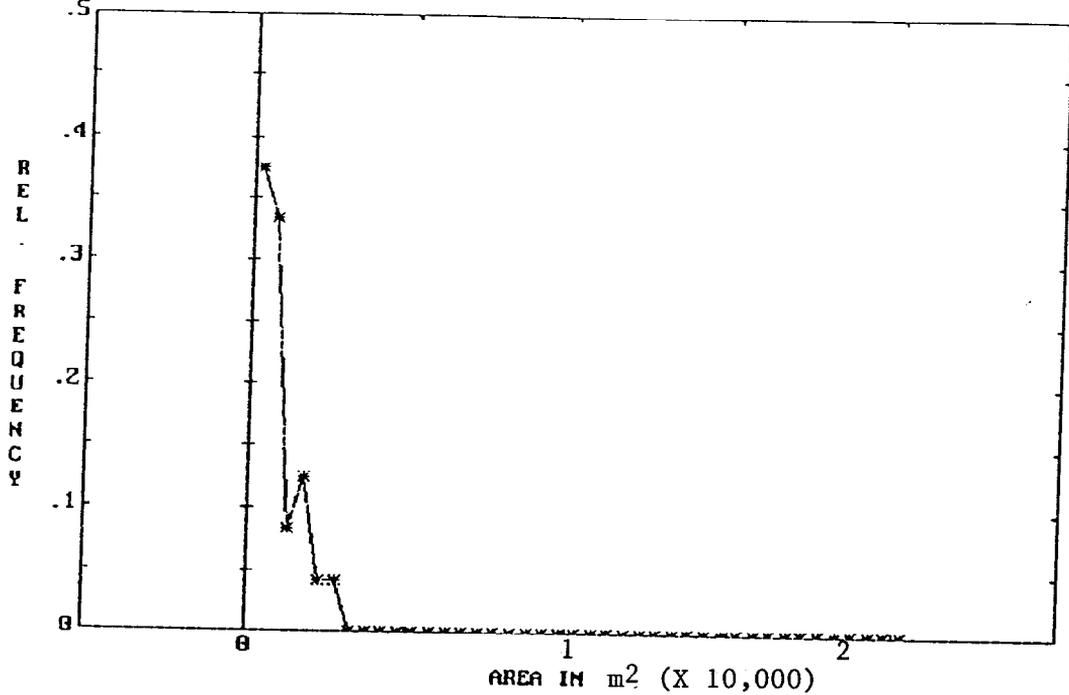


Figure 9. Distribution of sizes of openings around nests (above) and random points (below). Kolmogorov-Smirnov test shows $d = 0.220$, $P = 0.227$ so from the same population.

The proportion of nests in the plateau category is nearly significantly greater than the proportion of randomly selected points, and the proportion of nests in the midslope category is significantly smaller than the proportion of randomly selected points (Table 13). In both nest sites and randomly selected points, the most common topographic category is plateau, indicating an overall flat landscape.

The physiography of nest sites is similar to that of randomly selected points (Table 14). The slope is relatively small in both point categories, averaging less than five degrees above or below horizontal. The most common aspect in each point category is none, which corresponds to the plateau topographic category.

The percent cover of woody debris is significantly less at nests than at randomly selected points, but the difference is not great (Table 15). Seven species were significantly different, and three were strongly significantly different. Jack pine and blueberry (Vaccinium angustifolium) have greater indices of cover at nests than at randomly selected points, and bird's-foot violet (Viola pedata) has a smaller index of cover at nests than at randomly selected points (Table 15). The relative frequency of jack pine is significantly greater at nests than at randomly selected points, and the relative frequency of the violet is smaller at nests than at randomly selected points (Table 16). The greater relative frequency and percent

Table 13. Mean proportion of randomly selected points and nests that were in each topographic position in 20 sites.

TOPOGRAPHIC POSITION	RANDOM		NEST		PAIRED DIFFERENCE			P-VALUE	% ^a
	MEAN	SE	MEAN	SE	ACTUAL	SE			
Plateau	0.59	0.12	0.69	0.07	-0.10	0.05	0.078	16.6	
Upper Slope	0.10	0.02	0.16	0.05	-0.06	0.06	0.333	53.3	
Mid-slope	0.21	0.03	0.10	0.03	0.10	0.04	0.013	50.2	
Foot Slope	0.04	0.02	0.01	0.01	0.03	0.02	0.111	81.8	
Depression	0.04	0.02	0.04	0.03	-0.0003	0.03	0.992	0.7	
Knoll	0.02	0.01	0.00	0.00	0.02	---	---	100.0	

^a % = actual paired difference/random value * 100.

Table 14. Physiographic characteristics of randomly selected points and nests in 20 sites. Slope is reported in degrees of the angle above or below horizontal, and aspect is reported as the proportion of points in each aspect category.

VARIABLE	RANDOM			NEST			PAIRED DIFFERENCE			P-VALUE	% ^a
	MEAN	SE		MEAN	SE		ACTUAL	SE			
Slope	3.6	0.60		3.1	0.70		0.50	0.50		0.371	13.8
Aspect											
None	0.55	0.06		0.56	0.08		0.005	0.05		0.925	0.9
All	0.02	0.005		0.04	0.03		-0.02	0.03		0.386	146.3
North	0.12	0.02		0.17	0.06		-0.06	0.06		0.382	49.2
East	0.07	0.02		0.04	0.02		0.03	0.02		0.105	46.5
South	0.14	0.02		0.08	0.03		0.06	0.03		0.062	40.8
West	0.10	0.02		0.11	0.04		-0.005	0.03		0.879	4.8

^a % = actual paired difference/random value * 100.

Table 15. Mean number of plant species and mean index of cover (range = 0 - 5) for woody debris, bare ground and plant species in 1-m X 1-m plots centered at randomly selected points and nests in 20 sites.

VARIABLE	RANDOM		NEST		ACTUAL	PAIRED DIFFERENCE		
	MEAN	SE	MEAN	SE		SE	P-VALUE	% ^a
No. Species	7.40	0.31	6.92	0.40	0.48	0.37	0.204	6.5
Woody Debris	1.53	0.09	1.28	0.09	0.25	0.08	0.007	16.5
Bare Ground	1.42	0.08	1.29	0.07	0.13	0.10	0.242	8.9
<u>Pinus banksiana</u>	0.82	0.16	1.83	0.27	-1.01	0.25	0.0008	122.4
<u>Prunus serotina</u>	0.06	0.01	0.01	0.01	0.04	0.02	0.025	77.3
<u>Helianthemum canadense</u>	0.04	0.01	0.004	0.004	0.03	0.01	0.025	88.1
<u>Solidago spathulata</u>	0.11	0.02	0.04	0.02	0.07	0.03	0.036	65.5
<u>Viola pedata</u>	0.08	0.03	0.02	0.02	0.05	0.02	0.004	68.0
<u>Rubus sp.</u>	0.14	0.05	0.07	0.04	0.07	0.03	0.028	48.7
<u>Vaccinium angustifolium</u>	1.75	0.19	2.68	0.21	-0.93	0.18	0.00005	53.0

^a % = actual paired difference/random value * 100.

Table 16. Relative frequency of plants in 1-m X 1-m plots centered at randomly selected points and nests from 20 sites.

PLANT SPECIES	RANDOM		NEST		PAIRED DIFFERENCE			
	MEAN	SE	MEAN	SE	ACTUAL	SE	P-VALUE	% ^a
<u>Pinus</u> <u>banksiana</u>	0.26	0.04	0.48	0.07	-0.22	0.06	0.001	83.0
<u>Prunus</u> <u>serotina</u>	0.04	0.02	0.006	0.006	0.03	0.01	0.013	84.4
<u>Helianthemum</u> <u>canadense</u>	0.04	0.01	0.004	0.004	0.03	0.01	0.025	88.1
<u>Rubus</u> <u>sp.</u>	0.13	0.04	0.05	0.03	0.07	0.02	0.011	57.4
<u>Amelanchier</u> <u>sanguinea</u>	0.17	0.04	0.07	0.04	0.10	0.05	0.054	60.9
<u>Solidago</u> <u>spathulata</u>	0.10	0.02	0.04	0.02	0.07	0.03	0.040	63.8
<u>Viola</u> <u>pedata</u>	0.08	0.03	0.02	0.02	0.05	0.02	0.004	67.8

^a % = actual paired difference/random value * 100.

cover of jack pine in 1-m X 1-m plots at nests corroborates the greater density of jack pine at nests in the large circular plots.

There were no significant differences in soil characteristics between nests and randomly selected points (Tables 17 and 18). As at randomly selected points, the soil characteristics at nests indicate a well-drained soil condition.

Discussion

Comparison of plantations and wildfire sites

The physical description of plantations indicates that land managers accomplished most of their goal to replicate the wildfire habitat of the Kirtland's warbler. However, plantations and wildfire sites differed in a few important ways: jack pine density was 71% less, and percent cover of woody debris was 39% less in plantations. The data also suggest that plantations had 34% fewer openings. Percent cover and relative frequency of several ground vegetation species were also different.

The high density of jack pine in wildfire sites may be advantageous to the endangered species for two reasons. First, the high density of pines provides a greater foliage volume which is important as a forage resource for the insect prey base. Probst (1988) suggested this is a critical factor influencing occupancy of habitat. Second,

Table 17. Relative frequency of soil characteristics at randomly selected points and nests in 20 sites (rel. freq. = # cores with characteristic/ all cores).

SOIL CHARA.	RANDOM		NEST			PAIRED DIFFERENCE		
	MEAN	SE	MEAN	SE	ACTUAL	SE	P-VALUE	% ^a
Clay mottling	0.43	0.07	0.37	0.08	0.06	0.06	0.349	13.3
Clay banding	0.13	0.01	0.13	0.04	0.001	0.04	0.983	0.8
Fine sand	0.22	0.05	0.24	0.06	-0.02	0.04	0.542	11.4
Coarse sand	0.22	0.04	0.20	0.04	0.02	0.03	0.484	10.7
Gravel	0.68	0.06	0.65	0.06	0.03	0.05	0.629	4.0
Cobble	0.38	0.05	0.28	0.07	0.10	0.07	0.152	26.0
Dominant texture = coarse sand	0.02	0.02	0.02	0.01	0.005	0.02	0.737	20.5
Dominant texture = fine sand	0.06	0.03	0.08	0.02	-0.02	0.04	0.727	24.1
Dominant texture = medium sand	0.91	0.03	0.90	0.04	0.01	0.05	0.839	1.1

^a % = absolute paired difference/random value * 100.

Table 18. Measurements (in cm) of soil characteristics at randomly selected points and nests in 20 sites.

SOIL CHARA.	RANDOM				NEST				PAIRED DIFFERENCE			
	MEAN	SE	N	MEAN	SE	N	ACTUAL	SE	DF	P-VALUE	% ^a	
Depth of AO layer	7.6	0.5	20	7.8	0.6	20	-0.1	0.6	19	0.817	1.8	
Depth to clay mottling	117.9	2.7	19	114.0	4.8	16	1.4	5.2	15	0.786	1.2	
Cumulative clay mottling	45.6	2.7	19	41.5	3.8	15	4.4	5.2	14	0.409	9.7	
Depth to clay banding	97.5	7.9	13	117.7	12.6	9	-7.0	12.4	6	0.594	7.2	
Cumulative clay banding	30.8	8.0	13	17.6	7.3	8	9.7	10.5	6	0.389	31.5	
Depth to fine sand	99.5	8.9	14	86.9	8.0	14	16.3	11.9	10	0.200	16.4	
Depth to coarse sand	113.0	8.1	17	125.3	8.6	14	-8.9	10.5	12	0.410	7.9	
Depth to gravel	58.2	5.2	20	58.9	7.7	19	1.6	6.2	18	0.806	2.7	
Cumulative gravel	51.6	4.0	20	39.3	5.4	19	11.6	6.3	18	0.081	22.5	
Depth to cobble	88.8	8.2	18	72.7	11.6	14	30.4	10.8	11	0.016	34.3	

^a % = absolute paired difference/random value * 100.

the high jack pine density in wildfire sites provides dense cover for nests at the juxtaposition of pine clumps and openings. Nearly all nests are placed on such an edge (Walkinshaw 1983, Bocetti pers. obs.). To better replicate wildfire sites, land managers should increase the jack pine density of their plantations, and at the same time increase the number of openings. The increased pine density could be achieved by planting higher densities of pines in clumps at the edges of openings. The recent practice of hand-planting between trees of the two rows nearest the openings will approach the recommended pattern. The number of openings can be increased by decreasing the wavelength of the sine-wave pattern of rows, which would result in a greater number of smaller openings. The variable survivorship of trees should maintain the distribution of sizes of openings in plantations. Recall the distributions were similar in plantations and wildfire sites.

The percent cover and relative frequency of ground vegetation may influence warbler occupancy in the same ways as pine density, by providing forage resources for insects and by providing nest cover. The high percent cover of the sedge in plantations suggests that nest cover is less available. The sedge was the dominant nest cover for 2 of 51 nests, whereas shrub species such as bearberry, blueberry, sand cherry (Prunus pumila), and sweetfern (Comptonia peregrina) were the dominant cover for 47 of 51

nests. Sedge often grows in thick sod beds which can prevent the establishment of shrub species. Blueberry and bearberry have significantly lower percent cover in plantations, and bearberry occurs less frequently in plantations. The shrub species also provide greater foliage volume for insects. Warblers have been observed foraging on the ground in the shrub vegetation (Mayfield 1960, Walkinshaw 1983, Bocetti pers. obs.).

The lower percent cover of woody debris in plantations compared to wildfire sites is likely due to the harvest and site preparation methods of plantation management. Most stands are total-tree-harvested, which means that most of the branches as well as the tree trunks are chipped and removed from the site. The small amount of slash that remains is often cleared into piles and burned, or crushed during site preparation to allow planting equipment to traverse the site.

Land managers may be able to increase the percent cover of shrub species and woody debris by using harvest and site preparation methods that replicate wildfires. The Kirtland's Warbler Recovery Team recommends prescribed burning as a site preparation that simulates wildfire conditions, but the total-tree-harvest method may not provide enough fuel for hot prescribed burns, and the pile and burn method does not allow complete burning of the site. Hot burns on entire sites should allow the invasion of shrub

species, and the slash left on the ground will provide more woody debris. Chain, disc, and scalp scarification methods may provide the same disturbance as a hot burn such that shrub species can invade the site, but these techniques should be experimentally tested.

Soil and physiography characteristics are not expected to vary significantly between wildfire sites and plantations because these features are not caused by the method of jack pine regeneration. They can, however, have a major effect on the success of jack pine and ground vegetation regeneration. Barnes et al. (1989) found that species composition and percent cover of ground vegetation were correlated with elevation and soil moisture characteristics, as were the tree characteristics of the regenerating jack pine.

The relative importance of habitat characteristics to food availability and nest site availability for the Kirtland's warbler is unknown. The species diversity, abundance, and life history of insects in the jack pine plains ecosystem are virtually unknown. Therefore, it is difficult to assess if food is limiting to the warblers. The nest site characteristics of the endangered species are investigated below and compared to the habitat characteristics available, in an effort to determine which habitat characteristics are selected by warblers as the first step to understanding if nest sites are limiting.

Comparison of nests and randomly selected points

The data suggest that some habitat characteristics associated with Kirtland's warbler nests are used more or less than expected if nests were placed at random. The density of jack pine is 21% greater at nests. The height of the first live branch is 13% lower, and the diameter is 16% smaller on trees around nests. Nests occur in an opening 38% less often than expected under a random distribution. The percent cover of woody debris is 16% less at nests, and the percent cover and relative frequency of several ground vegetation species are different than expected if nests are placed at random. Nests are placed less frequently in the midslope category and more frequently in the plateau category than expected under random placement. Nest sites represent habitat characteristics used by both male and female warblers because nests are located within the territory established by the male, yet the specific nest site location is selected by the female.

The high density of jack pine at nest sites confirms that this habitat characteristic is advantageous to the endangered species. However, its relative importance as foraging material for insects or as nesting cover is still unclear. High jack pine density is likely critical to both breeding requirements. Walkinshaw (1983) noted that warblers start to nest in a stand once the lower jack pine branches reach those of neighboring trees, and he suggested

this feature was important as a component of nest cover. The height of the first live branch at nests is lower than expected if the nests are placed at random, supporting Walkinshaw's (1983) suggestion that jack pine provides an important component of nest cover. The smaller diameter of jack pine at nest sites may reflect a preference for younger (or slower growing) trees because they still have interlocking lower branches.

The ground vegetation species with higher percent cover and relative frequency at nests were remarkably similar to those found more often and at greater percent cover in wildfire sites, confirming the importance of these habitat characteristics to Kirtland's warblers. The higher percent cover and relative frequency of jack pine at nests corroborates the higher density of jack pine at nests. The higher percent cover of blueberry at nests verifies the importance of this shrub species. The bird's-foot violet seems to occur in sparsely vegetated or disturbed areas, and the lower percent cover and relative frequency of the bird's-foot violet at nests may reflect a tendency to avoid sparsely vegetated or disturbed areas. The rareness of this species makes it difficult to interpret the biological importance of the difference between nests and randomly selected points. Black cherry (Prunus serotina) and blackberry (Rubus sp.) have lower percent cover at nests, and both belong to the Rosa blanda Ecological Species Group

as defined by Barnes et al. (1989), which indicates more moist and fertile environmental conditions. Perhaps the warblers avoid such conditions because of the microclimate associated with the soil moisture (Zou pers. comm.), or because of the potential flooding of nests in less well-drained soils (Mayfield 1960).

Warbler nests have less percent cover of woody debris than expected if nests are placed at random. Nearly every nest site and randomly selected point has some woody debris, so the relative frequency is almost 1.00 for both point categories. The percent difference of woody debris at nests compared to randomly selected points is only 16.5%, so the biological significance is difficult to interpret. Perhaps woody debris has both costs and benefits. Many nests were placed next to some form of micro-structure, such as downed logs, soil mounds, or grass clumps. Woody debris is beneficial in this regard as a component of nest cover. However, ground squirrels (Citellus tridecemlineatus) and red squirrels (Tamiasciurus hudsonicus) may use the larger downed logs for dens or forage sites, and woody debris would be a cost in this regard as a refuge for nest predators.

Nest sites are closer to trees, and thus are surrounded by smaller open spaces, than expected if nests are placed at random. This may be a corollary to the finding that warblers choose higher tree densities, but the openings are an important feature. Kirtland's warblers place their nests

at or near the edge of openings (Mayfield 1960, Walkinshaw 1983, Bocetti pers. obs.). Of 126 nests, Walkinshaw (1983) shows that 32% of the nests are located within the pine growth, 17% are located exactly on the edge, and 51% are located in the opening, usually within 1 m of the edge. Only 20% of nests in this study are in openings (as defined by a rule that best distinguishes openings on aerial photos), and this is fewer than expected if nests are placed at random. The remaining 80% are within the pine clumps or at the edge, but nearly always within 1 m from the edge. Of the nests that are in openings, the patchiness, or distribution of sizes of openings, is no different than expected if the nests are placed at random. Further investigation of the characteristics of openings near the 80% of nests found just within the pine growth is required, such as a measurement of edge.

The physiography of nest sites is similar to randomly selected points. Mayfield (1960) and Zou et al. (1992) described the habitat used by Kirtland's warblers as overall flat or gently rolling, and the slope of both point categories supports this summary. Providing additional support, most points are in the topographic category, plateau. Anderson and Storer (1976) concluded that reproductive success is greater in flat compared to hilly terrain. Fewer nests are placed in the midslope category than expected if nests are placed at random. More nests are

placed in the plateau category, and this difference is nearly significantly different from random placement. More nests are placed at upper slopes, but not significantly so. The data suggest a tendency for warblers to place nests at or near flat areas rather than on slopes.

The soil characteristics of nest sites and randomly selected points are very similar. Mayfield (1960) characterized the sandy soil as loose and permeable to a depth of 1-2 m or more, and having a shallow humus layer that is at most 2-4 cm thick or lacking in many places. Zou et al. (1992) showed that ecosystems occupied by warblers have well-sorted sand soils with little (5-10 cm) or no textural bands, whereas ecosystems not occupied by warblers have soil with heavy textured layers (loam to clay). The data support Zou et al.'s (1992) conclusions about the soil characteristics of occupied ecosystems. Nest sites have soils dominated by medium sand and only small amounts of clay banding far below the surface, which indicates an excessively well-drained soil condition at the surface. The humus layer is thicker than Mayfield's (1960) findings, around 7 cm, and occurs consistently in both point categories. The depth to cobble is more shallow at nest sites than expected if nests are placed at random. This is a reflection of the glacial history of the sites, and supports Zou et al.'s (1992) finding that warblers occur in ecosystems within glacial outwash terrain.

Land managers should attempt to incorporate the habitat characteristics that are used by warblers more than expected if nests are placed at random, and avoid the characteristics that are used less than expected if nests are placed at random. The major findings of this analysis suggest that if land managers replicate features found in wildfire sites such as higher density of jack pine and greater percent cover and relative frequency of shrubby ground vegetation species, particularly blueberry, they will be providing the characteristics important to the warblers.

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MATING SUCCESS AND REPRODUCTIVE SUCCESS

OF MALE KIRTLAND'S WARBLERS

The Kirtland's warbler (Dendroica kirtlandii) was once thought to be a classic example of a monogamous species, having all the ecological and behavioral conditions for typical monogamous mating behavior (Selander 1965, Verner and Willson 1966, Orians 1969, Trivers 1972). It was thought that all males held territories in optimum habitat (Mayfield 1960, Brown 1969), attracted mates under a 1:1 sex ratio (Mayfield 1960, Walkinshaw 1983), and assisted in the care of the young (Leopold 1924, Mayfield 1960, Walkinshaw and Faust 1974, Walkinshaw 1977). However, exceptions to this monogamous mating strategy have been observed. Mayfield (1960) observed one case of polygyny. Walkinshaw (1983) described polygyny as very rare, noting four cases out of 163 males studied (2.45%). Radabaugh (1972) observed nine cases of polygyny from 1966 to 1968, involving seven males (20.6% of males studied) in a single study area. He suggested that the polygyny occurred when a stand was almost filled to capacity and was adjacent to an aging stand.

Recent research indicated that breeding habitat was limited (Probst 1986; Probst and Weinrich 1993, Kepler and Sykes, unpubl. data). Males had to compete for territories in optimum habitat, leaving some males to settle in marginal habitat. Some males failed to obtain a mate during the breeding season (Probst and Hayes 1987), while others failed to obtain a territory (Probst, unpubl.). Probst and Hayes (1987) determined that pairing success was correlated with habitat quality. They classified all habitat into marginal and suitable categories and identified males as paired or unpaired. They showed that pairing success was lower in marginal habitat. The frequency of polygyny was not investigated and was assumed to be minimal. Probst and Hayes (1987) postulated that polygyny would become more widespread as suitable habitat became scarce or dispersed. Clearly, Kirtland's warbler was not exclusively monogamous, and the proportion of males that were unmated, monogamous, or polygynous was unknown.

Walkinshaw (1983) described the reproductive success of Kirtland's warblers in naturally regenerated stands that were burned by wildfires. He estimated that fledging success was 0.8 fledgling per pair prior to cowbird control (1966-71), and 3.3 fledglings per pair after cowbird control (1972-77). Kelly and DeCapita (1982) investigated the effect of cowbird control on the number of young fledged and found an average of 2.76 young from 1972 to 1981. No

evaluation of the cowbird control program has been conducted since the habitat management program produced suitably-aged plantations in the mid-1980's. No work has been done to compare the reproductive success of males in various habitats, or to determine the recruitment of young in different habitats.

Walkinshaw (1983) calculated that 24.8% of nests were lost to predation. He found that most nest failures were due to predation rather than exposure, starvation or abandonment. He suggested that bluejays (Cyanocitta cristata), thirteen-lined ground squirrels (Citellus tridecemlineatus), red squirrels (Tamiasciurus hudsonicus), and garter snakes (Thamnophis sirtalis) were the primary nest predators. He also warned of increasing predation by house cats (Felis domesticus).

The purpose of this investigation is to determine the mating success and reproductive success of male Kirtland's warblers, as a supplement to the annual singing male census, and to evaluate habitat use in plantations and wildfire sites. Due to the substantial decrease in naturally regenerated, wildfire habitat, the recovery plan calls for the establishment of plantations as habitat for the endangered warbler (Byelich et al. 1976). The annual census of singing males provides an index of the Kirtland's warbler population (Weinrich 1989), but it is not a reliable index of habitat quality (Van Horne 1983). The census results

indicate which management practices attract singing males, but mating success and reproductive success of the males in each habitat type must be known to evaluate the plantations as sources or sinks. Pulliam (1988) warned that when there was more than one habitat type in a region, the productivity in each habitat type must be known because immigration may maintain the population levels of a sink. The study also provides an update on the success of the cowbird control program.

In addition to habitat type, biogeographic factors may influence Kirtland's warbler habitat use. Mayfield (1993) suggested that the size of a stand is very important to the warblers. He proposed that the larger stands, or complexes of stands, are more attractive to the species because the historical habitat was created by large wildfires, creating vast, open landscapes. Distance to the center of the range may influence habitat use because the distribution of the warbler population collapsed to the center of the range by 1975 (Byelich et al. 1976). Also, the age of a stand must be considered when mating success is investigated because females tend to settle in new stands slightly later than males (Probst 1988).

The objectives of this investigation are divided into two parts. Part I is designed to compare mating and reproductive variables between two habitat categories: plantations and wildfire areas. The wildfire areas are the

historical habitat of the Kirtland's warbler and serve as the guideline to evaluate plantations. The response variables are 1) mating success of males (proportion unmated, monogamous, or polygynous), 2) clutch size per nest, 3) number of young fledged per nest attempt, and 4) proportion of nests depredated. The influence of the following biogeographic variables on the above comparisons will be tested: stand age, stage of stand occupation, stand location (core or periphery), and stand isolation (isolated or within a complex). Part II is designed to evaluate plantations as sources or sinks, by combining the results of the landscape scale evaluation of male density in all habitat types (Chapter 2) with the results from Part I. The derived variables are 1) density of females, and 2) density of young fledged. The density of young fledged will be compared to the minimum density of young required to maintain the population of a stand from year to year as described by Pulliam (1988).

Methods

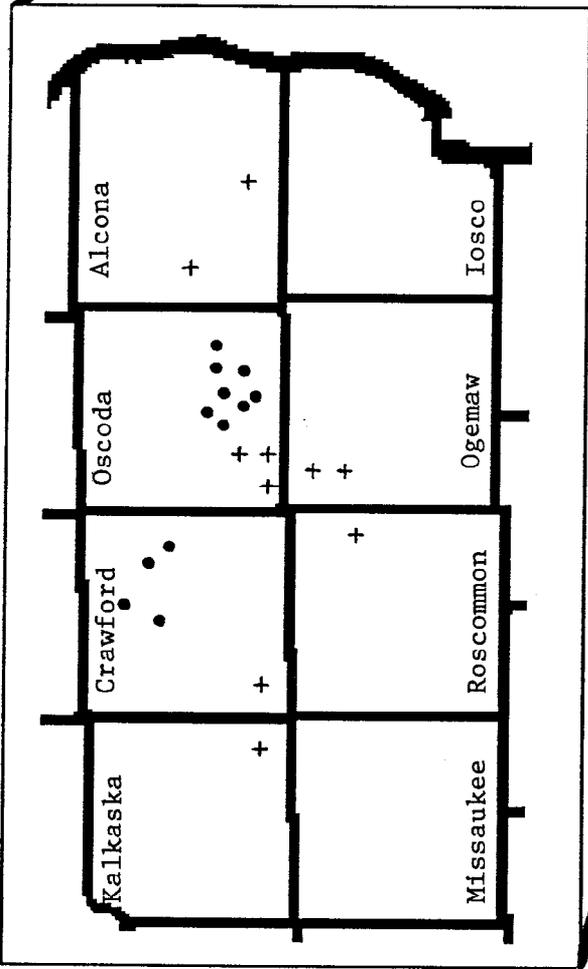
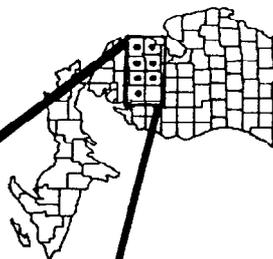
Part I

The study required a large population of uniquely marked warblers. Most birds were banded as part of another study conducted by the National Biological Survey, and some warblers were banded by me at each study site.

The field research was conducted during May through August of 1990, 1991, and 1992. Two years of preliminary data on mating success from 1988 and 1989 was used to supplement the data from the three complete field seasons. Study sites were distributed throughout the breeding range of the species, with about one-half the sites in each habitat category (Figure 10).

A two-stage sampling design was used, with the study sites as the primary sampling unit and the territorial male, or the nest, as the secondary sampling unit. Since inferences were made about habitat categories, the standard error was calculated only for the primary sampling units (sites), and unbiased estimates were assumed for the secondary sampling units (territorial males or nests). The means of the response variables were compared between habitat categories, with unequal variance t-tests and Satterthwaite's approximation of degrees of freedom, at $\alpha=0.05$. Power calculations based on preliminary and 1990 data were used to determine the minimum sample size needed of territorial males and nests.

Each field season began approximately 10-14 May with the arrival of male Kirtland's warblers. In 1990, study sites were selected prior to the arrival of the birds, based on the site treatment and history of occupation. In 1991 and 1992, a brief census period was required to find up to five sites in each habitat category that had at least four



+ = plantation study site
 • = wildfire study site

Figure 10. Distribution of study sites in Michigan.

singing males. In large tracts of habitat with many warblers, the site was defined by a randomly-selected cluster of singing males, but in smaller burns and plantations the site was defined by the boundary of the habitat.

Sites were selected with a range of ages and stages of occupation, and the effect of age and stage of occupation on mating success and reproductive success was investigated with regression analysis. Effects of stand location on mating success were evaluated by defining the core and periphery of the breeding range and comparing (with a t-test) the mean proportion of males in each mating status in the core versus in the periphery. The core of the breeding range was defined as the area less than half-way from the geographic center of the range to the edge of the range. The periphery was defined as the remaining area. Effects of stand isolation on mating success were evaluated by comparing (with t-tests) the mean proportion of males in each mating status in isolated stands (more than two miles from nearest warbler habitat) to the mean proportion of males in each mating status in stands that are part of a complex of habitat (less than two miles from the nearest warbler habitat).

Once the study sites were selected and most birds were banded, the territories of the singing males were plotted. During this time, the mating status of the male was

determined, and the nests were located. These activities continued through early July when breeding activity curtailed and song frequency diminished. Territories were delineated using focal animal sampling of singing males and plotting locations on enlarged, low flight, false-color infrared, aerial photographs (scale 1 inch: 250 feet).

Females were located by several methods. Some were located while territory boundaries were plotted, and others were located during systematic searches throughout the territory. Several cues were used to locate females, including the loud chip note of females and behavioral changes of the male associated with intersexual interactions such as changes in song type and song frequency or food-carrying. After each male was monitored for at least 120 bird-minutes during at least two days, the mating status of the male was inferred by the number of females located in his territory. Vigilance for additional females or for movements by males to other territories was continued even after the first female was found. Some cases of polygyny were discovered by knowing the identity of surrounding, singing males (some data provided by Probst), revealing a second territory of a study male. To better understand the polygynous behavior of male Kirtland's warblers, I summarized the proportion of males in each mating status by year, from 1988 to 1992. Habitat was less limiting each year, and if Probst and Hayes (1987) were correct, the

proportion of males that were polygynous should have decreased each year. Also, the change in status of individual males that were studied for more than one year was noted.

Nests were usually located early in the nesting cycle. They were located by following the singing male as he carried food to the incubating female, or by watching either parent deliver food to nestlings. Once the nest was located, an initial nest visit was conducted to determine the stage in the nesting cycle and clutch size. A second nest check was conducted on the sixth day of the nine-day nestling period to determine the number of nestlings. Since predation causes the loss of the entire nest, the sixth day nestling count provides the number of young fledged if the nest persists through fledging. Fledging was determined by the feeding behavior of the adults, by the high-noted chipping of the fledglings, or by the observation of a fledgling. Predation could be detected without precisely locating the nest. The adult feeding activity identified a small core area around the nest, and a sudden cessation of such feeding routines indicated the loss of the nest. Predation data is limited to the egg and nestling phases because after fledging the status of each fledgling could not be determined.

Part II

The number of young that must be produced every year to maintain the population of a stand is:

$$(1) \text{ productivity} = \frac{\# \text{ adults } (1 - \text{ survivorship of adults})}{\text{ survivorship of young}}$$

Annual survivorship of adults is estimated to be 0.58, and the first-year survivorship of young-of-the-year is estimated to be 0.30 (Kepler and Sykes, 1992 prelim. data). The survivorship data has not yet been analyzed by habitat type. If food availability differs between habitat types, the survivorship of adults and juveniles may vary by habitat type. If the number of polygynous nests varies between habitat types and the young from polygynous nests are smaller or weigh less due to reduced care, the juvenile survivorship may vary by habitat type. A brief investigation of the sensitivity of equation (1) to variation in adult and juvenile survivorship is conducted for each habitat type by changing the estimated survivorship values by ± 0.1 . The number of adults is estimated by the predicted density of warblers per 40 acres per year over the life of a stand from Chapter 2.

The observed density of females and the observed density of fledglings are calculated from the density of males in each habitat type (from Chapter 2) multiplied by the estimates of mating success and reproductive success in each habitat type from Part I.

Results

Part I

The proportions of males in each mating status on the three preliminary study sites (38 territorial males plotted in 1988-1989), as shown in Table 19, were similar to the proportions of males in each mating status on the nine plantations and 11 wildfire sites (108 territorial males plotted in 1990-1992), as shown in Table 20.

Comparing the mean proportions of males in each mating status (Table 20) between the two habitat categories revealed that there were more unmated males and fewer polygynous males in plantations compared to wildfire areas. While studying the mating success of territorial males, I found an unexpected result: most polygynous males (83%) were polyterritorial, as were 12% of unmated males and 6% of monogamous males (Table 21). Fewer males were polyterritorial in plantations than in wildfire sites (0.14 vs. 0.21, $p=0.20$), but not significantly so. From 1988 to 1992, habitat became less limiting, but there was no consistent trend in the mean proportion of males in each mating status in either habitat category (Table 22). Some males were seen in more than one year, and 34% of them changed mating status from year to year (Table 23).

Stand age did not have a significant effect on the proportion of males that were unmated ($r^2=0.109$, $p=0.133$) or polygynous ($r^2=0.070$, $p=0.235$). Stage of stand occupation

Table 19. Preliminary data on the proportions of territorial males in two wildfire areas and one plantation that are unmated (U), monogamous (M), and polygynous (P). Data collected in 1988-1989. Abbreviations for study sites are defined in Appendix B.

WILDFIRE SITES					PLANTATION SITES				
SITE	n	U	M	P	SITE	n	U	M	P
BHS ^a	15	0.00	0.66	0.34	SHP	6	0.50	0.50	0.00
MLB22 ^a	17	0.16	0.74	0.10					
mean		0.08	0.70	0.22	mean		0.50	0.50	0.00
SE		0.08	0.04	0.12	SE		--	--	--

^a Sites were studied in two separate years, and thus the reported values are means for the two years.

Table 20. Proportions of territorial males in 11 wildfire areas and nine plantations that are unmated (U), monogamous (M), and polygynous (P). Data collected in 1990-1992. Abbreviations for study sites are defined in Appendix B.

WILDFIRE SITES					PLANTATION SITES				
SITE	n	U	M	P	SITE	n	U	M	P
ML22	15	0.13	0.73	0.13	OMU21 ^a	8	0.07	0.86	0.07
ML16	4	0.00	0.75	0.25	WBU	3	0.33	0.67	0.00
ML11	3	0.00	0.67	0.33	FPK	3	0.00	1.00	0.00
ML5	5	0.00	0.80	0.20	PRU5	3	0.50	0.50	0.00
BHF	3	0.00	0.33	0.67	SHP	6	0.33	0.50	0.17
SBB	3	0.00	1.00	0.00	CLU	3	0.33	0.33	0.33
ML12	6	0.00	0.83	0.17	CLN	7	0.29	0.71	0.00
ML14	4	0.00	0.50	0.50	FPC	6	0.33	0.67	0.00
ML15	5	0.00	1.00	0.00	OMU28	10	0.30	0.70	0.00
ML17	4	0.25	0.75	0.00					
NBH	6	0.50	0.33	0.17					
mean		0.08 ^b	0.70	0.22 ^c	mean		0.28 ^b	0.66	0.06 ^c
SE		0.05	0.07	0.06	SE		0.05	0.07	0.04

^a Overlapping sites were studied at OMU21 in two separate years, and thus the reported values are means for the two years.

^b $P = 0.012$.

^c $P = 0.054$.

Table 21. Number of polyterritorial males / number of males in each mating status (unmated, monogamous, and polygynous) in each habitat category (wildfire and plantation). Data collected from 1988 to 1992.

HAB. CAT.	UNMATED	MONOGAMOUS	POLYGYNOUS	TOTAL
WILDFIRE	2 / 9	2 / 69	17 / 21	21 / 99
PLANTATION	1 / 17	4 / 39	3 / 3	8 / 59
TOTAL	3 / 26	6 / 108	20 / 24	29 / 158

Table 22. Number of sites studied each year and mean proportion of males that were unmated or polygynous in both habitat categories (wildfire = W and plantation = P) each year, as habitat became less limiting.

YEAR	SITES		UNMATED		POLYGYNOUS	
	W	P	W	P	W	P
1988	2	--	0.062	--	0.150	--
1989	2	1	0.100	0.500	0.292	0.000
1990	1	2	0.133	0.238	0.133	0.155
1991	5	5	0.000	0.233	0.290	0.067
1992	5	3	0.150	0.306	0.167	0.000

Table 23. Mating status of males seen in more than one year (unmated = U, monogamous = M, polygynous = P). Site and male abbreviations defined in Appendix B.

MALE ID.	SITE ID.	'88	'89	'90	'91	'92
GBYA	BHS	M	M			
RGAY	BHS	M	M			
ABGR	BHS	M	M			
AYGB	BHS	M	P			
ABRB	BHS	M	M			
GGAR	BHS	P	P			
AGYB	BHS	P	P			
RBAY	BHS	P	M			
AYJY	MLB22/12	U	M
RRYA	MLB22	M	M	M	M	
BRBA	MLB22	U	M	M	
BGBA	MLB22	M	M		
BYBA	MLB22	M	M	M	
BBBA	MLB22	M	M		
AGGR	MLB22	P	P		
JYRA	MLB22	M	M	
JJRA	MLB22	M	M	
RJRA	MLB22	M	M	
AYRJ	MLB22	M	M	
JRRA	MLB22	M	M	
JBRA	MLB22	P	M	
GYBA	SHP	U	U		
YRAG	SHP	U	M		
GAYG	SHP	M	U	U	
GBBA	SHP	M	P	M	
IARB	SHP	M	U	
YABJ	OMU	M	M	
AYJJ	OMU	M	M	
AYYJ	OMU	P	M	

was the number of years since the stand was first occupied, and it did not significantly influence the proportion of males that were unmated ($r^2=0.095$, $p=0.164$) or polygynous ($r^2=0.120$, $p=0.114$).

In plantations, stand location (core vs. periphery) did not have a significant effect on the proportion of males that were unmated (0.28 vs. 0.28, $p=0.99$) or polygynous (0.10 vs. 0.00, $p>0.20$). All wildfire sites were in the core of the breeding range.

For plantations, stand isolation (isolated vs. in complex) did not have a significant effect on the proportion of males that were unmated (0.29 vs. 0.26, $p=0.829$) or polygynous (0.04 vs. 0.08, $p=0.628$). Stand isolation also had no significant effect on the proportion of males that were unmated (0.25 vs. 0.04, $p=0.32$) or polygynous (0.08 vs. 0.26, $p=0.14$) in wildfire sites.

The comparison of reproductive success between habitat categories was based on three years of research, 1990-92. Nests were found in seven plantations and 10 wildfire sites. The mean clutch size was not significantly different in plantations and in wildfire areas (Table 24). The power (p') of the test was greater than 0.97 when the true difference (δ) was one. Stand age did not significantly influence clutch size ($r^2=0.069$, $p=0.307$), nor did stage of stand occupation ($r^2=0.006$, $p=0.761$). The mean number of young fledged per nest attempt (Table 25) was not

Table 24. Mean clutch size (number of eggs per nest) for each site and the grand means for each habitat category. Abbreviations for study sites are defined in Appendix B.

WILDFIRE SITES				PLANTATION SITES			
SITE	mean	s ²	n	SITE	mean	s ²	n
MLB22	4.56	0.50	9	SHP _a	4.50	0.33	4
MLB5	5.00	0.00	1	OMU21 _a	5.00	0.00	4
MLB11	4.50	0.33	4	WBU	4.00	0.00	1
BHF	4.00	0.00	1	FPK	4.00	0.00	1
SBB	5.50	0.50	2	CLN	5.00	0.00	2
MLB12	4.50	0.33	4	FPC	5.00	1.00	3
MLB14	4.00	0.00	2	OMU28	4.50	1.00	4
MLB15	4.00	0.00	1				
MLB17	5.00	0.00	2				
NBH	5.00	0.00	1				
grand mean	4.61			grand mean	4.57		
SE	0.16			SE	0.17		

^a Overlapping sites were studied at OMU21 in two separate years and SHP was studied for two years. Reported values are means for the two years.

Table 25. Mean number of young fledged per nest attempt for each site and the grand means for each habitat category. The abbreviations for study sites are defined in Appendix B.

WILDFIRE SITES				PLANTATION SITES			
SITE	mean	s ²	n	SITE	mean	s ²	n
MLB22	3.22	3.94	9	SHP	4.25	0.25	4
MLB5	5.00	0.00	1	OMU21 ^a	4.25	0.25	4
MLB11	3.00	4.67	4	WBU	4.00	0.00	1
BHF	3.00	0.00	1	FPK	4.00	0.00	1
SBB	5.50	0.50	2	CLN	2.50	12.50	2
MLB12	4.00	0.67	4	FPC	3.00	4.00	4
MLB14	2.00	8.00	2	OMU28	3.25	4.92	4
MLB15	2.00	8.00	2				
MLB17	3.00	2.00	2				
NBH	5.00	0.00	1				
grand mean	3.57			grand mean	3.61		
SE	0.40			SE	0.26		

^a Overlapping sites were studied at OMU21 in two separate years, and thus reported values are means for the two years.

significantly different in plantations and in wildfire areas. When $\delta = 1.42$, $p' = 0.81$. Stand age did not significantly influence the number fledged ($r^2 = 0.144$, $p = 0.147$), nor did stage of stand occupation significantly affect the number fledged ($r^2 = 0.073$, $p = 0.293$).

The proportion of nests lost to predation was calculated from eight plantations and 11 wildfire sites (73 nests or core areas). The mean proportion of nests and core areas lost to predation was not significantly different in plantations and in wildfire areas (Table 26). Prior to the third year of research, the mean proportion of nests depredated was significantly different between plantations and wildfire areas (0.03 vs. 0.23, $p < 0.02$). The mean predation rates for all habitats were similar during the first two years (0.14 in 1990 and 0.12 in 1991), and the proportions were similar. However, the mean predation rate for all habitats in 1992, the third year, was 0.27; the proportions (0.39 in plantations vs. 0.20 in wildfire areas) were not similar to the proportions in the first two years, and, in fact, showed the reverse trend. Stand age did not significantly influence predation rates ($r^2 = 0.00$, $p = 0.93$), nor did stage of stand occupation ($r^2 = 0.006$, $p = 0.754$).

A cowbird egg was found in a nest at Mack Lake Burn, section 5 on 24 June 1991. Perhaps the egg was laid too late during the incubation period, was laid after the

Table 26. Number of nests and core areas and the proportion depredated (a failed nest was assumed to be due to predation), for each site and the grand means for each habitat category. The abbreviations for study sites are defined in Appendix B.

SITE	WILDFIRE SITES		SITE	PLANTATION SITES	
	TOTAL NO.	PROPORTION LOST		TOTAL NO.	PROPORTION LOST
MLB22	14	0.214	OMU21 ^a	8	0.000
SBB	3	0.333	SHP ^a	6	0.167
BHF	3	0.333	PRU5	2	0.000
MLB16	1	0.000	FPK	3	0.000
MLB11	4	0.250	WBU	2	0.000
MLB5	4	0.250	CLN	3	0.667
MLB12	5	0.000	FPC	4	0.250
MLB14	2	0.500	OMU28	4	0.250
MLB15	2	0.500			
MLB17	2	0.000			
NBH	1	0.000			
mean proportion		0.216	mean proportion		0.167
SE		0.058	SE		0.082

^a Overlapping sites were studied at OMU21 in two separate years and SHP was studied for two years. Reported values are means for the two years.

warbler young fledged, or was infertile when it was laid. Young warblers did successfully fledge from this nest. A cowbird egg was found in a sparrow nest at Fletcher Road plantation in Crawford County on 11 June 1992. Cowbirds were being trapped and removed from both sites at the time.

Part II

From Chapter 2, the density of males was slightly greater in plantations than in wildfire sites (Table 9). Based on the proportions of males in each mating status, the sex ratio (male:female) for each habitat category was 1.00:0.78 in plantations and 1.00:1.14 in wildfire sites. The density of females (and nests) was the product of these ratios and the density of males in each habitat type. The density of females was lower in plantations than in wildfire sites (Table 27). Recruitment of young in each habitat category is the product of the density of females (nests) and the number of young fledged per nest. The density of fledglings is smaller in plantations (Table 27).

Table 27. Density of Kirtland's warblers per 40 acres per year over the life of a stand in each habitat type.

HABITAT TYPE	MALES	FEMALES	FLEDGLINGS
PLANTATIONS	0.21	0.16	0.58
WILDFIRE SITES	0.19	0.22	0.78

The density of young required to maintain a population in a given habitat type is sensitive to variation in adult and juvenile survivorship (Tables 28 and 29). If juvenile survivorship is below 0.27 in plantations or below 0.22 in wildfire sites, and the pooled estimate of adult survivorship is held constant, these habitats are no longer sources. Adult survivorship also affects this equilibrium point. Until the survivorship data (Kepler and Sykes 1992, prelim. data) is analyzed by habitat type, the average survivorship values from all habitats is used in this analysis. The density of adults per 40 acres per year over the life of a stand in each habitat type is the sum of the density of males and females. Therefore from equation (1), the density of young per 40 acres per year over the life of a stand that must be produced to maintain the population from year to year is:

for plantations:

$$\text{productivity} = \frac{(0.21 + 0.16)(1 - 0.58)}{0.30} = 0.52,$$

and for wildfire sites:

$$\text{productivity} = \frac{(0.19 + 0.22)(1 - 0.58)}{0.30} = 0.57.$$

These values are compared to the observed recruitment of young in each habitat type (Table 27). Because $0.58 > 0.52$ fledglings per 40 acres per year over the life of a plantation, plantations are considered sources. In this

Table 28. Density of young per 40 acres per year over the life of a plantation that must be produced to maintain the population from year to year, showing the effect of variation in adult and juvenile survivorship.

Surv.	Juvenile Survivorship																				
	.20	.21	.22	.23	.24	.25	.26	.27	.28	.29	.30	.31	.32	.33	.34	.35	.36	.37	.38	.39	.40
.48	.96	.92	.87	.84	.80	.77	.74	.71	.69	.66	.64	.62	.60	.58	.57	.55	.53	.52	.51	.49	.48
.49	.94	.90	.86	.82	.79	.75	.73	.70	.67	.65	.63	.61	.59	.57	.55	.54	.52	.51	.50	.48	.47
.50	.92	.88	.84	.80	.77	.74	.71	.69	.66	.64	.62	.60	.58	.56	.54	.53	.51	.50	.49	.47	.46
.51	.91	.86	.82	.78	.76	.73	.70	.67	.65	.63	.60	.58	.57	.55	.53	.52	.50	.49	.48	.46	.45
.52	.89	.85	.81	.77	.74	.71	.68	.66	.63	.61	.59	.57	.55	.54	.52	.51	.49	.48	.47	.46	.44
.53	.87	.83	.79	.76	.72	.70	.67	.64	.62	.60	.58	.56	.54	.53	.51	.50	.48	.47	.46	.45	.43
.54	.85	.81	.77	.74	.71	.68	.65	.63	.61	.59	.57	.55	.53	.52	.50	.49	.48	.46	.45	.44	.43
.55	.83	.79	.76	.72	.69	.67	.64	.62	.59	.57	.55	.54	.52	.50	.49	.48	.46	.45	.44	.43	.42
.56	.81	.78	.74	.71	.68	.65	.63	.60	.58	.56	.54	.53	.51	.49	.48	.47	.45	.44	.43	.42	.41
.57	.80	.76	.72	.69	.66	.64	.61	.59	.57	.55	.53	.51	.50	.48	.47	.45	.44	.43	.42	.41	.40
.58	.78	.74	.71	.68	.65	.62	.60	.58	.55	.54	.52	.50	.49	.47	.46	.44	.43	.42	.41	.40	.39
.59	.76	.72	.69	.66	.63	.61	.58	.56	.54	.52	.51	.49	.47	.46	.45	.43	.42	.41	.40	.39	.38
.60	.74	.70	.67	.64	.62	.59	.57	.55	.53	.51	.49	.48	.46	.45	.44	.42	.41	.40	.39	.38	.37
.61	.72	.69	.66	.63	.60	.58	.56	.53	.52	.50	.48	.47	.45	.44	.42	.41	.40	.39	.38	.37	.36
.62	.70	.67	.64	.61	.59	.56	.54	.52	.50	.48	.47	.45	.44	.43	.41	.40	.39	.38	.37	.36	.35
.63	.68	.65	.62	.60	.57	.55	.53	.51	.49	.47	.46	.44	.43	.41	.40	.39	.38	.37	.36	.35	.34
.64	.67	.63	.61	.58	.55	.53	.51	.49	.48	.46	.44	.43	.42	.40	.39	.38	.37	.36	.35	.34	.33
.65	.65	.62	.59	.56	.54	.52	.50	.48	.46	.45	.43	.42	.40	.39	.38	.37	.36	.35	.34	.33	.32
.66	.63	.60	.57	.55	.52	.50	.48	.47	.45	.43	.42	.41	.39	.38	.37	.36	.35	.34	.33	.32	.31
.67	.61	.58	.55	.53	.51	.49	.47	.45	.44	.42	.41	.39	.38	.37	.36	.35	.34	.33	.32	.31	.31
.68	.59	.56	.54	.51	.49	.47	.46	.44	.42	.41	.39	.38	.37	.36	.35	.34	.33	.32	.31	.30	.30

Table 29. Density of young per 40 acres per year over the life of a wildfire stand that must be produced to maintain the population from year to year, showing the effect of variation in adult and juvenile survivorship.

Adult	Juvenile Survivorship																				
	.20	.21	.22	.23	.24	.26	.26	.27	.28	.29	.30	.31	.32	.33	.34	.35	.36	.37	.38	.39	.40
.48	1.07	1.02	.97	.93	.89	.85	.82	.79	.76	.74	.71	.69	.67	.66	.63	.61	.59	.58	.56	.55	.53
.49	1.05	1.00	.95	.91	.87	.84	.80	.77	.75	.72	.70	.67	.65	.63	.61	.60	.58	.57	.55	.54	.52
.50	1.02	.98	.93	.89	.85	.82	.79	.76	.73	.71	.68	.66	.64	.62	.60	.59	.57	.56	.54	.53	.51
.51	1.00	.96	.91	.87	.84	.80	.77	.74	.72	.69	.67	.65	.63	.61	.59	.57	.56	.54	.53	.52	.50
.52	.98	.94	.89	.86	.82	.79	.76	.73	.70	.68	.66	.63	.61	.60	.58	.56	.55	.53	.52	.50	.49
.53	.96	.92	.88	.84	.80	.77	.74	.71	.69	.66	.64	.62	.60	.58	.57	.55	.54	.52	.51	.49	.48
.54	.94	.90	.86	.82	.79	.75	.73	.70	.67	.65	.63	.61	.59	.57	.55	.54	.52	.51	.50	.48	.47
.55	.92	.88	.84	.80	.77	.74	.71	.68	.66	.64	.61	.60	.58	.56	.54	.53	.51	.50	.49	.47	.46
.56	.90	.86	.82	.78	.75	.72	.69	.67	.64	.62	.60	.58	.56	.55	.53	.52	.50	.49	.47	.46	.45
.57	.88	.84	.80	.77	.73	.71	.68	.66	.63	.61	.59	.57	.55	.53	.52	.50	.49	.48	.46	.45	.44
.58	.86	.82	.78	.75	.72	.69	.66	.64	.61	.59	.57	.56	.54	.52	.51	.49	.48	.47	.45	.44	.43
.59	.84	.80	.76	.73	.70	.67	.65	.62	.60	.58	.56	.54	.53	.51	.49	.48	.47	.46	.44	.43	.42
.60	.82	.78	.75	.71	.68	.66	.63	.61	.59	.57	.56	.53	.51	.50	.48	.47	.46	.44	.43	.42	.41
.61	.80	.76	.73	.70	.67	.64	.61	.59	.57	.55	.53	.52	.50	.48	.47	.46	.44	.43	.42	.41	.40
.62	.78	.74	.71	.68	.65	.62	.60	.58	.56	.54	.52	.50	.49	.47	.46	.45	.43	.42	.41	.40	.39
.63	.76	.72	.69	.66	.63	.61	.58	.56	.54	.52	.51	.49	.47	.46	.45	.43	.42	.41	.40	.39	.38
.64	.74	.70	.67	.64	.61	.59	.57	.55	.53	.51	.49	.48	.46	.45	.43	.42	.41	.40	.39	.38	.37
.65	.72	.68	.65	.62	.60	.57	.56	.53	.51	.49	.48	.46	.45	.43	.42	.41	.40	.39	.38	.37	.36
.66	.70	.66	.63	.61	.58	.56	.54	.52	.50	.48	.46	.45	.44	.42	.41	.40	.39	.38	.37	.36	.35
.67	.68	.64	.61	.59	.56	.54	.52	.50	.48	.47	.45	.44	.42	.41	.40	.39	.38	.37	.36	.35	.34
.68	.66	.62	.60	.57	.55	.52	.50	.48	.47	.45	.44	.42	.41	.40	.39	.37	.36	.35	.34	.33	.33

habitat type, warblers maintain their population levels through reproduction plus provide excess young for dispersal. Wildfire sites are also sources because $0.78 > 0.57$ fledglings per 40 acres per year over the life of a wildfire site. These results must be used with caution because they are based on pooled estimates of survivorship.

Discussion

The mating success and reproductive success of males in each habitat category is used to evaluate plantations as suitable habitat for the endangered species. Due to the greater proportion of unmated males and the smaller proportion of polygynous males, plantations have fewer females and fewer nests per male than wildfire sites. Once a nest is initiated, the number of young produced per nest is very similar between plantations and wildfire areas. Due to the skew in the number of nests initiated, the number of young produced per male is much less in plantations than in wildfire areas. Perhaps females are settling in wildfire areas more than in plantations because there are more nest sites in wildfire areas, where shrubby ground cover is more frequent and has greater percent cover (see Chapter 3). Also, tree density is greater in wildfire sites, and in association with the patchy distribution of trees, wildfire sites provide more edge between dense clumps of trees and openings (see Chapter 3) where nests are most often placed

(Walkinshaw 1983). High tree density also provides greater inter-branch cover at the edge of a clump. The increased tree density and greater coverage of ground cover may also contribute to a more abundant and diverse insect prey base. Perhaps higher quality males are attracted to wildfire areas and females are choosing the higher quality males.

Even though the number of young produced per male is less in plantations than in wildfire sites, the productivity in plantations is enough to more than maintain the population of warblers in this habitat type. On average, plantations are sources rather than sinks. The warbler population growth is slower in plantations than in wildfire sites. As plantations are managed to more closely replicate the conditions in wildfire sites then perhaps productivity will increase to the level of wildfire sites and the population could increase faster. This predicted population increase has been realized only since 1987, as the area of suitably-aged habitat increased. Prior to 1987, the population was habitat limited (Probst and Weinrich 1993). The warblers were occupying marginal sites, such as the harvested stands (Chapter 2), which were likely habitat sinks. These conclusions are tentative because they are based on calculations using adult and juvenile survivorship estimates from all habitat types. If the survivorship values vary by habitat type, the conclusions may change. The analysis must be repeated after survivorship estimates

are made for each habitat type.

Reproductive success per nest is used to evaluate the cowbird control program. The program has succeeded because the reproductive success of Kirtland's warblers is not currently significantly affected by cowbird parasitism. The number of young fledged per nest is comparable to other non-parasitized passerine species (Nolan 1978). The number of nests parasitized is very few (1/48 nests with known number of young fledged).

The proportion of males that are polygynous does not seem to be affected by the scarcity of suitable habitat as suggested by Probst and Hayes (1987), or by the age and proximity of nearby sites as suggested by Radabaugh (1972). Polygyny is spatially and temporally widespread. It does not appear to be a biogeographic phenomenon because it occurs in stands of all ages, in all locations of the breeding range, in stands that are isolated, and in stands that are part of a complex.

The polyterritorial behavior of not only polygynous males but also of monogamous and unmated males suggests that the behavior is a viable reproductive strategy employed by males. It appears to be opportunistic because males change mating status from year to year.

It may be costly for females to become secondary mates, as suggested by anecdotal evidence of reduced weight and tarsus length of young produced in nests of polygynous males

(Bocetti, unpubl. data). Also, the females at those nests had resorbed pectoralis muscles and low body weights. Perhaps females pay an energetic cost as they attempt to compensate for reduced male care, and they pay a reproductive cost because the young are less healthy. Perhaps females become second mates because they are deceived by the male regarding his already-mated status. Alatalo et al. (1981) suggest that males are polyterritorial so that they may deceive females. The distance between territories of polyterritorial males is approximately one territory width or more, perhaps far enough apart that a female cannot hear singing from one territory to the other.

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DISTRIBUTION OF NEST SITES

In territorial bird species, two types of nest site distributions may be considered: the distribution of nests within territories, and the distribution of nests relative to other nests. The former may be described by the frequency distribution of distances from the nests to the nearest edge of the territory, and the latter may be described by the frequency distribution of distances between nests and their nearest neighboring nest.

The nest-to-nest pattern was first investigated by Tinbergen et al. (1967) who suggested that "spaced-out" nests should have lower predation risks. Other studies, of artificial nests, corroborated that a uniform distribution had lower predation rates than clumped or random distributions. In these studies, however, parents were absent (Andersson and Wiklund 1978), or predators were present in unusually high density (Picman 1988). Studies of natural nests have not confirmed Tinbergen et al.'s results (Blancher and Robertson 1985, Andrén 1991, Schieck and Hannon 1993). Andrén (1991) criticized artificial nest studies for using greater than natural densities of nests,

and suggested that predation is an overrated factor for explaining nest site dispersion in birds.

An additional explanation for nest site distributions involves the competing strategies of males and females to maximize reproductive success. A brief supposition regarding the possible, ideal nest distributions for each sex will elucidate the conflict between the sexes. Perhaps the ideal nest-to-nest pattern for a male is a clumped distribution of nests (females) that makes it easier for him to monopolize fertilizations, and the ideal nest-to-edge pattern is to place the nest(s) at the center of his territory to maximize the distance between his females and other males. Perhaps the ideal nest-to-nest pattern for females is a uniform distribution where females do not share resources (including male care), and if females want extra-pair fertilizations (EPF's), the ideal nest-to-edge pattern is to place the nest at the edge of the tending male's territory to increase the opportunities for EPF's. Male and female goals regarding nest placement may be in conflict, with each other or with other ecological constraints. The current variety of nest distributions in different species may reflect the various forms of evolutionary compromise between the sexes and other ecological factors.

Predation pressures and sexual selection pressures may not be mutually exclusive explanations for nest-to-nest distributions. For example, predation pressure may provide

the selective force by which aggressive females are favored, and this elevated aggression in females leads to greater female:female aggression, providing the mechanism for "spaced out" nest dispersion. The nest-to-nest distance may indeed be much greater than the detection distance of predators with area-restricted search patterns, but the distribution may still be ultimately influenced by predation pressure. Female:female aggression may also be the result of sexual selection pressures alone.

Some studies suggest that the within-territory nest distribution may favor the ideal male strategy. Møller (1990) suggested that males maximize the distance between females and other males, and concluded that males increase territory size during the female's fertile period to minimize the risk of intrusions and EPF's by other males. However, Dunn (1992) questioned this conclusion, suggesting possible alternative explanations for territory expansion during the nesting cycle, such as food abundance, male competition, or female choice for large territories. Møller's conclusion depended on the central location of females and nests, which he does not present as an observed or tested pattern. Mayfield (1960) observed that female Kirtland's warblers (Dendroica kirtlandii) settled in the center of the territory, but he did not test this hypothesis. Schieck and Hannon (1993) showed that female

willow ptarmigan (Lagopus lagopus) non-randomly placed their nests toward the centroid of the territory.

A few studies suggested that the nest-to-nest distribution may favor the ideal male strategy. Herremans (1993) found that wood warbler (Phylloscopus sibilatrix) territories, and thus nests, were clustered, and concluded that this pattern was due to the direct social advantage to males (increasing reproductive success) rather than to the clustering of food resources. Graves (1992) described a single, unusual case of aggregated nest placement in the Swainson's warbler (Limnothlypis swainsonii), whose breeding biology was otherwise poorly known, where two females placed their nests 2.8 m apart in the center of the male's territory.

I know of no studies that have shown nests to be non-randomly distributed toward the edge of territories. However, the within-territory pattern of nest placement has rarely been studied. Other evidence showing that females initiate or seek EPF's, suggests that nest placement near the edge of a territory may be important for some species. Recent studies found that females were seeking EPF's, most likely to obtain better genes for their offspring (swallow, Hirundo rustica: Møller 1988; black-capped chickadee, Parus atricapillus: Smith 1988; blue tit, Parus caeruleus: Kempenaers et. al. 1992). Two of these studies were on cavity-nesting species, and the availability of cavities was

likely a limiting ecological constraint that determined the pattern of nests within territories, thus masking the ideal female pattern.

Many studies suggest that the nest-to-nest distribution may favor the ideal female strategy. Aggression by a paired female can prevent the settlement of a second female in the same territory or vicinity (chaffinch, Fringilla coelebs: Marler 1956; willow ptarmigan, Hannon 1983; red-winged blackbird, Agelaius phoeniceus: Hurly and Robertson 1984, Searcy 1986; song sparrow, Melospiza melodia: Arcese 1989; pied flycatcher, Ficedula hypoleuca: Lundberg and Alatalo 1992). Anecdotally, I have observed intense aggression among female Kirtland's warblers and among female Nashville warblers (Vermivora ruficapilla) during the breeding season. However, none of the above studies shows that female aggression does more than prohibit the local settlement of another female. They do not show that female aggression produces an area of exclusion large enough to result in a non-random, uniform dispersion of nests. Schieck and Hannon (1993) found that willow ptarmigan nests are non-randomly over-dispersed (regular, according to Southwood 1978: 27), and they speculate that the pattern is due to the behavior of the hens. Yasukawa and Searcy (1981) show that despite female aggression, there is no evidence that red-winged blackbird nests initiated close together in time are spatially separated, i.e., they are not spaced differently

from random. This evidence is complicated by the temporal component because female aggression likely succeeds to disperse nests through time (Yasukawa and Searcy 1981).

Some studies suggest that neither the ideal male strategy nor the ideal female strategy is favored, but rather other ecological constraints are more important and thus mask the ideal nest distributions of both sexes. Lightbody and Weatherhead (1987) showed that female yellow-headed blackbirds (Xanthocephalus xanthocephalus) settled randomly in male territories, and Dale and Slagsvold (1990) suggested that female pied flycatchers arrived randomly with regard to area and settled with the first male they encountered. Davies (1992) showed that female dunnocks (Prunella modularis) settled randomly with regard to male territories because females settled first on the breeding grounds in relation to food abundance and distribution (Davies 1985).

A useful first step in understanding the process of nest placement with regard to the possible conflicting goals between males, females, and other ecological constraints, is to determine actual nest distributions. Both patterns of nest site placement are evaluated for the Kirtland's warbler. This species is a resource-defense, territorial songbird with male parental care and occasional polyterritorial polygyny. Females choose the nest sites after the males establish their territories (Mayfield 1960,

Walkinshaw 1983). For the distribution of nests within territories, three alternative hypotheses are evaluated: females place nests toward the center, females place nests toward the edge, or females place nests randomly with regard to territory boundary. For the distribution of nests relative to other nests, three alternative hypotheses are evaluated: nests are uniform (or regular as defined by Southwood 1978: 27), nests are clumped (or contagious as defined by Southwood 1978: 27), or nests are randomly distributed.

Methods

Territories of singing males were plotted during the breeding seasons of 1990-92 on false-color, infrared, aerial photographs with a scale of 1 inch equals 250 feet. All males were observed for at least 90 minutes on at least two days, beginning prior to 15 June. After this date territories tend to collapse as nesting attempts enter the nestling phase (Stefanski 1967). The territories were defined by connecting the outermost points at which the male was recorded, forming minimum convex polygons (White and Garrott 1990: 148 - 154). Nests or approximate nest locations, as indicated by the food-carrying behavior of the parent warblers, were found on all territories. Territories and nest sites were digitized with ArcInfo software and converted to raster format with a cell size of 5-m X 5-m.

The first analysis, investigating the distribution of nests within territories, included 85 territories from 21 study sites. The territory was treated as the primary sampling unit. The shortest distance from each cell to the territory perimeter was recorded, as was the maximum (MAX) of these distances for each territory. The distance from the nest to the nearest perimeter was also recorded. The MAX represents the distance from the perimeter to cells in the center of the territory. Both size and shape of the territory determine the number of, and distance value assigned to, cells in the center of the territory.

To evaluate the frequency of nests in concentric zones of a territory, I divided each territory into five zones based on distance to the perimeter. The boundaries between these zones were $0.2MAX$, $0.4MAX$, $0.6MAX$, and $0.8MAX$. For a given zone, let $\delta_i = 1$ if the nest in territory i was in the zone and 0 otherwise. Let $p_i =$ the proportion of territory i covered by the zone so that under the null hypothesis of random placement of nests, the $P(\delta_i = 1) = p_i$. Furthermore, let $d_i = \delta_i - p_i$. Then d_i is a random variable with expectation 0 under the null hypothesis that nests are distributed at random, and the mean of d_i , \bar{d} , and its standard error thus provide an appropriate basis for testing the null hypothesis that females place nests at random within territories. Finding that \bar{d} for a given zone is significantly less than 0 indicates a tendency to avoid the

zone when selecting nest sites, whereas a significantly positive value of \bar{d} indicates a tendency to settle more often in the zone than expected under the null hypothesis. Thus, t-tests using \bar{d} and its standard error were used to determine which zones, if any, were avoided or favored during nest site placement. Lack of independence among the five possible tests (one for each zone) and interpretation of significance to account for multiple comparisons is discussed below in Results. The p_i for each zone in each territory was determined with a computer program that randomly selected 100 locations in each territory and then recorded the proportion of those points that fell in each zone.

The computer program also determined the distance from each of those 100 random points to the territory perimeter, and then calculated the mean distance, \bar{x}_i , for each territory. To evaluate the mean distance from nests to territory perimeters, let $t_i = b_i - \bar{x}_i$ where b_i is the observed distance from the nest to the perimeter of the i^{th} territory and \bar{x}_i is the mean distance from random points to the perimeter of the i^{th} territory. Then t_i is a random variable, and the mean of the t_i , \bar{t} , and its standard error also provide an appropriate basis for testing the null hypothesis that females place nests at random within territories. Under the null hypothesis of random placement of nests, the expected value of \bar{t} is 0. Finding that \bar{t} is

significantly negative indicates that females place nests farther from the territory edge than expected under the null hypothesis of random nest placement, whereas a significantly positive value indicates that females place nests closer to the perimeter than expected under the null hypothesis. Thus, a t-test using \bar{t} and its standard error was used to determine if females place nests, on average, farther or closer to the territory perimeter than expected under random nest placement.

The second analysis, investigating the proximity of nest sites, included 15 study sites that had three or more nest sites. The primary sampling unit was the study site. The nearest-neighbor distance (NND) for each nest site and the standard deviation (SD) of NND's for each study site was recorded. The variability of NND's is a measure of the dispersion of nests. The mean SD's of random NND's were determined for each site with a computer program that randomly selected 100 locations within territories, using selection probabilities that replicate the observed distribution of nests within territories from the first analysis because the within territory restriction on nest placement might affect the proximity of nests. For comparison, the simulation was also run with no restriction on the selection of random points. For 100 iterations on each study site, a random nest site was chosen for each territory, and NND's were calculated. A SD of NND's was

determined for each iteration at each site, and a mean SD was calculated for all iterations at each site. Let the SD of observed NND's for the i^{th} study site = v_i , and the mean SD of random NND's for the i^{th} study site = \bar{n}_i . Furthermore, let $s_i = v_i - \bar{n}_i$. Then, s_i is a random variable, and the mean of s_i , \bar{s} , and its standard error provide an appropriate basis for testing the null hypothesis that females place nests randomly relative to other nests. Under the null hypothesis of random nest placement, the expected value of $\bar{s} = 0$. Finding that \bar{s} is significantly less than 0 indicates that the variation of NND's is less than expected under the null hypothesis of random placement of nests, i.e., the nests are more regularly spaced. Finding that \bar{s} is significantly greater than 0 indicates that the variation of NND's is greater than expected under the null hypothesis, meaning that nests are more clustered. A t-test using \bar{s} and its standard error was used to determine if the nests were dispersed in a non-random pattern relative to other nests.

Results

Distribution of nests within territories -- The observed proportion of nests in the outer zone was significantly smaller than the expected value under the null hypothesis of random nest placement (26% vs. 40%, $\bar{d} = -0.14$, $P = 0.003$), indicating a tendency for females to avoid the outer portion of the territory when choosing a nest location (Figure 11).

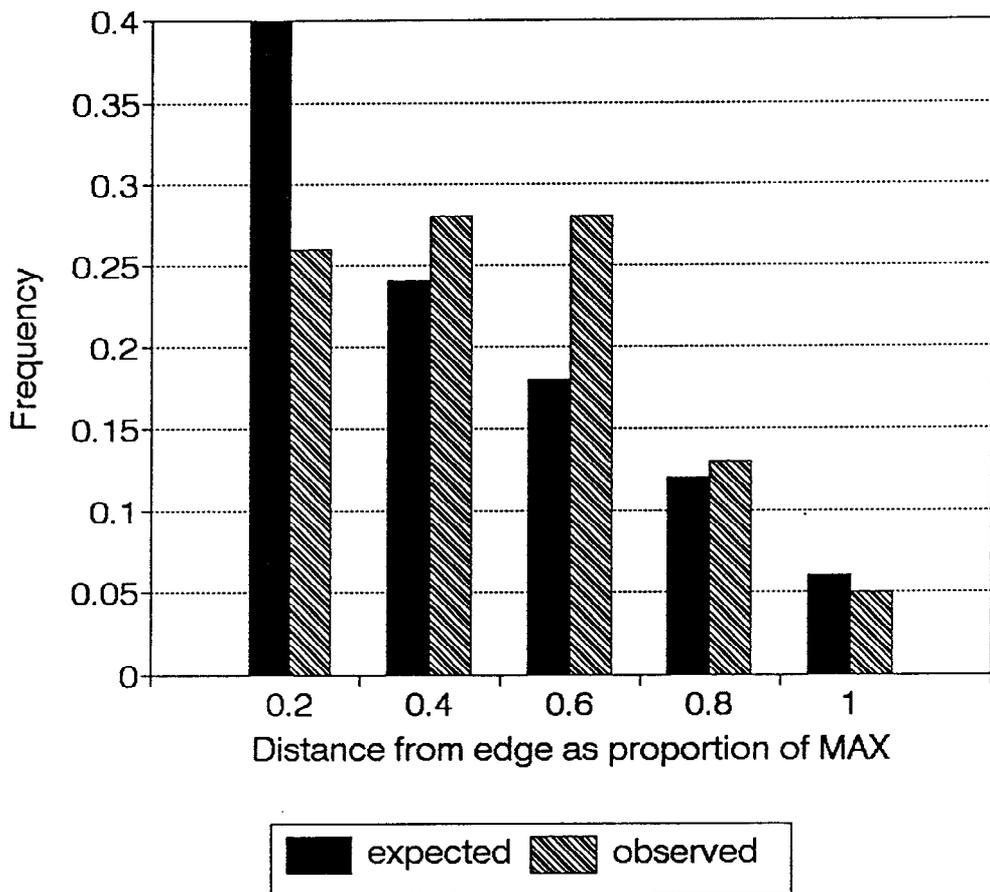


Figure 11. Frequency of nests in five zones defined by distance from the edge of territories (see text) and expected frequency under the hypothesis that nests are placed randomly within territories.

The observed proportion of nests in the third zone, bounded on the outside by 0.4MAX and on the interior by 0.6MAX, was significantly greater than the expected value under the null hypothesis (28% vs. 18%, $\bar{d} = 0.10$, $P = 0.030$), indicating a tendency for females to prefer this zone of the territory when selecting a nest location (Figure 11). The proportions in the other three zones were not significantly different from the expected values under the null hypothesis ($P = 0.362$, 0.839 , 0.501 in zones 2, 4 and 5, respectively). Because the five tests (one for each zone) were not independent and were evaluated with univariate tests, spurious results were possible. If each test was interpreted in isolation, the multiple comparison issue would be important. However, the trend indicated by all five zones was considered, and the general pattern suggested a tendency to settle in the middle zones of the territory and avoid the outer zones. In support of this interpretation, the mean nest-to-nearest-edge distance was 18.9 m, significantly farther ($P = 0.008$) from the edge than the expected value, 15.4 m, under the null hypothesis of random nest placement. The mean MAX distance was 48.1 m.

Distribution of nests relative to other nests -- As shown in Table 28, the observed SD's of NND's, v_i , were quite similar to the expected values under the null hypothesis of random nest placement, \bar{n}_i . The mean difference, \bar{s} , was 0.452 (SE =

Table 30. Observed standard deviation of nearest neighbor distances (v_i), the expected standard deviation of nearest neighbor distances under the null hypothesis of random nest placement (\bar{n}_i), and the "observed - expected" difference (s_i), for $i = 1$ to 15 Kirtland's warbler study sites.

Site	Observed SD (v_i)	Expected SD (\bar{n}_i)	Difference (s_i)
1	4.382	6.235	- 1.853
2	5.686	3.460	2.227
3	5.671	4.240	1.431
4	12.083	7.665	4.418
5	7.698	5.043	2.654
6	3.392	4.164	- 0.772
7	23.844	22.859	0.985
8	2.163	2.828	- 0.665
9	1.051	3.771	- 2.720
10	3.876	3.504	0.372
11	10.431	9.530	0.902
12	9.564	8.778	0.786
13	3.334	6.467	- 3.134
14	5.992	5.879	0.113
15	6.950	4.913	2.037

0.530, $P = 0.408$), which was not significantly different from zero, indicating that females do not choose nest sites different from random relative to the location of other nest sites. The simulation run without restrictions on the selection of random points was very similar to the original simulation, increasing the variation in NND's only slightly.

Discussion

The analysis of nest distribution within territories supports Mayfield's (1960) observation that female Kirtland's warblers preferentially place their nests toward the center of the territories established by the males. The data suggest that females avoid the edge of the territory, and prefer the zone midway between the edge and the center. It appears neither the ideal male strategy nor the ideal female strategy for nest placement within a territory is favored in this species. Perhaps the preference for the "middle" zone reflects the evolutionary compromise between the sexes. A male may have adequate distance between his female and other males such that he can sufficiently guard his paternity, and a female may be close enough to the perimeter that she may pursue EPF's, especially just prior to cuing her mate of her fertile status. Lumpkin (1980) and Arvidsson (1992) suggest that females control onset and rate of copulation, and thus guarding, by cuing males with copulation solicitation behaviors. In addition to the

competing strategies of the sexes, the distribution of nests within territories is likely influenced by other ecological factors. Schieck and Hannon (1993) propose alternative hypotheses for the placement of nests toward the centroid of the territory. First, they propose that nests are centrally located to decrease travel time and increase foraging efficiency during incubation. In a species such as the Kirtland's warbler with a prolonged incubation period (Mayfield 1960) and a nestling period, this may be an important selective force. Second, they propose that females may be avoiding the territory perimeter because conspicuous territorial disputes may attract predators to the territory boundaries. As a corollary to this hypothesis, it is possible that nests may be centrally located to decrease the vigilance distance for males and females as they forage during the incubation and nestling phases of the nesting cycle.

The analysis of nest proximity showed that the variation in nearest neighbor distances is not different from random. Because the simulation with no restrictions on random nest site selection is only very slightly different from the simulation that limited nest site selection according to the observed distribution in the first analysis, it seems that the within-territory pattern does not affect the pattern of female nest placement relative to other nests. It seems that neither the male nor female

ideal strategy of nest placement relative to other nests is favored in this species. Whether the observed pattern reflects some evolutionary equilibrium between the competing sexes or the importance of other ecological constraints that mask the competition between the sexes is unknown. The Kirtland's warbler has large, all-purpose territories (Mayfield 1960) and the distance between nests is, thus, quite large. It is doubtful that any predator would have a large enough area-restricted search pattern (Tinbergen et al. 1967) to account for this nest spacing. Therefore, I do not believe that predation is an important ecological factor influencing the distribution of nests relative to other nests. I have observed female:female aggression in the Kirtland's warbler, yet no site-wide spatial consequences are evident. Perhaps a temporal distribution of nests exists as suggested by Yasukawa and Searcy (1981). When females are competing for male parental care, the asynchrony of nests may allow the first female to monopolize the male's help. The polyterritorial, polygynous Kirtland's warbler males do seem to help the primary female more than the secondary female. Perhaps female aggression is important to the local expulsion of other females (competition for food or nest sites), but the size of the exclusive area is too small to result in a site-wide dispersion of females, especially in patchy habitat which is not "full".

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Summary of Major Findings

The landscape-scale evaluation of plantation use reveals that the density of male Kirtland's warblers (Dendroica kirtlandii) in plantations is 0.21 per 40 acres per year over the life of a stand, and the density of males in wildfire sites is 0.19 per 40 acres per year over the life of a stand. Harvested stands support 0.02 male per 40 acres per year over the life of a stand. This disparity suggests that harvested stands are less suitable than plantations and wildfire sites. Mean density deviation (an index of male density) is primarily influenced by habitat type, but the distance from a stand to the center of the range also affects mean density deviation.

The local-scale evaluation of plantation use reveals that plantations have more unmated males (28% vs. 8%) and fewer polygynous males (6% vs. 22%) than wildfire sites. The differences in mating success between habitat categories are not significantly influenced by stand location in the breeding range, by stand isolation, or by stand age. The reproductive success per nest is very similar between habitat categories. The clutch size is 4.61 eggs per nest

in plantations and 4.57 eggs per nest in wildfire sites. The number of young fledged per nest attempt is 3.57 young in plantations and 3.61 young in wildfire sites. Predation rates are lower in plantations, but not significantly so.

By combining results of the landscape-scale and local-scale evaluation of plantations, I calculated the density of females and density of young. Based on mating success data in each habitat category, sex ratios are calculated, and the density of females is extrapolated for each habitat category. The sex ratio is 1 male to 0.78 female in plantations, and 1 male to 1.14 females in wildfire sites. The density of females is 0.16 per 40 acres per year over the life of a stand in plantations, and 0.22 per 40 acres per year over the life of a stand in wildfire sites.

Females use plantations significantly less than wildfire sites. The density of females is the same as the density of nests attempts, so the reproductive success per nest attempt can be used to extrapolate the density of young fledged for each habitat category. The density of young fledged is 0.58 per 40 acres per year over the life of a stand in plantations and 0.78 per 40 acres per year over the life of a stand in wildfire sites. Plantations produce fewer young than wildfire sites due to the skew in the number of nests initiated. However, plantations produce enough young to replace the number of adults that fail to return each year

plus a surplus of young, thus serving as a source of young to the population of warblers.

The local scale evaluation of plantations reveals the differences and similarities of habitat characteristics between habitat categories. The important similarities between plantations and wildfire sites are: the distribution of sizes of openings among the jack pine (Pinus banksiana), the physiography, and the soils. Land managers have succeeded in selecting Kirtland's Warbler Management Areas that have landscape features of the natural habitat. They have also succeeded in producing a patchy pattern of jack pine regeneration that replicates the natural wildfire habitat. The important differences between habitat categories are: lower jack pine density, fewer openings, lower percent cover of shrubby ground vegetation species such as blueberry (Vaccinium angustifolium) and bearberry (Arctostaphylos Uva-ursi), lower relative frequency of bearberry, lower percent cover of woody debris, and higher percent cover of the sedge (Carex pennsylvanica) in plantations. The comparison of habitat characteristics of nest sites to the available habitat characteristics reveals that several of the above differences are important to the endangered species. Warblers select nest sites with higher jack pine densities and higher percent cover of blueberry than would be expected if the nests are placed at random.

They also choose nest sites with lower percent cover of woody debris than expected if nests are placed at random.

The theoretical evaluation of nest site dispersion revealed that females non-randomly select nest sites with regard to territory boundaries, but the pattern is not different from random with regard to nearest nests. The non-random distribution of nests within territory boundaries suggests that females avoid placing nests near the perimeter of territories, and select the middle zone for nest placement more than would be expected if the nests were placed at random.

Management Recommendations

Future demographic predictions should include separate categories for plantations and wildfire sites due to the significant differences in mating success and thus density of females and number of young produced in each habitat category. Estimates of survivorship should also differentiate between habitat types.

If management resources are limited, land managers should invest in habitat management near the core of the range before investing in the creation of peripheral sites. Plantations are much more suitable than harvested sites.

The methods of plantation management for the endangered species should be modified so that plantations more closely resemble wildfire sites and provide the habitat

characteristics used by the warblers. Instead of total tree harvest, branches could be left on site to provide fuel for hot prescribed burns. This will not only provide the conditions for shrubby ground vegetation, but also perhaps provide additional, natural jack pine regeneration.

Alternatively, new scarification methods should be tested to determine if they provide the same opportunity for shrubby ground vegetation species to invade the site. Jack pine regeneration methods should provide a greater density of pines, and provide more openings. This increased density may be achieved by planting jack pine in clumps along the edge of openings.

Suggestions for Future Research

At the landscape scale, additional variables can be tested to determine their influence on occupation of plantations and wildfire sites, as in Chapter 2. Such predictor variables include: harvest method, site preparation method, time from harvest to regeneration, time from site preparation to regeneration, density of snags, jack pine density, density of deciduous trees, or any others that land managers deem relevant. The analysis may be accomplished with a Geographical Information System (GIS) to assemble the data and the general linear model to test the data.

The territories of all the males studied could be digitized and submitted to a use-versus-availability analysis with GIS, to determine the relative importance of specific habitat characteristics. I have data for each male that describes the substrate used by the male throughout territory plotting. This analysis would complement the same analysis being done by National Biological Survey (Kepler and Sykes), and would increase the sample size significantly.

At the local scale, a survey of Kirtland's warbler habitat for insects would provide baseline data of the insect prey base available to the warblers. A foraging study would reveal which insects are used by the species, as well as the foraging behavior of the species. The sexes may forage at different levels in the substrate, and plantation management should provide the structure for both sexes to forage.

Also at the local scale, a survey of predator species and a study of predation pressure could be conducted. As land use changes continue to occur around the Kirtland's Warbler Management Areas, the abundance and distribution of potential predators is likely to change. In addition, it is another aspect of plantation evaluation. Plantations should provide optimum habitat for the warblers, but not for predators. This is not a high priority study, because the

reproductive success data suggest that predation pressures are not detrimental to the population at this time.

Once the population model for the species has been developed (currently being constructed by J. Bart), the model can be used for many fruitful analyses. The sensitivity of the species to various management scenarios may be tested. The delisting criteria can be evaluated, including the population goal of 1,000 breeding pairs. The viability of a second population can be explored.

A second phase of this study may be conducted around the year 2000, when the population is expected to reach a new carrying capacity and should be redistributed among the habitat categories. The managed habitat should hold a greater proportion of the population at that time. A second investigation of the mating success and reproductive success may be fruitful at that time for two reasons. First, the investigation will again provide an evaluation of habitat management. Many improvements in plantation management were instituted in the early 1990's and should be suitably-aged by 2000. The study would assess the success of the improvements. Second, the investigation will provide insight as to whether the frequency of polygyny was a result of the population dynamics at the time of the current study. The data in this study suggest that polygyny was not a result of habitat abundance and distribution, but only 5 years were used to search for a trend. The study would

investigate the frequency of polygyny under a new

distribution of warblers in the habitat.

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APPENDIX A

List of plant species found during
habitat analysis.

Table 31. Complete list of plant species found in 1-m X 1-m plots during a study of the characteristics of Kirtland's warbler habitat.

TREES	FORBS	GRASSES/SEDGE	MOSS/LICHEN
<i>Acer rubrum</i>	<i>Amelanchier sanguinea</i>	<i>Agropyron repens</i>	<i>Cladonia</i> spp.
<i>Amelanchier spicata</i>	<i>Anenome canadensis</i>	<i>Andropogon Gerardi</i>	<i>Polytridium juniperifolium</i>
<i>Crataegus</i> spp.	<i>Anenome cylindrica</i>	<i>Andropogon scoparius</i>	<i>Sphagnum</i> spp.
<i>Pinus banksiana</i>	<i>Anenome quinquefolia</i>	<i>Carex pensylvanica</i>	
<i>Populus grandidentata</i>	<i>Antennaria neglecta</i>	<i>Danthonia spicata</i>	
<i>Prunus pensylvanica</i>	<i>Apocynum androsaemifolium</i>	<i>Descampsia flexuosa</i>	
<i>Prunus serotina</i>	<i>Arctostaphylos Uva-ursi</i>	<i>Festuca ovina</i>	
<i>Prunus virginiana</i>	<i>Aster laevis</i>	<i>Oryzopsis asperifolia</i>	
<i>Quercus ellipsoidalis</i>	<i>Aster macrophyllus</i>	<i>Oryzopsis pungens</i>	
<i>Salix humilis</i>	<i>Aster ptarmicoides</i>	<i>Panicum linearifolium</i>	
	<i>Campanula rotundifolia</i>	<i>Poa</i> spp.	
	<i>Cirsium Hillii</i>	<i>Schizachne purpurascens</i>	
	<i>Clintonia borealis</i>	<i>Sorghastrum</i> spp.	
	<i>Comptonia peregrina</i>		
	<i>Convolvulus spithameus</i>		
	<i>Coreopsis lanceolata</i>		
	<i>Diervilla Lonicera</i>		
	<i>Epigaea repens</i>		
	<i>Equisitum hyemale</i>		
	<i>Fragaria virginiana</i>		
	<i>Gaultheria procumbens</i>		
	<i>Helianthemum canadense</i>		
	<i>Helianthus maximiliana</i>		
	<i>Hieracium aurantiacum</i>		
	<i>Hieracium floribundum</i>		
	<i>Hieracium paniculatum</i>		
	<i>Hieracium venosum</i>		

Table 31. (continued)

TREES	FORBS	GRASSES/SEDGE	MOSS/LICHEN
	<i>Houstonia longifolia</i>		
	<i>Hypericum perforatum</i>		
	<i>Krigia virginica</i>		
	<i>Liatris graminifolia</i>		
	<i>Lilium philadelphicum</i>		
	<i>Lithospermum carolinense</i>		
	<i>Maianthemum canadense</i>		
	<i>Melampyrum lineare</i>		
	<i>Mentha</i> spp.		
	<i>Polygala polygama</i>		
	<i>Potentilla simplex</i>		
	<i>Potentilla tridentata</i>		
	<i>Prunus pumila</i>		
	<i>Pteridium aquilinum</i>		
	<i>Rosa blanda</i>		
	<i>Rubus</i> spp.		
	<i>Rudbeckia</i> spp.		
	<i>Senecio pauperculus</i>		
	<i>Solidago hispida</i>		
	<i>Solidago spathulata</i>		
	<i>Spiraea</i> spp. (alba)		
	<i>Taenidia integerrima</i>		
	<i>Taraxacum officinale</i>		
	<i>Tragopogon pratensis</i>		
	<i>Vaccinium angustifolium</i>		
	<i>Vaccinium myrtilloides</i>		
	<i>Viburnum Rafinesquianum</i>		
	<i>Viola adunca</i>		
	<i>Viola pedata</i>		

APPENDIX B

Abbreviations for male identification and
study site identification.

Table 32. Abbreviations for colored bands placed on Kirtland's warblers for unique identification. The four letter band combination represents the bands on the upper left leg, lower left leg, upper right leg, then lower right leg.

ABBREVIATION	COLOR
A	Aluminum = Federal band
B	Blue
G	Green
I	Indigo = dark blue
J	Jet = black
R	Red
W	White
Y	Yellow

Example. BGYA = blue band on upper left leg, green band on lower left leg, yellow band on upper right leg, aluminum band on lower right leg.

Table 33. Abbreviations, counties, and legal descriptions (T = township, R = range, S = section) for wildfire sites.

ABBREV.	NAME	COUNTY	T	R	S
BHS	Bald Hill South	Crawford	27N	1W	20
BHF	Bald Hill Flats	Crawford	26N	1W	28
MLB5	Mack Lake Burn	Oscoda	25N	3E	5
MLB11	Mack Lake Burn	Oscoda	25N	3E	11
MLB12	Mack Lake Burn	Oscoda	25N	3E	12
MLB14	Mack Lake Burn	Oscoda	25N	3E	14
MLB15	Mack Lake Burn	Oscoda	25N	3E	15
MLB16	Mack Lake Burn	Oscoda	25N	3E	16
MLB17	Mack Lake Burn	Oscoda	25N	3E	17
MLB22	Mack Lake Burn	Oscoda	25N	3E	22
NBH	North Bald Hill	Crawford	27N	2W	14
SBB	Stephan Bridge Burn	Crawford	27N	2W	31 32

Table 34. Abbreviations, counties, and legal descriptions (T = township, R = range, S = section) for plantations.

ABBREV.	NAME	COUNTY	T	R	S
BLP	Byron Lake Plantation	Alcona	26N	5E	8
CLN	County Line North	Oscoda	25N	1E	25
CLU	County Line Unit	Oscoda	25N	1E	36
FPC	Fletcher Plantation	Crawford	25N	4W	29
FPK	Fletcher Plantation	Kalkaska	25N	5W	25
OMU21	Ogemaw Management Unit	Ogemaw	24N	1E	21
OMU28	Ogemaw Management Unit	Ogemaw	24N	1E	28
PRU5	Pine River Unit 5	Alcona	25N	7E	29
SHP	Saint Helen's Plantation	Roscommon	23N	1W	1
WBU	West Branch Unit	Oscoda	25N	1E	34