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Title: Patterns of Kirtland's Warbler Occurrence in Landscape Ecosystems of the Mack Lake Burn

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PATTERNS OF KIRTLAND'S WARBLER OCCURRENCE IN LANDSCAPE ECOSYSTEMS OF THE MACK LAKE BURN

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ABSTRACT

The major objectives of the 1988 field research were to determine the number of Kirtland's warblers occupying each of the major physiographic types and the local ecosystem types, to determine the specific characteristics of preferred warbler habitat, and to assess the quality of warbler habitat in different ecosystem types by studying individual warbler territories. In addition, the local ecosystem types, sampled in 1986-88, were contrasted by statistical analyses of physiographic, soil, and vegetation variables.

During the 1988 field season 31 (40%) of the warblers colonized the low-level outwash terrain and 47 (60%) occupied the high-level outwash and ice-contact terrain. Thirty-eight warbler territories were studied, 22 in the low-level terrain and 16 in the high-level terrain. Density of warblers was estimated for each ecosystem type by determining the average distance between territories. Ecosystem type 1 occupies the largest area in the low-level terrain, was the only one colonized in this physiographic type, and supported the largest warbler population of any ecosystem type. In the high-level terrain, 12 of the 16 territories studied were in ecosystem types 7 and 8, and 2 each were in ecosystems 6 and 10. The average distance between a male territory and its nearest neighbor was shortest for ecosystems 8 and 7 (269 and 365 m respectively), and longest (522 m) for ecosystem 10; ecosystem 1 was intermediate (435 m). The density of warblers was greatest in ecosystems 7 and 8, intermediate in 1, and least in 10. Based on this measure of warbler density, the highest quality ecosystems in 1988 are 7 and 8, 1 and 6 are second, and 10 is lowest of the ecosystems occupied.

Warblers in 1988 were found in ecosystem types 1, 6, 7, 8, and 10. These ecosystem types are characterized by (1) jack pine 2.5-4 m tall in patchy, relatively dense stands, (2) uplands with warm air and soil (not depressions or relict melt-water channels), (3) rolling terrain of outwash or ice-contact parent material and Grayling, Graycalm, Montcalm, or Rubicon soil series, and (4) vegetation of patchy, dense jack pine and northern pin oak together with a ground-cover layer dominated by *Vaccinium angustifolium* (low sweet blueberry), *Arctostaphylos uva-ursi* (bearberry), *Gaultheria procumbens* (wintergreen), *Andropogon* spp. (blue stem grasses), and mosses.

Large-scale aerial photographs (1:4500) were excellent for identifying physiographic features such as outwash plains, ice-contact landforms, and old melt-water stream channels. Tree species, such as jack and red pines, northern pin oak, and red maple could be recognized. But the identity and coverage of ground-cover species were problematical. Thus one can distinguish major physiographic types using aerial photographs, but their use in combination with ground reconnaissance is needed to determine and map local ecosystem types.

Reconnaissance in several areas outside Mack Lake, and plot sampling at Bald Hill, indicated that the ecosystem approach -- at both the broad physiographic level and the local ecosystem level -- can be used to distinguish high and low quality warbler habitat. This approach could be used effectively throughout the warbler's potential range in northern Lower Michigan to identify the most productive habitats where management could be centered to increase populations of the Kirtland's warbler.

INTRODUCTION

The project of 1988-89 (field season 1988) was a continuation and expansion of previous research to understand the landscape ecosystems of the Mack Lake burn as a basis for understanding the spatial and temporal patterns of occurrence of the Kirtland's warbler (*Dendroica kirtlandii*). Detailed background information on the Kirtland's warbler and its habitat were presented in the report of 1986 research (Barnes and Bosio 1986), our interim report of 1987 field research (Barnes et al. 1987), the final report of 1987 research (Barnes et al. 1989), and the Master's thesis of Zou (1988). Additional background material and a brief summary of the current situation is presented below.

Warbler Habitat and Territory

Species occur in different patterns in the landscape, i.e., the spatial and temporal arrangement of individuals of the species in different habitats. A habitat of a species is any portion of the surface of the earth where the species is able to colonize and live (Fretwell and Lucas 1970). The total area available to a species can be divided into different habitats. The area of any one habitat can be large or small, and different habitats of the same species may be of different sizes. A given habitat can consist of several subdivisions which are not contiguous and which are essentially homogeneous with respect to the physical and biological features. The physical and biological features are believed to be the most relevant to the behavior, reproduction, and survival of the species (Christian 1971, Chitty 1987, Keith 1983, Gibb 1981, Pearson 1971, Hansson 1979). Therefore, understanding physical and biological features of given habitats of a species is the key to understanding the pattern of a species occurrence. Landscape ecosystem approach provides a useful means to study the physical and biological features of habitats of a given species.

The earliest accounts of the study of dispersal of species over available habitats (i.e., the study of pattern of species occurrence) seem to be those of Howard (1920) who suggested several roles for territorial behavior in birds. Following this classic work, the relationship of territorial behavior to the habitat distribution has been studied extensively of different species (Stewart and

Aldrich 1951, Kluyver and Tinbergen 1953, Tinbergen 1957, Verner et al. 1986, and Clark and Weatherhead 1987). Fretwell and Lucas (1970) and Zimmerman (1982) stated that the habitats used by a species very in quality and suitability for reproduction of the species. Furthermore, Weatherhead and Robertson (1977) concluded that reproductive success of the redwinged blackbirds (*Agelaius phoeniceus*) was correlated positively with quality of the territory.

Summary of Previous Research

Research at Mack Lake was initiated in 1986 at the encouragement and enthusiastic support of Dr. Sylvia Taylor. Concern for the continuing low population of warblers gave impetus for detailed study of the bird's habitat. Much of the previous research had focused on the warbler's life history, biological characteristics, and territorial behavior (Mayfield 1960, Walkinshaw 1983). Less attention has been given to its habitat, although general relationships of vegetation type (jack pine and jack pine and oak forests) ground cover vegetation; height and density of jack pine, soil type, and patchiness of the jack pine cover (amount and distribution of openings) are known (Walkinshaw 1983, Byelich 1976, Probst 1986). Currently, the primary summer range of the warbler is in the lower peninsula of Michigan of ca 120 x 160 km. All nests have been found within 13 counties (Probst 1986). However, the warbler also was reported from Wisconsin in 1988 and 1989.

Population size of males, as determined by annual census, declined from 503 individuals in 1961 (Mayfield 1962) to 201 in 1971 (Mayfield 1973) (Table 1). From 1971 to the present, the male population has fluctuated around approximately 200 individuals. The mean number of singing males from 1971 through 1989 is 206 with the peak of 242 in 1980 and low points of 167 in both 1974 and 1987. Credit for saving the warbler from extinction and stabilizing its population is often given the cowbird control program whereby brown-headed cowbirds (*Molothrus ater*), that parasitize the nests of warblers, are trapped each summer (Ryel 1981). However, the significance of this program in saving the warbler has come under question, and some individuals maintain that it is the amount and quality of the habitat that is and will continue to be the most critical factor. In any event, ecologists such as Dr. Sylvia Taylor and

Table 1. Overall census record of male Kirtland's warblers, 1971-1989 and their occurrence at Mack Lake burn, 1986-1989.

Year	Estimate number of total male warblers[1]	Number of male warblers at Mack Lake burn (1986-1989)
1971	201	
1972	200	
1973	216	
1974	167	
1975	179	
1976	200	
1977	218	
1978	196	
1979	210	
1980	242	
1981	232	
1982	207	
1983	215	
1984	215	
1985	216	
1986	210	14
1987	167	38
1988	207	78
1989	212	101

[1]Personal communication from Jerry Weinrich, Michigan Department of Natural Resources, June 1988.

wildlife biologist and Kirtland's warbler expert, Jerry Weinrich, recognized immediately that the Mack Lake burn by wildfire in May 1980, and covering approximately 24,000 acres, would become first-class warbler habitat. However, only part of the burn is suitable warbler habitat. As of 1989, the part of this burn dominated by jack pine and oak forest now supports nearly half (48%) of the entire population in Michigan (and in the world).

Research was initiated in 1986 just as the first group of 14 warblers colonized the area. By June 1989 the population had increased to 101. Since 1986, it has been possible to identify and describe the major landscape ecosystem types of a major part of the burn (the entire burn area of ca 24,000 acres not all being suitable warbler habitat), and to associate the pattern of colonization by the warbler from 1986-1989 to (1) the 2 major physiographic types, and (2) the 11 local ecosystem types of the burn. In addition, the landscape ecosystem approach allows us to determine some of the reasons why the warbler apparently favors or avoids certain ecosystem types in both space and time. The entire research, conducted over a 3-year period and funded by the Wildlife Division of the Department of Natural Resources, has been an integrated whole whereby the research in 1988-89 is strongly based on previous work and itself continues to add to our understanding of the close relationships of the warbler to the geology, climate, and vegetation of the area.

This integrated approach, whereby landscape ecosystems are the focus or object-of-interest, rather than single factors such as vegetation or soil, was introduced in Michigan (Barnes et al. 1982, Pregitzer and Barnes 1984, Spies and Barnes 1985a) as a modification of a German multi-factor ecological method. It has been used for over 40 years to manage forest ecosystems and wildlife populations in the state of Baden-Württemberg in southwestern Germany. The details of this approach are given in Barnes et al. (1982).

Based on research in 1986 and 1987 we subdivided the area surrounding Mack Lake, in the heart of the burn and in jack pine-northern pine oak forest, into two major physiographic types, termed **low-level outwash terrain** and **high-level outwash and ice-contact terrain.** These areas are about equal in size (Figs. 1 and 2). The low-level outwash terrain surrounds Mack

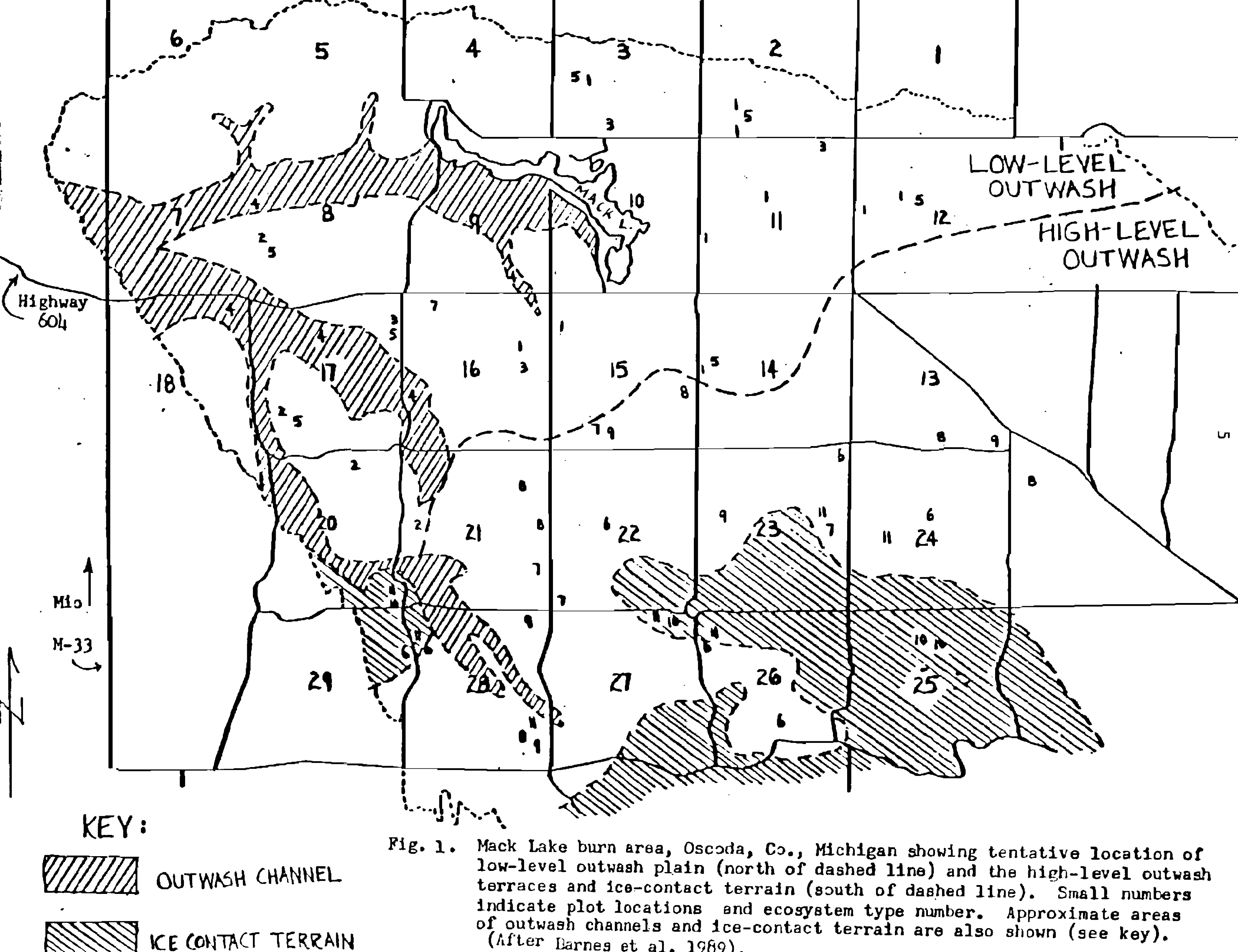

Fig. 1. Mack Lake burn area, Oscoda, Co., Michigan showing tentative location of low-level outwash plain (north of dashed line) and the high-level outwash terraces and ice-contact terrain (south of dashed line). Small numbers indicate plot locations and ecosystem type number. Approximate areas of outwash channels and ice-contact terrain are also shown (see key). (After Barnes et al. 1989).

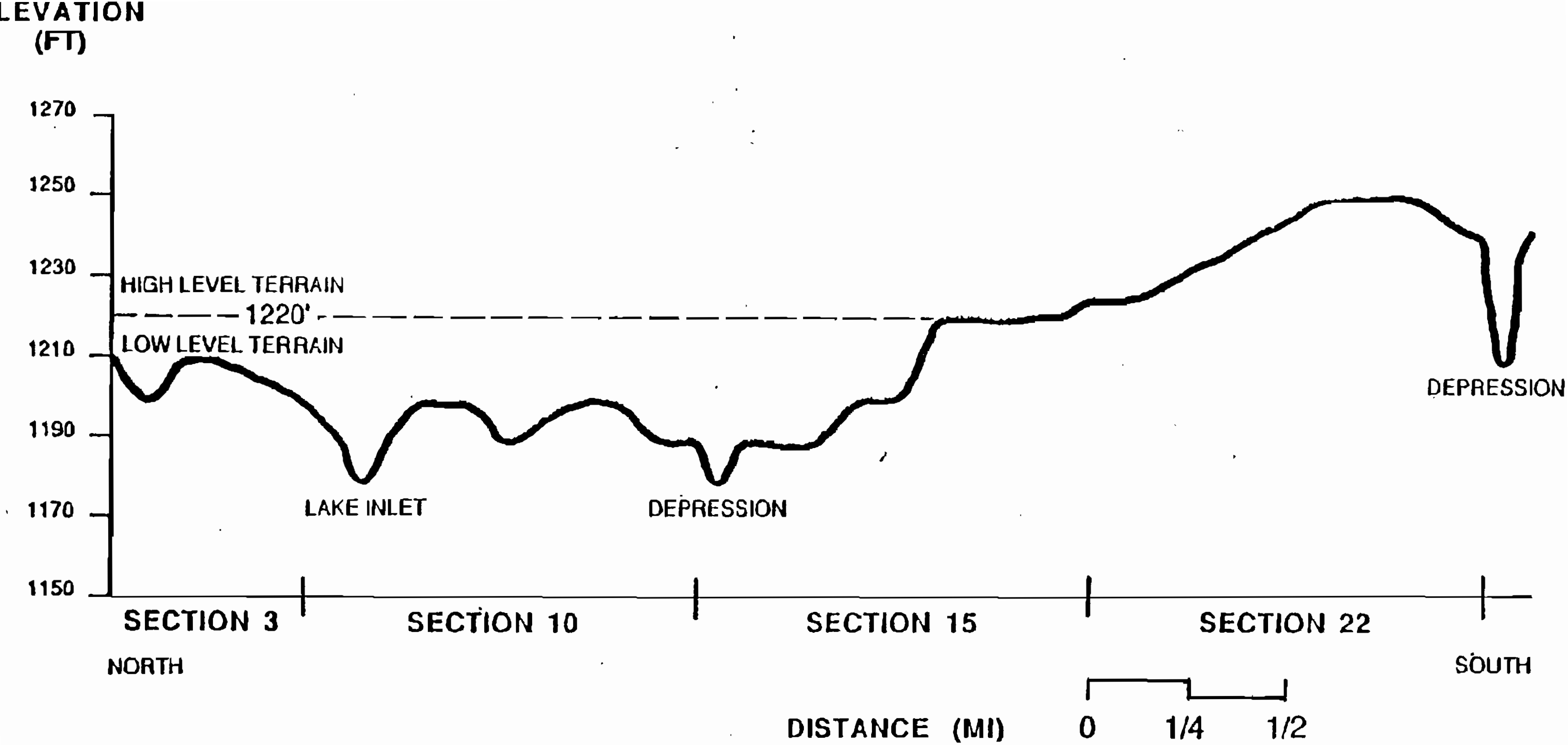

Fig. 2 ELEVATIONAL TRANSECT. N→S ALONG EAST SECTION LINE (FOWLER ROAD)

SECTIONS 3 (1/2 SEC.), 10, 15 & 22

MACK LAKE BURN OSCODA COUNTY, MICHIGAN

Lake; the landscape rises in elevation to the south in a series of outwash or kame terraces that were built adjacent to the receding glacial ice mass. Further south, pronounced ice-contact terrain was evident and characterized by high broad ridges, deep depressions, and small outwash plains -- features that are all typical of ice disintegration terrain. This area burned later in the day of May 10, 1980 which may account in part for its lesser value as warbler habitat. Based on intensive reconnaissance and plot sampling, we drew the boundary between the two major physiographic types at roughly the 1220 contour interval (Fig. 1); lands lower than this elevation were considered part of the low-level terrain. Within the low-level terrain one finds an extensive and gently rolling landscape, small depressions (pitted outwash) are a conspicuous feature. In addition, there are two major glacial melt-water channels that join together west of Mack Lake (Fig. 1). Within each of the major physiographic types we identified, classified, and described a series of local landscape ecosystems; the names and brief description of each ecosystem are presented in Table 2.

It was evident immediately in 1986 that the first 14 colonizing warblers strongly favored (71% to 29%) the high-level terrain that had the taller jack pines and a generally warmer climate (Barnes et al. 1989) (Fig. 3). However, 4 of the singing males were observed in the taller pine patches in the low-level outwash. In 1987, the number of male warblers increased to 38, and 61% were observed in the high-level terrain in local ecosystems 6, 7, 8, and 10 (Barnes et al. 1989). In addition, 65% of the female observations/nesting sites (determined by John Probst, USFS, North Central Forest Experiment Station, St. Paul, MN) were in the high-level outwash and ice-contact terrain. Zou (1988) showed that ecosystems colonized by the warblers were characterized by a patchy distribution of jack pines (dense patches and interspersed openings), whereas ecosystems avoided by warblers had a less patchy and more random distribution of pines. In addition, physiographic, soil and vegetative conditions of the individual ecosystems could be related to the presence or lack of warblers. For example, the greater occupancy of warblers in the high-level outwash terraces and ice-contact terrain (ecosystems 7, 8, 10), as compared to many parts of the low-level outwash plain, were attributed to (1) greater height of 'able 2. Local ecosystem types of the Mack Lake Burn.

I. Low-level outwash plains (Elevation 1160-1220 ft).

A. Upland topography (flat to gently sloping, depressions <5 ft); excessively to somewhat excessively drained.

1. Medium and medium-fine sand, very infertile soils.

2. Medium sand, infertile soils in areas of higher relative elevation between the major outwash channels.

3. Sand to loamy sand over bands of fine texture.

B. Channels and depressions; excessively to somewhat excessively drained

4. Outwash channels (usually 20-50 ft deep) with a distinct pebble/cobble layer.

5. Depressions (5-20 ft deep) with extreme microclimate; soils as in ecosystems 1, 2, or 3.

II. High-level outwash and ice-contact terrain (Elevation 1220-1280 ft).

A. High-level uplands (flat to moderately steep slopes); excessively to somewhat excessively drained.

6. Outwash, gently sloping topography, infertile, medium sand.

7. Outwash, flat topography, typically very infertile, >25% fine sand in top 50-70 cm.

8. Outwash, slightly infertile loamy sand to sand soils; 5-10 cm (cumulative) of fine textural bands.

9. Outwash, slightly to moderately infertile, loamy sand soil or a relatively thick textural band (>10 cm).

10. Ice-contact terrain, infertile sandy kamic hills.

B. Depressions.

11. Depressions (6-50+ ft) with extreme microclimate; soils as in ecosystems 6-10.

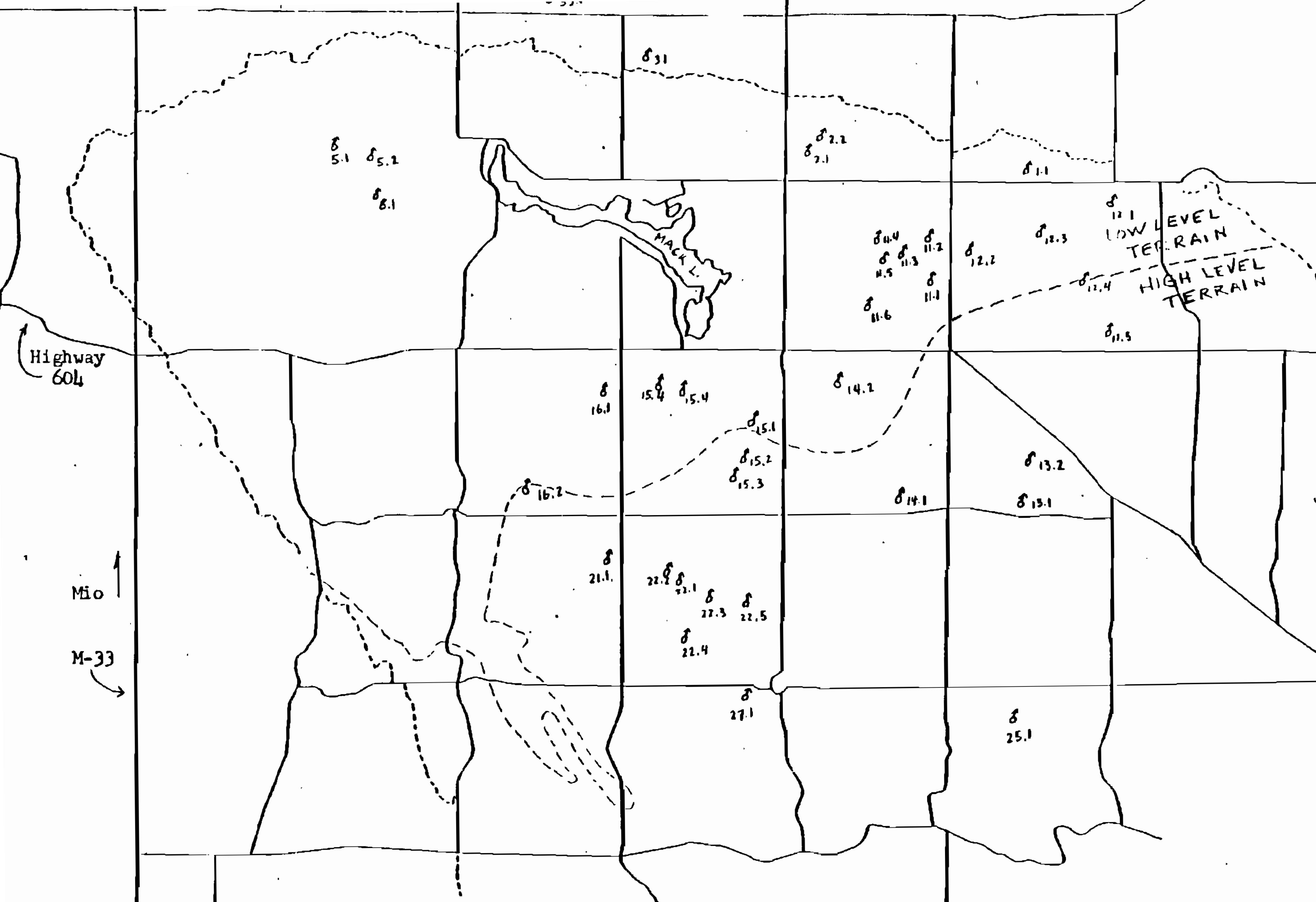

Fig. 3. Mack Lake burn area, Oscoda Co., Michigan. Territory locations of the 38 male Kirtland's warblers studied in 1988. Numbers indicate section number (in front of decimal point) and warbler number (following decimal point) in a given section.

jack pines, (2) greater density of pine regeneration, (3) greater patchiness of pine reproduction, (4) greater ground-cover species diversity, and (5) a generally warmer climate.

Problem

The pattern of warbler colonization of the low-level and high-level landscapes of the burn had been documented for 1986 and 1987, and we were especially interested to see that pattern in 1988 and compare it with the two previous years. In particular, would a greater number of warblers move into the low-level outwash area? This might be expected due to the increase in size of the pines in that area.

In addition, we needed to know more information about the specific sites the warblers occupied. Although from previous research it was clear that singing male warblers favored the high-level outwash and ice-contact terrain and ecosystems 6, 7, 8, and 10 of this area, the specific site and vegetative conditions of their territories was not known. Furthermore, in contrast to applications at other areas in Michigan, we had not been able to map the ecosystem types of the extensive Mack Lake burn due to lack of time and funds. Without such a map one cannot pinpoint for sure the ecosystem type of warbler occupancy and the specific soil and vegetation conditions within that ecosystem. In addition, detailed statistical analyses comparing all ecosystem types, like that done for other areas (Pregitzer and Barnes 1984, Spies and Barnes 1985a) had not been conducted. Analyses for selected ecosystem types were conducted by Zou (1988), and it was important to extend the quantitative analyses to all ecosystem types. By additional plot sampling we could simultaneously increase our data base for quantitative analyses to test ecosystem differences and also gain significant understanding of the specific characteristics of sites frequented by warblers. With the U.S. Fish and Wildlife Service team of Cameron Kepler and Paul Sykes conducting detailed studies at Mack Lake we could combine efforts to maximize our understanding of the specific habitat conditions of warbler territories.

We also wanted to examine the usefulness of low-level aerial photographs (that had just become available) in distinguishing similar ecosystems (for example, 6, 7, 8) and specific ecosystem characteristics (vegetation, physiography) that were favored or avoided by warblers. I was already clear that air photos could be used to distinguish major physiographic differences of the burn and some of the local ecosystem types such as those of depressions (types 5 and 11), large melt-water channels (type 4), and ice-contact terrain (type 10). However, it was not known how finely ecosystem types could be resolved by air photos.

How applicable is the landscape ecosystem approach, and specifically the Mack Lake ecosystem types, to other areas currently occupied by warblers? We hoped to gain at least a partial answer to this important question by visiting a few other areas and establishing plots to document similarities and differences between Mack Lake ecosystems and those of at least one other area.

Based on the above problem statement, the general and specific objectives of the research are presented below:

Objectives

Our general objectives were to gain a more precise understanding of (1) the landscape ecosystems occupied by the warbler in 1988 through field studies and study of aerial photographs and (2) the pattern of occupancy by the warbler in 1988. The specific objectives are:

1. to determine the major physiographic types and the specific ecosystem types occupied by the Kirtland's warbler in 1988 and to compare the 1988 occupancy with that in 1987 and 1986;
2. to determine the specific factors (physiography, local climate, soil, vegetation) of the ecosystems most closely associated with occupancy by the warbler (i.e., what are the specific attributes of preferred warbler habitat?);
3. to assess habitat quality by studying territories of individual warblers;
4. to determine, as far as possible, if low-level aerial photographs can be used to determine ecosystems or ecosystem components (physiography, vegetation) preferred or avoided by warblers in 1988; and
5. if possible, apply the ecosystem approach to the occurrence of warblers in other areas.

An additional objective of our research, stemming from previous research in 1986-87, was to compare and contrast the two physiographic types and the individual ecosystems using statistical analysis of physiographic, soil, and vegetative variables.

METHODS

Field sampling

The territories of 38 warblers were located by sightings of singing males (Fig. 3). Each of the territories was identified as to its ecosystem type (Table 2). Plant species in each territory were recorded. The percentage coverage of each plant species was estimated according to the method used in 1986 and 1987. The distance from a given territory and its closest neighbor was measured from their respective midpoints using the 1988 official census maps (Michigan DNR, Lansing, MI).

Twenty-seven plots were located and sampled -- 22 plots in the Mack Lake burn (Fig. 4) and 5 at the Bald Hill burn. Eighteen plots were located directly in the territory of a warbler; five of these plots were established and sampled at the Bald Hill site. Eight plots were located in sites where temperatures were recorded in 1987. The other one was located in ecosystem 9 in Section 22 at Mack Lake.

Plots were established using methods developed in 1986 and 1987 (Barnes et al. 1989, Zou 1988). Vegetative variables measured or recorded in each plot included jack pine density and coverage, oak height and coverage, number of oak clumps, coverage class of each plant species, and dominant jack pine height and growth in each year. Physiographic variables recorded at each plot were elevation, glacial origin, landform, aspect, slope %, length of slope, and position on slope. A physiographic sketch was drawn of the area surrounding each plot. A soil pit was located adjacent to each plot. Each soil pit was dug to at least 150 cm, and an auger was used to sample, wherever possible, to a depth of 400 cm. Soil samples from the major horizons in each pit were collected. Zou (1988) described in detail the variables recorded in each soil profile. Soil samples were air dried and textural analyses were conducted using a modified Day's hydrometer method (Day 1965, Grigal 1973).

Four representative depressions were chosen to record temperature. One of them was in low-level outwash in the burned area and another was in the high-level outwash in the burned area. The other two sites were separately located in the unburned areas in low-level outwash and in high-level outwash. Maximum-minimum thermometers were placed both at the bottom of

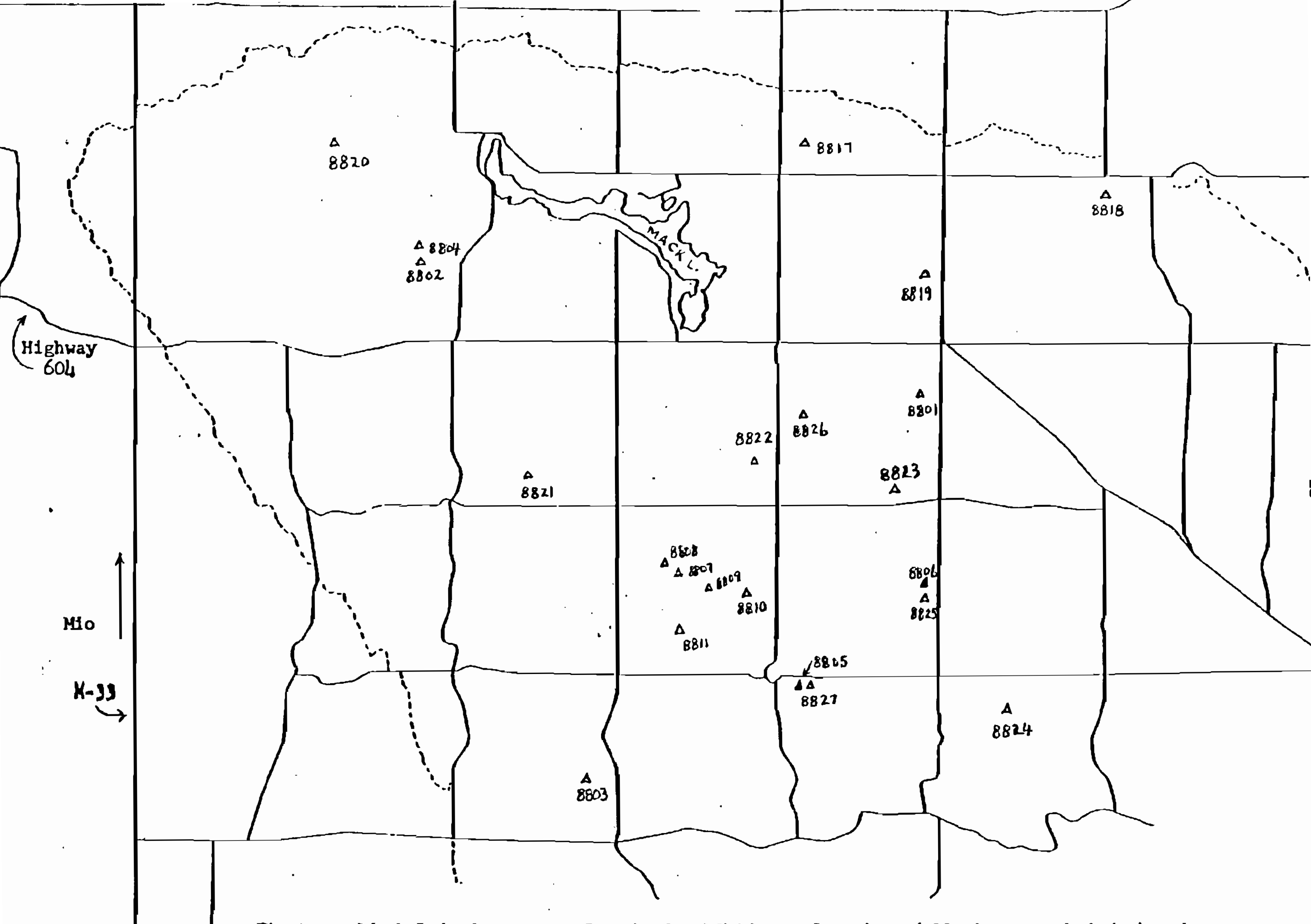

Fig. 4. Mack Lake burn area, Oscoda Co., Michigan. Location of 22 plots sampled during the summer of 1988. Five additional plots were sampled at the Bald Hill area.

each depression and at the edge of the depression in the north direction. The thermometers were positioned so that they faced north and were placed 20 cm above the ground. Maximum and minimum temperatures were recorded about once a week.

Color aerial photographs of scale 1:4500 were used to identify landforms, ecosystem types, and the preferred and avoided summer habitats of the warblers. Information obtained from the photographs was checked on the ground as far as possible.

Parts of the current warbler habitats in Bald Hill burn and the former (in 1940s and 1950s) habitats in the Lovells warbler site were examined. The applicability of the ecosystem approach in these areas and the comparability of Mack Lake ecosystem types at these areas was studied.

Data analysis

Distances between warbler territories of the same ecosystem type were organized by seven distance classes with midpoints varying from 175 to 1075 m (Table 3). The number of warblers by distance class was calculated for each ecosystem type.

Relative "habitat quality" for Mack Lake ecosystem types was assessed by the number of singing male warblers in each ecosystem type and by the proportion of warblers in the distance classes. Although Van Horne (1983) indicated that it is not sufficient to evaluate habitat quality only by density, we have no other data, such as the survival rate and reproduction of the warblers in each ecosystem, to provide a better estimate of habitat quality.

Data on soil variables and tree characteristics from all 11 ecosystem types for Mack Lake plots sampled in 1986, 1987, and 1989 (84 plots) were used in statistical analyses. Twenty-one variables of soil and tree characteristics were used. One-way Analysis of Variance (Neter et al. 1985) was conducted with the MIDAS program of the Statistical Research Laboratory of the University of Michigan. Alpha was set at 0.10 for all tests. The 90% level of significance was chosen because, in distinguishing ecosystem types, single factor measures are not seen to be as important as field integration of all available information. ANOVA assumes normality and homogeneity. These assumptions were tested with skewness and kurtosis coefficients. Normal

Table 3. Range and mean of classes used to estimate the nearest distance between adjacent warbler territories.

Class	Range (m)	Mean (m)
1	100-250	175
2	251-400	325
3	401-550	475
4	551-700	625
5	701-850	775
6	851-1000	925
7	1001-1150	1075

plots, Lilliefor's test, and Bartlett's test. When serious deviations from either normality or homogeneity were shown, variables were analyzed with the Kruskal-Wallis test (Conover 1980). Pairwise comparisons were made by Fisher's LSD when the assumptions of the parametric tests were met, or by the Mann-Whitney U-test when the assumptions were violated.

Eleven soils variables and ten tree variables were analyzed. In all cases a general one-way ANOVA or Kruskal-Wallis test was performed on data from all 11 ecosystem types. If this test determined a difference among the eleven ecosystem types, one complex contrast (comparing high-level versus low-level ecosystems) and 14 pairwise comparisons were performed. Three of the pairwise comparisons (1 v. 6, 3 v. 9, 5 v. 11) contrast the "similar" ecosystem types of the high- and low-levels with each other. The remaining pairwise contrasts were analyses within the high- or low-level groups.

Quantitative analyses for ground-cover vegetation for all 11 ecosystems were conducted on data from 64 sample plots from the 1986 and 1987 field seasons. Six ecological species groups (Barnes et al. 1982, Spies and Barnes 1985b) were developed (Barnes et al. 1989) and used in the analyses together with other vegetative data from the 64 plots. The coverage of each species within a group was summed over each of the 64 plots, and summed again for all species within each ecological species group. A mean coverage for each ecological species group was then obtained for each ecosystem type. One-way ANOVA was performed for the 11 ecosystem types on these data. Multiple comparisons were made between the types with Fisher's least Significance Difference (LSD) test at a 90% confidence level (alpha = 0.10). Residuals were tested for homogeneity with Bartlett's Test of Equal Variances. Residuals were tested for normality using Lilliefor's test, a normal plot, and a measure of skewness and kurtosis. A square root transformation was made on the data for the amount of bare ground, and the ecological species groups in order to meet the assumptions of normality and homogeneity. In only two cases, for ecological species groups, *Arctostaphylos uva-ursii* and *Ceanothus ovatus*, were the assumptions violated. The nonparametric Kruskal-Wallis test was used to make pairwise contrasts in these two cases. Statistical analyses were performed with the MIDAS program of the Statistical Research Laboratory of the University of Michigan.

RESULTS AND DISCUSSION

Pattern of the warbler occurrence in low-level vs. high-level terrain

A total 78 singing male warblers were found in 1988 in the Mack Lake burn (Fig. 5). Among these warblers, 31 (40%) were found in the low-level outwash, including 2 in the warbler management area, and 47 (60%) in the high-level outwash.

In 1986, 4 male warblers (29%) were found in the low-level outwash and 10 warblers (71%) in the high-level outwash (Fig. 6, Barnes et al. 1989). In 1987, 15 male warblers (39%) were found in the low-level outwash and 23 (61%) were in the high-level terrain (Fig. 7, Barnes et al. 1989). Thus, in 1987, the number of warblers increased for the burn as a whole and although a greater proportion still occupied the high-level terrain, there was a trend of increased usage of favorable parts of the low-level outwash. However, in 1988 the pattern of usage was virtually the same as in 1987, i.e., the proportion of warblers occupying low-level and high-level terrain was similar in both years.

During the first three years of colonization (1986-89), warblers favored the high-level terrain over the low-level terrain; the two areas are about the same size. The preference is probably primarily due to the taller pines in many ecosystems of the high-level terrain where soils are better and the temperature is somewhat warmer (Barnes et al. 1989). The low-level outwash has large areas of suitable warbler habitat, and we expected the trend of occupancy in 1988 to shift slightly from the high-level to low-level terrain as the jack pines increased in height in ecosystem type 1. However, in 1989 the two areas are about equally balanced. Of 101 singing males, 49% colonized the low-level outwash and 50% were recorded in the high-level terrain. Based only on the map of male warbler sightings, nearly all of the territories appear to be in ecosystem type 1. In succeeding years we expect not only that more warblers will colonize the burn, but that an increasingly higher proportion will occupy the low-level outwash terrain which is predominantly ecosystem type 1.

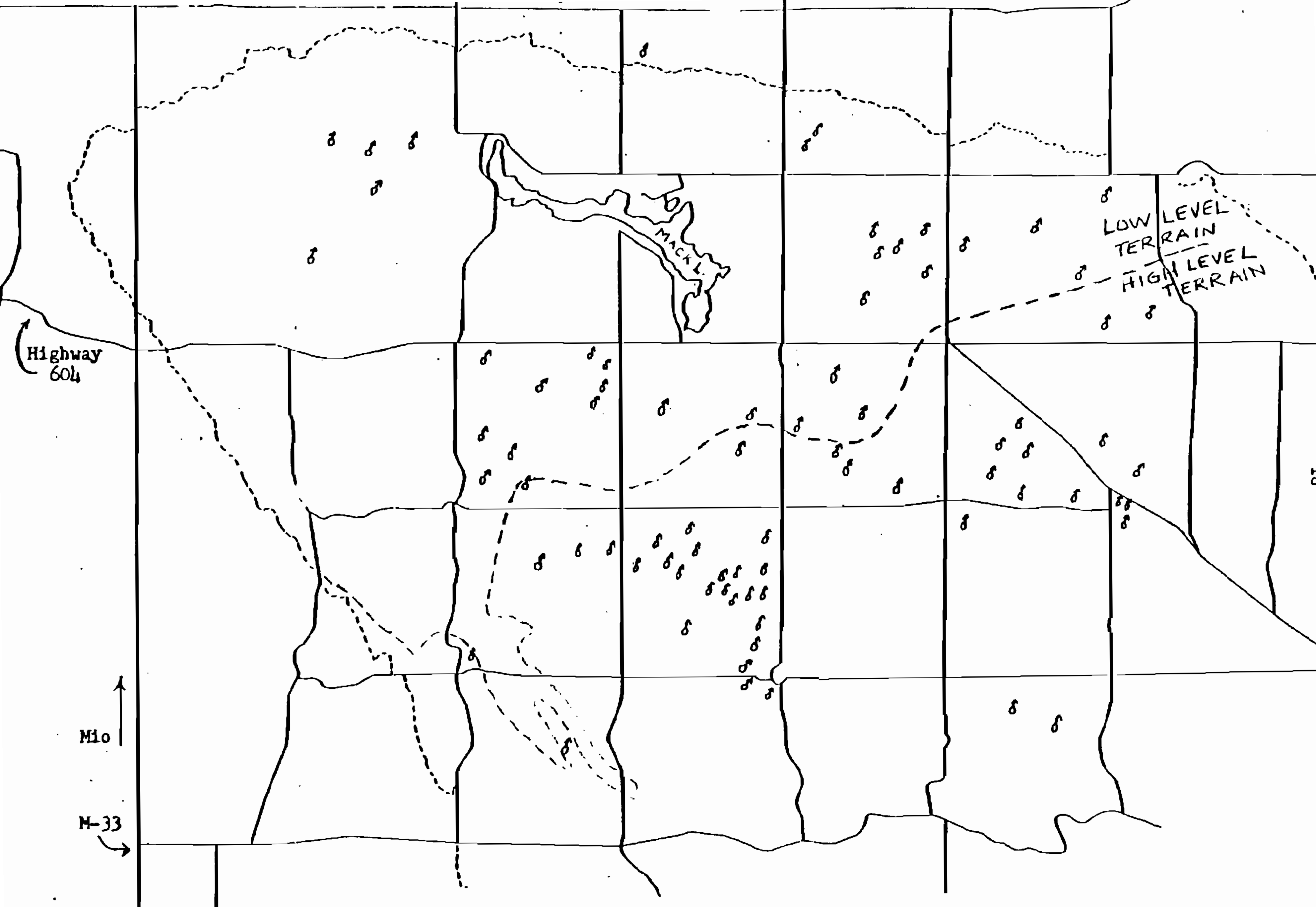

Fig. 5. Mack Lake burn area, Oscoda Co., Michigan. Location of male Kirtland's warblers in 1988 according to census: 78 males in burn and 2 additional males in adjacent management area.

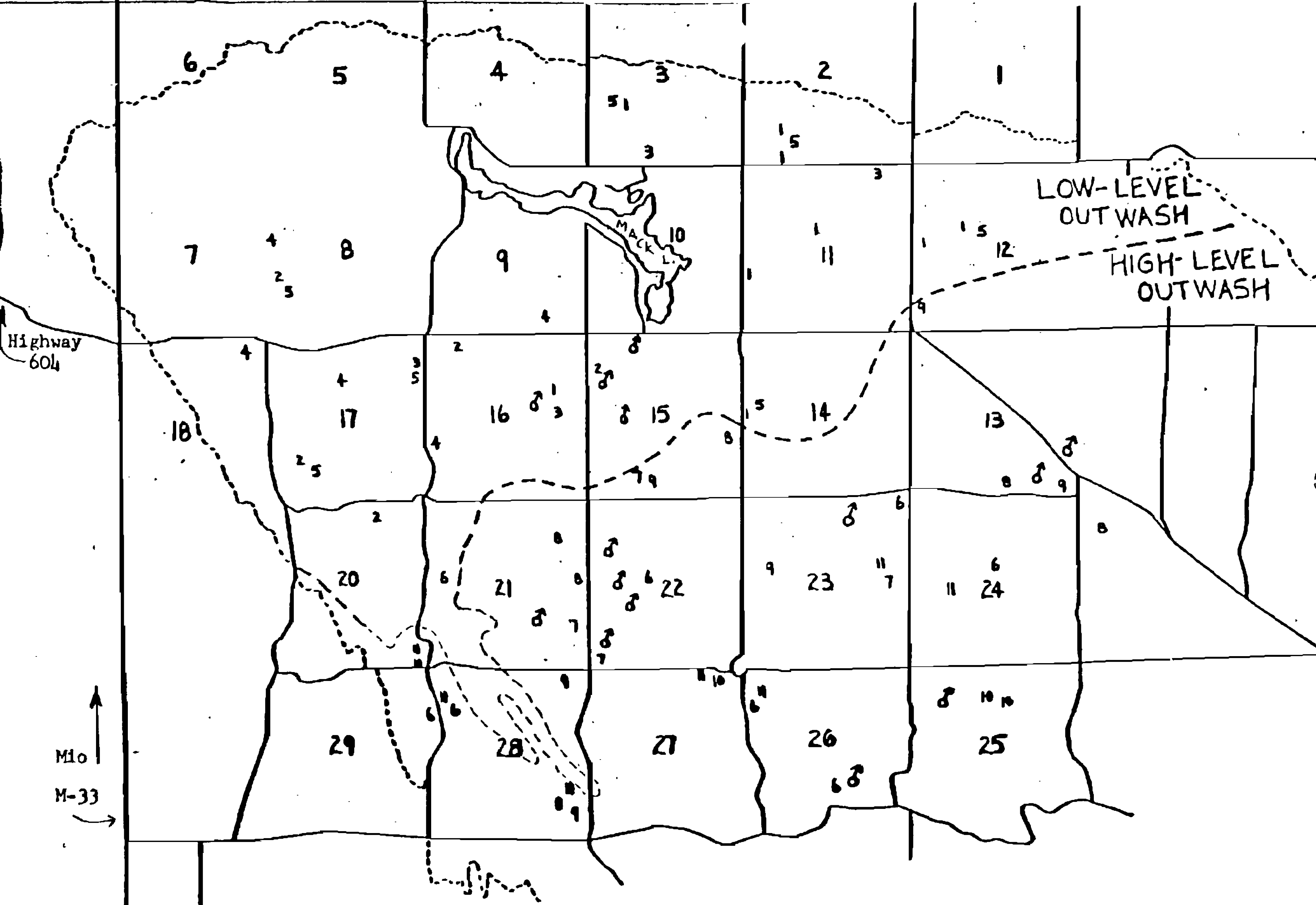

Fig. 6. Mack Lake burn area, Oscoda, Co., Michigan. Location of landscape ecosystem types (small numbers) and location of singing, male (♂) Kirtland's warblers, June, 1986 (After Barnes et al. 1989).

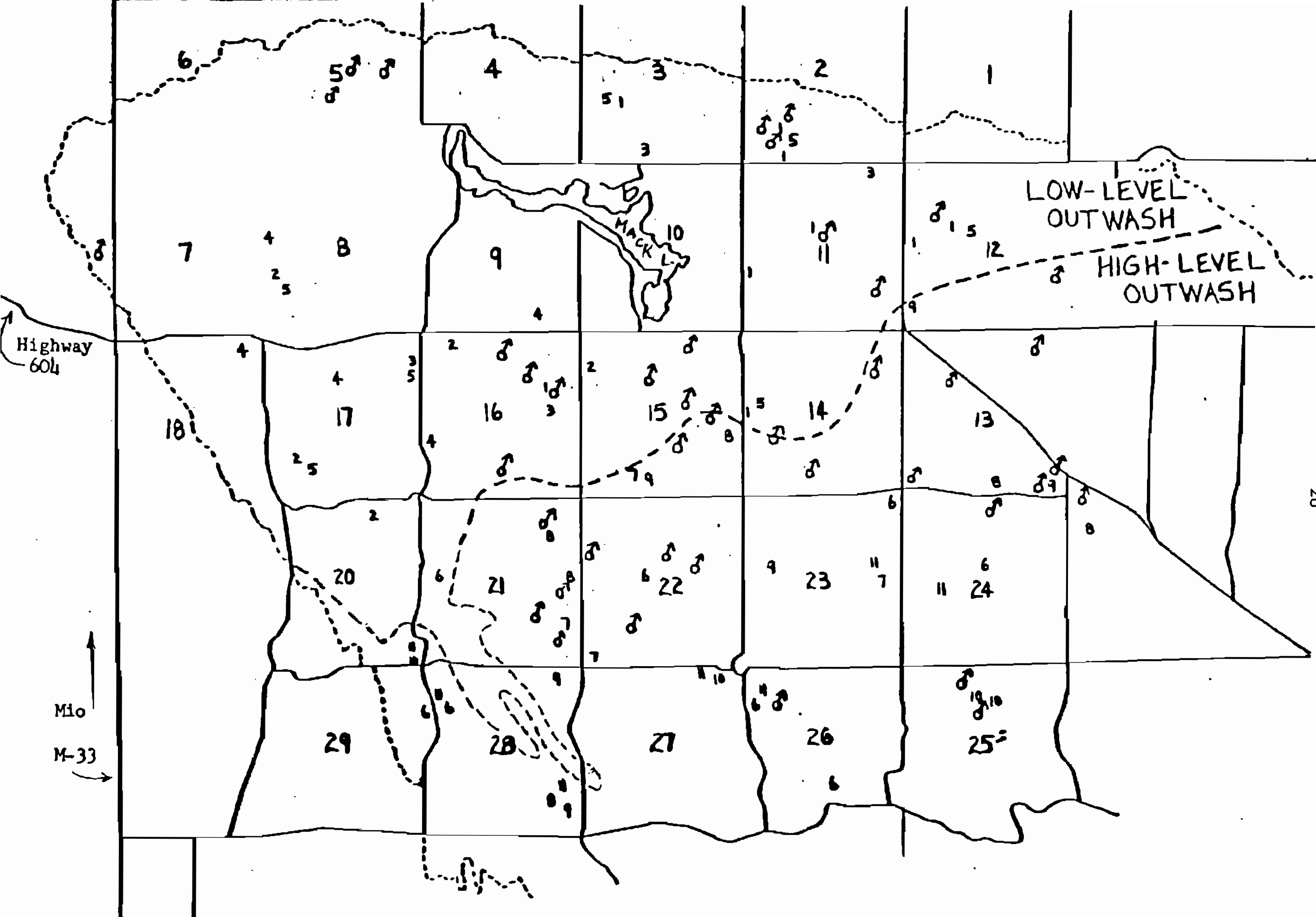

Fig. 7. Mack Lake burn area, Oscoda, Co., Michigan. Location of landsacpe ecosystem types (small numbers) and location of singing, male (♂) Kirtland's warblers, June, 1987 (After Barnes et al. 1989)

Occurrence of warbler territories in local ecosystem types

Similar to findings in field season 1987 (Barnes et al. 1987, Zou 1988), the Kirtland's warblers in 1988 occurred only in ecosystems 1, 6, 7, 8, and 10 (Table 4). None of the warblers appeared to have primary territory in ecosystem types 2, 3, 4, 5, 9, or 11. It is clear that warblers frequent ecosystem types 1, 6, 7, 8, and 10, whereas they did not occur in or perhaps avoided ecosystem types 2, 3, 4, 5, 9, and 11 in 1986, 1987, and 1988 (Figs. 6 and 7).

Table 4. Ecosystem type of 38 male Kirtland's warblers whose territories were specifically determined in 1988.

Ecosystem type	Number of warblers
1	22
6	2
7	5
8	7
10	2

Among the 38 warbler territories studied, 22 were located in the low-level outwash (ecosystem type 1 only) and 16 were in the high-level outwash and ice-contact terrain. Of these, 7 were located in ecosystem type 8, 5 in ecosystem 7, 2 were in ecosystem 6, and 2 in ecosystem 10 (Fig. 8).

Ecosystem 1 occupies the largest area of the study area and supported the largest warbler population of any ecosystem in 1988. The warblers colonize first in areas where jack pine is tall and relatively dense. Although the height of pines of this ecosystem is generally shorter and pine cover more sparse than in the high-level ecosystem types, areas of taller and denser pines do occur. These areas, from 1986 on, have supported warblers.

Ecosystem type 6 had only 2 (12.5%) of the territories studied in the high-level terrain. The soil of this ecosystem is dry and nutrient-poor; type 6 has shorter and sparser jack pines than the other high-level ecosystems. Ground vegetation coverage is low. Fewer plants of Vaccinium angustifolium (low sweet blueberry) were observed, especially in the extremely drought year in 1988 than in other high-level ecosystems.

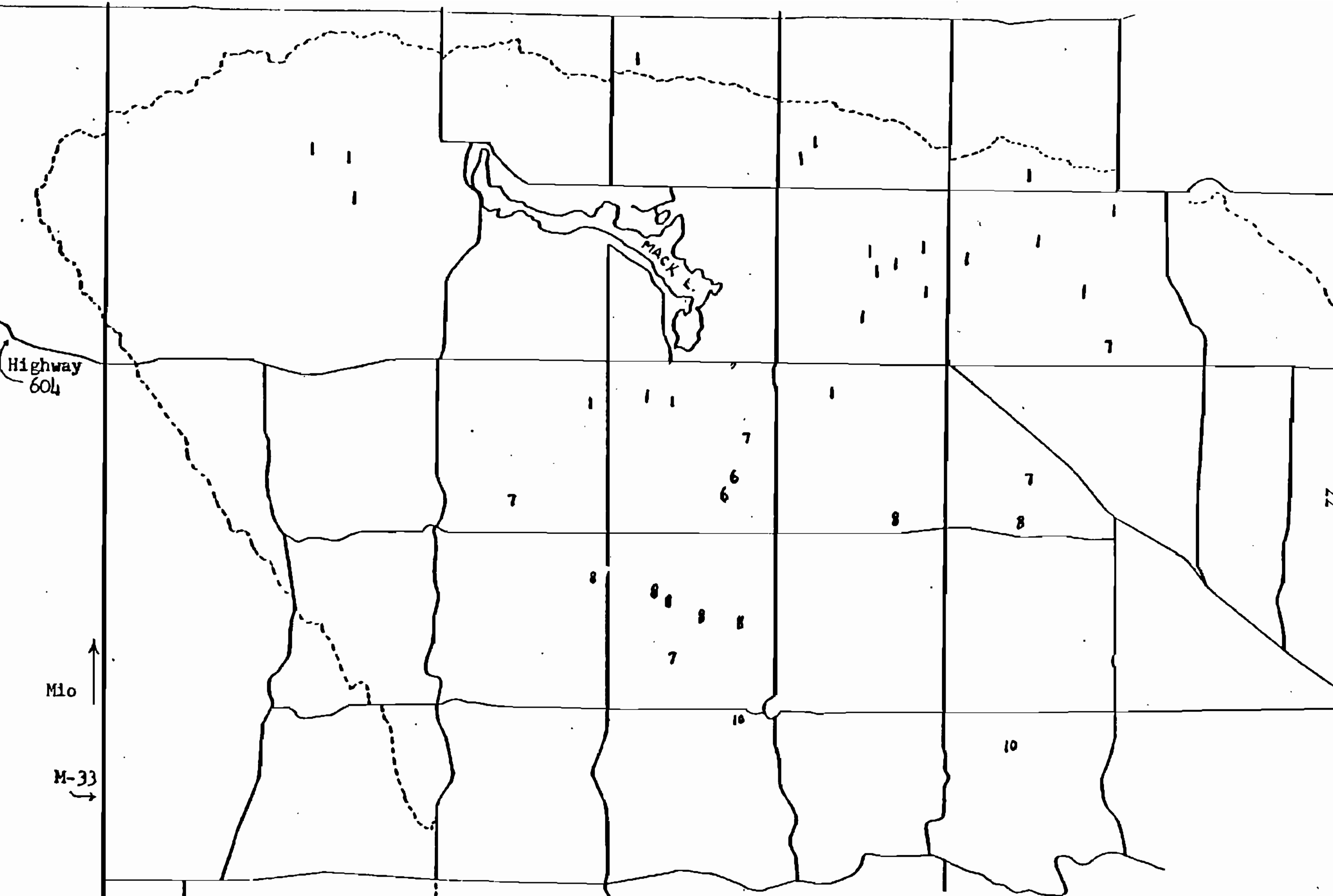

Fig. 8. Mack Lake burn area, Oscoda Co., Michigan. Location of 38 male Kirtland's warbler territories by ecosystem type that were studied in 1988. Numbers indicate locations of the territories and the ecosystem types in which they occur.

Ecosystem type 7 generally has the densest and tallest jack pines of all ecosystem types in the burn. However, it contributes only a small portion of the whole area of the high-level outwash. Nevertheless, 5 (31%) of 16 warblers studied in the high-level outwash had territories in this ecosystem.

Seven (44%) of the 16 male warbler territories in the high-level outwash were in ecosystem 8 -- one of the most favored ecosystems. The jack pines are dense and tall, although they are shorter than those in ecosystem type 7. Ecosystem type 8 is one of the major ecosystems of the high-level terrain, even so, it is still much smaller in area than ecosystem type 1 of the low-level outwash terrain.

As in 1987, 2 out of 16 male warblers were found in ecosystem type 10 in 1988. They were located in the same general area in both 1987 and 1988 (Figs. 8 and 9).

Characteristics of ecosystem types occupied by the warblers

In 1986, 1987, and 1988, the warblers were found only in areas of ecosystem types 1, 6, 7, 8, and 10 where the occurrence of jack pine was found to be distributed in a patchy (contagious) pattern (Zou 1988). These ecosystems account for over half, and possibly as much as two-thirds, of the total area of the Mack Lake burn. As a group, they exhibit, relatively tall and dense pine cover, a contagious pattern of jack pine occurrence, and the presence of northern pin oak; they lack severe microclimate.

Ecosystem type 1 is characterized by gently rolling terrain of the low-level outwash area. It has a high proportion of sand in the top 150 cm soil. An average of more than 60% of medium sand was typically found in soil at a depth ranging from 10-150 cm (Table 5). The average soil pH is 5.0 for the layer of 10-30 cm in depth. Soil moisture and nutrient conditions are the poorest of these five ecosystems. Soil series are Rubicon and Grayling. Jack pine is often low in density and was generally short in height. Average density was 268 per plot (10 x 20 m). The average height of jack pine in 1986 was 65.6 cm. Relatively few northern pin oaks occur in this ecosystem (Table 5). The dominant ground-cover species are *Vaccinium angustifolium*,

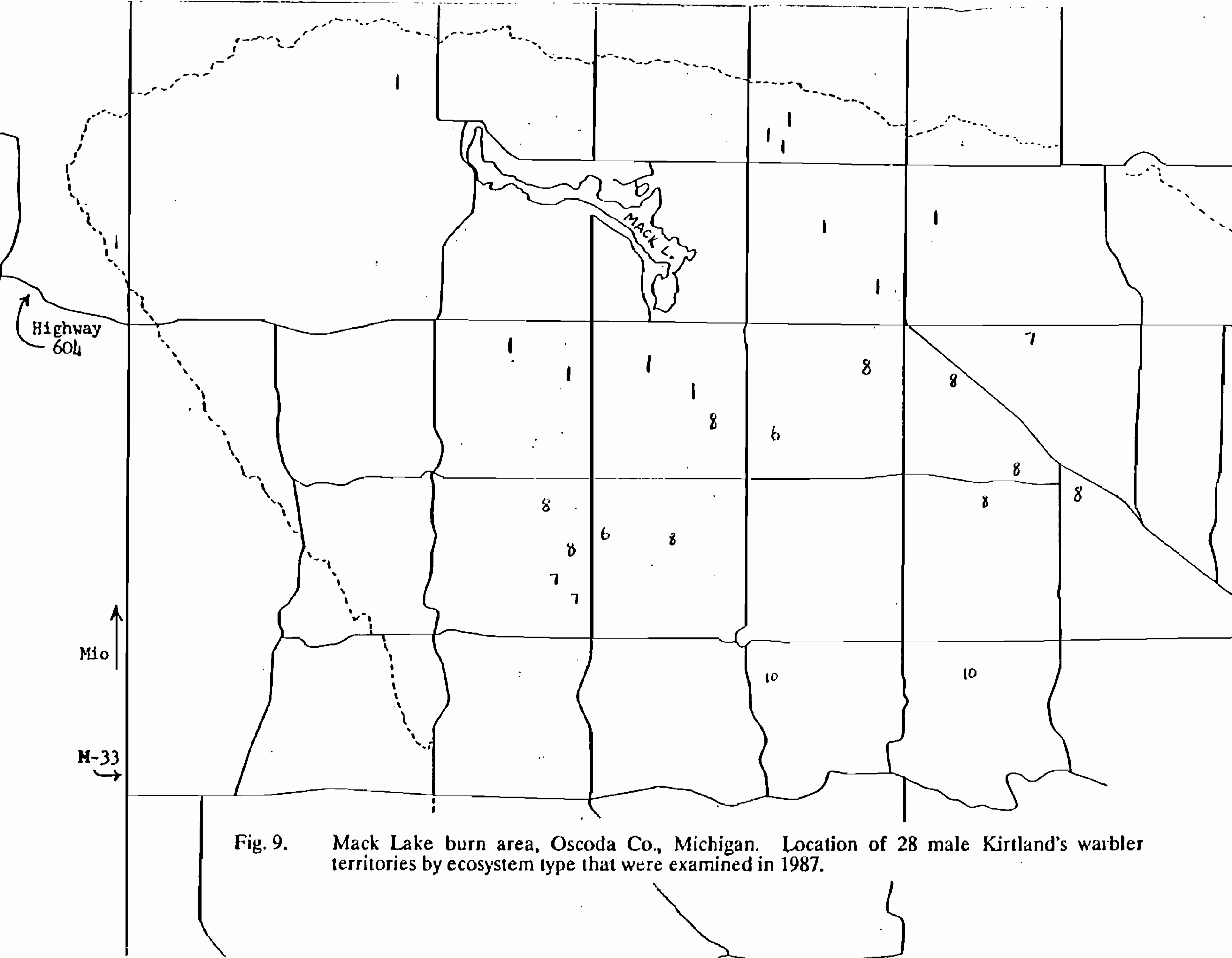

Fig. 9. Mack Lake burn area, Oscoda Co., Michigan. Location of 28 male Kirtland's warbler territories by ecosystem type that were examined in 1987.

Table 5. Mean and standard deviation of selected variables of physiography, soil, and ground-cover species in ecosystem types of the Mack Lake burn 1/

Variable	Ecosystem type										
	1	2	3	4	5	6	7	8	9	10	11
Percent of sand (10-30 cm)	92.1 (3.2)	91.2 (3.5	88.0 (3.9)	88.0 (2.2)	90.0 (6.5)	90.8 (1.5)	91.6 (2.8)	86.3 (2.3)	84.6 (7.4)	92.5 (2.0)	79.2 (26.4)
Percent of very coarse sand (10-30 cm)	1.1 (2.0)	2.2 (1.9)	2.3 (1.1)	0.9 (0.5)	1.4 (1.0)	1.1 (0.6)	1.0 (1.0)	0.9 (0.6)	1.0 (0.4)	1.0 (1.1)	1.2 (0.7)
Percent of medium sand (10-150 cm)	60.5 (8.5)	65.8 (2.0)	53.0 (16.7)	57.5 (19.4)	56.7 (12.4)	69.7 (5.4)	64.7 (8.1)	55.5 (9.5)	54.9 (11.1)	59.9 (6.9)	58.1 (8.6)
Depth to loam or clay band	>400	>400	137.0 (71.5)	>400	>400	>400	>400	>400	84.8 (23.0)	>400	>400
Total thickness of clay and loam (0-150 cm)(cm)	0	0	16.5 (17.1)	0	0	0	0	0	41.8 (15.4)	0	4.6 (12.1)
Percent of pebble and cobble (0-150 cm)	3.4 (7.5)	3.1 (5.5)	1.4 (1.4)	15.1 (9.3)	1.2 (2.6)	2.7 (3.2)	4.3 (6.5)	4.1 (4.7)	3.3 (2.9)	0.9 (0.8)	4.2 (8.9)
Elevation (m)	368.0 (2.2)	368.4 (0.5)	369.2 (2.1)	358.2 (3.6)	367.6 (2.1)	376.6 (3.7)	376.4 (6.0)	375.2 (4.1)	375.6 (3.4)	384.2 (4.8)	371.2 (8.4)
Percent of maximum slope	2.3 (1.6)	2.9 (2.1)	1.9 (0.9)	1.0 (0.8)	4.5 (3.2)	1.4 (2.1)	1.2 (1.1)	2.9 (1.6)	0.9 (0.7)	8.4 (7.2)	10.0 (5.3)
Depth of channel and depression (m)	0	0	0	7.6 (3.6)	3.3 (1.7)	0	0	0	0	0	9.5 (5.6)
Average pH (10-30 cm)	5.0 (0.3)	5.0 (0.4)	5.2 (0.2)	5.3 (0.1)	5.1 (0.2)	5.1 (0.3)	5.0 (0.1)	5.4 (0.3)	5.1 (0.2)	5.1 (0.4)	5.2 (0.2)
Height of 1st living JP branch (cm)	14.7 (5.4)	12.3 (6.1)	14.3 (2.9)	22.8 (7.1)	11.6 (9.7)	21.2 (8.6)	25.2 (6.9)	23.0 (5.0)	22.2 (6.7)	22.3 (7.9)	21.1 (5.3)
Number of oak clumps	0.9 (1.5)	6.3 (7.4)	5.0 (8.0)	1.2 (1.6)	1.1 (1.6)	8.6 (6.4)	5.8 (3.4)	7.0 (3.4)	3.8 (2.5)	11.5 (12.3)	10.0 (6.1)
Number of oak seedlings	0.6 (0.8)	3.3 (3.6)	2.8 (1.9)	1.2 (1.8)	1.1 (1.5)	6.2 (4.0)	9.2 (6.9)	6.6 (3.3)	11.0 (6.5)	15.5 (14.0)	3.0 (2.2)
Height of dominant oaks (cm)	17 (23)	97 (78)	131 (150)	20 (31)	33 (43)	82 (49)	247 (106)	190 (153)	134 (80)	139 (165)	71 (68)
Percent of coverage of oaks	2.2 (6.8)	3.3 (3.4)	10.5 (20.3)	0.7 (1.0)	0.1 (0.2)	3.4 (2.5)	18.0 (14.9)	5.9 (5.3)	3.4 (2.7)	14.4 (8.0)	1.9 (2.3)
Number of understory jack pines	1.9 (3.4)	1.5 (2.4)	0	4.6 (8.2)	0	3.4 (7.6)	14.2 (18.7)	28.4 (40.8)	4.0 (7.3)	18.8 (22.0)	0
Number of understory oaks	0.6 (1.9)	1.0 (2.0)	8.8 (15.0)	0.4 (0.9)	0	2.6 (5.3)	10.8 (9.0)	10.3 (13.3)	1.2 (2.9)	14.3 (8.0)	0.9 (2.3)

1/ Values are means and standard deviation (in parentheses) (From Zou 1988)

Andropogon gerardii, *A. scoparius* (blue stem grasses), *Prunus pumila* (sand cherry), *Arctostaphylos uva-ursii* (bearberry), and mosses (*Polytrichum* spp.) (Table 6).

Of the high-level ecosystem types, 6, 7, and 8 are part of the rolling outwash, whereas ecosystem type 10 is located in the ice-contact terrain, generally southeast of the outwash terrain (Fig. 1).

Similar to ecosystem type 1 in the low-level outwash, ecosystem type 6 is characterized by a high proportion of sand, 69.7% medium sand alone at 10-150 cm depth (Table 5). It is the poorest ecosystem type in moisture and nutrients in the high-level terrain. However, it is slightly richer in surface soil and also warmer than ecosystem 1. The average proportion of total sand at 10-30 cm depth in the surface soil of ecosystem type 6 is 90.8% compared with 92.1% in ecosystem type 1 (Table 5). Soil series is typically Grayling. Ecosystem 6 also has a higher coverage of vegetation, a significantly greater number of plant species, and a greater number of shrub species than ecosystem 1. The number of shrub species in ecosystem type 6 is 11 per plot compared with 5 in ecosystem 1. The northern pin oak is often one of the dominant species in this type.

Ecosystem type 7 is typically characterized by a high proportion of fine sand in the B or C horizons which are often mixed with several fine textured thin bands. The cumulative thickness of these thin bands is generally less than 5 cm. Soil moisture is relatively high because of the fine sand and small textured bands. The surface soil is nutrient poor, having 91.6% sand in the 10-30 cm layer. Soil series are mostly Graying and Graycalm. Jack pine reaches its greatest density and height in this ecosystem. Probably due to this high density, and despite its relatively good moisture status, this ecosystem has the lowest total number of species of any ecosystem except ecosystem 1. Ground vegetation is dominated by *Vaccinium angustifolium*, *Arctostaphylos uva-ursii*, *Quercus ellipsoidalis*, and mosses (Table 6). The high coverage of *Arctostaphylos uva-ursii* and mosses would be the key ground vegetative characters distinguishing ecosystem type 7 from other types in the area. Although it was among the first ecosystems colonized, it may not remain good warbler habitat for many years because of the rapid pine growth.

Table 6. Coverage means and standard deviations of selected ground-cover species of ecosystem types 1, 7, and 8 in the summer habitat of Kirtland's warbler at Mack Lake and Bald Hill in 1988.[1]

Species	Ecosystem type					
	1		7		8	
Andropogon spp.	17.9	(19.8)	5.4	(4.0)	0.4	(0.5)
Amelanchier spp.	2.9	(6.8)	0.7	(1.0)	0.6	(1.1)
Prunus pumila	4.6	(5.0)	2.3	(4.8)	2.5	(5.5)
Prunus virginiana	1.1	(3.0)	0.2	(0.7)	0.7	(1.3)
Quercus ellipsoidalis	2.5	(3.8)	15.8	(6.4)	15.3	(8.2)
Vaccinium angustifolium	43.0	(27.5)	60.6	(15.1)	53.6	(25.1)
Carex pennsylvanica	16.3	(14.8)	18.8	(11.6)	24.3	(15.4)
Oryzopsis pungens	3.3	(3.4)	8.8	(7.3)	3.4	(2.1)
Pteridium aquilinum	1.2	(2.2)	1.1	(1.8)	18.9	(9.9)
Arctostaphylos uva-ursii	7.0	(7.7)	16.9	(5.9)	1.1	(1.1)
Comptonia peregrina	2.7	(3.5)	1.8	(2.1)	5.9	(8.1)
Gaultheria procumbens	0.1	(0.5)	0.4	(0.7)	4.4	(7.8)
Prunus serotina	0.1	(0.2)	0		0	
Salix humilis	0.1	(0.2)	0		0.9	(0.7)
Symphorcarpus albus	0.2	(1.1)	0		0	
Fragaria virginiana	0.1	(0.2)	0		0	
Senecio pauperculus	0.1	(0.2)	0		0	
Solidago spp.	1.0	(2.9)	0.1	(0.2)	0.3	(0.4)
Viola adunca	0.1	(0.3)	0		0.2	(0.4)
Viola pedata	0.1	(0.3)	0		0	
Panicum spp.	1.6	(0.4)	2.6	(2.5)	1.2	(0.9)
Mosses	4.9	(6.5)	10.1	(9.1)	1.3	(1.8)
Lichens	5.0	(3.5)	6.4	(3.9)	6.1	(6.6)
Bare ground	5.3	(3.4)	3.1	(1.6)	2.5	(1.0)

[1]Values are means (in percent) and standard deviations (in parentheses).

Ecosystem type 8 is characterized by having a cumulative thickness of 5-10 cm fine textural bands of sandy loam to silt loam within the top 150 cm of soil. Soil series is commonly Montcalm. It had significantly less bare ground (more coverage of ground vegetation) than ecosystems 1, 2, 4, 6, 7, and 10. Ground vegetation is dominated by *Vaccinium angustifolium*, *Quercus ellipsoidalis*, *Pteridium aquilinum* (bracken fern), *Comptonia peregrina* (sweet fern), and *Gaultheria procumbens* (wintergreen). The constant occurrence of *Gaultheria procumbens*, the low coverage of *Arctostaphylos uva-ursii*, and the high coverage of ground vegetation help distinguish this type from others in the high-level terrain.

Ecosystem type 10, the ice-contact landform, is defined to encompass the upper slopes of depressions and tops of hills where there are less frost incidence and warmer temperature in general than the depressions (type 11). Soils are mostly sandy, but they often have several layers of thin textural bands at a depth less than 200 cm. Soil series are mostly Rubicon or Grayling. Ground vegetation is dominated by *Vaccinium angustifolium*, *Quercus ellipsoidalis*, and *Gaylussacia baccata* (black huckleberry). Other plant species include *Populus grandidentata* (bigtooth aspen), *Hamamelis virginiana* (witch hazel), and *Acer rubrum* (red maple).

In summary, Kirtland's warblers in 1988 were found in ecosystem types 1, 6, 7, 8, and 10 that are characterized by distinctive features of physiography, soil, and vegetation. Above all, presence of jack pine at least 6-8 ft tall is critical, and in addition its occurrence in patchy and relatively dense stands. Other features include: (1) uplands with warm air and soil (not depressions or relict melt-water channels), (2) rolling terrain of outwash or ice-contact parent material and Grayling, Graycalm, Montcalm, or Rubicon soil series, and (3) vegetation dominated by jack pine and northern pin oak together with a ground cover of *Vaccinium angustifolium*, *Arctostaphylos uva-ursii*, *Gaultheria procumbens*, mosses, and *Andropogon* spp. (blue stem grasses), and combinations of these species. Above all, physical factors (microclimate, physiography, soil, fire intensity) that promote tall, dense, and patchy jack pine appear to be extremely important.

Habitat quality and warbler territories

The "quality" of warbler habitat is a slippery subject. To date we can examine it using the number and density singing male warblers occupying the two major physiographic types and ecosystems within these types. We are unable to estimate quality by number of nests per unit area for a given ecosystem type or warbler fecundity per ecosystem type. Quality, by whatever yardstick, is a function of time. The major physiographic landscapes (the high-terrain, for example) and ecosystem types within them that provide suitable or high quality habitat in the first years of warbler occurrence in a burn or plantation may become less suitable with time, and other physiographic types and local ecosystems may increase in quality with time. And the characteristics that make up quality habitat also change over time.

In 1986, 71% of the warblers occupied the high-level terrain, especially ecosystems 7 and 8. Based only on occupancy, high-level terrain is high quality habitat, low-level terrain is lower quality habitat. In 1987 and 1988, about 60% of the warblers still occupied the high-level terrain, but the low-level area (primarily ecosystem 1) was supporting more and more warblers, i.e., becoming better quality habitat. In 1989, about the same number of warblers were observed in the low-level terrain as in the high-level terrain, i.e., the two physiographic types are about equal in overall habitat quality. Although the large area of ecosystem 1 in the low-level terrain is supporting more and more warblers, it may not support the most warblers per unit area.

In 1988, we attempted to determine the density of warblers in a given ecosystem and use this as a measure of habitat quality. Cameron Kepler and Paul Sykes of the U.S. Fish and Wildlife Service were able to help us identify individual warbler territories in 1988. Thus, we were able to make a quantitative estimate of habitat quality based on the distance between adjacent warbler territories: the shorter the distance between territories with an ecosystem type, the higher the density of warblers and the higher the quality of the habitat.

The average distance from a singing male territory to its nearest neighbor was the shortest for ecosystem types 8 and 7, 269 and 365 m respectively, and it was the longest, 522 m, for ecosystem type 10 (Table 7). Therefore, the density of the singing male warblers was the highest

Table 7. Means and standard deviations of distances between Kirtland's warbler territories to their nearest neighbor by ecosystem types.

Ecosystem types	1	7	8	10
Means (m)	435	365	269	522
Standard deviation (m)	317	153	207	42

in ecosystem types 7 and 8, and the lowest in ecosystem type 10 as is evident in Fig. 8. Ecosystem type 1 is intermediate.

The proportion of warblers per ecosystem type plotted over the distance class indicates that 72% and 40% of the warblers were nested next to one another by a distance of 100 to 250 m in ecosystem types 8 and 7 respectively (Fig. 10).[2] The warblers were most densely packed, i.e., had smallest territories, in ecosystems 7 and 8. None of the warblers were nested more than 700 m away from one another in these ecosystem types. In contrast, 36% of the singing male warblers were within a distance of 100-250 m in ecosystem type 1, and 24% of the warblers were nested away from their neighbors by a distance more than 700 m.

For the summer 1988 period, and based on warbler density only, we rank ecosystem types 7 and 8 as the highest quality habitat. Ecosystem type 1 is second, and ecosystem 10 is third. We did not have enough data to evaluate ecosystem 6. However, we believe it would rank as quality 2 because of its similarity of its physical and biological features to those of ecosystem 1 and its history of warbler occurrences from 1986 to 1988 (Barnes et al. 1987, Zou 1988).

An hypothesis suggested by Zou is that male warblers occupy territories in all three levels of ecosystem quality even before the saturation of occupancy in the ecosystems of highest quality (Fig. 11). Thus, in 1986 it may be that warblers occupied territories in ecosystems 1 and 6 (second level quality) before all the available areas of high quality habitat in ecosystems 7 and 8 was saturated. However, there is no evidence to pinpoint the sequence of establishment of territories in these ecosystems. Another explanation for warblers apparently establishing

[2]In Figure 10, the percentage of warblers for each of the ecosystem types 1, 7 and 8 (y axis) was plotted over the mean distance to the nearest neighbor's territory. For example, 40% of all warblers in ecosystem 7 were in the 100-250 m class (mean=175 m); 40% were in the 401-550 m class (mean=475 m), and 20% were in the 551-700 m class (625 m).

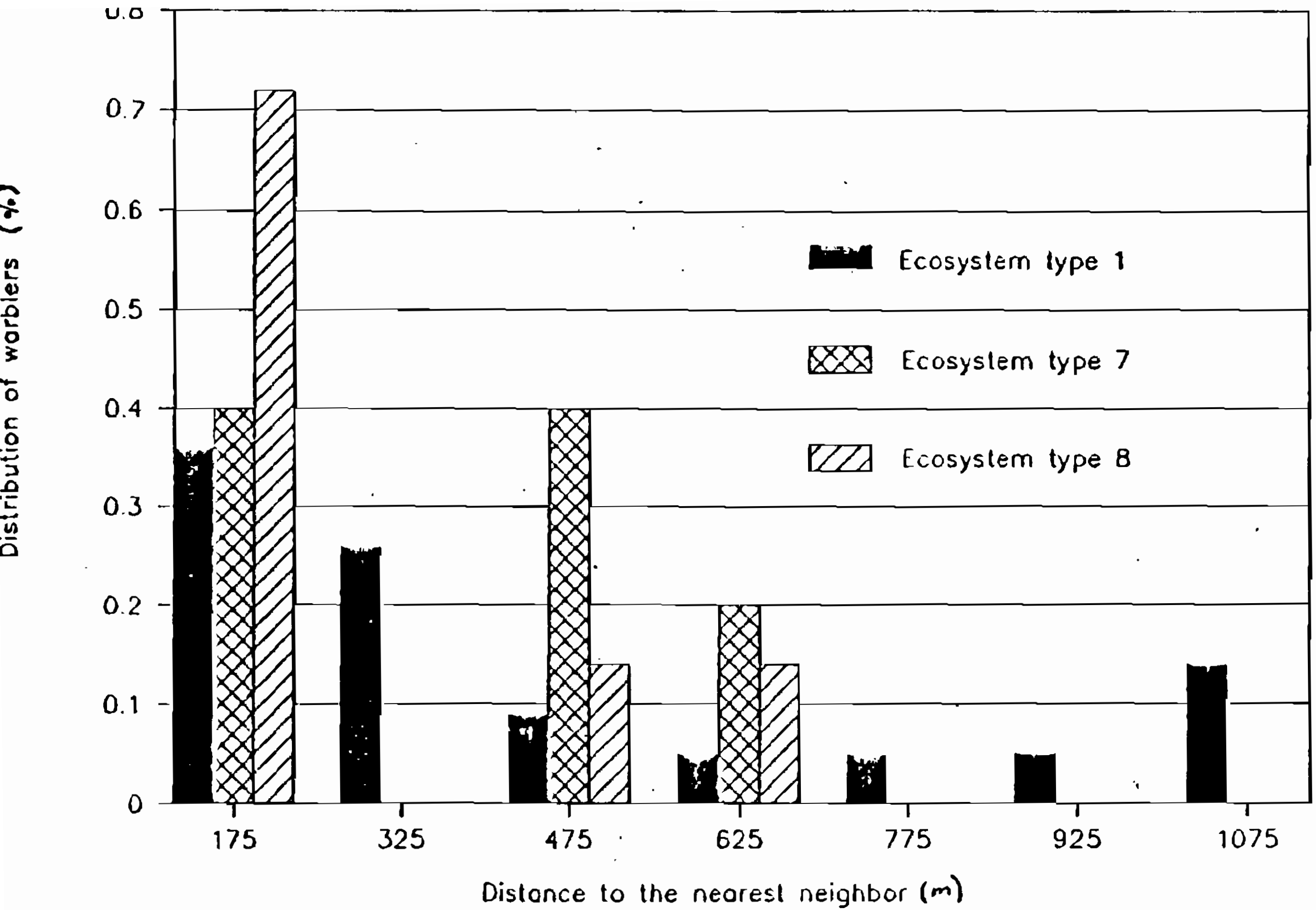

Fig. 10. Distribution of warblers (percent) according to the distance (m) to their nearest neighbor.

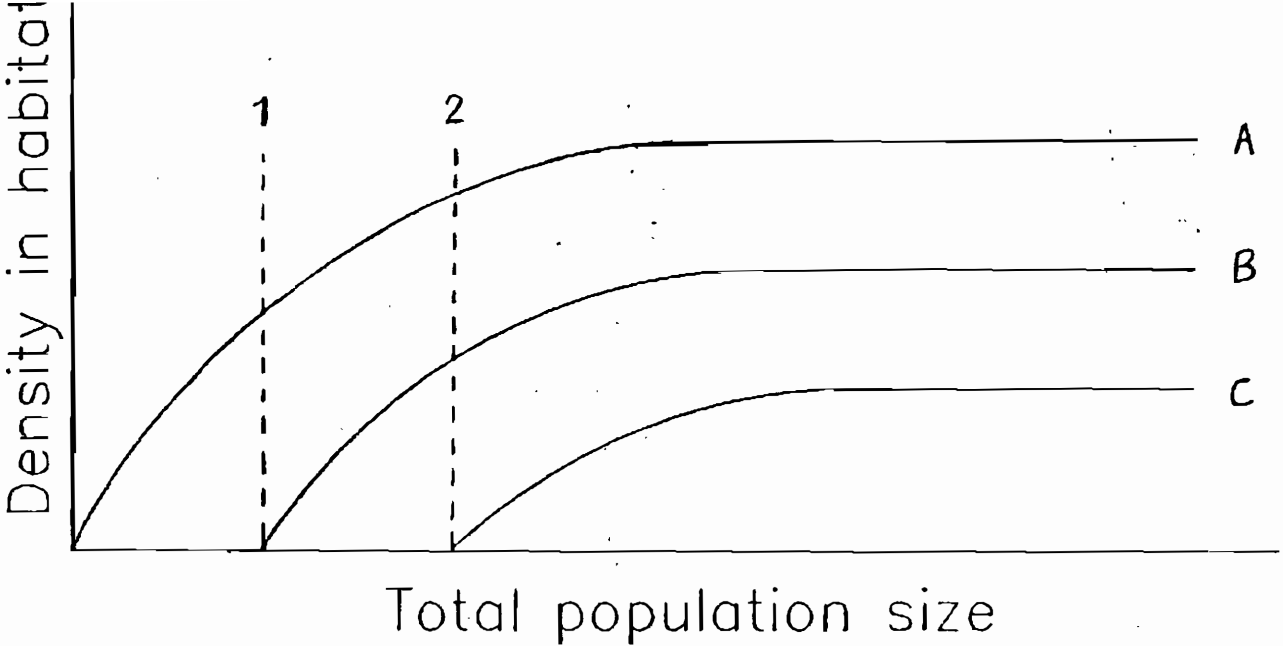

Fig. 11. Relationship between the density in habitat and the total population size of Kirtland's warblers at the Mack Lake burn. A = highest quality habitat; B = secondary quality habitat; C = lowest quality habitat. 1 and 2 indicate the total population size at which the warblers begin to move into the secondary and lowest quality habitats.

territories in lower quality ecosystems before saturating the high-quality ecosystems is that ecosystem types are not internally homogeneous in topography, soil, surface organic matter (fire intensity), and vegetation. Thus, some localities in so-called lower quality ecosystems (ecosystems 1 and 6, for example) may be equally as good (or better) in habitat (jack pine height, patchiness, etc.) as poor localities in the so-called high-quality ecosystems. More research, including mapping of ecosystem types, documenting the time of occupancy of each territory, and delineation of warbler territories and their characteristics, is needed to test these hypotheses.

In future research, particular attention should be directed to soil and air temperatures in relation to female nesting sites. Kirtland's warbler is a ground nesting bird. Thus it may be particularly sensitive to soil temperature that is controlled or indicated by air temperature (as in depressions), soil texture, and vegetative cover.

Applicability of aerial photographs

The large-scale, color aerial photographs are very useful in identifying generally suitable habitat for the warblers. However, it is very difficult to identify the specific ecosystem types that are not physiographically different (for example, ecosystems 6, 7, and 8). Information on physiography is most easily retrieved from aerial photographs. The general landforms of outwash plains, old stream channels, depressions, and ice-contact features are distinguishable in the photographs. Tree species such as northern pin oak, jack pine, red pine, red maple, old snags, and aspens also can be recognized. Ground vegetation in the photographs is fuzzy, and it is very difficult to distinguish the species and their respective coverages.

Using the color photographs, combined with on-the-ground checking, one could identify and map the general areas of outwash plains, channels, depressions, and ice-contact features. Therefore, one can distinguish the two major physiographic types and ecosystem types 1, 2, 4, 5, 10, and 11. Ecosystem types 3 and 9 might also be distinguished, but with difficulty, by the information from tree species and their density. It is very difficult to distinguish ecosystem types 6, 7, and 8 from one another. Thus, aerial photographs can be used to distinguish the low-level vs. high-level terrain, and some but not all of the specific ecosystem types. As in all other areas

Evaluation of the Distinctiveness of Low- and High-Level Terrain and The Ecosystem Types: Statistical Analyses.

The local ecosystem classification, developed by reconnaissance and plot sampling, is a set of hypotheses that require testing. Testing the distinctiveness of the ecosystem types is done by mapping and statistical analyses. Mapping was not done. However, univariate statistical analyses of soil and tree variables provide evidence for differences among the two physiographic types and the ecosystems. They also provide evidence for understanding the preference of warblers for the high- vs. low-level terrain and different ecosystem types within each of these major physiographic types. All significances cited are at the $P \leq 0.10$, unless otherwise indicated.

Overall, differences among ecosystem types are significant in many soil variables, including coarse sand, coarse plus very coarse sand, medium sand, fine sand, very fine sand, and silt plus clay. For vegetative variables, all were significantly different, especially the percent of oak coverage.

The difference among low- and high-level landscape appears biologically significant. High-level ecosystems have a significantly greater amount of silt plus clay than low-level systems at both 10-30 and 10-150 cm depths. This difference, coupled with that of warmer temperatures on the high-level terrain, are probably the most significant factors in influencing the greater occupancy by warblers in 1986, 1987, and 1988 in this area. Assuming equal severity of burn, these factors probably account in large part for the taller pines in the high-level terrain as compared to the low-level terrain. These major factors (landscape position and hence its air and soil temperature, soil texture, and presence of textural bands) can be used throughout the jack pine range in the High Plains District (Albert et al. 1986) to identify the best warbler habitats.

Analysis of tree variables (jack pine and oak) also revealed marked differences among the low- and high-level landscapes. Significant differences were found for: number of jack pine stems, mean growth of jack pine in 1985, 1984, 1983, 1980-82, and 1984-86; percentage jack pine coverage, and percentage of northern pin oak coverage.

The statistical analyses also bring out distinctive differences among ecosystems within the low-level area and within the high-level area. In the low-level terrain, ecosystem type 1 has significantly less silt and clay than types 3 and 4. Ecosystems 4 and 5 have significantly greater fine sand than type 1. Ecosystem 1 appears to have somewhat coarser soils than other low-level units, but place to place variation is very high. Ecosystem 1 has more stems of jack pine than any other ecosystem -- and 44% more than the closest other type in this regard. Yet, due to high inter-plot variation, it is only significantly different from ecosystem 5 in number of stems. It is also different from ecosystems 5 and 3 in percentage of jack pine coverage. The high variation in density was studied in 1986 and the marked differences cited by Barnes and Bosio (1986). These particular areas of tall and dense jack pines were the ones colonized first in the low-level outwash. The greater number of warblers observed in ecosystem type 1 than any other type in the low-level terrain is probably due to its warmer climate than units 4 and 5, its large areal extent compared to the limited areas of units 2 and 3, and within-ecosystem variation in soil textures and fire severity.

Ecosystem 6 of the high-level terrain most closely resembled ecosystem 1 in our reconnaissance and the two types were seen as a similar pair. Ecosystem 1 has significantly lower pH, less coarse sand and medium sand, but more fine sand and fine and very fine sand. No differences were found in silt and clay content. Thus, ecosystem 1 is not apparently better or worse than type 6 in soil characters -- confirming the similarity of these types within their respective low and high positions in the landscape.

Among high-level ecosystems, those favored by the warbler (7 and 8) generally have soils of heavier textures than ecosystem 6. Ecosystem 7 has significantly less coarse sand and more fine sand than unit 8. Type 8 has significantly greater silt and clay than either 6 or 7. In addition, type 8 has significantly greater very fine sand than types 7 and 9 and significantly greater fine sand and fine plus very fine sand than type 6. The pH of ecosystem 8 is also significantly higher than ecosystems 6 and 7. These analyses confirm field reconnaissance and field determinations of texture and pH.

Ecosystems 8 and 9 are only significantly different in silt plus clay in the 10-150 cm depth; 9 has 42% more silt plus clay than type 8. Besides being limited in area, type 9 has significantly fewer jack pines, less coverage of pines, and lacks a patchy distribution of pines.

The high-level ecosystems exhibit more differences than the low-level ecosystems in tree variables. Ecosystem type 7 is most similar to type 8. These systems have a greater number of jack pines compared to ecosystems 6 and 9. Ecosystem 11, the depression type, has fewer trees than ecosystem 6. Ecosystem 7 exhibits more stems, better growth (1984-86), and greater jack pine coverage (40% vs. 13%) than ecosystem type 6. The comparison of types 7 and 9 is similar to that of 7 vs. 6 except that growth differences which are significant for 1980-82 (before the trees in type 9 would have contacted the thick textural soil bands) become insignificant for 1984-86.

Ecosystem types 7 and 8 are very similar. Type 7 shows better growth for 1984 and 1985, and mean total height in 1986 is greater. Ecosystem 7 has a mean height of 85 cm in 1986, whereas ecosystems 6, 8, 9, and 10 have means between 71 and 74 cm; type 11, the depression ecosystem, has a mean of only 61 cm.

Analysis of herb and shrub ground-cover vegetation revealed a significantly greater number of total species and shrub species in high-level terrain ecosystems as compared to those of the low-level terrain. In addition, many differences among ecosystems were found. The ecosystems of relative high nutrient and moisture status (types 3, 5, 6, 9, and 11) had significantly less bare ground (more species coverage) than the drier and more nutrient poor ecosystems (especially types 1, 2, and 6). Paired ecosystems in low- vs. high-level terrain (1 and 6, 3 and 9, 5 and 11) were significantly different in number of shrub species; the low-level ecosystems always had fewer shrubs.

Each of the 6 ecological species groups (*Vaccinium angustifolium*, *Prunus pensylvanica*, *Gaultheria procumbens*, *Ceanothus ovatus*, *Arctostaphylos uva-ursii*, *Rosa blanda* [Barnes et al. 1989]), had a distinctive pattern of occurrence and coverage over the 11 ecosystem types. Four of the six groups (*Vaccinium*, *Prunus*, *Gaultheria*, *Rosa*) showed significant differences between the low- and high-level physiographic types. In particular, the *Rosa blanda* and *Prunus* *pensylvanica* groups were clearly in much greater abundance in the high-level terrain. Species of these groups were especially abundant in ecosystems lacking warblers (3, 9, 11). Based on our experience at Mack Lake and at other areas of the High Plains District (Albert et al. 1986) these groups may be used to identify ideas that are not suitable for warbler management. However, there are exceptions, ground-cover vegetation should not be used alone to indicate low quality habitat.

A key species of the *Rosa blanda* group, *Orozopsis asperifolia*, is consistently associated with the more fertile and clay-banded soils (Barnes et al. 1989) as well as other areas where warblers are not found. Its coverage was significantly greater in ecosystems 3 and 9 than in the other ecosystems.

The *Vaccinium angustifolium* group was well represented in all ecosystems, but was especially abundant in the channel-frost pocket ecosystem (type 4). Many species of this group (especially *Amelanchier sanguinea*, *Prunus pumila*, *Vaccinium angustifolium*) apparently have the ability to maintain their populations in a cold microclimate.

The statistical analyses of ground-cover vegetation confirmed field observations that ecological species groups can be very useful in indicating the local ecosystems and the broad physiographic types that are preferred by the warbler. However, vegetation should always be used in conjunction with physiographic and soil characters because of compensating factors that may affect the occurrence and coverage of individual plant species.

Although the univariate analyses largely confirm field observations and measurements, multivariate analyses of all ecosystems are needed to get a more comprehensive picture of the differences.

Applicability of the ecosystem approach to areas outside Mack Lake.

Several areas outside the Mack Lake burn were examined, including Bald Hill, Lovells, a jack pine plantation about 2 miles west and across I-75 from the MacMullan Conference Center, and other areas as well. Whereas some areas exhibited excellent habitat quality, other areas were unsuitable as warbler habitat or were relatively low quality. Based on the framework established at Mack Lake we believe the landscape ecosystem approach would be eminently useful to assess Kirtland's warbler habitat throughout the warbler's summer range in northern Lower Michigan. Existing management areas and other areas could be evaluated as to habitat quality based on physiographic, soil, and vegetative characters. This could be done first at the broad physiographic level and then at the local ecosystem level. Over the total area, however, the classification developed at Mack Lake would need to be revised and some new ecosystems added. For example, at the Lovells area the ground vegetation was obviously different from that in ecosystems encountered at Mack Lake.

Special attention was given to Bald Hill, and five ecosystem plots were established. We concluded that the relatively high occupancy of warblers at Bald Hill is due to the stand's wildfire origin (wildfire favored dense pine establishment and a patchy pine distribution) and to favorable physiographic, soil, and vegetation features that are similar to the high-quality ecosystems at Mack Lake. A major portion of the area is similar to ecosystem 7 of the Mack Lake; 5 plots were taken in this ecosystem type.

It is important to note that warblers in 1989 at just two areas, Mack Lake (101) and at Bald Hill (45), account for 69% of the total population. The landscape ecosystem approach provides the framework for identifying other high-quality landscapes for management. By applying the ecosystem approach throughout the warbler's range the best habitat could be identified; management could be concentrated in the best warbler habitat. The geographic information system techniques combined with the landscape ecosystem approach would be an excellent combination!

The general applicability of the ecosystem approach was also indicated by examination in 1989 of the jack pine plantation west and across I-75 from the MacMullan Conference Center. At the June 1989 meeting of the Recovery Team, Harold Mayfield mentioned to B. V. Barnes that this area of planted jack pine had been ideal in jack pine height for the warbler for some time, but no warblers had been found. Immediately following this conversation, I (BVB) drove to the site and examined the area. In only a few minutes, and even without a shovel to examine the soil, it was clear why the area was not favorable for the warbler. First, the area received cold air from up-slope and was unsatisfactory in microclimate. Second, northern pin oaks were rare, and the small stems still surviving exhibited branches and leaves killed by spring or summer frost. Third, the abundance of *Prunus serotina* and *Orozopsis asperifolia* indicated topographic and soil conditions too cold and moist for good warbler habitat despite the presence of pines of the right height. In addition, the jack pine plantation lacked the local patchiness characteristic of wildfires. The site was evidently moist enough to favor very high pine survival trees enhancing the systematic pattern of their occurrence. I do not know whether this area is or is not a part of a warbler management area. However, it is a good example of a site that by reconnaissance could quickly be dropped (or given low priority) from a list of possible areas to manage for the warbler.

In summary, the landscape ecosystem approach could be used successfully to prioritize lands for the management of the Kirtland's warbler throughout the potential range of the species in northern Lower Michigan. A two-stage process could be employed to identify suitable areas at the broad physiographic level and then identification of those areas having the greatest potential from a local ecosystem viewpoint.

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