INVESTIGATING MICHIGAN PRAIRIE WARBLER BREEDING TERRITORY HABITAT COMPOSITION, WITHIN-TERRITORY RESOURCE USE, AND FACTORS INFLUENCING OCCUPANCY

By

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ABSTRACT

INVESTIGATING MICHIGAN PRAIRIE WARBLER BREEDING TERRITORY HABITAT COMPOSITION, WITHIN-TERRITORY RESOURCE USE, AND FACTORS INFLUENCING OCCUPANCY

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Recent Prairie Warbler (*Dendroica discolor*) observations in Michigan are almost exclusively from Lake Michigan early-successional dune ecosystems in the Lower Peninsula. However, data describing breeding locations, population abundance, and habitat composition influencing breeding territory selection are largely unknown and thus critical information needs for this state-endangered, Neotropical migratory songbird. Understanding Prairie Warbler habitat selection during the breeding season will better inform conservation and management planning. Avian point counts were conducted in 9 study sites along the Lake Michigan coast in 2004 and 2005 to locate Prairie Warblers. Breeding territories were mapped using GPS and GIS. Plant composition was quantified within breeding territories and in unoccupied areas to determine whether geographic variation existed in vegetation associated with Prairie Warbler breeding areas from north to south. Logistic regression was used to develop a predictive model of Prairie Warbler occurrence. Using 1 m resolution imagery, distances from edge of territories and unoccupied areas to 7 environmental covariates were used as variables to forecast Prairie Warbler occupancy in the west Michigan dune ecosystems. Resource utilization functions (RUF) were developed to explore resource use by Prairie Warblers within highest-use areas of their breeding territories, thus relating geographic space use to environmental attributes as portrayed by 30 m land cover data. Comparisons were made across all breeding territories and for southern and northern sites exclusively to examine the potential for a north-to-south gradient

in resource use. Thirty-eight Prairie Warblers were detected, with high detection probability, in 5 of the 9 sites surveyed. Breeding areas tended to be clustered within sites, with breeding territory boundaries often adjacent to each other, suggesting potential for conspecific attraction. Results generally support previously observed relationships between Prairie Warbler occurrence and a mixture of herbaceous and low-growing woody vegetation. However, my study was the first to document a latitudinal gradient in Prairie Warbler habitat use related to vegetation composition; with northern territory space use correlated with denser, woody vegetation and southern territory space use associated with more open, grass dominated sites. Plant composition in areas occupied by Prairie Warblers was different from plant composition in unoccupied areas. However, those differences were not consistent from north to south. The best indicators of Prairie Warbler occupancy were proximity to other Prairie Warblers and proximity to shrub cover. I found an 80% probability of occupancy when another Prairie Warbler was within 91 m of an existing territory. I found a 39% probability of occupancy when shrubs were within 1 m. There were no significant environmental covariates from RUFs, however, four observations warrant attention: 1) northern sites have more woody vegetation cover than southern sites, and southern sites seem to be more open, 2) grass cover appears to be important on southern sites, potentially because shrubs are less ubiquitous, 3) higher soil moisture in northern territories was suggested as an important indicator of habitat use, and 4) lack of significant RUF coefficients suggest that the spatial resolution of land cover data used (30 m) may not have been appropriate to describe within territory space use for Prairie Warblers. Key among management recommendations, conservation professionals are encouraged to maintain existing, large areas of contiguous habitat with well dispersed shrubs to accommodate multiple breeding territories and thus maintain coastal Prairie Warbler population viability.

ACKNOWLEDGEMENTS

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CHAPTER 1

EXAMINING THE STATUS OF STATE-ENDANGERED PRAIRIE WARBLER POPULATIONS IN MICHIGAN

NEED FOR RESEARCH

Data describing Michigan's state-endangered Prairie Warbler (*Dendroica discolor*) populations are limited. The status of Michigan breeding locations, population abundance, and habitat composition influencing breeding territory selection are critical management and conservation needs for this state-endangered, Neotropical migratory songbird (Walkinshaw 1991, Nolan et al. 1999, Cooper 2000, Southwell 2001).

In recent years, the majority of Michigan breeding season observations have been reported from the western coastal counties along Lake Michigan (Brewer et al. 1991, Michigan Natural Features Inventory 2011). Gaining an understanding of where west Michigan Prairie Warbler breeding populations are specifically located, and in what abundance, will allow a baseline from which to monitor population status. Analyzing similarities and differences in plant composition between breeding locations will provide increased understanding of Michigan Prairie Warbler ecology. Describing habitat composition within breeding territories will help identify and specify Prairie Warbler habitat needs, thus informing conservation practitioners as they design long term management plans and are asked to respond to proposed land use changes (e.g., mining, wind tower siting, development).

Understanding the scale at which a species uses the landscape influences the way habitat composition data is collected (i.e., survey design) and ultimately provides for more relevant conservation and resource management recommendations for a species (Wiens 1989, Bohning-Gaese 1997) or the habitat on which it depends. Home range estimates describe an animal's use of space (Aebischer et al. 1993), however, resource use within an animal's home range is not often uniform (Marzluff et al. 1997). Exploring not only where Prairie Warblers are located, but also where specifically within the home range they are spending the majority of their time, is an important step in understanding key drivers of habitat selection in west Michigan coastal breeding areas. Linking habitat use information to the resource composition in those highest-used areas will increase our overall knowledge of this species and inform subsequent conservation actions.

Some have speculated that abundant Prairie Warbler habitat exists (Walkinshaw 1991, Cooper 2000, Southwell 2001), but habitat requirements for Prairie Warbler, and their selection strategies, may be more specific than previously anticipated. Examination of environmental factors (e.g., plant composition, proximity to specific land cover types or other Prairie Warblers) within breeding territories, compared to areas where Prairie Warbler are absent, will allow conservation practitioners to manage with a greater understanding of Prairie Warbler habitat selection strategies and thus how to maintain habitat for this state-endangered species in concert with other conservation objectives.

DISTRIBUTION AND POPULATION TRENDS

Prairie Warbler is one of many species that make an annual spring migration northward, over thousands of miles of land and water, to their breeding grounds. Prairie Warblers primarily winter in the West Indies but also in coastal Florida and coastal Central America including parts of Belize and Costa Rica (Dunn and Garret 1997). The core of the Prairie Warbler breeding range lies in the central southeastern United States with northern boundaries spanning from South Dakota, southern Ontario and southern New Hampshire (Walkinshaw 1991, Dunn and

Garret 1997) (Figure 1). They arrive on breeding grounds in the southeastern and south-central United States beginning in March. The Prairie Warblers that make their way to Michigan will have traveled farther than most, arriving at the northern edge of the breeding range during the first two weeks of May (Dunn and Garret 1997).

The first survey record for a Prairie Warbler in the United States (April 18, 1810) was from southwestern Kentucky in what was described by Alexander Wilson as “barrens” and “prairie country. . .evidently resembling and perhaps representative of the tall-grass prairie” (Mengel 1965). The bird’s name is derived from this description by Wilson (Nolan 1978). At the time of its discovery the species was likely a rare and local bird, with most populations scattered around the margins of its present range (Nolan 1978). Among other early records throughout the current breeding range, an 1839 record of a Prairie Warbler was noted by Abram Sager during travels between Detroit, Saginaw Bay and Jackson, Michigan (Wood 1951). It is thought that if a Michigan breeding populations existed at that time, it was likely disjunct (Nolan 1978).

Prairie Warblers were recorded nesting in the southern Lower Peninsula counties of Ottawa and Montcalm in the early 1900’s (Barrows 1912). Wood (1951) noted Berrien County as important to Prairie Warbler, as did Zimmerman and VanTyne (1959) in addition to reporting nesting records from the west Michigan counties of Ottawa, Muskegon, and Oceana. Wood (1951), Zimmerman and Van Tyne (1959), and Mayfield (1960) all reported occurrence in northeastern Lower Peninsula counties of Oscoda, Crawford, Otsego, Cheboygan, and Presque Isle, primarily associated with jack pine (*Pinus banksiana*) plains.

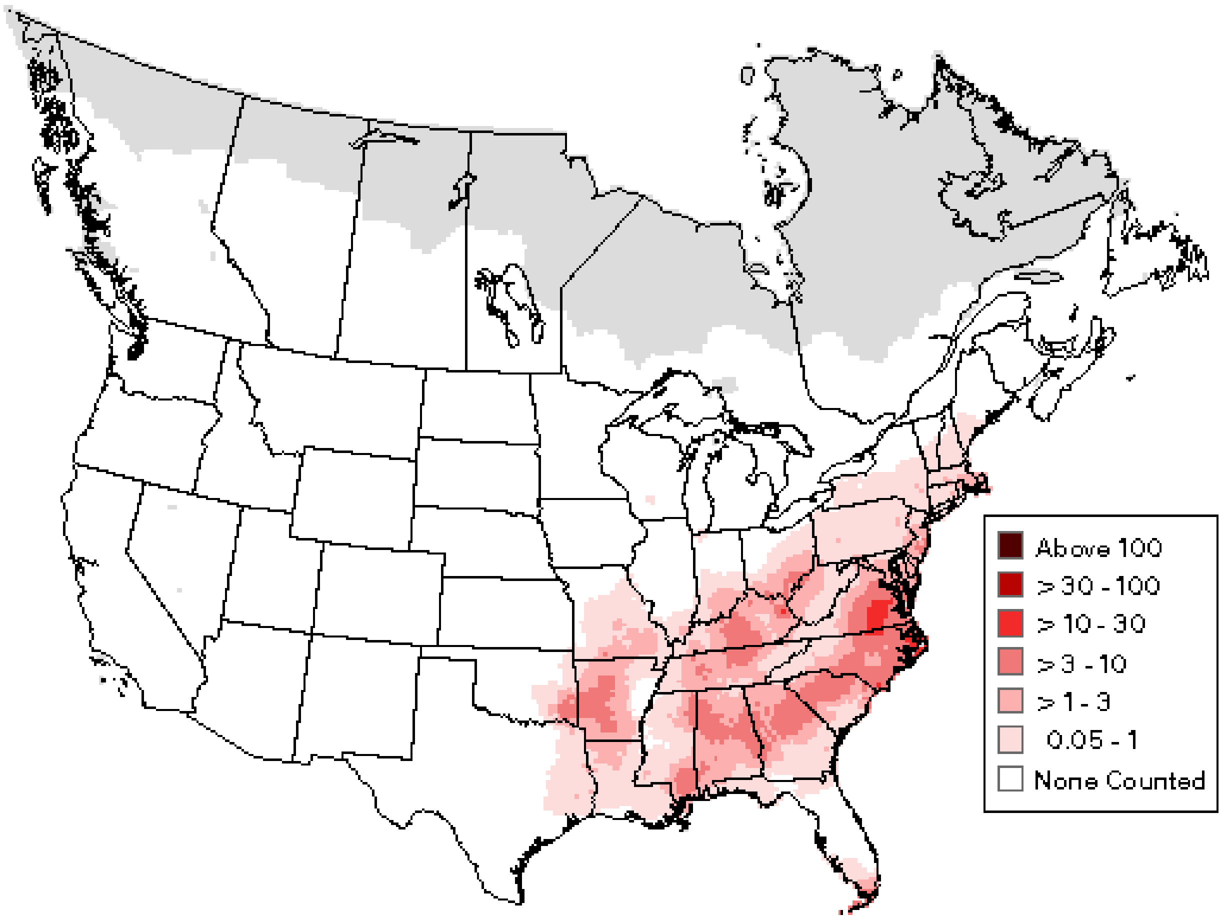

Fig. 1. North American Breeding Bird Survey summer Prairie Warbler distribution map (1994-2003). Numbers in legend refer to numbers of birds, with darkest colors representing greatest numbers observed. For interpretation of the references to color in this and all other figures and tables, the reader is referred to the electronic version of this dissertation.

Though globally secure (NatureServe 2011), Prairie Warbler populations have been declining nation-wide since 1970 (Robbins et al. 1986, Saurer et al. 2008). Midwest populations are of moderate to high management concern (Robinson et al. 1999). This trend holds true for Michigan populations (Michigan Natural Features Inventory 2011), which are thought to have always been small and localized (Nolan 1978). Between 1986 and 2011, Michigan has had occurrences confirmed in 18 out of 83 counties (Michigan Natural Features Inventory 2011) (Figure 2).

The North American Breeding Bird Survey's (BBS) best estimate of population change for Prairie Warbler over its range between 1966 and 2003 shows increases in New England, coastal regions of the Carolinas, southern Louisiana, southern Alabama and southern Georgia, the southern Florida panhandle and in other smaller patches within its current range (Saurer et al. 2008). The central Michigan Lake Michigan coast shows both decline and increase in Prairie Warblers (Figure 3).

PRAIRIE WARBLER ECOLOGY

Prairie Warbler breeding territories have been characterized throughout their range as open, brushy, early successional habitat with scrub-shrub species on poor soils with little or no tree canopy (Nolan 1978, Walkinshsaw 1991, Nolan et al. 1999, Cooper 2000). Overall, the Lake Michigan sand dunes have been denoted as critical breeding areas for this species in Michigan (Walkinshaw 1991). Wood (1951), Zimmerman and Van Tyne (1959), and Mayfield (1960) all suggested that Michigan's jack pine plains may be important to the species in the early- to mid-1900's.

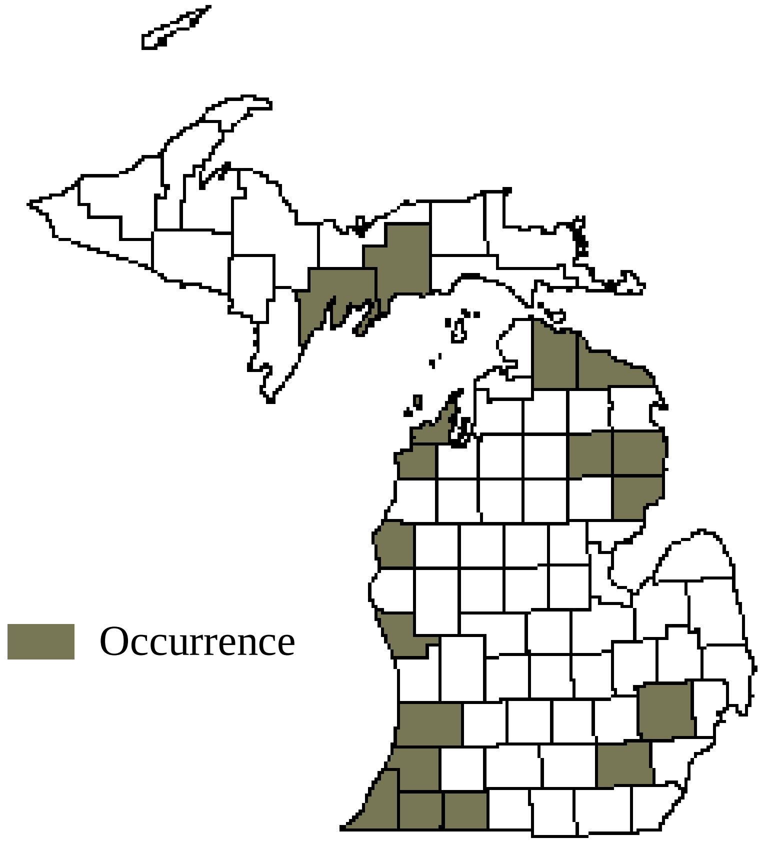

Fig. 2. Prairie Warbler occurrence confirmations by county in Michigan between 1986 and 2011. Data may not reflect true current distribution since much of the state has not been thoroughly surveyed. Data provided by Michigan Natural Features Inventory.

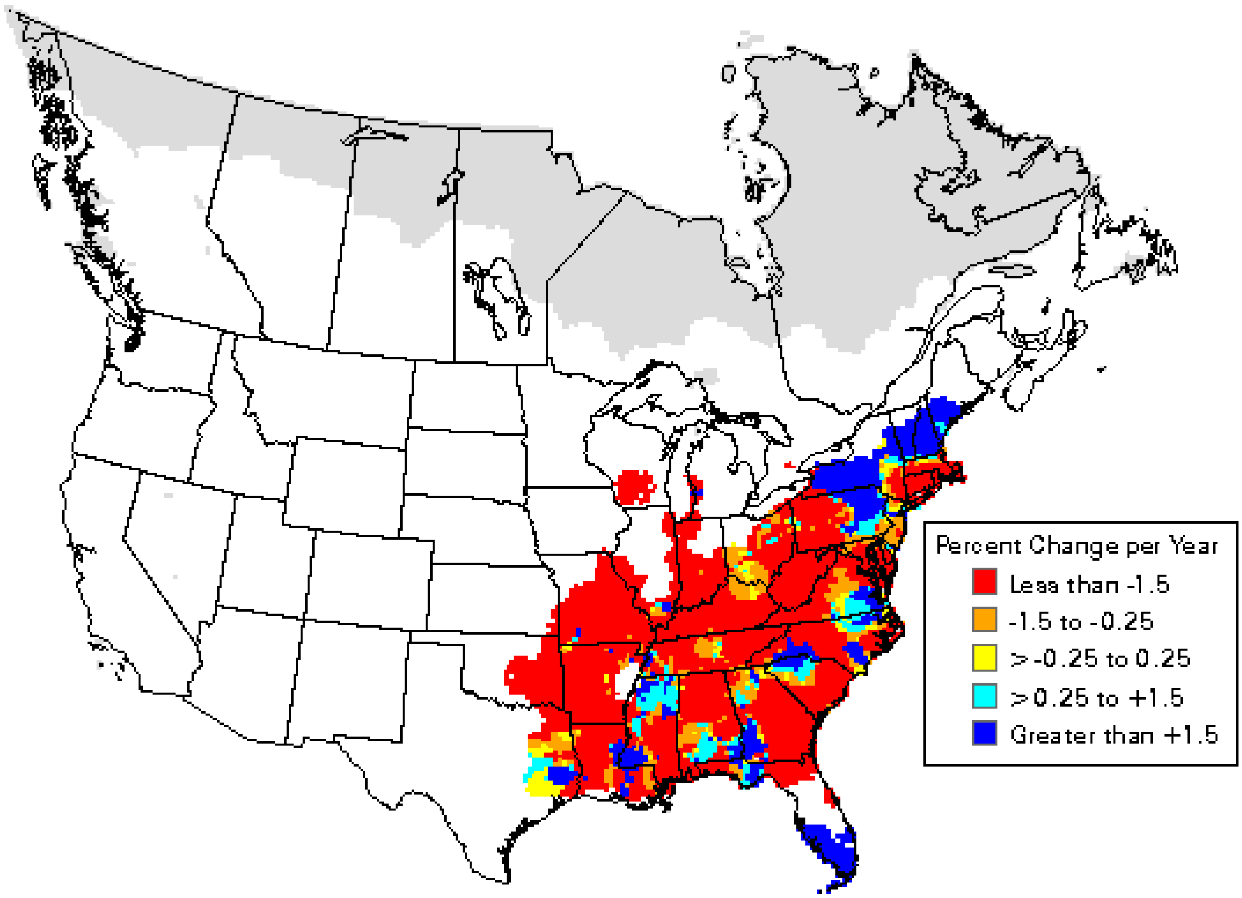

Fig. 3. North American Breeding Bird Survey trend map (1966-2003). Areas of increasing Prairie Warbler populations are shown in blue. Areas of population decline are shown in red.

Michigan populations have been observed breeding in three general vegetation types (Walkinshaw 1991, Cooper 2000), although this is not viewed as an exhaustive list of potential habitat:

- Early successional stages of Great Lakes sand dunes where deciduous or coniferous shrubs are intermixed with dune grass and other herbs,
- Early-successional, shrubby openings associated with previously-burned jack pine plains, and
- Previously burned conifer stands dominated by deciduous shrubs and small trees.

Prairie Warblers feed primarily on insects and sometimes spiders, snails, or worms; they are generalists. Nestlings are primarily fed caterpillars (Cooper 2000). The species forages by gleaning insects from leaves and branches and will occasionally take prey mid-air (DeGraaf et al. 1991, Nolan et al. 1999). A male will forage a few meters off the ground or from higher perches during the breeding season when he is advertising (Nolan 1978). Mean breeding season feeding height in Florida for breeding males is 2.19 m; for females 1.40 m (Prather 1994).

Territories are established in Michigan by males upon arrival in early May (Wood 1951, Nolan 1978, Nolan et al 1999). They advertise for females, who arrive about one week later, and defend their territory by singing from tall, exposed perches. Fall records suggest that Prairie Warblers tend to leave Michigan breeding grounds to migrate south by the third week of August (Wood 1951, Nolan 1978, Nolan et al. 1999).

Prairie Warbler breeding territory size varies between 0.24 – 3.5 ha (roughly half of a football field to about 8 football fields) (Nolan 1978). The species has been found to return to the same territory year after year until the land cover has succeeded beyond habitation (Nolan 1978). Males show a high rate of natal site fidelity (Nolan 1978).

Nests are open-cup, normally found 1-3 m (roughly 3 to 9 feet) off the ground, and are composed of woven plant fibers lined with hair or feathers (Cooper 2000). Nests are typically placed (dependent on geographic region) in a shrub, sapling, thicket, or fern clump. Typically, 3-5 eggs are laid in June, incubated solely by the female, and hatched within 11-15 days (Nolan 1978). Young are tended by both parents and fledge between 8-10 days, remaining dependent on the parents for an additional 30-35 days (Nolan 1978, Baicich and Harrison 1997).

After habitat loss and fragmentation in winter and breeding ranges, nest parasitism and predation are the two greatest threats to the Prairie Warbler. Primary predators of nestlings in Michigan include snakes, chipmunks and corvids (Nolan 1978). Females in Michigan populations usually only have one brood as the northern breeding season does not often provide ample time to re-brood. Brown headed cowbirds are known to be nest parasites (Nolan 1978, Nolan et al. 1999)

Males will sometimes have two territories (and two females). Females (rarely males) will move and change mates when a nest fails or before attempting a second brood (Nolan et al. 1999). Nolan's (1978) 20-year study on Indiana Prairie Warbler populations (1951-1972), indicated that 46% of 137 males were monogamous over one season; only 35% of 176 females exhibited season-long monogamy with a monogamous male.

Historical (early- to mid-1900's) Michigan occurrence patterns noted Prairie Warblers using the sandy outwash plains of the northeast Lower Peninsula; those areas now commonly associated with the federally endangered Kirtland's Warbler (Wood 1951, Zimmerman and Van Tyne 1959, Mayfield 1960). Records show that by the late 1950's, breeding Prairie Warblers were not as commonly observed the northeast Lower Peninsula (Mayfield 1960, Nolan 1978).

GOALS AND OBJECTIVES

The overarching goal of this research is to advance understanding of Prairie Warbler needs in the context of the western Michigan coastal landscape. This information will contribute to our understanding of Prairie Warbler resource use dynamics on the northern edge of the breeding range as well as provide this information at a spatial resolution that was previously unknown.

The chapters in this dissertation address the following objectives:

Chapter 2:

- Locate Prairie Warbler breeding areas along the west coast of Michigan,
- Quantify plant composition associated with Prairie Warbler breeding and unoccupied sites, and
- Determine whether geographic variation exists in the plant composition associated with Prairie Warbler breeding areas.

Chapter 3:

- Determine which land cover types can forecast Prairie Warbler occupancy in west Michigan dune landscapes,
- Develop resource utilization functions for Prairie Warbler breeding territories along Michigan's west coast, and
- Gain insight into how resource use may differ for Prairie Warblers between northern and southern coastal breeding territories in Michigan.

Chapter 4 will summarize research findings from Chapters 2 and 3 and translate findings into management recommendations.

Some repetition could occur between chapters, as chapters 2 and 3 are written in manuscript style, prepared with intent toward submission to peer-reviewed journals.

STUDY AREA

Nine study sites were located in the Lower Peninsula of Michigan along the Lake Michigan coast (Figure 4). Study sites were chosen because they were publically accessible and contained large areas of potential habitat for Prairie Warblers (identified by cover type (i.e., jack pine, sand dunes, scrub-shrub) (Nolan 1978, Nolan et al. 1999, Cooper 2000, Southwell 2001). Survey sites included six State Parks, Sleeping Bear Dunes National Lakeshore, Oval Beach (a public beach owned by the city of Saugatuck), and Kitchel-Lindquist Dunes Preserve (a publically-accessible preserve near Grand Haven). The distance between the southern-most site (Warren Dunes State Park) and the northern-most site (Sleeping Bear Dunes National Lakeshore) was approximately 386 km (240 miles).

The mean temperature during survey years (2004 and 2005) at Sleeping Bear Dunes between May 1-14 (Prairie Warbler estimated arrival on Michigan breeding grounds; Dunn and Garret 1997) was 11°C and 9°C, respectively. Mean temperatures at Warren Dunes were 14°C and 12°C, respectively. These year-specific temperatures compare closely to average annual temperatures at Sleeping Bear Dunes and Warren Dunes during May: 13°C and 14°C respectively (Figure 5). Average precipitation for the month of May at Sleeping Bear Dunes is 6.6 cm and at Warren Dunes is 8.1 cm (Figure 6). Temperatures increase throughout the Prairie Warbler breeding season in Michigan with variable rainfall.

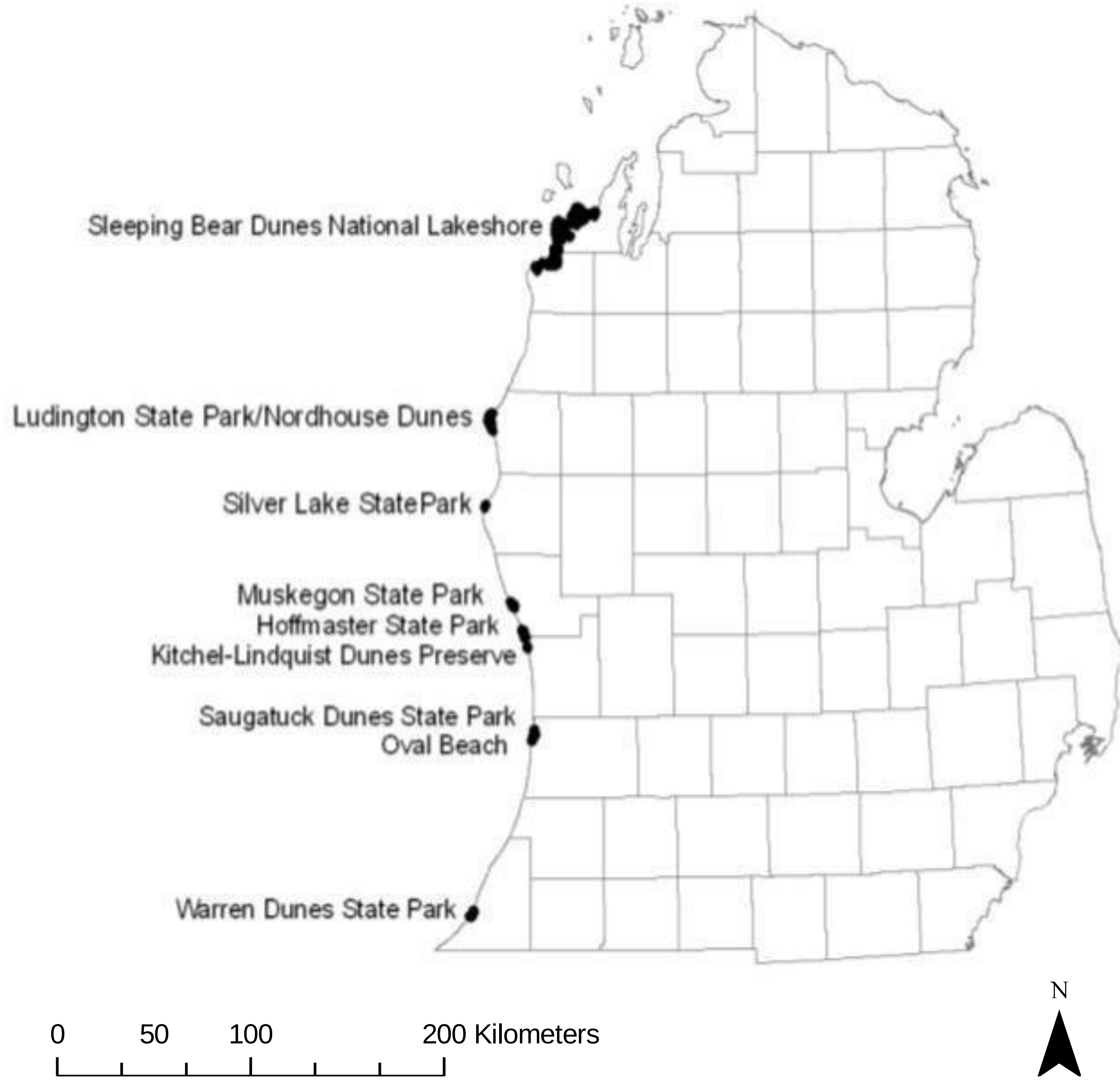

Fig. 4. Prairie Warbler and vegetation survey locations along the Lower Peninsula of Michigan. Surveys took place from May-August in 2004 and 2005. Distance between Warren Dunes State Park and Sleeping Bear Dunes National Lakeshore is approximately 386 km (240 miles).

Michigan's Great Lakes shoreline, foredune, and backdune forest systems are a relatively small but ecologically valuable component of the state's natural features (Albert 2000). Distinctive land cover types and hydrologic systems that support floral and faunal species in these areas provide stop-over resources for annually dependent migrating songbirds, hawks, and owls from South and Central America, as well as for native shorebirds (Brewer et al. 1991). The unique combinations of habitat structure and composition are instrumental and serve as breeding grounds for hundreds of these species.

Foredune vegetation communities consist of specialized plants and some shrubs adapted to sand burial and fast growth with deep, often rhyzomal, root systems that stabilize blowing sand. Pioneering grasses such as marram grass (*Ammophila breviligulata*) and sand-reed grass (*Calamovilfa longifolia*) allow sand to accumulate and stabilize. Common Michigan foredune shrubs include hearty, woody species such as sand cherry (*Prunus pumila*), red osier dogwood (*Cornus stolonifera*), bearberry (*Arctostaphylos uva-ursi*), several dune willows (*Salix* spp.), and creeping juniper (*Juniperus horizontalis*). These plants must tolerate extreme temperatures, low moisture levels, and low levels of nutrients in addition to blowing sand.

The foredune zone undergoes continual change due to natural weather events, erosion, and water level fluctuations. Larger dunes form behind the protective foredune, where sand accumulation is slower, allowing dune grasses, herbaceous plants and shrubs and forests to establish. Oaks (*Quercus* spp.), bigtooth aspen (*Populus grandidentata*) and sassafras *(Sassafras albidum)*, in addition to stands of jack pine (*Pinus banksiana*) and common juniper (*J.s communis*), grow closest to the shoreline on wind-ward slopes. In contrast, the landward side of the dunes is more moist and nutrient-rich, supporting mesic forest species like sugar maple (*Acer*

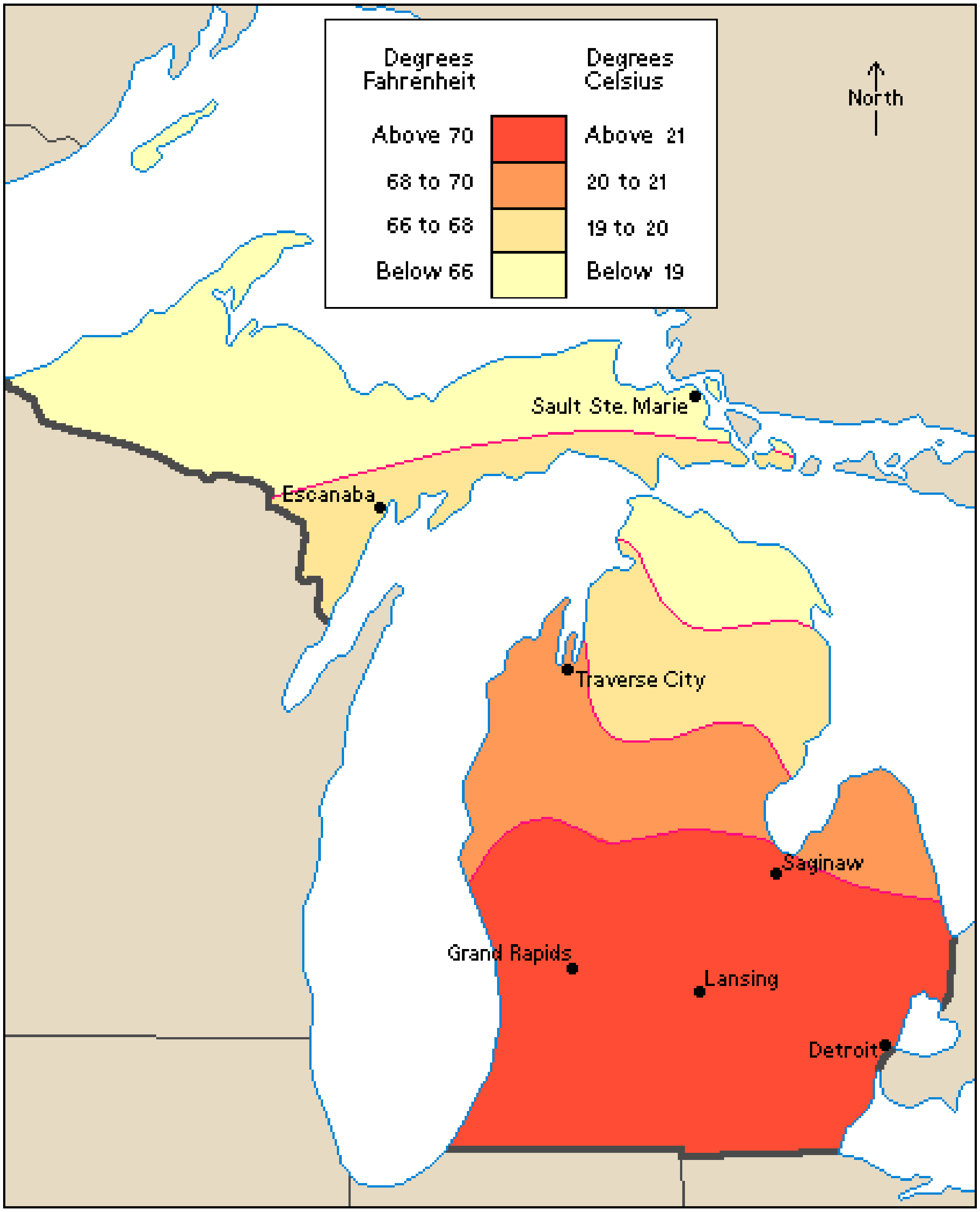

Fig. 5. Michigan average July temperature.

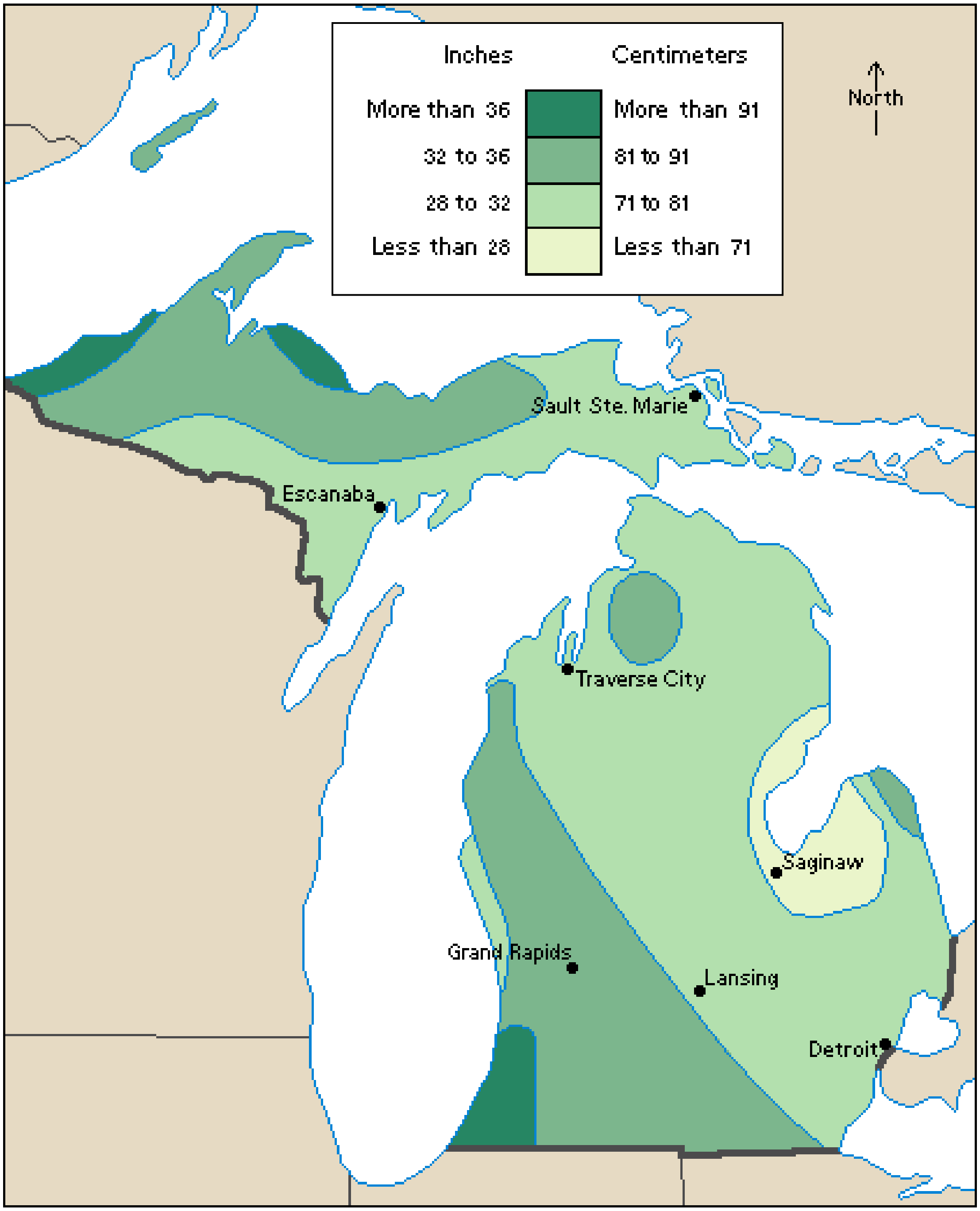

Fig. 6. Michigan average annual precipitation.

Saccharum), American beech (*Fagus grandifolia*), basswood (*Tilia americana*), and red oak (*Q. rubra*).

Anthropogenic effects from development patterns and introduction of non-native, fast-spreading plants are stressors on this fragile ecosystem. Incompatible development resulting in land use change could threaten the variety and availability of habitats, and thus threaten some of the only areas in which Prairie Warblers have been observed in Michigan in recent years (Brewer et al. 1991, Michigan Natural Features Inventory 2011).

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CHAPTER 2

UNDERSTANDING VEGETATION COMPOSITION IN MICHIGAN PRAIRIE WARBLER BREEDING AREAS

INTRODUCTION

The Prairie Warbler (*Dendroica discolor*) is one of 92 state-endangered species in Michigan (Michigan Natural Features Inventory 2011). Understanding plant composition in areas selected by Prairie Warblers in Michigan for breeding territories has been specifically identified as a critical information need to better understand habitat requirements for natural resource management and conservation planning (Nolan et al. 1999, Cooper 2000, Southwell 2001). Currently no quantifiable analysis of habitat selection exists for Prairie Warblers in Michigan (Walkinshaw 1991, Cooper 2000, Southwell 2001). Determining the composition of resources used by Prairie Warblers can aid our understanding of important elements associated with habitat use and needs in the broader context of the landscape. Information on within-territory habitat use will contribute to our understanding of habitat selection on the northern edge of the Prairie Warbler breeding range.

Prairie Warbler breeding territories have been characterized as open, brushy, early successional vegetation containing scrub-shrub plant species on poor soils with little or no tree canopy (Nolan 1978, Walkinshsaw 1991, Nolan et al. 1999, Cooper 2000). Lake Michigan sand dunes have been denoted as critical breeding areas (Walkinshaw 1991). Michigan Prairie Warbler populations have been noted to breed in three general vegetation types (Walkinshaw 1991), although this may not be an exhaustive list of potential breeding habitat in Michigan: 1) early successional stages of Great Lakes sand dunes where deciduous or coniferous shrubs are intermixed with dune grass and other herbs, 2) early-successional, shrubby openings associated with previously-burned jack pine plains, and 3) previously burned conifer stands dominated by deciduous shrubs and small trees. Prairie Warbler occurrences have been confirmed in 18 of 83 counties between 1986 and 2011 (Michigan Natural Features Inventory 2011) with more recent records associated almost exclusively with the west Michigan counties bordering Lake Michigan (Brewer et al. 1991, Michigan Natural Features Inventory 2011).

The goal of this research was to quantify breeding area information for Prairie Warblers along the eastern Lake Michigan coast. Objectives were to 1) locate Prairie Warbler breeding areas, 2) quantify plant composition associated with Prairie Warbler breeding areas and unoccupied sites, and 3) determine whether geographic variation existed in the plant composition associated with Prairie Warbler breeding areas.

STUDY AREA

Nine study sites were located in the Lower Peninsula of Michigan along the Lake Michigan coast (Figure 7). Study sites were chosen because they were publically accessible and contained potential Prairie Warbler habitat (identified by cover type (i.e., jack pine, sand dunes, scrub-shrub) (Nolan 1978, Nolan et al. 1999, Cooper 2000, Southwell 2001). Study sites included 6 State Parks, Sleeping Bear Dunes National Lakeshore, Oval Beach (a public beach owned by the city of Saugatuck), and Kitchel-Lindquist Dunes Preserve (a publically-accessible preserve near Grand Haven). The distance between the southern-most site (Warren Dunes State Park) and the northern-most site (Sleeping Bear Dunes National Lakeshore) was approximately 386 km (240 miles).

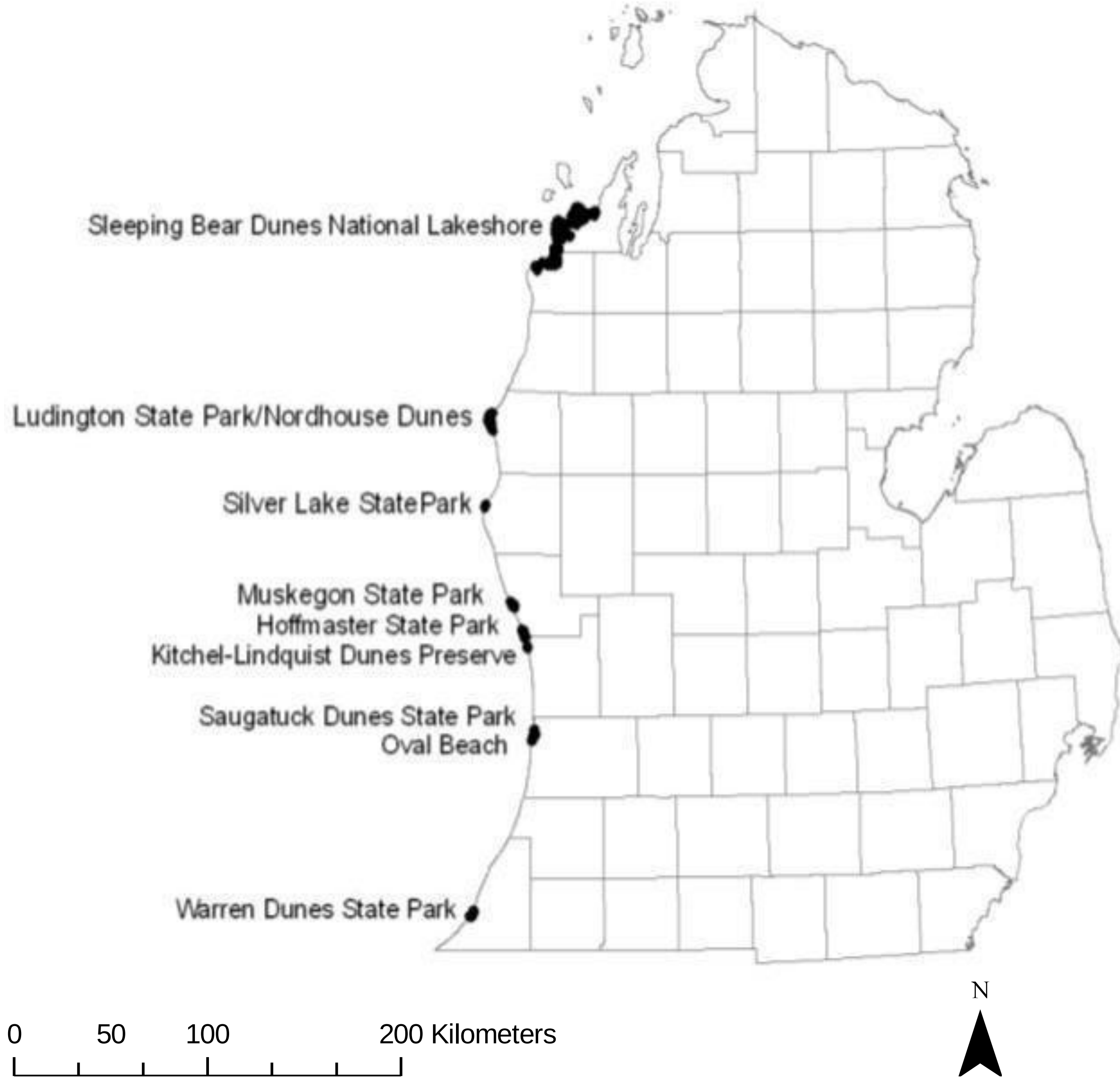

Fig. 7. Nine Prairie Warbler survey locations along the Lower Peninsula of Michigan. Surveys took place from May-August in 2004 and 2005. Distance between Warren Dunes State Park and Sleeping Bear Dunes National Lakeshore is approximately 386 km (240 miles). Prairie Warblers were detected in Sleeping Bear Dunes in 2004 and in Kitchel-Lindquist Dunes Preserve, Saugatuck Dunes State Park, Oval Beach and Warren Dunes State Park in 2005.

Michigan's Great Lakes shoreline, foredune, and backdune forest systems are a relatively small but ecologically valuable component of the state's natural features (Albert 2000). Foredune vegetation communities consist of specialized plants and some shrubs adapted to sand burial and fast growth with deep, often rhyzomal, root systems that stabilize blowing sand. Pioneering grasses such as marram grass (*Ammophila breviligulata*) and sand-reed grass (*Calamovilfa longifolia*) cause sand to accumulate and stabilize. Common Michigan foredune shrubs include hearty, woody species such as sand cherry (*Prunus pumila*), red osier dogwood (*Cornus stolonifera*), bearberry (*Arctostaphylos uva-ursi*), several dune willows (*Salix* spp.), and creeping juniper (*Juniperus horizontalis*). These plants must tolerate extreme temperatures, low moisture levels, and low levels of nutrients in addition to blowing sand (Hazlett 1991, Albert 2000).

The foredune zone undergoes continual change due to natural weather events, erosion, and water level fluctuations. Larger dunes form behind the protective foredune, where sand accumulation is slower, allowing dune grasses, herbaceous plants and shrubs and forests to establish. Oaks (*Quercus* spp), bigtooth aspen (*Populus grandidentata*) and sassafras *(Sassafras albidum)*, in addition to stands of jack pine (*P. banksiana*) and common juniper (*J. communis*), grow closest to the shoreline on wind-ward slopes. In contrast, the land-ward side of the dunes is more moist and nutrient-rich, supporting mesic forest species like sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), basswood (*Tilia americana*), and red oak (*Q. rubra*).

Anthropogenic effects from development patterns and introduction of non-native, fast-spreading plants are stressors on this ecosystem. Anthropogenic development could threaten the variety and availability of habitats, and thus threaten some of the only areas in which Prairie Warblers have been observed in Michigan in recent years (Michigan Natural Features Inventory

2011).

Prairie Warblers arrive on Michigan breeding grounds within the first 2 weeks of May (Dunn and Garret 1997). Mean temperature in 2004 and 2005 at Sleeping Bear Dunes during this time (May 1-14) was 11°C (52°F) and 9°C (49°F), respectively; Warren Dunes temperatures were 14°C (58°F) and 12°C (53°F), respectively. These year-specific temperatures compare closely to average annual temperatures at Sleeping Bear Dunes and Warren Dunes during May: 13°C (55°F) and14°C (57°F) respectively. Average precipitation for the month of May is 6.6 cm at Sleeping Bear Dunes and 8.1 cm at Warren Dunes. Temperatures increase throughout the Prairie Warbler breeding season in Michigan with variable rainfall. Fall avian observation records suggest that Prairie Warblers tend to leave breeding grounds to migrate south by the third week of August (Michigan Natural Features Inventory 2011).

METHODS

Avian Surveys

The Michigan Department of Natural Resources' (DNR) Integrated Forest Monitoring, Assessment and Prescription (IFMAP) land cover data were used to guide the selection of avian point count survey locations sampled in 2004 and 2005 (Michigan Department of Natural Resources 2001). The IFMAP data were derived from classified Landsat Thematic Mapper 5 and 7 imagery, dated 1999-2001. Overall accuracy of IFMAP data was 88% at Anderson Level 2 (major land cover classes; scale of 1:40,000) (Space Imaging 2004). The IFMAP land cover classes were aggregated from 35 classes into 9 similar, more general classes (Urban, Agriculture, Herbaceous-Shrub Upland, Upland Deciduous Forest, Upland Coniferous Forest, Water, Lowland Forest, Nonforested Wetland, Sand/Bare Soil) for the purposes of avian survey point selection. Survey points were equally distributed within 3 of the 9 land cover classes (Sand/Bare

Soil, Herbaceous-Shrub Upland, and Upland Coniferous Forest) to represent all possible land cover classes that Prairie Warblers have been known to inhabit in Michigan and throughout their breeding range (Nolan 1978, Nolan et al. 1999, Cooper 2000, Southwell 2001).

Avian point count survey locations were randomly chosen using a GIS random point generator (Jenness 2003) in suitable land cover types. Study site boundaries were acquired from state, federal or municipal entities. Two-hundred ninety-two point count survey points were established in Sleeping Bear Dunes in 2004. The number of survey points in each of the 8 sites south of Sleeping Bear Dunes (hereafter referred to as the southern sites) was selected in proportion to the total area of each site, totaling 172 point count survey points in 2005. Number of sampling sites in Sleeping Bear Dunes (2004) and southern sites (2005) were maximized based on the number of samples possible during the breeding season.

Locating Prairie Warblers was the primary objective of the point count surveys, therefore when a Prairie Warbler was detected while walking between point count locations, a GPS point was taken and added to the point count survey schedule. All avian survey points were at least 200 m apart. Prairie Warblers were identified using 10-minute point counts (Ralph et al. 1995, Cooper 2000) May 5 – July 28 in 2004 and May 3 – June 22 in 2005. Surveys took place from 30 minutes before sunrise (civil twilight) until 10:30AM in the absence of rain, heavy fog or high winds (Ralph et al. 1995). Point count locations were surveyed with a rotating time and observer schedule to reduce biases. All points were observed on at least 4 occasions.

Mapping Occupied Areas

Areas occupied by Prairie Warblers were mapped using GPS to provide descriptive spatial data estimating the shape and size of the area the birds were using for later vegetation sampling in those areas. Mapping began when Prairie Warbler presence was recorded during repeated point count surveys. Mapping visits continued until at least 25 registration (GPS) points per occupied area were collected. Registrations included male singing locations, feeding sites, or locations where defense of the area boundaries was observed. Though breeding was not confirmed, these areas were likely breeding territories. Each occupied area was visited for mapping at least 3 times. Each mapping visit lasted approximately 1 hour. The time of day a particular bird was mapped alternated so that early morning, mid-morning, and afternoon behaviors and movements were all included in the area's delineation.

The Animal Movement extension (Hooge and Eichenlaub 1997) was used in GIS to determine area size and shape based on registration points. Occupied area estimates were calculated using a fixed kernel home range estimator with least squares cross validation (Silverman 1986). Occupied areas were calculated at 95% and 50% probability contours. Fifty percent probability contours were chosen for use in vegetation sampling (described below) because these areas represented highest use.

Unoccupied Sites

Unoccupied survey points were chosen randomly from avian point count survey points on which Prairie Warblers were not detected. Unoccupied points were buffered by the average radius of the 50% probability contours (polygons) for each site (Table 1) to approximate occupied area for use in vegetation sampling. Occupied area size (assumed to be a breeding territory) tended to increase as area of the site increased, therefore the average territory radius for a site of similar total area was used to buffer unoccupied points on sites with no Prairie Warblers detected (Hoffmaster, Muskegon, Silver Lake and Ludington) (Table 1).

Vegetation Sampling and Survey Design

A 60 x 60 m grid was overlaid on each occupied area polygon using GIS. Three grid cells, occurring completely within the occupied area boundary, were randomly selected in each occupied area to serve as locations for vegetation sampling arrays. Survey arrays were centered

Table 1. Total area (ha) and potential habitat (ha)* of 9 study locations used to survey for Prairie Warblers in Michigan from May-August in 2004 and 2005.

Site	Territory (n)	Un-occupied (n)	Total Area (ha)	Potential Habitat (ha)	Average 50% Territory Radius (m)	Avian survey points (n)
Sleeping Bear Dunes National Lakeshore	20	27	28,808	5,289	56	292
Ludington State Park & Nordhouse Dunes	0	14	1,797	1,371	32	43
Silver Lake State Park	0	4	545	528	32	17
Muskegon State Park	0	4	410	160	32	23
Hoffmaster State Park	0	4	464	163	32	18
Kitchel-Lindquist Dunes Preserve	2	3	104	56	24	16
Saugatuck Dunes State Park	6	4	438	245	32	28
Oval Beach	2	2	42	16	19	8
Warren Dunes State Park	8	2	1,456	184	32	19
TOTAL	38	64	34,064	8,012	32	464

*Amount of potential habitat was calculated by summing sand, scrub-shrub herbaceous and conifer land cover classes derived from Michigan Department of Natural Resources Integrated Forest Monitoring, Assessment and Prescription land cover dataset. Site boundaries determined by state, federal or municipal parcel boundary GIS shapefiles.

in selected grid cells. Each unoccupied point was used as the center of an unoccupied vegetation sampling array, hereafter referred to as a plot.

Vegetation composition (presence – absence for each plant species) was measured in 0.5 m radius circles, serving as subsamples for 2 m- and 30 m-radius circles within each occupied area (Figure 8). The nested sampling design provides for flexibility in future analyses that could use multiple resolutions of satellite or aerial imagery (Urban 2001). Differences between occupied and unoccupied areas were quantified 1) within a site and 2) across sites. Plant species presence data by survey plot was transformed into relative abundances for each species to standardize sampling effort between plots. Relative abundances were calculated by dividing the number of times a plant species was present on each plot by the number of samples in the plot.

Statistical Analysis

Detection Probability

Detection probability generally can be defined as the probability of detecting the species one is surveying. The goal of calculating detection probability was to determine a level of confidence associated with the number of Prairie Warblers located on study sites based on the number of locations surveyed and the number of survey repetitions at each point count point. Using detection probability models is one way to compare field survey techniques and subsequent findings (i.e., species detections) to a more accurate and precise estimate of species occupancy in study areas. Detection-corrected estimates of occupancy were calculated using

Program PRESENCE (MacKenzie and Hines 2008). Models developed by MacKenzie et al. (2002) were used to calculate detection probability and estimate site occupancy for Prairie Warbler data collected in years 2004 and 2005 for Sleeping Bear Dunes and the southern sites, respectively. One sampling covariate, standardized Julian date, was used in the models to assess

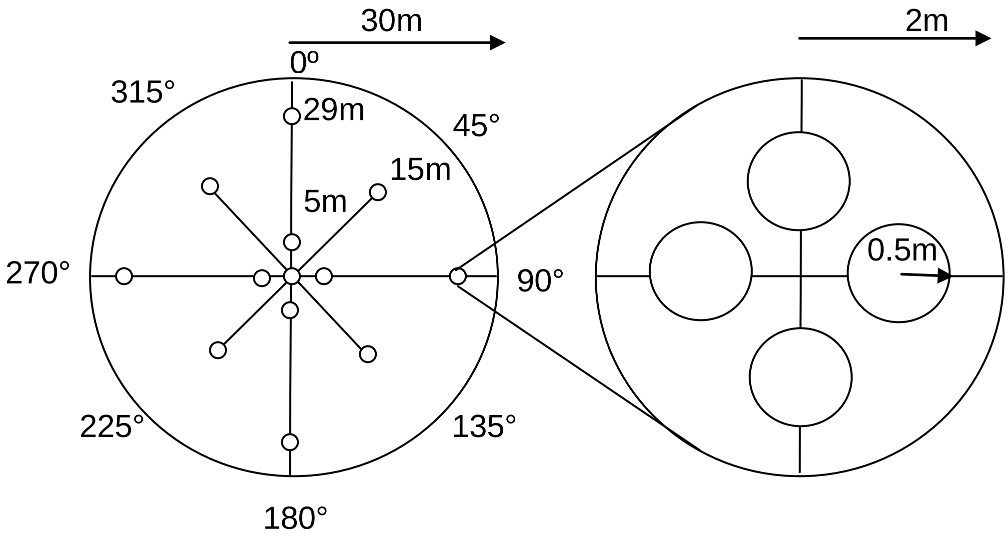

Fig. 8. Nested non-aligned block design used for vegetation sampling in Prairie Warbler territories and unoccupied sites. Vegetation sampling occurred in the 0.5 m circles. There were 52-0.5 m survey plots per 30 m radius plot.

whether date played a significant role in detection.

<u>Vegetation Analyses</u>

Exploratory analyses suggested that many plant species were not distributed across all survey plots with sufficient relative frequency to differentiate between Prairie Warbler presence and absence. To reduce the dimensionality of the vegetation data, a preliminary correspondence analysis was conducted in R (R Development Core Team 2008) using all plant species observed. Based on this analysis a subset of 46 plant species was selected for further analysis.

Using these 46 species, patterns in plant species composition were examined across the survey plots in a second correspondence analysis. Although there were 38 occupied and 64 unoccupied 30m radius vegetation survey arrays sampled (totaling 102 plots) (Figure 8), only the 76 survey plots on which Prairie Warblers were detected were used in this correspondence analysis (Sleeping Bear Dunes, Kitchel-Lindquist, Saugatuck, Oval Beach, Warren Dunes).

The goal of the correspondence analysis was to reduce the dimensionality of the dataset (76 plots x 46 plants data matrix) to describe how the plant composition differed across the 76 plots. Each axis generated by correspondence analysis represents a linear combination of the variables describing the abundances of each species. The amount of dimensional reduction represented by an axis is given by the eigenvalues of a matrix representing dissimilarities in species composition among plots (Legendre and Legendre 1998). The elements of the eigenvectors of this matrix associated with plant species represent the relative weighting of each plant species for a given axis.

A two-way analysis of variance (ANOVA), with an interaction term using the first 4 correspondence axes (dependent variables), was performed to determine 1) whether significant differences existed in areas where Prairie Warblers were present and absent and 2) whether those differences varied from north to south. A significant interaction between these 2 factors would indicate that the differences between areas where Prairie Warblers were present and absent varied between northern (Sleeping Bear Dunes) and southern sites.

RESULTS

Locating Prairie Warbler Breeding Areas

The greatest number of Prairie Warbler occupied areas was found in Sleeping Bear Dunes (n = 20). Eighteen occupied areas were collectively found in the southern sites, with Warren Dunes having the most (n=8), followed by Saugatuck Dunes State Park (n=6) and Kitchel-Lindquist Dunes Preserve and Oval Beach (n=2). Ludington State Park/Nordhouse Dunes, Silver Lake State Park, Muskegon State Park, and Hoffmaster State Park each had zero Prairie Warblers detected (Table 1). The average number of mapping visits per occupied area was 4.35. The average number of GPS registrations per territory was 38 (range 10 – 92 (SE = 3.4) across all sites; range 19 – 81 (SE = 3.7) in Sleeping Bear Dunes; range 10 – 81 (SE = 5.8) in the southern sites).

Detection Probability

Detection probability for Sleeping Bear Dunes was calculated using 292 point count locations with 5 sampling occasions per point in 2004. Prairie Warblers were detected at 28 point count locations in Sleeping Bear Dunes. The global model using standardized Julian date as a covariate on detection was overdispersed (c-hat = 1.947) and performed differently than expected based on bootstrap verification (chi-squared = 0.010). An intercept-only model, was subsequently calculated using the c-hat value from the global model to increase power in the detection probability model (MacKenzie et al. 2006). Both models performed equally well, leading to selection of the least parameterized model as the best model in this situation (Table 2). Detection probability for Prairie Warblers in Sleeping Bar Dunes was 0.340 (SE = 0.049),

Table 2. Detection probability and occupancy estimates for Prairie Warbler point count surveys in Sleeping Bear Dunes in 2004 (n = 292) and the 8 southern sites (n = 172).

			Occupancy		Detection Probability	
Model	AIC	AIC wt.	Psi	SE	p	SE
Sleeping Bear Dunes						
Psi(.),p(.)	362.988	0.500	0.123	0.023	0.340	0.049
Psi(.),p(Date)	362.480	0.500	0.122	0.023		
Southern sites						
Psi(.),p(.)	148.630	0.725	0.138	0.028	0.554	0.058
Psi(.),p(Date)	150.570	0.275	0.137	0.028		

indicating that the likelihood of detection, given that a Prairie Warbler occupy a site, is 0.34. Reliable survey methods should be able to detect a species 15% of the time when the species occupies an area (Bailey et al. 2004, O'Connel et al. 2006). Occupancy corrected for detection in Sleeping Bear Dunes was 0.123 (SE = 0.023; Table 2).

Detection probability for the southern sites in 2005 was based on 172 point count locations with 4 sampling occurrences per site. Prairie Warblers were detected at 22 southern point count locations. Similar to Sleeping Bear Dunes, I calculated an intercept-only and Julian model (Table 2). The intercept-only model ranked highest but was overdispersed (c-hat=1.694), suggesting more variation in the observed data than could be accounted for by the model. Detection probability on the southern sites was 0.554 (SE = 0.058). Occupancy corrected for detection probability was assessed at 0.138 (SE = 0.028).

Results indicate that Prairie Warbler detectability is relatively high (i.e, > 0.34) using the point count methodology. Hence, repeated sampling visits (i.e., > 3) should result in reasonably accurate occupancy status for a given location.

Vegetation Analysis

Correspondence axis 1 represented the largest amount of variability in the dataset. Axes 1 and 2 represent 15.1% and 11.3% of the variability in the dataset, respectively. Only results for correspondence axes 1 and 2 will be discussed below as they were the only axes where differences among breeding and non-breeding areas and differences between geographic locations were found.

Axis 1 is predominantly influenced by large, positive eigenvector loadings associated with tree species including sugar maple, Austrian pine (*P. nigra*), red pine (*P. resinosa*), jack pine, green ash (*Fraxinus pennsylvanica*), red oak and black cherry (*P. serotina*) (Table 3). Garlic mustard (*Alliaria petiolata*), considered a nonnative, invasive species, also had a large

Table 3. Plant species most influential in describing differences across vegetation survey plots. Plants are shown with correspondence analysis four-letter code, common name, genus species, and eigenvector loadings for axes 1 and 2 which represent 15.1% and 11.3% of the proportional variance in the dataset respectively. Large eigenvector loadings, driving differences, are bolded.

Spp	**Common name**	**Genus species**	**Axis 1**	**Axis 2**
ANSP	anenome spp	*Anemone spp.*	-0.05	0.09
AUPI	Austrian pine	*Pinus nigra*	**0.43**	0.02
BARB	barberry species	*Berberis species*	0.01	0.00
BEAR	bearberry	*Arctostaphylos uva-ursi*	-0.08	**0.40**
BLCA	bladder campion	*Silene latifolia*	-0.06	-0.05
BLCH	black cherry	*Prunus serotina*	**0.15**	-0.01
BOBE	bouncing bet	*Saponaria officinalis*	0.00	-0.12
BRFE	bracken fern	*Ptridium aquilinum*	0.00	-0.02
CHCH	choke cherry	*Prunus virginiana*	**0.08**	-0.05
CHWE	chickweed species	*Stellaria spp.*	-0.03	**-0.13**
COJU	common juniper	*Juniperus communis*	-0.04	**0.23**
COLU	columbine	*Aquilegia canadensis*	0.02	0.01
CRJU	creeping juniper	*Juniperus horizontalis*	-0.04	**0.50**
DWGR	dune wheat grass	*Agropyron dasystachyum*	-0.03	-0.08
FAHE	false heather	*Hudsonia tomentosa*	0.00	-0.06
FLSP	flowering spurge	*Euphorbia corollata*	0.00	-0.08
FMGR	fowl meadow grass	*Poa trivialis*	0.00	-0.02
GAMU	garlic mustard	*Alliaria petiolata*	**0.27**	0.00
GRAS	green ash	*Fraxinus pennsylvanica*	**0.19**	-0.01
GRSP	grass species	*grass spp.*	-0.01	0.13
HAWE	hawkweed	*Hieracium spp.*	-0.04	**0.13**
HOTA	horse tail	*Equisetum hyemale*	-0.03	**-0.17**
JAPI	jack pine	*Pinus banksiana*	**0.13**	0.00
JUGR	june grass	*Koeleria macrantha*	-0.05	**-0.14**
LIBL	little bluestem	*Schizachyrium scoparium*	-0.08	-0.08
LOTV	lily of the valley	*Convallaria majalis*	0.09	0.00
MAGR	marram grass	*Ammophila breviligulata*	-0.04	**-0.38**
MEAD	meadowsweet	*Spiraea alba*	0.02	-0.03
ORGR	orchard grass	*Dactylis glomerata*	-0.03	-0.09
PITH	pitcher's thistle	*Cirsium pitcheri*	-0.03	-0.06
POIV	poison ivy	*Toxicodendron radicans*	-0.01	**0.14**
QUGR	quack grass	*Agropyron repens*	0.01	-0.01
REOA	red oak	*Quercus rubra*	**0.15**	-0.03
REPI	red pine	*Pinus resinosa*	**0.25**	0.02
RTGR	red top grass	*Agrostis gigantea*	-0.01	**0.25**
RUBU	rubus species	*Rubus spp.*	0.01	0.10
RUSH	rush species	*Juncus spp.*	0.00	-0.10

Table 3. (cont'd)

SFSS	star.f.solomon's seal	*Smilacina stellata*	0.06	**0.16**
SNOW	snowberry, common	*Symphoricarpos albus*	0.01	0.01
SOGE	soapwort gentian	*Gentiana saponaria*	0.00	-0.03
SPKN	spotted knapweed	*Centaurea maculosa*	-0.08	0.05
SRGR	sand reed grass	*Calamovilfa longifolia*	-0.06	**-0.27**
SUMA	sugar maple	*Acer saccharum*	**0.71**	0.00
WHAS	white ash	*Fraxinum americana*	**0.06**	-0.03
WORM	wormwood	*Artemisia campestris*	-0.08	**-0.15**

positive eigenvector loading associated with axis 1. Choke cherry (*P. virginiana*) and white ash (*F. americana*), though not as strongly associated, are 2 additional tree species with positive loadings on axis 1.

Axis 2 was influenced by a broader diversity of plant types with large loadings (Table 3). Large, positive eigenvector loadings were associated with 3 shrub and 1 grass species: creeping juniper, bearberry, common juniper and redtop grass (*Agrostis gigantea*) (Table 3). Axis 2 had large negative loadings associated with other grasses including marram grass, sand reed grass and june grass (*Koeleria macrantha*). Three herbaceous plant species have large positive loadings on axis 2: starry false Solomon's seal (*Smilacina stellata*), poison ivy (*Toxicodendron radicans*) and hawkweed (*Hieracium* spp.), while several more herbs have large negative loadings on axis 2: horsetail (*Equisetum hyemale*), wormwood (*Artemisia campestris*) and various chickweed species (*Stellaria* spp.).

There was a significant interaction between sites where Prairie Warblers were present and absent and differences between sites from north to south existed for axis 1 ($p \leq 0.0001$) (Table 4). The ANOVA results for axis 2 also showed a significant interaction, indicating a significant difference between occupied and unoccupied sites as well as significant variation between those differences in occupied and unoccupied sites from north to south ($p \leq 0.0001$) (Table 4).

Means were plotted for axis 1 and illustrate the difference between southern sites where Prairie Warblers were present and absent (Figure 9). Plant species associated with sites where Prairie Warblers were present in the south were primarily negatively loaded on both axes 1 and 2 and included grass and herbaceous species like marram grass, sand reed grass, wormwood, horsetail and chickweed species (Table 3, Figure 10). However, plant species associated with southern sites where Prairie Warblers were absent, while not clearly defined, were primarily influenced by tree species positively loaded on axis 1. These species include sugar maple,

Table 4. Two-way analysis of variance (ANOVA) for correspondence axes 1-4 (dependent variables) to test for differences between areas where Prairie Warblers were present and absent (presence) and whether differences varied between northern Sleeping Bear Dunes and southern sites (site). Significant (α <0.05) results are bolded with axes 1 and 2 showing significant interactions. DF = degrees of freedom. SS = sum of squares. MS = mean square.

Axis 1	**DF**	**SS**	**MS**	**F Value**	**P Value**
presence	1	3.0620	3.0620	4.1042	**0.0465**
site	1	13.5960	13.5960	18.2211	**<0.0001**
presence:site	1	10.5210	10.5210	14.0999	**<0.0001**
Residuals	72	53.7250	0.7460		
Axis 2	**DF**	**SS**	**MS**	**F Value**	**P Value**
presence	1	7.2400	7.2400	49.0080	**<0.0001**
site	1	8.2211	8.2211	55.6500	**<0.0001**
presence:site	1	7.3923	7.3923	50.0390	**<0.0001**
Residuals	72	10.6366	0.1470	7.0000	
Axis 3	**DF**	**SS**	**MS**	**F Value**	**P Value**
presence	1	0.7214	0.7214	1.8293	0.1805
site	1	1.1754	1.1754	2.9806	0.0886
presence:site	1	0.3285	0.3285	0.8330	0.3645
Residuals	72	28.3938	0.3940	4.0000	
Axis 4	**DF**	**SS**	**MS**	**F Value**	**P Value**
presence	1	1.4060	1.4060	3.3036	0.0733
site	1	0.0756	0.0756	0.1777	0.6746
presence:site	1	0.0296	0.0296	0.0695	0.7929
Residuals	72	30.6442	0.4250	6.0000	

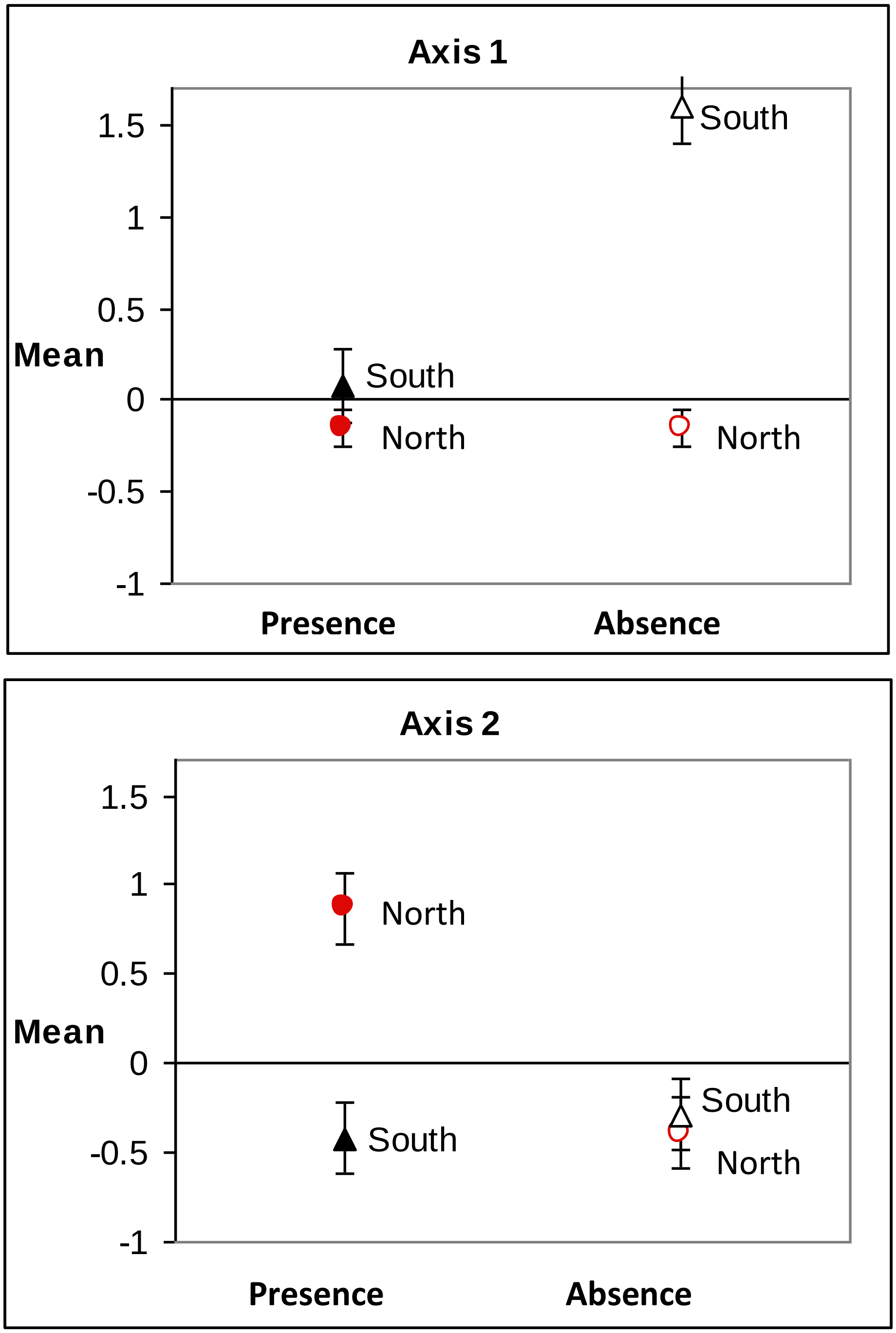

Fig. 9. Difference between Prairie Warbler occupied (solid shape) and unoccupied (hollow shape) areas in the north (red circles) vs. the south (black triangles). Mean eigenvector values were plotted for northern Sleeping Bear Dunes and southern sites with standard error bars for the first 2 correspondence axes.

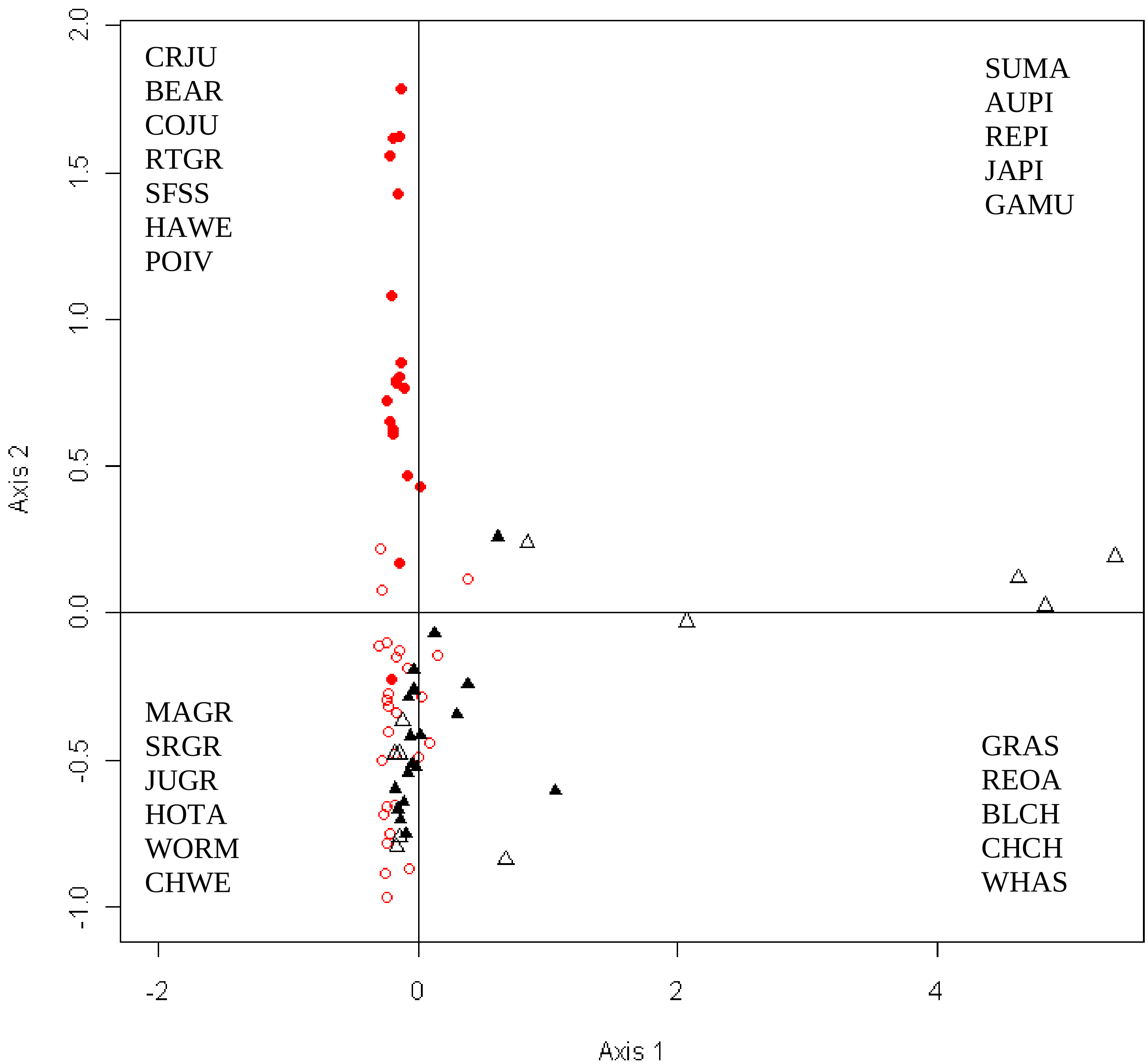

Fig. 10. Correspondence analysis plot for the 46 plant species. Plant species driving differences across Prairie Warbler presence and absence sites are represented by 4-letter codes in each quadrant (see Table 3 for plant species names and eigenvector loadings corresponding to axes). Sites occupied by Prairie Warbler in Sleeping Bear Dunes are represented by solid (red) circles and in southern sites by solid (black) triangles. Unoccupied sites in Sleeping Bear Dunes are represented by hollow (red) circles and in southern sites by hollow (black) triangles. Correspondence axis 1 (*x* axis) and 2 (*y* axis) represent 15.1% and 11.3% of the proportional variance in the dataset, respectively.

Austrian pine, red pine, jack pine, choke cherry, white ash, and garlic mustard (Table 3, Figure 10). This suggests that Prairie Warblers in the south may be avoiding areas with tree species and selecting areas with more grass and herbaceous plant species.

Means were plotted for axis 2 and illustrate the difference between northern areas in Sleeping Bear Dunes where Prairie Warblers were present and absent (Figure 9). Plant species associated with areas where Prairie Warblers were present in the north were positively loaded on axis 2 (and negative on axis 1). These plants included shrubs like creeping juniper, bearberry and common juniper (Figure 9). Redtop grass, hawkweed and poison ivy were also associated with areas where Prairie Warblers were present in Sleeping Bear Dunes (Table 3, Figure 10). Plant species associated with sites where Prairie Warblers were absent in the north were primarily negatively loaded on both axes 1 and 2 and included many of the same grass and herbaceous species present marram grass, sand reed grass, wormwood, horsetail, chickweed species). This suggests that Prairie Warblers in the north may be selecting sites with more shrub species than Prairie Warblers in the south.

Some of the same plants were common drivers between occupied and unoccupied southern sites and unoccupied areas of Sleeping Bear Dunes. While it can be difficult to summarize the complete variability of areas where Prairie Warblers (or any species) are absent, it is important that this study indicates that unoccupied areas are significantly different from areas where Prairie Warblers are present, both in the north and in the south. Additionally, plant composition associated with Prairie Warbler territories in the north is significantly different than plant composition associated with Prairie Warbler territories in the south.

DISCUSSION

The objectives of this study have been met. Prairie Warblers were located along the west Michigan shoreline with high detection probability. Plant composition varied across the plots surveyed and aspects of the differences can be related to specific relationships illustrated by correspondence analysis as outlined above. Plant composition in areas occupied by Prairie Warblers was found to be significantly different from plant composition in unoccupied areas. However, those differences were not consistent from north to south; Prairie Warblers breeding in northern areas had different plant species associated with them than did Prairie Warblers breeding areas in the southern part of the state. Overall, findings from this study should aid understanding of the differences in plant composition associated with Prairie Warbler breeding areas in different geographies along Michigan's west coast. Findings should better inform management and land use decision-making in areas this state-endangered species is, or could potentially be, using.

A main difference between northern and southern breeding areas tended to be the presence of shrubs versus grass; breeding areas in Sleeping Bear Dunes had more shrubs present than southern breeding areas did. Shrubs were largely absent on northern unoccupied plots, which shared some of the same plant species (grasses) as southern breeding areas, reinforcing the idea that there could be a change in habitat selection strategies from north to south along Michigan's west coast.

Why might these differences in vegetation from north to south exist and what does that mean for Prairie Warbler conservation and management? Michigan's climate and its glacial history yield a tension zone running east to west, roughly through the center of Michigan's Lower Peninsula, lending to some transition in vegetation community types distributed north to south along the lakeshore. Forest type transitions of primarily hardwood and associated herbaceous assemblages in the south, to mixed hardwood and coniferous forests with associated plant assemblages in the north are general descriptions of this transition. It is possible the north-to-south gradient in vegetation communities combined with differences in land use patterns (i.e., development, fragmentation) could result in different habitat selection strategies for Prairie Warblers north to south along the lakeshore. With regard to understanding these differences in the context of Prairie Warbler ecology, it may be important to gain additional insight into the specific plant assemblages serving the most essential functions in the breeding areas (i.e., nesting structure) so conservation and management actions consider these fine scale, high use habitat components. Reducing anthropogenic stressors on the dune ecosystem, such as incompatible development resulting in land use change and introduction of non-native, fast-spreading plants, may safeguard the variety and availability of habitats that exist, and thus protect some of the only areas in which Prairie Warblers have been observed in Michigan in recent years (Michigan Natural Features Inventory 2011).

This study's findings suggest that differences in vegetation composition between northern and southern breeding territories are a finer definition of habitat parameters for this species than has previously been documented. Learning more about the diversity of habitat Prairie Warblers may be using throughout Michigan could lend insight into future management opportunities. For example, surveying for Prairie Warblers in jack pine plains burned 10-20 years previously (i.e., Kirtland's Warbler habitat in the northeast Lower Peninsula). Prairie Warblers were more prevalent in the northeast Lower Peninsula in the early 1900's. Special attention to monitoring for Prairie Warblers in addition to Kirtland's Warblers during annual Kirtland's Warbler surveys is recommended to assess whether populations of Prairie Warblers may still be using parts of this area.

Nolan's (1978) 20-year study on Indiana Prairie Warbler populations (1951-1972) suggests that Prairie Warblers and their offspring will continue to return to the same breeding grounds until the area succeeds. Michigan's west coast may be providing a constant, or guaranteed, source of early successional habitat due to the disturbance inherent to the ecosystem. This could be the reason for their success in this region of the state. However, while the coastal areas surveyed in this study seem to support the majority of this species' population in Michigan (Michigan Natural Features Inventory 2011), surveys in other regions of the state could help better document the potential range of variability in plant composition associated with other areas Prairie Warblers find suitable.

This information will become increasingly important given the range of potential landscape composition changes projected in the Midwest and Great Lakes region under a changing climate (U.S. Global Change Research Program 2009). Michigan lies along the northern edge of the Prairie Warbler breeding range and the contribution of this study to Prairie Warbler ecology is the first of its kind in Michigan and the northern Great Lakes region. Understanding Prairie Warbler habitat selection strategies at the northern edge of the breeding range will expand our overall understanding of Prairie Warbler ecology for future natural resource management and conservation planning. Differences in habitat selection strategies we observe to the north and to the south of the glacial tension zone in Michigan, may be a unique opportunity to examine species adaptation strategies at the edge of adjacent plant communities, potentially informing adaptive behaviors as species ranges continue northward shifts under a changing climate.

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CHAPTER 3

PRAIRIE WARBLER OCCUPANCY AND RESOURCE USE IN MICHIGAN DURING THE BREEDING SEASON

INTRODUCTION

A diversity of migratory birds depend on the relatively small but ecologically valuable Lake Michigan shoreline, foredune, and backdune forest systems (Albert 2000). Migratory birds are known to use these dune ecosystems as stopover (Mehlman et al. 2005) and breeding habitats (Brewer et al. 1991). These unique systems (275,000 acres of sand dune along Michigan's Great Lakes shoreline; Michigan Sea Grant 2012), sustain specialized plant communities that are adapted to the extreme temperature and weather patterns inherent to dune landscapes (Albert 2000). State-endangered Prairie Warbler (*Dendroica discolor*) observations in Michigan are almost exclusively from the Lake Michigan early-successional dune ecosystems (Michigan Natural Features Inventory 2011). Describing plant composition in areas selected by Prairie Warblers is a critical information need (Nolan et al. 1999, Cooper 2000, Southwell 2001). Understanding Prairie Warbler habitat selection during the breeding season can inform conservation and management.

A breeding territory describes an animal's spatial and temporal use of space (Aebischer et al. 1993). However, resource use within a territory or home range is rarely uniform (Marzluff et al. 1997). Differential resource use can be quantified using utilization distributions (UD; van Winkle 1975, Kernohan et al. 2001). A UD is a continuous relative frequency distribution derived from point locations recorded for an animal over a period of time (van Winkle 1975). The highest value in the UD corresponds to the area(s) most heavily used by an animal. Utilization distributions have regularly been used to define core use areas within home ranges

(Samuel et al. 1985), assess animal interactions (Seidel 1992, Millspaugh et al. 2000), and incorporate geographically-referenced time budgets into home range calculations (Samuel and Garton 1987). Developing UDs for Prairie Warblers and relating the UDs to environmental covariates in a spatially explicit manner can be achieved using resource utilization functions (RUF) (Manly et al. 2003, Marzluff et al. 2004). RUFs enable continuous, rather than discrete (used-not used), resource use assessments across landscapes. The regression coefficients in the RUF indicate the importance of each resource to variation in the UD.

For Michigan Prairie Warbler populations, information on within-territory habitat use will contribute to our understanding of habitat selection strategies. Additionally, data on within-territory habitat use will provide information at a resolution previously not evaluated. Prairie Warbler breeding habitat is generally characterized as having little tree canopy cover and poor dry sandy soils that support nesting vegetation structure between 1 and 3 m tall (Cooper 2000, Dunn and Garrett 1997, Walkinshaw 1991). The first survey record for a Prairie Warbler in the United States (April 18, 1810) described habitat as “barrens” and “prairie country…evidently resembling and perhaps representative of the tall-grass prairie” (Mengel 1965). The bird’s name, derived from this description by Alexander Wilson (Nolan 1978), does not fully describe the diversity of locations the bird inhabits within its current breeding range.

Overall, the Lake Michigan sand dunes have been designated as critical breeding areas for this species in Michigan (Walkinshaw 1991). Mayfield (1960) also suggested that Michigan’s jack pine (*Pinus banksiana*) plains may be important. Michigan Prairie Warbler populations have been observed breeding in three general vegetation types (Walkinshaw 1991, Cooper 2000), although this is not viewed as an exhaustive list of potential habitat: 1) early successional stages of Great Lakes sand dunes where deciduous or coniferous shrubs are intermixed with dune grass and other herbs, 2) early-successional, shrubby openings associated with previously-burned jack pine plains, 3) previously burned conifer stands now dominated by deciduous shrubs and small trees.

The objectives of this study were to 1) determine which land cover types can forecast Prairie Warbler occupancy in west Michigan dune landscapes, 2) develop resource utilization functions for Prairie Warbler breeding territories along Michigan's west coast, and 3) gain insight into how resource use may differ for Prairie Warblers between northern and southern coastal breeding territories in Michigan.

STUDY SITE

Nine study sites were located throughout the Lower Peninsula of Michigan along the Lake Michigan coast (Figure 11). Study sites were chosen because they were publically accessible and contained potential Prairie Warbler habitat (identified by cover type (i.e., jack pine, sand dunes, scrub-shrub; Nolan 1978, Nolan et al. 1999, Cooper 2000, Southwell 2001). Study sites included six State Parks, Sleeping Bear Dunes National Lakeshore, Oval Beach (a public beach owned by the city of Saugatuck), and Kitchel-Lindquist Dunes Preserve (a publically-accessible preserve near Grand Haven) (Figure 11).

Foredune vegetation communities consisted of specialized plants adapted to withstand sand burial and exhibit fast growth with deep, often rhyzomal, root systems that stabilize blowing sand (Albert 2000). Pioneering grasses such as marram grass (*Ammophila breviligulata*) and sand-reed grass (*Calamovilfa longifolia*) cause sand to accumulate and stabilize. Common Michigan foredune shrubs include woody species such as sand cherry (*Prunis pumila*), red-osier dogwood (*Cornus stolonifera*), bearberry (*Arctostaphylos uva-ursi*),

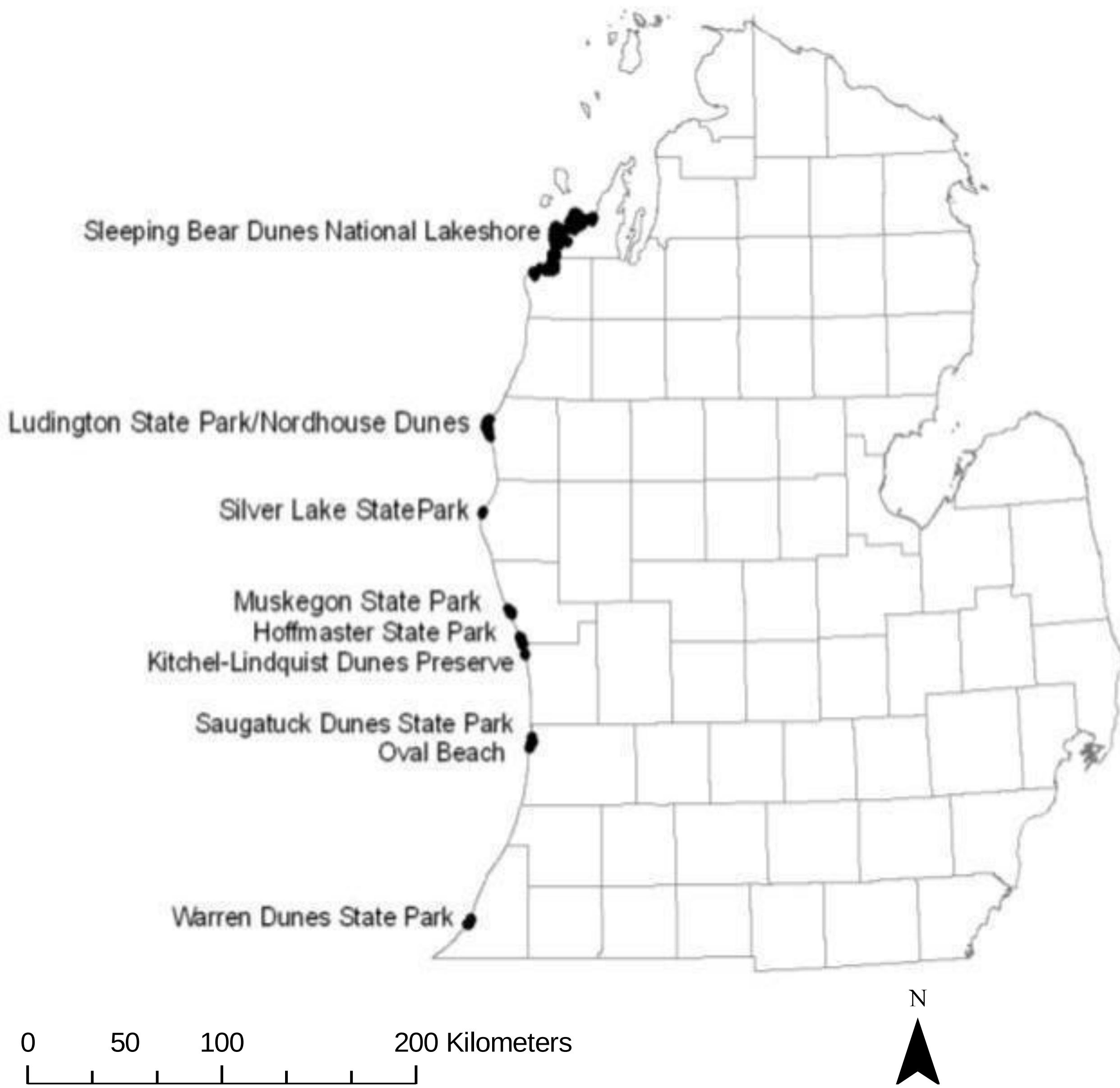


Fig. 11. Nine Prairie Warbler survey locations along the Lower Peninsula of Michigan. Surveys took place from May-August in 2004 and 2005. Distance between Warren Dunes State Park and Sleeping Bear Dunes National Lakeshore is approximately 386 km (240 miles). Prairie Warblers were detected in Sleeping Bear Dunes in 2004 and in Kitchel-Lindquist Dunes Preserve, Saugatuck Dunes State Park, Oval Beach and Warren Dunes State Park in 2005.

several dune willows (*Salix* species), and creeping juniper (*Juniperus horizontalis*). These plants must tolerate extreme temperatures, low moisture levels, and low levels of nutrients in addition to blowing sand.

The foredune zone undergoes continual change due to natural weather events, erosion, and water level fluctuations. Larger dunes form behind the protective foredune where sand accumulation is slower, allowing dune grasses, herbaceous plants, shrubs and forests to establish. Oaks (*Quercus* species), bigtooth aspen (*Populus grandidentata*) and sassafras *(Sassafras albidum)*, in addition to patches of jack pine and common juniper (*J. communis*), grow closest to the shoreline on wind-ward slopes. In contrast, the land-ward side of the dunes is moister and more nutrient-rich, supporting mesic forest species like sugar maple (*Acer Saccharum*), American beech (*Fagus grandifolia*), basswood (*Tilia americana*), and red oak (*Q. rubra*). Prairie warblers are most typically found in the early successional, transition zone between open sand and forest.

Anthropogenic effects from development and introduction of exotic invasive plants are stressors on the dune ecosystem. Anthropogenic development potentially threatens the variety and availability of habitats, thus threatening some of the only areas in which Prairie Warblers have recently been observed in Michigan (Michigan Natural Features Inventory 2011). Introduction of exotic invasive plants can alter the plant community composition and diversity (Levine et al., 2003); with potential negative consequences on Prairie Warbler habitat suitability.

Prairie Warblers arrive on Michigan breeding grounds within the first 2 weeks of May (Dunn and Garret 1997). The mean temperature in 2004 and 2005 at Sleeping Bear Dunes during this time (May 1-14) was 11°C and 9°C, respectively; Warren Dunes temperatures were 14°C and 12°C, respectively. These year-specific temperatures compare closely to average annual temperatures in Sleeping Bear Dunes and Warren Dunes during May: 13°C and 14°C, respectively. Average precipitation for May is 6.6 cm in Sleeping Bear Dunes and 8.1 cm in Warren Dunes. Temperatures increase throughout the Prairie Warbler breeding season in Michigan with variable rainfall. Fall avian observation records suggest that Prairie Warblers leave breeding grounds to migrate south by the third week of August (Michigan Natural Features Inventory 2011).

METHODS

Avian Surveys

I used Michigan Department of Natural Resources (DNR) Integrated Forest Monitoring, Assessment and Prescription (IFMAP; Michigan Department of Natural Resources 2001) land cover data to inform the selection of avian point count locations that were sampled in 2004 and 2005. The IFMAP data were derived from classified Landsat Thematic Mapper 5 and 7 imagery, dated 1999-2001. Overall accuracy was 88% for Anderson Level 2 categories (major land cover classes; scale of 1:40,000; Space Imaging 2004). I aggregated IFMAP data from 35 original land cover classes into 9 more general classes (Urban, Agriculture, Herbaceous-Shrub Upland, Upland Deciduous Forest, Upland Coniferous Forest, Water, Lowland Forest, Nonforested Wetland, Sand/Bare Soil). Equal numbers of survey points were distributed within 3 of the 9 land cover classes (Sand/Bare Soil, Herbaceous-Shrub Upland, and Upland Coniferous Forest) known to represent Prairie Warbler habitat throughout their breeding range (Nolan 1978, Nolan et al. 1999, Cooper 2000, Southwell 2001).

Avian point count locations were randomly chosen using a GIS random point generator (Jenness 2003) in suitable land cover types (Table 5). Study site boundaries were acquired

Table 5. Total area (ha) and potential habitat (ha)* of 9 study locations used to survey Prairie Warblers in Michigan from May-August in 2004 and 2005.

Site	Territory (n)	Un-occupied (n)	Total Area (ha)	Potential Habitat (ha)	Average 50% Territory Radius (m)	Avian survey points (n)
Sleeping Bear Dunes National Lakeshore	20	27	28,808	5,289	56	292
Ludington State Park & Nordhouse Dunes	0	14	1,797	1,371	32	43
Silver Lake State Park	0	4	545	528	32	17
Muskegon State Park	0	4	410	160	32	23
Hoffmaster State Park	0	4	464	163	32	18
Kitchel-Lindquist Dunes Preserve	2	3	104	56	24	16
Saugatuck Dunes State Park	6	4	438	245	32	28
Oval Beach	2	2	42	16	19	8
Warren Dunes State Park	8	2	1,456	184	32	19
TOTAL	38	64	34,064	8,012	32	464

* Amount of potential habitat was calculated for initial point count surveys by summing sand, scrub-shrub herbaceous and conifer land cover classes derived from Michigan Department of Natural Resources Integrated Forest Monitoring, Assessment and Prescription land cover dataset. Site boundaries determined by state, federal or municipal parcel boundary GIS shapefiles.

from state, federal or municipal entities. Two-hundred ninety-two point count survey points were established in Sleeping Bear Dunes in 2004 (5 sampling occurrences per point). The number of survey points in each of the 8 sites south of Sleeping Bear Dunes was selected in proportion to the total area of each site, totaling 172 point count survey points across those 8 sites in 2005 (4 sampling occurrences per point).

Locating Prairie Warblers was the primary objective of the point counts, therefore when a Prairie Warbler was detected while walking between point count locations, a GPS location was recorded and added to the point count schedule. All avian survey points were at least 200 m apart. Prairie Warblers were identified using 10-minute point counts (Ralph et al. 1995, Cooper 2000) May 5 – July 28 in 2004 and May 3 – June 22 in 2005. Surveys occurred from 30 minutes before sunrise (civil twilight) until 10:30AM in the absence of rain, heavy fog or high winds (Ralph et al. 1995). Point count locations were surveyed with a rotating time and observer schedule to reduce biases.

Territory Mapping

I conducted territory mapping in all areas occupied by Prairie Warblers in 2004 and 2005. Mapping began when Prairie Warbler presence was consistently recorded during repeated point count surveys. Mapping visits continued until ≥25 registration points (collected with GPS) per territory were collected. Registrations included male singing locations, feeding sites, or locations where defense of the territory boundaries was observed. Each territory was visited ≥3 times. Each mapping visit lasted approximately 1 hour. The time of day a bird was mapped alternated so that early morning, mid-morning, and afternoon behaviors and movements were all included in territory delineation.

Unoccupied Sites

Unoccupied survey points were chosen randomly from avian point count survey points on which Prairie Warblers were not detected. Unoccupied points were buffered by the average radius of the 50% use percentile, per site, as calculated from territories (Table 5). For sites without territories I used the average radius from the most proximate occupied site (Table 5). I used a fixed kernel home range estimator with least squares cross validation to estimate the 50% use percentile (Silverman 1986). Fifty percent probability contours were chosen to represent areas of concentrated use.

Occupancy Analysis

I used logistic regression to develop a predictive model of Prairie Warbler occurrence based on environmental covariates. I used 1 m National Agriculture Imagery Program (NAIP; United States Department of Agriculture 2005) imagery around each occupied and unoccupied point to quantify distances to specific cover types. Michigan NAIP imagery was collected between June and August, 2005. The images were available in county mosaics in natural color or color-infrared. The data met the 1:12,000 National Map Accuracy Standard (84% at Anderson level 4) (United States Bureau of the Budget 1947).

I explored the hypothesis that Prairie Warbler breeding territory occurrence was positively related to proximity of early successional land cover and to other Prairie Warbler territories. I defined 6 land cover types that could be identified from NAIP and were commonly observed around avian survey points: 1) developed, 2) sand, 3) grass, 4) shrub, 5) forest, and 6) water (Table 6). I measured distances from the nearest territory core area (50% use percentile) and from the edge of buffered unoccupied points to each land cover type using ArcMap 9.2 (ruler tool). I also measured the distance to nearest Prairie Warbler territory.

Table 6. Common, general land cover classes observed around Prairie Warbler breeding areas along Michigan's west coast.

Land Cover Type	**Definition**
Sand	Open, "bright"sand with no visible vegetation
Grass-herbaceous	Short and tall grasses and herbaceous vegetation indicated by "grayish" patches of sand that have no visible trees or large shrubs
Shrub	Patches of shrubs, saplings and occasional large trees that are disjunct from large, contiguous forest patches. This included large islands of "shrub" within the dune ecosystem.
Forest	Large, contiguous patches of dense canopy forest that boarder the sand dune ecosystem.
Lake Michigan	Water line visible in the NAIP image for Lake Michigan
Developed	Paved or unpaved roads, buildings, State campgrounds, State-owned parks with mowed lawns; note "developed" structures (e.g., cabin) under the canopy could not be detected
Closest Prairie Warbler occupied area	Kernel-estimated 50% territory probability contours (see Chapter 2)

I used distances to each land cover type and to Prairie Warbler territory as the predictor variables in a generalized logistic regression (Legendre and Legendre, 1998). Logistic regression is a special case of the generalized linear model (McCullaugh and Nelder 1983). It uses binary response variables (presence and absence) and estimates the probability of an effect (presence) given quantifiable circumstances (distances to land cover types or to another Prairie Warbler). I tested for multicollinearity among independent variables using Pearson correlations (Legendre and Legendre, 1998) in the R statistical and graphing environment (R Development Core Team 2011). Correlated variables were not included in the same candidate model.

I evaluated a full model (with all 6 independent variables) and a reduced model that included only significant variables ($\alpha < 0.05$). Model goodness-of-fit was assessed by calculating the amount of variation accounted for by each model. Coefficient significance was tested using Wald's chi-square test (z scores). A chi-squared test was used to determine whether the 2 models were significantly different from each other. Significant variables from the reduced model were plotted against the regressed occupied and unoccupied survey points to illustrate the probability of Prairie Warbler territory establishment as a function of distance to each variable.

Within-Territory Resource Utilization

I followed methods described by Marzluff et al. (2004) to explore resource use by Prairie Warblers within their breeding territories. I related geographic space use by Prairie Warblers, as portrayed by a UD, to environmental attributes using resource utilization functions (RUF; Manly et al. 2003, Marzluff et al. 2004). Utilization distributions can be related to environmental attributes using multiple regression (Marzluff 1986, Marzluff et al., 2004). The resulting regression equation is the RUF, where variation in the height of the UD (dependent variable) is attributed to variation in measured resources (independent variables) that underlie each UD location. The regression coefficients in the RUF indicate the magnitude and direction of animal responses to resources within a breeding territory.

I used R (R Development Core Team 2011) to calculate a UD for each Prairie Warbler breeding territory using a fixed-kernel estimation with least squares cross validation (LSCV) (Silverman 1986, Seaman and Powell 1996, Kernohan et al. 2001, Gitzen et al. 2006). Kernel-density estimation is favored over other territory estimation approaches (e.g., minimum convex polygon, bivariate-normal methods) for data with complex spatial patterns (Marzluff et al. 2004).

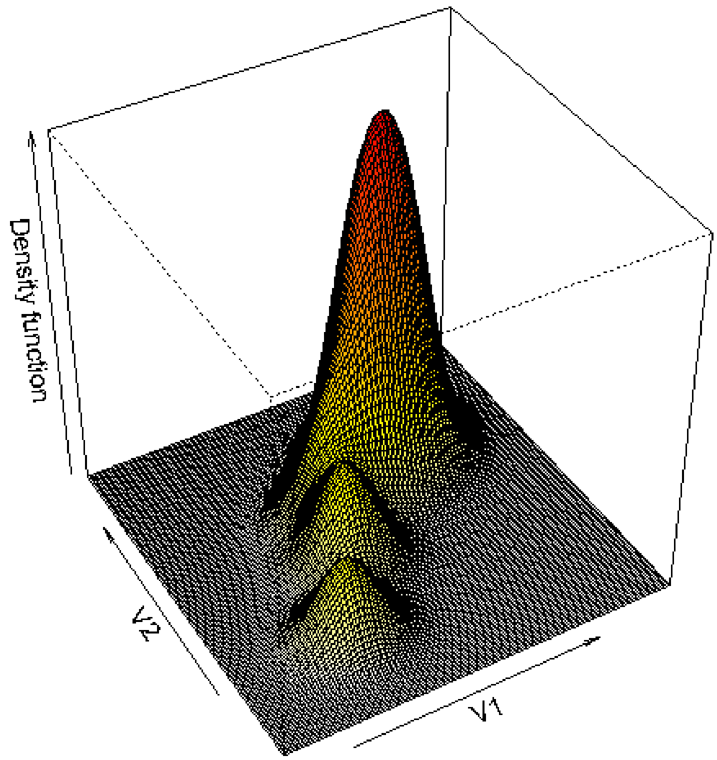
The kernel method is sensitive to choice of bandwidth (or smoothing parameter) (Silverman 1986, Seaman et al. 1999, Kernohan et al. 2001, Gitzen et al. 2006). The bandwidth controls the width of the individual kernels and therefore determines the amount of smoothing applied to the data (Kernohan et al. 2001). A large bandwidth value produces a smooth UD, which overestimates breeding territory size (Kernohan et al. 2001). Small bandwidths produce potentially fragmented breeding territories (Kernohan et al. 2001, Gitzen et al. 2006). Recent research indicates that the LCSV bandwidth performs best when distributions of registration points are in tight clumps (Millspaugh et al. 2006, Gitzen et al. 2006), consistent with Prairie Warbler registration points. The LSCV bandwidth also tends to perform better than other methods tested (e.g., solve-the-equation, plug-in) for estimating areas of peak use (e.g., measuring UD; Gitzen et al. 2006).

The kernel smoothing (KS) package was used in R, with least-squares-cross-validation (hlscv.diag R command) bandwidth. Hawth’s Tools (Beyer 2004) was used to calculate 99% breeding territory boundaries from Prairie Warbler registration points (Kernel Tools – Percent Volume Contour) and I subsequently used ArcMAP 9.3 to clip the UD with the 99% fixed-kernel territory boundary. This process resulted in a continuous UD surface that corresponded to the

99% territory. Cell size for the grid that represented each territory ranged from 2 - 8 m (varied depending on the size of the territory). I quantified the heights of the UD (e.g., Figure 12) for each grid cell in each breeding territory. The UD height was used as the response variable for the RUF.

I evaluated multiple land cover base map data sources (e.g., Michigan National Agricultural Imagery Program, Coastal Change Analysis Program (C-CAP), IFMAP, National Land Cover Database) for this project. Although I used 1 m NAIP county mosaics for the occupancy analysis, I chose 30 m C-CAP data for the within-territory analysis. The advantage of C-CAP imagery was that it was classified by 24 land cover types, which could be aggregated into land cover classes that theoretically influenced Prairie Warbler space use. The classified data provided an available, large-scale data source for repeating my analytical methods for all study locations (compared to NAIP unclassified images). C-CAP had a high accuracy rating and was deemed suitable for portraying the early successional components of the dune landscape important to Prairie Warblers.

The 30 m resolution C-CAP imagery was collected April 7, 2005 through October 1, 2006 (“leaf on” and “leaf off”), using Landsat Thematic Mapper and Landsat Enhanced Thematic Mapper (National Oceanic and Atmospheric Administration, Coastal Services Center 2008). The data met the 1:12,000 National Map Accuracy Standard (85% overall accuracy at Anderson level 4) (United States Bureau of the Budget 1947) with an overall accuracy assessment of 91.47% (National Oceanic and Atmospheric Administration, Coastal Services Center 2008). The C-CAP imagery contained 24 original land cover classes. I used 7 general land cover classes for this study: 1) developed, 2) sand, 3) grass, 4) shrub, 5) forest, 6) water, 7)



A.

B.

Fig. 12. (A) Example of multi-dimensional utilization distribution of a Prairie Warbler breeding territory compared to (B) territory mapping registration points for the same territory. The highest density of points in (B) is represented by the “highest” peak in (A).

wetland (Table 7). I quantified the percent of land cover classes for each cell within Prairie Warbler territories using a focal mean on a 3x3 neighborhood of cells.

I calculated a topographic wetness index (TWI) for the study area using the Topographic Wetness Index ArcScript in ArcGIS 9.3 (ESRI 2010). The TWI is a function of the natural logarithm of the ratio of local upslope contributing area and slope (ESRI 2010, Beven and Kirby 1979). The TWI was used as an index of soil moisture for 90 m cells within the study area and was calculated using a 30 m digital elevation model. High TWI values indicate wetness while low TWI values indicate dryness; TWI should thus portray wetness as influenced by topography.

I overlaid Prairie Warbler UDs and GIS layers of the independent variables (i.e., focal mean percent cover for each land cover class, focal mean of TWI, and nearest distance to other Prairie Warbler territory) and attributed each location in the UD with the independent variable value. Prior to RUF analysis (Handcock 2004, Handcock and Stein 1993), regression assumptions of normality, homoscedasticity and multicollinearity of independent variables were evaluated. The data were standardized to a mean of 0 and standard deviation of 1. I checked for multicolinearity among independent variables using a correlation matrix of Pearson correlation coefficients. I checked for homoscedasticity by evaluating residual plots. Normality was examined by viewing histograms of the data distribution for each independent variable. For right-skewed data, I used a Box Cox transformation (MASS package in R) to normalize the data.

The RUF is based on multiple linear regression (Legendre and Legendre, 1998) and produces maximum likelihood estimates for regression coefficients (Marzluff et al. 2004). Resource values at each cell within a breeding territory were regressed on the corresponding value of the UD at that cell. The sign associated with the regression coefficient for land cover

Table 7. Twenty-four original C-CAP land cover classes (30 m resolution) were reclassified into more general classes to represent resource attributes within Prairie Warbler breeding territories along the west coast of Michigan, 2004 and 2005.

Land Cover Type	**Definition**	**C-CAP classes merged (class number)**
Developed	The majority of "developed" land cover in selected survey sites is roads (often unpaved), parking lots and an occasional house or building. Some managed grasses or low-lying vegetation is planted in developed areas for recreation.	High- (2), Medium- (3),and Low-Intensity development(4). Developed Open Space (5)
Sand	Primarily composed of sand dunes. Generally, vegetation accounts for less than 10% of total cover.	Bare Land (20)
Grass	Areas dominated by grammanoid or herbaceous vegetation, generally greater than 80% of total vegetation. Although unlikely to occur, "cultivated crops" and "pasture/hay" were included in the event back-dune grassland was misclassified.	Grassland/Herbaceous (8), Cultivated Crops (6), Pasture/hay(7)
Shrub	Areas dominated by shrubs less than 5 m tall with shrub canopy typically greater than 20% of total vegetation. Includes tree shrubs, young trees in an early successional stage, or trees stunted from environmental conditions (12). Includes wetlands dominated by woody vegetation less than 5 m in height. Total vegetation coverage is greater than 20%. Species present could be true shrubs, young trees and shrubs, or trees that are small or stunted due to environmental condition.	Scrub/Shrub (12), Paulstrine Scrub/Shrub wetland (14)
Forest	Areas dominated by trees generally greater than 5 m tall and greater than 20% of total vegetation cover. Includes wetlands dominated by woody vegetation greater than or equal to 5 m in height where total vegetation coverage is greater than 20%.	Deciduous (9), Evergreen (10), Mixed Forest (11), Palustrine Forested Wetland(13)
Water	Areas of open water, generally with less than 25% over of vegetation or soil (e.g., Lake Michigan).	Open Water (21)
Wetland	Wetlands dominated by persistent emergent vascular plants, emergent mosses or lichens. Total vegetation cover is greater than 80%. Plants generally remain standing until the next growing season.	Palustrine Emergent Wetland (15)

types in this analysis indicates whether use increases (+) or decreases (-) with an increase in the quantity of the resource. For TWI, the sign designates increase in use with wetter (+) or drier (-) soil. Significance was estimated by noting whether the 95% confidence interval for the coefficient (mean ± SE*1.96) overlapped zero.

Mean standardized RUFs were assessed by comparing the regression coefficients in 3 ways: 1) across all 38 breeding territories (pooled), 2) for southern and northern sites exclusively to examine the potential for a north-to-south gradient in resource use (i.e., compare Sleeping Bear Dunes (n = 20) to the southern sites (n = 18)), and 3) individually for each of the 5 sites where Prairie Warblers were detected to assess more localized differences in site use. Comparison of standardized coefficients quantified the relative importance of each resource to space use in the breeding territory.

Relative availability of each covariate was compared across all territories (n = 38), for Sleeping Bear Dunes only (n = 20) and for the southern sites (n = 18). Mean TWI values for an area are on a possible scale from 0 to 224 (high = wet, low = dry). A *t*-test with Welch (1938) correction for unequal sample sizes was used to test for significant differences between mean percent land cover type for northern and southern territories. The Welch correction involves using degrees of freedom that are corrected for the sample size discrepancy (Zar 1996).

RESULTS

Thirty-eight Prairie Warblers were detected in breeding territories in 5 of the 9 sites surveyed (Table 5). The average number of mapping visits per territory was 4.35. The average number of GPS registrations per territory was 38 (range 10 – 92 (SE = 3.4) across all sites; range

19 – 81 (SE = 3.7) in Sleeping Bear Dunes; range 10 – 81 (SE = 5.8) in the southern sites). Breeding areas tended to be clustered within sites with breeding territory boundaries often adjacent to each other (e.g., Figure 13).

Occupancy Analysis

Percent cover of grass and shrubs were correlated (Pearson's correlation, $r = 0.817$). I removed the grass land cover variable because Prairie Warbler's are known to positively associate with shrub cover. Results from the fully parameterized logistic regression model indicated that distance to forest edge (forest; $z = -2.001$, $df = 116$, $P = 0.045$), distance to shrub (shrub; $z = -2.394$, $df = 116$, $P = 0.017$), and distance to closest Prairie Warbler occupied territory (praw; $z = -2.294$, df=116, $P = 0.022$) (Table 8) were negatively associated with Prairie Warbler occupancy along the western Michigan coastline. The negative association indicates that the probability of Prairie Warbler occupancy increased at shorter distances from the edge of another Prairie Warbler territory, to forest, and to shrub. My results confirm the hypothesis that Prairie Warbler breeding territories are associated with early successional woody land cover in the dune ecosystem. Additionally, my results indicate that Prairie Warblers establish breeding territories in close proximity to one another. The full model had an approximation of fit of 0.622 (1- residual deviance/null deviance), suggesting that 62% of the observed variability in the data was accounted for by this model.

I constructed a less parameterized logistic regression model using the 3 significant variables from the fully parameterized model (forest, shrub, distance to other prairie warbler territory). The reduced model indicated that distance to shrub ($z = -1.975$, $df = 119$, $P = 0.048$) and distance to closest Prairie Warbler territory ($z = -2.308$, $df = 119$, $P = 0.021$) were more

Fig. 13. Example of Prairie Warbler breeding territories calculated using a fixed kernel estimation with least squares cross validation. Eight breeding territories were mapped in Warren Dunes State Park, Berrien County, Michigan (southwest Michigan) in 2005.

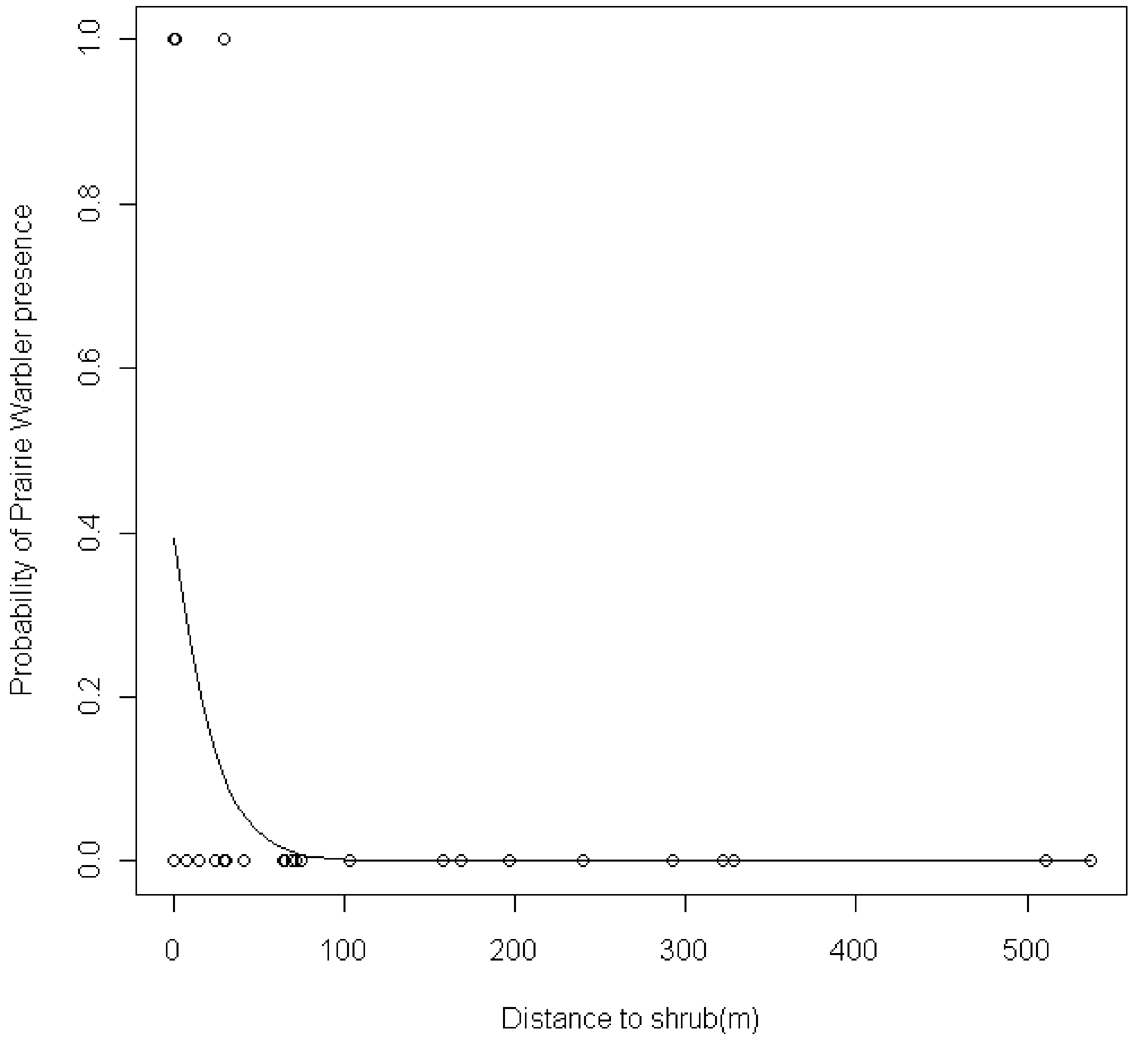
Table 8. Logistic regression results for land cover variables and Prairie Warbler presence-absence data. The full model contained 6 independent variables. The reduced model was calculated using significant variables from the full model. Coefficient significance was tested using Wald’s chi-square test (z scores). Approximation of fit was calculated as (1- residual deviance/null deviance) indicating the percent of variability explained by each model. X^2 notes whether the 2 models were significantly different (full residual deviance – reduced residual deviance, 3df).

	Full Model				**Reduced Model**			
	Estimate	SE	*z*	*P*	Estimate	SE	*z*	*P*
(Intercept)	1.788	0.749	2.387	0.017	2.086	0.516	4.044	0
forest	-0.003	0.001	-2.001	**0.045**	-0.002	0.001	-1.783	0.075
shrub	-0.117	0.049	-2.394	**0.017**	-0.086	0.043	-1.975	**0.048**
sand	0.020	0.017	1.211	0.226				
lake	-0.001	0.001	-0.781	0.435				
praw	-0.002	0.001	-2.294	**0.022**	-0.002	0.001	-2.308	**0.021**
developed	0.001	0.001	1.418	0.156				
Null deviance:		155.16	on 122 df		Null deviance:		155.16	on 122 df
Residual deviance:		58.6	on 116 df		Resid deviance :		62.62	on 119 df
Approximation of fit:		0.622			Approx. of fit:		0.596	
$X^2 = 0.259$								

*PRAW is distance to nearest Prairie Warbler occupied area important than forest cover to Prairie Warbler occupancy (Table 8). The approximation of fit for the reduced model was 0.596 (1- residual deviance/null deviance), suggesting that nearly 60% of the observed variation in the data was described using this model. Residual deviance for the reduced model was 62.62 on 119 degrees of freedom, which was larger than that of the full model (58.5, 116 *df*.), indicating that the full model performs better. However, results from these 2 models are similar; chi-square analysis showed that the fully parameterized model did not significantly differ from the less parameterized model ($P = 0.259$, $df = 3$; Table 8).

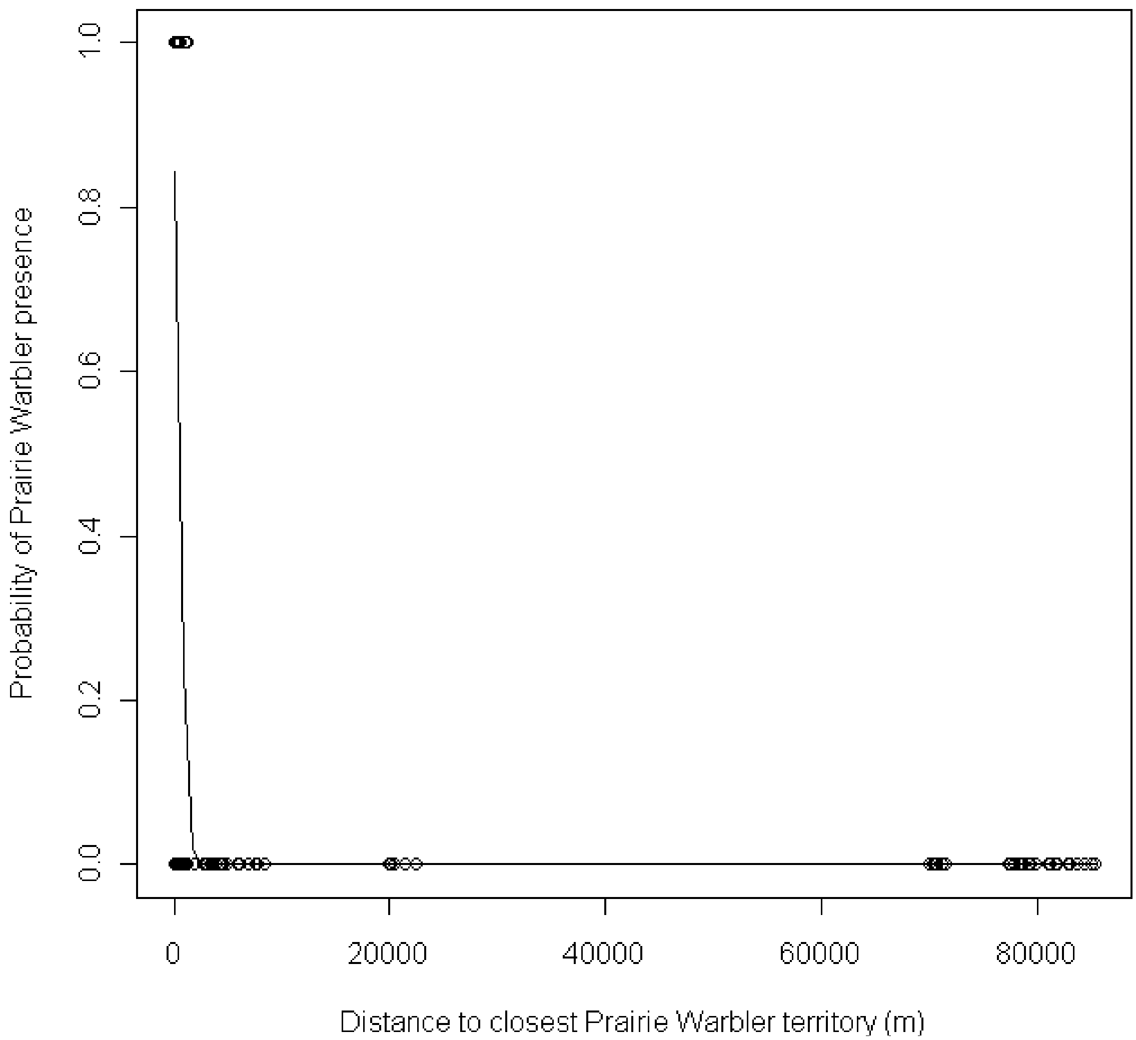
I plotted the relationships between Prairie Warbler occupancy probability and distance to the 2 significant predictors from the reduced model: shrub and distance to nearest Prairie Warbler territory (Figure 14). I found 0% probability of Prairie Warbler presence when shrubs were >103 m away from the edge of an existing Prairie Warbler territory. The probability of Prairie Warbler occupancy was 39% when shrubs were within 1 m (Figure 14). The model also predicts that Prairie Warblers will occupy sites that are <75 m away from shrubs, but probability of occupancy at these farther distances is low (1%). The farthest I measured shrubs from the edge of a Prairie Warbler territory in the field was 30 m.

Distance to the closest Prairie Warbler territory from the edge of another Prairie Warbler territory was the most significant predictor of Prairie Warbler presence (Table 8). I observed a 0% probability of Prairie Warbler presence when distance to another Prairie Warbler was beyond 1,284 m. However, I found an 80% probability of Prairie Warbler presence when another Prairie Warbler was within 91 m (Figure 14). These results indicate that Prairie Warbler breeding territories are clumped in the dune ecosystem, and because shrubs are relatively ubiquitous, I speculate that there is a conspecific attraction for territory establishment.



A.

Fig. 14. Probability of Prairie Warbler presence as a function of distance to (A) shrub and to (B) closest Prairie Warbler breeding territory; the two significant variables in the reduced logistic regression model.



B.
Fig. 14. (cont'd).

Resource Utilization Functions

None of the covariates I evaluated to describe within-territory Prairie Warbler space use were significant (i.e., Wald Test, P>0.05; Table 9). Similarly, RUFs for the north, south, and individual sites were not significant, although TWI may be informative (i.e., confidence interval does not overlap zero) on Sleeping Bear Dunes (Table 9). On the northern Prairie Warbler territories, resource use was positively correlated with moister sites (i.e., higher TWI values) (Table 9). These results suggest that habitat use within a Prairie Warbler territory is based on finer scale vegetation pattern than can be detected via C-CAP (30 m).

Northern and southern Prairie Warbler territories differed in cover type composition. Mean forest cover for Sleeping Bear Dunes (43%) was higher than that observed for southern territories (29%, Table 6; Welch's t = 2.28, df = 33, p = 0.029). Mean grass cover also differed between Sleeping Bear Dunes (32%) and southern territories (15%, Table 10; Welch's t = 2.83, df = 30, p = 0.008). Southern territories had greater mean percent sand than northern territories (65% vs. 40%; Table 10; Welch's t = -4.37, df = 35, p = 0.0001). I attribute these differences to higher TWI (noted in RUF output) that were observed in Sleeping Bear Dunes in that moister soils will likely support greater vegetation biomass.

Examination of the relationship among territory location and the amount of grass, forest and sand cover suggests a that northern Prairie Warbler territories contain more forest (Figure 15, solid circles) when grass cover is high, while southern Prairie Warbler territories contain more sand cover (Figure 15, hollow triangles) when grass cover is high. Thus, my results indicate that factors associated with space use by Prairie Warblers within a breeding territory vary by latitude, with more vegetated territories in the north.

Table 9. Estimates of standardized RUF coefficients (β) for Prairie Warblers across all territories (n = 38), Sleeping Bear Dunes only (n = 20) and southern sites (n = 18). Relative importance of resources is indicated by magnitude of β.

Resource Attribute	**Mean standardized RUF coefficients (β)**	**95% confidence interval**		***P* (β=0)***
All Territories (n=38)		**+**	**–**	
TWI	0.0164	0.0425	-0.0096	0.77
Grass	0.0595	0.1501	-0.0311	0.99
Developed	0.0015	0.0298	-0.0268	0.53
Shrub	0.0051	0.0444	-0.0342	0.59
Water	0.0077	0.0357	-0.0202	0.64
Forest	0.0018	0.0339	-0.0302	0.53
Wetland	-0.0084	0.0155	-0.0323	0.35
Sand	-0.0123	0.0146	-0.0393	0.29
Sleeping Bear Dunes (n=20)		**+**	**–**	
TWI	**0.0162**	**0.0321**	**0.0003**	0.53
Grass	0.0157	0.0319	-0.0005	0.53
Developed	-0.0171	-0.0013	-0.0330	0.47
Shrub	0.0256	0.0960	-0.0447	0.55
Water	-0.0122	0.0010	-0.0254	0.48
Forest	0.0220	0.0468	-0.0027	0.54
Wetland	-0.0051	0.0024	-0.0126	0.49
Sand	-0.0361	0.0022	-0.0744	0.44
Southern sites (n=18)		**+**	**–**	
TWI	0.0167	0.0696	-0.0362	0.66
Grass	0.1082	0.2990	-0.0826	0.99
Developed	0.0222	0.0787	-0.0343	0.71
Shrub	-0.0178	0.0093	-0.0448	0.33
Water	0.0299	0.0862	-0.0264	0.76
Forest	-0.0206	0.0406	-0.0817	0.31
Wetland	-0.0121	0.0385	-0.0627	0.39
Sand	0.0140	0.0489	-0.0208	0.63

*P-values test the null hypothesis that the standardized RUF coefficient (β) is zero, given sample sizes of n = 38, n = 20 and n = 18.

Table 10. Mean percent of each covariate by region. Relative availability of each covariate are compared across all territories (n = 38), for Sleeping Bear Dunes only (n = 20) and for the southern sites (n = 18). Mean TWI values indicate level of wetness for an area on a possible scale from 0 to 224 (high = wet, low = dry).

	TWI	SAND	FOREST	GRASS	SHRUB	DEVLP*	WETLND	WATER
All territories								
Min	15.91	1.17	0.01	0.01	0.01	0.01	0.01	0.01
Max	107.90	99.43	96.83	80.75	44.75	18.22	12.22	13.14
Mean	**50.81**	**51.92**	**36.12**	**23.59**	**3.35**	**2.13**	**0.81**	**0.67**
Sleeping Bear								
Min	14.68	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Max	91.91	98.91	96.71	87.81	47.31	27.36	9.91	17.76
Mean	**40.29**	**40.17**	**42.88**	**31.54**	**3.38**	**3.08**	**0.88**	**0.42**
Southern sites								
Min	17.29	2.45	0.01	0.01	0.01	0.01	0.01	0.01
Max	125.68	100.01	96.95	72.90	41.90	8.07	14.79	8.01
Mean	**62.49**	**64.97**	**28.60**	**14.76**	**3.31**	**1.08**	**0.73**	**0.95**
Warren Dunes								
Min	11.64	5.51	0.01	0.01	0.01	0.01	0.01	0.01
Max	116.26	100.01	94.51	79.26	30.51	0.01	5.51	12.51
Mean	**46.41**	**65.54**	**30.72**	**20.53**	**2.38**	**0.01**	**0.03**	**2.06**
Saugatuck								
Min	18.68	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Max	136.68	100.01	98.18	64.84	53.68	0.01	11.01	3.68
Mean	**65.50**	**60.53**	**31.98**	**11.18**	**4.75**	**0.01**	**0.76**	**0.06**
Oval Beach								
Min	24.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Max	122.01	100.01	100.01	61.01	61.01	39.01	16.51	11.01
Mean	**99.07**	**73.35**	**15.79**	**7.61**	**4.38**	**5.29**	**0.90**	**0.16**
Kitchel-Lindquist								
Min	29.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Max	134.01	100.01	100.01	83.51	33.01	33.51	61.51	0.01
Mean	**81.25**	**67.65**	**22.80**	**9.52**	**1.66**	**4.36**	**3.28**	**0.01**

*Developed land
** Southern sites include Warren Dunes State Park, Saugatuck Dunes State Park, Oval Beach and Kitchel –Lindquist Dunes Preserve.

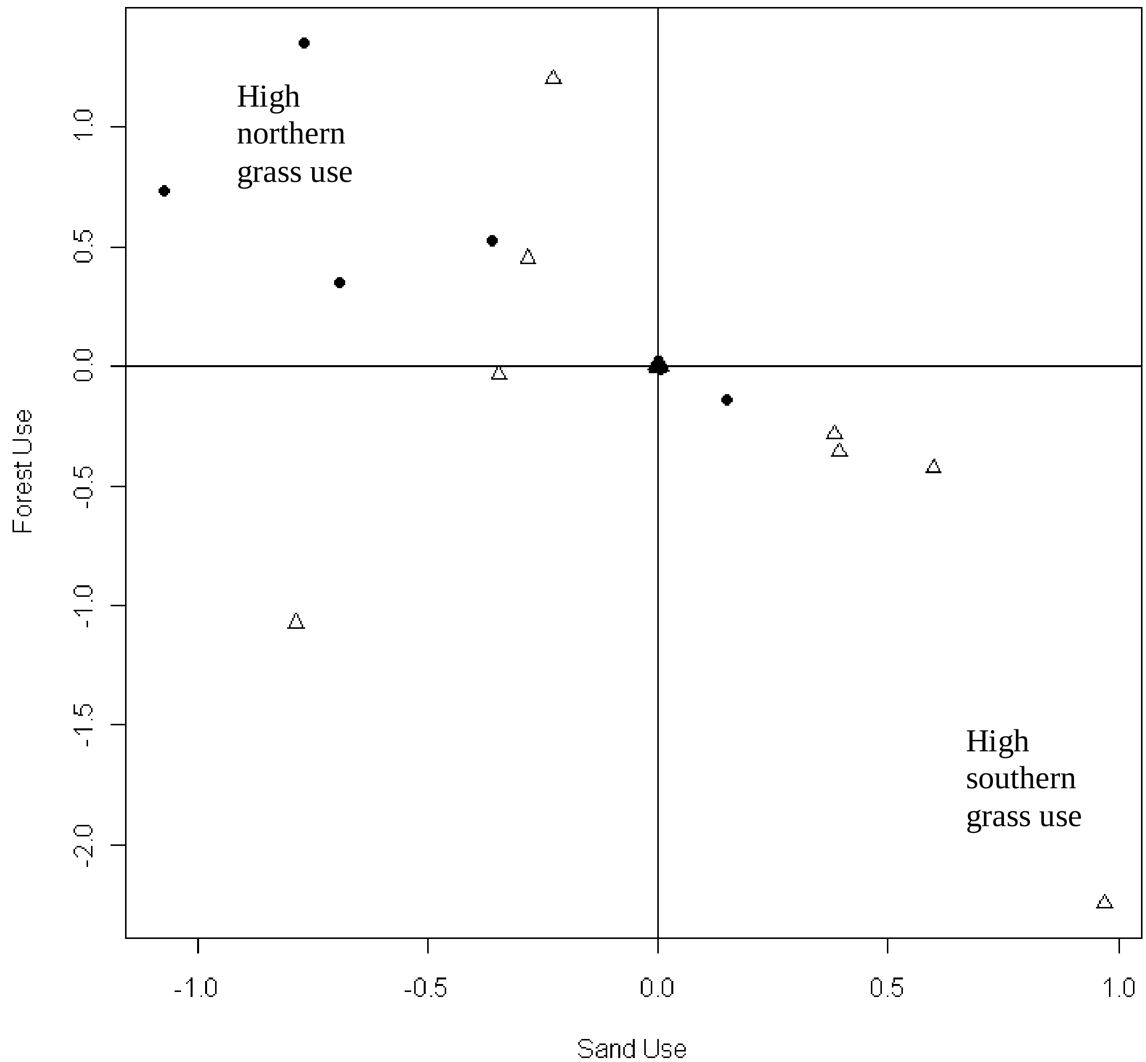


Fig. 15. Trend suggesting high northern forest use (solid circles) and high southern sand use (hollow triangles) by Prairie Warblers along Michigan's west coast. Prairie Warblers tended to use either forest or sandy areas of their breeding territories. Northern Prairie Warblers tended to concentrate use in grass when forest use was also high. Southern Prairie Warblers tended to concentrate use in grass when sand use was also high.

DISCUSSION

This research provides new information about Prairie Warbler resource utilization based on analysis of 38 west Michigan coastal breeding territories. The best indicators of Prairie Warbler occupancy were proximity to other Prairie Warblers and proximity to shrub cover type. I found an 80% probability of Prairie Warbler occupancy when another Prairie Warbler territory was within 91 m. I found a 39% probability of Prairie Warbler presence when shrubs were within 1 m of an existing Prairie Warbler territory. I found no significant environmental covariates from standardized RUFs, however, 4 observations warrant attention: 1) northern sites have more woody vegetation cover than southern sites, and southern sites seem to be more open, 2) grass cover appears to be important on southern sites, potentially because shrubs are less ubiquitous, 3) higher soil moisture in northern territories was suggested as an important indicator of habitat use, and 4) lack of significant (standardized) RUF coefficients suggests that the spatial resolution of land cover data (30 m C-CAP) may not have been appropriate to describe within territory space use for Prairie Warblers.

When determining which land cover types to use to assess Prairie Warbler resource use, I drew from Michigan casual observation records and species summaries (Brewer et al. 1991, Cooper 2000, Michigan Natural Features Inventory 2011), research in other breeding locations (Nolan 1978, Nolan et al. 1999, Cooper 2000, Southwell 2001) and my survey experience. Prairie Warblers require a specific combination of land cover features. Prairie Warblers glean insects from grass, herbaceous plants, shrubs and trees (Nolan 1978, Rappole et al. 1983) and they defend territories from and nest in shrubs and trees 1-3 m in height (Nolan 1978, Walkinshaw 1991, Dunn and Garrett 1997, Cooper 2000). Generally, my results support the previously observed relationships between Prairie Warbler occurrence and a mixture of herbaceous and low-growing woody vegetation. Additionally, my study was the first to document a latitudinal gradient in Prairie Warbler habitat use that was related to vegetation composition; with northern territory space use correlated with denser, woody vegetation and southern correlated with more open, grass dominated sites.

I found that proximity to another Prairie Warbler (within 91 m) was the most important predictor of occupancy in dune landscapes along the west coast of Michigan. Research suggests that conspecific attraction influences avian habitat selection and occupancy more than previously considered or reported (Danchin et al. 2004, Hahn and Silverman 2006, Betts et al. 2008). Studies on Kittiwakes (*Rissa tridactyla*) (Danchin et al. 1998) and Collared Flycatchers (*Ficedula albicollis*) (Doligez et al. 2002) have both shown that individuals will replicate habitat selection choices of conspecifics that experience high breeding success, using social cues as their primary decision-making strategy. Hahn and Silverman (2006) found that conspecific attraction was an important mechanism for breeding habitat selection for established populations of Redstarts (*Setophaa ruticilla*) in Michigan, but the effect was moderated by age, reproductive experience and timing of arrival. Harrison et al. (2009) warn that traditional habitat models, which consider only resource distributions and not social factors, may be inadequate tools for the conservation of Brewers Sparrows (*Spizella breweri breweri*) at the northern edge of their range.

Lack of significant RUF findings could imply little consistency in resource selection at the territory level, but more likely suggests that the data chosen to portray habitat conditions within a territory were likely not suited for this analysis. The 30 m C-CAP data was likely too coarse for describing Prairie Warbler habitat use within territories. Grass and sand land cover classes (as portrayed by 2006 C-CAP imagery) likely contained shrubs and saplings that would go undetected with 30 m resolution data. Finer-resolution land cover data may provide more useful insight into Prairie Warbler space use within a breeding territory. Key factors involved in habitat selection may not be detected without using the appropriate spatial scales of analysis (Orians and Wittenberg 1991). Using the grain at which organisms perceive resources is difficult to know but is certainly related to their sensory abilities (Vos et al. 2001) and thus should influence the scale at which resources are measured (i.e., the spatial resolution of land cover data). Marzluff et al. (2004) states that it would be prudent to select land cover data at a scale fine enough to capture important resource variation, even if one thinks this may not perceptible to the study organism.

MANAGEMENT RECOMMENDATIONS

The west Michigan dune landscape is providing a source of early successional habitat for Prairie Warblers that is maintained through wind and wave dynamics. Habitat fragmentation of dune ecosystems due to development or land conversion limits the amount of available habitat. Prairie Warblers occurred on 5 of the 9 dune ecosystems I surveyed along the western Michigan coastline and their 50% territory estimates ranged from an average radius of 19 - 56m, providing guidance on minimum area requirements for habitat management and restoration. The full suite of environmental factors useful for describing habitat suitability for Michigan coastal Prairie Warbler populations are unknown, however my results suggest that shrub cover should be abundant and well dispersed (<75 m separation) and that Prairie Warblers will likely occupy landscapes in a clumped pattern. Hence, Prairie Warbler habitat management plans should emphasize larger areas (i.e., multiple territories) of contiguous habitat with well dispersed shrubs.

New surveys for Prairie Warblers should be located in areas where Prairie Warblers have most recently been detected (Nolan 1978, Nolan et al., 1999). Prairie Warblers exhibit site fidelity, so offspring return to the same places year after year if breeding was successful, until habitat succeeds (Nolan 1978). The return rate to previous year's territory was 65% based on Nolan's 20-year Indiana study (Nolan 1978).

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CHAPTER 4

SYNTHESIS OF FINDINGS AND MANAGEMENT RECOMMENDATIONS FOR MICHIGAN PRAIRIE WARBLER POPULATIONS

INTRODUCTION

This chapter is written for natural resource managers and conservation practitioners. It summarizes background information for Prairie Warbler, the need for this study, and synthesizes research findings as context for conservation and management recommendations. Readers should consult referenced dissertation chapters, figures and tables for further detail on research methods and findings as indicated.

BACKGROUND AND RESEARCH NEED

The status of Michigan Prairie Warbler (*Dendroica discolor*) breeding locations, population abundance, and habitat composition influencing breeding territory selection are critical management and conservation needs for this state-endangered, neotropical migratory songbird (Walkinshaw 1991, Nolan et al. 1999, Cooper 2000, Southwell 2001).

Though globally secure (NatureServe 2011), populations of Prairie Warbler have declined throughout the breeding range (Robbins et al. 1986, Saurer et al. 2011). Midwest populations are of moderate to high management concern (Robinson et al. 1999). This trend holds true for Michigan populations at the northern edge of the breeding range (Michigan Natural Features Inventory 2011), though Michigan populations most likely always have been small and localized (Nolan 1978).

Michigan's earliest bird list (Sager 1839) reported Prairie Warbler somewhere between Detroit, Saginaw Bay, and Jackson. Prairie Warblers were recorded nesting in the southern

Lower Peninsula counties of Ottawa and Montcalm in the early 1900's (Barrows 1912). Wood (1951) noted Berrien County as important to Prairie Warbler, as did Zimmerman and VanTyne (1959) in addition to reporting nesting records from the west Michigan counties of Ottawa, Muskegon, and Oceana. Wood (1951), Zimmerman and Van Tyne (1959), and Mayfield (1960) all reported occurrence in northeastern Lower Peninsula counties of Oscoda, Crawford, Otsego, Cheboygan, and Presque Isle, primarily associated with jack pine (*Pinus banksiana*) plains.

Today, the majority of casual observations come from Lake Michigan dune habitat in the southwest and northwest Lower Peninsula (Michigan Natural Features Inventory 2011). Prairie Warbler became more rare in the Michigan jack pine plains after the 1960's (Nolan 1978, Walkinshaw 1991), was listed as state threatened in 1992 (Southwell 2001), and as state endangered in 1999 (Natural Resources and Environmental Protection Act 1994).

Prairie Warblers glean insects from leaves and branches of shrubs and trees and occasionally take prey mid-air (Nolan 1978, Rappole et al. 1983). Nestlings are primarily fed caterpillars (Nolan 1978). Mean breeding season feeding height in Florida for breeding males is 2.19 m; for females 1.40 m (Prather 1994). They build open cup nests in shrubs and trees 1-3 m in height (Nolan 1978, Walkinshaw 1991, Dunn and Garrett 1997, Cooper 2000,) and defend territories from the highest perches (shrubs or trees) in the area along territory boundaries (Nolan 1978). Males arrive on Michigan breeding grounds from the West Indies during the first two weeks of May with the female arriving about one week later (Wood 1951, Nolan 1978). Prairie Warblers typically depart Michigan breeding grounds in late August, with extreme early and late departure records of August 10 and September 23 respectively (Wood 1951, Nolan 1978).

Throughout their breeding range Prairie Warbler habitat preferences have generally been characterized as open, early-successional areas with scrub-shrub plant species found in poor soils and little or no tree canopy (Nolan 1978, Walkinshaw 1991, Nolan et al. 1999, Cooper 2000). Walkinshaw (1991) noted three distinct shrubby habitats in which Michigan Prairie Warblers had been recorded in recent decades: 1) early successional stages of Great Lakes dunes where deciduous or coniferous bushes are intermixed with dune grass and other herbs, 2) early-successional, shrubby openings associated with previously-burned jack pine plains, and 3) previously burned conifer stands dominated by deciduous shrubs and small trees.

Gaining an understanding of where west Michigan Prairie Warbler breeding populations are located (as the majority of occurrence records are reported from this region of the state; Michigan Natural Features Inventory 2011), and in what abundance, will allow a baseline from which to monitor population status. Describing habitat composition within breeding territories will help identify and specify Prairie Warbler habitat needs, thus informing conservation practitioners as they design long term management plans and are asked to respond to proposed land use changes (e.g., mining, wind tower siting, development).

Some have speculated that abundant Prairie Warbler habitat exists (Walkinshaw 1991, Cooper 2000, Southwell 2001), but habitat requirements for Prairie Warbler, and their selection strategies, may be more specific than previously thought. Examination of environmental factors (e.g., plant composition, proximity to specific land cover types or other Prairie Warblers) within breeding territories, compared to areas where Prairie Warbler are absent, will allow conservation practitioners to manage with a greater understanding of Prairie Warbler habitat selection strategies and thus how to maintain habitat for this state-endangered species in concert with other conservation objectives.

I chose to examine nine study sites located along the Lake Michigan coast throughout the Lower Peninsula of Michigan in 2004 and 2005 (Figure 4) to address the following needs for Michigan Prairie Warbler populations:

- Breeding location, distributions and relative abundance along Michigan's west coast, (Nolan 1978, Walkinshaw 1991, Felsing 1994, Cooper 2000, Southwell 2001),
- Breeding season plant composition associated with breeding territory selection and differences that exist in plant composition between territories and in unoccupied areas (Walkinshaw 1991, Nolan et al. 1999, Southwell 2001),
- An assessment of land cover predictors for Prairie Warbler occupancy (Nolan et al. 1999, Southwell 2001), and
- Insights into spatial resolution necessary to detect Prairie Warbler habitat needs.

SYNTHESIS OF FINDINGS

Population Distribution, Relative Abundance and Breeding Territory Sizes

My study sites were chosen because they were publically accessible and contained potential Prairie Warbler habitat (identified by cover type (i.e., jack pine, sand dunes, scrub-shrub; Nolan 1978, Nolan et al. 1999, Cooper 2000, Southwell 2001)). The nine study sites included 6 State Parks, Sleeping Bear Dunes National Lakeshore, Oval Beach (a public beach owned by the city of Saugatuck), and Kitchel-Lindquist Dunes Preserve (publically-accessible preserve near Grand Haven) (Figure 4).

The greatest number of Prairie Warbler occupied areas was found in Sleeping Bear Dunes (n = 20). Eighteen occupied areas were collectively found in southern sites, with Warren Dunes having the most (n = 8), followed by Saugatuck Dunes State Park (n = 6) and Kitchel-

Lindquist Dunes Preserve and Oval Beach (n = 2). Ludington State Park/Nordhouse Dunes, Silver Lake State Park, Muskegon State Park, and Hoffmaster State Park each had zero Prairie Warblers detected (Table 1). Though I did not monitor nests, these occupied areas were assumed to be breeding territories.

The average number of GPS registrations per breeding territory to estimate territory size and shape was 38 (range 10 – 92 (SE = 3.4) across all sites; range 19 – 81 (SE = 3.7) in Sleeping Bear Dunes; range 10 – 81 (SE = 5.8) in the southern sites). Breeding territories tended to be clustered within sites surveyed, with breeding territory boundaries often adjacent to each other (e.g., Figure 13; Appendix, Figures 16-22). Prairie Warbler mean 95% territory use percentile, as calculated from territories (Table 1, Table 11,) ranged from 1.01 ha in Oval Beach (n = 2, range 0.84 – 1.12; SD 0.245) to 3.170 ha in Sleeping Bear Dunes (n = 20, range 0.16 – 7.93 ha, SD = 2.281) (Table 11; Appendix, Figures 16-22), providing guidance on minimum area requirements for Prairie Warbler.

The smallest territory sizes recorded in the literature are: mean 0.47 ha (85 pair/ 40 ha tract in Maryland; Robbins et al. 1947), 0.24 ha on island in Georgia (Beer et al. 1956). Ranges of territory size in two adjacent long term study sites in Indiana (Nolan 1978) were: 3.5 and 0.5 ha (n = 111, mean = 1.62, SD = 0.72 ha) on younger successional stage site, and 2.4 and 0.4 ha (n = 60, mean = 1.47 ha, SD = 0.47 ha) on older successional stage site (more and larger trees).

Territories of young males are often smaller than older males (Nolan et al. 1999). Prairie Warbler territory sizes in Indiana were noted to be smallest when roughly square and compact, intermediate when oblong, and largest when very elongated (Nolan 1978, Nolan et al. 1999). Territories adjoining unsuitable habitat (where defense is thus unnecessary) tend to be larger (Nolan 1978, Nolan et al. 1999). These size comparisons were roughly consistent with average

Table 11. Mean area of Prairie Warbler 95% and 50% territory use percentiles (see Chapter 2 for methods). SD = standard deviation. Range of territory areas are shown for each southern survey site, mean across southern territories, mean across Sleeping Bear Dunes territories, and for each grouping of territories in the northern, central, and southern areas of Sleeping Bear Dunes (see Appendix for territory maps).

Mean territory area	95% (ha)	SD	range (ha)	50% (ha)	SD	range (ha)
Southern Sites (n = 18)	**1.769**	**0.910**	**0.537 - 3.971**	**0.297**	**0.237**	**0.107 -0.771**
Warren Dunes (n = 8)	2.139	0.965	1.368 - 3.971	0.355	0.251	0.128 - 0.771
Oval Beach (n = 2)	1.012	0.245	0.839- 1.185	0.117	0.014	0.107 - 0.128
Saugatuck Dunes (n = 6)	1.859	0.936	0.537 - 3.037	0.365	0.270	0.131 - 0.709
Kitchel-Lindquist (n = 2)	1.659	0.991	0.958 - 2.360	0.187	0.111	0.109 - 0.266
Sleeping Bear Dunes (n = 20)	**3.170**	**2.281**	**0.158 - 7.931**	**0.512**	**0.376**	**0.032 - 1.286**
North (n = 11)	3.023	2.053	1.058 - 6.897	0.547	0.424	0.120 - 1.286
Central (n = 6)	3.560	1.089	1.060 - 3.931	0.473	0.229	0.130 - 0.709
South (n = 3)	4.925	4.175	0.158 - 7.931	0.535	0.535	0.032 - 1.098

*southern sites are Warren Dunes and Saugatuck Dunes State Parks, Oval Beach, and Kitchel-Lindquist Dunes Preserve territory sizes recorded for the five sites where Prairie Warblers were found in this coastal, West Michigan study (Table 1, Table 11). I found Michigan coastal breeding territory size to increase with increasing size of the survey area available habitat (Appendix, Figures 16-22; Table 1).

West Michigan Coastal Habitat Composition

Generally, my results support the previously observed relationships between Prairie Warbler occurrence and a mixture of herbaceous and low-growing woody vegetation (Nolan 1978, Walkinshaw 1991, Nolan et al. 1999, Cooper 2000). However, my study was the first to document a latitudinal gradient in Prairie Warbler habitat use related to vegetation composition; with northern territory space use correlated with denser, woody vegetation and southern territory space use associated with more open, grass dominated sites.

Analysis of vegetation survey data (1 m diameter plots; see Chapter 2) showed that plant composition in areas occupied by Prairie Warblers was different from plant composition in unoccupied areas (Table 4, Figures 9 and 10). However, those differences were not consistent from north to south; Prairie Warbler breeding areas in the north had a different group of plants associated with them than did Prairie Warbler breeding areas in the southern part of the state (Table 3, Figures 9 and 10).

Prairie Warblers in Sleeping Bear Dunes were likely to be found in areas with woody cover assemblages including: bearberry (*Arctostaphylos uva-ursi)*, common juniper (*Juniperus communis)*, creeping juniper (*J. horizontalis*), and *Rubus* spp. Redtop grass (*Agtostis gigantean)*, hawkweed (*Hieracium spp.)*, and poison ivy (*Toxicodendron radicans)* were also commonly associated with areas of Prairie Warbler presence (Table 3, Figure 10).

Southern Prairie Warbler breeding territories were dominated by grasses and a mix of native and exotic herbaceous plants (Table 3); specifically, marram grass (*Ammophila* *breviligulata),* sand reed grass (*Calamovilfa longifolia),* wormwood (*Artemisia campestris),* horsetail (*Equisetum* spp.*)* and chickweed (*Stellaria* spp.) (Table 3, Figure 10). Many of these same plant species were associated with unoccupied areas in Sleeping Bear Dunes.

Plant species associated with southern sites where Prairie Warblers were absent, included sugar maple (*Acer saccharum),* Austrian pine (*P. nigra),* red pine (*P. resinosa)*, jack pine, choke cherry (*Prunus virginiana),* white ash (*Fraxinum Americana)*, and garlic mustard (*Alliaria petiolata)* (Table 3, Figure 10). This suggests that Prairie Warbler territories in the south were not associated with tree species and selected areas with more grass and herbaceous plant species. Southern territory plant composition suggested less dense vegetation overall, more open sand and more grass than northern Sleeping Bear Dunes territories.

Land cover analysis using 30 m Coastal Change Assessment Program (C-CAP; National Oceanic and Atmospheric Administration, Coastal Services Center 2008) imagery (Chapter 3) supported the difference in cover type composition in northern and southern Prairie Warbler territories. Mean forest cover for Sleeping Bear Dunes territories (43%) was higher than that observed for southern territories (29%, Table 10; Welch's $t = 2.28$, $df = 33$, $p = 0.029$). Mean grass cover also differed between Sleeping Bear Dunes territories (32%) and southern territories (15%, Table 10; Welch's $t = 2.83$, $df = 30$, $p = 0.008$). Southern territories had greater mean percent sand than northern territories (65% vs. 40%; Table 10; Welch's $t = -4.37$, $df = 35$, $p = 0.0001$). I attribute these differences in part, to higher topographic wetness index values that were observed in Sleeping Bear Dunes (see RUF output Chapter 3) in that moister soils will likely support greater vegetation biomass.

Assessing Occupancy

I found 0% probability of another Prairie Warbler being present when shrubs were >103 m away from the edge of an existing Prairie Warbler territory (Figure 14). The probability of another Prairie Warbler being present was 39% when shrubs were detected within 1 m of an existing Prairie Warbler territory (Figure 14). My model also predicted that Prairie Warblers will occupy sites that are <75 m away from shrubs, but probability of occupancy at these farther distances was low (1%). The farthest I measured shrubs from the edge of a Prairie Warbler territory in the field was 30 m.

Distance to the closest Prairie Warbler territory from the edge of another Prairie Warbler territory was the most significant predictor of Prairie Warbler presence (Table 8). I observed a 0% probability of Prairie Warbler presence when distance to another Prairie Warbler was beyond 1,284 m. However, I found an 80% probability of Prairie Warbler presence when another Prairie Warbler was within 91 m (Figure 14). These results indicate that Prairie Warbler breeding territories are clumped in the dune ecosystem, and because shrubs are relatively ubiquitous, I speculate there is a conspecific attraction (i.e., the tendency for Prairie Warblers to settle near one another) for territory establishment.

Research suggests conspecific attraction influences avian habitat selection and occupancy more than previously considered or reported (Danchin et al. 2004, Hahn and Silverman 2006, Betts et al. 2008). Studies on Kittiwakes (*Rissa tridactyla*) (Danchin et al. 1998) and Collared Flycatchers (*Ficedula albicollis*) (Doligez et al. 2002) have both shown that individuals will replicate habitat selection choices of conspecifics that experience high breeding success, using social cues as their primary decision-making strategy. Hahn and Silverman (2006) found conspecific attraction was an important mechanism for breeding habitat selection for established populations of Redstarts (*Setophaa ruticilla*) in Michigan, but the effect was moderated by age, reproductive experience, and timing of arrival. Harrison et al. (2009) warn that traditional habitat models, which consider only resource distributions and not social factors, may be inadequate tools for the conservation of Brewers Sparrows (*Spizella breweri breweri*) at the northern edge of their range.

Prairie Warblers were commonly found in the more stabilized early-successional, transition areas between open sand and forest edge or in patches of shrubs within dune blowouts. As referenced above, plant species associated with Prairie Warbler presence differed from north to south, but the commonality between territory establishment was availability of woody cover and most importantly, close proximity to other Prairie Warblers.

The full suite of environmental factors useful for describing habitat suitability for Michigan coastal Prairie Warbler populations are unknown, however my results suggest that shrub cover should be abundant and well dispersed (<75 m separation) and that Prairie Warblers will likely occupy landscapes in a clumped pattern. Hence, Prairie Warbler habitat management plans should emphasize larger areas of contiguous habitat with well dispersed shrubs to accommodate multiple territories.

Resource Utilization and Spatial Resolution Considerations

Resource Utilization Functions (RUF) indicate the importance of each land cover covariate (e.g., land cover type, soil moisture) within the breeding territories (Marzluff et al. 2004). I found no significant environmental covariates from RUFs, however, 4 observations warrant attention: 1) northern sites have more woody vegetation cover than southern sites, and southern sites seem to be more open, 2) grass cover appears to be important on southern sites, potentially because shrubs are less ubiquitous, 3) higher soil moisture in northern territories was suggested as an important indicator of habitat use, and 4) lack of significant RUF coefficients suggests that the spatial resolution of land cover data (30 m) may not have been appropriate to describe within territory space use for Prairie Warblers.

Lack of significant RUF findings could imply little consistency in resource selection at the territory level, but more likely suggest the data chosen to portray habitat conditions within a territory were likely not suited for this analysis. The 30 m C-CAP data used was likely too coarse for describing Prairie Warbler habitat use within territories. Grass and sand land cover classes (as portrayed by 2006 C-CAP imagery) likely contained shrubs and saplings that went undetected with 30 m resolution data. Finer-resolution land cover data may provide more useful insight into Prairie Warbler space use within a breeding territory.

Individual Prairie Warblers tended to vary in their use of specific resources. Further exploration of drivers behind resource use could provide greater insight into landscape patterns associated with Prairie Warbler breeding territory establishment, given the appropriate spatial data resolution is utilized (I suggest 1m). The characterization of use for RUFs describing Michigan Prairie Warbler populations will be an iterative process. Further refinement in how best to describe specific landscape conditions/covariates and then determine the correct model of use for those conditions should continue to be applied and reassessed to create better RUFs for this species. Increased understanding of factors associated with variation in each RUF coefficient will improve representation of how each coastal Prairie Warbler population uses resources. Once additional sources of difference or variation are found, additional or refined RUFs that target those factors could provide greater explanation of resource use in specific areas that may be applied in similar areas.

CONSERVATION AND MANAGEMENT RECOMMENDATIONS

Protect what we have. The threat of coastal habitat loss may be the biggest threat to coastal Michigan Prairie Warbler populations. The west Michigan dune landscape is providing a source of early successional habitat for Prairie Warblers that is maintained through wind and wave dynamics, therefore no specific land management technique to increase coastal west Michigan habitat appears to be needed. Land use changes that fragment current, large contiguous areas of habitat and surrounding land cover could pose new threats to coastal Prairie Warbler populations and potentially alter habitat suitability. As Southwell noted in her 2001 U.S. Forest Service Eastern Region report, "preservation of current habitat is a management necessity".

The extent to which land use changes such as urban development (Klepinger 2002), the siting of wind towers, or new cultivation of cropland (Johnson et al. 2003) could impact habitat suitability for Prairie Warbler (and other species) is not fully known. Land use development in west Michigan coastal communities is growing and lakeshore properties in Michigan continue to receive a disproportionate amount of development pressure relative to inland (United States Environmental Protection Agency 2001, 2008). The 2002 U.S. Census data confirm that Michigan's top 10 coastal cities are losing population while coastal rural areas are rapidly suburbanizing (United States Census Bureau 2002), indicating that people are moving out of cities and small towns to develop new coastal areas for cottages, primary residences and business (United States Census Bureau 2002). This type of development, while recognized as a source of economic development, degrades the solitude many come to find along Michigan's western lakeshore by limiting coastal access and fragmenting viewscapes of continuous natural beach (Klepinger 2002). These land use patterns, if continued, are predicted to cause greater fragmentation of natural systems (e.g., coastal wetlands, open dune, and forested dune; Klepinger 2002) for Prairie Warbler and other species.

Wind tower threats to migrating birds (Drewett et al. 2006, Klepinger 2007, American Bird Conservancy 2010) and bats (Johnston et al. 2003, Baerwald et al. 2008) are well documented and tower siting is under debate by the environmental community and landowners concerned with change to aesthetics, quality of life factors, or concern over economic land value brought about by wind tower siting.

New agricultural development that would fragment current land use has the potential to increase Brown headed cowbird (*Molothrus ater*) abundance and thus increase Prairie Warbler nest parasitism rates (Nolan 1978, Nolan et al. 1999). Throughout most of the breeding range, Prairie Warbler nests are known to be parasitized by cowbirds (Nolan 1978), though nest predation by snakes, chipmunks and corvids has been noted to be a bigger threat to Prairie Warbler than cowbird parasitism; predation “swamping out” effects of parasitism in Indiana (Nolan et a. 1999). Response of cowbird parasitism by female Prairie Warblers in Indiana was desertion of 48 (46%) of 105 nests. Parasitism probably has no effect on Prairie Warbler hatching success (hatching rate in Indiana study in unparasitized nests 95%, in parasitized nests 92%). Mean number of fledglings in 76 nests producing only Prairie Warblers was 3.36; in 9 nests also producing cowbirds, 0.78 warblers (a 73% reduction; Nolan 1978). Among 102 cowbird eggs observed in Prairie Warbler nests in Indiana (Nolan 1978), only 5% produced fledglings. Mean annual simulated cowbird-caused reduction of Prairie Warbler productivity in Indiana was 13.3% (Nolan 1978).

Habitat management plans including considerations for Prairie Warbler population viability should emphasize larger areas of contiguous habitat with well dispersed shrubs to

accommodate multiple territories. A comprehensive list of environmental factors describing habitat suitability for Michigan coastal Prairie Warbler populations is unknown, however my results suggest that shrub cover should be abundant and well dispersed. I found a 39% probability of Prairie Warbler occupancy when shrubs were detected within 1 m of an existing Prairie Warbler territory (Figure 14). My model also predicted that Prairie Warblers will occupy sites that are <75 m away from shrubs, but probability of occupancy at these farther distances was low (1%). The farthest I measured shrubs from the edge of a Prairie Warbler territory in the field was 30 m. Prairie Warblers will likely occupy landscapes in a clumped pattern. My findings show there was an 80% probability of Prairie Warbler presence when another Prairie Warbler was within 91 m. Mean 95% Prairie Warbler territory area estimates ranged from 1.01 in Oval Beach to 3.17 in Sleeping Bear Dunes (Table 11), providing conservation planning guidance for minimum area use requirements. Therefore, accommodating larger, contiguous areas of early successional habitat has the potential to accommodate larger populations of Prairie Warblers long term.

Surveys for Prairie Warblers should be located in areas where Prairie Warblers have been detected in recent years. All surviving male adults likely return to the previous year's territory (Nolan 1978) as long as early successional habitat remains. The male return rate to previous year's territory was 65% based on Nolan's 20-year Indiana study (Nolan 1978, Nolan et al. 1999). After returning (n = 75 cases), 27% of unmated males moved within 2 - 8 days. Known distance separating old and new territories ranged from 10 - 3,400 m (mean = 710 m, *n* = 12; Nolan 1978). Nolan noted that previous reproductive success, age, and number of previous moves, and territory suitability were not correlated with such moves. The female return rate was smaller; 19 of 105 females returned to the study area in one or more years following banding

(Nolan 1978, Nolan et al. 1999). Fourteen females nested on breeding territories that overlapped their territory from the preceding year (Nolan 1978). Distances between nesting sites for the 2 years ranged from 12 to 325 m (mean = 90 m) (Nolan 1978). Reproductive success and remaining on the study area after breeding were positively correlated with returns.

Prairie Warblers may disperse from their breeding territory once the nest has fledged, indicating the importance of surrounding habitat beyond the breeding territory before fall migration. Nolan (1978) showed that after breeding, 79% of 63 banded males were found before migration. Some males had stayed near or on the territory, some had moved and then returned to the territory and some spent the post-breeding time on a previous year's territory. These areas were not correlated with reproductive success, date that breeding ended, or date of molt. The same pattern was found for 43% of 54 females located post-breeding (Nolan 1978).

Future territory mapping, to estimate territory boundaries or utilization distributions (UD), should collect at least 30 registration (GPS) points if kernel-estimation techniques similar to the type used in this study will be used. Accurate kernel estimation assumes that sampling is sufficient to quantify relative differences in resource use (Garton et al. 2001). Seaman et al. (1999) suggests that with "adequate sample sizes" of >30 - 50 registration points, fixed kernel estimators better represent differential space use than other UD techniques and perform well at the outer boundary. Failure to secure an adequate sample size could have bearing on the kernel estimate of the territory UD and thus resource use estimates needed for future updates in analyzing Michigan Prairie Warbler populations.

Future survey, monitoring, or habitat protection design, using GIS applications to automate location or identification of potential habitat, should use spatial data with a resolution finer than 30 m. The 30 m, 2006 C-CAP data used in RUF analysis (Chapter 3) was likely too coarse for describing Prairie Warbler habitat use within territories. Grass and sand land cover classes (as portrayed by 2006 C-CAP imagery) used in my survey of land cover for RUF assessment likely contained shrubs and saplings that went undetected with 30 m resolution data. While on-the-ground vegetation surveys within breeding territories (and in unoccupied areas for comparison) were thorough, the more sparsely-distributed shrub and sapling component in southern territories the birds were likely using for nesting structure, did not translate as dominant drivers of Prairie Warbler presence in those areas. Prairie Warblers nest in shrubs and trees 1 - 3 m in height (Nolan 1978, Walkinshaw 1991, Dunn and Garrett 1997, Cooper 2000) and defend territories from the highest perches in the area, along territory boundaries (Nolan 1978). They prefer trees and shrubs with numerous branches, twigs and leaves distributed throughout (Nolan 1978). Nolan (1978) noted that among 577 nest plants in Indiana, about 27% were ≥5 m from nearest tree or shrub, 34% were in the middle of a small tree clump, 37% were at the edge of a large tree clump or woods, 2% were within woods. Among 608 nests in an Indiana study, 51% were placed in American elm, which constituted 25% of the early successional fallow fields in the study area (Nolan 1978). Placement of 555 Indiana nests were as follows: 47% in upright fork; 27% on twigs, against vertical branch; 18% on horizontal or diagonal branch; 5% in vines or wedged among small branches; 3% other. Though I did not search for nests, the 2 nests I observed during this study were in common juniper and red-osier dogwood (*Cornus stolonifera*), placed in forks of branches. Thus, based on Nolan's Indiana study and my own observations, I suggest that being able to discern the shrub component on the landscape is critical. Spatial resolution finer than 30 m will allow identification of these areas in future survey design and analysis using GIS and habitat modeling applications.

Prairie Warbler management plans should focus on the health and connectivity of whole systems (i.e., western Lake Michigan dune ecosystem and adjacent potential habitat) to provide access to a diversity of future habitat options, given overarching threats like invasive species and climate change and their unknown future impacts, to maintain and conserve landscapes important to Prairie Warbler. Michigan lies along the northern edge of the Prairie Warbler breeding range and the contribution of this study to Prairie Warbler ecology is the first of its kind in Michigan or the northern Great Lakes region. While understanding Prairie Warbler habitat selection strategies at the northern edge of the breeding range could expand our overall understanding of Prairie Warbler ecology, fiscal and staff limitations provide little capacity to address individual species management efforts. Additionally, the broader and overarching threats of invasive species and climate change to the dune ecosystem and surrounding systems, will challenge the adaptive tolerance of many niche-specific species and those already negatively affected by existing stressors (e.g., pests, disease, competition with invasive species).

The range of potential landscape composition changes projected in the Midwest and Great Lakes region under a changing climate (United States Global Change Research Program 2009, Lofgren et al. 2011) will be influenced by the projected 1- 3ºC degree temperature increase by the end of the 21st century as well as increases in heavy precipitation events and storm intensities with longer periods of drought between storm events (United States Global Change Research Program 2009). Addition of species moving into the Midwest will also contribute to competition for resources (Janetos et al. 2008).

While it is important to monitor rare species and design management plans with the needs of individual species in mind, an ever-evolving shift in focus from individual species management efforts toward protecting connected corridors of natural communities (Parmesan 1996, Union of Concerned Scientists 2010) and potentially their geophysical underpinnings (Anderson and Ferree 2010) will allow plants and animals the opportunity to move and adjust to a range future habitat and climate conditions. Protecting the ultimate drivers of biodiversity will be key to sustaining diverse, and thus healthy, systems over the long term.

Considering Climate Change Vulnerability Index (CCVI; NatureServe 2012) ratings for Prairie Warbler in the context of 1) species rarity rankings on a state and national level, 2) relative range position in Michigan compared to the full extent of the range, and 3) potential for breeding range shift into and out of the state should be included in future Prairie Warbler assessments and long term management planning (e.g., incorporation into State Wildlife Action Plan update considerations). The CCVI ratings for Prairie Warbler (as with all species) should be updated as new information becomes available. Examining how phenological changes are tracking with breeding season temperature or precipitation dynamics in Michigan may inform scoring.

Communicate with landowners adjacent to areas supporting Prairie Warblers, landowners with potential habitat, and the public who visits and uses state and federal parks to notify them of Prairie Warbler occurrence records and encourage conservation action and partnership when possible. Public awareness of rare (or common) species, their habitat needs, and research and conservation efforts underway, allow the public the opportunity to "buy in" to conservation and associate recommended conservation land use practices with their actions and the health and well-being of places they care about.

DATA LIMITATIONS

This study focused on West Michigan, coastal Prairie Warbler breeding habitat and cannot provide management recommendations for non-coastal occurrences. Casual observations in other areas of the state have been reported to the Michigan Breeding Bird Atlas Project (Brewer et al. 1991), Michigan Natural Features Inventory (2011), and on various birding list serves; specifically, Kirtland's Warbler (*D. kirtlandii*) breeding areas in the northeast Lower Peninsula, various locations in Washtenaw County, and north-central Mecosta County. Speculation on why Prairie Warblers are not more abundant on "inland" early successional areas similar to those where Prairie Warbler are found in Indiana, for example, cannot be made beyond re-stating that Michigan lies at the northern extent of the breeding range (Dunn and Garrett 1997), Prairie Warblers have never been abundant in the state (Nolan 1978), and populations have likely always been disjunct (Nolan 1978).

Some have speculated that "areas of apparently suitable habitat (i.e., jack pine plains)" exist but remain unoccupied (Cooper 2000) or that "much suitable habitat appears to be available" (Southwell 2001) or that "there appears to be no shortage of Prairie Warbler habitat in Michigan…unoccupied habitat that seems suitable remains" (Walkinshaw 1991). Prairie Warbler habitat requirements may be more specific than previously thought. The aforementioned accounts often link potential to increase Prairie Warbler abundance to Kirtland's Warbler management efforts and liken their habitat requirements (Cooper 2000, Walkinshaw 1991). These conclusions seem to be primarily based on reported Prairie Warbler use of jack pine plains prior to 1960, with Prairie Warbler likely using the open, shrubby areas found within jack pine stands as they were structured at that time.

The plant composition and structure of the jack pine plains in 1950's and 1960's was different than it is today. Fire suppression efforts had reduced the jack pine range at that time, and thus Kirtland's Warbler habitat availability (Olson 2002, Michigan Department of Natural Resources 2012). The logging, burning, seeding, and replanting of jack pine necessary for Kirtland's Warbler management increased the amount of jack pine forest over time, and changed the forest and understory composition as well as the landscape structure (Michigan Department of Natural Resources 2012).

Historically Prairie Warblers in Michigan were more common in the jack pine plains (Mayfield 1960) than they are today, with Mayfield noting Prairie Warblers nesting on 3 of 10 "Kirtlands Warbler areas" (specific locations or habitat conditions were not stated). Walkinshaw (1991) and Felsing (1994) note that Prairie Warbler populations in the northeast Lower Peninsula of Michigan likely peaked in the 1950's and 1960's. Timing of Mayfield's observations coincide with establishment of Kirtland's Warbler habitat management by the U.S. Forest Service and Michigan Department of Natural Resources between 1957 and 1962 (Michigan Department of Natural Resources 2012). These changes may have contributed to fewer Prairie Warbler observations in these areas after 1960. Brown headed cowbird prevalence in the area could have also contributed to fewer Prairie Warblers in the region.

CONCLUSIONS

In conclusion, protecting the early successional dune ecosystems from fragmentation will provide west Michigan coastal Prairie Warbler populations the opportunity to continue accessing these areas. Breeding territories have been found in groups along the lakeshore, suggesting the tendency for Prairie Warblers to settle near one another (conspecific attraction). Because Prairie

Warblers tend to return to the same breeding territories annually, continuing to maintain large, contiguous areas of early successional dune landscapes has the potential to accommodate larger populations of Prairie Warblers long term. Use of spatial data with resolution finer than 30 m (I recommend 1 m) may best identify potential habitat when using GIS applications. Threats of coastal development and subsequent potential for reduced habitat suitability due to area constraints, nest predation, and nest parasitism, compounded by threats Prairie Warbler may face on wintering grounds and along migratory routes (which were not examined in this study) may reduce Prairie Warbler abundance in some of the only areas in Michigan Prairie Warblers are currently observed.

Additions to our basic understanding of Prairie Warbler conservation could be gained through long-term examination of wintering habitat status and population dynamics there. Examination of potential changes in phenology (i.e., spring leaf-out and insect emergence) experienced along migratory routes and subsequent effects on breeding population viability and relative abundance would also be valuable. Further refinement of habitat models for Prairie Warbler should consider social factors in addition to resource distributions to explore the importance of conspecifics attraction in breeding site determination.

APPENDIX

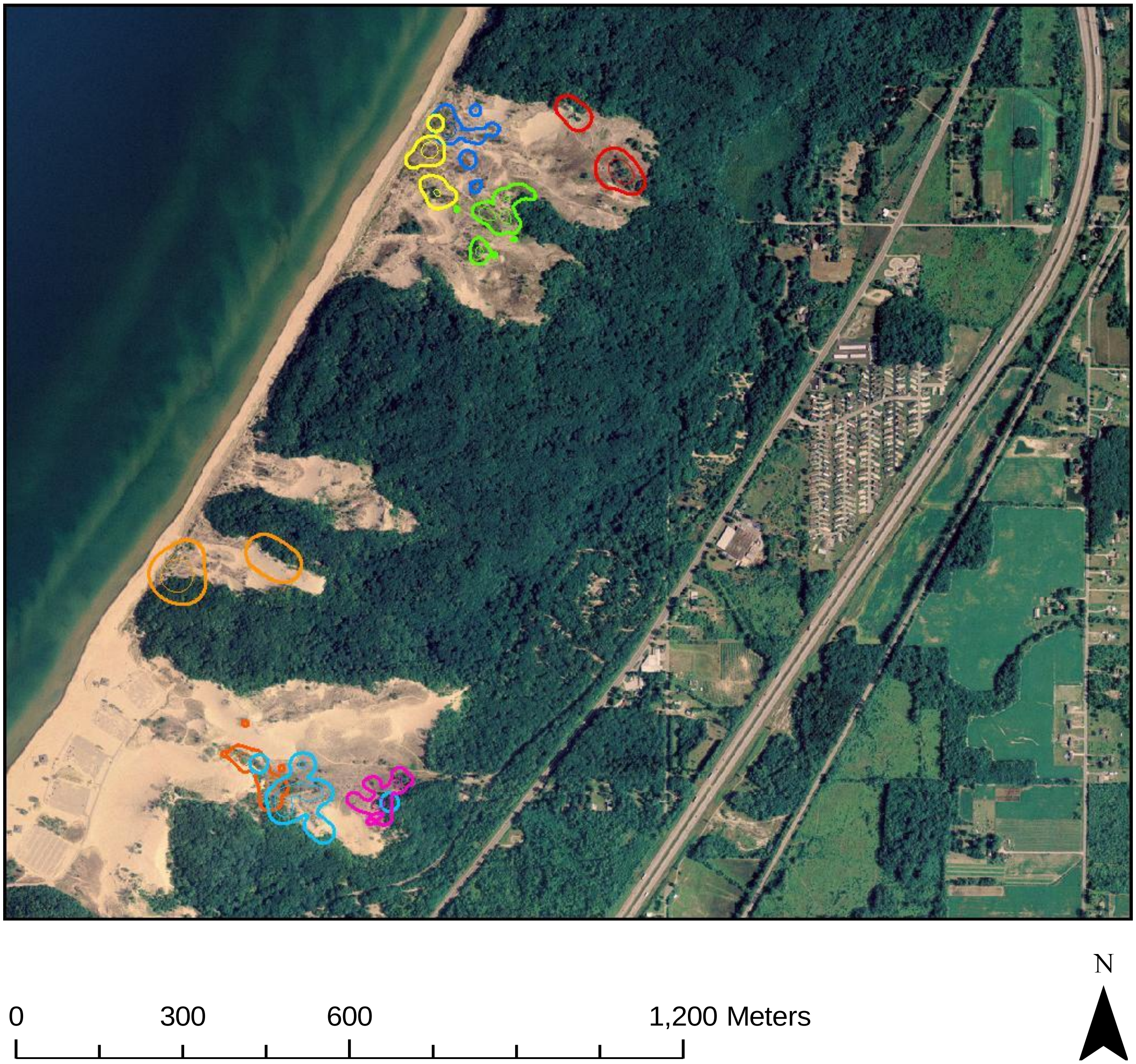

Fig. 16. Eight Prairie Warbler breeding territories mapped in 2005, Warren Dunes State Park, Berrien County, Michigan. Each breeding territory is designated by an individual color. The 95% use percentile for an individual Prairie Warbler with its interior 50% ("core") use percentile is shown overlaid on 1 m resolution, 2005 United States Department of Agriculture, National Agriculture Imagery Program, land cover data.

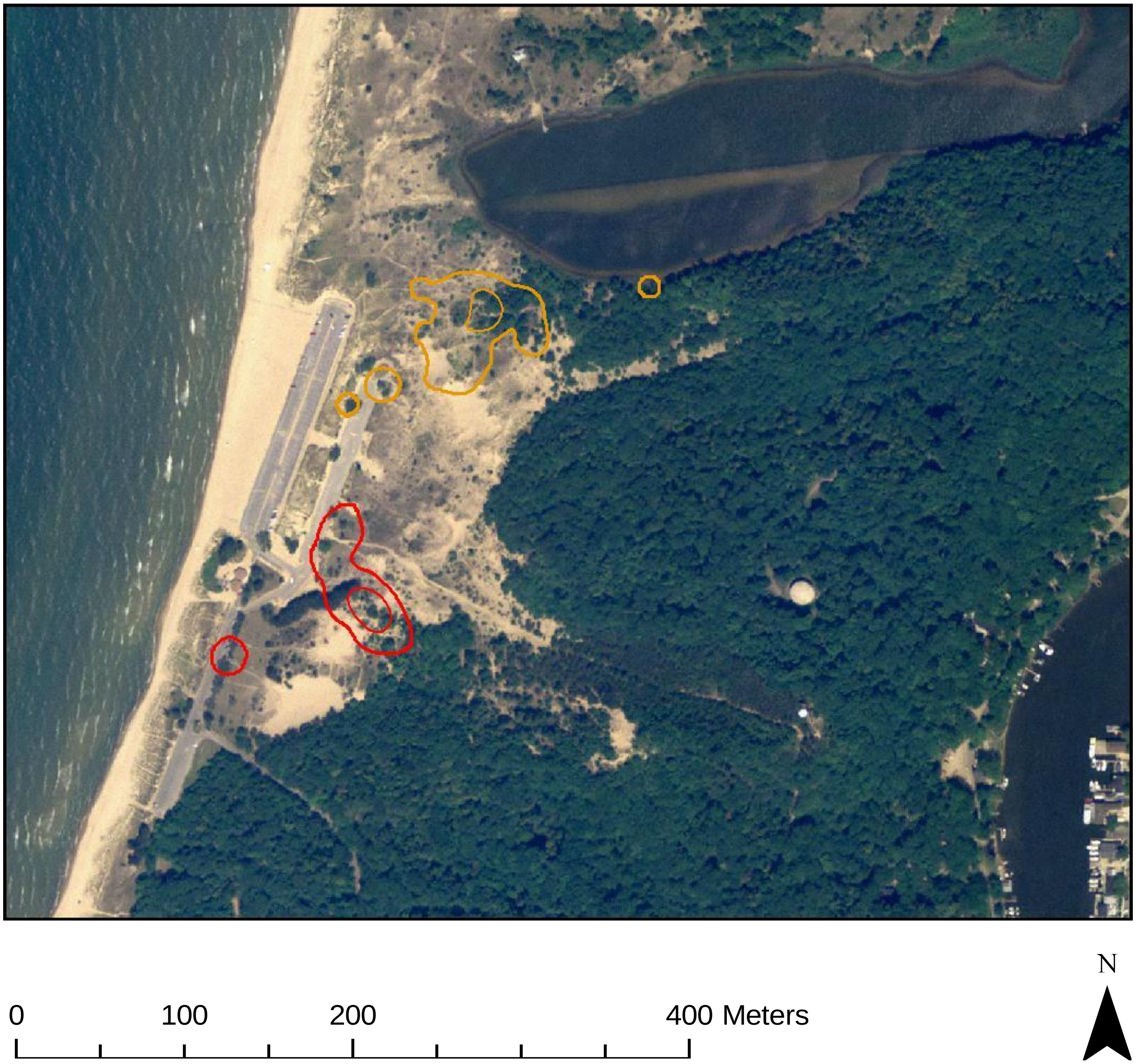

Fig. 17. Two Prairie Warbler breeding territories mapped in 2005, Oval Beach, Allegan County, Michigan. Each breeding territory is designated by an individual color. The 95% use percentile for an individual Prairie Warbler with its interior 50% (“core”) use percentile is shown overlaid on 1 m resolution, 2005 United States Department of Agriculture, National Agriculture Imagery Program, land cover data.

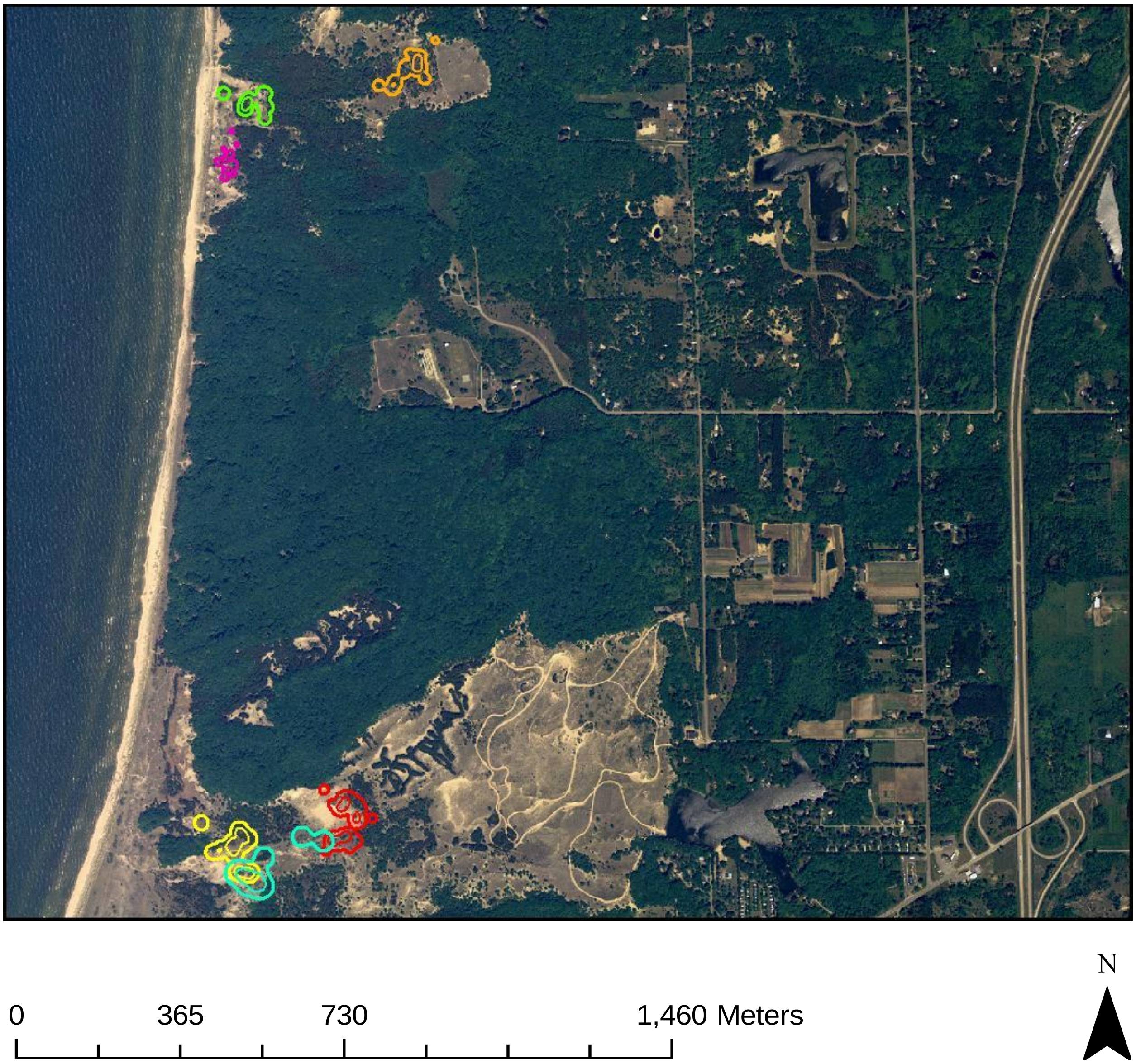

Fig. 18. Six Prairie Warbler breeding territories mapped in 2005, Saugatuck Dunes State Park, Allegan County, Michigan. Each breeding territory is designated by an individual color. The 95% use percentile for an individual Prairie Warbler with its interior 50% ("core") use percentile is shown overlaid on 1 m resolution, 2005 United States Department of Agriculture, National Agriculture Imagery Program, land cover data.

Fig. 19. Two Prairie Warbler breeding territories mapped in 2005, Kitchel-Lindquist Dunes Preserve, Ottawa County, Michigan. Each breeding territory is designated by an individual color. The 95% use percentile for an individual Prairie Warbler with its interior 50% ("core") use percentile is shown overlaid on 1 m resolution, 2005 United States Department of Agriculture National Agriculture Imagery Program land cover data.

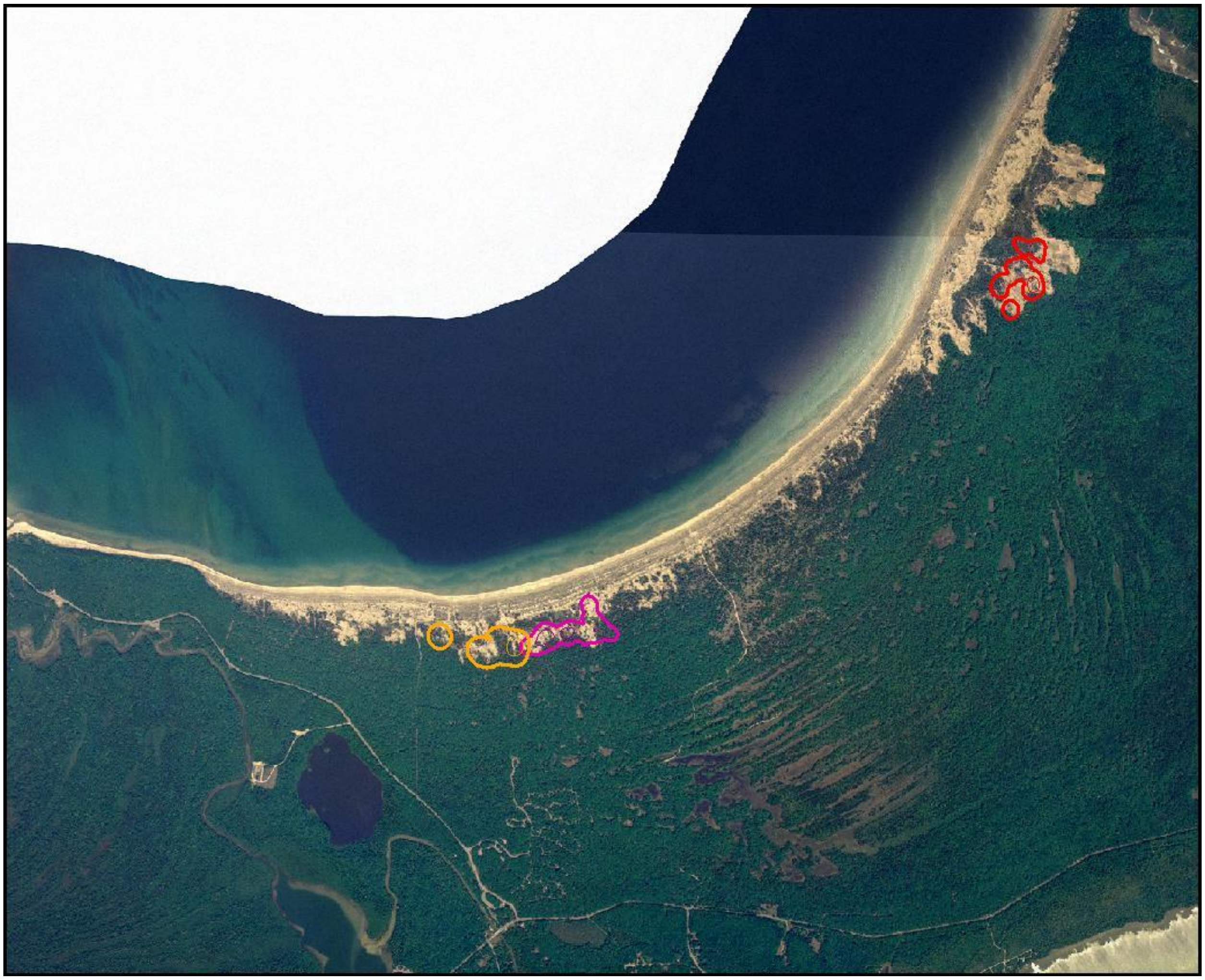

Fig. 20. Three Prairie Warbler breeding territories mapped in 2004, southern portion of Sleeping Bear Dunes National Lakeshore, Benzie County, Michigan. Each breeding territory is designated by an individual color. The 95% use percentile for an individual Prairie Warbler with its interior 50% ("core") use percentile is shown overlaid on 1 m resolution, 2005 United States Department of Agriculture National Agriculture Imagery Program land cover data.

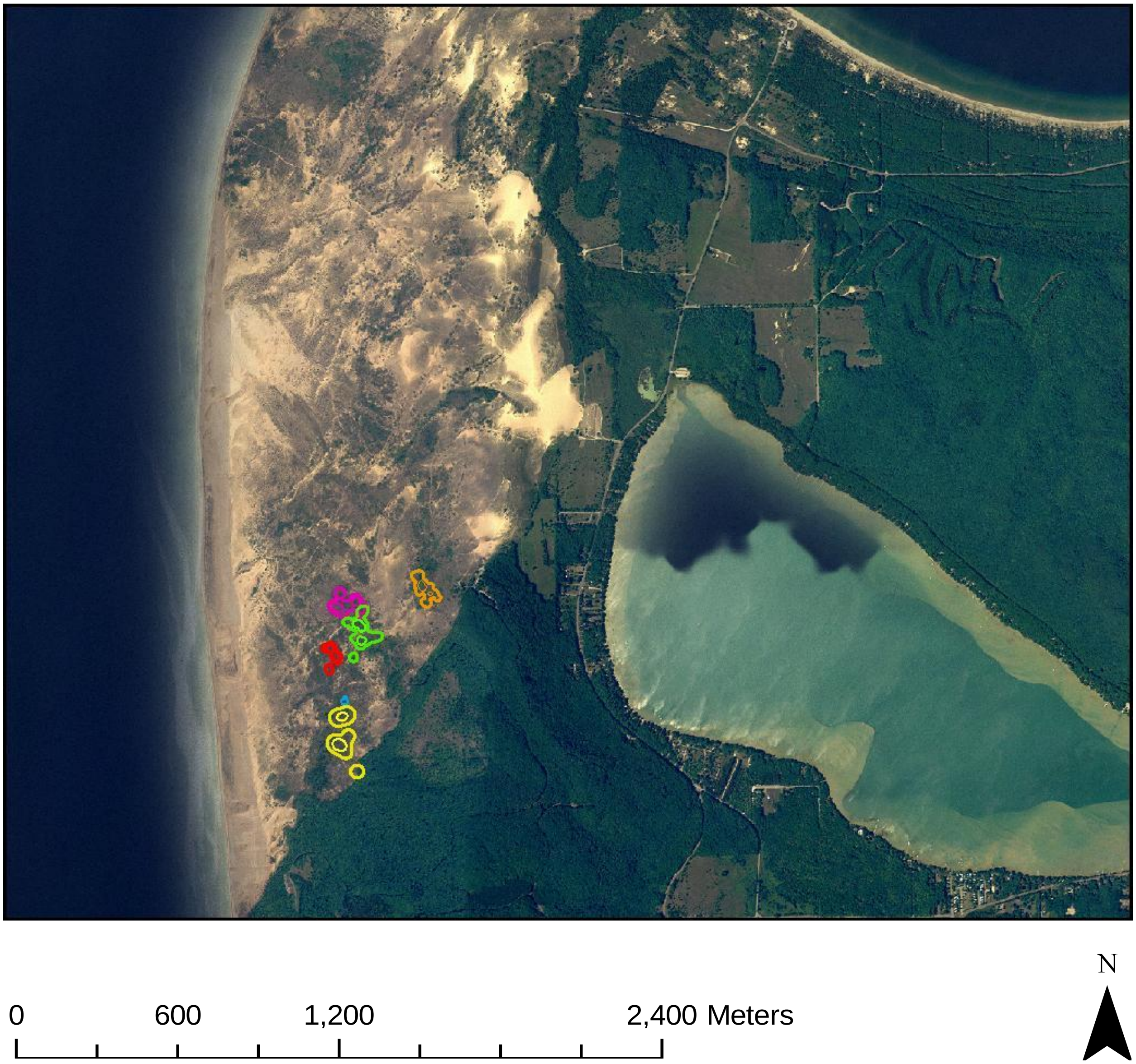

Fig. 21. Six Prairie Warbler breeding territories mapped in 2004, central portion of Sleeping Bear Dunes National Lakeshore, Leelanau County, Michigan. Each breeding territory is designated by an individual color. The 95% use percentile for an individual Prairie Warbler with its interior 50% ("core") use percentile is shown overlaid on 1 m resolution, 2005 United States Department of Agriculture National Agriculture Imagery Program land cover data.

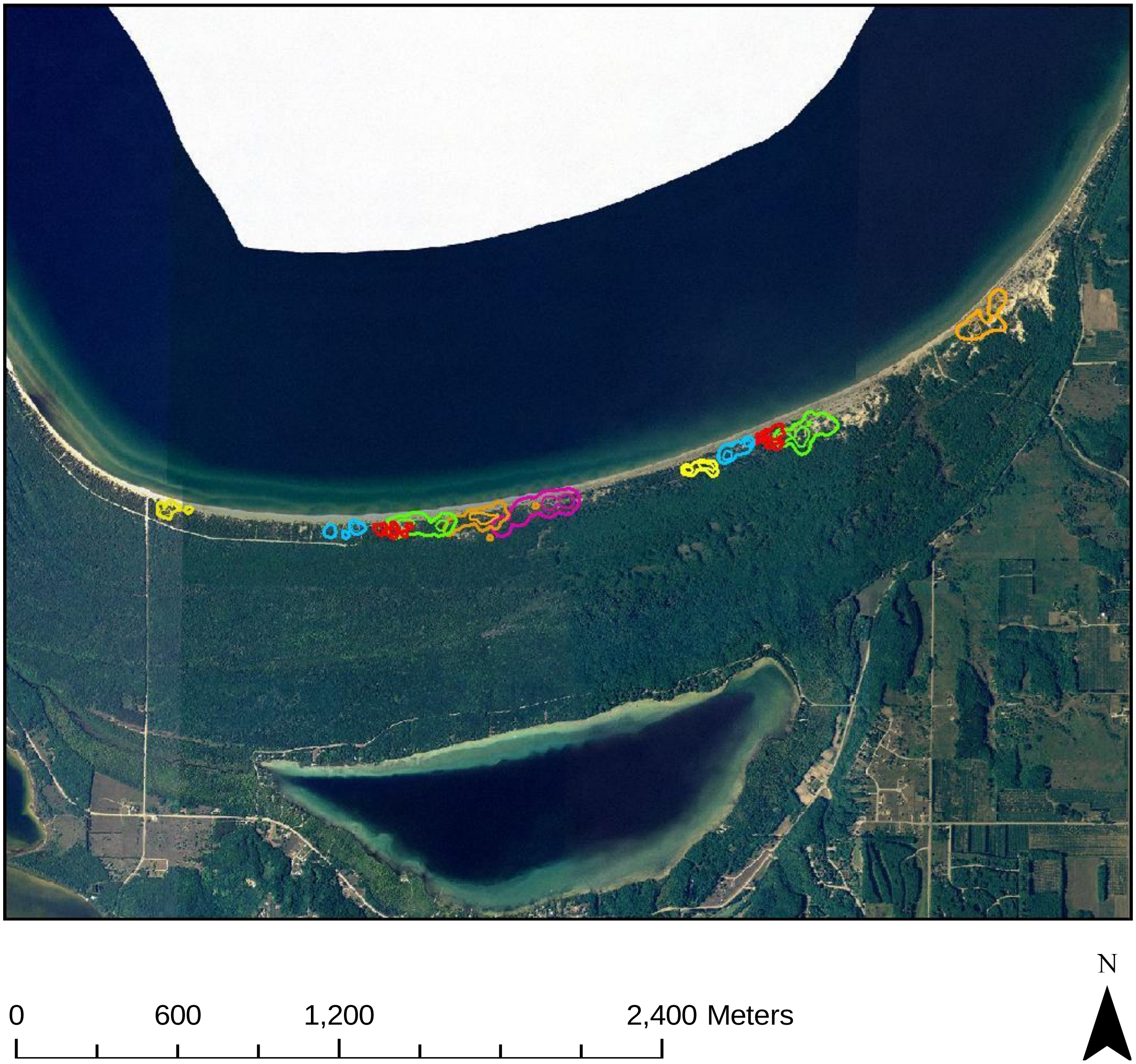

Fig. 22. Eleven Prairie Warbler breeding territories mapped in 2004, northern portion of Sleeping Bear Dunes National Lakeshore, Leelanau County, Michigan. Each breeding territory is designated by an individual color. The 95% use percentile for an individual Prairie Warbler with its interior 50% ("core") use percentile is shown overlaid on 1 m resolution, 2005 United States Department of Agriculture National Agriculture Imagery Program land cover data.

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