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THE EFFECTS OF LANDSCAPE CONTEXT AND COASTLINE COMPLEXITY ON BIRDS IN GREAT LAKES COASTAL WET MEADOWS

By

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A DISSERTATION

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in partial fulfillment of the requirements
for the degree of

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ABSTRACT

THE EFFECTS OF LANDSCAPE CONTEXT AND COASTLINE COMPLEXITY ON BIRDS IN GREAT LAKES COASTAL WET MEADOWS

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Landscape studies on birds have focused on effects of patch- and regional-level processes (e.g. area or fragmentation), but little is known about the effects of landscape context. Landscape context refers to the composition of the adjacent and surrounding landscape, and different contexts can have different effects on within-patch processes like species richness. To test for effects of landscape context, I censused birds along transects located in 40 Great Lakes coastal wet meadows during two breeding seasons (1997 and 1998). Twenty within-patch habitat characteristics (e.g. grass density) were measured each year. A GIS database was used to calculate 24 characteristics of the adjacent patches and the associated coastline. I used separate principal component analyses on each set of dependent variables (i.e. habitat, landscape and coastline) to reduce the number of variables and remove inter-correlations before using linear and logistic regressions. Regressions involved a two-stage approach to adjust bird variables for effects of patch-level variables before testing for effects of landscape context and coastline complexity.

Species richness, total abundance and most species were related to landscape and coastline components in consistent fashions. Higher richness and abundance were associated with complex contexts (high number of adjacent patches and patch types), wetland contexts, human-developed contexts, and less complex coastlines. Similarly,

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species turnover was lower in large patches located in complex or wetland contexts. Other analyses indicated that species richness and species composition of wet meadows located in coastal coves was not substantially different than wet meadows located out on coastal lobes.

These results indicate that conservation strategies for wetland birds in Great Lakes coastal regions should consider effects of landscape context. Specifically, patches located in complex and/or wetland contexts, but associated with simpler coastlines may be better conservation choices because they support the greatest numbers of species and birds. Similarly, wet meadows located in complex and/or wetland contexts more stable species composition (i.e. lower turnover rates). Without explicit knowledge about how landscape context affects species richness, abundance, and stability (turnover), managers will be unable effectively select conservation areas and unable to accurately predict how the species composition of these areas will change over time.

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My dissertation would not have been possible without the counsel and support of my major professor, Dr. Tom Burton, nor without the patience and support of my wife, Angie. Generous guidance and helpful suggestions were provided throughout my doctoral program by committee members Dr. Don Beaver, Dr. Jim Bence, and Dr. Jack Liu. Brian Keas and Joe Gathman provided suggestions for sampling and analysis and general encouragement. Brian Keas helped collect field data and construct the GIS database. This research also benefited from the advice and assistance of several individuals: Dr. Dave Ewert, Dr. Kevin Gutzwiller, Dr. Mic Hamas, and Daniel Rutledge. The Department of Geography at Michigan State University provided computer resources. Residents of Hessel, Cedarville, and DeTour graciously permitted me to work on private lands. This research was supported by grants from the Michigan Chapter of the Nature Conservancy (to Tom Burton); American Ornithologist's Union; the Michigan Polar-Equator Club; the George and Martha Wallace Ornithology Scholarship; the Graduate School and the Department of Zoology at Michigan State.

"I can do all things through Christ who strengthens me." Phillipians 4:13

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INTRODUCTION

Research in avian ecology over the last two decades has extensively explored the effects of landscape structure on species richness (e.g. Blake and Karr 1987; Pearson 1993; Freemark et al. 1995), patch selection (e.g. Gutzwiller and Anderson 1987a; Gutzwiller and Anderson 1992; Saab 1999), and breeding success (e.g. Robinson et al. 1995). Initially, research focused on how birds were affected by patch-level landscape characteristics such as patch area (Galli et al. 1976; Blake and Karr 1987; Brown and Dinsmore 1991), isolation (e.g. van Dorp and Opdam 1987; Brown and Dinsmore 1986), and edge effects (see Andren 1995 for review). More recent research addressed the importance of corridors (e.g. Dunning et al. 1995) and landscape connectivity (e.g. Haig et al. 1998) to the successful conservation of bird species. Substantial research effort has also centered on important regional-level processes such as forest fragmentation (e.g. Faaborg et al. 1995; Drolet et al. 1999; Rosenberg et al. 1999; Villard et al. 1999).

Based on information from these and similar studies, specific recommendations have been developed for the conservation and management of avian species (e.g. Martin and Finch 1995) and various strategies for the design and management of preserves (Schwartz 1999). However, such information is incomplete without considering potential effects of adjacent and surrounding landscape elements, or landscape context, on patches. Only recently have ecologists recognized that landscape context can affect patches in terms of species diversity (Webb and Hopkins 1984; Bloutin and Jobin 1998; Cantero et al. 1999; Liu and Ashton 1999), patch-use by species (Pearson 1993; Forys and Humphrey 1999) and the sustainability of economic and ecological processes (Risch et al. 1983; Liu and Ashton 1999) occurring within patches.

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Compared to other aspects of avian ecology, the importance of landscape context to birds has received little attention by researchers; but yet, consideration of landscape context has already helped clarify our understanding of some critical landscape processes. For example, predicting the occurrence of edge effects on birds (increased nest predation near edges) has been difficult because results of studies and experiments have been ambiguous (Paton 1994). However, accounting for characteristics of patches adjacent to edges (landscape context) has helped predict if and to what extent edge effects occur at a particular edge (see Andren 1995; Bayne and Hobson 1997). Landscape context can also explain variation in the bird species composition of habitats (Pearson 1993) and patches (Gutzwiller and Anderson 1987a; Estandes and Temple 1999; Saab 1999) as well as the occurrence of individual species. Unfortunately, studies which focus specifically on the effects of landscape context on birds are uncommon (but see Pearson 1993; Bayne and Hobson 1997), and this limits our understanding of avian ecology and hinders efforts to preserve avian diversity.

To ameliorate this lack of information, I conducted a landscape-scale study in a wetland-dominated, coastal region located along the northern shoreline of Lake Huron in the Upper Peninsula of Michigan. Birds were censused in 40 coastal wet meadow patches during 1998 and 1999. I also measured a suite of within-patch habitat characteristics along with characteristics of the adjacent patches, surrounding landscape, and associated coastline. For all analyses, bird variables were first adjusted for effects of patch area and within-patch habitat characteristics. Thus, any significant relationships with landscape context or coastline complexity are effects above and beyond those of area and habitat. Three sets of analysis were carried out, each designed to test for effects

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of landscape context and coastline complexity on a different aspect of avian biology. These analyses correspond to three specific chapters which are described below.

Chapter One addresses the primary objective of my research: to test for any apparent and strong associations between landscape context and measures of bird species richness and abundance. Recent research has demonstrated that the species composition of a patch may vary according to landscape context (e.g. Gutzwiller and Anderson 1987a; Pearson 1993; Estandes and Temple 1999; Saab 1999). For example, Friesen et al. (1995) described a negative relationship between bird species richness of forest patches and the number of adjacent houses, and some species avoided forest patches located in urban contexts altogether. Information about which contexts support the greatest number of species and/or the highest density of particular species would benefit conservation efforts, but this information is lacking for wetland-dominated landscapes such as the northern Lake Huron coastline.

Merely identifying the contexts that maintain high species richness (i.e. Chapter One), however, is not enough to ensure success of conservation efforts. Managers must also identify which landscape contexts facilitate a more stable species composition within a patch over time (i.e. lower species turnover rates). To help identify more stable contexts, Chapter Two tests for effects of landscape context and coastline complexity on the within-patch species turnover rates between 1997 and 1998. Information about species turnover rates will also help managers predict how the species composition of preserved or managed patches can be expected to change over time. Without this knowledge, manager's predictions about the future status of conservation areas are not based on accurate information and may lead to poor management decisions.

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Peninsula effects are defined as decreasing species richness with increasing distance from the mainland along a peninsula (Forman and Godron 1986; Milne and Forman 1986; Forman 1995). The northern Lake Huron coastline is highly interdigitated, and peninsular lobes and coves abound. In Chapter 3, I test predictions about species richness patterns along an interdigitated coastline that are based on the presence of peninsula effects. Specifically, peninsula effects predict that the species richness of wet meadows located in coves (near the mainland) should be higher than those located out on coastal lobes (far down the peninsula). Identifying positions along coastal lobes and coves that support higher species richness will further understanding of landscape context and also provide more detailed information relevant to the selection and management of wetland patches.

The information provided by this research will not only aid general understanding of landscape context effects, but will also directly benefit the regional management of the northern Lake Huron coastline. Although the wetlands associated with this section of coastline are some of the most undeveloped freshwater coastal wetlands remaining in the Great Lakes region, they are also currently threatened by residential and commercial development. These wetlands are a conservation priority because they represent critical migratory, breeding, and foraging habitat for a wide variety of bird species (Prince et al. 1992; Prince and Flegel 1995), many of which are declining regionally and/or locally (Brewer et al. 1991). Unfortunately, knowledge about the influence of landscape structure on birds in wetland-dominated landscapes is alarmingly scarce (see Freemark et al. 1995 and Weller 1999 for reviews), and, except for riparian forests (e.g. Gutzwiller and Anderson 1987a & b, Saab 1999), the effects of landscape context on birds in other wetland landsca

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wetland landscapes are practically unknown (but see Naugle et al. 1999). Without knowledge of the effects of landscape context on birds, the effectiveness and ultimate success of management schemes and conservation efforts in the Great Lakes and other regions are seriously compromised.

CHAPTER ONE

LANDSCAPE CONTEXT AND COASTLINE COMPLEXITY: EFFECTS ON SPECIES RICHNESS AND ABUNDANCE

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INTRODUCTION

Over the last decade, research in avian ecology has emphasized the importance of landscape composition and structure to species richness (e.g. Blake and Karr 1987; Pearson 1993; Freemark et al. 1995), patch selection (e.g. Gutzwiller and Anderson 1987a; Gutzwiller and Anderson 1992; Saab 1999), and breeding success (e.g. Robinson et al. 1995). Research initially focused on how birds were affected by landscape characteristics such as patch area (Galli et al. 1976; Blake and Karr 1987; Brown and Dinsmore 1991), isolation (e.g. van Dorp and Opdam 1987; Brown and Dinsmore 1986), and edge effects (see Andren 1995 for review) but has developed to address the importance of corridors (e.g. Dunning et al. 1995) and landscape connectivity (e.g. Haig et al. 1998) to the successful conservation of bird species. Substantial research effort has also centered on important regional-level processes such as forest fragmentation (e.g. Faaborg et al. 1995; Drolet et al. 1999; Rosenberg et al. 1999; Villard et al. 1999).

Based on information from these and similar studies, wildlife managers have developed specific recommendations for the conservation and management of avian species (e.g. Martin and Finch 1995) and various strategies for the design and management of preserves (Schwartz 1999). But no matter how detailed, such information is incomplete without considering effects of adjacent landscape elements, or landscape context, on patches. Ecologists have only recently recognized that landscape context can affect patches in terms of species diversity (Webb and Hopkins 1984; Bloutin and Jobin 1998; Cantero et al. 1999; Liu and Ashton 1999), patch-use by species (Pearson 1993; Forys and Humphrey 1999) and the sustainability of economic and ecological processes (Risch et al. 1983; Liu and Ashton 1999) occurring within patches.

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For birds, the importance of landscape context is just beginning to be understood, but already consideration of landscape context has furthered understanding of some important landscape processes. For example, understanding the occurrence of edge effects on birds (increased nest predation near edges) has been difficult because results of studies and experiments have been ambiguous (Paton 1994). However, accounting for characteristics of patches adjacent to edges (landscape context) has helped predict if and to what extent edge effects occur at a particular edge (see Andren 1995; Bayne and Hobson 1997). Landscape context can also explain variation in the bird species composition of habitats (Pearson 1993) and patches (Gutzwiller and Anderson 1987a; Estandes and Temple 1999; Saab 1999) as well as the occurrence of individual species. Friesen et al. (1995) described a negative relationship between bird species richness of forest patches and the number of adjacent houses, and some species avoided forest patches located in urban contexts altogether. Unfortunately, studies which focus specifically on the effects of landscape context on birds are uncommon (but see Pearson 1993; Bayne and Hobson 1997), and this limits our understanding of avian ecology and hinders efforts to preserve avian diversity.

To learn more about the effects of landscape context on species richness and species-occupancy in wetland-dominated landscapes, I censused birds in 40 coastal wet meadow patches and measured characteristics of the adjacent patches, surrounding landscape, and associated coastline. Variables describing bird species richness and abundance were first adjusted for wetland area, perimeter, and within-patch habitat characteristics so that effects of landscape context would not be confounded with these factors.

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My primary objective was to test for any apparent and strong associations between landscape context and measures of bird species richness and abundance, but my analyses were also guided by three *a priori* hypotheses about how context might influence within-patch composition of wet meadow bird communities. First, I expected that wet meadow patches located in more complex contexts (adjacent to a greater number of patches or patch types) would have greater species richness than those adjacent primarily to one patch type (Forman 1995). Second, I expected that wet meadows in human-developed contexts would have lower species richness than those adjacent to more natural patch types (Freisen et al. 1995); or, that some species would avoid wet meadows in human-developed contexts while other, more tolerant species would be more abundant in human-developed contexts (Blair 1996; Bolger et al. 1997; Bock et al. 1999). Third, I hypothesized that wet meadows associated with more complex and convoluted coastlines should have higher species richness than those associated with simpler coastlines (Nilsson 1987).

Compared to terrestrial landscapes, knowledge about the influence of landscape structure on birds in wetland-dominated landscapes is particularly scarce (see Freemark et al. 1995 and Weller 1999 for reviews). And, with the exception of riparian forests (e.g. Gutzwiller and Anderson 1987a & b, Saab 1999), the effects of landscape context on birds in other wetland landscapes are practically unknown (but see Naugle et al. 1999). The northern shoreline of Lake Huron where I conducted this research contains some of the most undeveloped freshwater coastal wetlands remaining in the Great Lakes region; but, like most wetland landscapes, they are threatened by residential and commercial development. These wetlands are a conservation priority because they serve as critical

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migratory, breeding, and foraging habitat for a wide variety of bird species (Prince et al. 1992; Prince and Flegel 1995), many of which are declining regionally and/or locally (Brewer et al. 1991). But, without knowledge of the effects of landscape context on birds, however, the effectiveness and ultimate success of management schemes and conservation efforts in the Great Lakes and other regions are seriously compromised.

METHODS

Study Area

I worked in 40 wet meadows that were part of northern Great Lakes marshes (Minc and Albert 1998) and located within 500 m of the highly convoluted, northern shoreline of Lake Huron in the Upper Peninsula of Michigan (Mackinac and Chippewa counties). Wet meadows selected for sampling met several additional criteria: they were seasonally or shallowly flooded; water levels were influenced by overall lake water levels; and vegetation was predominantly a mixture of hummock-forming grasses (*Calamagrostis canadensis*) and sedges (*Carex stricta* and *C. aquatilis*). The grass/sedge vegetation was interspersed with varying amounts of bulrush (*Scirpus* spp.), cattail (*Typha* spp.), and shrubs (*Salix* spp., *Alnus* spp., and *Myrica* spp.). Submersed (*Potomogeton* spp.) and floating (*Polygonum* spp., *Lemna* spp.) vegetation were often present in standing water between hummocks.

Bird Censuses

Permanent census transects (Verner 1985) oriented perpendicular to the coastline were established within each wet meadow. I censused each transect for breeding birds on multiple occasions (4 times during 1997; 5 times during 1998) between 15 May and 4 July. All censuses were conducted by a solitary individual (SKR) between 0530 and 1030

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EST. Before the first census each May, the order in which wet meadows were visited was randomized. This order was then systematically rotated for each successive census visit so that each wet meadow was equally censused during different times of the morning. Censuses were not conducted in unsuitable weather conditions (Robbins, 1981): temperatures < 0°C, strong winds, steady rainfall, or fog limiting visibility to < 300 m.

Because the hummocks and standing water often made it difficult to walk the transect quickly or quietly, I modified traditional protocols for line-transect sampling in grasslands (Verner 1985). Transects were walked at a slower than typical pace (0.5 km per hour). After progressing 50 m along the transect, I stopped and conducted a 10-minute count from that point. After 10 minutes had elapsed, I resumed walking the remainder of the transect. All birds seen or heard were recorded as either within the 100-m wide transect (fixed-width), or outside the transect but still within the perimeter of the wet meadow. Records were based on initial detections of individual birds known to be distinct in time and space.

Censuses were augmented by broadcasting recorded vocalizations of secretive birds (Virginia Rail, Sora, Yellow Rail, Least Bittern) to elicit responses (*sensu* Gibbs and Melvin 1993). Broadcasts were made during the last 2 minutes of the initial 10-minute point count. After completing the entire census transect, additional broadcasts were conducted while returning to the start of the transect to ensure that all individuals present along the transect were detected. Each 100-m segment received a broadcast of all three species' calls, and I randomized the order of the species' calls at each consecutive broadcast.

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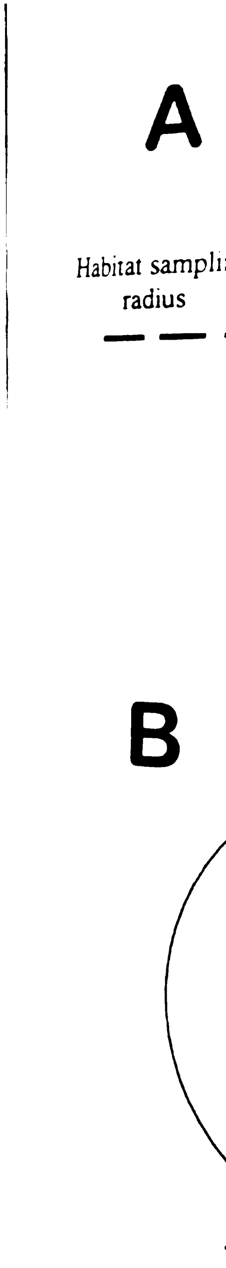
Habitat Characteristics

Because variation in within-patch habitat characteristics can influence bird species richness and abundance of wetlands (Craig and Beal 1992; Weller 1999), I measured 20 habitat characteristics along each bird census transect in late July after vegetation had reached mature height. Each bird census transect was divided into 50-m segments. Within each segment, four habitat-sampling radii were established radiating from the center of that segment (Figure 1A). Five sampling points were located at 10-meter intervals along each of the habitat-sampling radii (total of 20 points per 50-m segment of each bird transect). At each of these sampling points, I used three different types of sampling techniques: point-intercept sampling, frequency of cover types, and frequency of trees and snags (Figure 1B).

Point-intercept sampling. At each of the sampling points (Figure 1B), I passed a 2-m metal rod vertically through the vegetation. The rod was divided into eight 0.25-m sections (or strata), and I counted the number of hits, or touches, by vegetation in each of the 8 sections (*sensu* Rotenberry and Wiens 1980). Number of hits was used as an estimate of vegetation density. Grass density was calculated as the total number of hits by grasses or sedges in all eight 0.25-m strata; woody vegetation density was calculated as the total number of hits by woody vegetation in all strata; and total vegetation density was the total number of hits by all vegetation types in all strata. I estimated shrub foliage diversity by summing the number of 0.25-m sections of metal rod with at least one live woody hit (8 possible) and the number of sections containing at least one dead woody hit (up to 8 for a total possible of 16). I also used the metal rod to measure water depth, grass height, and hummock height at each of the sampling points.



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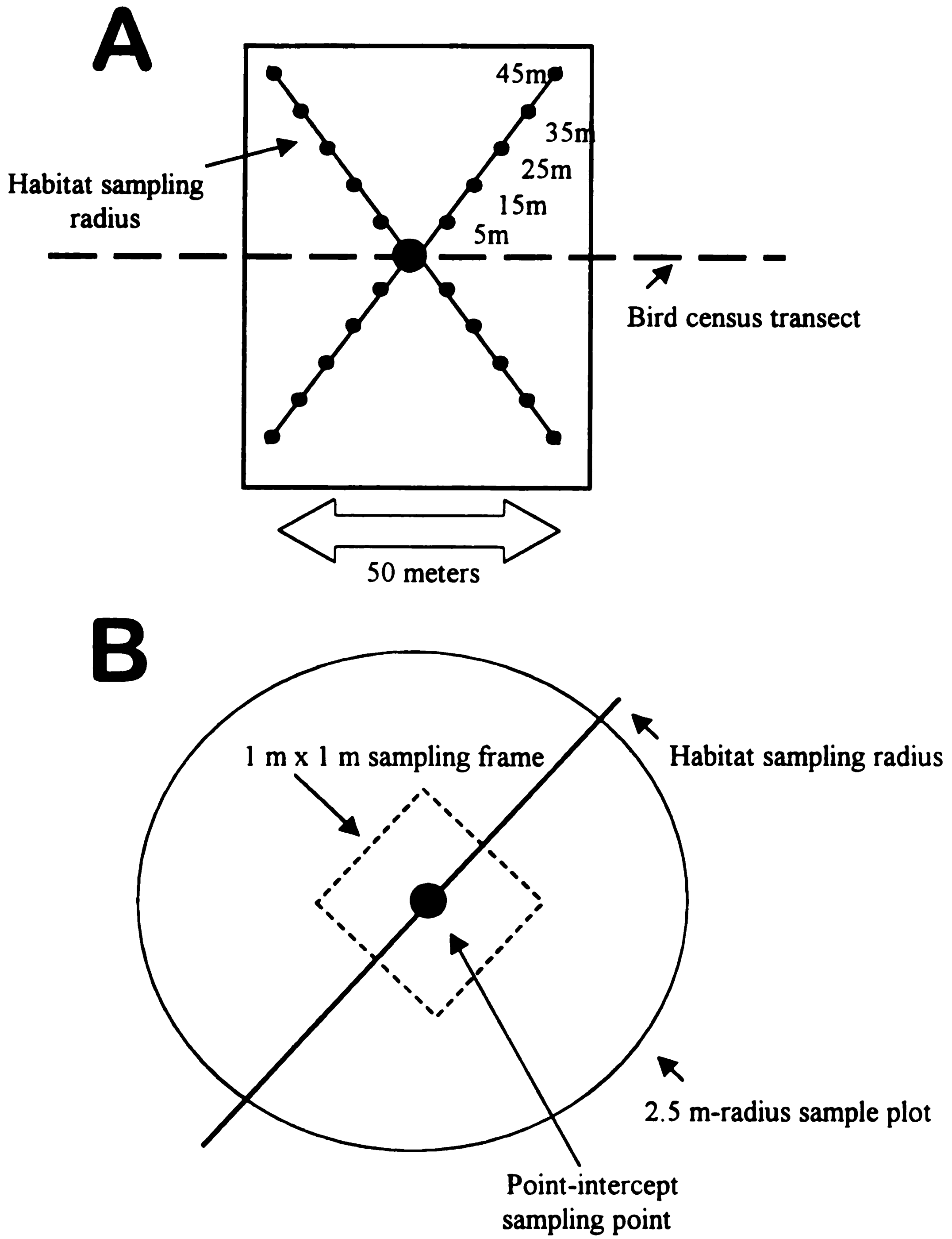

Figure 1. Diagram of habitat sampling procedures used in 40 Great Lakes coastal wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998. A) Locations of 20 habitat sampling points relation to center of 50-m transect segments. B) Details of 3 sampling techniques used at each of these 20 points.

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Because hummock formation resulted in a highly variable water depth, I standardized measurements by sampling between hummocks in the valley nearest to the sampling point. This was not a random approach, but it eliminated variation that would have occurred if the rod were positioned at the peak of a hummock at some points and in the valley between hummocks at others. At a remote site prior to conducting habitat sampling, I sampled seven 50-m sections of wet meadow habitat and determined that 20 measurements per 50m segment were sufficient to acquire stable estimates of the mean and variance for all variables using the metal rod.

Frequency of cover types. To estimate percent cover of various vegetation and cover types, I centered a 1-m^2 sampling frame on each of the point-intercept sampling points (Figure 1b). Within each frame, I recorded the presence or absence of graminoid vegetation (grass or sedge), cattail (*Typha* spp.), bulrush (*Scirpus* spp.), floating vegetation, submersed vegetation, willow (*Salix* spp.), alder (*Alnus* spp.), open water, and moss. Frequency of occurrence of each cover type was calculated as the proportion of the sampling points (20 per 50-m segment) at which that cover type was present.

Density of trees and snags. To estimate the density of trees and snags, I centered a 2.5-m radius circular plot on each point-intercept sampling point. All trees, shrubs, and snags within the plot were identified and counted. I calculated the frequency of occurrence of deciduous and coniferous stems (> 2.0 m in height) and the frequency of deciduous and coniferous snags (> 2.0 m in height) as the proportion of circular plots with that stem type present. Trees and shrubs were sampled in 1997 only, because there was little or no change in these habitat components between years.

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Calculation of Landscape Variables

Landscape context variables. Landscape context variables were derived using a geographic information system (ArcView; ESRI, Inc. 1998). Landuse/landcover of the entire coastal landscape (including wet meadow sites and adjacent habitats) was interpreted from color aerial photographs taken in 1992. Individual photographs were georeferenced, rectified and then mosaiked into a composite color image which was used as a template for digitizing landcover classes. The landcover classification scheme is detailed in Table 1. All landcover classifications were verified and updated by extensive visual ground-truthing during the spring of 1999.

The number of adjacent patches, the number of different adjacent patch types, and the number of patch interfaces were counted for each wet meadow patch. Number of interfaces was calculated as the number of discrete sections of a wet meadow perimeter where the adjacent patch type changed. Patch area, perimeter length, and the proportion of each wet meadow's perimeter adjacent to each particular landcover type were calculated in ArcView. Four other landscape context variables were calculated for the surrounding landscape (within 1-km of the edge of each wet meadow): percent of the surrounding landscape comprised of Lake Huron, percent of the surrounding landscape comprised of wet meadow habitat, density of roads (m/ha), and density of streams (m/ha).

Coastline complexity variables. Three measures of coastline complexity were derived from a vector coverage of the northern Lake Huron shoreline included in the U.S. Army Corps of Engineers Great Lakes coastal geomorphology database (Great Lakes Environmental Research Center). Three coastline vector segments representing three spatial scales -- 500-m, 1-km, and 2-km from the wet meadow perimeter -- were created

Table 1. Landcover classification system derived for the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

- Urban (Residential, Commercial, and Industrial)
- Agricultural (Cropland, Pasture, etc.)
- Non-Forested Openings
- Forested
- Lakes, Reservoirs, or other open water
- Forested Wetlands
- Inland Emergent Wetlands
- Coastal Wetlands:
  - Bulrush Marsh (*Scirpus* sp. wetland)
  - Cattail Marsh (*Typha* sp. wetland)
  - Wet Meadow
  - Fen Wetland
  - Sand Flats
  - Alvar Wetland
- Cobble Beaches
- Sand Beaches or Sand Dunes

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for each wet meadow using buffer operations in Arc/Info. Measures of complexity were calculated for each coastline segment separately. Total coastline was calculated directly from attribute tables. Sinuosity (total coastline divided by straight-line distance from end-point to end-point) and fractal dimension of each coastline segment were calculated using a Fortran program, Fract_Line (Lam and de Cola 1993).

Statistical Analysis

Habitat, landscape and coastline variables. Because many habitat, landscape, and coastline variables were inter-correlated, I used principal component analysis (PCA) to remove correlations and to reduce the number of variables for analysis (Proc Princomp, SAS Institute 1990). Principal component analysis was conducted three separate times: once each for the habitat, landscape and coastline variables resulting in three sets of principal components. Hereafter, these sets of components will be referred to as habitat, landscape and coastline components. Within each set, components with an eigenvalue > 1.0 were retained. Principal components were not rotated; and eigenvector coefficients, rather than factor loadings, were used to interpret components because factor loadings do not conserve the multivariate contributions of the original variables (Rencher 1992).

Bird variables. I analyzed data only for those birds detected within the 100-m transects. Species richness was the total number of different species detected during all census visits. Abundance (an estimate of density) was calculated as the mean number of birds per hectare of transect per visit. I calculated abundance for all birds (total bird abundance), all nesting birds, all non-nesting birds, and for individual species that were detected in > 2/3 of the wet meadows. Because wet meadows possess characteristics of both grasslands and wetlands, a species was designated in the nesting guild if it was an obligate or facultative nester in either grasslands (Vickery et al. 1999) or wetlands (based on life-history traits listed in Terres 1980). The non-nesting guild included species that nest exclusively in other habitats but still rely on wet meadows for other requirements such as foraging (e.g. Great Blue Heron). Nesting guilds are listed in Appendix A.

Linear and logistic regression models. Because I wanted to test for effects of landscape context and coastline complexity above and beyond variation in bird variables that could be explained by area and habitat effects, I adopted a two-stage regression approach (Morrison et al. 1998). In the first stage, a bird variable was regressed against patch area, perimeter-area ratio and 5 habitat principal components. Then, the residuals from this model were regressed against the 8 landscape and coastline components. For species richness variables, abundance variables, and abundance of species that occurred on > 2/3 of the wet meadows, I used stepwise linear regression for variable selection (Draper and Smith 1981). For species that occurred on less than 2/3 of the wet meadows, I used logistic regression (Trexler and Travis 1993) on presence/absence data. Instead of using residuals in the second stage of logistic regression, the habitat components selected in the first stage were forced into the model first before using stepwise selection on the landscape and coastline components (*sensu* Estandes and Temple 1999).

For each stage of linear and logistic regressions, I limited the number of explanatory variables to no greater than 8 (at least 5 observations per variable). For linear regression, variable selection was based on several criteria. First, models containing all possible subsets of variables selected by stepwise selection (using an F-to-stay = 0.15) were compared using prediction residuals (Draper and Smith 1981). This served as a method of validation, and the subset model with the lowest (best) sums of squares of prediction residuals was kept (PRESS: Draper and Smith 1981; Myers 1989). Other criteria for variable selection required that assumptions of regression (normality of residuals, constant variance) were satisfied and that all explanatory variables had significant *t*-statistics ($\alpha < 0.10$). For logistic regression, models containing all possible subsets of variables selected by stepwise selection were evaluated using Aikai's Information Criteria (AIC), and subset models with the lowest (best) AIC were kept (SAS Institute 1990). Additional criteria for variable selection required that the model pass a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989), that all explanatory variables had significant Wald χ^2-statistics ($\alpha < 0.10$), and that included components did not have unusually large coefficients or standard errors. Large coefficients and SEs indicate that the model is overfit or other problems such as complete separation or colinearity (Hosmer and Lemeshow 1989). These variable selection criteria were used for both stages of the regression procedures.

Transformation of variables. Many of the original habitat and landscape context variables were either count data or percentage data which are traditionally log or arcsine transformed. The reason for such transformations in the context of principal component analysis is to linearize the variables so that PCA can construct better linear combinations (maximized variance) of those variables. However, inspection of biplots of both transformed and untransformed variables revealed that transformations did not further linearize relationships between variables, and PCA using transformed variables did not result in qualitatively different principal components nor did those components explain more of the total variance in the original variables. Thus, I did not transform original variables prior to PCA. Similarly, counts of species richness and species' abundance were a

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not automatically log transformed. Log transformations on dependent variables were used only as necessary to linearize relationships between dependent and regressor variables, normalize residuals of regression models, or stabilize error variance (Rahbek 1997).

RESULTS

Bird Species Richness and Abundance

Species richness within wet meadows ranged from 1 to 19 in 1997 and from 1 to 16 during 1998. Over a two-year period, I made 2179 individual detections of 55 different species (Appendix A) during a total of 360 census visits to 40 wet meadow sites. Twenty-five species that potentially nest in wet meadow habitats (Appendix A) comprised just over 83% of all the detections. The most common species were the Yellow Warbler, Common Yellowthroat, Red-winged Blackbird, Swamp Sparrow, and Song Sparrow. Scientific names for all species are provided in Appendix A.

Habitat Characteristics

Although wet meadow sites were selected for inclusion in this study based on criteria of similar habitat features, the 20 habitat characteristics did vary both among sites and between years (see Table 2 for summary statistics). Five principal components based on habitat characteristics were retained for analysis, and they accounted for 74% and 77% of the total variation in the original habitat variables for 1997 and 1998, respectively (Appendices B and C). Preliminary analyses indicated that linear and logistic regression of bird variables using these principal components produced models with r^2 values that were not significantly different from models constructed using the original habitat variables (S. Riffell, unpublished data). Thus, principal components derived from original habitat components adequately accounted for habitat-related variance in bird variables.

Table 2. Summary statistics for habitat variables measured in 40 wet meadows along the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

			1997			1998	
Habitat Variable	Units	Mean	SE	Range	Mean	SE	Range
Water depth	cm	22.10	1.94	0.00-49.70	5.95	0.76	0.00-17.74
Hummock height	cm	23.85	1.47	0.00-42.54	23.51	1.41	0.00-40.81
Grass height	cm	105.40	3.27	59.95-151.52	109.47	3.29	58.16-154.83
Grass density	hits/point	5.53	0.41	0.58-12.38	5.81	0.39	0.34-13.22
Woody vegetation density	hits/point	0.28	0.04	0.00-1.08	0.28	0.04	0.00-1.04
Total vegetation density	hits/point	6.00	0.41	0.63-12.63	6.30	0.40	0.37-13.43
Shrub foliage diversity	str./patch	4.75	0.48	0.00-12.00	4.58	0.41	0.00-9.00
Frequency of cover types							
Graminoid	%	95.14	1.40	48.40-100.00	97.67	0.59	82.70-100.00
Cattail	%	7.43	2.25	0.00-72.90	6.76	2.31	0.00-75.90
Bulrush	%	18.15	3.50	0.00-90.00	19.12	3.40	0.00-91.40
Floating vegetation	%	10.26	1.99	0.00-58.30	2.88	1.22	0.00-47.90
Submersed vegetation	%	52.30	4.71	0.00-100.00	5.93	1.24	0.00-35.70
Willow	%	8.43	1.37	0.00-28.60	9.40	1.55	0.00-37.30
Alder	%	6.25	1.29	0.00-32.40	6.71	1.43	0.00-38.80
Open water	%	3.97	0.81	0.00-15.00	4.25	0.84	0.00-21.00
Moss	%	6.97	1.36	0.00-33.30	8.05	1.36	0.00-35.80
Frequency of trees and snags							
Coniferous trees	%	3.87	1.17	0.00-36.40	--*	--	--
Deciduous trees	%	1.91	0.45	0.00-9.60	--	--	--
Coniferous snags	%	1.56	0.40	0.00-8.30	--	--	--
Deciduous snags	%	1.09	0.51	0.00-17.00	--	--	--

* Not sampled in 1998 because distributions of trees and snags did not change over that time-interval.

Habitat components were biologically interpreted with respect to the contributions of the original variables (Table 3). Habitat components selected in two-stage regressions of bird variables were consistent with documented bird-habitat relationships in grasslands and wetlands (Weller 1999). However, because the focus of this study was bird-landscape relationships, bird-habitat relationships will not be discussed herein. Readers interested in further information about bird-habitat relationships in northern Lake Huron coastal wet meadows are referred to Table 3 and Appendices B and C where information about these components is given.

Landscape Components

The landscape surroundings of the 40 wet meadows varied from simple contexts (patch perimeter bordered by only 1 patch) to very complex contexts (patch perimeter bordered by as many as 11 different patches). Some wet meadows were bordered entirely by forest, others were bordered primarily by various wetland types, and still others by open water. Although the proportion of the wet meadow perimeter adjacent to urban patches ranged from 0 - 62%, less than 10% of most wet meadow perimeters were adjacent to urban patches. Additionally, most urban patches consisted of single-family residences, summer cabins, or boat dock and marinas which represented only a slight to moderate human-development of the landscape. The extensive agricultural, industrial, or commercial development that is characteristic of more populated regions of the Great Lakes were uncommon or lacking in this landscape. Summary statistics for landscape context variables are listed in Table 4. Principal component analysis identified 5 landscape context components (LAND1-LAND5) which comprised 78% of the total variance in the 16 original variables (Appendix D). Each of these components was comprised of a suite

Table 3. Habitat components derived from principal components analysis on original habitat variables.

	1997 Habitat Components
HAB1	*Grass Density and Height* Increasing hummock height, grass height & density, total vegetation density
HAB2:	*Trees vs. Deep Water and Bulrush* Increasing frequency of deciduous trees Decreasing water depth and frequency of bulrush
HAB3:	*Woody Vegetation* Increasing woody density, shrub foliage diversity, frequency of willow & alder
HAB4:	*Forested (deciduous) vs. Graminoid Coverage* Increasing frequency of deciduous trees and snags Decreasing graminoid coverage
HAB5	*Open Water and Floating Vegetation vs. Willow* Increasing frequency of moss, open water pockets, and floating vegetation Decreasing frequency of willow
	1998 Habitat Components
HAB1:	*Grass Density and Height* Increasing hummock height, grass height & density, total veg. density Decreasing frequency of bulrush
HAB2:	*Forested/shrubby vs Deep Water* Increasing woody, frequency of willow, trees, and snags Decreasing water depth

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Table 3. Continued.

HAB3:	*Shrubby, Open vs Graminoid Coverager*
	Increasing shrub foliage diversity, frequency of open water and deciduous snags Decreasing graminoid coverage
HAB4:	*Willowy vs Snags and Cattail*
	Increasing frequency of willow Decreasing deciduous snags and cattail
HAB3:	*Open Water and Floating Vegetation vs. Willow*
	Increasing frequency of floating vegetation, open water, moss, and coniferous trees Decreasing frequency of willow

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Table 4. Summary statistics for landscape context and coastline complexity variables measured for 40 wet meadows along the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

Variable	Units	Mean	SE	Range
	Landscape Context Variables			
# of adjacent patches	#/patch	4.08	0.37	1.00-11.00
# of adjacent patch types	#/patch	3.25	0.20	1.00-6.00
# of interfaces with other patches	#/patch	4.93	0.56	1.00-17.00
Percent of patch perimeter adjacent to:				
Urban	%	8.55	2.39	0.00-62.40
Non-forested opening	%	1.12	0.47	0.00-12.10
Forest	%	51.17	4.18	0.00-100.00
Open water	%	6.20	2.56	0.00-76.50
Forested wetland	%	9.13	2.42	0.00-68.00
Bulrush marsh	%	16.19	2.81	0.00-58.30
Cattail marsh	%	6.12	1.87	0.00-46.10
Total wetland	%	32.31	3.76	0.00-96.94
Surrounding landscape (within 1-km of patch perimeter):				
Amount of wet meadow	%	3.70	0.48	0.00-11.00
Amount of Lake Huron	%	31.35	2.71	4.70-71.00
Stream density	m/ha	4.90	0.30	0.30-10.37
Road density	m/ha	12.04	1.10	0.10-32.93
	Coastline Complexity Variables			
Total coastline				
500-m	m/ha	6.15	0.40	0.30-12.18
1-km	m/ha	13.35	0.85	4.41-33.82
2-km	m/ha	33.87	2.33	11.85-79.33
Sinuosity				
500-m	--*	2.84	0.25	1.08-8.35
1-km	--	2.83	0.23	1.06-7.57
2-km	--	2.82	0.20	1.06-6.99
Fractal dimension				
500-m	--**	1.17	0.02	1.01-1.42
1-km	--	1.16	0.01	1.01-1.39
2-km	--	1.15	0.01	1.01-1.28

* Sinuosity is the ratio of total length (total coastline) divided by the distance between the two endpoints. Sinuosity of 1.00 indicates a straight line.

** Fractal dimension is unitless.

of intercorrelated, and often conceptually related, original variables which permitted me to interpret and name (*sensu* Saab 1999) each component (see Table 5).

The first component (LAND1) represented a contrast of *complex contexts vs. simple, forested contexts.* High values of LAND1 were associated with wet meadows that were adjacent to a large number of patches and patch types and that had proportionally more perimeter bordered by wetlands, and low values of LAND1 were associated with patches primarily surrounded by forest habitat. The second component (LAND2) was a contrast between *Lake Huron and stream contexts vs. forested wetland contexts.* High values of LAND2 were associated with wet meadows where a relatively high proportion of the surrounding landscape was comprised of Lake Huron and also contained relatively high stream densities. Low values of LAND2 indicated that a relatively high proportion of wet meadow perimeters was bordered by forested wetland.

The third principal component (LAND3) represented a gradient of increasingly *human-developed contexts.* High values of LAND3 were associated with relatively higher proportions of urban and cattail marsh perimeters as well as greater density of roads within the surrounding landscape. Anthropogenic effects often facilitate the development and spread of cattails in wetlands (Newman et al. 1998), so it is not surprising that cattail perimeters were correlated with other measures of human impact. The fourth principal component (LAND4) was a contrast of *wetland contexts vs. open water contexts.* High values of LAND4 were associated with wet meadow perimeters bordered by relatively higher proportions of bulrush marsh and all wetland types as a group, while low values indicated wet meadow perimeters were bordered by relatively higher proportions of open water and were less connected to other wetlands. The last component (LAND5),

Table 5. Landscape components and coastline components derived from principal components analysis on original variables.

	Landscape Context Components
LAND1	*Complex Contexts vs. Simple, Forested Contexts* Increasing number of patches, patch types, and total wetland perimeter Decreasing forested perimeter
LAND2:	*Lake and Stream Contexts vs. Forested Wetland Contexts* Increasing proportion of Lake Huron and density of streams in the surrounding landscape Decreasing forested wetland perimeter.
LAND3:	*Human-developed Contexts* Increasing Urban and Cattail Perimeter and Road Density
LAND4:	*Wetland Contexts vs. Open Water Contexts* Increasing bulrush marsh and total wetland perimeter Decreasing open water perimeter
LAND5	*Forested Contexts vs. Aquatic Contexts* Increasing forested perimeter Decreasing open water and wetland perimeters; increasing proportion of Lake Huron in the surrounding landscape
	Coastline Complexity Components
COAST1:	*Highly Fractal and Complex Coastlines* Increasing fractal dimension, sinuosity and total coastline length at all three spatial scales

Table 5. Continued.

COAST2:	*Increasing Total Coastline*
	Increasing length of total coastline (all scales)
COAST3:	*Scale Contrast / Sinuosity*
	Increasing sinuosity and total coastline (1-km and 2-km scales) Decreasing fractal dimension, sinuosity and total coastline (500-m)

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represented a contrast of *terrestrial, forested contexts vs. aquatic contexts*. High values of LAND5 were associated with wet meadows that were primarily adjacent to forested habitats while low values of LAND5 were associated with wet meadows adjacent to bulrush marshes and other wetlands and/or surrounded by a greater proportion of open water.

Coastline Components

Three measures of coastline complexity were calculated at three spatial scales for coastline segments associated with each wet meadow. These segments varied from simple, nearly straight coastlines to highly convoluted and complex coastlines (Table 4). Complexity measures were highly inter-correlated and principal components analysis identified three components which contained 77% of the variance in the original variables (Appendix E and Table 5). The first coastline component (COAST1) represented *highly fractal and complex coastlines* at all scales. Large values of COAST1 indicated wet meadows that were associated with highly fractal coastline segments at all three scales. These segments also tended to be highly sinuous with high amounts of total coastline. High values of the second component (COAST2) indicated wet meadows associated with coastline segments with high amounts of *total coastline* length at all three spatial scales. The third component (COAST3) represented a *scale contrast*. High values of COAST3 indicated wet meadows with high values of total coastline and sinuosity for associated coastline segments at scales of 1-km and 2-km, but low values of all three coastline metrics for segments at the scale of 500-km.

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Bird-Landscape Relationships

For 22 of the 26 species and bird variables tested, landscape context or coastline components significantly explained variation above and beyond that explained by models containing area, PAR and habitat components during at least 1-yr of the study. The improvement in variance explained (r^2) ranged from 5% to 40% (Table 6). Because of the large number of models involving community- or species-level bird variables, results will be summarized in two ways. First, I will summarize the landscape and coastline components which were selected in regression models of community level variables. Models involving total species richness and total abundance will be described first, followed by models involving nesting and non-nesting guild variables. Second, I will summarize results of species-specific models by each landscape and coastline component in turn.

Total species richness and total abundance. Area, perimeter-area ratio (PAR) and habitat components alone explained 63% and 64% of the variance in species richness in 1997 and 1998, respectively (Table 6) in the first stage of linear regressions. Landscape and coastline components significantly increased the variance explained to 75% in 1997 and 78% in 1998. In both years, higher species richness was observed in wet meadows located in more complex contexts (LAND1) and more human-developed contexts (LAND3). High species richness was also associated with less fractal coastlines (COAST1: Table 6) in 1997, and with less sinuous coastlines (COAST3) and aquatic contexts (LAND5) in 1998.

Habitat components explained 38% and 10% of the variance in total bird abundance in 1997 and 1998, respectively. Addition of landscape and coastline

Table 6. Comparison of within-patch habitat effects and effects of landscape context and coast
models of wet meadow birds in 40 wet meadows associated with the nor
counties, Michigan. (+) or (-) indicates the dir

Table 6. Comparison of within-patch habitat effects and effects of landscape context and coastline complexity in two-stage regression models of wet meadow birds in 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan. (+) or (-) indicates the directions of the relationship between that component and the bird variable.

	Habitat-only models		Models including landscape components	
Bird variable	# of PCs in model	R^2	Significant landscape components	R^2
Total species richness				
1997 (log transformed)	Area (+), PAR (-), HB3 (+), HB4 (+)	0.63	LAND1 (+), LAND3 (+), COAST1 (-)	0.75
1998 (log transformed)	Area (+), HB3 (+), HB5 (+)	0.64	LAND1 (+), LAND3 (+), LAND5 (-), COAST3 (-)	0.78
Total Bird Abundance				
1997 (log transformed)	HB1 (+), HB3 (+), HB4 (+)	0.38	LAND1 (+)	0.50
1998 (log transformed)	HB3 (+)	0.10	LAND1 (+), LAND2 (+), LAND5 (-), COAST2 (-)	0.50
Nesting Species Richness				
1997 (log transformed)	Area (+), PAR (-), HB1 (+), HB3 (+), HB4 (+)	0.75	LAND1 (+)	0.84
1998 (log transformed)	Area (+), HB3 (+), HB5 (-)	0.69	LAND2 (+), LAND3 (+), LAND5 (-), COAST1 (-)	0.81
Nesting Bird Abundance				
1997 (log transformed)	HB1(+), HB3 (+)	0.33	LAND1 (+), LAND5 (-), COAST2 (-)	0.55
1998 (log transformed)	Area (+), HB3 (+)	0.16	LAND2 (+), LAND3 (+), LAND5 (-), COAST1 (-)	0.27

Table 6. Continued.

Bird variable	Habitat-only models
Non-nesting	# of PC

Table 6. Continued.

	Habitat-only models		Models including landscape components	
Bird variable	# of PCs in model	R^2	Significant landscape components	R^2
Non-nesting Species Richness				
1997	Area (+), HB4 (+)	0.34	--	--
1998	HB3 (+), HB5 (-)	0.31	LAND1 (+)	0.37
Non-nesting Bird Abundance				
1997	HB2 (+), HB4 (-)	0.33	--	--
1998	HB3 (+), HB5 (-)	0.19	--	--
Abundance (log # individuals)				
Common Yellowthroat				
1997	HB3 (+)	0.17	COAST1 (-)	0.40
1998	HB2 (+)	0.24	LAND5 (-), COAST2 (-)	0.36
Swamp Sparrow				
1997	Area (+), HB1 (+)	0.41	LAND2 (-), COAST1 (-)	0.53
1998	PAR (-), HB1 (+), HB4 (+)	0.42	LAND5 (-)	0.53
Song Sparrow				
1997	PAR (+), HB1 (-)	0.32	--	--
1998	PAR (+), HB1 (-)	0.28	LAND4 (-), LAND5 (-)	0.57

Table 6 Continued

Habitat-only models

Table 6. Continued.

Bird variable	Habitat-only models		Models including landscape components	
	# of PCs in model	R^2	Significant landscape components	R^2
Presence/Absence				
Great Blue Heron				
1997	--	--	LAND1 (+), COAST1 (-)	0.24
1998	HB2 (-)	0.16	LAND3 (-)	0.27
American Bittern				
1997	Area (+), HB1 (+)	0.37	COAST2 (-)	0.44
1998	Area (+), HB1 (+), HB5 (-)	0.27	--	--
Mallard				
1997	HB1 (+)	0.23	COAST1 (+)	0.32
1998	Area (+), HB3 (+)	0.37	COAST2 (+)	0.43
Virginia Rail				
1997	Area (+), HB1 (+), HB4 (+)	0.33	--	--
1998	Area (+)	0.27	LAND1 (+)	0.34
Sora				
1997	Area (+), HB1 (+), HB2 (-)	0.39	COAST3 (+)	0.44
1998	Area(+)	0.15	COAST3 (-)	0.23

Table 6 Continued

Habitat-only models

Table 6. Continued.

	Habitat-only models		Models including landscape components	
Bird variable	# of PCs in model	R^2	Significant landscape components	R^2
Common Snipe				
1997	--	--	--	--
1998	--	--	--	--
Northern Flicker				
1997	Area (+)	0.10	--	--
Downy Woodpecker				
1997	HB4 (+)	0.16	--	--
1998	HB1 (+), HB5 (-)	0.29	--	--
Eastern Kingbird				
1997	Area (+), HB4 (-)	0.32	LAND5 (-), COAST3 (+)	0.46
Alder Flycatcher				
1997	HB3 (+)	0.35	--	--
1998	HB3 (+), HB5 (-)	0.17	LAND4 (+), COAST3 (-)	0.43
Sedge Wren				
1998	Area (+)	0.40	LAND4 (+)	0.49
Cedar Waxwing				
1997	Area (+), HB4 (+)	0.15	COAST3 (+)	0.29
1998	HB2 (+), HB5 (-)	0.18	--	--

Table 6 Continued

Bird variable	Habitat-only models
Yellow Warbler	# of PC

Table 6. Continued.

Bird variable	Habitat-only models		Models including landscape components	
	# of PCs in model	R^2	Significant landscape components	R^2
Yellow Warbler				
1997	HB3 (+), HB4 (+)	0.26	--	--
1998	HB3 (+), HB4 (+), HB5 (-)	0.26	LAND1 (+), LAND5 (-), COAST3 (-)	0.57
Red-winged Blackbird				
1997	Area (+), HB1 (+)	0.47	LAND1 (+)	0.65
1998	HB2 (-), HB4 (+), HB5 (-)	0.46	LAND1 (+), LAND4 (+)	0.61
American Goldfinch				
1997	Area (+)	0.11	--	--
1998	Area (+), HB1 (+), HB3 (+), HB4 (+)	0.53	COAST2 (-)	0.57
Savannah Sparrow				
1997	Area (+), HB5 (-)	0.39	--	--
Chipping Sparrow				
1997	--	--	COAST1 (-)	0.12

components significantly increased the variance explained to 50% in both years (Table 6). Total abundance was positively associated with complex contexts (LAND1) in both years. In 1998, total abundance was also associated with lake and stream contexts (LAND2), aquatic contexts (LAND5) and less total coastline length (COAST2).

Nesting and non-nesting guilds. Area, PAR, and habitat components explained 75% and 69% of the variation in nesting species richness in 1997 and 1998, respectively (Table 6). Inclusion of landscape and coastline components significantly increased the explained variance to 84% in 1997 and 81% in 1998. In 1997, higher nesting species richness was associated with complex contexts (LAND1). In 1998, higher nesting species richness was associated with lake and stream contexts (LAND2), human-developed contexts (LAND3), aquatic contexts (LAND5) and less fractal coastlines (COAST1). Components selected in models for nesting bird abundance generally mirrored those selected in richness models (Table 6).

Area and habitat components explained approximately 30% of the variation in non-nesting species richness and abundance. Landscape and coastline components did not significantly increase the variance explained for any non-nesting guild variable with the exception of non-nesting species richness which was associated with complex contexts (LAND1) in 1998 (Table 6).

Community and species-specific responses. Landscape and/or coastline components significantly explained additional variation above and beyond that explained by area, perimeter, and habitat components for most of the species during at least one year (Table 6) with the exception of Common Snipe, Northern Flicker, and Downy Woodpecker. Landscape and coastline components selected in models were highly inconsistent between years (e.g. Common Yellowthroat related to COAST1 in 1997 and LAND5 and COAST2 in 1998; see Table 6), but were highly consistent with regard to the direction of relationships observed for particular principal components. Thus, both community-level and species-level results of models will be summarized by component (see Table 7) in the following text.

LAND1: Complex contexts vs. simple, forested perimeters. When selected in regression models, this component was always positively associated with bird variables. No negative associations with this component were observed. In addition to species richness and total bird abundance (both years) and nesting bird species richness and abundance (1997), the presence/absence of 4 bird species (Great Blue Heron, Virginia Rail, Yellow Warbler, and Red-winged Blackbird) were positively associated to LAND1 during one or both years (Tables 6 & 7). Compared to wet meadows primarily surrounded by forest, these 4 species were more likely to be detected in wet meadows in complex contexts (adjacent to a greater number and diversity of patches).

LAND2: Lake Huron and stream contexts vs. forested wetland contexts. This component was related to four bird variables (Table 7). In 1997, Swamp Sparrow abundance was negatively related to this component. In contrast, nesting bird species richness and abundance of nesting and total birds in 1998 were positively associated with this component.

LAND3: Human-developed contexts. Five bird variables were associated with this variable (Table 7). Total species richness was positively associated with human-developed contexts during both years, and thus with wet meadows which had relatively more adjacent urban landuse, adjacent cattail marsh, and more roads in the surrounding

Table 7. Results of regression modeling summarized by principal component. Models for each of the listed bird variables contained that component as a significant predictor ($P < 0.10$). (+) indicates landscape or coastline characteristics that are positively associated with that component; (-) indicates characteristics that are negatively associated.

Positive Relationships	Negative Relationships
LAND1: Complex Contexts (+) vs. Simple, Forested Contexts (-)	
Total Species Richness 1997 & 1998	None
Total Abundance 1997 & 1998	
Nesting Bird Species Richness 1997	
Nesting Bird Abundance 1997	
Non-nesting Bird Species Richness 1998	
Great Blue Heron 1997	
Virginia Rail 1998	
Yellow Warbler 1998	
Red-winged Blackbird 1997 & 1998	
LAND2: Lake and Stream Contexts (+) vs. Forested Wetland Contexts (-)	
Total Abundance 1998	Swamp Sparrow 1997
Nesting Bird Species Richness 1998	
Nesting Bird Abundance 1998	
LAND3: Human-developed Contexts (+)	
Total Species Richness 1997 & 1998	Great Blue Heron 1998
Nesting Bird Species Richness 1998	
Nesting Bird Abundance 1998	
LAND4: Wetland Contexts (+) vs. Open Water Contexts (-)	
Alder Flycatcher 1998	Song Sparrow 1998
Sedge Wren 1998	
Red-winged Blackbird 1998	

Table 7. Continued.

Positive Relationships	Negative Relationships
LAND5: Forested Contexts (+) vs. Aquatic Contexts (-)	
NONE	Total Species Richness 1998
	Total Abundance 1998
	Nesting Bird Species Richness 1998
	Nesting Bird Abundance 1997 & 1998
	Eastern Kingbird 1997
	Yellow Warbler 1998
	Common Yellowthroat 1998
	Swamp Sparrow 1998
	Song Sparrow 1998
COAST1: Highly Fractal and Complex Coastlines (+)	
Mallard 1997	Total Species Richness 1997
Cedar Waxwing 1998	Nesting Species Richness 1998
	Nesting Bird Abundance 1998
	Great Blue Heron 1997
	Common Yellowthroat 1997
	Swamp Sparrow 1997
	Chipping Sparrow 1997
COAST2: Increasing Total Coastline (+)	
Mallard 1998	Total Bird Abundance 1998
	Nesting Bird Abundance 1997
	American Bittern 1997
	American Goldfinch 1998
	Common Yellowthroat 1998
COAST3: Scale Contrast / Sinuosity (+)	
Sora 1997	Total Species Richness 1998
Eastern Kingbird 1997	Sora 1998
Cedar Waxwing 1997	Alder Flycatcher 1998
	Yellow Warbler 1998

landscape. In 1998, nesting bird species richness and abundance were positively associated with human-developed contexts. In contrast, presence/absence of Great Blue Heron (1998) was negatively associated with human-developed contexts.

LAND4: Wetland contexts vs. open water contexts. Relationships between bird variables and LAND4 were predominantly positive relationships (Table 7). During 1998, Alder Flycatcher, Sedge Wren, and Red-winged Blackbird were all more likely to be detected in wet meadows adjacent to bulrush marsh or other wetland types. In contrast, higher Song Sparrow abundance (1998) was observed in wet meadows bordered by a relatively higher proportion of open water.

LAND5: Terrestrial, forested contexts vs. aquatic contexts). This component was negatively associated with a total of 10 bird variables, and no positive relationships were observed (Table 7). In addition to total species richness and abundance and nesting bird species richness and abundance, this component was negatively related to five species: Common Yellowthroat (1998), Swamp Sparrow (1998), Song Sparrow (1998), Eastern Kingbird (1997) and Yellow Warbler (1998). These species were more abundant or more likely to be detected in wet meadows bordered by higher proportions of aquatic habitats relative to terrestrial habitats.

COAST1: Highly fractal and complex coastlines. Significant relationships between COAST1 and bird variables were predominantly negative (Table 7). In addition to total species richness (1997) and nesting bird species richness and abundance (1998), Common Yellowthroat (1997), Swamp Sparrow (1997), Great Blue Heron (1997) and Chipping Sparrow (1997) were less abundant or less likely to be detected in wet meadows associated with highly fractal or complex coastlines. In contrast, the presence of Mallard

(1997) was positively associated with highly fractal coastline segments (high values of COAST1).

COAST2: Total coastline. Significant relationships between COAST2 and bird variables were also predominantly negative (Table 7). Total bird abundance (1998), nesting bird abundance (1998), Common Yellowthroat abundance (1998) and the probability of detecting American Bittern (1997) and American Goldfinch (1998) were negatively associated with the total amount of coastline within the surrounding landscape. Conversely, the probability of detecting Mallard (1998) positively associated with the total amount of coastline surrounding wet meadows (COAST2).

COAST3: High total coastline and sinuosity at 1-km/2-km scale vs. complex coastlines at 500-m scale. Relationships between COAST3 and bird variables were mixed (Table 7). This component was positively related to the probability of detecting Sora (1997), Eastern Kingbird (1997), and Cedar Waxwing (1997), but was negatively associated with the probability of detecting Sora (1998), Alder Flycatcher (1998) and Yellow Warbler (1998) and total species richness (1998).

DISCUSSION

Effects of Area and Perimeter

Much previous work has focused on the importance of patch area as a predictor for species richness in both wetlands (Brown and Dinsmore 1991) and grasslands (Herkert 1994; Vickery et al. 1994; Helzer and Jelinski 1999). Most recently, Helzer and Jelinski (1999) demonstrated that the perimeter-to-area ratio (PAR) may be a more appropriate predictor of bird species richness and occurrence in wet grasslands than area, but further research is needed to confirm their findings. Because I included both area and PAR in the first stage of regressions, my results can help identify the relative importance of these two related patch features to the conservation of wetland birds in Great Lakes coastal wetlands. Although not the primary focus of this paper, the relevance of this information to conservation planning warrants further discussion.

In contrast to what Helzer and Jelinski (1999) observed, area occurred more frequently in linear and logistic regression models than did PAR, suggesting that area is better predictor (Table 6) for Great Lakes coastal wet meadows. Total species richness, nesting birds, non-nesting birds, and 12 species were positively associated with area: American Bittern, Mallard, Virginia Rail, Sora, Northern Flicker, Eastern Kingbird, Sedge Wren, Cedar Waxwing, Red-winged Blackbird, American Goldfinch, Savannah Sparrow, and Swamp Sparrow. In contrast, perimeter-to-area ratio (PAR) occurred in models for only 4 variables. Species richness in 1997 was negatively associated with PAR indicating that patch shape (amount of edge relative to area) explained a significant amount of variation in species richness above and beyond habitat and area. Swamp Sparrow were negatively associated with PAR during one year, but positively associated with area in the other. PAR was a positive predictor for the abundance of Song Sparrow, a known edge denizen. These results underscore the potential importance of perimeter-to-area ratios for patch selection in some species of wetland and grassland birds. But, they also indicate that teasing apart the separate effects of area and PAR may be difficult and that area may still be the better predictor for many grassland/wetland bird communities. Based on my results, it would be premature to dismiss the importance of area in favor of PAR.

Importance of Landscape Features

Landscape and coastline components significantly increased the variation explained in the large majority of models. Because I used a two-stage regression approach, effects of landscape context and coastline complexity described herein represent true landscape-effects, and not merely effects due to correlations with area, perimeter or other habitat characteristics. Thus, I can confidently assert that landscape context, in the sense of characteristics of the adjacent landscape and surrounding coastline, can explain variation in bird richness and species' distributions in Great Lakes coastal wet meadows that is not explained by area and habitat characteristics.

Overall, landscape variables selected in linear and regression models for a particular bird variable were not consistent from year-to-year. This is a common problem with habitat and landscape studies (e.g. Brown and Dinsmore 1991; Villard et al. 1999). One cause is that birds may select habitats based on a suite of characteristics at a variety of spatial scales (Pearson 1993; Freemark et al. 1995; Weller 1999) either in concert or in a temporal and/or spatial hierarchy (*sensu* Saab 1995). This problem is exacerbated in Great Lakes coastal habitats because patch-level characteristics (e.g. water depth or duration of flooding) can and often do fluctuate widely from year-to-year (Bedford 1992). In such dynamic systems, birds may use different landscape cues in one year compared to the next based on changes in underlying habitat conditions at the patch scale. Another factor contributing to these inconsistencies are characteristics of the statistical methods themselves. Stepwise regression techniques only recover the combinations of independent variables that best explain the variance in bird variables. As with most other multivariate techniques (e.g. ordination, discriminant analysis, etc.), there is no assurance that these variables have direct causal relationships to bird variables. In situations where the organism of interest is likely to use multiple characteristics as selection criteria, one variable (e.g. grass density) may be selected by regression techniques in one year; and another variable (e.g. adjacent forest) may be selected the next year. But in reality, the bird may be using a combination of the two factors measured by researchers during both years. In light of low annual consistency in regression models, species-specific associations with landscape and coastline components should be used to generate hypotheses only and, although they may possibly represent causal relationships, it would be unwarranted to construe them as such.

However, more robust conclusions about the general effects of landscape context on birds are possible. The relationships between landscape and coastline components and bird variables were consistent such that sign (direction) and magnitude of the regression coefficients were remarkably similar across different bird variables (see Table 6). For example, in every instance where complex contexts (LAND1) was selected as an explanatory variable, it was positively associated with that bird variable, and no negative associations were observed (Table 7). Additionally, bird/component relationships were usually readily explained by existing knowledge and/or theories of landscape ecology. These properties of the responses I observed lend credence to my conclusions and indicate that these relationships are not spurious results of the modeling process. Rather they likely represent at least generalizable, predictive relationships, and potentially causal mechanisms for some species. Following, I highlight four general patterns of bird response to landscape context which were consistent across bird variables.

Complex contexts. My first hypothesis was that the species richness of a patch should increase with the number of adjacent patches and patch types (Forman 1995). Increased species richness of wet meadow birds was positively associated with a principal component (LAND1) representing a gradient of increasing number of adjacent patches and patch types, or diverse landscape contexts (Table 6), and this association occurred in both years. One could posit that larger patches tend to have more adjacent patches and patch types simply because they are larger or have more perimeter, and that the effects of complex contexts are in reality effects of area and/or perimeter. However, this is highly unlikely because the two-stage regressions removed effects of both area and perimeter in the first stage.

Forman (1995) first predicted this relationship, and suggested that different adjacent patch types each have unique species pools from which they contribute colonizers to the species richness pool of the patch in question. Although my results are consistent with this mechanism, I also observed significant relationships between the number of adjacent patches and the abundance and occurrence of several species (Table 7). Thus this colonization mechanism, while a likely possibility, is not by itself sufficient to account for the patterns observed in Great Lakes coastal wetlands. A second alternative mechanism is that a greater number of adjacent patches provide a more diverse, more stable or more abundant suite of food resources for birds located immediately adjacent to breeding habitat. Many wetland bird species depend on adjacent habitats for foraging (e.g. Red-winged Blackbirds [Orians 1980]; see also Szaro and Jackle 1984), and a diversity of resources (i.e. diversity of adjacent patch types) would also stabilize available food resources in highly variable systems (Skagen and Knopf 1994) like Great Lakes coastal wetlands. This would increase the intrinsic habitat quality of wet meadows located in complex contexts, allow smaller territories (Anderson and Titman 1992) and, hence, greater abundance of birds within the same patch (Gill 1995).

Human-developed Contexts. In contrast to my original hypothesis that species richness would decrease in increasingly developed contexts, total species richness during both years and nesting birds in 1998 were higher in human-development contexts (Table 7). A possible reason is that even the most urbanized wet meadows in the region are only developed to an intermediate degree. Thus, they may not be degraded enough to exclude wet meadow breeders (such as American Bittern), but the developed context may attract additional species (e.g. American Robin *sensu* Blair 1996) such that species richness is highest at moderate levels of impact. Low to moderate levels of human impacts can also repel potential predators (*sensu* Bowers and Breland 1996), such as the Great Blue Heron (see next paragraph) which could, in turn, make those wet meadows more attractive to breeding birds. More research is necessary to determine if such patterns consistently occur in moderately-developed landscape contexts.

The probability of detecting Great Blue Heron was lower in wet meadows located in more developed contexts, but this was the only species or bird variable that was negatively related to developed contexts. Great Blue Herons nest in forest habitats that are disjunct from the wet meadows I studied, but did use wet meadows regularly for foraging (S. K. Riffell, personal observations). Hence, human-developed contexts may exclude herons or other wading birds from valuable foraging territories, but this too, warrants further investigation.

Because negative effects of human-developed contexts were largely absent in these wet meadows, urban impacts do not appear to be a primary factor in determining habitat use in this region. However, I warn that potentially negative effects of urbanization should not be ignored. Negative responses by birds to development-related impacts have been well-documented in other regions and habitats (Freisen et al. 1995; Blair 1996; Bolger et al. 1997), and the lack of a relationship I observed could reflect the generally low levels of development in the northern Lake Huron region. Also, I did not measure breeding success, so it is not known whether human-developed contexts impact breeding success in these wet meadows. Impacts on breeding success would not necessarily be apparent in richness or presence/absence data because the abundance of relatively unimpacted wet meadow habitat (source habitat) in the region could be supplying many surplus breeders. These surplus breeders would be relegated to patches in developed contexts and maintain high abundance in these impacted sites (sink habitats) despite the lower breeding success therein (Pulliam 1988).

Wetland contexts. Although I did not theorize *a priori* that wetland contexts (connected, adjacent wetlands) would be an important predictor of bird distributions in Great Lakes coastal wetlands, the combined responses to landscape components 2, 4, and 5 suggest that wetland connectivity may indeed be very important for birds. Three species, Alder Flycatcher, Sedge Wren, and Red-winged Blackbird, were associated with wetland contexts compared to open water contexts (LAND4; Table 7). Similarly, 14 bird variables (5 species) were associated with aquatic contexts compared to terrestrial, forested contexts (LAND5; Table 7).

Wetland and/or aquatic contexts may confer advantages to birds breeding in wet meadows in two major ways. First, adjacent wetlands may improve the foraging resources available to birds. Red-winged Blackbirds are known to use adjacent habitat, rather than the breeding patch, for foraging (Orians 1980) and likely other species do as well (Szaro and Jackle 1984). Adjacent wetlands and aquatic habitats may be a more productive source of plants, insects and other invertebrates that are important food resources for breeding birds compared to terrestrial forests (Verner and Willson 1966; Tilton and Schwegler 1978; Mitsch and Gosselink 1993) or open water habitats (Tilton and Schwegler 1978; Gathman et al. 1998). Emergence of invertebrates is often synchronized such that each species emerges *en masse* over a short time-period (few days to a few weeks: Orians 1980), and a particular species would only be available to breeding birds for a short time. Wetland contexts with a large variety of adjacent wetland types would contain more invertebrate species and, hence, a more constant supply of emerging invertebrates. Also, invertebrate abundance within wet meadow patches may decrease over the course of the summer because of decreasing oxygen concentrations and decreasing water levels (Kaldec and Smith 1992), so an adjacent wetland which remains inundated (like bulrush marsh) would provide needed resources in mid- to late-summer that open water would not. Wet meadows bordered by open water may also be less protected from lake winds, storm-related fluctuations in water level, and temperature fluctuations (Herdendorf 1992). For these reasons, wet meadows connected to other types of wetlands (in a wetland context) may provide higher quality habitat for birds. Similarly, three bird variables were positively related to contexts with a relatively higher proportion of Lake Huron and higher stream densities (LAND2). These types of aquatic habitats likely serve many of the same functions just discussed.

Second, wetland and aquatic contexts may provide protection from predators. Predator densities and predation rates are typically higher in upland habitats compared to wetland habitats (Picman 1988). Thus, adjacent forest and upland habitats may serve as a source of terrestrial predators (e.g. squirrels or raccoons) that could access the wet meadow via the shared boundary. Also, the physical structure of adjacent trees may provide perches for visual-searching predators (e.g. corvids; Bergin et al. 1997) and/or brood parasites (e.g. Brown-headed Cowbirds; Hauber and Russo 2000) permitting them to scan deep into the interior of the wet meadow and enhancing their ability to detect nests. In contrast, inundated wetlands or open water do not provide either form of access for these predators and can restrict access merely by the presence of standing water (Jobin and Picman 1997). Any or all of these mechanisms could decrease predation rates within a wet meadow and enhance its attractiveness to breeding birds.

Of the species related to wetland contexts (LAND4 or LAND5), not all were true wetland obligates (e.g. Sedge Wren), but many were facultative species (e.g. Song Sparrow, Eastern Kingbird) which can and often do breed very successfully in entirely terrestrial habitats. This underscores the importance of wetland contexts and wetland connectivity (Taylor et al. 1993; Haig et al. 1998) to breeding birds in general including facultative and even non-wetland birds. Whether or not these birds have higher breeding success in wetlands than in their more commonly occupied terrestrial habitats is not currently known, and future studies that tested this question would yield valuable information.

Significant relationships to wetland contexts were observed almost exclusively during 1998 (Table 7). Overall lake levels were approximately 30 cm lower in 1998 than in 1997 (NOAA, unpublished data). Consequently, many of the wet meadows that had been inundated during the breeding season in 1997 were merely saturated or entirely dry during much of 1998 (Table 2). Because lower water levels may lead to less invertebrate production from within the wet meadow, one would expect birds to seek out wet meadows located in a wetland context where additional invertebrate resources were available from the adjacent landscape, and relationships observed in 1997 and 1998 are consistent with this expectation. In landscapes with high inter-annual variability in habitat quality like Great Lakes coastal wetlands, birds may change habitat selection criteria according to underlying habitat conditions. Preserving complexes of connected wetland types is critical to providing the resources necessary for bird communities over the entire range of annual conditions that are likely to occur in such systems.

Effects of Coastline Complexity. My third hypothesis was that coastline complexity (i.e. coastlines that were more fractal or more sinuous) would be positively associated with species richness and other bird variables. Although a few bird variables were positively related to coastline components, relationships with coastline components were predominantly negative (Table 7), exactly opposite of what I hypothesized. These results are surprising because landscape theory predicts that highly complex landscapes should be more stable (Forman 1995) and hence, have higher biodiversity in patches. Also, complex coastlines are correlated with greater wetland resources (Nilsson 1978; Kent and Wong 1982) are important for many wetland birds (Weller 1999).

One possible explanation for why birds were associated with less complex coastlines is that, for the northern Lake Huron coastline, fractal dimension (i.e. COAST1) was negatively related to the amount of coastal wetlands in the surrounding landscape (Figure 2), and thus, to wetland contexts. This contrasts the positive relationship between coastline fractal dimension and wetland area predicted by others (Kent and Wong 1982). Wetland contexts are important for many species (see discussion earlier), so the negative responses to COAST1 may reflect this relationship.

Information about migratory forest songbirds in terrestrial landscapes may provide a second explanation for why many wet meadow birds were negatively related to complex coastlines. As a group, migratory songbirds are highly-sensitive to habitat fragmentation (see Faaborg et al. 1995), and Flather and Sauer (1996) observed that migratory songbirds were less abundant in forested landscapes with high complexity or high fractal dimension. Complex landscapes also had, on average, smaller patch sizes. In this study, COAST2 (total coastline length) was similarly inversely correlated to mean patch size (Figure 3) in the surrounding landscape, and the majority of the species with negative relationships to coastline components were migratory songbirds (Table 7). Thus, patches in these landscapes may be avoided by birds because they are in a landscape context which they perceive as very fragmented (*sensu* Flather and Sauer 1996).

These two mechanisms could account for the negative relationships between birds and coastline components I observed, but some species were positively related to coastline complexity. Interpretation is further complicated because responses to COAST3 (a contrast of scale) were mixed indicating that responses may be scale-specific, and the critical scale may vary from species to species. More research is needed about how

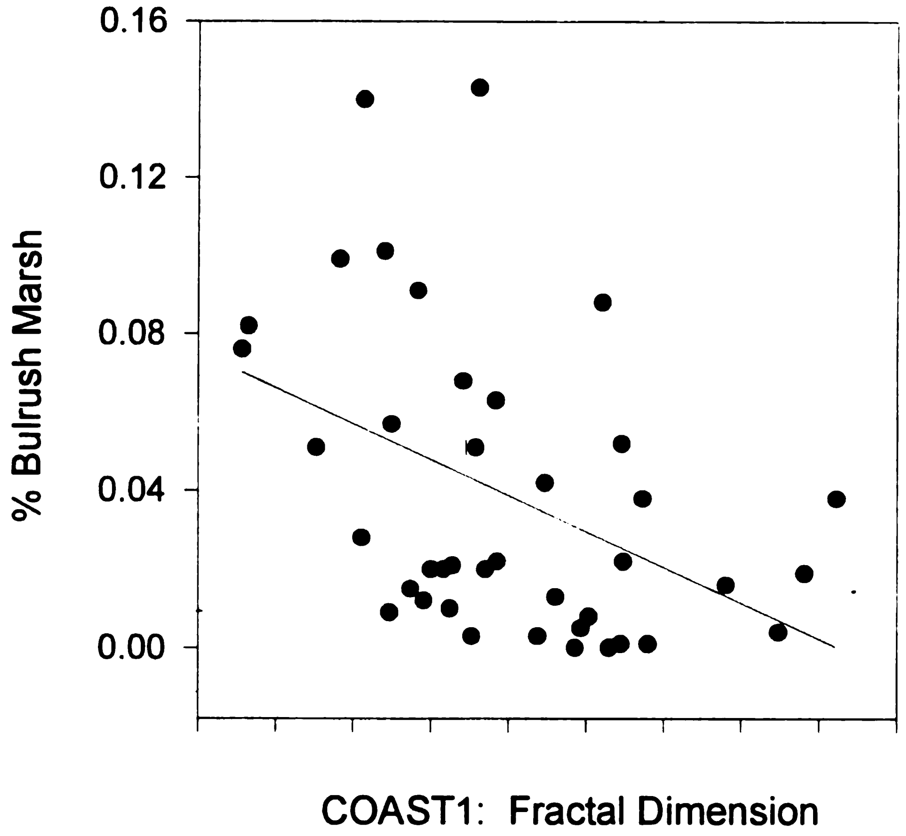

Figure 2. Relationship between the the fractal dimension of the coastline (COAST1) and the percent of the surrounding landscape (1-km from perimeter of the wet meadow) comprised of bulrush marsh.

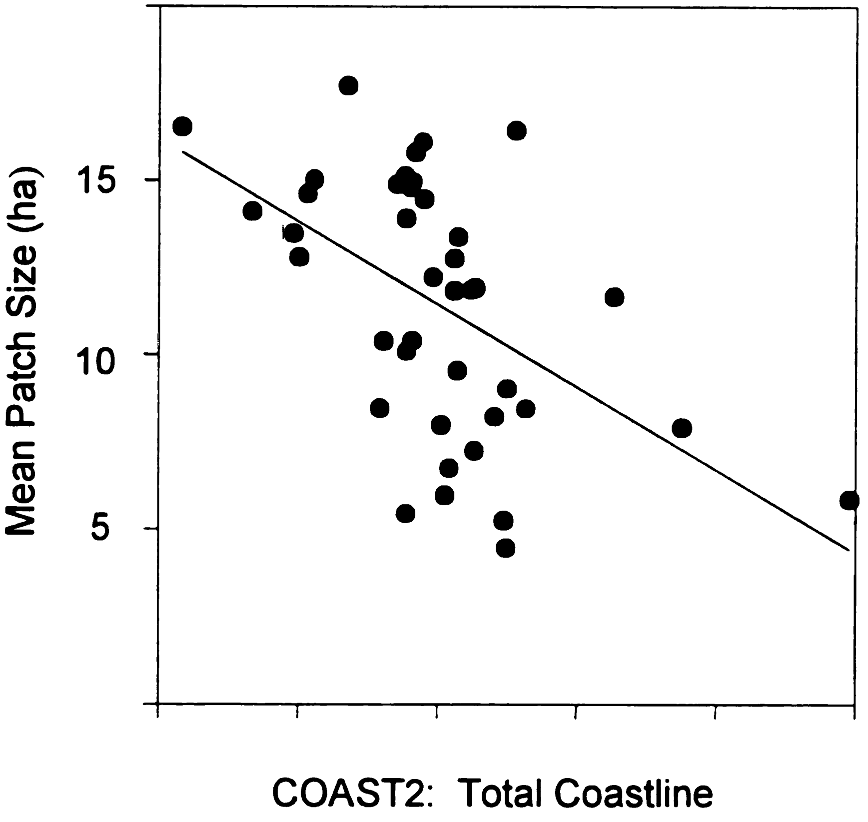

Figure 3. Relationship between the the total coastline length (COAST2) and the mean patch size (ha) in the surrounding landscape (1-km from perimeter of the wet meadow).

coastline complexity and fractal dimension of landscapes affect bird distributions. Understanding these landscape characteristics will be difficult because responses to coastline characteristics may be year- and/or scale-specific and complicated by the effects of different life-history traits (Hanson and Urban 1992) on avian response.

IMPLICATIONS FOR CONSERVATION AND RESEARCH

These results have implications for conserving birds in Great Lakes coastal wet meadows, but they apply to other regions and habitats as well. Because Great Lakes coastal wet meadows are emergent wetlands dominated by grasses and sedges, they possess habitat features and bird species that are characteristic of both wetlands and grasslands. Thus, my recommendations apply more broadly to the general management and conservation of avian communities in both wetland and grassland habitats.

Habitat, landscape, and coastline components selected by regression models were generally not consistent between years, and this illustrates the importance of long-term, multi-year studies (Wiens 1981). This problem is further compounded in dynamic systems like Great Lakes coastal wetlands because birds may alter habitat selection criteria as overall habitat conditions change from year to year. Thus, only long-term, multi-year research projects can identify the entire complement of habitat types and landscape structures needed to conserve wetland bird communities over time in dynamic landscapes. Unfortunately, such long-term studies do not exist, and management of wetland birds must be guided by results from short-term studies such as mine until longer-running studies have been completed. Fortunately, the direction of responses were remarkable consistent across species despite inter-annual inconsistencies within species, for most landscape components. This strengthens the conclusions that can be drawn about the effects of landscape structure on wet meadow birds in general, and, in the absence of long-term studies, some preliminary management guidelines can be drawn.

First, area and perimeter were important predictors of both species richness and the occurrence of many bird species (Table 5). The importance of patch size has been well-documented in wetlands (Brown and Dinsmore 1986; Weller 1999) as well as in other habitats (e.g. grasslands [Herkert 1994; Vickery et al. 1994] and forests [e.g. Blake and Karr 1987]). Similarly, patches with low perimeter-to-area ratio contain less edge- and more interior-habitats (Helzer and Jelinski 1999). Management plans should continue to focus on preserving large habitat patches with relatively little perimeter, although the importance of small wetlands should not be ignored (Gibbs 1993; Semlitsch and Bodie 1998; Schwartz 1999).

Plans for the conservation of wetland birds should go further, however, and consider the landscape context of patches. Wet meadows adjacent to a large number of patches and/or patch types should be given priority over wet meadows in simple landscape contexts because patches in complex contexts consistently had higher species richness and were more likely to contain several species. My results also demonstrated that wet meadows connected to other types of wetlands (i.e. in a wetland context) were consistently associated with the presence or absence of not only obligate wetland/grassland species, but also certain facultative wetland species. This relationship was markedly more important in 1998 when water levels were low. Wetland conservation schemes should strive to protect entire wetland complexes and preserve connections among wetland types rather than focusing on portions of wetlands or individual wetland types.

Considering landscape context could greatly enhance the effectiveness of conservation efforts. For example, even small wet meadow patches could be valuable if located in complex, wetland contexts which would then provide a stable set of resources in low-water years. Similar relationships may operate in many other landscapes, and these recommendations could likely be implemented in conservation efforts with a high probability of success. However, further research about the effects of landscape context is needed to fully understand these processes and insure the success of conservation efforts. Without detailed information about the effects of landscape context on within-patch diversity and process, conservation funds and efforts will not be fully effective, predictions of landscape change will not be accurate, and critical ecosystem functions could be compromised.

CHAPTER TWO

LANDSCAPE CONTEXT AND COASTLINE COMPLEXITY: EFFECTS ON SPECIES TURNOVER RATES

INTRODUCTION

Species turnover is the change in species composition of a patch or community due to extinction, immigration, or both (Diamond and May 1977). Each individual extinction (loss of a species) or immigration (addition of a new species) represents one turnover event, and the sum of these events over a unit of time as a percentage of the total species pool is the turnover rate. MacArthur and Wilson (1967) focused attention on the importance of turnover to maintenance of species richness within island communities. According to their theories of island biogeography, turnover rates on islands decrease with increasing island area and increasing isolation (distance to the mainland or nearest island), and these turnover processes interact to produce a predictable, equilibrium number of species for each island.

Since that time, avian biologists have used island biogeography as a tool for explaining patterns of avian species richness and as a framework for understanding the effects of fragmentation in terrestrial habitat patches (see Faaborg et al. 1995 for review). But surprisingly, little attention has been paid to patch-level turnover rates in avian communities despite the importance of turnover to the success of conservation efforts (see Rice et al. 1983; Gutzwiller and Anderson 1987b). Habitats with lower turnover rates contain relatively more stable communities where individual species are less likely to go extinct, and hence are more effective choices for habitat preservation. Also, managers must be able to predict how rapidly communities can be expected to change, and must also be able to predict the nature of these changes (Russell et al. 1995). Without an understanding of what drives turnover within avian communities, such predictions are not possible.

Studying avian turnover in most non-oceanic habitat islands is problematic because they are not true islands, and the relatively straight-forward theories of island biogeography often do not sufficiently explain observed patterns (e.g. Gutzwiller and Anderson 1987b). Although area and isolation may influence turnover in avian communities, both internal features of the habitat (Gutzwiller and Anderson 1987b) and changes in habitat features over time (e.g. Weller 1994; Patten and Rotenberry 1998) can influence patch-level turnover of species. Human-induced factors can also alter these processes, not only by affecting habitat features, but also by promoting invasion of new predators (Savidge 1987), influencing survival in migratory and wintering habitats (e.g. Conway et al. 1995), or otherwise disrupting extinction and colonization processes.

The landscape context of a patch refers to the characteristics of the adjacent habitats and surrounding landscape, and it is unknown how context affects turnover rates within patches. Some processes critical to avian biology such as edge-related nest predation can be influenced by the characteristics of the adjacent patches (Andren 1995; Bayne and Hobson 1997). Also, recent studies have described effects of landscape context on species richness and species-occupancy of patches for riparian forest patches in the western United States (Gutzwiller and Anderson 1987a; Saab 1999), forest fragments in a Canadian agricultural landscape (Freisen et al 1995), and Chilean forest remnants (Estandes and Temple 1999). These patterns in species richness could be caused by effects of landscape context altering patch-level turnover rates (colonization and/or extinction), but such research has not been conducted.

It is not difficult to theorize how landscape context could influence turnover in avian communities. If the surrounding habitat is inhospitable, it could effectively isolate patches which are not geographically distant (Wiens 1996). Certain contexts may increase predation or mortality (Andren 1995; Bayne and Hobson 1997), provide fewer foraging resources, or otherwise render a patch less-suitable as habitat. Breeding individuals may be less likely to return to patches in unfavorable contexts the following year. This would raise turnover rates in unfavorable contexts. Alternatively, breeding individuals may be more likely to return to patches in favorable contexts because their breeding success would be enhanced (Blancher and Robertson 1985; Bensch and Hasselquist 1991). This would lower turnover rates in favorable contexts.

I tested whether or not landscape context influenced avian turnover rates in 40 Great Lakes coastal wet meadows over a 2-yr time-interval. Turnover rates were first adjusted for area and within-patch habitat characteristics, and then I tested for additional effects of landscape context. These analyses were designed to answer three major questions: (1) Does landscape context affect avian turnover rates in wet meadows? (2) Does the complexity of the associated coastline affect avian turnover rates? and (3) Does island biogeography predict avian turnover rates?

These wetlands are associated with the northern shoreline of Lake Huron and are some of the most undisturbed remaining wetlands in the Great Lakes regions. They are critical habitat for migratory and breeding birds (Prince and Flegel 1995), and some of these species are declining locally and/or regionally (Brewer et al. 1991). These wet meadows are currently threatened by commercial and residential development, so understanding the processes that drive turnover rates in these wet meadows is critical. Unfortunately, information about turnover in wetland bird communities is lacking. Without this understanding, it will be impossible to predict how the bird communities of the region can be expected to change. As a result, the success of management and conservation efforts will be hindered.

METHODS

Study Area

Data from 40 wet meadows (sedge- and grass-dominated wetlands) associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties were used for these analyses. Sites were selected based on specific vegetational and geographical criteria. These criteria and a detailed description of the vegetation are listed in *Chapter One, Methods, Study Area.*

Bird Censuses

The presence or absence of each bird species was determined each year using line-transect censuses in each wet meadow. All birds seen or heard within the perimeter of the wet meadow patch were recorded. Each transect was censused 4 times in 1997 and 5 times in 1998. Only the first 4 visits of 1998 (corresponding temporally to the 4 visits in 1997) were included in these analyses. A detailed description of censusing protocol is listed in *Chapter One: Methods, Bird Censuses.*

Habitat Characteristics

Because within-patch habitat characteristics (e.g. Gutzwiller and Anderson 1987b) could influence patch-level turnover in bird communities, I measured 20 habitat characteristics along each census transect in both 1997 and 1998. Details of the habitat sampling methods, as well as habitat variable definitions, are listed in *Chapter One: Methods, Habitat Characteristics.*

Calculation of Landscape Variables

Landscape context variables included the number of adjacent patches, the number of adjacent patch types, and the proportion of the wet meadow perimeter bordered by each patch type. The classification system used for delineating patches is listed in Table 1. Landscape context variables also included the density of roads and streams in the surrounding landscape. Coastline complexity measures were calculated for three coastline segments associated with each wet meadow: 500-m, 1-km, and 2-km from the perimeter of each wet meadow. Total coastline, sinuosity, and fractal dimension were calculated for each coastline segment using ArcView software and a Fortran program, Fract_Line (Lam and De Cola 1993). Detailed description of how these variables were measured is listed in *Chapter One: Methods, Calculation of Landscape Variables*.

Statistical Methods

Habitat Variables. Great Lakes coastal wetlands are influenced by overall lake water levels which can fluctuate greatly from one year to the next (Bedford 1992). Thus, there is the potential that mean water depth and, consequently, other within-patch habitat characteristics changed from 1997 to 1998. I tested to see if such changes occurred using two-tailed, paired-*t* tests on each of the 20 habitat characteristics (Ott 1988). The null hypothesis was that the mean of a particular habitat characteristic was not different in 1998 compared to 1997. The alternative hypothesis was that it did change. When the assumptions of the parametric *t*-test were not clearly satisfied, I used the Wilcoxon signed-rank test instead (Ott 1988). I used $\alpha = 0.10$ for all tests involving habitat characteristics.

Because species turnover could have been affected by changes in habitat characteristics (Patten and Rotenberry 1998), unchanging (or average) habitat characteristics (Gutzwiller and Anderson 1987b), or some combination of both, I conducted a principal components analysis (PCA) separately on two different sets of variables. First, I identified the set of habitat characteristics that changed significantly and calculated the difference in the mean of that characteristic in 1998 and the mean of that characteristic in 1997 (see Table 8). Then I conducted a PCA on this set of variables. Components derived from this PCA will be referred to hereafter as habitat change components. Second, I took the mean value for all 20 habitat characteristics over the two year period and conducted a second PCA on this set. Components derived from this PCA will be hereafter referred to as mean habitat components. Within each set, components with an eigenvalue > 1.0 were retained.

Landscape and Coastline Variables. Because landscape context and coastline complexity variables were intercorrelated, I used principal components analysis to remove the correlations and reduce the number of variables. I conducted two separate PCA's, one each on the landscape context variables and the coastline complexity variables. These analyses are described in detail in *Chapter One, Methods, Statistical Analysis.* The same, identical landscape and coastline components are used in the present analysis.

Calculation of Turnover Rates. I calculated turnover rate following the formula of Diamond and May (1977):

$$\text{turnover rate}_{97\text{ to }98} = (\#\text{ extinctions}_{98} + \#\text{ immigrations}_{98}) / \text{total }\#\text{ of species}_{97+98}$$

Table 8. Summary statistics for mean habitat variables and habitat change variables for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

	Mean		Change			
Habitat Variable	$\bar{X}$	Range	$\bar{X}$	Range	Test statistic*	P
Water depth	14.02	0.00-33.72	-16.15	-31.97-4.91	$t = 10.21$	< 0.001
Hummock height	23.68	4.14-39.02	-0.34	-27.73-26.75	$t = -0.21$	0.837
Grass height	107.43	59.05-153.18	4.08	-11.33-27.66	$t = 2.72$	0.010
Grass density	5.67	0.46-12.58	0.28	-3.20-2.30	$T_- = 250$	0.051
Woody vegetation density	0.28	0.00-0.99	0.00	-0.37-0.34	$t = 0.20$	0.839
Total vegetation density	6.15	0.50-12.83	0.30	-3.39-2.39	$T_- = 257$	0.040
Shrub foliage diversity	4.66	0.00-9.50	-0.18	-5.00-5.00	$t = -0.47$	0.638
Frequency of cover types						
Graminoid	97.03	84.95-100.00	1.41	-4.50-15.20	$T_- = 71$	0.024
Cattail	7.09	0.00-74.40	-0.67	-15.20-12.20	$T_+ = 85$	0.289
Bulrush	19.41	0.00-90.70	-0.60	-21.80-12.40	$t = -0.61$	0.543
Floating vegetation	6.57	0.00-53.10	-7.38	-35.70-2.60	$T_+ = 13$	< 0.001
Submersed vegetation	29.11	2.55-51.20	-46.36	-98.70-35.70	$t = -8.51$	< 0.001
Willow	8.91	0.00-31.60	0.97	-11.90-13.90	$t = 1.12$	0.269
Alder	6.48	0.00-32.85	0.46	-13.20-15.40	$t = 0.55$	0.586
Open water	4.11	0.00-17.15	0.28	-12.40-11.80	$t = 0.35$	0.727
Moss	7.51	0.00-31.35	1.08	-17.60-29.40	$t = 0.72$	0.471
Frequency of trees and snags						
Coniferous trees	3.87	0.00-36.40	--**	--	--	--
Deciduous trees	1.91	0.00-9.60	--	--	--	--
Coniferous snags	1.56	0.00-8.30	--	--	--	--
Deciduous snags	1.09	0.00-17.00	--	--	--	--

* Test statistic is either student's *t* or Wilcoxon T.

**Not sampled in 1998 because distributions of trees and snags did not change over that time-interval.

where # extinctions = the number of species detected in a patch in 1997 that were not detected in that patch in 1998; # of immigrations = the number of species detected in 1998 that were not detected in 1997; and total # of species = the total number of different species detected in a patch over both years (or # species detected in 1997 + # immigrations).

A species was considered present in a patch if it was detected within the perimeter of the wet meadow patch during at least one of the four census visits during a year. I used unlimited-distance records rather than fixed-width records (birds detected within the 100-m wide transect) because this would have overestimated true patch turnover. For example, a species recorded within the transect in 1997 could move its territory the next year such that it was located just outside the 100-m wide transect. Although that species persisted in the patch, it would have been erroneously recorded as an extinction if only fixed-width data had been used. Using data collected within the patch perimeter but over an unlimited transect width avoids this problem.

Because the factors that influence the turnover of species which nest in the wet meadows might differ from the factors that influence the turnover of accidental species or species which use the wet meadows primarily for foraging (e.g. Great Blue Heron), I calculated 3 different turnover rates. Total species turnover rate was calculated based on all species detected in the wet meadow regardless of nesting requirements. Nesting species turnover was calculated using only that subset of species that can potentially breed in wet meadows (Appendix A). Because habitat features of coastal wet meadows are characteristic of both wetlands and grasslands, nesting species include obligate and facultative grassland species (Vickery et al. 1999) in addition to obligate and facultative wetland birds (based on information in Terres 1980). Non-nesting species turnover was calculated using only occurrences of those species not included in the nesting guild (Appendix A).

Regression modeling. Because I wanted to test for effects of landscape context and coastline complexity on avian turnover rate above and beyond that which could be explained by area and habitat effects, I adopted a two-stage regression approach (Morrison et al. 1998) similar to that used in Chapter One. In the first stage, I regressed turnover rate against area, perimeter-area ratio (PAR), habitat change components and mean habitat components. The residuals from this model were then regressed against landscape and coastline components. Landscape and coastline components significantly influenced turnover rates if a component explained a significant portion of the variation in these residuals (*t*-statistic with $P < 0.10$).

At each stage, I used a stepwise selection procedure. Rather than let the stepwise algorithm select the variables unsupervised, I set the F-to-stay value at $P < 0.15$ to select a *suite* of variables. I then evaluated models involving all possible subsets of this suite of variables to find the best model (Draper and Smith 1981). The best model (1) met the assumptions of regression (constant variance, normal residuals, etc.); (2) had the lowest sum of prediction residuals (a form of validation [Myers 1987]); and (3) all explanatory variables had *t*-ratios significant at $P < 0.10$. Transformations were conducted if and only when necessary to satisfy the assumptions of regression (Rahbek 1997).

RESULTS

Habitat Characteristics

Although wet meadows included in this study were selected because they shared similar vegetation structure and composition, there was still considerable variation among sites (see Tables 2 and 8). Five mean habitat components were retained from principal component analysis, and these five components accounted for 75% of the total variation in the original mean values (Appendix F).

Several habitat characteristics did change significantly from 1997 to 1998 (Table 8). Mean water levels were significantly lower in 1998 relative to 1997 ($P < 0.001$), and consequently so were the percent cover of submerged ($P < 0.001$) and floating ($P < 0.001$) vegetation (Table 8). Conversely, mean grass cover ($P < 0.024$), mean grass height ($P = 0.010$), mean grass density ($P = 0.051$) and total vegetation density ($P = 0.040$) increased in 1998 (Table 8). Two habitat change components were retained from principal component analysis on these 7 variables, and they accounted for 56% of the total variation in the original habitat change variables (Appendix G).

Each mean habitat component and habitat change component was influenced primarily by a set of correlated and often biologically- or structurally-related variables, so I interpreted each component (Table 9).

Landscape Context Components

The context of wet meadows within the surrounding landscape varied from very simple contexts (patches bordered entirely by a single habitat type) to complex contexts (patches bordered by a diversity of habitat types: see Table 4). Principal component analysis identified 5 components which accounted for 78% of the total variation

Table 9. Mean habitat components and habitat change components derived from original variables which were retained for analysis.

Principal Component	Interpretation
	Mean Habitat Components
PC1	Increasing hummock height, grass height, grass density, and vegetation density
	Decreasing bulrush frequency
PC2	Increasing frequency of trees, snags, and alder and woody vegetation density
	Decreasing water depth and bulrush frequency
PC3	Increasing woody vegetation density, shrub foliage diversity, and frequency of willow
PC4	Increasing frequency of open water, deciduous trees and snags
	Decreasing frequency of graminoid vegetation
PC5	Increasing frequency of coniferous trees, moss, open water and floating vegetation
	Decreasing frequency of willow
	Habitat Change Components
CHANGE1	+: Increased grass height, grass density , little or no decrease in water depth
	-: Increased frequency of submersed vegetation, decreased water depth
CHANGE2	+: Increased grass height and frequency of floating vegetation; little or no change in water depth
	-: Increased frequency of graminoid vegetation, decreased (or little change) in grass density, decreased water depth

(Appendix D). Similarly, coastline complexity varied from very simple coastline segments to very sinuous, highly fractal segments (Table 4). PCA identified 3 coastline components which accounted for 77% of the total variation in coastline characteristics (Appendix E). Interpretations and names for landscape and coastline components are listed in Table 5.

Changes in Species Richness

I estimated species richness using over 3000 individual detections at 40 sites during 320 census visits. Total species richness declined significantly from a mean of 9.08 species/patch (range: 1-22) in 1997 to 8.25 species/patch (range: 1 to 18) in 1998 (paired-*t* = -2.05, df = 39, P = 0.048). Nesting species richness declined significantly from a mean of 7.30 species/patch (range: 1 to 18) in 1997 to 6.75 species/patch (range: 1 to 16) in 1998 (paired-*t* = -1.84, df = 39, P = 0.074). Species richness of non-nesters also declined from a mean of 1.78 species/patch (range: 1 to 7) to 1.50 species/patch (range: 1-5) species/patch, but this decline was not significant (paired-*t* = -1.10, df = 39, P = 0.279).

Turnover Rate

Total species turnover rate. All 40 sites experienced at least one turnover event (extinction or immigration) between 1997 and 1998 (Table 10), and mean turnover in the wet meadows averaged 0.56 turnover events/species (range: 0.19 - 0.86). The first stage of the regression procedure indicated that turnover rate was negatively associated with log(area) and mean habitat component 3 (MHAB3: greater density of woody vegetation, greater shrub foliage diversity, and coverage of willow). Total turnover was positively associated with mean habitat component 4 (MHAB4: more open water, deciduous trees

Table 10. Extinctions, immigrations, and turnover rate for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

Wet Meadow	Extinctions	Immigrations	Total Species	Turnover Rate
1	1	2	16	0.188
2	5	3	18	0.444
3	5	3	13	0.615
4	2	2	5	0.800
5	7	2	24	0.375
6	1	4	8	0.625
7	0	2	3	0.667
8	4	3	10	0.700
9	2	2	10	0.400
10	2	2	13	0.308
11	4	2	7	0.857
12	5	3	14	0.571
13	3	0	6	0.500
14	3	0	7	0.429
15	3	2	13	0.385
16	6	2	17	0.471
17	2	2	6	0.667
18	5	6	22	0.500
19	1	1	3	0.667
20	3	2	9	0.556
21	4	0	7	0.571
22	6	2	20	0.400
23	6	3	11	0.818
24	1	4	14	0.357
25	2	2	6	0.667
26	7	5	19	0.632
27	2	3	9	0.556
28	9	2	21	0.524
29	5	4	15	0.600
30	1	3	13	0.308
31	6	4	12	0.833
32	5	0	6	0.833
33	4	2	9	0.667
34	3	6	11	0.818
35	8	2	12	0.833
36	2	2	13	0.308
37	2	4	14	0.429
38	1	1	3	0.667
39	0	2	7	0.286
40	5	2	11	0.636

and snags, less coverage of graminoid vegetation). Area and habitat components explained 36% of the variability in turnover rate (Table 11).

Landscape components described an additional 14% of the variation in total species turnover rate (Table 11). Turnover rate was negatively associated with LAND1 and positively associated with LAND5. Total species turnover rate was lower in complex contexts (patches adjacent to a large number of patches and patch types), and turnover rate was lower in wetland contexts (patches with perimeters adjacent to proportionately more open water and wetland habitats) compared to terrestrial forest contexts. Coastline components were not related to total species turnover rate.

Nesting species turnover rate. Nesting species turnover was not related to area. Similar to total species turnover rate however, nesting species turnover was negatively associated with MHAB3 and positively associated with MHAB4 (Table 11). Nesting species turnover was also positively related to LAND5. Thus, turnover rates of nesting species were lower in wetland contexts (bordered by a relatively higher proportion of open water and/or wetland habitats) compared to terrestrial, forested contexts.

Non-nesting species turnover rate. Turnover rate of non-nesting species was negatively related to area (r^2 =- 0.10; Table 11). Mean habitat components, habitat change components, landscape components and coastline components did not explain significant amounts of remaining variation in non-nesting species turnover rates.

DISCUSSION

Average Habitat Conditions vs. Changes in Habitat Conditions

Great Lakes coastal wetlands are dynamic habitats in that water levels fluctuate from year-to-year (Bedford 1992), and vegetation characteristics can change in response

Table 11. Results of logistic regression on bird species turnover rates in wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998. For all regressions, n = 40.

Turnover Rate	Habitat Variables	r^2	Landscape Components	r^2
All Species	Area (-) HPC3 (-) HPC4 (+)	0.36	LAND1 (-) LAND5 (+)	0.50
Nesting Species	HPC3 (-) HPC4 (+)	0.21	LAND5 (+)	0.27
Non-Nesting Species	Area (-)	0.10	--	--

to these fluctuations. Lake Huron water levels were approximately 20 cm lower in 1998 than in 1997 (NOAA). Consequently, many habitat characteristics including water level, grass density, and coverage of submerged and floating vegetation were significantly different in 1998 (see Table 8). Because these specific features provide many services critical to breeding birds (e.g. protection from predators [Jobin and Picman 1997], foraging substrates [Brewer et al. 1991; Weller 1999], etc.), one would intuitively expect these changes to be a major driver of turnover in these wet meadows (Weller 1994). However, regression models selected only mean habitat components, and not habitat change components, as predictors of avian turnover (Table 11).

Although this suggests that average habitat conditions influence turnover rates (Gutzwiller and Anderson 1987b), I caution that this does not imply that changing habitat conditions are unimportant to turnover rates, breeding success or other aspects of avian ecology. First, this study was conducted over a short time-interval (2 yrs), and the impact of these habitat changes on turnover rates and bird distributions may not be apparent over such a short interval. Second, the magnitude of most habitat changes were correlated with the mean of that habitat characteristic over the study period (the greater the water depth on average, the greater the potential for large changes), or were correlated with area (Table 12). Because of these correlations, mean habitat components may explain, not only variation in turnover due to average habitat conditions, but also some of the variation due to changing habitat conditions. Thus, mean habitat components may have been selected as the best predictors by regression techniques even though habitat change components may have also influenced turnover rates. I caution that the potential importance of yearly fluctuations in water levels and other habitat characteristics on

Table 11. Correlation coefficients and P-values for correlations between habitat change components and area, perimeter-area ratio, and mean habitat components for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

Area and Mean Habitat Components	Habitat Change PC1	Habitat Change PC2
log(Area)	-0.021	-0.311
	0.899	0.051
Perimeter-area ratio (PAR)	-0.151	0.285
	0.354	0.074
Mean habitat PC1	0.127	-0.179
	0.437	0.268
Mean habitat PC2	0.363	0.560
	0.022	0.000
Mean habitat PC3	0.078	-0.316
	0.634	0.047
Mean habitat PC4	0.149	0.208
	0.360	0.197
Mean habitat PC5	-0.019	0.210
	0.909	0.193

turnover rates and avian community dynamics within Great Lakes coastal wetlands should still be considered in both future research and conservation efforts.

Effects of Habitat Characteristics on Turnover Rates

Turnover rates were lower in wet meadows characterized by relatively denser woody vegetation, a more diverse shrub layer (< 2-m in height) and more willow shrubs (MHAB3). Wet meadows with these characteristics offer more vertical substrates for foraging and more woody vegetation required by shrub-nesting species like the Yellow Warbler, and woody wet meadows may be more likely to consistently attract these species year after year compared to sites with little shrubby vegetation. Alternatively, the structure of shrub vegetation and shrub-dominated wetlands is less affected by changing water levels than more herbaceous-dominated wetlands, or at least changes in shrub-dominated wetlands have a longer lag time (Burton 1985). Thus, species turnover rates could be lower in shrubby wet meadows because the overall habitat structure and vegetative composition does not change as rapidly.

Turnover rates were higher in wet meadows characterized by increased frequency of pockets of open water and interspersed deciduous trees and snags and a decreased frequency of graminoid coverage (MHAB4). Two factors could account for this relationship. First, wet meadows possessing more homogeneous grass coverage may simply attract wetland/grassland breeding birds (e.g. Swamp Sparrow, American Bittern) more consistently than those where graminoid vegetation is heterogeneous or interspersed with deciduous trees and open water. Second, interspersed trees and snags may provide perches for predators (like corvids; Bergin et al. 1997) or brood parasites (Hauber and Russo 2000) within the meadow and, thus, elevate nest predation rates by allowing visual-searching predators to penetrate deep into the interior of the wet meadow patch. Similarly, open pockets of open water may disrupt the protective cover of the graminoid vegetation making bird nests easier to locate. Breeding wetland birds that suffer predation events are not likely to return to the same patch in the following year (Blancher and Robertson 1985; Bensch and Hasselquist 1991), and either of these mechanisms could result in increased turnover rates.

Effects of Landscape Context

While recent studies have demonstrated that characteristics of the adjacent landscape can affect species richness (Pearson 1993; Estandes and Temple 1999; Saab 1999; Chapter One), patch selection by species (Friesen et al. 1994), and edge-related nest predation (Andren 1995; Bayne and Hopson 1997), mine is the first study to relate adjacent habitats to within-patch turnover rates. Turnover rates were lower in patches adjacent to a proportionately greater number and diversity of patches (complex contexts: LAND1). Turnover rates were also lower for sites adjacent to proportionately more water and wetland habitats (a wetland context) compared to patches surrounded by forest habitats (a terrestrial context; LAND5).

The effect of a diverse landscape context was first predicted by Forman (1995) who theorized that species richness of a patch should increase with the number of adjacent patches because each adjacent patch contributes different colonizers to the patch in question. The logical extension of this theory is that turnover rates should be lower in patches surrounded by a variety of patch types because there is an increased probability of replacing species which abandon the patch with colonizers from adjacent patches. Previous analyses (Chapter One) indicated that bird species richness was indeed higher for wet meadows in diverse contexts. The decreased turnover rates for meadows in complex contexts supports this mechanism and suggests that adjacent patches may indeed serve as sources for colonizers. Because of the effects of adjacent patches on colonization rates, wet meadows in complex contexts may maintain higher species richness and have lower annual turnover rates.

However, previous results suggested that other explanations may also be appropriate (see Chapter One) because patches located in complex contexts also had greater abundance (Table 7). Colonization mechanisms predict increased species richness, but not increased abundance. A possible explanation is that complex contexts may provide a more diverse, and hence, more stable, suite of resources for foraging. This would increase the intrinsic habitat quality of a patch and allow breeding bird densities to be greater (Anderson and Titman 1992; Gill 1995), and could also account, at least in part, for the decreased turnover rates observed in complex contexts. More stable food resources would attract potential breeders more consistently, and breeding pairs would be less likely to abandon these patches in low water years when production of invertebrates and plants within the meadow itself is low. More research will be required to test if one or both potential mechanisms are responsible for the patterns I observed.

The second relationship was that turnover rates were lower in patches located in an aquatic/wetland context compared to those in a terrestrial context (Table 11). Wetland contexts similarly contained greater species richness, total bird abundance and abundance of several species (Chapter One, Table 7). Two mechanisms may interact to account for this relationship. First, many species that breed in wet meadows often forage in nearby habitats (e.g. Red-winged Blackbird [Orians 1980]), and wetland habitats provide an abundant supply of aquatic invertebrates (Tilman and Schwegler 1978; Gathman et al. 1999). Emergence of aquatic invertebrates is highly seasonal such that different species emerge over a short time-interval (few days to a few weeks: Orians 1980). Diverse wetland contexts contain more invertebrate species, and would thus provide a consistent supply of emerging invertebrates over the duration of the bird-breeding season. Wetland contexts would be especially important during low water years (like 1998) when the wet meadows are not flooded, and hence, invertebrate densities and emergence are substantially lower within the meadow itself. In such years, adjacent wetlands would insure that food resources remained available, and breeding birds would be less likely to abandon wet meadows during dry years. This would lower turnover rates in patches located in wetland contexts.

Second, adjacent wetlands may provide protection from predators simply because water prevents access by many terrestrial predators (Jobin and Picman 1997). Predation rates, and presumably either predator densities or predator efficiency, are higher in upland habitats than in wetland habitats (Picman 1988). Adjacent upland habitats may provide access to the wet meadow by upland predators whereas adjacent wetland may buffer the wet meadow from these predators. Also, visual-searching predators and brood parasites can use trees at forest edges to search the wet meadow for nests (Bergin et al. 1997; Hauber and Russo 2000), and adjacent wetlands do not provide this type of structure. If the potential for nest predation is higher in forested, terrestrial contexts, then breeding individuals would be less likely to return to a meadow where they had bred unsuccessfully the year before (Blancher and Robertson 198; Bensch and Hasselquist 1991), hence, increasing turnover rates in terrestrial contexts.

One might argue that these observed effects are really an indirect effect of area and/or perimeter. Large wet meadows, or oddly shaped meadows with a relatively longer perimeter, would be adjacent to a greater number of patches and patch types, and would be more likely to be adjacent to wetland habitats, simply because they were larger. However, the two-stage regression design removed effects of area and perimeter (in the form of perimeter/area ratio) before I tested for the effects of landscape context, so this is unlikely. Thus, these results represent a true "context effect" above and beyond effects of area and perimeter.

Effects of Coastline Complexity

Ecological theory suggests that complex, or highly fractal, landscapes are more stable because the diversity of the landscape dampens environmental and biological oscillations (Forman 1995). Additionally, some researchers have noted that some wetland species and habitats tend to be more abundant along complex coastlines (Nilsson 1978; Kent and Wong 1984). Thus, I hypothesized that turnover rates should be lower in wet meadows associated with complex or highly fractal coastline segments. However, my results did not support this because coastline components were not related to turnover rates.

Coastline components were significant predictors of species richness and presence/absence in these same Great Lakes wet meadows (see Chapter One, Table 7), so it is still possible that birds do use coastline features as a habitat selection criteria, at least to some extent. If birds do use coastline features as habitat selection criteria, then these features may serve only to increase or decrease the maximum species richness of a particular patch. In Great Lakes coastal wet meadows, coastline features were not related to turnover rates.

Turnover in Nesting vs. Non-nesting Species

Regression analysis selected different variables as predictors for turnover rates in nesting and non-nesting birds which suggests that different factors influence colonization and extinction events in these two groups of species. Turnover of nesting birds was related to habitat characteristics and landscape context. The importance of patch-level habitat characteristics to nest site selection (Knopf and Sedgewick 1992) and nesting success (e.g. Picman 1988) of wetland/grassland birds has been well-documented, so it is not surprising that habitat characteristics are related to turnover rates of nesting species. Turnover of nesting birds was also lower in wetland contexts. Wetland contexts could decrease turnover rate through effects on nesting success described earlier: either the higher quality foraging resources or the protection from nest predators that would be afforded by wetland contexts would increase nesting success and thus lower turnover.

In contrast, turnover of non-breeding birds was lower in larger patches, but was not related to any other habitat or landscape component. Foraging birds (such as Great Blue Herons) traveling from other habitats may be more likely to forage in large wet meadows simply because of a sampling effect. They would be more likely to encounter a large wet meadow than a small wet meadow, or perhaps these species would be simply more likely to be detected by an observer in large patches. Similarly, the probability of detecting that same species again the following year would be greater in larger wet meadows, and observed turnover rates would be lower in large meadows. It is also possible that larger patches are more likely to contain the food resources required by foraging birds. Effects of area would account for this as well.

The habitat and landscape components selected in the model for total species richness represented a combination of the variables selected in the individual models for nesting and non-nesting species turnover (Table 11). Thus, turnover of nesting species and turnover of non-nesting species may be independent processes governed by a different suite of factors: habitat and landscape context for the former, and area for the latter. This is not surprising because nesting birds require different characteristics (e.g. nesting substrates, long-term food availability, etc.) than do non-nesting or foraging birds (e.g. proximity to their nesting habitat, immediate food supply), and these characteristics may be associated with different habitat features and landscape contexts. Biologists and managers should realize that conservation criteria aimed at decreasing turnover rates for one group of birds would not be effective at decreasing turnover rates in the other.

One landscape component in the overall turnover model, diverse contexts (LAND1), was not included in either the nesting or non-nesting turnover models. Complex contexts could have influenced turnover rates of either nesting species, non-nesting species, or both and still not have been selected as a predictor if it was secondary in importance to the other factors (habitat characteristics and wetland context for nesters, area for non-nesters). Only when turnover of nesters and non-nesters are combined into a single turnover rate, however, the combined effects of complex contexts may have been great enough for the stepwise algorithm to select that component.

Relevance of Island Biogeography

Island biogeography predicts that turnover rate should decrease with increasing island (or patch) area and with increasing isolation (farther from the mainland or nearby patches of the same type), and that these processes interact to maintain a predictable equilibrium number of species (MacArthur and Wilson 1967). Researchers have made repeated attempts to use this theory to predict the species richness and turnover patterns of birds in various types of non-oceanic "island" patches (Faaborg et al. 1995), but these attempts have met with only varying success for two major reasons. First, colonization and extinction rates can be influenced by within-patch habitat features (Gutzwiller and Anderson 1987b), by changes in habitat features (Weller 1994), or by human-induced changes (Savidge 1987; Patten and Rotenberry 1998) such that mainland avian populations are rarely at equilibrium. In the Great Lakes coastal wet meadows I studied, this assumption was clearly not satisfied. On average, species richness decreased between 1997 and 1998 which would not be expected if the region were truly at equilibrium.

Second, the habitats surrounding these wet meadows are not inhospitable for birds as is the case for the oceanic islands systems used to develop island biogeography (MacArthur and Wilson 1967). In fact, adjacent habitats are used by many wetland species throughout the breeding season (Weller 1999). If these aspects of wetland habitat "islands" are considered, it is quite reasonable to expect landscape context to influence turnover rates and for island biogeography to poorly predict these turnover rates. This is precisely what was observed for bird communities in Great Lakes coastal wet meadows. Total species turnover rate was inversely related to area. However, further analyses indicated that this was due primarily to turnover of non-nesting species whereas turnover of nesting species was related, not to area, but to habitat characteristics and landscape context.

Isolation was not related to turnover rates either. As an *a posteriori* analysis, I calculated two measures of isolation for each wet meadow: distance to nearest wet meadow and proportion of the surrounding landscape (within 1-km of patch perimeter) comprised of wet meadow. I then went back, and to each stage of each regression model, added both measures of isolation to the stepwise algorithm. Neither isolation measure was significant for any of the three turnover rates. This is not surprising because the northern Lake Huron coastline is relatively undisturbed and contains a great deal of wet meadow habitat. In fact, no wet meadow was farther than 1.2 km from another wet meadow patch and most inter-patch distances were much smaller. These distances are easily traversed by vagile organisms like birds, so these wet meadows may not be functionally isolated at all.

Turnover of bird communities in Great Lakes coastal wet meadows was influenced by many of the same variables that were significantly related to species richness (compare Table 5, Chapter 1, and Table 10, this chapter). Thus, the theory of island biogeography applies to these wetlands in that the processes of colonization and extinction (through turnover rates) are linked to and help determine species richness. However, the more specific tenets that area and isolation predict turnover rates (and species richness) did not apply to birds in Great Lakes coastal wet meadows. Rather, turnover rates in coastal wetlands are more likely driven by habitat conditions and landscape context.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Although recommendations based on my results are most appropriate for managing avian diversity in Great Lakes coastal wetlands, they may apply to other habitats as well. Wet meadows are similar to both wetlands and grasslands in terms of both habitat characteristics and breeding bird species, so species turnover may be influenced by similar factors in other grassland and wetland habitats in other landscapes.

My results indicate that managers should not assume that island biogeography is an appropriate model for predicting turnover rates or for formulating conservation plans. Oftentimes, the primary target of management plans in both grasslands and wetlands are nesting species. In Great Lakes wetlands, turnover of nesting species was influenced by habitat characteristics and landscape context, whereas turnover of non-nesting species was related only to area. Thus, programs aimed at preserving species which breed in wetland or grasslands should not rely solely on predictions of island biogeography, but consider critical features of the habitat and a patch's context in the landscape in addition to wetland area and isolation.

In Great Lakes coastal wet meadows, annual turnover of birds would be minimized in large wet meadows located in a wetland context where they are adjacent to other aquatic- and wetland-habitat types. Wet meadows should also contain a relatively greater density and diversity of woody vegetation in the shrub layer, be comprised of homogeneous, relatively unbroken stands of grasses and sedges, and lack deciduous trees and snags in the interior of the wet meadow. Wet meadows meeting these criteria would attract both breeding and non-breeding species consistently from year-to-year, and community composition would be more stable.

Future studies should be conducted over 5-yrs, 10-yrs, or longer if possible. My interpretations are based on only one time-step (2 yrs) which is often not long enough to identify long-term patterns because relationships can fluctuate from year-to-year (Wiens 1981). However, because such long-term studies are currently lacking for the Great Lakes region, recommendations based on short-term studies such as mine should be heeded until longer-term studies have been completed. Scientists and managers alike should seek to identify and preserve habitat patches with lower turnover rates because this represents more stable communities less likely to lose species (biodiveristy) to extinction (Russell et al. 1995). Without understanding turnover rates and the factors that influence this process, effective long-term management of wetland birds is difficult because without this knowledge, it is impossible to predict how communities will change over time.

CHAPTER THREE

PENINSULA EFFECTS IN A COASTAL LANDSCAPE: ARE COVES MORE SPECIES RICH THAN LOBES?

INTRODUCTION

The phenomenon of decreasing species richness with increasing distance along peninsula lobes is called a peninsula effect (Forman and Godron 1986). Peninsula effects have been identified for a variety of taxa on large peninsulas like Baja California (e.g. Taylor and Regal 1978) and Florida (e.g. Keister 1971), but this pattern has not been consistently observed on all peninsulas or for all taxa (Taylor 1987). Review of the evidence (Forman 1995) suggests that these patterns may be caused by mechanisms of colonization and extinction related to dispersal rates and island biogeography (MacArthur and Wilson 1967; Taylor and Regal 1978), a gradient in climate or environmental factors from the mainland to the peninsula tip (Taylor and Regal 1978), or a combination of both (Milne and Forman 1986).

Attention to peninsula effects has been focused on the continental scale, but little is known about the presence or absence of peninsula effects at smaller, more regional scales like a Great Lakes coastline. This is surprising in light of commonness of highly interdigitated landscapes in both coastal and terrestrial regions and the utility of such knowledge for conservation planning. Milne and Forman (1986) found that plant species richness decreased along 9 peninsulas 375 m to 16,000 m in length in coastal Maine, but other studies at this scale are lacking. If such patterns are ubiquitous at both the continental and regional scales, such information would be extremely valuable in setting conservation priorities.

The theory of island biogeography can be extended to peninsular landscapes if patches located on lobes are considered analogous to far islands and patches located within coves can be considered analogous to near islands. These analogies suggest two predictions (see Figure 4): (1) species should accumulate faster with area (steeper slopes) in lobe patches compared to cove patches; and (2) cove patches should be generally more species rich (higher intercepts). I tested these predictions along the northern coast of Lake Huron in Michigan. I compared bird species richness of coastal wet meadows located within coves (*sensu* near islands) to species richness of wet meadows located on peninsula lobes (*sensu* far islands). Before testing for differences in species richness, I controlled for variation related to habitat and landscape characteristics.

METHODS

Study Area

I worked in wet meadows located along the highly convoluted, northern shoreline of Lake Huron in the Upper Peninsula of Michigan (Mackinac and Chippewa counties). All wet meadows were seasonally or shallowly flooded grasslands, were within 500-km of the coastline, were influenced by lake water levels; and were dominated by a mixture of tussock-forming grasses (*Calamagrostis canadensis*) and sedges (*Carex stricta* and *Carex aquatilis*). Wet meadows were interspersed with varying amounts of bulrush (*Scirpus* spp.), cattail (*Typha* spp.), and shrubs (*Salix* spp., *Alnus* spp, and *Myrica* spp.). Submersed (*Potomageton* spp.) and floating (*Polygonum* spp., *Lemna* spp.) vegetation were often present in standing water between hummocks.

Bird Censuses

Within each of the wet meadows, I established a 100-m wide, permanent transect (Verner 1985) which I censused censused multiple times between 15 May and 4 July of each year (4 times during 1997; 5 times during 1998). Census techniques are described in detail in *Chapter One, Methods, Bird Censuses.*

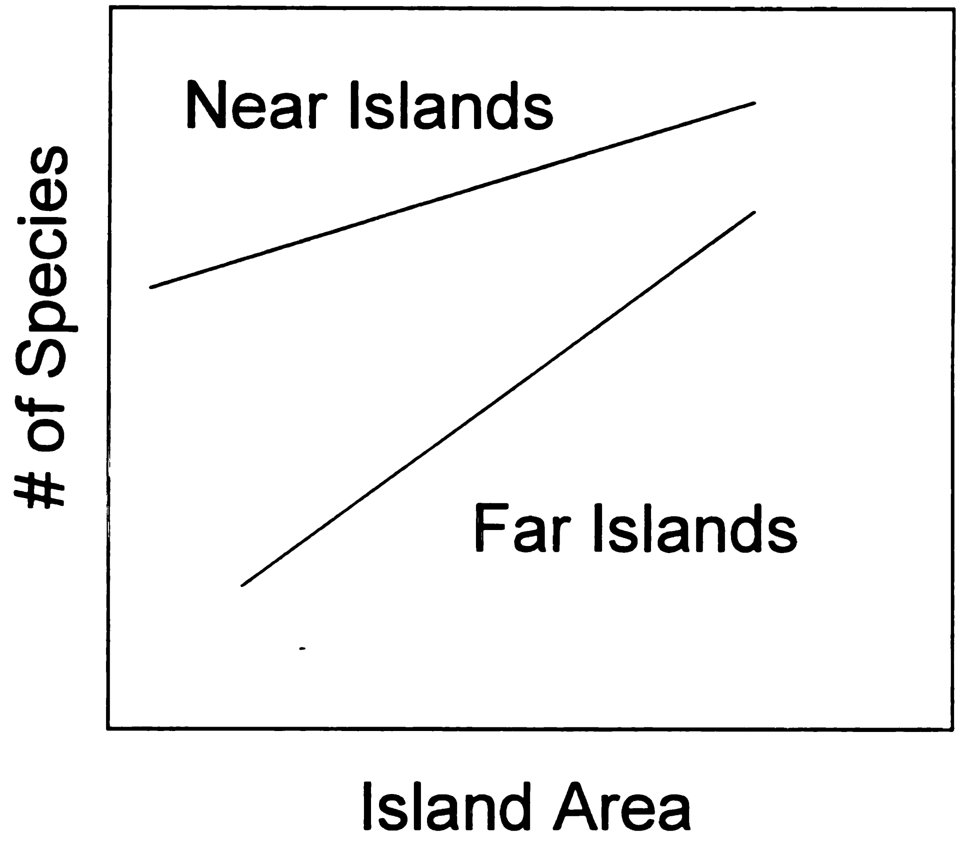

Figure 4. Theoretical species-area relationships as predicted by island biogeography. Wet meadows located in coves are analogous to near islands; wet meadows located on lobes are analogous to far islands.

Habitat Characteristics

Because variation in habitat characteristics can influence bird species richness (e.g. Craig and Beal 1992), I measured 20 habitat characteristics along each bird census transect in late July after vegetation had reached mature height. Within each segment, I estimated grass height and density, density and diversity of shrub vegetation, water depth and hummock height using point-intercept sampling techniques (*sensu* Rotenberry and Wiens 1980). Percent cover of vegetation types (e.g. bulrush, cattail, open water, etc.) was estimated as the frequency of occurrence in 1-m^2-sampling plots. Frequency of trees and snags were estimated from 2.5-m radius sampling plots. Detailed description of habitat sampling techniques are in *Chapter One, Methods, Habitat Sampling.* Habitat variables are listed in Appendices H and I.

Landscape Characteristics

Surrounding landuse of the northern Lake Huron shoreline was interpreted into an ArcView GIS from 1:24,000-scale color aerial photographs taken in 1992. Accuracy was verified by extensive ground-truthing. Wet meadow areas, perimeters and the proportion of the perimeter adjacent to specific patch types were calculated in ArcView. Buffer operations were used to calculate density of wet meadow, Lake Huron, roads and streams within 1-km of the wet meadow border. For each wet meadow, 3 coastline segments (500-m, 1-km, and 2-km from each wet meadow perimeter) were derived from a vector coverage of the Great Lakes shoreline (Great Lakes Environmental Research Center). For each segment, I calculated total coastline length, sinuosity, and fractal dimension (Lam and De Cola 1993). Further details about the derivation of landscape and coastline variables are in *Chapter One, Methods.*

Construction of Bird Variables

I analyzed data only for those species which were detected within the 100-m wide transects. Three different measures of species richness were calculated: total species richness (the total number of different species detected within the wet meadow during a particular year); nesting species richness (the total number of nesting species detected within the meadow during a year); and non-nesters species richness (total number of non-nesting species detected within a year). Because wet meadows have characteristics of both wetlands and grasslands, a species was designated as a nesting species if it was an obligate or facultative grassland (Vickery et al. 1999) or wetland (based on Terres 1980) nester. I also calculated total bird abundance and abundance of species occurring on > 2/3 of the wet meadows. Abundance was calculated as the average number of individuals detected divided by the total transect area.

Statistical Analysis

Site Selection. Of the 40 wet meadows censused for breeding birds, I identified 30 which were clearly located either in a cove or out on a lobe (see Figure 5). Wet meadows not clearly located in either a cove or lobe were excluded from these analyses. Initial examination of the species-area curve for these wet meadow patches revealed that the range of patch areas was much higher for cove sites than for lobe sites (Figure 6). Because it is inappropriate to compare regression lines or other statistics which are estimated over disparate ranges, I restricted statistical analysis to 21 sites that were less than 5 ha (Figure 6). For cove sites, n = 10; for lobe sites, n = 11. The center of lobe patches was located at a mean of 817 m (standard error = 221.7 and ranging from 157 m to 2268 m) from the mainland.

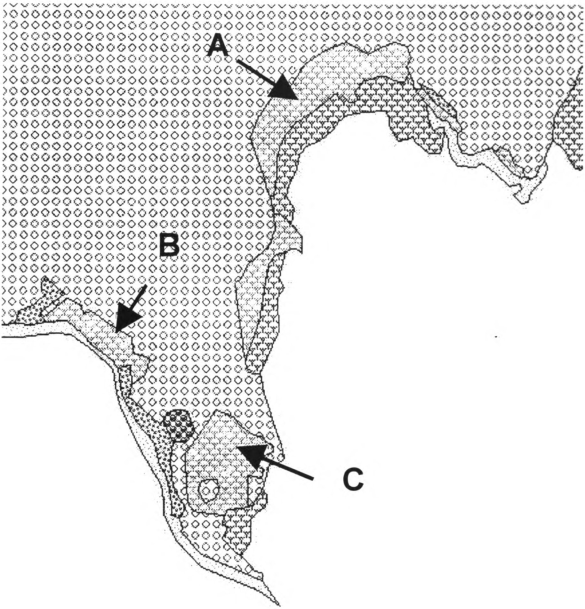

Figure 5. Diagram of northern Lake Huron shoreline. A = wet meadow patch distinctly located within a cove. B = wet meadow patch not clearly located in either a lobe or out on a cove. C = wet meadow patch distinctly located out on a lobe. Only wet meadow meeting either criterion A or C were included in this analysis.

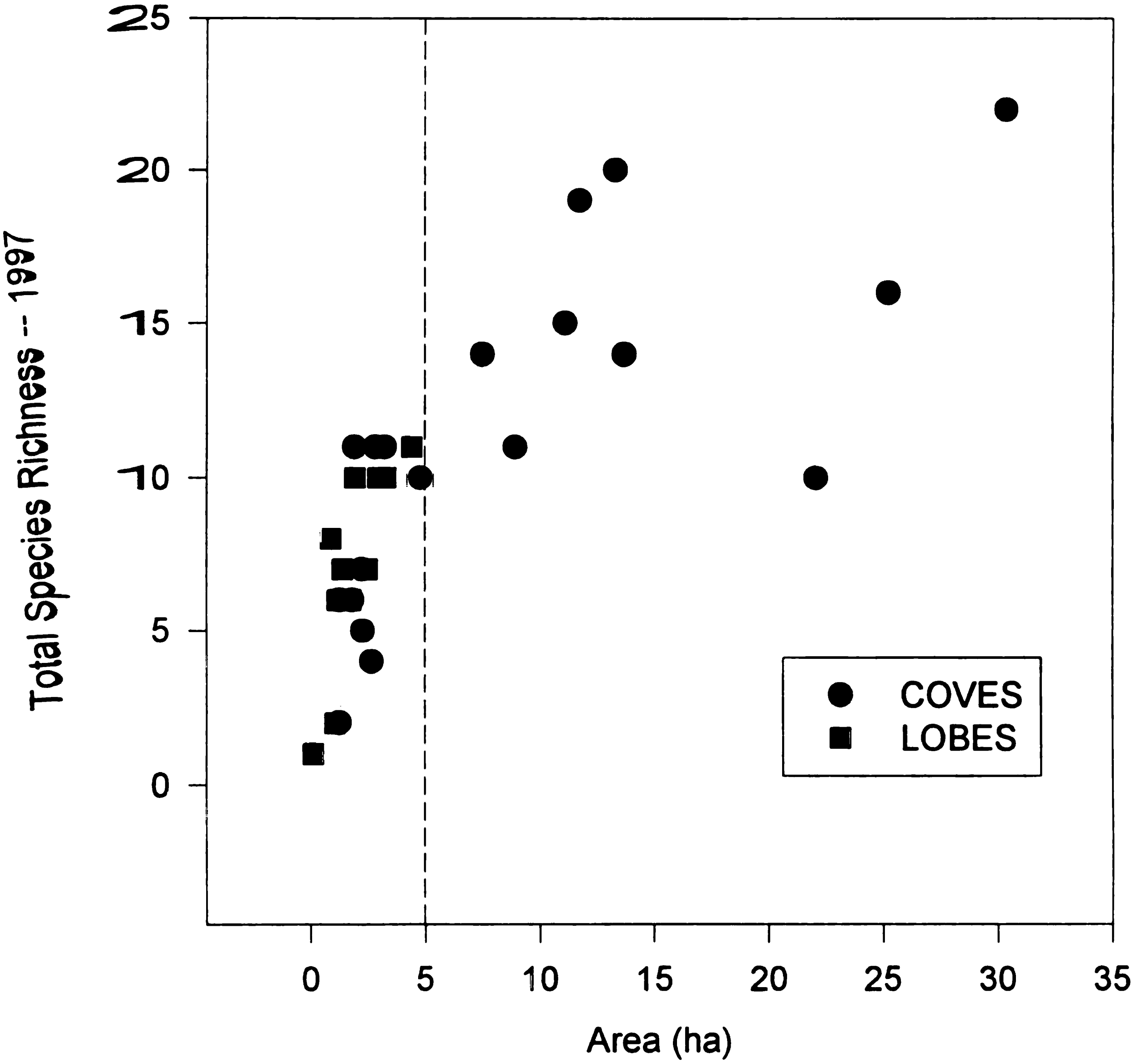

Figure 6. Species-area relationships in 30 wet meadows located in coves or out on lobes. Sites to the left of dashed line are ones retained for analysis.

Habitat, Landscape, and Coastline Characteristics. Habitat characteristics (e.g. Craig and Beal 1992), landscape characteristics (e.g. Brown and Dinsmore 1986; Naugle et al. 1999, *Chapter One*), and coastline characteristics (*see Chapter One)* can affect patterns of bird species richness and could thus be confounded with or mask true peninsula effects. To ameliorate this, I accounted for effects of these variables before testing for effects of coves and lobes. To reduce the number of variables, I conducted 4 separate principal component analyses: once each for 1997 habitat characteristics, 1998 habitat characteristics, landscape variables, and coastline variables. For each of the 4 sets of variables, I retained components with eigenvalues > 1 for further analysis.

Species-area Regressions. To test hypotheses about differences in species-area relationships of coves and lobes, I used a two-stage regression approach (Morrison et al. 1998) to account for habitat and landscape effects. Because of small sample size and limited degrees of freedom, I restricted the number of habitat/landscape components to one. Using Proc RSquare (SAS Institute, Inc, 1989), I identified the principal that was the best, single predictor of each richness variable from a set of variables including area, perimeter-area ratio, habitat components, landscape components, and coastline components. The best predictor had the highest r^2, a linear relationship with the richness variable, and satisfied all assumptions of regression. Each richness variable was then regressed against this best predictor, and the residuals from this regression were saved and used as the dependent variable in a second regression.

In the second-stage of regression, I used these adjusted richness variables (residuals) to test for differences in species richness patterns between cove patches and lobe patches. I conducted separate adjusted species richness vs. area regressions for cove and lobe patches and then tested for differences in the slope and intercept parameters. I tested two null hypotheses for each year and richness variable combination: (1) the intercept of the species-area regression for cove patches would be equal to or less than the intercept of the species-area regression for lobe patches; and (2) the slope of the species-area regression for cove patches would be equal to or greater than the slope of the species vs. area regression for lobe patches. The alternate hypotheses were that species-area regressions involving cove patches would have higher intercepts but smaller slopes than regressions involving lobe patches. I tested for differences in slopes and intercepts between regressions involving cove and lobe patches using one-tailed *t*-tests described by Zar (1984: eqs. 18.1 and 18.25). For all statistical tests, I used $\alpha = 0.10$ to improve statistical power (Westmoreland and Best 1985; Riffell et al. 1996).

Species-area relationships are typically expressed on a log-log scale by transforming both species number and area. However, I did not conduct transformations unless it was necessary to meet the assumptions of regression. The species-area curve involving all 31 cove and lobe patches demonstrated the classical curvilinear relationship, but my analyses were restricted to only the linear part of the relationship (Figure 3). Thus, I suspected that the assumptions of regression might be satisfied without transformations (*sensu* Rahbek 1997). I evaluated each model with respect to the assumptions of linear regression (Ott 1988): linear relationship between X and Y; constant variance of residuals; and normality of residuals. For all richness variables and all years, untransformed data met these assumptions, and transformations did not improve on these criteria relative to the untransformed model. In many instances, transformations introduced blatant violations of regression assumptions.

To assess the ability of the *t*-tests to detect true differences in slopes and intercepts, I calculated minimum detectable differences (δs [Zar 1984]). For these analyses, δs represent the smallest absolute difference in a slope or intercept that would have been detected at $\alpha = 0.10$ at a power of 80%. I calculated the median and range of δs for tests involving slopes and intercepts.

Species' abundance and presence/absence. For total bird abundance and abundance of species that occurred on at least 2/3 of the sites, I used traditional linear models to test for differences in abundance between cove and lobe sites. I restricted the number of covariates to one covariate for each abundance variable (see above). I identified the single, best predictor from the set of habitat, landscape, and coastline components. The final linear model included one covariate (the best predictor) and cove/lobe designation as the main effect. I used $\alpha = 0.10$ and two-tailed F-statistics for hypothesis tests about coves and lobes.

For species occurring on < 2/3 of the sites, I used presence/absence data. Before testing for differences between coves and lobes, I identified the single, best predictor from among the habitat, landscape and coastline components using a forward selection procedure in a generalized linear model (PROC GENMOD: SAS Institute Inc, 1997). This best predictor was then included as a covariate with cove/lobe position as the main effect. To test for significant effects of cove/love position, I used Wald χ^2 statistics. All test statistics and P-values were based on Type III sums of squares. Tests based on Type III sums of squares account for effects of other variables in the model. Hence, they test for effects of cove/lobe position above and beyond effects of the habitat or landscape covariate.

RESULTS

Habitat Characteristics

Although wet meadows were selected based on similar habitat features, the habitat variables I measured did vary among wet meadows. Habitat characteristics are summarized elsewhere (*Chapter One and Two, Tables 2 & 8*) and are beyond the scope of this chapter. Principal component analysis identified 6 components in 1997 (Appendix H) and 5 components in 1998 (Appendix I) to be retained for subsequent analyses. These components accounted for 81% and 79% of the variation in the original variables.

Habitat characteristics generally did not differ significantly between cove and lobe patches during either 1997 or 1998. Frequency of moss and submersed vegetation were greater in lobe patches than in cove patches ($P < 0.10$) in 1998, but not it 1997. None of the other 18 habitat characteristics I measured were significantly different between lobes and coves in either year. These two significant tests are less than the 4 significant tests (2 years x 20 habitat variables x 0.10 = 4) expected due to chance.

Landscape and Coastline Characteristics

Landscape and coastline characteristics varied among wet meadows. However, discussion of these characteristics is beyond the scope of this paper. Readers are referred to Chapters One and Two for detailed descriptions. For these analyses, PCA identified 5 landscape components (Appendix J) and 3 coastline components (Appendix K). These components accounted for 87% and 84% of the variation in the original variables.

Species Richness

I detected a total of 39 species over two years in the 21 wet meadows. Species residuals vs. area regressions were generally significant ($P < 0.10$) for total species richness and nesting species richness in coves and lobes separately (Table 12), indicating a relationship between richness and area independent of habitat effects for these richness measures. Richness of non-nesting species was not significantly related to area (Table 12).

Intercepts from cove-patch regressions were not different from lobe-patch regressions (Table 12). For non-nesting species richness in 1998, the slope was greater for lobe sites than for cove sites as predicted ($P = 0.086$). However, intercepts did not differ in 1997 for any other variable. This single significant test is only 1 out of a total of 12 tests on slopes and intercepts. Additionally, regression parameters did not differ between coves and lobes in a consistent direction. Thus, there is little evidence of peninsula effects on species-area relationships.

Minimum Detectable Effect Sizes

For tests involving slopes from species residuals - area regressions, the mean minimum detectable effect size (δs) in slopes was 1.643 (range: 0.816 - 2.362). The mean δ for intercepts was 1.804 (range: 0.896-2.594). Increases in slopes and intercepts this large or larger would have been detected with a statistical power of 80% at an $\alpha = 0.10$. These δs are quite large. Tests would have been reliably significant (80% power) only when lobe slopes were 72% - 182% steeper than the cove slopes or when lobe intercepts were 34% - 129% smaller than cove intercepts. Thus, I would not have detected small or subtle peninsula effects had they occurred.

Individual Species

I conducted a total of 20 tests on abundance and presence/absence data for a total of 11 different species (Table 13). Some species occurred frequently enough for statistical analysis during only one year. Swamp Sparrow abundance was higher in cove patches

Table 12. Coefficients of adjusted species-area regression for cove and lobe wet meadows associated with the northern shoreline of Lake Huron, Chippewa and Mackinac counties, Michigan. For all regressions, cove n = 10 and lobe n = 11.

Parameter	Coves	Lobes	Difference	*t*	P-value
	Total Species Richness -- 1997 (HABPC3)				
Slope	1.59	1.36*	0.23	0.241	0.594
Intercept	-3.72	-2.80	-0.92	-0.391	0.649
	Total Species Richness -- 1998 (LANDPC5)				
Slope	1.29*	2.00*	-0.71	-0.700	0.247
Intercept	-2.59	-4.41	1.82	0.721	0.241
	Nesting Species Richness -- 1997 (LANDPC1)				
Slope	0.86	1.42*	-0.56	-0.751	0.232
Intercept	-1.58	-3.24	1.66	0.884	0.195
	Nesting Species Richness -- 1998 (HABPC3)				
Slope	2.02*	1.06*	0.96	1.540	0.929
Intercept	-4.71	-2.24	-2.47	-1.592	0.935
	Non-nesting Species Richness -- 1997 (LANDPC5)				
Slope	0.44	0.27	0.17	0.348	0.563
Intercept	-0.69	-0.71	0.02	0.017	0.493
	Non-nesting Species Richness -- 1998 (LANDPC5)				
Slope	-0.04	0.71	-0.75	-1.428	0.086
Intercept	-0.09	-1.22	1.13	0.849	0.204

* Indicates that the slope for that particular species-area regression was significant ($P < 0.10$).

Table 13. Results of regression on species abundance and presence absence variables in 21 wet meadows located in either coves or lobes of the northern shoreline of Lake Huron, Chippewa and Mackinac counties, Michigan.

Variable	Covariate	Position Parameter	F or χ^{2*}	*P*-value
		Abundance Variables		
Total Abundance				
1997	HAB3 (+)	-0.56	0.59	0.453
1998	LAND5 (-)	0.08	0.00	0.948
Common Yellowthroat				
1997	HAB4 (-)	0.28	1.82	0.195
1998	HAB2 (+)	-0.18	0.71	0.411
Swamp Sparrow				
1997**	HAB2 (+)	0.04	0.04	0.836
1998	HAB1 (+)	0.66	5.43	0.032
Song Sparrow				
1997	Area (-)	-0.44	-3.93	0.008
1998	Area (-)	-0.50	0.26	0.619
		Presence/absence Variables		
Great Blue Heron				
1997	LAND1 (+)	4.89	4.88	0.027
American Bittern				
1997	LAND5 (-)	1.86	1.81	0.178
1998	HAB2 (+)	1.17	0.79	0.373
Mallard				
1997	LAND1 (+)	-0.15	0.02	0.883
Virginia Rail				
1997	COAST2 (+)	2.24	2.29	0.130
Alder Flycatcher				
1997	HAB3 (+)	0.28	0.08	0.780
1998	--	-0.59	0.45	0.504

Table 13. Continued.

Variable	Covariate	Position Parameter	F or χ^{2*}	*P*-value
Yellow Warbler				
1997	LAND5 (-)	0.96	0.78	0.371
1998	LAND5 (-)	0.30	0.09	0.770
Red-winged Blackbird				
1997	LAND1 (+)	0.74	0.38	0.537
1998	HAB2 (-)	2.02	3.07	0.080
American Goldfinch				
1998	HAB3 (+)	7.82	8.73	0.003

* Abundance variables use a standard least squares F-statistic. Presence/absence variables use a Wald χ^2-statistic

** Data for 1997 Swamp Sparrow abundance is based on presence/absence data.

than in lobe patches during 1998. Similarly, the probability of detecting Great Blue Heron (1997), Red-winged Blackbird (1998) and American Goldfinch (1998) was also higher in cove patches. In contrast, the abundance of Song Sparrow (1997) was greater in lobe patches. I observed a total of 5 significant tests which is approximately 2.5 times the number (0.10 x 20 tests = 2) of significant tests expected by chance alone.

DISCUSSION

Habitat Characteristics

Habitat characteristics such as grass density (e.g. Herkert 1994), vertical structure (e.g. Rotenberry and Wiens 1980) and heterogeneity (Rotenberry and Wiens 1980; Craig and Beal 1992) can influence both the likelihood that a species will be present and the ability of species to be detected by sight and sound (Waide and Nairns 1988). Thus, features of the habitat can influence species richness and estimates of species richness. Additionally, habitat characteristics may vary with any environmental gradient present between cove and lobe patches, and this variation could mask or be confounded with true cove vs. lobe differences. In this study, only 2 out of the 20 measured habitat characteristics were significantly different between cove and lobe patches, and these were both during one year. Two significant tests could easily be accounted for by chance. Thus, there were few, if any major habitat differences between coves and lobes. Although this does not preclude the presence of environmental differences between coves and lobes in an unmeasured variable (e.g. air temperature or wind velocity), a gradient was not reflected in 20 major habitat characteristics. This evidence, and my technique of removing habitat- and landscape-related variation in species richness using principal components, reduces the likelihood that habitat characteristics were confounded with the cove/lobe designation.

Species Richness vs. Area Regressions

I detected only one statistically significant difference in intercepts (non-nesting species richness in 1998), and no significant differences in slopes (Table 12). While this one significant test was consistent with the prediction that species-area slopes would be steeper in lobe patches, regression parameters did not differ between cove and lobe regressions in a consistent manner. Additionally, this one significant result can also be accounted for by chance. Because of the low power of my tests; however, I cannot rule out the possibility that small, subtle peninsula effects might still be present in Great Lakes coastal wet meadows. However, because of the lack of consistent patterns in the regression parameters, it is highly doubtful that large differences in the species-area relationships of cove and lobe patches actually existed, and also unlikely that any large peninsula effects were present at this scale in this system.

There are several factors which may explain why peninsula effects were absent, or only very subtle, in this study. One reason may be that there was little difference in habitat characteristics between cove and lobe sites. Gradients in habitat or environmental conditions along the peninsula may sometimes produce peninsular gradients in species richness (e.g. Taylor and Regal 1978; Milne and Forman 1987). Because habitat differences were slight or absent in my study area, it is unlikely that habitat-driven peninsula effects could have occurred, although differences in environmental variables I did not measure (e.g. wind speeds) might have existed. Theoretically, peninsula effects should still be present because of the effect of distance from the mainland on colonization rates (MacArthur and Wilson 1967; Figure 4), but the northern Lake Huron coastline consists of relatively small peninsulas 100 m to 3 km in length. Peninsula effects have been observed at this scale for plants (Milne and Forman 1987), but birds are highly vagile organisms capable of traversing (and hence colonizing) these distances easily. For this reason peninsula effects may not exist for birds at this spatial scale or be so subtle that they are difficult to detect. Additionally, in this region migrating birds arrive traveling north in the springtime, and thus encounter the tips of these peninsulas first after crossing the lake. This order of arrival may increase the likelihood of a species colonizing a lobe patch and offset existing peninsula effects.

Response of Individual Species

Great Blue Heron, Red-winged Blackbird, American Goldfinch, and Swamp Sparrow were more abundant or more likely to be detected in cove patches than in lobe patches, but none were consistently related to cove/lobe position during both years. These species may prefer cove sites for several reasons. American Goldfinch may be more likely to be detected in cove patches simply because they are closer to the mainland, terrestrial habitats they typically inhabit, or they may simply avoid habitats close to open water such as those on coves. Similarly, Red-winged Blackbirds regularly use upland habitat (among others) for foraging (Orians 1980), and cove patches were likely near to more of these types of habitats. Great Blue Heron use wet meadows primarily for foraging, and cove sites may be closer to their forested nesting habitats. Or, cove patches may be closer to habitats Heron use for retreat when threatened. Swamp Sparrow and Red-winged Blackbird were the only wetland/grassland breeding species that were more abundant in cove patches. Although the habitat features were not generally different between cove and lobe wet meadows, cove patches may buffer many environmental factors I did not measure. For instance, wind speeds and air temperatures may vary less in cove patches than in lobe patches, but without further research this is only speculation. One species, Song Sparrow, was more abundant in lobe patches compared to those in coves. Song Sparrows are known for their affinity for edges (Terres 1980), and may perceive peninsula tips as edge habitats. Another possibility is that, as a generalist species, Song Sparrows may prefer lobes to avoid interspecific competition because other species (like the conspecific Swamp Sparrow) may be less abundant in lobes.

Although I observed over twice as many significant tests for abundance and presence/absence as predicted by chance, still only 4 of the 11 species were significantly associated with either cove patches or lobe patches. Additionally, total abundance did not differ between cove patches and lobe patches. Although there may be a few species which discriminate between coves and lobes at this scale, this difference between coves and lobes does not appear to be important for birds in Great Lakes coastal wet meadows. More studies should be conducted at a variety of spatial scales and with greater replication in order to identify more completely the suite of species which exhibit peninsula effects.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Because coves were not significantly more species rich than lobes and few species were more abundant in coves, cove patches would not be considered superior conservation choices in the northern Lake Huron coastal region. However, I caution that dismissing the presence or importance of cove vs. lobe effects in this region or other regions would be unwise because they have been demonstrated in other systems for other taxa (e.g. Taylor and Regal 1978; Milne and Forman 1987). In this study, I addressed only avian richness patterns, and did not investigate other taxa. Avian reproductive parameters like pairing success, clutch size or reproductive success could vary between cove and lobe patches, but these differences would not necessarily have been reflected in differences in species richness. Additionally, statistical power (ability to detect effects) was quite low, and only large peninsula effects would have been detected. Research about the effects of cove and lobe locations on all aspects of avian ecology and other taxa should continue. Until such research is completed, the extent of peninsula effects will remain unknown.

An important caveat is that all of the wet meadows larger than 5 hectares in the region were located in coves, and the importance of large patches to the reproductive success of birds (e.g. Hoover et al. 1995; Burhans and Thompson 1999), persistence of populations (Forman 1995), and conservation reserve design (Schwartz 1999) have been well established. Based on this information, conservation plans for the northern Lake Huron coastline should target large wetlands located in coastal coves. There may also be subtle differences in habitat characteristics or environmental conditions between lobes and coves (e.g. more floating vegetation in cove patches), and such differences could represent a difference in habitat quality for wildlife. Without further research, however, the importance of these differences will not be fully understood.

SUMMARY AND RECOMMENDATIONS

Based on my results, conservation planning for birds in the northern Lake Huron coastline should focus not simply on large wetlands but go further and consider the landscape context of particular patches. Two specific types of landscape contexts were clearly beneficial to birds. Patches located in complex contexts (adjacent to a large number of patches and patch types) and in wetland contexts contained significantly higher species richness than patches of similar size in simple and terrestrial contexts. Complex contexts and wetland contexts were also associated with lower rates of within-patch species turnover were thus not only more species-rich but also more stable and predictable in terms of species composition. For these reasons, conservation plans should seek to preserve whole wetland complexes rather than individual wetlands so that preserves contain the landscape contexts that maximize both species diversity and population persistence.

Effects of other types of landscape context were less clear. For example, species richness was higher in more human-developed contexts, but effects of human-developed contexts were generally lacking for individual species and totally absent for species turnover rates. However, the potentially negative impacts of human development in the northern Lake Huron shoreline should not be dismissed because negative effects of human activities on birds have been well-documented (Freisen et al. 1995; Blair 1996; Bolger et al. 1997). Also, the degree of human development the northern Lake Huron shoreline is slight compared to the heavy commercial and industrial impacts that are common in other parts of the Great Lakes region. Thus, some species with an affinity for human-developed areas may have been attracted (e.g. American Robin *sensu* Blair 1996) without excluding sensitive species. For these reasons, human-related impacts on birds in the region should remain a serious management concern and a primary focus of research.

Another less than general trend involved coastline complexity. Richness and most bird species were associated with simpler coastlines, but a few bird species were associated with more complex coastlines. In the northern Lake Huron region, highly complex and fractal coastlines were negatively correlated to mean patch sizes and amount of coastal wetland in the surrounding landscape. Hence, wet meadows associated with complex coastlines were located in landscape contexts which contained less wetland and appeared more fragmented. For these reasons, many birds may have avoided these patches. Coastline complexity was not an important predictor of turnover. Conservation priorities which emphasize simpler coastlines would benefit a large number of species, but would not benefit other species like Mallards which were associated with complex coastlines. More research is needed before the effects of coastline complexity on wetland birds can be fully understood, and management decisions based on coastline features should not be made until such research is complete.

Peninsula effects on birds appeared to be absent in the northern Lake Huron coastline in that species richness of wet meadow patches located in coves was not significantly different from patches located out on lobes. Although some species were associated with either coves or lobes, responses were not consistent. One important caveat, however, was that all the large (>5 ha) wet meadows were located in coastal coves. For birds, peninsula effects do not provide predictions useful for conservation and management, but future research about peninsula effects on other taxa or other aspects of avian biology would be worthwhile.

Habitat, landscape, and coastline components selected in regression models were generally not consistent between 1997 and 1998, and this illustrates the importance of long-term, multi-year studies (Wiens 1981). This problem is further compounded in dynamic systems like Great Lakes coastal wetlands because birds may alter habitat selection criteria as overall habitat conditions change from year to year (e.g. wetland contexts were more important in a low water year). Thus, longer-running, multi-year research projects are needed to identify the entire complement of habitat types and landscape contexts needed to conserve wetland bird communities over time in dynamic landscapes. Unfortunately, such long-term studies do not exist, and management of wetland birds must be guided by results from short-term studies such as mine until longer-running studies have been completed.

APPENDICES

Appendix A. List of bird species detected in 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

Common Name	Scientific Name	Wet Meadow Nester*
Pied-billed Grebe	*Podilymbus podiceps*	
Green Heron	*Butorides striatus*	
Great Blue Heron	*Ardea herodias*	
Black-crowned Night Heron	*Nycticorax nycticorax*	
American Bittern	*Botaurus lentiginosus*	Nester
Mute Swan	*Cygnus olor*	
Canada Goose	*Branta canadensis*	
Mallard	*Anas platyrhynchos*	Nester
Black Duck	*Anas rubripes*	Nester
Blue-winged Teal	*Anas discors*	Nester
Wood Duck	*Aix sponsa*	
Common Merganser	*Mergus merganser*	
Cooper's Hawk	*Accipiter cooperii*	
Bald Eagle	*Haliaeetus leucocephalus*	
Northern Harrier	*Circus cyaneus*	Nester
Sandhill Crane	*Grus canadensis*	Nester
Virginia Rail	*Rallus limicola*	Nester
Sora	*Porzana carolina*	Nester
Killdeer	*Charadrius vociferus*	Nester
Common Snipe	*Gallinago gallinago*	Nester
Mourning Dove	*Zenaida macroura*	Nester
Ruby-throated Hummingbird	*Archilochus colubris*	
Belted Kingfisher	*Cerlye alcyon*	
Northern Flicker	*Colaptes auratus*	
Red-naped Sapsucker	*Sphyrapicus varius*	
Hairy Woodpecker	*Picoides villosus*	
Downy Woodpecker	*Picoides pubescens*	
Eastern Kingbird	*Tyrannus tyrannus*	Nester
Great-crested Flycatcher	*Myiarchus crinitus*	
Yellow-bellied Flycatcher	*Empidonax flaviventris*	
Alder Flycatcher	*Empidonax alnorum*	Nester
American Crow	*Corvus brachyrhynchos*	
Black-capped Chickadee	*Poecile atricapillus*	
Marsh Wren	*Cistothorus palustris*	Nester
Sedge Wren	*Cistothorus platensis*	Nester
Gray Catbird	*Dumatella carolinensis*	
American Robin	*Turdus migratorius*	
Cedar Waxwing	*Bombycilla cedrorum*	
Black-and-white Warbler	*Mniotilta varia*	

Appendix A. Continued.

Common Name	Scientific Name	Wet Meadow Nester*
Nashville Warbler	*Vermivora ruficapilla*	
Yellow Warbler	*Dendrioca petechia*	Nester
Chestnut-sided Warbler	*Dendrioca pensylvanica*	
Common Yellowthroat	*Geothlypis trichas*	Nester
Bobolink	*Dolichonyx orzyivorus*	Nester
Red-winged Blackbird	*Agelaius phoeniceus*	Nester
Northern Oriole	*Icterus galbula*	
Common Grackle	*Quiscalus quiscula*	Nester
American Goldfinch	*Carduelis tristas*	
Savannah Sparrow	*Passerculus sandwichensis*	Nester
LeConte's Sparrow	*Ammospiza leconteii*	Nester
Chipping Sparrow	*Spizella passerina*	
White-throated Sparrow	*Zonotrichia albicollis*	
Lincoln's Sparrow	*Melospiza lincolnii*	Nester
Swamp Sparrow	*Melospiza georgiana*	Nester
Song Sparrow	*Melospiza melodia*	Nester

* Designation as nesting species indicates species is either obligate or facultative wetland or grassland nesting bird. Designations are based on Vickery et al. (1999), life-histroy traits described in Terres (1980), and personal observations (S. Riffell).

Appendix B. Eigenvectors of the first 5 principal components derived from the 1997 habitat variables for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	PC1	PC2	PC3	PC4	PC5
Eigenvalue	4.70	3.94	2.60	1.72	1.22
Percent variance explained	23.51	19.71	12.99	8.59	6.08
Water depth	0.23	-0.33	0.18	-0.11	-0.03
Hummock height	0.30	-0.13	0.16	-0.08	0.08
Grass height	0.42	0.08	0.10	-0.06	-0.04
Grass density	0.34	0.28	0.01	-0.03	0.12
Woody vegetation density	-0.21	0.13	0.46	-0.07	-0.12
Total vegetation density	0.32	0.30	0.04	-0.01	0.09
Shrub foliage diversity	-0.11	0.04	0.51	-0.02	0.17
Frequency of cover types					
Graminoid	-0.04	0.20	-0.19	-0.53	0.13
Cattail	0.14	0.10	-0.20	0.20	-0.26
Bulrush	-0.27	-0.34	-0.06	0.02	-0.21
Floating vegetation	0.24	-0.14	0.18	0.19	0.39
Submersed vegetation	0.26	0.28	0.05	-0.18	-0.00
Willow	0.04	-0.18	0.43	-0.04	-0.35
Alder	-0.16	0.28	0.31	-0.02	-0.20
Open water	0.01	-0.17	0.20	0.19	0.52
Moss	-0.24	0.18	-0.05	-0.00	0.34
Frequency of trees and snags					
Coniferous trees	-0.27	0.19	0.02	-0.19	0.29
Deciduous trees	-0.06	0.30	0.07	0.46	-0.19
Coniferous snags	-0.16	0.25	0.15	-0.19	-0.01
Deciduous snags	-0.05	0.23	-0.02	0.51	0.14

Appendix C. Eigenvectors of the first 5 principal components derived from the 1998 habitat variables for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	PC1	PC2	PC3	PC4	PC5
Eigenvalue	5.63	3.63	2.37	1.90	1.19
Percent variance explained	28.13	18.14	11.87	9.51	5.95
Water depth	0.05	-0.37	0.25	-0.05	-0.13
Hummock height	0.38	-0.00	0.01	0.07	0.02
Grass height	0.39	-0.02	0.01	0.14	0.01
Grass density	0.39	0.06	0.04	0.14	0.15
Woody vegetation density	-0.12	0.32	0.26	0.28	-0.17
Total vegetation density	0.39	0.11	0.08	0.13	0.12
Shrub foliage diversity	-0.15	0.17	0.38	0.33	-0.10
Frequency of cover types					
Graminoid	0.00	0.22	-0.40	0.25	0.19
Cattail	0.15	-0.03	-0.05	-0.35	-0.14
Bulrush	-0.35	-0.19	0.07	0.02	-0.04
Floating vegetation	0.17	-0.20	0.33	0.19	0.39
Submersed vegetation	-0.24	-0.16	0.18	0.05	0.17
Willow	-0.03	-0.11	0.09	0.46	-0.49
Alder	-0.04	0.42	0.25	-0.03	-0.01
Open water	0.05	-0.29	0.44	-0.06	0.23
Moss	-0.27	0.04	0.02	-0.08	0.32
Frequency of trees and snags					
Coniferous trees	-0.14	0.25	0.07	-0.07	0.41
Deciduous trees	0.09	0.32	0.20	-0.26	-0.21
Coniferous snags	-0.03	0.34	0.11	0.03	0.13
Deciduous snags	0.11	0.13	0.30	-0.48	-0.19

Appendix D. Eigenvectors of the first five principal components derived from the landscape context variables for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	LAND1	LAND2	LAND3	LAND4	LAND5
Eigenvalue	4.14	2.67	1.94	1.59	1.28
Percent variance explained	27.58	17.78	12.97	10.61	8.55
# of adjacent patches	0.40	0.16	-0.23	-0.24	0.15
# of adjacent patch types	0.42	0.13	-0.17	-0.21	0.04
# of interfaces	0.38	0.11	-0.24	0.27	0.18
% of patch perimeter adjacent to:					
Urban	0.18	0.03	0.58	-0.03	-0.05
Non-forested opening	0.23	0.16	0.07	-0.15	0.19
Forest	-0.34	0.10	-0.23	0.03	0.51
Open water	-0.15	0.05	0.08	-0.56	-0.48
Forested wetland	0.16	-0.43	-0.16	-0.01	-0.06
Bulrush marsh	0.09	0.26	-0.30	0.50	-0.24
Cattail marsh	0.28	-0.20	0.34	0.08	-0.09
Total wetland	0.33	-0.21	-0.18	0.40	-0.28
% of wet meadow in surrounding landscape (within 1-km of patch perimeter)	-0.03	0.30	0.24	0.10	0.18
% of Lake Huron in surrounding landscape (within 1-km of patch perimeter)	0.04	0.46	0.00	0.06	-0.28
Road density	0.25	-0.16	0.31	0.19	0.39
Stream density	0.08	0.50	0.18	0.16	-0.01

Appendix E. Eigenvectors of the first three principal components derived from the coastline complexity variables for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	COAST1	COAST2	COAST3
Eigenvalue	3.27	2.60	1.05
Percent variance explained	36.32	28.93	11.70
Total coastline			
500-m segments	0.20	0.51	-0.21
1-km segments	0.16	0.56	0.20
2-km segments	0.16	0.42	0.59
Sinuosity			
500-m segments	0.45	0.01	-0.34
1-km segments	0.29	-0.27	0.46
2-km segments	0.20	-0.40	0.38
Fractal dimension			
500-m segments	0.43	-0.10	-0.30
1-km segments	0.45	-0.02	-0.08
2-km segments	0.44	-0.12	0.07

Appendix F. Eigenvectors of the first five principal components derived from mean habitat variables for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

Habitat Variable	PC1	PC2	PC3	PC4	PC5
Eigenvalue	5.49	3.85	2.50	1.89	1.18
Percent variance explained	27.44	19.24	12.51	9.46	5.90
Water depth	0.13	-0.37	0.19	-0.06	-0.02
Hummock height	0.37	-0.05	0.12	-0.05	0.01
Grass height	0.40	0.03	0.06	-0.07	-0.05
Grass density	0.38	0.17	-0.00	-0.03	0.12
Woody vegetation density	-0.16	0.23	0.41	-0.13	-0.15
Total vegetation density	0.37	0.21	0.03	-0.01	0.09
Shrub foliage diversity	-0.12	0.10	0.52	-0.08	0.03
Frequency of cover types					
Graminoid	-0.00	0.19	-0.26	-0.48	0.14
Cattail	0.13	0.04	-0.22	0.23	-0.22
Bulrush	-0.31	-0.26	0.03	0.01	-0.02
Floating vegetation	0.21	-0.19	0.26	0.13	0.38
Submersed vegetation	0.28	0.19	0.03	-0.18	0.13
Willow	0.01	-0.16	0.40	-0.26	-0.37
Alder	-0.09	0.39	0.25	0.01	-0.07
Open water	0.03	-0.21	0.29	0.32	0.43
Moss	-0.26	0.12	-0.7	0.06	0.33
Frequency of trees and snags*					
Coniferous trees	-0.20	0.24	0.01	-0.06	0.43
Deciduous trees	0.02	0.33	0.06	0.37	-0.30
Coniferous snags	-0.08	0.32	0.12	-0.12	0.11
Deciduous snags	0.03	0.21	0.03	0.55	-0.05

* Frequency of trees and snags are mean values for 1997 because these variables did not change over one year.

Appendix G. Eigenvectors of the first two principal components derived from habitat variables that changed significantly between 1997 and 1998 for 40 wet meadows associated with the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan, 1997-1998.

Habitat Variable	CHANGE1	CHANGE2
Eigenvalue	2.17	1.78
Percent variance explained	31.04	25.41
Δ Water depth	0.24	0.56
Δ Grass height	0.36	0.42
Δ Grass density	0.58	-0.37
Δ Total vegetation density	0.58	-0.33
Δ Frequency of cover types		
Graminoid	-0.16	-0.39
Floating vegetation	0.14	0.34
Submersed vegetation	-0.30	-0.03

Appendix H. Eigenvectors of the first 6 principal components derived from the 1997 habitat variables for 21 wet meadows located in lobes or coves of the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	HAB1	HAB2	HAB3	HAB4	HAB5	HAB6
Eigenvalue	5.36	4.36	2.73	1.59	1.15	1.05
Percent variance explained	26.79	21.78	13.63	7.97	5.73	5.25
Water depth	-0.34	-0.21	0.10	-0.10	-0.19	-0.12
Hummock height	-0.36	-0.08	0.11	-0.10	-0.18	-0.12
Grass height	-0.37	0.17	0.09	-0.03	0.04	-0.00
Grass density	-0.23	0.34	-0.00	-0.02	-0.09	0.35
Woody vegetation density	0.29	0.08	0.37	-0.15	-0.13	0.09
Total vegetation density	-0.20	0.35	0.05	-0.01	-0.11	0.36
Shrub foliage diversity	0.21	0.02	0.45	-0.12	-0.05	0.14
Frequency of cover types						
Graminoid	0.13	0.25	-0.26	-0.36	0.02	-0.14
Cattail	-0.06	0.11	-0.13	0.53	0.24	-0.36
Bulrush	0.17	-0.38	0.04	0.15	-0.21	0.09
Floating vegetation	-0.18	-0.17	0.11	0.21	0.33	0.25
Submersed vegetation	-0.19	0.34	-0.02	-0.16	0.16	-0.07
Willow	0.00	-0.12	0.52	0.04	0.01	-0.22
Alder	0.24	0.26	0.25	0.04	-0.11	-0.25
Open water	0.03	-0.11	0.18	-0.11	0.65	0.34
Moss	0.25	0.02	-0.26	0.16	0.18	0.10
Frequency of trees and snags						
Coniferous trees	0.33	0.02	-0.21	-0.08	-0.19	0.32
Deciduous trees	0.07	0.22	0.24	0.49	-0.05	0.15
Coniferous snags	0.20	0.24	0.08	-0.22	0.35	-0.32
Deciduous snags	0.08	0.34	0.00	0.30	-0.18	-0.01

Appendix I. Eigenvectors of the first 5 principal components derived from the 1998 habitat variables for 21 wet meadows located in lobes or coves of the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	HAB1	HAB2	HAB3	HAB4	HAB5
Eigenvalue	6.13	4.66	2.11	1.61	1.22
Percent variance explained	30.64	23.31	10.57	8.06	6.09
Water depth	-0.06	-0.33	0.10	0.24	0.33
Hummock height	0.32	-0.20	0.06	-0.11	-0.09
Grass height	0.33	-0.21	0.07	-0.07	0.07
Grass density	0.38	-0.11	0.03	0.00	-0.08
Woody vegetation density	0.00	0.37	0.28	-0.19	0.04
Total vegetation density	0.38	-0.04	0.08	0.00	-0.06
Shrub foliage diversity	-0.09	0.31	0.36	-0.17	0.22
Frequency of cover types					
Graminoid	0.16				
Cattail	0.21	-0.36	-0.03	0.40	-0.06
Bulrush	-0.36	-0.04	0.17	0.06	0.10
Floating vegetation	0.00	-0.32	0.29	0.08	-0.37
Submersed vegetation	-0.27	-0.10	0.21	0.02	-0.23
Willow	-0.04	-0.09	0.49	-0.29	0.32
Alder	0.14	0.35	0.25	0.20	-0.00
Open water	-0.21	-0.20	0.08	0.27	-0.00
Moss	-0.32	0.08	-0.12	0.23	0.01
Frequency of trees and snags					
Coniferous trees	-0.14	0.26	-0.22	.01	-0.33
Deciduous trees	0.15	0.19	0.31	0.38	-0.08
Coniferous snags	0.11	0.27	0.03	0.01	-0.08
Deciduous snags	0.18	0.19	0.09	0.47	-0.19

Appendix J. Eigenvectors of the first 5 principal components derived from the landscape context variables for 21 wet meadows located in coves or lobes of the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	LAND1	LAND2	LAND3	LAND4	LAND5
Eigenvalue	4.87	3.00	2.02	1.56	1.10
Percent variance explained	32.44	20.01	13.45	10.40	7.31
# of adjacent patches	0.40	0.20	-0.03	-0.16	-0.08
# of adjacent patch types	0.42	0.07	-0.07	-0.14	-0.06
# of interfaces	0.40	0.12	-0.13	-0.16	-0.03
% of patch perimeter adjacent to:					
Urban	0.22	-0.09	-0.32	0.46	-0.38
Non-forested opening	0.19	0.25	-0.14	0.02	0.03
Forest	-0.33	0.26	0.11	0.18	0.25
Open water	-0.15	0.00	-0.42	-0.47	-0.09
Forested wetland	0.21	-0.30	0.12	-0.31	0.49
Bulrush marsh	0.06	0.00	0.61	-0.05	-0.40
Cattail marsh	0.25	-0.30	-0.22	0.15	0.27
Total wetland	0.26	-0.28	0.44	-0.14	0.02
% of wet meadow in surrounding landscape (within 1-km of patch perimeter)	0.12	0.35	0.08	0.22	0.54
% of Lake Huron in surrounding landscape (within 1-km of patch perimeter)	0.17	0.44	0.02	-0.11	-0.07
Road density	0.23	-0.23	0.05	0.50	0.04
Stream density	0.12	0.41	0.16	0.14	0.01

Appendix K. Eigenvectors of the first 3 principal components derived from the coastline complexity variables for 21 wet meadows located in coves or lobes of the northern shoreline of Lake Huron in Chippewa and Mackinac counties, Michigan.

Habitat Variable	COAST1	COAST2	COAST3
Eigenvalue	4.20	2.40	1.21
Percent variance explained	46.67	26.70	13.47
Total coastline			
500-m segments	0.13	0.54	-0.33
1-km segments	0.09	0.62	0.12
2-km segments	0.11	0.49	0.53
Sinuosity			
500-m segments	0.41	0.03	-0.37
1-km segments	0.42	-0.13	0.34
2-km segments	0.31	-0.25	0.48
Fractal dimension			
500-m segments	0.40	-0.04	-0.34
1-km segments	0.41	-0.02	-0.03
2-km segments	0.44	-0.09	-0.21

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