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Peninsula Effects on Birds in a Coastal Landscape: Are Coves More Species Rich than Lobes?

Sam Riffell[1*], Brian Keas[2], Thomas Burton[3]

[1] Department of Wildlife, Fisheries & Aquaculture, Mississippi State, MS, 39762 USA

[2] Department of Biological & Allied Health Sciences, Ohio Northern University, Ada, OH, 45810 USA

[3] Zoology Department, Michigan State University, East Lansing, MI, 48824 USA

[*] corresponding author: sriffell@cfr.msstate.edu

Abstract

Peninsula effects - decreasing richness with increasing distance along peninsula lobes - have been identified for many taxa on large peninsulas. Peninsula effects are caused by differences in colonization and extinction predicted by island biogeography or by environmental gradients along the peninsula. We compared species-area regressions for cove patches (i.e., mainland) to regressions for lobe patches (i.e., on peninsula tips) for wet meadow birds along a highly interdigitated shoreline (northern Lake Huron, USA). We conducted analysis both with and without accounting for variation in habitat and landscape characteristics (i.e., environmental gradients) of wet meadows. Species-area regressions for coves did not differ from lobes, nor did these results differ when we accounted for gradients. Similarly, few species were more abundant in coves. Peninsula effects may have been lacking because lobe patches were located ≈ 800 m on average from the mainland, and birds are highly mobile and can easily sample patches over these distances. One important caveat was that wet meadow patches > 5 ha were located in coves, so coves would still be important considerations in conservation plans because of the contribution of large patches to reproductive success, dispersal and population dynamics.

Keywords:

birds, coastal wetlands, Great Lakes, peninsula effect

1 Introduction

The phenomenon of decreasing species richness with increasing distance along peninsula lobes is called a peninsula effect (Simpson 1964, Forman and Godron 1986, Forman 1995). 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., Kiester 1971), but this pattern has not been consistently observed on all peninsulas or for all taxa (Tubelis et al. 2007 for review). Review of the evidence (Forman 1995, Tubelis et al. 2007) suggests that these patterns may be caused by mechanisms of colonization and extinction (geometry hypothesis as per Jenkins and Rinne 2008) 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 (e.g., habitat hypothesis as per Jenkins & Rinne 2008, and also 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 regional scales like a Great Lakes shoreline. This is surprising in light of the commonness of highly interdigitated landscapes in both coastal and terrestrial regions and the utility of such knowledge for conservation planning. At smaller scales, peninsula effects have been observed in plant species richness in coastal Maine peninsulas (Milne and Forman 1986), forest bird species richness in Brazilian savannas (Silva 1996) and riparian eucalypt forests in Australia (Tubelis et al. 2007). But, other studies at smaller scales are lacking. If such patterns are ubiquitous at both the continental and regional scales, such information would be extremely valuable in setting conservation priorities.

We compared bird species richness of coastal wet meadows located within coves to species richness of wet meadows located on peninsula lobes along the highly interdigitated, northern shoreline of Lake Huron in Michigan to test for the presence and cause of peninsula effects. If peninsula effects are caused by differences in colonization and extinction rates (i.e., geometry hypothesis, Jenkins and Rinne 2008, McArthur and Wilson, 1967), then patches located on lobes could be considered analogous to far islands and patches located within coves could be considered analogous to near islands. The geometry hypothesis makes two predictions. First, species should accumulate faster with area (steeper slopes) in lobe patches compared to cove patches because of lower colonization rates of cove patches. Second, cove patches should be generally more species rich (larger intercepts) because of higher colonization rates (see Figure 1 for graphical depiction of these predictions). Conversely, the habitat hypothesis predicts similar patterns between lobe and cove patches that result from differences habitat features between cove and lobe patches. We differentiated between the two possible explanations by testing predictions of the habitat hypothesis and controlling for variation related to habitat and landscape characteristics that might vary along the peninsular gradient (Taylor and Regal 1978, Tubelis et al. 2007) before testing predictions of the geometry hypothesis.

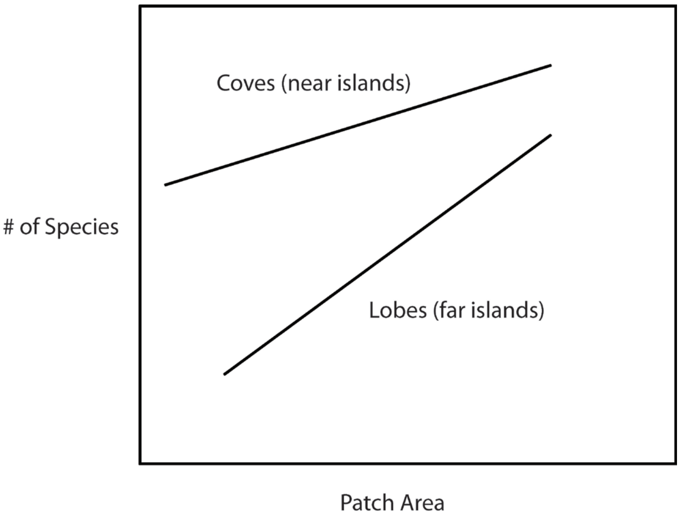

Figure 1: Theoretical shape of species-area relationships in cove vs. lobe patches as predicted by the geometry hypothesis.

2 Methods

2.1 Study Area

We worked in wet meadows located along the highly convoluted, northern shoreline of Lake Huron in the Upper Peninsula of Michigan (Mackinac and Chippewa counties, see Figure 2A). All wet meadows were seasonally or shallowly flooded grasslands, within 500 m of the shoreline, influenced by lake water levels, and 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* sp. and *Ourrica* spp.). Submersed (*Potomageton* spp.) and floating (*Polygonum* spp., *Lemna* spp.) vegetation were often present in standing water between hummocks.

2.2 Bird Counts

We established 200-m wide, permanent line transects (Riffell et al. 2003) in each of the wet meadows and recorded birds multiple times between 15 May and 4 July of each year (4 times in 1997; 5 times in 1998). All counts were conducted between 0530 and 1030 EST. Transect length varied with the size of the individual wetlands. We minimized variation due to weather (we did not sample when temperatures were < 0°C; or when strong winds, steady rainfall, or fog limiting visibility to < 300 m were present [Riffell et al. 2001, 2003]), all counts were conducted by one observer (SR), and counts were augmented by broadcasting recorded vocalizations of secretive species (Gibbs and Melvin 1993).

2.3 Habitat Characteristics

Because variation in habitat characteristics along peninsular gradients can influence bird species richness (Taylor and Regal 1978, Tubelis et al. 2007), we measured 20 habitat characteristics along each bird transect in late July after vegetation had reached mature height (Riffell et al. 2001, Riffell et al. 2003). We used a combination of point-intercept techniques (Rotenberry and Wiens 1980) to estimate water depth, hummock height and vegetation density, frequency of occurrence in 1m^2 quadrats to estimate percent cover of various vegetation types, and frequency of occurrence in 2.5m radius circular plots to estimate density of trees and snags. Our habitat sampling methods are described in detail elsewhere (Riffell et al. 2001). Habitat variables are listed in Table 1.

Table 1: Eigenvectors of principal components derived from the 1997 and 1998 habitat variables for 21 wet meadows associated with the northern Lake Huron shoreline, Michigan. Coefficients in boldface contributed most strongly to interpretation.

	1997						1998				
Habitat Variable	HPC1	HPC2	HPC3	HPC4	HPC5	HPC6	HPC1	HPC2	HPC3	HPC4	HPC5
Eigenvalue	5.36	4.36	2.73	1.59	1.15	1.05	6.13	4.67	2.53	1.60	1.21
Percent variance extracted	26.8	21.8	13.6	8.0	5.7	5.3	30.6	23.3	10.7	8.0	6.0
Water depth	**-0.34**	-0.21	0.10	-0.10	-0.19	-0.12	-0.05	**-0.34**	0.09	0.23	**0.31**
Hummock height	**-0.36**	-0.08	0.11	-0.10	-0.18	-0.12	**0.32**	-0.20	0.11	-0.09	-0.00
Grass height	**-0.37**	0.17	0.09	-0.03	0.04	-0.00	**0.33**	-0.21	0.05	-0.08	0.05
Grass density	-0.23	**0.34**	-0.00	-0.02	-0.09	**0.35**	**0.38**	-0.10	0.01	0.00	-0.10
Shrub density	0.29	0.08	**0.37**	-0.15	-0.13	0.09	0.01	**0.37**	0.28	-0.18	0.03
Total vegetation density	-0.20	**0.35**	0.05	-0.01	-0.11	**0.36**	**0.38**	-0.04	0.06	0.00	-0.08
Shrub foliage diversity	0.21	0.02	**0.45**	-0.12	-0.05	0.14	-0.09	**0.30**	**0.37**	-0.16	0.24
Frequency of cover types:											
Graminoid	0.13	0.25	-0.26	**-0.36**	0.02	-0.14	0.16	0.21	**-0.35**	-0.05	**0.39**
Cattail	-0.06	0.11	-0.13	**0.53**	0.24	**-0.36**	0.09	-0.05	-0.03	**0.48**	**-0.47**
Bulrush	0.17	**-0.38**	0.04	0.15	-0.21	0.09	**-0.36**	-0.04	0.18	0.07	0.12
Floating vegetation	-0.18	-0.17	0.11	0.21	**0.33**	0.25	0.00	**-0.32**	0.28	0.09	**-0.39**
Submersed vegetation	-0.19	**0.34**	-0.02	-0.16	0.16	-0.07	-0.27	-0.10	0.21	0.03	-0.22
Willow	0.00	-0.12	**0.52**	0.04	0.01	-0.22	-0.03	-0.09	**0.49**	-0.29	0.29
Alder	0.24	0.26	0.25	0.04	-0.11	-0.25	0.14	**0.35**	0.25	0.21	0.00
Open water	0.03	-0.11	0.18	-0.11	**0.65**	**0.34**	-0.21	-0.21	0.08	0.27	0.03
Moss	0.25	0.02	-0.26	0.16	0.18	0.10	**-0.32**	0.08	-0.11	0.23	0.04
Frequency of trees & snags:											
Coniferous trees	**0.33**	0.02	-0.21	-0.08	-0.19	**0.32**	-0.15	0.27	-0.22	0.03	**-0.32**
Deciduous trees	0.07	0.22	0.24	**0.49**	-0.05	0.15	0.15	0.19	**0.30**	**0.39**	-0.09
Coniferous snags	0.20	0.24	0.08	-0.22	**0.35**	**-0.32**	0.12	0.27	0.04	0.01	-0.05
Deciduous snags	0.08	**0.34**	0.00	**0.30**	-0.18	-0.01	0.18	0.19	0.08	**0.47**	-0.18

2.4 Landscape Characteristics

Surrounding land use of the northern Lake Huron shoreline was interpreted into an ArcView GIS from 1:24,000-scale color aerial photographs taken in 1992. We classified the landuse/landcover of each patch in the coastal landscape (wet meadow sites and surrounding habitats) into one of 15 patch types (Riffell et al. 2003) and verified and updated these classifications by extensive visual ground-truthing in spring 1999. We used this GIS to calculate wet meadow area, wet meadow perimeter, perimeter/area ratio (Helzer and Jelinski 1999) and the proportion of the perimeter adjacent to specific patch types. Buffer operations were used to calculate density of wet meadow, Lake Huron, roads and streams within 1km of the wet meadow border. Landscape characteristics are listed in Table 2 (see also Riffell et al. 2003).

Table 2: Eigenvectors of principal components derived from landscape variables measured for 21 wet meadows associated with the northern Lake Huron shoreline, Michigan.

Habitat Variable	LPC1	LPC2	LPC3	LPC4	LPC5
Eigenvalue	4.87	3.00	20.02	1.56	1.10
Percent variance explained	32.4	20.0	13.5	10.4	7.3
# 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
Proportion 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
Characteristics of the surrounding landscape (within 1-km):					
Proportion wet meadow	0.12	**0.35**	0.08	0.22	**0.54**
Proportion Lake Huron	0.17	**0.44**	0.02	-0.11	-0.07
Stream density	0.12	**0.41**	0.16	0.14	0.01
Road density	0.23	-0.23	0.05	**0.50**	0.04

2.5 Statistical Analysis

2.5.1 Site Selection

Of the 40 wet meadows counted for breeding birds, we identified 30 which were clearly located either in a cove or out on a lobe (for example, see Figure 2B). Wet meadows not clearly located in either a cover or lobe were excluded from analyses. Initial examination of the species-area curve for these wet meadow patches revealed that the range of patch area was much higher for cove sites than for lobe sites (i.e., most larger wet meadows were in coves, see Figure 3). Because it is inappropriate to compare regression lines or other statistics which are estimated over disparate ranges, we restricted statistical analysis over a range (< 5 ha) that included both lobe and cove sites. This resulted in 21 sites that were retained for analysis (cove sites n = 10; lobe sites n = 11). Centers of lobe patches were located a mean distance of 817 m from the mainland (ranging from 157 m – 2268 m).

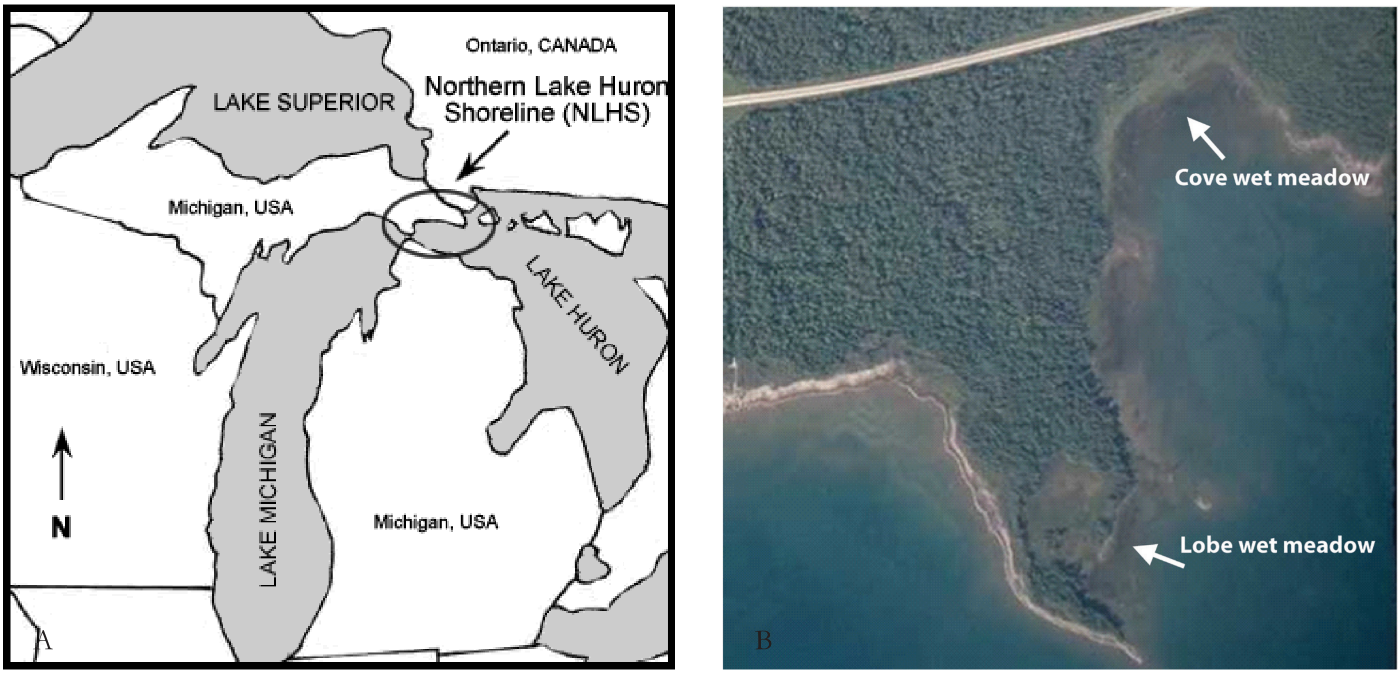

Figure 2: (A) Location of northern Lake Huron shoreline study area. (B) Portion of the northern Lake Huron shoreline (Michigan, USA) containing wet meadows located both in coves and out on lobes of the interdigitated shoreline. Photo credit: Michigan State University.

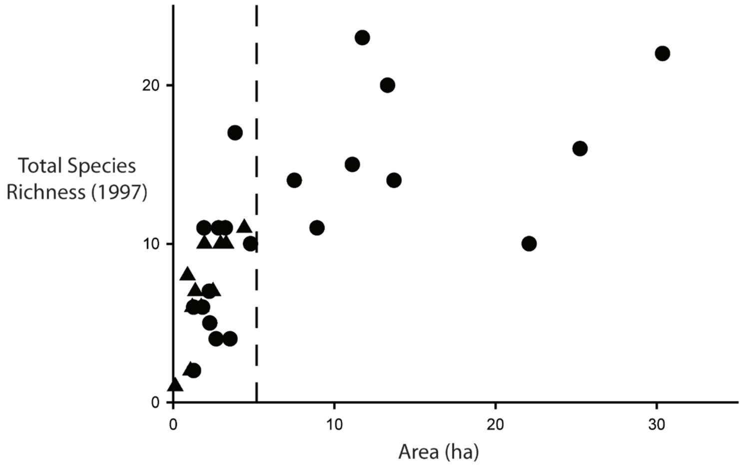

Figure 3: Species-area relationships in 30 wet meadows located in coves (circles) or out on lobes (triangles) along the northern Lake Huron shoreline, Michigan, USA. Twenty-one sites to the left of the dashed line were retained for analysis.

2.5.2 Analysis of Habitat and Landscape Variables

To test for differences in habitat and landscape characteristics between cove and lobe sites that might be confounded with true peninsula effects, we used Welch's *t*-tests to compare each habitat and landscape variable between cove and lobe sites. We used $\alpha = 0.10$ for all tests.

Because we wanted to use habitat and landscape variables in subsequent tests for peninsula effects (see below), we used principal component analysis (PCA) to reduce the number of variables and avoid problems associated with collinearity. We conducted three separate principal component analyses: once each for 1997 habitat characteristics and 1998 habitat characteristics, and a third PCA for landscape variables (Tables 1 and 2). For each of the 3 sets of variables, we retained components with eigenvalues > 1 for further analysis.

2.5.3. Construction of Bird Variables

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

2.5.4 Species-area Regressions

Habitat characteristics (e.g., Riffell et al. 2001) and landscape characteristics (e.g., Brown and Dinsmore 1986, Naugle et al. 1999, Riffell et al. 2003) can potentially affect patterns of bird species richness and could thus be confounded with or mask true peninsula effects if they differ between lobe and cover sites. To ameliorate this, we conducted tests for peninsula effects both with and without accounting for effects of these variables.

To test hypotheses about differences in species-area relationships of coves and lobes, we 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; we restricted the number of habitat/landscape components to one. Using Proc RSquare (SAS Institute, Inc. 1989), we identified the principal component that was the best, single predictor of each richness variable from a set of variables including area, perimeter-area ratio, habitat components, and landscape 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 the best predictor, and the residuals from this regression were saved and used as the dependent variable in the second regression.

In the second-stage of regression, we used these adjusted richness variables (residuals) to test for differences in species richness patterns between cove patches and lobe patches. We conducted separate adjusted species richness vs. area regressions for cove and lobe patches and then tested for differences in the slope and intercept parameters. We 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 the 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 (Figure 1). The alternate hypotheses were that species-area regressions involving cove patches would have higher intercepts but smaller slopes than regressions involving lobe patches. We 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). We also compared slopes and intercepts on unadjusted data (i.e., a single stage regression without covariates). For all statistical tests, we 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, we did not conduct transformations unless it was necessary to meet the assumptions of regression. The species-area curve involving all 30 cove and lobe patches demonstrated the classical curvilinear relationship, but our analyses were restricted to only the linear part of the relationship (Figure 3). Thus, we suspected that the assumptions of regression might be satisfied without transformations (sensu Rahbek 1997). We 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.

2.5.5. Species' abundance and presence/absence

For total bird abundance and abundance of species that occurred on at least 2/3 of the sites, we used traditional linear models to test for differences in abundance between cove and lobe sites. We restricted the number of covariates to one covariate for each abundance variable (see above). We identified the single, best predictor from the set of habitat and landscape components. The final linear model included one covariate (the best predictor) and cove/lobe designation as the main effect. For species occurring on < 2/3 of the sites, we used presence/absence data. Before testing for differences between coves and lobes, we identified the single, best predictor from among the habitat and landscape 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/lobe position, we used Wald χ^2 statistics. All test statistics and *P*-values were based on Type III sums of squares which 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. We also conducted these tests without the habitat and landscape covariates (unadjusted data). We used $\alpha = 0.10$ for all tests.

3 Results

3.1 Habitat Characteristics

Although wet meadows were selected based on similar habitat features, the habitat variables we measured did vary among wet meadows. Habitat characteristics are summarized elsewhere (Riffell et al. 2001) and are beyond the scope of this paper. Principal component analysis identified 6 components in 1997 and 5 components in 1998 (Table 1) 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 ($t_{13.3}$=-1.92, *P*=0.077) and submersed vegetation (t_{16}=-1.96, *P*=0.067) were greater in lobe patches than in cove patches in 1998, but not in 1997. None of the other 18 habitat characteristics we 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.

3.2 Landscape Characteristics

Landscape characteristics varied among wet meadows. However, discussion of these characteristics is beyond the scope of this paper (see Riffell et al. 2003). For these analyses, PCA identified 5 landscape components (Table 2). These components accounted for 84% of the variation in the original variables.

Wet meadow patches on lobes had a greater number of adjacent patches ($t_{17.5}$ = -1.80, *P* = 0.089), more adjacent non-forested openings (t_{10}= -2.03, *P* = 0.070) and a greater proportion of the surrounding landscape comprised of Lake Huron ($t_{18.5}$= -3.75, *P* = 0.001). This is twice the number of significant tests (15 habitat variables x 0.10 = 1.5) expected due to chance. None of the other landscape characteristics differed between cove and lobe patches.

3.3 Species Richness

We 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 3). Because richness-area relationships were consistent between analysis that included habitat or landscape components and those using unadjusted richness estimates, these relationships are likely true area effects independent of habitat or landscape effects on species richness. Richness of non-nesting species was not significantly related to area (Table 3).

We observed little evidence of peninsula effects on species-area relationships. Intercepts from cove regressions were not different from lobe regressions (Table 3). For non-nesting species richness in 1998, the slope was greater for lobe sites than for cove sites as predicted ($P = 0.086$) when using richness adjusted for habitat and landscape characteristics. However, slopes did not differ for any other richness variable in either year. This single significant test is out of a total of 24 tests on slopes and intercepts. Additionally, regression parameters did not differ between coves and lobes in a consistent direction.

Table 3: Coefficients of unadjusted and adjusted species-area regressions for cove and lobe wet meadows associated with the northern shoreline of Lake Huron, Chippewa and Mackinac counties, Michigan (cove n = 10 and lobe n = 11). Selected habitat and landscape components are in parentheses. * indicates that the slope for that particular species-area regression was significant ($P < 0.10$).

Parameter	Coves	Lobes	Difference	*t*	*P*-value
		Total Species Richness – 1997 (Unadjusted)			
Slope	1.72*	2.10*	-0.38	-0.39	0.351
Intercept	3.12	3.00	0.12	0.68	0.255
		Total Species Richness – 1997 (HABPC3)			
Slope	1.59	1.36*	0.23	0.24	0.594
Intercept	-3.72	-2.80	-0.92	-0.53	0.699
		Total Species Richness – 1998 (Unadjusted)			
Slope	2.28*	2.63*	-0.35	-0.31	0.380
Intercept	1.66	2.14	-0.48	-0.23	0.588
		Total Species Richness – 1998 (LANDPC5)			
Slope	1.29*	2.00*	-0.71	-0.70	0.247
Intercept	-2.59	-4.41	1.82	0.98	0.171
		Nesting Species Richness – 1997 (Unadjusted)			
Slope	1.24	1.63*	-0.39	-0.46	0.327
Intercept	3.08	2.55	0.53	0.36	0.362
		Nesting Species Richness – 1997 (LANDPC1)			
Slope	0.86	1.42*	-0.56	-0.75	0.232
Intercept	-1.58	-3.24	1.66	1.20	0.123

Table 3: Continued

Parameter	Coves	Lobes	Difference	*t*	*P*-value
		Nesting Species Richness – 1998 (Unadjusted)			
Slope	1.93*	1.67*	0.26	0.36	0.637
Intercept	1.50	2.20	-0.70	-0.52	0.695
		Nesting Species Richness – 1998 (HABPC3)			
Slope	2.02*	1.06*	0.96	1.54	0.929
Intercept	-4.71	-2.24	-2.47	-1.59	0.977
		Non-nesting Species Richness – 1997 (Unadjusted)			
Slope	0.48	0.47	0.01	0.00	0.500
Intercept	0.04	0.45	-0.41	0.09	0.466
		Non-nesting Species Richness – 1997 (LANDPC5)			
Slope	0.44	0.27	0.17	0.16	0.563
Intercept	-0.69	-0.71	-0.02	-0.02	0.507
		Non-nesting Species Richness – 1998 (Unadjusted)			
Slope	0.34	0.96	0.62	1.07	0.850
Intercept	0.16	-0.06	0.24	0.21	0.419
		Non-nesting Species Richness – 1998 (LANDPC5)			
Slope	-0.04	0.71	-0.75	-1.43	0.086
Intercept	-0.09	-1.22	1.13	1.15	0.133

* Abundance variables use a standard least squares F-statistics. Presence/absence variables use a Wald X2-statistic.

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

3.4 Individual Species

We conducted 40 tests on abundance and presence/absence data for 11 different species (Table 4). Some species occurred frequently enough for statistical analysis during only one year. When including a habitat or landscape component, Swamp Sparrow abundance was higher in cove patches 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. Not accounting for habitat or landscape components did not change these results, with the exception of Great Blue Heron which did not differ between coves and lobes when landscape components were not included. We observed a total of 10 significant tests which is approximately 2.5 times the number (0.10 x 40 tests = 4) of significant tests expected by chance alone.

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Table 4: 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	Unadjusted	-0.62	0.52	0.478
1997	HAB3 (+)	-0.56	0.59	0.453
1998	Unadjusted	-0.55	0.16	0.691
1998	LAND5 (-)	0.08	0.00	0.948
Common Yellowthroat (*Geothlypis trichas*)				
1997	Unadjusted	0.25	1.15	0.297
1997	HAB4 (-)	0.28	1.82	0.195
1998	Unadjusted	-0.18	0.56	0.462
1998	HAB2 (+)	-0.18	0.71	0.411
Swamp Sparrow (*Melospiza georgiana*)				
1997**	Unadjusted	-0.67	0.53	0.465
1997**	HAB2 (+)	-0.17	0.02	0.876
1998	Unadjusted	0.89	9.24	0.007
1998	HAB1 (+)	0.66	5.43	0.032
Song Sparrow (*Melospiza melodia*)				
1997	Unadjusted	-0.50	9.93	0.005
1997	Area (-)	-0.44	-8.93	0.008
1998	Unadjusted	-1.24	1.25	0.277
1998	Area (-)	-0.50	0.26	0.619
		Presence-Absence Variables		
Great Blue Heron (*Ardea herodias*)				
1997	Unadjusted	-0.65	0.40	0.525
1997	LAND1 (+)	4.89	4.88	0.027
American Bittern (*Botaurus lentiginosus*)				
1997	Unadjusted	-0.65	0.40	0.252
1997	LAND5 (-)	1.86	1.81	0.178
1998	Unadjusted	-0.65	0.40	0.252
1998	HAB2 (+)	1.17	0.79	0.373

Table 4: Continued

Variable	Covariate	Parameter	F or χ^2	*P*-Value*
Mallard (*Anas platyrhynchos*)				
1997	Unadjusted	0.59	0.44	0.507
1997	LAND1 (+)	-0.15	0.02	0.883
Virginia Rail (*Rallus limicola*)				
1997	Unadjusted	-0.66	0.40	0.529
1997	LAND1 (+)	0.24	1.37	0.242
Alder Flycatcher (*Empidonax alnorum*)				
1997	Unadjusted	-0.18	0.04	0.835
1997	HAB3 (+)	0.28	0.08	0.780
1998	Unadjusted	-0.59	0.45	0.504
1998	--	-0.59	0.45	0.504
Yellow Warbler (*Setophaga petechia*)				
1997	Unadjusted	-0.22	0.06	0.801
1997	LAND5 (-)	0.96	0.74	0.377
1998	Unadjusted	0.18	0.04	0.835
1998	LAND5 (-)	0.30	0.08	0.770
Red-winged Blackbird (*Agelaius phoeniceus*)				
1997	Unadjusted	0.18	0.04	0.835
1997	LAND1 (+)	0.74	0.04	0.537
1998	Unadjusted	-1.41	2.28	0.119
1998	HAB2 (-)	2.02	2.63	0.080
American Goldfinch (*Spinus tristis)*				
1998	Unadjusted	-1.91	3.55	0.045
1998	HAB3 (+)	-7.82	8.73	0.003

4 Discussion

4.1 Habitat and Landscape Characteristics

Both habitat characteristics such as grass density vertical structure and heterogeneity (Rotenberry and Wiens 1980, Craig and Beal 1992, Herkert 1994) and characteristics of the surrounding landscape (Riffell et al. 2003) can influence 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, habitat and landscape components could have influenced 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 (i.e., the habitat hypothesis; Jenkins & Rinne 2008). In this study, habitat characteristics did not differ between coves and lobes. The only differences between lobes and coves for landscape characteristics were that lobe patches had more adjacent habitat types, more adjacent non-forested openings and more open water from Lake Huron in the surrounding landscape. These differences were not surprising given lobe patches were by definition projecting out into the lake. Thus, there were few 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), no gradient was reflected in 35 major habitat and landscape characteristics. Plus, results of tests for cove and lobe differences in species richness did not generally differ when we accounted for habitat and landscape components compared to unadjusted analyses. This evidence further reduces the likelihood that habitat characteristics were confounded with the cove/lobe designations.

4.2 Species Richness vs. Area Regressions

We only detected one difference in intercepts (non-nesting species richness in 1998), and no differences in slopes (Table 4). Although this one significant test was consistent with the prediction that species-area slopes would be steeper in lobe patches (sensu the geometry hypothesis; Jenkins & Rinne 2008); it could also be a single spurious result, especially as regression parameters for other richness variables did not differ between coves and lobes in a consistent direction or magnitude. Because of small sample size (and consequently likely low power), we cannot rule out the possibility that small peninsula effects might still be present in Great Lakes coastal wet meadows. Yet, because of the lack of consistent patterns in the regression parameters, it is unlikely 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.

One hypothesized mechanism for differences between lobe and cove patches (essentially peninsula effects) is gradients in habitat or environmental conditions along the peninsula may sometimes produce peninsular gradients in species richness on a large scale (e.g., Taylor and Regal 1978; Milne and Forman 1987). Because habitat differences were slight or absent in our study area, it is unlikely that habitat-driven peninsula effects could have occurred (habitat hypothesis; Jenkins & Rinne 2008), although differences in environmental variables we did not measure (e.g., wind speeds) might have existed. A second hypothesis is the geometry hypothesis (Jenkins & Rinne 2008) which states that peninsula effects should be present because of the effect of distance from the mainland on colonization rates (see also MacArthur and Wilson 1967), but the northern Lake Huron shoreline 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) and birds (Silva 1996, Tubelis et al. 2007), but birds are highly vagile organisms capable of traversing (and hence colonizing) these distances easily. For this reason peninsula effects at this spatial scale may not always exist for birds or be so subtle that they are difficult to detect. Additionally, in this region migrating birds arrive travelling north in the springtime, and thus peninsula tips may first intercept birds after crossing the lake (Gutzwiller and Anderson 1992). This could potentially increase the likelihood of a species colonizing a lobe patch and offset existing peninsula effects. A third hypothesis is that peninsula effects are artefacts of past climatic or geologic events. However, the history hypothesis (Jenkins & Rinne 2008) is not likely a factor for the northern Lake Huron shoreline because the short peninsulas (relative to continental peninsulas like Baja California; e.g., Wiggins 1999) we studied have been subject to the same climatic and geological forces over time.

4.3 Responses 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 (Poole 1995), or they may simply avoid habitats close to open water such as those on lobes. Similarly, Red-winged Blackbirds regularly use upland habitats (among others) for foraging (Orians 1980), and cove patches were likely near to more of these types of habitats. Great Blue Herons 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 Herons use for retreat when threatened (Poole 1995). Swamp Sparrow and Red-winged Blackbird were the only wetland/grassland breeding species that were more abundant in cove patches. Although habitat features were not generally different between cove and lobe wet meadows, cove patches may buffer many environmental factors we did not measure. Further research is needed to test these possibilities.

Song Sparrow was the only species 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 congeneric Swamp Sparrow) may be less abundant in lobes.

Although we 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, the difference in bird communities between coves and lobes does not appear to be important in Great Lakes coastal wet meadows. More research at a variety of spatial scales and with greater replication should be conducted to identify more completely the suite of species which exhibit peninsula effects.

4.4 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 Heron coastal region. However, we caution that dismissing 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, we 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 difference in species richness.

An important caveat is that all of the wet meadows larger than 5 ha in the region were located in coves (Figure 3), and the importance of large patches to the reproductive success of birds (e.g., Ribic et al. 2009), 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 shoreline should target large wetlands located in coastal coves. There may also be subtle differences in habitat characteristics or environmental conditions between lobes and coves, and such differences could represent a difference in habitat quality of wildlife. Without further research, however, the importance of these differences will not be fully understood.

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