Grasshopper Sparrow Distribution, Habitat Associations,
and Use as an Indicator Species for Grassland Birds in Southwestern Minnesota

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Dedication

This thesis is dedicated to R. A. Mauck, who inspired me to major in biology as an undergraduate despite all my best intentions to the contrary.

Abstract

Reductions in grassland habitat due to agricultural conversion have caused severe declines in populations of many grassland bird species. Effective grassland bird conservation requires efficient use of limited funding. Techniques advocated by conservationists include: 1) focusing management activities on a single indicator species that represents the habitat and management requirements of other species, 2) managing existing preserved habitat for appropriate vegetation structure to ensure desired population responses, and 3) identifying areas of high value for species of interest through remotely sensed data. In Minnesota, the Grasshopper Sparrow (*Ammodramus savannarum*) has been identified as a species of conservation interest and potential management indicator species. My objectives were to: 1) assess the extent to which the Grasshopper Sparrow and seven other passerines might serve as grassland bird indicators, 2) identify local-scale habitat associations of these species, and 3) develop and assess the suitability of landscape-scale species distribution models for the Grasshopper Sparrow. To address these objectives I conducted bird and vegetation surveys on 71 grassland sites in southwestern Minnesota during 2013–2014, examined patterns of community composition and species-specific habitat associations, and modeled Grasshopper Sparrow density. I found that the Grasshopper Sparrow could reasonably be used as a management indicator for five of seven grassland species. Inclusion of a second indicator species could improve representation of the entire group of species. Grasshopper Sparrow density was positively associated with distance to trees and negatively associated with vegetation height, vegetation density, and percent tree cover.

Grasshopper Sparrow density also exhibited nonlinear relationships with litter and percentages of shrub, dead vegetation, and bare ground cover. Judicious selection of explanatory variables offered an efficient approach to determination of species' habitat requirements and predicting their occurrences. Finally, using both local-scale habitat and remotely sensed landscape variables produced a better model than using variables at either scale alone.

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CHAPTER 1. EVALUATING THE GRASSHOPPER SPARROW (*AMMODRAMUS SAVANNARUM*) AS A MANAGEMENT INDICATOR SPECIES

Funding constraints have highlighted the need for efficient approaches to manage remaining wildlife habitat. One such approach is to monitor a single species that serves as an indicator of management effectiveness. The Grasshopper Sparrow (*Ammodramus savannarum*) is an obligate dry upland prairie species that has been identified as a potential indicator species in Minnesota. To evaluate whether this species (or another) would make a suitable indicator for grassland birds in southwestern Minnesota, I examined the strength of correlations in the density and occurrence of Grasshopper Sparrows and those of other grassland species: Sedge Wren (*Cistothorus platensis*), Savannah Sparrow (*Passerculus sandwichensis*), Henslow's Sparrow (*Ammodramus henslowii*), Dickcissel (*Spiza americana*), Bobolink (*Dolichonyx oryzivorus*), Western Meadowlark (*Sturnella neglecta*), Brown-headed Cowbird (*Molothrus ater*) and a composite of all grassland obligates encountered, not only those listed here. I calculated correlation coefficients to measure linear association of density, conducted logistic regression analyses to predict occurrence from density, and used generalized linear models to predict density from occurrence. I then compared avian community composition between grassland sites with and without Grasshopper Sparrows. Overall, density of the composite group was most strongly correlated with densities of individual species; no single species was a good predictor for all other species. Grasshopper Sparrow, Savannah Sparrow, and Bobolink density significantly predicted the greatest numbers of other species' densities and occurrences. Bobolink, Dickcissel, and

Grasshopper Sparrow occurrence significantly predicted the greatest numbers of other species' densities. Density of all species except Sedge Wren and Brown-headed Cowbird were significantly higher at sites with Grasshopper Sparrows. Therefore, the Grasshopper Sparrow is a reasonable choice as an indicator species within this region. However, a better approach would be to select multiple, complimentary indicator species to ensure that species not well-indicated by Grasshopper Sparrows are adequately represented.

INTRODUCTION

Human land use change is one of the greatest threats to biodiversity today. This is especially true in temperate grasslands (Hoekstra et al. 2005). In North America alone, greater than 50% of native prairie habitat has been converted to human land use (Hoekstra et al. 2005), in particular agriculture (Askins et al. 2007). While so much grassland is being turned to crop production, very little is being set aside for protection (Hoekstra et al. 2005). The result has been increasing habitat fragmentation and habitat loss that has greatly impacted grassland species (Herkert 1994; Herkert *et al*. 2003). Between 1966 and 2014, grassland bird populations have declined more dramatically than almost any other group of birds breeding in the Midwest (Herkert 1995; North American Bird Conservation Initiative U.S. Committee 2014). Veech (2006) found that during the years 1982-2002, 1633 populations representing 36 species declined in the Great Plains region of the U.S.

The need to focus conservation efforts in grasslands and other habitats has resulted in various approaches that aim to efficiently prioritize areas to be set aside as reserves. The focal-species approach calls for identifying the range of threats to biodiversity and using the species most sensitive to those threats as the basis for conservation planning (Lambeck 1997). In theory, protecting the most-sensitive species will incidentally provide full protection for all other species. However, there has been a great deal of concern over the practical utility of this and similar methods that rely on managing overall biodiversity through the protection and monitoring of a subset of organisms (Roberge & Angelstam 2004), and many studies have examined the utility of these methods (Simberloff 1998; Andelman and Fagan 2000; Garson *et al*. 2002; Favreau *et al*. 2006; Ficetola *et al*. 2007; Rodrigues and Brooks 2007).

One major flaw of the focal-species approach is that no single species, guild, or taxon will have the same requirements as all other groups and therefore cannot serve as representative indicators of biodiversity (Lambeck 2002; Lindenmayer *et al*. 2002). This problem has been documented in the prairie ecosystems of North America, where the use of non-representative indicators has been common because most prairie conservation in North America has focused on protecting waterfowl habitat for the purpose of hunting (Koper & Schmiegelow 2006; Skinner & Clark 2008; Johnson et al. 2012). As a result, most of the protected grassland is associated with prairie wetlands. Many prairie organisms prefer drier upland areas. Although many waterfowl use upland prairie as nesting habitat, benefits to non-game upland species through the protection and management of these areas have been largely incidental and some practices such as predator control may be detrimental to them (Johnson et al. 2012). Therefore, because ducks do not serve as an adequate umbrella species for conservation of all dry upland prairie birds (Koper & Schmiegelow 2006; Skinner & Clark 2008), it is necessary to find a suitable representative for these species that can be used as an indicator of their habitat, distribution, and responses to management activities.

Several different evaluation methods have been proposed to identify suitable indicators (Wiens et al. 2008). Small endemic birds with moderate abundances and diverse habitat preferences are ideal candidates for modelling bird species richness at a global scale (Carrascal et al. 2012). However, I am explicitly interested in those species which are restricted to dry prairie environments so the requirement for flexible habitat preferences is of less importance. Instead, we can identify groups of similar species that share characteristics such as habitat preference (Bishop & Myers 2005) and find a suitable indicator species from within that group. Fleishman *et al*. (2000) recommend that an ideal indicator would be somewhat rare; highly sensitive to disturbance; co-occur with a high percent of other species; and would parallel the abundance of other species, not just their presence or absence.

Grasshopper Sparrows (*Ammodramus savannarum*) have been proposed as a possible indicator for other dry upland prairie birds and possibly other taxa with similar habitat requirements (Ringelman *et al*. 2005; Quamen 2007). This species is characterized by several traits that would make it a suitable indicator. Due to population declines consistent with other grassland bird species (Herkert 1994; Sauer and Link 2002; Nocera and Koslowsky 2011), Grasshopper Sparrows have been identified as a species of conservation concern at state and regional levels within the Midwestern United States (Bakker 2005; Ringelman *et al*. 2005; Minnesota Department of Natural Resources 2006; Minnesota Prairie Plan Working Group 2011). This species is moderately abundant (0.20 - 0.25 birds/ha; Quamen 2007), which means its abundance is well suited for statistical analysis. Grasshopper Sparrows exhibit similar variability in abundance as Henslow's Sparrows and Savannah Sparrows (Dornak 2010). The responses of Grasshopper Sparrows to haying (Nocera & Koslowsky 2011), grazing (Sutter & Ritchison 2005), and trees in the landscape (Grant et al. 2004) demonstrate that this species is sensitive to disturbance. Furthermore, Grasshopper Sparrows' habitat requirements exhibit a great deal of overlap with other upland prairie species because they are dry prairie specialists (Vickery 1996; Slater 2004). For instance, Wiens (1969) found evidence that Grasshopper Sparrows, Savannah Sparrows, and Eastern Meadowlarks used habitats with similar litter and vegetation characteristics.

To determine if the Grasshopper Sparrow (or another species) would make a suitable indicator for dry upland prairie birds, I collected bird survey data in two years to compare occurrences and abundances (as suggested by Fleishman et al. 2000) of seven dry upland prairie species in southwestern Minnesota. Grasshopper Sparrow, Dickcissel (*Spiza americana*), and Savannah Sparrow (*Passerculus sandwichensis*) have been documented to use dry or dry-mesic prairie habitat (Sample & Hoffman 1989). Bobolink (*Dolichonyx oryzivorus*) and Western Meadowlarks (*Sturnella neglecta*) also use upland prairie habitat (McCracken & Rowan 2005). I expected that Grasshopper Sparrow occurrences and annual abundance would be closely correlated with the abundances of these four other species because they share upland prairie habitat. I also compared the occurrences and abundances of these species to those of the Henslow's Sparrow (*Ammodramus henslowii*) which is likewise a grassland obligate that co-occurs with Grasshopper Sparrows (Dornak 2010), but which is also tolerant of wet meadow and idle hayfield habitat (Herkert 2015). I expected that this species would be less closely correlated with the other grassland obligates because while it may be present at dry upland sites, it would also likely be present at wetter sites. As a further comparison, I compared the occurrences and abundances to those of Sedge Wren (*Cistothorus paltensis*). This species is frequently associated with wet prairie (Shaffer et al. 2015b), so I expected its abundance to be inversely related to the abundances of the other species.

In addition, I compared the abundances of all of these obligate grassland species to the abundance of Brown-headed Cowbird (*Molothrus ater*), a habitat generalist, because this species is a brood parasite that has an impact on nest success of other species (Patten et al. 2006). I expected that Brown-headed Cowbird abundance would be positively correlated with the abundances of all of these species, including Sedge Wren, because the cowbird's reproductive strategy relies on its ability to locate the nests of other species and therefore requires it to stay in proximity to them during the early breeding season (USGS Northern Prairie Research Center 2013).

METHODS

Field Methods

Study sites.—During 2013 and 2014, I surveyed 71 sites within the Prairie Parkland Province of the Minnesota Department of Natural Resources (MN DNR) Southern Region in southwestern Minnesota (Fig. 1). Sites were chosen in conjunction with MN DNR and The Nature Conservancy (TNC) collaborators, on the basis that selected sites would have the potential to support breeding populations of Grasshopper Sparrows and other grassland birds. I used several sources of information to identify potential sites, including: 1) core areas and corridors identified in the Minnesota Prairie Landscape Conservation Plan (Minnesota Prairie Plan Working Group 2011); 2) Grassland Bird Conservation Areas (Granfors 2010a; Johnson *et al*. 2010); areas predicted by habitat models as likely to harbor Grasshopper Sparrows (e.g., Granfors 2010b); areas where Grasshopper Sparrows have been recorded consistently by the Minnesota Breeding Bird Atlas project, Minnesota County Biological Survey, eBird, or the U.S. Geological Survey (USGS) Breeding Bird Survey (BBS); 4) additional areas with reported Grasshopper Sparrow occurrences and suitable habitat such as Important Bird Areas (IBAs); and 5) U.S. Department of Agriculture (USDA) National Agricultural Statistics Service (NASS) Cropscape data files that identify grassland. Forty acres was set as the minimum area threshold to represent the minimum reasonable management area. Sites were selected to represent a broad range of geographic extent, landscape types, habitat characteristics, anticipated abundance of Grasshopper Sparrows, and ownership.

Of the 71 sites visited, 48 were on public lands, 17 were privately owned, and six were owned by The Nature Conservancy (Appendix A). I visited 48 sites (51 discrete management units) in 2013 and 49 sites (53 discrete management units) in 2014, with 26 sites visited in both years (Appendix A). Each site was visited only once during a breeding season because occurrence rates for grassland bird species increase only marginally with a second visit (Quamen 2007). Exceptions were made when the first visit occurred under suboptimal weather conditions or during the first week of each field season, when observers were still familiarizing themselves with survey methodology. When two surveys were conducted at a single site, I used results from only one survey for each species. Whether I used the first or second visit was determined by whether the species of interest was considered an early-season breeder or a late-season breeder (as defined by Igl and Johnson 1997).

Bird surveys.—Breeding bird surveys were conducted in 2013 and 2014 from late May to early July, which coincides with the peak breeding season of most breeding birds in this region. Surveys were conducted between 30 minutes prior to sunrise and 10 a.m. to coincide with peak hours of bird activity. Counts of birds were based primarily on the number of breeding pairs on territories or home ranges. Generally, nearly all indicated pairs were observed as territorial males or as segregated pairs. I used the total-area count method for surveying breeding birds; this is a minor modification of the strip-transect procedures used by Stewart & Kantrud (1972) and Igl & Johnson (1997). Each site was surveyed by one or two observers walking slowly (1.0–1.5 km h^{-1}) on foot and documenting all birds encountered. This method allows one or two observers to efficiently cover one large field or several smaller fields within four hours after sunrise. Strip width varied depending on field size and shape but never exceeded 100 m on either side of the transect line. As recommended by Stewart & Kantrud (1972), deviations from the route were allowed and were sometimes necessary to adequately survey all portions of the fields (e.g., in rolling topography, around large wetlands) or to track down elusive individuals to confirm identification. Large or wide-ranging birds (e.g., raptors) that flush from the field upon the observer's arrival or during the survey were recorded as being within the field. In fields that were surveyed by two observers, observers compared field notes at the end of the survey to prevent duplication in the counts of large or wide-ranging birds or birds that occur along the shared survey boundary.

Statistical Analysis

From these data I calculated transect-specific density and occurrence rates for each species. For each species pair, I used density and occurrence of one species as predictor variables for density of another species, and density of one species as a predictor of the occurrence of the other species. However, occurrence of one species could not be used to predict occurrence of another species because I was unable to account for differences in transect area. Due to the greater time spent and area covered on longer transects, an observer is more likely to encounter more species than on shorter transects.

I ran statistical analyses in program R version 3.1.1 (R Core Team 2014) using the aod (Lesnoff & Lancelot 2012), zoo (Zeileis & Grothendieck 2005), and ggplot2 (Wickham 2009) packages.

As a measure of linear association between species densities, I calculated correlation coefficients. I also compared each species to an amalgamated group (ALLGRASS) that included all obligate grassland species observed at least once in the study, including: Gray Partridge (*Perdix perdix*), Ring-necked Pheasant (*Phasianus colchicus*), Northern Harrier (*Circus cyaneus*), Upland Sandpiper (*Bartramia longicauda*), Marbled Godwit (*Limosa fedoa*), Vesper's Sparrow (*Pooecetes gramineus*), Le Conte's Sparrow (*Ammodramus leconteii*), and Eastern Meadowlark (*Sturnella magna*), in addition to Grasshopper Sparrow, Sedge Wren, Savannah Sparrow, Henslow's Sparrow, Dickcissel, Bobolink, Western Meadowlark, and Brown-headed Cowbird (Igl & Johnson 1997). However, when I calculated correlation coefficients between ALLGRASS and the individual species, the species of interest was temporarily removed from the ALLGRASS value so that no species was used to relate to its own density.

I conducted logistic regression analyses, predicting the occurrence of one species from the density of another. I used generalized linear models to predict the density of one species from the occurrence of another species.

Finally, I used analysis of variance to compare the mean densities of each species at sites where Grasshopper Sparrows were observed with densities at sites where Grasshopper Sparrows were not observed.

RESULTS

Density as a predictor of density

Overall, the strongest predictor of the density of individual grassland bird species was the amalgamated group ALLGRASS, which used the densities of all other grassland species as a predictor, with a mean correlation coefficient of 0.36 (Table 1.1). Of the individual species, Grasshopper Sparrow (mean absolute value correlation coefficient of 0.15), Savannah Sparrow (mean absolute value correlation coefficient of 0.12), and Bobolink (mean absolute value correlation coefficient of 0.12) were the best predictors for all other species. Not all of the correlation coefficients were statistically significant, nor in the case of Grasshopper Sparrow and Bobolink were all the significant correlation coefficients positive. In particular, Grasshopper Sparrow showed a significant negative relationship with Sedge Wren (correlation coefficient = -0.16).

Density as a predictor of occurrence

Bobolink density significantly predicted the occurrence of five other species (Dickcissel, Grasshopper Sparrow, Henslow's Sparrow, Savannah Sparrow, and Sedge Wren; Table 1.2). Savannah Sparrow density significantly predicted occurrence of four other species (Brown-headed Cowbird, Bobolink, Sedge Wren, and Western Meadowlark) as did Grasshopper Sparrow density (Dickcissel, Henslow's Sparrow, Savannah Sparrow, and Western Meadowlark occurrences). Dickcissel density significantly predicted occurrence of three species (Bobolink, Grasshopper Sparrow, and Savannah Sparrow), as did Henslow's Sparrow density (Bobolink, Grasshopper Sparrow, and Sedge Wren), Sedge Wren density (Bobolink, Dickcissel, and Grasshopper Sparrow), and Western Meadowlark density (Dickcissel, Grasshopper Sparrow, and Savannah

Sparrow). Brown-headed Cowbird density did not significantly predict the occurrence of any other species, probably because it was so rarely recorded on my transects. Also, Grasshopper Sparrow occurrence was the most frequently well predicted, with all six other species except Brown-headed Cowbird serving as significant predictors.

Occurrence as a predictor of density

Bobolink occurrence could be used to predict the densities of five other species (Dickcissel, Grasshopper Sparrow, Henslow's Sparrow, Savannah Sparrow, Sedge Wren; Table 1.3). Dickcissel occurrence was a significant predictor of the densities of four species (Bobolink, Grasshopper Sparrow, Savannah Sparrow, and Western Meadowlark). Grasshopper Sparrow occurrence was a significant predictor of the densities of four other species (Dickcissel, Henslow's Sparrow, Savannah Sparrow, and Western Meadowlark). Henslow's Sparrow occurrence significantly predicted the densities of three other species (Bobolink, Grasshopper Sparrow, and Sedge Wren). Savannah Sparrow occurrence significantly predicted the densities of three species (Bobolink, Sedge Wren, and Western Meadowlark). Sedge Wren occurrence significantly predicted the densities of four species (Brown-headed Cowbird, Bobolink, Dickcissel, and Grasshopper Sparrow). Western Meadowlark occurrence significantly predicted the densities of four species (Grasshopper Sparrow, Henslow's Sparrow, Savannah Sparrow, and Sedge Wren). Brown-headed Cowbird occurrence was a significant predictor only of the density of Western Meadowlark. Also, Grasshopper Sparrow density was the most frequently well-predicted, with occurrences of all other species except Brown-headed Cowbird and Savannah Sparrow serving as significant predictors.

Bird density with and without Grasshopper Sparrow

Densities of all species except Sedge Wrens and Brown-headed Cowbirds were significantly higher at sites with Grasshopper Sparrows than at sites without Grasshopper Sparrows (Table 1.4; Fig 1.1). Sedge Wren density was significantly higher at sites without Grasshopper Sparrows than at sites with Grasshopper Sparrows and Brown-headed Cowbird density did not differ between sites with and without Grasshopper Sparrows.

DISCUSSION

My results support the idea that the Grasshopper Sparrow could reasonably serve as an indicator species for the occurrence and density of other grasslands birds, based on the criteria suggested by Fleishman et al. (2000). The Grasshopper Sparrow was the individual species with the highest mean absolute value of correlation coefficients between its density and that of the other grassland species. Furthermore, the densities of all species except Sedge Wren were significantly higher at sites with Grasshopper Sparrows than at sites without them. Even though Sedge Wren density was negatively correlated with that of Grasshopper Sparrows, it was still the strongest correlation exhibited for the Sedge Wren. In addition, Grasshopper Sparrow density could also be used as a significant predictor of Dickcissel, Henslow's Sparrow, Savannah Sparrow, and Western Meadowlark occurrences. The densities of these same four species could also be predicted from the occurrence of Grasshopper Sparrows.

In addition to meeting Fleishman et al.'s (2000) criteria of co-occurrence and similar abundances, it is important that these different metrics (occurrence or density of the indicator species) can be used to predict the occurrence or density of other species because they represent a range of monitoring investment paired with a range of usefulness in the resulting information outcomes. Surveys that estimate density are more labor intensive than merely assessing occupancy but are simultaneously more useful for monitoring populations (Ralph et al. 1993; Mackenzie & Nichols 2004; Grouios & Manne 2009). Therefore, although using density to predict density is the most labor intensive method, it provides the most information. Conversely, using density to predict occurrence is sub-optimal because it reveals the least information about how the population of the predicted species may be faring and yet it takes the most effort to get that little bit of information. Even so, information about occurrence may be adequate for some land managers (Ralph et al. 1993; Mackenzie & Nichols 2004; Grouios & Manne 2009). Instead, using occurrence to predict density is preferable because it takes less effort to collect the data, but provides more information. This could be ideal for land managers with limited resources.

In addition, I propose a more comprehensive approach to indicator species. Instead of using just a single indicator species for dry upland prairie birds, I would suggest using more than one species. More diverse indicator groups that incorporate more than a single species, guild or taxon have been shown to be better representatives of overall biodiversity (Lambeck 1997; Roberge and Angelstam 2004; Sarkar *et al*. 2005; Larsen et al. 2009; Larsen *et al*. 2012). For instance, in every case except that of the Brown-headed Cowbird, using a combined density from all other grassland bird species was the most strongly correlated metric, with a mean correlation coefficient double or even triple that of any of the higher-performing individual species (Table 1.1). However, if resources and training time are limited, it may be more efficient to select a smaller cohort of grassland birds that could be combined to provide more complete coverage for all grassland birds. One possibility would be to consider Grasshopper Sparrows and Sedge Wrens, because density of Sedge Wrens is not adequately indicated by the presence or density of Grasshopper Sparrows and Sedge Wrens are associated with a different type of grassland habitat. This would ensure that the species was adequately protected, along with other grassland species that share the Sedge Wren's wetter, more densely vegetated habitat. Another option would be to combine indicator metrics of the Grasshopper Sparrow and either the Savannah Sparrow or Bobolink, both of which are positively correlated with Sedge Wren. This combination would also provide full coverage for my set of species of interest. However, dropping the Grasshopper Sparrow and using the combination of Bobolink and Savannah Sparrow would be problematic because then the Western Meadowlark would not be receiving adequate coverage. This is problematic because the Western Meadowlark is a species that has exhibited especially severe declines (Igl & Johnson 1997).

One very important caveat is that although the Grasshopper Sparrow may be indicative of the presence of other grassland birds on grassland sites such as I investigated, and therefore could serve as an indicator species; one should not conclude that managing existing grasslands to benefit Grasshopper Sparrows will benefit any of the other species. Individual species of grassland birds vary dramatically in response to vegetation characteristics such as height, density, and patchiness (Knopf 1996) and therefore the disparate needs of different species need to be considered separately (Johnson et al. 2012).

TABLES

Table 1.1. Correlation coefficients between densities of grassland bird species. The group ALLGRASS includes all grassland species observed at least once in the study, including: Eastern Meadowlark, Gray Partridge, Le Conte's Sparrow, Marbled Godwit, Northern Harrier, Ring-necked Pheasant, Upland Sandpiper, and Vesper Sparrow, in addition to Brown-headed Cowbird (BHCO), Bobolink (BOBO), Dickcissel (DICK), Grasshopper Sparrow (GRSP), Henslow's Sparrow (HESP), Savannah Sparrow (SAVS), Sedge Wren (SEWR), and Western Meadowlark (WEME; Igl & Johnson 1997), however, as I calculated correlation coefficients between ALLGRASS and an individual species, the species was temporarily removed from the ALLGRASS so that no species was used to correlate with its own density. The mean absolute value shows that the strongest overall predictors are ALLGRASS, Grasshopper Sparrow, Savannah Sparrow and Bobolink. Within the table grassland bird species of interest are listed using standardized four-letter American Ornithologists' Union alpha codes. Asterisks indicate $p < 0.05$.

Response Species	Predictor Species								
	GRSP	SEWR	SAVS	HESP	DICK	BOBO	WEME	BHCO	ALLGRASS
GRSP		-0.16*	0.18*	0.13*	0.23*	0.16*	0.20*	-0.02	0.25*
SEWR	-0.16*		0.15*	0.09	-0.08	0.14*	-0.03	0.04	0.44*
SAVS	0.18*	0.15*		0.06	0.13*	0.16*	0.10	0.09	0.48*
HESP	0.13*	0.09	0.06		0.02	0.22*	-0.01	-0.04	0.39*
DICK	0.23*	-0.08	0.13*	0.02		-0.13*	0.10	-0.02	0.32*
BOBO	0.16*	0.14*	0.16*	0.22*	-0.13*		0.00	-0.01	0.74*
WEME	0.20*	-0.03	0.10	-0.01	0.10	0.00		0.19*	0.20*
BHCO	-0.02	0.04	0.09	-0.04	-0.02	-0.01	0.19*		0.10
ALLGRASS	0.25*	0.44*	0.48*	0.39*	0.32*	0.74*	0.20*	0.10	
MeanAbs[1]	0.15	0.10	0.12	0.08	0.10	0.12	0.09	0.06	0.36

[1]This indicates the mean absolute value of correlation coefficients as a measure of the strength of the relationships between the predictor species and all other species except ALLGRASS.

Table 1.2. Regression coefficients associated with logistic regression equations using the density of one species to predict the occurrence of another species. Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1). Statistically significant *p*-values are marked with an asterisk.

Response Species	Predictor Species							
	GRSP	SEWR	SAVS	HESP	DICK	BOBO	WEME	BHCO
GRSP		-1.98*	1.84	4.05*	3.48*	0.74*	6.67*	-3.40
SEWR	-1.14		1.99*	3.34*	-0.24	0.74*	-2.52	-2.40
SAVS	2.71*	0.90		2.03	1.55*	1.00*	4.80*	0.11
HESP	3.17*	1.36	1.30		0.59	1.01*	0.26	-5.63
DICK	2.41*	-2.12*	1.78	0.75		-1.67*	7.21*	-1.77
BOBO	0.82	4.61*	3.00*	5.24*	-1.42*		0.62	-2.63
WEME	2.67*	-1.21	2.02*	-0.42	1.13	0.35		8.53
BHCO	-0.98	1.85	4.27*	-5.70	-3.67	0.72	5.29	

Table 1.3. Regression coefficients associated with generalized mixed models that use occurrence of one species to predict the density of another species (birds per 100 ha). Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1). Statistically significant *p*-values are marked with an asterisk.

Response Species		Predictor Species							
		GRSP	SEWR	SAVS	HESP	DICK	BOBO	WEME	BHCO
GRSP			-4.37*	2.61	2.40*	9.11*	7.96*	2.77*	-0.21
SEWR		-3.94		3.16*	2.50*	-0.94	8.21*	-1.09	-0.14
SAVS		10.78*	2.40		1.59	6.56*	10.42*	2.42*	0.01
HESP		14.86*	4.03	2.16		2.70	11.24*	0.12	-0.25
DICK		10.03*	-4.18*	2.89	0.54		-14.20*	3.90*	-0.11
BOBO		3.09	6.94*	3.49*	2.28*	-6.22*		0.30	-0.18
WEME		10.84*	-2.66	3.22*	-0.29	5.01*	3.38		0.61*
BHCO		-3.39	6.95	11.00*	-1.95	-6.09	8.10	3.97	

Table 1.4. Means, standard deviations, and results from one-way analysis of variance for densities of grassland bird species of interest at sites with and without Grasshopper Sparrows (GRSP). Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1). Statistically significant *p*-values are marked with an asterisk.

Species	GRSP absent		GRSP present		F (1, 334 df)	*p*	r.sq
	Mean	SD	Mean	SD			
SEWR	0.10	0.01	0.06	0.02	6.28	0.013*	0.02
SAVS	0.05	0.01	0.07	0.01	3.97	0.047*	0.01
HESP	0.02	0.01	0.04	0.01	6.91	0.009*	0.02
DICK	0.04	0.02	0.13	0.02	18.27	0.000*	0.05
BOBO	0.28	0.02	0.36	0.03	5.41	0.021*	0.02
WEME	0.02	0.01	0.05	0.01	13.90	0.000*	0.04
BHCO	0.01	0.00	0.00	0.00	0.56	0.455	0.00
ALLGRASS	0.55	0.04	0.76	0.05	15.30	0.000*	0.04

FIGURES

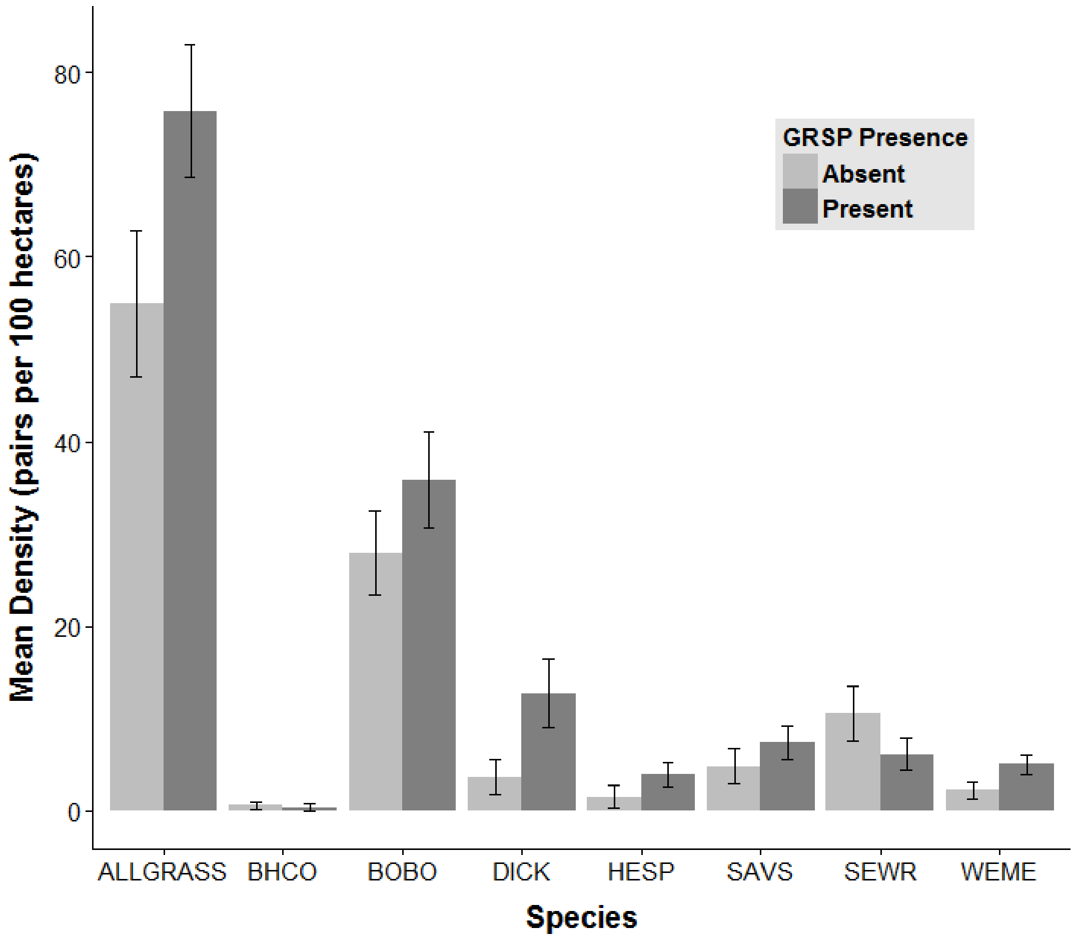


Figure 1.1. Density of all species except Sedge Wren and Brown-headed Cowbird are significantly higher at sites with Grasshopper Sparrows than at sites without Grasshopper Sparrows. Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1). Error bars represent 95% CI.

CHAPTER 2. LOCAL-SCALE HABITAT ASSOCIATIONS OF GRASSLAND BIRDS IN SOUTHWESTERN MINNESOTA

Conservation of obligate grassland species requires not only the protection of a sufficiently large quantity of habitat, but also the provision of necessary vegetation characteristics for particular species. As a result, land managers must understand which habitat characteristics are important for their species of interest. I used a principal components analysis to determine the most important vegetation characteristics in southwestern Minnesota for eight obligate grassland-breeding bird species: Grasshopper Sparrow (*Ammodramus savannarum*), Sedge Wren (*Cistothorus platensis*), Savannah Sparrow (*Passerculus sandwichensis*), Henslow's Sparrow (*Ammodramus henslowii*), Dickcissel (*Spiza americana*), Bobolink (*Dolichonyx oryzivorus*), Western Meadowlark (*Sturnella neglecta*), and Brown-headed Cowbird (*Molothrus ater*). I used the first four principal components to model occurrence of these species and calculated correlation coefficients with vegetation variables as a measure of linear association. I assessed curvilinear relationships with loess plots. Principal components 1-4 account for 12-22% of the variation among sites and some combinations of them were predictive of occurrences of all species except Brown-head Cowbirds. For all species except Henslow's Sparrow and Brown-headed Cowbird, the original vegetation measurements exhibited slightly stronger and much more easily-interpreted relationships with species' densities, in particular curvilinear relationships, than did principal components. As a whole, grassland birds showed the strongest positive associations with greater distance to trees, fewer trees within 100m, and less bare ground, although individual species showed different patterns of correlation and most species were tolerant of a wide variety of habitat conditions. The Grasshopper Sparrow, a species of particular interest in Minnesota, showed negative associations with increasing vegetation height, vegetation density, and presence of trees in addition to nonlinear relationships with litter and percentages of shrub, dead vegetation, and bare ground cover. Judicious selection of explanatory variables negated the need for the principal components analysis, thereby providing an avenue for more efficient habitat monitoring.

INTRODUCTION

The pressures of a growing global human population have increased rates of land conversion from native ecosystems to human use while the rate of habitat protection remains static (Hoekstra *et al*. 2005). Land conversion has been particularly prevalent in temperate grassland, resulting in precipitous declines in the extent of this habitat type across much of North America, Europe, and South America (Askins *et al*. 2007). More than 50% of native temperate grasslands in North America had been converted to human use by 2005 (Hoekstra *et al*. 2005).

The loss of grassland habitat has caused corresponding declines in the populations of grassland-specific species (Samson & Knopf 1994). Obligate grassland-breeding birds, which require grassland for all aspects of their life history (Vickery *et al*. 1999), have experienced declines among the most severe seen for any avian group (North American Bird Conservation Initiative U.S. Committee 2014).

The issue of habitat loss is further compounded in remnant grasslands by habitat degradation. Barriers to visibility (Eason & Stamps 1992) or movement decrease the suitability of potential habitat for these grassland specialists (Harris & Reed 2002; Hamer *et al*. 2006) because they are adapted to open habitats characterized by lack of vertical stratification (Mengel 1970). For instance, the vertical complexity added to the habitat by woody vegetation has a strong negative effect on obligate grassland bird occurrences (Grant *et al*. 2004; Thompson *et al.* 2014). Trees have been introduced to the grassland landscape through intentional planting and unintended encroachment (Fuhlendorf *et al*. 2002) due to fire suppression and modified grazing patterns (Samson & Knopf 1994; Askins *et al*. 2007). Such interference with natural disturbance regimes that have historically maintained grassland has also allowed the accumulation of litter, shrubs, and taller, denser vegetation through the process of succession (McCracken & Rowan 2005; Holimon *et al*. 2012). In addition, some invasive species such as smooth brome (*Bromus inermis*) compound the structural issues of succession both through dense growth patterns that decrease the heterogeneity of the habitat and by negatively impacting litter decomposition rates (Askins *et al*. 2007). In particular, these structural changes reduce the suitability of habitat for those species that require shorter, sparser vegetation (Powell 2006).

To conserve such sensitive grassland bird species, researchers and management agencies frequently determine that large natural areas of open grassland need to be protected (Askins *et al*. 2007). However, it is important to ensure not only the protection of sufficient area of habitat, but that those protected areas provide the necessary vegetation characteristics for obligate grassland species. Vegetation characteristics are critical for the success of grassland bird conservation because they affect predation, brood parasitism, and food availability mechanisms that have repercussions for habitat use, survival, and reproductive success (Rodewald & Yahner 2001; Dunford & Freemark 2005; Koper & Schmiegelow 2006). However, not all birds react in the same way to these vegetation characteristics; vegetation preferences are species-specific (Scott *et al*. 2002). With this in mind, land managers need to understand which habitat characteristics are important for their species of interest because management and monitoring are both expensive and labor intensive.

The objective of this study is to determine which vegetation characteristics are most important for the occurrence and density of obligate grassland bird species in southwestern Minnesota. I focused on seven grassland bird species: Grasshopper Sparrow (*Ammodramus savannarum*), Sedge Wren (*Cistothorus paltensis*), Savannah Sparrow (*Passerculus sandwichensis*), Henslow's Sparrow (*Ammodramus henslowii*), Dickcissel (*Spiza americana*), Bobolink (*Dolichonyx oryzivorus*), and Western Meadowlark (*Sturnella neglecta*). In addition, I included the Brown-headed Cowbird (*Molothrus ater*) in my analysis because, although it is only a facultative grassland species, it is a brood parasite and co-occurs with other grassland birds and can have negative impacts on the nesting success of those species. Therefore it may be helpful to land managers to know the habitat associations of this species, as well.

I chose habitat characteristics to measure based on a comprehensive review of vegetation measures studied in conjunction with grassland birds. This review showed nine variables were especially relevant to occurrence, density, abundance, and habitat selection (Fisher & Davis 2010). These nine variables include percent cover of bare ground, grass, dead vegetation, forbs, and shrubs; as well as vegetation density and volume; litter depth; and vegetation height. In addition, woody vegetation is a landscape-scale vegetation characteristic that has an influence on habitat use and suitability (Grant *et al*. 2004; Caplat & Fonderflick 2009). I included measures of the distance to the nearest tree and the percentage of tree cover within the larger landscape at a scale of 100m.

To determine the most important vegetation characteristics, I used a principal components analysis. This technique is well suited to identify the most important explanatory variables when a large number of variables have been measured (Johnson 1981; Vaughan & Ormerod 2005). Principal components have been used to identify vegetation characteristics of habitat used by Black-tailed Godwits (Groen *et al*. 2012), insectivorous forest birds in Brazil (Stratford & Stouffer 2015), and forest birds in California (Lee & Rotenberry 2015), to name just a few recent instances.

METHODS

Field Methods

Study sites.— See chapter 1 for a description of the study sites.

Bird surveys.—I collected breeding bird abundance data as described in the data collection methodology outlined in chapter 1.

Habitat measures.—I collected data on habitat characteristics to relate the occurrence and abundance of breeding grassland birds to a variety of habitat characteristics at several scales. I returned to sites for vegetation surveys after the initial bird surveys; however, in 2013 there was one instance when the landowner did not give permission for a visit to measure vegetation, and in 2014 one site could not be accessed a second time for vegetation surveys due to the route being blocked off by installation of a new fence. In 2014 nine transects could not be surveyed for vegetation because water levels rose prohibitively high between visits.

The number of points sampled along each transect was proportional to the square root of the transect length, with a starting density of two points for every 100 m. This method allowed for more sampling points at larger sites, while accounting for expected homogeneity within the site. The first sample point along each transect was determined randomly, with the first sampling point falling between 0 and 50 m from the start of the transect. The remaining points were spaced at equal intervals along the transect.

I assigned each transect to one of three broad habitat classes: upland grassland, low grassland, or wet meadow. At each sampling point, I collected information on local features to assess habitat condition. Local features included height-density (Visual Obstruction Readings [VORs]; Robel *et al*. 1970), litter depth, and visual estimates of the coverage of dominant vegetation (grass, forb, shrub, dead vegetation [DeadVeg], and bare ground [BareGround]) in a 4-m radius circular plot around the sampling point, percent tree cover within 100 m of the point [Trees100], and distance to nearest tree

[DistToTree]. Summary information for these vegetation variables is included in Table 2.1.

Because birds were recorded along belt transects whereas vegetation measurements were recorded only for points along the center of each transect, and due to the heterogeneity of many of my sites, the conditions encountered by birds could vary significantly from the recorded vegetation measurements. For instance I recorded some unusually high litter depths (above 15 cm) that may have been restricted to only a small portion of the total area surveyed.

Statistical Analysis

I ran statistical analyses in program R version 3.1.1 (R Core Team 2014) using the car (Fox & Weisberg 2011), zoo (Zeileis & Grothendieck 2005), and ggplot2 (Wickham 2009) packages. The ten vegetation variables were subjected to a principal component analysis to assess their usefulness in distinguishing sites and describing habitat associations of the birds.

For the purposes of my principal components analysis, missing values were replaced with mean values so that I did not lose an entire observation when only a single vegetation measurement was missing. I also standardized values for each variable. Vegetation characteristics were averaged within each transect, and I treated each transect as if independent of other transects within the same site. Both years were combined because the general pattern of associations did not differ between years. To assess linear associations, I calculated correlation coefficients between species' densities and the principal components.

I modeled occurrence with linear regression, using a null model (no explanatory variables except an intercept) and all possible combinations of the first four principal components. The best model for each species was selected by using the lowest Akaike's Information Criterion (AIC).

As a measure of linear association between species and vegetation variables, I calculated correlation coefficients. I assessed curvilinear relationships by plotting density of each species of interest against each vegetation measurement and using locally weighted scatterplot smoothing to fit curves to the plots. For each plot, span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

RESULTS

Principal Components Analysis

Factor loadings for the first four principal components are presented in Table 2.2A, but correlation coefficients with explanatory variables are more useful for interpreting the components and are presented in Table 2.2B. Principal component 1 (PC1) accounted for 22% of the variation among sites and contrasted sites with high percentages of bare ground and non-graminoids from sites with high percentages of grass, litter, and distance to trees and high VOR readings (Table 2.2B, Fig. 2.1). Principal component 2 (PC2) accounted for 21% of the variation among sites and contrasted sites with high percentages of grass cover and far from trees from sites that had taller, denser vegetation (reflected by VOR) and a higher percentage of forbs (Table 2.2B, Fig. 2.1). Principal component 3 (PC3) accounted for 16% of the variation among sites and contrasted sites with more trees within 100 m and higher percentage of grass cover from sites that were farther from trees and had more forb cover (Table 2.2B, Fig. 2.1). Principal component 4 (PC4) accounted for 12% of the variation in sites and essentially distinguished between sites with more residual dead vegetation (DeadVeg and Litter) and sites that had more live vegetation (a combination of grasses, forbs, and shrubs) (Table 2.2B, Fig. 2.1).

PC 1 and 2 were useful for distinguishing among the three broad habitat types that I identified. Low grassland sites had a mean PC2 score of -0.37±1.38 (SD), whereas upland sites had a mean PC2 score of 0.90±1.11 (Fig. 2.2). PC1 values were always greater than -1.0 for wet meadow sites (mean 0.83±1.48sd; Fig. 2.2).

PC1 through PC4 were useful for predicting densities of all species except Brown-headed Cowbird and Henslow's Sparrow (Table 2.3). Grasshopper Sparrow density was most strongly correlated with PC2 and PC3. Sedge Wren density was most strongly correlated with PC2, PC3, and PC1. Savannah Sparrow density was most strongly correlated with PC2, PC3, and PC1. Dickcissel density was most strongly correlated with PC3. Bobolink density was most strongly correlated with PC3, PC1 and PC2. Western Meadowlark density was most strongly correlated with PC4 and PC1, and the composite density of all grassland birds was most strongly correlated with PC3, PC1 and PC4.

However correlations between densities and principal components were generally low (maximum correlation coefficient in absolute value= 0.31), and consistent with these low correlations it is difficult to see associations in the species density plots (Fig. 2.3).

From analysis of mean PC scores for sites where each species was present, we can see that bird densities differed primarily along mean PC2 scores, but not along mean scores for PC1, PC3 or PC4 (Fig. 2.4). Three species groupings emerged from PC2, with Grasshopper Sparrow, Savannah Sparrow and Western Meadowlark having the closest PC scores (Fig. 2.4). These three species were differentiated along the PC4 axis (Fig. 2.4).

In contrast, the second set of species (Brown-headed Cowbird, Bobolink, Dickcissel, and Henslow's Sparrow) was most closely aligned along the PC2 axis, but their mean PC scores are separated along the PC1 axis (Fig. 2.4). Finally, Sedge Wren was particularly separated from the other two groups along the PC2 axis (Fig. 2.4). Although these groupings were evident upon examination of the mean PC scores for sites where the individual species were present, when we looked at the PC scores of sites independently, it was apparent that there was a great deal of variation in the system, in that most species occurred on transects with a wide variety of PC scores (Fig. 2.5).

PC1 through 4 were also useful for predicting occurrences of all species except Brown-headed Cowbird (Table 2.4). For Brown-headed Cowbird, the null model had the lowest AIC score. Savannah Sparrow and Sedge Wren occurrences were best modeled by PC1, PC2 and PC3, the same three PCs that were most strongly correlated with their densities. For all other species, the best model of occurrence did not include the same set of PCs that were most strongly correlated with the density of that species. Grasshopper Sparrow occurrence was best predicted by the model that included all four PCs. Henslow's Sparrow occurrence was best modeled by PC1, PC3, and PC4. Dickcissel occurrence was best predicted by the model that included PC1 and PC4. Bobolink occurrence was best predicted by the model that included PC1, PC3 and PC4. Western Meadowlark occurrence was best modeled by the combination of all four PCs.

Linear Correlations with Vegetation Characteristics

As a whole, grassland birds showed the strongest positive associations with greater distance to trees, fewer trees within 100m, and less bare ground (Table 2.5). However, individual species showed different patterns of correlation. Grasshopper Sparrow densities showed stronger correlations with distance from trees and shorter, sparser vegetation (Table 2.5). Sedge Wren density showed strongest correlations with taller, denser vegetation that included more standing dead vegetation, less bare ground, fewer shrubs, and more forbs and litter (Table 2.5). Savannah sparrows had highest densities at sites that had greater distance to trees, less standing dead vegetation, fewer shrubs, and more grass coverage (Table 2.5). Dickcissel densities were most strongly associated with sites with a higher percentage of dead vegetation, denser vegetation, greater distance to trees, and less bare ground cover (Table 2.5). Bobolink densities showed a stronger correlation with greater distance from trees and lower percentage of standing dead vegetation (Table 2.5). Higher densities of Western Meadowlark were most strongly associated with greater distances to trees and less bare ground (Table 2.5). Densities of Henslow's Sparrows and Brown-headed Cowbirds did not show significant correlations with any of the measured vegetation characteristics (Table 2.5).

Nonlinear Relations to Vegetation Characteristics

It is important to note that these correlations measured only linear relationships and therefore did not take into account any curvilinear relationships. I used loess smoothing to examine the relationships more closely. In my interpretation of the results, I was careful not to go beyond where the sample size was thin. Grasshopper Sparrow density increased with increasing percent shrub cover, to ~4% shrub (Fig. 2.6E). Similarly, a small amount of dead vegetation corresponded to higher Grasshopper Sparrow densities (Fig. 2.6F). The relationship between Grasshopper Sparrow density and bare ground was curvilinear, with Grasshopper Sparrow density peaking at about 8% bare ground (Fig. 2.6G). Because the relationship was curvilinear it did not show up as a significant linear correlation in Table 2.5. While Grasshopper Sparrow density did not show a strong linear correlation with litter depth (Table 2.5), there was a noticeable pattern that, above about 5 cm of litter depth, Grasshopper Sparrow density declined slightly (Fig. 2.6A). Grasshopper Sparrow density also declined with height, especially up to about 45 cm (Fig. 2.6B). Grasshopper Sparrow density decreased with increasing Visual Obstruction Readings, consistent with a linear relationship (Fig. 2.6H). Also Grasshopper Sparrow density decreased as the proportion of trees within 100 m increased (Fig. 2.6J) and analogously increased with increasing distance to nearest tree (Fig. 2.6I). Grass and forb densities did not show any relationship with the density of Grasshopper Sparrows (Fig. 2.6C, D).

Sedge Wren density increased slightly with increasing litter (Fig 7A). Sedge Wren density increased with increasing vegetation height to about 60 cm (Fig. 2.7B).

Sedge Wren density increased with increasing forb cover (Fig. 2.7D) and with increasing dead vegetation (Fig. 2.7F) and VOR (Fig. 2.7H). Sedge Wren density decreased with increasing grass cover (Fig. 2.7C) and was highest at sites with no shrub cover (Fig. 2.7E). Sedge Wren density was relatively unaffected by bare ground (Fig. 2.7G), distance to trees (Fig. 2.7I), and trees within 100 m (Fig. 2.7J).

Savannah Sparrow density increased with increasing grass cover beyond about 70% grass cover (Fig. 2.8C) and increased with increasing distance to trees (Fig. 2.8I). Savannah Sparrow density peaked at about 5% dead vegetation (Fig. 2.8F) and 1% bare ground coverage (Fig. 2.8G). Savannah Sparrow density was highest at the lowest values of shrub cover (Fig. 2.8E). Savannah Sparrow density decreased with increasing VOR (Fig. 2.8H) and with increasing forb cover to about 20% forb cover (Fig. 2.8D). Savannah Sparrow density decreased slightly with increasing height (Fig. 2.8B). Savannah Sparrows were almost always absent when tree coverage was above seven percent (Fig. 2.8J). Savannah Sparrow density was relatively unaffected by litter depth (Fig. 2.8A).

Henslow's Sparrow density was relatively unaffected by all vegetation characteristics (Fig. 2.9).

Dickcissel density was slightly higher at intermediate values of vegetation height (Fig. 2.10B). Dickcissel density increased slightly with greater grass coverage (Fig. 2.10C). Dickcissel density was slightly higher at low percentages of shrub cover (Fig. 2.10E) and low percentages of bare ground (Fig. 2.10G). Dickcissel density increased with increasing VOR to a VOR value of about 5 (Fig. 2.10H). Dickcissel density increased with increasing distance to trees (Fig. 2.10I) and decreased from 0 to 5% tree cover within 100 m (Fig. 2.10J). Dickcissel density was relatively unaffected by litter depth (Fig. 2.10A), forb cover (Fig. 2.10D), and dead vegetation (Fig. 2.10F).

Bobolink density also increased with increasing litter to about 5 or 10% litter, and possibly declining thereafter (Fig. 2.11A). Although the range in height was limited, there is some suggestion that density may increase to about 35 cm (Fig. 2.11B). Bobolink density increased up to about 2% bare ground coverage, then decreased to about 4% bare ground, after which density remained constant (Fig. 2.11G). Bobolink density increased with increasing distance to nearest tree up to about 200m (Fig. 2.11I). In general, Bobolink density decreased with increasing proportion of trees within 100 m (Fig. 2.11J). Bobolink density decreased with increasing dead vegetation to about 10% dead vegetation, after which the density was relatively stable (Fig. 2.11F). Bobolink density was relatively unaffected by grass cover (Fig. 2.11C), forb cover (Fig. 2.11D), shrub cover (Fig. 2.11E), and VOR (Fig. 2.11H).

Western Meadowlark density increased very slightly with increasing grass cover (Fig. 2.12C) and increased with increasing distance to trees (Fig. 2.12I). Western Meadowlark density decreased slightly with greater litter depth (Fig. 2.12A) and decreased slightly with increasing vegetation heights (Fig. 2.12B). Western Meadowlark density decreased beyond about 7% shrub cover (Fig. 2.12E). Western Meadowlark density also decreased with increasing dead vegetation (Fig. 2.12F). Western Meadowlark density was relatively unaffected by forb cover (Fig. 2.12D), bare ground (Fig. 2.12G), and VOR (Fig. 2.12H).

Brown-headed Cowbird density was relatively unaffected by all vegetation characteristics (Fig. 2.13).

Grassland bird density was slightly higher at intermediate values of litter (Fig. 2.14A) and increased with increasing vegetation height up to 60 cm (Fig. 2.14B). Grassland bird density peaked at sites with about 1% bare ground (Fig. 2.14G). Grassland bird density increased with increasing distance to trees to about 200 m (Fig. 2.14I) and decreased with increasing percentage of trees within 100 m (Fig. 2.14J). Grassland bird density was slightly higher at sites with very few shrubs (Fig. 2.14E). Grassland bird density decreased with increasing dead vegetation to about 10% dead vegetation (Fig. 2.14F). The overall density of all grassland birds was relatively unaffected by grass cover (Fig. 2.14C), forb cover (Fig. 2.14D), and VOR (Fig. 2.14H).

DISCUSSION

My results showed that PC1-4 were useful for predicting occurrences of all species except Brown-headed Cowbird and for predicting densities of all species except Brown-headed Cowbird and Henslow's Sparrow. However correlations between densities and principal components were generally modest (maximum correlation coefficient in absolute value=0.32). In addition, different species were most closely associated with different vegetation characteristics and hence best predicted by different principal components. However, the fact that the first major principal components did not capture large fractions of the total variability in the explanatory variables indicates that there was little redundancy among those variables. Such limited redundancy suggests that the choices I made regarding which variables to measure (based on the body of literature relating to grassland bird habitat measurements, in particular: Grant *et al*. (2004), Fisher & Davis (2010)) were sound. Vaughan & Ormerod (2005) suggest a method of clustering variables before conducting a PCA as a means of simplifying interpretations and potentially reducing costs associated with subsequent monitoring. However, their methodology is applicable only in cases where a large number of variables have already been measured and hence a great deal of time and money has already been invested. My approach of limiting the number of variables examined before beginning field work provides an even more efficient alternative.

I also saw that while some principal components varied considerably among sites, the mean density of birds did not vary closely in response. For instance, although there is considerable overlap between PC scores of upland grassland and lowland grassland sites, PC2 effectively differentiates between those sites at the extremes (Fig. 2.2), and is the primary distinguisher between densities of different species (Fig. 2.4). However, while PC1 was useful for distinguishing wet meadow sites from non-wet meadow sites (Fig 2), this did not correspond to differences in species densities (Fig. 2.4). Also, mean PC3 and PC4 were not correlated with species presence (Fig. 2.4). Furthermore, despite the differences in mean PC2 scores between different species, when we consider the full range of PC values at sites occupied by any one species, it is evident that there is significant overlap in the PC values at sites where the different species occur. Any particular species may be present at a wide range of sites, regardless of the PC values of those sites. As suggested by Johnson (1981), the principal components may have little relation to the species of interest or its needs.

Therefore I focused my analysis on the original variables rather than on the PCA scores as indicated by Johnson (1981). Consistent with the summary by Shaffer *et al*. (2015a), I found that Grasshopper Sparrows were negatively associated with vegetation height. This trend also seems appropriate because after a certain vegetation height, I typically did not encounter many of the obligate grassland bird species. Shaffer *et al*. (2015a) identified litter depth and shrub density to be particularly important vegetation characteristics for this species, and The Birds of North America account (Vickery 1996) additionally noted a negative relationship with shrub density. In contrast, my results showed a non-significant correlation with percent shrub cover, but a pattern of slightly higher Grasshopper Sparrows at very low levels of shrub cover than at higher levels of shrub cover or no shrub cover. A few shrubs or other tall vegetation may provide males with singing perches necessary for territory establishment and defense, but more than that may be a deterrent for the species (Slater 2004). Furthermore a few shrubs may increase the ability to detect birds (pers. obs.). In addition, my results indicate that the presence of trees on the landscape is negatively correlated with Grasshopper Sparrow density. This finding supports the previous literature (Vickery 1996; Shaffer *et al*. 2015a) that suggests open grassland is important for this species. My results showed several individual points that have much higher than expected Grasshopper Sparrow densities given the fairly short distance to a tree (Fig. 2.6A), but a single small tree nearby could be less problematic than many trees farther away. My examination of curvilinear relationships also indicates that a small amount of dead vegetation may be beneficial to the Grasshopper Sparrow (Fig. 2.6A), perhaps because it corresponds with an optimum length of time since last fire or other disturbance event. Similarly, some bare ground (about 7-9%) corresponds with higher Grasshopper Sparrow densities, probably because a small amount is good for foraging, but too much and the birds are exposed and may not have enough cover for nesting.

Consistent with the summary by Shaffer *et al*. (2015b), I found that tall, dense vegetation with a high percentage of forb cover is important for the Sedge Wren. While they also found forb cover to be particularly important, I found that dead vegetation and litter depth were possibly more important than forb cover. This positive relationship with residual vegetation is also documented in the Birds of North America account (Herkert *et al*. 2001).

Swanson's (2015) summary of Savannah Sparrows suggests that litter, height and density (VOR) are important for this species. I found that Savannah Sparrow density was negatively correlated with VOR, though not with height or litter depth. Instead, I observed correlations with presence of trees, percent shrub cover, and percent grass cover, all of which are correspondingly recorded to be important in the Birds of North America account of this species (Wheelwright & Rising 2008).

For Henslow's Sparrows, my results showed no significant correlations with the vegetation characteristics that I measured. In contrast, Herkert (2015) identified height, density and litter depth as important vegetation characteristics for this species and the Birds of North America account (Herkert *et al*. 2002) additionally suggested that forb density, absence of trees, and presence of dead vegetation are also key components of habitat. However, the species is a relatively recent arrival in my study area (Herkert *et al*. 2002) and was relatively rare in my surveys. Therefore, the species may be too uncommon to be present at all sites that could provide preferred habitat.

The vegetation characteristics that I found to be most strongly correlated with Dickcissel density were dead vegetation, bare ground, VOR and distance to trees. Similarly, Shaffer *et al*. (2015c) identified height and density (VOR) as important for this species. They also concluded that litter depth and forb coverage are important habitat characteristics. The Birds of North America account (Temple 2002) supports my finding that the presence of trees is negative for this species: the account identified proximity to wooded areas as being negatively correlated with habitat suitability. However, the Birds of North America account (Temple 2002) also identified density, height, litter, and forb cover as important vegetation characteristics.

For the Bobolink, I found that the key vegetation characteristics correlated with breeding pair density were absence of trees and dead vegetation. In contrast, the summary by Shaffer *et al*. (2015d) identifies vegetation height and density, and litter, forb, and shrub cover as key vegetation characteristics for this species. The Birds of North America account, consistent with my findings, identified a high proportion of non-forested habitat as an important component of Bobolink habitat, and in agreement with the Shaffer *et al*. (2015d) summary, found density, litter, and forb cover to be important. In accordance with my finding that dead vegetation was negatively correlated with the density of Grasshopper Sparrows, the Birds of North America account identified hay fields more than eight years since plowing or reseeding as suitable habitat for this species, and such sites may be more likely to have residual dead vegetation if they were not mown during the previous fall or spring.

Consistent with Shaffer *et al*.'s (2015e) summary of the Western Meadowlark and the Birds of North America account for this species (Davis & Lanyon 2008), I found that absence of trees and a high percentage of grass cover are correlated with the density of this species. Although Shaffer *et al*. (2015e) and Davis & Lanyon (2008) conclude that a high litter component is important for this species, I did not find this to be the case. However, I did find that a residual dead vegetation (which often occurs simultaneously with high litter), was negatively correlated with Western Meadowlark density.

I found no significant correlations between Brown-headed Cowbird density and the vegetation characteristics that I recorded, although height, density, litter depth, forb cover, grass cover, shrub cover and tree density have all been found to be important vegetation characteristics for this species as summarized by Shaffer *et al*. (2003). This species is associated with edge habitat (Lowther 1993), so my methodology of walking along belt transects into the grassland starting several meters in from the roadside may not adequately sample this species.

In summary, although my results are generally consistent with previous accounts of vegetation characteristics preferred by each of these species, the low correlation coefficients and the wide variance in my results indicate that most species are tolerant of a wide variety of habitat conditions. In addition, judicious selection of explanatory variables negated the need for the PCA, thereby providing an avenue for more efficient habitat monitoring.

TABLES

Table 2.1. Variables included in the analysis of habitat associations for each of the seven species of interest (Grasshopper Sparrow, Sedge Wren, Savannah Sparrow, Henslow's Sparrow, Dickcissel, Bobolink, Western Meadowlark, and Brown-headed Cowbird) in southwestern Minnesota. Ranges, means, medians, standard deviation (SD) and first and third quartiles are intended to give context to land managers for relative terms (denser, less, higher) used to describe species' habitat associations.

Variable	Variable description	Range	Mean	Median	SD	1st Quartile	3rd Quartile
Litter	Depth of residual plant litter (cm)	0.00-16.67	5.00	4.75	2.50	3.40	6.17
Height	Height of vegetation (cm)	7.00-108.75	40.40	39.17	11.91	33.75	45.00
Grass	Percent cover of grass within 4 m	14.00-100.00	69.78	71.67	15.87	59.17	81.25
Forbs	Percent cover of forbs within 4 m	0.00-82.00	18.00	14.27	13.13	8.40	25.00
Shrub	Percent cover of shrubs within 4 m	0.00-30.25	3.13	0.50	4.99	0.00	4.88
DeadVeg	Percent cover of standing dead vegetation within 4 m	0.00-36.00	6.23	4.00	6.67	2.00	7.75
BareGround	Percent cover of bare ground within 4 m	0.00-22.03	2.08	1.00	3.79	0.00	2.00
VOR	Vegetation density estimated by visual obstruction reading	0.55-8.83	3.40	3.38	1.33	2.42	4.35
DistToTree	Distance to nearest tree (m)	16.67-480.50	147.43	151.81	74.12	92.45	188.41
Trees100	Estimated percent tree cover within 100 m	0.00-25.00	2.48	0.50	4.14	0.00	3.33

Table 2.2. (A) Factor loadings for each variable of each of the top four principal components. (B) Correlation coefficients between the variables and the principal components.

Table 2.2A. Factor loadings for the first three principal components

Variable	PC1	PC2	PC3	PC4
Litter	-0.37	-0.09	-0.05	0.42
Height	-0.18	-0.57	0.02	-0.29
Grass	-0.49	0.29	0.39	-0.15
Forbs	0.37	-0.33	-0.42	-0.19
Shrub	0.21	-0.03	0.21	-0.13
DeadVeg	0.00	-0.19	-0.20	0.73
BareGround	0.41	0.22	0.03	-0.10
VOR	-0.32	-0.53	0.05	-0.20
DistToTree	-0.30	0.25	-0.48	-0.25
Trees100	0.24	-0.23	0.59	0.13

Table 2.2B. Correlation coefficients between PC values and vegetation variables

Variable	PC1	PC2	PC3	PC4
Litter	-0.55	-0.12	-0.10	0.46
Height	-0.28	-0.81	0.04	-0.32
Grass	-0.71	0.44	0.48	-0.16
Forbs	0.54	-0.50	-0.51	-0.20
Shrub	0.32	0.02	0.11	-0.14
DeadVeg	0.00	-0.30	-0.18	0.80
BareGround	0.61	0.30	0.08	-0.11
VOR	-0.48	-0.75	0.09	-0.22
DistToTree	-0.43	0.35	-0.62	-0.27
Trees100	0.35	-0.32	0.75	0.14

Table 2.3. Correlation coefficients between the densities of grassland birds of interest and the four principal components. Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1). Asterisks represent $p < 0.05$.

Species	PC1	PC2	PC3	PC4
GRSP	0.02	0.28*	-0.23*	-0.07
SEWR	-0.16*	-0.31*	-0.18*	0.02
SAVS	-0.11*	0.18*	-0.13*	-0.05
HESP	-0.10	-0.04	-0.08	-0.11
DICK	-0.08	-0.09	-0.15*	0.06
BOBO	-0.14*	0.12*	-0.17*	-0.19*
WEME	-0.08	0.13*	-0.07	-0.20*
BHCO	0.02	-0.02	-0.05	-0.02
ALLGRASS	-0.23*	0.01	-0.28*	-0.16*

Table 2.4. Logistic Regression Models using PCs to predict species occurrences. Best model for each species is indicated in bold. Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1).

Species	**PC**	**AIC**	**ΔAIC**
GRSP	Null	423.872	51.093
GRSP	PC1	423.064	50.285
GRSP	PC2	397.829	25.050
GRSP	PC3	406.245	33.466
GRSP	PC4	421.726	48.947
GRSP	PC1 + PC2	396.766	23.987
GRSP	PC1 + PC3	405.192	32.413
GRSP	PC1 + PC4	420.859	48.080
GRSP	PC2 + PC3	377.377	4.598
GRSP	PC2 + PC4	395.469	22.690
GRSP	PC3 + PC4	403.607	30.828
GRSP	PC1 + PC2 + PC3	375.750	2.971
GRSP	PC1 + PC2 + PC4	394.470	21.691
GRSP	PC1 + PC3 + PC4	402.496	29.717
GRSP	PC2 + PC3 + PC4	374.420	1.641
GRSP	**PC1 + PC2 + PC3 + PC4**	**372.779**	**0.000**
SEWR	Null	389.343	38.134
SEWR	PC1	375.478	24.268
SEWR	PC2	370.424	19.215
SEWR	PC3	387.466	36.257
SEWR	PC4	391.310	40.101
SEWR	PC1 + PC2	353.048	1.839
SEWR	PC1 + PC3	373.045	21.836
SEWR	PC1 + PC4	377.421	26.212
SEWR	PC2 + PC3	368.721	17.511
SEWR	PC2 + PC4	372.371	21.161
SEWR	PC3 + PC4	389.437	38.228
SEWR	**PC1 + PC2 + PC3**	**351.209**	**0.000**
SEWR	PC1 + PC2 + PC4	354.902	3.693
SEWR	PC1 + PC3 + PC4	375.005	23.796
SEWR	PC2 + PC3 + PC4	370.692	19.483
SEWR	PC1 + PC2 + PC3 + PC4	353.113	1.904
SAVS	Null	373.776	18.603
SAVS	PC1	373.662	18.489

Species	PC	AIC	ΔAIC
SAVS	PC2	364.424	9.250
SAVS	PC3	366.980	11.807
SAVS	PC4	375.725	20.551
SAVS	PC1 + PC2	363.979	8.806
SAVS	PC1 + PC3	366.390	11.217
SAVS	PC1 + PC4	375.608	20.434
SAVS	PC2 + PC3	356.373	1.200
SAVS	PC2 + PC4	366.305	11.132
SAVS	PC3 + PC4	368.939	13.766
SAVS	**PC1 + PC2 + PC3**	**355.173**	**0.000**
SAVS	PC1 + PC2 + PC4	365.838	10.665
SAVS	PC1 + PC3 + PC4	368.354	13.180
SAVS	PC2 + PC3 + PC4	358.271	3.098
SAVS	PC1 + PC2 + PC3 + PC4	357.066	1.893
HESP	Null	270.861	7.501
HESP	PC1	264.122	0.761
HESP	PC2	272.617	9.256
HESP	PC3	270.812	7.451
HESP	PC4	270.491	7.131
HESP	PC1 + PC2	265.768	2.407
HESP	PC1 + PC3	263.730	0.369
HESP	PC1 + PC4	263.733	0.372
HESP	PC2 + PC3	272.635	9.275
HESP	PC2 + PC4	272.304	8.943
HESP	PC3 + PC4	270.560	7.200
HESP	PC1 + PC2 + PC3	265.480	2.119
HESP	PC1 + PC2 + PC4	265.422	2.061
HESP	**PC1 + PC3 + PC4**	**263.360**	**0.000**
HESP	PC2 + PC3 + PC4	272.415	9.054
HESP	PC1 + PC2 + PC3 + PC4	265.129	1.769
DICK	Null	346.663	9.670
DICK	PC1	340.531	3.538
DICK	PC2	348.662	11.669
DICK	PC3	347.059	10.066
DICK	PC4	343.283	6.291
DICK	PC1 + PC2	342.530	5.537
DICK	PC1 + PC3	340.758	3.765
DICK	**PC1 + PC4**	**336.993**	**0.000**

Species	PC	AIC	ΔAIC
DICK	PC2 + PC3	349.056	12.064
DICK	PC2 + PC4	345.276	8.283
DICK	PC3 + PC4	343.827	6.834
DICK	PC1 + PC2 + PC3	342.758	5.765
DICK	PC1 + PC2 + PC4	338.992	1.999
DICK	PC1 + PC3 + PC4	337.308	0.315
DICK	PC2 + PC3 + PC4	345.817	8.825
DICK	PC1 + PC2 + PC3 + PC4	339.305	2.312
BOBO	Null	353.021	25.048
BOBO	PC1	343.906	15.933
BOBO	PC2	353.430	25.457
BOBO	PC3	346.590	18.617
BOBO	PC4	344.486	16.514
BOBO	PC1 + PC2	344.248	16.275
BOBO	PC1 + PC3	337.722	9.749
BOBO	PC1 + PC4	334.843	6.870
BOBO	PC2 + PC3	347.246	19.274
BOBO	PC2 + PC4	345.030	17.057
BOBO	PC3 + PC4	336.995	9.023
BOBO	PC1 + PC2 + PC3	338.245	10.272
BOBO	PC1 + PC2 + PC4	335.282	7.310
BOBO	**PC1 + PC3 + PC4**	**327.973**	**0.000**
BOBO	PC2 + PC3 + PC4	337.781	9.809
BOBO	PC1 + PC2 + PC3 + PC4	328.575	0.602
WEME	Null	366.682	25.625
WEME	PC1	367.194	26.137
WEME	PC2	354.122	13.064
WEME	PC3	365.023	23.966
WEME	PC4	356.169	15.111
WEME	PC1 + PC2	354.247	13.190
WEME	PC1 + PC3	365.375	24.318
WEME	PC1 + PC4	356.515	15.458
WEME	PC2 + PC3	351.986	10.929
WEME	PC2 + PC4	342.652	1.595
WEME	PC3 + PC4	354.877	13.820
WEME	PC1 + PC2 + PC3	351.857	10.799
WEME	PC1 + PC2 + PC4	342.733	1.676
WEME	PC1 + PC3 + PC4	355.034	13.976

Species	**PC**	**AIC**	**ΔAIC**
WEME	PC2 + PC3 + PC4	341.237	0.180
WEME	**PC1 + PC2 + PC3 + PC4**	**341.057**	**0.000**
BHCO	**Null**	**96.692**	**0.000**
BHCO	PC1	98.688	1.997
BHCO	PC2	98.669	1.977
BHCO	PC3	98.238	1.546
BHCO	PC4	98.685	1.994
BHCO	PC1 + PC2	100.665	3.974
BHCO	PC1 + PC3	100.229	3.537
BHCO	PC1 + PC4	100.682	3.990
BHCO	PC2 + PC3	100.201	3.510
BHCO	PC2 + PC4	100.663	3.971
BHCO	PC3 + PC4	100.231	3.540
BHCO	PC1 + PC2 + PC3	102.192	5.500
BHCO	PC1 + PC2 + PC4	102.659	5.968
BHCO	PC1 + PC3 + PC4	102.222	5.531
BHCO	PC2 + PC3 + PC4	102.195	5.504
BHCO	PC1 + PC2 + PC3 + PC4	104.185	7.494

Table 2.5. The correlation coefficients between the densities of grassland birds of interest and the individual variables.

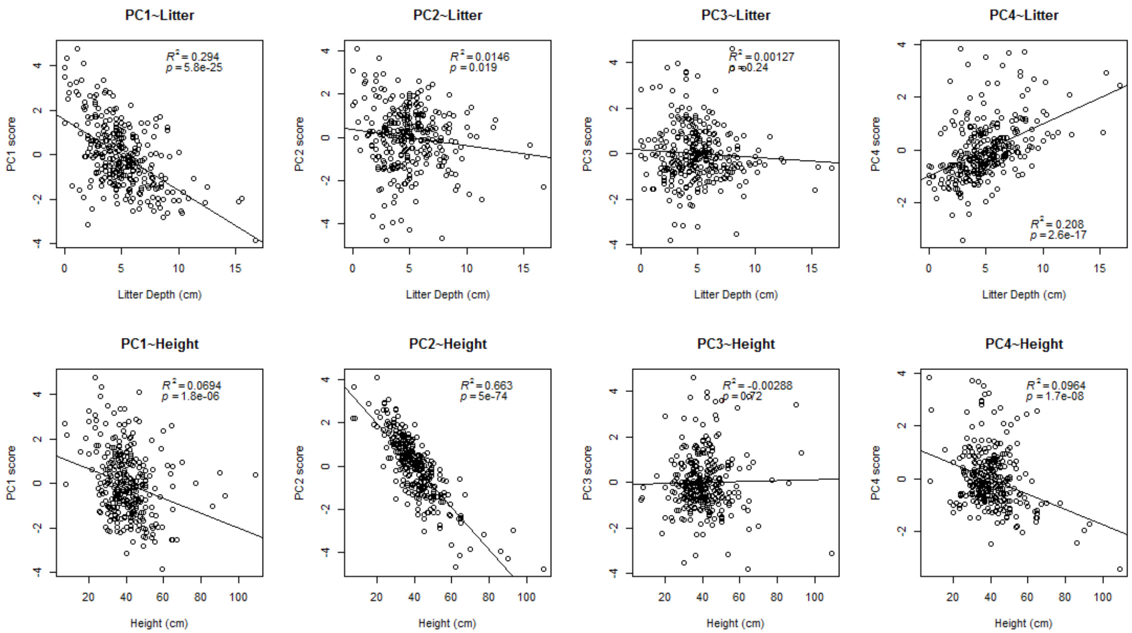
Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1).

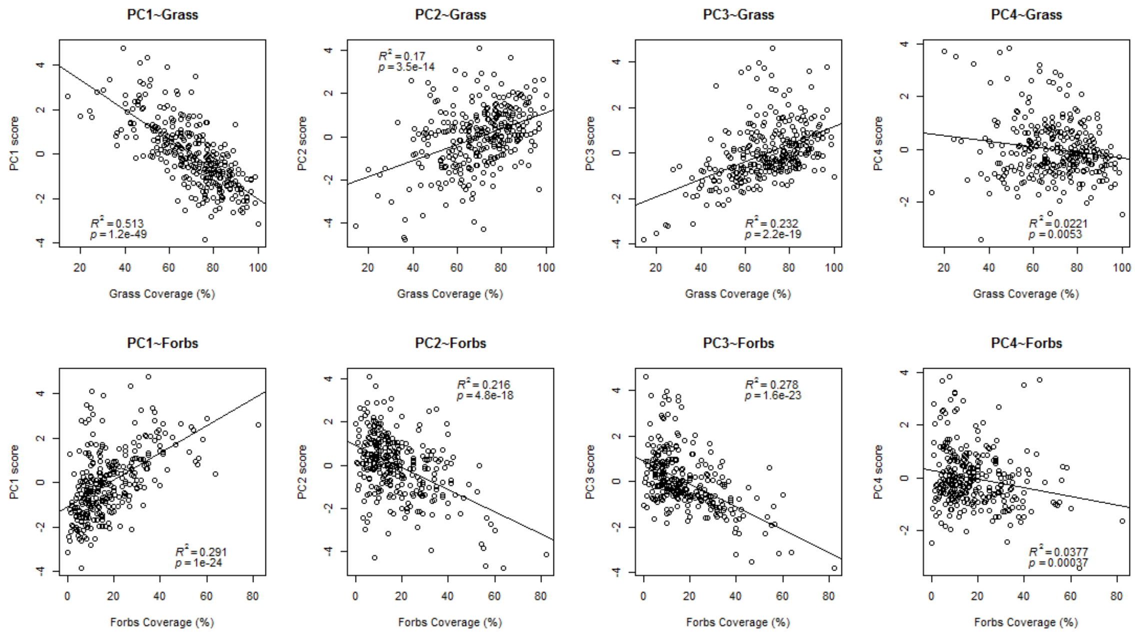
Statistically significant *p*-values are marked with an asterisk.

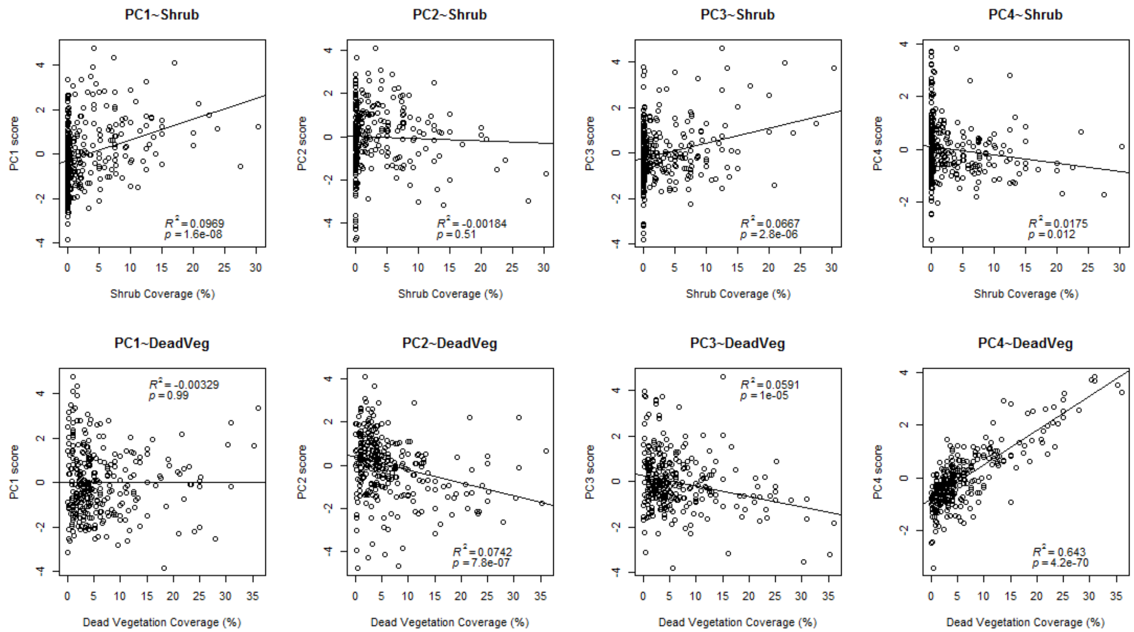
Species	Litter	Height	Grass	Forbs	Shrub	DeadVeg	BareGround	VOR	DistToTree	Trees100
GRSP	-0.08	-0.25*	0.00	0.03	0.03	-0.05	0.03	-0.22*	0.30*	-0.23*
SEWR	0.12*	0.32*	-0.10	0.12*	-0.15*	0.17*	-0.14*	0.30*	0.06	-0.09
SAVS	0.00	-0.09	0.11*	-0.04	-0.16*	-0.07	-0.03	-0.12*	0.21*	-0.17*
HESP	0.01	0.05	0.03	0.06	-0.05	-0.08	-0.11	0.09	0.10	-0.09
DICK	0.04	0.03	-0.08	0.05	-0.03	0.14*	-0.14*	0.13*	0.12*	-0.08
BOBO	0.04	0.03	0.09	0.00	0.02	-0.18*	-0.10	-0.07	0.25*	-0.27*
WEME	-0.09	-0.06	0.12*	-0.01	-0.10	-0.20*	0.03	0.01	0.12*	-0.17*
BHCO	0.07	-0.01	-0.05	0.09	0.02	-0.06	-0.03	-0.02	-0.01	-0.04
ALLGRASS	0.07	0.10	0.05	0.06	-0.10	-0.08	-0.19*	0.07	0.32*	-0.30*

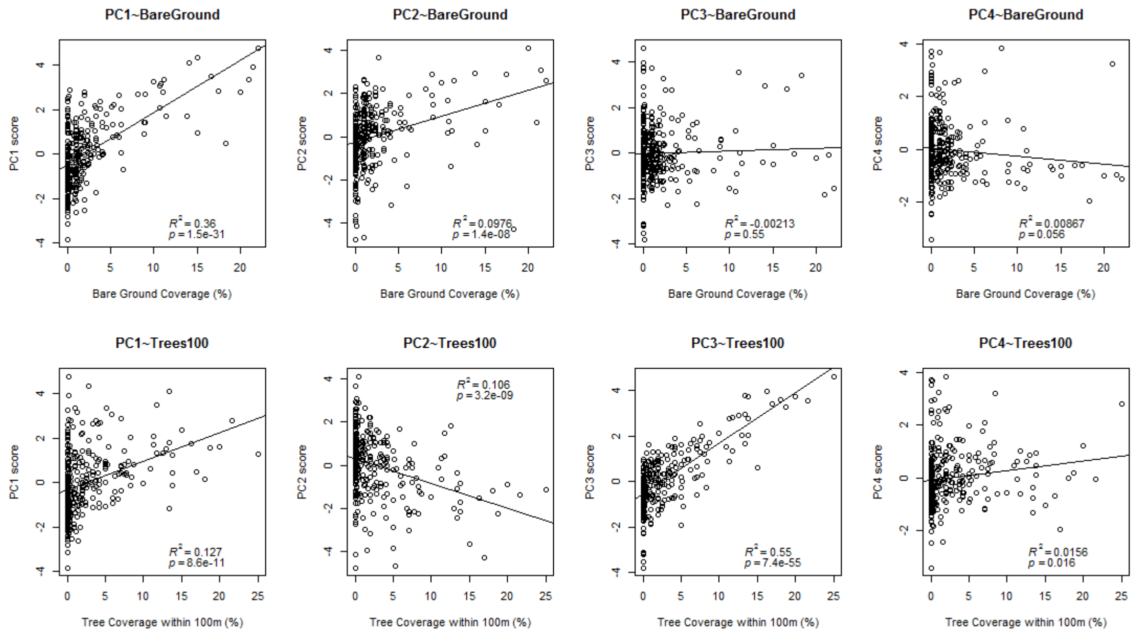
FIGURES

Figure 2.1. Principal component scores in relation to vegetation variables.




PC1~Grass
PC1 score
R² = 0.513
p = 1.2e-49
Grass Coverage (%)
PC2~Grass
PC2 score
R² = 0.17
p = 3.5e-14
Grass Coverage (%)
PC3~Grass
PC3 score
R² = 0.232
p = 2.2e-19
Grass Coverage (%)
PC4~Grass
PC4 score
R² = 0.0221
p = 0.0053
Grass Coverage (%)
PC1~Forbs
PC1 score
R² = 0.291
p = 1e-24
Forbs Coverage (%)
PC2~Forbs
PC2 score
R² = 0.216
p = 4.8e-18
Forbs Coverage (%)
PC3~Forbs
PC3 score
R² = 0.278
p = 1.6e-23
Forbs Coverage (%)
PC4~Forbs
PC4 score
R² = 0.0377
p = 0.00037
Forbs Coverage (%)


PC1~Shrub
PC2~Shrub
PC3~Shrub
PC4~Shrub
PC1 score
PC2 score
PC3 score
PC4 score
R^2 = 0.0969
p = 1.6e-08
R^2 = -0.00184
p = 0.51
R^2 = 0.0667
p = 2.8e-06
R^2 = 0.0175
p = 0.012
Shrub Coverage (%)
PC1~DeadVeg
PC2~DeadVeg
PC3~DeadVeg
PC4~DeadVeg
R^2 = -0.00329
p = 0.99
R^2 = 0.0742
p = 7.8e-07
R^2 = 0.0591
p = 1e-05
R^2 = 0.643
p = 4.2e-70
Dead Vegetation Coverage (%)


PC1~BareGround
PC1 score
$R^2 = 0.36$
$p = 1.5e-31$
Bare Ground Coverage (%)
PC2~BareGround
PC2 score
$R^2 = 0.0976$
$p = 1.4e-08$
Bare Ground Coverage (%)
PC3~BareGround
PC3 score
$R^2 = -0.00213$
$p = 0.55$
Bare Ground Coverage (%)
PC4~BareGround
PC4 score
$R^2 = 0.00867$
$p = 0.056$
Bare Ground Coverage (%)
PC1~Trees100
PC1 score
$R^2 = 0.127$
$p = 8.6e-11$
Tree Coverage within 100m (%)
PC2~Trees100
PC2 score
$R^2 = 0.106$
$p = 3.2e-09$
Tree Coverage within 100m (%)
PC3~Trees100
PC3 score
$R^2 = 0.55$
$p = 7.4e-55$
Tree Coverage within 100m (%)
PC4~Trees100
PC4 score
$R^2 = 0.0156$
$p = 0.016$
Tree Coverage within 100m (%)

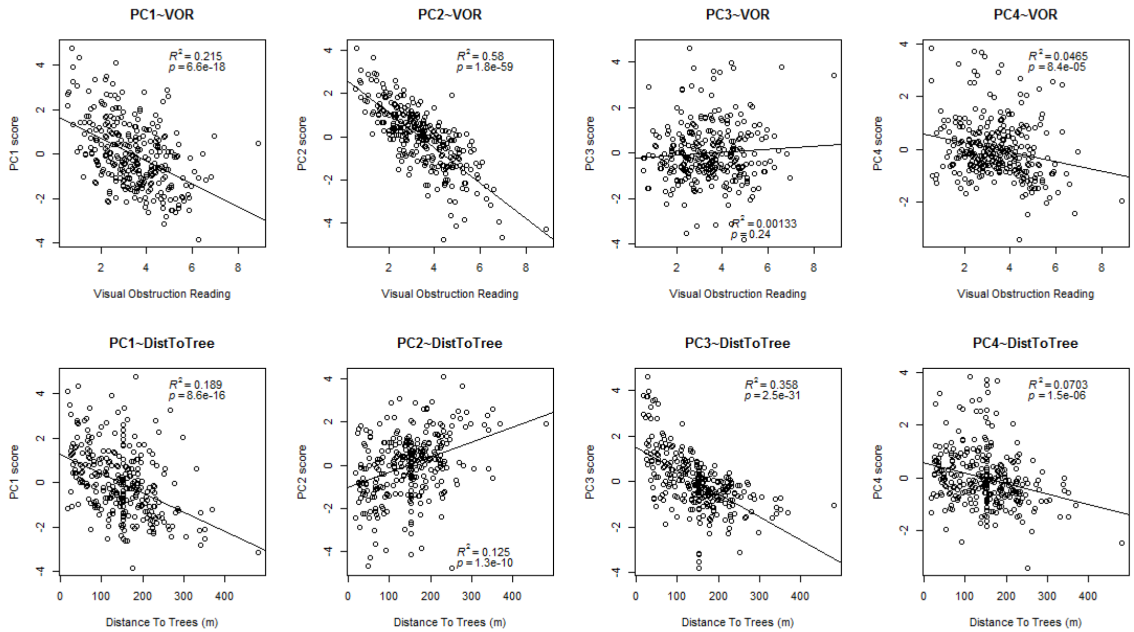

PC1~VOR
$R^2 = 0.215$
$p = 6.6e-18$
PC1 score
Visual Obstruction Reading
PC2~VOR
$R^2 = 0.58$
$p = 1.8e-59$
PC2 score
Visual Obstruction Reading
PC3~VOR
$R^2 = 0.00133$
$p = 0.24$
PC3 score
Visual Obstruction Reading
PC4~VOR
$R^2 = 0.0465$
$p = 8.4e-05$
PC4 score
Visual Obstruction Reading
PC1~DistToTree
$R^2 = 0.189$
$p = 8.6e-16$
PC1 score
Distance To Trees (m)
PC2~DistToTree
$R^2 = 0.125$
$p = 1.3e-10$
PC2 score
Distance To Trees (m)
PC3~DistToTree
$R^2 = 0.358$
$p = 2.5e-31$
PC3 score
Distance To Trees (m)
PC4~DistToTree
$R^2 = 0.0703$
$p = 1.5e-06$
PC4 score
Distance To Trees (m)

Figure 2.2. The distribution of Upland Grassland (Green), Low Grassland (Black) and Wet Meadow (Red) sites in relation to the principal components 1 and 2. PC1 separates wet meadow sites from non-wet meadow sites, while PC2 separates Low grassland sites from upland grassland sites.

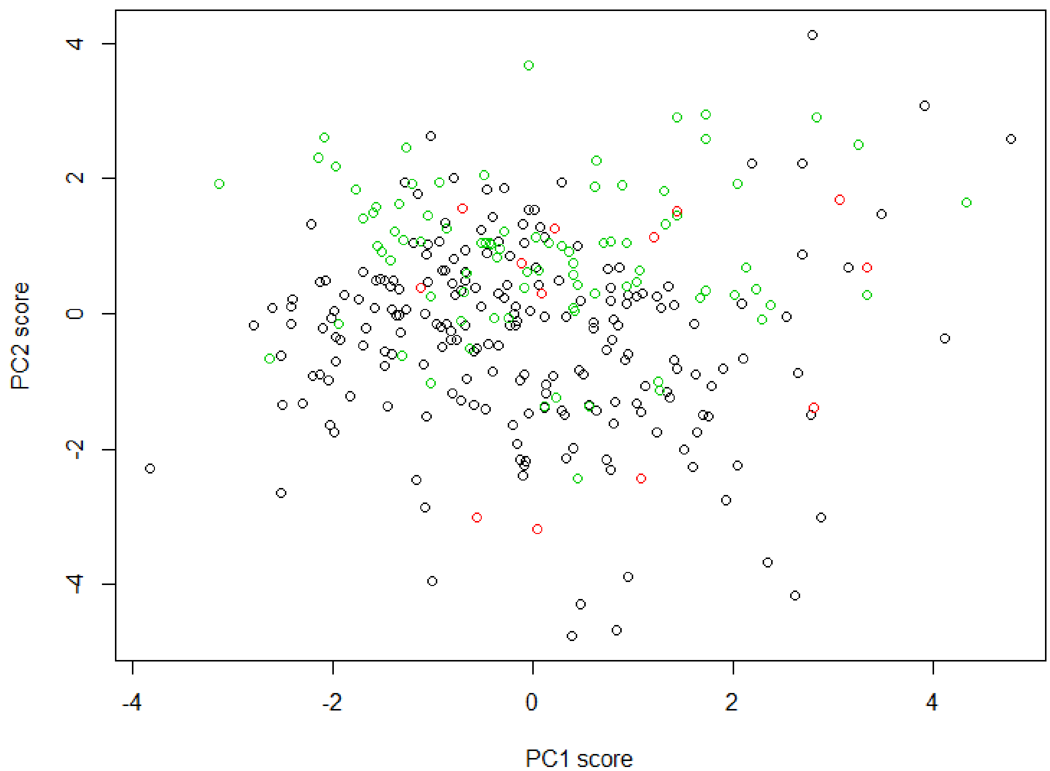
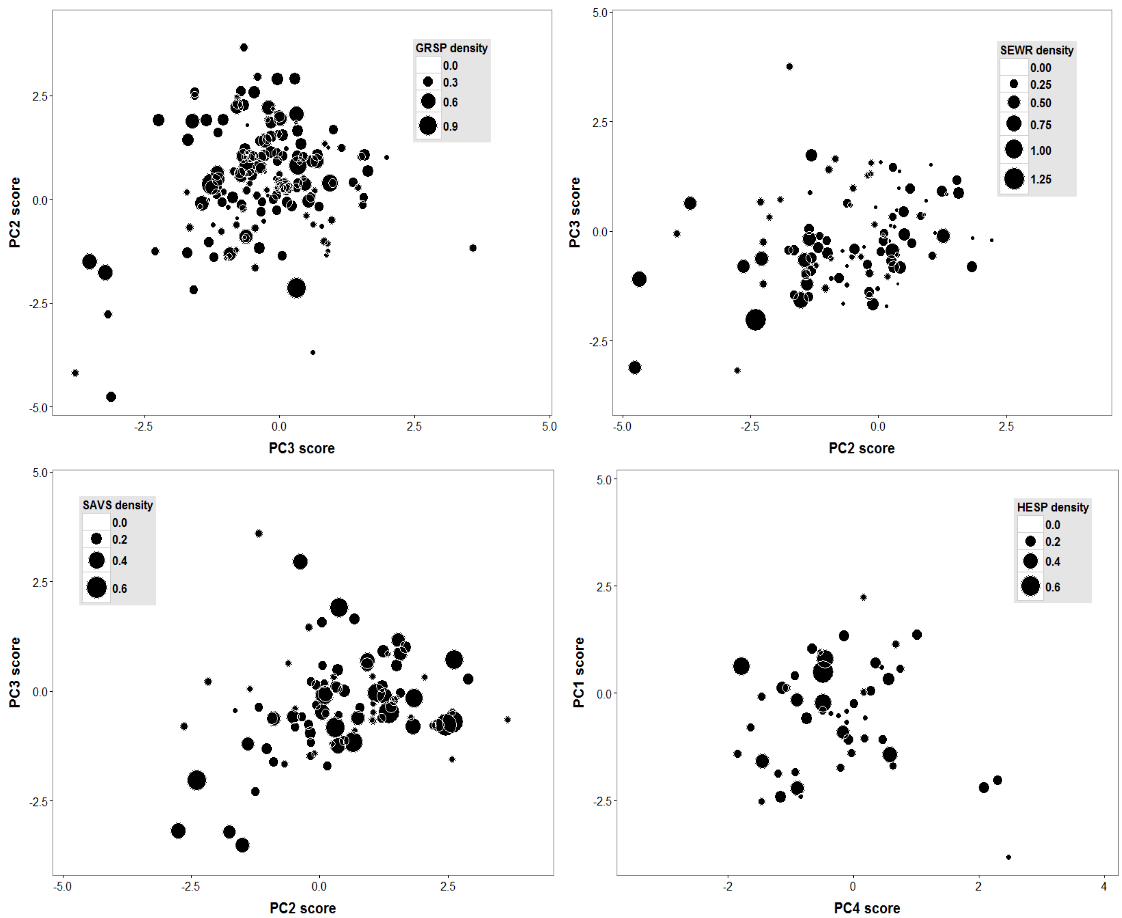


Figure 2.3. Relative density of the species of interest indicated by size of bubble. Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1).   Principal components were chosen for the axes on the basis of highest correlations with the species of interest's density (see Table 2.3).



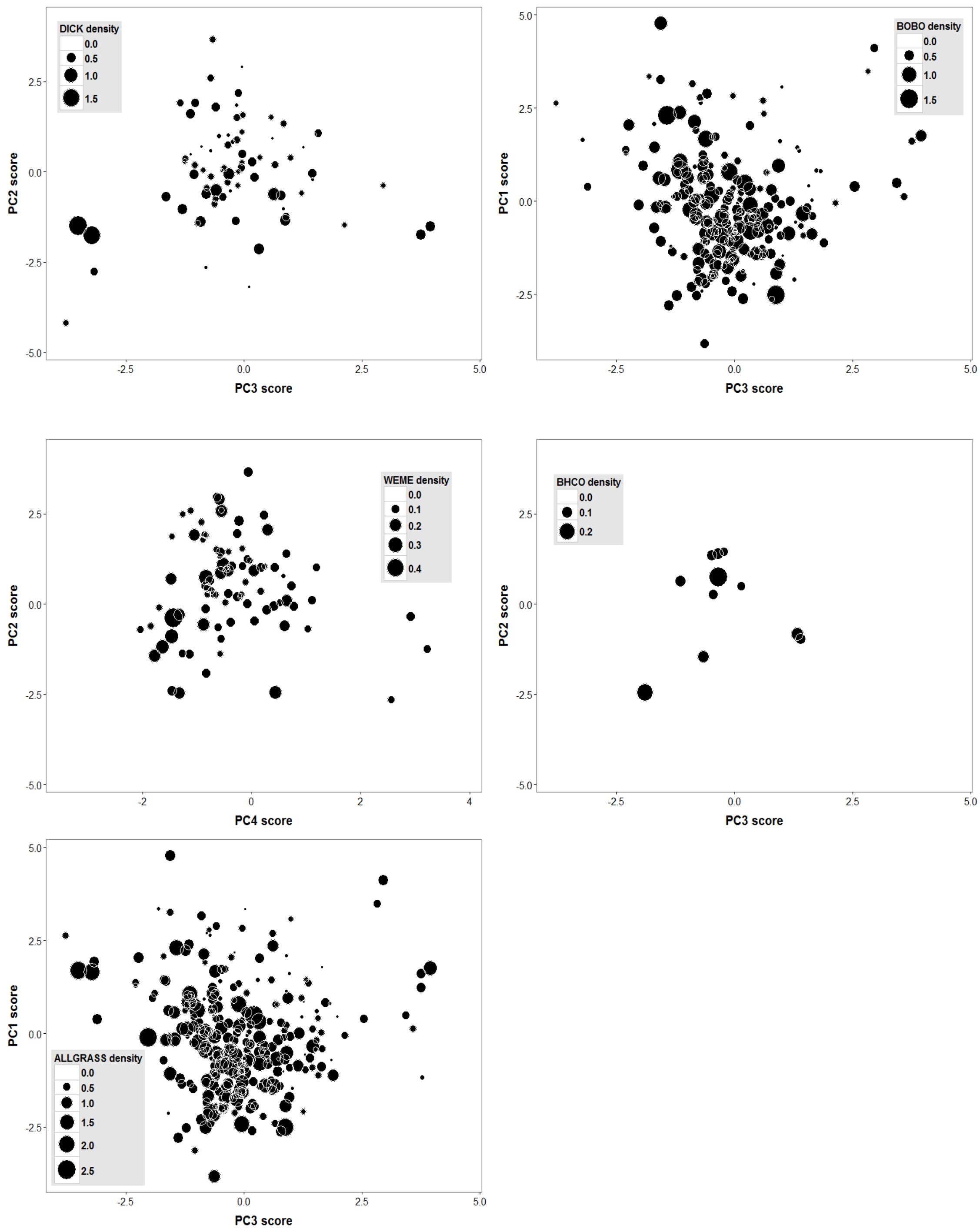

DICK density
0.0
0.5
1.0
1.5
PC2 score
PC3 score
BOBO density
0.0
0.5
1.0
1.5
PC1 score
PC3 score
WEME density
0.0
0.1
0.2
0.3
0.4
PC2 score
PC4 score
BHCO density
0.0
0.1
0.2
PC2 score
PC3 score
ALLGRASS density
0.0
0.5
1.0
1.5
2.0
2.5
PC1 score
PC3 score

Figure 2.4. The mean PC scores for the sites where each species of interest was observed. Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1).

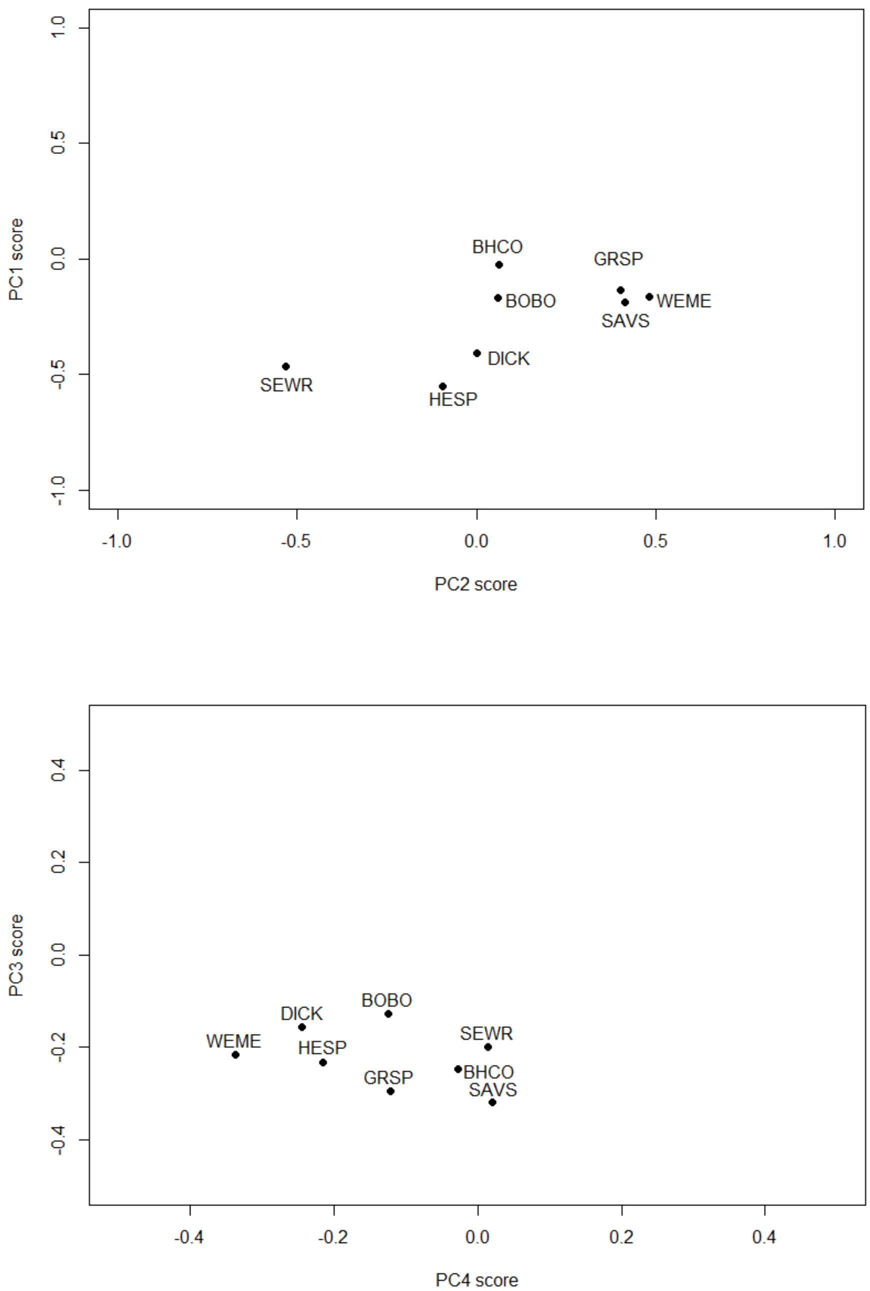


Figure 2.5. PC1 and PC2 scores for sites where each species of interest was observed. Grassland bird species are listed using standardized four-letter American Ornithologists' Union alpha codes (See Table 1.1).

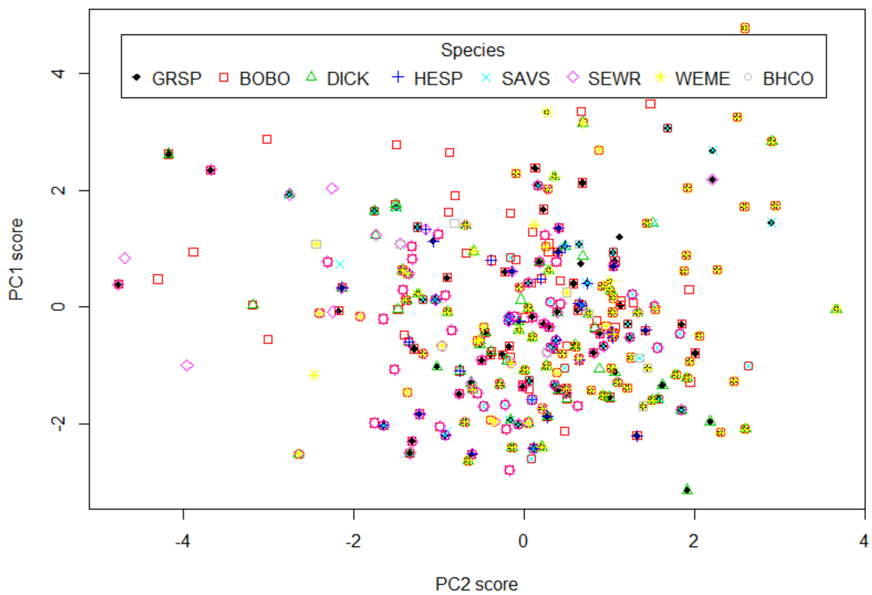


Figure 2.6. Loess plots of Grasshopper Sparrow (GRSP) density in relation to vegetation variables. Span was chosen to minimize AIC$_c$ value using loess.as from the fANCOVA package (Wang 2010) in R.

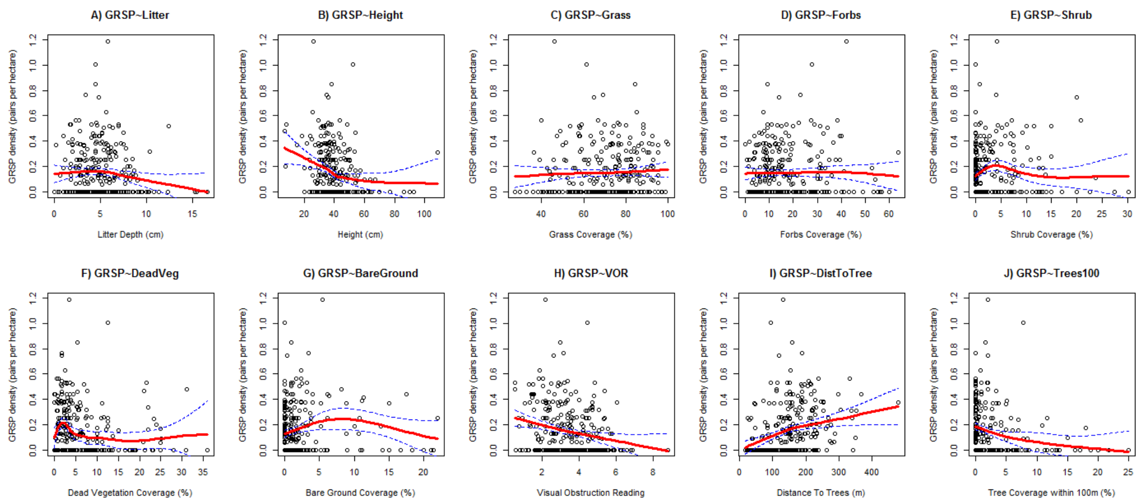


Figure 2.7. Loess plots of Sedge Wren (SEWR) density in relation to vegetation variables. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

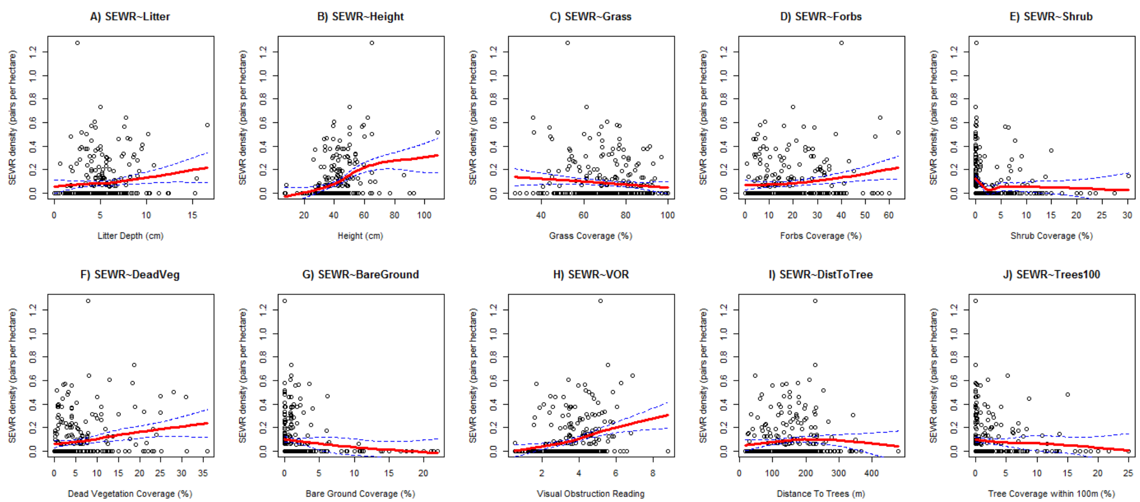


Figure 2.8. Loess plots of Savannah Sparrow (SAVS) density in relation to vegetation variables. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

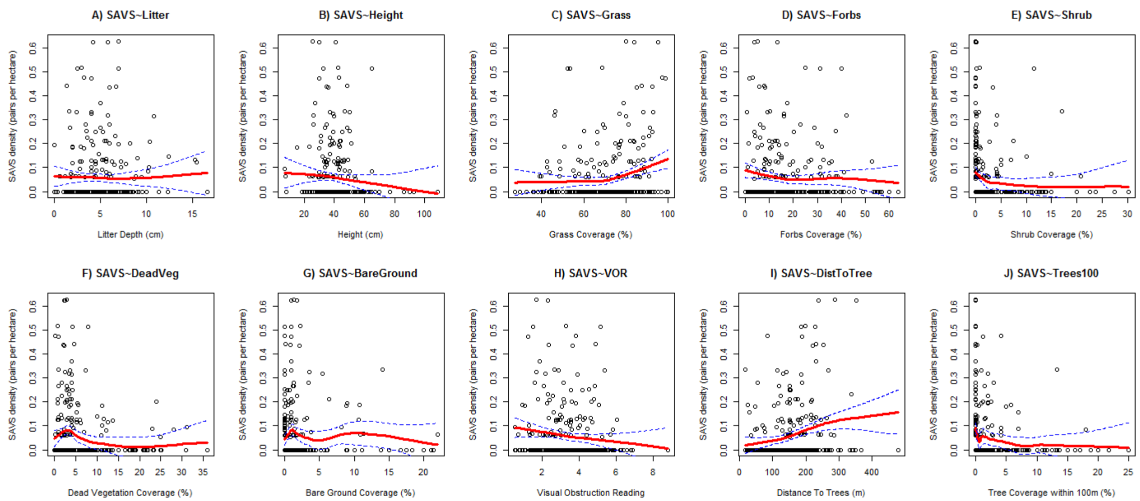


Figure 2.9. Loess plots of Henslow's Sparrow (HESP) density in relation to vegetation variables. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

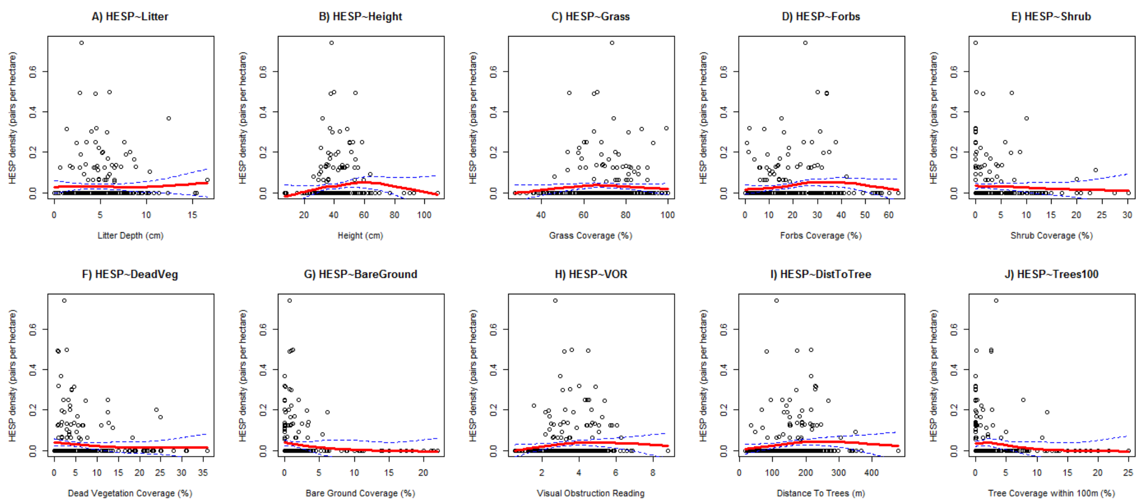


Figure 2.10. Loess plots of Dickcissel (DICK) density in relation to vegetation variables. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

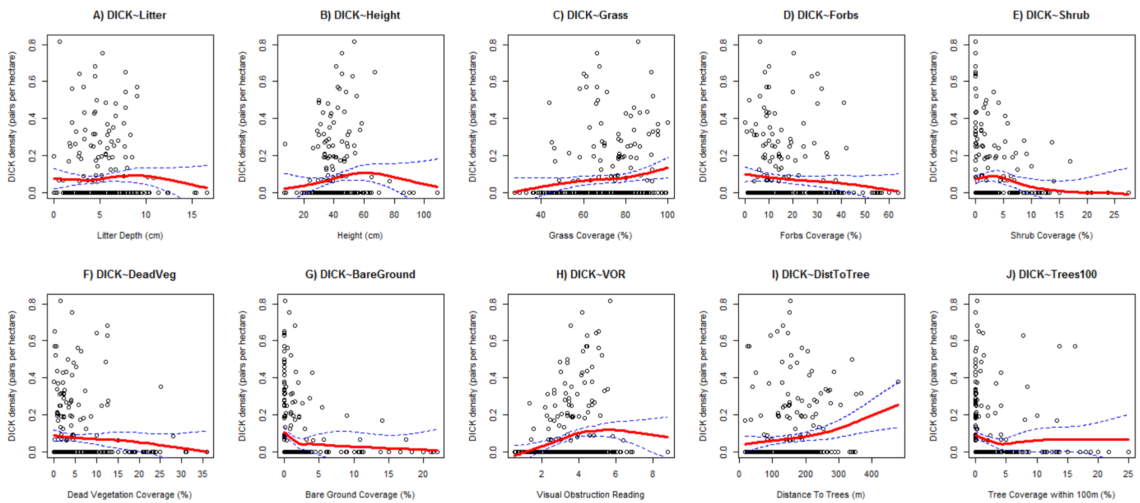


Figure 2.11. Loess plots of Bobolink (BOBO) density in relation to vegetation variables. Span was chosen to minimize AIC$_c$ value using loess.as from the fANCOVA package (Wang 2010) in R.

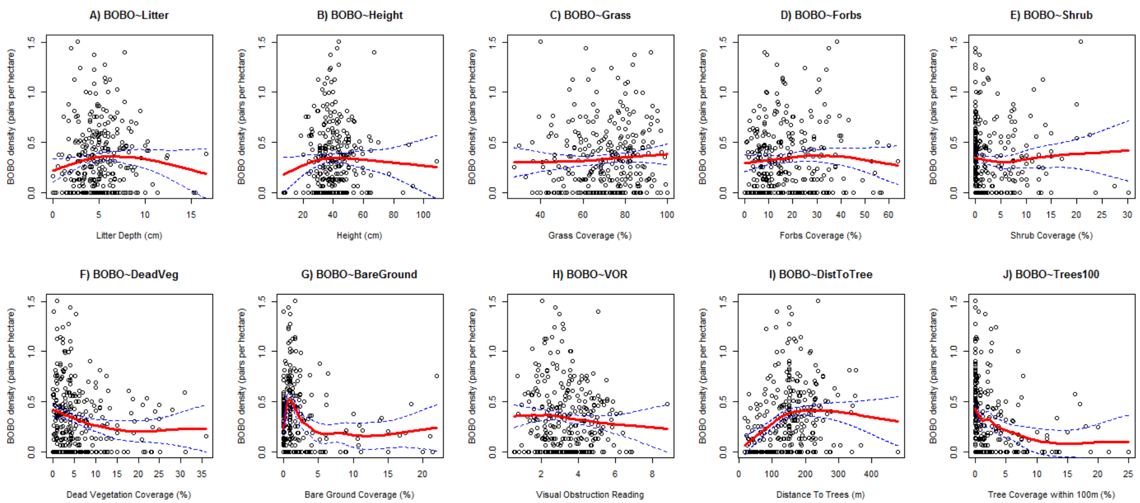


Figure 2.12. Loess plots of Western Meadowlark (WEME) density in relation to vegetation variables. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

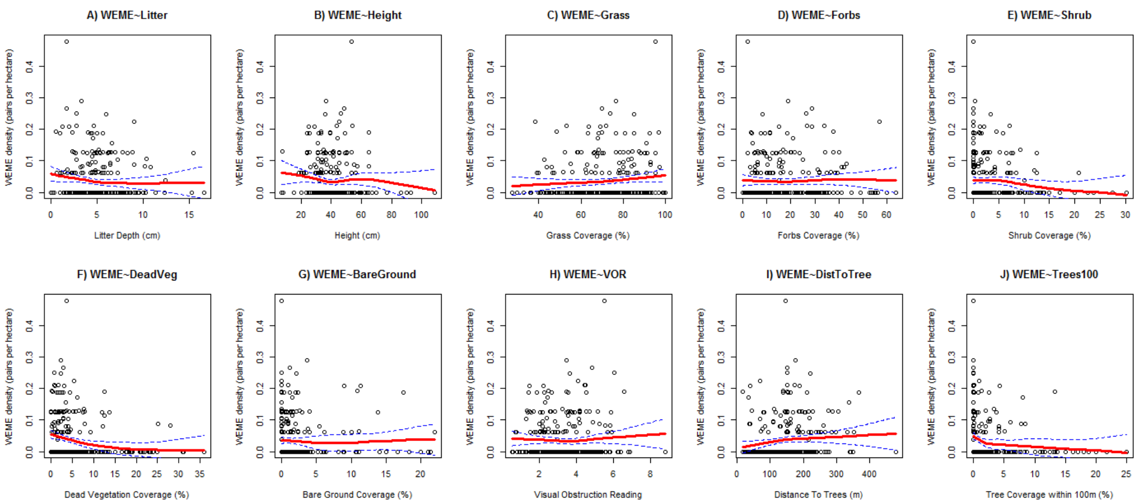


Figure 2.13. Loess plots of density of Brown-headed Cowbirds (BHCO) in relation to vegetation variables. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

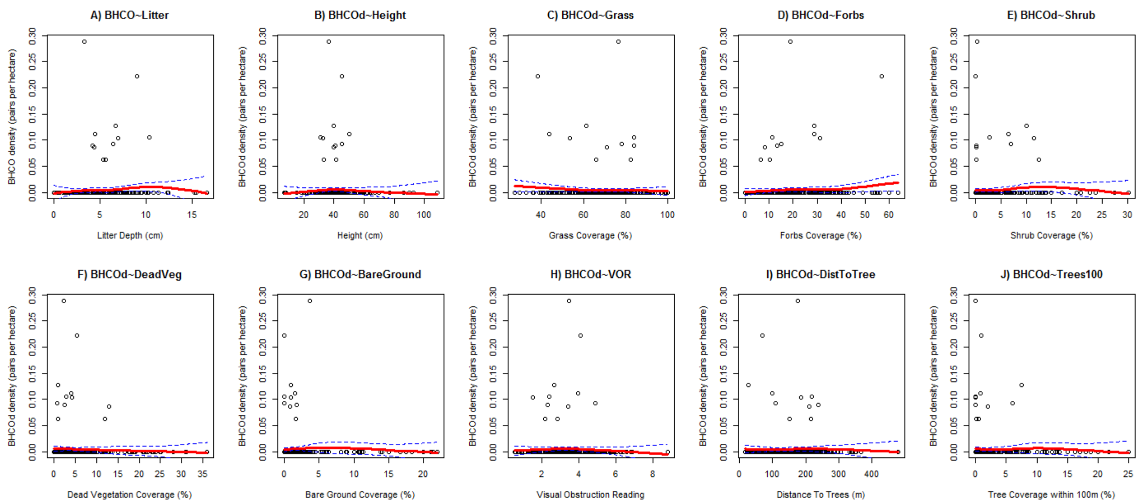
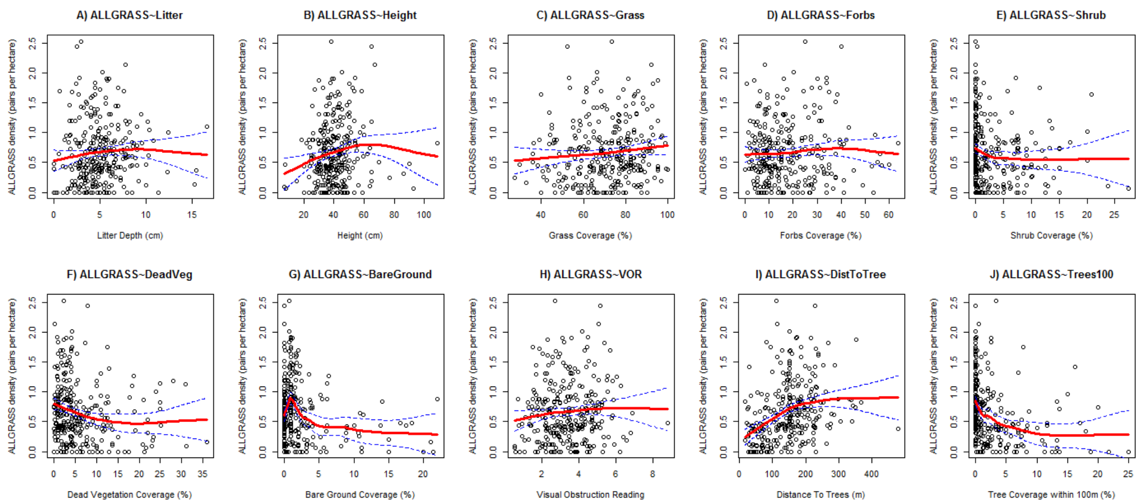


Figure 2.14. Loess plots of density of all grassland birds (ALLGRASS) in relation to vegetation variables. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.



CHAPTER 3. MODELING GRASSHOPPER SPARROW DENSITY IN SOUTHWESTERN MINNESOTA: ARE LANDSCAPE-SCALE COVARIATES SUFFICIENT?

Most species distribution models rely on landscape-scale covariates to determine the suitability of potential species habitat, yet wildlife species also respond to local-scale habitat characteristics. This is especially problematic when agencies are attempting to identify areas of special interest for a particular species across a large geographic area. Grasshopper Sparrows are one such species, having been designated a species of conservation concern by MN DNR. Bird and vegetation surveys were conducted at 71 grassland sites in 2013 and 2014, and landscape covariates were analyzed within 400m, 800m, and 1600m buffers around each site. I created candidate sets of models with local-scale covariates only, landscape-scale covariates only, and a combination of local- and landscape-scale covariates. The best model for each was selected with the second-order Akaike's information criterion (AIC_c), and then the three top performing models were compared, also using AIC_c. The model that included a combination of local- and landscape-scale variables outperformed the models that contained covariates of only a single scale. I used the top-performing landscape-only model to create a predictive map of Grasshopper Sparrow densities across the project area, and compared predicted to observed densities. My model explained only 11 percent of the variation in observed Grasshopper Sparrow densities, even though it was being validated by the same data set used to create the predictive model. In comparison, the top-performing combined-scale model was able to predict 21 percent of variation in Grasshopper Sparrow density.

INTRODUCTION

Grassland birds have shown concerning rates of population decline over the last half century (Igl & Johnson 1997; North American Bird Conservation Initiative U.S. Committee 2014), primarily as the result of habitat loss and fragmentation (Herkert 1994; Herkert *et al*. 2003). As a whole, the grassland bird population has declined by nearly 40% since 1968 (North American Bird Conservation Initiative U.S. Committee 2014). One grassland obligate, the Grasshopper Sparrow (*Ammodramus savannarum*) has declined by 5.5% per year in the Midwest from 1966 to 1993, for a total loss of 77% of the original population. In this same region, only one tenth of one percent of the original tallgrass prairie remained as of the late 1990s (Samson et al. 1998) and more recently rates of grassland conversion to corn/soy ranged from 1% to 5.4% per year between 2006 and 2011 in response to elevated commodity prices (Wright & Wimberly 2013).

Given that resources such as time and money are limited, commonly suggested measures to reverse these declines include focusing on priority areas for particular species of concern (Williams et al. 2002; Johnson et al. 2010), such as the Grasshopper Sparrow (Bakker 2005; Ringelman *et al*. 2005; Minnesota Department of Natural Resources 2006; Minnesota Prairie Plan Working Group 2011). As a result, resource managers need to know where high concentrations of these species can be found. One tool that has proved useful for determining “hot spots” for particular species is the use of spatially explicit models of species-habitat relationships (Dunning et al. 1995; Turner et al. 1995). These models typically rely on remotely sensed landscape-scale variables such as landcover to predict density of a species of interest (Williams et al. 2002). Remotely gathered data are relatively easily acquired and can be applied across a wide geographic range (Williams et al. 2002).

However, most such models of species density are based on landscape-scale components and do not include finer-scale variables such as vegetation components (Johnson et al. 2010). This is problematic because habitat selection occurs at multiple scales (Johnson 1980; Jones 2001). A variety of studies have found that, at least in some cases, landscape-scale variables have little, if any, explanatory power for grassland bird abundances (e.g., Fletcher & Koford 2002; Bakker et al. 2002; Jacobs et al. 2011) and this is especially true for the less-common species such as Grasshopper Sparrow (Murray et al. 2008). While landscape-scale components alone may not be adequate to predict species distributions, models that incorporate both local and landscape-scale covariates may offer a substantial improvement (Fletcher & Koford 2002; Cunningham & Johnson 2006; Winter et al. 2006; Quamen 2007; Renfrew & Ribic 2008; Thompson et al. 2014).

Due to its severe decline, the Grasshopper Sparrow has increasingly been the focus of regional conservation efforts. The U.S. Fish and Wildlife Service has identified this species as a surrogate species for the Eastern Tallgrass Prairie (Blomquist et al. 2013; Ruth 2015). Within Minnesota, it has been identified as both a Species in Greatest Conservation Need (SGCN) by the Minnesota State Wildlife Action Plan (Minnesota Department of Natural Resources 2006) and a Target Conservation Species by Minnesota Audubon (Pfannmuller 2014). Although species distribution modeling has been done for this species (Quamen 2007; Drum et al. 2015), the existing models are either out of date (e.g., Quamen 2007) considering the extensive land use change that occurred from 2006 to 2011 within the region (Wright & Wimberly 2013) or rely exclusively on landscape-scale data (e.g., Drum et al. 2015). Given the interest in this species and the lack of current models involving proximate habitat information, my primary objectives were to 1) develop and assess the relative suitability of Grasshopper Sparrow density models using local-scale variables only, landscape-scale variables only, and a combination of variables at the two scales; and 2) use the top-performing landscape-only model to map estimated densities of Grasshopper Sparrows throughout the study area. I expected that multi-scale models would provide the greatest predictive power, and that local-only models would offer more predictive power than landscape-only models.

METHODS

Field methods

For a description of field methods for data collection, please refer to chapter 1. For the purposes of this chapter, I measured Grasshopper Sparrow density along 222 transects at 71 sites, 26 of which were visited in both 2013 and 2014.

Landscape-scale information

I secured 2012 landcover data from USDA National Statistics Service Cropland Data Layer (USDA National Agricultural Statistics Service Cropland Data Layer 2012). I combined cover classes into grassland, cropland, trees, developed, and other (see Appendix C for reclassification scheme). I conducted focal mean analyses (ArcGIS 10.0; ESRI) to evaluate the proportion of each combined landcover class within buffers of radius 400, 800, and 1600 meters from the edges of each surveyed area at the 71 monitored sites. These landscape variables will henceforth be referred to by a combination of the habitat class and buffer distance, e.g., Grass400 is grassland within 400 meters. Results from these focal mean analyses were used as input variables for the Grasshopper Sparrow density models.

Statistical Methods

I analyzed the density of Grasshopper Sparrows using local- and landscape-scale habitat as explanatory variables. I conducted statistical analyses in program R version 3.1.1 (R Core Team 2014). I developed models that included local-only, landscape-only, and combined-scale variables to compare the relative value of models at different scales and hence different levels of utility for land managers. From the top-performing model I then developed a predictive GIS landscape-only model that could be used for identification of hotspots of Grasshopper Sparrow density within my study area. As a final measure, I assessed the suitability of both my predictive model and a predictive model, developed by the USFWS Habitat and Population Evaluation Team (HAPET; Drum et al. 2015) in comparison to my actual observations. See below for more detailed descriptions of individual analyses.

Linear regression modeling for local-only model.—I used linear regression models to examine the effect of local-scale variables on Grasshopper Sparrow density. Candidate variables—which included vegetation height (Height), visual obstruction reading (VOR), percent cover of trees within 100 meters (Trees100), distance to nearest tree (DistToTree), litter depth (Litter), percent shrub cover within a 4 meter radius of the point (Shrub), percent standing dead vegetation cover within a 4 meter radius of the point (DeadVeg), and percent bare ground cover within a 4 meter radius of the point (BareGround)—were selected on the basis of linear correlation coffeicients or evidence of curvilinear relationships with Grasshopper Sparrow density based on loess plots (see Chapter 2). I assessed the level of correlations among these variables using Pearson's r statistic. To reduce the problematic effects of collinearity, I used a threshold-based pre-selection to exclude highly correlated variables (Dormann et al. 2013). For pairs of variables with correlations $|r| \geq 0.60$, I retained only the variable that had a stronger correlation with Grasshopper Sparrow density. I constructed a balanced model set with all combinations of the remaining local-scale variables (Table 3.1). When quadratic terms were included in the model the corresponding linear term was also included. I then selected the best model with the second-order Akaike's information criterion (AIC_c; Anderson & Burnham 2002), using the AICcmodavg package in R (Mazerolle 2015).

Linear mixed effects modeling for landscape-only model.—I used the nlme package in R (Pinheiro et al. 2015) to create linear mixed effects models examining the effects of landscape-scale variables on Grasshopper Sparrow density. I examined percent grass cover, percent crop cover, percent tree cover, and percent developed land as potential landscape variables. I assessed the level of correlation of these variables with Grasshopper Sparrow density using Pearson's r statistic, and rejected variables with $p > 0.05$. I then checked the level of correlation among the remaining landscape variables using Pearson's r statistic, to ensure that the remaining set of variables did not exhibit collinearity. I then identified the most predictive scale of each variable to improve model performance using AIC and used only that scale for candidate models (Drum et al. 2015). I ran simple linear models to determine if quadratic terms provided additional explanatory power, retaining only those quadratic terms with $p < 0.05$. I then constructed a balanced model set with all combinations of the remaining landscape variables (Table 3.3). Each candidate model included the landscape variables of interest as fixed effects and site as a random effect. When quadratic terms were included in the model the corresponding linear term was also included. The best model was selected with the second-order Akaike's information criterion (AIC_c; Anderson & Burnham 2002), using the AICcmodavg package in R (Mazerolle 2015).

Linear mixed effects modeling for combined-scale model.—I used the nlme package in R (Pinheiro et al. 2015) to create linear mixed effects models examining the combined effects of local- and landscape-scale variables on Grasshopper Sparrow density. Each candidate model included the local-scale variables from the top-performing local-scale-only model (height, distance to nearest tree, litter depth, and percent dead vegetation) as fixed effects and site as a random effect. Due to the fact that DistToTree was incorporated in the base local-only model, I also checked that this variable was not strongly collinear with percent tree cover. However, I found relatively low correlation coefficients (|*r*| < 0.30) and therefore retained both variables (Dormann et al. 2013). I then constructed a balanced model set with all combinations of the landscape variables identified during the landscape-only variable selection process as additional fixed effects (Table 3.5). When quadratic terms were included in the model the corresponding linear term was also included. The best model was selected with the second-order Akaike's information criterion (AIC_c; Anderson & Burnham 2002), using the AICcmodavg package in R (Mazerolle 2015).

Comparison of local-only, landscape-only and combined-scale Models.—I removed random effects from the landscape-only and combined-scale models to compare my three models. I then selected the top-supported model with AIC_c, using the AICcmodavg package in R (Mazerolle 2015).

Predictive GIS model.—I created a binary raster grid of grassland in ArcGIS 10.0 (ESRI) using the reclassified 2012 Cropland Data Layer. I then calculated the percentage of grass in an 800-meter buffer around each $30m^2$ pixel that was classified as grassland. I used the landscape-only mixed effects model to calculate the predicted density of Grasshopper Sparrows at each grassland pixel and assumed that non-grassland pixels had a Grasshopper Sparrow density of 0 (Fig. 3.1).

Comparison of predicted vs. observed GRSP densities.—I calculated the expected Grasshopper Sparrow density for each of the 71 grassland sites sampled for birds by using the zonal statistics as table tool in ArcGIS 10.0 (see Appendix D for priority ranking of sites based on predicted density). I compared observed densities to expected densities at each site using linear regression. I would expect an R^2 value of 1 for a model that yielded predictions exactly equal to true density (Johnson et al. 2006, Drum et al. 2015). I also compared both my observed densities and model predictions to predictions calculated from the landscape-only model of Grasshopper Sparrow density developed by USFWS HAPET (Drum et al. 2015). Finally, I used a chi-square test to examine the relationship between my model's high expected density sites (> 8 pairs per 100 hectare) and Grasshopper Sparrow occurrence.

RESULTS

Linear regression modeling for local-only model

The 23 candidate models included various combinations of the variables Height, DistToTree, $Litter^2$, $DeadVeg^2$, $Shrub^2$, and $BareGround^2$ (Table 3.1). The top model ranked only 0.62 AIC_c units better than the next best supported model (Table 3.1). The top model indicated that Grasshopper Sparrow density increased with increasing distance to nearest tree, litter depth, and nonlinearly with dead vegetation, and with decreasing vegetation height, dead vegetation, and nonlinearly with litter depth (Table 3.2). This model explained a small but significant proportion of variance in Grasshopper Sparrow density (adjusted $R^2 = 0.16$, $F(6, 229) = 10.69$, $p < .001$).

Linear mixed effects modeling for landscape-only model

The initial analysis indicated that Grass800, Crop800, Tree400, and the quadratic terms for Grass800 and Crop800 were the variables most closely related to Grasshopper

Sparrow density. The candidate models included 17 combinations of these five variables (Table 3.3). The top model ranked 3.89 AIC_c units better than the next best supported model (Table 3.2). The top model indicated that Grasshopper Sparrow density increased with increasing percent grassland within 800m, which could be modeled by the regression equation y = 0.012 + 0.002x, where x is the grass cover in percent within 800m, and site was encorporated as a random effect (Table 3.4). This model explained a modest but significant proportion of variance in Grasshopper Sparrow density (adjusted $R^2 = 0.11$, $F(1, 304) = 37.86$, $p < .001$).

Linear mixed effects modeling for combined-scale model

The candidate model set included 17 combinations of the variables from the top-performing local-only model (Height, DistToTree, Litter^2, and DeadVeg^2), Grass800, Crop800, Tree400 Grass800^2, and Crop800^2 as fixed effects (Table 3.5). Site was encorporated into each candidate model as a random effect. The top three models each included only a single landscape-scale variable (Grass800, Tree400, or Crop800), and the best-supported model ranked only 1.40 AIC_c units better than the next best supported model (Table 3.5). In fact, a total of nine models were well supported ($\Delta AIC_c < 4$; Winter et al. 2006). The top-performing model contained the combination of the top-performing landscape-only and local-only models, indicating that Grasshopper Sparrow density increased with increasing percent grassland within 800 meters of the site and with local-scale increases in distance to nearest tree, litter depth, and nonlinearly with dead vegetation, and with decreasing vegetation height, dead vegetation, and nonlinearly with litter depth (Table 3.6).

Comparison of local-only, landscape-only and combined-scale models

The best-supported model was the combined scale model that included the top-performing sets of local and landscape scale variables (Table 3.7). This combined-scale model performed 17 AIC_c units better than the local-only model and 30 AIC_c units better than the landscape-only model. This model explained a small but significant proportion of variance in Grasshopper Sparrow density ($R^2 = 0.23$, $F(7, 298) = 12.50$, $p < .001$).

Predictive GIS landscape-only model

Predicted Grasshopper Sparrow density was mapped across the MN DNR Region 4 with the landscape-only regression equation $y = 0.012 + 0.002x$, where x is the grass cover in percent within 800m (Fig. 3.1).

Comparison of predicted vs. observed GRSP densities

Although the combined-scale model was the top-performing model, it is useful to assess the functionality of the more commonly used landscape-scale model with its more easily attainable explanatory variables. My observed densities were not very similar to predictions made with the landscape-only mixed effects model (Fig. 3.2). However, predictions from my model were more similar to observed densities than were predictions generated by the more complicated HAPET model (Fig. 3.3). My model and the HAPET model explained only 11 and 5 percent of the observed variation in Grasshopper Sparrow density, respectively (adjusted R^2). Although my model contained only a single covariate, the two models demonstrated a substantial amount of similarity in their predictions (Fig. 3.4).

A chi-square test of independence was performed to examine the relation between sites that my model predicted would have high densities and Grasshopper Sparrow occurrence. The relation between the variables was significant, $\chi^2(1, n=97 \text{ sites}) = 7.70$, $p < 0.01$. Sites with the highest expected Grasshopper Sparrow densities (> 0.08 pairs per hectare) had Grasshopper Sparrows present in 65 percent of cases whereas sites with lower expected Grasshopper Sparrow densities had Grasshopper Sparrows present in only 21 percent of cases.

DISCUSSION

The top-performing landscape-only and combined-scale models both included the term for percent of grassland within an 800-m buffer of the site as the only landscape-scale variable of importance. This further demonstrates that the value of a grassland is enhanced by increased grassland area and proximity to other grasslands (Sample & Mossman 1997; Johnson et al. 2010).

The top performing local-only model included terms for height, distance to trees, litter, litter^2, dead vegetation and dead vegetation^2 (Table 3.2). However, several of my local-only models performed very similarly. I had support for nine models ($\Delta AIC_c < 4$; Winter et al. 2006) which included various combinations of the nonlinear terms for shrub cover and bare ground cover in addition to the covariates specified in the top model (vegetation height, distance to trees, litter, litter^2, dead vegetation and dead vegetation^2; Table 3.2). This means that it may be worthwhile to include shrub cover, shrub cover^2, bare ground, and bare ground^2 cover for the purposes of local-only modeling of Grasshopper Sparrow density.

As I expected, my results show that models that have both local-scale and landscape-scale components outperformed models based on variables at a single scale. My combined-scale model performed 17 AIC_c units better than the local-only model and 30 AIC_c units better than the landscape-only model. These findings are supported by several other studies that reported the importance of both local- and landscape-scale variables for models of Grasshopper Sparrow density (Fletcher & Koford 2002; Cunningham & Johnson 2006; Quamen 2007; Renfrew & Ribic 2008).

My findings differ from the results of Bakker et al. (2002), who examined occurrence and density models for seven grassland bird species. Bakker et al. (2002) found that, while multi-scale models were top-performing for Grasshopper Sparrow occurrence, this pattern did not hold true for Grasshopper Sparrow density: some local variables (such as VOR and litter depth) were included in the top-performing density model but no landscape-scale variables (such as percent grass and tree cover in 400m, 800m, or 1600m) were included. However, one of their key findings from their analysis of four other grassland obligate species that occurred within both tallgrass and mixed-grass prairie was that there were within-species regional differences in habitat use and, therefore, associations found in mixed-grass prairie could not be extrapolated to tallgrass prairie. Their Grasshopper Sparrow model was developed in mixed-grass prairie because they did not have an adequate sample size for analysis in tallgrass prairie. Therefore, my model is not directly comparable to theirs because mine was developed in the tallgrass prairie.

When looking at previous work in tallgrass prairie, my results are more comparable. Quamen (2007) found that Grasshopper Sparrow density was best modeled by a combination of local and landscape scale variables. At the local scale, Quamen found that percecnt tree cover within 100 meters had a significant relationship with Grasshopper Sparrow density. While I also measured this variable, it did not perform as well as distance to nearest tree, with which it was colinear ($r = 0.62$). Like me, Quamen found no significant relationship between Grasshopper Sparrow density and VOR. In contrast, Quamen did not find significant relationships between Grasshopper Sparrow density and height or litter depth, which were two variables that were included in the top-performing local-only model. At the landscape scale, Quamen's model included percent tree cover and grass cover within 400m of survey locations. I similarly found evidence for the importance of grass cover, though I found a slightly stronger relationship between Grasshopper Sparrow density and percent grassland at 800m ($r = 0.33$) rather than at 400m ($r = 0.30$). Although tree cover was not included in my top model, I did find support for tree cover within 400 m ($\Delta AIC_c < 4$;Winter et al. 2006). I chose not to include tree cover (and cropland cover, which also had a $\Delta AIC_c < 4$) because combinations of the top variables resulted in considerably larger ΔAIC_c.

Several reasons may explain why my model predictions differ from Quamen's. First of all, Quamen based his landscape data on 2001-2003 landcover imagery and land use has changed dramatically in the Midwest since his analysis (Wright & Wimberly 2013). Not only does this mean that Quamen's predictive maps may no longer identify appropriate habitat in some areas, but it is also possible that birds' habitat selection criteria will change if availability of high quality sites is more restricted. Second, Quamen covered a larger geographic area than I did, using a single model to predict Grasshopper Sparrow density across western Minnesota and northwestern Iowa. A more narrow geographic scope is likely to yield more accurate predictions given the potential for regional variation (Bakker et al. 2002; Evans et al. 2014) in avian communities due to differences in species ranges, climate, landscape structure, and land use history, among others. In addition, Quamen included survey sites located in cropland as well as grassland, while my study sites were located almost exclusively in grassland. This smaller regional scope, more current land cover data, and greater focus on grassland habitat mean that my results are more closely calibrated to current conditions in southwestern Minnesota.

Another notable difference in my model predictions compared to Quamen's predictions are my much lower expected Grasshopper Sparrows densities. Quamen found higher average densities of Grasshopper Sparrows in grasslands, with 20 - 25 pairs/100 ha (as compared to 15 pairs/100 ha in my study) and had predictions as high as 83 pairs/100 ha (as compared to 25 pairs/100 ha). Such lower densities may be expected due to the differences in our survey methodologies: line transects may result in more conservative density estimates than cicular-plot counts (Bollinger et al. 1988). Hence, my predicted densities are expected to be lower, though still proportional, to those of Quamen's model.

Despite these differences, my mapping outcomes are very similar to those produced by Quamen in southwestern Minnesota. Quamen identified several areas of high predicted bird densities and protection that concur with my predicted areas of high Grasshopper Sparrow densities. These areas include the Inner Coteau and Coteau Moraine, Minnesota River Valley, and Northern Minnesota River Prairie (Quamen 2007 Fig. 12).

The explanatory power (as measured by R^2) of my top-performing model (23%) is on par with other models of grassland bird density reported in the literature (Table 3.8). Models in Fletcher and Koford (2002) explain 20-30% of variation in Grasshopper Sparrow densities based on 20 grasslands; Bakker et al. (2002)'s model explains 17% of variation in Grasshopper Sparrow densities based on 380 grasslands; Winter and Faaborg (1999) explain 67% of variation in Grasshopper Sparrow density based on 13 grasslands. Models based on landscape variables alone (both my model and the model produced by HAPET), were not as successful as combined-scale models at predicting Grasshopper Sparrow density. These models explained only 11 and 5 percent of the observed variation in Grasshopper Sparrow density, respectively. The inclusion of local-scale variables with landscape-scale variables almost doubled the explanatory power. Given the poor performance of landscape-only models, I suggest that the addition of local-scale vegetation data could greatly improve the predictive ability of spatially explicit species density models.

Unfortunately, the necessary infromation on local-scale habitat characteristics is not available for the large geogrpahic regions typically covered by spatially explicit population models that rely on remotely sensed data. It would be time- and labor-intensive to collect the necessary field data to improve these models. Future advances in remote sensing may make the acquisition of local-scale habitat characteristics more feasible, but in the meantime, where such adjustments are not feasible, it is still possible to gather useful information from landscape-only predictive modeling. My results showed that Grasshopper Sparrow presence could be roughly predicted on the basis of how much grassland exists in the surrounding landscape at a scale of 800 m. Furthermore, simple models may perform on par with more complex models: my simple landscape-only model, which contained a single explanatory variable, was highly correlated ($|r| > 0.72$) with the HAPET model, which included seven explanatory variables.

TABLES

Table 3.1. Local-only linear regression models of Grasshopper Sparrow density in southwestern Minnesota in 2013 and 2014. Candidate models were selected on the basis of linear correlation coefficients and evidence of curvilinear relationships from loess plots. Models are ranked according to differences in Akaike's Information Criterion (AIC_c).

Model[a]	**Δ AIC_c**[b]	**w_i**[c]	**Model Likelihood**	**K**[d]
Height + DistToTree + Litter^2 + BareGround^2	0.00	0.21	1.00	8
Height + DistToTree + DeadVeg^2	0.62	0.15	0.73	6
Height + DistToTree + DeadVeg^2 + BareGround^2	0.80	0.14	0.67	8
Height + DistToTree + Litter^2 + BareGround^2 + DeadVeg^2	1.11	0.12	0.57	10
Height + DistToTree + Litter^2	1.79	0.09	0.41	6
Height + DistToTree + Shrub^2 + Litter^2 + DeadVeg^2	2.88	0.05	0.24	10
Height + DistToTree	3.37	0.04	0.19	4
Height + DistToTree + DeadVeg^2 + Shrub2	3.39	0.04	0.18	8
Height + DistToTree + Shrub^2 + BareGround^2 + DeadVeg^2	3.77	0.03	0.15	10
Height + DistToTree + Litter^2 + BareGround^2	4.00	0.03	0.14	8
Height + DistToTree + Litter^2 + BareGround^2 + Shrub^2 + DeadVeg^2	4.09	0.03	0.13	12
Height + DistToTree + Litter^2 + Shrub^2	4.51	0.02	0.10	8
Height + DistToTree + BareGround^2	4.53	0.02	0.10	6
Height + DistToTree + Shrub^2	5.83	0.01	0.05	6
Height + Trees100 + VOR + DistToTree	5.97	0.01	0.05	6
Height + DistToTree + Litter^2 + BareGround^2 + Shrub^2	6.96	0.01	0.03	10
Height + DistToTree + Shrub^2 + BareGround^2	7.34	0.01	0.03	8
DistToTree	19.67	0.00	0.00	3
Height	29.76	0.00	0.00	3

Model[a]	Δ AIC$_c$[b]	w_i[c]	Model Likelihood	K[d]
DeadVeg^2	40.80	0.00	0.00	4
BareGround^2	46.74	0.00	0.00	4
Litter^2	46.90	0.00	0.00	4
Shrub^2	48.38	0.00	0.00	4

[a] The linear term was also included for each squared variable

[b] Δ AIC$_c$ represents the difference in Akaike's Information Criterion corrected for small sample size between the current model and the top-performing model.

[c] Relative likelihood of the current model (*i*) based on AIC$_c$ value, (equals AIC$_c$ weight)

[d] Number of parameters in the model

Table 3.2. Parameter estimates ($\hat{\beta}$ and SE) from the top-supported local-only linear regression model describing Grasshopper Sparrow density at grassland sites in southwestern Minnesota in 2013 and 2014. Test statistics (t and p) are from the final model and indicate relative support for individual variables, but model selection was based on AIC_c (Table 3.1).

Parameter	$\hat{\beta}$	SE	t	p
Intercept	0.1938	0.0536	3.618	0.0003
Height	-0.0035	0.0009	-3.986	0.0001
DistToTree	0.0008	0.0001	5.454	0.0000
Litter	0.0126	0.0118	1.069	0.2861
Litter^2	-0.0015	0.0009	-1.685	0.0931
DeadVeg	-0.0104	0.0045	-2.297	0.0223
DeadVeg^2	0.0004	0.0002	2.431	0.0156
Adjusted R^2: 0.1601				
F-statistic: 10.69 on 6 and 299 df				
p-value: 9.144e-11				

Table 3.3. Landscape-only linear mixed effects models of Grasshopper Sparrow density in southwestern Minnesota in 2013 and 2014. Site is included as a random effect for all models. Candidate models were selected on the basis of correlation coefficients and evidence of curvilinear relationships. Models are ranked according to differences in Akaike's Information Criterion (AIC_c).

Model[a]	**Δ AIC_c**[b]	**w_i**[c]	**Model Likelihood**	**K**[d]
Grass800	0.00	0.82	1.00	4
Tree400	3.89	0.12	0.14	4
Crop800	5.36	0.06	0.07	4
Grass800 + Crop800	9.88	0.01	0.01	5
Grass800 + Tree400	11.26	0.00	0.00	5
Crop800 + Tree400	14.40	0.00	0.00	5
$Grass800^2$	17.97	0.00	0.00	5
Grass800 + Crop800 + Tree400	21.19	0.00	0.00	6
$Crop800^2$	25.43	0.00	0.00	5
$Grass800^2$ + Crop800	28.91	0.00	0.00	6
$Grass800^2$ + Tree400	29.55	0.00	0.00	6
Grass800 + $Crop800^2$	29.69	0.00	0.00	6
$Crop800^2$ + Tree400	34.20	0.00	0.00	6
$Grass800^2$ + Crop800 + Tree400	40.30	0.00	0.00	7
Grass800 + $Crop800^2$ + Tree400	41.06	0.00	0.00	7
$Grass800^2$ + $Crop800^2$	48.82	0.00	0.00	7
$Grass800^2$ + $Crop800^2$ + Tree400	60.21	0.00	0.00	8

[a] The linear term was also included for each squared variable

[b] Δ AIC_c represents the difference in Akaike's Information Criterion corrected for small sample size between the current model and the top-performing model.

[c] Relative likelihood of the current model (i) based on AIC_c value, (equals AIC_c weight)

[d] Number of parameters in the model

Table 3.4. Parameter estimates ($\hat{\beta}$ and SE) from the top-supported landscape-only linear mixed effects model describing Grasshopper Sparrow density at grassland sites in southwestern Minnesota in 2013 and 2014. Test statistics (*t* and *p*) are from the final model and indicate relative support for individual variables, but model selection was based on AIC_c (Table 3.3).

Parameter	$\hat{\beta}$	SE	DF	*t*	*p*
Intercept	0.012	0.044	234	0.278	0.782
Grass800	0.002	0.001	70	2.992	0.004

Table 3.5. Combined-scale linear mixed effects models of Grasshopper Sparrow density in southwestern Minnesota in 2013 and 2014. Candidate models were selected on the basis of linear correlation coefficients and evidence of curvilinear relationships from loess plots. Models are ranked according to differences in Akaike's Information Criterion (AIC_c).

Model[a]	ΔAIC_c[b]	w_i[c]	Model Likelihood	K[d]	Res.LL[e]
Grass800	0.00	0.569	1	10	76.30
Tree400	1.40	0.283	0.496	10	75.60
Crop800	2.74	0.145	0.254	10	74.93
Grass800 + Crop800	11.41	0.002	0.003	11	71.68
Grass800 + Tree400	12.26	0.001	0.002	11	71.25
Crop800 + Tree400	14.46	0.000	0.001	11	70.15
$Grass800^2$	17.87	7.50E-05	0.000	11	68.44
Grass800 + Crop800 + Tree400	22.11	9.01E-06	1.58E-05	12	67.41
$Crop800^2$	22.90	6.05E-06	1.06E-05	11	65.93
$Grass800^2$ + Crop800	30.15	1.62E-07	2.84E-07	12	63.39
$Grass800^2$ + Tree400	30.21	1.57E-07	2.75E-07	12	63.36
Grass800 + $Crop800^2$	31.43	8.52E-08	1.50E-07	12	62.75
$Crop800^2$ + Tree400	34.51	1.83E-08	3.21E-08	12	61.21
$Grass800^2$ + Crop800 + Tree400	41.07	6.89E-10	1.21E-09	13	59.02
Grass800 + $Crop800^2$ + Tree400	42.27	3.78E-10	6.63E-10	13	58.42
$Grass800^2$ + $Crop800^2$	50.29	6.83E-12	1.20E-11	13	54.41
$Grass800^2$ + $Crop800^2$ + Tree400	61.21	2.91E-14	5.11E-14	14	50.05

[a] The local-only model and a random effect of site was also included for each candidate model. Where a squared variable was included, a linear term was also included.

[b] ΔAIC_c represents the difference in Akaike's Information Criterion corrected for small sample size between the current model and the top-performing model.

[c] Relative likelihood of the current model (i) based on AIC_c value, (equals AIC_c weight)

[d] Number of parameters in the current model

[e]Restricted log-likelihood of the current model

Table 3.6. Parameter estimates ($\hat{\beta}$ and SE) from the top-supported combined-scale mixed effects model describing Grasshopper Sparrow density at grassland sites in southwestern Minnesota in 2013 and 2014. Test statistics (*t* and *p*) are from the final model and indicate relative support for individual variables, but model selection was based on AIC_c (Table 3.5).

Parameter	$\hat{\boldsymbol{\beta}}$	**SE**	***t***	***p***
Intercept	0.0808	0.0697	1.160	0.2473
Height	-0.0025	0.0009	-2.790	0.0057
DistToTree	0.0005	0.0001	3.427	0.0007
Litter	0.0131	0.0111	1.189	0.2355
Litter^2	-0.0012	0.0008	-1.494	0.1366
DeadVeg	-0.0072	0.0044	-1.636	0.1032
DeadVeg^2	0.0003	0.0001	1.835	0.0678
Grass800	0.0016	0.0008	2.034	0.0457

Table 3.7. Comparison of top-performing local scale only, landscape scale only, and combined scale linear regression models of Grasshopper Sparrow density in southwest Minnesota in 2013 and 2014. Models are ranked according to differences in Akaike's Information Criterion (AIC_c).

Model	**Δ AIC_c**[a]	**w_i**[b]	**Model Likelihood**	**K**[c]
Combined Scale Model	0	1.00	1.00	9
Local Scale Model	17.17	0.00	0.00	8
Landscape Scale Model	30.31	0.00	0.00	3

[a] Δ AIC_c represents the difference in Akaike's Information Criterion corrected for small sample size between the current model and the top-performing model.

[b] Relative likelihood of the current model (*i*) based on AIC_c value, (equals AIC_c weight)

[c] Number of parameters in the model

Table 3.8. Results of published studies of models for Grasshopper Sparrow, including location and published R^2 values for each scale assessed. The range in R^2 values reported for other grassland bird species in the same article are indicated within parentheses.

Study	Location	Local-only	Landscape-only	Combined-scale
Winter and Faaborg 1999	Missouri	0.67		
		(0.26-0.77)		
Bakker et al. 2002	South Dakota	0.17		
		(0.10-0.48)		
Fletcher and Koford 2002	Iowa	0.20		0.30
		(0.06-0.40)		(0.11-0.44)
Quamen 2007[a]	Minnesota and Iowa	++	+	+++
		(++)	(+)	(+++)
Murray et al. 2008	Wisconsin			N/A
				(0.18-0.26)
Drum et al. 2015[b]	Prairie Pothole Region		0.71	
			(0.00-0.89)	
My Study	Minnesota	0.18	0.11	0.23

[a]Quamen 2007 used BIC rather than reporting R^2. More plus signs indicate stronger BIC support of the model scale represented.

FIGURES

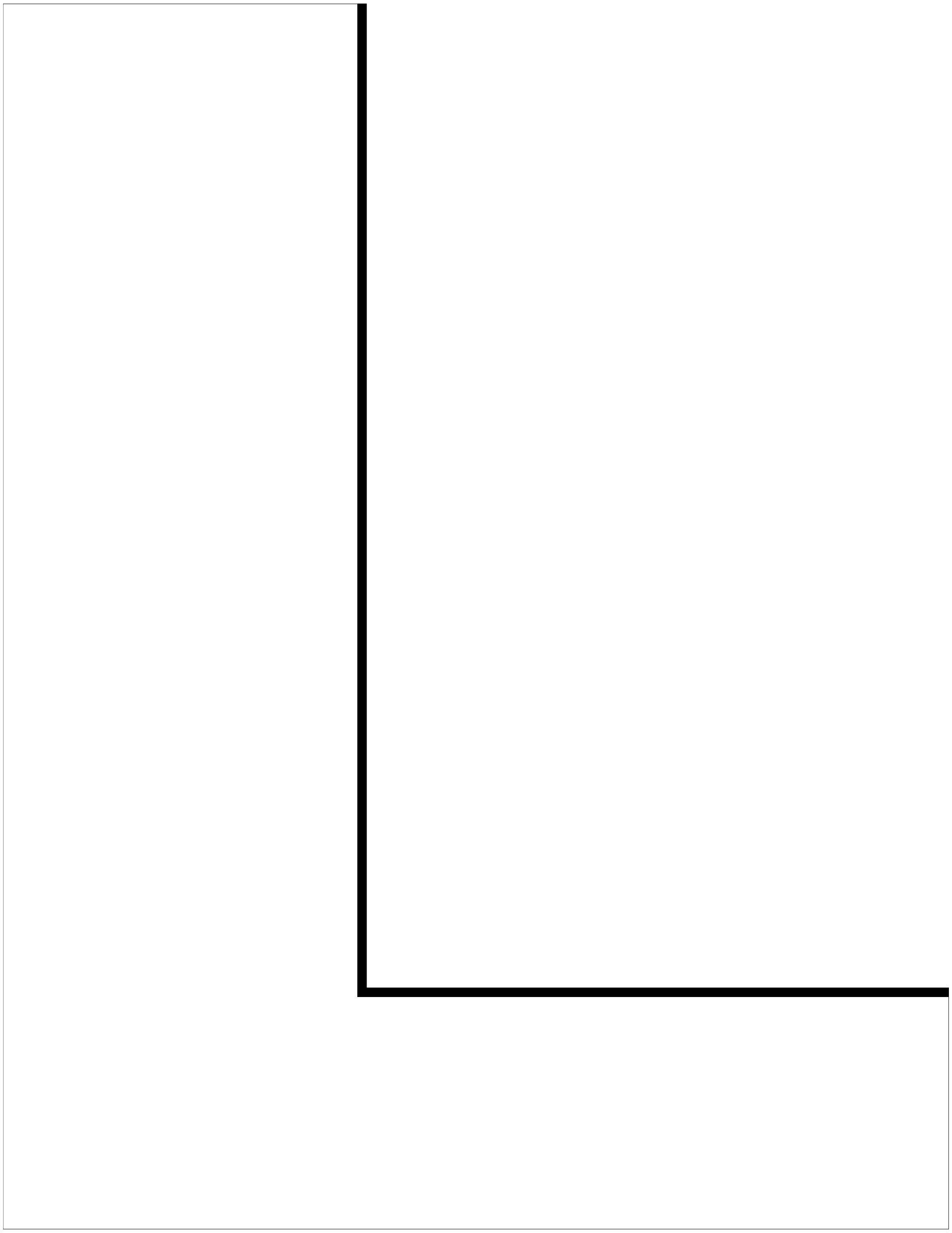


Figure 3.1. Predicted Grasshopper Sparrow densities in MN DNR Region 4. Density was predicted for each 30 m grassland pixel using the regression equation y = 0.012 + 0.002*x*, where *x* is the grass cover in percent within 800 m.

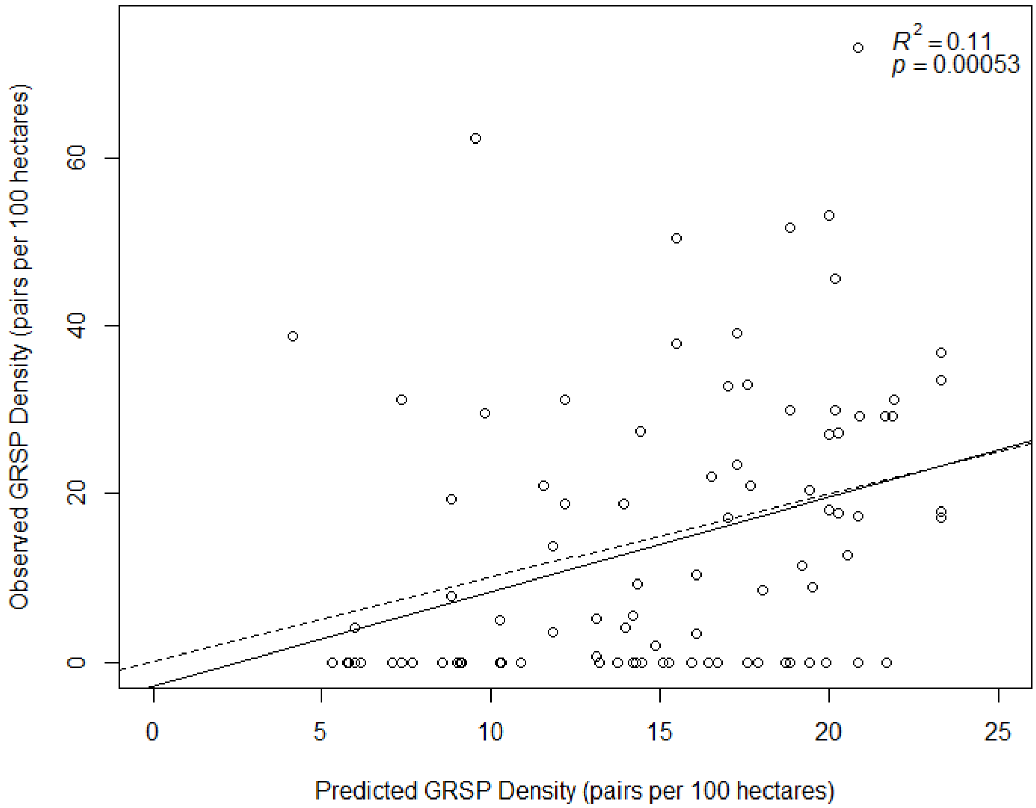


Figure 3.2. Comparison of observed versus predicted Grasshopper Sparrow densities at 71 sites in southwestern Minnesota. Predictions are based on the top-performing landscape-only mixed effects model. Solid line indicates regression line; dashed line indicates a 1 to 1 line.

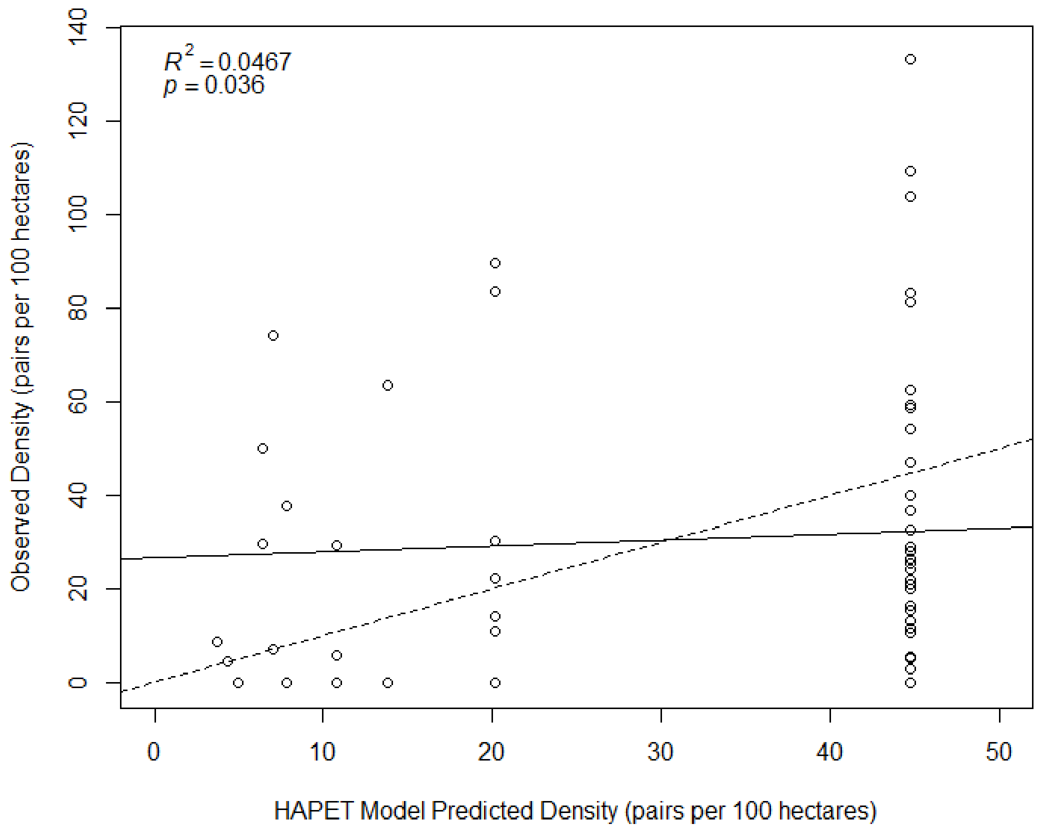


Figure 3.3. Comparison of observed versus HAPET model-predicted Grasshopper Sparrow densities at 71 sites in southwestern Minnesota. Solid line indicates regression line; dashed line indicates a 1 to 1 line.

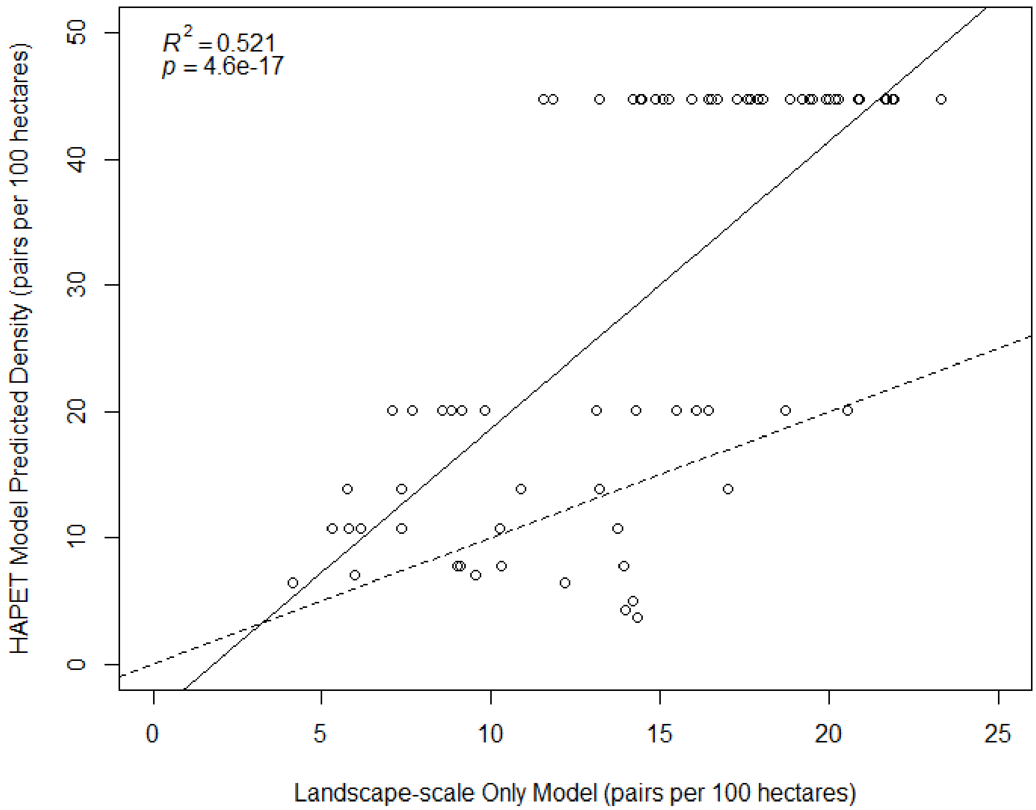


Figure 3.4. Comparison of predicted Grasshopper Sparrow densities at 71 sites in southwestern Minnesota. Predictions are based on my top-performing landscape-only model and the landscape model developed by HAPET. Solid line indicates regression line; dashed line indicates a 1 to 1 line.

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APPENDICES

Appendix A. *Grassland study sites and management units visited in the 2013 and 2014 field seasons.*

Site	***Management Unit***	***SiteID***	***Ownership***	***'13***	***'14***
Altona WMA		*ALDNR*	*WMA*	*Y*	*Y*
Artichoke Lake WPA		*ARFWS*	*WPA*	*N*	*Y*
Beaver Falls WMA		*BFDNR*	*WMA*	*N*	*Y*
Belle Lake Cattle Co.		*BLPVT*	*Private*	*Y*	*Y*
Big Stone Lake State Park		*BSDNR*	*State Park*	*Y*	*N*
Big Stone NWR		*BSFWS*	*NWR*	*N*	*Y*
Bloom WPA		*BLFWS*	*WPA*	*Y*	*Y*
Blue Mounds State Park		*BMDNR*	*State Park*	*Y*	*Y*
Bonanza Prairie SNA		*BODNR*	*SNA*	*N*	*Y*
Burbank WMA		*BUDNR*	*WMA*	*Y*	*N*
Camden State Park		*CMDNR*	*State Park*	*Y*	*Y*
Chetomba Creek WMA		*CCDNR*	*WMA*	*Y*	*Y*
Chetomba Creek WMA	*2014 Grazed*	*CCGDNR*	*WMA*	*Y*	*Y*
Chippewa Prairie TNC	*North*	*CHNOTNC*	*TNC*	*Y*	*Y*
Chippewa Prairie TNC	*South*	*CHSOTNC*	*TNC*	*Y*	*Y*
Cobb River WPA	*Duncanson*	*CRDUFWS*	*WPA*	*Y*	*N*
Cottonwood Lake WPA		*CLFWS*	*WPA*	*Y*	*N*
David B. Vesall WMA		*DVDNR*	*WMA*	*N*	*Y*
Easement 11G	*2014 Burn*	*11BPVT*	*Private*	*N*	*Y*
Easement 11G		*11PVT*	*Private*	*N*	*Y*
Easement 166H		*166PVT*	*Private*	*N*	*Y*
Easement 22G		*22PVT*	*Private*	*Y*	*Y*
Easement 296H		*296PVT*	*Private*	*Y*	*Y*
Easement 331G		*331PVT*	*Private*	*N*	*Y*
Easement 51G		*51PVT*	*Private*	*Y*	*N*
Easement 58G		*58PVT*	*Private*	*Y*	*N*
Elm Creek Easement	*2014 Burn*	*ECBPVT*	*Private*	*N*	*Y*
Elm Creek Easement		*ECPVT*	*Private*	*N*	*Y*
Fort Ridgely State Park		*FRDNR*	*State Park*	*N*	*Y*
Glynn Prairie SNA		*GPDNR*	*SNA*	*Y*	*Y*
Hawk Creek 35 Easement		*HCPVT*	*Private*	*Y*	*Y*
Hole in Mountain WMA		*HMDNR*	*WMA*	*N*	*Y*
Hole-in-the-Mountain TNC		*HMTNC*	*TNC*	*Y*	*N*
Holthe Prairie SNA		*HPDNR*	*SNA*	*Y*	*N*
Hunter WPA		*HUFWS*	*WPA*	*Y*	*Y*
Joseph A. Tauer SNA		*JTDNR*	*SNA*	*N*	*Y*

Site	***Management Unit***	***SiteID***	***Ownership***	***'13***	***'14***
Klabunde WMA		*KLDNR*	*WMA*	*N*	*Y*
Lac qui Parle WMA		*LPDNR*	*WMA*	*Y*	*Y*
Lake Augusta WPA		*LAFWS*	*WPA*	*Y*	*N*
Lamberton WMA		*LMDNR*	*WMA*	*N*	*Y*
Lincoln WPA		*LIFWS*	*WPA*	*Y*	*N*
Miller Hills WPA		*MHFWS*	*WPA*	*Y*	*Y*
Minneopa State Park		*MIDNR*	*State Park*	*Y*	*N*
Mound Spring Prairie SNA	*A*	*MSPADNR*	*SNA*	*Y*	*N*
Mound Spring Prairie SNA	*B*	*MSPBDNR*	*SNA*	*N*	*Y*
Mound Spring WMA		*MSDNR*	*WMA*	*N*	*Y*
Northern Tallgrass Prairie NWR	*Touch the Sky*	*TPTSFWS*	*NWR*	*Y*	*Y*
Pierce Lake WPA		*PLFWS*	*WPA*	*Y*	*Y*
Pipestone NM	*2014 Burn*	*PIBNPS*	*NM*	*Y*	*N*
Pipestone NM		*PINPS*	*NM*	*Y*	*Y*
Plover Prairie TNC		*PPTNC*	*TNC*	*Y*	*Y*
Prairie Banks: Camp Release 32		*32PVT*	*Private*	*Y*	*Y*
Prairie Banks: Carney		*CRPVT*	*Private*	*Y*	*N*
Prairie Banks: Moulton 5		*M5PVT*	*Private*	*Y*	*N*
Prairie Banks: Petersburg26		*26PVT*	*Private*	*Y*	*N*
Prairie Banks: Schellberg		*SCPVT*	*Private*	*Y*	*N*
Prairie Coteau SNA		*PCDNR*	*SNA*	*Y*	*Y*
Randall WPA		*RAFWS*	*WPA*	*N*	*Y*
Red Rock Prairie TNC		*RRTNC*	*TNC*	*N*	*Y*
Rock Ridge Prairie SNA		*RRDNR*	*SNA*	*Y*	*N*
Salt and Pepper WMA		*SPDNR*	*WMA*	*Y*	*N*
Schaefer Prairie TNC		*SFTNC*	*TNC*	*N*	*Y*
Sibley State Park		*SIDNR*	*State Park*	*Y*	*N*
Sioux Nation WMA		*SNDNR*	*WMA*	*N*	*Y*
Slaughter Slough WPA		*SSFWS*	*WPA*	*Y*	*N*
Split Rock Creek State Park		*SRDNR*	*State Park*	*N*	*Y*
Storden WPA		*STFWS*	*WPA*	*Y*	*Y*
String Lake WPA		*SLFWS*	*WPA*	*N*	*Y*
Talcot Lake WMA		*TADNR*	*WMA*	*Y*	*Y*
Timber Lake WMA	*2014 Burn*	*TIBFWS*	*WMA*	*Y*	*Y*
Timber Lake WMA		*TIFWS*	*WMA*	*Y*	*Y*
Toe WMA		*TODNR*	*WMA*	*N*	*Y*
Wang 14 Easement		*14PVT*	*Private*	*Y*	*Y*

Site	*Management Unit*	*SiteID*	*Ownership*	*'13*	*'14*
Wang 30 Easement		*30PVT*	*Private*	*Y*	*Y*
Watonwan WPA		*WAFWS*	*WPA*	*Y*	*N*
Wolf Lake WPA		*WLFWS*	*WPA*	*Y*	*N*
TOTAL # units visited				*51*	*53*
TOTAL # Sites				*48*	*49*

Appendix B. *The results of an ANOVA between densities (birds per 100 ha) of one species at sites with and without the predictor species present (ALLGRASS has been adjusted to be ALLGRASS minus the density of predictor species so that a species was not used to predict its own density). Each cell contains three values: birds per 100 ha at sites with the predictor species present, birds per 100 ha at sites with the predictor species absent, and in bold the difference (in birds per 100 ha) between sites with and without predictor species recorded.*

Response Species	*Predictor Species*							
	BHCO	*BOBO*	*DICK*	*GRSP*	*HESP*	*SAVS*	*SEWR*	*WEME*
ALLGRASS	*64.1*	*26.3*	*60.1*	*54.6*	*59.5*	*51.8*	*52.8*	*58.9*
	101.8	*80.2*	*81.6*	*75.8*	*100.0*	*96.2*	*90.3*	*81.7*
	37.7	***53.8***	***21.4***	***21.2***	***40.4***	***44.4***	***37.4***	***22.8***
BHCO		*0.6*	*0.5*	*0.5*	*0.5*	*0.4*	*0.5*	*0.3*
		0.4	*0.3*	*0.3*	*0.2*	*0.4*	*0.3*	*0.9*
		-0.2	***-0.1***	***-0.2***	***-0.3***	***0.0***	***-0.1***	***0.6***
BOBO	*31.6*		*35.4*	*27.7*	*30.2*	*28.6*	*29.1*	*30.9*
	39.8		*21.3*	*35.9*	*41.6*	*39.2*	*37.4*	*34.4*
	8.2		***-14.1***	***8.1***	***11.3***	***10.5***	***8.3***	***3.5***
DICK	*8.5*	*12.7*		*3.6*	*7.9*	*6.2*	*8.6*	*6.8*
	2.4	*6.6*		*12.7*	*10.6*	*12.8*	*7.7*	*11.9*
	-6.1	***-6.1***		***9.1***	***2.7***	***6.6***	***-0.9***	***5.0***
GRSP	*14.8*	*12.3*	*12.1*		*12.5*	*11.3*	*15.9*	*11.5*
	11.4	*15.5*	*22.2*		*27.4*	*22.1*	*12.1*	*22.4*
	-3.3	***3.2***	***10.1***		***14.9***	***10.8***	***-3.9***	***10.9***
HESP	*2.8*	*1.1*	*2.6*	*1.5*		*2.3*	*1.9*	*2.8*
	0.9	*3.4*	*3.2*	*3.9*		*3.9*	*4.4*	*2.5*
	-1.9	***2.3***	***0.5***	***2.4***		***1.6***	***2.5***	***-0.3***
SAVS	*5.7*	*3.6*	*5.4*	*4.8*	*5.8*		*5.1*	*5.2*
	16.8	*7.1*	*8.3*	*7.4*	*8.0*		*8.2*	*8.4*
	11.0	***3.5***	***2.9***	***2.6***	***2.2***		***3.2***	***3.2***
SEWR	*8.0*	*3.2*	*9.2*	*10.4*	*7.6*	*7.5*		*9.0*
	14.9	*10.1*	*5.1*	*6.1*	*11.7*	*9.9*		*6.3*

Response Species	*Predictor Species*							
	BHCO	*BOBO*	*DICK*	*GRSP*	*HESP*	*SAVS*	*SEWR*	*WEME*
	7.0	***7.0***	***-4.1***	***-4.3***	***4.1***	***2.4***		***-2.6***
WEME	*3.5*	*3.4*	*2.7*	*2.2*	*3.6*	*2.9*	*4.0*	
	7.5	*3.7*	*6.6*	*5.0*	*3.7*	*5.3*	*2.9*	
	4.0	***0.3***	***3.9***	***2.8***	***0.1***	***2.4***	***-1.1***	

Appendix C. *Landcover input classification*

Assigned Land Cover Classification	NASS Cropscape Cover Classification
Grassland	Other Hay/Non Alfalfa, Sod/Grass Seed, Switchgrass, Grassland Herbaceous, Pasture/Hay, Herbaceous Wetlands
Trees	Forest, Christmas Trees, Deciduous Forest, Evergreen Forst, Mixed Forest, Woody Wetlands, Tree Crops (including: Cherries, Peaches, Apples, Citrus, Pecans, Almonds, Walnuts, Pears, Pistachios, Prunes, Olives, Oranges, Pomegranates, Nectarines, Plums, Apricots and Other Tree Crops)
Developed land	Developed, Developed/Open Space, Developed/Low Intensity, Developed/Med Intensity, Developed/High Intensity
Other	Shrubland (Shrubland, Grapes), Barren (Barren, Fallow/Idle crop land), Water (Water, Wetlands, Aquaculture, Open Water) and No Data (Clouds/NoData, Nonag/Undefined, Perennial Ice/Snow)
Cropland	All other categories

Appendix D. *Grasshopper Sparrow priority areas. Landcover was determined from reclassification of USDA National Statistics Service Cropland Data Layer (USDA National Agricultural Statistics Service Cropland Data Layer 2012; see Appendix C for reclassifications). Grasshopper Sparrow density was then predicted for each 30m grassland pixel using the regression equation y = 0.012 + 0.002x, where x is the grass cover in percent within 800 m, which was determined to be the top-performing landscape-scale model of Grasshopper Sparrow density using an information-theoretic approach (see Chapter 3 for a full discussion of methodology and results). Each of our 71 sites was then ranked according to predicted Grasshopper Sparrow density, and then separated into five quantile classes that represented areas from high to no priority.*

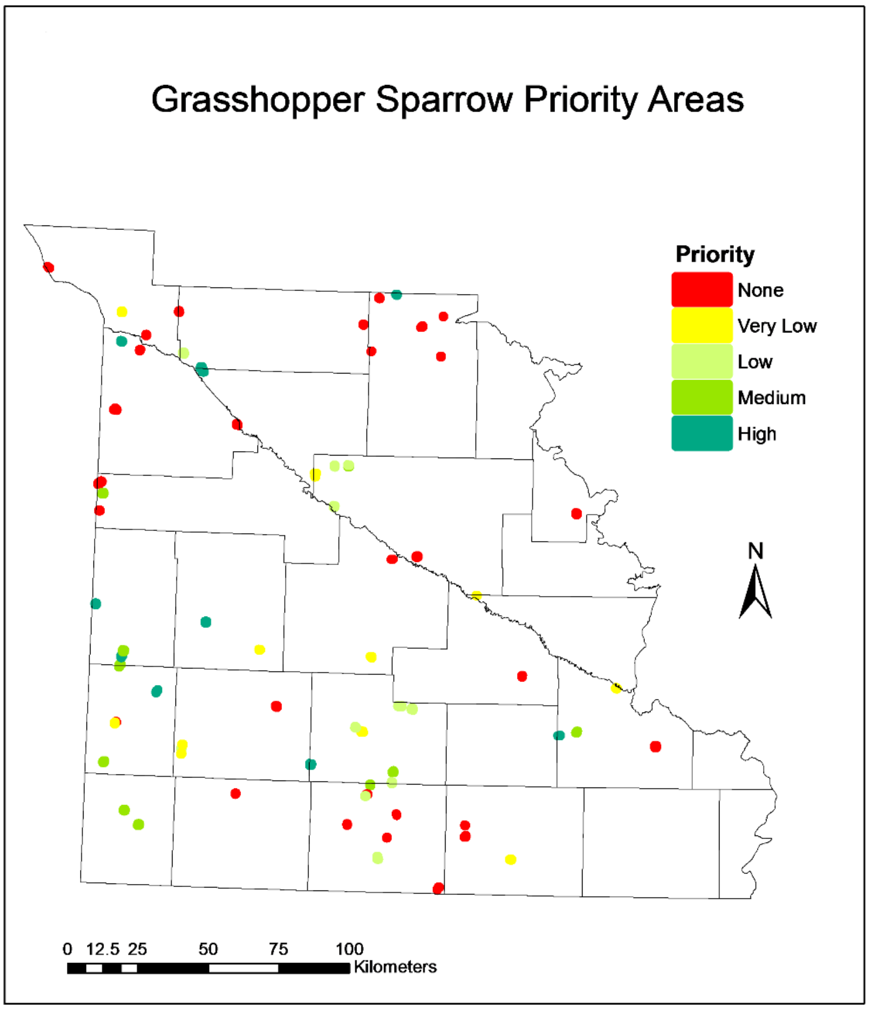

Figure 1. A map of priority areas for breeding Grasshopper Sparrows within the identified project area. Sites are ranked on the basis of density (pairs per hectare) averaged across the years (2013 and/or 2014) in which they were surveyed, using 5 quantile classes.