

Spatiotemporal variability of populations and suitable breeding habitat in three grassland
sparrows: a multiscale approach

By

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ABSTRACT

Henslow's Sparrows (*Ammodramus henslowii*) are not only uncommon, but they are also unpredictable in grasslands that appear suitable. Furthermore, the extent, distribution, and year-to-year variability of their breeding habitat has not yet been characterized. In this dissertation, resettlement behavior was analyzed using two measures of population variability, prevalence of occurrence and variation in abundance, first at the Breeding Bird Survey (BBS) route level (Chapter 2), then across multiple spatial resolutions (Chapter 3). Variability of Henslow's Sparrow populations was compared to that of two other grassland sparrow species, Grasshopper Sparrows (*A. savannarum*) and Savannah Sparrows (*Passerculus sandwichensis*). In both analyses, Henslow's Sparrows showed lower prevalence and higher variation in abundance than the other two species at the BBS route level and across all but the broadest spatial resolutions. Henslow's Sparrows do not occur consistently at extents of less than 120 000 km², suggesting nomadic behavior. To relate patterns of habitat turnover to the nomadic behaviors described in the first two research chapters, ecological niche models were used to identify the extent and distribution of suitable breeding area across three years (2008–2010), and then to characterize turnover in suitability between 2 sets of years (2008–2009 and 2009–2010; Chapter 4). Turnover varied across time and species, such that losses and gains fluctuated in dominance within species and between years. Turnover of both gains and losses was similar among species and relatively low in 2008–2009; however, in 2009–2010, Henslow's Sparrows showed much higher losses and lower gains, and more clustering of this turnover across broad regions compared to the other two species. Overall, conversion (i.e., state change) of grasslands was relatively low, accounted for a greater proportion of losses than gains of suitable area for all species, and varied within losses among species. In variable years when turnover is high, Henslow's Sparrows may be more nomadic compared to mild years, when turnover and movements are low. Results presented here provide a more complete understanding of the broad-scale dynamics of Henslow's Sparrow populations and their habitat, information that may be key to successful conservation of this and ecologically similar grassland species.

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CHAPTER 1

Introduction

This research focuses on improving the understanding of the response of a rare habitat specialist (Henslow's Sparrow, *Ammodramus henslowii*) to broad-scale habitat changes, and of the extent to which natural and anthropogenic influences affect the amount and distribution of its breeding habitat. This dissertation enhances the current knowledge of the breeding biology of this species and two other grassland sparrows (Grasshopper, *A. savannarum*, and Savannah, *Passerculus sandwichensis*, sparrows). More generally, this study illustrates nomadic species' distributional ecology on a range-wide scale, providing a novel example of whole-range methodology that can be extended to any other taxa.

General habitat requirements.—Henslow's Sparrows are an obligate grassland-nesting species that has a sparse and patchy breeding distribution across Midwest and portions of the northeastern US (Pruitt 1996, Herkert et al. 2002, Sauer et al. 2011). Although this species nests in a variety of “broadly-named” habitats (e.g. tallgrass prairies, marshes (Hyde 1939), swamps (Sutton 1928, Stone 1984), weedy pastures (Eifrig 1919), reclaimed surface mines (Bajema et al. 2001), etc.), it actually requires a unique suite of habitat characteristics: large, open grasslands (Hyde 1939, Smith 1968, Thogmartin et al. 2006) where vegetation litter density and depth are well developed (Wiens 1969, Robbins 1971, Cully and Michaels 2000, Bajema et al. 2001), standing dead residual vegetation is present, forbs and woody-stem density are sparse or entirely lacking, and standing live vegetation is tall and dense (Wiens 1969, Robbins 1971).

These aspects of vegetation height (Wiens 1969, Herkert 1994b) and density (Wiens 1969, Zimmerman 1988) are typical of natural and relatively infrequent fire and grazing disturbances. Changes in frequency or intensity of disturbance easily alter vegetative structure, and can result in avoidance of an area by the species. An increase in disturbance reduces preferred above-ground vegetation, whereas decreases encourage woody encroachment (Graber 1968, Bollinger 1995, Cully and Michaels 2000).

Furthermore, the years immediately following disturbance generally present unsuitable habitat for this species; 2–3 years of no disturbance are required before habitat is suitable once more to attract breeding pairs (Powell 2006). Across the landscape, disturbances are temporally and spatially discontinuous, producing a landscape across which suitable habitat may shift significantly through time. Henslow's Sparrows are area-sensitive (i.e., requiring a minimum habitat extent; Herkert 1994a, Winter and Faaborg 1999), generally avoid edge habitat near roads (Patten et al. 2006), and are suspected to require habitat patches with some degree of connectivity.

Grasshopper and Savannah sparrows have more extensive breeding ranges and wider breadths of preferred habitat compared to Henslow's Sparrows, and are more likely take advantage of habitat in earlier stages of succession (Wiens 1973). In summer months, Grasshopper Sparrows are observed across most of the US, east of the Rocky Mountains, with some extension of their range into western states (e.g., Idaho, Washington, Nevada, California) and southern Canada, overlapping that of Henslow's Sparrow completely (Sauer et al. 2011). Grasshopper Sparrow preferred habitat may vary with geography; however, the species typically prefers moderately open grassland, recently burned prairies, and restored surface mine-lands (Herkert 1994b, Vickery 1996). This species selects habitat for its vertical structure, choosing larger areas (>30ha) with more bare ground, less litter layer, and sparser vegetation than those areas preferred by Henslow's (Whitmore 1981) or Savannah sparrows (Wiens 1969). Areas with heavy shrub cover are generally avoided (Vickery 1996, Dieni and Jones 2003) in the East, but tolerated and perhaps selected for in western, arid grasslands (Wiens 1973).

Savannah Sparrows have the broadest breeding range of the three species, occurring across all of northern US and southern Canada. This species also uses the widest variety of breeding habitats: open country, grassy meadows, cultivated fields, grazed pastures, roadsides, coastal grasslands, sedge bogs, salt marshes, and tundra (Wiens 1969). Savannah sparrows prefer a well-developed litter layer with areas of bare ground (Wiens 1969, Dieni and Jones 2003). In both Grasshopper and Savannah sparrows, habitat

preferences appear to have spatial association (e.g., difference is shrub preference by Grasshopper Sparrows; Wiens 1973; Vickery 1996).

Conservation status.—Population trend data suggest that Henslow's Sparrows have declined over most of the breeding range in the last century (Sauer et al. 2011); however, recent reports suggest that some populations appear stable, or even increasing in portions of their range (Herkert 2007, Sauer et al. 2011). Notwithstanding current population estimates, Henslow's Sparrows remain classified as "Near Threatened" by the BirdLife International (2012a) and are listed as endangered or threatened in 12 states (Pruitt 1996, Burhans 2002), although they do not have federal listing (Herkert et al. 2002). Grasshopper and Savannah sparrows show continual declines survey-wide (Sauer et al. 2011); however, both are classified as species of "Least Concern" by the BirdLife International (2012b,c) on the basis of range size and extent.

Grassland bird population declines can be attributed in large part to monumental (>99%) loss of native tallgrass prairie, a result of 200 years of agriculture, development, and grazing (Knopf 1994, Fuhlendorf and Engle 2001, Smith and Owensby 1978), such that 13 species within this critically endangered biome (Noss et al. 1995) have incurred serious losses (Knopf 1994, Peterjohn and Sauer 1999, Robbins et al. 2002, Powell 2006). More recently, management practices for cattle on tallgrass prairie have emphasized yearly spring burnings and high density cattle stocking; although this scheme may be optimal for cattle production, it produces a perpetually early-succession prairie that is sub-optimal for many prairie bird species (Robbins et al. 2002). This broad conversion of prairie to large-scale agriculture and grazed pastures has altered natural disturbance regimes region-wide, and has rendered most of the native habitat unusable by Henslow's Sparrows. Nonetheless, range-wide assessments of the amount and distribution of habitat for this species have yet to be developed. Throughout this dissertation, "conversion" is used broadly, but refers to the state change of grassland to non-grass land cover types.

Breeding behavior.—Henslow's Sparrows present a unique behavior, such that they are observed inconsistently from year to year, although vegetation at nest sites appears unchanged (Hyde 1939, Wiens

1969, Skipper 1998, Ingold et al. 2009). Site fidelity (used interchangeably with philopatry and resettlement throughout this dissertation) is the likelihood that individuals or populations return to nest sites or areas used in previous years. In studies that focus on individual returns to previously-used nest sites, Henslow's Sparrows exhibit low (Skipper 1998, Monroe and Ritchison 2005) or nonexistent site fidelity (Pruitt 1996) compared to other grassland species: Savannah Sparrows (Bédard and LaPoint 1984), Grasshopper Sparrows (Skipper 1998), Bobolinks (*Dolichonyx oryzivorus*, Gavin and Bollinger 1988), Dickcissels (*Spiza americana*, Zimmerman and Finck 1989). Site fidelity is higher in species whose habitat does not change much between years, or in species that have broad habitat preferences, such that minor changes to environmental conditions do not render habitat unsuitable. Site fidelity has particular advantages: familiarity with an area increases the probability of finding food, defending a territory from conspecifics, and avoiding predators (Hinde 1956); however, for species that use highly variable habitats or have narrow habitat preferences, returning to previously-used areas may not be possible if the suitability of these areas has been reduced to suboptimal conditions. For these species, it is advantageous to settle new sites.

Nomadism is a special form of resettlement that is characterized by irregular movements of individuals, groups of individuals, or whole populations to different areas from year to year or within seasons (Sinclair 1984, Dean 1997). Nomadism develops most commonly in species when limiting resources fluctuate spatiotemporally and become patchy and unpredictably available across a region (Sinclair 1984, Dean 1997), hence making it ineffective for individuals to return consistently to the same areas (Andersson 1980). Such conditions are common in arid environments where resources are ephemeral and associated with unpredictable precipitation, and in intercontinental grasslands where disturbances (fire and grazing; Jones et al. 2007) and dynamic weather patterns regulate annual growth and structural development of the vegetation (Bragg 1995).

Nomadic predictors appear to vary by spatial scale, species biology, and environmental conditions. At fine scales, nomadism at the individual level may be determined by age (Newton and

Marquis 1982), mate loss (Greenwood and Harvey 1982), or unsuccessful breeding attempts in past years (Greenwood and Harvey 1982, Newton and Marquis 1982, Gavin and Bollinger 1988). Among populations and across broader spatial scales, nomadism may be driven by conspecific attraction (Stamps 1987, 1988, Ahlering et al. 2006) or habitat loss (Fuhlendorf and Engle 2001). Diet, however, has multiscale influences and is considered the best predictor of nomadism in birds. This behavior appears most commonly in granivorous birds (Andersson 1980, Dean 1997) and rodent specialists (Lack 1954) where food abundance fluctuates cyclically (Andersson 1980).

Objectives.—Previous research has focused on understanding the dynamics of Henslow's Sparrows at local and regional levels; however, there is currently a pressing need for landscape (i.e., range-wide) analysis of Henslow's habitat. It is not known whether the low, local site fidelity is transferred to broader regions, or if it occurs across the full breeding distribution. If Henslow's Sparrows are not returning consistently to breeding areas, what ecological factors may be responsible for these movements? What is more, for conservation management to be efficient and effective, both the current extent of suitable habitat and the breeding behavior and habitat use of this species must be considered. If territory selection and establishment cannot be predicted consistently because of multi-scale nomadism, special efforts must be made to design a configuration of patches of suitable habitat that accounts for this behavior.

The objectives of this dissertation were threefold. In Chapter 2, abundance data from the Breeding Bird Survey (BBS) were used to create two variables (prevalence of occurrence and variation in abundance) to characterize spatiotemporal population variability in Henslow's, Grasshopper, and Savannah sparrows within the Henslow's Sparrow's breeding range at a single spatial scale (the BBS route level). Chapter 3 is an expansion of the analysis of Chapter 2 to include a spectrum of spatial resolutions and extents ranging from 0.5 km^2 to $0.5 \times 10^6 \text{ km}^2$, or 6 orders of magnitude of area, and to present a novel method by which to analyze multi-resolution prevalence of occurrence data. These first two chapters characterize the consistency to which Henslow's Sparrows return to previously-used nest

areas, and make inferences about possible causes for this variability. In Chapter 4, ecological niche modeling was used to identify the extent, distribution, and between-year dynamics of suitable habitat of these species and relate these results to the patterns described in Chapters 2 and 3.

Chapter 2 has been published (Dornak, L. L. 2010. Breeding patterns of Henslow's Sparrow and sympatric grassland sparrow species. *Wilson Journal of Ornithology* 122:635–645), and Chapter 3 has been accepted for publication (Dornak, L. L., N. Barve, and A. T. Peterson. 2012. Spatial scaling of prevalence and population variation in three grassland sparrows. *Condor* (*in press*)). Chapter 4 is being prepared, with co-authors, A. Townsend Peterson and Jorge Soberón, for submission.

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CHAPTER 2

Breeding patterns of Henslow's Sparrow and sympatric grassland sparrow species

ABSTRACT.—Henslow's Sparrows (*Ammodramus henslowii*) are reported to show irregular patterns of return to breeding areas. I present data supporting these reports at range-wide extents, while testing potential biases inherent in the North American Breeding Bird Survey data. Two measures of population variability were used to show that Henslow's Sparrows are less likely to use breeding areas predictably and consistently, but have similar variance in numbers at occupied sites relative to other sympatric grassland sparrow species. I illustrate how restricting analyses to single-observer-collected BBS data results in subtle but significant effects not detected in data aggregated from multiple observers through the study period. The most conservative analysis (single-observer, restricted distribution) showed that Henslow's Sparrows exhibited lower prevalence of occurrence than Grasshopper ($P < 0.001$) and Savannah Sparrows ($P < 0.001$) but no difference in variation of abundance ($P > 0.05$). These results suggest that Henslow's Sparrows are not returning to previously used breeding habitat from year-to-year. Grassland management should consider the behavior documented in this study and attempt to incorporate this facet of Henslow's Sparrow biology into decisions that involve broad-scale landscape design.

INTRODUCTION

Artificial grazing regimes, drainage of wetlands, large-scale agriculture, and alteration of natural fire regimes have changed North American landscapes, and left behind only relict tracts of native prairie (Hyde 1939; Knopf 1988, 1994). The full extent of these impacts on native flora and fauna has only recently begun to be appreciated. Shifts are likely occurring continent-wide, but the most dramatically impacted habitat has been native grasslands. Since European settlement, 99.9% of native prairies have been lost (Samson and Knopf 1994) or altered (Vickery et al. 1994) in North America, and they are now termed a critically endangered habitat (Noss et al. 1995). Thirteen bird species within this biome have suffered serious declines, far surpassing those of any other North American biome (Knopf 1994,

Peterjohn and Sauer 1999, Robbins et al. 2002, Powell 2006), probably the result of continued conversion (i.e., state change) of prairie habitat to an artificial landscape.

Henslow's (*Ammodramus henslowii*), Grasshopper (*A. savannarum*), and Savannah (*Passerculus sandwichensis*) sparrows are obligate grassland nesters (Vickery et al. 1994) with population declines across part or all of their breeding ranges (Peterjohn and Sauer 1999, Wells and Rosenberg 1999). None has national threatened or endangered species status, but Henslow's and Grasshopper sparrows were listed as Birds of Conservation Concern (BCC) in 2008 (USDI 2008) and as Species of Continental Importance (Rich et al. 2004). However, the species' behavior and habitat use, as it relates to landscape configuration, must be understood more fully before successful management can be achieved.

Hyde (1939:23) was the first to note the unpredictability of Henslow's Sparrows appearance in breeding areas, writing "its presence in a given season cannot be certainly predicted," a sentiment that has been repeated by other authors (Wiens 1969, Skipper 1998, Ingold et al. 2009). Most studies report low (Skipper 1998, Monroe and Ritchison 2005) or nonexistent site fidelity for Henslow's Sparrows in breeding areas (J.L. Zimmerman cited in Pruitt 1996). This behavior is atypical compared to Grasshopper and Savannah sparrows which exhibit higher nest site fidelity (Bédard and LaPointe 1984, Wheelright and Rising 1993). The aforementioned studies have used site fidelity as a measurement of return rates to breeding areas in consecutive years, and have necessarily concentrated at only a few sites. Thus, a broader-scale assessment of annual resettlement patterns in breeding areas is necessary but lacking in the literature.

Henslow's Sparrows may be also erratic and opportunistic in selection of sites for breeding on a broad spatial scale. Previous research on this species has focused at local and regional scales, with a few exceptions (e.g., Herkert 2007). The only studies that have used landscape-level analysis were limited to sections of the species' range (Bajema and Lima 2001, Cunningham and Johnson 2006, Thogmartin et al. 2006), and little information exists to provide a range-wide perspective on this species.

I examined abundance data from the entire breeding range for Henslow's Sparrows, and compared it to similar data for Grasshopper and Savannah sparrows. The focus was not to compare habitats used by each species; instead, I analyzed patterns of resettlement in habitat the birds already had assessed as suitable for nesting. Grasshopper and Savannah sparrows were chosen for comparison, not because of similarity or dissimilarity of habitat choices, but because they are obligate grassland sparrow species that nest within Henslow's Sparrows' breeding range.

I used the North American Breeding Bird Survey (BBS) data (Sauer et al. 2007) to address two objectives. First, I examined how Henslow's Sparrow populations vary in time and space. BBS data have been criticized for biases, and a secondary objective was to assess the impact of using different subsets of the BBS data to answer this question. This information is critical to understanding this species' natural history, as well as any conservation implications that may be derived.

METHODS

Study area.—The study area included the entire breeding ranges of Henslow's, Grasshopper, and Savannah sparrows (Fig. 1). All bird abundance data were derived from the BBS, a monitoring system created in the 1960s with the goal of understanding long-term trends in North American breeding bird populations (Sauer et al. 2007). BBS data are collected annually, on fair-weather June mornings, on 4,100 standardized roadside census routes across the United States, Canada and, most recently, Mexico. Sampling points are spaced evenly along the survey route (Robbins et al. 1986), which is 39.4 km in length; 50 sampling points are located every 0.8 km along the route. Observers record all birds seen or heard during 3 min at each stop. Data are available for all years between 1966 and the present, but I used data from 2000–2007 to assure maximal route density and consistency.

Count data.—I used two measures to describe the magnitude of yearly fluctuations of resettlement across the ranges of these species: prevalence of occurrence (proportion of years present) and variation in abundance. The former describes how consistently a species returns to a given BBS route year after year, and is calculated as the ratio of the number of years in which a species was detected on a

route to the number of times during the study period the route was surveyed. The latter measures year-to-year variation in the number of individuals at the site and is estimated as the coefficient of variation: the standard deviation data divided by the mean abundance for each route across all years in which the route was surveyed. Routes sampled in only 1 year of the study period were excluded from analyses because the coefficient of variation was undefined. These two variables describe the consistency of occurrence and abundance, but saturation effects of variation in abundance may influence my results.

The BBS data were divided and analyzed in four groups to consider potentially inherent biases. (1) BBS routes were considered across the entire breeding range of each species. (2) Analysis was constrained to BBS routes within the recorded breeding range of Henslow's Sparrows. I examined BBS route data collected by single observers across all years in the study period, removing possible biases originating from differences in observer consistency. These analyses were conducted (3) across the entire range of each species, and (4) only within Henslow's Sparrows' distributional area. The smallest data set had 56 routes and, to have equal samples sizes for each analysis, I randomly selected 50 routes per species for each data set.

Statistical analysis.—Shapiro-Wilk normality tests and Levene's test for homogeneity of variances were performed on all data sets. At least one sample within each data set had non-normally distributed data and unequal variances. Both negative and positive skews were common within datasets, and transformation of the data was not possible. Thus, I used Kruskal-Wallis nonparametric analysis of variance to test for differences among means, which provided conservative and consistent testing for differences among all groups. Kruskal-Wallis test statistics were evaluated with $\alpha = 0.05$. Mann-Whitney *U*-tests were performed to differentiate between significant groups whenever significant χ^2 values were obtained. I used the non-parametric Kendall's tau statistic to analyze the relationship between prevalence of occurrence and variation in abundance. A Bonferroni correction was applied to Mann-Whitney *U*-tests and Kendall's tau correlations, and all effects were reported at $\alpha = 0.0167$. Statistical analyses were performed using SPSS, Version 16.0 (2007). All maps were created in ArcGIS, version 9.2 (ESRI 2009).

RESULTS

Prevalence of occurrence.—Significant differences were found among species in all data sets tested for prevalence of occurrence ($P < 0.001$). There were significant differences between species for the multiple-observer data set, both at the full extent of the species' ranges and within the distribution of Henslow's Sparrows (Table 1). Mann-Whitney U -tests for the full extent of the species' ranges indicated the median prevalence of occurrence for Henslow's Sparrows (0.50) was lower than for Grasshopper (0.78, $P = 0.006$), and Savannah (1.00, $P < 0.001$) sparrows; Grasshopper Sparrows did not differ significantly in prevalence from Savannah Sparrows ($P = 0.022$, Table 2). Results constrained to within Henslow's Sparrow's distributional area were similar, and significant for all comparisons (Tables 1–2, Fig. 2).

There were significant among-group differences in the single-observer data sets for both the full-range extent and within Henslow's Sparrow's distributional area ($P < 0.001$, Table 1). Median Henslow's Sparrows prevalence (0.50) for full-range extents was significantly lower than for Grasshopper (0.88, $P < 0.001$), and Savannah (1.00, $P < 0.001$) sparrows (Table 2). Grasshopper Sparrows had lower prevalence than Savannah Sparrows ($P = 0.005$, Table 2). The same results occurred when these data were restricted to Henslow's Sparrow's distributional area (Tables 1–2, Fig. 3).

Variation in abundance.—Results were less consistent between data sets than for prevalence comparisons. There were differences between species ($P = 0.011$, Table 1) for the multiple-observer data set across the full extent of the species' ranges. Grasshopper Sparrows had higher variability in abundance (median = 0.54) than Henslow's Sparrows (0.42, $P = 0.004$), but no significant differences existed between Henslow's and Savannah (0.50, $P = 0.070$) sparrows, or between Savannah and Grasshopper sparrows ($P = 0.18$, Table 2, Fig. 4). No differences were apparent between the species (Table 1, Fig. 2) when the data were limited to Henslow's Sparrow's distributional area.

The single-observer data sets revealed a similar pattern, but with significant differences between species in analysis of the full extent ($P = 0.002$) and within Henslow's Sparrow's distribution ($P = 0.018$,

Table 1). There was no difference between Henslow's Sparrows and Grasshopper (0.44, $P = 0.090$) or Savannah ($P = 0.21$, Table 2) sparrows. Grasshopper Sparrows, however, did have higher variability (median = 0.47) than Savannah Sparrows (0.39, $P < 0.001$). The same results were obtained for analyses limited to single-observer routes within Henslow's Sparrow's distribution (Tables 1–2, Fig. 3).

Correlation of prevalence and variation.—Prevalence of occurrence was significantly and positively correlated to variation in abundance for Henslow's Sparrows in the multiple-observer ($\tau = 0.37$, $P < 0.001$) and single-observer ($\tau = 0.32$, $P = 0.003$) datasets. This relationship did not hold for either Grasshopper or Savannah sparrows in any data set (all $P > 0.05$).

DISCUSSION

Resettlement.—Site fidelity describes the likelihood of an individual's return to a particular site from year to year. Often, the decision for adult birds to return to a particular site is based on the individual's experiences, or the experiences of conspecifics, at the site in previous years (Hildén 1965). This measurement is ideal for finer-scale analyses, but broad-scale studies require consideration of resettlement of an area by groups of individuals. More importantly, global patterns exhibited by these groups across space and time can provide insight into differences across their geographic ranges.

Previous studies have evaluated nest site fidelity in Henslow's, Grasshopper, and Savannah sparrows (Bédard and La Point 1984, Skipper 1998, Jones et al. 2007), although, to my knowledge, this study is the first to examine variation in resettlement patterns across their breeding ranges. Henslow's Sparrows, in all analyses, had the lowest prevalence of occurrence among the three species. They were, as a group, less likely to return to a BBS route from 1 year to the next. When Henslow's Sparrows were detected, with the exception of one test, they had variability in abundance not distinguishable from those of Grasshopper and Savannah sparrows. Both Grasshopper and Savannah sparrows had greater numbers of high-prevalence routes than Henslow's Sparrows. These across-species differences in variation in occurrence might be best explained by habitat choices and social behavior of each species.

Henslow's Sparrows require large, open grasslands (Hyde 1939, Smith 1968, Thogmartin et al. 2006). Vegetation structure, including aspects of vegetation height (Wiens 1969, Herkert 1994a) and density (Wiens 1969, Zimmerman 1988), is an important factor for nest site selection in Henslow's Sparrows (Graber 1968, Bajema and Lima 2001, Powell 2006). Fields must remain relatively undisturbed for several consecutive years to achieve vegetation structure typical of Henslow's Sparrow's breeding habitat. Thus, this sparrow avoids fields frequently disturbed by haying (Graber 1968, Cully and Michaels 2000), burning, or grazing on frequent rotations (Bollinger 1995). Similarly, Grasshopper and Savannah sparrows prefer natural habitat to managed landscapes (Owens and Myers 1973, Dale et al. 1997). These species are less strict in their habitat preferences, unlike Henslow's Sparrows, and take advantage of a greater variety of habitat, including grazed, cultivated (Owens and Myers 1973), and hay fields (Graber 1968, Dale et al. 1997).

These differences in habitat preferences among the species may explain differences in prevalence of occurrence. The narrowness of Henslow's Sparrows' breeding habitat preferences within the dynamic grassland biome possibly motivates groups of individuals to seek unused habitat when previously settled locations are no longer suitable (Reinking et al. 2000). For example, an area that is optimal habitat in 1 year may experience a disturbance, such as a late summer burn, resulting in unsuitable habitat for subsequent breeding seasons, thereby encouraging Henslow's Sparrows to seek new nesting locations. Settling suitable habitat when encountered upon arrival in the breeding area, rather than homing to a previously used site and then relocating, would also be advantageous for species that use highly variable resources (Johnson and Grier 1988). Grasshopper and Savannah sparrows, on the contrary, using a wider variety of habitats (Smith 1968, Wiens 1969, Owens and Meyers 1973, Dale et al. 1997), may resettle an area in successive breeding seasons, even though the habitat has been altered from previous years. For species whose nesting habitat is unpredictable and patchy, the ability to be opportunistic and flexible when choosing a nesting location may be advantageous (Wiens 1973, Cody 1985, Johnson and Grier 1988).

Henslow's Sparrows, in the relatively few areas where they occurred consistently, showed higher variation in abundance. In areas where they were not consistently present, they showed less variation in abundance, thus, creating a positive association between prevalence and variability. This pattern might be explained by the effect of clustering, combined with opportunistic settling. The earliest literature on Henslow's Sparrows noted the tendency of the species to nest in loose colonies, especially when occupying large patches of habitat (Hyde 1939, Graber 1968, Wiens 1969). Individuals of nomadic species, such as Henslow's Sparrows, arriving to an area may use the presence of conspecifics which have already settled there as a means to evaluate habitat quality, especially when knowledge of nest success from previous years within that nesting location is lacking (Bollinger and Gavin 1989, Ahlering et al. 2006). Thus, clustering when paired with opportunistic location selection may produce a pattern of irregularity of settlement with regularity of abundance. Unlike Henslow's Sparrows, no significant relationship exists between variability, prevalence, and abundance in either Grasshopper or Savannah sparrows.

Biases in BBS data.—Use of BBS data is a timely and cost-effective way of answering relatively short-term, broad-scale questions (Sauer et al. 2005, Winter et al. 2006). The BBS is the only source for range-wide, standardized data in North America; it is commonly used to estimate abundances and year-to-year fluctuations across species' breeding ranges (Bibby et al. 2000, Diefenbach et al. 2003, Herkert 2007). Although the BBS is widely used, it is not without potential bias.

One criticism of the BBS is that of change of observers across time. Link and Sauer (1998) suggested that differences in ability among observers may influence trends detected along routes over time. I found that results differed when data were limited to single-observer routes. Specifically, Savannah Sparrows had significantly higher prevalence rates than Grasshopper Sparrows in the single-observer data set, a difference not detected in analyses of the multiple-observer data set. The difference was significant in both the full extent of the species' ranges and in the restricted area; thus, reduced to Henslow's Sparrow's distributional area, the effect was not a result of geographic extent. Removing

routes surveyed by multiple observers also affected variation in abundance. There were contrasting differences between species across the full extents of the species' ranges. Grasshopper Sparrows had the highest variability, but the ranks of the other two species shifted. The multiple-observer data set in analyses constrained to within the Henslow's Sparrow's distribution showed no species differences, but the single-observer data set revealed significant results.

Thus, results of several analyses changed when the route data collected by multiple observers were removed. This variation is likely a result of change in observers and their relative abilities (Link and Sauer 1998). Sauer et al. (1994) suggested abundance patterns are best represented by analyses of single-observer data only. However, even single observers may, through time, improve in identification and detection skills, for example by learning a song (Link and Sauer 1998) or the opposite (e.g., with declining hearing abilities); these effects cannot be measured, but may be reduced by comparisons with multiple-observer data.

Detection.—Other concerns not addressed within the analyses of this paper should be considered. In addition to concerns of multiple-observer or geographic effects, it is possible that Henslow's Sparrows are not detected as easily as Grasshopper or Savannah sparrows. The species may be too rare in some areas, resulting in detection difficulties (Wells and Rosenberg 1999, DeVault et al. 2002). In other locations where individuals are more abundant, lack of activity (Diefenbach et al. 2007, Confer et al. 2008), or failure to detect individuals may cause discrepancies, thereby affecting count data.

Henslow's Sparrow's cryptic appearance and secretive behavior (Hyde 1939), in addition to its insect-like song (Leftwich and Ritchison 2000), may lead to detection problems during surveys. Detection may be further restricted when singing declines after mate pairing (Leftwich and Ritchison 2000) or as a result of Henslow's Sparrows' proclivity for nocturnal singing (Walk et al. 2000). Henslow's Sparrows may not nest near roadsides as a response to present woody vegetation (Patten et al. 2006) or traffic volume (Forman et al. 2002), yet BBS data are collected entirely from roadside routes. It is possible that populations of birds are not surveyed accurately because of species' behavior and surveying techniques.

Bajema et al. (2001) suggest applying a correction factor to estimate Henslow's Sparrow abundance to counter these detection problems.

Conservation implications.—Henslow's Sparrow was once thought to be prevalent throughout the western extent of its breeding range, although it now occupies less than 1% of this original area (Robbins et al. 2002). Its need for regular, though infrequent, habitat disturbance to maintain a particular seral stage may facilitate this decline in present human-dominated landscapes (Pruitt 1996). This habitat in the pre-European landscape was maintained by fire (natural and artificial), and grazing by large herbivores, creating a mosaic of habitats on the landscape (Knopf 1994, Umbanhowar 1996). Burning, grazing, and mowing have all been recommended as suitable management practices (Pruitt 1996), but the timing, extent, and frequency of these disturbances are critical factors that affect suitability of the habitat for breeding Henslow's Sparrows (Herkert 1994a, Powell 2006). The patterns documented in this study are strongly suggestive of a species that has adapted to be able to track optimal sites in a shifting habitat mosaic.

Henslow's Sparrows are also considered area-sensitive, and are affected by patch size of breeding habitat (Herkert 1994b, Walk and Warner 1999, Oleary and Nyberg 2000, Thogmartin et al. 2006). The current approach of conserving large isolated patches of high-quality habitat may be too narrowly focused on this concept. Renfrew and Ribic (2008), in a study of Bobolinks (*Dolichonyx oryzivorus*), Grasshopper, and Savannah sparrows, concluded that patch-size might only be particularly restrictive when the entire landscape is heavily fragmented. Thus, conserving smaller areas in addition to large, contiguous habitat patches within the landscape matrix would create more total grassland habitat and better suit Henslow's Sparrows, as it enhances the overall quality of the landscape and fosters its nomadic movements and colonial behavior (Horn and Koford 2006, Ribic et al. 2009). Acquiring smaller, but functioning, plots may be easier and more economical, thus producing more immediate conservation impacts. Ultimately, losses of suitable grassland nesting habitat on regional scales may result in

extinction of obligate grassland species (Vickery et al. 1994), and particularly Henslow's Sparrows, which appear to move much more broadly across regional landscapes than the other two species analyzed.

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Table 1. Kruskal-Wallis test results for comparisons of Henslow's, Grasshopper, and Savannah sparrows between multiple- and single-observer groups, and between data collected across: the full extent of each species' breeding range versus restricted to Henslow's Sparrow's distributional area. Breeding Bird Survey data were collected from 2000–2007 on 50 randomly selected routes. (*) indicates significant results ($P \leq 0.05$).

	Full extent of species' ranges				Henslow's Sparrow distributional area			
	Multiple observers		Single observer		Multiple observers		Single observer	
	<i>H</i>	df	<i>P</i>	<i>H</i>	df	<i>P</i>	<i>H</i>	df
Prevalence of occurrence	26.9	2	<0.001*	39.9	2	<0.001*	45.1	2
Variation in abundance	9.0	2	0.011*	12.6	2	0.002*	8.1	2

Table 2. Mann-Whitney *U*-test results for comparisons of Henslow's (HESP), Grasshopper (GRSP), and Savannah (SASP) sparrows between multiple- and single-observer groups, and between data collected across two different geographic extents: the full extent of each species' breeding range and restricted to Henslow's Sparrow's distributional area. Breeding Bird Survey data were collected from 2000–2007 on 50 randomly selected routes. One comparison for variation in abundance is lacking because of nonsignificant results found with the Kruskal-Wallis analysis. (*) indicates significant results ($P \leq 0.0167$).

	Full extent of species' ranges						Henslow's Sparrow distributional area					
	Multiple observers			Single observer			Multiple observers			Single observer		
	<i>U</i>	<i>z</i>	<i>P</i>	<i>U</i>	<i>z</i>	<i>P</i>	<i>U</i>	<i>z</i>	<i>P</i>	<i>U</i>	<i>z</i>	<i>P</i>
Prevalence of occurrence												
<i>Henslow's - Grasshopper</i>	856.5	-2.7	0.006*	649.5	-4.2	<0.001*	582.0	-4.7	<0.001*	625.5	-4.4	<0.001*
<i>Henslow's - Savannah</i>	505.0	-5.2	<0.001*	422.5	-5.9	<0.001*	364.5	-6.3	<0.001*	347.0	-6.4	<0.001*
<i>Grasshopper - Savannah</i>	938.0	-2.3	0.022	879.0	-2.8	0.005*	998.5	-1.9	0.045	933.5	-2.5	0.014*
Variation in abundance												
<i>Henslow's - Grasshopper</i>	830.5	-2.9	0.004*	1003.5	-1.7	0.09	-	-	-	1152.5	-0.7	0.50
<i>Henslow's x Savannah</i>	987.5	-1.8	0.070	1068.0	-1.3	0.21	-	-	-	1009.0	-1.7	0.10
<i>Grasshopper - Savannah</i>	1056.5	-1.3	0.18	697.0	-3.8	<0.001*	-	-	-	815.0	-3.0	0.003*

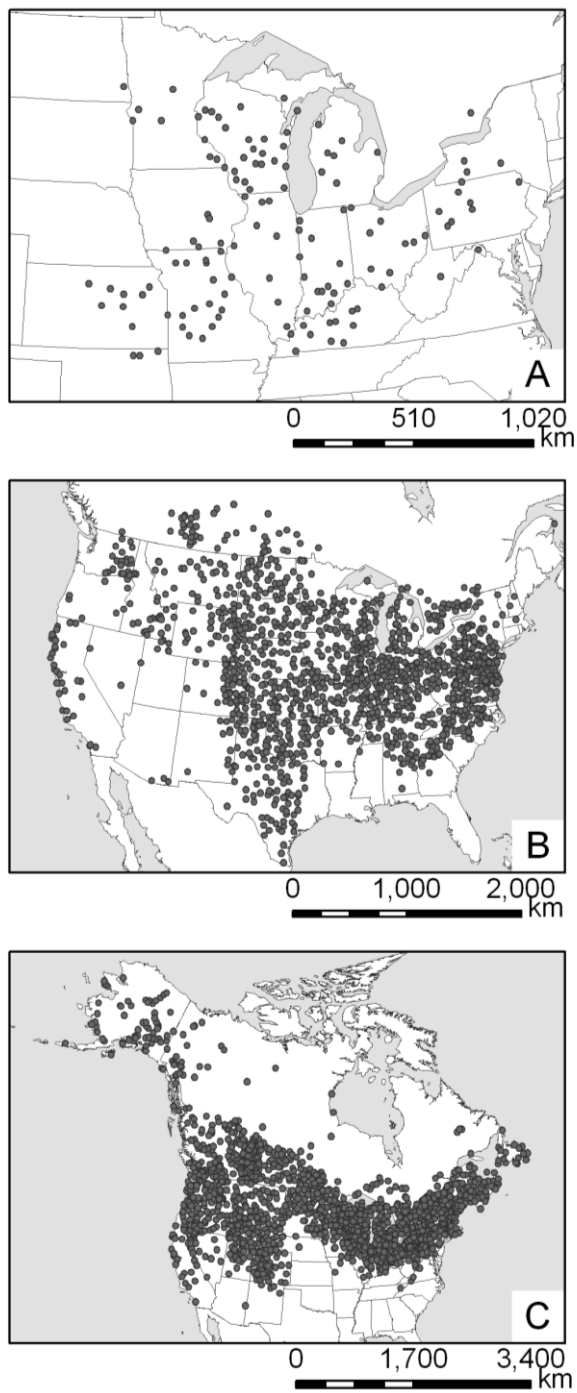


Figure 1. Henslow's (A), Grasshopper (B), and Savannah (C) sparrow distributions from Breeding Bird Survey route data collected during 2000–2007. Henslow's, Grasshopper, and Savannah sparrows were observed on 132; 1387; and 1765 routes, respectively.

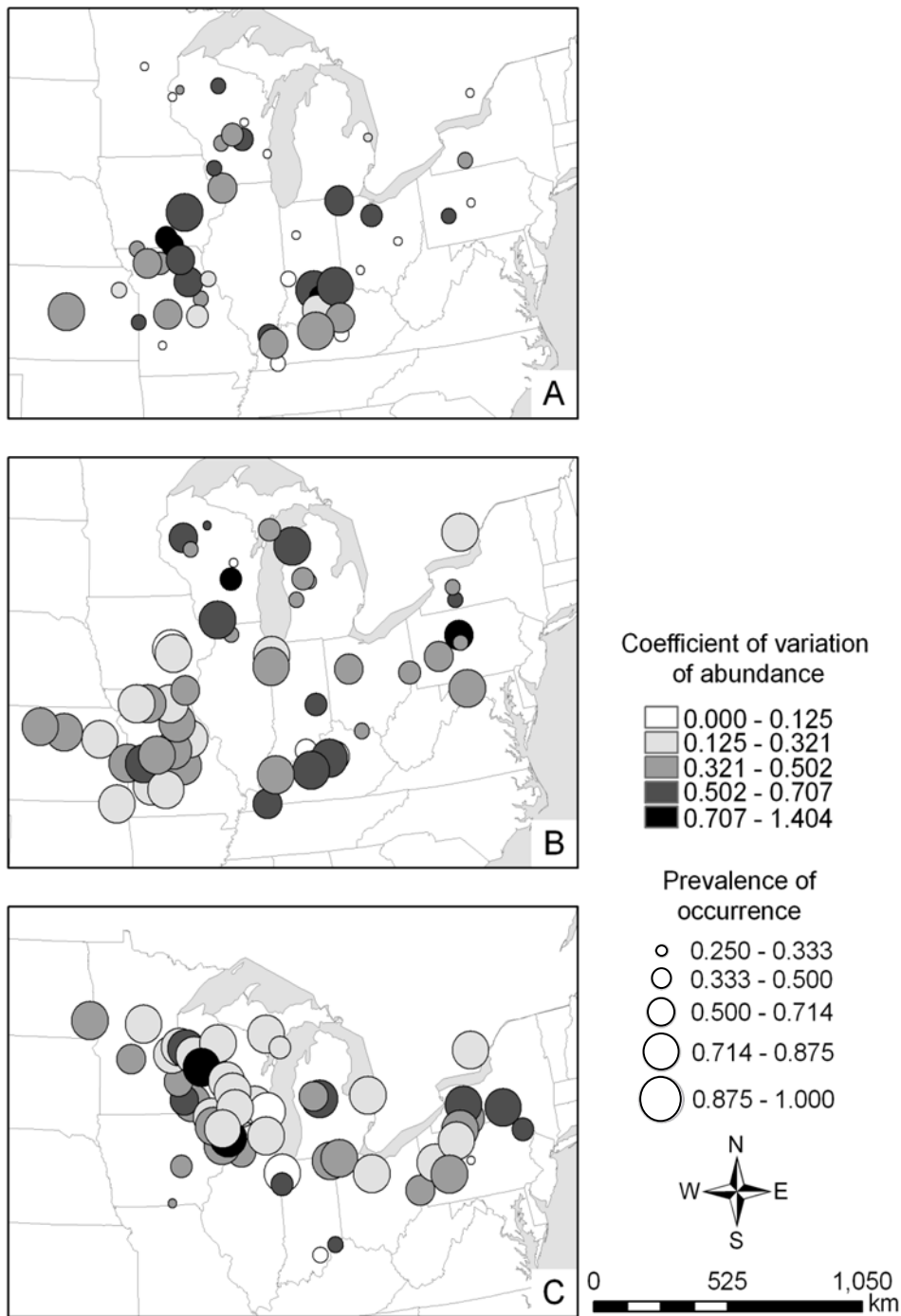


Figure 2. Henslow's (A), Grasshopper (B), and Savannah (C) sparrow distributions, showing prevalence (circle size) and abundance (shading of circles). Data are restricted to within the Henslow's Sparrow's breeding distribution and were collected by multiple observers from 2000–2007 on 50 randomly selected Breeding Bird Survey routes.

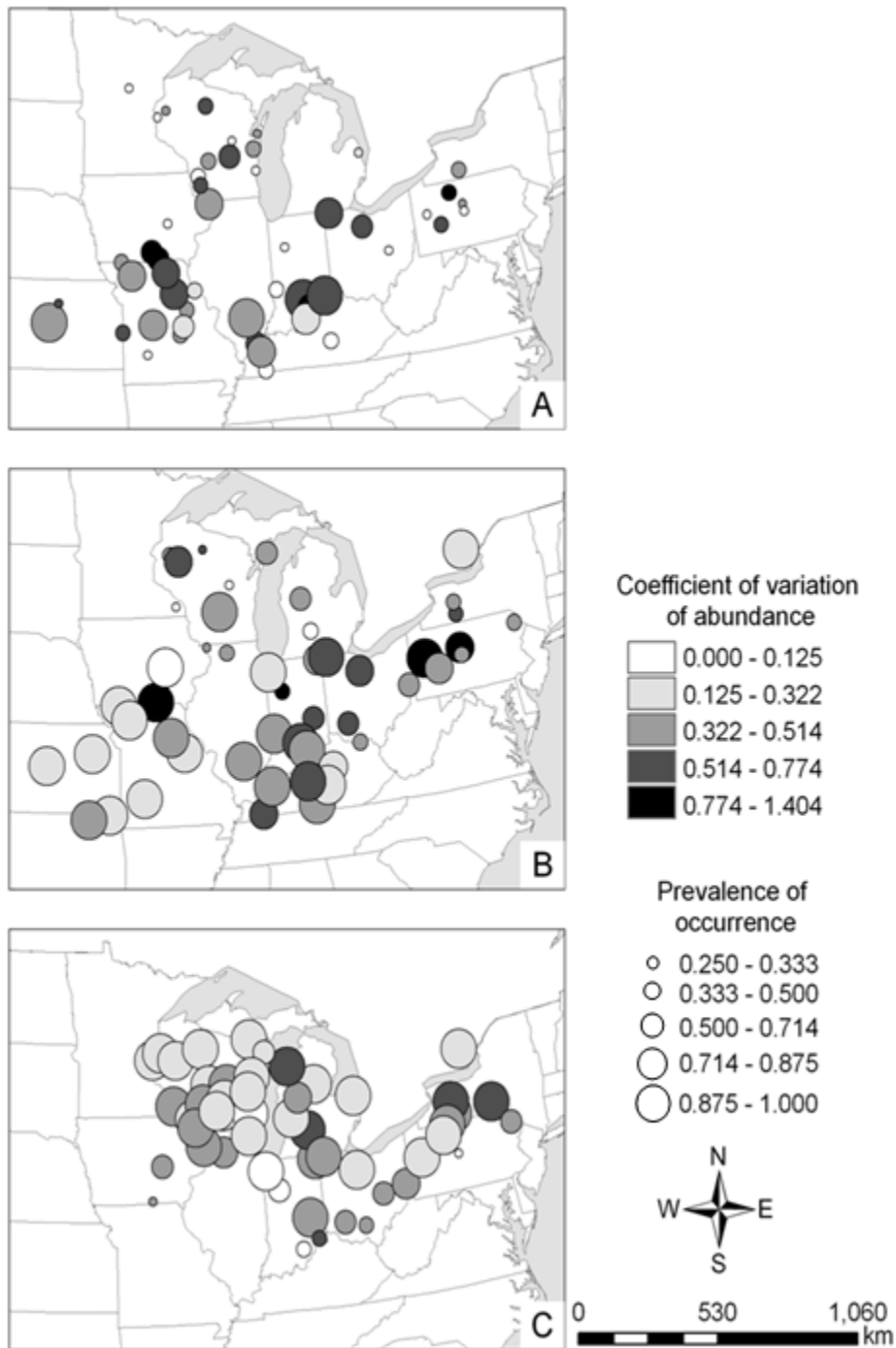


Figure 3. Henslow's (A), Grasshopper (B), and Savannah (C) sparrow distributions, showing prevalence (circle size) and abundance (shading of circles). Data are restricted to within the Henslow's Sparrow's breeding distribution but were collected by single observers only for given routes, from 2000–2007 on 50 randomly selected Breeding Bird Survey routes.

CHAPTER 3

Spatial scaling of prevalence and population variation in three grassland sparrows

ABSTRACT.—Henslow’s Sparrows (*Ammodramus henslowii*) are distributed in tallgrass prairies in central North America; however, this species is restricted further to specific habitats within these prairies—large extents with relatively little woody vegetation, but accumulation of standing grasses and forbs, conditions that result from infrequent disturbances by fire, mowing, or grazing. Henslow’s Sparrows have been documented to be unpredictable at breeding sites from year to year, but studies to date have considered only local spatial scales. Here, we compared resettlement behavior (prevalence of occurrence and variation in abundance) of Henslow’s Sparrows to that of two other grassland sparrow species, Grasshopper Sparrows (*A. savannarum*) and Savannah Sparrows (*Passerculus sandwichensis*), across multiple spatial resolutions. Henslow’s Sparrows showed lower prevalence and higher variation in abundance than the other two species. Indeed, Henslow’s Sparrows do not occur consistently at extents of less than 120 000 km², suggesting nomadic characteristics of where they breed from year to year. We suggest that these patterns reflect Henslow’s Sparrows’ responses to frequently changing habitat, such that this species is tracking spatiotemporal changes in optimal habitat that result from disturbances broadly across regional landscapes.

INTRODUCTION

Henslow’s Sparrows (*Ammodramus henslowii*) breed on remnants of tallgrass prairie and similar grassland habitats scattered across the Midwest and portions of northeastern North America (Pruitt 1996, Herkert et al. 2002). This species, once common (Robbins et al. 2002), is now recorded only infrequently on North American Breeding Bird Survey (BBS) routes across much of its original breeding range (Sauer et al. 2011). Its breeding habitat, formerly relatively contiguous in prairies and coastal marshes from the northeastern seaboard to the western limit of tallgrass prairie (Hyde 1939, Pruitt 1996), is now patchy, with few documented core areas. Henslow’s Sparrows are not only uncommon, but they are also

unpredictable in grasslands that appear suitable (Hyde 1939, Wiens 1969, Skipper 1998). For example, this species may be present one year, but not return to the area in subsequent years, even though the vegetation appears unchanged, for reasons that are unclear. An earlier analysis (Dornak 2010) found that Henslow's Sparrow breeding sites were less predictable from year to year, compared to Grasshopper (*A. savannarum*) and Savannah (*Passerculus sandwichensis*) sparrows, on BBS routes. That study concluded that Henslow's Sparrows were possibly nomadic because birds were not consistently resettling at the same sites for breeding.

Nomadism is the irregular or undirected dispersal of individuals following patchy and unpredictably available resources across a landscape (Sinclair 1984, Dean 1997), and is in effect temporal turnover of populations (Allen and Saunders 2002). Nomadism can occur among individuals, groups of individuals, or entire populations (Andersson 1980), and across multiple spatial scales (Dean 1997). It is most commonly observed in species that live in highly variable environments, such as the North American grasslands (Bragg 1995), where the ability to track resources (e.g., food or suitable nesting sites) and colonize new breeding areas quickly in response to changing environmental conditions is advantageous (Cody 1985, Igl and Johnson 1999)

The Dornak (2010) analyses examined nomadism only at one spatial scale; however, it remains unclear if this trend can be observed over multiple scales, and (most importantly) at what scales the differences in prevalence between these grassland species are manifested. The present study investigates these questions using comparisons of occurrence and variation in abundance patterns among Henslow's, Grasshopper, and Savannah sparrows at spatial resolutions spanning six orders of magnitude (0.5–511 360 km²). These three species were chosen for comparison because they are all obligate grassland nesters (Vickery et al. 1999), they have variable tolerances to grassland succession (Wheelwright and Rising 1993, Vickery 1996, Powell 2006), and they have been observed to exhibit different levels of fidelity to nest sites (Bédard and LaPoint 1984, Skipper 1998, Jones et al. 2007). Although we note that these

species differ with respect to microhabitat preferences, our focus is on predictability of occurrence of each species within their respective microhabitats.

METHODS

Study area. —Our analysis was restricted to the overall known extent of Henslow's Sparrows' breeding occurrence (Figure 1), which subsumes the site-to-site variation that is the subject of this paper. Although Grasshopper and Savannah sparrow breeding distributions extend more broadly, restricting the area analyzed to the distribution of Henslow's Sparrows reduces variation resulting from irrelevant processes manifested beyond the range of the focal species (Dornak 2010). The reduced area covers $2.1 \times 10^6 \text{ km}^2$, and is dominated by agriculture, pasture, and croplands, interspersed with patches of woodlands, shrub, wetlands, urban and developed areas, fallow pastures, and native prairie.

Occurrence data. —Occurrence data were extracted from the BBS database (Sauer et al. 2011). The BBS is conducted annually on >4000 roadside census routes across the US, southern Canada, and northern Mexico, and is the only broad-scale, standardized, long-term system that monitors breeding bird trends in North America (Sauer et al. 2011). Each 39.5 km route has 50 stops (observation points) distributed every 0.8 km. Each year in June, observers record all birds seen or heard at each stop for 3 minutes (Sauer et al. 2011). Fifty BBS routes per species were used, representing almost all routes (see below) on which Henslow's Sparrows have been detected, and paralleling past analyses (Dornak 2010). Although the system is not without inherent bias (T. R. Cooper, pers. comm.), for studies extending across entire breeding distributions, the BBS is the only distribution-wide, standardized database for North America; as such, BBS data are most appropriate as the basis for the analyses of this study. To control for biases in observer consistency (Dornak 2010), only data from BBS routes conducted by single observers across the study period were used, which reduced the sample size of routes on which this species has been detected to 50. Two metrics were used to describe yearly resettlement patterns of the species: prevalence of occurrence and coefficient of variation in abundance (Dornak 2010). Prevalence of occurrence describes the consistency of resettlement of an area by the species across years. It was derived

by dividing the total number of years that a species was observed on a route by the total years that the route was surveyed. The coefficient of variation of numbers of individuals of the species detected is a standardized metric of variation, calculated as standard deviation divided by the mean abundance.

Spatial scale gradient. —All analyses are based on regroupings of records of sparrow species within and among stops on BBS routes to develop a multiple-scale approach crossing orders of magnitude. We analyzed data (1) below the spatial scale of individual BBS routes by creating subgroups of BBS stops, (2) at the route level, and (3) above the route level by combining routes within regions (Figure 2). That is, within each BBS route in the sample, the finest resolution was offered by the 50 stops individually (each representing sampling of $\sim 0.5 \text{ km}^2$), which were then grouped into 25 pairs of consecutive stops ($\sim 1.14 \text{ km}^2$ per pair). To construct increasingly broader spatial scales, stops were aggregated into 10 groups of 5 stops ($\sim 3.06 \text{ km}^2$ per group), 5 groups of 10 stops ($\sim 6.26 \text{ km}^2$ per group), 2 groups of 25 stops ($\sim 15.86 \text{ km}^2$ per group), and finally the full BBS route ($\sim 32.02 \text{ km}^2$; Figure 2).

Coarser resolutions were developed by dividing the species' range into quadrants of equal areas. The Henslow's Sparrow breeding distribution ($2\,109\,744 \text{ km}^2$) was divided into 64 ($30\,780 \text{ km}^2$ per region), 16 ($126\,126 \text{ km}^2$ per region), and 4 equal regions ($511\,360 \text{ km}^2$ per region; Figure 2). All three species' occurrences were analyzed across this same suite of areas. Hence, prevalence and variability could be visualized across a spectrum of spatial resolutions and extents ranging from 0.5 km^2 to $0.5 \times 10^6 \text{ km}^2$, or 6 orders of magnitude of area. We note that the route-based areas and the quadrant-based areas are not completely compatible and consistent with one another as the smaller above-route quadrants varied in sample size of routes and thoroughness of sampling, for this reason, one confirmatory rarefaction test was based only on extents at and below that of entire routes (see below).

Statistical analysis. —Tests for normality and homogeneity of variances were conducted initially for all levels of analysis. Because most samples were either non-normally distributed or had non-homogenous variances, non-parametric analyses were used throughout. Kruskal-Wallis rank sums tests were used to assess differences between species at particular resolutions within the original data sets (i.e.,

not the rarefied data sets, see below); when significant differences resulted, *post hoc* Mann-Whitney *U*-tests were used to differentiate between groups of species. Kruskal-Wallis results were evaluated using $\alpha = 0.05$. To control for Type-I errors when multiple significance tests are performed, Bonferroni corrections were applied to all Mann-Whitney *U*-tests, so results are reported at $\alpha = 0.0167$. Statistical analyses were performed using SPSS, version 17.0 (SPSS 2008) and with R (R Development Core Team 2011). However, because successive resolutions are not independent of one another, creating potential for bias, testing was explored in further depth, as follows.

Prevalence values were plotted across the spectrum of spatial resolutions as curves connecting (0, 0) (no area, no presence) and (511 360 km², 1) (full range, constant presence). As a hypothetical example, these curves would be highly convex in a species with very consistent local occurrence patterns, for example *Turdus migratorius*, but concave in highly nomadic species with consistent occurrence only at broad extents (Figure 3). To compare these curves in terms of their concave *versus* convex nature, and bearing in mind that the same data that make up the data for one spatial resolution participate in making up the data at the next-coarser resolution, making different resolutions non-independent, we calculated the area under each species' curve as a means of building comparisons across spatial scales. To permit statistical comparisons of these areas, we used a 50% bootstrap subsampling of the data that are used to estimate the curves (i.e., the stop-level BBS detection data) to generate 1000 replicates from which to generate distributions of areas reflecting the intrinsic variability in the data. To avoid violating assumptions of independence, we used area-under-the-curve analysis to consider all resolutions concurrently. We also applied this method to coefficients of variation of abundance values to compare differences among the species. These calculations were generated using programs developed by N. Barve that are available upon request from the authors.

Tests for biases. —Henslow's Sparrows are observed less often per BBS stop and are more difficult to detect than either Grasshopper or Savannah sparrows (Dornak 2010). Henslow's Sparrows also appear to be less abundant than the other two species analyzed herein. We argue that the effect of the

differences in detection and abundance are similar, such that, within our analyses, a species with low detectability will present a pattern of occurrence similar to that of one with low abundance. We conducted tests to verify that the low prevalence of Henslow's Sparrows is not simply a consequence of lower numbers of individuals or lower detectability of similar numbers of individuals. To this end, we treated detection and abundance as a single phenomenon and subsampled Grasshopper and Savannah sparrow individual occurrences at the stop level across the study period to produce a data set that matched abundances overall to the Henslow's Sparrow BBS data. Because we resampled randomly from Grasshopper and Savannah sparrow occurrence data to equal Henslow's Sparrow abundances, we effectively manipulated overall numbers without changing the spatial structure; then, we tested whether that spatial structure differed among species. We reassembled rarefied data sets into presence-absence data sets, and analyzed as described above. Because of the random nature of the resampling method, abundances at some stops were reduced, but abundances were eliminated entirely on other stops. The resampling was randomized and repeated to generate 200 rarefied data sets for each of Grasshopper and Savannah sparrows. We feel that our methods of reducing the abundances of Grasshopper and Savannah sparrows also reduced the effects of detection differences among the species, such that prevalence patterns presented in our results reflected natural phenomena and not density biases. We restricted these analyses to AUC, and did not repeat the Kruskal-Wallis and Mann-Whitney U-test comparisons.

Spatial resolutions and associated prevalence values were constructed from the rarefied data as described above, and median prevalence was calculated for each resolution; however, owing to inconsistencies between the route-based and quadrant-based data, we conducted these analyses for resolutions only at and below the route level. Areas under the curve were generated for each rarefied subset, applying the same parameters used with the original data sets. To consider intrinsic variability in the data underlying each curve for each of these 200 rarefied data sets per species, we again used 50% bootstrap subsampling to generate 1000 randomized values. These 1000 bootstrap values were averaged and used to create a histogram of the distribution of each of the 200 rarefied data sets. We compared the

observed area for Henslow's Sparrows to those of the bootstrapped distributions. Because the data in the coarser (regional) resolutions mask patterns that emerge at finer resolutions, and in light of the inconsistencies of above-route resolutions noted above, this analysis was limited to resolutions of 0.5 km² (stop) through 32.02 km² (route).

RESULTS

Prevalence of occurrence. —At most spatial resolutions, prevalence was lowest in Henslow's Sparrows and higher in the other two species. Significant differences between species were found at all spatial resolutions ($P < 0.001$) except 125 126 km² ($P = 0.185$) and 511 360 km² (Table 1). Analysis for the latter resolution did not merit further consideration because all species had a median prevalence of 1.0, so no differences could be detected. However, for all resolutions at or below 30 780 km², Henslow's Sparrows had significantly lower prevalence of occurrence compared to both Savannah and Grasshopper sparrows ($P < 0.01$, Table 1). The consistency with which Henslow's Sparrows returned to sites at these extents varied: 22% (0.5 km²), 50% (32.02 km²), and 63% (30 780 km²); the species was not consistently present (i.e., prevalence >75%) at sites until the resolution was broadened to cover 126 126 km². Comparatively, Grasshopper and Savannah sparrows were consistently prevalent at much finer resolutions the 32.02 km² (87%) and 3.06 km² (77%) resolutions, respectively (Figure 3). Grasshopper Sparrows had significantly lower prevalences compared to Savannah Sparrows at all resolutions through 32.02 km² (Table 1, Figure 3). However, as mentioned above, these comparisons are complicated because prevalences at different spatial resolutions are not independent of one another.

The prevalence curve comparisons offer a means of comparing the species without the complication of non-independence of successive spatial resolutions. The curves were significantly different among all comparisons of species ($P < 0.001$). The Henslow's Sparrow curve was significantly lower than those curves of Grasshopper ($z = -38.72$; $P < 0.001$) and Savannah ($z = -38.72$; $P < 0.001$) sparrows; similarly, the Grasshopper Sparrow curve was lower than that of Savannah Sparrows ($z = -21.95$; $P < 0.001$).

Finally, we used rarefaction analyses to check that the prevalence differences described above were not an artifactual consequence of overall lower abundance and/or detectability. We found that, at least at finer spatial resolutions, Henslow's Sparrow prevalences were still significantly ($P < 0.005$) less consistently present at sites than either of the other two species, even when the abundances of the other two species were rarefied (Figure 4). As a result, we conclude that the result of less consistent occurrence of Henslow's Sparrows is indeed a reality, and not an artifact.

Variation in abundance.—Significant differences among species in tests for variation in abundance were found only at two resolutions, 32.02 km² ($P = 0.049$) and 126 126 km² ($P = 0.005$; Table 1). At 32.02 km², Grasshopper Sparrows (median = 0.43) had higher ranked variability in abundance than Savannah Sparrows (0.32, $P = 0.010$). At 126 126 km², Henslow's Sparrows (0.53) had higher ranked variability than Savannah Sparrows (0.23, $P = 0.002$; Table 1). Variation in Grasshopper Sparrows (0.41) was almost significantly larger than Savannah Sparrows at 126 126 km² extent ($P = 0.017$; Table 1).

Comparisons of areas under curves revealed significant differences between species ($P < 0.001$). The Henslow's Sparrow curve was significantly higher than those for both Grasshopper ($z = -25.79$; $P < 0.001$) and Savannah ($z = -38.72$; $P < 0.001$) sparrows; hence, Henslow's Sparrow abundance was more variable than the other grassland sparrows. The curve for Grasshopper Sparrows was significantly higher than that for Savannah Sparrows ($z = -38.72$; $P < 0.001$; Figure 5). We did not conduct rarefaction manipulations for population variation owing to confusion as to how best to manipulate individual occurrences in this case.

DISCUSSION

Comparisons of species.—Henslow's Sparrows do not use breeding areas consistently from year to year across their geographic distribution; as a consequence, they showed significantly lower prevalence of occurrence compared to Grasshopper and Savannah sparrows at most spatial resolutions analyzed. At local scales (0.5 km²), prevalences were low for all three species; however, as spatial resolution coarsened, Grasshopper and Savannah sparrow prevalences increased, but Henslow's Sparrow

prevalences remained low. Indeed, Henslow's Sparrows returned to entire BBS routes (30.02 km^2) only in 50% of years sampled, and were at times conspicuously absent even from broader regions ($30\,780 \text{ km}^2$ at 63% prevalence). Statistical comparisons at individual resolutions, though informative, violate assumptions of independence between tests; therefore, the area-under-the-curve may characterize better prevalence of occurrence for the three species across multiple spatial resolutions. The prevalence curve of Henslow's Sparrows was more concave—having less area beneath the curve—than the curves of Savannah and Grasshopper sparrows, thus supporting the idea that Henslow's Sparrows are indeed less prevalent than the other two obligate grassland-nesting sparrows. These results were confirmed even after adjusting for differences in detectability or abundance among the three species.

No clear pattern emerged from tests of differences in variation between species at individual spatial resolutions; only at two spatial resolutions were differences significant between species. The area-under-the-curve proved to be more useful, showing that Henslow's Sparrows were more variable overall (highest curve) than both Grasshopper and Savannah sparrows, the latter species having the lowest variation (lowest curve). Henslow's Sparrows thus showed the most variation in year-to-year abundance, and exhibited the lowest prevalence of the three species. Savannah Sparrows, conversely, showed the smallest variation in abundance, and the highest prevalence of occurrence.

Results from this study corroborate patterns of occurrence suspected by previous researchers (Hyde 1939, Wiens 1969, Skipper 1998) and documented in a preliminary manner by Dornak (2010). Not only are Henslow's Sparrows less prevalent and more variable than the other two sparrow species, but they are not predictably present until extents of $120\,000 \text{ km}^2$ are considered; these contrasts among species are not simple consequences of lower abundance or detectability. So then, why is Henslow's Sparrow's prevalence lower than that of Grasshopper and Savannah sparrows across multiple spatial resolutions, when all three species are obligate grassland nesters? These observations might indicate that too much habitat exists for too few individuals to fill (Cody 1985), or some unusual life-history strategy adapted to life in a spatially and temporally dynamic landscape.

Our results support strongly the hypothesis that Henslow's Sparrows exhibit nomadic behavior among breeding seasons across multiple spatial resolutions. Nomadism is a special form of dispersal that is characterized by irregular movements of individuals, groups of individuals, or whole populations to different areas from year to year or within seasons (Sinclair 1984, Dean 1997). Nomadism develops most commonly in species when limiting resources fluctuate spatiotemporally and become patchy and unpredictably available across a region (Sinclair 1984, Dean 1997).

Nomadism has a variety of predictors that appear to be linked to spatial scales. At fine scales, factors such as age, mate loss (Newton and Marquis 1982), unsuccessful breeding attempts in a previous year (Harvey et al. 1979, Greenwood and Harvey 1982, Newton and Marquis 1982), and conspecific attraction (Stamps 1987, 1988, Ahlering et al. 2006) can influence whether individuals or groups of individuals return to previously-used breeding areas. At broader scales, factors such as regional weather patterns (Wiens 1986, Johnson and Grier 1988, Kantrud and Faanes 1979), precipitation in arid landscapes (Davies 1984, Dorfman and Kingsford 2001), and land use (Milton 1994) affect resource distributions and may impact population variation and regional distributions of species. Some factors have cross-scale influences; food resources, for example, can cause fine-scale movements in birds tracking insect emergence (Dean 1997), or broad-scale variability in species following high seed masts (Andersson 1980, Sinclair 1984, Dean 1997) or microtine densities (Martin 1989, Korpimäki and Norrdahl 1991).

We suspect that Henslow's Sparrows may be responding to multiple factors causing nomadic movements across spatial scales (Allen and Saunders 2006). At finer resolutions, patch-to-patch movements may be the result of conspecific attraction and patch-level land uses. Henslow's Sparrows are loosely colonial (Hyde 1939, Wiens 1969) and may require an aggregation of conspecifics to settle an area, or use presence of conspecifics to make decisions about the suitability of a patch (Stamps 1987, 1988, Ahlering et al. 2006). Patch-level disturbance may also result in year-to-year settlement variation: Henslow's Sparrow habitat occurs primarily on managed lands (Herkert et al. 1996) where burning,

grazing, and haying are common disturbances and may alter the suitability between management units. Recently (i.e., around 1 yr) disturbed areas are not optimal for Henslow's Sparrows (Powell 2008), although some males may use such areas (Swengel 1996, Herkert and Glass 1999). As time since disturbance accumulates, plant biomass (standing live, dead, and thatch) increases, and the habitat becomes more attractive. Over succeeding years, more males establish territories, thus increasing abundance on the patch and conspecific attraction. When the habitat is disturbed once again, however, habitat suitability is reduced and the cycle is repeated. Therefore, species that select habitats regulated by short disturbance cycles should be expected to have lower prevalence of occurrence and high variation in abundance across years, particularly when the spatial grain of the disturbance regime is large (Robbins et al. 2002). Henslow's Sparrows are known not to return to previously-used nest areas, although the sites appear unchanged. We propose that conspecific attraction may influence nest area settlement before individuals return sites used the previous year (i.e., opportunistic settling, Johnson and Grier 1988).

At broader spatial scales, weather patterns and regional land use variation may also contribute to the prevalence patterns we identified across spatial resolutions. The interior of the US experiences high year-to-year variation in precipitation and temperature (Bragg 1995). Grasslands respond to extreme or unseasonable weather conditions (e.g., periods of drought or late-onset springs) rather quickly (Wiens 1986), and can influence the distributions of opportunist species across broad areas (Igl and Johnson 1999). Land use change (i.e., conversion of native grasslands to rangeland or hayfields) has altered the structure, species diversity, density, and biomass of these grasslands and created patch-level homogeneity within management units (Fuhlendorf and Engle 2001). The result may be all-or-nothing suitability when extreme weather patterns determine growth and structure of the vegetation, and consequently the region-wide timing of haying or burning of these lands. Although we did not analyze annual weather patterns or the spatiotemporal variability of managed grasslands, we suspect that interactions of these factors contribute to the broad-scale, inter-annual movements of Henslow's Sparrows across their breeding distribution.

Nomadism occurs most commonly in species that specialize on a particular food resource or whose food occurs ephemerally (Andersson 1980, Sinclair 1984, Dean 1997), a frequent occurrence in arid/semi-arid environments (Davies 1984). Northern Harriers (*Circus cyaneus*, Martin 1989), Tengmalm's Owls (*Aegolius funereus*, Korpimäki et al. 1989), and Short-eared Owls (*Asio flammeus*, Korpimäki and Norrdahl 1991) feed on microtines that have cyclic or randomly fluctuating populations; White ibises (*Eudocimus albus*) track emergence of shallow and ephemeral wetlands to forage on invertebrate prey (Frederick and Ogden 1997). We believe that Henslow's Sparrows are unusual in that their nomadic behavior may be associated solely with the spatial and temporal patchiness of suitable breeding area related directly to structural characteristics of the vegetation, and not to distribution of food resources. Grassland sparrows, including the species analyzed here, feed primarily on insects during the breeding season (Wheelwright and Rising 1993, Vickery 1996, Herkert et al. 2002). Because this resource is typically superabundant (Wiens 1974, Rotenberry and Wiens 1979) and shared among the species, it is not likely a cause of nomadism for Henslow's Sparrows. Instead, Henslow's Sparrows appear to be tracking disturbance cycling across the landscape (Dornak 2010), essentially moving among resource 'hot spots' (Cody 1985), characterized by patches that have been idle or only lightly disturbed in 2+ years (Powell 2006). We are unaware of other species known to exhibit nomadism for reasons not related directly or indirectly to food resource distribution and availability.

Why then do Henslow's Sparrows exhibit nomadic behavior, but Grasshopper and Savannah sparrows do not? We attribute this contrast to differences in breadth of preferred habitat among these species. Grasshopper and Savannah sparrows, which do use native prairies, also exploit grazed, cultivated, or hayed fields, even occupying shrubby areas and marshes in portions of their ranges (Graber 1968, Owens and Myers 1973, Vickery 1996, Dale et al. 1997). These species show greater tolerance of divergence from pristine grassland, as well as of different (and particularly earlier) stages of grassland succession, such that they can take advantage of more recently disturbed areas. Nomadism may be energetically expensive and result in delayed nesting, and even nest failure, should individuals not find

suitable sites. For species with broader habitat preferences like those of Grasshopper and Savannah sparrows, philopatry is advantageous, as familiarity with an area increases the probability of finding food, defending a territory from conspecifics, and avoiding predators (Hinde 1956). It should not be surprising then, that these species would have higher prevalences than Henslow's Sparrows.

The support for nomadism in Henslow's Sparrows that has been assembled is strong. We believe it unlikely that the patterns presented here reflect other phenomena, such as population cycling, rather than low permanence and mobile populations. Population cycling is the regular fluctuation of populations on multi-year cycles, best documented in microtine rodents with synchrony that develops in predators that specialize on them (Lack 1954, Ims and Steen 1990). These cycles are regulated by food and nutrient variability (Lack 1954, Batzli and Pitelka 1971) and predator-prey interactions (Lack 1954). Although population cycling could present as low prevalence, it is not an adequate explanation for the patterns we observed. First, as noted above, food resources are not highly variable, but rather are considered superabundant (Wiens 1974, Rotenberry and Wiens 1979). Second, for predation to regulate Henslow's Sparrow populations, (1) we would expect this species to have specialized predators, which it does not and instead is preyed upon by generalist, opportunist species (Wray et al. 1982, Pietz and Granfors 2000); or (2) its populations should reach peak densities (Lack 1954), which they have not in recent times (Sauer et al. 2011). What is more, those predators that do commonly parasitize or depredate grassland ground breeding birds are more common and have a greater impact on species that nest nearer to edges. Henslow's Sparrows select for sites away from edges, and thus are less affected by predation and nest parasitism (Herkert 1994a, Pruitt 1996, Winter et al. 2000). Third, other factors shown to regulate populations in cycling species, such as disease outbreaks or density-dependent crashes, have never been recorded in Henslow's Sparrows. Fourth, if Henslow's Sparrow populations did exhibit any cycling, BBS trend analysis would show both positive and negative trends across years; instead, they report small, declines to somewhat stable populations from year to year of this species (Sauer et al. 2011).

Caveats.—Our results may have been influenced by several factors. First, the broadest resolution (511 360 km²) had a very small sample size ($n = 4$), which likely influenced both determination of true variation in abundance and strength of hypothesis testing at that extent. Moreover, both Grasshopper and Henslow's sparrow variation in abundance peaked at 126 126 km². These values surely contributed to differences found in both between-resolution and scale-independent analyses; it is unknown whether these values are random artifacts of smaller samples sizes or imperfect detection (Royle et al. 2005), or whether they truly represent patterns at these resolutions, since no such spike was found in Savannah Sparrows.

Some biases inherent in the BBS methodology (change of observer, geographic influences, and non-consecutive years) were addressed within the methodology of this study, based on results of previous analyses (Dornak 2010). However, it has been suggested that certain factors can affect population comparisons based on observational data, such as detectability, differences in abundance, and observer ability to sample grassland habitats. Henslow's Sparrows are visually and behaviorally cryptic (Hyde 1939), which may impair detection. When they are not singing, they are difficult or impossible to detect. When they do sing, however, they perch atop vegetation, and their songs—although short and insect-like (Hyde 1939)—carry across the grassland over distances of at least 150 m (pers. observ.); therefore, detections based on song alone may not be a limiting factor in detecting Henslow's Sparrows. Still, Henslow's Sparrows may not be recorded consistently because observation times (3 min) at each BBS stop may not be long enough to assure that males present at a location would indeed sing (Diefenbach et al. 2007). Coupling this factor with possible declines in singing frequency after mate pairing (Leftwich and Ritchison 2000), Henslow's Sparrows may be difficult to detect, especially since BBS routes are surveyed in June, after pair-bonds have formed (Sauer et al. 2011). To assuage concerns of this nature within our study, we rarefied Grasshopper and Savannah sparrow occurrence data sets to mimic abundances and detectability of Henslow's Sparrows, and then used these subsampled datasets to test for biases within our analyses. Differences in abundance and detection are similar population phenomena — even if low detectability implies more individuals present, we see no reason why those individuals would

be detected with a clumped spatial structure. Hence, our rarefaction manipulation mimicked both lower numbers of individuals and lower detectability, and yet differences among species were still apparent. Reducing the data sets did lower the prevalence curves of Grasshopper and Savannah sparrows, but not sufficiently to change the results of the cross-scale analysis. We thus conclude that differences of detectability and abundance between these species did not bias the qualitative results of our analyses.

A final consideration is that all BBS routes are located along roads. Forman et al. (2002) found that grassland birds avoid habitat adjacent to high-traffic roadways. However, these findings were specific to roads with >15 000 vehicles per day. BBS routes, on the other hand, are generally located along rural, low-traffic roads (Sauer et al. 2011), which are less likely to inhibit either the observers' ability to hear singing males or the sparrows' use of habitat near the fence line (pers. observ.). Henslow's Sparrows, however, may avoid roadsides if fence lines are heavy with woody vegetation, since it decreases habitat attractiveness, exacerbating any detection problems (Patten et al. 2006).

Conservation implications.—Henslow's Sparrow populations have declined over much of their distribution (Sauer et al. 2011), apparently in response to habitat loss and fragmentation (Pruitt 1996). Some surveys have shown a recent trend reversal, with stable or increasing populations reported for specific states (e.g., Illinois; Herkert 2007b), in wintering populations (National Audubon Society 2002), and even distribution-wide (T. R. Cooper, pers. comm., Sauer and Link 2011). Although these reports are promising, they do not consider substantial losses in coming years in Conservation Reserve Program (CRP) grasslands that currently function to augment Henslow's Sparrow breeding habitat and that may be responsible for recent population recovery (Cooper 2007, Herkert 2007, Herkert 2007b).

A central goal of Henslow's Sparrow conservation planning for the breeding range is to manage grassland habitat so as to allow for sustained or growing populations (T.R. Cooper, pers. comm.). An assumption underlying this goal, however, is that Henslow's Sparrows exhibit typical breeding behavior: migration to breeding range, territory selection and establishment, pair formation and nesting, and migration to wintering range. If territory selection and establishment cannot be predicted consistently

because of multi-scale nomadism, as in the case of Henslow's Sparrows, however, special efforts must be made to design a configuration of patches of suitable habitat that accounts for this behavior.

At finer scales, techniques such as patch rotation should be encouraged to increase patch-level heterogeneity, which may be more compatible with the species' nomadic movement. Patch rotation on three-year cycles limits cattle stocking to a subset of the pasture, allows for structural development of herbaceous vegetation, and restricts woody growth, all of which promote suitable breeding habitat for Henslow's Sparrows (Wiens 1969, Herkert 1994b, Powell 2006). This management regime considers the spatial and temporal disturbance pattern that creates the shifting mosaic and "out-of-phase" succession across patches, and would support locally nomadic populations of Henslow's Sparrows (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004). Traditionally, core areas (>800 ha) fall under "large-scale" management (Sample et al. 2003); however, we suggest that these areas need to be managed to promote patch-level heterogeneity.

At regional scales in light of the species' nomadism, focus should be on configuration of locally managed areas integrated across broader regions. Ideally, these efforts would create a landscape-level mosaic of moderately-sized and well-dispersed habitat patches, and potentially buffer the effects of extreme weather conditions. This configuration should help to support regionally nomadic populations that do not nest consistently within core breeding areas. What is more, broad-scale management for Henslow's Sparrows that incorporates this shifting-patch mosaic will benefit species that use other phases of grassland succession. Fuhlendorf and Engle (2001) suggested that species that use remarkably different habitat co-occur across the grasslands thanks to the temporal and spatial heterogeneity. We suspect that this management regime would have far-reaching, positive impacts on avian diversity on North American grasslands. For management at this scale to be implemented efficiently and with limited financial costs and wasted effort, detailed and dynamic maps of suitable breeding habitat across Henslow's Sparrow's full distribution will be necessary, which will have to take local landscape dynamics into account directly.

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TABLE 1 Comparisons of Henslow's, Grasshopper, and Savannah sparrows across multiple spatial resolutions (in km²). Breeding Bird Survey data were collected from 2000–2007.

Spatial resolution										
Kruskal-Wallis rank sums tests										
Prevalence		0.5	1.14	3.06	6.26	15.86	32.02	30 780	126 126	511 360
	H	32.97	39.73	87.95	44.50	45.72	53.23	19.76	3.37	-
	df	2	2	2	2	2	2	2	2	-
	P	< 0.001†	< 0.001†	< 0.001†	< 0.001†	< 0.001†	< 0.001†	< 0.001†	0.185	-
Coefficient of variation										
	H	5.37	3.82	2.43	3.99	3.55	6.03	5.31	10.56	5.05
	df	2	2	2	2	2	2	2	2	2
	P	0.068	0.148	0.297	0.136	0.169	0.049†	0.07	0.005†	0.08
Mann-Whitney U-tests										
Prevalence										
<i>Henslow's -</i>	U	783.0	858.5	713.0	762.0	726.0	648.5	220.5	-	
<i>Grasshopper</i>	z	-3.23	-2.71	-3.71	-3.37	-3.63	-4.19	-2.72	-	
	P	0.001*	0.007*	<0.001*	0.001*	<0.001*	<0.001*	0.006*	-	
<i>Henslow's -</i>	U	428.5	328.5	42.0	302.0	286.0	268.0	136.5	-	
<i>Savannah</i>	z	-5.67	-6.37	-8.34	-6.54	-6.71	-7.05	-4.22	-	
	P	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	-	
<i>Savannah -</i>	U	872.5	755.5	222.0	739.0	800.0	771.0	253.0	-	
<i>Grasshopper</i>	z	-2.60	-3.41	-7.09	-3.53	-3.22	-3.68	-2.07	-	
	P	0.009*	0.001*	<0.001*	<0.001*	0.001*	<0.001*	0.039	-	
Coefficient of variation										
<i>Henslow's -</i>	U	-	-	-	-	-	1149.5	-	57.0	-
<i>Grasshopper</i>	z	-	-	-	-	-	-0.70	-	-0.84	-
	P	-	-	-	-	-	0.487	-	0.401	-
<i>Henslow's -</i>	U	-	-	-	-	-	1049.0	-	15.5	-
<i>Savannah</i>	z	-	-	-	-	-	-1.39	-	-3.07	-
	P	-	-	-	-	-	0.165	-	0.002*	-
<i>Savannah -</i>	U	-	-	-	-	-	875.0	-	21.0	-
<i>Grasshopper</i>	Z	-	-	-	-	-	-2.59	-	-2.39	-
	P	-	-	-	-	-	0.01*	-	0.017*	-

† indicates significant differences among species ($P = 0.05$) with Kruskal-Wallis tests.

* indicates significant differences ($P = 0.0167$) with Mann-Whitney U -tests. Note that comparisons are presented only at spatial resolution where tests showed significance in Kruskal-Wallis tests.

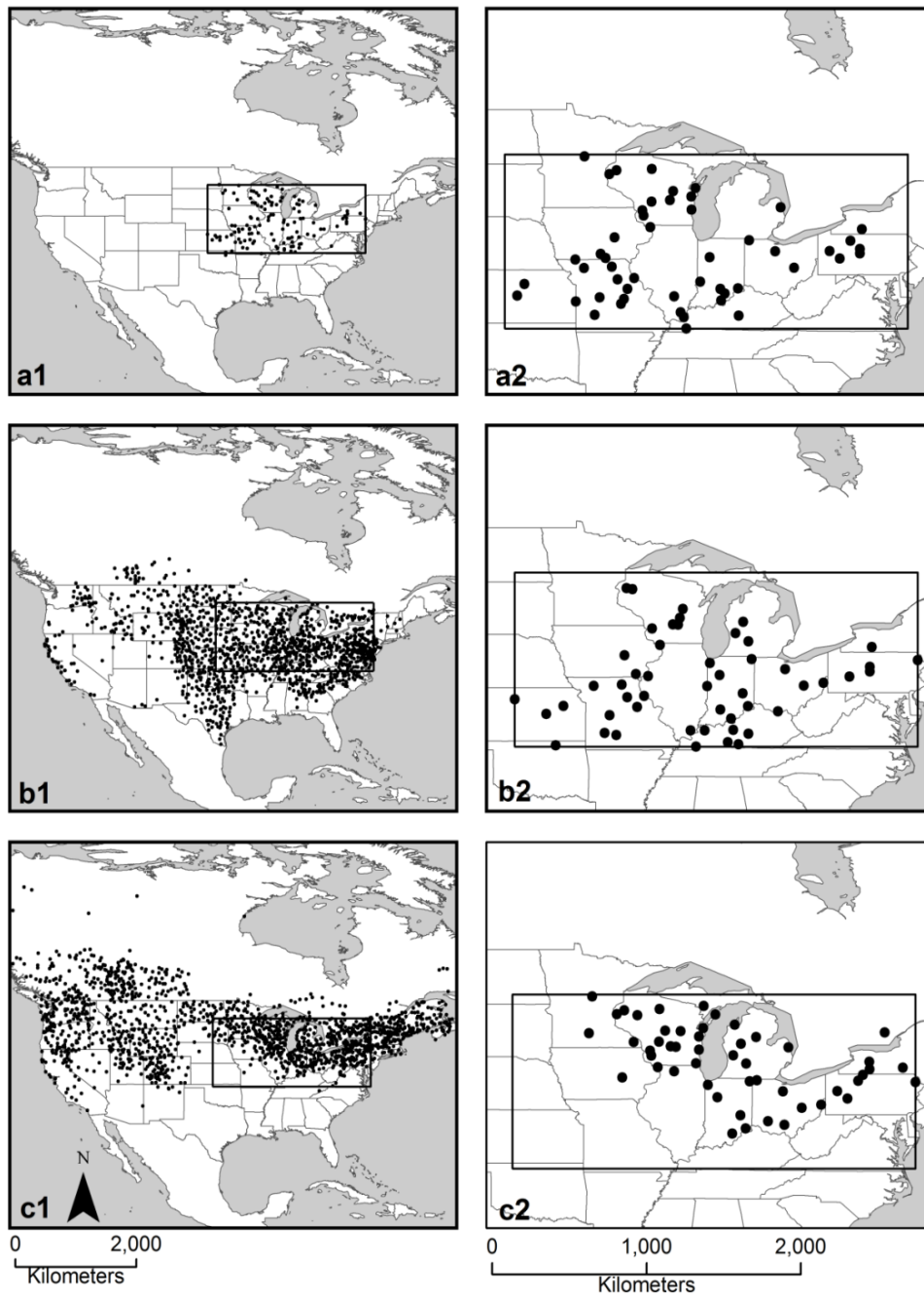


Figure 1. Henslow's (a), Grasshopper (b), and Savannah (c) sparrow breeding distributions (1) and Breeding Bird Survey routes used in our analyses (2) restricted to the Henslow's Sparrow's breeding distribution and single-observer routes.

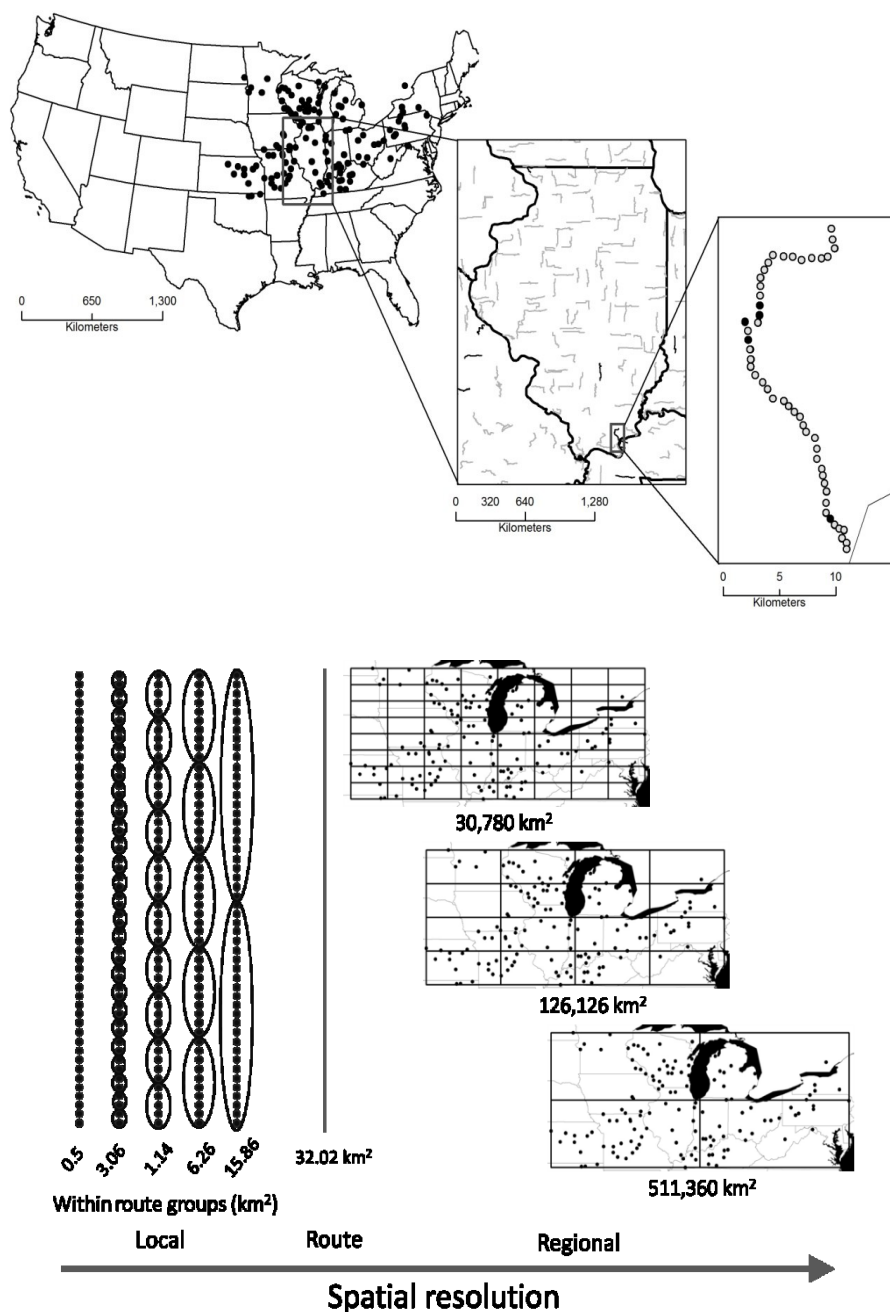


Figure 2. Top: map of U.S. showing North American Breeding Bird Survey (BBS) routes (points) where Henslow's Sparrows were detected during 2000–2007. First inset shows all BBS routes where Henslow's Sparrows were detected (black lines) in Illinois. Second inset shows specific BBS stops where Henslow's Sparrows were recorded on one example route. Bottom: illustration of groups of stops and routes used in comparisons across spatial resolutions.

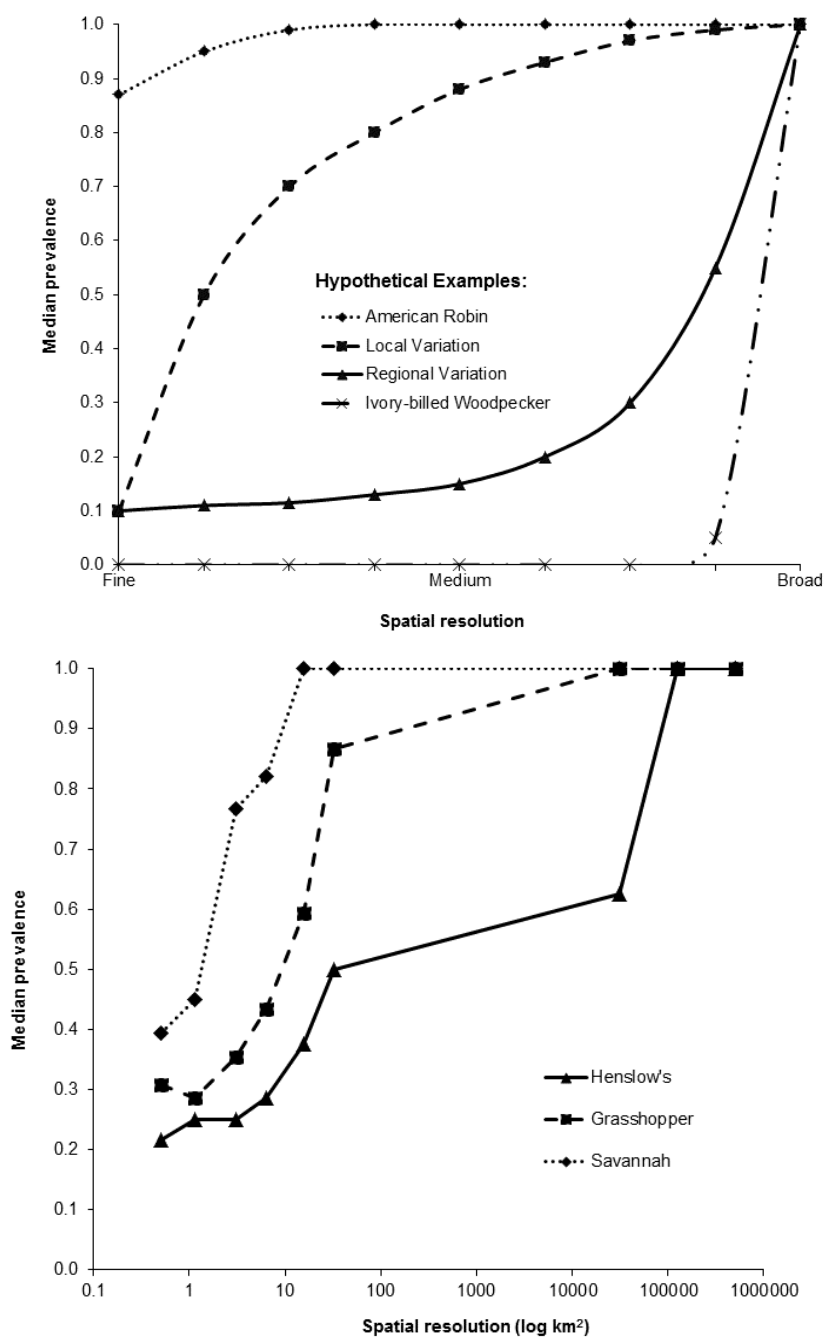


Figure 3. Patterns of prevalence across spatial scales. Top: hypothetical examples, illustrating the range of variation from American Robins (*Turdus migratorius*) (ubiquitous and constantly present at most sites) to the fabled Ivory-billed Woodpecker (*Campephilus principalis*), which never seems to be in any particular place. Bottom: observed patterns in the three species of grassland sparrows.

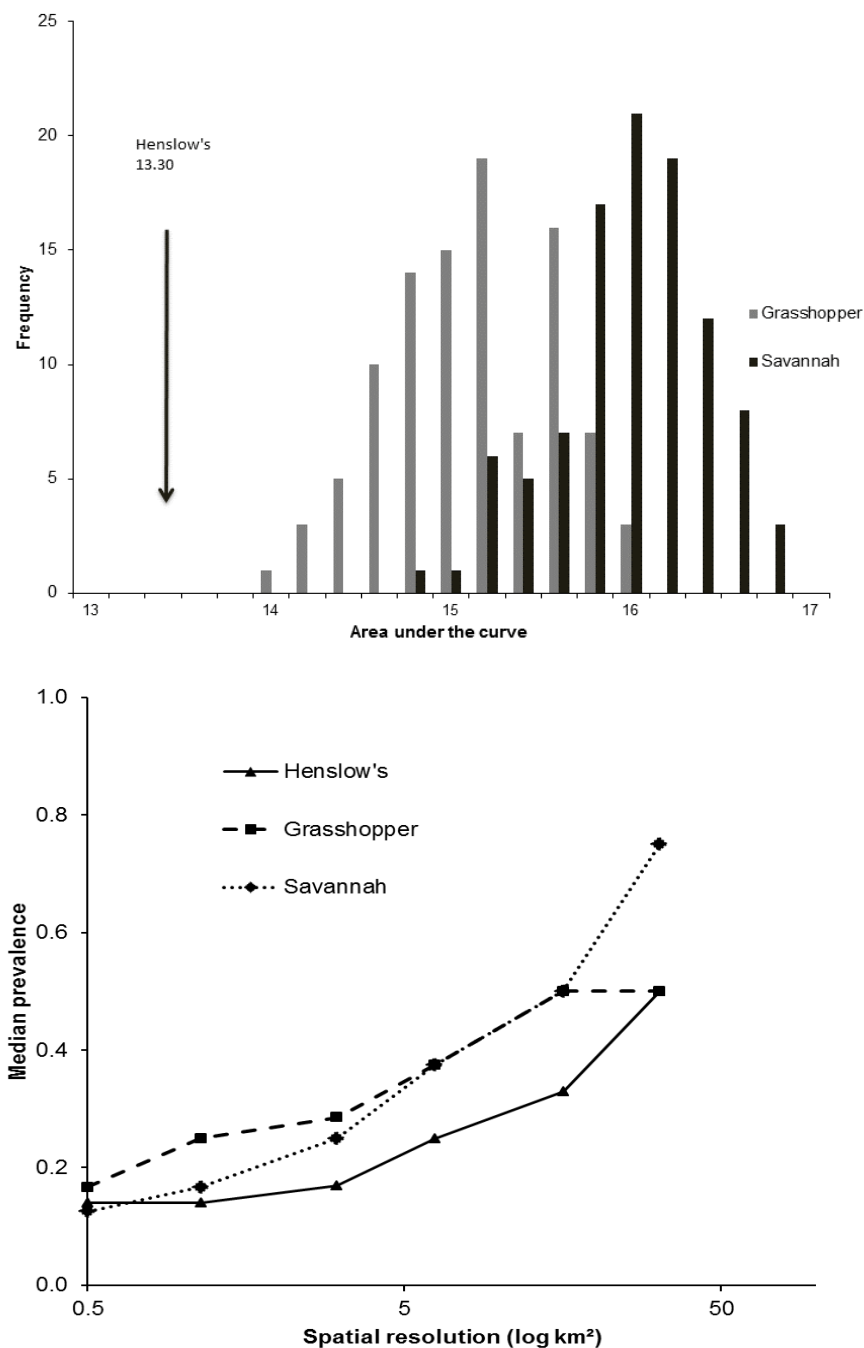


Figure 4. Top: frequency of mean bootstrapped values of area under the prevalence curve across 6 spatial resolutions (0.5 – 32.02 km²) for rarefied population data for Grasshopper and Savannah sparrows, and showing the observed value for Henslow's Sparrow. Bottom: median prevalence by spatial resolution of rarefied abundance data for Grasshopper and Savannah sparrow populations, compared to Henslow's Sparrow.

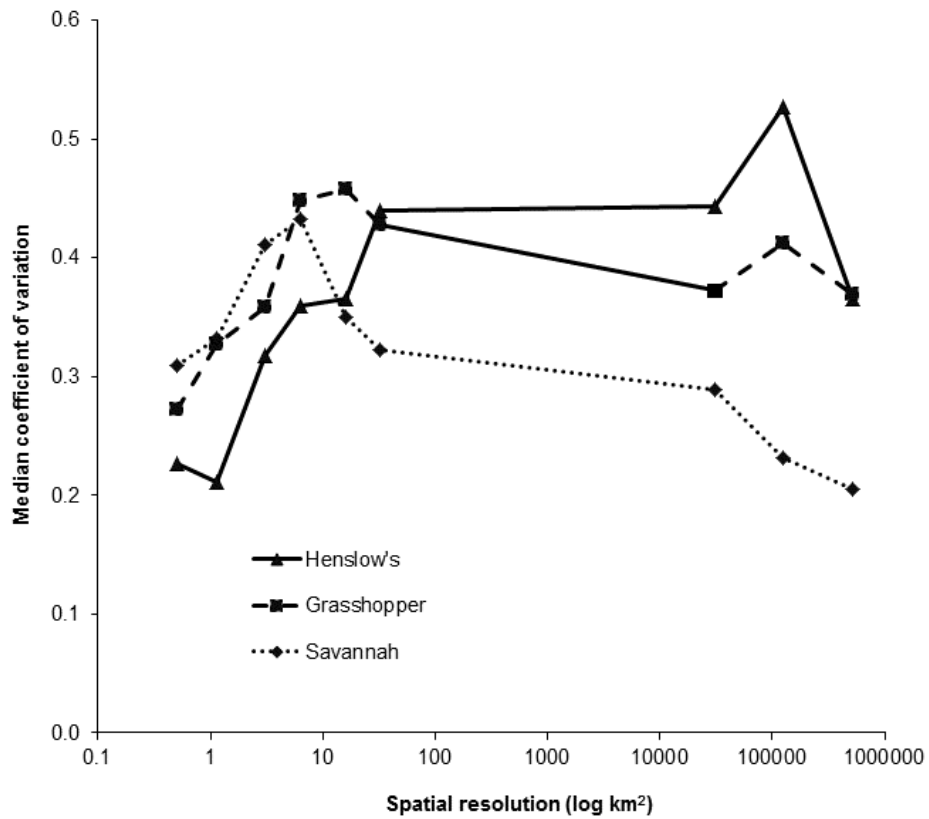


Figure 5. Patterns of coefficient of variation across spatial scales in three grassland sparrow species.

CHAPTER 4

Distribution and spatiotemporal variability of suitable breeding habitat in three grassland sparrows

ABSTRACT.—Henslow's Sparrows (*Ammodramus henslowii*) are a nomadic species that breeds across the tallgrass prairies, selecting for vegetation structure characterized by infrequent disturbances. Much of this native habitat has been converted or fragmented, and is no longer available for breeding birds. Furthermore, what remains may not be stable temporally. Here, we used ecological niche models to identify the extent and distribution of suitable breeding area across three years (2008–2010) for this species and two other grassland sparrows that occur within the Henslow's Sparrow breeding distribution: Grasshopper (*Ammodramus savannarum*) and Savannah (*Passerculus sandwichensis*) sparrows. What is more, we characterized change (or turnover) in suitability between 2 sets of years (2008–2009 and 2009–2010) and relate patterns of this turnover to nomadic behaviors affirmed in recent studies. Using the differences between years, we found that turnover varied across time and species, such that losses and gains fluctuated in dominance within species and between years. Turnover of both gains and losses was similar among species and relatively low in 2008–2009; however, in 2009–2010, Henslow's Sparrows showed much higher losses and lower gains, and more clustering of this turnover across broad regions compared to the other two species. Overall, conversion (i.e., state change) of grasslands was relatively low, accounted for a greater proportion of losses than gains of suitable area for all species, and varied within losses among species. We suggest that in variable years when turnover is high, Henslow's Sparrows may be more nomadic compared to mild years, when turnover and movements are low.

INTRODUCTION

Henslow's Sparrow (*Ammodramus henslowii*) is an obligate grassland-nesting species of the Midwestern and northeastern portions of North America (Pruitt 1996, Vickery et al. 1994, Herkert et al. 2002). They require large (~10–60ha), open grasslands (Hyde 1939, Smith 1968, Thogmartin et al. 2006) with aspects

of vegetation height (Wiens 1969, Herkert 1994b) and density (Wiens 1969, Zimmerman 1988) typical of natural and relatively infrequent fire and grazing disturbances (with no less than two years between disturbances). Changes in frequency or intensity of disturbance easily alter vegetative structure, and can result in avoidance of an area by the species. An increase in disturbance reduces preferred above-ground vegetation, whereas prolonged lack of disturbance encourages woody encroachment (Graber 1968, Bollinger 1995, Cully and Michaels 2000). As regards Henslow's Sparrows, the years immediately following disturbance (fire, grazing, haying) generally present unsuitable habitat for this species, with suitability peaking 2–3 years after disturbance (Powell 2006). Across the landscape, disturbances are thought to be temporally and spatially discontinuous, producing a landscape across which suitable habitat may be patchy and may shift significantly through time.

Henslow's Sparrow populations have been in gradual decline across much of their distribution for decades (Sauer et al. 2011). Reports of these trends are not consistent across states or regarding winter or breeding populations, with some trends even showing local stability or increase (Herkert 2007, National Audubon Society 2002). Declines are attributed broadly to monumental (>99%) loss of native tallgrass prairie, a result of 200 years of agriculture, development, and grazing (Knopf 1988, Knopf 1994). More recently (~ last 30 years), management practices for cattle on the tallgrass prairie that maintain early succession characteristics (e.g., annual spring burns and early cattle stocking) are not suitable for nesting Henslow's Sparrows (Robbins et al. 2002). Broad conversion, or state change, of prairie to large-scale agriculture and heavily-grazed, overstocked pastures has altered natural disturbance regimes region-wide, and has rendered most native habitat unusable by Henslow's Sparrows. Nonetheless, range-wide assessments of the amount and distribution of suitable habitat for this species have yet to be developed.

What is more, changes in disturbance regimes may have influenced the breeding and dispersal behavior of Henslow's Sparrows. The unpredictability of this species in returning to seemingly suitable areas has been noted by many authors (Hyde 1939, Wiens 1969, Skipper 1998, Ingold et al. 2009), and two recent studies have identified nomadic behavior in this species (Dornak 2010, Dornak et al. 2012).

That is, Henslow's Sparrows were not returning to breeding areas from year to year. Dornak et al. (2012) concluded that the nomadic movements may be the result of multi-scale predictors; patch dynamics and conspecific attraction at fine scales, and annual weather patterns and land management regimes at broader scales; however, regardless of scale, the major factor driving these movements is likely turnover of habitat. Turnover can occur when a suitable habitat patch is disturbed such that it is rendered undesirable for breeding birds the next year. If this patch remains undisturbed throughout the following year or two, it may become suitable again once preferred vegetative structures are restored.

This paper has two main goals: (1) to identify the extent, distribution, and between-year dynamics of suitable habitat of Henslow's Sparrows (i.e., to what extent does inter-annual turnover in suitability occur and how is that turnover distributed across the landscape), and (2) to relate patterns of turnover to the nomadic behaviors identified by Dornak (2010) and Dornak et al. (2012). Here, we use ecological niche modeling based on fine-resolution occurrence data related to detailed remote-sensing imagery to define suitable sites for breeding Henslow's Sparrows over three years. Ecological niche models estimate niches by comparing environmental characteristics of known occurrences of the species across a landscape with those of the broader landscape, to define a set of conditions under which the species can ostensibly maintain populations. These conditions can then be mapped in a GIS to outline potential distributional areas (Peterson et al. 2011). In this study, such models are used to estimate where, and to what extent, turnover of suitable Henslow's Sparrow habitat occurs. To understand whether patterns of turnover observed for Henslow's Sparrows are atypical, we compared this species to two other grassland sparrows, Grasshopper (*Ammodramus savannarum*) and Savannah (*Passerculus sandwichensis*) sparrows. We chose these two species because both use grassland in various stages of succession for breeding, their breeding ranges overlap that of Henslow's Sparrow, and both were used previously in prevalence analyses by Dornak et al. (2012).

METHODS

Study region.—Ecological niche models were developed across areas of ~29.5 million km² that bounds the Henslow's Sparrow extent of breeding occurrence in the United States. Although the species' range extends marginally into southern Canada, key data sets used in analyses covered the United States only, so models were restricted to the United States. Models were developed for Grasshopper and Savannah sparrows within the same extent; although their ranges extend beyond the extent covered here, we limit consideration of these species to the geographic and ecological conditions within the breeding distribution of Henslow's Sparrows to limit comparisons to grasslands found only within this range.

Occurrence data.—Occurrence data were drawn from the North American Breeding Bird Survey (BBS; Sauer et al. 2011) and eBird (eBird 2012) data sets. The BBS is a continent-wide survey that uses standardized techniques to monitor long-term trends in North American breeding bird species. Each year in June, the BBS runs ~4100 roadside censuses, each transect 39.5 km long, with 50 observation points (stops) distributed every 0.8 km (Sauer et al. 2008). Although approximate route-start coordinates are easily accessible, stop-level locality data sets have not been digitized completely. Hence, to produce a data set of stop-level coordinates, we used detailed stop descriptions to which BBS staff kindly provided access, in combination with National Agriculture Imagery Program (NAIP) imagery, Google Earth, Google Street View, Cropland Data Layer (CDL) data sets, and ArcGIS base maps, to georeference each point. Points were analyzed for placement; those points with high uncertainty or obvious error were removed (e.g., “roadside” points in the middle of a corn field or open water, etc.).

eBird data were downloaded directly from the Avian Knowledge Network (<http://www.avianknowledge.net/>). eBird is a citizen-science based approach to collecting bird observations (abundance and distribution). Advantages to using eBird are that these data are not restricted to roadside observations (although access is an obvious consideration); data are recorded continuously through the year; and observations are collected globally (eBird 2012). These data should be used with caution, however, since contributor experience ranges from amateur to professional, and eBird offers no

information regarding observer experience. A two-stage verification system does flag automatically possibly erroneous identifications, which are then verified later by local experts (Sullivan et al. 2009). All eBird occurrence data for the three species were downloaded with associated coordinate information. We filtered data to remove duplicate records; records marked “not valid” under the “Record Review Status;” and any record collected before May and after July, since these records may represent migrating individuals. Like BBS occurrence data, eBird points were analyzed for obvious placement error.

Land cover data.—Land cover datasets have proven useful in assessing wildlife habitat (Roseberry and Sudkamp 1998, Thogmartin 1999), and in delineating different land cover types (Hollister et al. 2004). Open cover types, however, like rangeland, wetlands, and barren areas, can show poor classification accuracy (Hollister et al. 2004). Therefore, instead of using these less-than-accurate specific classes, non-grassland classes (e.g., forest, cropland, developed, etc.) were used to eliminate extraneous data from the imagery, effectively masking out irrelevant areas, and increasing model accuracy. This information was not used in model calibration.

Cropland Data Layer (CDL) data were acquired from the National Agriculture Statistics Service (NAAS) CropScape portal (Han et al. 2012; <http://nassgeodata.gmu.edu/CropScape>). CDL is a country-wide, crop-specific land cover data set composed of 133 different crop and land cover categories. It is produced annually, and state by state, which makes it more likely than the National Land Cover Data (NLCD) to record year-to-year land cover changes. The CDL is produced primarily from India’s Advanced Wide Field Sensor (AWiFS), although some states use various ancillary data to augment AWiFS (e.g., NASA’s Landsat 5 TM and 7 ETM+, NLCD). CDL data are available for all states since 2008, at fine spatial resolutions (56 m before 2010, 30 m from 2010 to present) in raster formats.

Because CDL does not include a specific category for native grasslands/prairie, we recoded cover types in ArcMap10 to create a category representing *possible* grasslands, including the union of Pasture/Grass, Fallow/Idle Cropland, Grassland Herbaceous, Pasture/Hay, and Herbaceous Wetlands, versus all remaining categories. We note that CDL grass classification are not without error (see

Discussion); however, after some experimentation, this data set proved the best available for the needs of our analyses.

Henslow's Sparrows are area-sensitive, meaning that they have minimum patch size requirements of 10–55 ha (Sampson 1980, Herkert 1994, Walk and Warner 1999, Winter and Faaborg 1999). To consider this sensitivity, we removed areas too small to function as breeding habitat from the CDL layer before using it as a mask. We chose 10 ha, which represented the smallest identifiable area used by Henslow's Sparrows (Sampson 1980).

Environmental data.—Raster layers were used to link occurrence points with environmental conditions present at the location and time of occurrence. These datasets consisted of multi-temporal series of Enhanced Vegetation Index (EVI) summaries derived from the MODIS sensor (Huete et al. 1999) at a native spatial resolution of 250 m. EVI is developed from differences in spectral reflectance: red, near-infrared, and blue spectral bands are combined with two coefficients, and soil adjustment and gain factors, to characterize the structure and growth of the vegetation. Compared to its predecessor, the Normalized Difference Vegetation Index (NDVI), EVI is more sensitive to higher biomass, and corrects for soil reflection and atmospheric influences (Huete et al. 1999). Like NDVI, EVI is correlated with precipitation (strongly) and temperature (weakly), and therefore was used in place of climate metrics (Nagler et al. 2007) which are not available at such fine spatial resolutions. Reflectance data are collected daily and composited into 16-day summary images. We used data collected between 22 March and 1 November in each year (2007–2010) to characterize “green-up” and “brown-down” cycles while avoiding periods presenting snow cover. Here, green-up refers to the period in Spring beginning when vegetation leafs-out until growth is at its peak. Brown-down refers to the period from peak growth until the vegetation senesces.

In total, we used 8 summaries of variables to characterize environments (mean, maximum, minimum, range, ‘green-up,’ ‘brown-down,’ difference green-up, difference brown-down). The green-up and brown-down layers were produced as follows. A temporal EVI profile was created for each point in

the data set, from which we determined the date of the inflection point, using the average EVI for each date. If the profile was bimodal, the date associated with the highest peak was selected. We then calculated the rise-over-run for each pixel: the difference of the EVI at inflection point and the EVI of the first date in the time series divided by the number of images between the first date and the inflection point minus one. The brown-down layer was calculated as the difference between the inflection point and the EVI of the last image date, divided by the number of images between the inflection point and the last date. Difference rasters were used to characterize inter-annual change in the green-up and senescence layers between two adjacent years (e.g., the green-up raster from 2009 was subtracted from the green-up raster in 2010).

Model calibration.—We used two algorithms to develop occurrence-environment models: the Genetic Algorithm for Rule-set Prediction (GARP; Stockwell and Nobel 1992) and a general-purpose maximum entropy model (Maxent; Phillips et al. 2006). GARP and Maxent use different algorithms to derive models, each with its unique set of advantages and disadvantages (Elith et al. 2006, Peterson et al. 2007). We ran a set of preliminary models using both algorithms to test performance. Although both algorithms produced models with similar significance, GARP had lower proportion of successful test point predictions so we chose Maxent for all final models.

Maxent is a generative machine-learning method that attempts to model the species' environmental distribution by finding the distribution of maximum entropy (i.e., closest to uniform). This technique fits a probability distribution to presence-only input data such that entropy is maximized for that distribution, but subject to constraints imposed by the known occurrences of the species (Phillips et al. 2006). All models were developed using random seed, 10,000 maximum iterations, 10 replicates via bootstrapping, and extrapolation and clamping deselected to avoid unrealistic model projections. All other parameters were left on default settings.

Model evaluation.—Numbers of occurrence records were limited, so traditional methods of model evaluation (e.g., data splitting) were not practical. Instead, we took advantage of our multi-year

occurrence data and the nomadic nature of the species to test whether a model based on occurrences and environments in one year can anticipate distributional patterns in another year. We used independent occurrence data sets for model calibration (BBS data) and evaluation (eBird data). To this end, we first defined the critical threshold for each model, converting the continuous Maxent output to a binary result that represented suitable or unsuitable areas and to remove the lowest 5% of model predicted values such that noise and errors in the occurrence data were accounted for (Peterson et al. 2008). Then, we used cumulative binomial probability calculations to determine whether model predictions were better than random expectations (Peterson et al. 2011). We calculated $[P = 1 - \binom{n}{k} p^k (1 - p)^{n-k}]$, the probability of getting at least k successful eBird predictions out of n eBird points used for testing with p as an underlying probability of success, calculated as the proportion of area predicted suitable.

Special considerations.—It is important to consider the accessible area for a species prior to model development; this area, symbolized as **M**, is the set of sites that has been sampled by a species over relevant time periods. Defining this area incorrectly can have undesirable effects on model results (Barve et al. 2011) such as over-estimation of suitable area (Phillips et al. 2006, Phillips and Dudík 2008) and false significance in model evaluation (Barve et al. 2011, Lobo et al. 2008). However, defining **M** is not simple, nor is a “correct” method available yet (Barve et al. 2011). Effectively, we forced models to distinguish between suitable and unsuitable grasslands, rather than between grassland and non-grasslands (forest, agriculture, urban, etc.). We took two measures to restrict areas corresponding to a hypothesis of **M** for breeding Henslow’s Sparrows. First, we buffered each Henslow’s Sparrow BBS observation during 2000–2010 by 300 km, and clipped the environmental layers to this extent. Second, to reduce this extent still further, we masked out all areas within this extent not identified by the CDL as possible grassland (see above), as other cover types are not suitable for this species. We restricted Grasshopper and Savannah sparrow models to the same area to make models for these species that were comparable to those for Henslow’s Sparrows (Wheelwright and Rising 1993, Vickery 1996); however, for processing after model development, we restricted Savannah Sparrow models still further, as the species does not

breed in the southern portion of this area. Therefore, we restricted all subsequent analyses of Savannah Sparrows between -101.0° and -71.7° longitude and 49.4° and 40.0° latitude (Fig. 1; Sauer et al. 2011).

Because of small sample sizes, accounting for spatial autocorrelation in the traditional sense was not feasible, as sample sizes would have been reduced to impractical levels. However, we assessed each point visually, making certain that no single pixel included multiple points, and that nearby points fell in visually distinct management units.

Turnover of suitability.—Here, we define turnover as change (loss or gain) between years. We made comparisons for each species, assessing losses and gains separately, for two years (2008–2009 and 2009–2010). We calculated proportional losses and gains relative to the total area predicted as suitable, total area of CDL grass cover, and total study area; however, the results across these areas were similar; therefore, we present only results that relate to total area predicted suitable area for species area turnover, and total area of CDL grass cover for CDL change.

To understand factors contributing to loss or gain of suitability, we identified the proportion of gains and losses where change occurred but that was not the result of land cover conversion (i.e., state change from grassland to other cover types). For areas where turnover was the product of conversion, we identified land cover types responsible for that change.

We analyzed the distribution of turnover across the study area to identify the degree to which changes were clustered (i.e., spatially autocorrelated) across multiple resolutions (0.083° – 4°). Dispersion analyses are typically done using points rather than raster grids, with either quadrat- or distance-based methods. Our data sets, however, are not typical, owing to their type (raster grids) and size (~250,000 points after raster-to-point conversion), so applications of these methods required adaptation of data and methods. After considerable experimentation, a quadrat-based method that calculated a variance-to-mean ratio appeared to be the most appropriate method by which to estimate turnover dispersion with regard to a Poisson distribution. Although distance-based methods such as Ripley's K would be ideal, computer processing power available was insufficient.

To apply a point pattern analysis, we first converted raster grids to point shape files and associated each point with x-y coordinates, such that tables of point localities could be imported into the ‘quadratcount’ function of the ‘spatstat’ package (Baddeley and Turner 2005) within R (R Development Core Team 2011). Then, to circumvent the data set size problems, we used a tiling method to divide points into subsets appropriate to each resolution. To ensure that our results were not influenced by edge effects, we selected only tiles that were within the boundaries of the point distribution completely. To reduce processing time at finer resolutions, we sampled a proportion of the tiles (e.g., 1% of the 34,658 0.083°-resolution tiles), whereas at broader resolutions, we used all tiles available. A consequence of analyzing Savannah Sparrows within a smaller study area was that analysis at the coarsest resolution (4°) was not possible, so all analyses for this species were restricted to 2°.

The ‘quadratcount’ function split each tile into a predefined set of square grids (e.g., 2x2, 3x3, etc.), within which points were counted. These grids were sized such that the area of each grid was proportional across resolutions (e.g., 2x2 grid at 1/12°, 3x3 grid at 1/18°, 12x12 grid at 1/2°, etc.; Fig. 1). From these grid counts, we derived the variance-to-mean ratio by tile. Variances exceeding means indicate clumping of points, whereas tiles with variances less than means are closer to uniform or over-dispersed in pattern.

We are careful to state explicitly that our turnover characterization was not tested for statistical significance, for two reasons. First, we chose a best, single ecological niche model for each species from which to estimate change, such that no variation was available on which to base testing. Second, turnover analysis was highly intensive computationally—multiple model runs would have been impractical and would have lengthened processing time considerably. Consequently, we present descriptions of patterns, which we assess qualitatively for correspondence to our expectations.

RESULTS

General descriptions.—We modeled niches and distributions across three years for three grassland bird species. All between-year predictions (2008 model projected to 2009 conditions, 2009 model projected to

2010 conditions, etc.) performed significantly better than random expectations ($P \leq 0.002$). Although the study area for all species was between 31.9° and 49.3° latitude and -102.2° and -69.6° longitude, most of the area identified as suitable for each species was concentrated between 33.7° and 49.3° latitude and -101.1° and -91.0° longitude, the approximate extent of the tallgrass prairie ecosystem.

Modeled suitable area for Henslow's Sparrow in 2008 was concentrated in eastern Kansas, northeastern Oklahoma, western Missouri, and southern Iowa, with local suitable areas in Minnesota, Wisconsin, Kentucky, and Ohio. Some additional areas at the margins of the calibration area were predicted suitable (e.g., North Dakota and South Dakota, central Nebraska, northern Texas); however, these areas may be overly peripheral to make much contribution to the species' breeding distribution. Suitable area in 2009 was similar to that in 2008, albeit with less predicted area in the northern regions: North Dakota and Michigan. Predictions for 2010 were consistently more restricted compared to 2008 and 2009, concentrated in northeastern Oklahoma, southeastern Kansas, Missouri, and southern Iowa. Total suitable area was considerably smaller in 2010 (7.3 million km²) compared to 2009 (17.2 million km²; Fig. 2).

Suitable areas for Grasshopper Sparrows in 2008 and 2009 were similar, and concentrated in eastern Kansas, northern Arkansas, eastern Oklahoma, and northern Texas; isolated suitable areas were in Ohio, Wisconsin, Minnesota, Kentucky, South Dakota, Nebraska, and Alabama. Predicted areas in 2008 extended further west than in 2009, to include Nebraska, North Dakota, and South Dakota. Unlike Henslow's Sparrow models, predicted areas along the margins of the study area are well within the documented range of the species' breeding extent, and therefore should be considered functional breeding areas. In 2010, the distribution of suitable area is similar to that in 2008, except that more suitable area becomes available in North Dakota, South Dakota, and western Minnesota (Fig. 3).

In 2008, within the more-restricted study area for Savannah Sparrows, suitable areas were concentrated in the western part of the region, mostly in South Dakota, Minnesota, southern Iowa, Missouri, and southern Wisconsin. Local suitable areas were in northern Kentucky and eastern Ohio.

Predicted areas for 2009 and 2010 matched those areas in 2008, but extended more broadly throughout North Dakota. As with Henslow's Sparrows, we question whether the southwestern portion (i.e., northern Missouri) of the predicted (Fig.4) is relevant to this species.

General description of turnover.—We describe turnover as the change between suitable and unsuitable conditions between years; with regard to CDL, it is the change between grass and non-grass land cover categories. All estimates of turnover excluded changes resulting from gain or loss of urban or forest land cover, for reasons described in the Methods. For Henslow's Sparrows between 2008 and 2009, stable area was notable across the region, and losses of suitable habitat were dispersed with stable areas relatively evenly across the western portion of the distribution. Gains in suitability were restricted primarily to central South Dakota, central Minnesota, eastern Kansas, central Oklahoma, and northern Texas. Stable areas were intermixed with losses and gains across much of the study area. Losses in 2009–2010 occurred across a broader region and in greater amounts compared to 2008–2009, including extensive areas in eastern Kansas and western Missouri, and in disjunct areas in central Nebraska, central South Dakota, and northern Kentucky. Gains were minimal across the region, and were notable only in northeastern Oklahoma. Much less stable area was visible in 2010, although isolated areas occurred in northeastern Oklahoma, southwestern Missouri, and along the Iowa-Missouri border (Fig. 2).

Turnover of suitable area as well as stable areas in 2008–2009 for Grasshopper Sparrows was similar to that observed for Henslow's Sparrows, with losses occurring between Oklahoma and North Dakota, extending east into Missouri and southern Iowa. Gains were more local, concentrated between eastern Kansas and north-central Texas. Losses in 2009–2010 were again similar to patterns in Henslow's Sparrows, but were more sparse. Gains were prominent in North Dakota and South Dakota, and moderate across eastern Kansas; stability was notable across northern Texas, eastern Oklahoma, eastern Kansas, much of Missouri, and southern Iowa (Fig. 3).

Loss of suitable areas for Savannah Sparrows in 2008–2009 was light and scattered across South Dakota and Wisconsin, and between Minnesota and Missouri. Gains of area were restricted primarily to

North Dakota and South Dakota. Stable areas occurred across much of the distribution, although notably absent for North Dakota. In 2009–2010, losses were minor, but were scattered across the same areas identified in 2009. Gains of suitable area were notably greater and more extensive compared to 2008–2009, showing increases across North Dakota, South Dakota, Minnesota, Iowa, and Missouri, and in a small cluster in northern Kentucky. Stable areas were less common and concentrated along the Iowa-Missouri border (Fig. 4).

Turnover of CDL (i.e., change between grass and non-grass cover) was sparse across much of the region; however, broad areas of losses and gains occurred along the western border of the study area in both 2008–2009 and 2009–2010. Losses were visible on the regional scale in North Dakota, South Dakota, northern Missouri, southern Iowa, and southern Wisconsin. Gains were predominant in eastern Kansas and in an isolated area along the North Dakota-South Dakota border. Gains and losses were intermixed and substantial in central Kansas and the Texas Panhandle. In 2009–2010, losses were apparent in Minnesota and Wisconsin, but were comingled with gains throughout the region, particularly in South Dakota, central Kentucky, northern Texas, and central Kansas, where turnover was extensive. Gain of CDL grass occurred primarily across the eastern half of the Dakotas (Fig. 5).

Percent turnover.—In comparisons of the species in 2008–2009, stable area was roughly equal to areas of turnover for all species. Within turnover area, we noted little difference between proportional loss and gain of suitable habitat in any species. The largest disparity between loss (31%) and gain (16%) was in Grasshopper Sparrows. The three species showed losses and gains of similar magnitude in this first temporal transition. In 2009–2010, however, differences were more pronounced. The proportion of stable area was lowest for Savannah Sparrows (27%), followed by Henslow's (36%), and Grasshopper (50%) sparrows. Percent loss (51%) was greater than percent gain (14%) in Henslow's Sparrows, whereas in Grasshopper and Savannah sparrows, gain (32% and 60%, respectively) was greater than loss (18% and 13%, respectively). Differences between percent gain (11% in 2009 and 10% in 2010) and loss (13% in 2009 and 2010) of CDL grass in proportion to total CDL appeared negligible (Table 1).

Henslow's Sparrows had greater losses and fewer gains in 2009–2010 compared to 2008–2009. The opposite was true for Grasshopper and Savannah sparrows, which showed fewer losses and greater gains between 2008–2009 and 2009–2010. Losses and gains of CDL grass were similar over time (Table 1).

Turnover within grasslands.—Proportion of turnover occurring within grass-dominated areas varied among species and between years. Overall, turnover from conversion was low (<15% of total area) for all species. Both loss (2009–2010 only) and gain of suitable area for Henslow's Sparrows and gain of area for Grasshopper and Savannah Sparrows, occurred primarily in grass-dominated (>70%) pixels in both sets of years. Conversion accounted for almost half of losses for Henslow's Sparrows (2008–2009 only), and the majority of losses for Grasshopper, and Savannah sparrows. Loss of suitable area from conversion was higher than gain from conversion for all species and in both sets of years. Considering conversion by CDL category, in pixels that showed turnover from conversion (i.e., when the proportion of grass fell below 70%), CDL grass cover still composed the majority of this area; hence, turnover as a result of conversion from grass to non-grass categories was minuscule ($\leq 6\%$). Within these categories, corn, soybeans, and other hay were the dominant crops that replaced grassland, except in 2008–2009 losses for Henslow's Sparrows, where woody wetland and shrubland were primary (Table 1).

Index of dispersion of turnover.—In 2008–2009, we observed almost no variation among species or CDL in losses or gains, although we noted stronger clustering at coarsest resolutions in all species for areas where loss of suitable habitat or CDL grass occurred. Patterns for 2009–2010 showed greater differentiation among species and CDL, particularly in areas of loss. Turnover was more clustered spatially in Henslow's Sparrows than in any other species. Index values for Henslow's Sparrows in 2009–2010 was 1.5–2 times greater than those from 2008–2009 across the coarse spatial resolutions (1–4°; Fig. 6).

DISCUSSION

This study presents a broad view of turnover of suitable breeding habitat for three grassland sparrows. We characterized turnover using estimates of percent gain and loss, identification of approximate causes, and analyses of spatial dispersion across multiple resolutions in three years for each species. The general result supports the idea that grasslands are not static; rather, they vary greatly between years and across broad areas as regards suitability for nesting birds. Although this concept is not new (Igl and Johnson 1999, Ahlering 2005, Winter et al. 2005), the implications of these dynamics and their effects on different species have yet to be considered in detail across species' ranges.

We have identified broad, stable areas within the breeding distributions of each species from year to year; however, we also noted large areas where gains and losses are prominent. For example for Henslow's Sparrows in 2010, stable areas extended from northeastern Oklahoma into southeastern Kansas and across much of Missouri, yet areas of transient suitability covered large areas of eastern Kansas and northern Missouri. What is more, we found inconsistencies in the degree and direction of turnover, such that losses and gains fluctuated in dominance within species, among species, and through time. The clearest result was that Henslow's Sparrow's suitable habitat losses exceeded gains in both years; through time, Henslow's and Savannah sparrow habitat was less stable and showed more regional turnover in 2009–2010 compared to 2008–2009.

Turnover within grasslands.—Overall, proportions of turnover resulting from conversion were relatively low, suggesting that, when loss or gain of suitable area occurred, it was more likely the result of structural change within grasslands and not from conversion of grass to non-grass land cover types. Conversion accounted for a larger proportion of loss than gain of suitable area, likely because it is uncommon for cropland to be converted back to grassland. What is more, in 2008–2009, when losses were low for all species, conversion accounted for more equal proportions of that change; however, in 2009–2010, when losses were high for Henslow's Sparrow and low for Savannah Sparrows, these species had disparate proportions of turnover: Henslow's Sparrows losses were confined within grasslands, but

Savannah Sparrow losses were attributed predominately to land cover conversion. Conversion, as calculated herein, does not imply fully that all grassland within a loss or gain pixel was converted, only that grassland no longer represents 70% grass coverage, and as such grass area may still make up the land cover majority in pixels classified as ‘converted;’ therefore, estimates of suitable area turnover regarding conversion are probably much lower.

Turnover and prevalence.—In addition to estimating percent change and grass-to-crop conversion, we also characterized the spatial dispersion of turnover (i.e., degree of clustering) for each species across nine spatial resolutions. We found few differences among species in 2008–2009 in either losses or gains, although clustering of losses for all species appeared to exceed clustering of gains. In 2009–2010, however, Henslow’s Sparrows had greater clustering of loss areas compared to the other species; this effect was clearest at broadest resolutions.

A major motive for this study was to explore the possibility that turnover patterns explain the nomadic movements described by Dornak (2010) and Dornak et al. (2012). In those analyses, prevalence patterns of Henslow’s, Grasshopper, and Savannah sparrows were compared across multiple spatial resolutions; Henslow’s Sparrows showed markedly lower prevalence compared to other species at most spatial resolutions, from which we concluded that Henslow’s Sparrow populations may be moving nomadically across their breeding distribution from year to year in response to suitable breeding habitat availability.

For turnover to explain nomadism at broad scales, we would expect that substantial portions of Henslow’s Sparrow’s habitat would be unstable at any point in time, such that broad areas of turnover (particularly losses) would be clustered and itinerant from year to year. These patterns should differ markedly from patterns identified in Grasshopper and Savannah sparrows, which should show greater stability and less clustering of turnover. Because we were limited to three years of environmental data, and because methods used in Dornak et al. (2012) do not specify in which years movement occurred, we do not have direct evidence that turnover drives nomadic behavior in Henslow’s Sparrows. However, in

2009–2010, Henslow’s Sparrow habitat losses were greater overall and more clustered than for Grasshopper and Savannah sparrows. These differences were not discernible in 2008–2009, such that we do not know whether one of these years was anomalous, or whether regionally-moderated turnover (as in 2009–2010) occurs cyclically or sporadically. We suggest that in mild years (e.g., 2008–2009) where turnover is low, Henslow’s Sparrows may be less likely to exhibit nomadic behavior; however, for more dramatic turnover years, we expect to see lower return rates of breeding Henslow’s Sparrows to areas used in the previous year. To understand this relationship more thoroughly, we need a longer temporal span of analyses, from which we can identify turnover patterns across this landscape more clearly, and relate year-to-year patterns to independent data on sparrow population stability or turnover.

Caveats.—The data used to generate our models are not without bias. For example, BBS and eBird data sets used to train and test our models, respectively, may contain identification and georeferencing errors. The potential for identification error is most relevant to Henslow’s Sparrows, which are cryptic visually, and sing short, insect-like songs, making them difficult to detect when present (Hyde 1939), or easily confused with Grasshopper Sparrows when environmental conditions impair vocal identification. However, we consider our methods, as well as protocols within the BBS and eBird projects, sufficient to reduce erroneous identifications and provide adequate signal-to-noise ratios.

Some error may have originated from BBS and eBird data point georeferencing. BBS occurrence points were taken either directly from coordinate information provided within BBS route maps (~10%), or were georeferenced manually from stop descriptions or points on topographical maps. Descriptions were often hand-written and occasionally (~30%) not thorough enough to assign coordinates to points with confidence. All eBird points were downloaded with coordinate data; however, upon close inspection, some of these points included obvious errors (e.g., over open water). Therefore, to limit introduced error, we excluded any points (and in some cases, entire BBS routes) with high uncertainty (e.g., points that had illegible, incomplete, or missing descriptions or descriptions that included landmarks not identifiable from areal imagery). On occasion (~20%), points were repositioned within adjacent MODIS pixel

footprints that represented the observation point best, in view of additional data provided with the record. We are confident that our quality-control methods were appropriate to reduce overall error considerably and not introduce new error into the data sets.

In processing the environmental data for the turnover analysis, we found previously unappreciated problems within the CDL dataset. As described in our methods, we focused our analyses on pixels where $\geq 70\%$ of the pixel was classified as CDL grass, hence removing pixels influenced strongly by roads, urban areas, forest, etc. This method worked well for removing non-grass areas for model development; however, when models were combined to detect habitat change, we saw large areas that appeared to change between grass and urban (or forest). When turnover was to urban, we identified three possible sources of error that caused false gains and losses: (1) shifts in road networks, (2) change in spatial resolution, and (3) classification differences between years. Forest conversion rates in the US are relatively low ($\sim 1\%$; Masek et al. 2011), particularly on the scale that occurred in our data, and grass-to-forest conversion is neither likely nor quick. Therefore, we attributed these errors almost entirely to classification error and spatial resolution changes. To correct for both problems, we removed any change pixel that intersected road networks or where forest class accounted for $>30\%$ of the area before turnover was analyzed.

Conversion of grass to non-grass land cover was low ($<15\%$ across all species); within this conversion, CDL grass categories composed the majority of this area, even though these areas are noted as losses or gains that resulted from conversion. We note two factors that may have influenced these estimates. First, we used zonal majority procedures in ArcMap10 to identify the land cover class assigned to each loss pixel. This function would not have accounted for other land cover classes present within the pixel that were not the majority, which tends to eliminate minority classes and overemphasize variation. As a consequence, in some sense, some information was not recorded. Second, misclassification of land cover classes within the CDL data set could have resulted in misidentification of grass cover types. Overall, classification accuracy of CDL data was good ($\sim 72\text{--}95\%$ for the Great Plains region in 2009);

however for the idle/fallow class, accuracy was much more variable (user accuracy 22–100%, mean 69%; USDA 2011). Accuracy assessments for other grass classes were not available for CDL data, but we expect similar rates. For all non-agricultural land cover, CDL metadata refer users to consider the NLCD data assessments; overall NLCD accuracy (Level II 68–82%) and grass type class accuracies (Level II user accuracy 47–84%, mean 66%) are comparable to CDL (Wickham et al. 2010). It is possible that the small proportions of gains that resulted from conversion in our analyses may reflect this classification error.

Management considerations.—Native grasslands in North America have experienced massive conversion and fragmentation; indeed, only ~4% of prairies remain since European settlement. Tallgrass prairies have been most impacted, with >99% of the original extent now lost (Samson and Knopf 1994). Such losses have affected obligate grassland birds to a degree that species without the ability to adapt to anthropogenic changes have suffered marked population declines (Robbins et al. 2002, Sauer and Link 2011). Over the last 100 years, Henslow's Sparrow's breeding range has expanded and retracted in response to fluctuating extents of North American grasslands (Hyde 1939). Recent population estimates show declines (Sauer and Link 2011), implying range retractions. Although other factors have certainly contributed to these declines (e.g., wetland drainage and woody plant succession; Knopf 1994), recent changes are most likely the result of the industrialization of American agriculture (Fuhlendorf and Engle 2001) and cattle production (Smith and Owensby 1978, Zimmerman 1997, Robbins et al. 2002)

In the last 50 years, mechanization (e.g., combine harvesters), fire frequency, and grazing regimes revolutionized American agriculture and increased crop and cattle yields substantially (Robinson and Sutherland 2002); however, it also resulted in monumental loss of temporal and spatial landscape diversity. Industrialized equipment for haying requires large, rectilinear fields, which necessitates alteration of field margins to accommodate machinery navigation, and ultimately results in loss of small, native habitat patches (Hart 1968, Corry and Nassauer 2002). Prescribed burns are used to encourage growth and increase nutrition and palatability of grasses, prevent woody encroachment, and discourage

unwanted forbs (McClain 1983, Rohrbaugh et al. 1999). Standard practice is to burn annually or biennially in early spring (e.g., March or April), then follow with ‘intensive early stocking’ of cattle (May-July; Smith and Owensby 1978, Robbins et al. 2002). The result is faster weight gain of cattle over shorter time periods, but also heavy grazing that produces structurally homogenous pastures (Smith and Owensby 1978). This spatial homogeneity is good for cattle production, but creates areas that are worthless for species that do not tolerate frequent disturbances that reduce or eliminate accumulation of standing vegetation, structural heterogeneity, and species diversity (e.g., Henslow’s Sparrows). Alternative management regimes use prescribed burns in late summer and less frequently, and stock cattle at lower densities for longer periods (“season-long stocking”). Season-long stocking creates uneven grazing patterns that leave non-uniform fuel loads, and thus irregular burn patterns and more historic patch-level heterogeneity (Smith and Owensby 1978).

Here, we have developed one example in which spatial homogeneity may influence regional patterns of turnover. The objectives of this paper were to characterize patterns of turnover and relate them to nomadic behavior described recently for Henslow’s Sparrows (Dornak et al. 2012), such that any commentary beyond that scope is *post hoc* and can serve only to erect hypotheses for future research. In this example, we show how the current, broad-scale land management regimes, coupled with fluctuating environmental conditions, may account for regional turnover.

Most of the breeding habitat available for grassland species, and particularly for Henslow’s Sparrows, is on lands managed for purposes other than conservation of grassland birds (e.g., hay fields, grazed pastures, switchgrass, etc.; Herkert et al. 1996). Each species in this study has different vegetative structural requirements, including plant diversity, height, and density, but all are affected by the current land management paradigm that promotes homogeneity across landscapes. In this example, pastures and hay fields are roughly homogeneous with regard to vegetation structure, composition, density, and biomass (Fuhlendorf and Engle 2001), each managed specifically for livestock or hay production. Most of the area in the states in this study is under private ownership (USGSA 1998), and many land owners

adhere to farming practices that value production over species diversity (e.g., annual spring burns, early intensity stocking; Smith and Owensby 1978, Rohrbaugh et al. 1999). Although each land unit is managed independently, all units are influenced regionally by environmental conditions that regulate burning, grazing, or haying treatments to some degree. The result is broad-scale annual homogeneity in land use classes; by this rationale, broad-scale turnover patterns would emerge, particularly where land classes are clustered.

In the broadest sense, spatial heterogeneity buffers variation in temporal habitat suitability (Benton et al. 2003), resulting in more stable habitat at multiple spatial resolutions. Valuing plant species diversity, structural diversity, and landscape heterogeneity over broad-scale uniformity will necessitate rotational patch management, such that disturbance patterns mimic those of pre-settlement patterns to promote a mosaic of dispersed patches in asynchronous succession across the landscape, and create fine-scale patch nonconformity that would transfer to broader-scale heterogeneity (Fuhlendorf and Engle 2001). Heterogeneity within management units, produced by burning, haying, or grazing of patches within fields creates multi-successional habitat that fosters species diversity. For example, recently disturbed patches would be desirable to Grasshopper Sparrows (Wiens 1969, Herkert 1994), Bobolinks (*Dolichonyx oryzivorus*; Skinner 1975), and Upland Sandpipers (*Bartramia longicauda*; Powell 2006), whereas undisturbed areas would attract Sedge Wrens (*Cistothorus platensis*; Skinner 1975), Bell's Vireo (*Vireo bellii*; Powell 2006), and Henslow's Sparrows (Wiens 1969, Herkert 1994, Powell 2006). At regional or landscape scales, heterogeneity would promote stability in suitable breeding habitat for all species, and potentially brake population declines.

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Table 1. Proportion of turnover for Henslow's, Grasshopper, and Savannah sparrows for two pairs of years (2008–2009 and 2009–2010) by gains and losses. Turnover is categorized to show proportions that occurred within grassland owing to structural changes in these areas ('within grassland') and proportion resulting from grassland conversion ('conversion'). This 'conversion' category was subdivided further to show Cropland Data Layer (CDL) categories that contributed to this conversion.

	Henslow's		Grasshopper		Savannah	
	Loss	Gain	Loss	Gain	Loss	Gain
2008–2009						
Total turnover	26.89	19.11	31.09	15.51	23.39	30.29
Within grassland	14.99	15.94	19.69	13.13	8.84	25.25
From conversion	11.90	3.17	11.39	2.38	14.55	4.73
Conversion by CDL category						
Possible grass*	5.80	2.67	5.81	2.02	5.36	1.74
Corn	1.48	0.09	1.10	0.03	1.71	0.07
Soybeans	1.30	0.08	1.12	0.03	1.35	0.06
Wheat	0.45	0.04	0.44	0.05	0.33	0.02
Alfalfa	0.39	0.01	0.27	0.01	0.54	0.01
Other hay	1.46	0.02	1.64	0.01	1.37	0.05
Open water	0.13	0.02	0.09	0.01	0.12	0.03
Deciduous forest	0.50	0.18	0.53	0.16	0.27	0.05
Shrubland	0.05	0.01	0.07	0.02	0.01	0.00
Woody wetland	0.09	0.02	0.06	0.01	0.08	0.01
Misc.	0.27	0.03	0.25	0.02	0.20	0.01
2009–2010						
Total turnover	50.81	13.68	17.9	32.31	13.22	59.91
Within grassland	36.44	12.81	9.65	30.83	2.56	56.80
From conversion	14.37	0.87	8.24	1.48	10.66	3.11
Conversion by CDL category						
Possible grass*	9.05	0.86	5.25	1.44	5.27	1.70
Corn	1.53	<0.01	0.70	<0.01	1.42	0.01
Soybeans	1.30	<0.01	0.66	<0.01	0.88	0.01
Wheat	0.37	<0.01	0.16	<0.01	0.05	<0.01
Alfalfa	0.55	<0.01	0.40	<0.01	0.81	<0.01
Other hay	1.11	<0.01	0.81	<0.01	0.61	0.01
Open water	0.10	<0.01	0.04	<0.01	0.04	0.01
Deciduous forest	0.07	<0.01	0.03	<0.01	0.06	0.01
Shrubland	0.07	<0.01	0.05	<0.01	0.01	0.00
Woody wetland	0.06	<0.01	0.03	<0.01	0.04	<0.01
Misc.	0.18	<0.01	0.11	<0.01	0.07	<0.01

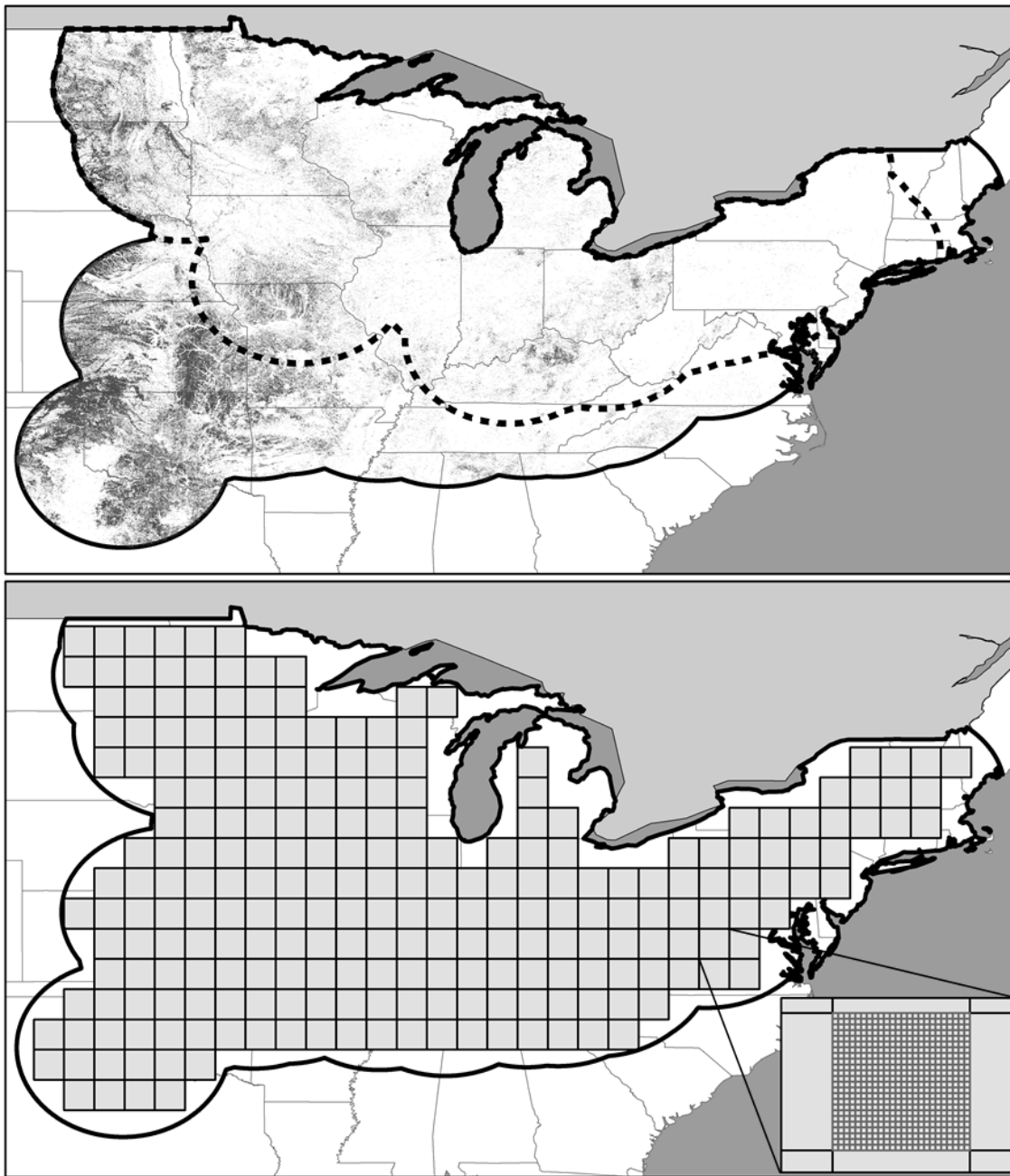


Figure 1. Top: the grassland mask (Cropland Data Layer) for an example year (2008), and the two spatial extents used in this study: the solid line marks the boundary of the training region used for all three species for model development and the area used for turnover comparisons for Henslow's and Grasshopper sparrows. The dashed line identifies the area to which we restricted Savannah Sparrow turnover analyses. Bottom: the tile scheme (e.g., 1°) and associated grids (inset; 24×24) used in point pattern analyses.

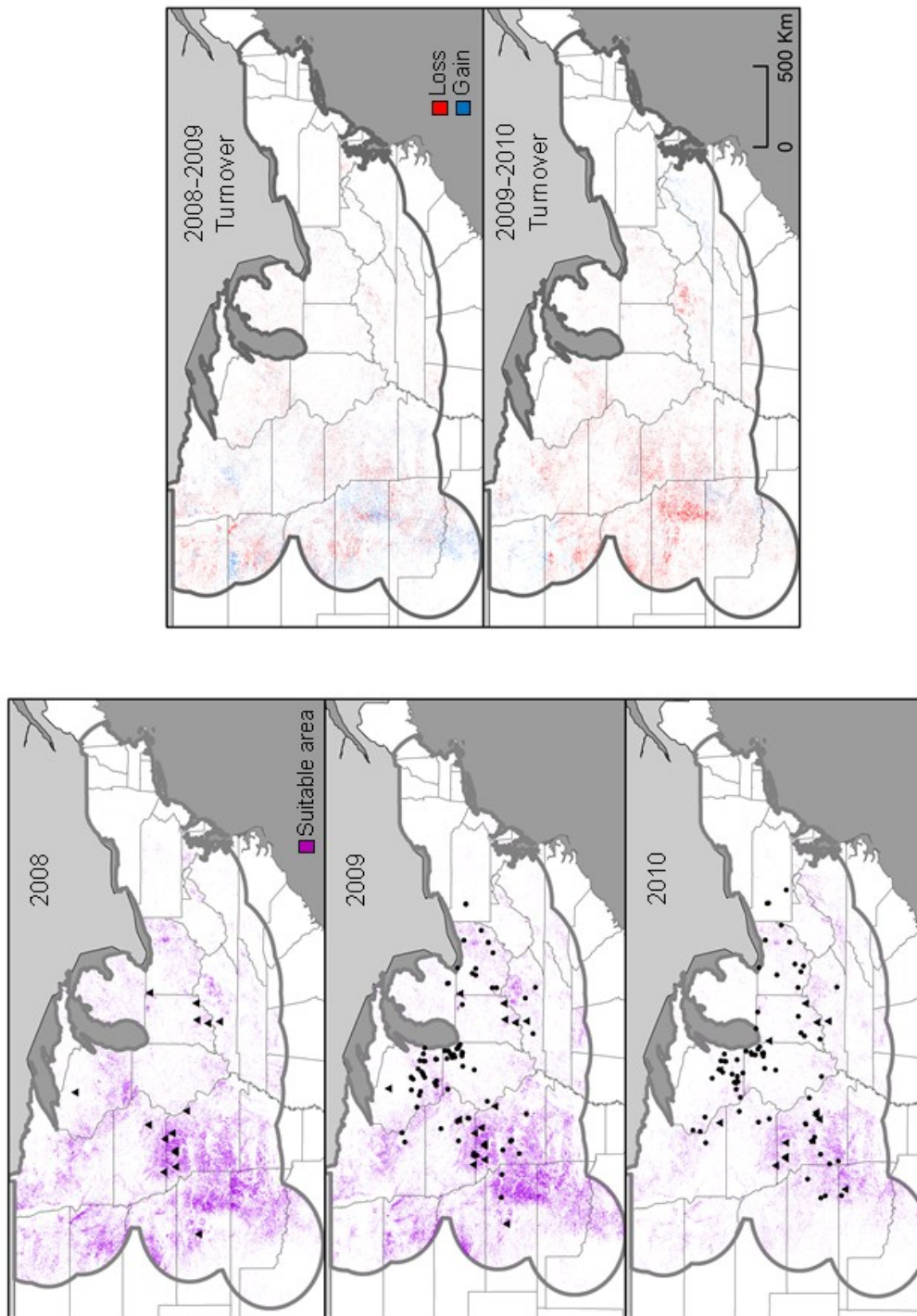


Figure 2. Left three panels: Henslow's Sparrow suitable areas (purple) for three years (2008–2010); black triangles show training occurrence data (Breeding Bird Survey) in all years, and black dots show testing occurrence data (eBird) for 2009 and 2010. Right two panels: turnover of suitable area (losses in red, gains in blue) between two sets of years (2008–2009 and 2009–2010).

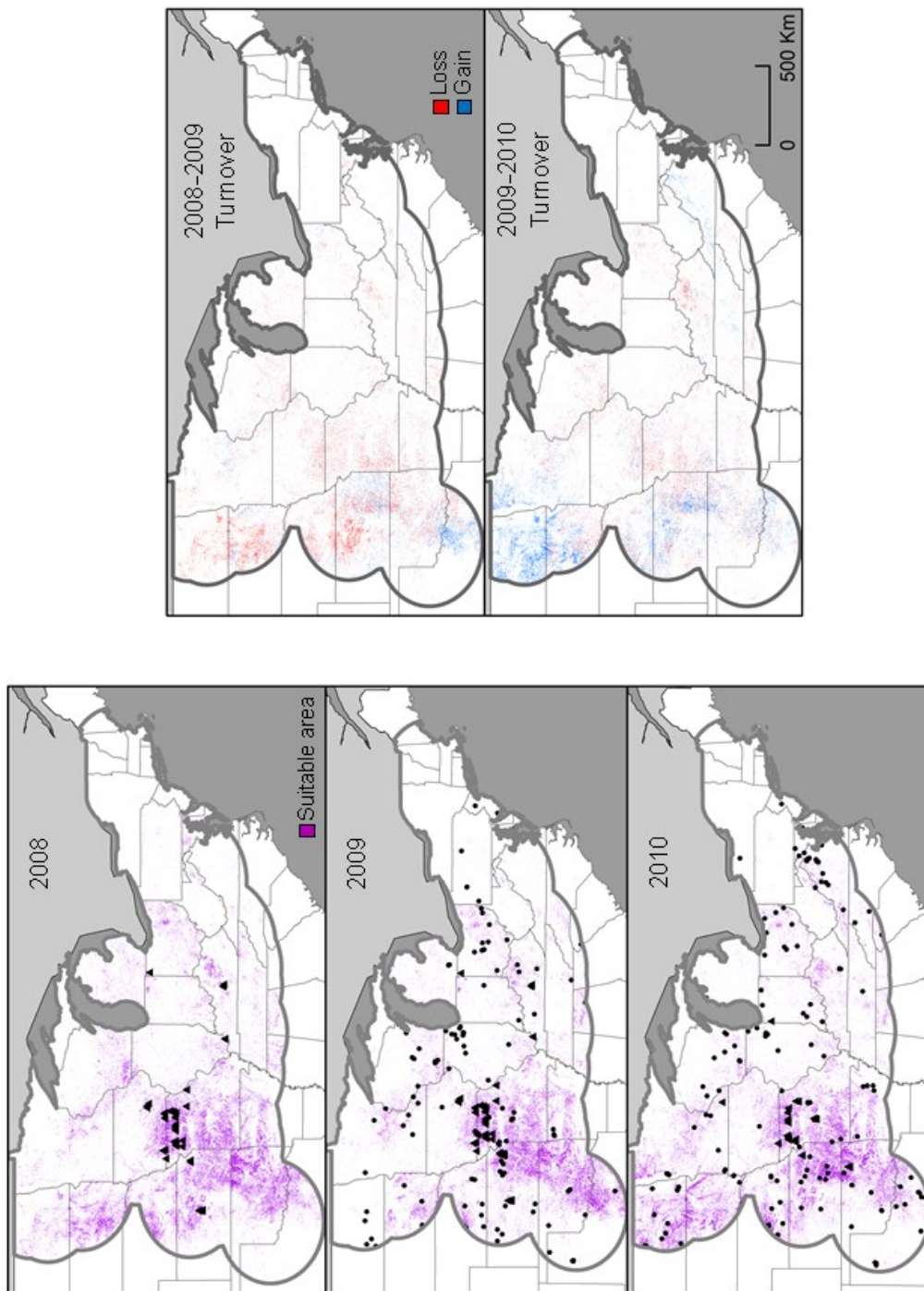


Figure 3. Left three panels: Grasshopper Sparrow suitable areas (purple) for three years (2008–2010); black triangles show training occurrence data (Breeding Bird Survey) in all years, and black dots show testing occurrence data (eBird) for 2009 and 2010. Right two panels: turnover of suitable area (losses in red, gains in blue) between two sets of years (2008–2009 and 2009–2010).

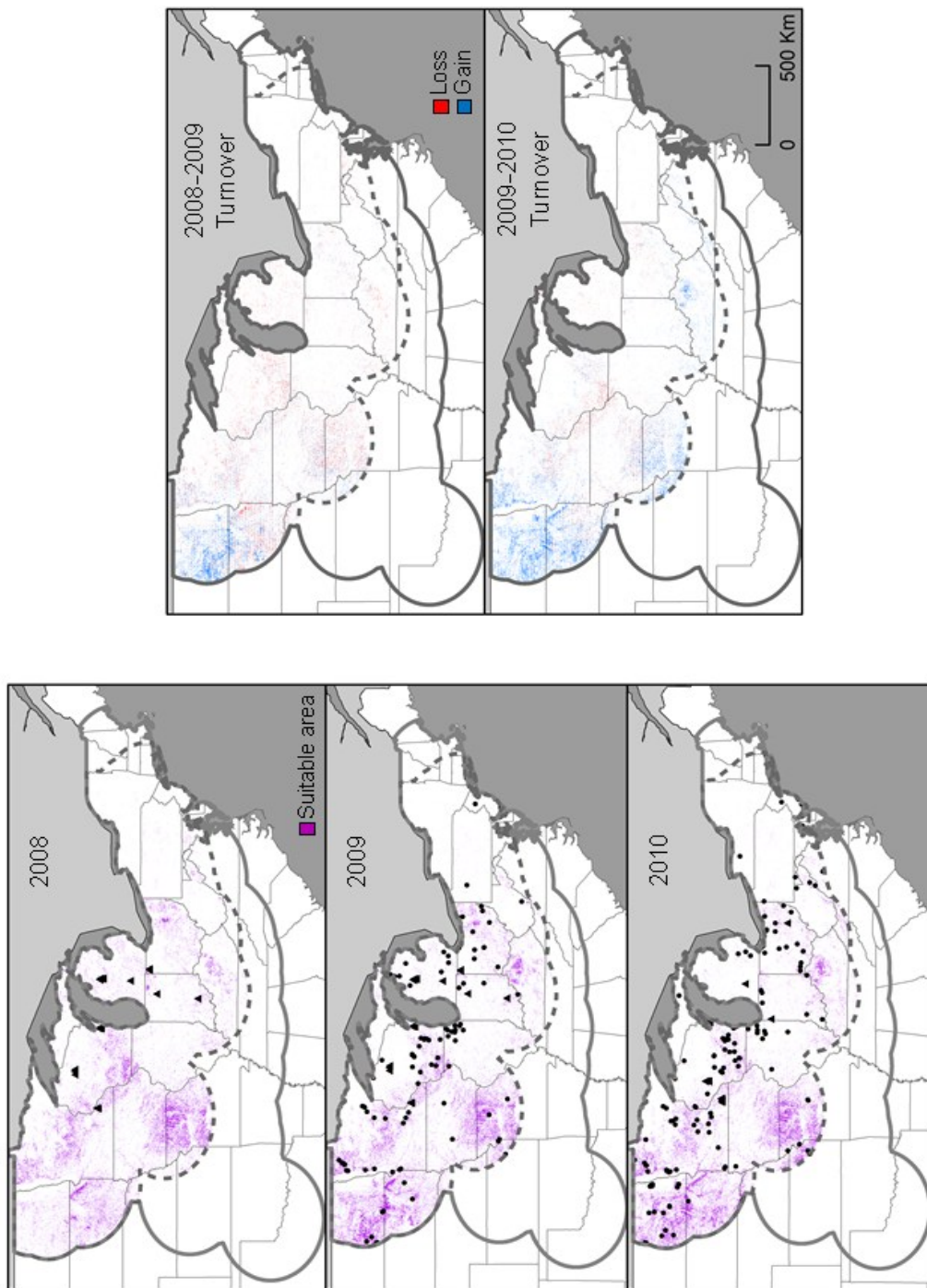


Figure 4. Left three panels: Savannah Sparrow suitable areas (purple) for three years (2008–2010); black triangles show training occurrence data (Breeding Bird Survey) in all years, and black dots show testing occurrence data (eBird) for 2009 and 2010. Right two panels: turnover of suitable area (losses in red, gains in blue) between two sets of years (2008–2009 and 2009–2010).

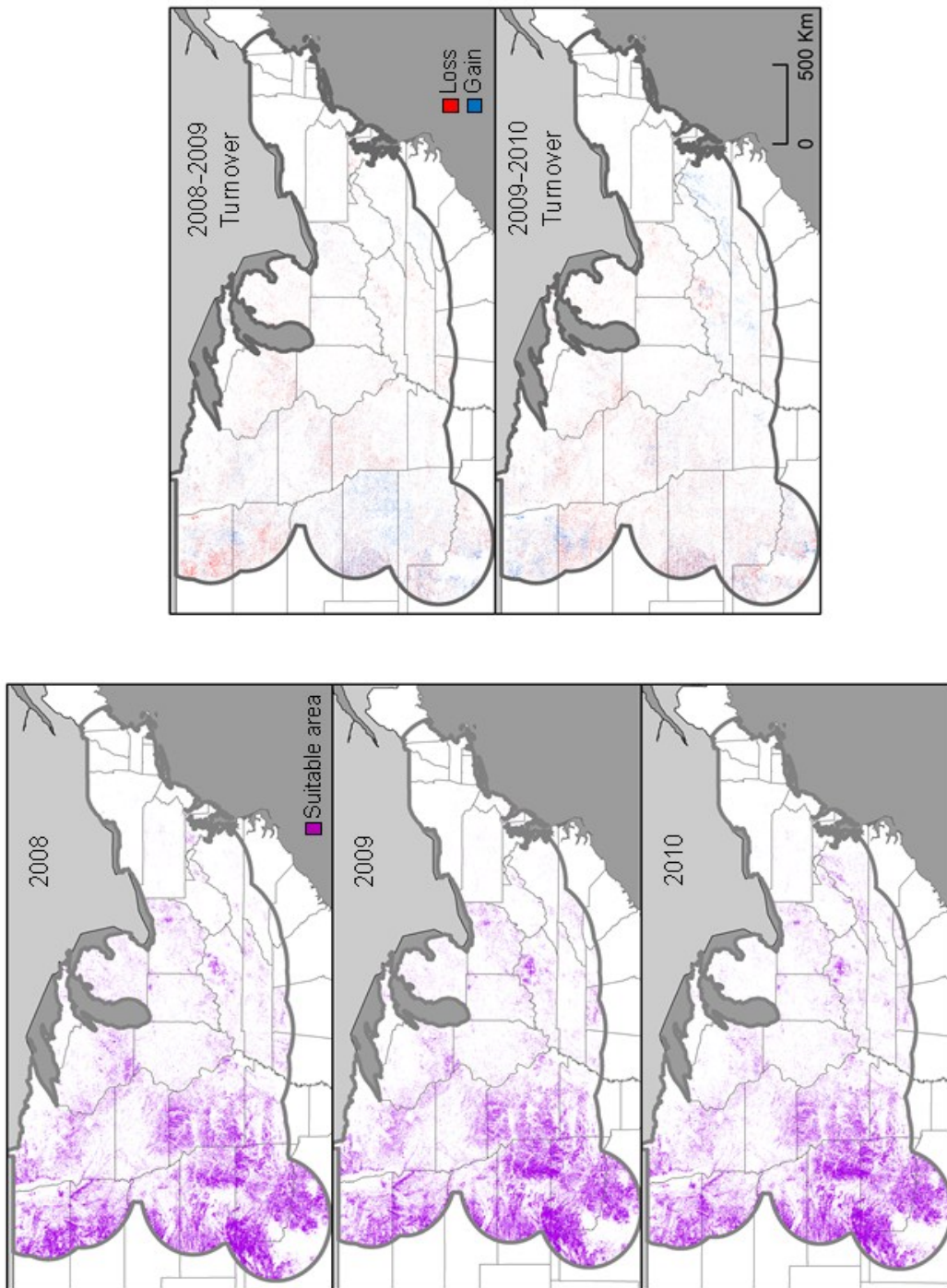


Figure 5. Left three panels: Cropland Data Layer possible grass area (purple) for three years (2008–2010). Right two panels: turnover of grass area (losses in red, gains in blue) between two sets of years (2008–2009 and 2009–2010).

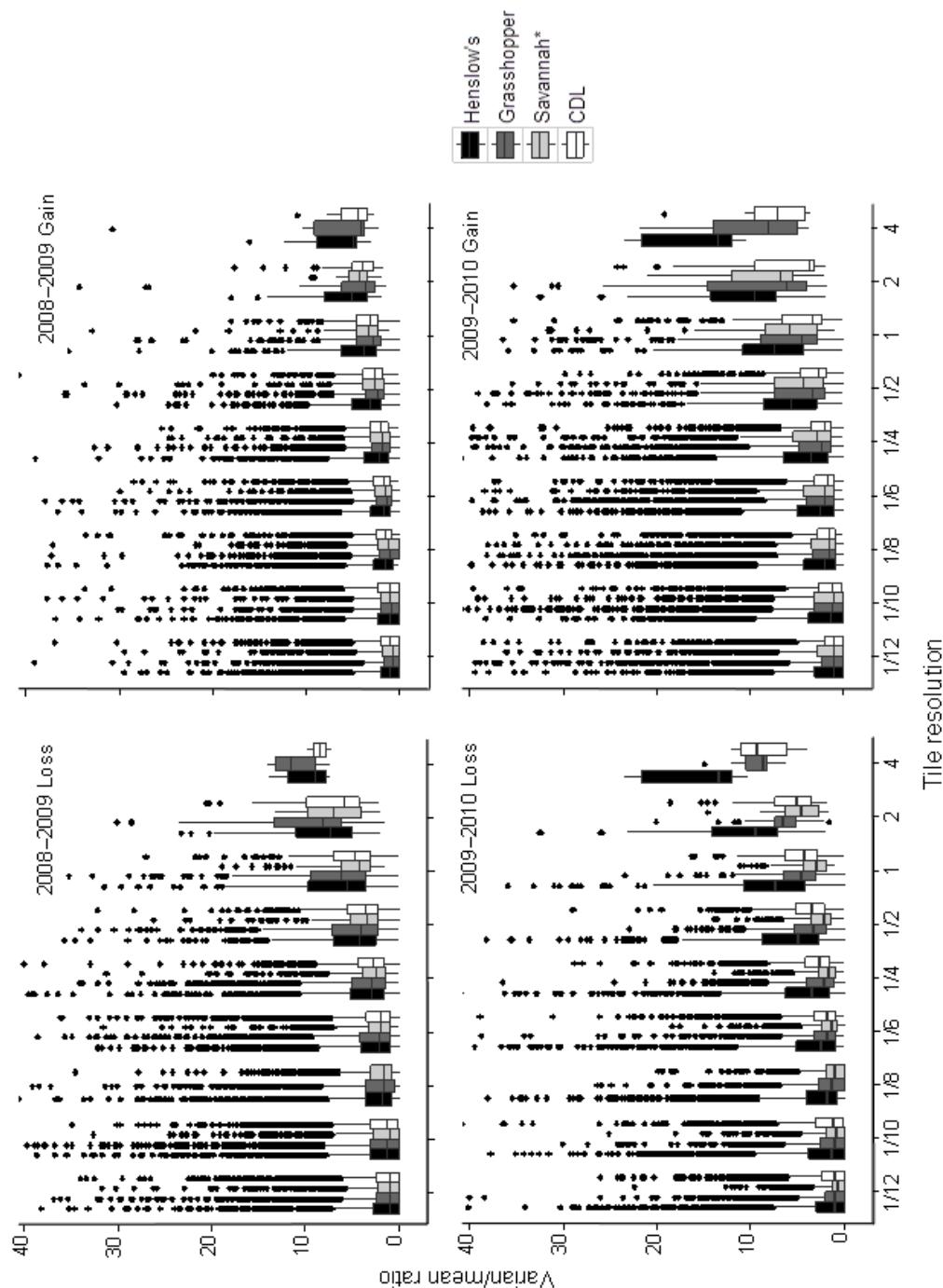


Figure 6. Index of dispersion of turnover losses and gains represented as variance/mean ratio by for three species (Henslow's, Grasshopper, and Savannah sparrows) and the Cropland Data Layer for two sets of years (2008–2009 and 2009–2010) and across 9 spatial resolutions (1/12–4°). * Analyses restricted to a smaller extent for Savannah Sparrows.

CHAPTER 5

Conclusions

General findings.—In Chapter 2, two variables, prevalence of occurrence and variation in abundance, were used to compare population variation of Henslow's, Grasshopper, and Savannah sparrows in space and time at a single spatial resolution (BBS route). Of these species, Henslow's Sparrows had the lowest prevalence, followed by Grasshopper Sparrows. Variation in abundance was not distinguishable among the species; however, it was positively correlated with prevalence of occurrence, such that where populations occurred more consistently, they showed higher variation in abundance. This research provides the first, range-wide evidence that Henslow's Sparrows may be settling new areas from year to year rather consistently as a result of highly variable nest habitat. Furthermore, conspecific clustering may explain low variation in abundance where prevalence is high. A second, minor objective of Chapter 2 was to demonstrate the impact of using BBS data without considering the effects of geographic or observer bias. In these analyses if the signal of the variation was strong, like that of prevalence, these biases may have little effect on overall results; however, for weak signals, like variation in abundance, analyses may yield misleading trends.

In Chapter 3, the analysis of Chapter 2 was expanded to test whether patterns observed at the BBS route level could be identified across multiple spatial resolutions. Here, differences were tested using two methods: standard, nonparametric Kruskal Wallis and Mann-Whitney U-tests that consider each resolution independently, and a new variation of an older method (area-under-the-curve) that tests all spatial resolutions concurrently. Indeed, the results from these analyses showed that Henslow's Sparrow had lower prevalence of occurrence compared to Grasshopper and Savannah sparrows across spatial resolutions. Comparisons of variation of abundance at individual resolutions yielded inconsistent results; however, when all resolutions were considered together, Henslow's Sparrows had more overall variation in abundance than Grasshopper or Savannah sparrows. To verify that these patterns were not the result of

bias caused by differences in detection and abundance, Grasshopper and Savannah sparrow data sets were resampled to match the abundances observed in Henslow's Sparrows and reanalyzed using area-under-the-curve. Although differences between the species were smaller, Henslow's Sparrows still had lower overall prevalence.

In Chapters 2 and 3, year-to-year fluctuations in Henslow's Sparrow populations across multiple spatial resolutions were identified, with results that suggest this species may be responding to multiple factors causing nomadic movements (Allen and Saunders 2006). Nomadism in Henslow's Sparrows may be associated with the spatial and temporal patchiness of suitable breeding area related directly to structural characteristics of the vegetation, but that this behavior may be driven by factors across spatial scales. At finer scales, patch-level land use and conspecific attraction may be responsible for patch-to-patch movements; however, at regional scales, weather patterns and land use variation may account for broad-scale movement between years.

In Chapter 4, extent, distribution, and annual turnover of suitable breeding habitat for each species was characterized to understand better the relationship between nomadism and landscape-level environmental dynamics. In general, there was stability across broad areas for each species, and turnover of suitable area varied among species and between years. Specifically, suitable areas for Henslow's Sparrows had greater losses in both years and were less stable overall between years. Proportions of turnover resulting from conversion (i.e., state change) were relatively low, suggesting that, when loss or gain of suitable area occurred, it was more likely the result of structural change within grasslands and not from conversion of grass to non-grass land cover types. Dispersion of turnover also varied between species and among years, such that there was little difference among the species in 2008–2009; however, in 2009–2010, clustering of both losses and gains of Henslow's Sparrow's suitable area exceeded that of the other two species. Although a pattern of turnover could not be established from just two sets of years, it is possible that there may be both mild years where total turnover is low, and years that experience high regionally-moderated change. In the latter, there may be more broad-scale movement in Henslow's

Sparrow breeding populations. I also suspect that variability between years is caused by annual weather fluctuations that ultimately influence vegetation growth and agricultural operations on a regional scale.

Together, these chapters have characterized (1) a relatively unique behavior in Henslow's Sparrows, and (2) the dynamic nature of their breeding habitat. My research identified potential breeding areas across the full extent of Henslow's Sparrow's summer range. These maps, when paired with a more complete understanding of how this species uses grasslands across the landscape, will be quite valuable to conservation planners and resource managers.

Conservation considerations.—Native grasslands, particularly tallgrass prairies, have experienced massive conversion, and now constitute <1% of what occurred before European settlement (Samson and Knopf 1994). Such losses have affected obligate grassland birds to a degree that species without the ability to adapt to anthropogenic changes have suffered marked population declines (Robbins et al. 2002, Sauer and Link 2011). What is more, the broad conversion of prairie to large-scale agriculture and grazed pastures has altered natural disturbance regimes region-wide, and has rendered most of the native habitat unusable by Henslow's Sparrows, and as such, populations have declined over much of their distribution (Sauer et al. 2011), in response to habitat loss and fragmentation (Pruitt 1996). Recent trend analyses show apparent stability in populations, and even suggest small annual increases (Sauer and Link 2011); however, these reports should not warrant a reduction, or dismissal, of conservation efforts. Instead, it is important to anticipate and identify future challenges facing the conservation of Henslow's Sparrows and other grassland species. Currently, there is a need to assess whether there is now, and will continue to be, enough grassland to maintain populations at current levels, and whether suitable grassland is distributed spatially and available temporally to accommodate nomadic populations.

As regards maintenance of sufficient grassland acreage, no other government initiative has done more to conserve US grasslands than the Conservation Reserve Program (CRP). CRP was created by the Food Security Act of 1985 specifically to retard soil erosion on highly erodible cropland by providing rental payments and cost-share assistance to landowners in 10–15 year contracts to remove their land

from agricultural production and establish long-term, native vegetation cover specific to their region (Wu and Weber 2012, USDAa). Since its creation, this program has improved the quality of soil, air, water, and wildlife habitat (Wu and Weber 2012). What is more, CRP has been credited with the recent Henslow's Sparrow population reversals (Herkert 2007b). Unfortunately, these trends do not consider projected CRP losses and rising commodity prices that will undoubtedly result in broad-scale CRP conversion to cropland.

As of 2011, just over 30 million acres of farmland was enrolled in CRP contracts, the lowest enrollment since 2000 (Wu and Weber 2012, USDAb). CRP has cycled twice through periods of increase and decrease since 1985, and recent projections suggest continued declines. Enrollment (or re-enrollment) is affected by two broad factors: federal spending and commodity prices. Because CRP is a government-regulated program, it is subject to, and threatened by, cuts to federal spending. With no funding for rental payments and assistance, total available contracts are reduced and reversion of CRP to cropland is likely. Prices of agricultural commodities, particularly corn and soy, and the increasing attractiveness of biofuel production, will influence enrollment decisions, possibly more substantially than projected budget cuts. Since 2007, the continual decline in CRP enrollment appears to coincide with fluctuating commodity prices (Wu and Weber 2012). At best, the future of CRP is uncertain, and the broad-scale effects on wildlife populations are unknown.

Species that exhibit nomadism present particular challenges to conservation and management. Because their habitat is often disjunct spatially and temporally ephemeral, directing management efforts is not easy (Skagen and Knopf 1994). Although this dissertation is the first to show support for broad-scale nomadism in Henslow's Sparrows, this behavior may not be a new phenomenon in this species, such that it may have manifested alongside the development of the tallgrass prairie system. Native Americans, American Bison (*Bison bison*) movement, and fire (artificial and natural), along with climatic conditions, were keystone elements that determined the structure, species diversity, and spatiotemporal heterogeneity of this system (Axelrod 1985; Kay 1998). Forest clearing and other landscape modifications, fire, and

broad-scale grazing of millions of migrant bison created a shifting mosaic of grasslands in varied successional stages across the landscape for > 12 000 yr. before European settlement (Pyne 1995; Shaw 1995; Arcese and Sinclair 1997). Species with temporally-restricted habitat preferences that evolved within this dynamic system would have responded to disturbances with low site fidelity. If these disturbances were unpredictable and frequent enough, this strategy would have been stable evolutionarily (Dean 1997).

Today, most of the remaining Henslow's Sparrow breeding habitat is distributed primarily across privately-owned lands (e.g., rangeland, hayfields, switchgrass fields; Herkert et al. 1996), notwithstanding scattered prairie preserves (e.g., Tallgrass Prairie National Preserve, Midewin National Tallgrass Prairie, etc.) and reclaimed strip mines (Bajema et al. 2001). Although these tracts are obviously important, both for their size and because they can be managed specifically for species diversity, they may be too few and too dispersed to maintain all Henslow's Sparrow populations should the CRP dissolve or enrollment suffer serious declines. On privately-owned lands, species diversity and conservation is not generally the priority of the landowner. Management practices for cattle emphasize annual spring burns and intense stocking; hay and switchgrass plantings are harvested yearly and in early summer. Both practices remove standing vegetation and produce a perpetually early-succession prairie that is sub-optimal for many bird species (Robbins et al. 2002). Regionally, pastures and hayfields are roughly similar with regard to vegetation structure, composition, density, and biomass (Fuhlendorf and Engle 2001), such that management paradigms and regional weather patterns may create a spatiotemporally homogenous matrix and distribution of habitat that does not support roaming sparrow populations.

The key to Henslow's Sparrow conservation with consideration for their nomadic tendencies may be to concentrate efforts on the landscape matrix, with particular focus on creating patch-level, "out-of-phase" succession and multi-scale heterogeneity, potentially mimicking conditions under which the North American grasslands developed (i.e., under the influence and interaction of grazing and fire; Axelrod 1985; Kay 1998; Fuhlendorf and Engle 2001). For regional effects to manifest, coordination must begin at

the local level and within the management unit. For example, patch rotation on three-year cycles limits cattle stocking to a subset of the pasture, allows for structural development of herbaceous vegetation, and restricts woody growth, all of which promote suitable breeding habitat for Henslow's Sparrows (Wiens 1969; Herkert 1994; Powell 2006). This management regime considers the spatial and temporal disturbance pattern that creates the shifting mosaic and "out-of-phase" succession across patches, and would support nomadic populations of Henslow's Sparrows (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004). What is more, benefits would extend beyond Henslow's Sparrows and to species with habitat preferences of all stages of grassland succession. However, if CRP enrollment declines as expected in the coming years, other incentives should be in place to encourage non-traditional (i.e., rotational) land management.

Future directions.—A dissertation is never complete, or so it feels; and as such, there are several 'next steps' that I hope to address. First, because my data sets were limited temporally to three years, I could not describe long-term trends of turnover fully; therefore, the obvious next step will be to add models as new MODIS imagery and BBS data become available, and thereby identify better the patterns of turnover across a broader set of years.

Second, with the methods used in this dissertation to estimate prevalence of occurrence, I could not identify between which years populations were most variable; however, to compare between-year movements to turnover, I will need to develop an alternate method to determine when and where population movements occur. Then, I can test whether years of high turnover are correlated with years of high population variability.

Third, in Chapter 4 I identified core suitable breeding areas and areas that are stable temporally; however, I also showed where regional turnover was occurring, which I suspect is the result of annual weather variation. Between years, weather in the intercontinental US may be highly dynamic, such that droughts, summer heat waves, or extreme and prolonged winters are not uncommon. Recent studies (Albright et al. 2010a,b, Albright et al. 2011) have addressed the effects of extreme weather events on

avian communities, and found that species richness and population abundance are affected by short-term heat waves and drought. Grasslands can respond quickly to these and other events (e.g., prolonged winters), as evidenced by development of vegetation and onset of green-up (Wiens 1986). It may be that variation in precipitation and temperature affect structure of the vegetation, and consequently its attractiveness to Henslow's Sparrows, at the time when individuals are selecting nesting areas. I plan to develop methods that will test whether turnover of suitability is correlated to seasonal weather events.

Fourth, in my dissertation proposal I planned a chapter that would test the ability of the BBS to survey Henslow's Sparrow habitat and the tallgrass prairie system; however, as the dissertation progressed, I felt that this chapter did not fit well with the overall continuity of the project. Several studies have addressed this question for habitats other than grasslands: recent studies have evaluated the ability of the BBS to sample different land cover types accurately, with mixed results (Niemuth et al. 2007, O'Connell et al. 2007, Walz-Salvador et al. 2008). However, no study has as yet analyzed the ability of BBS routes to represent accurately tallgrass prairie cover type. For this follow-on project, I will mentor an undergraduate student who will complete this analysis and take lead authorship of the resulting manuscript. In this project, the student will determine whether grasslands, and particularly Henslow's Sparrows suitable habitat, is represented proportionally by the BBS. These comparisons will help to determine whether robust conclusions about Henslow's Sparrow population levels and trends can be drawn from BBS-collected data.

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