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RESEARCH ARTICLE

The future demographic niche of a declining grassland bird fails to shift poleward in response to climate change

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Abstract

Context Temperate grasslands and their dependent species are exposed to high variability in weather and climate due to the lack of natural buffers such as forests. Grassland birds are particularly vulnerable to this variability, yet have failed to shift poleward in response to recent climate change like other bird species in North America. However, there have been few studies examining the effect of weather on grassland bird demography and consequent influence of climate change on population persistence and distributional shifts.

Objectives The goal of this study was to estimate the vulnerability of Henslow's Sparrow (*Ammodramus henslowii*), an obligate grassland bird that has been declining throughout much of its range, to past and future climatic variability.

Methods We conducted a demographic meta-analysis from published studies and quantified the relationship between nest success rates and variability in breeding season climate. We projected the climate-demography relationships spatially, throughout the breeding range, and temporally, from 1981 to 2050. These projections were used to evaluate population dynamics by implementing a spatially explicit population model.

Results We uncovered a climate-demography linkage for Henslow's Sparrow with summer precipitation, and to a lesser degree, temperature positively affecting nest success. We found that future climatic conditions—primarily changes in precipitation—will likely contribute to reduced population persistence and a southwestward range contraction.

Conclusions Future distributional shifts in response to climate change may not always be poleward and assessing projected changes in precipitation is critical for grassland bird conservation and climate change adaptation.

Keywords Climate change vulnerability assessment · Demographic modeling · Grassland

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birds · Nest success · Poleward shift · Precipitation · Species distribution modeling

Introduction

Grassland ecosystems dominated central North America previous to European settlement, but are now one of the most extensively human-altered ecosystems (Samson et al. 2004). The conversion of prairies to agriculture and rangeland has affected native fauna, including grassland birds, which have declined more than any other bird group over the past 35–40 years (Sauer et al. 2014). While issues surrounding land-use and grassland management related to bird conservation have received considerable attention (Askins et al. 2007), less work has investigated the effect of climate variability on grassland bird populations. A range-wide assessment of grassland birds found a high probability that population declines of grassland bird species will be exacerbated by modern climate change, with more than half of North America's grassland birds facing additional pressures due to climate change (North American Bird Conservation Initiative 2010). Analyses of Christmas Bird Count data found that grassland birds were the only group of birds failing to shift north during the past 40 years in response to warmer winters (Niven et al. 2010). It is unknown whether this lack of a systematic northward shift is due to a lack of available grassland habitat in northerly regions or whether grassland birds are simply less sensitive to climate variability compared to other bird species (VanDerWal et al. 2013; Gillings et al. 2015).

Grassland ecosystems are characterized by treeless expanses and occur in regions of low topographic complexity where the rate of climate change is greatest (Dobrowski et al. 2013). Compared to other biomes, the velocity of temperature change has been highest in temperate grasslands and savannas (Loarie et al. 2009), and future climate projections suggest a higher likelihood of drought and elevated summer temperatures in many prairie systems (Meehl et al. 2007). Understanding the demographic sensitivity of grassland birds to historic and future climate variability is critical for understanding the potential implications of future climate change for these species.

At regional scales, climate variables such as mean precipitation and temperature have been found to be important predictors of grassland bird abundance and occurrence throughout the upper Midwestern United States (Thogmartin et al. 2006). However, the effects of weather on reproductive parameters of grassland birds appear to vary by species. Lark Bunting (*Calamospiza melanocorys*) clutch size, nest survival, and productivity were found to be sensitive to precipitation (Skagen and Yackel Adams 2012). In contrast, Henslow's Sparrow (*Ammodramus henslowii*) nest success was sensitive to breeding season temperature while Savannah Sparrow (*Passerculus sandwichensis*) and Grasshopper Sparrow (*Ammodramus savannarum*) nest success showed little response to weather (Stauffer et al. 2011). Conrey et al. (2016) found lower nest success after hot, dry, or stormy days within a season and across years in drier and warmer breeding seasons for five grassland bird species. Despite these findings, few of these studies evaluated the sensitivity of grassland bird demography to long-term climate variability or assessed the vulnerability of species to future climate change at range-wide scales.

Climate change vulnerability assessments (CCVA) represent an approach for gauging historical and predicting future responses of species and populations to climate change, with a primary goal of interpreting ecological responses in a way that can inform management strategies and reduce vulnerability (Williams et al. 2008; Pacifici et al. 2015). Whether a species is directly vulnerable to climate change is a combination of intrinsic sensitivity to climate variability—often defined in terms of physiological or demographic limits—and exposure to region-specific changes in climatic means and extremes (Moritz and Agudo 2013). To date, most CCVA approaches have relied on species distribution models (Franklin 2010) based primarily on occurrence data, and although these approaches are critical for capturing changes in future bioclimatic space, they are limited by a lack of inference on species demography. The goal of this study was to conduct a CCVA for Henslow's Sparrow, a grassland bird of high conservation concern, with the goal of estimating both demographic sensitivity to past climate variability and exposure to future climate conditions. As an obligate grassland bird (Vickery et al. 1999), Henslow's Sparrow is an exemplary species for evaluating demographic sensitivity and regional exposure of grassland birds to historic and future climate change. Our objectives were to conduct a demographic meta-analysis to quantify nest success sensitivity to historical patterns of temperature and precipitation and develop a spatially explicit and range-wide assessment of the influence of future climate variability on population persistence.

Methods

Study species

Henslow's Sparrow is a short-distance migrant breeding in grasslands of the central United States and overwintering in the southern United States. Despite recent overall population increases from land enrollment in federal conservation programs (Cooper 2012), regional populations of Henslow's Sparrow are still declining and several states have the species listed as endangered, threatened, or a species of concern (Cooper 2012). Henslow's Sparrow historically bred in native prairie, but the species has been found to breed in surrogate grasslands that include hayfields, pastures, and agricultural lands in federal conservation programs (Cooper 2012). Henslow's Sparrow is area-sensitive (Ribic et al. 2009b) and grasslands of ~100 ha or larger are most likely to sustain populations (Herkert et al. 1993) with density estimates at 20–90 birds per 100 ha (Cooper 2012).

Climate change vulnerability assessment

Our CCVA consisted of a series of steps for quantifying demographic sensitivity. First, we conducted a literature review of Henslow's Sparrow demographic studies to identify available demographic rates. Second, we collected data for spatial environmental variables considered to be biologically relevant to demographic rates. Third, we created a statistical model to assess the relationship of the demographic rate with the environmental variables and projected the demographic rate spatially, throughout the breeding range of Henslow's Sparrow, and temporally, from 1981 to 2050. The final step was to model the population dynamics of Henslow's Sparrow through time and space by implementing a population model at annual time steps. The population model allowed us to incorporate the statistical projections of demographic rates and dispersal to estimate the persistence of Henslow's Sparrow populations across their range and into the future.

Demographic meta-analysis

In our literature review, we considered both survival and nest success as demographic parameters, but studies on survival (adult and juvenile) were scarce. Therefore, we focused on estimates of nest success (Fig. 1). We used studies that had sample sizes of $\geq$10 nests (Benson et al. 2013) and provided daily survival rates (DSR) calculated using either the Mayfield method (Mayfield 1961) or the logistic-exposure method (Shaffer 2004). DSR was used to calculate overall nest success by raising DSR to the power of 24, the most common number of days in the nesting period found in the studies (Online Appendix 1). When studies only provided overall nest success, DSR was back-calculated using the nesting period provided in the study. When only the number of failures and the number of exposure days were provided, we calculated DSR using the Mayfield method (Mayfield 1961). For estimates of nest success that were calculated with covariates, we contacted authors to provide DSR calculated without covariates. We matched nest success studies spatially and temporally to environmental data sets; when specific study site locations were unavailable, we used county centerpoints. We found 26 studies of Henslow's Sparrow nest success from across the breeding range (Fig. 1). Nest success values ranged from 0.10 to 0.57 with an average nest success of 0.25 ± 0.11 (SD) (Online Appendix 1).

Environmental variables

We focused on collecting environmental variables across the Henslow's Sparrow breeding range. We defined the breeding range as the NatureServe boundary (BirdLife International and NatureServe 2014), buffered by 150 km to include all of the nest success studies (Fig. 1). We focused on five climate variables that we and our scientific advisory board considered a priori to be biologically relevant for grassland bird nest success (Table 1).

Body condition on arrival to the breeding grounds and reproductive success have been linked to weather and food resources on the wintering grounds for other migratory birds (e.g., Hostetler et al. 2015). Because

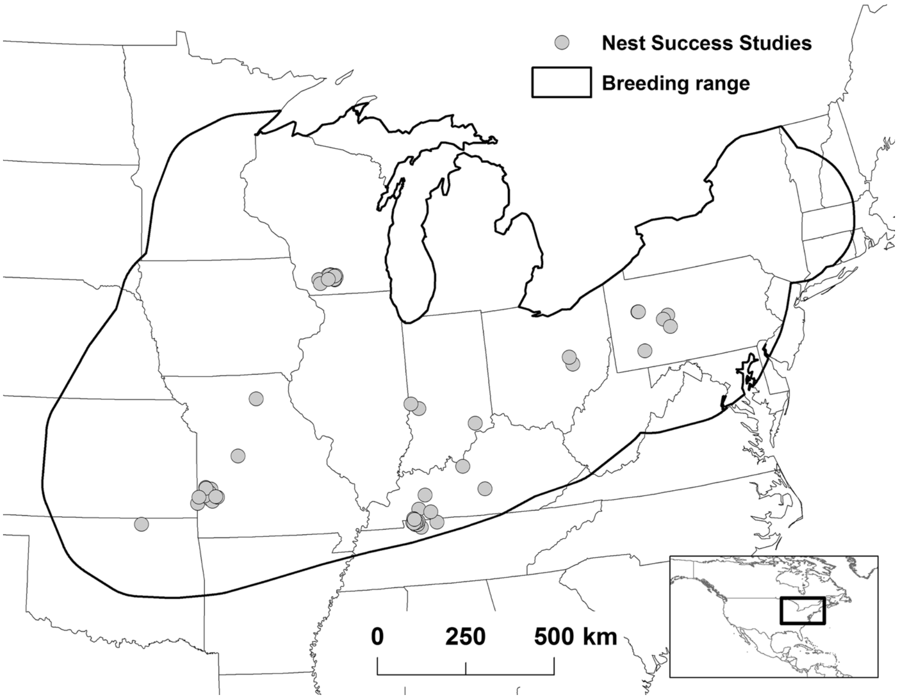

Fig. 1 Henslow's Sparrow (*Ammodramus henslowii*) nest success study locations and breeding range used in the model. Studies are listed in Online Appendix 1

there is no information connecting breeding populations to specific wintering ground locations for Henslow's Sparrows, we averaged the climate variables across the entire winter range.

For assessing population-specific exposure to climatic variation, we quantified mean climate variables for the historical time period (1981–2011) using the 4-km resolution gridded climate surface for precipitation (mm) and maximum temperature (°C) developed from the Parameter-elevation Regression on Independent Slopes Model (PRISM; PRISM Climate Group-Oregon State University 2014). Breeding season variables were estimated from daily PRISM data (which goes back to 1981) and bioyear and wintering grounds precipitation were collected from monthly data. The Henslow's Sparrow breeding season was defined as May 15–August 15 and the bioyear was defined as the year (July–June) preceding the breeding season in which the nest success data were collected. We also computed the number of extreme events across the breeding season at individual weather stations and then used the procedure outlined in Notaro et al. (2014) to interpolate the number of extreme events across the breeding range. We defined the extremes as the 90th percentile or above of daily precipitation and temperature for each location.

We hypothesized that the amount of grassland and/or the amount of urbanization around the breeding sites could affect overall nest success (Marzluff et al. 2001; Pidgeon et al. 2003). As such, we calculated the total amount of grassland (as defined by the NLCD grassland/herbaceous and pasture/hay categories; Fry et al. 2011) and housing density (Radeloff et al. 2010) within a 2.5 km buffer surrounding each site. The 2.5 km buffer size is comparable to the resolution of the population model (see below).

Statistical analysis

To evaluate the effect of weather and land cover variables on nest success and create annual time steps of projected nest success throughout the range, we used binomial generalized linear models (GLM) with a logit link function weighted by the number of nests (Shaffer 2004). The response variable was nest success taken from site/year combinations of studies in the literature (values given in Online Appendix 1). All environmental variables for each site and year were scaled and centered. We developed models for all possible combinations of a priori variables (Table 1) and used Akaike's Information Criterion for small sample sizes (AIC_c) to rank models (Burnham and Anderson 2002).

Table 1 Predictor variables for the statistical model of Henslow's Sparrow (*Ammodramus henslowii*) nest success, time periods of data, descriptions of data, and rationale for each variable

Climate variables	Time period	Description	Rationale
Breeding season precipitation	May 15$_t$–August 15$_t$	Total precipitation (mm) during the breeding season	Positive; higher hatching rates with higher precipitation[a] Negative; higher precipitation during nestling stage affects parent's ability to acquire food[b]
Bioyear precipitation	July$_{t-1}$–June$_t$	Total precipitation (mm) during the preceding year	Positive; wetter conditions in the preceding year lead to higher primary productivity in breeding season[c] and more nests[c,d]
Breeding season temperature	May 15$_t$–August 15$_t$	Average daily maximum temperature (°C) during the breeding season	Positive; better able to thermoregulate, increased foraging success[a]; insects more active, less time foraging and more time nest guarding[e] Negative; reduced nest survival (interacting with forest cover) mediated through increased predator activity (especially snakes)[f]
Extreme precipitation events	May 15$_t$–August 15$_t$	Number of days in the 90th percentile or above for precipitation at each site	Positive; depresses predator activity (e.g., snakes)[g] Negative; reduces foraging success, adults may desert nest and chicks die of exposure, and drowns nestlings/washes away nests[a]
Extreme temperature events	May 15$_t$–August 15$_t$	Number of days in the 90th percentile or above for temperature at each site	Negative; nest failure for a wide variety of reasons[h]
Overwinter climate variables			
Summer precipitation	April$_{t-1}$–Sept$_{t-1}$	Total precipitation (mm) across the entire wintering range from April through September	Positive; Potential carryover consequences of winter conditions to nest success in the following breeding season. Low precipitation during the grass growing season (April-September) can depress seed production leading to poor winter condition of Henslow's Sparrow[i]
Winter precipitation	Dec$_{t-1}$–February$_t$	Total precipitation (mm) across the entire wintering range from December through February	Positive; Potential carryover consequences of winter conditions to nest success in the following breeding season. Drought conditions during the winter could decrease winter insect abundance/activity leading to poor winter condition of Henslow's Sparrow[i]
Land cover variables			
Total grassland (ha) within 2.5 km buffer	2006	Grassland area defined as NLCD grassland/herbaceous and pasture/hay categories[j]	Positive; more grassland surrounding the nest site would lead to higher nest success[k]
Housing density (housing units per km^2) within 2.5 km buffer	Annually$_t$	Housing density converted to annual time steps[l]	Negative; higher density of houses surrounding the nest site would lead to lower nest success[m]

t is the year the nest success data were collected

[a] Skagen and Yackel Adams (2012)

[b] Siikamaki (1996)

[c] Chase et al. (2005)

[d] Rotenberry and Wiens (1991)

[e] Stauffer et al. (2011)

[f] Cox et al. (2013)

[g] Stauffer (2008)

[h] McKechnie and Wolf (2010)

[i] Johnson et al. (2011)

[j] Fry et al. (2011)

[k] Pidgeon et al. (2003)

[l] Radeloff et al. (2010)

[m] Marzluff et al. (2001)

A variable was considered uninformative and removed from the top models if its 85% confidence interval overlapped zero (Arnold 2010). If there was more than one competing model, we used model-averaging to develop our parameter estimates (Burnham and Anderson 2002). There have been recent concerns about the practice of model-averaging (Cade 2015). However, multi-collinearity among our predictor variables was low, our variables were standardized, and we felt that the importance of including all potential climate variables into our demographic predictions outweighed the concerns about model-averaging. We used the final model to predict nest success means and variances across the breeding range at annual time steps from 1981 to 2050 as inputs in the population model (see below).

Future climate variables from the top model were calculated for the years 2012–2050 from the World Climate Research Program's (WCRP) Coupled Model Intercomparison Project phase 5 (CMIP5) multimodel data set, downloaded as daily data for each year from the Bias Corrected and Downscaled WCRP CMIP5 Climate Projections archive at http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/dcpInterface.html (Maurer et al. 2007; Brekke et al. 2013). The daily data from each year were used to calculate the breeding season variables. To ensure continuity between PRISM (historic years) and CMIP5 data (future years), we calculated future climate variables using the "delta method" (see Online Appendix 2 for methods).

Future nest success was predicted for each of 19 General Circulation Models (GCM) and in two Representative Concentration Pathways (RCP): RCP 4.5 and RCP 8.5 (Online Appendix 3). RCP 8.5 predicts increasing emissions while RCP 4.5 predicts stable or decreasing emissions throughout the century (Harris et al. 2014). Spatially explicit population models were run using the following models of future climate data: model-averaged data from all 19 GCMs for RCP 4.5 (results in Online Appendix 4); model-averaged data from all 19 GCMs for RCP 8.5; a GCM that represents low extremes of precipitation and temperature (INM-CM4 RCP 8.5; Hamann 2016; Wang et al. 2016); a GCM that represents high extremes of precipitation and temperature (GFDL-ESM2M RCP 8.5; Hamann 2016; Wang et al. 2016). To visualize climate conditions, nest success trends in each period were created (see Online Appendix 2 for methods). All statistical analyses and processing of environmental data were conducted using the R statistical platform v. 3.1.1 (R Development Core Team 2015).

Spatially explicit population model

We developed a spatially explicit population model (SEPM) using HexSim, an individual-based modeling platform operating on a hexagonal spatial grid (Schumaker 2015). HexSim allowed us to implement the SEPM through time, incorporating user-defined demographic parameters and habitat (Schumaker 2015). We used a grid of 5-km wide hexagons that covered the breeding range of Henslow's Sparrow, where each hexagon represented a potential population of Henslow's Sparrows. We considered each hexagon with a minimum 100 ha patch (Herkert et al. 1993) of grassland habitat (defined from NLCD, see above) as suitable for a potential population.

Our SEPM consisted of five life-cycle events in each annual time step (Fig. 2). The reproduction event used predicted nest success from the statistical model (above) and the number of births was estimated from the literature (Table 2). Post-fledging, adult breeding season, and over-winter/migration survival rates were estimated from the literature for Henslow's Sparrow and other similar species (Table 2). The inter-annual movement event (Fig. 2) represented the distance an individual would move from one breeding season to the next and were estimated from limited banding data available.

Simulations were initiated in 1981 and continued in annual time steps to 2050. We calculated the probability of persistence for each hexagon and year as the proportion of 500 model iterations in which a population (i.e., 20 or more birds; Herkert 1994) was present. Probability of persistence values were calculated for mid-century projections by averaging values from 2040 through 2050. This time period was used to approximate mid-century populations without being strongly influenced by conditions in any single year. Specific and more detailed methods of the HexSim model are provided in Online Appendix 2.

Model validation

For purposes of model validation, we estimated probability of occurrence (as opposed to probability of persistence values calculated above) using model-

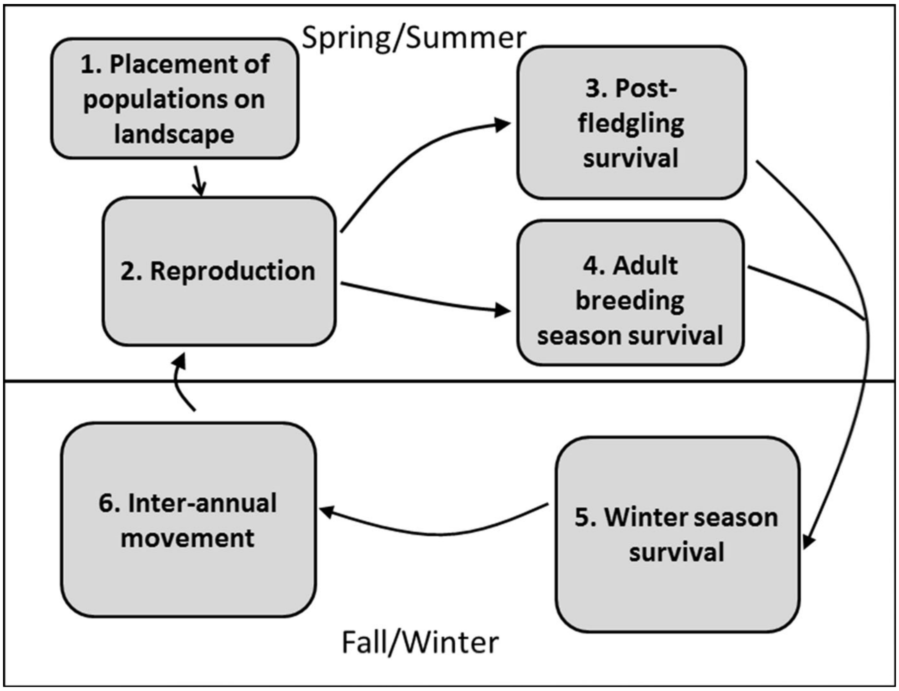

Fig. 2 HexSim model events for each year of the spatially explicit population model for Henslow's Sparrow (*Ammodramus henslowii*). Step 1 is completed once at the beginning of the model run and steps 2–6 are completed at each annual time step in the model

derived predictions at the scale of the hexagon averaged for the contemporary time period (2001–2011). We calculated probability of occurrence values from the demographic model output as the proportion of 500 model iterations in which 1 or more bird(s) was present. We compared probability of occurrence values to independent presence points with Breeding Bird Survey (BBS) routes (Pardieck et al. 2014) using classification performance measures. We assumed presence on a BBS route if a Henslow's Sparrow was detected in the years 2001–2011. BBS routes were buffered by 5 km, the resolution of the SEPM, and probability of occurrence values from the model output were averaged across buffered BBS routes. Model performance was assessed using the area under the curve (AUC) of the Receiver Operating Characteristic (ROC), classification sensitivity, classification specificity, and proportion of correctly classified routes (Mouton et al. 2010). We used a threshold for these measures that maximized the sum of sensitivity and specificity. AUC is threshold-independent and is expressed as a proportion with values >0.5 representing better than random classification. Model evaluation analyses were conducted in R (R Development Core Team 2015) using the SDMTools package (VanDerWal et al. 2015).

We recognized that BBS routes may not be the most accurate representation of Henslow's Sparrow presence on the landscape because detection probability for the species is low and BBS categorizes the data as having "an important deficiency" (Sauer et al. 2014). Additionally, we expected that data showing species trends across years may be more comparable to outcomes from a population model than simple presence records. Thus, we also did a comparison of the SEPM output to BBS trends data (e.g., increasing vs. decreasing) from 1966 to 2013 (Sauer et al. 2014).

To separate the effects of habitat from the effects of climate, we also ran simulations of a null model that removed environmental variation due to climate. The null model allowed us to see if the patterns of population persistence were influenced by habitat availability versus climate. Instead of using nest success survival values predicted from the statistical model, we used only the mean and variation from the nest success studies (Online Appendix 1) to define a distribution and pulled nest success rates for each hexagon-year from that distribution. However, with

Table 2 Input values and methods used in the spatially explicit population model

Demographic parameter	Mean ± SD used in model	Method	Substitute species	Range from literature	Citations
Reproduction					
Nest success	Dynamic	Used predictions from statistical model	–		Nest success studies; Fig. 2, Online Appendix 1
No. of births	3.65 ± 0.39	Values drawn from a normal distribution binned to integers	–	2.6–4	Nest success studies; Fig. 2, Online Appendix 1
Post-fledging survival	0.5 ± 0.15	Values drawn from a normal distribution	Dickcissel, Grasshopper Sparrow, Lark Bunting	0.21–0.57	Yackel Adams et al. (2001), Berkeley et al. (2007), Suedkamp Wells et al. (2007), Hovick et al. (2011)
Adult breeding season survival	0.95	Constant	–		Pulliam (1988)
Migration + winter survival	0.67 ± 0.2	Values drawn from a normal distribution	Grasshopper Sparrow, Savannah Sparrow	0.3–0.83	Thatcher et al. (2006), Perlut et al.(2008), Stauffer (2008), Johnson et al. (2011), Michel et al.(2011), Perlut and Strong (2011)
Inter-annual movement	50 ± 12.5 km	Values drawn from a lognormal distribution; random direction, no autocorrelation in dispersal direction	–	14–52 km	U.S. Bird Banding Laboratory, Laurel, Maryland, USA; Our scientific advisory board

When sufficient data was unavailable for Henslow's Sparrow (*Ammodramus henslowii*), other species were added or substituted. Citations provided are for all species data used

just the average nest success, populations failed to stabilize after an initial burn-in period. As a result, we iteratively increased survival values in the null model until population growth was stable ($\lambda \sim 1$).

Results

Nest success in relation to climate

Eight models with five variables were in the top model set: breeding season precipitation, breeding season maximum temperature, housing density, temperature on the overwinter grounds (April–September), and total grassland area (Table 3). However, only breeding season precipitation and breeding season maximum temperature had 85% confidence intervals that did not overlap zero and remained in the final model set. Adjusted R^2 values for model 1 and model 2 are 0.27 and 0.34, respectively. We used model averaging across the top two models to develop parameter estimates for breeding season precipitation and maximum temperature (Table 3). The relative variable importance values in the final model were 0.88 for breeding season precipitation and 0.31 for breeding season maximum temperature. We found that nest success was positively associated with both breeding season precipitation ($\widehat{\beta} = 0.28$, SE $= 0.1$; Fig. 3a) and maximum temperature ($\widehat{\beta} = 0.21$, SE $= 0.11$; Fig. 3b). Predicted nest success in the contemporary period (2001–2011) was highest in the southwest part of the breeding range (Fig. 4; Online Appendix 5). Nest success trends for each cell in the hindcast and forecast periods can be found in Online Appendix 6.

Population model predictions

For the contemporary time period, Henslow's Sparrow populations were more likely to occur in the

Table 3 Model selection results for the Henslow's Sparrow (*Ammodramus henslowii*) nest success models in the top model set and the null model

Model	AIC$_c$	ΔAIC$_c$	logLik
Breeding season precipitation	**125.2**	**0**	**−60.34**
Breeding season precipitation + Breeding season maximum temperature	**125.3**	**0.05**	**−59.082**
Breeding season precipitation + Housing density	126	0.77	−59.442
Breeding season precipitation + Breeding season maximum temperature + Overwinter precipitation from April to September	126	0.8	−58.05
Breeding season precipitation + Breeding season maximum temperature + Housing density	126.4	1.18	−58.237
Breeding season precipitation + Overwinter precipitation from April to September	126.5	1.29	−59.698
Breeding season precipitation + Total grassland	126.8	1.59	−59.851
Breeding season precipitation + Overwinter precipitation from April-September + Total grassland	126.9	1.69	−58.492
Null Model	130.9	5.67	−64.352

The top two models (in bold) were the models in the final model set because parameters in the other models were found to be uninformative based on 85% confidence intervals

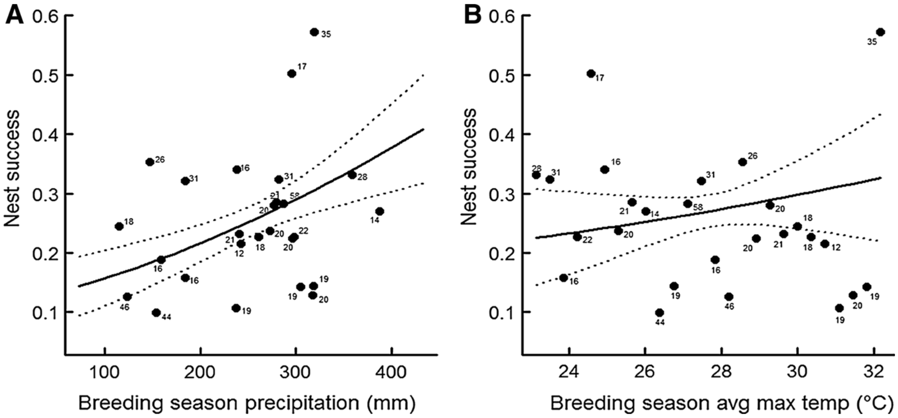

Fig. 3 Predictor variable effects from the final statistical model of Henslow's Sparrow (*Ammodramus henslowii*) nest success. *Y*-axes are the fitted nest success values from the model. *Solid lines* are based on the β-estimates for that variable. *Points* are actual nest success values. *Labels* next to *points* represent the number of nests

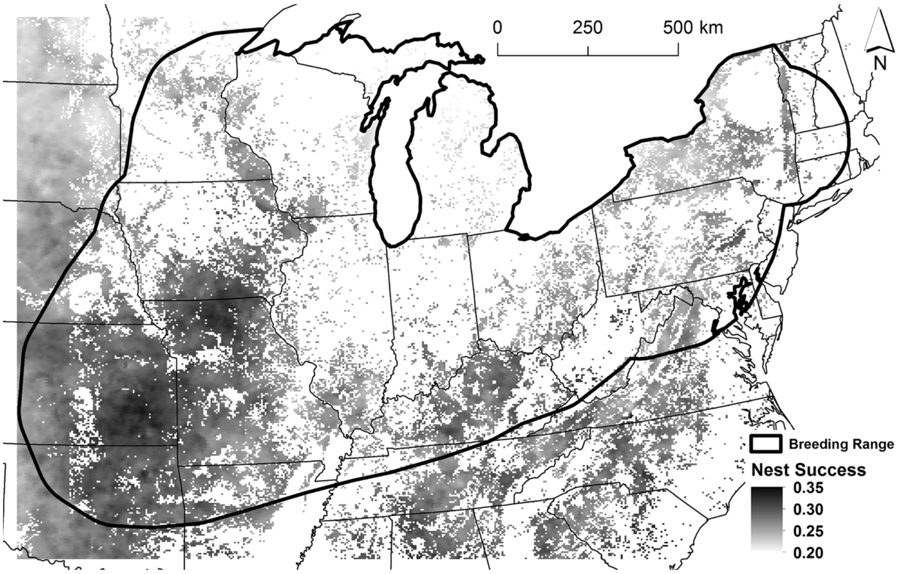

Fig. 4 Predicted Henslow's Sparrow (*Ammodramus henslowii*) nest success values from the statistical model, averaged over the years 2001–2011 (annual values were used in the demographic model). Only hexagons considered habitat (maximum grassland patch ≥100 ha) have values. The *thick black line* represents the breeding range where initial populations in the population model were placed

southwestern portion of the range with lower occurrence in the northern and eastern parts of the range (Fig. 5a; Online Appendix 5). We found that the probability of persistence by mid-century was predicted to contract into the southwestern part of the range with populations in the rest of the range having low probabilities of persistence (Fig. 6; Online Appendix 5). Results from individual GCMs that represent the extremes of precipitation and temperature show similar geographic patterns to the model-averaged results, but the range of the probability of persistence varied across individual GCMs (Fig. 6; Online Appendix 5). Results from the null model indicate the importance of climate in the model; the model produced evenly distributed probabilities of persistence across the range, a pattern very different from the models that included climate.

To assess model performance, we used 165 BBS routes that detected Henslow's Sparrows (presence) and 1095 routes that failed to document a detection (absence). The demographic model had an AUC score of 0.62 and the model correctly classified 75% of the routes. Classification sensitivity was 0.44 and specificity was 0.81 showing there was a higher proportion of correctly classified absences than presences. The average probability of occurrence in regions where BBS trends showed decreasing species presence was 0.1 while the average probability of occurrence in regions where BBS trends showed increasing species presence was 0.32 (Fig. 5; Online Appendix 5).

Discussion

Across a broad geographic region, we found that the Henslow's Sparrow was sensitive to inter-annual variation in temperature and precipitation, resulting in elevated nest success rates during warmer and wetter breeding seasons with precipitation having the larger relative effect. Studies have examined the effect of anthropogenic warming on species ranges and extinctions (Thomas et al. 2004), but less is known about the potentially important role of precipitation (Beale et al. 2013; Illán et al. 2014). At a continental scale, grassland species have failed to shift northward with increasing temperatures like other groups of birds (Niven et al. 2010), and our results suggest that a greater sensitivity to heterogenous changes in precipitation could help account for this difference. By combining climate-demography sensitivities with model-based predictions of exposure to climate variability, we found that the range-wide vulnerability of Henslow's Sparrow to future climate change will be potentially impacted by future changes in precipitation.

In many regions of the breeding range of Henslow's Sparrow, climate models have predicted declines in summer precipitation (Melillo et al. 2014), and our vulnerability assessment suggests future changes in precipitation could lead to a range-wide decline in demographic suitability, with the exception of the southwestern portion of the range. Over geographic

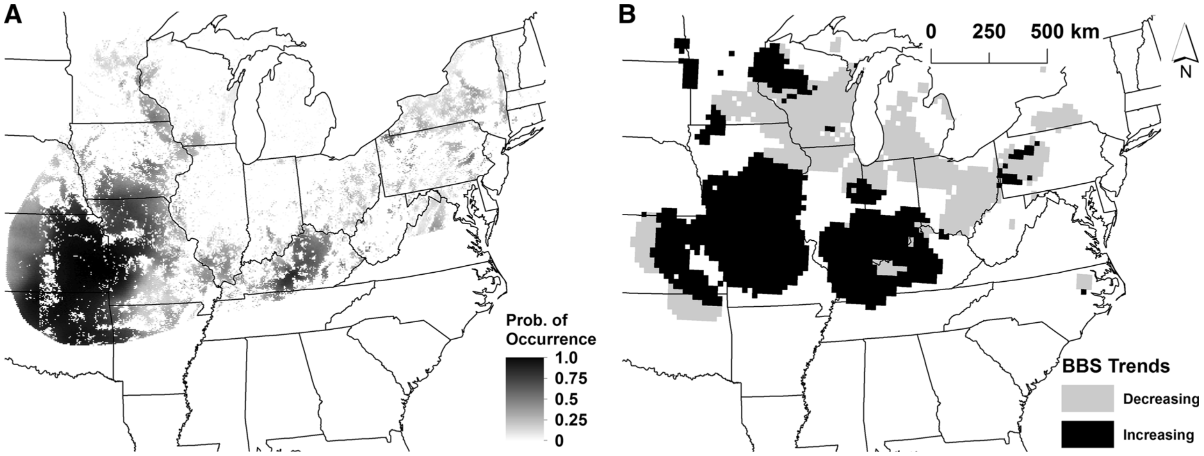

Fig. 5 **a** Henslow's Sparrow (*Ammodramus henslowii*) probability of occurrence values from the spatially explicit population model output averaged over the years 2001–2011. Probability of occurrence is the probability out of 500 model runs that a cell will have at least one bird present. **b** Breeding Bird Survey trends data from the years 1966 to 2011

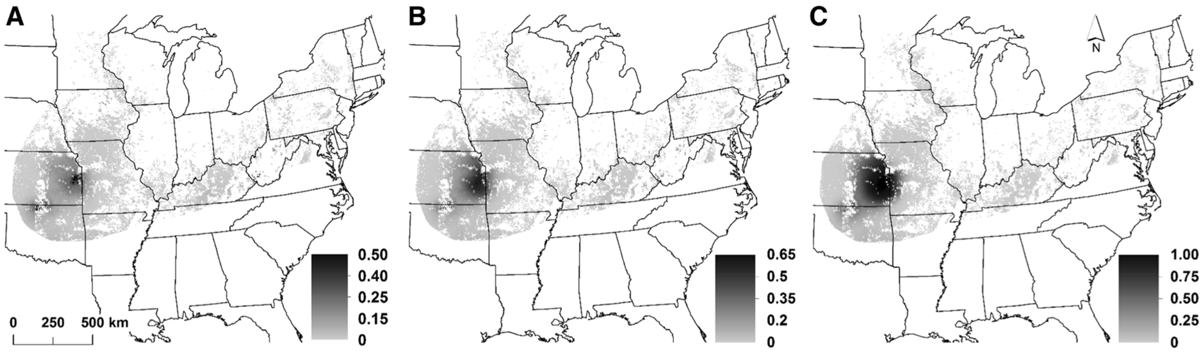

Fig. 6 Henslow's Sparrow (*Ammodramus henslowii*) probability of persistence values from the spatially explicit population model output averaged over the years 2040–2050 for RCP 8.5. Climate data for the nest success predictions were **a** the low extreme GCM for temperature and precipitation (INM-CM4); **b** the model-averaged climate data; and **c** the high extreme GCM for temperature and precipitation (GFDL-ESM2). Probability of persistence is the probability out of 500 model runs that a cell will have at least 20 birds present, the minimum number considered a population

scales, changes in precipitation are highly variable and difficult to predict (Trenberth et al. 2014), but most climate model projections agree that drying will occur under increasing greenhouse gas concentrations, especially for arid regions (Burke et al. 2006; Sheffield and Wood 2008; Dai 2012). In grassland ecosystems, precipitation is a critical driver of vegetation productivity (Vicente-Serrano et al. 2013) and increased precipitation is associated with higher insect availability and biomass (Rotenberry and Wiens 1991; Skagen and Yackel Adams 2012). Biotic interactions could also be playing an important role in these predicted changes. For example, grassland bird nest depredation could be influenced by changes in precipitation that affect vegetation growth as predators might avoid moving through denser and taller grasses (Ribic et al. 2012) or have increased availability of alternative food sources (Chase et al. 2005; Stauffer 2008). Higher temperatures can lead to increased foraging success (Skagen and Yackel Adams 2012). Insects are more active in warmer temperatures meaning there is less time needed for foraging and more time can be spent nest guarding (Stauffer et al. 2011). Although our study does not provide a rigorous assessment of which of these mechanisms are more important, our results suggest that Henslow's Sparrow nest success is influenced by climate, particularly precipitation, and future patterns of climate variability could promote a southwestward contraction in their demographic niche.

Climate models vary in their predictions of temperature and precipitation and thus, the magnitude of changes in future nest success varied among GCMs. In our models, projections of higher predicted precipitation and temperature led to higher predicted nest success and increased probability of persistence. The low-extreme GCM model resulted in the lowest probabilities of persistence and induced the strongest range contraction. Thus, the overall range of predicted persistence values varied among GCMs, and ensemble model averaging produced intermediate results. Under all future projections, the geographic pattern of population persistence remained similar among GCMs. Additionally, models based on the RCP 4.5 pathway showed a patchier pattern of probability of persistence, but with overall results similar to that of the models based on RCP 8.5. Our models consistently predicted a "hotspot" of persistence for populations of Henslow's Sparrows in the southwest portion of the range, but the overall range of persistence probabilities proved sensitive to the uncertainty in future precipitation and temperature projections.

Regions of high persistence, as defined by our modeling approach, could be considered to be more demographically suitable. However, in comparison with independent occurrence data from the BBS, we were not able to predict contemporary presences accurately. A possible reason for this incongruence could be that in areas where Henslow's Sparrows are present, but have been declining, our models predicted a more rapid demographic decline than is actually occurring. Additionally, the null model results demonstrated that the average nest success across the range was not sufficient to maintain populations and that patches of relatively high nest success, promoted by suitable climate conditions, were required for population persistence. The results from the null model also verified that the patterns of high population persistence in the southwest portion of the range were driven by optimal climate conditions in that region and not simply due to the availability of more habitat in that portion of the range.

Limited data availability for certain parts of the Henslow's Sparrow life cycle affected our ability to include those aspects in our statistical and demographic models. No relationship was found to suggest that a carryover effect of wintering climate on nest success exists, but wintering climate was averaged each year across the entire wintering range. Linking breeding populations to corresponding overwintering locations may improve statistical models and predictions of nest success. Similarly, we were unable to model the effect of climate on post-fledging or adult overwinter/migration survival because empirical data were limited; only a few studies of adult survival over the wintering period were available (Thatcher et al. 2006; Johnson et al. 2011). There is also little data available on inter-annual movement distances and while our dispersal distances represent the best available data, the lack of long-distance inter-annual movement events prevent populations from tracking climate shifts. Many of these parameters with limited data should be sensitive to climatic variability and extreme weather, and including those relationships in our models could improve model predictions.

Predicted spatial distributions of high nest success and population persistence were similar over broad geographic scales, but also showed important regional differences, highlighting the importance of the SEPM to assess population-level outcomes even when complete demographic information is missing for key vital rates. The SEPM allowed us to incorporate existing knowledge about habitat, current population size, range extent, dispersal, local extinction/colonization, and estimates of other demographic parameters to gain a better understanding of the consequences of climate variability for population persistence, through its influence on nest success.

While Henslow's Sparrow nest success was shown to be sensitive to climate, land cover was not identified as an important variable in our model selection. A lack of response by Henslow's Sparrow to landscape context has been found in other studies (Bajema and Lima 2001; Ribic et al. 2009a); Henslow's Sparrow are more likely to use patches so large that the patches themselves are considered a "landscape" and thus a response to surrounding land use may be less influential (Bajema and Lima 2001). However, a potential issue for modeling grassland bird habitat is that grassland habitat quality is difficult to quantify using remote-sensing derived land cover products at the spatial scales required to study range-wide species distributions. NLCD may be a high-resolution dataset at this geographic extent, but is limited in its ability to distinguish appropriate grassland habitat (Thogmartin et al. 2004). As such, the generalized land cover categories (e.g., grassland/herbaceous and pasture/hay) may not accurately represent Henslow's Sparrow habitat throughout the range, even with focusing on hexagons having large patches of grasslands. Improved data sets on grassland habitat quality could enhance modeling efforts for many grassland species and better match species' perception of available habitats (Sample et al. 2003). Additionally, future projections of grassland cover are unavailable or unreliable and were not incorporated into our future projections, allowing for individuals in the model to only move among current grassland habitat. While this limitation led to conservative estimates of the future spatial extent of demographically suitable habitat, large increases in grassland habitat in the future are unrealistic given regional land use trends of declining grassland that are likely to continue or remain static (Samson et al. 2004).

It has been assumed that environmental conditions along the periphery of a species' range are less favorable than conditions at the core of the range (Gaston 1990; Brown et al. 1995), with range boundary populations being smaller, more variable, and less likely to receive immigrants from the core (Channell and Lomolino 2000). As a result, it has been assumed that as a species' range contracts, it will contract toward the center with peripheral populations going extinct and core populations remaining (Brown 1995; Lawton 1995). However, Channell and Lomolino (2000) found that many species persist at the periphery of their range following range collapses. Our results support this prediction, showing the climatic conditions at the southwestern range edge of Henslow's Sparrows to be more demographically suitable now and into the future, provided no new grassland habitat becomes available. Although changing climate conditions have produced broad expectations of poleward range shifts for many species (Parmesan and Yohe 2003; Bateman et al. 2016), recent studies have suggested that range shifts can be geographically complex (VanDerWal et al. 2013; Gillings et al. 2015; Bateman et al. 2016). Using a CCVA, our study suggests that a possible reason for a lack of poleward shift for grassland birds is a result of heterogeneous changes in precipitation and their influence on demographic processes. Incorporating future changes in climate, especially the role of changing precipitation, is important for assessing the future vulnerability of grassland-dependent species.

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