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Research Paper

Climate change and land management implications for a declining Neotropical migratory songbird breeding in the North American Great Plains

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ABSTRACT. Anthropogenic climate change and habitat loss pose major threats to grassland breeding birds, the most rapidly declining group of birds in continental North America. Although previous studies have investigated grassland breeding bird responses to land management, few empirical studies explore their responses to climatic variation or its interactions with land management, which warrant urgent conservation attention. We evaluated the effects of climate and land management parameters on an indicator species for grassland breeding birds, the Grasshopper Sparrow (*Ammodramus savannarum*), a Neotropical migrant of conservation concern whose global population has declined by more than two thirds since 1970. We quantified Grasshopper Sparrow responses to climate variation, land management actions, and their interactions in the Platte River Valley, Nebraska, in the North American Great Plains, using six years of mark-recapture data collected via the Monitoring Avian Productivity and Survivorship (MAPS) protocol. We implemented generalized linear mixed models to estimate avian population trends (adult abundance and productivity) in response to changes in precipitation and temperature as well as cattle grazing, haying, and prescribed burning. Our models showed that climatic variation, especially spring precipitation, was the most important driver of avian population trends. Grasshopper Sparrow abundance declined with increasing spring precipitation, but prescribed burns helped mitigate this effect and were positively related to productivity, especially during years of lower spring temperatures. Our findings demonstrate the vulnerability of grassland bird population trends to ongoing and predicted climate change as well as the potential of land management actions to mitigate some negative effects of climate change on grassland breeding birds.

Conséquences du changement climatique et de la gestion des terres sur un passereau migrateur néotropical en diminution dans les Grandes Plaines d'Amérique du Nord

RÉSUMÉ. Les changements climatiques d'origine anthropique et la perte d'habitat constituent des menaces majeures pour les oiseaux de prairie nicheurs, groupe d'espèces qui diminue le plus rapidement en Amérique du Nord continentale. Bien que des études antérieures aient examiné les réactions des oiseaux de prairie nicheurs suivant la gestion des terres, peu d'études empiriques ont exploré leurs comportements à la suite de variations climatiques ou leurs interactions avec l'aménagement des terres, qui méritent pourtant une attention urgente pour la conservation. Nous avons évalué les effets du climat et des paramètres de gestion des terres sur une espèce représentative des oiseaux de prairie nicheurs, le Bruant sauterelle (*Ammodramus savannarum*), un migrateur néotropical dont la population mondiale a diminué de plus des deux tiers depuis 1970. Nous avons quantifié les réactions des Bruants sauterelles aux variations climatiques, aux mesures de gestion des terres et à leurs interactions dans la vallée de la rivière Platte, au Nebraska, dans les Grandes Plaines d'Amérique du Nord, en utilisant six ans de données de marquage-recapture collectées au moyen du protocole MAPS (Monitoring Avian Productivity and Survivorship). Nous avons conçu des modèles linéaires généralisés à effets mixtes pour estimer la démographie (abondance des adultes et productivité, ou nombre de jeunes) en réponse aux changements de précipitation et de température ainsi qu'au pâturage du bétail, à la fenaison et au brûlage dirigé. Nos modèles montrent que la variation climatique, en particulier les précipitations printanières, était le facteur principal agissant sur les tendances démographiques. Le nombre de Bruants sauterelles a diminué avec l'augmentation des précipitations printanières, mais les brûlages dirigés ont aidé à atténuer cet effet et étaient positivement liés à la productivité, surtout lors des années de températures printanières plus basses. Selon nos résultats, les populations d'oiseaux de prairie sont vulnérables aux changements climatiques en cours et prévus, et des mesures de gestion des terres adéquates peuvent atténuer certains effets négatifs des changements climatiques sur les oiseaux de prairie nicheurs.

Key Words: *Ammodramus savannarum*; avian demography; climate; conservation; Grasshopper Sparrow; grassland breeding birds; management; Monitoring Avian Productivity and Survivorship

INTRODUCTION

Anthropogenic climate change is affecting biodiversity worldwide, including over half of North American bird species, and its effects are expected to intensify in the coming years (Foden et al. 2013, Langham et al. 2015). Under current climate change predictions, North American breeding birds will encounter increasingly novel climates characterized by large seasonal and spatial climate variation that may pose serious threats to their populations (La Sorte et al. 2019). At the same time, agricultural expansion and intensification (Rickletts et al. 1999, Samson et al. 2004) has been driving worldwide declines in habitat and terrestrial biodiversity (Millennium Ecosystem Assessment 2005, Butchart et al. 2010). One of the world's largest temperate grassland ecosystems, the Great Plains has incurred more habitat loss and hydrological change than any other North American ecosystem because of agricultural expansion and intensification (Sohl et al. 2019). Consequently, birds breeding in the Great Plains have suffered the steepest declines of any region on the continent (Rosenberg et al. 2016, NABCI 2017). Ongoing climate change is expected to cause further declines in Great Plains breeding birds by driving range contractions and shifts (Gorzo et al. 2016). However, few empirical studies in the Great Plains have assessed breeding bird responses to climatic variation or their interactions with habitat management, limiting our ability to deal with these threats through adaptive management and conservation planning.

Great Plains grasslands are disturbance-dependent ecosystems that were historically shaped by seasonal flooding, wildfires, and ecosystem engineers such as American bison (*Bison bison*) and black-tailed prairie dogs (*Cynomys ludovicianus*; Currier 1982, Collins 1990, Anderson 2006). These natural disturbances have been virtually eliminated since the European colonization of the Great Plains and subsequent extirpation of bison, prairie dogs, and other ecosystem engineers from most of their native range as well as the damming of rivers and suppression of wildfires. Today, land management practices such as prescribed burning, cattle grazing, and haying may partially mimic the natural disturbances of the past (Gibson and Hulbert 1987, Briggs and Knapp 1995, Briggs et al. 2005). Such disturbances maintain habitat for a wide variety of grassland breeding birds and other taxa by creating heterogeneity in grassland structure, species composition, and successional state (Thogmartin et al. 2006, Fuhlendorf et al. 2006, 2009). Grassland structure and composition are critical components of breeding bird habitat quality, and may vary dramatically from year to year depending on land management actions and climatic variation (Patterson and Best 1996, Fuhlendorf and Engle 2004, Winter et al. 2005, Coppedge et al. 2008, Gorzo et al. 2016).

Grassland breeding bird species have evolved to specialize in particular ecological niches within disturbance gradients, such that land management practices have significant consequences for their breeding success (e.g., Delaney et al. 2002, Reinking 2005, Sutter and Ritchison 2005, Coppedge et al. 2008, Rahmig et al. 2009). Henslow's Sparrows (*Centronyx henslowii*), for example, tend to nest in mature tallgrass prairies three or more years postdisturbance, e.g., grazing, haying, burning, which harbor significant levels of nesting material (Herkert 1998, Thogmartin et al. 2006, Fuhlendorf et al. 2009). Upland Sandpipers (*Bartramia longicauda*), by contrast, tend to forage and nest in

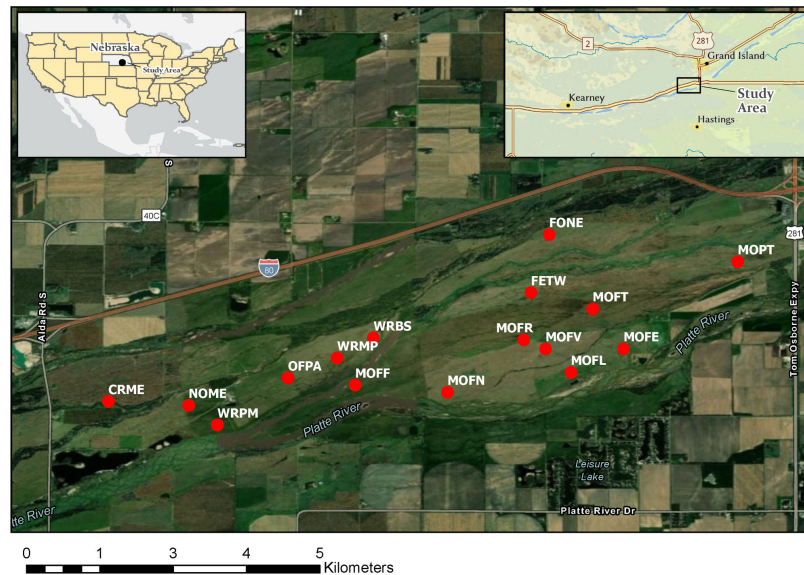
grasslands with more recent disturbances (Dechant et al. 2002, Thogmartin et al. 2006, Fuhlendorf et al. 2009). Studying grassland birds' responses to land management enables science-based conservation efforts, but few empirical studies have examined the role that climatic factors, e.g., precipitation or temperature, play in moderating, mitigating, or enhancing the intended effects of land management actions on birds (Jones et al. 2007, Yarnell et al. 2007, Archibald 2008, Kim et al. 2008).

Ongoing anthropogenic climate change is predicted to strongly affect temperature and precipitation levels in the Great Plains, now and in the future (Ojima et al. 2012, Gorzo et al. 2016). Grassland bird populations as a group have exhibited > 50% declines in abundance since 1970 (Rosenberg et al. 2019), and effective conservation planning will require information about avian responses to climatic variation as well as land management. Here, we examine the effects of climate and land management variables on the Grasshopper Sparrow (*Ammodramus savannarum*), an indicator species whose densities are effective predictors of the densities of many other grassland breeding bird species, such as Eastern and Western Meadowlarks (*Sturnella magna*, *S. neglecta*), Bobolinks (*Dolichonyx oryzivorus*), Henslow's Sparrows, and Dickcissels (*Spiza americana*; Thogmartin et al. 2006, Rosenberg et al. 2016, Elliot and Johnston 2018). A Neotropical migrant whose wintering range extends from southern United States and Mexico to Central America and the Caribbean, the Grasshopper Sparrow has an extensive breeding range in North America, but is uncommon to rare in many parts of its range (Vickery 1996). Its global population has fallen by nearly 70% since 1970, leading to its designation as a species of conservation concern by the U.S. Fish and Wildlife Service (Ruth 2015, Rosenberg et al. 2016). Grasshopper Sparrow breeding abundance peaks in the central Great Plains (Sauer et al. 2014), but its Nebraska population has been declining nearly 2% annually (Silcock and Jorgensen 2018) as grasslands continue to be converted to monoculture crops.

Grasshopper Sparrows forage exclusively on the ground, hunting grasshoppers, other arthropods, and seeds (Martin et al. 1951, Vickery et al. 1999). To maximize their foraging success during the breeding season, they tend to select relatively dry, sparsely vegetated sites in tallgrass prairies with patchy bare ground (Delaney et al. 1985, Vickery et al. 1999), which tend to be associated with frequent disturbance (Vickery 1996, Balent and Norment 2003, Ruth 2015). Studies in other systems have found correlations between Grasshopper Sparrow abundance and frequent burning and grazing (Swengel and Swengel 2001, Guiliano and Daves 2002, Sutter and Ritchison 2005, Fuhlendorf et al. 2006), with abundance peaking around one to two years after burning (Fuhlendorf et al. 2006, Powell 2006, 2008). Grasshopper Sparrows construct highly cryptic nests that typically feature overhanging grasses and a side entrance (Vickery et al. 1999, Fogarty et al. 2017), camouflage that provides some protection against predators, and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Vickery et al. 1999).

Here, we assess breeding Grasshopper Sparrow population responses to climatic variation and land management in tallgrass prairie in the Platte River Valley in the central Great Plains. Our main objective was to elucidate their vulnerability to ongoing and future climate change and to investigate the ability of targeted

Fig. 1. Map of Grasshopper Sparrow sampling locations in the central Platte River Valley, Nebraska Great Plains.



land management to mitigate those impacts. We hypothesized that climatic variation would strongly influence Grasshopper Sparrow abundance, because changes in precipitation and temperature affect soil moisture and vegetation growth that are critical to successful foraging and breeding (Rahmig et al. 2009, Ahlering and Merkord 2016). Specifically, we predicted that higher temperatures would be associated with bird declines (Gorzo et al. 2016) in association with decreased food availability and increased physiological stress on birds, and that higher precipitation levels would be correlated with declining population trends (Kim et al. 2008) in association with flooding and plant growth in excess of ideal foraging or breeding conditions for this species. We further hypothesized that managed disturbances, which regulate biomass production and vegetative structure, could magnify or mitigate the impacts of climatic variation on bird abundance and productivity (Fuhlendorf and Engle 2004, Thogmartin et al. 2006, Kim et al. 2008).

METHODS

Study system

We investigated Grasshopper Sparrow abundance and productivity on ~2025 ha of lowland tallgrass prairie in the central Platte River Valley, Nebraska (40.798°N, -98.416°W, ~600 m asl). A globally recognized Important Bird Area (Poague 2019), the central Platte River Valley features riparian wet meadows and lowland tallgrass prairies that provide breeding and stopover habitat for a high diversity of birds, particularly migratory waterbird and grassland breeding species (Lingle and Hay 1982, Sharpe et al. 2001, Kim 2005, Johnsgard and Brown 2013). A remnant of the critically endangered North American Central and Southern Mixed Grasslands ecoregion, where 95% of native habitat has been converted to agriculture and other human uses, this landscape harbors the highest floristic diversity of any North American grassland (Barbour et al. 1980). The Platte River

extends the westward reach of eastern tallgrass prairie habitat by raising the water table and increasing available subsurface moisture for the long roots of perennial prairie grasses (Currier 1982, Kaul and Rolfsmeier 1993, Kaul et al. 2006). Habitat in this region was historically structured by disturbances caused by Plains bison (*Bison bison bison*), wildfires, and seasonal floods that prevented woody encroachment and maintained early successional vegetation (Williams 1978, Anderson 2006). European colonization in the late 19th century fundamentally altered wildlife in this region by causing extinctions, extirpations, and population reductions of many native species and subspecies such as the Eskimo Curlew (*Numenius borealis*), Great Plains wolf (*Canis lupus nubilus*), American bison, black-tailed prairie dog, and Greater Prairie-Chicken (*Tympanuchus cupido*). Many nonnative species were subsequently introduced, both accidentally and deliberately, including cattle, exotic grasses, and other plants and animals that have major impacts on surviving native species (Willson and Stubbendieck 2000). Seasonal flood pulses were also substantially reduced through extensive damming of the Platte River (Currier 1982, Junk et al. 1989).

Study design

We carried out fieldwork on two adjacent river islands, Mormon and Shoemaker islands, which constitute the largest contiguous expanse of prairie habitat remaining in the central Platte River Valley (Krapu et al. 2014). Land management practices in our study area included rotational cattle grazing (resting every three to four years), and haying (every two to four years), and patch burning (every two to six years). During our sampling period, burning took place in the spring prior to the bird breeding season, while grazing periods often overlapped with the breeding season. Haying occurred after the breeding season in the late summer or fall. We sampled birds at a total of 16 grassland sites (Fig. 1), of which three sites were sampled for six consecutive years, while 13 were sampled for periods between one to five years. Of the 16 total sites, 10 were grazed, four were hayed, and two were neither

Table 1. Grasshopper Sparrow (*Ammodramus saviannarum*) sampling locations (Monitoring Avian Productivity and Survivorship [MAPS] stations) in the central Platte River Valley, Nebraska Great Plains: site names and characteristics 2002–2007.

Site	Size (ha)	Years MAPS stations were active	Grazed/ Hayed	Burned
CRME	117	2003, 2004	Neither	Spring 2004
FETW	104	2005, 2006, 2007	Grazed	Spring 2005
FONE	130	2003, 2004, 2005, 2006, 2007	Grazed	Spring 2001, Spring 2005
MOFE	118	2002, 2003, 2004, 2005, 2006, 2007	Hayed	Spring 2000, Spring 2006
MOFF	94	2002, 2004, 2005, 2006, 2007	Grazed	Spring 2001, Spring 2006
MOFL	118	2003	Hayed	Spring 2000
MOFN	118	2002, 2004, 2005, 2006, 2007	Grazed	Spring 2003, Spring 2007
MOFR	104	2003, 2006, 2007	Grazed	Spring 2002, Spring 2004
MOFT	130	2002, 2003, 2004, 2005, 2006, 2007	Grazed	Spring 2004, Spring 2007
MOFV	103	2002, 2005, 2006	Hayed	Spring 1996
MOPT	103	2005, 2006, 2007	Grazed	Spring 2005
NOME	55	2003, 2004, 2005, 2006, 2007	Hayed	Spring 2000, Spring 2004, Spring 2007
OFPA	49	2003, 2004, 2007	Grazed	Fall 1998, Spring 2007
WRBS	29	2002, 2003, 2004, 2006	Grazed	Spring 2002, Spring 2003
WRMP	33	2005	Grazed	Spring 2002
WRPM	14	2002, 2003, 2004, 2005, 2006, 2007	Neither	Spring 2000, Spring 2007

grazed nor hayed. All of the sites were burned at least once during the years in which the data were collected (Table 1). Sites (hereafter pastures) ranged in size from 14 to 130 ha (mean = 88.7 ha, median = 103.5 ha), and were delineated by physical barriers including fencing, sloughs, river channels, and roads.

Bird sampling

We analyzed mark-recapture data collected annually from May 2002 to August 2007, using methods standardized by the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante and Kaschube 2009, DeSante et al. 2017) under U.S. federal bird banding permit 23224. Twelve mist nets (12 x 3 m, 30 mm mesh) were set up in each pasture in areas ranging in size from 180 x 200 m to 450 x 480 m (mean = 287 x 323 m). In accordance with MAPS protocols, each sampling occasion consisted of a netting period of six hours following sunrise (~0600) approximately once every 10 days. Effort was consistent for each sampling occasion and across years. Starting in 2005, most pastures were netted in a 300 x 300 m grid, with three rows of four nets. We identified birds captured and fitted each with a uniquely numbered USGS aluminum band, and recorded sex, age, and biometric measurements before releasing them on site (Pyle 1997).

Quantifying climate and land management parameters

We considered both climate and management parameters as independent variables (Table 1). We generated climate parameters using temperature and precipitation measurements from the National Oceanic and Atmospheric Administration (NOAA 2017) online database for the city of Grand Island, Nebraska (located approximately 20 km northeast of our research site). We created four variables to estimate yearly climatic variation: average temperature and total precipitation for the spring (March-May) of the current year, and average temperature and total precipitation for the previous year (January-December).

To investigate the effects of management actions, we created three management variables that represented time (months) since disturbances (grazing, haying, and burning) at sampling sites. For this analysis, we capped months since disturbance at 240 months (20 years), because management actions that occurred earlier than this were unlikely to have any predictable effect on habitat structure (Collins 2000). To investigate the effects of management intensity in the case of grazing, we created two additional management variables that quantified grazing via the cattle stocking rate on grazed pastures. We measured stocking rate in animal unit months per hectare (AUM/ha), which is defined as the forage requirement for one animal unit (mature cow and calf pair) for a 1-month period (Hamilton 2007, Johnson et al. 2011). Our first stocking rate variable quantified AUM/ha at each study site at the time of data collection (hereafter referred to as current stocking rate). Our second variable represented the average AUM/ha at each site for the sampling year plus the four years preceding data collection, i.e., grazing history. Sites that were not grazed during MAPS data sampling were given a value of 0.

Statistical analysis

We analyzed Grasshopper Sparrow capture data across all 16 sites using R Studio version 3.4.0 (R Core Team 2017). We removed recaptures of individuals that occurred during the same year and at the same site from the dataset to avoid double-counting. Pastures in this study were often grazed for the first or second half of the summer, meaning that the values of variables such as months since grazing and current stocking rate could change for a single pasture within a banding season. To address this issue, each banding season was separated into two sampling periods for analysis, which broadly correspond to the first and second halves of the bird breeding season. The first sampling period covered MAPS periods 3–6, roughly the end of May until the beginning of July, and the second covered MAPS periods 7–10, or the beginning of July until the beginning of August. We quantified two different response variables: (1) the number of unique adult Grasshopper Sparrows captured, an index of abundance

Table 2. Individual Grasshopper Sparrow (*Ammodramus savannarum*) adult (n = 982) and juvenile (Hatch-Year; n = 463) birds captured and released at each sampling location 2002–2007.

Site	Adults							Hatch-years						
	2002	2003	2004	2005	2006	2007	Total	2002	2003	2004	2005	2006	2007	Total
CRME		2	4				6			1				1
FETW				13	13	5	31				3	3	6	12
FONE		35	28	28	36	23	150		48	20	20	14	34	136
MOFE	24	12	6	1	3	4	50	19	2	0	0	5	0	26
MOFF	22		10	3	17	2	54	28		3	0	6	1	38
MOFL		38					38		17					17
MOFN	14		38	19	28	7	106	5		14	17	3	9	48
MOFR		5			5	1	11		1		1	1	0	3
MOFT	3	5	9	17	29	23	86	0	0	3	6	1	10	20
MOFV	5			27	35		67	1			4	4		9
MOPT				16	34	15	65				4	13	0	17
NOME		18	19	7	16	5	65		10	11	1	4	11	37
OFPA		27	24			29	80		3	12			4	19
WRBS	11	19	17		46		93	33	12	3		14		62
WRMP				5			5				1			1
WRPM	11	14	7	11	18	14	75	4	2	2	1	3	5	17
Total	90	175	162	147	280	128	982	90	95	69	58	71	80	463

(hereafter, abundance); and (2) the probability of a captured bird being a hatch-year bird, an index of productivity (hereafter, productivity; Foster et al. 2017, Saracco et al. 2019).

Before constructing candidate models, we tested for correlations among independent variables. Variables that were highly correlated ($r > 0.6$) were not included in the same model. We created a series of candidate models as generalized linear mixed models in the R package glmmTMB (Brooks et al. 2017). We employed a negative binomial distribution for the abundance models to account for overdispersion of our count data (O'Hara and Kotze 2010), and used a binomial distribution for productivity models. We created model sets consisting of management variables, and additive and/or interactive combinations of management and climate variables we developed a priori. For the productivity model set, we used the values of management variables from period 1 only, because this corresponds with the time that most birds are nesting. We included site in all models as a random effect to account for variations among sites not otherwise accounted for in our models. Variables were scaled and centered before fitting them to models, by subtracting the mean of each variable and dividing the result by the variable's standard deviation (Bring 1994). Our null model included site as a random effect, but no management or climate variables.

We used Akaike's Information Criterion (Akaike 1973) adjusted for small sample size (AIC_c ; Hurvich and Tsai 1989) to assess the fit of each model, which was determined by evaluating AIC_c values and Akaike weights (w_i) in the R package MuMIn (Barton 2019). We created a confidence set of models with a $\Delta AIC_c < 2$ of the best fitting model (Burnham and Anderson 2002). We assessed the relative importance of predictor variables by measuring the cumulative AIC_c weights of models containing the variable, and by comparing model-averaged standardized regression coefficients (β) and their 95% confidence intervals.

RESULTS

We analyzed data from 1445 Grasshopper Sparrows (Table 2), including 982 adults and 463 juveniles. We captured 1040 birds on grazed pastures (mean per pasture = 104.0 ± 25.9 SE, $n = 10$ pastures), 306 on hayed pastures (mean = 76.5 ± 9.0 SE, $n = 4$ pastures), and 99 on pastures that were not grazed or hayed (mean = 49.5 ± 60.1 SE, $n = 2$). The number of Grasshopper Sparrows captured per year varied between 180 in 2002 and 351 in 2006 (mean = 242.5 ± 25.7 SE). Climate parameters (precipitation and temperature) had the greatest effects on Grasshopper Sparrow population responses. Spring precipitation was the strongest predictor of avian abundance, and the interaction of spring temperature and months since burning was the strongest predictor of avian productivity. We found no evidence of year affecting the number of captures, beyond the yearly variations in climate already accounted for in our models. Similarly, we found no association between abundance in grazed versus hayed pastures. Adding year or pasture type (grazed versus hayed) as predictor variables to our models decreased their ΔAIC_c by at least 2, indicating that they had little effect on abundance (Burnham and Anderson 2002). Thus, we did not include variables representing year or management type in the final model set.

Abundance

Our top models predicting adult Grasshopper Sparrow abundance all included spring precipitation ($\Delta AIC_c < 2$, $n = 3$, Table 3). The highest-ranked model was spring precipitation alone ($w_i = 0.283$). Our second-ranked model included the interaction of spring precipitation with months since haying ($\Delta AIC_c = 1.55$). Our third-ranked model included the interaction of spring precipitation and grazing history ($\Delta AIC_c = 1.98$). Although both spring climatic and management variables were present in our strongest abundance models (Table 3), climatic variables representing the previous year were absent. Spring precipitation ($\beta = -0.034$, C.I. = $-0.055, -0.009$, Table 4) had a negative impact on adult abundance.

Table 3. AIC ranking of top candidate models (of 24 total) that predict Grasshopper Sparrow (*Ammodramus savannarum*) abundance (top 4 models plus null model) and productivity (top 3 models plus null model) in response to climate and land management variables and their interactions.

Response variable Model [†]	K [‡]	AIC _c [§]	ΔAIC _c	w _i [¶]
Abundance				
precip.spring	4	751.59	0	0.283
hay.months x precip.spring	6	753.14	1.545	0.131
grazing.history x precip.spring	6	753.58	1.983	0.105
temp.spring + precip.spring + current. stocking.rate	6	753.73	2.134	0.097
null	3	757.24	5.648	0.017
Productivity				
burn.months x temp.spring	5	1723.67	0	0.918
temp.spring x precip.spring	5	1728.53	4.859	0.081
temp.year x precip.year	5	1737.51	13.831	0.001
null	2	1763.79	40.119	0

[†] All models include site as a random effect.

[‡] The number of parameters in the model.

[§] Akaike's Information Criterion for small samples.

^{||} The difference between this model's AIC_c and the AIC_c of the top model.

[¶] Akaike weight.

Table 4. Model-averaged climate and land management parameter estimates within 2 ΔAIC of top model.

Parameter	Estimate	95% confidence intervals	Cumulative model weight
Abundance			
precip.spring	-0.03375	-0.055 to -0.009	0.822
hay.months	-0.0267	-0.077 to 0.03	0.142
grazing.history	0.02875	-0.011 to 0.069	0.138
hay.months x precip.spring	0.01431	-0.008 to 0.037	0.131
grazing.history x precip.spring	0.00854	-0.012 to 0.029	0.105
Productivity			
temp.spring	-0.4865	-0.771 to -0.178	0.999
burn.months	-0.8178	-1.176 to -0.459	0.918
burn.months x temp.spring	0.40451	0.087 to 0.721	0.918

Productivity

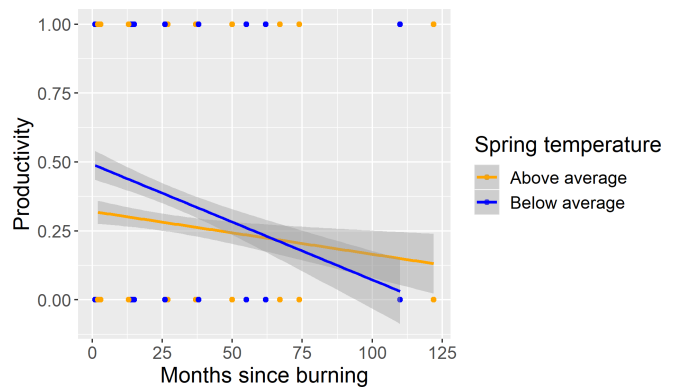
The interaction of time since burning and spring temperature was the strongest predictor of avian productivity ($w_i = 0.918$, Table 3). No other model was within 2 ΔAIC_c, making this by far the most competitive model in our model set. Grasshopper Sparrow productivity was negatively related to months since burning ($\beta = -0.818$, C.I. = -1.176, -0.459), meaning that productivity was highest in recently burned areas. The effect size of months since burning on productivity decreased with increasing spring temperature (Fig. 2).

DISCUSSION

Our results demonstrate the vulnerability of Grasshopper Sparrows (and by extension, other grassland breeding birds) to ongoing and future climate change, and indicate the potential of particular land management strategies to mitigate some of the negative impacts of climate change. Both spring precipitation and

temperature levels had significant effects on Grasshopper Sparrow population trends. Spring precipitation, the strongest predictor of adult Grasshopper Sparrow abundance (Table 2), was negatively related to adult bird abundance but did not have a measurable effect on productivity. By contrast, productivity was higher in sites that had been recently burned, and this trend was more pronounced after cooler springs (Fig. 2). Although both abundance and productivity responded positively to moderate disturbance caused by management actions, increased temperatures lessened this effect for productivity but had no effect on abundance. The existence of different drivers of abundance and productivity raises the possibility that a particular set of conditions could drive these demographic variables in different directions, setting the stage to create either population sources or sinks that function as ecological traps (Schlaepfer et al. 2002, Foster et al. 2017).

Fig. 2. Grasshopper Sparrow productivity and 95% confidence intervals in response to grassland regeneration time (months) since burning, based on linear regression of mark-recapture data on number of individual juveniles captured per day (n = 463); Productivity during years of above-average spring temperature and below-average spring temperature from 2002-2007 are plotted separately.



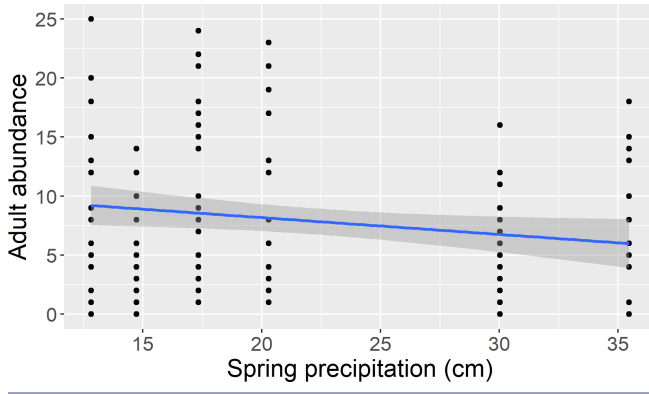
Abundance

Although identifying the mechanisms driving these patterns are beyond the scope of this research, we can use the results to hypothesize what they might be. We hypothesize that increasing spring precipitation was related to decreasing bird abundance because higher spring precipitation is conducive to plant growth in excess of ideal conditions for this species, which tends to avoid tall and dense vegetation (Patterson and Best 1996). Spring precipitation has a strong influence on bird breeding season vegetation structure, an important factor for habitat selection for Grasshopper Sparrows and other grassland birds (George et al. 1992, Fletcher and Koford 2002, Winter et al. 2005). Even small changes in spring precipitation have an important effect on vegetation structure and biomass production in tallgrass prairie (Coppedge et al. 1998), and generally interact with management activities (Rahmig et al. 2009, Ahlering and Merkord 2016). Several other studies (Derner and Hart 2007, Augustine and Milchunas 2009) have documented the effects of spring precipitation on vegetation structure and biomass production in other North American grassland ecosystems. Grasshopper

Sparrows' foraging success depends in part on the presence of sparse grassland with patchy bare ground, allowing them optimal access to their arthropod prey (Vickery et al. 1999).

The negative effect of spring precipitation on Grasshopper Sparrow abundance is consistent with findings by Kim et al. (2008) in the same study system that showed Grasshopper Sparrow population density in grazed pastures increased with drier conditions (as measured by the Palmer Drought Severity Index of the current year) from 1980 to 1996. Abundance increased along with a site's grazing history in our study. This effect was stronger after wetter springs because the resulting increase in vegetation growth may be associated with decreased overall Grasshopper Sparrow abundance (Fig. 3), but increased the importance of grazing as a tool to maintain vegetation structure at the levels conducive to higher Grasshopper Sparrow abundance. By contrast, a study in the Badlands and Prairies Bird Conservation Region about 560 km northwest of our study site in dry short-grass prairie, found that Grasshopper Sparrows were negatively affected by drier conditions (Gorzo et al. 2016). Drought conditions may magnify the impact of grazing in creating portions of short vegetation and exposed bare ground (Teague et al. 2004).

Fig. 3. Adult Grasshopper Sparrow abundance and 95% confidence intervals in response to spring precipitation levels, based on linear regression of mark-recapture data on number of individual adults captured per day (n = 982).



Productivity

The results of our productivity models were likely influenced to some extent by postfledging movements of young birds to areas with more bare ground and greater foraging potential. Little is known about postfledging dispersal of Grasshopper Sparrows, though a study by Anthony et al. (2013) in Maryland recorded an average dispersal distance of 346 m for juvenile Grasshopper Sparrows in the first few months after fledging, and concluded that the majority of juveniles remain in their natal area prior to their preformative molt. Our study sites were as close as 300 m to each other, but often much farther apart (Fig. 1)

Prescribed fire has been previously demonstrated to increase productivity for Grasshopper Sparrows (Rahmig et al. 2009, Hovick et al. 2012, Roberts et al. 2017) and other grassland birds (Roberts et al. 2017). The mechanisms driving this response are

understudied; it is possible that recently burned areas promote more successful foraging by decreasing vegetation density and increasing the amount of bare ground that Grasshopper Sparrows depend on for movement during foraging (Vickery et al. 1999, Fletcher and Koford 2002). It is also possible that recent burning increases the density of prey items available. Jonas and Joern (2007) found that the highest densities of grasshoppers in tallgrass prairies in Kansas occurred within one year of a burn. This may contribute to an increased probability of nestling survival, as adults can more effectively feed nestlings, as well as to higher postfledging survival for juveniles learning to forage.

The positive effect of prescribed fire on productivity was more pronounced after cooler springs (Fig. 2). Cooler spring temperatures and recent fire both serve to improve structural habitat characteristics for Grasshopper Sparrows by reducing standing biomass and increasing the amount of bare ground (Gibson and Hulbert 1987, Briggs and Knapp 1995, Coppedge et al. 1998, Fletcher and Koford 2002, Flanagan and Johnson 2005, Flanagan et al. 2013). During seasons with higher temperatures, the benefits provided by more recently burned areas were slightly negated, likely due to the cost of greater physiological stress incurred by nestlings and fledglings in areas with sparser vegetation. With temperatures in this region expected to increase in the future as a result of climate change (Ojima et al. 2012), the positive effect of prescribed fire on grassland bird productivity may become less pronounced. Dense vegetation can provide shelter from high temperatures, which can exceed 38 °C, and associated thermal stress conditions that can lead to nest failure. Greater vegetation cover may contribute to cooler microclimates that aid the nest survival of ground-nesting birds (Carroll et al. 2015, Fogarty et al. 2017). For an adult Grasshopper Sparrow, choosing quality breeding territory may represent a trade-off between recently burned areas with shorter vegetation and bare ground patches that provide greater foraging opportunities, and less-disturbed areas with taller, denser vegetation that can shield nestlings and fledglings from hot summer temperatures and potential predators through visual and olfactory concealment (Fogarty et al. 2017).

CONCLUSION

Predicted climate change patterns in the Great Plains include more frequent droughts and extreme precipitation events (Touma et al. 2015), which are already underway and will have increasingly important consequences for avian population trends and other biodiversity in the future (Langham et al. 2015). In recent years, precipitation levels in the study area have increased significantly, which may contribute to driving further Grasshopper Sparrow and other bird declines (Rosamond, Goded, Soltan, et al. *unpublished manuscript*). By contrast, higher rainfall may positively influence this species in drier ecosystems (Gorzo et al. 2016), illustrating how the impacts of climatic variation on avian population trends are often area and ecosystem-dependent. Land management actions to promote increased adult and juvenile Grasshopper Sparrow abundance must consider their respective ecoregions, ecosystems, and environmental conditions. In our case, land management strategies that include frequent burning and moderate grazing appear to maintain vegetation structure for breeding Grasshopper Sparrows (Powell 2008, Fuhlendorf et al. 2009).

Our findings thus demonstrate the need to incorporate climate factors together with local and regional site characteristics in conservation strategies that consider future climate change scenarios (Gibson and Hulbert 1987, Teague et al. 2004, Rahmig et al. 2009). Our findings also highlight both the potential and the limits of land management actions to locally mitigate negative impacts of climate change on grassland species of conservation concern. In our case, the influence of land management on Grasshopper Sparrow population trends was more constrained in years with low precipitation and high spring temperatures. These constraints highlight an increasing body of evidence that demonstrates the urgent need to make fundamental changes toward reducing the destruction of native grasslands, greenhouse gas emissions, and other factors contributing to species declines and climate change (Ripple et al. 2017).

Positive avian abundance responses may be used to track habitat conditions attractive to breeding birds, whereas habitat quality may be demonstrated by demographic data, such as evidence of breeding success (van Horne 1983, Foster et al. 2017, Saracco et al. 2019). This study focused on drivers of the population dynamics of a species of conservation concern that is also an effective indicator of the densities of other grassland breeding bird species (Elliot and Johnson 2018). Future studies should explore the mechanisms by which climatic variation affects this species and other grassland breeding birds, for example, by specifically investigating food availability and foraging success, thermal stress, and vegetation structure and composition as they affect bird population trends. Such studies would provide additional insights into grassland bird ecology and inform targeted conservation actions.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/1515>

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