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Weather Constrains the Influence of Fire and Grazing on Nesting Greater Prairie-Chickens☆,☆☆

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ABSTRACT

Grasslands are highly imperiled as a result of widespread conversion for agriculture and alteration from human development. Remaining grasslands are susceptible to mismanagement, development and fragmentation, and variable weather associated with global climate change. Understanding the response of declining grassland species to these challenges will be important for informed conservation and management. We assessed Greater Prairie-Chicken *(Tympanuchus cupido)* survival and nest site selection in tallgrass prairie characterized by interacting fire and grazing disturbance and oil and gas infrastructure. We found that Greater Prairie-Chicken survival was most affected by weather variability (expressed in our models as solar radiation) while most other variables had little influence. Focal disturbance did not affect survival directly, but vegetation height, which is greatly influenced by fire and grazing processes, was positively associated with nest survival. Greater Prairie-Chickens chose nesting locations that maximized time post fire while minimizing tree cover and distance to leks. Future conservation efforts for Greater Prairie-Chickens should focus on variable fire regimens that create areas of residual biomass to increase vegetation height and potentially reduce the effects of solar radiation while decreasing woody vegetation that is avoided by nesting females. However, even the best management practices may prove to be futile in the southern Great Plains if climate change continues to create unfavorable nest survival conditions. Management that creates and maintains suitable nesting sites through the use of interacting fire and grazing should maximize the potential for high reproduction in years when local weather variables are favorable.

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Introduction

Grasslands are one of the most imperiled ecosystems in the world (Hoekstra et al., 2005), and loss of grassland environments is widespread. As a consequence, many grassland species are in decline and of conservation concern. Grassland birds specifically have experienced major population declines over the last half century (Vickery et al., 1999; Sauer et al., 2012). In addition to habitat loss, global changes in climate and an increase in energy infrastructure in rangeland ecosystems threaten conservation of remaining grassland organisms (Kuvlesky et al., 2007; Pruett et al., 2009; Hovick et al., 2014a). To improve future conservation and management of grasslands and their associated biota, there is a need to understand the relative impacts of management, anthropogenic structures, and a changing climate.

Grasslands are disturbance dependent ecosystems that rely on grazing and fire processes to drive and shape ecosystem structure and function (Collins & Wallace, 1990; Anderson, 2006). Traditionally, the application of fire and grazing in rangelands has been under a utilitarian paradigm and goals have been production based, which often results in homogenous systems that are largely devoid of heterogeneity (Fuhlendorf et al., 2012). Although these practices have been mostly successful at limiting heavily grazed and ungrazed areas, they have limited disturbance-driven heterogeneity and biodiversity (Fuhlendorf et al., 2012). More recently, however, the focus of conservation in rangelands has begun a paradigm shift that promotes the conservation of pattern and process through the restoration of natural disturbances (Derner et al., 2009; Fuhlendorf et al., 2009; Fuhlendorf et al., 2012). The use of interacting fire and grazing (i.e., pyric herbivory) can increase the breadth of niches available in

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Table 1
Climatic variables from the Tallgrass Prairie Preserve, OK, measured at a standardized Oklahoma Mesonet weather station. Variables are summarized to contrast weather patterns from the 15 years before the study with weather events that occurred during the 3-year study. Maximum temperature (°C) is the average maximum temperature for each day of the month, rainfall (cm) is the sum of all rainfall events in the month, solar radiation ($W \cdot m^{-2}$) is the overall average of the averaged daily solar radiation recorded for every day of the month, and > 32 represents the number of days in the month where temperatures exceeded 32°C. Ranges are given parenthetically below the average value for each variable.

	15 years previous (1996–2010)				3 years of study (2011–2013)			
Month	Max temp.	Rainfall	Solar radiation	>32	Max temp.	Rainfall	Solar radiation	> 32
April	30.44	9.83	18.97	0.43	32.60	16.41	18.53	0.33
	(28-34)	(3.18-17.40)	(17.45-20.99)	(0-5)	(32-34)	(9.07-25.60)	(16.34-19.70)	(0-1)
May	31.67	11.56	21.60	0.93	32.78	12.88	21.17	1.33
	(29-35)	(2.46-17.02)	(17.44-24.1)	(0-7)	(32-34)	(6.88-24.21)	(18.41-24.90)	(1-2)
June	33.57	15.60	23.57	4.86	36.48	7.49	25.92	13.33
	(32-37)	(2.39-32.41)	(20.19-25.54)	(0-15)	(36-38)	(7.34-7.59)	(25.75-26.22)	(8-21)
July	36.87	8.92	24.31	17.36	40.74	10.16	25.03	24.67
	(34-41)	(1.37-17.60)	(22.2-26.92)	(8-26)	(37-43)	(1.07-22.58)	(23.6-25.74)	(12-31)
August	38.26	8.02	21.67	18.79	41.29	9.53	21.38	20.00
	(34-42)	(0.03-24.03)	(18.64-24.4)	(7-28)	(36-44)	(8.64-10.52)	(20.95-21.76)	(13-25)

rangelands, thereby favoring diversity and potentially improving long-term stability in these systems (Otsfeld et al., 1997; Wiens, 1997; Fuhlendorf et al., 2006; Hovick et al., 2014b). As a result, recent studies in the Great Plains have called for management that promotes patchy disturbance (Patten et al., 2007; With et al., 2008; Augustine & Sandercock, 2011; McNew et al., 2012). Concurrently with this paradigm shift, new challenges are emerging as energy development in rangelands is increasing and global climate change is creating more variable weather patterns (Lyon & Anderson, 2003; Holloran et al., 2010; Obermeyer et al., 2011; IPCC, 2013).

Energy extraction processes and the associated infrastructure can have many negative direct and indirect effects on native rangelands species (Kociolek et al., 2011; Obermeyer et al., 2011; Douglas et al., 2012). Although the direct effects are often most obvious and well documented (Kunz et al., 2007; Wolfe et al., 2007; Kociolek et al., 2011), the avoidance or displacement associated with energy infrastructure can be much greater than direct habitat loss resulting from development (Zeiler & Grünshauchner-Berger, 2009; Pearce-Higgins et al., 2012; Hovick et al., 2014a; Winder et al., 2014). Additionally, the increased direct and perceived fragmentation to grasslands that results from anthropogenic structures may exacerbate future challenges associated with greater climate variability and mismanagement by reducing species' abilities to shift to suitable habitats (Pruett et al., 2009; Lawler et al., 2013).

Climate-driven changes have increased biodiversity loss and understanding how species respond to a warming and more variable climate is a central challenge facing ecologists (Dawson et al., 2011). Climate changes are now occurring at unprecedented rates (IPCC, 2013), which raises concerns for extinctions in species that are unable to adjust (Veneir et al., 1999). Moreover, changes are not uniform in space or time and patterns can be complex as a result of interplay between region-specific and species-specific factors that are affected by local management (Tingley et al., 2012). Greater investigation of species' responses to current weather conditions can improve predictions of species' responses to future climate change and potentially inform conservation efforts allowing organisms to persist.

Increasing climate variability, management that promotes homogeneity, and the construction of new energy structures in previously unfragmented rangelands are all challenges facing Greater Prairie-Chickens (*Tympanuchus cupido;* hereafter "prairie-chicken"). Prairie-chickens have been referred to as an indicator and umbrella species of the tallgrass prairie ecosystem (Poiani et al., 2001; Pruett et al., 2009), and they have experienced one of the greatest distribution contractions and population declines of any grassland species (Schroeder & Robb, 1993; Robbins et al., 2002). Remaining prairie-chicken populations are highly susceptible to human alterations of the landscape because of their complex life history traits and need for large, open, and unfragmented landscapes (Johnsgard, 2002; PIF, 2012). Yet the effects of these potential threats have gone mostly unexamined. Previous research has proposed that rangeland practices that promote heterogeneity should be implemented, but few have investigated prairie-chicken survival or habitat use in landscapes with interacting fire and grazing (Patten et al., 2007; McNew et al., 2012). Furthermore, until recently no research had investigated the effects of energy development on prairie-chickens (Winder et al., 2013; Winder et al., 2014; McNew et al., 2014), and few studies have examined the effects of oil and gas infrastructure (Jarnevich & Laubhan, 2011). Moreover, the influence of climatic variables on prairie-chicken nest survival is largely unknown and because this is a Pleistocene relic species that is well adapted to cold environments, it may be particularly vulnerable to a warming climate at the southern extent of its range (Johnsgard 1983; Storch, 2007).

We examined prairie-chicken nest survival and nest site selection in tallgrass prairie characterized by interacting fire and grazing and anthropogenic structures associated with oil and gas extraction. Our specific objectives were to 1) test the influence of grassland management (i.e., fire and grazing), energy infrastructure, and weather variables on nest survival of prairie-chickens, and 2) examine the relative role of management, energy infrastructure, and lek sites on nest site selection by prairie-chickens.

Methods

Study Site

We examined prairie-chicken nest survival and selection across approximately 30 000 ha of tallgrass prairie composed of The Nature Conservancy's Tallgrass Prairie preserve (hereafter, the preserve) and an adjacent private ranch. Both properties are managed with fire and grazing in a way that creates heterogeneity, but management is done at different scales. The private ranch creates heterogeneity through grazing and fire deferment across pastures, whereas the preserve allows fire and grazers to interact within pastures. At the preserve this takes place across two different units. One has native bison *(Bison bison)* and is ~9 500 ha, while the other unit is managed with cattle *(Bos taurus)* and has five subunits that vary in size (430–980 ha) and the proportion burned (range: 12–100%). Both units are moderately stocked (2.1–2.4 animal unit month/ha-1), and all animals are contained by exterior fences for organizational purposes without any interior pasture fencing. To address potential differences between the two properties that may affect survival, we used variables

Table 2
Summary statistics for noncorrelated variables used to examine nest survival of Greater Prairie-Chickens at the Tallgrass Prairie Preserve, OK, USA, 2011–2013.

Parameter/classification	Mean (SE)	Range	Definition
Anthropogenic			
Distance to road (m)	228.85 (29.00)	2.48-925.67	Distance from a nest to all road types (no paved roads in study area)
Well density	12.24 (1.25)	0.00-27.07	Wells per square kilometer measured in 2-km radius of the nest
Distance to power-pole (m)	1178 (89.72)	107.71-2602.67	Distance from a nest to the nearest power-pole
Management			
Months post fire	21.19 (1.80)	2.00-46.00	Months elapsed since the last fire at the nest site
Forb	41.85 (3.67)	3.00-86.00	Forb canopy cover in a 0.5-m^2 quadrat placed over the nest bowl
Litter	80.60 (4.40)	3.00-98.00	Litter cover in a 0.5-m^2 quadrat placed over the nest bowl
Litter depth	4.49 (0.54)	0.00-14.00	Litter depth in a 0.5-m^2 quadrat placed over the nest bowl
Vegetation height (cm)	65.49 (2.66)	26.00-119.00	Tallest piece of vegetation in a 0.5-m^2 quadrat placed over the nest bowl
Vegetation density	3.79 (0.13)	1.75-5.90	Cumulative score of Nudd's board reading taken at nest site
Weather			
Maximum temperature (°C)	83.70 (1.45)	44.00-101.00	Daily maximum temperature recorded on site
Relative humidity	71.88 (1.92)	43.00-98.00	Average daily relative humidity recorded on site
Precipitation (cm)	0.36 (0.18)	0.00-10.97	Daily precipitation total recorded on site
Solar radiation	23.73 (0.96)	3.45-30.67	Daily maximum solar radiation measured in $W \cdot m^2$ on site

measured at nest sites. Additionally, in preliminary analysis we tested for overall survival differences between properties and found none, so we conducted the final analysis by grouping nests from both properties (β_{ranch} = -0.36, SE = 0.37, CI -1.08 to 0.36).

Data Collection

We trapped prairie-chickens using walk-in funnel traps during the springs of 2011–2013 (Schroeder & Braun, 1991). Trapping started in mid-March and concluded in early May each year. We focused on leks (i.e., central display areas where males gather to attract females) with the most displaying males but attempted to trap all available leks with ≥ 5 males. We monitored traps each morning 1 hour before sunrise until lekking activity ceased or until we were forced to flush birds in order to retrieve trapped individuals.

Table 3
Models explaining the effects of temporal, anthropogenic, management, and local weather variables on Greater Prairie-Chicken nest survival at the Tallgrass Prairie Preserve, OK, USA, 2011–2013.

Model	ΔAIC_c[1]	k[2]	w[3]	Deviance
Temporal models				
Linear trend	0.00	2	0.52	214.96
Null	1.71	1	0.22	218.68
Quadratic trend	1.72	3	0.22	214.66
Year effects	5.09	3	0.04	218.03
Anthropogenic models				
Null	0.00	1	0.36	218.68
Distance to power-pole	0.38	2	0.30	217.05
Distance to road	1.35	2	0.19	218.02
Well density	1.74	2	0.15	218.41
Management models				
Vegetation height	0.00	2	0.25	216.19
Null	0.48	1	0.19	218.68
Months post fire	0.69	2	0.18	216.87
Litter depth	1.23	2	0.13	217.42
Vegetation density	1.87	2	0.10	218.06
Forb	2.29	2	0.08	218.48
Litter	2.38	2	0.07	218.57
Weather models				
Solar radiation	0.00	2	0.71	210.73
Maximum temperature	2.62	2	0.19	213.35
Precipitation	5.44	2	0.05	216.17
Null	5.94	1	0.04	218.68
Relative humidity	7.91	2	0.01	218.63
Best models				
Solar radiation + veg. height[4]	0.00	3	0.29	208.50
Solar radiation	0.21	2	0.26	210.73
Solar radiation + linear trend	0.76	3	0.20	209.26
Global	1.00	4	0.17	207.48
Linear trend	4.44	2	0.03	214.96
Linear trend + veg. height	4.61	3	0.03	213.11
Veg. height	5.67	2	0.02	216.19
Null	6.15	1	0.01	218.68

[1] Akaike's Information Criterion adjusted for small sample sizes. Numbers are based on differences from the best model within each model set.
[2] Number of parameters in each model.
[3] Model weight.
[4] AIC_c for best model = 214.54.

We attached necklace-style radio transmitters to adult female prairie-chickens at the time of capture. We used series A4100 transmitters weighing approximately 16 g (~1.5 % of the bird's body weight) and having an expected life span of 900 days (Advanced Telemetry Systems, Isanti, MN). Females were then monitored every 1 to 3 days with daily checks after we determined they had localized in an area. We flushed females intentionally after they localized in the same area for 3 consecutive days to observe nest contents and record exact nest locations using a handheld GPS unit. Additionally, we marked nests by placing a large rock 5 and 10 m south of nest sites. To minimize disturbance after finding nests, females were monitored every 2 days at distances > 100 m by triangulation of the radio signal. Once we determined that the female was no longer tending the nest, we revisited the nest site to determine nest fate. A nest was classified as successful if ≥ 1 egg hatched.

We measured vegetation at nest sites using a 0.5 m^2 quadrat centered over the nest location (Daubenmire, 1959). Canopy cover was estimated for the following plant functional groups: grasslike, forb, litter, bare ground, and shrub. We measured vegetation height using the tallest stalk within each quadrat, and litter depth was measured in the northwest corner of each quadrat. Additionally, we visually estimated vegetation density using a Nudd's board adapted for grassland/shrubland use (Nudds, 1977; Guthery et al., 1981).

Weather variables were collected on-site at an Oklahoma Mesonet station (Brock et al., 1995). The weather station collects a variety of weather variables every 5 minutes, 365 days of the year. For the purposes of this study, we included weather variables that have been shown to affect nest survival in grouse or that we hypothesized may influence the ability of a predator to locate nests (Grisham et al., 2013; Hovick et al., 2014c). The variables of interest included maximum daily temperature, minimum daily temperature, daily precipitation total, average daily relative humidity, average daily barometric pressure, and average daily solar radiation. During the course of our 3-year study, climatic conditions were highly variable both within and across breeding seasons (Table 1).

Finally, we used ArcGIS 10.0 (ESRI 2011) and GeoEye-1 satellite imagery taken in 2010 to measure tree cover and distances to and densities of anthropogenic structures such as roads, oil and gas wells, and power poles. We digitized images to mark known well locations and used local expertise and ground-truthing to identify

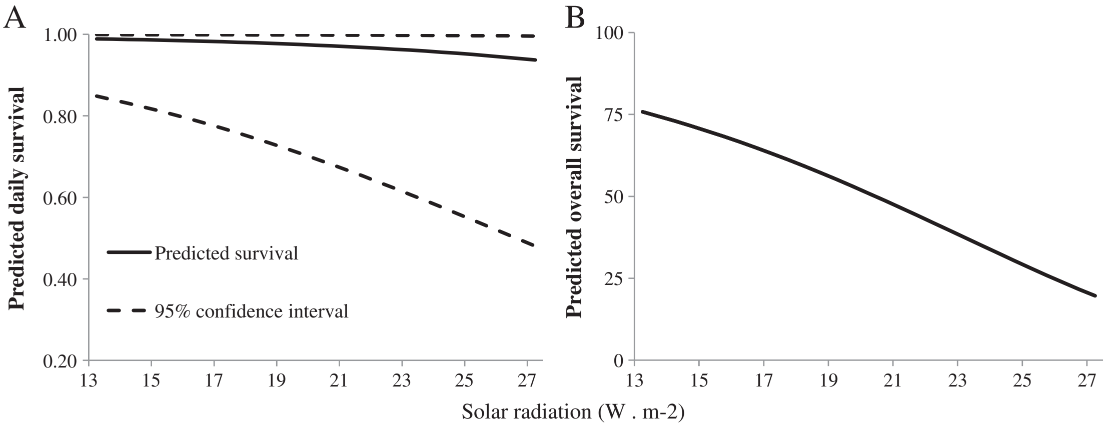

Fig. 1. Logistic regression curves showing **(A)** predicted daily survival rates of nesting Greater Prairie-Chickens as a function of solar radiation and **(B)** predicted overall survival as a function of solar radiation assuming a 25-day incubation period for nesting Greater Prairie-Chickens. Solar radiation range is based on the values recorded at the on-site OK-Mesonet weather station at the Tallgrass Prairie Preserve, OK, USA from 2011–2013.

recently constructed infrastructure that was not on current imagery. Additionally, anthropogenic structures and burn-patch perimeters were recorded with a Trimble handheld GPS unit throughout the preserve.

Data Analysis

Nest Survival

We used the nest survival model in program MARK to quantify the effects of management, anthropogenic structures, and local weather variables on nesting prairie-chickens (White & Burnham, 1999; Dinsmore et al., 2002). Our first step was to create four model groups based on temporal trends, management, anthropogenic structures, and weather variables. We then used Pearson's correlation to assess multicollinearity among variables within each group, retaining one variable from any highly correlated variable pairs ($r >$ 0.6; Coppedge et al., 2008). As a result, we used five management, three anthropogenic, and four weather variables to examine nest survival (Table 2). We then ran single-variable models in all four groups and ranked them on the basis of their relative importance (AIC weight [w_i]) and in comparison to a null model. Single-variable models from each group that had greater relative importance than the null model and were within two AIC_c units of the best model for their respective model set were considered strongly supported and used to produce a "best" model set. To gauge the relative importance of each variable in the best model set, we ran all single, two-way, and three-way combinations of models using the strongly supported variables. Additionally, we ran a global model that included all parameters and null model (intercept only) for comparison (Loss & Blair, 2011). This method created the opportunity for each variable to be included in the same number of models within the best model set and allowed us to rank the relative importance of each variable on prairie-chicken survival. We calculated model-averaged parameter weights for each variable that was strongly supported by summing AIC weights (w_i) in the best model set and then dividing by the total number of models that each variable occurred in (Burnham and Anderson 2002). This allowed us to determine which parameters were most informative despite multiple competitive models ($\Delta AIC_c \leq 2$) and helped us to overcome the lack of a goodness of fit measure for nest survival modeling (Arnold 2010).

Nest Site Selection

We used resource selection functions in program R to determine nest site selection of prairie-chickens (R Development Core Team, 2014). Resource selection functions (RSFs) are defined as any function that is proportional to the probability of use by an organism (Manly et al., 1993). The RSF method is highly applicable to natural resource management and can be a powerful tool when linked to a

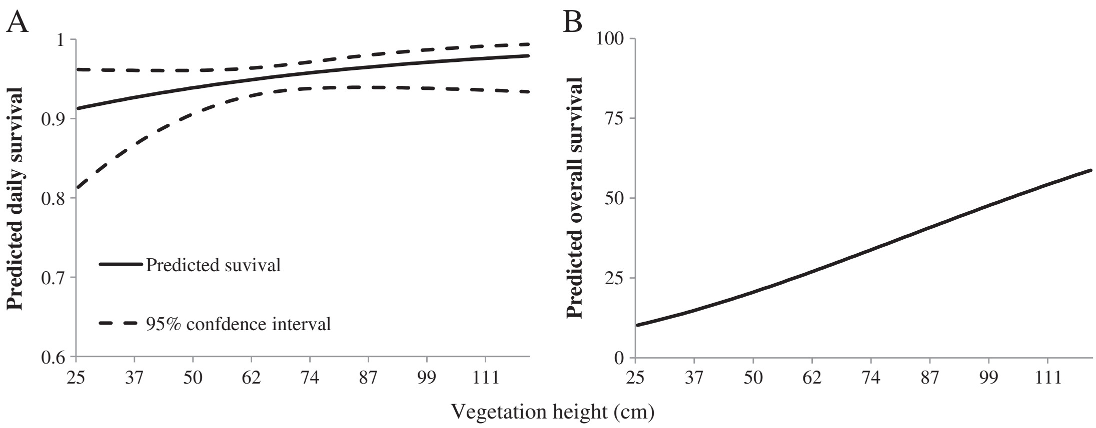

Fig. 2. Logistic regression curves showing **(A)** predicted daily survival rates of nesting Greater Prairie-Chickens as a function of vegetation height and **(B)** predicted overall survival as a function of vegetation height assuming a 25-day incubation period for nesting Greater Prairie-Chickens. Vegetation heights are based on the values recorded at the Tallgrass Prairie Preserve, OK, USA from 2011–2013.

Table 4
Resource selection models investigating the influence of management, anthropogenic structures, and lek sites on Greater Prairie-Chicken nest site selection at the Tallgrass Prairie Preserve, OK, USA, 2011–2013.

Model	ΔAIC_c^1	k^2	w^3	Deviance
Fire + distance to lek + trees [d]	0.00	4	0.860	193.73
Global	4.70	7	0.080	192.07
Fire	5.60	2	0.050	203.45
Trees	12.70	2	0.001	210.62
Distance to lek	14.80	2	<0.001	212.70
Null	16.00	1	<0.001	215.94
Distance to road	16.20	2	<0.001	214.10
Well density	17.80	2	<0.001	215.68
Distance to power pole	18.00	2	<0.001	215.92
Anthropogenic	20.20	4	<0.001	213.89

[1] Kaike's Information Criterion adjusted for small sample sizes. Numbers are based on differences from the best overall model.
[2]Number of parameters in each model.
[3]Model weight.
[4]AIC_c for best model = 201.73.

geographical information system (Boyce et al., 2002). We employed a binomial generalized linear model for our use versus availability sampling design where we assigned three random (available) points to each nest site point (use) (Allred et al., 2011). We randomly distributed three points within a 2-km radius buffer surrounding each nest site and random point because our preliminary data showed that bird movement averaged approximately 1.5 km from leks to nest sites and 90% of nests were within 2200 m of leks. Therefore a 2-km buffer represented a realistic "available" area for nest site selection in this population. We then used the information gathered within the random and nest site buffers to populate the binomial generalized linear model. Similar to nest survival models, we examined management-related and anthropogenic structure parameters that have been identified as potential influences for nest selection in prairie-chickens or other gallinaceous birds (Hagen et al., 2004; Aldridge & Boyce, 2007; McNew et al., 2012). We did not use weather variables to examine nest selection because the resolution of that data was too great to examine nest locations and nearby random locations. Additionally, we used remote sensing to identify random locations and, as such, we did not report fine-scale vegetation parameters but instead used months post fire-grazing, which affects many of the fine-scale vegetation parameters in a predictable way (Fuhlendorf & Engle, 2004; Allred et al., 2011; McGranahan et al., 2012). Finally, we used Pearson's correlation to assess multicollinearity among variables within each group, retaining one variable from any highly correlated variable pairs ($r > 0.6$). As a result, we used six total covariates to examine prairie-chicken nest selection in this landscape that included time since fire, distance to leks, tree cover, oil well density, distance to power pole, and distance to nearest road. We created one model set for nest site selection by comparing univariate models of all parameters of interest to a null, global, anthropogenic (i.e., additive model including all human structures) and an additive model using variables from univariate models that had greater importance weights than the null model (Loss and Blair 2011). We evaluated all nest selection models following the guidance of Burnham and Anderson (2002) using Akaike's Information Criteria for small samples (AIC_c) and model weights (AIC weight [w_i]).

Results

We attached transmitters to 40 female prairie-chickens and found a total of 47 nests (36 first attempts and 11 re-nests) from 2011–2013. The constant daily survival rate (DSR) for all nests and years combined was 0.9525 and, when exponentiated over the 25-day incubation period, indicated that prairie-chicken nests in this population have an ~30% chance of surviving until hatch. Similarly, using mean covariate estimates from our most supported model from the best model set, we found that prairie-chicken nests had an ~34% chance of surviving the 25-day incubation period.

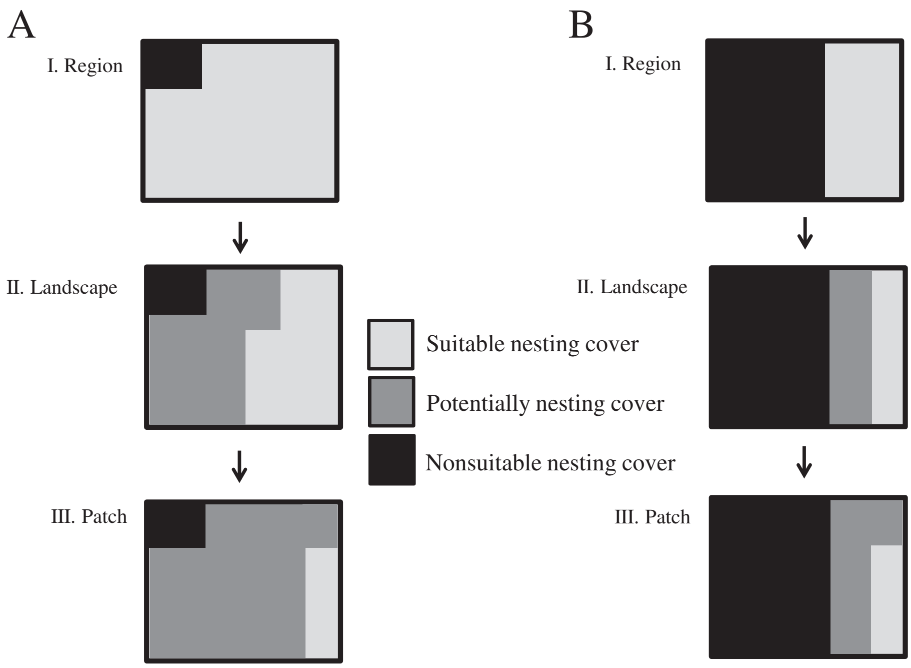

Fig. 3. Conceptual model of two theoretical rangelands because our data suggest that filters exist at varying scales to influence prairie chicken habitat selection. Contiguous grassland **(A)** would likely benefit from management actions at finer scales (i.e., patch) because fewer filters exist to prevent prairie-chicken selection at the broadest scales (i.e., region). Actions such as an altered burning regimen, a reduced herbicide application, or reduced stocking rates may be beneficial. In contrast, management in landscapes similar to much of the Great Plains **(B)** would benefit from a focus on region-scale habitat suitability with little focus on the patch level (i.e., nesting conditions), thereby increasing the amount of potential nesting cover with proper management actions (e.g., tree removal, restored disturbance regimes, addition of grasslands).

We used 12 covariates to examine the effects of management, anthropogenic structures, and local weather on the survival of 47 prairie-chicken nests with known fates. We found that local weather variables had the greatest influence on prairie-chicken survival while distance to and density of energy infrastructure had relatively less effect on estimated nest survival rates (Table 3). Survival of prairie-chicken nests was most affected by solar radiation (parameter importance weight = 0.23), vegetation height (parameter importance weight = 0.13), and a linear temporal trend (parameter importance weight = 0.11), although vegetation height and the linear temporal trend did have confidence intervals that slightly overlapped with zero and subsequently could have no effect on survival (Table 3). Solar radiation had a negative influence on nest survival (β = -0.13 on a logit scale, SE = 0.06, CI = -0.24 to -0.02; Fig. 1), there was a trend toward a positive influence of vegetation height (β = 0.02, SE = 0.01, CI = -0.005 to 0.036; Fig. 2), and there was a trend toward a linear decrease in survival throughout the breeding season (β = -0.22, SE = 0.12, CI = -0.45 to 0.007).

We used 48 nest site locations to determine resource selection by nesting prairie-chickens and found that time since fire, tree cover, and distance to lek sites were most influential in determining nest locations. In contrast, oil and gas infrastructure in this landscape had relatively little impact on prairie-chicken nest placement (Table 4). Of the covariates we examined, months since fire had the greatest impact of all parameters examined and prairie-chickens sought nesting areas that maximized the amount of time elapsed since an area had previously burned (β = 0.64, SE = 0.18, CI = 0.30 to 1.00). Furthermore, prairie-chickens selected nesting locations with minimal tree cover (β = -0.57, SE = 0.32, CI = -1.34 to -0.05) and sites that minimized distances from leks (β = -0.40, SE = 0.20, CI = -0.81 to -0.02).

Discussion

Rangeland practices that restore heterogeneity to grasslands have been shown to be an effective strategy for promoting diversity of avian communities (Fuhlendorf et al., 2006; Hovick et al., 2014b; 2014d) and have been suggested as a likely method for stabilizing declining prairie-chicken populations (Patten et al., 2007; McNew et al., 2012). Our research in structurally heterogeneous grasslands resulting from interacting fire and grazing found that prairie-chickens may benefit from variable disturbance regimens. Our justification for this is twofold. First, prairie-chickens tended to have higher survival in areas with greater time post fire and grazing, and second, prairie-chickens avoided nesting in areas with relatively greater amounts of tree cover. Therefore prairie-chickens require disturbance (i.e., fire) to reduce woody vegetation or expansion into grasslands while maintaining areas that have gone unburned and grazed in multiple years for nesting cover. Importantly, while fire and grazing did directly influence nest site selection, they were less important in determining nest survival and, instead, local weather variables appear to be the most influential. These results are consistent with an emerging body of evidence emphasizing the importance of thermal environments and climatic conditions on gallinaceous bird habitat use and survival (Guthery et al., 2005; Fields et al., 2006; Grisham et al., 2013; Larsson et al., 2013; Hovick et al., 2014c).

Our findings reveal that increased solar radiation (indicating fewer clouds and brighter days) decreased the probability of nest survival. Solar radiation likely impacted nest survival through increased operative temperatures (Hovick et al., 2014c)—an incorporation of energy flow between an animal and its environment that depends on solar radiation, air temperature, wind, and humidity (Dzialowski, 2005)—which can increase stress on incubating females and potentially kill embryos if nests are exposed for prolonged periods of time (Webb, 1987). Solar radiation may have had greater effects during the course of our study than during average weather years as both maximum temperature and solar radiation reached levels outside the range recorded at the onsite weather station over the past 2 decades (Table 1). However, weather experienced during the course of this study may become more frequent as climate change predictions for the southern Great Plains are forecasting more extreme weather events with an increase in overall temperature (IPCC, 2013). Conservation efforts that vary focal disturbance across broad scales can maximize thermal refugia and potentially limit the heat stress experienced by nesting prairie-chickens (Hovick et al., 2014c).

Our estimated nest survival rates were within the range of previously reported rates for prairie-chickens with a constant nest survival estimate of 29.6% for a 25-day exposure period. For comparison, if we extrapolated our daily survival estimate across a 35-day exposure period similar to previous research done in the Flint Hills (Augustine & Sandercock, 2011; McNew et al., 2012), our overall nest survival estimate would be 18.2%, which despite being low, is still greater than rates recently reported in portions of the Flint Hills (e.g., 2–16%; McNew et al., 2012). Additionally, nest survival was much lower during our study than the 50% threshold recommended to maintain stable populations (Westemeier, 1979). Low nest survival in this population appears to be closely linked to local weather variables, a finding that has been reported for populations in Kansas and Nebraska (Fields et al., 2006; Anderson 2012). However, these effects may be exacerbated in Oklahoma as this is the southernmost extant population of Greater Prairie-Chickens, making them especially susceptible to warming trends, extreme heat events, and other factors that commonly confront populations on a species distribution boundary (Sexton et al., 2009).

Prairie-chicken nest selection in this contiguous, grassland landscape was dependent on fire regimens, with females selecting areas that maximized the time since a site had burned. In addition, females selected areas that minimized tree cover, which illustrates the importance of maintaining fire in grasslands, especially grasslands in the southern Great Plains that are threatened by conversion to Eastern red cedar (*Juniperus virginiana*) woodland through fire suppression (Briggs et al., 2002). This creates a paradox because prairie-chickens require nesting patches that have gone unburned, but fire is necessary to prevent woody vegetation from invading grassland environments. Additionally, conservation for species with large home ranges such as the Greater Prairie-Chicken can be challenging and needs to occur at appropriate scales (Noss et al., 1996). As such, we created a simple conceptual figure to elucidate the differences and challenges in attempting to manage for a species at fine scales without consideration of the status and condition of habitat at the broadest scale (e.g., watershed, region) (Fig. 3A). Despite the potential limitations of simplifying a complex issue, we attempt to illustrate that conservation efforts at fine scales have high potential to influence prairie-chicken populations when landscapes are primarily contiguous grasslands (i.e., Flint Hills), which is supported by recent research from the Flint Hills suggesting conservation that alters disturbance regimens to affect nest site conditions can be highly effective (McNew et al., 2012, 2013). In contrast, conservation efforts at fine scales in landscapes with high amounts of fragmentation are unlikely to improve the outlook for long-term population persistence and efforts would be better spent focusing on a reduction of fragmentation at broad scales (e.g., tree removal) (Fig. 3B).

Anthropogenic structures had relatively little influence on prairie-chicken nest survival or nest site selection, which contrasts the overall trends associated with grouse and energy infrastructure (Lyon & Anderson, 2003; Walker et al., 2007; Zeiler & Grünshanchner-Berger, 2009; Harju et al., 2010; Hagen et al., 2011; Hovick et al., 2014a).

Several factors likely influenced our results. First, use of home ranges throughout the year or long-term lek data may be more adequate measures of the influence of structures on grouse habitat use and behavior because nesting hens may use cues at scales that do not reflect behavior throughout the rest of the year (Walker et al., 2007; Harju et al., 2010; Hagen et al., 2011; Winder et al., 2014). Second, much of the energy infrastructure in this region has been on the landscape for > 50 years and it is possible that new infrastructure and old infrastructure influence prairie-chickens differently as some research suggests they are capable of acclimating to structures over time (Hagen et al., 2011). Finally, most grouse species exhibit high-site fidelity, which may confound any perceived avoidance of structures in breeding areas (e.g., leks), but structures may affect the long-term persistence by exhibiting a lag effect through an eventual decline as later generations begin to avoid previously used sites (Walker et al., 2007).

Overall, our results suggest that the influence of fire and grazing on nesting prairie-chickens is constrained by local weather variables in the southern Great Plains. However, nest survival tended to increase with taller vegetation and prairie-chickens preferentially selected nest sites in areas with greater time since fire. These findings illustrate the importance of maintaining residual biomass and support previous work suggesting that practices such as annual burning coupled with early intensive stocking is detrimental to prairie-chicken populations (Robinson et al. 2002). Moreover, prairie-chickens selected nest sites in areas with relatively less tree cover, so the use of variable fire regimens that can reduce woody vegetation while maintaining portions of the landscape that have gone unburned for multiple years may be the most beneficial. Our findings support previous recommendations to improve conservation efforts for prairie-chickens by promoting interacting grazing and fire disturbances that can increase structural heterogeneity (Patten et al., 2007; Augustine & Sandercock, 2011; McNew et al., 2012). As this research shows, when weather conditions are highly variable and extreme, they can have a greater influence on nest survival than other land use practices, but promoting variable fire and grazing disturbances may maximize reproduction when weather conditions are favorable.

Management Implications

Greater Prairie-Chickens are experiencing precipitous population declines throughout much of the Flint Hills region, and these declines are likely associated with management (Robbins et al., 2002; McNew et al., 2012). Annual burning followed by early intensive stocking removes residual biomass and limits the ability of prairie-chickens to conceal their nests and may in part be responsible for increased rates of nest predation. Our findings suggest that a variable fire and grazing disturbance regimen that allows for areas with residual biomass but consistent fire that prohibits expansion of woody vegetation can benefit prairie-chicken populations, while maintaining production and potentially buffering against production losses associated with a more variable climate (Allred et al., 2014). Future rangeland management that promotes multiple uses needs to recognize that no single state exists to meet all objectives and that production and conservation can coexist when the focus is on the conservation of patterns and processes rather than single objectives (Fuhlendorf et al., 2012). Practices that do promote heterogeneity will create suitable nesting sites that can maximize the potential for reproduction when other variables such as weather allow.

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