



## RESEARCH ARTICLE

**Interactive effects between nest microclimate and nest vegetation structure confirm microclimate thresholds for Lesser Prairie-Chicken nest survival****Blake A. Grisham,<sup>1\*</sup> Alixandra J. Godar,<sup>1#</sup> Clint W. Boal,<sup>2#</sup> and David A. Haukos<sup>3#</sup>**<sup>1</sup> Department of Natural Resources Management, Texas Tech University, Lubbock, Texas, USA<sup>2</sup> U.S. Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Lubbock, Texas, USA<sup>3</sup> U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan, Kansas, USA

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**ABSTRACT**

The range of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) spans 4 unique ecoregions along 2 distinct environmental gradients. The Sand Shinnery Oak Prairie ecoregion of the Southern High Plains of New Mexico and Texas is environmentally isolated, warmer, and more arid than the Short-Grass, Sand Sagebrush, and Mixed-Grass Prairie ecoregions in Colorado, Kansas, Oklahoma, and the northeast panhandle of Texas. Weather is known to influence Lesser Prairie-Chicken nest survival in the Sand Shinnery Oak Prairie ecoregion; regional variation may also influence nest microclimate and, ultimately, survival during incubation. To address this question, we placed data loggers adjacent to nests during incubation to quantify temperature and humidity distribution functions in 3 ecoregions. We developed a suite of a priori nest survival models that incorporated derived microclimate parameters and visual obstruction as covariates in Program MARK. We monitored 49 nests in Mixed-Grass, 22 nests in Sand Shinnery Oak, and 30 nests in Short-Grass ecoregions from 2010 to 2014. Our findings indicated that (1) the Sand Shinnery Oak Prairie ecoregion was hotter and drier during incubation than the Mixed- and Short-Grass ecoregions; (2) nest microclimate varied among years within ecoregions; (3) visual obstruction was positively associated with nest survival; but (4) daily nest survival probability decreased by 10% every half-hour when temperature was greater than 34°C and vapor pressure deficit was less than –23 mmHg during the day (about 0600–2100 hours). Our major finding confirmed microclimate thresholds for nest survival under natural conditions across the species' distribution, although Lesser Prairie-Chickens are more likely to experience microclimate conditions that result in nest failures in the Sand Shinnery Oak Prairie ecoregion. The species would benefit from identification of thermal landscapes and management actions that promote cooler, more humid nest microclimates.

**Keywords:** empirical distribution functions, humidity, Kansas, Lesser Prairie-Chicken, microclimate, nest survival, New Mexico, temperature, Texas, *Tympanuchus pallidicinctus*

**Los efectos de la interacción entre el microclima de los nidos y la estructura de la vegetación confirman los umbrales microclimáticos en la supervivencia de los nidos de *Tympanuchus pallidicinctus*****RESUMEN**

La distribución geográfica de *Tympanuchus pallidicinctus* incluye 4 ecoregiones únicas a lo largo de 2 gradientes ambientales distintos. La ecoregión de Sand Shinnery Oak Prairie en el sur del altiplano de Nuevo México y Texas está ambientalmente aislada y es más cálida y seca que las ecoregiones de Short-Grass Prairie, Sand Sagebrush Prairie y Mixed-Grass Prairie en Colorado, Kansas, Oklahoma, y el noreste de Texas. Se sabe que el clima influye en la supervivencia de los nidos de *T. pallidicinctus* en la ecoregión de Sand Shinnery Oak Prairie; la variación regional también podría afectar el microclima de los nidos y su supervivencia durante la incubación. Para abordar esta pregunta, pusimos medidores automáticos junto a los nidos durante la incubación para cuantificar las funciones de distribución de la temperatura y la humedad en 3 ecoregiones. Desarrollamos un conjunto de modelos *a priori* sobre la supervivencia de los nidos que incorporó parámetros microclimáticos derivados y obstáculos visuales como covariables en el programa MARK. Monitoreamos 49 nidos en la ecoregión de Mixed-Grass, 22 nidos en Sand Shinnery Oak y 30 nidos en Short-Grass entre 2010 y 2014. Nuestros resultados indicaron que 1) la ecoregión de Sand Shinnery Oak Prairie fue más cálida y seca durante la incubación que las ecoregiones de Mixed-Grass y Short-Grass; 2) el microclima de los nidos varió entre años en las ecoregiones; 3) los obstáculos visuales estuvieron asociados positivamente con la supervivencia de los nidos; pero 4) la probabilidad de supervivencia diaria de los nidos disminuyó 10% cada media hora cuando la temperatura era mayor a 34°C y el déficit en la presión de vapor era menor a –23

mmHg durante el día (06:00 a 21:00 h). Nuestro resultado más importante confirmó los umbrales microclimáticos para la supervivencia de los nidos bajo condiciones naturales a través de la distribución de *T. pallidicinctus*, aunque la especie es más propensa a experimentar las condiciones microclimáticas que resultan en el fracaso de los nidos en la ecoregión de Sand Shinnery Oak Prairie. La especie podría beneficiarse de la identificación de paisajes térmicos y acciones de manejo que promuevan microclimas más frescos y húmedos en los nidos.

*Palabras clave:* funciones de distribución empírica, humedad, Kansas, microclima, Nuevo México, supervivencia de los nidos, temperatura, Texas, *Tympanuchus pallidicinctus*.

## INTRODUCTION

Egg production is energetically costly, and additional energy is expended to protect eggs from unfavorable environmental conditions and predators at nests. Behavioral (e.g., nest-site selection) and physiological (e.g., gular flutter; Table 1) mechanisms may be combined to protect eggs. For precocial, ground-nesting birds (e.g., Galliformes), unfavorable environmental conditions during incubation (e.g., extreme heat) likely influence egg and nest survival in 2 ways. First, precocial species do not incubate eggs until the entire clutch is laid, thus exposing eggs to environmental stressors before the parents begin incubation. Second, unfavorable environmental conditions may cause stress on incubating parents, resulting in additional trips off the nest for water or food, leading to decreased nest attentiveness or even abandonment. Energy expenditure is exacerbated in extreme nesting environments, due to increased time spent maintaining body and egg temperature (via gular fluttering or shivering; Andreev 1999, Piersma et al. 2003, Saalfeld et al. 2012). Concomitantly, nest survival may be affected by the incubating parent's ability to choose nest vegetation that conceals nests from predators while simultaneously protecting eggs from the elements (Martin and Ghalambor 1999, Mayer et al. 2009).

Environmental stressors on incubating parents and eggs are likely an important component of nest survival in mating systems in which the female is solely responsible for incubation, as in the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Nest survival is critical to population persistence in Lesser Prairie-Chickens because survival of juveniles from hatch to the following breeding season has been identified as the key demographic parameter associated with population declines (Hagen et al. 2009). Despite the wavering status of the species on the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2016), and attention to habitat management and conservation, evidence suggests that Lesser Prairie-Chicken populations have not recovered (McDonald et al. 2015). Therefore, understanding the role of environmental stressors on nest survival may identify fine-scale interactions between nest vegetation and microclimate that have not been incorporated into previous assessments of nest ecology (Pitman et al. 2006, Davis 2009, Grisham et al.

2014, Fritts et al. 2016) and thus improve conservation actions for the species.

Microclimate at nests, and the role of microclimate on nest survival, is important for this species because timing of breeding varies little throughout the range (Boal et al. 2014), despite inconsistent environmental conditions among ecoregions during this time (Grisham et al. 2016a). According to 30 yr climate means, the Sand Shinnery Oak Prairie ecoregion (Figure 1) receives less precipitation, has lower humidity, and is warmer at the start of incubation in early May than the other 3 ecoregions ("ecoregion" *sensu* McDonald et al. 2012). Greater Prairie-Chickens (*T. cupido*) nesting in the southern part of their range in Oklahoma apparently select nest sites on the basis of vegetation cues, nest failure being associated with nests with higher temperatures (Hovick et al. 2014). Similar relationships among nest microclimate, nest vegetation, and nest survival might be expected for Lesser Prairie-Chickens, especially in the hottest part of their distribution.

A recent meta-analysis of nesting habitat selection by Lesser Prairie-Chickens suggests that females across all 4 ecoregions select nesting habitats that have similar vegetation structure (Hagen et al. 2013). Visual obstruction is supported as an indicator of Lesser Prairie-Chicken nest-site selection (Davis 2009, Grisham et al. 2014) and nest survival (Pitman et al. 2005, Grisham et al. 2014). However, simultaneous comparisons of visual obstruction and microclimate on nest survival are lacking for this species, despite contemporary evidence that microclimate (Hovick et al. 2014) and seasonal weather patterns (Grisham et al. 2013) may be critical components of nest survival for prairie grouse. The goal of the present study was to quantify nest microclimate conditions and assess the influence of microclimate and nest vegetation on nest survival for Lesser Prairie-Chickens among 3 ecoregions.

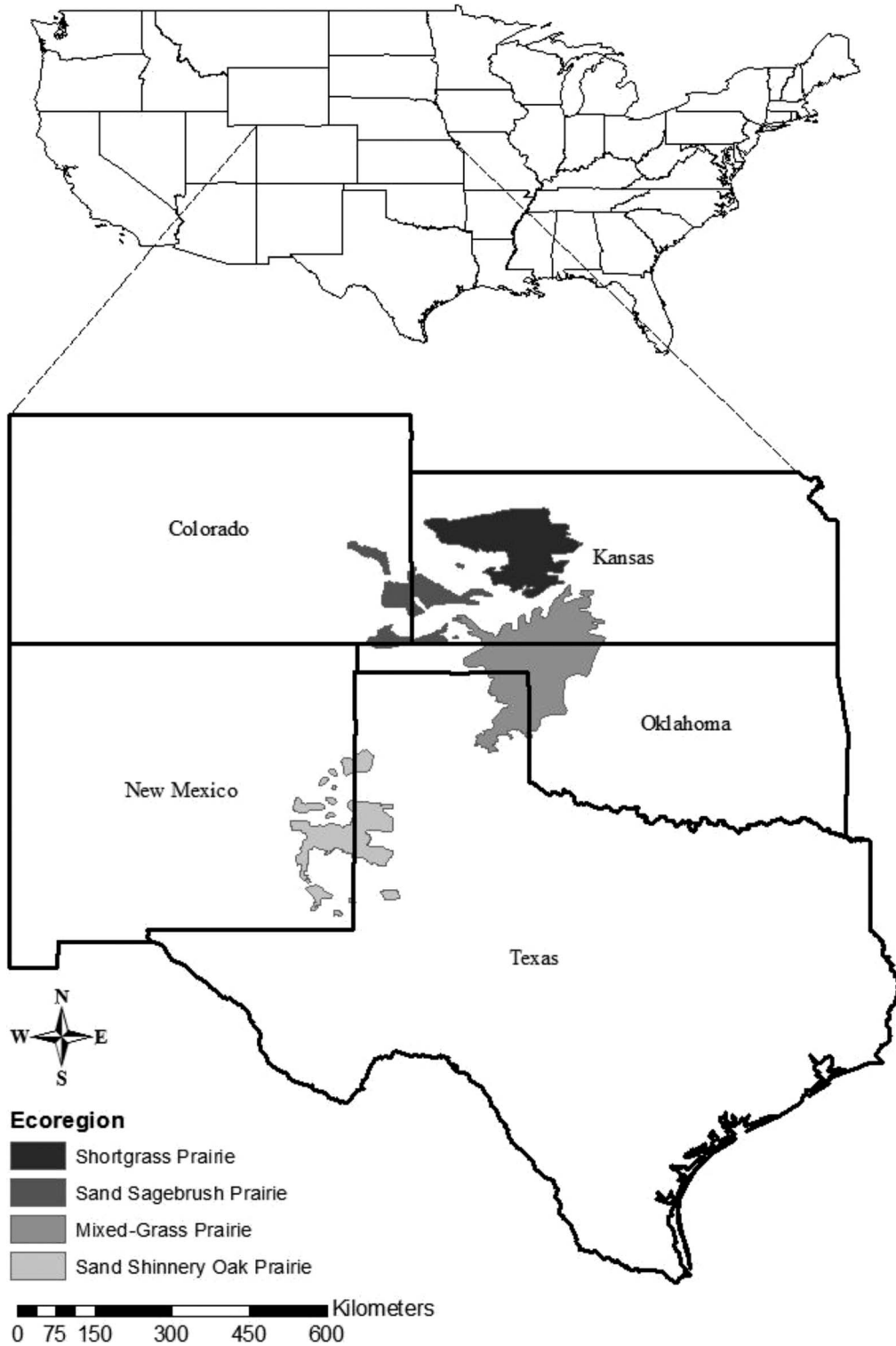
Our first objective was to compare microclimate (temperature and humidity) at nests (i.e. within 5–10 cm of the edge of the nest bowl) (1) among ecoregions (Mixed-Grass, Short-Grass Prairie/CRP Mosaic [hereafter "Short-Grass"], and Sand Shinnery Oak Prairies); (2) among years within ecoregions (2010–2012 in Sand Shinnery Oak Prairie, 2013–2014 in Mixed-Grass and Short-Grass); and (3) between nest attempts (first and

**TABLE 1.** Description and notation of 9 derived microclimate parameters and the mechanistic basis of their potential influence on Lesser Prairie-Chicken nest survival at 101 nest locations in the Mixed-Grass Prairie, Sand Shinnery Oak Prairie, and Short-Grass Prairie ecoregions, 2010–2014. Data were derived from ibutton data loggers placed within 5–10 cm of each nest.

Parameter	Description	Notation	Mechanism
DayTemp	Mean temperature (°C) outside of nest during daylight hours (about 0600–2100 hours)	DayTemp	Increased energy expenditure and potential water loss to incubating female due to gular flutter (hyperthermia) or shivering (hypothermia)
DayVPD	Mean vapor pressure deficit (VPD; mmHg) outside of nest during daylight hours (about 0600–2100 hours)	DayVPD	Egg desiccation, attracting olfactory nest predators
NightTemp	Mean temperature (°C) outside of nest during nighttime hours (about 2101–0559 hours)	NightTemp	Increased energy expenditure and potential water loss to incubating female due to gular flutter (hyperthermia) or shivering (hypothermia)
NightVPD	Mean VPD (mmHg) outside of nest during nighttime hours (about 2101–0559 hours)	NightVPD	Evaporative water loss to incubating female, attracting olfactory nest predators
Percent extreme heat and arid values	Percentage of recordings where temperature was >34°C and VPD was less than –23 mmHg during daylight hours (about 0600–2100 hours)	HotandArid	Increased energy expenditure and potential water loss to incubating female due to gular flutter (hyperthermia), egg desiccation and death, decreased female attentiveness, and increased time spent off nest
Percent extreme negative cold and arid values	Percentage of recordings where temperature was <15°C and VPD was less than –23 mmHg during all hours	ColdandArid	Increased energy expenditure of incubating female due to shivering (hypothermia)
Percent extreme heat and humid values	Percentage of recordings where temperature was >34°C and VPD was less than –23 mmHg during daylight hours (about 0600–2100 hours)	HotandHumid	Increased energy expenditure to incubating female due to gular flutter (hyperthermia)
Percent extreme cold and humid values	Percentage of recordings where temperature was <15°C and VPD was >0.27 mmHg during all hours	ColdandHumid	Increased energy expenditure of incubating female due to shivering (hypothermia)
Percent most frequent nest conditions	Percentage of recordings where outside conditions matched the most frequent nest conditions (26–31°C; –11 to –3.69 mmHg)	Mean	If microclimate conditions outside of nest are similar to conditions inside nest, then energy allocation to gular flutter or shivering is reduced
Visual obstruction reading	100% visual obstruction at nest (Robel et al. 1970)	VOR	Concealment from potential nest predators and environmental conditions

renewed). We hypothesized that conditions during incubation would be hottest and least humid in Sand Shinnery Oak Prairie, following the latitudinal temperature trends. We also expected considerable interannual variability in microclimate within the 3 ecoregions, with more pronounced temperature extremes in the Sand Shinnery Oak Prairie (Grisham et al. 2013). We expected nest temperature and humidity to differ between first and re-nest attempts within and among ecoregions.

Our second objective was an ecoregion-level assessment of the influence of microclimate on nest survival. We expected microclimate to influence nest survival similarly among the 3 ecoregions. We hypothesized that humidity would explain nest survival to a greater extent than other microclimate parameters for all 3 ecoregions (Grisham et al. 2013, Dunn and Milne 2014). We expected nest survival probabilities to decrease as temperatures increased and humidity decreased across all ecoregions (Grisham et al.



**FIGURE 1.** Historically, the range of Lesser Prairie-Chickens encompassed the entire western portion of the Southern Great Plains, but the current distribution is restricted to 4 distinct geographic ecoregions.

2013, Dunn and Milne 2014, Hovick et al. 2014). Our final hypothesis was that microclimate would be more important for nest survival than vegetation around the nest site as measured by visual obstruction reading (VOR; Pitman et al. 2005, Hagen et al. 2013, Grisham et al. 2014, 2016a). Our goal was to rank microclimate parameters in the context of the most supported measurement of nest survival for the species (i.e. VOR) while simultaneously assessing whether (1) microclimate influenced nest survival differentially among ecoregions, (2) VOR and microclimate had additive effects on nest survival, and (3) VOR and microclimate have interactive effects on nest survival.

## METHODS

### Study Areas

The Mixed-Grass Prairie ecoregion study areas in Kiowa and Comanche counties in south-central Kansas consist of mixed-grass prairie on loamy soils. The Sand Shinnery Oak Prairie ecoregion study areas in New Mexico and Texas are a matrix of grassland, cropland, and gently undulating sandhills dominated by sand shinnery oak (*Quercus havardii*) and sand sagebrush (*Artemisia filifolia*) with mixed grasses and forbs. The Short-Grass Prairie ecoregion study area in Logan and Gove counties in northwest Kansas area is a mosaic of short-grass and mixed-grass prairies, Conservation Reserve Program (CRP) grasslands, and row-crop agriculture on silt loam soils. Relevant weather data and drought severity rankings for each ecoregion are included in the Appendix. Wolfe et al. (2016), Dahlgren et al. (2016), and Grisham et al. (2016b) provide comprehensive reviews of the key plant species, climate data, population size, species management, and land cover and land use for Lesser Prairie-Chickens in the 3 ecoregions.

### Capture

We captured females with walk-in funnel traps (Haukos et al. 1989, Schroeder and Braun 1991, Grisham et al. 2015) and magnetic drop-nets (Wildlife Capture Services, Flagstaff, Arizona, USA). Upon capture, we assessed sex by pinnae length, presence of eye comb, and other plumage characteristics (Copelin 1963). We identified second-year birds as those having white spotting within 2.5 cm of the tip of the 9th and 10th primaries, whereas the absence of white spotting indicated after-second-year birds (Copelin 1963). We affixed a uniquely numbered aluminum leg band to all captured birds and equipped each female with a 9 g, necklace-style, very-high-frequency (VHF) radio-transmitter (American Wildlife Enterprises, Monticello, Florida, USA); a 15 g, necklace-style, VHF radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA); or a 22 g, rump-mounted, platform terminal transmitter (PTT; Microwave Transmitters, Co-

lumbia, Maryland, USA) and then released the bird at the capture site. Preliminary data from the Mixed-Grass Prairie and Short-Grass Prairie ecoregions indicated no differences in female and nest survival among transmitter types (D. Haukos personal observation).

### Nest Location

We determined nest locations of VHF radio-tagged females by approaching the female via homing when their approximate locations remained unchanged for  $\geq 3$  days (Pitman et al. 2006). For females with PTTs, we waited until GPS locations indicated that the female had begun incubation (when downloaded data indicated the female was stationary for  $\geq 3$  days) and used the GPS locations to locate the nest. We wore rubber boots and latex gloves to reduce scent and scent trails when we approached the nest. We spent as little time as possible at the nest ( $< 5$  min) and avoided leaving dead-end scent trails at nests. We revisited a nest to assess nest fate only when we verified that the female was off the nest. At each nest, we counted the number of eggs present at first discovery and remotely monitored nests daily until fate was evident, categorizing each nest as successful ( $\geq 1$  egg hatched) or unsuccessful (all eggs depredated or nest abandoned).

At first nest check, we placed one Maxim Integrated Semiconductor data logger (Maxim Integrated Products, Sunnyvale, California, USA; hereafter "ibutton") outside the nest bowl, but in the same vegetative substrate that constituted the nest bowl. Each data logger recorded air temperature and relative humidity at 10 min intervals until nest fate was determined. For example, if the nest bowl was located in bluestem (*Andropogon* spp.), we placed the ibutton within 5–10 cm of the edge of the nest bowl in a random direction in the same plant. We positioned each ibutton on the ground in the plant substrate and concealed it with camouflage duct tape and plant substrate. We collected each ibutton within 3 days of nest failure or success. We calibrated ibuttons in an Envirotronics System Plus HRZ environmental control chamber (Weiss Envirotronics, Grand Rapids, Michigan, USA) prior to deployment in the field. For each 10 min measurement, we calculated the vapor pressure deficit (VPD), which is the difference between the amount of moisture in the air and how much moisture the air can hold when saturated (mmHG), by using the paired temperature and relative humidity measurements from each data logger (Anderson 1936). VPD is a better measure of aridity than relative humidity, which is not a reliable measure of atmospheric moisture unless the temperature and relative humidity measurements are identical (Anderson 1936). We quantified nest vegetation structure within 3 days following nest failure or success (Pitman et al. 2005, Grisham et al. 2014). We estimated VOR from a distance of 4 m and a height of 1 m, using a Robel pole at the nest bowl (Robel et al. 1970).



## Statistical Analysis

**Microclimate conditions.** We compiled ibutton data by ecoregion (Mixed-Grass Prairie, Short-Grass Prairie, and Sand Shinnery Oak Prairie), year (2010–2014), and nest attempt (first, reneest) and then calculated summary statistics for temperature and VPD using Proc Means in SAS 9.3 (SAS Institute, Cary, North Carolina, USA). We compared empirical distribution functions of nest temperature and VPD (1) among ecoregions, (2) among years within an ecoregion, and (3) between nest attempts among and within ecoregions. Empirical distribution functions are defined as the distribution of the cumulative data points in the sample and converge to a probability of 1 (Zar 2010). We used a Kolmogorov-Smirnov test to assess differences in empirical distribution functions for temperature and VPD for each comparison.

For each assessment, we reported the Kolmogorov-Smirnov statistic, the asymptotic Kolmogorov-Smirnov statistic, the maximum deviation (MD), and the percentage of observations that fell to the left of the MD. The MD was the value that maximized differences in the empirical distribution function among parameters. A greater proportion of observations to the left of the MD for temperature meant that the distribution function was cooler. Conversely, more observations to the left of the MD for VPD meant that the distribution function was more arid.

We did all pairwise comparisons (i.e. 2 class levels) for each objective using a 2-sample Kuiper statistic in PROC NPARIWAY in SAS 9.3. For all pairwise comparisons, we report the Kuiper statistic, asymptotic Kuiper statistic, *P* value, MD, and percentage of observations that fell to the left of the MD for temperature and VPD.

**Nest survival.** We assessed nest survival using the logit-link function in the nest survival model (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999). Our data met the assumptions of the nest survival model because we used radio-telemetry to find and accurately age and check nests. Nests in this assessment were aged correctly, we correctly determined the nest fates, our nest checks did not influence nest survival, and we assumed that nest fates were independent because each nest was  $\geq 500$  m from any other nest we monitored (Dinsmore et al. 2002). We used the date when the female's location had remained the same for 3 consecutive days as the date the nest was found (*i*); the day before the nest hatched or failed as the last day the nest was checked alive (*j*); and the date of hatch or failure as the last day the nest was checked (*k*; Dinsmore et al. 2002). During our study, nests were active from April 16 to July 7, which resulted in 83 estimates of daily nest survival. However, we eliminated the first 3 days of every nest from this analysis because we did not place ibuttons in the nest until the female had incubated the nest  $\geq 3$  consecutive days. April 19 was the first day in our field

assessment when an ibutton was collecting data. Therefore, nests for both stages of this analysis were active during April 19–July 7, which resulted in 80 estimates of daily nest survival. We used the mean incubation period of 28 days (Hagen and Giesen 2005, Boal et al. 2014) to estimate nest survival across the incubation period (Grisham et al. 2014).

We developed 29 a priori models using 9 derived microclimate parameters (Table 1) from the ibuttons. Boal et al. (2014) found that nest microclimate in the Sand Shinnery Oak Prairie ecoregion was (1) consistent and predictable with time of day (i.e. night was cooler and more humid than midday), (2) warmer as the nesting season progressed, and (3) without a temporal pattern of relative humidity as the nesting season progressed. Thus, we did not include time-varying microclimate parameters (i.e. parameters specific to a given nest-exposure day at each nest) in the nest survival assessment to avoid model over-parameterization and facilitate comparison between microclimate data (multiple values at each nest location) and VOR (one measurement per nest). Our derived parameters reduced temporal autocorrelation in the dataset by combining 10 min data points into trends. Our derived parameters are appropriate for drawing an inference about the relationship between microclimate and nest survival because nests initiated later in the year are more likely to have higher mean values as well as a larger proportion of extreme temperature values (Boal et al. 2014), and these trends are naturally built into the nest survival model because nests included in the analysis are standardized by the first nest found in the dataset (Dinsmore et al. 2002).

We grouped all nests by ecoregion to assess whether microclimate disproportionately affected nest survival across ecoregions. We did not separate first nest from renests in this analysis because of the low sample size of renests. Our microclimate candidate models were developed using information presented in Flanders-Wanner et al. (2004), Fields et al. (2006), Grisham et al. (2013), Dunn and Milne (2014), and Hovick et al. (2014) that suggested temperature and humidity as limiting factors for various aspects of Holarctic grouse reproductive ecology. We also included several exploratory models that included the proportion of extreme temperature and VPD measurements to assess whether extreme microclimate conditions influenced nest survival (Table 1). We included one model for each derived microclimate parameter ( $n = 9$ ), one model that included VOR as a predictor of nest survival, one model that incorporated variation in nest survival among ecoregions, 9 models that included VOR and each microclimate parameter as additive effects, and 9 models that included VOR and each microclimate parameter as interactive effects. We included VOR as a main additive and interactive covariate in our nest survival models

**TABLE 2.** Evaluation of ecoregion-specific empirical distribution functions for Lesser Prairie-Chicken nest temperature and vapor pressure deficit (VPD) in Mixed-Grass Prairie (Mixed;  $n = 42$  nests), Sand Shinnery Oak Prairie (SSOP;  $n = 18$  nests), and Short-Grass Prairie (Short;  $n = 28$  nests) ecoregions, 2010–2014.

Parameter	Assessment	Pairwise	KS	KSa	K	Ka	P	MD <sup>a</sup>	Percentage of observations		
									Mixed	SSOP	Short
Temperature	Ecoregion		0.09	51.76	–	–	–	29°C	82% <sup>b</sup>	58%	88%
		SSOP-Mixed	–	–	0.27	49.29	<0.001	29°C	–	58%	88%
		Mixed-Short	–	–	0.08	20.16	<0.001	17°C	12%	–	20%
		SSOP-Short	–	–	0.29	51.31	<0.001	29°C	–	58%	88%
VPD	Ecoregion		0.09	52.71	–	–	–	–13.70 mmHg	20% <sup>c</sup>	45%	15%
		SSOP-Mixed	–	–	0.26	47.01	<0.001	–12.53 mmHg	19%	46%	–
		Mixed-Short	–	–	0.10	28.01	<0.001	–18.39 mmHg	14%	–	7%
		SSOP-Short	–	–	0.26	47.01	<0.001	–13.77 mmHg	–	45%	15%

Abbreviations: KS = Kolmogorov-Smirnov critical value, KSa = Kolmogorov-Smirnov test statistic, K = Kuiper critical value, Ka = Kuiper test statistic, MD = maximum deviation.

<sup>a</sup> MD is the value where the empirical distribution function among ecoregions differs the most.

<sup>b</sup> Interpretation: 82% of the temperature observations in the Mixed-Grass Prairie ecoregion were located to the left of the MD (29°C), 58% of the temperature observations in the SSOP ecoregion were located to the left of the MD (29°C), and 88% of the temperature observations in the Short-Grass Prairie ecoregion were located to the left of the MD (29°C), where a greater percentage of observations to the left of the MD indicates that the ecoregion was cooler.

<sup>c</sup> Interpretation: 20% of the VPD observations in the Mixed-Grass Prairie ecoregion were located to the left of the MD (–13.70 mmHg), 45% of the temperature observations in the SSOP ecoregion were located to the left of the MD (–13.70 mmHg), and 15% of the temperature observations in the Short-Grass Prairie ecoregion were located to the left of the MD (–13.70 mmHg), where a greater percentage of observations to the left of the MD indicates that the ecoregion was more arid.

because VOR is strongly supported as the critical indicator of nest-site selection (Hagen et al. 2013) and nest survival for the species (Grisham et al. 2014).

We used second-order Akaike's Information Criterion for small sample sizes ( $AIC_c$ ),  $\Delta AIC_c$  values, and Akaike weights ( $w_i$ ) to select the best-approximating model (Burnham and Anderson 2002) for our analysis. We considered any model with  $\Delta AIC_c \leq 2$  to be competitive. We model-averaged parameter estimates across competing models and used the delta method (Powell 2007) to calculate standard errors and 95% confidence intervals (CIs) in instances with multimodel support (no single model with  $w_i > 0.90$ ).

## RESULTS

### Capture

We located 56 nests (17 in 2013, 32 in 2014; 4 renests) from 45 radio-tagged females in the Mixed-Grass Prairie ecoregion; 26 nests (17 in 2010, 3 in 2011, 6 in 2012; 3 renests) from 41 radio-tagged females in the Sand Shinnery Oak Prairie ecoregion; and 32 nests (7 in 2013, 25 in 2014; 8 renests) from 31 radio-tagged females in the Short-Grass Prairie ecoregion. The low sample size of nests from radio-tagged females in the Sand Shinnery Oak Prairie was primarily due to few nest attempts in 2011 (3 of 15 radio-tagged females initiated nests; Grisham et al.

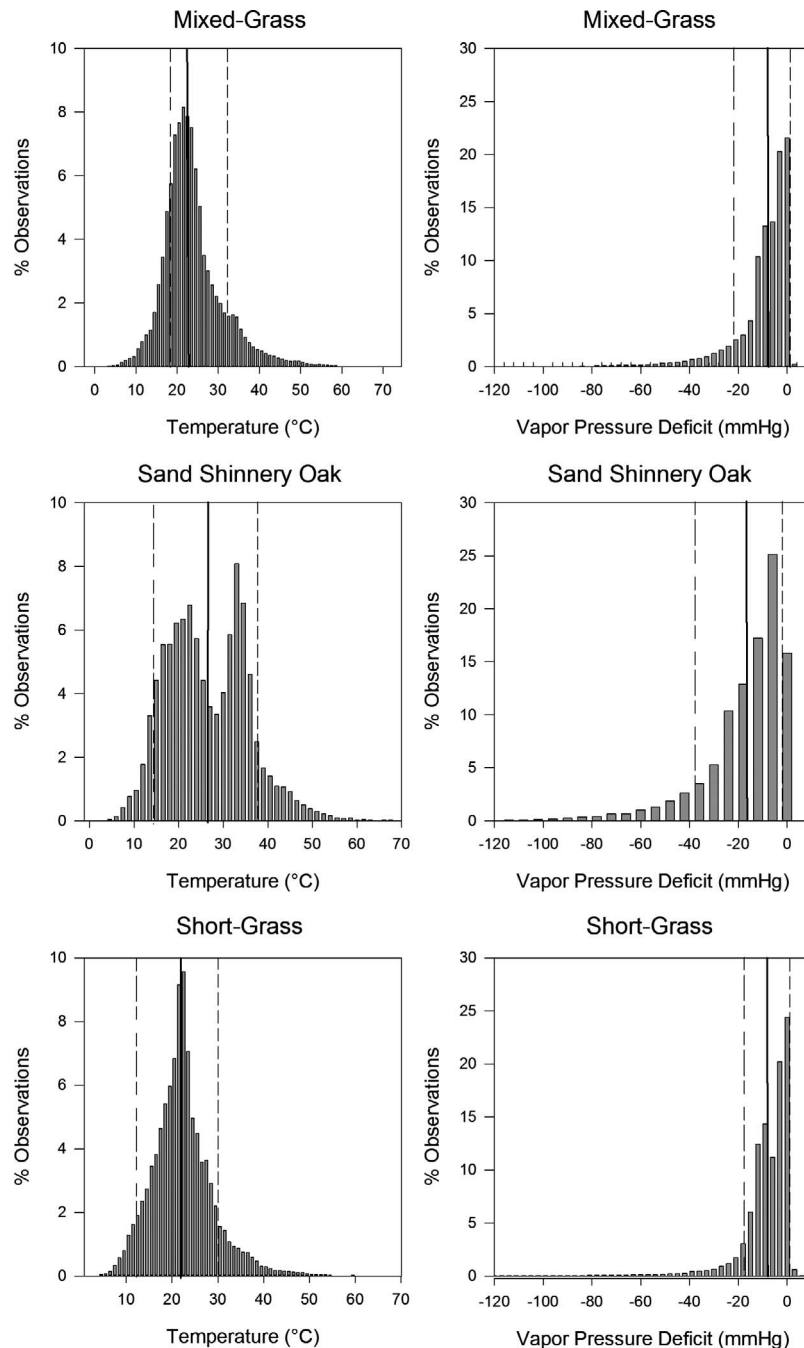
2014) and subsequent population declines following the drought of 2011.

### Microclimate Conditions

We collected 159,362 recordings of temperature and VPD from 49 nests in 2013–2014 in the Mixed-Grass Prairie ecoregion; 40,256 recordings of temperature and VPD from 22 nests in 2010–2012 in the Sand Shinnery Oak Prairie ecoregion; and 113,310 recordings of temperature and VPD from 30 nests in 2013–2014 in the Short-Grass Prairie ecoregion. We eliminated 7, 4, and 2 nests from the Mixed-Grass Prairie, Sand Shinnery Oak Prairie, and Short-Grass Prairie ecoregions, respectively, because of lost or damaged ibuttons.

**Ecoregion.** Empirical distribution functions of temperature followed the latitudinal gradient, indicating that temperature during incubation was hotter for incubating females in the Sand Shinnery Oak Prairie ecoregion compared to the northern ecoregions (Table 2; Figure 2). Likewise, empirical distribution functions for VPD followed the longitudinal gradient, and the Mixed-Grass Prairie ecoregion was the most humid ecoregion during incubation, followed by the Short-Grass Prairie and Sand Shinnery Oak Prairie ecoregions (Table 2; Figure 2).

**Year.** There was considerable interannual variability in empirical distribution functions for temperature and VPD between and among years in all ecoregions (Table 3;



**FIGURE 2.** Empirical distribution of temperature (left column) and vapor pressure deficit (right column) recordings from Lesser Prairie-Chicken nests in the Mixed-Grass Prairie ( $n = 159,362$ ), Sand Shinnery Oak Prairie ( $n = 40,256$ ), and Short-Grass Prairie ( $n = 113,310$ ) ecoregions. Vertical lines indicate the lower 10th percentile, mean, and upper 90th percentile of observations.

Figures 3–5). Conditions at nests in the Mixed-Grass Prairie ecoregion were cooler and less arid in 2013 compared to 2014 (Table 3; Figure 3). The Sand Shinnery Oak Prairie ecoregion was cooler and less arid in 2010 compared to 2011 and 2012 (Table 3; Figure 4); 2011 in the Sand Shinnery Oak Prairie ecoregion was the hottest, most arid year across all ecoregions (Figure 4). The Short-Grass

Prairie ecoregion was cooler and less arid in 2014 compared to 2013 (Table 3; Figure 5).

**Nest attempt.** Temperature and VPD distributions differed between nest attempts and among ecoregions (Table 4; Appendix Figures 6 and 7). In general, temperatures were cooler during first nest attempts in the Mixed- and Short-Grass Prairie ecoregions, but not in



**TABLE 3.** Evaluation of yearly empirical distribution functions for Lesser Prairie-Chicken nest temperature and vapor pressure deficit (VPD) in Mixed-Grass Prairie ( $n = 42$  nests), Sand Shinnery Oak Prairie (SSOP;  $n = 18$  nests), and Short-Grass Prairie ( $n = 28$  nests) ecoregions, 2010–2014.

Parameter	Assessment	Pairwise	KS <sup>a</sup>	KSa	K	Ka	<i>P</i>	MD <sup>a</sup>	Percentage of observations				
									2010	2011	2012	2013	2014
Temperature	Mixed-Grass SSOP	2013–2014	–	–	0.19	39.32	<0.001	26°C	–	–	–	82% <sup>b</sup>	68%
			0.04	9.18	–	–	–	31°C	62%	41%	73%	–	–
		2010–2011	–	–	0.36	6.66	<0.001	22°C	37%	0.01%	–	–	–
		2010–2012	–	–	0.21	15.05	<0.001	31°C	62%	–	73%	–	–
		2011–2012	–	–	0.37	6.75	<0.001	22°C	–	4%	43%	–	–
VPD	Short-Grass	2013–2014	–	–	0.14	21.87	<0.001	23°C	–	–	–	57%	70%
		Mixed-Grass SSOP	2013–2014	–	–	0.18	35.74	<0.001	–13.98 mmHg	–	–	–	9% <sup>c</sup>
	2010–2011		–	–	0.59	10.90	<0.001	–15.19 mmHg	40%	99%	46%	–	–
	2010–2012		–	–	0.12	9.29	<0.001	–15.19 mmHg	40%	99%	–	–	–
	2011–2012		–	–	0.53	9.47	<0.001	–4.70 mmHg	73%	–	86%	–	–
	2011–2012		–	–	0.53	9.47	<0.001	–15.19 mmHg	–	99%	47%	–	–
	Short-Grass	2013–2014	–	–	0.09	14.53	<0.0001	–8.05 mmHg	–	–	–	52%	43%

Abbreviations: KS = Kolmogorov-Smirnov critical value, KSa = Kolmogorov-Smirnov test statistic, K = Kuiper critical value, Ka = Kuiper test statistic, MD = maximum deviation.

<sup>a</sup> The MD is the value where the empirical distribution function among years differs the most.

<sup>b</sup> Interpretation: 82% of the temperature observations in 2013 in the Mixed-Grass Prairie ecoregion were located to the left of the MD (26°C), and 68% of the temperature observations in 2014 in the Mixed-Grass Prairie ecoregion were located to the left of the MD (26°C), where a greater percentage of observations to the left of the MD indicates that the year was cooler.

<sup>c</sup> Interpretation: 9% of the VPD observations in 2013 in the Mixed-Grass Prairie ecoregion were located to the left of the MD (–13.98 mmHg), and 27% of the VPD observations in 2014 in the Mixed-Grass Prairie ecoregion were located to the left of the MD (–13.98 mmHg), where a greater percentage of observations to the left of the MD indicates that the year was more arid.

the Sand Shinnery Oak Prairie ecoregion (Table 4; Appendix Figure 6). Empirical distribution functions of VPD differed between first and reneat attempts in all ecoregions, but microclimate conditions during reneat attempts in the Sand Shinnery Oak Prairie and Short-Grass Prairie ecoregions were more humid (Table 4; Appendix Figure 7). By contrast, microclimate conditions during reneat attempts in the Mixed-Grass Prairie ecoregion were more arid compared to first nest attempts (Table 4; Appendix Figure 7).

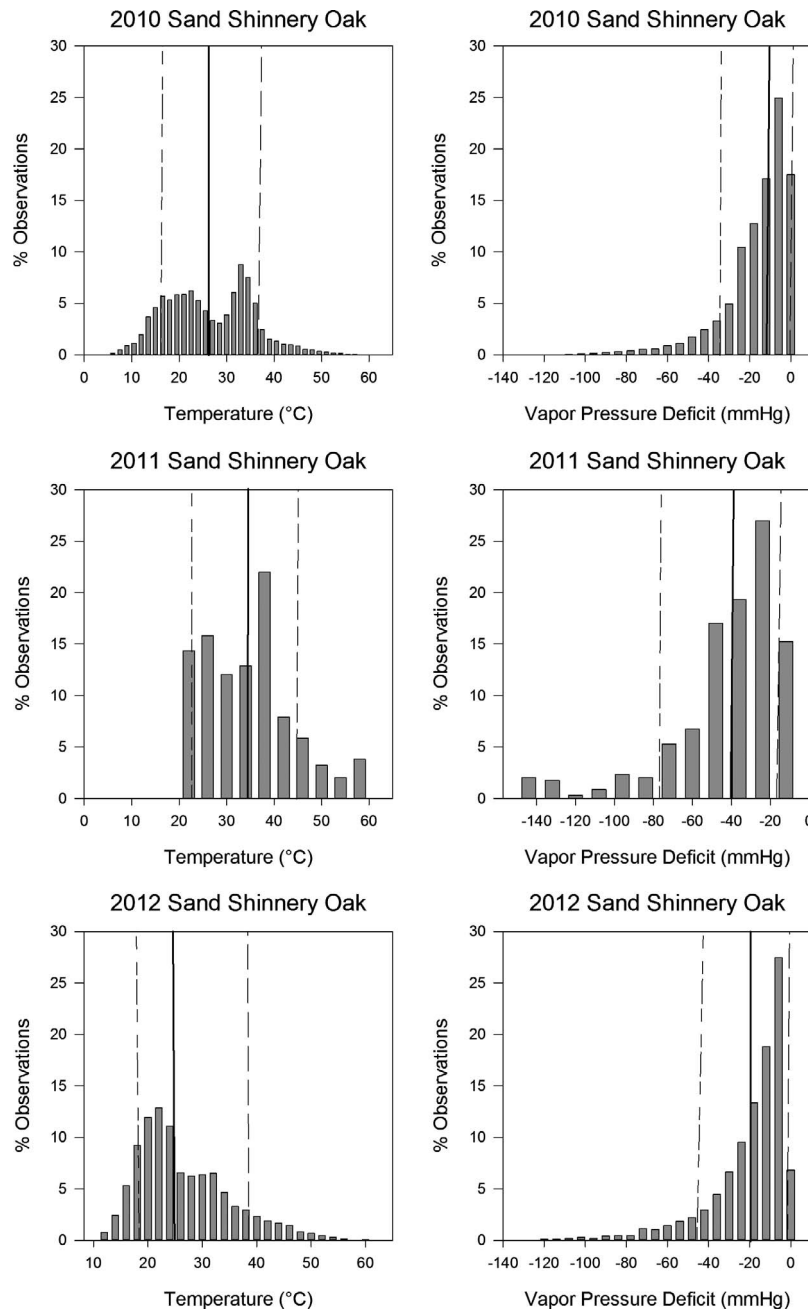
### Nest Survival

There was a high degree of model-selection uncertainty across our suite of 29 candidate models (Table 5). The top competing model ( $S_{VOR*HotandArid}$ ) received 40% of the  $AIC_c$  weight. In this model, the proportion of extreme hot and arid measurements had a negative effect on survival ( $\beta_{HotandArid} = -0.05$ ) whereas VOR had a positive effect on survival ( $\beta_{VOR} = 0.003$ ). However, the interactive effect was negative ( $\beta_{VOR*HotandArid} = -0.0007$ ), which suggests that VOR was unable to compensate for extreme hot, arid conditions at nests. The model that incorporated interactive effects of VOR and VPD during the daylight hours ( $S_{VOR*DayVPD}$ ) received some model support ( $\Delta AIC_c = 1.31$ ), as did the model that incorporated additive effects of VOR and the proportion of hot and arid measurements ( $\Delta AIC_c = 1.92$ ). The model that incorporated only VOR received minimal support within our candidate set ( $\Delta AIC_c$

$= 7.09$ ) but explained nest survival to a greater extent than all microclimate parameters, aside from hot and arid conditions and mean daily temperature. However, the effect size for VOR was an order of magnitude smaller ( $\beta_{VOR} = 0.001$ ) than the effect size for proportion of hot and arid observations ( $\beta_{HotandArid} = -0.04$ ), but not mean daily VPD ( $\beta_{HotandArid} = -0.002$ ). There was no evidence of an ecoregion-level difference in nest survival ( $\Delta AIC_c = 8.27$ ). Based on our model-averaged parameter estimates, the probability of daily nest survival ( $\pm$  SE) was  $0.971 \pm 0.007$  (95% CI: 0.95–0.98) for the Mixed-Grass Prairie ecoregion,  $0.973 \pm 0.008$  (95% CI: 0.95–0.98) for the Sand Shinnery Oak Prairie ecoregion, and  $0.970 \pm 0.01$  (95% CI: 0.95–0.98) for the Short-Grass Prairie ecoregion. Assuming a 28-day exposure period (i.e. the incubation period), the probability of a nest surviving the incubation period was 44% in the Mixed-Grass Prairie ecoregion, 43% in the Short-Grass Prairie ecoregion, and 46% in the Sand Shinnery Oak Prairie ecoregion ( $0.970$ – $0.973^{28}$ ).

### DISCUSSION

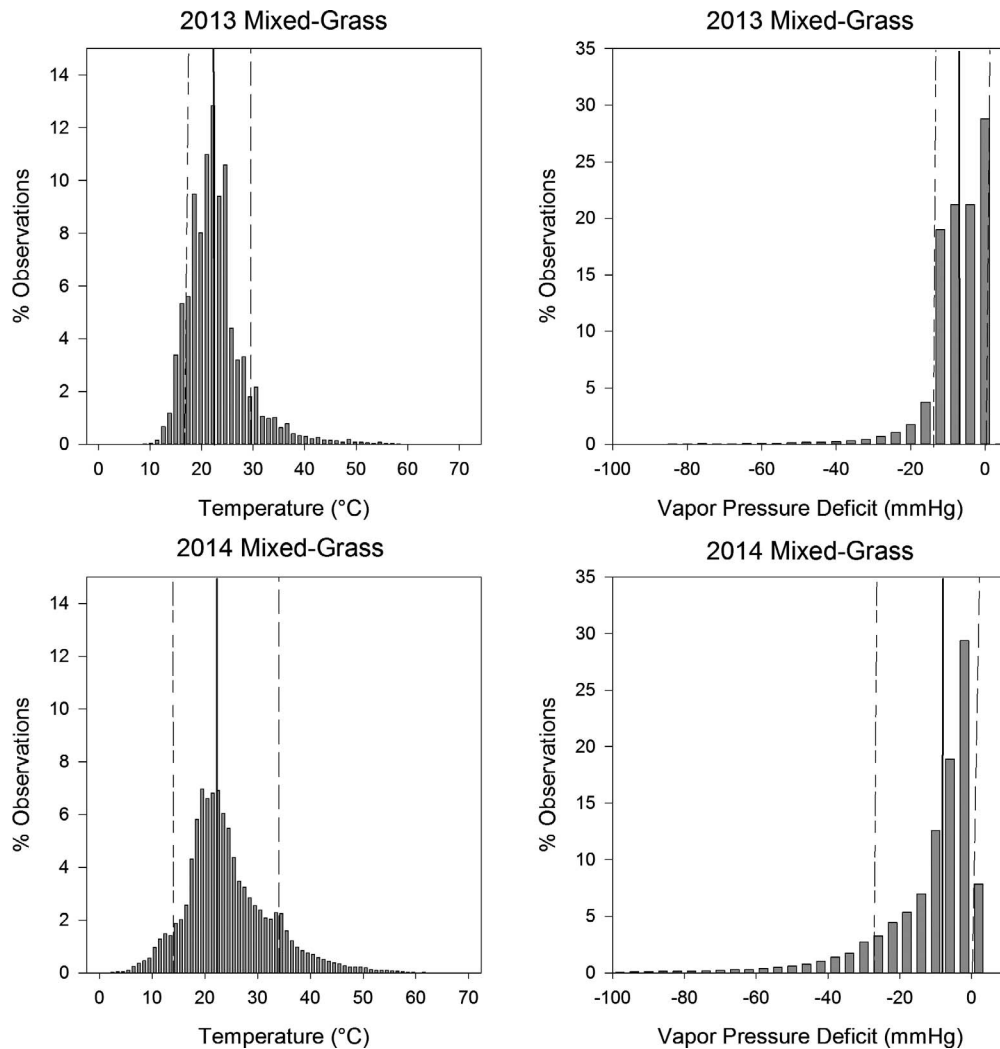
Our study was the first fine-scaled, range-wide assessment of nest microclimate and the interactive effects between microclimate and visual obstruction on nest survival of a prairie grouse species. Our major finding was that visual obstruction was a good predictor of nest survival, but daily survival probabilities decreased dramatically when tem-



**FIGURE 3.** Empirical distribution of temperature (left column) and vapor pressure deficit (right column) recordings from Lesser Prairie-Chicken nests in the Sand Shinnery Oak Prairie ecoregion in 2010 ( $n = 33,882$ ), 2011 ( $n = 341$ ), and 2012 ( $n = 6,033$ ). Vertical lines indicate the 10th percentile, mean, and upper 90th percentile of observations.

perature was  $>34^{\circ}\text{C}$  and VPD was less than  $-23$  mmHg during the day (about 0600–2100 hours). Daily nest survival probability decreased by 1% as the proportion of extreme hot and arid conditions increased by 4%. Based on this relationship, the daily nest survival probability decreased by 10% every half-hour when conditions were beyond the estimated threshold of  $34^{\circ}\text{C}$ . Hyperthermia is a severe risk for developing embryos (Webb 1987); Ring-

necked Pheasant (*Phasianus colchicus*) and chicken (*Gallus gallus domesticus*) eggs can typically survive exposures of  $\sim 2$  hr to temperatures between  $16^{\circ}\text{C}$  and  $41^{\circ}\text{C}$ , or several hours of exposure to temperatures between  $36^{\circ}\text{C}$  and  $39^{\circ}\text{C}$  (Webb 1987). Evidence from our study suggests that during the drought years of 2011 and 2012 in the Sand Shinnery Oak Prairie ecoregion, 2013 in the Short-Grass ecoregion, and 2014 in the Mixed-Grass



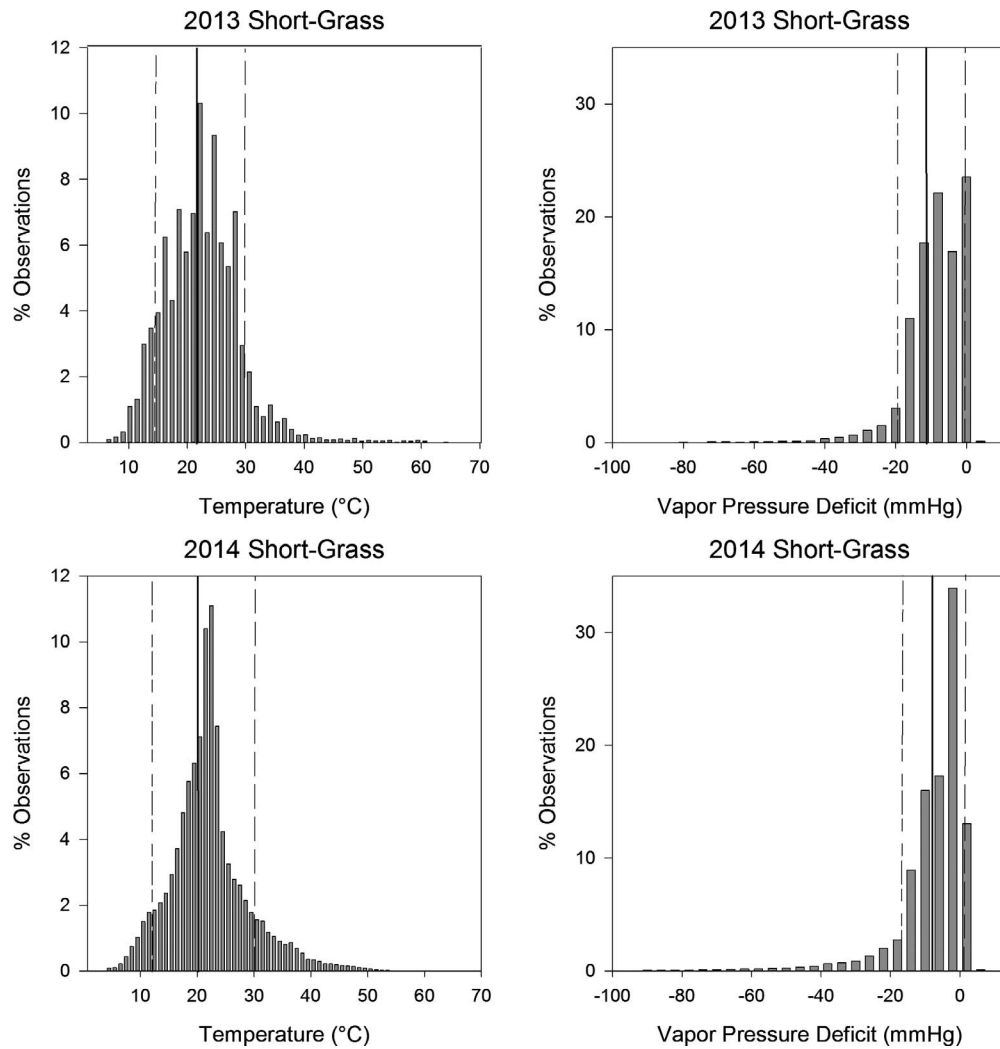
**FIGURE 4.** Empirical distribution of temperature (left column) and vapor pressure deficit (right column) recordings from Lesser Prairie-Chicken nests in the Mixed-Grass Prairie ecoregion in 2013 ( $n = 69,488$ ) and 2014 ( $n = 89,731$ ). Vertical lines indicate the 10th percentile, mean, and upper 90th percentile of observations.

ecoregion, Lesser Prairie-Chickens were exposed to temperatures and humidity that exceeded not only their own tolerance levels, but likely that of their eggs. Although we were unable to identify the exact mechanism responsible for nest failures when microclimate conditions were beyond what is suitable for eggs and females, multiple scenarios for nest failure exist for precocial, ground-nesting birds like Lesser Prairie-Chickens.

The first scenario is egg death prior to incubation, while eggs were left unprotected until the entire clutch was laid and the female did not attempt incubation. Second, eggs could have survived the laying period, but thermal stress on females during incubation caused abandonment and subsequent egg death (Boal et al. 2014). Third, egg death could have occurred prior to incubation, with females attempting incubation, only to abandon nests later in the

incubation period (Blomberg et al. 2015). In 2 drought years, Grisham et al. (2014) reported 6 nest abandonments in 2009, and only 3 incubation attempts out of 15 radio-marked females in 2011 in the Sand Shinnery Oak Prairie ecoregion (both drought years). Grisham et al. (2014) confirmed that females abandoned nests during incubation, but they were unable to determine whether nest failures were a result of egg death prior to incubation or thermal stress on the incubating female.

Video evidence from 3 Lesser Prairie-Chicken nests and camera-trap data at water sources in Texas suggest that Lesser Prairie-Chickens have developed 2 unique behavioral mechanisms to help alleviate thermal stress on themselves and their nests (Boal et al. 2014, Gickhorn 2015). First, video and ibutton data from Texas suggest that female Lesser Prairie-Chickens left the nest when ambient



**FIGURE 5.** Empirical distribution of temperature (left column) and vapor pressure deficit (right column) recordings from Lesser Prairie-Chicken nests in the Short-Grass Prairie ecoregion in 2013 ( $n = 28,672$ ) and 2014 ( $n = 84,638$ ). Vertical lines indicate the 10th percentile, mean, and upper 90th percentile of observations.

thermal conditions did not put the eggs at risk (Boal et al. 2014). Females monitored by Boal et al. (2014) left the nest twice a day, once at dawn and again at dusk. Time spent off nest ranged from 20 min to 1 hr. While females were off the nest, temperature and relative humidity inside the nest tended to decrease, with more noticeable changes in microclimate conditions in the evenings. Second, video-monitored females engaged in gular flutter, indicating thermal stress (Weathers and Schoenbaechler 1976). Gular flutter started when temperature outside of the nests was  $\geq 23^{\circ}\text{C}$  (range:  $23\text{--}35^{\circ}\text{C}$ ) and relative humidity was  $\leq 77\%$  (range:  $39\text{--}77\%$ ; Boal et al. 2014). Because these behaviors were consistent among years and in various environmental conditions, Boal et al. (2014) suggested that gular flutter was likely a mechanism used to prevent and regulate hyperthermia via evaporation of water in the trachea.

Gular flutter is energetically costly to incubating females because of associated water loss, especially if female prairie-chickens obtain water largely through metabolic processes, as has been suggested (Snyder 1967). However, Gickhorn (2015) reported that female Lesser Prairie-Chickens' use of water sources was highest before and during the breeding season. We confirmed multiple visits to water sources, including visits at dawn and dusk, by nesting females in the present study. Robinson et al. (2016) empirically linked water use and embryo development in nesting Lesser Prairie-Chickens, which explained visits to water before incubation. Our studies now suggest that females' continued visits to water during incubation were likely due to thermal stress. We speculate that one indirect benefit of free water use and gular flutter is a subsequent increase in nest relative humidity when water is evaporated

**TABLE 4.** Evaluation of empirical distribution functions for Lesser Prairie-Chicken first-nest and reneest temperature and vapor pressure deficit (VPD) in Mixed-Grass Prairie (MG;  $n = 38$  nests, 4 reneests), Sand Shinnery Oak Prairie (SSOP;  $n = 15$  nests, 3 reneest), and Short-Grass Prairie (SG;  $n = 20$  nests, 8 reneests) ecoregions, 2010–2014.

Parameter	Assessment	Pairwise	KS	KSa	K	Ka	P	MD <sup>a</sup>	Percentage of observations					
									MG First	MG Reneest	SSOP First	SSOP Reneest	SG First	SG Reneest
Temperature	Nest Attempt		0.09	37.22	–	–	–	29°C	82% <sup>b</sup>	85%	56%	76%	89%	83%
	Mixed-Grass First-Reneest	–	–	0.17	12.33	<0.001	21°C	47%	32%	–	–	–	–	
	SSOP First-Reneest	–	–	0.44	16.68	<0.001	19°C	–	–	30%	7%	–	–	
	Short-Grass First-Reneest	–	–	0.16	17.25	<0.001	18°C	–	–	–	–	31%	14%	
VPD	Nest Attempt		0.09	36.87	–	–	–	–12.74 mmHg	23% <sup>c</sup>	12%	47%	49%	19%	15%
	Mixed-Grass First-Reneest	–	–	0.2	14.11	<0.001	–6.15 mmHg	51%	32%	–	–	–	–	
	SSOP First-Reneest	–	–	0.27	10.25	<0.001	–5.50 mmHg	–	–	70%	89%	–	–	
	Short-Grass First-Reneest	–	–	0.13	13.79	<0.001	–1.10 mmHg	–	–	–	–	79%	87%	

Abbreviations: KS = Kolmogorov-Smirnov critical value, KSa = Kolmogorov-Smirnov test statistic, K = Kuiper critical value, Ka = Kuiper test statistic, MD = maximum deviation.

<sup>a</sup> The MD is the value where the empirical distribution function among nests within and among ecoregions differs the most.

<sup>b</sup> Interpretation: 82% of the temperature observations for first nests in the Mixed-Grass Prairie ecoregion were located to the left of the MD (29°C), 85% of the temperature observations for reneests in the Mixed-Grass Prairie ecoregion were located to the left of the MD (29°C), 56% of the temperature observations for first nests in the SSOP ecoregion were located to the left of the MD (29°C), 76% of the temperature observations for reneests in the SSOP ecoregion were located to the left of the MD (29°C), 89% of the temperature observations for first nests in the Short-Grass Prairie ecoregion were located to the left of the MD (29°C), and 83% of the temperature observations for reneests in the Short-Grass Prairie ecoregion were located to the left of the MD (29°C), where a greater percentage of observations to the left of the MD indicates that conditions at nests were cooler.

<sup>c</sup> Interpretation: 23% of the VPD observations for first nests in the Mixed-Grass Prairie ecoregion were located to the left of the MD (–12.74 mmHg), 12% of the VPD observations for reneests in the Mixed-Grass Prairie ecoregion were located to the left of the MD (–12.74 mmHg), 47% of the VPD observations for first nests in the SSOP ecoregion were located to the left of the MD (–12.74 mmHg), 49% of the VPD observations for reneests in the SSOP ecoregion were located to the left of the MD (–12.74 mmHg), 19% of the VPD observations for first nests in the Short-Grass Prairie ecoregion were located to the left of the MD (–12.74 mmHg), and 15% of the VPD observations for reneests in the Short-Grass Prairie ecoregion were located to the left of the MD (–12.74 mmHg), where a greater percentage of observations to the left of the MD indicates that conditions at nests were more arid.

out of the trachea to reduce heat stress (Grisham 2012, Boal et al. 2014, Grisham et al. 2014, Gicklhorn 2015). Although it appears that Lesser Prairie-Chickens benefited from the addition of free water on the landscape, our major finding indicated that visual obstruction was a good predictor of nest survival except in extreme microclimate conditions. Among the multiple nest-failure scenarios listed above, the available evidence suggests that egg death prior to incubation was the most likely cause of nest failures in extreme conditions (i.e. drought), due to lack of cover that protected eggs from direct sunlight and desiccating winds.

Vegetation in Texas failed to foliate during the 2011 drought, leaving eggs exposed to the elements prior to incubation (Grisham et al. 2013). Lack of suitable cover via vegetation explained why visual obstruction was not supported over extreme microclimate conditions. Birds with lek-centric breeding systems select nest sites within 3–5 km of leks. Female Lesser Prairie-Chickens, Greater Prairie-Chickens, and Greater Sage-Grouse (*Centrocercus urophasianus*) all selected nest sites within close proximity to brood-rearing habitat while avoiding anthropogenic structures (Haukos and Smith 1989, Pitman et al.

2005, Dinkins et al. 2014, Grisham et al. 2014). At finer scales (i.e. within 2–4 m of nest plant) within 3–5 km of leks, females of the same species selected for nesting cover that protected eggs from the elements (Hovick et al.

**TABLE 5.** Model ranking of 29 a priori candidate models used to estimate nest survival for 101 Lesser Prairie-Chicken nests in the Mixed-Grass Prairie, Sand Shinnery Oak Prairie, and Short-Grass Prairie ecoregions, 2010–2014.

Model	$\Delta AIC_c$ <sup>a</sup>	$w_i$	Model likelihood	K	Deviance
VOR*HA <sup>b</sup>	0	0.40	1	6	513.60
VOR*DayVPD	1.31	0.20	0.5	6	514.91
VOR+HA	1.92	0.15	0.38	5	517.54
HA	3.16	0.08	0.20	4	520.79
DayTemp	5.98	0.02	0.05	4	523.62
VOR+DayTemp	6.53	0.01	0.03	5	522.16
VOR+NightTemp	6.88	0.01	0.03	5	522.50
VOR	7.09	0.01	0.02	4	524.72
VOR*NightTemp	7.78	0.01	0.02	6	521.39

<sup>a</sup> Lowest  $AIC_c$  value = 525.65,  $\Delta AIC_c$  = differences in  $AIC_c$ ,  $w_i$  = model weights, K = number of parameters.

<sup>b</sup> For parameter notation and definitions, see Table 1. Models with  $w_i < 0.01$  are not shown.



2014, present study) while facilitating protection and escape from predators (Conover et al. 2010, Hovick et al. 2014, Fritts et al. 2016). Our findings, when combined with information in Hagen et al. (2013), suggest that visual obstruction and microclimate were both important components of nest habitat and survival. We argue that visual obstruction was the selection cue for nesting females at finer scales, and our findings indicate that except in severe drought, vegetation was capable of protecting the nest from the elements. Hovick et al. (2014) implied that nest temperature was the causal mechanism in nest success for Greater Prairie-Chickens, although vegetation structure was likely the nest selection cue. Therefore, environmental conditions are likely to affect vital rates, and thus demography and persistence, of Lesser Prairie-Chickens in the Sand Shinnery Oak Prairie ecoregion more than in the other ecoregions, because ~50% of all temperature and VPD observations were  $\geq 30^{\circ}\text{C}$  and less than or equal to  $-15$  mmHg.

Admittedly, differences in empirical distribution functions among ecoregions were influenced by the historic drought in the Sand Shinnery Oak Prairie ecoregion in 2011 (Huber and Gullede 2011, Nielsen-Gammon 2012, Rupp et al. 2012), as well as drought in the Mixed-Grass and Short-Grass Prairie ecoregions, but overlapping 95% CIs for nest survival suggested no difference in daily nest survival probabilities among all 3 ecoregions. The dynamic interannual variation we found in nest survival is consistent with the boom–bust reproductive strategy of the species (Hagen et al. 2009), in that each ecoregion in our assessment had 1 yr of high nest survival with 1 yr (Mixed-Grass Prairie and Short-Grass Prairie) or 2 yr (Sand Shinnery Oak Prairie) of poor nest survival (Grisham et al. 2014, Lautenbach 2015). We suspect that regional and interannual variation in microclimate may explain the boom–bust productivity pattern of the species (Hagen et al. 2009), given that the limited number of years of our assessment was adequate to capture the range of environmental conditions the species was exposed to in all 3 ecoregions and the subsequent effects on nest survival. Current climate-change forecasts predict hotter and drier conditions on the Great Plains during incubation and brood rearing (Grisham et al. 2016a). Our results offer fine-scale, nest-location-specific support to earlier evidence that Lesser Prairie-Chicken productivity has the potential to decrease with changes in spring phenology and warmer, more arid conditions due to climate change (Fields et al. 2006, Grisham et al. 2013). However, nest survival in the eastern and northern portions of the species' range is less likely to be affected by naturally cooler, more humid climates that decrease the probability of egg death or nest abandonment.

Our study is the first to identify the approximate environmental thresholds for nest survival in Lesser

Prairie-Chickens in relation to nest vegetation. Our major finding confirms that except during extreme drought, visual obstruction was a good predictor of nest survival. We also confirmed a positive relationship between visual obstruction and nest survival in all 3 ecoregions. This finding was consistent with most previous research (Haukos and Smith 1989, Pitman et al. 2005, Davis 2009, Grisham et al. 2014; but see Fritts et al. 2016). Visual obstruction was an important predictor of nest survival in studies when the majority of nests were located in either sand sagebrush or shinnery oak (Davis 2009, Grisham et al. 2014) but not in studies in which the majority of nests were located in grasses (Fritts et al. 2016). Fritts et al. (2016) suggested that native grasses provide greater visual obstruction than shrubs, thus increasing the amount of potential nesting locations when grasses are widely available. In the present study, grasses were unavailable for nesting during drought years in the Sand Shinnery Oak Prairie ecoregion (Grisham et al. 2014), although residual grasses were available in the Mixed- and Short-Grass ecoregions (Lautenbach 2015). In the Sand Shinnery Oak Prairie ecoregion, shrubs provided thermal refugia (Patten et al. 2005, Bell et al. 2010) and visual obstruction (Davis 2009, Hagen et al. 2013, Grisham et al. 2014) for nesting females during drought years, but grasses were selected for nesting over shrubs when available (Grisham et al. 2014, Fritts et al. 2016). Thus, in the final synthesis, latitudinal and longitudinal differences in microclimate conditions (present study), interannual plant composition (Grisham et al. 2014, Lautenbach 2015, Fritts et al. 2016), and subsequent vegetation composition and structure among ecoregions (Hagen et al. 2013, present study) explain the conflicting relationships between nest survival and visual obstruction among previous studies.

### Management Implications and Future Directions

Lesser Prairie-Chicken populations would benefit from research that identifies thermal landscapes (i.e. distribution of temperature and relative humidity at multiple spatial scales; Johnson 1980) and land management techniques (e.g., prescribed fire, grazing, tree removal, herbicide application) that promote cooler, more humid microclimates for nesting and brood-rearing activities (Patten et al. 2005, Bell et al. 2010). Populations would also benefit from improving and maintaining suitable visual obstruction (about 3.7–4.4 dm; Hagen et al. 2013, Fritts et al. 2016) for nesting activities (Hagen et al. 2013). Our results indicate that identification of thermal refugia has higher priority in the Sand Shinnery Oak Prairie ecoregion, but our recommendation for identification of thermal landscapes is warranted for all populations, given expected climate change throughout the distribution (Grisham et al. 2016a).

Sand shinnery oak provides critical nesting habitat and thermal refugia and promotes high adult survival (Patten et al. 2005, Bell et al. 2010, Fritts et al. 2016). The herbicide tebuthiuron is commonly used to reduce or eliminate shinnery oak in favor of grasses and forbs for cattle forage (Peterson and Boyd 1998). Although Haukos (2011) recommended best management practices for tebuthiuron application in the Sand Shinnery Oak Prairie ecoregion, widespread misuse (e.g., spraying during drought, doses  $\geq 1.0 \text{ kg ha}^{-1}$ ; Haukos 2011) of tebuthiuron continues (P. McDaniel personal communication), killing sand shinnery oak. Our results stress the importance of sand shinnery oak to this system. Lesser Prairie-Chicken populations in the Sand Shinnery Oak Prairie ecoregion would benefit if tebuthiuron application were completely avoided during drought years (including prolonged drought), because otherwise plants are defoliated during incubation and brood-rearing activities (Peterson and Boyd 1998), reducing the availability of thermal refugia.

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**Ethics statement:** All methods were approved under Kansas State University Institutional Animal Care and Use Protocol no. 3241 and Texas Tech University Institutional Animal Care and Use Protocol no. 1052-08. Any use of trade names, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

**Author contributions:** B.G., C.B., and D.H. conceived and designed the experiments. B.G. performed the experiments. B.G., C.B., and D.H. developed or designed the methods. B.G. and A.G. analyzed the data and wrote the paper. C.B. and D.H. contributed substantial materials, resources, or funding.

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## APPENDIX

### Study Area Descriptions

**Mixed-Grass Prairie ecoregion.** Dominant vegetation within the region included little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), sideoats grama (*B. curtipendula*), buffalograss (*Buchloe dactyloides*), sand dropseed (*Sporobolus cryptandrus*), Louisiana sagewort (*Artemisia ludoviciana*), western ragweed (*Ambrosia psilostachya*), sand sagebrush (*Artemisia filifolia*), and eastern red cedar (*Juniperus virginiana*; Lauver et al. 1999). The study area in Clark County in south-central Kansas was located along the ecotone of the Mixed-Grass and Sand Sagebrush Prairie ecoregions; the study area also included considerable alkali flats along drainages. Dominant vegetation in the area included little bluestem, sideoats grama, blue grama, hairy grama, big bluestem (*Andropogon gerardii*), alkali sacaton (*Sporobolus airoides*), Russian thistle (*Salsola* sp.), kochia (*Kochia scoparia*), annual sunflower (*Helianthus annuus*), and sand sagebrush (Lauver et al. 1999).

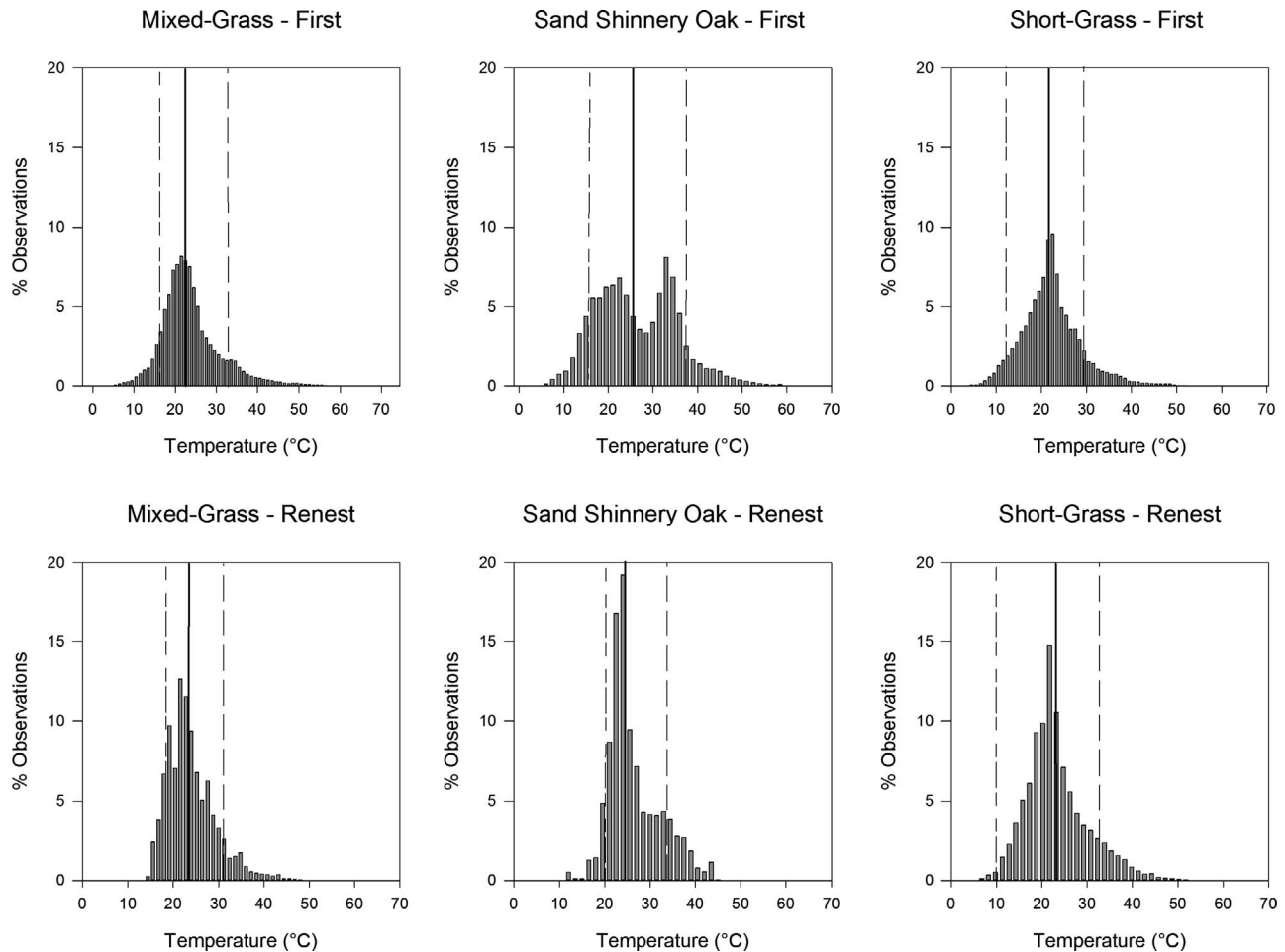
Average high temperatures for the study area during the nesting season were 22°C (range: 8–34°C) in April; 29°C (range: 14–40°C) in May; and 32°C (range: 19–39°C) in June. Average low temperatures were 3°C (range: –6°C to 18°C) in April; 8°C (range: –4°C to 20°C) in May; and 17°C (range: 10–24°C) in June. Total precipitation in 2013 was 14.47 cm in April, 21.32 cm in May, and 22.41 cm in June

(annual precipitation = 41.0 cm). Total precipitation in 2014 was 10.41 cm in April, 11.67 cm in May, and 13.5 cm in June (annual precipitation = 41.16 cm). The study area was listed as “mid-range” on the Palmer Drought Severity Index at the end of the nesting season in 2013 (June 7; <http://www.ncdc.noaa.gov/temp-and-precip/us-weekly/20130601>) and 2014 (<http://www.ncdc.noaa.gov/temp-and-precip/us-weekly/20140607>). The region was primarily used for ranching/pastureland, with row-crop agriculture interspersed throughout the region.

**Sand Shinnery Oak Prairie ecoregion.** Strahan (2008) provides a complete floristic survey of the plants located in sand shinnery oak prairies. Average high temperatures for the study area during the nesting season were 25°C (range: 22–27°C) in April; 29°C (range: 27–30°C) in May; and 35°C (range: 34–37°C) in June. Average low temperatures were 9°C (range: 8–10°C) in April; 13°C (range: 12–15°C) in May; and 19°C (range: 19–21°C) in June. In general, 2010 was the wettest year during the study, with 3.17 cm in April, 3.00 cm in May, and 13.56 cm in June (annual precipitation = 53.34 cm); whereas 2011 was the driest year, with 0.00 cm in April, 0.05 cm in May, and 0.00 cm in June (annual precipitation = 0.60 cm); and 2012 received 1.24 cm in April, 1.70 cm in May, and 5.86 cm in June (annual precipitation = 27.56 cm) (<http://www.mesonet.ttu.edu>; Mallet Station). The study area was listed as “moderately moist” on the Palmer Drought Severity Index at the end of the nesting season in 2010 (June 7; <http://www.ncdc.noaa.gov/temp-and-precip/us-weekly/20100605>) and as “extreme drought” in 2011 (<http://www.ncdc.noaa.gov/temp-and-precip/us-weekly/20110604>) and 2012 (<http://www.ncdc.noaa.gov/temp-and-precip/us-weekly/20120602>).

The major land uses in this region were cattle production, row-crop agriculture, and oil and natural gas extraction. Although the New Mexico and Texas study areas were separated by a political boundary, there were no genetic or other biological differences between Lesser Prairie-Chickens in these states; thus, the study sites consisted of a single population (Corman 2011, Oyler-McCance et al. 2016).

**Short-Grass Prairie ecoregion.** Dominant vegetation in the region included blue grama, hairy grama, buffalograss, little bluestem, sideoats grama, big bluestem Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annuum*), sand milkweed (*Asclepias arenaria*), 9-anther dalea (*Dalea enneandra*), and western ragweed (Lauver et al. 1999). The grass species planted within the CRP fields included little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indiangrass (*Sorghastrum nutans*; Fields et al. 2006). After original planting, the fields were interseeded with forbs, including white sweetclover (*Melilotus alba*), yellow



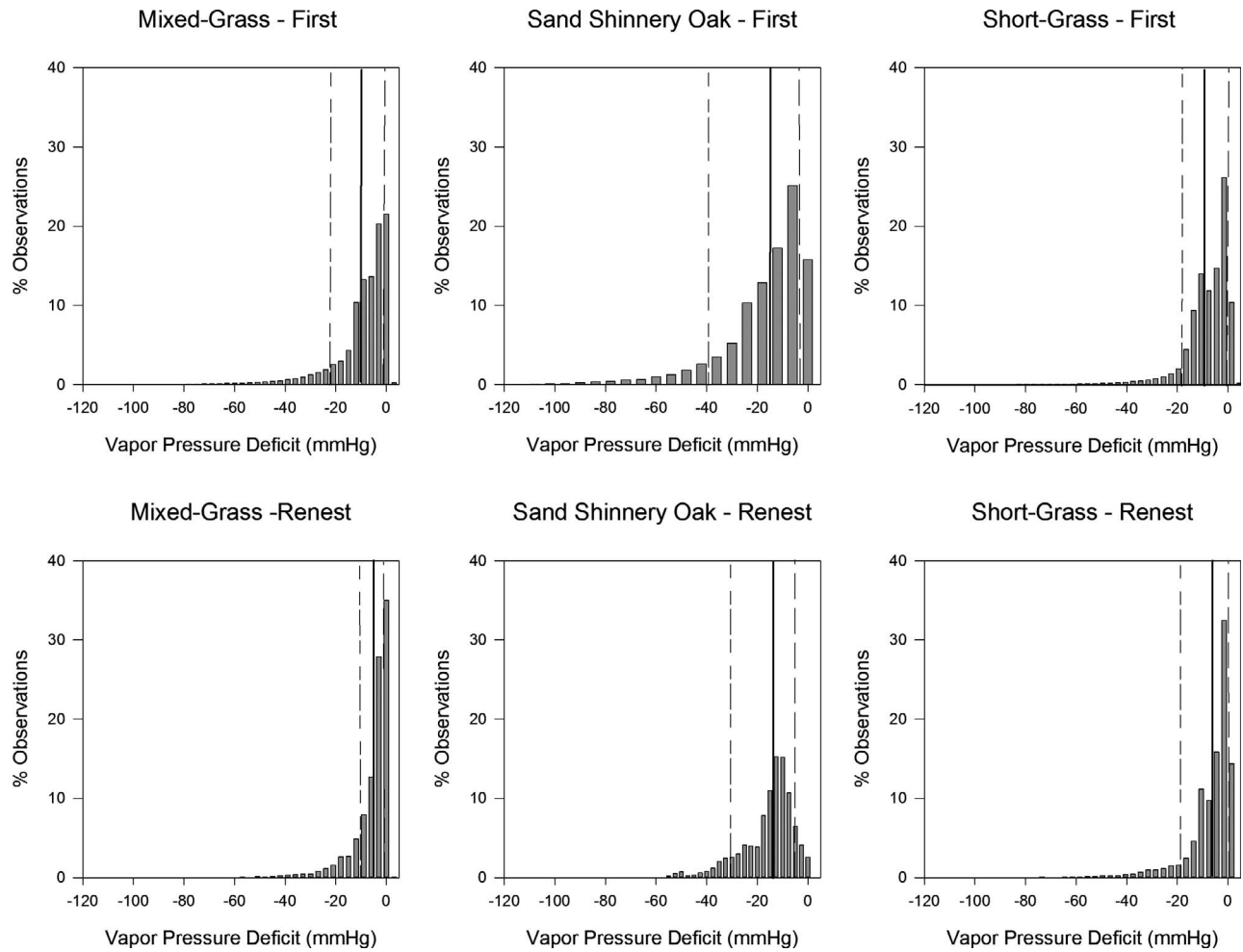
**APPENDIX FIGURE 6.** Empirical distribution of temperature recordings from Lesser Prairie-Chickens' first ( $n = 267,888$ ; top row) nests and renests ( $n = 45,041$ ; bottom row) in the Mixed-Grass Prairie ( $n = 12,426$ ), Sand Shinnery Oak Prairie ( $n = 3,297$ ), and Short-Grass Prairie ( $n = 29,318$ ) ecoregions. Vertical lines indicate the 10th percentile, mean, and upper 90th percentile of observations.

sweetclover (*M. officinalis*), Maximilian sunflower (*Helianthus maximiliani*), Illinois bundleflower, purple prairie clover (*Dalea purpurea*), and prairie coneflower (*Ratibida columnifera*; Fields et al. 2006).

Average high temperatures for the study area during the nesting season were 18°C (range: 0.6–33°C) in April; 26°C (range: 4–37°C) in May; and 32°C (range: 15–43°C) in June. Average low temperatures were 0.69°C (range: –8°C to 11°C) in April; 8°C (range: –3°C to 18°C) in May; and 15°C (range: 5–22°C) in June. Total precipitation in 2013 was 1.65 cm in April, 5.54 cm in May, and 5.00 cm in June (annual

precipitation = 52.67 cm). Total precipitation in 2014 was 2.33 cm in April, 0.41 cm in May, and 27.82 cm in June (annual precipitation = 55.93 cm). The study area was listed as “severe drought” on the Palmer Drought Severity Index at the end of the nesting season in 2013 (June 7; <http://www.ncdc.noaa.gov/temp-and-precip/us-weekly/20130601>) and 2014 (<http://www.ncdc.noaa.gov/temp-and-precip/us-weekly/20140607>). The dominant land uses in this region were livestock grazing, row-crop agriculture, and CRP. Wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), and corn (*Zea mays*) were the major crops in the region.





**APPENDIX FIGURE 7.** Empirical distribution of vapor pressure deficit recordings from Lesser Prairie-Chickens' first ( $n = 267,888$ ; top row) nests and renests ( $n = 45,041$ ; bottom row) in the Mixed-Grass Prairie ( $n = 12,426$ ), Sand Shinnery Oak Prairie ( $n = 3,297$ ), and Short-Grass Prairie ( $n = 29,318$ ) ecoregions. Vertical lines indicate the 10th percentile, mean, and upper 90th percentile of observations.