

The relative contribution of climate to changes in lesser prairie-chicken abundance

BETH E. ROSS,^{1,5,†} DAVID HAUKOS,² CHRISTIAN HAGEN,³ AND JAMES PITMAN⁴

¹Division of Biology, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan, Kansas 66506 USA

²U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan, Kansas 66506 USA

³Oregon State University, Bend, Oregon 97702 USA

⁴Western Association of Fish and Wildlife Agencies, Emporia, Kansas 66801 USA

Citation: Ross, B. E., D. Haukos, C. Hagen, and J. Pitman. 2016. The relative contribution of climate to changes in lesser prairie-chicken abundance. *Ecosphere* 7(6):e01323. 10.1002/ecs2.1323

Abstract. Managing for species using current weather patterns fails to incorporate the uncertainty associated with future climatic conditions; without incorporating potential changes in climate into conservation strategies, management and conservation efforts may fall short or waste valuable resources. Understanding the effects of climate change on species in the Great Plains of North America is especially important, as this region is projected to experience an increased magnitude of climate change. Of particular ecological and conservation interest is the lesser prairie-chicken (*Tympanuchus pallidicinctus*), which was listed as “threatened” under the U.S. Endangered Species Act in May 2014. We used Bayesian hierarchical models to quantify the effects of extreme climatic events (extreme values of the Palmer Drought Severity Index [PDSI]) relative to intermediate (changes in El Niño Southern Oscillation) and long-term climate variability (changes in the Pacific Decadal Oscillation) on trends in lesser prairie-chicken abundance from 1981 to 2014. Our results indicate that lesser prairie-chicken abundance on leks responded to environmental conditions of the year previous by positively responding to wet springs (high PDSI) and negatively to years with hot, dry summers (low PDSI), but had little response to variation in the El Niño Southern Oscillation and the Pacific Decadal Oscillation. Additionally, greater variation in abundance on leks was explained by variation in site relative to broad-scale climatic indices. Consequently, lesser prairie-chicken abundance on leks in Kansas is more strongly influenced by extreme drought events during summer than other climatic conditions, which may have negative consequences for the population as drought conditions intensify throughout the Great Plains.

Key words: climate change; drought; lesser prairie-chicken; population model; *Tympanuchus pallidicinctus*.

Received 14 July 2015; revised 11 September 2015; accepted 5 December 2015. Corresponding Editor: B. Maslo.

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⁵Present address: U.S. Geological Survey, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, South Carolina 29634 USA.

† **E-mail:** bross5@clemson.edu

INTRODUCTION

As environmental conditions are predicted to change and become more variable within the current century (IPCC 2013), forecasting the effects of projected climate variability on future wildlife populations is critical for managing species of conservation concern. Managing for species using current weather patterns fails to incorporate

the projected changes associated with future climatic conditions. Indeed, without incorporating potential changes in climate into conservation strategies, management and conservation efforts may fall short or waste valuable resources (Nichols et al. 2011).

Some of the greatest increases in climate variability are projected to occur in the Great Plains of North America (IPCC 2013, Cook et al. 2015).

The effects of climate may be intensified through agricultural practices in the region (Stohlgren et al. 1998), which are projected to increase in the future (Sohl et al. 2012). Additionally, weather conditions in the Great Plains can cause decreases in important population demographic parameters such as reproduction (Grisham et al. 2013, Grisham and Boal 2015) or juvenile (Pitman et al. 2006) and adult survival (Plumb 2015). Many avian species endemic to the Great Plains region are decreasing in response to changes in climate (Peterson 2003), which may be affected by a decoupling of food availability (e.g., insect abundance) and brood rearing (Pitman et al. 2006). As many of these populations are already at reduced abundance, they are especially susceptible to the projected intensification of drought in the region (Willi et al. 2006). Therefore, understanding the effects of past drought events on changes in abundance of species in the region will help inform conservation planning in a changing climate.

A sentinel species of conservation concern in the Great Plains is the lesser prairie-chicken (*Tympanuchus pallidicinctus*), which was listed as threatened under the U.S. Endangered Species Act in May 2014, but as of this publication date, was ruled as listed unlawfully. Currently, the lesser prairie-chicken persists in Kansas, Colorado, New Mexico, Texas, and Oklahoma with the core of the range and >70% of the population occurring in Kansas (McDonald et al. 2014a). Intensive, range-wide annual population abundance estimates are only available from 2012 onward, and little information is available on causes of long-term trends in abundance. As the current species abundance is estimated to be relatively low (i.e., 29,162 individuals 90% confidence intervals = 21,661–41,017), and highly variable, the concern related to extinction or extirpation of small populations is warranted (Willi et al. 2006). The greatest decreases of the lesser prairie-chicken are occurring in the Mixed-Grass Prairie and Sand Sagebrush (*Artemisia filifolia*) Prairie Ecoregions. The population has been increasing in areas with a mosaic of Short-Grass and Conservation Reserve Program (CRP) land cover (Garton et al. 2016), with climate change potentially contributing to these regional changes in abundance and occupied range (Dahlgren et al. 2016).

The reduction in abundance of the lesser prairie-chicken has been attributed to changes

in natural stressors (e.g., recent drought conditions, McDonald et al. 2014b) as well as human-induced change (e.g., changes in land use, Fuhlendorf et al. 2002). The landscape of the Great Plains, especially Kansas, is experiencing changes in precipitation and temperature, which are projected to increase in variation in the future (Karl et al. 2009, Cook et al. 2015). Projected increases in temperature and decreases in relative humidity are expected to reduce nest success of lesser prairie-chickens such that fecundity will fall below the threshold necessary for population persistence by 2050 in the Sand Shinnery Oak Prairie Ecoregion (Grisham et al. 2013). Due to projected changes in climate, these populations in the southern portion of the range may be forced to find potentially less suitable habitat and may experience accelerated declines in population abundance (Grisham et al. 2013). Alternatively, northern populations have shown slow, but persistent, northern expansion of their range. Therefore, understanding these possible shifts in the range and population dynamics of the lesser prairie-chicken relative to climate variation is critical for implementing management practices for species conservation.

The goal of this study was to assess the effects of climate variability on abundance of lesser prairie-chickens on leks, the communal display and mating grounds used by grouse that can be used as an index to total population abundance (Walsh et al. 2004, Garton et al. 2016). To achieve our goal, we (1) quantified the effects of changes in climate indices on abundance of lesser prairie-chickens on leks in Kansas from 1981 to 2014 and (2) assessed the proportion of variation in lesser prairie-chicken abundance explained by changes in climate.

METHODS

Study area

As the Kansas Department of Wildlife, Parks, and Tourism is the only agency within the current range of the lesser prairie-chicken to conduct consistent, long-term, broad-scale surveys to monitor lesser prairie-chicken populations, and Kansas is the core of the current range, we limited our analysis to this region. Lesser prairie-chicken surveys included three ecoregions in western (Short-Grass/CRP mosaic), southwestern (Sand Sagebrush Prairie), and

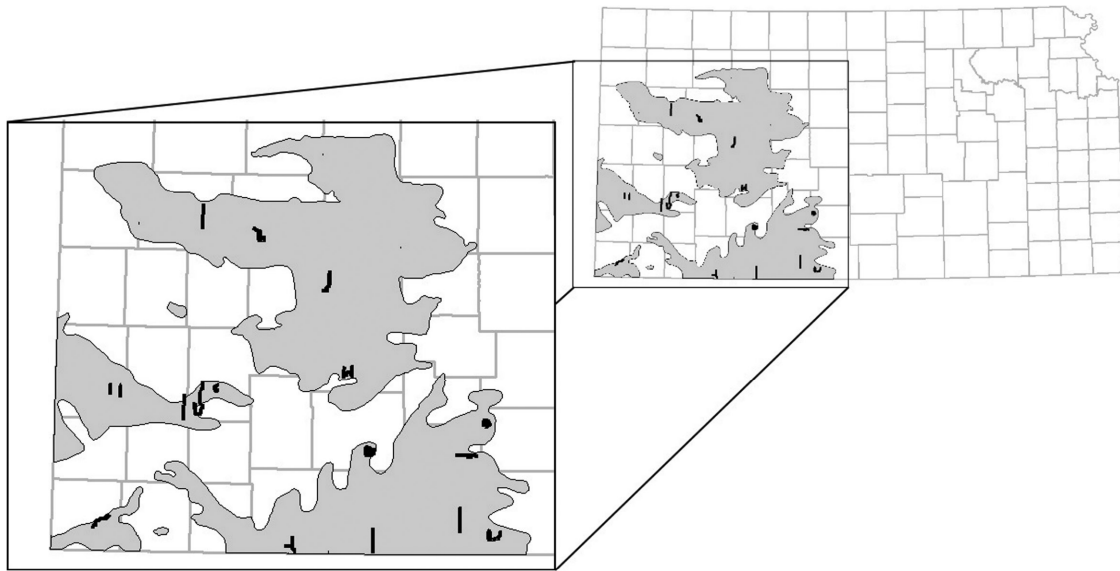


Fig. 1. Survey routes (in black) for lesser prairie-chicken leks in Kansas from 1981 to 2014. The range of the species in Kansas is shown in gray.

south-central Kansas (Mixed-Grass Prairie), covering a large portion of the species' core range (Fig. 1; McDonald et al. 2014b). Land use in western Kansas consisted of row-crop agriculture, grazing, and land enrolled in the U.S. Department of Agriculture CRP. Southwestern Kansas was dominated by sand sagebrush prairie, and primarily consisted of range and cropland. Surveys in south-central Kansas were located within the Red Hills region, which primarily consisted of grassland with pockets of row-crop agriculture in bottomlands. Typical cropland in Kansas consists of winter wheat, grain sorghum, alfalfa, and limited area of corn (both irrigation and dryland).

Lek survey counts

Surveys for lesser prairie-chickens in Kansas began with single transects in three counties in 1967 and increased to 17 transects in 15 counties covering $\sim 520 \text{ km}^2$ by 2014. To conduct a survey, observers drove a 16-km transect and stopped every 1.6 km for 3-min auditory surveys to identify leks. Surveys generally started between 05:00 and 07:00 hours. After completing the driving route, the observer then returned to each lek, flushed the birds, and counted all the lesser prairie-chickens on the lek. Observers generally conducted surveys twice each season

between March 20 and April 20. Lekking males are most likely to be detected with this survey methodology as transient males and females are likely not a large proportion of the observed birds. Mixed-species leks and leks with hybrids between lesser and greater prairie-chickens may occur on three routes or fewer in northwestern Kansas (Bain and Farley 2002). These mixed leks are difficult to distinguish in flush counts and may have been included in counts of lesser prairie-chickens.

While inference from lek counts can be problematic, they can also be used as an index to population abundance if certain assumptions are met (Walsh et al. 2004, Garton et al. 2016). Our model controls for imperfect detection, and leks were surveyed up through 90 min after sunrise to control for issues related to lek attendance rates.

Effects of climate variation

We used three climatic indices as surrogates for climate condition: the Palmer Drought Severity Index (PDSI), the El Niño Southern Oscillation (ENSO), and the Pacific Decadal Oscillation (PDO). These climatic indices range from quick turnover rates (PDSI) of a few months to slow turnover rates (PDO) of several decades. The variety of time scales allowed us to determine the relative time scale on which

changes in climate variability might be affecting lesser prairie-chicken abundance. Additionally, we were specifically interested in understanding how short-term, extreme drought events, relative to more gradual climatic changes, affect lesser prairie-chicken abundance.

We created four variables for PDSI to denote years with extreme wet or drought conditions in either spring or summer. Covariates were created as binary variables (1 or 0) for spring (April–May) and summer (June–July) of each year in which there was a high value of PDSI (>3) or low value of PDSI (<-3 ; e.g., a year with an extreme drought in summer would be coded as a 1 for that year). Values of PDSI >3 are classified by the National Climatic Data Center as “Very Moist Spells” and values of PDSI <-3 are classified as “Severe Droughts” (NCDC 1994). PDSI variables were developed for the following three different climatic regions in Kansas: northwestern Kansas, central-western Kansas, and south-central Kansas (climate divisions 4, 7, and 8; NCDC 1994). The ENSO variable, based on data for the Oceanic Niño Index (National Weather Service Climate Prediction Center 2014), was included for three-month periods from December, January, February; April, May, June; May, June, July; and June, July, August. The PDO data (Mantua 2014) were averaged from November to April, which correlates with climate changes in the Great Plains (Mantua and Hare 2002). The slow turnover of the PDO also coincides with a 20-yr cycle of drought in the Great Plains that has occurred during the last century with intense droughts in the 1930s, 1950s, 1970s, 1990s, and 2010s (Trenberth et al. 1988, Chen and Newman 1998, Grisham et al. 2016). Lesser prairie-chicken population fluctuations seem to correspond to this 20-yr drought periodicity (Grisham et al. 2013), though this has yet to be explicitly tested in relation to specific climatic variables and other population drivers.

The above variables were implemented using a 1-year lag effect, e.g., a low value of PDSI in 2002 would affect population abundance in 2003, based on the timing of surveys relative to the growing season. Additionally, a 2-year lag effect (e.g., a low value of PDSI in 2002 would affect population abundance in 2004) was included for each of the above variables as juvenile males are less likely to attend traditional leks in their first

year (Haukos and Smith 1999); thus, affecting our ability to detect effects of climate variation on abundance the following spring.

Hierarchical model

We implemented a Bayesian hierarchical model (Royle 2004) to estimate and quantify drivers of abundance at leks throughout the range of the lesser prairie-chicken in Kansas. The data for this model were specified as coming from a binomial distribution as

$$y_{i,j,t} \sim \text{Binomial}(N_{i,t}, p_{i,j,t}) \quad (1)$$

where $y_{i,j,t}$, the count data from lek surveys at stop i , visit j , and year t , are distributed binomially with parameters $N_{i,t}$, the estimated abundance on leks, and $p_{i,j,t}$, the combined probability of detection. We assumed that detection probability varied by year and site with a random effect for survey occasion. Because of the survey methodology, we were unable to separate detection probability associated with identifying individual leks versus counting available individuals on each lek (where the probability an individual is available to be detected may be <1). We subsequently refer to detection probability as “combined detection probability” to clarify this distinction. We truncated the data to 1981 due to the limited number of surveys conducted before that time, but note that this starting date predates the most contemporary population peak that likely occurred in the mid-1980s (Garton et al. 2016).

We constructed a process model to describe changes in climate variability that might affect abundance of males of the lesser prairie-chickens on leks, which would in turn be representative of greater changes to the population as a whole. The abundance at leks was linked to the observation model where $N_{i,t}$ (from Eq. 1) was defined as coming from a Poisson distribution as $N_{i,t} \sim \text{Poisson}(\lambda_{i,t})$, and the parameter $\lambda_{i,t}$ was estimated as

$$z_{i,t} = \log(\lambda_{i,t}) = \beta_0 + \mathbf{x}'_{i,t} \boldsymbol{\beta} + \gamma_i \quad (2)$$

where β_0 was an intercept and $\boldsymbol{\beta}$ was the matrix of regression coefficients for 1- and 2-yr lag effects

for PDSI, ENSO, PDO. The $\gamma_i \sim N(0, \sigma_\gamma^2)$ were random effects for each site.

We compared the proportion of variance explained by the climatic variables relative to a null model with only the random effects of site (σ_γ^2) and a model with both random effects and climatic variables. The total proportion of variation explained by both the random effects and climatic variables was calculated as

$$R_{GLMM(c)}^2 = \frac{\sigma_f^2 + \sigma_\gamma^2}{\sigma_f^2 + \sigma_\gamma^2 + \sigma_e^2 + \sigma_d^2} \quad (3)$$

where σ_γ^2 was the variance of the random effect from Eq. 2, σ_f^2 was the variance calculated from the fixed effect variables, and σ_d^2 was the distribution-specific variance. The conditional R^2 value shown here can also be interpreted as the variance explained by the entire model (Nakagawa and Schielzeth 2013). We compared the conditional R^2 to the marginal R^2 (Nakagawa and Schielzeth 2013) of the intercept-only model with no environmental variables specified as

$$R_{GLMM(m-intercept)}^2 = \frac{\sigma_\gamma^2}{\sigma_f^2 + \sigma_\gamma^2 + \sigma_e^2 + \sigma_d^2}. \quad (4)$$

and the marginal R^2 of the model with only environmental variables specified as

$$R_{GLMM(m-environment)}^2 = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_\gamma^2 + \sigma_e^2 + \sigma_d^2}. \quad (5)$$

Because we did not know which climatic variables would influence lek abundance a priori, we used the stochastic search variable selection (SSVS) to determine the β to include in our model the traditional model selection using Deviance Information Criterion is not appropriate for complicated Bayesian hierarchical models (O'Hara and Sillanpaa 2009, Hooten and Hobbs 2015). The variables $\gamma_k \sim \text{Bern}(q_k)$ indicated when the β_k were included in the model; when $\gamma_k = 1$ the k th variable was included and not included when $\gamma_k = 0$. We specified the conditional prior on β_k as a mixture of two Gaussians, $\beta_k | \gamma_k \sim (1 - \gamma_k) \times N(0, c_1) + \gamma_k \times N(0, c_2)$ with the

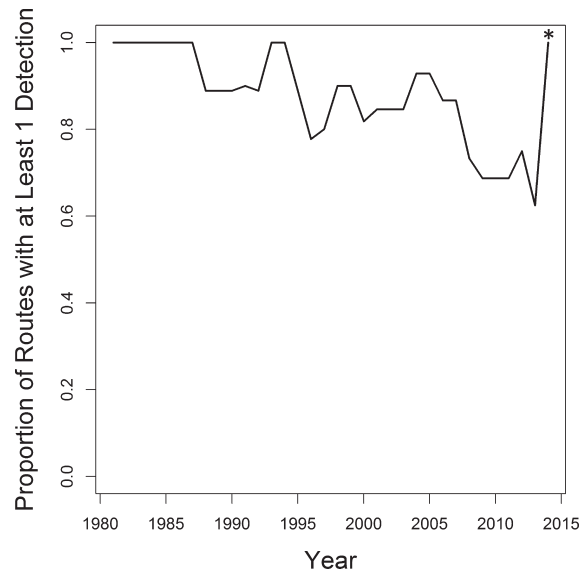


Fig. 2. Proportion of routes with at least one detection of a lesser prairie-chicken in Kansas from 1981 to 2014. The "*" indicates a decrease in the number of routes surveyed from 16 in 2013 to 8 in 2014.

constant $c_1 = 0.01$ and $c_2 = 10$. These values were chosen for c_1 and c_2 to allow for vague priors for β_k if β_k was included in the model, and tuning the values of c_1 and c_2 yielded similar results. Ultimately, using SSVS allowed us to assign a mean probability of inclusion for each variable of interest based on the number of inclusions ($\gamma_k = 1$) out of the total number of Markov Chain Monte Carlo (MCMC) samples (O'Hara and Sillanpaa 2009, Hooten and Hobbs 2015). We based inference on those variables with a probability of inclusion of 0.5 or higher (Walli 2010, Malsiner-Walli and Wagner 2011).

We used MCMC and a Gibbs sampler in JAGS (Plummer 2012) with the package runjags (Denwood 2014) in program R (R Core Team 2013) to obtain posterior distributions for the parameters. We discarded the first 50,000 samples as burn-in and ran 3,000,000 iterations from three chains thinned to every 1000 sample and collected 1000 samples. As we did not have a priori data to support particular effect sizes, detection probabilities, or residuals, we specified vague prior distributions as $\beta \sim \text{Normal}(0, 100)$, $p_{i,t} \sim \text{Uniform}(0, 1)$, and $\gamma_i \sim \text{Normal}(0, 9)$. JAGS code for the hierarchical model and SSVS procedure can be found in Appendix S1.

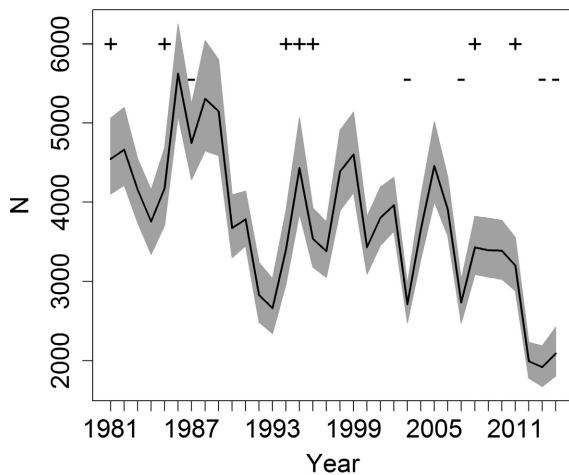


Fig. 3. Estimates of total abundance on surveyed lesser prairie-chicken leks in Kansas from 1981 to 2014. Years denoted as “high” Palmer Drought Severity Index (PDSI) in spring are indicated with a “+” while years denoted as “low” PDSI in summer are indicated with a “-”.

RESULTS

From 1981 to 2014, 31,557 birds were observed on 8–17 routes with most routes having at least one detection (Fig. 2). Lesser prairie-chicken abundance at leks in Kansas was greatest during the late 1980s, followed by a slight decrease in abundance during the early 1990s (Fig. 3). The population fluctuated throughout the 1990s

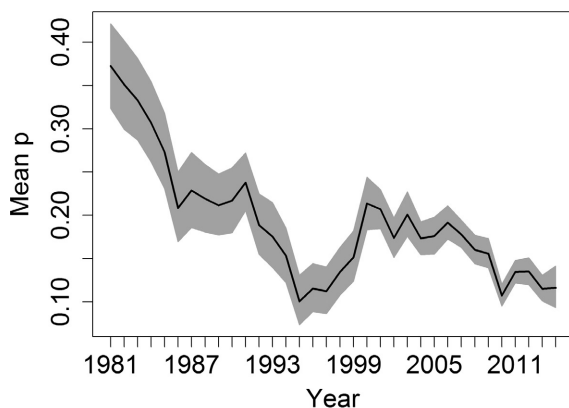


Fig. 4. Estimates of combined detection probability (probability of detecting a lek and probability of detecting individuals on a lek) of males on lesser prairie-chicken leks in Kansas from 1981 to 2014.

and 2000s, and decreased significantly from 2011 to 2012. Overall, the population has been relatively stable on the survey routes in Kansas since the early 1990s, exhibiting high variability but generally returning to a population of approximately 3500–4000 males on surveyed leks. Fewer surveys conducted early in the study likely led to lower precision associated with the estimates of detection probability from the 1980s and 1990s. Combined detection probability consisting of leks and the number of males on leks was generally low, with the mean detection probability estimated around 0.2 for most years (Fig. 4), though detection probability did decrease from 1981 to 1994.

The results from the SSVS procedure indicated two important variables for inference, high PDSI in the spring and low PDSI in the summer of the previous year (but not for 2 yr prior). The remaining variables had a probability of inclusion

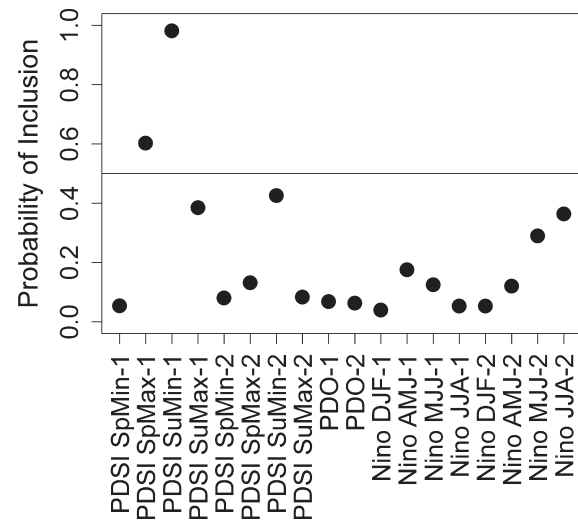


Fig. 5. Inclusion probabilities from stochastic search variable selection procedure indicating which climatic variables likely affect (above 0.5) lesser prairie-chicken abundance on leks in Kansas from 1981 to 2014. Climatic variables considered were 1-yr lag effects of Palmer Drought Severity Index (PDSI) values during wet (“Max”) and dry (“Min”) springs (“Sp”) and summers (“Su”), Pacific Decadal Oscillation (PDO), and El Niño Southern Oscillation (ENSO) from December to February (“DJF”), April to June (“AMJ”), May to July (“MJJ”) and June to August (“JJA”). The effects of 2-yr lags were also included (“-2”) for all the above variables.

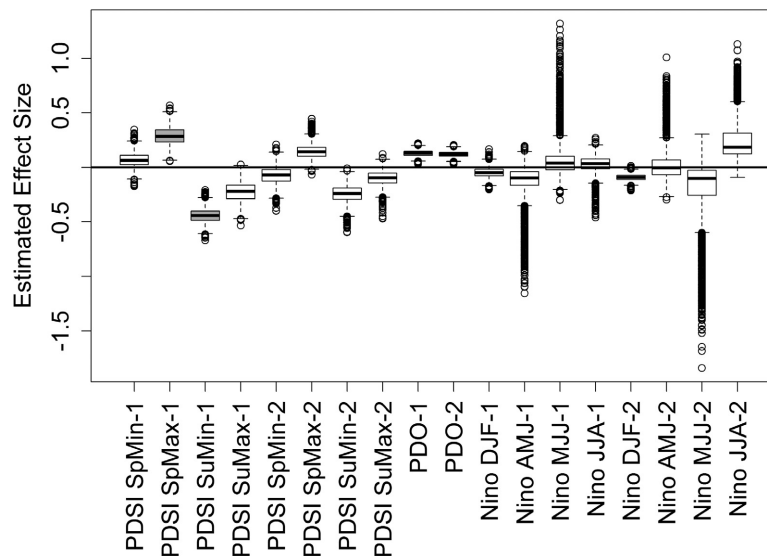


Fig. 6. Boxplots of β coefficients for all climatic variables considered in model of lesser prairie-chicken abundance on leks in Kansas from 1981 to 2014. Climatic variables considered were 1-yr lag effects of Palmer Drought Severity Index (PDSI) values during wet (“Max”) and dry (“Min”) springs (“Sp”) and summers (“Su”), Pacific Decadal Oscillation (PDO), and El Niño Southern Oscillation (ENSO) from December to February (“DJF”), April to June (“AMJ”), May to July (“MJJ”) and June to August (“JJA”). The effects of 2-yr lags were also included (“-2”) for all the above variables. Both high PDSI in spring (“PDSI SpMax”) and low PDSI in summer (“PDSI SuMin”; both shown in grey) were statistically significant and had a probability of inclusion over 0.5.

of <0.50 , and while some were statistically significant (i.e., 95% credible intervals did not include zero), they were not included for further inference because of their low probability of inclusion (Fig. 5). Both the high spring and low summer PDSI variables (1-yr lag) had a significant relationship with abundance on leks, with high PDSI (>3) in spring positively correlated with abundance on leks and low PDSI (<-3) in summer negatively correlated (Fig. 6), indicating increases in abundance following wet, cool conditions during spring and decreases in abundance on leks after dry, warm conditions during summer. When overlaid with abundance estimates, years with high PDSI in the previous spring are often followed by an increase in abundance and years with low PDSI in the previous summer are followed by a decrease in abundance (e.g., Region 4, Fig. 3).

The proportion of variation explained by only the high spring and low summer PDSI variables was relatively small (conditional $R^2 = 12.6\% \pm 3.4\%$), and the intercept and variation among sites (random effect of site) ex-

plained considerably more of the variation in the process (marginal $R^2 = 71.2\% \pm 4.0\%$). Combined, the total proportion of variation explained by the model was quite high (conditional $R^2 = 83.8\% \pm 1.9\%$).

DISCUSSION

Our results indicate that short-term, extreme climatic events (springs with recorded values of extremely high PDSI and summers with values of extremely low PDSI) generally have a larger effect on lesser prairie-chicken lek populations than long-term climatic events (e.g., PDO) over the time period of our study. We hypothesize that the positive effect of high spring PDSI on male lesser prairie-chicken abundance on leks the following breeding season is due to effects of precipitation on vegetation in the early growing season, with increased precipitation providing favorable growing conditions for cool season grasses and forbs (Waller et al. 1986). If high spring PDSI increases opportunities for earlier nest initiation through an increase

in either resources or habitat cover, these earlier nests have a greater probability of success (Fields et al. 2006, Grisham et al. 2014, Lautenbach 2015), and lesser prairie-chicken abundance would likely increase. Other grouse species (black grouse, *Tetrao tetrix*) advance egg-laying and hatching in response to a mismatched shift in climate, though asymmetric changes in climate in Norway cause decreased chick survival through colder post-hatching conditions in early summer (Ludwig et al. 2006). While our analysis was not developed to detect the effects of asymmetric shifts in climate, those variables related to variation in summer temperature and precipitation (ENSO JJA or ENSO JJA 1-yr lag) and mild summer conditions (PDSI summer maximum or PDSI summer maximum 1-yr lag) were not identified as significant drivers of population abundance.

Alternatively, extreme drought conditions during the summer likely have negative impacts on brood survival through direct (e.g., severe dehydration) and indirect (e.g., decreased food availability) effects on chicks. Lesser prairie-chicken chicks experience the lowest survival during the first 7 d after hatching, and cannot thermoregulate efficiently during this time (Pitman et al. 2006). Extreme drought combined with high temperatures can also lead to decreased survival in chicks due to exposure (Hannon and Martin 2006). Because lesser prairie-chicken chicks feed on a high insect diet, drought can also reduce the availability of insects and food resources for chicks and juveniles (Hagen et al. 2005). Drought conditions during the summer could have cascading consequences, reducing habitat quality and survival of juveniles throughout the subsequent year. Drought may delay nest initiation, increase nest abandonment, and reduce nest success for lesser prairie-chickens (Grisham et al. 2014, Lautenbach 2015). In other grouse species, high summer temperatures reduce reproduction through decreased resources (Selås et al. 2011), and variation in annual precipitation describes 75% of annual variation in population size of the greater sage-grouse (Blomberg et al. 2012). During years without extreme drought conditions, we predict that current populations may expand in response to environmental conditions if local habitat

quantity and quality are available. Indeed, the amount of grassland (i.e., native grassland and CRP combined) in the lesser prairie-chicken range in Kansas has remained relatively stable since the 1960s (Spencer 2014), though climate has fluctuated considerably.

The correlation of high spring PDSI and low summer PDSI with lesser prairie-chicken abundance, but not other variables included in the model, may indicate that at least abundance of males, and likely female abundance as well (Winder et al. 2014), responds to climatic changes on a shorter temporal scale rather than climatic indices that operate on a longer time scale such as the ENSO and PDO. Granted, variability in PDSI is likely somewhat correlated with ENSO and PDO, however, separating the components of these longer temporal scale changes that contribute to PDSI would be difficult. Because the lesser prairie-chicken is a relatively short-lived species and exhibits a relatively fast life-history strategy (Sæther and Bakke 2000), individuals may be opportunistically breeding and nesting earlier when climatic conditions allow. Lesser prairie-chicken population dynamics are most sensitive to variation in reproductive parameters and juvenile survival (Hagen et al. 2009), and other grouse species have greater variation in recruitment than adult survival (Blomberg et al. 2012). However, adult survival may be an important driver of population dynamics in the southern portion of the lesser prairie-chicken range (Pruett et al. 2011). Environmental conditions for successful recruitment may be infrequent in the semi-arid range of the lesser prairie-chicken, resulting in boom-bust fluctuations (Garton et al. 2016). Increases in climatic variability will likely intensify boom-bust dynamics of lesser prairie-chickens, especially under scenarios with increased drought conditions (Cook et al. 2015). If the frequency of years with high spring PDSI decreases, the probability of the species being extirpated will increase, as the years with favorable conditions could be insufficient to overcome the frequency or duration of years with low summer PDSI (Grisham et al. 2013). Incorporating the effects of PDSI on lesser prairie-chickens is important for future management scenarios (Nichols et al. 2011).

The inference for our study is limited to our sites in Kansas, but the study area does incorporate over 70% of the total range of lesser prairie-

rie-chickens and three distinct ecoregions with lesser prairie-chicken habitat (Van Pelt et al. 2013). Our abundance estimates only provide an index to abundance of the species at route locations, not values for state- or range-wide abundance. We also assume that males and females respond similarly to the included environmental conditions. If PDSI is affecting lesser prairie-chickens through changes in breeding or nesting behavior, and not via adult survival, we would expect that chicks of both sexes would be affected equally. Additionally, while some of the covariates included in our model may have been correlated, it is likely that correlation among the variables would not affect our interpretation of the SSVS results as SSVS is relatively robust to correlated covariates (Walli 2010, Malsiner-Walli and Wagner 2011). If correlation exists among covariates, the SSVS procedure has less power to detect variables of importance, and yields a conservative interpretation of results, thus making it less likely that we would have been able to detect effects of PDSI (Walli 2010, Malsiner-Walli and Wagner 2011).

The combined probability of detection did decrease during the first decade of our analysis, likely due to two possible causes. Survey routes may have been chosen during early years of the survey because they were known to contain active leks, and biologists may have increased their search effort knowing a priori that leks were present. Additionally, oil wells and other causes of anthropogenic noise pollution increased throughout this time period concurrent with development in the region, reducing the surveyor's ability to detect leks using sound. Decreases in detection should not have caused any systematic bias in our abundance estimates, but likely reduced precision of parameter estimates.

Our results indicate that short-term increases in spring PDSI may positively affect lek abundance in the following year, but our results do not indicate a response to long-term drought (i.e., through correlation with ENSO or PDO). Rather, if there was a relationship with ENSO or PDO, the response to long-term drought would result in annual decreases in abundance on leks for the duration of the drought, and continued annual declines would correlate more with PDSI than PDO. While incorporating variation in pro-

jected climate scenarios will likely help explain variation in lesser prairie-chicken abundance (Nichols et al. 2011), climate variation did not explain the majority of variation in our models. Future management actions would benefit from also accounting for drivers of lesser prairie-chicken abundance other than climate, as climate explained a relatively small proportion of the variance relative to a model with only an intercept and random site effects. As the variation among sites explained considerably more variation in the model than climate, our results may suggest that differences among sites (fine-scale) have a larger impact on lesser prairie-chicken abundance on leks, and perhaps the whole population, than broad-scale population dynamics. If fine-scale effects have a larger impact on abundance than climate variation, then maintaining sufficient quantity of quality habitat at a local scale is important for persistence of the species (Fuhlendorf et al. 2002). Indeed, conservation efforts for the lesser prairie-chicken that focus on improvement of habitat (Van Pelt et al. 2013) may be useful in offsetting projected changes in climate. While fine-scale effects may influence population abundance, continued study of the effects of climate change and the incorporation of climate variability in lesser prairie-chicken management is still important given the high variability in abundance of the population and the small population size.

ACKNOWLEDGMENTS

Earlier drafts of this manuscript were improved with comments by D. Dahlgren, L. Martin, M. Pendergast, J. Sutton, S. Supp, and E. Weiser and six anonymous reviewers. We thank J. Kramer, M. Mitchener, D. Dahlgren, J. Predergast, and S. Hyberg for their assistance with the project. Funding for the project was provided by Kansas Wildlife, Parks, and Tourism (Federal Assistance Grant KS W-73-R-3), USDA Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62), and the USDA Natural Resources Conservation Service through the Lesser Prairie Chicken Initiative. We thank the biologists from the Kansas Department of Wildlife, Parks, and Tourism for collecting the lek survey data. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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