



Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

Landscape composition creates a threshold influencing Lesser Prairie-Chicken population resilience to extreme drought

Beth E. Ross^{a,b,*}, David A. Haukos^c, Christian A. Hagen^d, James C. Pitman^e^a Division of Biology, Kansas State University, Manhattan, KS, 66506, USA^b U.S. Geological Survey, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson, SC, 29634, USA^c U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Manhattan, KS, 66506, USA^d Oregon State University, 500 SW Bond St., Ste 107, Bend, OR, 97702, USA^e Western Association of Fish and Wildlife Agencies, Emporia, KS, 66801, USA

HIGHLIGHTS

- Drought and land cover change interact to reduce Lesser Prairie-Chicken abundance.
- Our estimates of abundance indicate a decreasing population from 1978 to 2010.
- Decreased grassland reduces population resilience to extreme drought events.
- A threshold of cropland:grassland exists below which the population declines.

ARTICLE INFO

Article history:

Received 11 January 2016

Received in revised form 7 March 2016

Accepted 7 March 2016

Keywords:

Climate change

Land-cover change

Lesser Prairie-Chicken

Threshold models

Resilience

ABSTRACT

Habitat loss and degradation compound the effects of climate change on wildlife, yet responses to climate and land cover change are often quantified independently. The interaction between climate and land cover change could be intensified in the Great Plains region where grasslands are being converted to row-crop agriculture concurrent with increased frequency of extreme drought events. We quantified the combined effects of land cover and climate change on a species of conservation concern in the Great Plains, the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). We combined extreme drought events and land cover change with lek count surveys in a Bayesian hierarchical model to quantify changes in abundance of male Lesser Prairie-Chickens from 1978 to 2014 in Kansas, the core of their species range. Our estimates of abundance indicate a gradually decreasing population through 2010 corresponding to drought events and reduced grassland areas. Decreases in Lesser Prairie-Chicken abundance were greatest in areas with increasing row-crop to grassland land cover ratio during extreme drought events, and decreased grassland reduces the resilience of Lesser Prairie-Chicken populations to extreme drought events. A threshold exists for Lesser Prairie-Chickens in response to the gradient of cropland:grassland land cover. When moving across the gradient of grassland to cropland, abundance initially increased in response to more cropland on the landscape, but declined in response to more cropland after the threshold ($\delta = 0.096$, or 9.6% cropland). Preservation of intact grasslands and continued implementation of initiatives to revert

* Corresponding author at: U.S. Geological Survey, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson, SC, 29634, USA. Tel.: +1 864 656 4141.

E-mail addresses: bross@usgs.gov, beross@ksu.edu (B.E. Ross), dhaukos@ksu.edu (D.A. Haukos), christiran.hagen@oregonstate.edu (C.A. Hagen), jim.pitman@wafwa.org (J.C. Pitman).

<http://dx.doi.org/10.1016/j.gecco.2016.03.003>

2351-9894/Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

cropland to grassland should increase Lesser Prairie-Chicken resilience to extreme drought events due to climate change.

Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Understanding responses of wildlife populations to landscape and climatic variation is key for determining how resilient populations are to environmental change. Resilience can be defined as the capacity of a system to absorb disturbances without changing structurally or functionally (Holling, 1973) or the ability of a system to return to a pre-disturbed state (Pimm, 1984). Understanding population resilience is critical for conserving species with dynamic fluctuations in abundance that are linked to habitat quality. Where quality is driven by highly variable or extreme environmental events, such as drought, understanding resilience to extreme climatic events is crucial for fully appreciating the population dynamics of a species (Juguet et al., 2006). Additionally, understanding how changes in habitat affect species resilience during extreme climatic events can aid in mitigation efforts for species of conservation concern (Godfree et al., 2011; Oliver et al., 2013).

In addition to understanding the resilience of a species, projecting the combined effects of climate and land cover change on future wildlife populations is critical for managing species of conservation concern. Habitat loss and degradation interact with climate change to affect demographic rates of populations (Selwood et al., 2014), especially in highly dynamic ecosystems (Diffenbaugh et al., 2005), yet responses of populations to climate and land cover are typically quantified independently. The effects of landscape and climate change on wildlife may be compounded in areas such as the Great Plains of North America (Samson et al., 2004), where climate change is coupled with land cover change. For example, in the Northern Great Plains, land cover change has modified near-surface temperatures (Mahmood et al., 2006). Land cover change also causes shifts in avian community structure, as only a few grassland bird species respond positively to increases in agricultural cover (Coppedge et al., 2001). Bird species in the Great Plains are also likely to be disproportionately affected by projected temperature increases in the region (Peterson, 2003; Grisham et al., 2013).

Understanding how population dynamics are influenced by climatic variation and land cover change in the context of resilience is critical for predicting how a species may recover from extreme climatic events, such as drought (Oliver et al., 2013). If habitat management can decrease the recovery time for a population to return to pre-disturbed states after an extreme climatic event, conservation efforts can be targeted accordingly. For example, several prairie grouse species have large natural fluctuations in population abundance (Hudson et al., 1998; Williams et al., 2004; Garton et al., 2016), and are affected by extreme climatic events (Ross et al., in press). While fluctuations may exist naturally in prairie grouse populations, long-term, persistent declines are occurring for some species (Garton et al., 2016). Particularly, the loss and degradation of habitat (Fuhlendorf et al., 2002) and changes in climate (Grisham et al., 2013) may be causing these declines.

A sentinel species of conservation concern in the Great Plains is the Lesser Prairie-Chicken (*T. pallidicinctus*), which was listed as “threatened” under the Endangered Species Act in May 2014. Although the listing decision was vacated on procedural grounds by judicial review in September 2015, the concerns and impacts that prompted the initial listing decision remain. While affected by changes in climate (Grisham et al., 2013, in press; Ross et al., in press) and land cover (Fuhlendorf et al., 2002), no study we are aware of has simultaneously quantified the relative contribution of both of these factors to Lesser Prairie-Chicken population dynamics. Lesser Prairie-Chicken abundance declines during periods of drought throughout their range (Grisham et al., 2013, in press; Rodgers, 2016; Ross et al., in press), but are also negatively affected by changes in land cover and landscape fragmentation (Crawford and Bolen, 1976; Fuhlendorf et al., 2002). Landscape fragmentation decreases Lesser Prairie-Chicken home range size (Merchant, 1982), reduces recruitment (Hagen and Giesen, 2005), and subsequently, causes population declines independent of drought (Fuhlendorf et al., 2002). Due to a gap in knowledge about the interactive effects of various environmental conditions and land-cover change on the population, proposed management for Lesser Prairie-Chickens focuses primarily on habitat manipulation and improvements without accounting for potential future climatic states.

Our goal was to assess the resilience of Lesser Prairie-Chicken populations to the effects of drought, land cover change, and their interaction. We used threshold models, trends in the standard deviation of abundance, and return times following population declines to estimate shifts in resilience. Additionally, we quantified a population threshold for the landscape-scale cropland:grassland ratio of land cover.

2. Methods

2.1. Study area

Kansas has the largest abundance of Lesser Prairie-Chickens (McDonald et al., 2014). Furthermore, the Kansas Department of Wildlife, Parks, and Tourism is the only agency with long-term survey data of the species. Lesser Prairie-Chicken surveys incorporated three ecoregions in western (Short-Grass Prairie/Conservation Reserve Program Mosaic), southwestern (Sand Sagebrush Prairie), and south-central Kansas (Mixed-Grass Prairie), covering a large portion of the species' core range

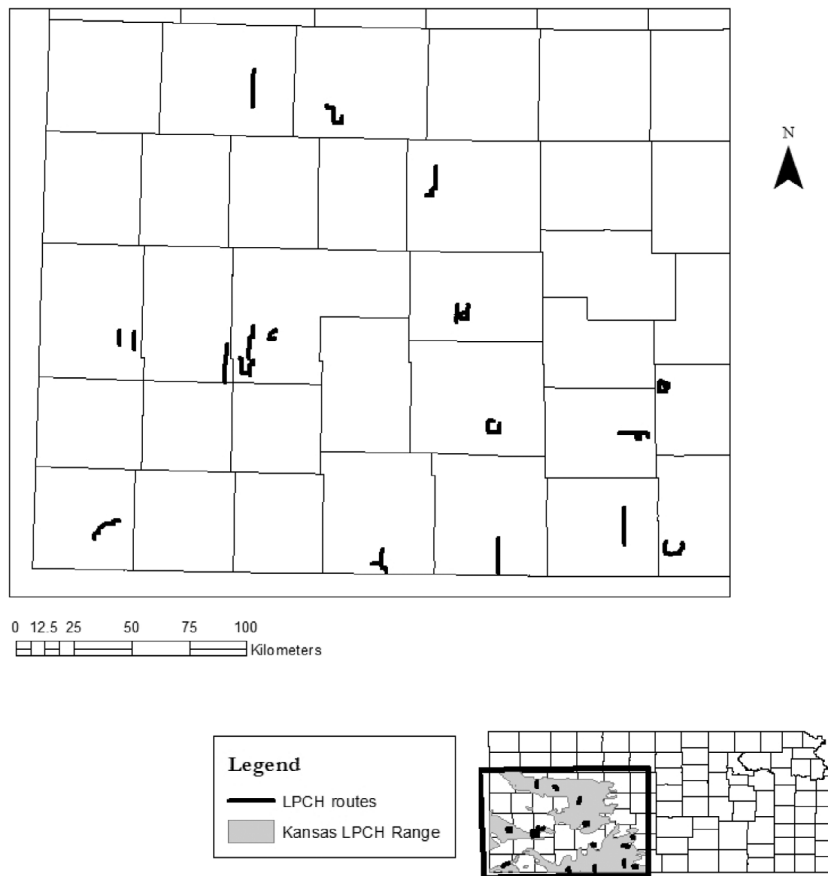


Fig. 1. Survey routes (in black) for Lesser Prairie-Chicken leks in Kansas from 1978 to 2014. The range of the species in Kansas is shown in gray.

(Fig. 1; McDonald et al., 2014). Land cover in western Kansas consisted of row-crop agriculture, native grassland, and former cropland enrolled in the U.S. Department of Agriculture Conservation Reserve Program (CRP). Southwestern Kansas was dominated by sand sagebrush (*Artemisia filifolia*) prairie, and primarily consisted of grassland with intermixed 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 consisted of winter wheat, grain sorghum, alfalfa, soybeans, and limited areas of corn.

2.2. Lek survey counts

Surveys for Lesser Prairie-Chickens in Kansas began with single transects in six counties in 1964, increasing to 17 transects in 15 counties covering $\sim 520 \text{ km}^2$ by 2014. To conduct a survey, observers drove a 16-km transect stopping every 1.6 km for three-minute auditory surveys to identify leks. Surveys generally started between 0500 and 0700. After completing the driving route, the observer then returned to each lek, flushed the birds, and counted all 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. Additionally, previous studies in Kansas have shown high lek fidelity for male Lesser Prairie-Chickens (92% for adult males; Hagen et al., 2005a). Mixed-species leks and leks with hybrids between Lesser and Greater Prairie-Chickens (*Tympanuchus cupido*) may co-occur on 3 routes or fewer in northwestern Kansas (Bain and Farley, 2002). Species composition of mixed leks are difficult to distinguish in flush counts; thus, a few Greater Prairie-Chickens or hybrids may have been included in counts of Lesser Prairie-Chickens on routes in northwestern Kansas.

Lek counts can be used as an index to population abundance if certain assumptions are met (Walsh et al., 2004; Garton et al., 2016). Our model incorporated detection probability, and leks were surveyed up through 90 min after sunrise during the peak lek attendance period (March to April) to control for issues related to lek attendance rates, which improves the validity of the lek count as a population index and allows inference about population dynamics.

2.3. Environmental variables

We conducted land cover classification using LandSat imagery for 1978, 1985, 1988, 1994, 2003, 2009, and 2013, providing data on land cover types for the years prior to and following implementation of the CRP (McLachlan, 2012; Spencer, 2014). The contemporary purpose of CRP is to reduce soil erosion, improve water quality, and increase wildlife habitat through incentive-based voluntary conservation efforts of land owners. Although many CRP lands within the distribution of the Lesser Prairie-Chicken were seeded in non-native grass mixes, seed mixes used on CRP lands in Kansas were primarily native (Rodgers, 2016).

Land cover was classified into four categories: grassland, cropland, urban, and water. The grassland category consisted of both CRP and native grassland for the purpose of this study (McLachlan, 2012; Spencer, 2014). Enrollment into CRP took place primarily in specified years: 1986 and 1987 with re-enrollment in 1996 and 1997 and again in 2006 or 2011 (10 or 15-year contracts); therefore, we assumed that CRP portion of the grassland cover in years between enrollment periods remained relatively constant.

For each year in which land cover classification was performed, we estimated the effects of land cover by calculating the proportion of land covered by cropland to land covered by grasslands (native or CRP) within a 3-km buffer for each survey route, as male Lesser Prairie-Chickens spend the majority of time within 3 km of their lekking site during the breeding season (Hagen and Giesen, 2005). Additionally, the 3-km buffer allowed us to assess land cover change at a broad spatial scale with similar spatial features rather than the site-specific scale. We standardized this ratio to have a mean of 0 with variance of 1 to aid in model convergence.

Because land cover is easier to manipulate than climate, land-use management is a feasible tool for conserving the Lesser Prairie-Chicken population in Kansas. We therefore implemented a piecewise linear and step-wise function in our covariate for land cover to test the effects of different ratios of land cover. Both of these functions allowed us to estimate a change point in the standardized ratio of cropland:grassland, indicating a management threshold below which Lesser Prairie-Chickens respond differently to changes in land cover. Implementing this threshold function on land cover alone, and not the interaction of land cover and climate, provides information to managers about the effects of land cover independent of current weather conditions and aligns better with current conservation practices using relatively long contracts (i.e., greater than 5 years; Van Pelt et al., 2013).

We used the Palmer Drought Severity Index (PDSI), which correlates with Lesser Prairie-Chicken population abundance in Kansas (Ross et al., in press), to identify extreme drought conditions during the breeding season of the Lesser Prairie-Chicken. We created a covariate for PDSI based on previous research where extreme drought conditions (low values of PDSI, < -3) during the summer (June–July) had the greatest influence on Lesser Prairie-Chicken survey counts (Ross et al., in press). The PDSI covariate was developed for the following 3 different climatic regions in Kansas: northwestern Kansas, central-western Kansas, and south-central Kansas (climate divisions 4, 7, and 8; Vose et al., 2014; NCDC, 1994). The covariates for land cover and PDSI 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 breeding season.

2.4. Hierarchical model of Lesser Prairie-Chicken Abundance

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. Data for this model were specified as coming from a binomial distribution

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

where the $y_{i,j,t}$ consisted of 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 $p_{i,t}$, 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 less than 1). We subsequently refer to detection probability as “combined detection probability” to clarify this distinction. We did not use data prior to 1978 due to the limited number of surveys conducted before that year.

We constructed process models to describe changes in climate and land cover that might affect abundance of male Lesser Prairie-Chickens on leks, which would be representative of greater changes to the whole population. We modeled the abundance at leks as $N_{i,t} \sim \text{Poisson}(\lambda_{i,t})$, and implemented three models: a basic linear model with PDSI and cropland:grassland ratio as covariates, a linear model with an interaction between PDSI and cropland:grassland, and a piecewise linear (hockey stick) model (Qian and Cuffney, 2012; Qian, 2014; Wagner and Midway, 2014). The piecewise linear model allowed for a threshold or change point along the gradient of cropland:grassland, causing a potential change in the effect of cropland:grassland (i.e., a change in the estimated slope) after a certain amount of cropland was present on the landscape. The linear model with an interaction was defined as

$$z_{i,t} = \log(\lambda_{i,t}) = \beta_0 + \beta_1 x_{\text{PDSI}} + \beta_2 x_{\text{land}} + \beta_3 x_{\text{PDSI} * \text{land}} + \varepsilon_{i,t} \quad (2)$$

and the piecewise linear model was defined as

$$z_{i,t} = \log(\lambda_{i,t}) = \beta_0 + \beta_1 x_{PDSI} + (\beta_2 + \delta I(x_{land} - \phi))(x_{land} - \phi) + \varepsilon_{i,t} \quad (3)$$

where in each case β_0 was an intercept and β_1 and β_3 were the coefficients for PDSI and the interaction of PDSI and land cover, respectively. The slope of the coefficient for land cover, β_2 , was then modified in the threshold model by adding or subtracting (depending on a positive or negative estimated effect) the intensification coefficient, δ , after the change point or threshold, ϕ . The intensification coefficient describes the potential change in β_2 in response to crossing the threshold value, and could be estimated at any real number value (i.e., positive, negative, or equal to zero). For the piecewise linear model (Eq. (3)), the indicator function, $I(a) = 0$ when $a < 0$, or $x - \phi < 0$, and $I(a) = 1$ when $a \geq 0$, or $x - \phi \geq 0$. The $\varepsilon_{i,t} \sim N(0, \sigma)$ were random effects for site and time. The linear model without the interaction term was used to compare data fit to the piecewise linear model, however, we still wanted to quantify the strength of interaction between PDSI and land cover. Additionally, we tested a model with a step-function threshold (Qian and Cuffney, 2012); however, this model failed to converge and was removed from further model inference.

To compare among our models, we assessed the fit of each model by comparing residuals and predicted values to a 1-to-1 line. We used this approach because comparing change point models is largely based on identifying the model that best represents the underlying pattern rather than the most parsimonious predictive model (Qian and Cuffney, 2012). Additionally, traditional model comparison metrics such as DIC are not necessarily appropriate for complex hierarchical models (Hooten and Hobbs, 2015).

To determine how resilient the Lesser Prairie-Chicken population in Kansas is to climate and land cover change, we (1) estimated the recovery time for the population after an extreme drought event (Oliver et al., 2013) and (2) used model output to quantify trends in the standard deviation of annual abundance through time averaged over sites (Carpenter and Brock, 2006; Scheffer et al., 2012). While there is some uncertainty associated with how to quantify shifts in resilience of a system, evaluating changes in the standard deviation is an accepted approach to identifying potential changes in resilience (Scheffer et al., 2012). Larger standard deviations in abundance indicate time periods of less resilience, and a consistent change in standard deviation indicates a potential shift in resilience (Scheffer et al., 2012).

We used Markov Chain Monte Carlo (MCMC) and a Gibbs sampler in JAGS (Plummer, 2012, Appendix B) with the package runjags (Denwood, in press) in program R (R Core Team, 2015) to obtain posterior distributions for the parameters. We discarded the first 150,000 samples as burn-in, used a thinning rate of 500 and saved 1000 samples from 3 chains. Convergence of chains was evaluated with a Gelman–Rubin statistic, and convergence attained when the potential scale reduction factors were < 1.05 for all monitored parameters (Gelman et al., 2014). We specified the prior distributions as $\beta \sim N(0, 10)$, $\delta \sim N(0, 10)$, $\varepsilon_{i,t} \sim N(0, 15)$, and $\phi \sim U(l, u)$ where l and u represent the lower and upper values for the standardized cropland:grassland ratio.

3. Results

From 1978 to 2014, 31,557 individual birds were observed on 8 to 17 routes with most routes having at least 1 detection. Estimated abundance from all models indicated Lesser Prairie-Chickens on leks in Kansas decreased by 61% from 1978 to 2014 (from 5108 males in 1978 to 2002 males in 2014) with one of the largest declines between 2010 and 2012, corresponding to severe drought conditions during this time period (Fig. 2). After extreme drought events, Lesser Prairie-Chicken abundance took 1 to 4 years to return to previous population states and has not yet returned to the abundance levels prior to the 2012 drought (Fig. 2). All models indicated that the population exhibited considerable variation in abundance throughout the study period, though variation was greatest towards the beginning of the study period. 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 available males on leks was generally low, with the mean detection probability estimated below 0.4 for most years (Fig. 3). The number of routes with at least one detection generally declined during the study period, though this increased in 2014 when fewer routes were surveyed (Fig. A.1).

When using real vs. generated data and residuals to compare models, we found support for both the piecewise linear and basic linear model (Fig. A.2; ratio of 0.957 for real vs. generated data for piecewise linear model, 0.961 for basic linear model, and 0.929 for interaction model). The plots of residuals for each of the three models were comparable and did not indicate support for one model over another, though there was slightly more variation associated with the residuals for the model with the interaction (Fig. A.3). Inference related to parameter estimates (e.g., estimates of comparable beta parameters), abundance, and detection probability from all models was relatively similar.

The piecewise and basic linear models indicated a significant negative effect of low values of summer PDSI, such that hot, dry summer reduced abundance on leks in the subsequent spring (i.e., 95% credible intervals did not include 0). In addition, the interaction model indicated a significant interaction between low values of summer PDSI and the cropland to grassland ratio. Thus, Lesser Prairie-Chicken abundance decreased more during years with severe drought conditions in areas with greater cropland to grassland ratios, indicating a decrease in resilience to variation in climate with decreases in grassland land cover (Fig. 4). The piecewise linear model estimated a significant threshold of land cover at a cropland:grassland of -0.69 ($\phi = -0.69$, 95% CI = $-0.73, -0.37$ standardized scale; $\phi = 0.096$ on transformed scale, or 9.6% cropland in a

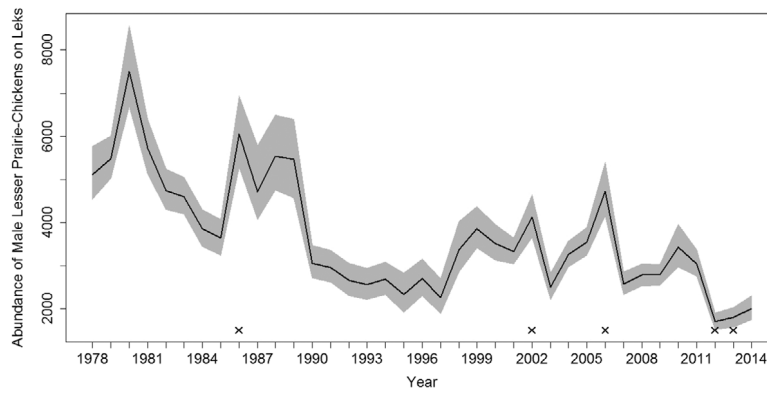


Fig. 2. Estimates of total abundance of Lesser Prairie-Chickens from the piecewise linear model on surveyed leks in Kansas from 1978 to 2014 with 95% credible intervals shown in gray. Years with extreme drought events are indicated with a “x”.

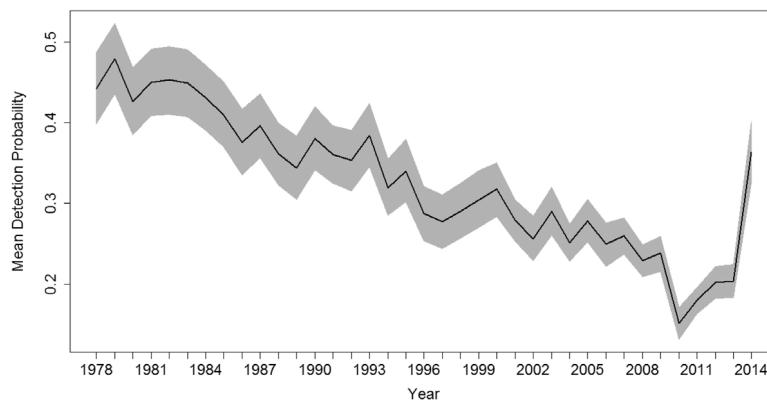


Fig. 3. Estimates of combined detection probability (probability of detecting a lek and probability of detecting individuals on a lek) of males on Lesser Prairie-Chicken leks in Kansas from 1978 to 2014.

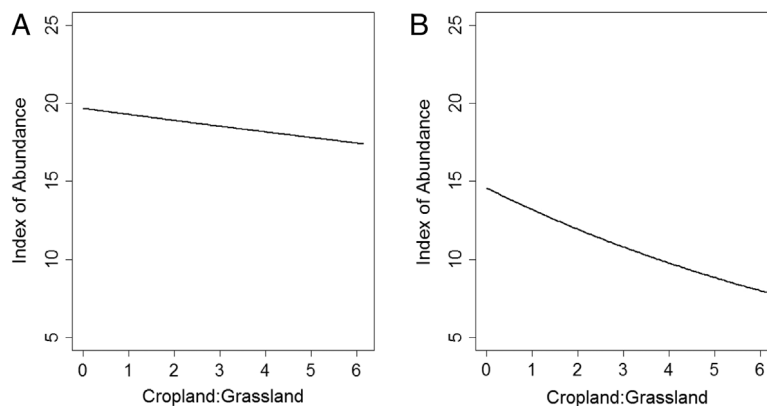


Fig. 4. Changes in relative abundance of male Lesser Prairie-Chickens on leks in Kansas from 1978 to 2013 during years without severe drought (PDSI value of < -3) during summer (A) and with severe drought during summer (B) over the range of values for cropland:grassland.

3 km buffer around leks). Resilience was considerably higher when there was 20 times greater grassland than cropland, and below this threshold, decreased as cropland was added to the landscape. Prior to the threshold, abundance increased in response to more cropland on the landscape ($\beta = 0.88$; 95% CI = 0.47, 1.20); however, once the threshold was reached, abundance decreased significantly as more cropland was added ($\delta = -0.93$; 95% CI = $-1.26, -0.56$; Fig. 5). The resilience of the population through time, as inferred from the standard deviation of abundance, was relatively low from 1978 to 1990 in all models (larger standard deviation), but primarily increased from 1990 to 2014 (smaller standard deviation; Fig. 6), though this may be confounded with survey precision (i.e., low detection probabilities).

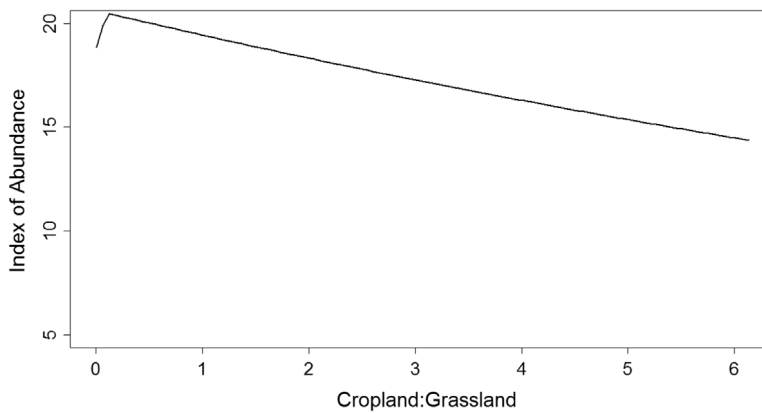


Fig. 5. Changes in relative abundance of male Lesser Prairie-Chickens on leks in Kansas in response to an estimated threshold of land cover (cropland:grassland).

When comparing the abundance of N_t to N_{t-1} , there was considerable spread along the 1-to-1 line (Fig. A.4), indicating low resilience in the population at high abundance. Additionally, there were large variations in abundance from one year to the next, especially at high abundances, with points higher on the x-axis falling well below or above the 1-to-1 line, indicating large decreases in abundance after years of high abundance.

4. Discussion

Our models of Lesser Prairie-Chicken abundance since 1978 indicated a significant decrease in resilience to extreme drought events intensified by decreases in grassland cover at the landscape level. Lesser Prairie-Chicken abundance in Kansas declined from high levels in 1978 to contemporary record lows from 2011 to 2014. Decreases in abundance on leks coincided with extreme drought in the preceding year, and was intensified by changes in land cover. Because resilience of extreme drought events is driven by land cover, the response of Lesser Prairie-Chickens to drought likely varies spatially. Typically, the abundance of the species remained relatively stable after initial decreases in response to extreme drought events. However, the population has yet to recover from an event in 2012, and often took several years to return to previous abundance levels after initial decreases. Regardless of recovery rate from this most recent drought, we expect that resilience will be reduced if projected frequency in extreme drought events (Cook et al., 2015) and grassland conversion in the Great Plains continues to increase (Claassen et al., 2011).

Variation in climate and extreme climatic events affect other species of grouse as well (Ludwig et al., 2006; Selås et al., 2011; Blomberg et al., 2012). Understanding the interaction of climatic events and land cover change could guide more effective management actions for these species. Grouse may also be affected by other environmental effects such as fire (Greater Prairie-Chickens, McNew et al., 2012), disease (West Nile Virus and Greater Sage-Grouse, Taylor et al., 2013), and parasite load (Red Grouse [*Lagopus lagopus*], Cattadori et al., 2005), which could be intensified by climate or land cover change. Given the results of our study and the biological similarity of many species of grouse, it is likely that climate is interacting with other limiting factors to cause declines in other grouse populations.

As land use exceeded a threshold of the amount of cropland on the landscape (ratio of 1:10, cropland:grassland), the population declined. While a small amount of cropland on the landscape likely provided some winter forage for the population, exceeding the threshold reduced available quality grassland habitat. The latter provides usable space for the critical life stages of nesting and brood-rearing for the species (Hagen et al., 2009). The presence of more grassland on the landscape, and thus less cropland, likely provided increased resources for Lesser Prairie-Chickens during extreme summer drought events. Increased grassland availability could have increased nest success and brood survival by providing high-quality nesting habitat, forage for chicks, and increased cover from predation (Hagen et al., 2005b). Additionally, grassland resources may have prevented delays in nesting or re-nesting attempts of females during extreme drought conditions (Grisham et al., 2014), potentially through more favorable microclimate in grasslands (Lautenbach, 2015). Overall, it appears that a reduction in grassland habitat could reduce resilience of Lesser Prairie-Chickens through several mechanisms.

The resilience of the Lesser Prairie-Chicken was lower during first half of the study (until 1990), and gradually increased during the study, but has decreased again during the last two years of the study. While initial values of standard deviation of abundance may be confounded with detection probability, the decrease in standard deviation during the last two years of the study does not follow the same trend in detection probability. During times of relative population stability (the mid-1990s to mid-2000s), the standard deviations of abundance were relatively low (Fig. 6), indicating greater resilience (Carpenter & Brock 2006; Scheffer et al., 2012). By contrast, during times of large population fluctuations (the early- to mid-1980s and mid-2000s through 2010s), the standard deviation was comparatively higher, indicating less resilience by comparison. The change in standard deviation corresponds to extensive conversion of sand sagebrush prairie to row-crop agriculture in southwest Kansas in the early to mid-1980s, peak levels of CRP during the mid-1990s to mid-2000s, and a decrease in CRP

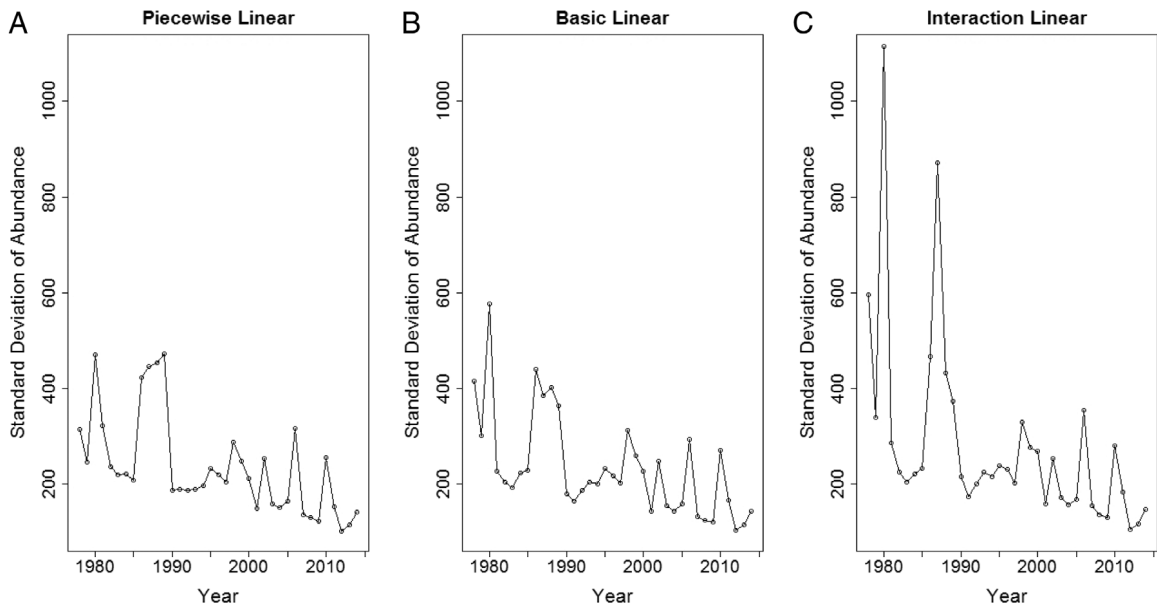


Fig. 6. Plots of standard deviation through time for the piecewise linear (A) basic linear (B) and interaction linear (C) models for Lesser Prairie-Chickens in Kansas from 1978 to 2014.

from the mid-2000s to 2010s (Spencer, 2014), indicating that resilience of the population may be affected by landscape-level land-cover patterns. We suggest that monitoring programs that are designed to track variation in abundance are needed, because detecting sustained levels of high variation would indicate a potential shift of the species to a different state (e.g., decreased resilience and a decrease in abundance; Scheffer et al., 2012). Additionally, quantifying changes in the standard deviation of population abundance relative to “boom-and-bust” dynamics of Lesser Prairie-Chickens can provide additional insight into management actions, and allow managers to understand if the population is undergoing a shift to a lower abundance state or simply a natural fluctuation in abundance. Our results comparing N_{t-1} to N_t indicated that populations rarely maintained high levels of abundance after years of high abundance independent of extreme drought events or land cover change, supporting previous descriptions (e.g. Williams et al., 2004; Garton et al., 2016) of large natural fluctuations in Lesser Prairie-Chicken abundance. These large fluctuations may be due to density dependence or the formation of satellite leks, whereby lek counts are reduced but abundance may be increasing.

The combined probability of detection decreased during the first decade of our analysis, and we attribute this to three possible causes. First, the initial survey routes may have been chosen subjectively because they were known to contain active leks and were still surveyed despite the lack of a detection for up to 20 years, as the number of routes with leks declined throughout the survey (Fig. A.1). Second, continued development of anthropogenic noise pollution increased throughout this time period concurrent with development in the region (Spencer, 2014), potentially reducing the ability of surveyors to detect leks using sound. Third, population declines resulted in the number of males per lek being reduced, causing a potential decline in detection probability.

Current management strategies for the Lesser Prairie-Chicken are primarily based on habitat conservation and improvements (Hagen et al., 2013; Van Pelt et al., 2013). Our results indicate that reductions to the cropland to grassland ratio below 1:10 would likely improve population resilience to drought events. Further research is needed to fully understand what land cover practices most effectively offset extreme drought events and the mechanisms by which Lesser Prairie-Chickens benefit from increased grassland cover. Efforts to restore grassland (e.g., through CRP initiatives and prairie restoration) and an increased emphasis on retaining existing CRP would likely benefit Lesser Prairie-Chicken populations, especially with increased frequency of drought in the future. Improved monitoring of grassland conversion in the near-term would improve our understanding of Lesser Prairie-Chicken resilience to land cover and climate change. Additionally, habitat quality for Lesser Prairie-Chickens (e.g., Hagen et al., 2013; Haukos and Zavaleta, 2016) was not considered in the analyses and could be included in future analyses. Through a combined understanding of the threshold of cropland:grassland concurrent with the interaction of land cover and extreme drought events, conservation efforts may help boost resilience of the Lesser Prairie-Chicken in Kansas during projected future climate change. Neglecting to incorporate climate change into population abundance models related to land cover for Lesser Prairie-Chickens underestimates the importance of land cover in sustaining populations.

Acknowledgments

Earlier drafts of this manuscript were improved with comments by L. Martin, A. Ricketts, J. Sutton, and E. Weiser. We thank J. Kramer, M. Mitchener, D. Dahlgren, J. Prendergast, 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 (RWO 62, KSCFWRU) 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. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.03.003>.

References

- Bain, M.R., Farley, G.H., 2002. Display by apparent hybrid prairie-chickens in a zone of geographical overlap. *Condor* 104, 683–687.
- Blomberg, E.J., Sedinger, J.S., Atamian, M.T., Nonne, D.V., 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. *Ecosphere* 3. <http://dx.doi.org/10.1890/ES11-00304.1>. Article 55.
- Carpenter, S.R., Brock, W.A., 2006. Rising variance: a leading indicator of ecological transition. *Ecol. Lett.* 9, 311–318.
- Cattadori, I.M., Haydon, D.T., Hudson, P.J., 2005. Parasites and climate synchronize red grouse populations. *Nature* 433, 737–741.
- Claassen, R., Carriazo, F., Cooper, J.C., Hellerstein, D., Ueda, K., 2011. Grassland to Cropland Conversion in the Northern Plains. Technical report. U.S. Department of Agriculture Economic Research Service.
- Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American southwest and great plains. *Sci. Adv.* 1, 1–7.
- Coppedge, B.R., Engle, D.M., Masters, R.E., Gregory, M.S., 2001. Avian response to landscape change in fragmented southern great plains grasslands. *Ecol. Appl.* 11, 47–59.
- Crawford, J.A., Bolen, E.G., 1976. Effects of land use on Lesser Prairie-Chickens in Texas. *J. Wildl. Manage.* 40, 96–104.
- Denwood, M., 2016. Interface utilities, parallel computing methods and additional distributions for MCMC models in JAGS. *J. Stat. Softw.* (in press).
- Diffenbaugh, N.S., Pal, J.S., Trapp, R.J., Giorgi, F., 2005. Fine-scale processes regulate the response of extreme events to global climate change. *Proc. Natl. Acad. Sci.* 102, 15774–15778.
- Fuhlendorf, S.D., Woodward, A.M., Leslie, D.M., Shackford, J.S., 2002. Multi-scale effects of habitat loss and fragmentation on Lesser Prairie-Chicken populations of the U.S. Southern Great Plains. *Landsc. Ecol.* 17, 617–628.
- Garton, E.O., Hagen, C.A., Beauprez, G.M., Kyle, S.C., Pitman, J.C., Schoeling, D.S., Van Pelt, W.E., 2016. Population dynamics of the Lesser Prairie-Chicken. In: Haukos, D.A., Boal, C.W. (Eds.), *Ecology and Management of Lesser Prairie-Chickens*. CRC Press, Boca Raton, pp. 49–76.
- Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B., 2014. *Bayesian Data Analysis*. CRC Press, Boca Raton.
- Godfree, R., Lepschi, B., Reside, A., Bolgers, T., Robertson, B., Marshall, D., Carnegie, M., 2011. Multiscale topoeadaphic heterogeneity increases resilience and resistance of a dominant grassland species to extreme drought and climate change. *Global Change Biol.* 17, 943–958.
- Grisham, B.A., Boal, C.W., Haukos, D.A., Davis, D.M., Boydston, K.K., Dixon, C., Heck, W.R., 2013. The predicted influence of climate change on lesser prairie-chicken reproductive parameters. *PLoS One* 8. <http://dx.doi.org/10.1371/journal.pone.0068225>.
- Grisham, B.A., Borsdorf, P.K., Boal, C.W., Boydston, K.K., 2014. Nesting ecology and nest survival of lesser prairie-chickens on the southern high plains of Texas. *J. Wildl. Manage.* 78, 857–866.
- Grisham, B.A., Godar, A.J., Griffin, C.P., 2016. Climate change. In: Haukos, D.A., Boal, C.W. (Eds.), *Ecology and Management of Lesser Prairie-Chickens*. CRC Press, Boca Raton (in press).
- Hagen, C.A., Grisham, B.A., Boal, C.W., Haukos, D.A., 2013. A meta-analysis of lesser prairie-chicken nesting and brood-rearing habitats: implications for habitat management. *Wildl. Soc. Bull.* 37, 750–758.
- Hagen, C.A., Giesen, K.M., 2005. Lesser prairie-chicken (*Tympanuchus pallidicinctus*). In: Poole A.A., (Ed.), *Birds of North America Online*. Ithaca. <http://dx.doi.org/10.2173/bna.364>.
- Hagen, C.A., Pitman, J.C., Sandercock, B.K., Robel, R.J., Applegate, R.D., 2005a. Age-specific variation in apparent survival rates of male lesser Prairie-Chickens. *The Condor* 107, 78–86.
- Hagen, C.A., Salter, G.C., Pitman, J.C., Robel, R.J., Applegate, R.D., 2005b. Lesser prairie-chicken brood habitat in sand sagebrush: invertebrate biomass and vegetation. *Wildl. Soc. Bull.* 33, 1080–1091.
- Hagen, C.A., Sandercock, B.K., Pitman, J.C., Robel, R.J., Applegate, R.D., 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. *J. Wildl. Manage.* 73, 1325–1332.
- Haukos, D.A., Zavaleta, J.C., 2016. Habitat. In: Haukos, D.A., Boal, C.W. (Eds.), *Ecology and Management of Lesser Prairie-Chickens*. CRC Press, Boca Raton, pp. 99–132.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hooten, M.B., Hobbs, N.T., 2015. A guide to bayesian model selection for ecologists. *Ecol. Monograph* 85, 3–28.
- Hudson, P.J., Dobson, A.P., Newborn, D., 1998. Prevention of population cycles by parasite removal. *Science* 282, 2256–2258.
- Jiguet, F., Julliard, R., Thomas, C.D., Dehorter, O., Newson, S.E., Couvet, D., 2006. Thermal range predicts bird population resilience to extreme high temperatures. *Ecol. Lett.* 9, 1321–1330.
- Lautenbach, J.M., 2015. Lesser Prairie-Chicken Reproductive Success, Habitat Selection, and Response to Trees (MS thesis). Kansas State University, Manhattan.
- Ludwig, G.X., Alatalo, R.V., Helle, P., Lindén, H., Lindström, J., Siitari, H., 2006. Short-and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proc. R. Soc. B* 273, 2009–2016.
- Mahmood, R., Foster, S.A., Kelling, T., Hubbard, K.G., Carlson, C., Leeper, R., 2006. Impacts of irrigation on 20th century temperature in the northern great plains. *Glob. Planet. Change* 54, 1–18.
- McDonald, L., Beauprez, G., Gardner, G., Griswold, J., Hagen, C.A., Hornsby, F., Klute, D., Kyle, S., Pitman, J., Rintz, T., et al., 2014. Range-wide population size of the lesser Prairie-Chicken: 2012 and 2013. *Wildl. Soc. Bull.* 38, 536–546.
- McLachlan, M.M., 2012. *Playa Lakes Joint Venture Landcover Accuracy Assessment Report*. Lafayette, Colorado, USA.
- McNew, L.B., Prebyl, T.J., Sandercock, B.K., 2012. Effects of rangeland management on the site occupancy dynamics of prairie-chickens in a protected prairie preserve. *J. Wildl. Manage.* 76, 38–47.
- Merchant, S.S., 1982. *Habitat Use, Reproductive Success, and Survival of Female Lesser Prairie-Chickens in Two Years of Contrasting Weather* (MS Thesis). New Mexico State University, Las Cruces.
- NCDC. 1994. Time bias corrected divisional temperature-precipitation-drought index. Documentation for dataset TD-9640. Available from DBMB, NCDC, NOAA, Federal Building, 37 Battery Park Ave., Asheville, North Carolina 28801.

- Oliver, T.H., Brereton, T., Roy, D.B., 2013. Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography* 36, 579–586.
- Peterson, A.T., 2003. Projected climate change effects on rocky mountain and great plains birds: generalities of biodiversity consequences. *Global Change Biol.* 9, 647–655.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. *Nature* 307, 321–326.
- Plummer, M., 2012. JAGS version 3.3.0 user manual.
- Qian, S., Cuffney, T., 2012. To threshold or not to threshold? that's the question. *Ecol. Indic.* 15, 1–9.
- Qian, S., 2014. Ecological threshold and environmental management: a note on statistical methods for detecting thresholds. *Ecol. Indic.* 38, 192–197.
- R Core Team. 2015. R: a language and environment for statistical computing. Vienna.
- Rodgers, R.D., 2016. A history of Lesser Prairie-Chickens. In: Haukos, D.A., Boal, C.W. (Eds.), *Ecology and Management of Lesser Prairie-Chickens*. CRC Press, Boca Raton, pp. 15–38.
- Ross, B.E., Haukos, D., Hagen, C., Pitman, J., 2016. The relative contribution of climate to changes in Lesser Prairie-Chicken abundance. *Ecosphere* (in press).
- Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60, 108–115.
- Samson, F.B., Knopf, F.L., Ostlie, W.R., 2004. Great plains ecosystems: past, present, and future. *Wildl. Soc. Bull.* 32, 6–15.
- Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J., van de Leemput, I., Levin, S., van Nes, E., et al., 2012. Anticipating critical transitions. *Science* 338, 344–348.
- Selwood, K.E., McGeoch, M.A., Mac Nally, R., 2014. The effects of climate change and land-use change on demographic rates and population viability. *Biol. Rev.* 90, 837–853.
- Selås, V., Sonerud, G.A., Framstad, E., Kålås, J.A., Kobro, S., Pedersen, H.B., Spidsø, T.K., Wiig, Ø., 2011. Climate change in norway: warm summers limit grouse reproduction. *Popul. Ecol.* 53, 361–371.
- Spencer, D.A., 2014. A Historical Record of Land Cover Change of the Lesser Prairie-Chicken Range in Kansas (MS Thesis). Kansas State University, Manhattan.
- Taylor, R.L., Tack, J.D., Naugle, D.E., Mills, L.S., 2013. Combined effects of energy development and disease on Greater Sage-Grouse. *PLoS ONE* 8, e71256.
- Van Pelt, W.E., Kyle, S., Pitman, J., Klute, D., Beauprez, G., Schoeling, D., Janus, A., Haufler, J., 2013. The Lesser Prairie-Chicken Range-wide Conservation Plan. Western Association of Fish and Wildlife Agencies. Cheyenne, WY.
- Vose, R.S., Applequist, S., Durre, I., Menne, M.J., Williams, C.N., Fenimore, C., Gleason, K., Arndt, D., 2014. Improved historical temperature and precipitation time series for U.S. climatic divisions. *J. Appl. Meteorol. Climatol.* 53, 1232–1251.
- Wagner, T., Midway, S.R., 2014. Modeling spatially varying landscape change points in species occurrence thresholds. *Ecosphere* 5, 145–161.
- Walsh, D.P., White, G.C., Remington, T.E., Bowden, D.C., 2004. Evaluation of the lek-count index for greater sage-grouse. *Wildl. Soc. Bull.* 32, 56–68.
- Williams, C.K., Ives, A.R., Applegate, R.D., Ripa, J., 2004. The collapse of cycles in the dynamics of North American grouse populations. *Ecol. Lett.* 7, 1135–1142.