Implications of climatic heterogeneity for conservation of the Lesser Prairie-Chicken (Tympanuchus pallidicinctus)

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Abstract. A geographic range is a heterogeneous matrix where the natural capability to support resident species varies from detrimental to optimal. Given this, the first priority for species conservation should be to determine where optimal environments exist. We used MaxEnt species distribution modeling to distinguish climatic characteristics associated with persistent leks from those at random locations in order to characterize the niche and potential distribution of the imperiled Lesser Prairie-Chicken (Tympanuchus pallidicinctus). Annual, brood period, and winter precipitation were the most important characteristics of the niche across the entire range, but maximum temperature during nesting was a key characteristic in the southern part of the range. Habitat suitability across the geographic range was multimodal but also consistent with a center-periphery pattern. Western Kansas and Oklahoma and east-central New Mexico contributed more than expected, whereas all other areas contributed less than expected, to habitat suitability of the geographic range. Lesser Prairie-Chickens appear constrained on the western edge of their range by abiotic factors, namely aridity, unfavorable temperatures and sandy soils. Conversely, they appear constrained on the eastern edge by biotic factors, namely transition from mid-grass to tallgrass prairie that results in dominance by the Greater Prairie-Chicken (Tympanuchus cupido). Conserving Lesser Prairie-Chickens will depend on maintaining persistent populations in western Kansas and Oklahoma and east-central New Mexico, as well as expanding its distribution across Texas. Aridity, unfavorable temperatures, and a paucity of habitat make eastern Colorado and southeastern New Mexico challenging areas for persistence of this species. Climate change may make it more difficult for populations in New Mexico and adjacent parts of Texas to persist, but more favorable for populations in eastern Colorado. The potential difficulties for populations in the southern part of the range will make it increasingly important to conserve populations in western Kansas and Oklahoma.

Key words: climate; geographic range; Lesser Prairie-Chicken; MaxEnt; niche; species distribution model.

INTRODUCTION

The center-periphery hypothesis posits that environmental conditions contributing most to species persistence occur in the center of its geographic range (i.e., the historic extent of the species distribution) with decreased contributions toward the periphery (Haldane 1956, Brown 1984, Hall et al. 1992, Brown et al. 1996, Guo 2005). An analysis of breeding bird surveys by Brown et al. (1995) demonstrated this pattern, but also found extensive multimodality; a few locales supported high population densities, but most did not. The contrast between the center
and periphery, however, does not discount the value of the range periphery. It might contain the best remaining populations or habitat in the wake of anthropogenic disturbance (Lomolino and Channell 1998) and may support populations or provide stepping stones key to metapopulation persistence (Gilpin 1980, Kiett et al. 1997). Thus, the geographic range of a species may best be considered a heterogeneous matrix in which suitability varies from detrimental to optimal. Given this, areas important to persistence potentially may occur anywhere (Senft et al. 1987, Brown et al. 1995, Lomolino and Channell 1998).

Recognizing the heterogeneity of geographic ranges is especially important when considering locations to pursue recovery and conservation of imperiled species. A hierarchy of three criteria can be used to focus the selection process: historic distribution, habitat, and environmental characteristics. Historic distribution alone has several shortcomings. Often surveys from which distributional boundaries were derived were not systematic and were limited both spatially and temporally (e.g., Ligon 1927). Thus, some occupied locations may have been missed. Conversely, characteristics where the species was observed might have been used to include unsurveyed areas as part of the species range, when in reality these areas never were occupied. Lastly, historic surveys generally were insufficient to assess species persistence.

Knowing distribution and abundance of suitable habitat (i.e., habitat that provides requirements for survival) can reduce ambiguity about persistence. Organisms generally persist longest where their habitat occurs in large patches that are close to one another (Prugh 2009). However, the ability of suitable habitat to contribute to persistence is dependent on environmental characteristics, such as climate, that provide needed resources at crucial times (Pulliam 1988). In short, not all suitable habitat is created equal.

Availability of suitable habitat is particularly pertinent in the case of the Lesser Prairie-Chicken (Tympanuchus pallidicinctus) (LPC), a candidate for listing as threatened under the federal Endangered Species Act. Development of fossil fuel and renewable energy resources, conversion of native prairie to agriculture, and poor grazing practices have reduced the distribution of this species to <20% of its historic range (Hagan and Giesen 2005) and undoubtedly will continue to affect persistence of LPC for the foreseeable future.

Increasing numbers and distribution of LPC through habitat and population restoration will be challenging because sites are limited where: (1) suitable habitat currently is adequate or can be increased enough to support persistent populations, (2) anthropogenic disturbance is minimal or can be cost-effectively mitigated, and (3) private landowners (on whose land the majority of LPC habitat is found) are willing to cooperate in conservation efforts. Additionally, reintroductions of prairie grouse have not been particularly successful. Less than one-third of reported reintroductions have resulted in populations that persisted for more than a few generations (Reese and Connelly 1997, Snyder et al. 1999) and establishment of a reintroduced LPC population has yet to be documented (H. Whitlaw, personal communication). Thus, it is crucial to select sites where LPC have the best opportunity for long-term persistence.

Species distribution modeling can help determine where conservation might be most profitable (Guisan and Thuiller 2005, Elith and Leathwick 2009). These models characterize the niche, environmental conditions that allow recruitment to be greater than or equal to mortality (Chase and Leibold 2003), and the potential distribution, the geographic region where those conditions occur (James et al. 1984). A primary benefit of species distribution models is they provide a systematic, consistent means of measuring habitat suitability across a species range.

Here we employ MaxEnt (Phillips et al. 2006), one of the best performing species distribution models (Elith et al. 2006) to determine how climatic characteristics associated with LPC persistence (Appendix) differ between locations of persistent leks (mating grounds) and all locations where leks could possibly occur. Specifically, we (1) identify which climate variables best describe the niche of LPC across its range and within subdivisions of that range, (2) map the potential distribution of LPC, and (3) compare the potential among subdivisions to support LPC. We then examine the implications of our findings for conservation of this species.
METHODS

The Bayesian foundation of MaxEnt

MaxEnt is based on the principle of maximum entropy in which the best approximation of an unknown probability distribution is defined as the one closest to uniform but subject to constraints (Jaynes 1957). With MaxEnt, that translates to a distribution that encompasses all locations in which expected values of a predictor variable equal or exceed the average value at locations where the species of interest is known to occur (Phillips et al. 2006). A Bayesian approach is used to achieve this; the probability of a value of a predictor variable (x) given the species of interest being present (y = 1), p(x|y = 1), is used to predict the probability of species’ occurrence given the value of the predictor variable, p(y = 1|x) (Elith et al. 2011). To do this, characteristics of occurrences (in this study, persistent leks) were compared against the same characteristics at randomly selected locations within LPC habitat (hereafter “background”) that represent the available range of values of predictor variables (in this study, climate characteristics).

Occurrence and background locations

We obtained locations, survey dates, and counts at leks in 4 of 5 states where LPC were historically found: Oklahoma, Kansas, Colorado, and New Mexico (Table 1, Fig. 1). Data on individual leks were not available from Texas because of confidentiality agreements between Texas Department of Parks and Wildlife and private landowners.

Three methods were used by resource agencies to survey LPC: (1) listening at designated points along transects, then counting LPC at identified leks (if locations were accessible), (2) completely searching defined geographic areas, then counting LPC at identified leks, and (3) annually revisiting and counting LPC at known leks. Use of these methods varied among states but consistency in four key components made counts comparable: sampling units (leks), weather conditions (calm, clear), observation periods (one-half hour before to 2 hours after dawn during the breeding season: late March–early May), and number of annual visits (usually 1, never more than 3). The low number of annual visits could have inflated the error of omission; LPC may have been using the lek, but were not present when the observer arrived. To compensate for this, we considered LPC as being present if ≤2 years separated previous and subsequent observations of LPC from the survey in which they were not observed.

Occurrence data needed to meet four criteria to ensure model accuracy. First, leks had to have been active within the 30 year period (1971–2000) of climate measurements. Second, they had to represent populations in equilibrium with their environment (Elith and Leathwick 2009). To meet this assumption, we used only leks that supported persistent populations (“persistent leks”), those in which LPC were present for ≥5 consecutive years, the maximum lifespan of this species (Campbell 1972). Third, occurrences could not be autocorrelated. To test for this, we compared counts taken during the same years between each pair of leks ≤20 km from each other. If significantly (P < 0.05) correlated, one randomly chosen lek of the pair was removed from the sample.

Lastly, occurrence data needed to be collected

Table 1. Surveys of Lesser Prairie-Chickens (Tympanuchus pallidicinctus) (LPC) in five climate zones found in four of five states historically occupied by this species. Data from Texas were unavailable for our analysis. Persistent leks were defined as mating grounds in which LPC were present for ≥5 consecutive years. Numbers in parentheses in LPC/km² field are the number of survey routes that were available to determine population densities.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Persistent leks</th>
<th>Annual surveys/persistent lek (SD)</th>
<th>LPC/persistent lek (SD)</th>
<th>LPC/km² (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southeastern New Mexico</td>
<td>14</td>
<td>13.3 (3.5)</td>
<td>6.1 (0.74)</td>
<td>0.05 (2)</td>
</tr>
<tr>
<td>East-central New Mexico</td>
<td>213</td>
<td>8.1 (7.3)</td>
<td>9.7 (0.32)</td>
<td>0.53 (29)</td>
</tr>
<tr>
<td>Eastern Colorado</td>
<td>42</td>
<td>13.7 (7.5)</td>
<td>8.7 (0.55)</td>
<td>0.24 (1)</td>
</tr>
<tr>
<td>Western Kansas/Oklahoma</td>
<td>40</td>
<td>28.1 (7.4)</td>
<td>14.0 (0.83)</td>
<td>0.52 (4)</td>
</tr>
<tr>
<td>Eastern Kansas/Oklahoma</td>
<td>54</td>
<td>21.3 (14.1)</td>
<td>12.1 (0.56)</td>
<td>0.3 (15)</td>
</tr>
</tbody>
</table>
Fig. 1. The geographic range and 5 climate zones used to model the niche and potential distribution of the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) (LPC). Gray shading is LPC habitat derived from Gap Analysis landcover types known to be used by this species. Black dots are persistent leks (LPC present ≥5 continuous years). Zone boundaries were the edge of the geographic range or county boundaries in which LPC population surveys were conducted. The boundary of the geographic range was adapted from Davis et al. (2008). The inset shows where the geographic range is located in North America.
randomly or systematically to avoid creating models that reflected heavily sampled more than preferred locations. Our data did not meet this criterion, so we followed Phillips et al. (2009) and randomly selected background locations in the same proportion as occurrences within subdivisions of the study area. We delineated five subdivisions (“climate zones”) that differed from each other in temperature or precipitation (Fig. 1). Southeastern New Mexico was in a higher quintile of annual mean temperature than east-central New Mexico, whereas eastern Colorado, western Kansas/Oklahoma, and eastern Kansas/Oklahoma were in different quintiles of annual precipitation (Fig. 2). Proportions of occurrences (i.e., persistent leks) from each climate zone were based on population densities, instead of numbers of leks, because most leks were used by \( \geq 1 \) LPC. At least some surveys in each climate zone were conducted systematically thereby providing data from which lek densities could be calculated (Table 1). Lek densities were then multiplied by the mean number of LPC counted per lek to estimate population densities. The proportion of persistent leks and background locations to be used in the model was the population density for each climate zone divided by the sum of population densities for all zones.

**Habitat data**

The extent of our analysis was limited to habitat used by LPC within its geographic range (Davis et al. 2008). A habitat layer was created in ArcMap 9.3.1 (Environmental Science Research Institute, Redlands, CA) by extracting grass-shrub landcover types known to be used by LPC (Appendix) from GAP Analysis raster databases (http://gapanalysis.usgs.gov/). These databases were based on satellite imagery from the mid- to late 1990s. Accuracy was 55–60\%, which is considered adequate for modeling at a regional scale (e.g., our climate zones) (Lowry et al. 2005).
Predictor variables

Nine measures of climate related to LPC demographics were used to differentiate conditions at persistent leks from background locations (Table 2; Appendix). Precipitation and temperature data were derived from raster layers available from the PRISM Climate Group (http://www.prism.oregonstate.edu). Precipitation variables included 30 year means (1971–2000) for amounts produced annually as well as during winter (November–March), nesting (April–May), and brood rearing (June–August). Additionally, a coefficient of variation was calculated for annual precipitation. Temperature variables included 30-year means for daily maximum and minimum temperatures during the nesting period and mean daily maximum temperature during the brood rearing period. A raster of mean potential annual evapotranspiration (PET) was obtained from MODIS imagery (http://modis.gsfc.nasa.gov/). Cells used for modeling were extracted from the PRISM and MODIS rasters using the LPC habitat layer as a mask.

The LPC model

MaxEnt offers a myriad of options for modeling (see www.cs.princeton.edu/~schapire/maxent/ and Elith et al. [2011] for detailed explanations). We chose the following: (1) the entire sample of occurrences was modeled first, followed by the subsets of each climate zone; (2) regularization, an algorithm to smooth distributions and increase generalization of results, was varied from 0.1 (closer to training data) to 5 (more generalized); (3) model iterations ceased at 500 or when log loss of deviance per iteration was $<10^{-5}$; (4) variables in linear (continuous values), quadratic (squared values), and product (multiplied with other variables) formats were used to determine constraints via the mean, variance and covariance, respectively; (5) the model considered best was that which had the largest area under the receiver operating curve (AUC) and highest gain; (6) the importance of predictor variables was measured by permuting training data to increase gain and also by jackknife sampling, in which each predictor variable was used alone in, and then excluded from, models (jackknife sampling also minimized confounding effects of correlated variables, such as annual and winter precipitation [Phillips et al. 2006]); (7) all predictor variables were included in initial model runs, but those whose permutation importance was $<10$% or whose jackknife values were not among the top 50% of variables were eliminated during subsequent runs; (8) response curves created by modeling each predictor variable in isolation of others were used to determine the range of values where the probability of LPC being present was $\geq 0.5$; (9) model fits were tested via 10-fold cross-validation using clamped data (test

Table 2. Climate variables used as predictors for modeling the niche and potential distribution of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*). See Niche characteristics of Lesser Prairie-Chickens (Appendix) for a more detailed overview.

<table>
<thead>
<tr>
<th>Climate variable</th>
<th>Potential effect on population persistence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precipitation</td>
<td></td>
</tr>
<tr>
<td>Annual</td>
<td>Positive: cover and forage</td>
</tr>
<tr>
<td></td>
<td>Negative: hypothermia, less favorable habitat</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>Negative: variable recruitment that might adversely affect persistence.</td>
</tr>
<tr>
<td>Winter</td>
<td>Positive: cover and forage during nesting and brood rearing.</td>
</tr>
<tr>
<td>Nesting</td>
<td>Negative: depletion of energy reserves for thermoregulation.</td>
</tr>
<tr>
<td>Brood rearing</td>
<td>Negative: hypothermia</td>
</tr>
<tr>
<td>Temperature</td>
<td>Positive: invertebrate abundance</td>
</tr>
<tr>
<td>Nesting</td>
<td></td>
</tr>
<tr>
<td>Mean daily maximum</td>
<td>Negative: hyperthermia, egg desiccation.</td>
</tr>
<tr>
<td>Mean daily minimum</td>
<td>Negative: hypothermia</td>
</tr>
<tr>
<td>Brood rearing</td>
<td>Negative: hyperthermia</td>
</tr>
<tr>
<td>Mean daily maximum</td>
<td></td>
</tr>
<tr>
<td>Evaporation</td>
<td>Negative: organismal/egg/forage desiccation.</td>
</tr>
<tr>
<td>Potential evapotranspiration</td>
<td></td>
</tr>
</tbody>
</table>

data values limited to the range of training data); and (10) predicted habitat suitability based on occurrence and background locations within the 5 climate zones was projected to all habitat cells within the geographic range.

Logistic values produced by MaxEnt for each cell represented habitat suitability and were used to analyze the part-to-whole relationship (Gianpietro 2004) between the entire range and six subdivisions. These subdivisions were the five climate zones and the LPC range in Texas. Texas was included because expanding the distribution of LPC across it will reconnect the metapopulation in Kansas and Oklahoma with the one in east-central New Mexico. We created bivariate density functions by graphing cumulative MaxEnt values against cumulative area for the geographic range as well as for each subdivision and quartile of MaxEnt values of each subdivision. The slope of the curve for the geographic range represented the expected value under an assumption that all subdivisions had equal value. For each subdivision and quartile, the ratio of cumulative MaxEnt value to cumulative area for each added cell represented observed values, which were subtracted from the expected value. Means and 95\% confidential intervals for differences between observed and expected values were calculated. Positive means indicated contributions to the suitability of the geographic range were more than expected, whereas negative means indicated contributions were less than expected. Differences (P ≤ 0.05) in contributions among subdivisions were determined with two-way analysis of variance and post-hoc Tukey tests.

**RESULTS**

We obtained data for 694 leks of which 363 were persistent (i.e., LPC were present for ≥5 consecutive years) and uncorrelated with other leks (Table 1). Occurrence data used in our model consisted of 191 of the 363 persistent leks that included all leks located in southeastern New Mexico (n = 14) and western Kansas/Oklahoma (n = 40) and random subsets of persistent leks in eastern Colorado (n = 35 of 42), east-central New Mexico (n = 60 of 213), and eastern Kansas/Oklahoma (n = 35 of 54).

Climate at persistent leks across the geographic range was characterized by increasing precipitation and decreasing maximum temperatures from southwest to northeast (Fig. 3). Precipitation during winter and nesting was half the amount in New Mexico as in eastern Kansas/Oklahoma. Conversely, annual precipitation was twice as variable in southeastern New Mexico as in eastern Colorado, Kansas, and Oklahoma. Temperatures generally were highest in New Mexico but exceptions were minimum nest and maximum brood period temperatures, which were higher in eastern Kansas/Oklahoma than in east-central New Mexico. Temperatures were consistently lowest in eastern Colorado.

Climate variables that differentiated persistent leks from background were consistent for all values of regularization. Here, we present results from the most generalized models we created, those in which regularization was set at 5. Across the geographic range, the niche of LPC was characterized by annual, brood period, and winter precipitation (Table 3). Brood period precipitation had the highest permutation importance, but winter precipitation produced the strongest jackknife values (i.e., highest when included alone, lowest when excluded). The range of values for annual, brood, and winter precipitation in which the probability of presence was ≥0.5 were 38–44, 17–21, and 6–10 cm, respectively.

Within individual climate zones, temperature in the south and precipitation in the north differentiated persistent leks from background locations (Table 3). Maximum temperature during nesting had the highest permutation importance in southeastern and east-central New Mexico and the strongest jackknife values in southeastern New Mexico. Winter precipitation produced the strongest jackknife values for all climate zones other than southeastern New Mexico. Other variables that characterized the niche of LPC within individual zones included annual precipitation (eastern Colorado, Kansas, Oklahoma), brood period precipitation (eastern Colorado, eastern Kansas/Oklahoma), and maximum temperature during the brood period (east-central New Mexico).

Variables in which the probability of presence was ≥0.5 differed between the geographic range and individual climate zones in several cases (Fig. 4). Values in which the probability of
presence was ≥0.5 for precipitation generally were higher in Kansas and Oklahoma and lower in southeastern New Mexico than across the geographic range. Conversely, maximum temperatures during nesting were lower in Kansas, Oklahoma, and eastern Colorado and higher in southeastern New Mexico.

The geographic range contained 8.46 million ha of LPC habitat; over 40% was in Texas and 26% was in eastern Kansas/Oklahoma (Table 4, Fig. 5). Habitat suitability per unit area differed among the six subdivisions ($F_{5, 103,175} = 2743.88, P < 0.0001$) with higher than expected contributions limited to western Kansas/Oklahoma and east-central New Mexico (Fig. 6). Almost all cells within western Kansas/Oklahoma were in the highest quartile and over half of the cells of east-central New Mexico were in the two highest quartiles (Table 4). The contribution per unit area from all other zones was less than expected particularly in eastern Colorado and southeastern New Mexico where most cells contributed little to the overall suitability of the geographic range (Table 4, Fig. 6).

DISCUSSION

Our choice of data and approach to modeling addressed many potential pitfalls that can plague species distribution models. Our sample of occurrences was more than enough to provide reliable results (Hernandez et al. 2006) and
represented the breadth of environmental conditions that characterize the range of LPC. Our analysis was focused, using a limited number of well-chosen variables to describe the climate envelope of LPC (Duncan et al. 2009). Importantly, the choice of variables was based on empirical data from an abundance of studies and surveys conducted throughout the geographic range during a variety of climatic regimes (Appendix). Thus, it is improbable that our knowledge of the niche of LPC was constrained by the unknown effect of factors such as dispersal barriers or biotic interactions (Jimenez-Valverde et al. 2008).

We chose GAP to map habitat because it was the only dataset that encompassed the entire geographic range and included specific vegetative types used by LPC. Its relatively low accuracy might elicit concern, but that weakness was tempered by habitat patterns consistent with previous studies (Ligon 1927, Sullivan 2000, Hagan and Giesen 2005), field observations, and more intensive mapping efforts. For example, LPC habitat in the Texas panhandle, shown by GAP as scattered in the southwest and more connected in the northeast, is consistent with field observations (S. Kyle, personal communication). In southeastern New Mexico, GAP recognized 55% of the habitat identified by a map of LPC habitat that was created via remote imagery and extensive field sampling (Neville et al. 2005). Importantly, there was no error of commission indicating the pattern of habitat identified by GAP was consistent with Neville et al. (2005).

It was not unexpected that the range wide niche of LPC was characterized by precipitation, given the association between precipitation (particularly two winters prior to surveys of gallinaceous birds) and population size (Bailey 1999). Grasses upon which LPC depend require consistent interannual precipitation to replenish and maintain densities. In turn, grasses provide LPC with cover to reduce mortality and forage to fuel natality.

The transition of dominant niche characteristics from temperature in the south to precipita-
Fig. 4. Range of values in which a probability of presence ≥0.5 was predicted by MaxEnt for four climate variables that characterized the niche of the Lesser Prairie-Chicken (Tympanuchus pallidicinctus) across the geographic range and within five climate zones.

Table 4. Habitat (ha) across the geographic range of Lesser Prairie-Chickens (Tympanuchus pallidicinctus) (LPC) and within six subdivisions of the geographic range. Habitat suitability is categorized into quartiles of MaxEnt logistic values. The contribution of each subdivision to the suitability of the geographic range was calculated by subtracting the ratio of cumulative MaxEnt value to cumulative area for each added cell (the observed value) from the slope of the bivariate density function of the cumulative MaxEnt value and cumulative area for the geographic range (the expected value).

<table>
<thead>
<tr>
<th>Geographic extent</th>
<th>MaxEnt values</th>
<th>Total habitat (ha)</th>
<th>Contribution to suitability (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Entire geographic range</td>
<td>2,136,768</td>
<td>2,173,376</td>
<td>2,093,618</td>
</tr>
<tr>
<td>Southeastern New Mexico</td>
<td>61,760</td>
<td>37,376</td>
<td>49,536</td>
</tr>
<tr>
<td>East-central New Mexico</td>
<td>5,440</td>
<td>39,168</td>
<td>85,760</td>
</tr>
<tr>
<td>Eastern Colorado</td>
<td>84,928</td>
<td>12,160</td>
<td>33,792</td>
</tr>
<tr>
<td>Western Kansas/Oklahoma</td>
<td>0</td>
<td>4,480</td>
<td>59,584</td>
</tr>
<tr>
<td>Eastern Kansas/Oklahoma</td>
<td>581,568</td>
<td>684,160</td>
<td>489,600</td>
</tr>
<tr>
<td>Texas</td>
<td>633,152</td>
<td>1,086,144</td>
<td>1,054,770</td>
</tr>
</tbody>
</table>
tion in the north underscores the importance of intrarange analyses. Comparing overlap in values in which the probability of presence was >0.5 between climate zones and the geographic range provides a benchmark for how well zone characteristics reflect the range wide niche. Three zones displayed substantial differences from the geographic range (Fig. 4). Southeastern New Mexico was characterized by lower precipitation and higher maximum temperatures. These factors, combined with the high potential evapotranspiration and variable patterns of precipitation (Fig. 3), likely explain why historically LPC were not as abundant in this zone as in other parts of the geographic range (Ligon 1953, Sands 1968). Eastern Colorado was characterized by cool temperatures which may benefit LPC during nesting by reducing the potential for hyperthermia and desiccation (Table 2, Figs. 2, 3, and 4; Appendix). However, they also may cause LPC to divert energy to thermoregulation that would otherwise be invested in reproduction. Additionally, cool temperatures might delay germination of plants and hatching of insects,
thereby limiting food resources during critical reproductive periods. Eastern Kansas/Oklahoma was characterized by high precipitation which would be expected to enhance reproduction and survival of LPC. However, it also contributes to the transition from mid-grass to tall grass prairie, and a resulting dominance by the Greater Prairie-Chicken \( (Tympanuchus cupido) \) (Robb and Schroeder 2005).

The potential distribution found by our model had two characteristics that commonly define geographic ranges (Brown et al. 1996). First, constraints that define one edge (western) of the geographic range are abiotic, namely aridity, unfavorable temperatures, and a cessation of sandy soils that support vegetation types used by LPC (Appendix). Conversely, constraints that define the opposite edge (eastern) are biotic, namely conditions that favor the Greater Prairie-Chicken more than LPC. Additionally, habitat suitability across the geographic range, although multimodal, was consistent with a center-periphery pattern (Haldane 1956, Brown 1984, Hall et al. 1992, Guo et al. 2005). The more centrally-located western Kansas/Oklahoma zone provides the highest habitat suitability per unit area whereas the edges of the geographic range are characterized by habitat with low suitability (Tables 1 and 4, Figs. 5 and 6). Of interest, Jackson and DeArment (1963) conjectured that the southeastern part of the range in Texas historically might have been used by LPC as a
winter range. Low suitability found by our analysis suggests this supposition may have been largely without merit.

Several of our findings provide direction for conservation. First, the high density of suitable habitat of western Kansas/Oklahoma warrants vigilance, not complacency. A substantial amount of habitat in this zone has been lost to agriculture, but it still has density and suitability of habitat found nowhere else in the geographic range. Conservation of core areas such as this is the most cost-effective way to ensure continued persistence of any species.

Our results indicate focused conservation also is warranted in east-central New Mexico, the only other zone whose contribution to range wide suitability was greater than expected. In particular, populations in this zone possess genetic structure and reproductive strategies markedly different from the northern part of the range (in particular, western Oklahoma); demographic isolation and local fragmentation of habitat were implicated as causative factors (Van Den Bussche et al. 2003, Patten et al. 2005a). Climate may contribute to regional variation in these characteristics as well (Ellsworth et al. 1994, 1996). If so, reintroductions in the southern part of the range likely will be more successful if founding individuals come from populations, such as those of east-central New Mexico, adapted to warmer and drier conditions (Kleiman 1989).

Increasing the distribution of LPC should be considered within the context of eventually reconnecting populations in east-central New Mexico with those in western Kansas/Oklahoma. Starting points could be near the northeastern corner and western border of the panhandle of Texas where small scattered populations remain. Increasing populations along the western border also would strengthen the isolated metapopulation of east-central New Mexico.

The contrast between the abundance of habitat and the paucity of LPC in Texas (Texas Parks and Wildlife Department, unpublished data) highlights the importance of building on our analysis with an examination of anthropogenic disturbances that contributed to the current population status (Sullivan et al. 2000). The density of highly suitable habitat does not match that of Western Kansas/Oklahoma, but the abundance of habitat suggests mitigation of anthropogenic impacts might be worthwhile.

In contrast, unfavorable climate characteristics and a paucity of habitat in eastern Colorado and southeastern New Mexico make these areas challenging for LPC persistence. Populations in western Kansas/Oklahoma might provide adequate demographic support for LPC in the southern part of eastern Colorado. However, the low potential for LPC persistence in southeastern New Mexico because of a paucity of suitable habitat is exacerbated by surrounding oil and gas development that effectively blocks populations from east-central New Mexico or west Texas immigrating to this area. Further, mitigating oil and gas impacts within southeastern New Mexico likely would not be particularly beneficial. Returning all of the approximately 14,000 wellpads and access roads found within or near LPC habitat to natural conditions would add 11,200 ha, but the amount and suitability of habitat would still be well below that of more central parts of the geographic range.

Our model was based on climate from the latter 20th century, but future conditions may differ markedly because of global climate change. The wide range of projected temperature increases (1.3–3.9°C over 80–100 years [Allen et al. 2009]) and uncertainty concerning precipitation (Stocker et al. 2013) precludes specific predictions. However, some general trends can be anticipated. Higher temperatures, increased evaporation, and decreased precipitation in the southwestern United States (Christenson et al. 2004, Stocker et al. 2013) will make it more challenging to maintain persistent populations in New Mexico and adjoining parts of Texas. Conversely, increased temperatures may make eastern Colorado more favorable for LPC. The wide temperature tolerance found for nesting LPC in western Kansas/Oklahoma (Fig. 4) suggests these populations will face low risk from climate change. However, with potential population decreases elsewhere, the need to conserve LPC in this part of the geographic range will grow in importance.

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Historically, Lesser Prairie-Chickens (Tympanuchus pallidicinctus) (LPC) were found throughout the southern great plains from central Kansas to southeastern New Mexico, occupying grass-shrub habitats in sandy soils with shinnery oak (Quercus havardii), sand sage (Artemisia filifolia), and big, little, and sand bluestem (Andropogon gerardii, Schizachyrium scoparium, A. hallii, respectively) as dominant species (Hagen and Gieson 2005). They display high interannual fidelity to their mating grounds (leks) (Riley et al. 1994). Most year-round activity occurs ≤3.2 km, and nesting often is ≤1.8 km, from leks (Campbell 1972, Giesen 1994, Hagen et al. 2005, Pitman et al. 2006a). Nesting and brood rearing (late March–August) is most successful where vegetation affords a high degree of vertical and horizontal cover that protects LPC from predation, extreme temperatures, and desiccating winds (Riley et al. 1992, Giesen 1994, Johnson et al. 2004, Hagen et al. 2005, Patten et al. 2005b,
Pitman et al. 2005).

Fat reserves average <5% of the body weight of grouse, so daily foraging is critical to meeting energy needs (Thomas and Popko 1981, Thomas 1982, Dehaley and Moss 1996). Important dietary components include seeds, acorns, and cultivated grains during fall and winter (Davis et al. 1981, Riley et al. 1993), forbs during spring (Davis et al. 1981), and invertebrates during summer (Jamison et al. 2002, Hagen et al. 2005). Invertebrate abundance is positively related to forb cover (Jamison et al. 2002) which in turn responds to grazing (McNaughton 1985) and to precipitation, particularly that which occurs during the winter preceding, and the spring of, the nesting season (Muldavin et al. 2008, Xia et al. 2010).

Wide population fluctuations are common among LPC (Johnsgard 1983) and demographics are considered to be largely influenced by a strong relationship between precipitation and recruitment. Precipitation affects vegetative growth, and in turn, food and cover (Campbell 1972, Riley et al. 1992, Pitman et al. 2005, Giesen 2000, Patten et al. 2005b).

Jackson and DeArment (1963) speculated LPC from the panhandle historically migrated to central Texas (>100 km distance) during winter; however, most documented movements have been ≤10 km (Campbell 1972, Riley et al. 1994, Hagen 2003, Pitman et al. 2006b). Range expansion occurs incrementally during fall through natal dispersal (Pitman et al. 2006b) and during spring through establishment of new leks by subordinate males when populations are high (Dunn and Braun 1985, Haukos and Smith 1999). Conversely, ranges contract when leks become inactive because of declining populations.