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STRATEGIC CONSERVATION FOR LESSER PRAIRIE-CHICKENS AMONG LANDSCAPES OF VARYING ANTHROPOGENIC INFLUENCE

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ABSTRACT

In the southwestern Great Plains, variable weather and subsequent primary productivity influences population dynamics of many species, including the lesser prairie-chicken (*Tympanuchus pallidicinctus*). Large and spatially heterogeneous grasslands are more likely to provide quality habitat among both dry and wet years. Unfortunately, conversion of native grasslands to cropland, woody encroachment, and the establishment of vertical anthropogenic features (cell towers, oil wells, transmission lines, etc.) have made large intact grasslands rare. We estimated the distribution of lesser prairie-chickens using data from individuals marked with GPS transmitters in Kansas and Colorado, USA, and empirically derived relationships with anthropogenic structure densities and grassland composition. On average, ~10% of the estimated current lesser prairie-chicken range was available as habitat. Our results indicated that preserving or restoring large intact grasslands will most benefit lesser prairie-chickens. However, mechanisms that degrade and fragment grassland habitat vary regionally throughout the lesser prairie-chicken range and spatially explicit conservation strategies are needed. In Northwest Kansas, conversion of cropland to Conservation Reserve Program (CRP) grasslands can increase habitat abundance for lesser prairie-chickens. In contrast, in the Red Hills of Kansas, extensive woody encroachment on former large intact grasslands can limit available habitat. Based on predictions from our species distribution model, we provide spatially explicit prescriptions for

CRP enrollment and tree removal in locations most likely to benefit lesser prairie-chickens. Spatially incentivized CRP sign up has the potential to provide 498 km^2 of additional habitat and the strategic application of tree removal has the potential to restore 1,154 km^2. Tree removal and CRP enrollment are conservation tools that can align with landowner goals and much more likely to be effective in regions where >90% of land is privately owned.

KEY WORDS Conservation Reserve Program, grassland, hierarchy theory, prairie grouse, Random Forest, species distribution.

INTRODUCTION

The ability of a landscape to provide resources for birds in a non-equilibrium grassland system is not only contingent on the status quo of the landscape, but also potential interacting weather and ecological disturbance scenarios (Wiens 1974, Winter et al. 2005). Provision of optimal resources (food or cover) at any point may be outweighed by the lack of available habitat during other life stages or years (Wiens 1974). Broad grassland-dominated landscapes can allow grassland birds to cope with variable weather and resulting spatially inconsistent habitat quality through movement and may facilitate persistence among boom-and-bust reproductive years (Wiens 1974, Ross et al. 2016a)

In the unpredictably variable environment of the southwestern Great Plains, persistence of the grassland obligate lesser prairie-chicken relies upon a boom-or-bust life history strategy where annual population growth fluctuates strongly with periods of favorable environmental conditions (Sala et al. 1988; Garton et al. 2016; Ross et al. 2016a, b). The boom-or-bust strategy likely evolved as an adaption to, and consequence of, temporal environmental instability buffered by the historic broad availability of grasslands (Mengel 1970, Wiens 1974, Ross et al.

2016b). Unfortunately, large grassland-dominated landscapes available for lesser prairie-chicken populations and other grassland birds have become rare due to conversion of native grasslands to cropland, establishment of anthropogenic features, and woody encroachment due to grassland management practices (Hagen et al. 2011, Rodgers 2016, Lautenbach et al. 2017, Plumb et al. 2019). The extent of functional habitat lost due to grassland conversion and presence of anthropogenic features is not known. These factors contribute to the long-term decline of lesser prairie-chickens at varying levels of influence across the species' range (Garton et al. 2016, Ross et al. 2016a).

To estimate effects of grassland habitat loss, knowledge of how grassland composition (proportion of grassland in a landscape) and anthropogenic feature densities constrain the distribution of lesser prairie-chickens at multiple broad scales and among years of variable climate are needed. It remains unclear what constrains the distribution of lesser prairie-chickens and how much available habitat is distributed in Kansas and Colorado, which support >80% of extant lesser prairie-chickens (McDonald et al. 2014). To fill knowledge gaps, a machine learning approach can provide spatially explicit predictions of potential habitat of lesser prairie-chickens (Cutler et al. 2007).

Once an empirically-derived species distribution is estimated, the predicted distribution could be used to spatially prioritize management practices. For *Tympanuchus spp*. populations, it is unlikely that a universal management practice will benefit populations similarly across their range, with a 40-cm annual precipitation gradient from Kansas to Colorado (McNew et al. 2013, PRISM 2016). For example, two management interventions that could increase habitat include tree removal in south central Kansas and restoration of cropland to grassland through the USDA Conservation Reserve Program (CRP) in northwest Kansas (Lautenbach et al. 2017, Sullins et al.

2018). Both conservation practices can be profitable for producers in the lesser prairie-chicken range of Kansas and Colorado where >90% of the species occupied range is privately owned. However, tree removal and enrollment in CRP will only benefit lesser prairie-chickens when surrounding landscapes can support sustainable populations. Conservation practices should be strategically applied within large grassland areas having limited anthropogenic structures (Winder et al. 2015, Plumb et al. 2019, Sullins et al. 2018).

Therefore, our first objective was to predict the distribution of lesser prairie-chicken habitat in Kansas and Colorado based on grassland composition, tree occurrence, and anthropogenic feature density constraints. We used a Random Forest model that incorporated locations from marked lesser prairie-chickens and available locations to create spatially-explicit predictions of use through the northern extent of the lesser prairie-chicken range. Our second objective was to use the predicted distribution to identify locations at which tree removal and the enrollment of cropland into the CRP would have the greatest benefit to lesser prairie-chicken populations (Kraft 2016, Lautenbach et al. 2017, Sullins et al. 2018).

STUDY AREA

Our study area encompassed the northern half of the extant lesser prairie-chicken range including portions of the Short-Grass Prairie/CRP mosaic (SGP), Mixed-Grass Prairie (MGP), and Ecoregions (SSP; Figure 1, McDonald et al. 2014). A longitudinal annual precipitation gradient spanned from east (~69 cm) to west (~37 cm) across the extent of Kansas into eastern Colorado with a concomitant transition from mixed- to short-grass prairie (PRISM 2016). Pockets of sand sagebrush (*Artemisia filifolia*) prairie were interspersed on sandy soils, especially in the southwest portion of the study area. Mosaics of CRP and row-crop agriculture were associated in areas with arable soils. Most of the large remaining grasslands were restricted

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to areas of poor or rocky soils and areas with rough terrain that were unsuitable for cultivation (Spencer et al. 2017). Anthropogenic development was present in the form of oil wells, transmission lines, county roads, major roads, and other vertical features (e.g., cell towers, windfarms, grain elevators, etc.). Within the study area, data were collected at 6 study sites that varied in anthropogenic feature densities including 3 in Colorado (Prowers/Baca, Cheyenne, Comanche National Grasslands[NG]) and 3 in Kansas (Red Hills/Clark, Northwest, Cimarron NG; Figure 1, Table S1, see supplemental material for further description each of study site). Temperatures ranged from -26 to 43° C (extreme minimum and maximum temperature), with average daily minimum and maximum temperatures of 5° C and 21° C, respectively, during data collection (15 March 2013 to 15 March 2016; NOAA 2016).

METHODS

Capture and marking

We captured lesser prairie-chickens at all study sites during lekking seasons (March to mid-May) and uniquely marked individuals with rump-mounted 22-g GPS (global positioning system) satellite PTT transmitters (SAT-PTT; PTT-100, Microwave Technology, Columbia, MD, USA, or North Star Science and Technology, King George, VA, USA; Robinson et al. 2018). These GPS transmitters had a spatial error of ±18 m; within the 30-m × 30-m resolution pixels used in our analyses. GPS locations were recorded every 2 hours during the day, with a 6-hour and 8-hour gap during summer and winter, respectively. Every other bird was tagged with a 15-g very-high-frequency transmitter (VHF; A3960, Advanced Telemetry System, Isanti, MN, USA). We attached VHF transmitters as a necklace with whip antennae down the middle of the back and estimated diurnal locations four times per week using triangulation and Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary).

Study sites were delineated using minimum convex polygons (MCP) around all marked bird locations. We then buffered the MCP by the average net displacement distance (16.18 km) to estimate the area available to all GPS marked lesser prairie-chickens (Earl et al. 2016). To model species distribution and potentially limit autocorrelation issues, we randomly selected two used locations weekly from each marked bird (Segurado et al. 2006). We then separated location data from GPS and VHF marked individuals to create a model training and independent validation data samples, respectively. We randomly generated one pseudo absence record for each location used by lesser prairie-chickens throughout each study site to account for the lack of true absence data; our response variable was relative probability of use (Barbet-Massin et al. 2012).

Landcover Covariates

We obtained landcover type classifications at a 30-m × 30-m resolution from the 2011 National Landcover database (NLCD) and a shapefile identifying the distribution of Conservation Reserve Program (CRP) grasslands provided under agreement with the U.S. Department of Agriculture, Farm Service Agency (Homer et al. 2015). We created continuous rasters of grassland and shrubland composition from the NLCD land cover classification using focal-point statistics in ArcGIS 10.2. We created surfaces using multiple windows that estimated grassland composition within 0.4 km–5 km to represent potential scales of selection for lesser prairie-chickens. Throughout, we refer to the scale used as the length of the radius (e.g., 5-km scale).

We examined multiple scales because of the uncertainty of the scale at which emergent and extrahierarchical properties of the landscape would best predict lesser prairie-chicken occupancy (King 1997). We bounded scales assessed to be ≤5 km based on past lesser prairie-chicken literature, which included demographic influences at the 3-km scale and selection of nest sites within 4.8 km of capture lek (Giesen et al. 1994, Ross et al. 2016b).

Anthropogenic Feature Covariates

To estimate the distance to, and densities of, anthropogenic features, we acquired shapefile layers of oil wells, transmission lines, major roads, county roads, and cell phone towers (see Supplemental Materials for sources of anthropogenic feature data). In ArcGIS 10.2, we used the Euclidean distance tool to generate rasters depicting distance to feature and focal statistics tool to estimate summed densities of features within circular radii (0.5 km, 1 km, 2 km) of each pixel. The range of radii was selected to encompass known avoidance distances (~0.5–2 km) published in past literature (Pruett et al. 2009, Hagen et al. 2011, Plumb et al. 2019).

Species Distribution Modeling and Validation

Prediction.—Lesser prairie-chicken occurrence was predicted using a Random Forest method (package ‘randomForest’; Liaw and Wiener 2002,) in R (R Development Core 2017). Random Forest is a classification and regression tree method that uses bootstraps to handle over-fitting (Cutler et al. 2007).

We first assessed multicollinearity of all variables at $\alpha = 0.05$ using a leave one out assessment. Then, the most influential scales of variables were identified using a model improvement ratio based on predictions from a global model of all variables at all scales that also included distance to anthropogenic feature (MIR; Evans et al. 2011). Ranks were estimated using the mean decrease in out-of-bag error standardized from 0 to 1. The scale (grassland composition 0.4–5-km radius circles, anthropogenic features = 0.5–2-km radius circles) achieving the greatest MIR was used in the final model for each variable. Predictions of presence or absence were generated based on majority votes across all trees using the final model. An occurrence threshold was estimated following Jimenez-Valverde and Lobo (2007) to identify the model output probability (0–1) where occurrence or non-occurrence were most discrete and to identify potential habitat.

Validation.— We validated the model using VHF location data that were not used to train the predictive model and collected concurrently with GPS locations. Models were validated based on accuracy, specificity, and sensitivity of the model in predicting presence or pseudoabsence of locations from the independent validation set. We also estimated an area under the ROC curve (AUC; Delong et al. 1988).

Spatial Prioritization of Tree Removal

To identify priority areas where tree removal would most likely restore lesser prairie-chicken habitat within the MGP, we defined potential habitat from the Random Forest model using both grassland composition and anthropogenic features. We used the threshold that included the top 95% predicted values (values > 0.33) from VHF locations in the validation to incorporate a greater area for potential conservation than obtained following Jimenez-Valverde and Lobo (2007). We then derived a layer depicting tree densities from Falkowski et al. (2017), following methods of Lautenbach et al. (2017; see Supplemental Materials for tree canopy cover). Areas where predicted habitat overlapped with trees densities >2/ha, were most likely to be restored as habitat through tree removal. Last, we identified predicted habitat areas affected by low, medium, and high canopy coverage identified in Falkowski et al. (2017).

Spatial Prioritization of CRP Enrollment

To identify areas where applying CRP would most likely benefit lesser prairie-chickens, we first predicted the distribution of habitat using the occurrence threshold estimated from the

Random Forest model, based on avoidance of anthropogenic features (Jimenez-Valverde and Lobo 2007). Previous research indicated that CRP in landscapes (4-km radius) with <56 cm of annual average precipitation and >60% grassland were most likely to be used by lesser prairie-chickens (Sullins et al. 2018). We multiplied binary layers detailing areas of predicted habitat, a layer indicating where landscapes were >60% grassland, areas receiving <56 cm of annual average precipitation, and areas that are currently in CRP to indicate priority areas for conservation as well as cropland as indicated from NLCD 2011 to indicate priority areas for enrollment (Homer et al. 2015).

We then estimated the composition of priority enrollment and conservation of CRP by tillage risk. To identify tillage risk, we used a layer developed by Smith et al. (2016) that predicts areas of high and low tillage risk based on soil, climate, and topography related variables. We identified areas of low (0.00–0.32), medium (0.33–0.66), and high (0.67–1.00) tillage risk.

RESULTS

We randomly selected a subset of 9,895 locations from 170 lesser prairie-chickens marked with GPS satellite transmitters and monitored from 2013–2016 to build our species distribution model. Two used locations per week were sampled from an average of 29.16 (SD = 36.35; range = 2–136) weeks for each individual. Only locations from female lesser prairie-chickens were used from the Red Hills/Clark and Northwest study sites; however, small sample sizes from study sites in Colorado and Cimarron NG required the use of both male and female individuals for analyses.

Grassland composition at the 5-km scale had the greatest model variable importance (1.0) and was 38% more important than at the 4-km scale (Figures S1 and S2). For all anthropogenic features (county roads, major roads, oil wells, transmission lines, and other vertical features) densities estimated at the 2-km scale (e.g., number of transmission lines within 2-km radius) had the greatest model variable importance with a mean importance of 0.28, which was 150% greater than densities estimated at the 1-km scale. Grassland composition within 5 km and anthropogenic features within 2 km were used as covariates in the final model to predict available habitat.

Grassland composition was 79% greater in model importance compared to the next predictor in the final model. Peak relative probability of use occurred at ~77% grassland composition; similar to the 76% mean of used locations (Figure 2, Table 1). Having lower model importance than grassland composition were densities of county roads, vertical point features, transmission lines, and major roads in respective order of model importance (Figure S2). Overall, the relative probability of use decreased as cumulative densities of anthropogenic features increased (Figure 2). However, the raw predicted probability of use increased from 0 to 5 km/12.6 km^2 of county roads then declined sharply as densities increased beyond 5 km/12.6 km^2 and was close to zero at densities >10 km/12.6 km^2 (Figure 2). When county road densities surpassed a threshold of 8–10 km/12.6 km^2, it indicated an urban environment based on visual observations.

In addition to the county road threshold of ~8 km/12.6 km^2, all other anthropogenic features displayed patterns of sharp decreases in relative probability of use after surpassing a density (Figure 2). Based on the raw probability distribution, the occupancy threshold for vertical point feature densities occurred at ~2 vertical features/12.6 km^2 (Figure 2). A similar threshold was estimated for oil wells with areas having >2 oil wells/12.6 km^2 having 8 times lower relative probability of use. The threshold for major roads and transmission lines was achieved at 0.15 km/12.6 km^2; relative probability of use decreased abruptly when surpassed.

Prediction—The predicted relative probability of use output from the Random Forest model is depicted in Figure 1. The model predicted a greater area of lesser prairie-chicken habitat in the MGP than in the SGP or SSP Ecoregions (McDonald et al. 2014). An occurrence threshold for the model was estimated at a model output probability of 0.60 for the model incorporating both grassland composition and anthropogenic structures and 0.70 for the model including only anthropogenic structure densities based on maximizing the sum of model sensitivity and specificity (Jimenez-Valverde and Lobo 2007).

The percentage of potential habitat (>0.6 predicted occurrence threshold) within the northern extent of presumed range of the lesser prairie-chicken as delineated in McDonald et al. (2014) was 16% (3,099/14,790 km^2) in the MGP Ecoregion, 9% (2,613/27,899 km^2) in the SSP Ecoregion, and 8% (3,671/43,641 km^2) in the SGP Ecoregion. In the SGP Ecoregion of northwest Kansas, optimal habitat appears constrained to patches within 12 km of the Smoky Hill River in Gove and Logan counties; northeast Finney County; and northeast Wallace County. The model also predicted a substantial amount of habitat in the western most extent of the SGP in Kiowa and Cheyenne Counties of Colorado where a large expanse of undeveloped sand sagebrush prairie occurs within what is technically delineated as the SGP Ecoregion. Within the delineated SSP Ecoregion, predicted habitat is largely clumped in the western extent as well. In the MGP of Kansas and northern Oklahoma, USA, habitat was more uniformly distributed (Figure 1).

Validation— We used subsampled VHF locations (2 locations per week from 113 individuals) to validate our predictions (n = 4,043). Model performance was good with an estimated accuracy of 84%. The model correctly predicted 83% of VHF locations as habitat (sensitivity) and 83% of pseudoabsences as nonhabitat (specificity). The receiver operating curve

AUC was 0.91 suggesting a fairly strong dichotomy between predicted habitat and nonhabitat (Delong et al. 1988).

Spatial Prioritization of Tree Removal

We estimated that 1,154 km^2 of habitat for lesser prairie-chickens could be gained by tree removal and an alteration of land management practices to prevent further woody encroachment in the MGP of Kansas and northern Oklahoma (Figure 3). Of the potential habitat, 12% is affected by low canopy cover (1–5%), 8% by medium canopy cover (6–15%), and 1% by high canopy cover (>15%). Priority areas for tree removal were largely clustered to the eastern extent of the lesser prairie-chicken range.

Spatial Prioritization of CRP Enrollment

Our model suggests that 1,570 km^2 of current CRP provides habitat for lesser prairie-chickens and should remain CRP (Figure 4). There were 4,189 km^2 of cropland that reside in areas where enrollment would benefit lesser prairie-chickens. However, based on our results enrolling cropland into CRP would be most beneficial when increasing grassland composition within 5-km to approximately 80% in areas receiving less than 56cm of precipitation. Predicted effects of anthropogenic features resulted in a 7,211 km^2 decrease in priority cropland for enrollment and 4,312 km^2 decrease in priority areas to conserve CRP and highlights the importance of considering anthropogenic feature densities. Our model highlighted areas on the Lane, Ness, and Finney county lines in addition to areas near our study sites.

The proportion of area that was predicted as high, medium, and low risk for tillage varied among priority areas for enrollment and conservation. Priority areas for enrollment were 7%, 32%, and 61% of low, medium, and high risk to tillage respectively. Priority areas to conserve CRP were comprised of 25%, 48%, and 28% of low, medium, and high risk respectively.

Discussion

We provide an empirically-driven species distribution estimate that identifies grassland strongholds remaining within Kansas and Colorado that likely provide quality habitat for lesser prairie-chickens and species that fall under its ecological umbrella (Brennan and Kuvlesky 2005). Although, our model focused on the distribution of lesser prairie-chickens, the use of broad-scale grassland composition and anthropogenic feature densities as predictors makes these predictions important for several grassland obligate birds (Veech 2006, Mahoney and Chalfoun 2016, Plumb et al. 2019). Our model indicates how the broad-scale availability of large grasslands unencumbered by anthropogenic features is limited within the study area and likely imposes strong constraints on the distribution of grassland-obligate wildlife; especially those requiring large spatial extents for populations to persist (e.g., lesser prairie-chicken).

We estimated the presence of 9,383 km^2 of available habitat (>0.60 relative probability of use) for lesser prairie-chickens in Kansas and Colorado. There is potential to increase available habitat by 1,154 and 4,189 km^2 through strategic removal of trees and enrollment of cropland into CRP grasslands. Area of predicted habitat was greatest in the SGP, followed by the MGP, and the SSP ecoregions. However, the model likely overestimated the amount of habitat in the far western extent where short-grass prairie is largely contributing to the grassland composition of the model and may not provide habitat due to insufficient vertical structure (Giesen et al. 1994). In contrast, the area in the far northwestern extent of the lesser prairie-chicken range is predominantly sand sagebrush prairie that is free of anthropogenic features and may become more important for lesser prairie-chickens given climate change projections (Grisham et al. 2016).   Based on our predictions, it appears lesser prairie-chickens at current population abundance are constrained to areas having >70% grassland within a 5km radius (78.5km^2) and with minimal anthropogenic features (e.g., <10 vertical features in 12.6 km^2).

We suggest that grassland abundance in a landscape influences the occurrence of lesser prairie-chickens both directly, as extrahierarchical boundaries, and indirectly through emergent properties operating at finer scales (King 1997). Occurrence of lesser prairie-chickens is a product of the finer scale provision of lekking, nesting, brooding, and nonbreeding habitats that are properly abundant and configured to allow the establishment of a home range at subsequently broader scales (Hagen et al. 2013, Winder et al. 2015, Robinson et al. 2018). In addition to the spatial heterogeneity needed to satisfy all life-stage needs, the vertical cover requirement (e.g., 25–80 cm tall herbaceous cover) must also be realized among dry and wet years in a dynamic grassland ecosystem (Sala et al. 1988, Ross et al. 2016b). Habitat must also be abundant enough, and properly configured when fragmented, for dispersal to facilitate demographic and genetic rescue at even broader scales (Simberloff 1994, Ross et al. 2016b). Our estimate of optimal grassland area (77% of 78.5 km^2 landscape) lie between the 49 km^2 and 202 km^2 estimates of habitat to support a single lek and overall population respectively (Haukos and Zaveleta 2016). The estimate also falls within a range of scales at which CRP enrollment and prescribed grazing influenced lesser prairie-chicken occupancy (Hagen et al. 2016). Our predictions are based on the landscape rather than a single contiguous patch of grassland and suggest that landscapes that have limited vertical structures (e.g. oil wells, trees) and ≥60.5 km^2 of grassland within a 78.5 km^2 area would be optimal assuming that the grasslands are managed properly.

Effects of Anthropogenic Feature Densities

The presence of vertical structures at high densities can make a landscape that would otherwise function as habitat unavailable to lesser prairie-chickens (Hagen et al. 2011, Plumb et al. 2019). Lesser prairie-chickens have evolved mechanisms to avoid vertical structures likely to minimize risk of predation from perching raptors (Reinert 1984, Manzer and Hannon 2005). Vertical structures avoided by lesser prairie-chickens include trees, transmission lines, oil wells, wind turbines, and cell phone towers (Pitman et al. 2005, Hagen et al. 2011, Lautenbach et al. 2017, Plumb et al. 2019). The avoidance of tall vertical features is not absolute and largely contingent on the density of features at a landscape scale, life-stage of individual birds, and may be reduced if access to high-quality habitat outweighs the presence of vertical features (Lautenbach et al. 2017, Plumb et al. 2019). For example, lesser prairie-chickens avoid areas having >2 trees/ha at the 16-ha scale when nesting and areas having >8 trees/ha otherwise (Lautenbach et al. 2017). Such constitutive relationships and interactions among life stages likely drive the complex hierarchical system from which population occupancy emerges. Although there is considerable variation of the effect of anthropogenic features on lesser prairie-chickens based on life-stage and landscapes in which they occur, we provide evidence of thresholds where anthropogenic feature densities may overall act as constraints.

The lack of avoidance of county roads suggests that they do not affect lesser prairie-chicken occurrence at low densities (<15 km/12.6 km^2). Locations of roads in upland areas may additionally be a result of overlapping desirable conditions for road placement and lesser prairie-chicken habitat. We expect this to partially be a function of county roads being largely gravel surfaced and often occurred in upland areas of relatively greater elevation that are more likely used by lesser prairie-chickens (Lautenbach 2015). Additionally, traffic volume on certain roads may dictate avoidance more than presence of the road itself (Blickley et al. 2012).

Spatial Prioritization of Tree Removal

To increase the amount of potential habitat for lesser prairie-chickens, we identified strategic areas where tree removal, mostly eastern red cedar (*Juniperus virginiana*), would have maximum benefits. However, it is imperative that trees are not merely removed, then allowed to return (estimated encroachment: +2.3% forest cover/year; Briggs et al. 2002). We suggest that on-site tree removal follow Lautenbach et al. (2017) and implementation of a prescribed fire component following the mechanical removal of trees (Ortmann et al. 1998). Additionally, lower canopy cover areas could be prioritized first followed by medium and high percent canopy coverage areas to be cost effective.

Mechanical removal of trees at low (1–5%), medium (6–15%), and a high canopy cover (>15%) are estimated to cost US\$15,863/km^2, US\$40,046/km^2, and US\$103,572/km^2, respectively (Lautenbach et al. 2017; C. Hagen, Lesser Prairie-Chicken Initiative, personal communication). Based on these estimates to remove trees, it will cost US\$10.2 million in identified priority areas (157.80 km^2) of low percent canopy cover, US\$17.3 million in medium percent canopy cover areas (108.35 km^2), and US\$5.1 million to remove areas (9.85 km^2) having high percent canopy cover. Overall, it would cost US\$32.6 million to remove trees in priority areas. Our predictions do not account for trees killed in the Anderson Creek and Starbuck fires of 2016 and 2017, which burned 2,841 km^2 in northern Oklahoma and in Barber, Comanche, Clark and Meade counties of Kansas, respectively. A substantial number of the trees killed by the fire remain standing as skeletons, which will likely still be avoided by lesser prairie-chickens if skeletons provide perches for raptors (Reinert 1984). It is likely that some post-fire treatment will be needed to prevent recolonization of this area by woody species (Lautenbach et al. 2017).

Spatial Prioritization of CRP Enrollment

The underlying ability of CRP to benefit both producer and grassland wildlife is likely the reason for its conservation success in areas >90% privately owned (Johnson 2005, Sullins et al. 2018). To build on the underlying conservation success of CRP on working lands, current continuous CRP signup programs were developed that pay more per acre than traditional CRP signup (Stubbs 2014). Increased payments are used to encourage further management within CRP tracts to benefit pollinators, waterfowl, and upland game birds by requiring interseeding with native forbs and desired native grasses (North American Bird Conservation Initiative 2015). Although CRP can benefit wildlife, the future of CRP remains uncertain and its ability to provide habitat for lesser prairie-chickens is contingent on renewal of the program with each new Farm Bill and the enrollment and reenrollment of CRP grasslands in contracts that typically span 10-15 years (Stubbs 2014).

We provide empirical insights that could be used to incentivize strategic placement and conservation of CRP where surrounding landscapes are favorable for lesser prairie-chickens. Priority areas identified in our model could be directly declared ‘wildlife priority zones’ within the Farm Service Agency’s Environmental Benefit Index system that is currently used to rank areas for CRP enrollment. Both within CRP field management and spatially targeted approaches provide mechanisms to benefit wildlife populations at broad scales as there is >700,000 ha of CRP grassland within the estimated lesser prairie-chicken range (Sullins et al. 2018).

Rental payments for general CRP signup within the study area average US$7,463/$km^2$ (US$30.3/acre) based on the 2018 farm bill with rental rates averaging $2,472 less per km^2(-US$10/acre) in Colorado compared to Kansas (United States Department of Agriculture website: https://www.fsa.usda.gov/). Based on our model estimates of 1,570 km^2 of current CRP

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providing habitat for lesser prairie-chickens, US$11.7 million annually in rental rates will conserve these areas for lesser prairie-chickens in addition to providing several other ecological services (Johnson 2005). Enrollment of half of the 4,189 km^2 of cropland within the priority area would cost an additional US$15.6 million annually in rental rates and would cost US$19.2 million to establish (US$9,143/$km^2$ [US$37/acre] establishment fee; Young and Osborn 1990).

Conclusion

Broad scale (78.5 km^2) grassland composition and anthropogenic feature densities appear to exert constraints on the distribution of lesser prairie-chickens and likely other grassland- obligate wildlife in our study area. The study area was >95% privately owned and using tree removal and CRP at landscape scales may be the best management options to improve habitat availability for lesser prairie-chickens (Lautenbach et al. 2017, Sullins et al. 2018). Comparing costs of tree removal to CRP enrollment suggest that CRP enrollment may be more cost efficient; however, because lesser prairie-chickens use habitat at a landscape scale, comparison of area gained from tree removal and CRP enrollment are not directly comparable. Using both tools in areas with voluntary landowner participation will be best for conserving lesser prairie-chickens and other grassland-dependent wildlife.

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Table 1. Mean and standard deviation of grassland composition (5-km radius scale) and anthropogenic feature densities (2-km radius scale) estimated at lesser prairie-chicken locations (*n* = 9,895) from 2013–2016, and at random locations (*n* = 9,895) distributed within dispersal range of Kansas and Colorado, and throughout the entire extent analyzed for the species distribution model. The units for linear features (roads and transmission lines) are displayed as linear km densities within the 2 km (12.6 km^2) of each location while the vertical features (e.g., cell towers, large buildings, wind turbines, and oil wells) are represented by the densities of individual features. Estimates for the entire extent are based on the mean and variance of all pixel values estimated using a moving window analysis within the study area.

	Used		**Random**		**Entire Extent**	
Variables	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Grassland composition	0.76	0.18	0.55	0.26	0.51	0.27
Anthropogenic features						
County roads (km/12.6km^2)	3.90	2.36	4.38	2.81	4.98	3.53
Major roads (km/12.6km^2*)*	0.09	0.39	0.31	0.70	0.34	0.73
Oil wells/12.6km^2	2.42	3.89	2.95	5.04	3.49	6.67
Transmission lines (km/12.6km^2)	0.06	0.31	0.23	0.66	0.43	0.98
Vertical point features/12.6km^2	2.43	3.91	3.16	5.28	3.82	7.41

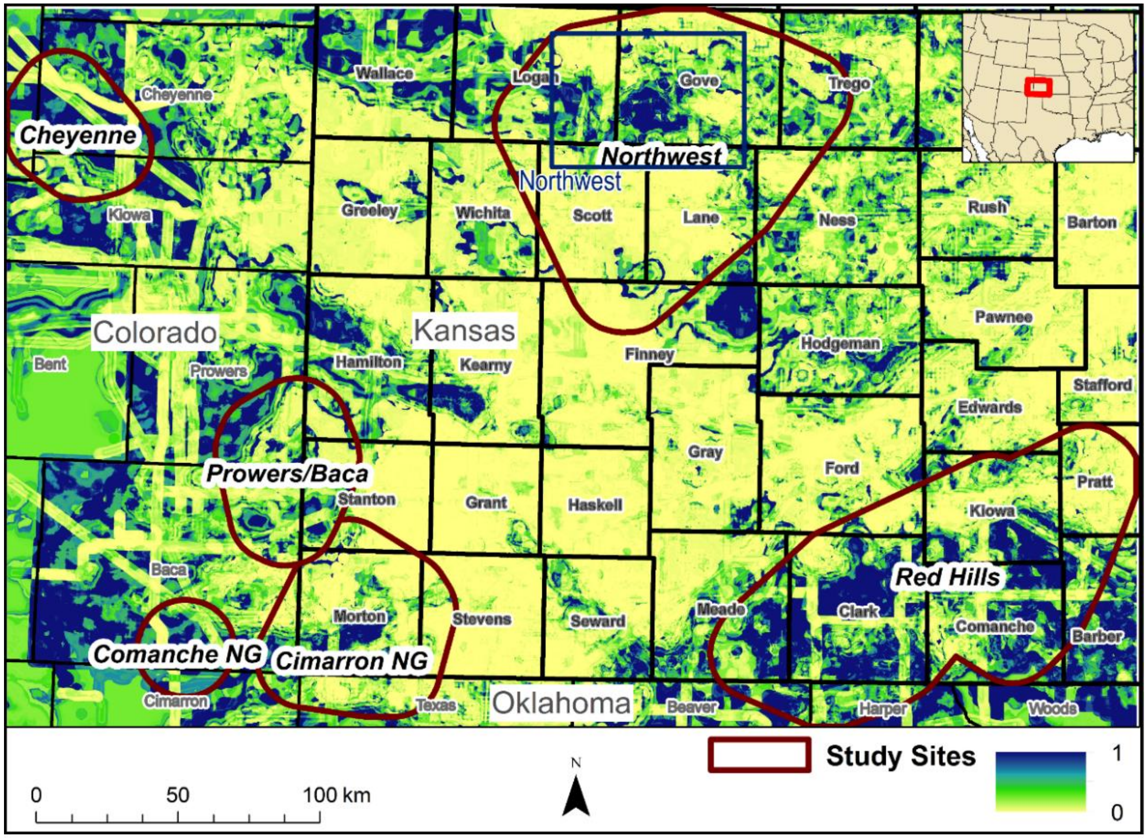

Figure 1. Locations of the 6 study sites where lesser prairie-chickens were marked, captured, and monitored in Kansas and Colorado, USA during 2013–2016 to estimate species distribution using a Random Forests model relative to presumed occupied range of lesser prairie-chickens. Study sites were established by creating minimum convex polygons from the subset of locations used by lesser prairie-chickens marked with GPS satellite transmitters then buffering the minimum convex polygons with the average net displacement during dispersal (16.18 km) following Earl et al. (2016). Values range from 0 (yellow) to 1(dark blue) indicating the relative probability of use by lesser prairie chickens and predict the extent of habitat based on grassland composition within 5 km and anthropogenic feature densities within 2 km. The species distribution model encompasses 3 of 4 ecoregions used by the lesser prairie-chicken including the Short Grass Prairie/CRP mosaic (Northwest study site), Mixed Grass Prairie (Red Hills study site), and Sand Sagebrush Prairie Ecoregions (Cimarron NG, Comanche NG, Prowers/Baca, and Cheyenne study sites) as defined in McDonald et al. (2014).

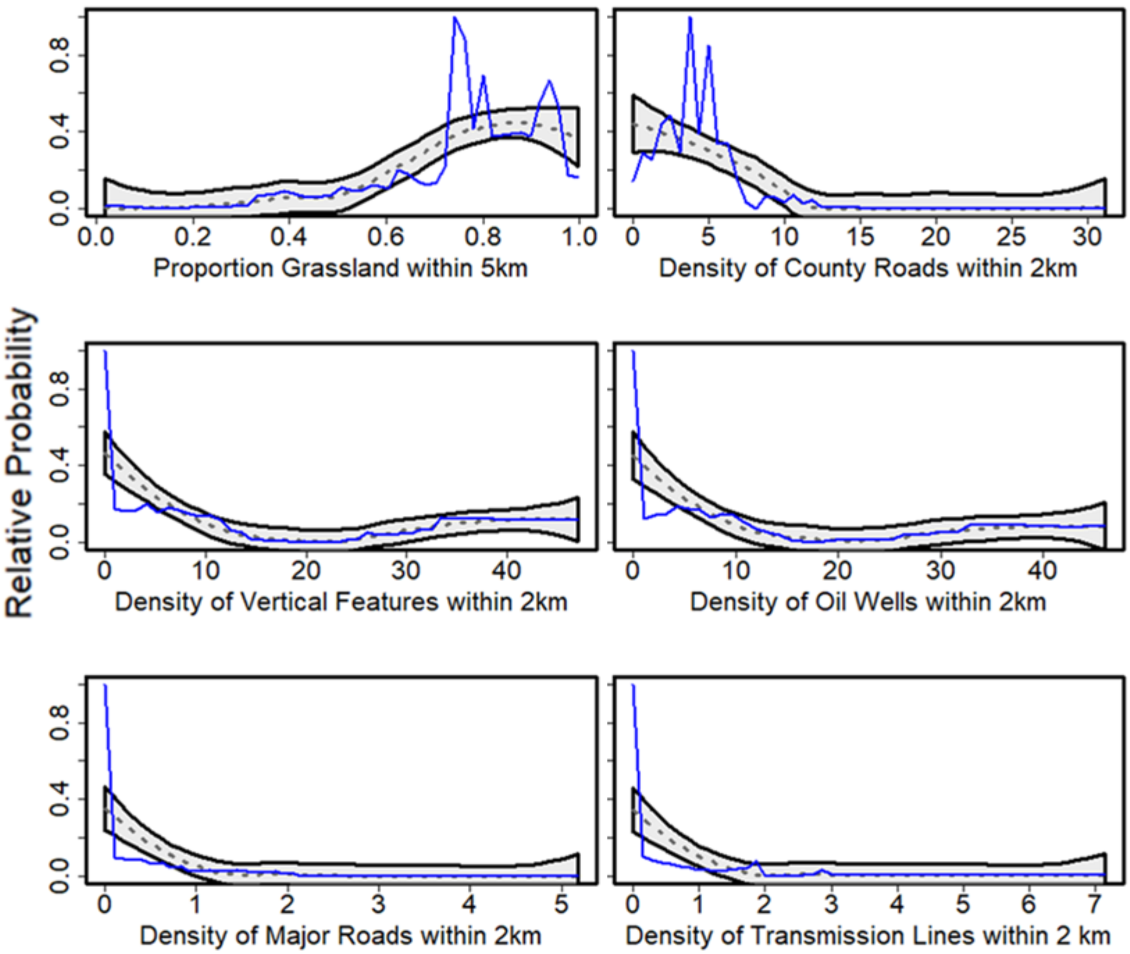

Figure 2. Partial dependence plots for all grassland composition and anthropogenic feature densities used to predict the distribution of lesser prairie-chickens in Kansas and Colorado as depicted in Figure 1 based on data from 2013-2016. A loess polynomial regression is plotted in as a dashed grey line with 95% prediction intervals highlighted in grey and the raw relative probability of use distribution is plotted a blue line.

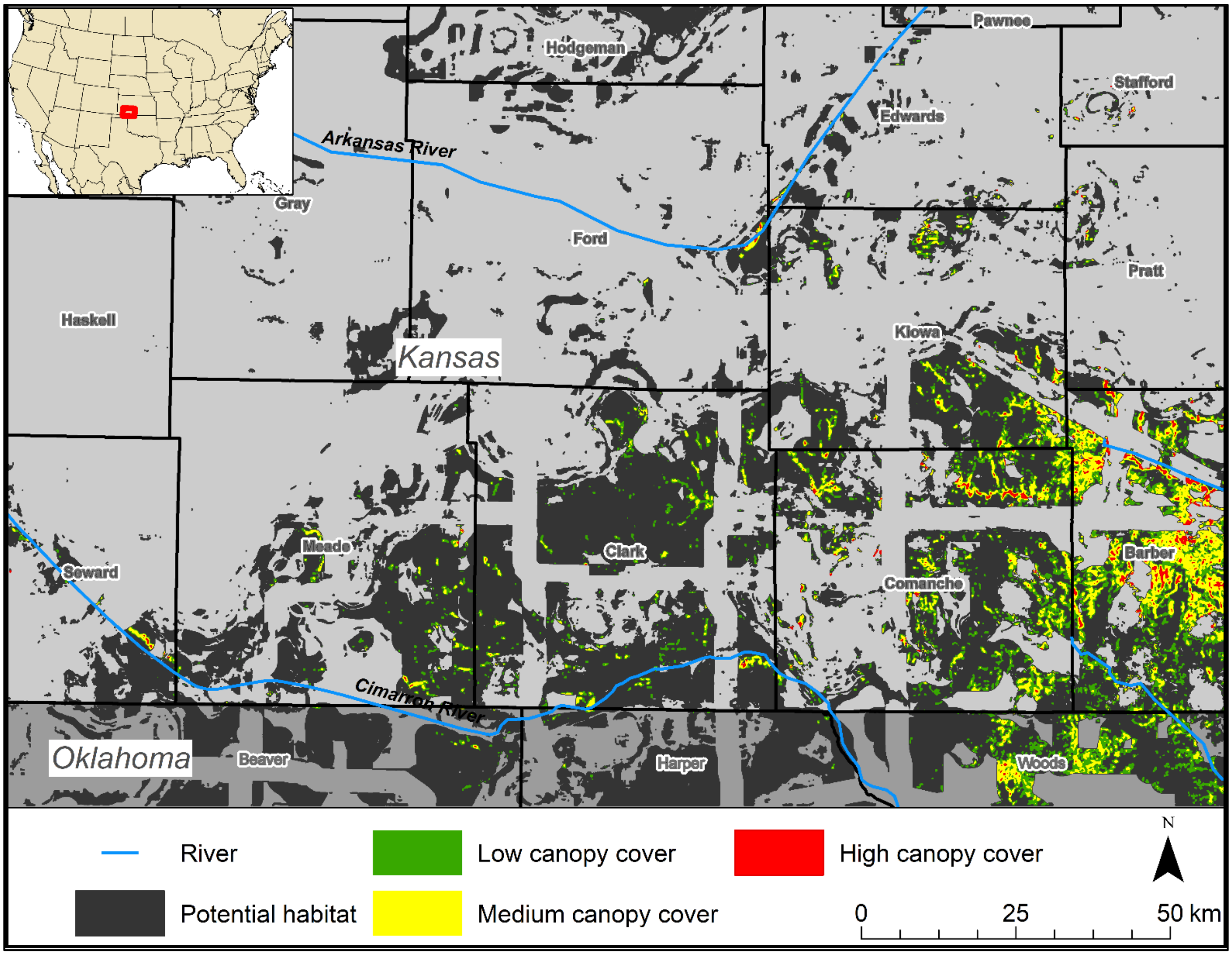

Figure 3. Predicted areas of low (1–5%), medium (6–15%), high (>15%) tree canopy cover where tree removal is most likely to restore lesser prairie-chicken habitat in Kansas and Colorado based on grassland composition within 5 km and anthropogenic feature densities. Areas having a high priority for tree removal are where the top 66% of predicted values from the Random Forests model occurred and where there was >2 trees/ha (Falkowski et al. 2017, Lautenbach et al. 2017).

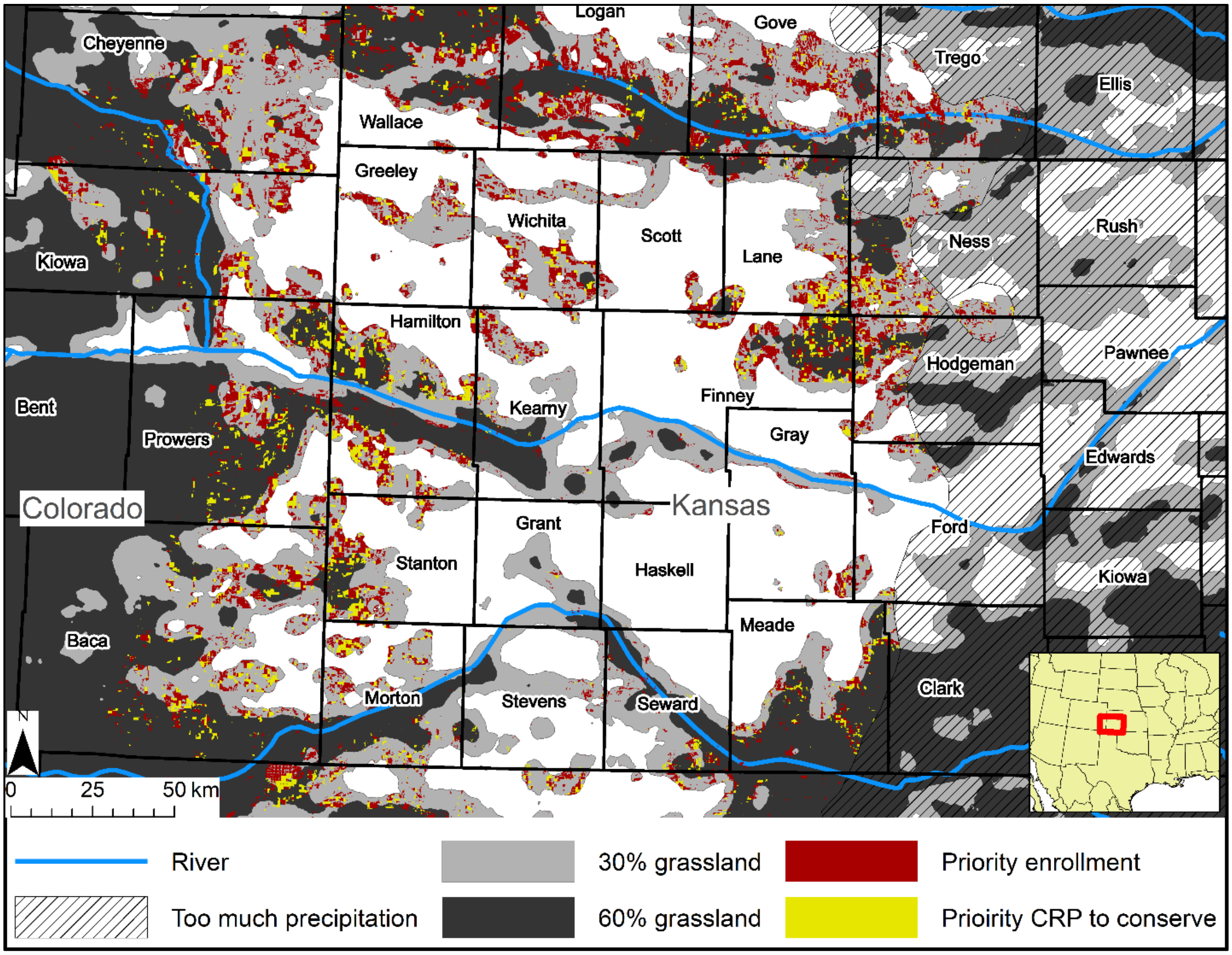

Figure 4. Predicted areas where current priority CRP grasslands (yellow) and cropland that could be converted to CRP (red) is most likely to be used by lesser prairie-chickens in Kansas and Colorado. Priority areas that are currently enrolled CRP grassland and areas currently cultivated were in locations having greater than 30% native working grassland (light grey) within 4 km and where the top 30% of values from a Random Forests model using only anthropogenic features occurred. Also, shown are areas that had greater than 60% native working grassland (dark grey) within 4km.

Supplemental Material

2/14/19

STUDY AREA

The study site in northwest Kansas (9,557 km^2) was located in Gove and Logan counties (Figure 1). The portion of the study site occurring in Logan County was comprised of relatively more short-grass prairie and less precipitation than the Gove County portion to the east as the transition between semi-arid and temperate precipitation levels divided the study site (Plumb 2015). The study site was a mosaic of CRP (7.4%), cropland (36%), and native short-grass or mixed-grass prairie (54%; Robinson et al. 2018). Research was mostly conducted on private, working grasslands, but also included the Smoky Valley Ranch (SVR) in Logan County, owned and operated by The Nature Conservancy. Historical ecological drivers that maintained grasslands at the Northwest study site included periods of drought, bison grazing, and fire. However, fire is largely absent from the current landscape and grazing by cattle is within fenced pastures. A full season, rotational grazing operation for both cow/calf and yearling herds was the dominant system used among local ranchers. A significant portion of CRP was hayed prior to and during the study due to drought conditions, a few tracts were inter-seeded and disked, and others were undisturbed and idle. Annual precipitation was 39 cm, 48 cm, and 49 cm in 2013, 2014, and 2015, respectively which was below the 30-year long term average of 50 cm (NOAA 2016).

The Red Hills/Clark study site (9,537 km^2) included locations in Clark County and on the border of Comanche and Kiowa counties. Location one was in western Clark County, Kansas, on the transition between of the MGP and SSP ecoregions. The Clark site was 77% grassland, 14% cropland, and 5.5% CRP (Robinson et al. 2018) and largely comprised of 2 privately owned ranches; one in the Cimarron River floodplain dominated by loamy fine sands, fine sandy loams, and fine sands with the other in rolling hills 20 km north on mostly silty clay, clay loam, and silt loam (Soil Survey Staff 2017). Rotational grazing systems for both cow/calf and yearling herds were used in this area. Stocking rates were set to utilize 50% of available forage produced each growing season on the study ranches. The Red Hills site was in the MGP of Comanche and Kiowa counties and represented the eastern boundary of the lesser prairie-chicken range. The Red Hills study site was 87% grassland, 8.9% cropland, and 2.2% CRP (Robinson et al. 2018). The site was comprised of large contiguous grasslands maintain by both cow/calf and yearling (season long) grazing systems. Research efforts focused on a large ranch that implemented a patch-burn grazing system wherein large pastures were divided into thirds or fourths and a portion was sequentially burned annually.

The Cimarron NG study site (3,575 km^2) encompassed the Cimarron National Grasslands, which was managed for multiple uses by the U.S. Forest Service (USFS). Grassland was abundant within the USFS managed portion of the study site; however, the surrounding matrix for which lesser prairie-chickens can disperse encompassed a substantial amount of cropland. The Cimarron NG study site depicted in Figure 1 was 32.3% grassland, 47.1% cropland, and 16.7% CRP grassland. The study site incorporates areas that were heavily cultivated in the early 1900s. The area was severely degraded by soil erosion during the 1930s Dustbowl and many farms and ranches were abandoned. The land first became part of the Franklin Roosevelt administration’s national soil conservation program and later a National Grassland in the 1960s. The area has been restored to resemble a pre-cultivation sand sagebrush grassland state; however, trees may be more abundant along riparian areas than prior to European settlement (Cable et al. 1996, McDonald et al. 2014, Raynor et al. 2017).

The 3 study sites in Colorado received less annual average precipitation in comparison to the sites in Kansas. The Prowers County study site (2,556 km^2) was comprised of dwindling patches of grassland (largely CRP) within a landscape mosaic of dryland and irrigated row-crop agriculture. The study site was composed of 43% cropland, 28% native working grassland, and 25% CRP (Homer et al. 2015). Prowers County was dominantly comprised of loamy soils (Soil Survey Staff 2017) and received 43 cm of precipitation annually (PRISM 2016). Most CRP tracts were enrolled into the program in the mid-1980s. Many tracts had recently undergone mid-contract management. To meet management requirements, typically 1/3 of the CRP fields were disked creating linear strips of disturbed and undisturbed grass (J. Reitz, Colorado Parks and Wildlife, pers. comm.).

The study site in Cheyenne County (1,989 km^2) was comprised of large expanses of lightly and heavily grazed sand sagebrush prairie where 30-year precipitation averages were lowest of all study sites (37 cm, PRISM 2016). The Cheyenne County study site was composed of 99% native working grassland and 1% cropland both largely occurring on sandy soils (Homer et al. 2015, Soil Survey Staff 2017). The Comanche NG landscape (915 km^2) was 71.2% grassland, 13.2% cropland, and 13.0% CRP and managed for multiple uses similar to the Cimarron NG study site but differed by having a surrounding matrix that was predominantly grassland.

The Red Hills/Clark study site was located in the MGP Ecoregion while the Logan and Gove study sites were located in the SGP Ecoregion of their current range (McDonald et al. 2014). The Cheyenne County and Prowers County study sites each represented isolated portions of their current range in Colorado and occurred within the SSP Ecoregion; however, if classified by land-cover characteristics, the Prowers County study site would more resemble the Short-Grass Prairie/CRP Mosaic Ecoregion (Hagen and Giesen 2005, McDonald et al. 2014).

METHODS

Anthropogenic Feature Covariates

All shapefiles were converted to raster files with 30-m × 30-m pixels in ArcGIS 10.2 to enable creation of continuous density of anthropogenic feature surfaces. For point features, overlapping features in the same 30-m pixel were summed. For linear features, we first buffered lines by 30 m, then converted to rasters. To convert back to length estimates, we divided the number of pixels by 2 and multiplied by the size of the 30-m length of each pixel. We use the radius of the window to describe scales used below (e.g., 2-km scale indicates everything within a 2-km radius) except when describing the length of linear features, which are reported as km of feature/km^2 of the scale assessed.

We used outside sources to validate the location of anthropogenic features within the extent of study sites using basemap aerial imagery provided in ArcGIS 10.2 (product of: ESRI, i-cubed, USDA FSA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGP). Operating oil well locations since the 1930s were derived from a shapefile created by the Kansas Geological Survey that is updated weekly (http://www.kgs.ku.edu/PRS/petroDB.html). We queried and used only active wells that were producing. Oil well locations in Colorado were obtained from the Colorado Oil and Gas Conservation Commission, which updated data daily; we queried wells that had statuses of active, producing, or temporarily abandoned. Locations of active oil wells in Oklahoma were obtained from the National Energy Technology Laboratory Energy Data Exchange (https://edx.netl.doe.gov/dataset /Oklahoma-well-locations-and-operators) and the available shapefile was created using data compiled by the Oklahoma Corporation Commission which was updated yearly.

Road and electric transmission locations in Kansas were obtained from the Kansas Geographic Information Systems Data Access and Support Center (DASC; http://www.kansasgis.org/) as shapefiles. Locations of roads in Oklahoma and Colorado were gathered per county from the USDA geospatial data gateway (https://gdg.sc.egov.usda.gov/) and based on Topologically Integrated Geographic Encoding and Referencing (TIGER) 2010 census data. To account for potential differences in behavioral avoidance of more heavily and lighter travelled roads, we placed roads into two categories; major roads and county roads. Major roads included all federal and state highways receiving heavy use and were largely paved while county roads included the smaller secondary roads, which were almost entirely gravel surfaced.

Transmission line data in Colorado were obtained from a shapefile displaying all transmission lines in the western USA available on arcgis.com (Hanser 2011). Locations of transmission lines in Oklahoma were identified from data used in the Oklahoma lesser prairie-chicken spatial planning tool (Horton et al. 2010). Due to presumed security threats, electric distribution line data were not publicly available and was only obtained for Kansas from the Kansas Corporation Commission. Cell phone tower locations for all study areas were downloaded from arcgis.com and derived from data provided by the Federal Communications Commission (FCC). All linear feature densities were estimated by summing the number of pixels where a linear feature (e.g., road or transmission line) was present using focal statistics in ArcGIS 10.2 then converted back to kilometers to estimate the linear km of features within each landscape (e.g., 4.5 km/12.6 km^2). All vertical point features included cell towers, large buildings, wind turbines, and oil wells, but did not include transmission or distribution lines.

Spatially Explicit Tree Canopy Cover and Tree Density Estimation

A percent cover of conifer and mesquite (*Prosopis* spp.) raster layer (30-m resolution) was available through the Kansas Biological Survey (http://kars.ku.edu/). In this layer, spatial wavelet analysis was used to identify conifer tree canopy cover and model estimates were correlated (r = 0.98) and had a root mean square error of 4% in comparison with field measured canopy cover (Falkowski et al. 2017). To calibrate this layer to tree density (trees/ha), we first adjusted the scale of canopy cover estimates to match the 16-ha scale of Lautenbach et al. (2017), lesser prairie-chickens did not nest in 16-ha areas having >2 trees/ha. To adjust the scale, we used focal point statistics (e.g., moving window analysis) to estimate average canopy coverage at the 16-ha scale from the Falkowski et al. (2017) layer. We then used raster calculator in ArcGIS 10.2 to convert canopy cover to tree density using the function provided in Lautenbach et al. (2017; percent canopy coverage = 0.786 + 0.389*trees/ha). Finally, we created a binary raster that identified pixels occurring in areas having tree densities >2 trees/ha at the 16-ha scale. Lautenbach et al. (2017) identified this density as a threshold separating nesting habitat from non-habitat for lesser prairie-chickens.

ADDITIONAL DISCUSSION

Comparison to a Climate-based Prediction of Distribution

Our predicted distribution complements a previous climate-based species distribution model (Dunn and Milne 2014). Within the domain of optimal climate for lesser prairie-chickens predicted by Dunn and Milne (2014), limited grassland composition at the 5-km scale and high anthropogenic features densities at the 2-km scale may preclude lesser prairie-chicken occupancy. Suggesting that areas that are of optimal climatic condition are not available for use by lesser prairie-chickens due to limited grassland availability and anthropogenic development.

Surprisingly, a high proportion of the region predicted to be optimal based on climate predictors in the Dunn and Milne (2014) model were in areas of limited grassland composition or high densities of anthropogenic features and were not optimal based on our predictions. Our results suggest that lesser prairie-chickens are confined to climatic regions of lower habitat quality.

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Table S1. Environmental conditions at 6 study sites used in the Random Forests species distribution model using location data from GPS transmittered lesser prairie-chickens monitored from 2013–2016 in Kansas and Colorado. The units for linear features (roads and transmission lines) are displayed as kilometers within a 2-km radius while the vertical point features (e.g., cell towers, large buildings, wind turbines, and oil wells) are represented by independent features.

	Study Area					
Site Characteristics	**Red Hills/Clark**	**Northwest**	**Prowers/Baca**	**Cheyenne**	**Comanche NG**	**Cimarron NG[6]**
***Latitude*[1]**	37.4534	38.7076	37.6357	38.6989	37.0615	37.1591
***Longitude*[1]**	-99.244	-100.568	-102.106	-103.001	-102.485	-101.803
***N*[2]**	4,228	3,312	1,263	488	16	588
Annual Precipitation	63.1	51.7	43.2	38.0	42.2	44.3
Soils	variable, fine sand to Clay	silt loam, clay loam, fine sandy loam	loam	sand, sandy loam	sand, loamy fine sand, sandy loam	sand, loamy fine sand, sandy loam
Dominant Plants[3]	little bluestem sand dropseed Louisiana sagewort western ragweed sideoats grama	sideoats grama blue grama sand dropseed western wheatgrass little bluestem	sideoats grama blue grama little bluestem Field bindweed	blue grama sand dropseed sand sagebrush Russian thistle	blue grama sand dropseed sand sagebrush annual buckwheat	sand dropseed blue grama plains yucca sand sagebrush
Anthropogenic features and rankings[4]	4	5	2	1	3	6
County roads (km)	3.72 ± 2.78	4.28 ± 2.39	5.99 ± 2.6	3.87 ± 3.53	7.05 ± 3.75	4.74 ± 2.51
Major roads (km)	0.36 ± 0.76	0.28 ± 0.66	0.27 ± 0.63	0.32 ± 0.71	0.22 ± 0.58	0.37 ± 0.76
Oil wells	3.34 ± 4.71	3.19 ± 5.42	0.07 ± 0.46	0.23 ± 1.33	0.29 ± 1.28	7.02 ± 7.14
Transmission lines (km)	0.3 ± 0.78	0.26 ± 0.69	0.002 ± 0.04	0.23 ± 0.6	0.46 ± 0.82	0.14 ± 0.48
Vertical point features	3.62 ± 5.03	3.41 ± 5.59	0.11 ± 0.49	0.25 ± 1.34	0.29 ± 1.28	7.16 ± 7.20
Grassland Composition[5]	0.67 ± 0.23	0.40 ± 0.21	0.47 ± 0.21	0.79 ± 0.18	0.84 ± 0.16	0.49 ± 0.20

[1]Latitude and longitude are from the centroid of the study site.
[2] N is the number of bird locations subsampled for each site
[3] dominant plants were determined from point-step transects (see diet chapter) and from Cable et al. (1996)
[4]Anthropogenic feature densities were estimated within a 2km radius for each 30x30m pixel then averaged. Rankings are based on the sum of anthropogenic densities at each site with 1 having lowest and 6 having the greatest anthropogenic feature densities.
[5]Grassland composition was estimated within a 5 km radius for each 30x30m pixel within each study site

[6]Soil and dominant plants for the Cimarron national grasslands were identified from Birds of Cimarron National Grassland (Cable et al. 1996)

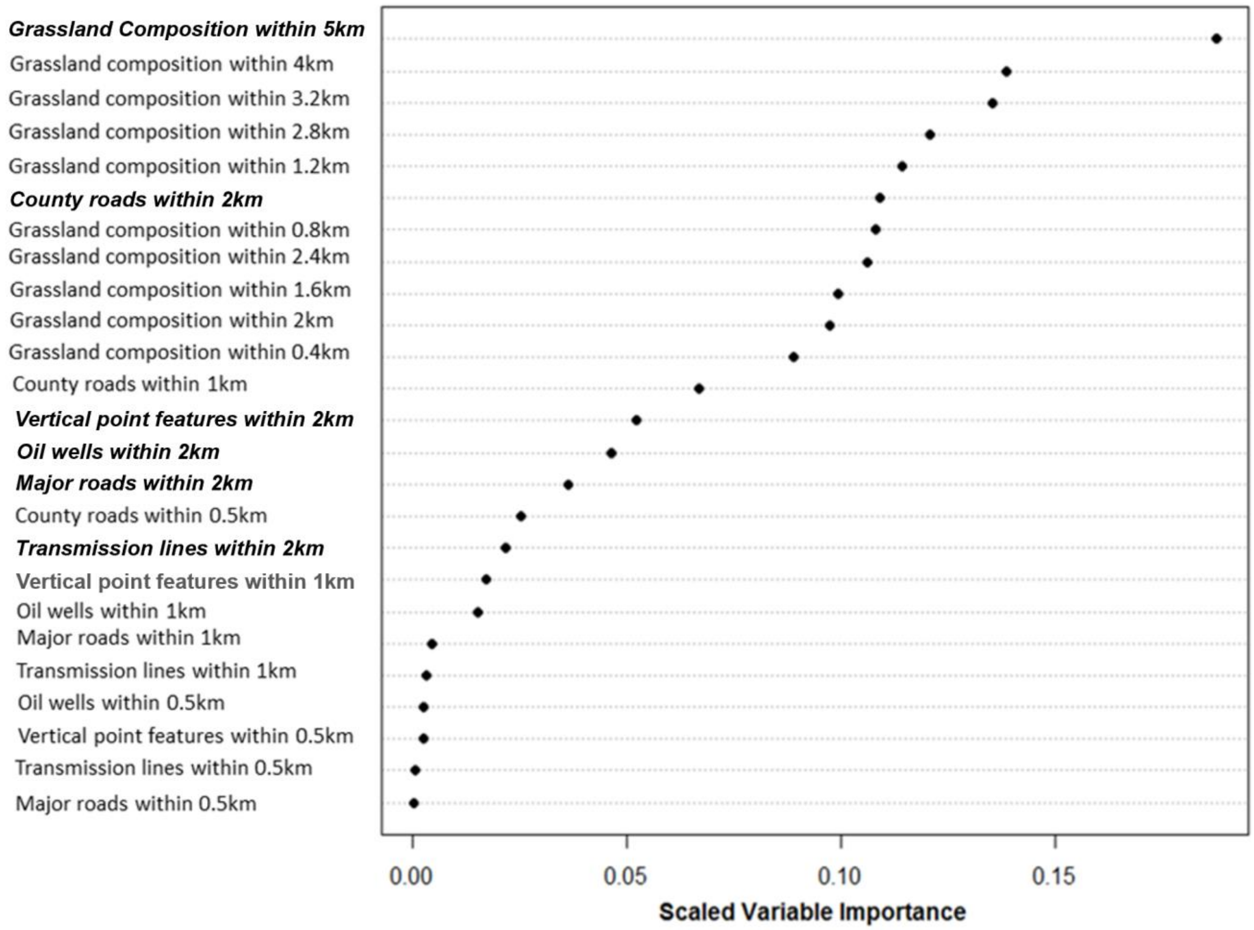

Figure S1. Model-scaled variable importance (Evans et al. 2011) used to identify scales for modeling grassland composition and anthropogenic features for lesser prairie-chickens in Kansas and Colorado. The scale exhibiting the greatest model variable importance for each variable (e.g., grassland composition, oil well density) was used in the final Random Forest model and are shown in bold and italicized. All variable names describe the variable and the radius within which the variable was estimated (e.g. grassland composition within a 5km radius). Vertical point features included all tall features including cell towers, large buildings, wind turbines, and oil wells.

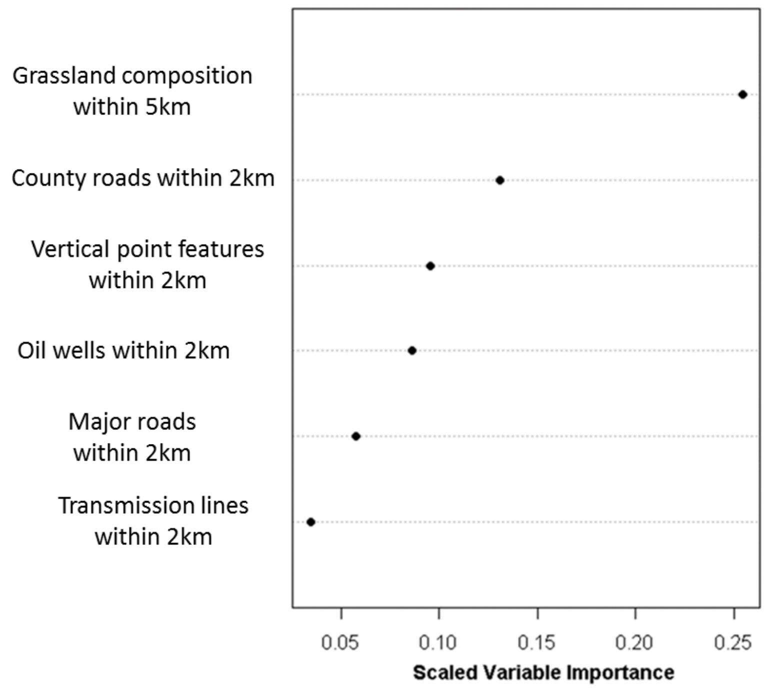

Figure S2. Model scaled variable importance (Evans et al. 2011) among variables used in the final species distribution model. The scale exhibiting the greatest model variable importance for each variable (e.g., grassland composition within 5 km, oil well density within 2 km) was used in the final Random Forest model based on the output in Figure 2. All variable names describe the variable and the radius within which the variable was estimated (e.g., grassland composition within a 5-km radius). Vertical point features included all tall features including cell towers, large buildings, wind turbines, and oil wells.