

## Strategic conservation for lesser prairie-chickens among landscapes of varying anthropogenic influence

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### ARTICLE INFO

#### Keywords:

Conservation reserve program  
Grassland  
Prairie grouse  
Random Forest  
Species distribution  
Working lands

### ABSTRACT

For millennia grasslands have provided a myriad of ecosystem services and have been coupled with human resource use. The loss of 46% of grasslands worldwide necessitates the need for conservation that is spatially, temporally, and socioeconomically strategic. In the Southern Great Plains of the United States, conversion of native grasslands to cropland, woody encroachment, and establishment of vertical anthropogenic features have made large intact grasslands rare for lesser prairie-chickens (*Tympanuchus pallidicinctus*). However, it remains unclear how the spatial distribution of grasslands and anthropogenic features constrain populations and influence conservation. 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. Our model suggested decreased probability of use in 2-km radius (12.6 km<sup>2</sup>) landscapes that had greater than two vertical features, two oil wells, 8 km of county roads, and 0.15 km of major roads or transmission lines. Predicted probability of use was greatest in 5-km radius landscapes that were 77% grassland. Based on our model predictions, ~10% of the current expected lesser prairie-chicken distribution was available as habitat. We used our estimated species distribution to 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 4189 km<sup>2</sup> of additional habitat and strategic application of tree removal has the potential to restore 1154 km<sup>2</sup>. Tree removal and CRP enrollment are conservation tools that can align with landowner goals and are much more likely to be effective on privately owned working lands.

### 1. Introduction

Conservation on working lands may require not only efforts to protect remaining tracts of high biodiversity but efforts to strategically apply management practices that simultaneously consider human well-

being and wildlife (Samson et al., 2004; Kareiva and Marvier, 2012). Since the start of the Progressive Era > 100 years ago, those that have strived to protect wildlife and wild areas have disagreed on whether to preserve by protecting and leaving areas alone, or by conserving wildlife friendly habitat through human imposed management (Fox,

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1981; Miller et al., 2011). More recently, this discussion has evolved to include ideas on land sparing versus land sharing and a “new conservation” that demonstrates human benefit to gain conservation success through public approval (Miller et al., 2011; Kareiva and Marvier, 2012; Kremen, 2015). Such considerations are relevant for prairie-grouse (*Tympanuchus* and *Centrocercus* spp.) management that occurs in areas that are either privately owned or leased for agricultural production (Ciuzio et al., 2013). To improve landowner participation, slogans such as “what’s good for the bird, is good for the herd” have been developed to disseminate wildlife-friendly land management practices to more widespread audiences (Wiklund, 2015). Outside of efforts to preserve large remaining tracts of grassland, the “new conservation” approach may be the best, and only, foreseeable option in the Great Plains of Kansas and Colorado, USA, where historical ecological drivers that once maintained habitat for numerous grassland dependent species have been greatly altered (Askins et al., 2007). Management that closely mimics site-specific historical ecological drivers is likely the best option to manage for biodiversity in grasslands; however, due to the extent of alterations and global change, more novel approaches to provide grassland on working lands may be beneficial. For example, free-ranging bison (*Bison bison*) have been replaced by cattle in fenced pastures, fire has largely been removed from the landscape, woody species are encroaching, the climate is changing, and increased food, fiber, and energy needs for growing human populations have greatly changed the Great Plains since pre-European settlement (Samson et al., 2004; Haukos and Boal, 2016).

It is estimated that grasslands have decreased 46% worldwide and only 4.5% of grasslands are protected (Hoekstra et al., 2005). In the Great Plains of North America, grasslands have decreased by an estimated 70% (Samson et al., 2004). This is especially problematic for grassland-dependent wildlife that need broad grassland availability to cope with weather driven variation in habitat availability (Wiens, 1974, Sala et al., 1998, Winter et al., 2005). Large grassland-dominated landscapes available for lesser prairie-chicken (*Tympanuchus pallidicinctus*) 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).

Knowledge of how grassland composition (i.e., proportion of grassland in a landscape) and anthropogenic feature densities constrain the distribution of lesser prairie-chickens at multiple scales and among years of variable climate are needed. It remains unclear what constrains the distribution of lesser prairie-chickens and how available habitat is distributed in Kansas and Colorado, which together 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 can be used to identify grassland strongholds to be protected and areas within those strongholds that can be spatially prioritized for conservation on working lands.

Two conservation actions that could increase habitat include tree removal in south-central Kansas and conversion of cropland to perennial grassland through the USDA Conservation Reserve Program (CRP) in northwest Kansas and eastern Colorado (Lautenbach et al., 2017; Sullins et al., 2018). For *Tympanuchus* spp., it is unlikely that a universal management practice will benefit populations similarly across their range, with a 40-cm annual precipitation gradient in our study area from Kansas to Colorado (McNew et al., 2013; PRISM, 2016). Therefore, we propose two distinct conservation practices that are spatially dependent, but potentially capable of large-scale application on working lands. Both conservation practices can be profitable for producers in the lesser prairie-chicken range of Kansas and Colorado where > 95% of the species-occupied range is privately owned (Becerra et al., 2016). 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 where they are most likely to reap benefits within large grassland areas having limited anthropogenic structures (Winder et al., 2015; Sullins et al., 2018; Plumb et al., 2019).

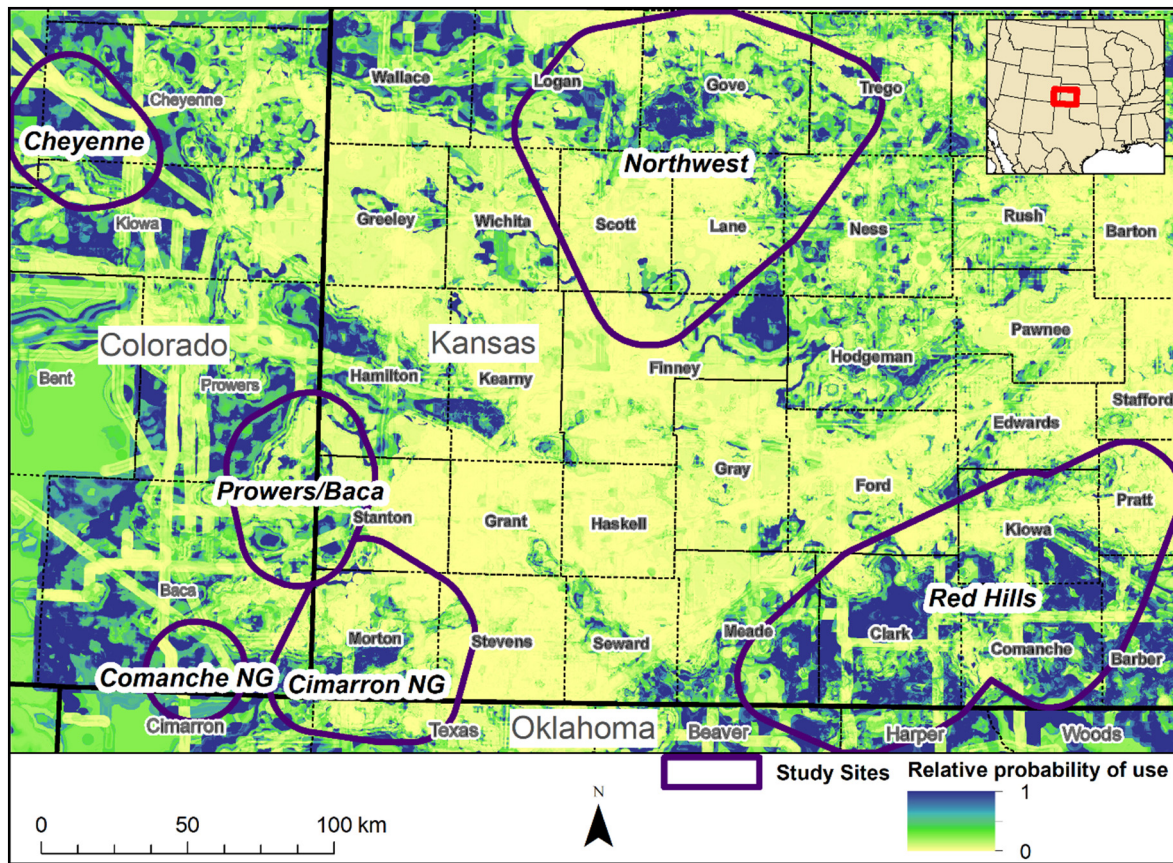
Merely protecting a grassland as a wildlife-friendly grassland is not possible due to the dependence of the grassland itself, and its quality for wildlife, on ecological drivers that have been greatly altered (Askins et al., 2007). Alterations to ecological drivers (processes) that once maintained quality grasslands in this area have led to declines and distribution shifts in several grassland bird species (Peterjohn and Sauer, 1999). For example, there is evidence that prairie-grouse (*Tympanuchus* spp.), grasshopper sparrows (*Ammodramus savannarum*), and Henslow’s sparrows (*A. henslowii*) exhibit declining trends in traditional portions of their range but have increased in areas where cropland has been converted to ungrazed grassland through the Conservation Reserve Program (CRP; Herkert, 1998, Johnsgard, 2001, Rodgers and Hoffman, 2005). The benefit of CRP for these species is a clear example, albeit by accident, of “new conservation” because the program incentivizes landowners to take land out of agricultural production. The financial benefit of CRP makes this a favorable tool for wildlife conservation.

Tree removal is another management practice that can benefit both cattle producer and prairie grouse by expanding grasslands that provide cover for prairie grouse and forage for cattle (Lautenbach et al., 2017; Severson et al., 2017). Deploying such management practices have promise of being well received and implemented by producers; however, because of various environmental and abiotic constraints, and our inability to preserve a pre-European settlement state at an appropriate scale, most conservation benefits are site dependent and therefore, must be spatially targeted (Samson et al., 2004; Ciuzio et al., 2013).

We provide an example of strategic conservation to target management practices on privately owned land that may benefit both producer and lesser prairie-chickens alike. 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 enrollment of cropland into the CRP would have the greatest benefit to lesser prairie-chicken populations (Lautenbach et al., 2017; Sullins et al., 2018).

## 2. Study area

Our study area encompassed the northern portion of the extant lesser prairie-chicken distribution including portions of the Short-Grass Prairie/CRP mosaic (SGP), Mixed-Grass Prairie (MGP), and Sand Sagebrush Prairie Ecoregions (SSP; Fig. 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 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,



**Fig. 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. \(2016; A\)](#). 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 (B). 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. \(2014\)](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Cimarron NG; [Fig. 1](#), Table S1, see supplemental material for further description of each 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](#)).

### 3. Methods

#### 3.1. Capture and marking

We captured lesser prairie-chickens at all study sites on leks during spring (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](#)) or a 15-g very-high-frequency transmitter attached as a necklace with whip antennae down the middle of the back (VHF; A3960, Advanced Telemetry System, Isanti, MN, USA). We alternated attachment of GPS and VHF transmitters on every other bird captured. The GPS transmitters had a spatial error of  $\pm 18$  m, which was less than the  $30\text{-m} \times 30\text{-m}$  ( $900\text{ m}^2$ ) resolution pixels used in our analyses. We limited VHF location data to those with error polygons  $< 1000\text{ m}^2$  ([Robinson et al., 2018](#)). Locations were recorded every

2 h during the day for GPS transmitters, with a 6-hour and 8-hour nocturnal gap during summer and winter, respectively. 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 using Location of a Signal software to estimate error polygons (Ecological Software Solutions LLC, Hegymagas, Hungary).

#### 3.2. Landcover covariates

We obtained landcover type classifications at a  $30\text{-m} \times 30\text{-m}$  resolution from the 2011 National Landcover database (NLCD) and a shapefile identifying the distribution of Conservation Reserve Program (CRP) grasslands in 2014 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  $0.4\text{ km}–5\text{ km}$  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  $\leq 5\text{ km}$  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, 1994, Ross et al., 2016a). We used the 0.4-km radius as a minimum scale because it is less than estimates for habitat requirements in Haukos and Zaveleta (2016).

### 3.3. 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).

### 3.4. Species distribution modeling and validation

**Predicted species distribution.**— 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. 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 marked lesser prairie-chickens (Earl et al., 2016). Average net displacement distance provides an estimate of dispersal distance that is not based on circular movement but linear distance away from initial capture location, which we used to infer areas available to the lesser prairie-chickens at the population level (Earl et al., 2016). We randomly generated one pseudo absence location for each location used by lesser prairie-chickens throughout the estimated available area and to account for the lack of true absence data; the response variable was relative probability of use (Barbet-Massin et al., 2012).

Lesser prairie-chicken occurrence was predicted using a Random Forest method (package ‘randomForest’; Liaw and Wiener, 2002, 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 (MIR) based on predictions from a global model of all variables at all scales that also included distance to anthropogenic feature (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 receiver operating characteristic curve to evaluate the predictive power of the model (AUC; DeLong et al., 1988).

### 3.5. 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 tree densities > 2 per ha were most likely to be restored as habitat through tree removal based on a habitat relationship in Lautenbach et al. (2017). Last, we identified predicted habitat areas affected by low (1–5%), medium (6–15%), and high (> 15%) canopy coverage identified in Falkowski et al. (2017).

### 3.6. 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 > 30% 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 > 30% grassland, areas receiving < 56 cm of annual average precipitation, and areas that were 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). Priority areas for conservation included CRP grasslands that provided habitat for lesser prairie-chickens based on our model. Priority areas for enrollment were areas that were cropland but if enrolled as CRP would likely provide habitat.

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 for descriptive purposes.

## 4. Results

We randomly selected a subset of 9895 locations from 170 lesser prairie-chickens marked with GPS satellite transmitters monitored from 2013 to 2016 to build our species distribution model. We sampled two locations a week from an average of 29.16 (SD = 36.35; range = 2–136) weeks for each individual. The model included only locations from female lesser prairie-chickens 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 (Figs. 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 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. We used grassland composition within 5 km and anthropogenic features within 2 km 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

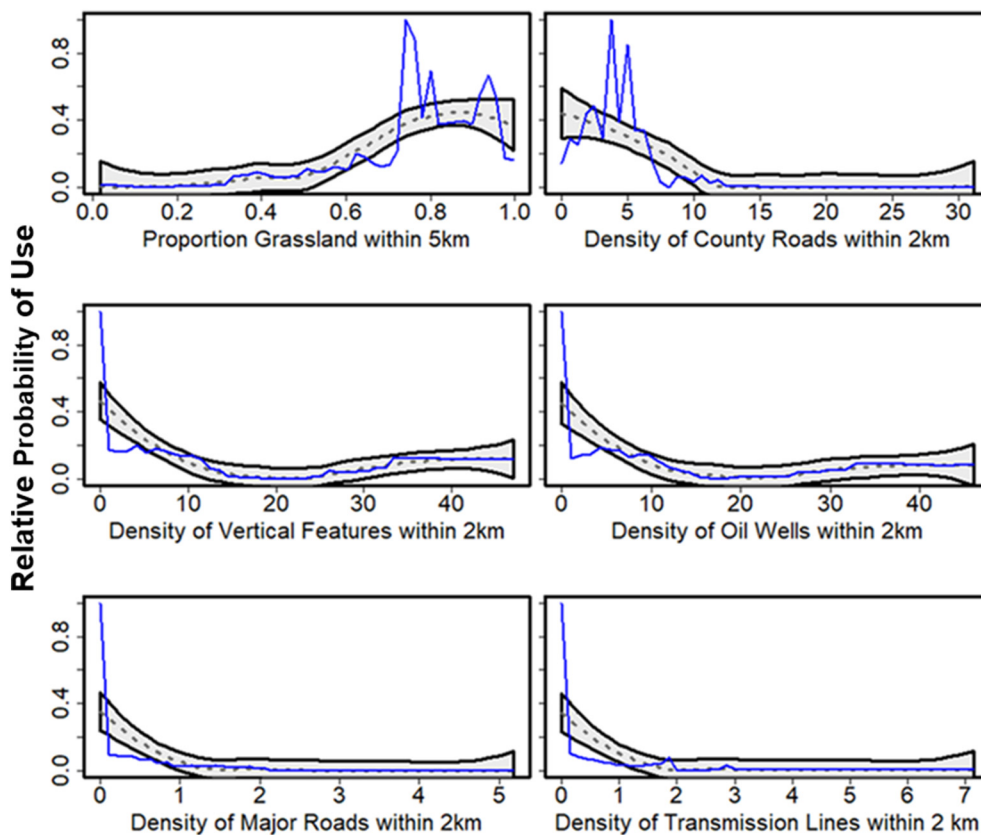


Fig. 2. Partial dependence plots for all grassland composition and anthropogenic feature densities used to predict the distribution of lesser prairie-chickens in Kansas and Colorado, USA, as depicted in Fig. 1 based on data from 2013 to 2016. A loess polynomial regression is plotted in as a dashed grey line with 95% prediction intervals highlighted in grey and the raw relative probability of use distribution is plotted as a blue line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Mean and standard deviation of grassland composition as a proportion of a 5-km radius scale and anthropogenic feature densities (2-km radius scale) estimated at lesser prairie-chicken locations ( $n = 9895$ ) from 2013 to 2016, and random locations ( $n = 9895$ ) distributed within dispersal range of Kansas and Colorado, USA, 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 ( $12.6 \text{ km}^2$ ) 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.

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

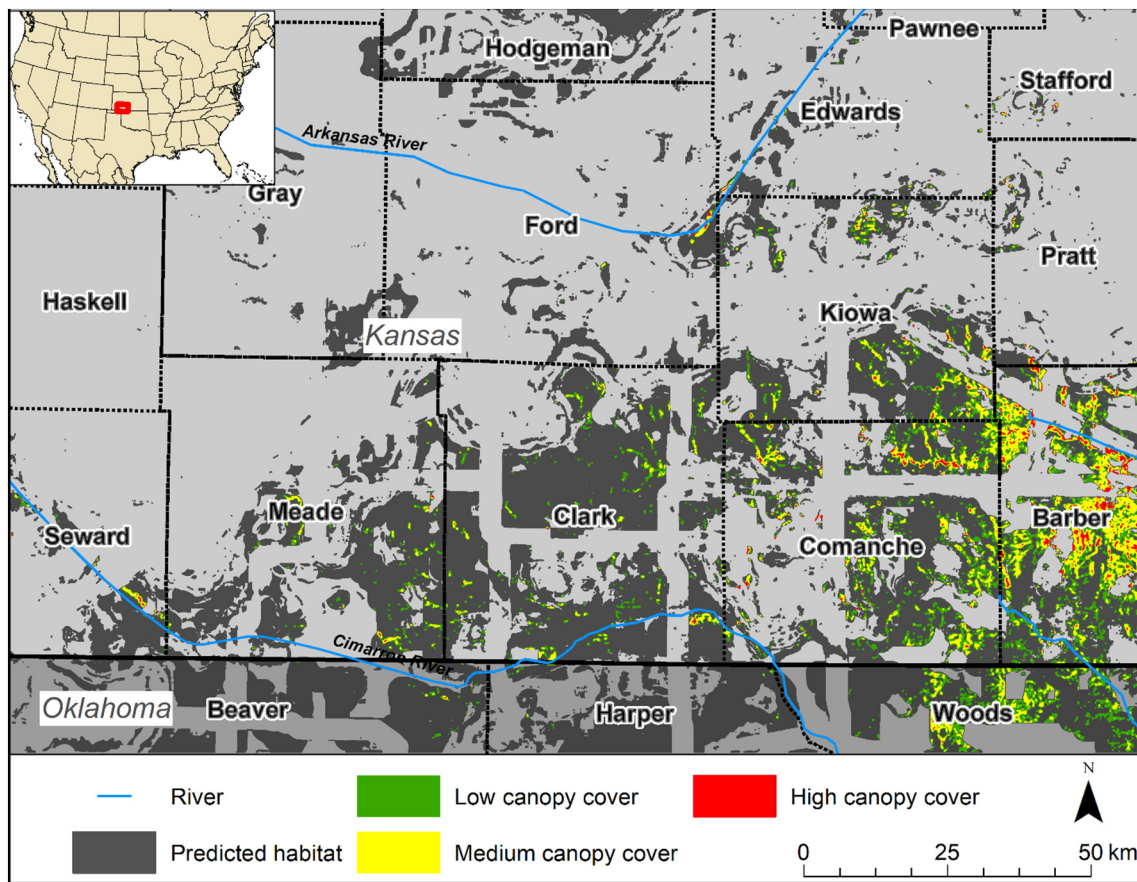
probability of use occurred at ~77% grassland composition; similar to the 76% mean of used locations (Fig. 2, Table 1). Having lower model importance than grassland composition were densities of county roads, vertical point features, transmission lines, and major roads in decreasing order of model importance (Fig. S2). Overall, the relative probability of use decreased as cumulative densities of anthropogenic features increased (Fig. 2). However, the raw predicted probability of use increased from 0 to 5 km per  $12.6 \text{ km}^2$  of county roads then declined sharply as densities increased beyond 5 km per  $12.6 \text{ km}^2$  and was close to zero at densities  $> 10 \text{ km}$  per  $12.6 \text{ km}^2$  (Fig. 2). When county road densities surpassed a threshold of 8–10 km per  $12.6 \text{ km}^2$  area, it

indicated an urban environment based on visual observations.

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

**Predicted species distribution.**— The predicted relative probability of use output from the Random Forest model predicted a greater area of lesser prairie-chicken habitat in the MGP than in the SGP or SSP Ecoregions (Fig. 1; 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 in Kansas and Colorado as delineated in McDonald et al. (2014) was 16% (3099/ $14,790 \text{ km}^2$ ) in the MGP Ecoregion, 9% (2613/ $27,899 \text{ km}^2$ ) in the SSP Ecoregion, and 8% (3671/ $43,641 \text{ km}^2$ ) 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



**Fig. 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, USA, based on grassland composition within 5 km and anthropogenic feature densities (A). Areas having a high priority for tree removal were the top 66% of predicted values from the Random Forests model and where tree densities were > 2 trees/ha (Falkowski et al., 2017, Lautenbach et al., 2017, B).

Kansas and northern Oklahoma, habitat was more uniformly distributed (Fig. 1).

**Validation.**— We used subsampled VHF locations (2 locations per week from 113 individuals) to validate our predictions ( $n = 4043$ ). 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 area under the receiver operating characteristics was 0.91 suggesting a fairly strong dichotomy between predicted habitat and nonhabitat (DeLong et al., 1988).

#### 4.1. Spatial prioritization of tree removal

Based on our identification of areas with limited anthropogenic influence and adequate grassland availability, we estimated that 1154 km<sup>2</sup> 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 (Fig. 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.

#### 4.2. Spatial prioritization of CRP enrollment

Our model suggests that 1570 km<sup>2</sup> of current CRP provides habitat for lesser prairie-chickens and should remain CRP if lesser prairie-chickens are a priority (Fig. 4). There were 4189 km<sup>2</sup> 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 < 56 cm of precipitation. Predicted effects of anthropogenic features resulted in a 7211 km<sup>2</sup> decrease in priority cropland for enrollment and 4312 km<sup>2</sup> 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.

## 5. Discussion

We provide empirical evidence that can be used to preserve remaining grassland strongholds of low anthropogenic feature densities as well as spatially target management practices that are likely to acquire voluntary participation on working lands. 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 9383 km<sup>2</sup> of available habitat (> 0.60 relative probability of use) for

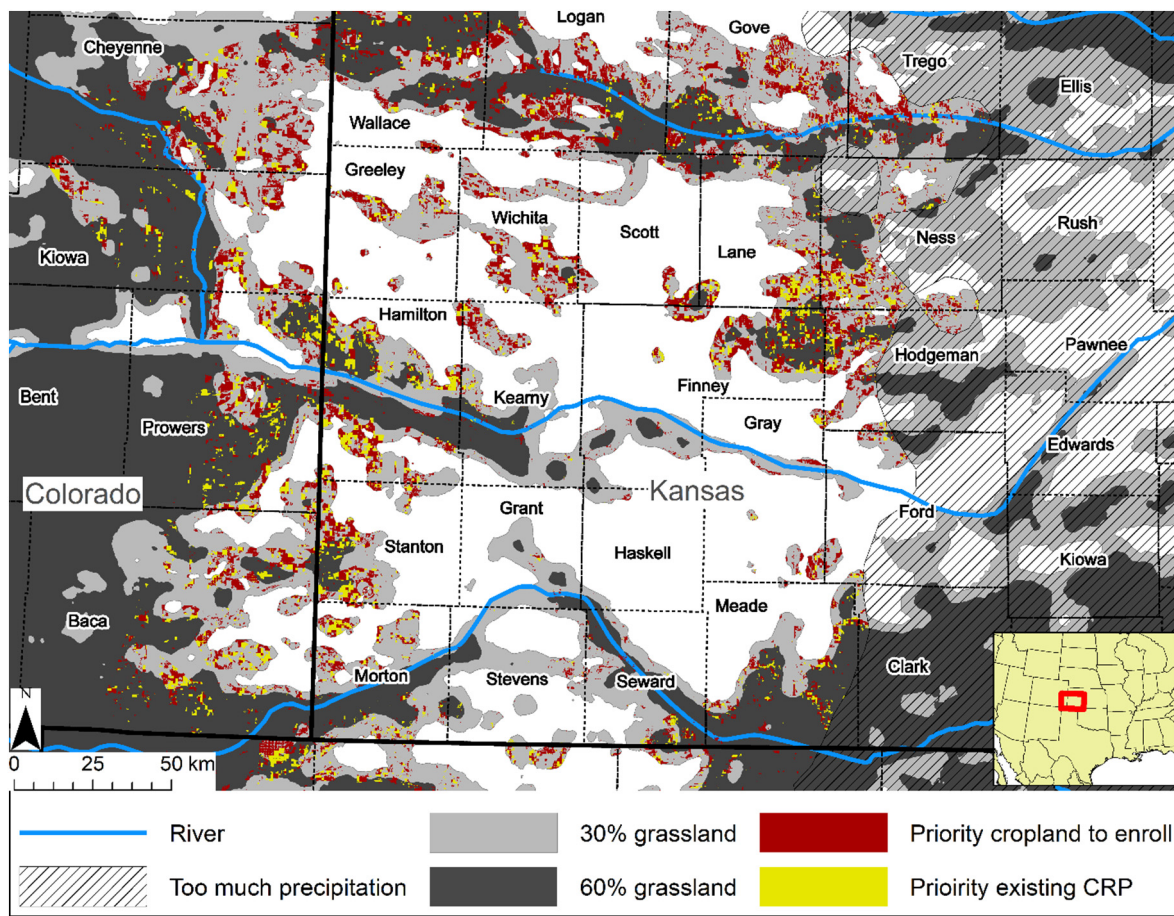


Fig. 4. Predicted priority areas where current CRP grasslands (yellow) and cropland that could be enrolled in CRP (red) were most likely to be used by lesser prairie-chickens in Kansas and Colorado, USA (A). Priority areas occur in locations having  $> 30\%$  native working grassland (light grey) within 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  $> 60\%$  native working grassland (dark grey) within 4 km (B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lesser prairie-chickens in the study area. There is potential to increase available habitat by 1154 and 4189 km<sup>2</sup> (57%) through strategic removal of trees and conversion of cropland to CRP grasslands. Area of predicted habitat was greatest in the SGP ecoregion, followed by the MGP and SSP ecoregions. However, the model likely overestimated the amount of available habitat in the far western extent of the distribution where short-grass prairie is largely contributing to the grassland composition of the model and may not provide habitat due to insufficient vegetation structure (Giesen, 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 5-km radius (78.5 km<sup>2</sup>) and with minimal anthropogenic features (e.g.,  $< 10$  vertical features in 12.6 km<sup>2</sup>).

In the working landscapes of the Southern Great Plains, the need for strategic conservation is critical (Samson et al., 2004). Future expected increases in global food and energy needs may take a further toll on biodiversity in this region. There has been much discussion on whether approaches that would “spare” land parcels and allow for intensification of production elsewhere or whether landscapes should be “shared” to provide large areas that are marginal for both agriculture and biodiversity (Kremen, 2015). We did not explicitly test these ideas but the optimization of lesser prairie-chicken habitat at 77% grassland, the purported population increase following low intensity agriculture at the

turn of the century, and the underlying spatial variability in farming suitability suggest that a combination of “sparing” and “sharing” strategies may be best (Kremen, 2015; Rodgers, 2016). Diet analyses have also demonstrated the use of some crops and crop pests as foods (Sullins et al., 2018). Our results and past literature highlight the utility of large grassland areas adjacent to low intensity row crop agriculture for lesser prairie-chickens. Our model does not account for the influence of dispersal on population persistence. Successful conservation will likely need to consider how the cropland matrix, adjacent to, and within grassland dominated landscapes facilitates successful dispersal. Having a matrix that facilitates movement by grassland dependent wildlife from one optimal habitat patch to another is likely important (Simberloff, 1994; Kremen and Merenlender, 2018).

Grassland abundance in a landscape likely 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 availability of lekking, nesting, brooding, and nonbreeding habitats that are properly abundant and configured to allow the establishment of home ranges and populations 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 vegetation structure 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., 2016a; 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., 2016a). Our estimate of optimal grassland area (77% of 78.5 km<sup>2</sup> landscape) lies between the 49 km<sup>2</sup> and 202 km<sup>2</sup> 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 established CRP grasslands and prescribed grazing influence 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  $\geq 60.5$  km<sup>2</sup> of grassland within a 78.5 km<sup>2</sup> area would be optimal – assuming the grasslands are managed properly.

### 5.1. 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 is 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 act as overall constraints.

The lack of avoidance of county roads suggests that they do not affect lesser prairie-chicken occurrence at low densities (< 15 km per 12.6 km<sup>2</sup>). 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 higher 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).

Although our reported avoidance density thresholds are specific for lesser prairie-chickens, there are other grassland birds that avoid anthropogenic structures and exhibit area sensitivity (Ribic et al., 2009; Ludlow et al., 2015; Londe et al., 2019). The area sensitivity of several grassland songbirds likely make them more susceptible to the fragmentation effects of anthropogenic structures and infrastructure (Ribic et al., 2009). Some grassland birds may not be negatively affected by anthropogenic structures and more species-level information is needed (Ludlow et al., 2015). However, our model predictions identify areas where anthropogenic feature densities are minimal and due to the lesser prairie-chicken's strong sensitivity to anthropogenic features may provide an estimate based on a worst case scenario for many grassland birds.

### 5.2. Spatial prioritization of tree removal

To increase the amount of potential habitat for lesser prairie-chickens, we identified strategic areas where tree removal, primarily 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. Based on cost estimates in Lautenbach et al. (2017), it would cost US\$32.6 million to remove trees in priority areas in Kansas and Colorado (more details in supplemental material). Tree removal in predicted priority areas would likely benefit cattle producers by increasing available forage and therefore may be more likely to be implemented (Ciuzio et al., 2013; Severson et al., 2017).

### 5.3. Spatial prioritization of CRP enrollment

The underlying ability of CRP to benefit both producer and grassland dependent wildlife is likely the reason for its conservation importance in areas > 95% privately owned (Johnson, 2005; Sullins et al., 2018). To build on the underlying conservation importance of CRP on working lands, current continuous CRP sign-up programs were developed that pay more per acre than traditional CRP sign-up (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). Based on our model estimates of 1570 km<sup>2</sup> of current CRP 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; more details in supplemental material). Financial support may be necessary to maintain conservation gains achieved through CRP, as voluntary participation can decline when financial incentives are removed (Mascia and Mills, 2018). Efforts to connect CRP, or other forms of grassland restoration, with existing community actions and social movements may be other options for increasing participation on private lands (Kremen and Merenlender, 2018).

## 6. Conclusion

For grassland birds in the Great Plains, conservation on working lands is the only feasible option to provide habitat at a relevantly broad scale. Implementation of conservation practices that simultaneously create wildlife habitat and improve human well-being will be the most likely to positively affect wildlife populations (Samson et al., 2004; Kareiva and Marvier, 2012). Broad scale (78.5 km<sup>2</sup>) 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 due to their likelihood of achieving voluntary participation (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, lesser prairie-chickens use of habitat at a landscape scale make tree removal and CRP enrollment not directly comparable. Efforts to preserve remaining habitat matched with strategic management efforts that take into account human well-being have the greatest potential to conserve lesser prairie-chickens and other grassland-dependent wildlife on working lands.



## Acknowledgement

We thank Kent Fricke, three anonymous reviewers, and the associate editor for providing reviews that improved the quality of the manuscript. We thank K. Schultz and A. Chappell for capturing and providing GPS data from lesser prairie-chickens captured on the Cimarron National Grasslands. B. Anderson, S. Baker, S. Bard, G. Brinkman, K. Broadfoot, R. Cooper, J. Danner, J. Decker, E. D. Entsminger, R. M. Galvin, N. Gilbert, A. Godar, G. Gould, B. Hardy, S.P. Hoffman, D. Holt, B. M. Irle, T. Karish, A. Klais, H. Kruckman, K. Kuechle, S. J. Lane, E. A. Leipold, J. Letlebo, E. Mangelinckx, L. McCall, A. Nichter, K. Phillips, J. K. Proescholdt, J. Rabon, T. Reed, A. Rhodes, B. E. Ross, D. Spencer, A. M. Steed, A. E. Swicegood, P. Waldron, B. A. Walter, I. Waters, W. J. White, E. Wiens, J. B. Yantachka, and A. Zarazua, provided much needed assistance with data collection. We greatly appreciate the logistic and technical support provided by J. C. Pitman, J. Kramer, M. Mitchener, D. K. Dahlgren, J. A. Prendergast, C. Berens, G. Kramos, and A. A. Flanders. Funding for the project was provided by Kansas Wildlife, Parks, and Tourism (Federal Assistance Grant KS W-73-R-3); United States Department of Agriculture (USDA) Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62); and USDA Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.108213>.

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