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Research Paper

Assessing range-wide habitat suitability for the Lesser Prairie-Chicken

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ABSTRACT. Population declines of many wildlife species have been linked to habitat loss incurred through land-use change. Incorporation of conservation planning into development planning may mitigate these impacts. The threatened Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) is experiencing loss of native habitat and high levels of energy development across its multijurisdictional range. Our goal was to explore relationships of the species occurrence with landscape characteristics and anthropogenic effects influencing its distribution through evaluation of habitat suitability associated with one particular habitat usage, lekking. Lekking has been relatively well-surveyed, though not consistently, in all jurisdictions. All five states in which Lesser Prairie-Chickens occur cooperated in development of a Maxent habitat suitability model. We created two models, one with state as a factor and one without state. When state was included it was the most important predictor, followed by percent of land cover consisting of known or suspected used vegetation classes within a 5000 m area around a lek. Without state, land cover was the most important predictor of relative habitat suitability for leks. Among the anthropogenic predictors, landscape condition, a measure of human impact integrated across several factors, was most important, ranking third in importance without state. These results quantify the relative suitability of the landscape within the current occupied range of Lesser Prairie-Chickens. These models, combined with other landscape information, form the basis of a habitat assessment tool that can be used to guide siting of development projects and targeting of areas for conservation.

Évaluation de la qualité d'habitat dans l'ensemble de l'aire du Tétras pâle

RÉSUMÉ. Les baisses de population de nombreuses espèces fauniques ont été associées à la perte d'habitat consécutive aux changements d'utilisation des terres. L'incorporation de la planification de la conservation dans la planification du développement pourrait modérer ces impacts. Le Tétras pâle (*Tympanuchus pallidicinctus*) est une espèce menacée qui fait face à la perte d'habitat naturel et à des niveaux élevés de développement énergétique dans l'ensemble de son aire multi autorités. L'objectif de notre étude était d'explorer les relations existantes entre les occurrences de l'espèce et les caractéristiques du paysage ainsi que les effets anthropiques qui influencent sa répartition, au moyen de l'évaluation de la qualité de l'habitat utilisé pour la parade (aire de lek), un habitat à usage particulier. Les aires de lek ont été relativement bien inventoriées, bien que de façon non constante, par toutes les autorités concernées. Les cinq États dans lesquels se trouve le Tétras pâle ont tous coopéré dans l'élaboration d'un modèle de qualité de l'habitat Maxent. Nous avons créé deux modèles : l'un comprenant l'État comme variable explicative et l'autre ne la comprenant pas. Lorsque l'État était inclus dans le modèle, il se révélait la variable explicative la plus importante, suivi par le pourcentage de couverture du sol correspondant aux classes de végétation connues ou pressenties dans un rayon de 5000 m autour d'une aire de lek. Sans l'inclusion de l'État dans le modèle, la couverture du sol se révélait la variable explicative la plus importante de la qualité des leks. Parmi les variables anthropiques explicatives, la condition du paysage - une mesure de l'impact humain calculée à partir de plusieurs facteurs - était la plus importante et se classait au troisième rang en l'absence de l'État. Ces résultats quantifient la qualité relative du paysage de l'aire occupée actuellement par le Tétras pâle. Les présents modèles, combinés à d'autres informations sur le paysage, forment la base d'un outil d'évaluation de l'habitat pouvant être utilisé afin d'orienter l'emplacement des projets de développement et la conservation de milieux.

Key Words: *conservation planning; energy development; habitat suitability; land cover; Maxent; prairie grouse; species distribution modeling; Tympanuchus pallidicinctus*

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INTRODUCTION

Land-use change resulting in habitat loss is one of the primary factors affecting population declines of many wildlife species (Morrison et al. 2007). Minimization of the effects of land development and land-use change on species' conservation may be possible if conservation planning can be included in development decisions. However, this is only possible if data to inform conservation needs are available at the time decisions are being made. Models of species distribution and habitat suitability can be created using fewer than 25 locations to successfully guide future field surveys (Pearson et al. 2007) and can inform conservation decisions related to land-use conversion (Marini et al. 2009, Thorn et al. 2009).

In general, logistical constraints and sparse, clustered, or observational (rather than probabilistically sampled) data often limit statistical analyses that can be conducted and the interpretive value of results for rapid conservation management decisions. Thus, decisions are often based on models made with readily available data, ranging from presence-only to binary models (presence-absence) to count-based models (abundance). Models based on nonrandom data may be misleading because of sampling biases, such as nonrandom road surveys (Elith et al. 2011). Nonrandom presence-only data are often all that are available, especially for rare species, and when implemented carefully can lead to useful models as indicated in the application mentioned above. Maxent, a machine learning method that uses the principal of maximum entropy to identify relationships between available environment and observed locations (Phillips et al. 2006, Phillips and Dudik 2008), is part of a suite of techniques known as species distribution modeling, and identifies relationships between observations of species and the available environment to predict habitat suitability at unknown locations (Guisan and Thuiller 2005, Franklin 2010).

The Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) is a prairie grouse species distributed on the Great Plains of the United States, including the states of Colorado, Kansas, New Mexico, Oklahoma, and Texas. Lesser Prairie-Chickens have experienced an estimated 90% reduction in range since the 1800s (Taylor and Guthery 1980, Hagen et al. 2004) and evidence suggests population changes vary greatly across the region (Holt 2012, McDonald et al. 2014, Garton et al. 2016). As a result, the Lesser Prairie-Chicken was petitioned for protection under the Endangered Species Act in 1995, and the species was listed as threatened across its range in May 2014 (U.S. Fish and Wildlife Service 2014). Biologists cite the loss of native prairie as the main cause of decline for Lesser Prairie-Chickens. Among other things, losses can occur from grazing practices resulting in reduced vegetation structure and woody vegetation encroachment, which fragment and deteriorate habitat (Hagen and Giesen 2005).

In addition to loss of native habitat, an emerging and potentially critical threat is energy development within the current distribution of the Lesser Prairie-Chicken (Pruett et al. 2009, Hagen et al. 2011, Jarnevich and Laubhan 2011). The North American Great Plains is currently undergoing rapid land-use change as a result of increasing energy development throughout the region (Allred et al. 2015, American Wind Energy Association 2015). This development has the potential to impact the habitat of species in the region, and cause declines or hasten declines of species' populations. Several recent studies have documented avoidance of anthropogenic structures and human disturbance by prairie grouse species (*Centrocercus* and *Tympanuchus* spp.; Holloran 2005, Pitman et al. 2005, Walker et al. 2007, Pruett et al. 2009, Grisham et al. 2014). The number of Greater Sage-Grouse (*C. urophasianus*) males displaying at leks decreased with increasing natural gas field-related disturbances around leks (Holloran 2005, Walker et al. 2007). Additionally, male attendance at leks and the number of active Sage-Grouse leks declined at a faster rate within natural gas fields compared with areas outside natural gas fields (Holloran 2005, Walker et al. 2007). In Kansas and Texas, Lesser Prairie-Chicken nests were located further than expected from transmission lines, improved roads, and oil or gas wellheads even though otherwise-suitable habitat surrounded these features (Pitman et al. 2005, Grisham et al. 2014). Pruett et al. (2009) examined the avoidance behavior of Lesser and Greater Prairie-Chickens (*T. cupido*) to power lines and highways in Oklahoma and found birds avoided the power lines and few nests were found within 2 km of the power lines. Other studies in northcentral Kansas, at the center of the Greater Prairie-Chicken extant range, found that although nest site selection and survival were not negatively affected by proximity to wind turbines (McNew et al. 2014), females avoided wind turbines that could lead to local extirpation of the species in proximity to wind turbines (Winder et al. 2014). In Texas, Timmer et al. (2014) found the density of Lesser Prairie-Chicken leks decreased as the density of active oil and gas wells and paved roads increased.

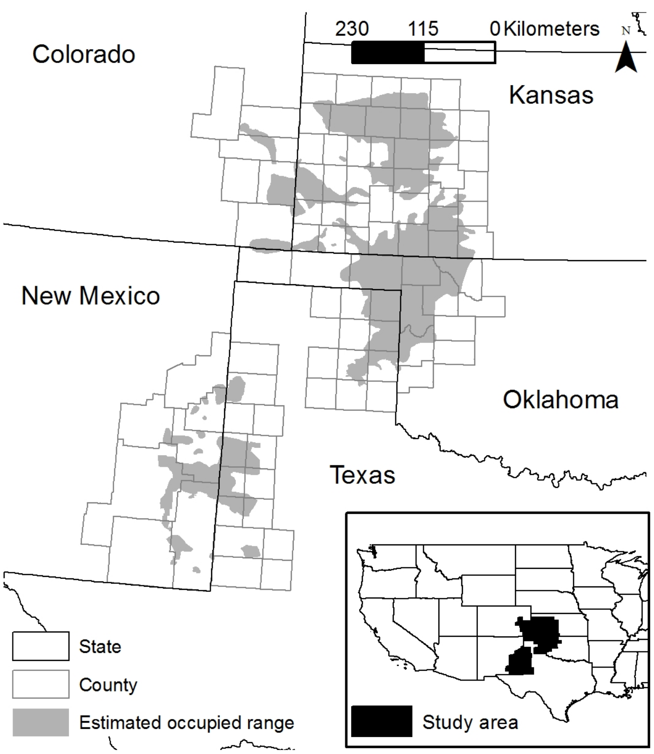
The distribution and population of Lesser Prairie-Chickens have been monitored by state wildlife biologists and managers through lek surveys, but until recently a considerable amount of interstate variation existed in survey methodologies (D. M. Davis, R. E. Horton, E. A. Odell, R. D. Rodgers, and H. A. Whitlaw 2008, *unpublished manuscript*). Nesting habitat is considered a factor limiting population size (Wisdom and Mills 1997), although nesting site data are only available from a few, localized research studies. On the other hand, landscape features indicative of lekking activity are not thought to limit the population, but lek data is available across much more of the species' range. Breeding habitats are closely associated with lek sites (Hagen and Giesen 2005, Pitman et al. 2006), and leks have been used as a surrogate for nesting habitat over broad spatial extents in the past (Jarnevich and Laubhan 2011). Given that lek data are the only somewhat consistent data available range wide, we chose to focus our modeling efforts on this single life history event. Even so, the available data for Lesser Prairie-Chicken management decisions vary in terms of survey effort, methodology, and spatial coverage, and many are derived from nonrandom sampling. For example, some states have set routes that are monitored with a set protocol, while others visit historic and currently known lek locations (see Van Pelt et al. 2013 for detailed descriptions of each states' monitoring efforts). Until recently, surveys also lacked specific absence data or information on survey extents and effort. Therefore, Maxent is an appropriate technique to estimate relationships between environmental characteristics and lek occurrence because much of the available data for Lesser Prairie-Chicken populations consist of presence-only locations from nonrandom samples with an unknown sampling frame.

The objectives of our study were to predict habitat suitability for Lesser Prairie-Chicken leks and to explore relationships of occurrence with landscape characteristics and anthropogenic effects that may influence their distribution. We used Maxent to develop habitat suitability models for Lesser Prairie-Chicken leks using existing data merged from multiple collection efforts throughout the current occupied range. We then applied these models to all counties intersecting the 2012 estimated occupied range of the Lesser Prairie-Chicken (Van Pelt et al. 2013) to identify areas of higher habitat suitability for the species. Our overarching goal in reaching these objectives was to inform management decisions related to identifying locations for habitat conservation and developing a habitat conservation program for Lesser Prairie-Chickens.

METHODS

Our study extent included the 2012 estimated occupied range of the Lesser Prairie-Chicken buffered by 16.1 km as defined by the Lesser Prairie-Chicken Interstate Working Group and mapped on the Southern Great Plains Crucial Habitat Assessment Tool web site (Fig. 1; Van Pelt et al. 2013). We expanded the area to county boundaries to match political jurisdictions for management applications. This resulted in a 28,420,417 ha area, covering 89 counties in Colorado, New Mexico, Kansas, Oklahoma, and Texas.

Fig. 1. Location map showing the estimated occupied range (Van Pelt et al. 2013) and the study area consisting of 89 counties in the five state region historically occupied by Lesser Prairie-Chickens.



Data sets

All five states encompassing the historic range cooperated in an effort to compile lek location data from across the species' range. We selected lek locations from each state that had been observed between 2002 and 2012 to limit issues related to changes in land use since the time of observation. The definition of a lek, i.e., number of birds required to be present at the time of observation, varied by state, and given that some locations were opportunistic and not revisited we did not require leks to be observed in multiple years. We removed lek locations within 100 m of each other from different years and used only the most recent location to avoid pseudo-replication in the data. Because of potential issues related to coordinate accuracy as reported by the states collecting data, we dropped any locations that state representatives, headed by the coauthor from each state agency, believed had a spatial accuracy less than 100 m, i.e., removed leks with location data uncertainty such that it may have been assigned to an incorrect grid cell. We developed the lek model using a grid cell resolution of 210 m. These criteria resulted in 1402 unique locations including 76 in Colorado, 669 in New Mexico, 189 in Kansas, 185 in Oklahoma, and 283 in Texas. The sample size difference by state results from both the actual distribution of leks on the landscape, i.e., real differences in lek occupancy that exist between states, and artifacts from different historical survey methodologies discussed above and availability of data (sampling bias and privacy issues).

Potential predictor variables were chosen based on the life history of the species, and included land-cover metrics, topography, and anthropogenic features for a total of 15 predictors (Table 1). Our models were partially limited by the availability of consistent quality land-cover data throughout the range. We used three different sets of land-cover data based on which land-cover data set was determined as best for each state by the state representatives. We began with National Land Cover Dataset (NLCD) vegetation classes for all states (Fry et al. 2011), focusing on shrubland, grassland/herbaceous, and pasture/hay classes as important, but because of errors in this dataset we replaced it for Texas and New Mexico. For Texas, we used the Texas Ecological Systems Classification Project data set (Elliot et al. 2014); for New Mexico, we used the southwest regional gap analysis project land cover (USGS National Gap Analysis Program 2004). We also included a metric quantifying the amount of land in the conservation reserve program (CRP), because this land-use type has been important in previous models (Jarnevich and Laubhan 2011).

Because of the large number of land-cover classes, the quality of the classifications at a fine thematic scale, and our interest in the spatial context of location, experts from each state classified their land cover into known or suspected used and unused classes based on annual lek surveys and monitoring data (see Appendix 1 for more details and a list of the classes). To explore what landscapes may be important to the occurrence of leks, we created vegetation predictors of percent known used, percent suspected used, and percent CRP summarizing a 1600 m diameter neighborhood and a 5000 m diameter neighborhood around each location. These distances cover the range in reported area around leks used by Lesser Prairie-Chickens (newer estimate around 1.5 km from Pitman et al. 2006, Boal and Pirius 2012, and Grisham et al. 2014 to older estimates of 4.8 km used by Fuhlendorf et al. 2002). Known used consisted of vegetation broadly classified as

Table 1. All predictor variables considered in Lesser Prairie-Chicken lek suitability models including the variable name, steps taken to create the variables, the source of the original data, if the variable was included and, if not, the identity of the predictor with which it was correlated, a justification for inclusion, and the range in values (minimum to maximum) in the training data including both presence and background locations. FAA indicates Federal Aviation Administration.

Variable	Creation step	Source	Included	Justification	Range in values
Distance to FAA structure	Euclidean distance (meters) to FAA obstructions taller than 50 feet using ArcGIS Spatial Analyst tools.	Federal Aviation Administration, January 2011	Yes	Robel et al. 2004, Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011	1 m to 31.2 km
Distance to highway	Euclidean distance (meters) using ArcGIS Spatial Analyst tools to highways.	ESRI ArcGIS Data and Maps, version 10, “mroads” layer from the North America Streetmap dataset including interstates, freeways, state and county highways	Yes	Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011	0 to 24.4 km
Distance to all roads	Euclidean distance (meters) using ArcGIS Spatial Analyst tools to roadways.	ESRI ArcGIS Data and Maps, version 10, North America Streetmap database subset to named roads (field “DISP_NAME”; except for Kansas, which is from 2010 Kansas Department of Transportation data)	Yes	Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011	0 to 10.8 km
Distance to transmission lines	Euclidean distance (meters) using ArcGIS Spatial Analyst tools to any transmission lines.	Platts “North America Electric Transmission Lines GIS Layer,” obtained April 2011	Yes	Robel et al. 2004, Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011	0 to 46.3 km
Distance to wells	Euclidean distance (meters) using ArcGIS Spatial Analyst tools to wells.	Well data compiled from each state government in 2011, removing those with indication no longer active or plugged.	Removed because of correlation with well density (Appendix 2)	Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011	0 to 37.4 km
Well density (800m, 1600m)	Point statistics in ArcGIS Spatial Analyst neighborhood functions, summing the number of points in a circle with an 800m radius and with a 1600m radius	Well data compiled from each state government in 2011, removing those with indication no longer active.	Retained 1600m (Appendix 2)	Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011	800 m radius: 0 to 31.2 km 1600 m radius: 0 to 24.4 km
Average EVI	Average of average annual Enhanced Vegetation Index (EVI) from 2000 to 2009	MODerate resolution Imaging Spectroradiometer (MODIS) Vegetation Indices: http://ladsweb.nascom.nasa.gov/data/search.html	Yes		1 to 6083
Average minimum EVI	Average of minimum annual Enhanced Vegetation Index (EVI) from 2000 to 2009	MODerate resolution Imaging Spectroradiometer (MODIS) Vegetation Indices	Removed because of correlation with average EVI		-289 to 3293
Average maximum EVI	Average of maximum annual Enhanced Vegetation Index (EVI) from 2000 to 2009	MODerate resolution Imaging Spectroradiometer (MODIS) Vegetation Indices	Removed because of correlation with average EVI		0 to 7843
Topographic Ruggedness Index (TRI)	Topographic Ruggedness Index calculated following Riley et al. (1999); resampled to 240 m	National Elevation Dataset 1 arc-second Digital Elevation Model (http://ned.usgs.gov/index.html)	Yes	Riley et al. 1999, Hagen et al. 2004, Hagen and Giesen 2005	0 to 25
State	Categorical value for each of the five states	National Atlas of the United States, State Boundaries of the United States: National Atlas of the United States, Reston, VA. (http://nationalmap.gov/)	Yes	States differ in management strategies and CRP land treatment	Na
Percent “known used” (Appendix 1)	Focal Statistics (suitable_2010, Sum) / Focal Statistics (constant, Sum) * 100, Calculated for a 5000 m radius and a 1600 m radius, then resampled to 210 m	Regional land cover map derived from the Southwest Regional Gap Land Cover Dataset in New Mexico, the National Land Cover Dataset for Colorado, Kansas and Oklahoma, and Ecological Mapping Systems of Texas.	Retained 5000 m (Appendix 2)		0 to 100%

(con'd)

Percent conservation reserve program (CRP) land	Focal Statistics (suit_*, Sum) / Focal Statistics (constant, Sum) * 100, Calculated for a 5000 m radius and a 1600 m radius, then resampled to 210 m	Conservation Reserve Program information summarized from 2012	Retained 5000m (Appendix 2)	0 to 66.3%
Percent "suspected used" (Appendix 1)	Focal Statistics (suit_*, Sum) / Focal Statistics (constant, Sum) * 100, Calculated for a 5000 m radius and a 1600 m radius, then resampled to 210 m	Regional land cover map derived from the Southwest Regional Gap Land Cover Dataset in New Mexico, the National Land Cover Dataset for Colorado, Kansas and Oklahoma, and Ecological Mapping Systems of Texas.	Merged with "known used"	Na (merged with "known used")
Landscape condition	Comer, P. J. and J. Hak. 2012, http://yale.databasin.org/pages/natureservemethodsdetail	WGA landscape condition data created from Landfire, wells, roads, transmission lines, railroad, and vertical structures. It is a measure of human impact (cropland counts as impact). Scale is 1-10,000 with higher values less impacted.	Yes	1 to 8398

WGA indicates Western Governor's Association

"shrubland, steppe and savanna systems" while suspected used consisted of vegetation broadly classified as "grassland systems" (Appendix 1). Introduced grasses also contributed to the two categories. We collapsed known used and suspected used into a single predictor after preliminary runs, resulting in a single land-cover variable represented by percent of area within 5000 m with land cover classified as either known used or suspected used (see Appendix 2). We created predictors for well density using counts of active wells in an 800 m and 1600 m diameter neighborhood around the locations, which we later restricted to a 1600 m area based on preliminary runs (Table 1; see Appendix 2). These distances were based on expert opinion and the set back recommendations from anthropogenic features in Hagen et al. (2011). Other anthropogenic variables included distance to active wells, roads, highways, transmission lines, tall structures, and landscape condition (a measure of human impact integrating several anthropogenic factors; Table 1). Additional predictors included topographic ruggedness index (a measure of topographic heterogeneity in the region around a focal cell), state, and enhanced vegetation index (EVI; a spectral vegetation index that calculates photosynthetically active vegetation while accounting for effects from atmospheric and soil influences; Huete et al. 2002). All predictors were created at a 210 m resolution to match decisions regarding the minimum mapping unit for modeling leks as described in Table 1.

Modeling

To develop species distribution models, we used Maxent (version 3.3.3k). Maxent requires presence locations of a species, background or pseudo-absence locations representative of the sampled environment, and environmental predictors. It utilizes the principle of maximum entropy to determine statistical relationships between presence locations and the environment by comparing the environment where an organism is found to the available environment. We implemented Maxent within the Software for Assisted Habitat Modeling (SAHM; version 1.0; Morisette et al. 2013).

Predictor importance and response curves in Maxent are sensitive to cross-correlations, so we removed variables with high correlations of $|r|>0.7$ using the maximum of the Pearson's, Spearman's, and Kendall's correlation coefficients (Dormann et al. 2013). The three methods use different ways to identify correlations, which is useful given that Maxent utilizes linear and nonlinear relationships. We retained the variable from correlated pairs that was thought to be most directly related to Lesser Prairie-Chicken presence, indicating which predictor was retained and why others were dropped in Table 1.

All five states contributed lek data with varying degrees of completeness because of landowner confidentiality requirements. Colorado and Kansas provided all known lek locations that were collected with a GPS unit, and some locations were omitted for Oklahoma, New Mexico, and Texas. However, we do not know the exact number of locations or the specific areas of omitted data within these states. Thus, we limited the random selection of the 10,000 background locations to within 10 km of a recorded lek so that we did not sample areas outside the known sampled area (a 3,672,555 ha area; Phillips et al. 2009, VanDerWal et al. 2009). We chose 10 km because it extended the available area to several pixels beyond each presence location, allowing for enough environmental variation between presence locations and background locations to produce a meaningful model while still minimizing the inclusion of potentially unsampled areas. The number of background points required to adequately represent the available environment is estimated to be 10,000 (Phillips and Dudik 2008, Barbet-Massin et al. 2012).

We fit the lek model 25 times, withholding a different random 30% of presence locations during each of the 25 replicate model runs. We also set the maximum number of iterations to 5000 to allow models to converge. Otherwise we used the default settings for Maxent. However, in preliminary models we noticed signs of overfitting in the models including very complex response curves and large differences between receiver operating characteristic area under the curve (AUC) values calculated for training and testing data (i.e., > 0.05). We therefore tested alternate values of the regularization parameter that controls model complexity in Maxent and chose a value of two for subsequent runs. We ran models that both included and excluded state as a predictor to account for the potential differences in sample sizes between states mentioned above. Models including state assumed that differences in number of observed leks were an artifact of sampling bias as described above, and the state variable was meant to account for this difference. Models excluding state assumed that these differences reflected actual differences in occupancy, i.e., sample size differences arose because of environmental conditions differing between states. Because truth is probably some combination of these hypotheses, the two model scenarios provided bounds around the expected answer.

We evaluated models by examining the AUC value for the test data, which generally ranges between 0.5 and 1 and is a measure of discrimination ability of the model (Fielding and Bell 1997). Values less than 0.5 are no better than random, values between 0.5 and 0.7 are rather low accuracy, values between 0.7 and 0.9 are useful for some purposes, and values above 0.9 represent high accuracies (Swets 1988). Maxent provides two different evaluations of variable contribution to models. Permutation importance is calculated on the converged model only by examining change in AUC when randomly permuting the values among the presence and background data for each variable while holding the other variables constant. This metric provides a model-independent measure of the relative influence of each predictor in each model. The second contribution criterion is variable contribution, which is calculated based on the additive regularized training gain (positive addition or negative subtraction) at each iteration of the algorithm as it reaches convergence. Maxent also produces a multidimensional environmental similarity surface (MESS) when projecting the model onto new locations, e.g., such as from our constrained background locations to counties encompassing the historic range. The MESS surface includes increasingly negative values as the environmental conditions at the new location depart from those used in developing the model by comparing the range in values for each environmental variable at the locations used to develop the model (presence and background) to the value at the new location (Elith et al. 2010). We used this surface as a measure of uncertainty in predictions, classifying any negative value as a location with novel environmental conditions, i.e., conditions that were outside the range of parameters used to train the model.

To compare model results and provide a simplified product, we discretized the model predictions into suitable and unsuitable classes using three threshold rules produced in Maxent. The rules included the minimum training presence, which determines the minimum predicted value for any presence location used to train the model to use as the threshold; five percentile training presence threshold, which orders the predicted values for the presence locations used to train the model and selects the value that would misclassify the bottom 5%; and the 10 percentile training threshold, which misclassifies the bottom 10%. Because Maxent produces maps with a continuous index of relative habitat suitability rather than a probability, using these thresholds highlight areas in four different classes of relative suitability, with the 10% being the highest class followed in order by 5%, minimum training presence, and unsuitable.

RESULTS

As expected, several predictor variables were correlated. Our reduced, uncorrelated set included 11 predictors (Table 1; Appendix 3). The lek model performed well with an average test AUC value of 0.79 (Table 2). The lek locations used to train the model captured much of the available environment in the region of interest, with only 2.7% of the study area containing novel environments. New Mexico and Oklahoma contributed most to the novel area (Figs. 2 and 3).

Table 2. Metrics for the different Lesser Prairie-Chicken lek suitability models including AUC values for the test and the training data sets, percent of the study area classified as novel, three threshold values to discretize the model (minimum training presence [MTP], 5 percentile training presence threshold, [5 per.] and the 10 percentile training presence [10 per.]), and the percent of the study area (estimated occupied range [EOR]) and total area classified as suitable by the thresholds.

Model	AUC		Novel %	Threshold method	Threshold value	% EOR Suitable	Area suitable (ha)
	Test	Train					
With State	0.79	0.81	2.7	MTP	0.025	86	24,473,586
				5 per.	0.173	40	11,296,572
				10 per.	0.234	28	7,805,854
Without State	0.78	0.79	2.7	MTP	0.021	90	25,684,016
				5 per.	0.189	45	12,906,209
				10 per.	0.255	34	9,512,251

Fig. 2. Lesser Prairie-Chicken lek suitability model predictions including state as a predictor for the study area including (a) the continuous habitat suitability index with areas exhibiting novel environmental conditions overlaid and (b) three different thresholds used for binary classification of the model results into suitable and unsuitable habitat, including minimum training presence (MTP), 5 percentile, and 10 percentile thresholds.

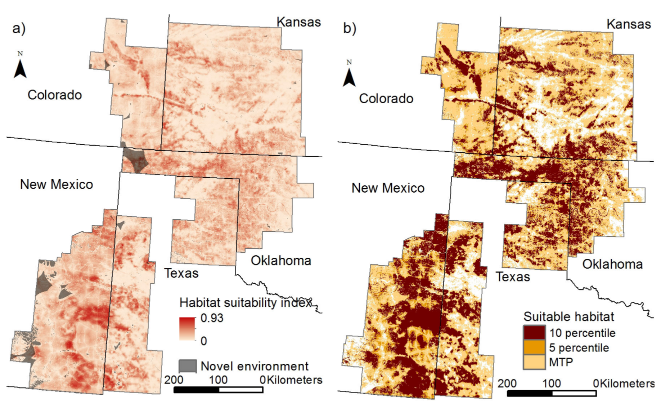
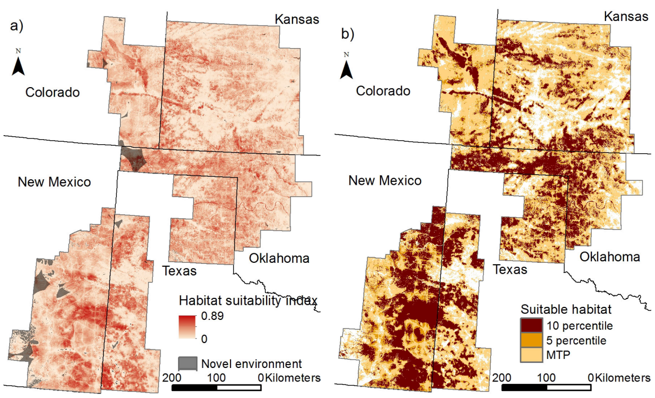


Table 3. Variable importance as measured by permutation importance and percent contribution for the top two Lesser Prairie-Chicken lek suitability models. The top three predictors are highlighted in bold. Permutation importance is calculated by randomly permutating the values for presence and background locations for each predictor while holding all other predictors constant. The percent contribution is calculated based on the path the variable follows in reaching convergence. CRP indicates conservation reserve program; FAA indicates Federal Aviation Administration.

Variable†	With State		Without State	
	Percent contribution	Permutation importance	Percent contribution	Permutation importance
State	**35.9**	**34.5**	n/a	n/a
Known or suspected used land cover within 5000 m	**21.9**	**31**	13	**19.8**
Mean annual enhanced vegetation index	**11.6**	3.9	**20.5**	10.9
Topographic ruggedness index	9	**9.4**	**22.9**	**20.3**
Landscape condition	7.8	2.4	**22**	**17.7**
Distance to highways	3.3	2.6	4.2	5.5
Distance to transmission lines	3	4.1	4.9	6.4
Distance to secondary roads	2.7	2.3	5.2	5.4
Percent CRP within 5000 m neighborhood	2.1	5.5	1.1	3.4
Distance to FAA structure	1.7	2.8	3.8	6.7
Active well density with 1600 m neighborhood	1	1.4	2.5	3.9

†Variables explained in Table 1.

Fig. 3. Lesser Prairie-Chicken lek suitability model predictions without state as a predictor for the study area including a) the continuous habitat suitability index with areas exhibiting novel environmental conditions overlaid and b) three different thresholds used for binary classification of the model results in to suitable and unsuitable habitat, including minimum training presence (MTP), 5 percentile, and 10 percentile thresholds.



For the model including state, relative ranking of the top two important predictors was the same regardless of method used to calculate importance, with state and land cover contributing at least 50% (Table 3). State was the most important predictor in the model, with the New Mexico category, which also had the largest sample size, associated with the greatest lek suitability. The univariate response for the other state categories were similar, but the Colorado response was associated with higher suitability when the marginal effect was calculated (varying one variable while holding all others constant at their mean value). Topographic ruggedness was also a high predictor, ranking third according to permutation importance, and closely followed by average EVI. With removal of state, topographic ruggedness index and landscape condition increased in importance, forming the top three predictors along with land cover and again followed by EVI. In both models there was a general trend of increasing suitability with increasing percentage of known or suspected used land cover, and a decreasing suitability with increasing topographic ruggedness.

Anthropogenic features also contributed to the models. In the model with state, all anthropogenic predictors except landscape condition had a relative contribution of less than 5% based on permutation importance. However, if viewed in aggregate their contribution is 13.2% (sum of highways, transmission lines, Federal Aviation Administration structures, and well density). With removal of state, importance of anthropogenic features besides landscape condition increased, with an additional four features having contributions > 5% and a total sum of 27.9%. Of the anthropogenic features, landscape condition was most important, followed by transmission lines. Examining the response curves (data not shown), landscape condition had a sharp increase in suitability followed by a slow, noisy decrease. Distance from transmission lines, highways, secondary roads, and Federal Aviation Administration structures followed a similar pattern, with a sharp increase in suitability as distance increased (up to roughly 2.5 km [with a noticeable drop in steepness around 150 m], 1.2 km, 3 km, and 23 km, respectively) followed by a more variable pattern dependent on the specific variable. Active well density had a negative relationship with suitability, with a small decrease with even one well followed by a very precipitous decline in suitability with more than 5 wells in the 1600 m area around a lek. Variable importance as measured by a change in training gain using a jackknife test was similar for both training and testing data.

The habitat suitability index for the study area discriminated areas within each state as having relatively high suitability compared with other areas within our study region (Fig. 2a). As expected, the three different thresholds we examined to discretize the continuous habitat suitability index to suitable and unsuitable habitat classifications differed. The minimum training presence classified 86% of the study area as suitable, while the 10 percentile threshold decreased this amount to 28% of the study area (Tables 2 and 4, Figs. 2b and 3b). There were minimal differences in spatial predictions when state was removed (Tables 2 and 4, Figs. 2a and 3a).

Table 4. The total amount of the study area (area suitable) and the percent of estimated occupied range (EOR) classified as suitable by the thresholds for each state. Values are calculated for the two suitability models, the one with state included as a predictor and the one without state. MTP indicates minimum training presence.

Model	State	Area suitable (ha)			% EOR suitable		
		MTP	5 per.	10 per.	MTP	5 per.	10 per.
With State							
	CO	2,860,992	870,344	493,695	93	28	16
	KS	6,872,667	2,303,264	1,509,102	79	26	17
	NM	5,626,992	3,524,243	2,508,011	92	58	41
	OK	3,602,578	1,999,512	1,446,533	90	50	36
	TX	5,510,357	2,599,210	1,848,513	85	40	28
Without State							
	CO	2,897,445	1,344,552	872,113	95	44	28
	KS	7,575,983	2,761,974	1,948,378	87	32	22
	NM	5,489,255	3,084,874	2,244,086	90	51	37
	OK	3,757,205	2,179,175	1,650,769	93	54	41
	TX	5,964,128	3,535,634	2,796,906	92	54	43
Disagreement							
	CO	82,762	622,013	492,421	2.7	19.8	15.5
	KS	796,997	932,203	815,643	9.1	10.7	9.3
	NM	175,192	750,661	736,148	2.8	12.0	11.8
	OK	185,057	443,986	468,267	4.4	10.1	11.1
	TX	569,794	1,114,606	1,124,030	8.7	16.8	17.0

Examining the model predictions for each state, Colorado and Oklahoma always had the lowest area of predicted suitable habitat, but the percent of the study area for the state that was suitable was high (93 and 90%, respectively; Table 4). With the more conservative threshold values (5 and 10 percentile), Texas and New Mexico had the largest amount of suitable habitat. Comparing the two models, Colorado, Kansas, and Texas all had increased area predicted as suitable when state was removed (Appendix 4).

DISCUSSION

Given the threats facing declining Lesser Prairie-Chicken populations (U.S. Fish and Wildlife Service 2014), there is a recent interest in the use of spatial models to relate landscape features with density or occurrence or to identify suitable habitat (Gregory et al. 2011, Jarnevich and Laubhan 2011, Timmer et al. 2014). These models are particularly useful when there is a need for science-based decisions to balance energy development and habitat requirements for species of conservation concern, such as Lesser Prairie-Chickens (Jarnevich and Laubhan 2011). Maximum entropy models estimate the statistical relationship between the environment where a species occurs, i.e., presence-only data, and the available environment (Elith et al. 2011). Gregory et al. (2011) developed hierarchical entropy models to categorize Greater Prairie-Chicken lek suitability in eastern Kansas to target areas for conservation efforts. Jarnevich and Laubhan (2011) also developed Maxent models of environmental and anthropogenic features to predict relative habitat suitability for Lesser Prairie-Chicken leks in Kansas to guide energy development. Timmer et al. (2014) developed spatially-explicit models, based on hierarchical distance sampling, to relate Lesser Prairie-Chicken lek density with anthropogenic and vegetative features in Texas. Previous models of prairie-chicken lek habitat have been built for a subset of the entire range (e.g., Jarnevich and Laubhan 2011, Timmer et al. 2014), but produced similar results to our range-wide assessment. All models highlighted the importance of anthropogenic features in predicting habitat suitability for Lesser Prairie-Chicken leks. Further, range-wide models such as ours identify species relationships with biotic and abiotic variables and their response to disturbance across the entire range, providing important information of range-wide patterns for conservation and management.

Although state was the most important predictor when included, our results suggest vegetation type (percent used or suspected used) was important as expected in the lek suitability model. Including state as a predictor did not greatly alter model results, and its importance was likely partly driven by sampling bias. These results are not surprising because Lesser Prairie-Chickens conduct most of their daily activities and complete their life cycle within 1.5 km of known leks (Pitman et al. 2006, Boal and Pirius 2012, Grisham et al. 2014). Therefore, lek suitability should increase in landscapes that contain high amounts of vegetation classes known to be used by Lesser Prairie-Chickens, i.e., shrubland or grassland systems, for other life stages such as those described by Hagen et al. (2013). Woodward et al. (2001) found suitable composition of vegetation in a 4.8 km area around leks varied between New Mexico, Texas, and Oklahoma for Lesser Prairie-Chicken populations, but had similar patterns of vegetation and land use. Here, we found that suitability increased with increasing amounts of known or suspected used land cover within a 5000 m around a lek. Landscapes, on average, comprised 86.5% native vegetation, which generally consisted of shrubland though the amount varied by state (Woodward et al. 2001). In Texas, Timmer et al. (2014) found percent grassland, total percent of grassland and shrubland, paved road density, and active oil and gas well density were the best predictors of lek density. They observed an inverse relationship between the anthropogenic variables and lek density. However, more complex relationships were observed for the vegetative variables, e.g., a quadratic relationship for percent grassland that varied by region. In Cochran County, Texas, lek density was highest in native shinnery oak (*Quercus havardii*) rangeland interspersed with some cultivated land (5-37% grain sorghum fields; Crawford and Bolen 1976).

Although avoidance of anthropogenic features has been demonstrated in Kansas, Oklahoma, and Texas (Robel et al. 2004, Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011, Grisham et al. 2014), the relative impact of these features remains unknown across the remainder of the Lesser Prairie-Chicken's distribution. In Kansas, nest sites were located further from utility lines, buildings, and improved roads than expected at random (Pitman et al. 2006). Pruett et al. (2009) found few Lesser Prairie-Chicken nests within 2 km of a power line in an Oklahoma study and only one Greater Prairie-Chicken nest within 2 km of the power line. Hagen et al. (2011) found a general pattern of avoidance to anthropogenic features in monthly home ranges in Kansas, and a before-after-control-impact design revealed that Lesser Prairie-Chicken monthly use areas were less likely to include utility lines. Although the causative agents behind avoidance of anthropogenic features remain unknown, it may be due to the functional elimination of suitable habitat (Robel et al. 2004) through general avoidance of noise, the potential for predators to perch on features, or a neophobic response to these features from evolving on a landscape devoid of tall structures. Our models provide evidence that these factors are important across the entire range of Lesser Prairie-Chickens, with a positive relationship between suitability and distance to features over distances examined in the above studies.

The Lesser Prairie-Chicken data available to create the models had several biases related to sampling. We attempted to control for some of the problems by limiting selection of background points, but the bias may still have affected model results. By limiting background point selection to areas we knew were sampled, we left out areas on the edges of the historic range that could still potentially provide some habitat. Inclusion of these other areas could potentially alter model results and variable relationships. Several different methods of assessing uncertainty in the model can be used to guide model usage. Locations where the two models did not overlap, had high standard deviation among replicate runs, or had novel environments, e.g., portions of New Mexico and Oklahoma, would be good places to target sampling to improve future modeling efforts (Crall et al. 2013). Predictor variables also had uncertainty, such as the three land cover data sets that were merged to create the land cover predictor. These were created at different points in time, which may affect model results. However, the NLCD evaluation, visualization and analysis tool indicated minimal land cover change for each state within our study region for 2001 to 2011 (0.46% of Kansas, 3.62% of Texas, 2.12% of Oklahoma, 1.34% of Colorado, and 0.95% of New Mexico; https://www.sciencebase.gov/catalog/item/541369e9e4b0239f1986bcc6). By collapsing to two categories (known or suspected used versus not used), we may have minimized some of these land cover differences. All three data sets were created during our sampling time frame.

Recently a range-wide aerial survey for Lesser Prairie-Chickens has been developed and is now operational (McDonald et al. 2014). As these data continue to be collected, they could provide the basis for better species distribution models which could incorporate abundance information to move beyond simple habitat suitability models. The data have already been used to estimate probability of occupancy range-wide (L. McDonald, F. Hornsby, T. Ritz, and G. Gardner 2013, *unpublished data*). Additionally, some nest data have been aggregated across the five state range and could be used to develop models for nesting habitat suitability. Adding another life history event would provide another layer of information that managers could use to inform decision making.

Management implications

Loiselle et al. (2003) cautioned against overpredicting suitable habitat because this may misguide conservation efforts. Using a higher threshold value such as 5 or 10 percentile training presence could minimize false-positive errors by limiting locations in less optimal habitat. However, these thresholds misclassify some known leks as being in unsuitable habitat. These models can then be used for targeting of conservation actions such as easements and management contracts. Using the moderate 5 percentile threshold, more than 50% of the study area was classified as unsuitable and focusing development within these areas could potentially minimize impact to Lesser Prairie-Chickens. The three thresholds presented provide a way to rank habitat suitability depending on management objectives, with the 10 percentile threshold highlighting areas with the highest relative suitability compared to the others.

These results have been integrated with other information regarding Lesser Prairie-Chicken habitat including focal areas determined by teams in each state as priority locations with intact suitable habitat (with suitability based on the Maxent models), habitat corridors, and the estimated occupied range based on state surveys to produce a coarse scale map to classify the historic range into four classes of conservation priority. This tool, the Southern Great Plains Crucial Habitat Assessment Tool (http://kars.ku.edu/maps/sgpchat/), can be used to guide siting of development and targeting of conservation. This tool is a component of the Western Association of Fish and Wildlife Agencies mitigation framework as described in the Lesser Prairie-Chicken Range-wide Conservation Plan (Van Pelt et al. 2013).

CONCLUSION

These models represent a collaborative effort across management agencies to work toward the conservation of a threatened species. We used existing data for a single, well-observed range-wide habitat use, lekking, to make inferences about general habitat requirements for a species. These results provide information that can be used to meet management objectives and potentially guide further sampling efforts in the absence of other information. Information on habitat use for other life stages could be useful in better quantifying seasonal habitat needs (D'Elia et al. 2015). These analyses represent a means to utilize existing data from multiple sources for a single use to make inferences regarding locating energy development and conservation efforts.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/807

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Appendix 1. Originally we used the National Land cover Database (NLCD) for all five states, calculating percent of the area around a pixel that was shrubland, percent grassland/ herbaceous, and percent pasture/ hay. These vegetation data, however, resulted in what was agreed as great over-prediction in the southwest driven by the NLCD shrubland classification including large expanses of unused vegetation. Texas had recently developed a new land cover, Ecological Mapping Systems of Texas for Texas (Elliot et al. 2014), which was thought to be more accurate for the region than the NLCD. For New Mexico the most accurate land cover was believed to be the Southwest Regional Gap Land Cover Dataset. Cover categories were selected by each state's biologists as known used or suspected used (included below) with other categories assumed as unused. Lek location data were examined in relation to the vegetation categories along with biological knowledge.

Table A1.1. Land cover classes in the National Land Cover Dataset for Colorado, Kansas, and Oklahoma.

Class	Area (ha)
Shrubland (Dwarf Scrub and Shrub/ Scrub)	703,436
Grassland/ Herbaceous	7,350,080
Pasture/ Hay	233,199

Table A1.2. Classes included from the Southwest Regional Gap Land Cover for New Mexico.

Class	Area (ha)
Apacherian-Chihuahuan Mesquite Upland Scrub	1,156,120
Apacherian-Chihuahuan Semi-Desert Grassland and Steppe	549,528
Chihuahuan Creosotebush, Mixed Desert and Thorn Scrub	627,038
Chihuahuan Gypsophilous Grassland and Steppe	4,784
Chihuahuan Mixed Salt Desert Scrub	29,570
Chihuahuan Sandy Plains Semi-Desert Grassland	14,432
Chihuahuan Stabilized Coppice Dune and Sand Flat Scrub	11,946
Chihuahuan Succulent Desert Scrub	447
Coahuilan Chaparral	8,064
Colorado Plateau Mixed Low Sagebrush Shrubland	217
Inter-Mountain Basins Montane Sagebrush Steppe	160
Inter-Mountain Basins Semi-Desert Grassland	715
Inter-Mountain Basins Semi-Desert Shrub Steppe	67,798
Madrean Juniper Savanna	15,304
Mogollon Chaparral	4,001
Rocky Mountain Gambel Oak-Mixed Montane Shrubland	3,168
Rocky Mountain Lower Montane-Foothill Shrubland	7,100
Southern Rocky Mountain Juniper Woodland and Savanna	37,141
Southern Rocky Mountain Montane-Subalpine Grassland	875
Western Great Plains Foothill and Piedmont Grassland	448
Western Great Plains Mesquite Woodland and Shrubland	108,558
Western Great Plains Shortgrass Prairie	2,470,784

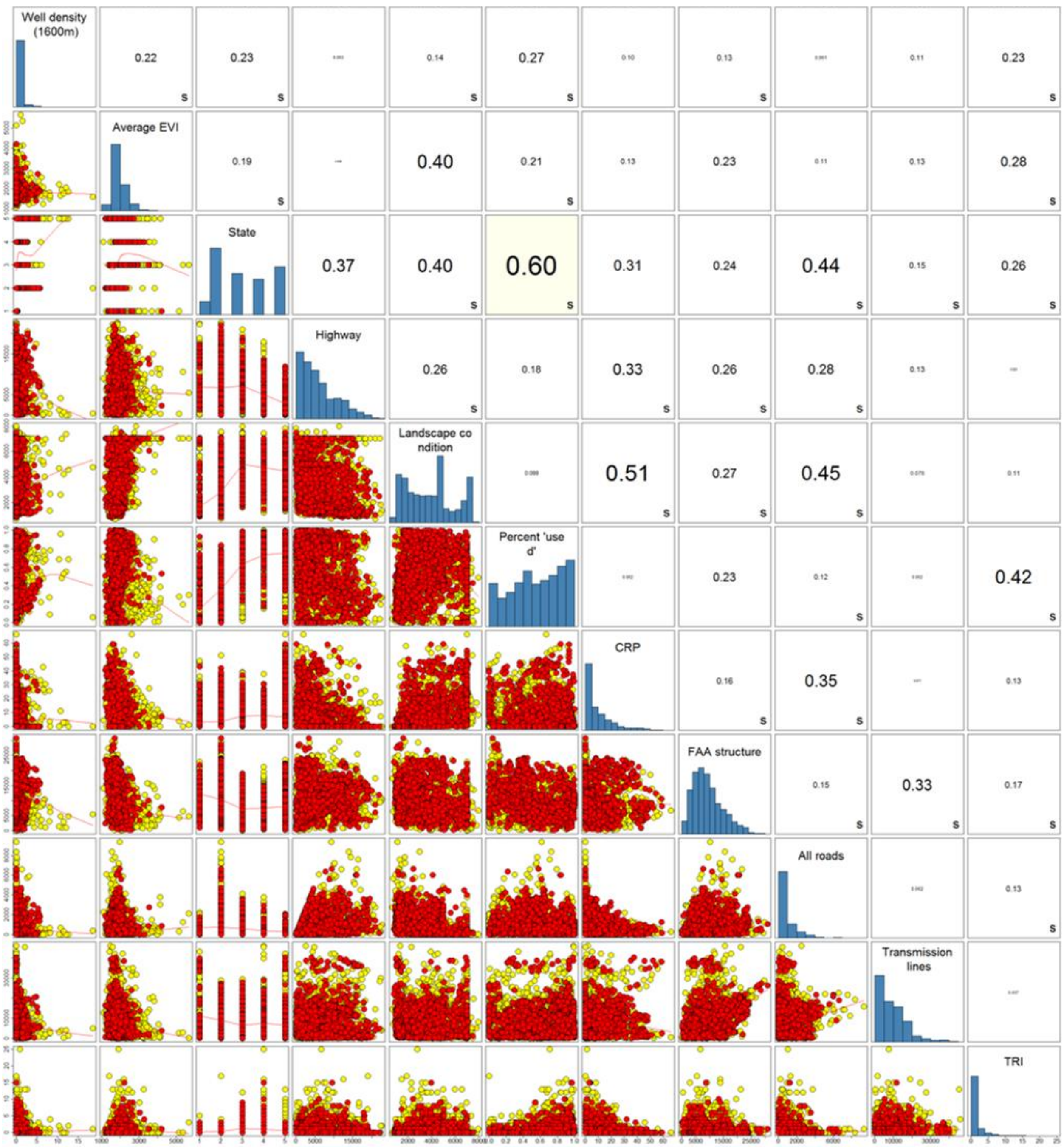
Table A1.3. Classes from the Ecological Mapping Systems of Texas for Texas.

Class	Area (ha)
CRP / Other Improved Grasslands	2,341,747
High Plains: Sand Prairie	310,563
High Plains: Sandhill Shinnery Duneland	35,312
High Plains: Sandy Deciduous Shrubland	195,982
High Plains: Sandy Shinnery Shrubland	35,232
High Plains: Shortgrass Prairie	963,522
Native Invasive: Deciduous Shrubland	52,794
Native Invasive: Sand Sage Shrubland	459,313
Rolling Plains: Mixed Grass Prairie	840

Appendix 2. Metrics for the different lesser prairie-chicken lek suitability models including two different vegetation neighborhood sizes (1,600 m and 5,000 m) and three different layers related to wells (count within 1,600 m, count within 800 m, and distance to nearest well). Metrics in the table include AUC values for the test and the training data sets, percent of the historic area classified as novel, two threshold values to discretize the model (minimum training presence [MTP] and the 10 percentile training presence [10 per.]), and the percent of the historic area classified as known used by the thresholds. Distance to wells resulted in a much greater amount of novel area, so we only retained well density. Assessment metrics were similar for the remaining models. Experts agreed that the 1,600 m vegetation models were over predicting known used habitat, so we chose 5,000 m. Well count within 1,600 m performed slightly better than well count within 800 m.

Model		AUC			Threshold value		Known used (%)	
Vegetation neighborhood	Well layer	Test	Train	Novel %	MTP	10 per.	MTP	10 per.
1,600m	Count 1600m	0.819	0.836	32.1	0.018	0.179	74	13
	Count 800m	0.814	0.839	31.1	0.019	0.182	73	12
	Distance to	0.827	0.844	49.8	0.022	0.18	64	9
5,000m	Count 1,600m	0.805	0.829	35	0.024	0.2	52	10
	Count 800m	0.803	0.829	34.1	0.021	0.198	56	10
	Distance to	0.81	0.838	50.7	0.023	0.189	46	9

Appendix 3. Correlation matrix produced by the Software for Assisted Habitat Modeling CovariateCorrelationAndSelection module showing the 11 predictor variables that were uncorrelated below the 0.7 threshold we used. The diagonal shows a histogram for each predictor. Above the diagonal is the correlation coefficient for each pair, with text scaled by size of the coefficient. Where an 'S' is present in the bottom right the value is the Spearman rank coefficient; otherwise it is the Pearson's coefficient. Below the diagonal is a scatterplot of the presence (red) and background (yellow) locations for each pair.



Appendix 4. Lesser prairie-chicken lek suitability agreement between models including and excluding state as a categorical variable, including agreement between a) the minimum training presence threshold, b) the five percentile threshold, and c) the ten percentile threshold. The 'maybe suitable' category indicates locations where one model classified a location as suitable while the other classified it as unsuitable.