Integrating land surface phenology with cluster density and size improves spatially explicit models of animal density

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ABSTRACT

Models of animal density often use coarse landcover categories that homogenize vegetation attributes, thereby limiting specificity of results. Alternatively, models including land surface phenology (LSP) metrics derived from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery capture continuous time-series data describing plant growth and senescence. LSP metrics may better discriminate the vegetation conditions influencing species habitat and distribution. Additionally, applications modeling animal density often use clusters (i.e., groups of individuals) but omit differences in cluster sizes. Ignoring how cluster size varies with landscape characteristics risks misrepresenting the spatial distribution of an animals' density. Using lesser prairie-chickens (LEPC; *Tympanuchus pallidicinctus*) as an example, we integrated the spatial distributions of cluster density and cluster size with LSP metrics to better predict its density in Texas, USA. We modeled LEPC cluster density using hierarchical distance sampling and cluster size with zero-truncated generalized linear modeling. Variables included landcover categories, LSP metrics, human infrastructure and topography. Models incorporating LSP metrics received most support and identified conservation areas that landcover models missed. Cluster density associated with LSP metrics, road density, oil and gas well density, topography, and grassland to shrubland ratio. Cluster size associated with topography and LSP metrics. Omitting the spatial distribution of cluster size underestimated LEPC density. Our approach generates geospatial predictions for prioritizing LEPC protection, habitat restoration, and evaluating impacts from development or phenological change. This study demonstrates the utility of integrating LSP metrics, cluster density and cluster size for predicting species density across large and heterogeneous landscapes.

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1. Introduction

Recent advances in ecological modeling build relationships between animal density and environmental variables while accounting for bias caused by incomplete detectability (Royle et al., 2004; Sillett et al., 2012). These models often use thematic landcover categories to characterize vegetation or landscape characteristics at local- to regional-scales (e.g., Sillett et al., 2012; Blank, 2013; Krementz et al., 2014; Timmer et al., 2014). Thematic landcover categories can oversimplify the vegetation conditions that dictate an animal's density (Viña et al., 2008). Further, thematic maps tend to be produced infrequently (i.e., 5- and 10-year intervals) risking temporal mismatches between animal observations and landscape composition (Lepers et al., 2005; Xian et al., 2009). An additional challenge is that detection-based models usually treat clusters (i.e., groups or aggregations) of individuals as the sample unit, ignoring that clusters vary by the number of individuals within them. By failing to account for cluster size, and only considering cluster density, models risk misrepresenting the spatial distribution of an animal's density (Hefley et al., 2013).

We addressed both of these issues while building density-habitat relationships for lesser prairie-chickens (LEPC; *Tympanuchus pallidicinctus*) within Texas, USA. This species was recently listed as Threatened, but that decision was later vacated by the U.S. District Court for the District of West Texas (USFWS, 2014, 2016). Much interest exists in recovering LEPCs, an outcome requiring knowledge of where most LEPCs occur and where their highest-quality habitat remains within a five-state area encompassing their remaining populations and historical range. Armed with knowledge of density-habitat relationships, land managers can guide future conservation actions for LEPC more effectively. Unfortunately, previous work has relied on coarse and oversimplified thematic landcover categories that can limit understanding of the environmental conditions conducive to predicting the abundance or occurrence of LEPCs and ignored the spatial variation in cluster size (Jarnevich and Laubhan, 2011; Timmer et al., 2014; Jarnevich et al., 2016).

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Our approach focused on incorporating remotely sensed land surface phenology (LSP) data which describes plant growth and senescence dynamics. Such data are captured using a time-series of the normalized difference vegetation index (NDVI) from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery (de Beurs and Henebry, 2004; Tan et al., 2011; Henebry and de Beurs, 2013). Ecologists commonly rely on vegetation indices like NDVI for modeling the amount and quality of a species' habitat (Mueller et al., 2008; Pettorelli et al., 2011). However, LSP metrics differ from their NDVI foundation, by identifying the beginning and end of a growing season, growing season length and other phenological characteristics for each pixel (Gao et al., 2008; Tan et al., 2011). We selected five annual LSP metrics to model LEPC density: amplitude of plant productivity (NDVI amplitude), timing of productivity (greenup day and peak date), length of the growth cycle (season length), and the timing of plant senescence (browndown day). These LSP metrics enable characterization of important differences in grassland vegetation and habitat conditions (Tuanmu et al., 2011; Wang et al., 2013). In contrast to thematic maps, LSP provides a more spatially and temporally comprehensive measure of vegetation conditions, which likely corresponds to animal habitat and occurrence at local and regional scales (Tan et al., 2011). We also used thematic data from the 2011 National Land Cover Database (NLCD) to compare and contrast LEPC density predictions based on thematic and LSP data sources.

Hierarchical distance sampling has been used to generate spatially explicit models of LEPC lek density across large landscapes while accounting for incomplete detection of LEPCs (Timmer et al., 2014). This previous work, however, did not model individual LEPC density and therefore could not predict total LEPC abundance. Our efforts are unique, as we characterized and integrated the spatial distributions of cluster density and cluster size within a hierarchical distance sampling framework that accounts for detection bias. Our approach results in estimates of LEPC total abundance and enhances the specificity of spatially explicit predictions of LEPC density because we accounted for imperfect detection in predictions of cluster density and size-biased detection (i.e., larger clusters are more detectable than small ones) in predictions of cluster size.

Specifically, the issue is that in distance sampling, clusters of individuals are detected and treated as the sample unit to maintain independence of samples for modeling a detection function, resulting in estimates of cluster density (Buckland et al., 2001). Cluster density is then transformed to individual density by multiplying it by an estimate of mean cluster size (Buckland et al., 2001). This ignores, however, that clusters do not have equal contributions to total abundance because the number of individuals within each cluster varies. For example, LEPC lek sizes (i.e., clusters) can vary from 2 to >20 individuals (Haukos and Smith, 1999; Sullivan et al., 2000).

When calculating mean density of individuals or total abundance, using an estimate of mean cluster size is appropriate (Buckland et al., 2001). However, if a spatially explicit description of individual density is needed, then knowledge of the spatial distribution of both cluster density and cluster size is required, especially if those processes are organized by different environmental features within a spatially heterogeneous landscape (Hefley et al., 2013). In addition, larger clusters are often more detectable than smaller ones, causing bias in estimated cluster size (known as size-biased detection; Buckland et al., 2001). This bias is adjusted by regression of detection probability against cluster size (Buckland et al., 2001). By extending this regression with covariables describing the spatial distribution of cluster size, we simultaneously deal with size-biased detection and spatially variable cluster size.

Therefore, our work provides unbiased estimates of spatially explicit individual LEPC density in Texas by characterizing and integrating the spatial distributions of cluster density and cluster size. Because many animal species occur in clusters, developing a technique that explicitly considers cluster size forms an important contribution. Our study appears to be the first to demonstrate the utility of remotely sensed LSP metrics (i.e., timing of plant growth and senescence) in modeling animal density and estimating population size. Previous wildlife studies have used LSP metrics developed from time-series satellite vegetation indices to predict habitat suitability (Viña et al., 2008; Tuanmu et al., 2011). Including LSP metrics improved spatially explicit models of LEPC density beyond those attainable with thematic landcover categories. By accounting for two forms of detection bias (i.e., incomplete detection of clusters and size-biased detection of clusters) and incorporating LSP metrics, we generate bias-corrected predictions (i.e., maps) of individual LEPC density over the LEPC range in Texas. Our predictions can guide future management actions and land use planning for advancing conservation of LEPCs. Our approach offers a mechanism for range-wide LEPC monitoring and analysis (habitats and populations), while exemplifying methods useful for improving the conservation of other species that cluster or are otherwise influenced by land surface phenology.

2. Methods

2.1. Study area

Prior to 1980, LEPCs occurred in at least 34 Texas counties. By 2010, their occupied range declined to portions of 20 Texas counties (Davis et al., 2008). The current occupied range in Texas is divided into two primary populations (Corman, 2011). One population occurs near the northeastern edge of the Llano Estacado Plateau from the Oklahoma Panhandle south through the Canadian River, Washita River, and North Fork of the Red River valleys (Jackson and DeArment, 1963). The other population occurs to the southwest on the Llano Estacado Plateau along the New Mexico border and extends west into eastern New Mexico (Grisham et al., 2014). The locations of these two populations were indicated as the northeastern and southwestern regions in our sampling frame (Fig. 1; Timmer et al., 2013, 2014).

2.2. Aerial survey

Our sampling frame was a grid composed of 285, 7.2-km × 7.2-km blocks overlaid on the occupied range of LEPCs in Texas (Fig. 1; Davis et al., 2008; Timmer et al., 2013, 2014). Blocks composed of vegetation not considered LEPC habitat (e.g., riparian woodlands, cotton fields) were excluded.

Surveyed blocks were selected using a stratified random design (details available in Timmer et al., 2013, 2014). The survey was split across 2 years to accommodate survey logistics (Fig. 1); the northeastern region was surveyed during spring 2010 (17 March–3 June) and the southwestern region during spring 2011 (1 March–4 May; Timmer et al., 2013, 2014).

We placed 18 evenly spaced transects (400-m spacing, north-south orientation) across each block (McRoberts et al., 2011; Timmer et al., 2013, 2014). Observers search within 200 m of the transect on the side in which they were seated. Surveys were conducted during early March through early June (LEPC breeding season) from sunrise until approximately 2.5 h post-sunrise at ≈15 m above ground level and a target speed of 60 km/h (McRoberts et al., 2011; Timmer et al., 2013, 2014). Most surveys were conducted using an R-22 helicopter with two observers, while some flights were conducted from an R-44 helicopter with four observers (Robinson Helicopter Co., Torrance, CA). Surveys used a line-transect based distance sampling approach (Buckland et al., 2001). When LEPCs were detected, the observers recorded the number of individuals in the cluster and the coordinates of the cluster's center (Timmer et al., 2013, 2014). These coordinates were used to measure perpendicular distance from the transect to the cluster. Detected clusters included both males and females at lek (breeding) and non-lek (non-breeding) locations (Timmer et al., 2013).
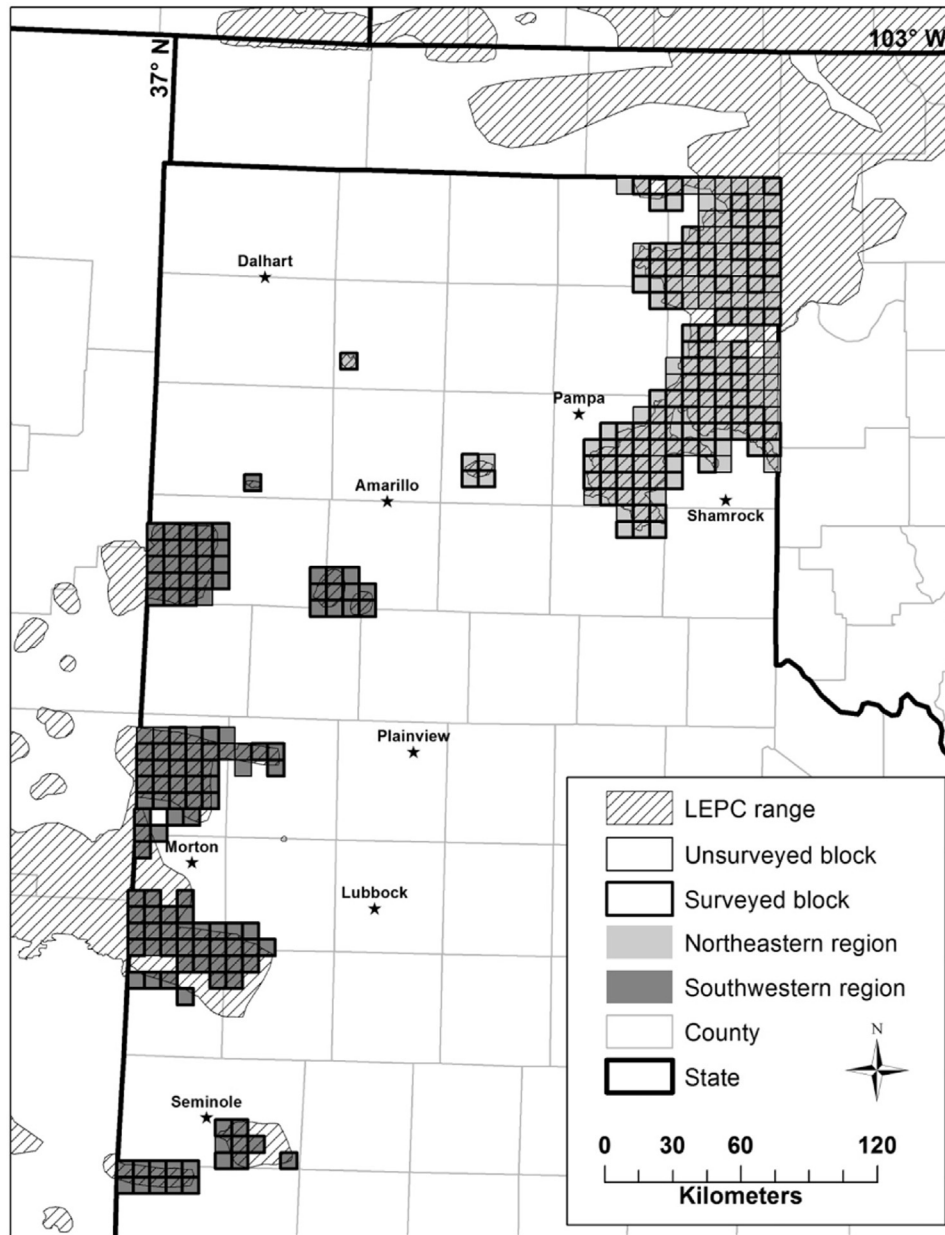
Fig. 1. Sampling frame of 285, 7.2-km × 7.2-km blocks (208 blocks surveyed) encompassing occupied range of lesser prairie-chickens (LEPC) in Texas, USA.

2.3. Remotely sensed variables

For each NLCD and MODIS pixel, we calculated the mean of human infrastructure, topography, landcover and LSP variables (Appendix A, Table S1) within a 2000-m radius, while retaining the original pixel size (30 m or 250 m, respectively). This procedure accounted for surrounding landscape conditions in an area equivalent to a typical LEPC home range (≈1250 ha; Taylor and Guthery, 1980a; Hagen et al., 2004) and for edge effects (Turner et al., 1989). We divided each surveyed block into four 3.6-km × 3.6-km quadrats. We calculated the mean and SD of the pixels within each quadrat for each variable (Raster package v. 3.1.2; R Core Team, 2015). These explanatory variables were used to model cluster density and cluster size (as separate response variables).

2.3.1. Infrastructure and topography

Human infrastructure and topography included two categories of roads, active oil and natural gas wells (hereafter wells), percent slope and topographic roughness (Appendix A, Table S1; Pitman et al., 2005; Pruett et al., 2009; Hagen, 2010; Timmer et al., 2014). We used TIGER road layers from the U.S. Census Bureau to estimate the density of primary roads (highway density), along with primary and secondary roads (road density; Appendix A, Table S1). To evaluate the effect of energy development on LEPC density, we calculated active well density concurrent to our survey (Appendix A, Table S1; IHS Energy, https://www.ihs.com/). Active wells concurrent to our survey were wells completed and in production by December 2011. The topographic variables, mean slope percent and roughness (SD of elevation within 2000 m of each pixel; Appendix A, Table S1), were developed from a 30-m digital elevation model (DEM) obtained from the National Elevation Dataset (NED; http://ned.usgs.gov/).

2.3.2. Landcover

We used landcover categories known to be important to LEPC density (Fuhlendorf et al., 2002; Hagen et al., 2004; Pitman et al., 2005; Timmer et al., 2014) from the 2011 NLCD (30-m pixels; Appendix A,

Table S1). NLCD was chosen because it is repeatedly updated, has known classification accuracy and covers the LEPC range (Jin et al., 2013). For characterizing landscape conditions in each quadrat, we calculated the percent of grassland, shrubland and cropland cover using the Geospatial Modelling Environment software (Beyer, 2012). We assumed that juxtaposition and arrangement of landcover types was important to LEPC density (Fuhlendorf et al., 2002; Hagen et al., 2004; Winder et al., 2015). Therefore, we derived two additional predictor variables to characterize the ratio and aggregation of grasslands and shrublands within each quadrat (Appendix A, Table S1). The ratio of grassland to shrubland was quantified as the ln(shrubland proportion + 0.0035) − ln(grassland proportion + 0.0035). To measure the degree of grassland and shrubland aggregation, we calculated the percentage of like adjacency for grassland and shrubland pixels (FRAGSTATS; McGarigal et al., 2012).

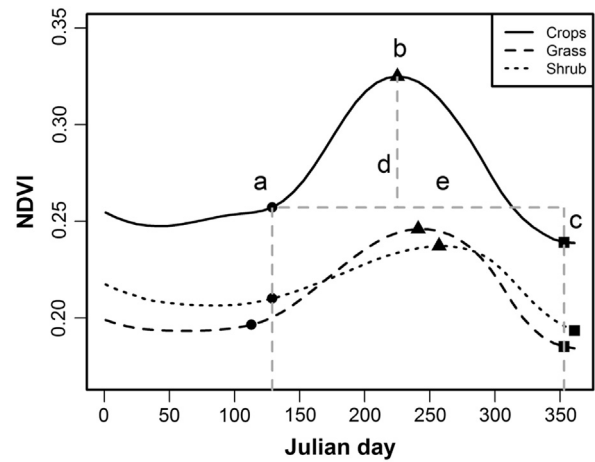### 2.3.3. MODIS land surface phenology

The MODIS satellite sensor revisits each portion of the Earth's surface every 2 to 3 days, capturing spectral reflectance data useful for calculating NDVI. NDVI is sensitive to changes in plant vigor, leaf area index and greenness, enabling it to measure the timing and magnitude of vegetation growth cycles (Huete et al., 2002; Gundin-Garcia et al., 2012). The MODIS for North American Carbon Program (NACP) developed 14 annual LSP metrics from 2000 to 2012 using 8-day NDVI composite images at 250-m pixel scale covering all of the Earth's terrestrial surfaces (MOD09Q1P_NDVI; http://accweb.nascom.nasa.gov/index.html). We compared and contrasted density model outcomes for LEPC using MODIS NACP derived LSP metrics with more commonly used NLCD categories.

The remotely sensed LSP metrics were developed using the TIMESAT model, which extracts annual LSP measurements from high temporal frequency time-series NDVI (Tan et al., 2011). The TIMESAT model uses time-series from years surrounding a growing season (Tan et al., 2011). This approach improves accuracy in the characterization of phenology (Tan et al., 2011). TIMESAT further reduces the potential negative effects arising from cloud contaminated or noise dominated pixels. TIMESAT accomplishes this by temporally smoothing time series vegetation indices with semi-local fitting functions such as asymmetric Gaussian or double logistic approaches (see Gao et al., 2008).

We selected five of the 14 LSP metrics to model LEPC density based on LEPC biology and LSP data correlations. Biologically, the five LSP metrics characterize the timing, duration, and magnitude of increased plant production, and appear effective for discriminating differences in plant composition, land use and animal habitat (Tuanmu et al., 2011; Wang et al., 2013; You et al., 2013). These five variables represent levels of productivity (NDVI amplitude), timing of productivity (greenup day and peak date), length of the growing cycle (season length), and the timing of plant senescence (browndown day) on a site (Appendix A, Table S1; Fig. 2; Tan et al., 2011). Crall et al. (2013) used similar LSP metrics to improve habitat suitability estimates for non-native invasive plants which exhibit differences from native vegetation in growth cycle. The nine unused LSP metrics were correlated with the others ($r \geq 0.70$). We used the mean and SD of LSP metrics developed for years 2001 to 2012 for each of the five metrics to incorporate inter-annual variability and avoid data gaps for pixels with no detectable growth period in a given year (Tuanmu et al., 2011). We anticipated these LSP metrics would characterize prairie habitat conditions and variables important to LEPC density and for distinguishing native prairie from intensively grazed and cultivated lands in the study area.

2.4. Modeling cluster density

We used hierarchical distance sampling to model LEPC cluster density and account for incomplete detection (multinomial-Poisson mixture model; Royle et al., 2004; Sillett et al., 2012). Hierarchical distance sampling simultaneously models the detection and cluster

Fig. 2. MODIS NDVI curves for cropland (Crops; $n = 46$), shrubland (Shrub; $n = 46$) and grassland (Grass; $n = 46$) from randomly selected locations in the study area. Derived land surface phenology metrics are a) the time at which the growing season starts (greenup day; black dot), b) the time at which NDVI reaches its maximum value (peak date; black triangle), c) the time at which NDVI ends its decrease (browndown day; black square), d) the difference between the maximum and annual base NDVI (amplitude; gray vertical line), and e) the time from the start to the end of the growing season for a given year (season length; gray horizontal line).

density processes and allows the effects of a given variable, on either process, to be disentangled (Royle et al., 2004; Sillett et al., 2012). Data were analyzed in Program R using the distsamp function of package unmarked (Fiske and Chandler, 2011; R Core Team, 2015). To model the detection function, we binned the distance data into 7 intervals (i.e., 0–35 m, 35–50 m, 50–70 m, 70–90 m, 90–120 m, 120–150 m, 150–200 m; Timmer et al., 2014).

We used Akaike's Information Criterion (AIC) to evaluate the evidence for each model (Burnham and Anderson, 2002). We considered models plausible if ΔAIC (difference in AIC compared to lowest AIC of the model set) was <2 and excluded models containing uninformative variables (i.e., $P > 0.150$; Burnham and Anderson, 2002). We evaluated the goodness-of-fit of the most supported model(s) using a Freeman-Tukey χ^2 procedure with 1000 bootstrap replicates (parboot; Fiske and Chandler, 2011; Krementz et al., 2014). We selected best detection function(s) based on AIC (Buckland et al., 2001). We then developed three model sets for cluster density: 1) a model set that combined infrastructure, topography and landcover (hereafter, landcover model set); 2) a model set that combined infrastructure, topography and LSP (hereafter, phenology model set); and 3) a model set that combined infrastructure, topography, landcover and LSP (hereafter, combination model set). This approach enabled comparison of models composed of landcover variables with those composed of LSP variables. We excluded pairs of variables from occurring in the same model if the absolute value of Pearson's correlation coefficient was >0.60. All variables used in the analysis were standardized ([observation–mean]/SD; Appendix A, Table S2).

For each model set, model selection followed a three-stage approach. First, we selected the most supported combination(s) of infrastructure and topography variables. Second, we selected the most supported combination(s) of landcover or phenology variables. These sets of models considered the possibility that shrubland cover or season length may influence the detection process because shrublands have increased horizontal cover which may reduce detectability, and a longer growing season was associated with areas containing more shrubland (Pearson's $r = 0.463$, $n = 1140$, $P < 0.001$) than grassland (Pearson's $r = 0.260$, $n = 1140$, $P < 0.001$). Third, we combined the most supported models from the first two steps to select our most supported model for each model set (Appendix A, Table S2). Finally, we combined the models receiving the most support from the third step to examine infrastructure, topography,

Table 1
Variable coefficients for most supported models of lesser prairie-chicken cluster density for each model set, 2010–2011, Texas, USA.

	Landcover Model (AIC = 1311.591)			Phenology model (AIC = 1273.217)			Combination model (AIC = 1250.472)			Combination model 2 (AIC = 1251.140)		
	β[a]	SE	P	β[a]	SE	P	β[a]	SE	P	β[a]	SE	P
Density[b]												
Intercept	−3.330	0.167	<0.001	−3.211	0.204	<0.001	−3.048	0.212	<0.001	−3.023	0.208	<0.001
Topographic roughness	−0.671	0.100	<0.001	−0.746	0.113	<0.001	−0.736	0.119	<0.001	−0.784	0.119	<0.001
Grassland to shrubland ratio	0.296	0.182	0.104				−0.297	0.194	0.126	−0.091	0.208	0.661
Grassland to shrubland ratio^2	−0.396	0.079	<0.001				−0.340	0.082	<0.001	−0.286	0.080	<0.001
Ratio × roughness	−0.567	0.191	0.003				−0.603	0.208	0.004	−0.616	0.213	0.004
Total grassland and shrubland	0.761	0.113	<0.001									
Road density	−0.232	0.125	0.064	−0.208	0.125	0.095	−0.215	0.123	0.081	−0.213	0.124	0.086
Well density	−1.367	0.337	<0.001	−1.301	0.323	<0.001	−1.486	0.349	<0.001	−1.493	0.350	<0.001
NDVI amplitude				0.140	0.116	0.226	0.196	0.116	0.091	0.186	0.116	0.109
NDVI amplitude^2				−0.212	0.079	0.007	−0.185	0.082	0.023	−0.213	0.082	0.009
Browndown day				0.234	0.189	0.215	0.292	0.194	0.133	0.286	0.192	0.137
Browndown day^2				−0.911	0.230	<0.001	−0.795	0.225	<0.001	−0.795	0.225	<0.001
Season length				0.859	0.182	<0.001	0.846	0.179	<0.001	0.554	0.146	<0.001
Browndown SD				−1.034	0.244	<0.001	−0.868	0.250	0.001	−0.850	0.249	0.001
Detection												
Intercept	4.189	0.117	<0.001	4.305	0.155	<0.001	4.310	0.156	<0.001	4.192	0.117	<0.001
Season length				−0.485	0.183	0.008	−0.500	0.186	0.007			
Shrubland	−0.253	0.083	0.002							−0.261	0.082	0.002

[a] All predictor variable values were standardized ([observation − mean] / SD).
[b] Predictor variable definitions provided in Appendix A, Table S1.

landcover and LSP variables together (combination model set; Appendix A, Table S3).

Following Timmer et al. (2014), our landcover model set included quadratic terms for grassland and shrubland. To better model the optimal mix of grassland and shrubland, we included the ratio of shrubland to grassland as a quadratic relationship. In our phenology model set, we included quadratic terms for NDVI amplitude and browndown day. We considered models in which topographic roughness interacted with NDVI amplitude, season length, shrubland, grassland or the ratio of
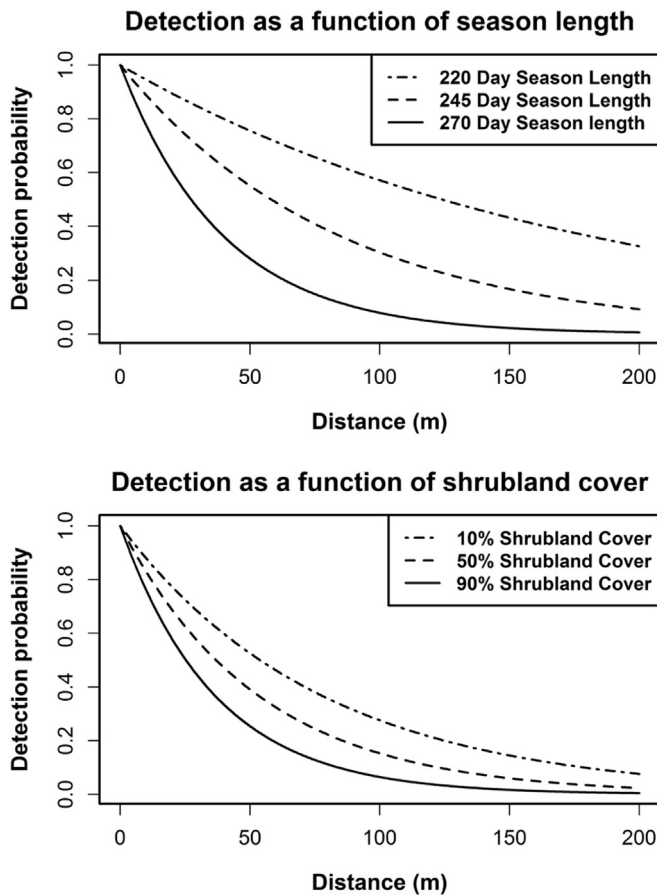
Fig. 3. Detection probability of lesser prairie-chicken clusters decreased as season length or shrubland cover increased, 2010–2011, Texas, USA.
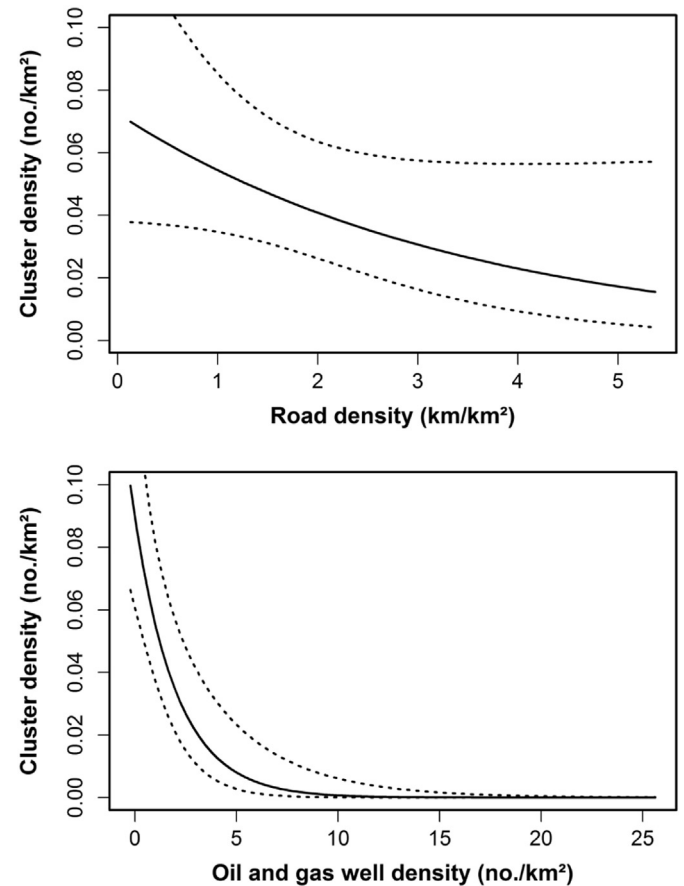
Fig. 4. Cluster density of lesser prairie-chickens declined with increases in road density and oil and natural gas well density, 2010–2011, Texas, USA. Prediction based on the best model from the combination model set. All other variables in the model were held at their means. The dotted lines represent 95% confidence intervals.

shrubland to grassland because plant communities differing by topographic relief may exhibit similar phenological or landcover characteristics.

2.5. Modeling cluster size

To correct for size-biased detection, we estimated detection probability based on our most supported hierarchical distance sampling model from each model set and regressed it against cluster size (Buckland et al., 2001). An unbiased estimate of mean cluster size was then estimated as the predicted cluster size given a detection probability of one. This technique assumes that individuals within clusters detected near transects are accurately counted and all clusters near transects are detected (Buckland et al., 2001).

As with cluster density, cluster size may be influenced by environmental features (Hefley et al., 2013). Therefore, we modeled cluster size as a function of estimated detection probability and infrastructure, topography, landcover and/or LSP using zero-truncated generalized linear modeling (vglm function of the VGAM package; Zuur et al., 2009; R Core Team, 2015). We assumed a zero-truncated negative binomial distribution (posbinomial; R Core Team, 2015) because detected clusters cannot have zero individuals and data were overdispersed (Zuur et al., 2009). Model selection for cluster size followed the same process as model selection for cluster density except we used AIC corrected for small sample size (AIC$_c$; Burnham and Anderson, 2002). For each model set, we used the detection probability from the most supported cluster density model from each respective model set.

2.6. Spatially explicit prediction of density and total abundance

We converted predicted density for each quadrat (12.96 km^2) into abundance. We estimated total abundance in the sampling frame by summing the estimated abundances for each quadrat. To characterize the uncertainty in our estimates, we used a nonparametric bootstrap procedure with 1000 replicates. We resampled the data by survey quadrat, refit the hierarchical distance sampling model, predicted cluster density for each quadrat, refit the cluster size model and then predicted cluster size for each quadrat. We estimated coefficients of variation (bootstrapped SE/predicted density) for each quadrat as an indicator of the reliability of the prediction. We approximated 95% confidence intervals (CI) with the 2.5 and 97.5 percentiles of the bootstrapped distribution.

3. Results

We surveyed 208, 7.2-km × 7.2-km blocks (832, 3.6-km × 3.6-km quadrats; Fig. 1). We detected 175 clusters of LEPCs (0.016 clusters/km^2, SD = 0.054) with 96 classified as leks. Mean cluster size was 3.4 LEPCs per cluster ($n = 173$, SD = 3.51; cluster size was unknown for 2 detections). Cluster size was similar among regions ($t = 1.159$, df = 171, $P = 0.248$). All LEPC clusters were detected within 200 m of transects (Appendix A, Fig. S1).

3.1. Cluster density

The most supported model from the phenology model set was 38.4 AIC units better than the most supported model from the landcover
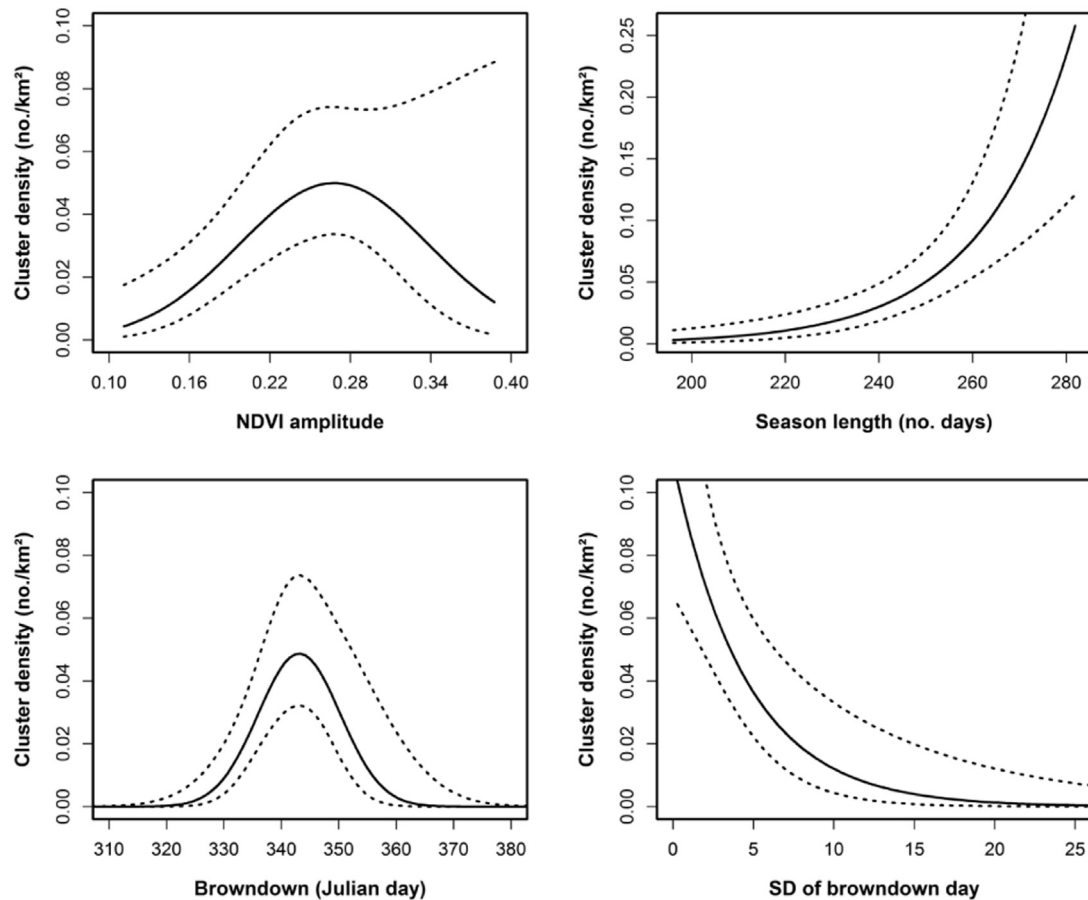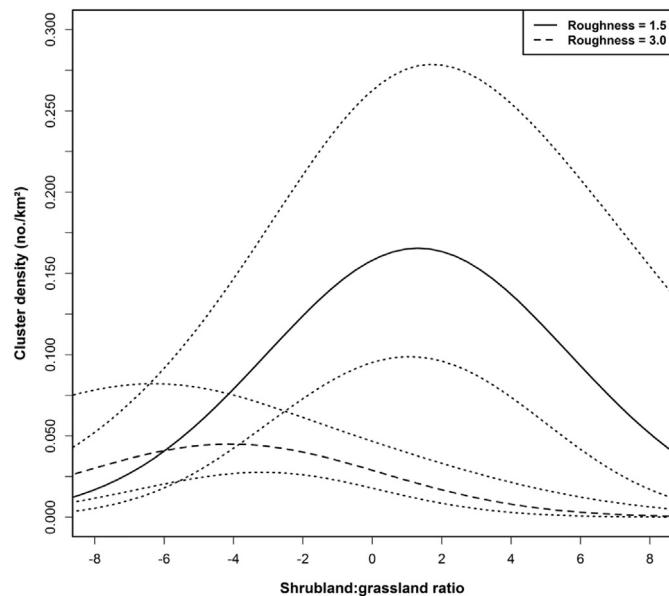

Fig. 5. Cluster density of lesser prairie-chickens exhibited quadratic relationships with NDVI amplitude and browndown day, increased as season length increased, and decreased as the variability of browndown day increased, 2010–2011, Texas, USA. Prediction based on the best model from the combination model set. All other variables in the model were held at their means. The dotted lines represent 95% confidence intervals.

model set (Table 1 and Appendix A, Table S2). Goodness-of-fit tests indicated both models had adequate fit (landcover model set, $P = 0.276$; phenology model set, $P = 0.236$). By combining infrastructure, topography, landcover and LSP (combination model set, Table 1 and Appendix A, Table S3), we improved upon the most supported model from the phenology model set by 28.7 AIC units.

Two models from the combination model set were competitive (Table 1 and Appendix A, Table S4) and goodness-of-fit tests indicated both had adequate fit ($P = 0.231$ and $P = 0.240$). These two models contained the same explanatory variables for density, but differed in the detection function (Table 1). The detection function was best described by a negative-exponential, with one model indicating that detectability varied by season length and the other by shrubland cover (Table 1). For example, at 100 m from the transect, detectability was ≈ 0.57 when vegetation exhibited a 220 day season length but declined to ≈ 0.08 when season length increased to 270 days (Fig. 3). The second model indicated that at 100 m from the transect, detectability was ≈ 0.28 when shrubland cover was 10% but declined to ≈ 0.06 when shrubland cover increased to 90% (Fig. 3).

Cluster density relationships were similar among the most supported models from the three model sets (Table 1). The most supported combination models indicated cluster density declined as road density and well density increased (Table 1; Fig. 4). Well density had the greatest influence on LEPC cluster density, indicating >5 wells/km^2 were associated with cluster densities of <0.01/km^2 (Fig. 4). LEPC cluster density exhibited quadratic relationships with browndown day and NDVI amplitude (Table 1) peaking in areas with mean browndown of ≈ 343 days and mean NDVI amplitude of ≈ 0.27 (Fig. 5). As season length increased from 260 to 280 days, LEPC cluster density increased ≈ 2.8 fold (Fig. 5). LEPC cluster density decreased ≈ 3.1 fold as browndown SD increased from 5 to 10 (Fig. 5). Cluster density exhibited a quadratic relationship with shrubland to grassland ratio which interacted with topographic roughness (Table 1). This interaction indicated that as topographic roughness increased, cluster density peaked in areas composed of more grassland than shrubland (Fig. 6). In the least rugged areas, cluster density peaked in areas composed of more shrubland (Fig. 6).
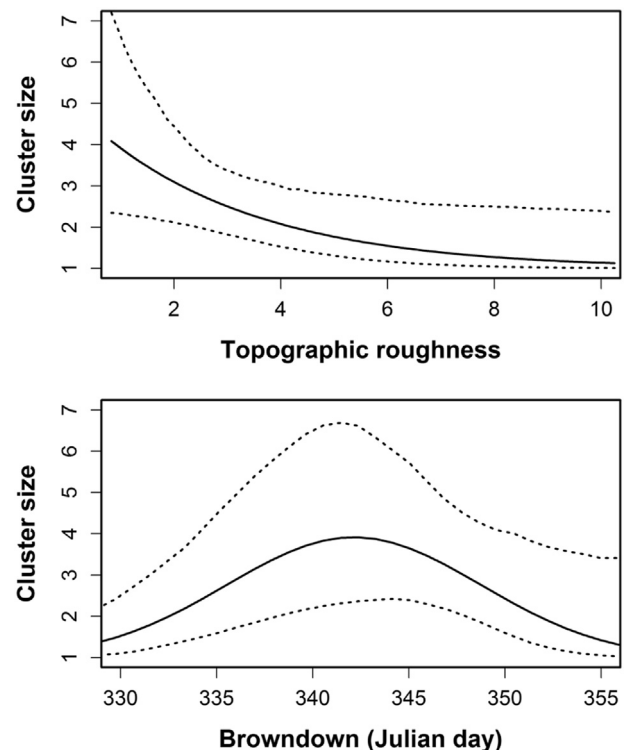
3.2. Cluster size

In the landcover model set, none of the landcover variables related to cluster size. The most supported model from the landcover model set ($AIC_c = 695.644$) indicated that detectability was inversely related to cluster size ($\beta = -1.074$, SE $= 0.366$, $P = 0.003$) and as topographic roughness increased, cluster size decreased ($\beta = -0.258$, SE $= 0.135$, $P = 0.056$). The most supported model from the phenology model set ($AIC_c = 694.422$) indicated that detectability was inversely related to cluster size ($\beta = -0.993$, SE $= 0.3542$, $P = 0.005$), and cluster size was inversely related to browndown SD ($\beta = -0.474$, SE $= 0.311$, $P = 0.127$) and topographic roughness ($\beta = -0.224$, SE $= 0.144$, $P = 0.118$). It also indicated that cluster size exhibited a quadratic relationship with browndown day (linear: $\beta = 0.203$, SE $= 0.258$, $P = 0.432$; quadratic: $\beta = -0.957$, SE $= 0.455$, $P = 0.036$).

The most supported model from the combination model set ($AIC_c = 693.361$) indicated that detection probability was inversely related to cluster size ($\beta = -1.045$, SE $= 0.351$, $P = 0.003$). Observed mean cluster size was 3.4 LEPCs per cluster ($n = 173$, SD $= 3.51$) but when corrected for sized-biased detection, it was 2.3 per cluster (SE $= 0.16$; see equations in Buckland et al., 2001:74). This model indicated that as topographic roughness increased, cluster size decreased ($\beta = -0.306$, SE $= 0.143$, $P = 0.032$; Fig. 7). Cluster size exhibited a quadratic relationship with browndown day (linear: $\beta = 0.154$, SE $= 0.254$, $P = 0.544$; quadratic: $\beta = -1.012$, SE $= 0.453$, $P = 0.025$) and was predicted to peak in areas with a mean browndown of ≈ 342 days (Fig. 7).

3.3. Total abundance

We estimated total abundance of LEPCs in our sampling frame as 2036 (CV $= 29.0$%; 95% CI $= 1578–3872$) based on the most supported

Fig. 6. Cluster density of lesser prairie-chickens exhibited a quadratic relationship with the ratio of shrubland to grassland (ln(shrubland proportion + 0.0035) − ln(grassland proportion + 0.0035)), which interacted with topographic roughness, 2010–2011, Texas, USA. Prediction based on the best model from the combination model set. All other variables in the model were held at their means. The dotted lines represent 95% confidence intervals.

Fig. 7. Lesser prairie-chicken cluster size decreased as topographic roughness increased and exhibited a quadratic relationship with browndown day, 2010–2011, Texas, USA. Predictions based on the best cluster size model from the combination model set. For topographic roughness, browndown day was held constant at 342 days and for browndown day, topographic roughness was held constant at 1. The dotted lines represent 95% confidence intervals.

landcover model, 2117 (CV = 27.3%; 95% CI = 1419–3637) based on the most supported phenology model, and 2101 (CV = 27.6%; 95% CI = 1573–3771) based on the most supported combination model. The most supported landcover model predicted fewer LEPCs in the northeastern region than the most supported phenology model (Fig. 8). Predictions in the southwestern region were similar among all the models with the most notable difference west of Muleshoe, Texas (Fig. 8). In both regions, spatial predictions from the most supported combination model were similar to those from the most supported phenology model (Fig. 8).

4. Discussion

Modeling LEPC cluster detection and density using hierarchical distance sampling benefited from LSP metrics, showing improved model performance when compared to models based on landcover types (Table 1 and Appendix A, Table S2). By incorporating the spatial distribution of cluster density and size, our predictions improved the spatial specificity of models (Fig. 8). These results identify the specific locations to target for protecting and conserving LEPCs. Results also provide better parameters describing quality habitat, thereby steering selection of
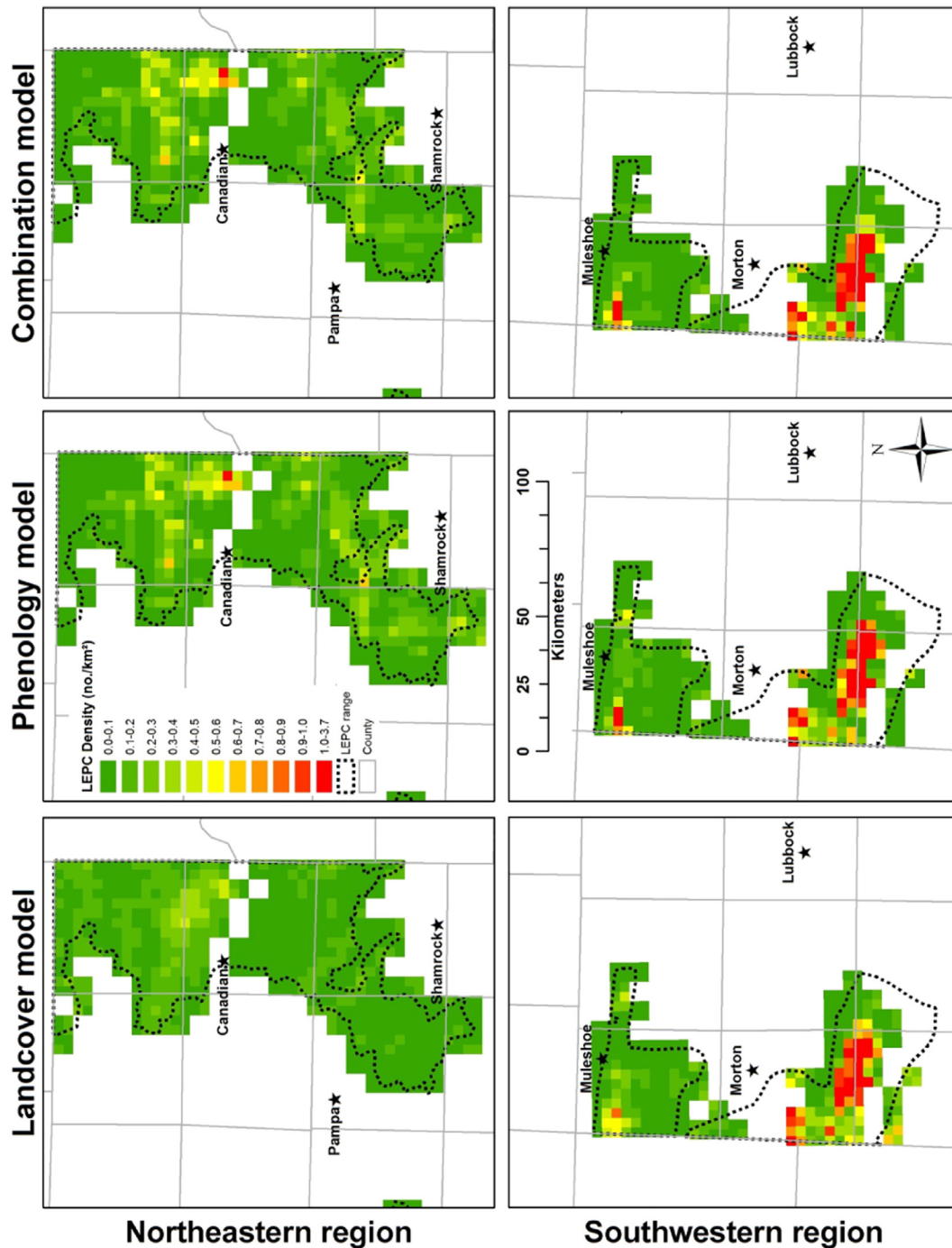

Fig. 8. Lesser prairie-chicken (LEPC) density (no./km²) per quadrat for models receiving most support from three model sets, 2010–2011, Texas, USA. The combined model included landcover and land surface phenology (LSP) metrics. Incorporating LSP metrics improved specificity of spatial predictions.

sites to reintroduce LEPCs, while forming restoration targets. Although landcover-based models have proven useful for predicting the abundance and distribution of LEPCs (Timmer et al., 2014), the classification process for generating landcover data risks oversimplifying the very differences in vegetation conditions that can dictate animal density. Indeed, landcover classes can poorly distinguish among heterogeneous shrubland and grassland conditions, thereby generalizing model outcomes and reducing the utility of results for management and conservation. Shrublands and grasslands also experience frequent, but heterogeneous disturbance from drought, fire, livestock grazing, cultivation, urbanization or other human development (Hovick et al., 2015). Such spatial and temporal land-use patterns and change creates a variety of conditions that often become categorized as one landcover type. However, many of these altered habitat conditions may not support LEPC populations (Taylor and Guthery, 1980b).

MODIS captures imagery at a low spatial resolution (250 m) but at a high temporal frequency (every 2 to 3 days) which is necessary for calculating LSP metrics (Tuanmu et al., 2011). Encouragingly, previous work demonstrates that LSP metrics developed from time-series vegetation indices such as NDVI can improve animal habitat models even in comparison to higher spatial resolution data derived from Landsat (Viña et al., 2008; Tuanmu et al., 2011). We found growing season length, browndown day, and browndown SD were important LSP metrics for describing LEPC cluster density (Table 1). This is because warm- and cool-season grasses, shrubs, and various crop types grow and senesce at different times and have varying season lengths (Wardlow et al., 2007; Wang et al., 2013). LSP metrics helped discriminate native prairie vegetation from highly altered shrubland, grassland or cropland sites unsuitable for LEPCs, while landcover classes did not. For this reason, the landcover model likely underestimated LEPC density within critical habitat areas in the northern portion of the study area (Fig. 8). We considered this a primary advantage of developing models using LSP metrics, in addition to their potential application to much larger areas such as the LEPC's historical five-state range.

LEPC cluster density and size peaked in areas with plant senescence (browndown) occurring at ≈342 days (Figs. 5 and 7). Areas with late senescence dates (i.e., >365 days) are probably associated with crops like winter wheat, while earlier senescence dates (i.e., <325 days) are likely dominated by perennial native and non-native grasses or crops such as cotton, sorghum or corn. Mean senescence dates (≈342 days) may indicate a specific mixture of native cool- and warm-season grasses and shrub species that support superior habitat conditions for LEPCs (Bradley et al., 2007; Wardlow et al., 2007; Wang et al., 2013). The variability of plant senescence (browndown SD) in an area also helped to discriminate LEPC habitat. As browndown SD increased, we found cluster density (Fig. 5) and size decreased. Greater values of browndown SD were associated with a greater mixture of cropland cover within an area (Pearson's $r = 0.549$, $n = 1140$, $P < 0.001$) compared to areas composed of native grasses and shrubs. Areas with a larger browndown SD were also indicative of landscapes with heterogeneous land-uses. The relationship between browndown SD and cluster size observed in the phenology model set indicated larger clusters of LEPCs occurred in areas with less cropland and more contiguous habitat conditions.

Areas with longer growing seasons indicated more shrubland cover (Pearson's $r = 0.463$, $n = 1140$, $P < 0.001$) than grassland cover (Pearson's $r = 0.260$, $n = 1140$, $P < 0.001$). As the amount of croplands in an area increased, growing season length shortened (Pearson's $r = -0.858$, $n = 1140$, $P < 0.001$). Reduced detectability in areas with a longer growing season (Fig. 3) was likely a result of those areas containing more shrublands that increased horizontal cover. Longer growing seasons were also indicative of greater LEPC cluster density (Fig. 5). Season length helped models eliminate some cropland areas and likely helped characterize appropriate mixtures of shrubs and grasses supporting LEPCs.

NDVI amplitude, which measures annual productivity (Ricotta et al., 1999), exhibited a quadratic relationship with cluster density, peaking at ≈0.27 NDVI amplitude (Fig. 5). On this landscape, the lowest NDVI amplitudes occur in sparsely vegetated areas and the highest occur in croplands, neither being quality LEPC habitat. Thematic landcover variables fail to characterize such gradients. For example, an area composed of bare ground with 20% grass cover and an area composed of 80% grass cover would be classified into the same NLCD grassland category, though these grassland compositions affect LEPC density quite differently.

As previously acknowledged, variables representing human infrastructure and development were associated with reduced LEPC cluster density (Pitman et al., 2005; Pruett et al., 2009; Hagen, 2010; Jarnevich and Laubhan, 2011; Timmer et al., 2014). These variables were important in our models as well. Cluster density declined in landscapes with increased road density and well density (Fig. 3; Table 1). Of all the variables used, oil and natural gas well density had the greatest magnitude of effect on LEPC cluster density (>1.7 times more than other variables in most supported models; Table 1). Though few wind energy facilities existed within the LEPC range in Texas concurrent to this study, future work should incorporate electrical-transmission line and wind turbine densities into models of LEPC density, as they pose a growing concern for sustainable LEPC conservation (Pruett et al., 2009; USFWS, 2014).

The cluster density model was refined by including a quadratic relationship with grassland to shrubland ratio and an interaction with topographic roughness. In rougher terrain, LEPC cluster density peaked in areas composed of more grassland than shrubland (Fig. 6). This is likely because shrublands occurring in rougher terrain were composed of species like juniper (*Juniperus* spp.) or mesquite (*Prosopis glandulosa*) that are not components of quality LEPC habitat (Fuhlendorf et al., 2002; Hagen et al., 2004). We also found smaller LEPC clusters were associated with rougher terrain (Fig. 7). This further indicated increased topographic roughness (e.g., canyon slopes or other steep irregular terrain) was not conducive to abundant LEPCs, likely because vegetation structure or composition was unsuitable for foraging, nesting and other activities. Additionally, none of the landcover variables were related to cluster size, probably because they lacked the specificity for describing vegetation conditions dictating cluster size.

Modeling the relationships between cluster size and environmental conditions improved the description of where LEPCs were most abundant. Relying only on the size-bias corrected mean cluster size would underestimate LEPC density in the most suitable areas (Fig. 9). In areas with flat terrain and plant senescence occurring on day 343, the size-bias corrected mean cluster size was nearly twofold smaller than the spatially explicit cluster size. Indeed, relying on size-bias corrected mean cluster size alone would have underestimated individual LEPC density by ≈18% on average, in areas predicted to have ≥0.5 LEPC/km² (Fig. 9). Thus, it is important to consider models of spatially explicit cluster size.

We estimated 2101 (CV = 27.6%; 95% CI = 1573–3771) LEPCs in the sampling frame based on the most supported combination model. Using a conventional distance sampling-based analysis of the same dataset, Timmer et al. (2013) estimated the total abundance of LEPCs in the sampling frame as 1822 (CV = 23%). Previous work by Timmer et al. (2013, 2014) estimated 294 leks (CV = 19%) using conventional distance sampling and 236 leks (CV = 13.8%) using hierarchical distance sampling. As expected, the spatially explicit model improved the precision of lek abundance estimates (Hedley and Buckland, 2004). Including a spatially explicit description of cluster size limited gains in precision on total abundance (CV of 27.6% with the technique used here and 23% with conventional distance sampling). This is because the analysis technique used by Timmer et al. (2013) did not consider additional uncertainty caused by the overdispersion of cluster size, as our analysis did.

Some investigators seek validation of predictions using raw counts, yet our predictions defy validation with raw counts, because the "raw counts" (i.e., observed data) are biased by the detection process. This bias results in fewer groups of LEPC being detected than actually occur
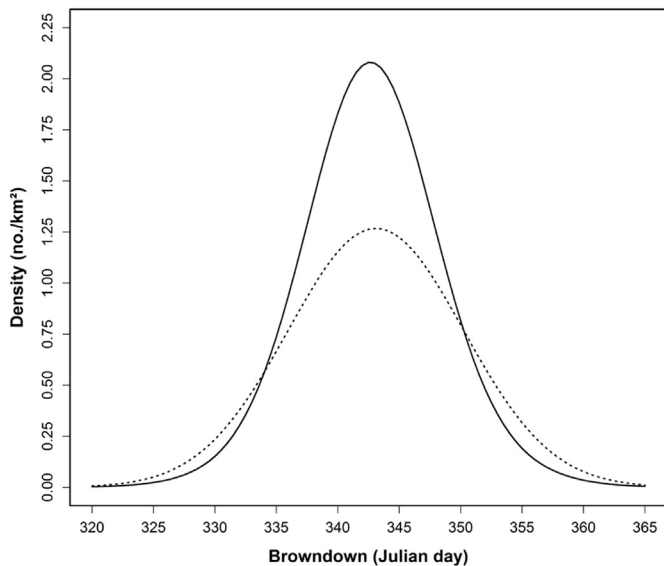
Fig. 9. Individual lesser prairie-chicken (LEPC) density based on cluster size as a function of land surface phenology metrics (solid line) and size-bias corrected mean cluster size (dotted line), 2010–2011, Texas, USA. Topographic roughness, road density, and oil and natural gas well density were held at minimum values and all other variables in the model were held at their means. Models relying on mean cluster size would underestimate LEPC density.

(i.e., some groups are missed by observers). It also results in larger cluster sizes than actually occur due to size-biased detection (e.g., observers are more likely to see larger groups than smaller groups of LEPCs). Indeed, the point of producing a model-based prediction to begin with is to correct for these detection processes.

The techniques used here improved upon previous mapping efforts by providing individual LEPC density instead of occurrence or lek density, accounting for covariate effects on detectability, and incorporating variables describing subtle nuances of vegetation conditions that thematic maps cannot (Jarnevich and Laubhan, 2011; Van Pelt et al., 2013; Timmer et al., 2014; Jarnevich et al., 2016). Although spatially

explicit models of LEPC lek density already exist for Texas (Timmer et al., 2014), conservation practitioners should continue improving models in which critical conservation actions are based. For example, the most supported phenology-based model suggested more LEPCs (≈ 175 individuals) occur in the northeastern population than indicated by the most supported landcover-based model (Fig. 8). Basing conservation decisions upon the most supported landcover model would misinform conservation practitioners, potentially causing them to focus management efforts elsewhere (Fig. 8).

Maps of individual LEPC density accounting for detection biases and relying on vegetation metrics (i.e., LSP) that are not overly simplistic can better guide management and conservation actions. Such predictions help prioritize land protection, identify areas for habitat restoration, and evaluate potential impacts from proposed development or landscape change. For example, well density in a seven county area (Ochiltree, Lipscomb, Roberts, Hemphill, Gray, Wheeler and Donley) of the northeastern population of LEPCs increased from an average of 1.035 wells/km^2 in 2011 to 1.333 wells/km^2 in 2015. Road density increased slightly from 1.433 km/km^2 in 2011 to 1.437 km/km^2 in 2015. Assuming all other variables remained constant, the model predicts 39.6 (95% CI = 16.6–91.0) fewer LEPCs in the seven county area in 2015 than 2011 given the changes in infrastructure (Fig. 10). In quadrats where well density increased >75%, the model suggests LEPC density would decline by 45–75% (Fig. 10).

Creating range-wide maps of individual LEPC density would be invaluable to conservation planning efforts. A range-wide (across five U.S. States) monitoring effort for LEPCs using distance sampling from helicopters began in 2012 (McDonald et al., 2014). Data from that effort could be combined with LSP metrics to build a range-wide map of individual LEPC density. However, LSP metrics for a functional plant group may vary by latitude (Henebry, 2013; Wang et al., 2013) which would require expanded modeling efforts to consider interactions between latitude and LSP metrics.

Temporal variation in weather, such as periodic drought and subsequent changes in growing season conditions may also impact LEPC habitat and demographics (Grisham et al., 2014). Therefore, annual dynamics of phenological characteristics (Tsalyuk et al., 2015) may be useful in describing demographic dynamics of LEPC or other prairie
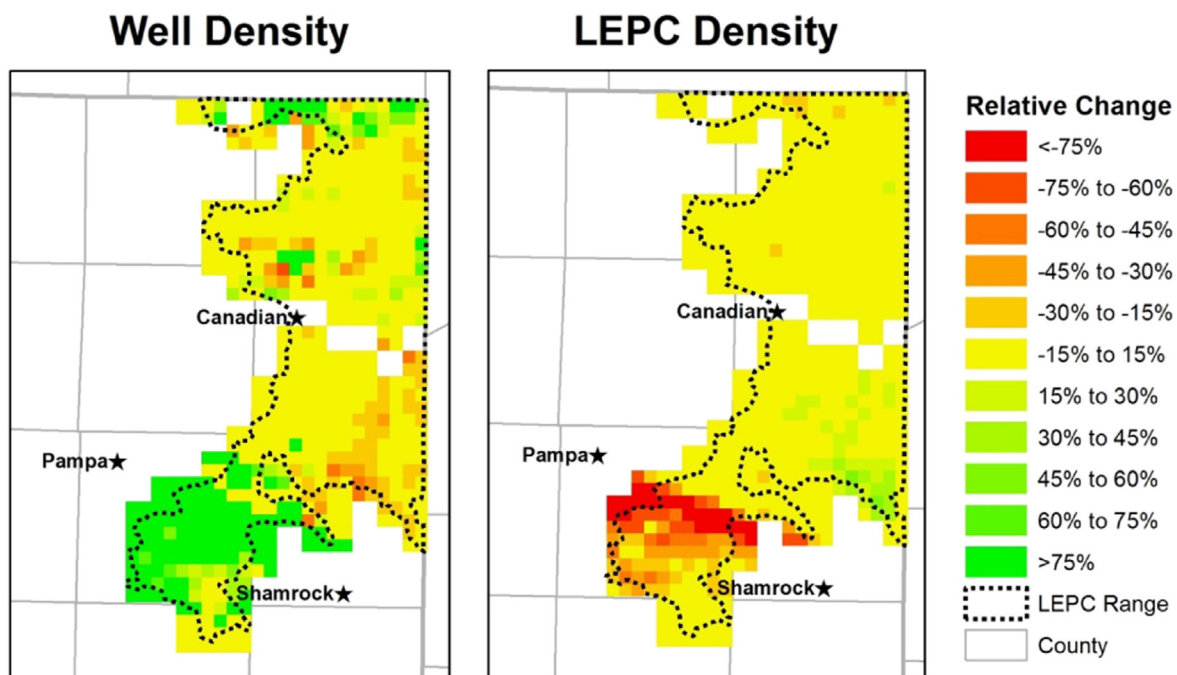
Fig. 10. Relative change in oil and natural gas well density (between 2011 and 2015) and its predicted effect on lesser prairie-chicken (LEPC) density in a seven county area (Ochiltree, Lipscomb, Roberts, Hemphill, Gray, Wheeler and Donley) of the northeastern population. Predictions of LEPC were based on the best cluster density and cluster size models.

grouse. Future work could couple population density or other population parameters with annual LSP metrics to estimate spatially explicit population dynamics or range-wide population trends. Determining inter- and intra-annual relationships between plant phenology and animal density in native shortgrass prairie ecosystems will ultimately enhance estimates of future climate change impacts on LEPC and other prairie organisms.

5. Conclusions

Thematic maps of landcover risk oversimplifying vegetative conditions beneficial for modeling the density or occurrence of terrestrial animals, especially in frequently disturbed landscapes such as grasslands and shrublands (Hovick et al., 2015; Viña et al., 2008). In contrast, phenology-based methods capture subtle differences in plant growth cycles and vegetative conditions that influence an animal's habitat preferences. By combining land cover and LSP metrics for estimating species abundance and predicting habitat quality, our work offers numerous advantages. First, this mixture of data improved the specificity in species-habitat predictions. Second, since mean cluster size misrepresents how individual animals distribute themselves among groups in a population, we show how LSP metrics enable discerning these patterns in cluster size, thereby better characterizing the environmental conditions predicting LEPC density. Third, we illustrate the application of free, global and readily available data for addressing species abundance and habitat questions. Fourth, we offer a realistic solution and sustainable method for range-wide LEPC monitoring and analysis. In the future, changing plant phenologies may indicate changing climatic conditions (Cleland et al., 2007), land use or disturbance regimes, enabling models incorporating LSP metrics to predict the response of animals to climate and land use changes. Such work centers on quantifying and monitoring LEPC habitats and populations through time. In aggregate, the modeling and monitoring methods we exemplified are transferable to mapping range-wide animal density and estimating the total abundance of other animals responding to phenological changes in their habitats. Such information is especially lacking for threatened and endangered species.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rse.2017.06.046.

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