Multi-scale occupancy estimation for the lesser prairie-chicken: 2012–2016

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All photos except top-left come from the Lesser Prairie-Chicken Initiative website (http://lpcinitiative.org/prairie-community/the-habitat/four-vegetation-types/)
Top-left: Shinnery Oak Prairie in winter, New Mexico. Photo by L. McDonald
Top-right: Sand Sagebrush Prairie, Colorado. Photo by Colorado Natural Heritage Program
Bottom-left: Mixed Grass Prairie, Kansas. Photo by D. Haukos
Bottom-right: Shortgrass/CRP Mosaic, Kansas. Photo by M. Waechter

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EXECUTIVE SUMMARY

The range-wide monitoring program for the lesser prairie-chicken (*Tympanuchus pallidicinctus*) conducted by the Western Association of Fish and Wildlife Agencies plays an important role in landscape conservation initiatives for the recovery of the species. Methodologies to evaluate lesser prairie-chicken responses to habitat conditions and conservation practices are necessary to evaluate the success of these initiatives. We adapted the data collected as part of the range-wide monitoring program (2012–2016) to apply a multi-scale occupancy model based on 15-km × 15-km grid cells and 7.5-km × 7.5-km quadrants to meet the following objectives:

1. Quantify the range-wide annual variation in the probability of occupancy of the lesser prairie-chicken at two spatial scales over the five years of study.
2. Identify the most important predictors of lesser prairie-chicken occupancy (including anthropogenic land uses, drought-related climatic conditions, conservation actions, and vegetative landcover) throughout the entire range and within each of four ecoregions.
3. Map the probability of lesser prairie-chicken occupancy range-wide as a function of the most important predictor variables.

Range-wide, we found that the probability of occupancy at the large scale (15-km × 15-km grid cells) was relatively constant across years at 0.31 (90% confidence interval = 0.26, 0.36). Given occupancy of the large grid cell, the probability of occupancy at the small scale (7.5-km × 7.5-km quadrants) oscillated across years, but with no clear trend over time. Small-scale occupancy was greatest in the Shortgrass/CRP Mosaic ecoregion (typically between approximately 0.3 – 0.4) and relative to the other three ecoregions (typically < approximately 0.2). We used model predictions to evaluate *a priori* hypotheses for covariate effects on site occupancy. We found strong positive relationships range-wide between occupancy and shrubland landcover, the amount of land enrolled in the Conservation Reserve Program (CRP), grassland landcover, and the size of grassland-landcover patches; and these relationships were generally consistent at both scales of occupancy. There was weaker evidence range-wide of negative relationships between occupancy and woodland landcover or anthropogenic development. We continued the investigation of multi-scale covariate relationships within each of four ecoregions. The ecoregion-specific analyses generally agreed with the results of the range-wide analysis, but provided additional insight into the effect of covariates that were found to be ecoregionally important. Mapping the unconditional probability of small-scale occupancy relative to the important covariates provided a spatially explicit representation of habitat suitability range-wide. The results of this work provide insight into the range-wide dynamics of lesser prairie-chicken occupancy, suggesting that presence of lesser prairie-chickens at the scales we examined varied somewhat by ecoregion, but was relatively constant over five years. Furthermore, although our study was observational in nature, our results demonstrate that the presence of lesser prairie-chickens was related to human-related landscape characteristics, suggesting the possibility to affect occupancy through management and conservation efforts.

INTRODUCTION

The range-wide conservation plan for the lesser prairie-chicken (LEPC, *Tympanuchus pallidicinctus*) outlined threats from habitat loss and fragmentation, climate change, and anthropogenic development, as well as conservation efforts for species recovery (Van Pelt et al. 2013). The LEPC range-wide monitoring program provides a unified framework for estimating long-term population status and trend, and monitoring the success of conservation efforts (McDonald et al. 2014). The data from the LEPC range-wide monitoring program were adapted to allow occupancy estimation at the scale of 7.5-km × 7.5-km quadrants nested within each of the 15-km × 15-km grid cells (Adachi et al. 2015, Hagen et al. 2016). We developed a series of covariates to represent *a priori* hypotheses for the effects of landscape composition and configuration, anthropogenic development, drought-related climatic conditions, and conservation efforts on LEPC occupancy patterns at two spatial scales. We extended the predictive multi-scale occupancy model of Hagen et al. (2016) to investigate additional covariate relationships for all data collected from 2012–2016. The predictive multi-scale models were used to investigate second-order habitat relationships (Johnson 1980, Haukos and Zavaletta 2016) using the theory of hierarchical habitat use (Cody 1985), where habitat use at the small-scale (56.25 km^2) scale is conditional on habitat use at the large-scale (225 km^2). The relationships between occupancy and covariates of interest have implications for landscape conservation at multiple scales (George and Zack 2001), perhaps suggesting management actions that could maintain or increase the range-wide extent of occurrence of LEPC.

Hagen et al. (2016) examined the adaptability of one year of data from the current range-wide aerial survey (McDonald et al. 2015; hereafter "RW-survey") to estimate LEPC occupancy at two scales: 15-km × 15-km grid cells and 7.5-km × 7.5-km quadrants nested within the larger grid cells. They evaluated two datasets—the first dataset was limited to 2015 data from the original RW-survey design, and the second dataset was adapted to include repeated temporal replicates from 2015 data to estimate occupancy (Hagen et al. 2016). The probability of occupancy was estimated at multiple spatial scales for both datasets. The primary results indicated that precision was not enhanced significantly when supplemented with repeated temporal replicates (Hagen et al. 2016). For this analysis, we continued to pursue the multi-scale occupancy modeling effort using data from the original design of the RW-surveys for the years 2012–2016, which allowed for the evaluation of annual differences due to extreme variation in drought-related climatic conditions.

Hagen et al. (2016) continued and conducted an exploratory evaluation of the potential of the multi-scale occupancy model to predict the effects of habitat and conservation practices on LEPC occupancy using a limited set of predictive covariates. Continuing this effort, we expanded the predictive covariates to include additional covariates for habitat composition and configuration, anthropogenic development, drought-related climatic conditions, and conservation efforts; and we examined the effects of the expanded list of covariates over multiple years of data. Our objectives were to (1) quantify the range-wide annual variation in the probability of occupancy of the LEPC at two spatial scales over the five years of study, (2) identify the most important predictors of LEPC occupancy throughout the entire range and within each of four ecoregions, and (3) map the probability of LEPC occupancy range-wide as a function of the most important predictor variables.

METHODS

Study Area

The study area spanned the entire estimated occupied range of the lesser prairie-chicken in 2011 (8 million ha), including portions of five U.S. states: Colorado, Kansas, New Mexico, Oklahoma, and Texas (McDonald et al. 2014; Figure 1). Due to expected geographic variation in

LEPC habitats, distribution, and abundance, the study area was subdivided into four ecoregions for ecoregion-level analyses: Shinnery Oak Prairie (SOPR), Sand Sagebrush Prairie (SSPR), Mixed Grass Prairie (MGPR), and Shortgrass/CRP Mosaic (SGPR; Figure 1).

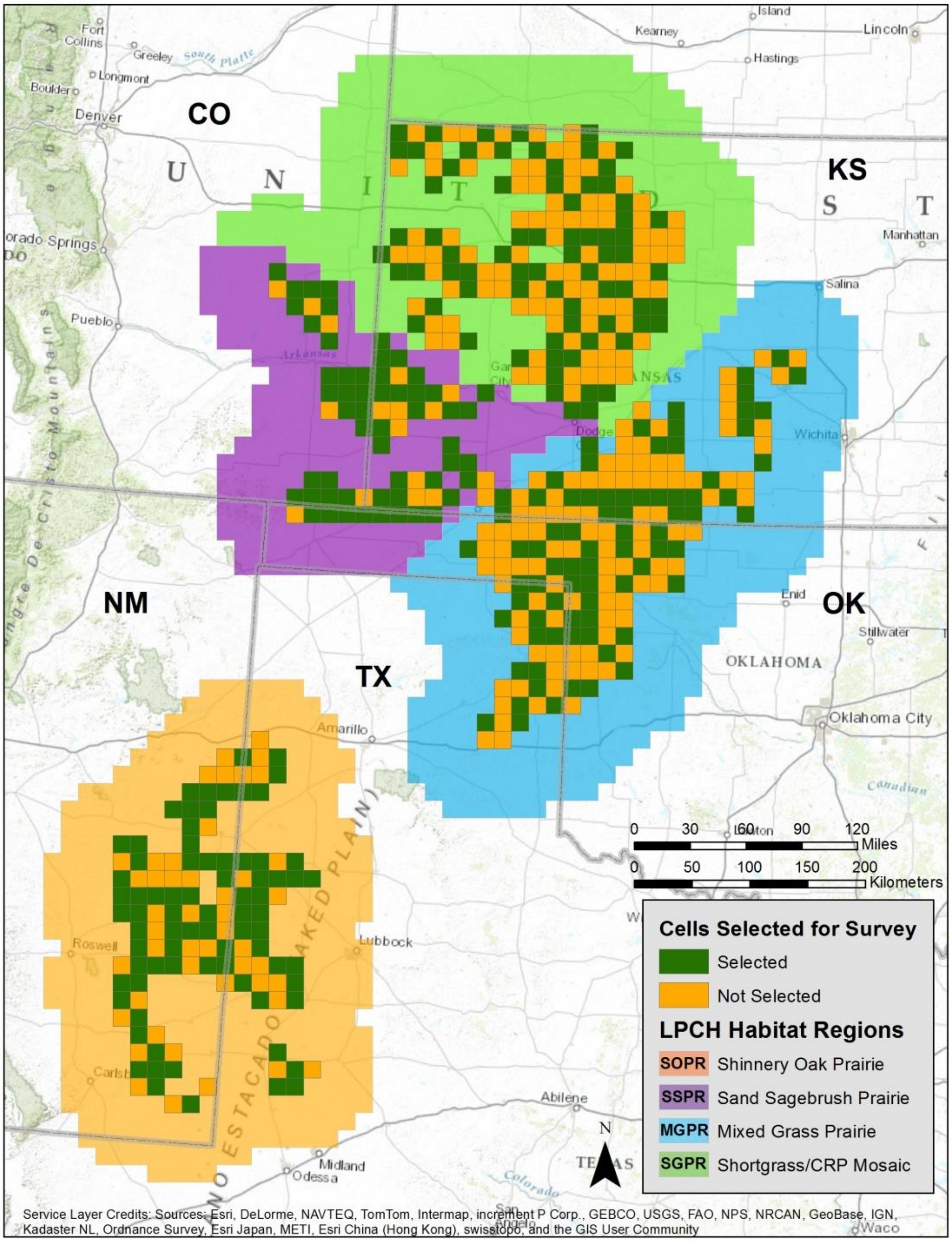

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Figure 1. Study area map showing 15-km × 15-km grid cells surveyed for lesser prairie-chickens, 2016. The colored areas surrounding each ecoregion indicate an approximate 77.7-km (30-mi) buffer into which the survey may be expanded in the future.

Data Collection

Covariate development

We derived covariates that described anthropogenic land uses, drought-related climatic conditions, conservation actions, and vegetative landcover at two spatial scales (225 km^2 grid cells and 56.25 km^2 quadrants) within a Geographic Information System (see Table A1, Appendix A for descriptions, sources, and references for covariate data). As possible, the values of covariates were allowed to vary from year to year, meaning the value of a grid- or quadrant-level covariate could change annually as updated source datasets were available (e.g., 5% of the grid cell was enrolled in prescribed grazing practices one year, but 8% was enrolled in the next year). However, covariates representing primary road density, transmission line density, and landcover types sourced from NLCD (see Table A1) were assumed to be constant through time. We attributed the entire sampling frame of 15-km × 15-km grid cells and 7.5-km × 7.5-km quadrants with the value of each covariate each year for the purpose of modeling and mapping the occupancy distribution.

Vegetation-related covariates described both landscape composition (the percentage of each grid cell or quadrant covered by selected vegetation types) and landscape configuration (the mean patch size of selected vegetation types within a grid cell or quadrant). We included landscape-composition covariates at both spatial scales and describing cropland, grassland, shrubland, mesquite (*Prosopis* spp.) woodland, eastern red cedar (*Juniperus virginiana*) woodland, and wetland vegetation types (Table A1). We also combined some of our covariates to define broader vegetation-related groups with biological relevance to LEPC. We defined native habitat as grassland or shrubland vegetation classes and defined general habitat as native habitat, land enrolled in the Conservation Reserve Program (CRP), or pasture lands (Table A1). We included covariates describing the landcover of woodland with canopy closure >1%, >5%, and >10% (Table

A1). We included landscape-configuration covariates at only the larger spatial scale (225 km^2 grid cells) and only those describing the mean patch size of cropland, grassland, native habitat, and general habitat vegetation types (Table A1).

We considered five covariates representing anthropogenic development at both spatial scales (225 km^2 grid cells and 56.25 km^2 quadrants), including FAA (Federal Aviation Administration) vertical structures, oil and gas wells, primary roads, transmission lines, and landcover associated with anthropogenic development (Table A1).

We developed covariates to represent conservation actions at both spatial scales (225 km^2 grid cells and 56.25 km^2 quadrants), including the landcover of Lesser Prairie-Chicken Initiative (LPCI) prescribed grazing practices, the amount and patch size of CRP-enrolled land, and the amount of land enrolled in conservation agreements administered by the Western Association of Fish and Wildlife Agencies (WAFWA; Table A1). We developed covariates describing drought-related climatic conditions at both spatial scales (225 km^2 grid cells and 56.25 km^2 quadrants). For each grid cell and year, we used the U.S. drought monitor to measure the number of summer drought weeks (classified as severe, extreme, or exceptional drought; Table A1) and the number of spring green weeks (not classified as abnormally dry, moderate, severe, extreme, or exceptional drought; Table A1).

Model Justification and Hypotheses

For the second objective, identifying the most important predictors of LEPC occupancy, we used predictive models and the method of multiple working hypotheses (Chamberlin 1965) to evaluate *a priori* hypotheses for the effects of landscape structure, anthropogenic development, conservation practices, and drought-related climatic conditions on site occupancy at the scale of 56.25 km^2 quadrants and 225 km^2 grid cells. We used predictive models to evaluate strength of evidence for covariate relationships at two spatial scales for which the LEPC may respond differently (Fuhlendorf et al. 2002, Haukos and Zavaletta 2016). The covariate relationships may be useful for informing conservation practices at different spatial scales and for identifying the habitat factors that influence the distribution of a species (Hagen et al. 2016, Pavlacky et al. 2017). The two spatial scales represented a continuum within second order habitat use (Johnson 1980), and the modeled relationships may represent suitable habitat for the LEPC at the landscape scale (Haukos and Zavaletta 2016). Landscape-level habitat loss and fragmentation are among the most important factors for the long-term population dynamics of the LEPC (Van Pelt et al. 2013, Haukos and Zavaletta 2016). The primary management question for landscape structure involved distinguishing between the composition and configuration of habitat to better understand the relative importance of habitat loss and fragmentation on range contraction and expansion. To the extent that habitat fragmentation is more important than habitat loss, the negative effects of habitat loss may be partially offset by managing for large patch sizes in the landscape (Kareiva and Wennergen 1995). We used known habitat associations of the LEPC to develop a species-oriented approach to investigate the landscape ecology of the species (Turner et al. 2001, Fischer and Lindenmayer 2007). We used patterns of landscape composition (i.e., landcover of unique vegetation types) to make inference about processes of habitat loss, and patterns of landscape configuration (i.e., mean patch size of unique vegetation types) to make inference about processes of habitat fragmentation. We investigated all model subsets of the landscape composition covariates for the small-scale occupancy (56.25 km^2 scale) and all subsets of the landscape composition and configuration covariates for the large-scale occupancy (225 km^2 scale; Table A1) to determine which aspects of landcover mosaics are favored by the LEPC in terms of core habitat patch configuration and between-patch matrix composition. We predicted landscape configuration and the mean patch size of grassland, shrubland, or native habitat would be important for the site occupancy of the LEPC (Hagen et al. 2016); but we were uncertain whether lands enrolled in CRP would contribute to core habitat patches or function as between-patch matrix habitat. We hypothesized that LEPC would respond negatively to increases in the landcover and patch size of cropland (Haukos and Zavaletta 2016). We also considered an alternate hypothesis that LEPC would respond positively to landscape heterogeneity (Fahrig et al. 2011), wherein the probability of occupancy would be highest at intermediate values of cropland landcover or patch size (Ross et al. 2016a). We also investigated curvilinear responses for grassland, shrubland, and native habitat to represent hypotheses for landscape heterogeneity involving non-linear responses to suitable habitat at the landscape scale. Finally, we investigated possible interactions between ecoregion (as a factor) and continuous landscape composition and configuration covariates because we hypothesized that habitat-occupancy relationships likely varied by ecoregion.

We developed hypotheses for anthropogenic disturbance using covariates for vertical structures, oil and gas wells, primary road density, transmission lines, and landcover associated with anthropogenic development (Table A1). We predicted LEPC occupancy would decline with increasing anthropogenic development (Bartuszevige and Daniels 2016). In addition, we investigated specific anthropogenic threats and hypothesized LEPC occupancy would decline with increasing oil and gas, transmission line, and primary road development (Hagen et al. 2011, Van Pelt et al. 2013), as well as vertical structures.

We evaluated hypotheses for conservation efforts in the ecoregions using covariates for CRP-enrolled land, LPCI-prescribed grazing, and WAFWA conservation easements. We predicted LEPC occupancy would increase with increasing landcover of the LPCI core conservation practices, including prescribed grazing and CRP-enrolled land (Bartuszevige and Daniels 2013, USFWS 2011, Hagen et al. 2016). We evaluated three hypotheses for LEPC responses to CRP in tandem with landscape composition covariates, including the (1) contribution of CRP-enrolled land to the landcover and patch configuration of general habitat, (2) additive area of CRP-enrolled land as between-patch matrix habitat, and (3) additive effect of mean patch size of CRP-enrolled land. The first hypothesis would be supported if models containing covariates for general habitat were supported over models containing covariates for native habitat. In addition to the above hypotheses, we evaluated quadratic relationships for the landcover and patch size of CRP-enrolled land to investigate whether occupancy has highest at intermediate amounts or sizes of CRP-enrolled lands. In addition to independent hypotheses for the positive effects of prescribed grazing and WAFWA conservation easements, we investigated whether LEPC occupancy increased with the combination of LPCI prescribed grazing and WAFWA conservation easements. We investigated interactions with the ecoregion factor and conservation covariates to evaluate whether the effect of conservation efforts varied by ecoregion. We evaluated all-model subsets of the conservation covariates with the landscape structure, anthropogenic development, and drought-related climatic covariates to evaluate support for the relative effects of conservation efforts in the ecoregions.

Because climate change in the Southern Plains is expected to influence the population viability of the LEPC (Grisham et al. 2016), we investigated hypotheses for the effects of spatial and temporal variation in drought on the range dynamics of the LEPC. The interaction between spring precipitation and vegetation cover has the potential to influence key population vital rates, such as nest survival and recruitment (Grisham et al. 2016). We predicted that LEPC range expansion would be correlated with spatial and temporal variation in the number of non-drought weeks during spring (Table A1). Drought during the summer months may have large influences on invertebrate prey availability, and together with extreme temperatures, have potential consequences for recruitment and adult survival (Grisham et al. 2016). We hypothesized that LEPC range contraction may be correlated with the spatial and temporal variation in the number of drought weeks in the summer (Table A1). We evaluated hypotheses for interactions between the drought-related covariates and covariates describing landscape structure and conservation efforts to understand mechanisms for range expansion and contraction in the ecoregions. In addition, we investigated interactions between the ecoregion factor and continuous drought-related covariates to evaluate the hypothesis that the effects of climatic conditions varied from ecoregion to ecoregion.

Sampling Design and Field Surveys

Our sampling design and field methodology are detailed by McDonald et al. (2014) and Hagen et al. (2016) and summarized here. McDonald et al. (2014) used a spatially balanced sampling procedure to select 15-km × 15-km grid cells to survey for LEPC. The survey effort varied annually and by ecoregion, but approximately 250–300 total grid cells were surveyed each year (McDonald et al. 2014, Hagen et al. 2016). We subdivided each grid cell into four quadrants (7.5-km × 7.5-km each). During 2012–2016, the range-wide survey crew flew a single 7.5-km line transect through each quadrant during March, April, or May and recorded detections of prairie-chickens within 300 m of the line using a double-observer method. LEPC, greater prairie-chickens (*Tympanuchus cupido*), and their hybrids co-occur in portions of the SGPR ecoregion, but are not reliably distinguishable during aerial surveys. Therefore, on-the-ground visits were conducted to verify species identification in areas where mixed-species groups were possible (McDonald et al. 2014, Hagen et al. 2016).

Statistical Analysis

Sampling framework for multi-scale occupancy

We aggregated and summarized data recorded in the database of the WAFWA LEPC range-wide monitoring program (McDonald et al. 2014) such that large-scale occupancy corresponded to the detection of LEPC on 15-km × 15-km grid cells and small-scale occupancy corresponded to the detection of the species in four quadrants (7.5-km × 7.5-km) nested within the grid cells (Hagen et al. 2016). The encounter history was arranged by treating independent observers in the helicopter as independent sampling occasions to estimate the probability of detection (Hagen et al. 2016). We pooled the encounters of LEPC across the observer in the front-left seat and the pilot in the front-right seat (first occasion or search). Similarly, we pooled the encounters across the observers in the back-left seat and back-right seat (second occasion or search). This yielded an encounter history with two occasions or searches of a quadrant. For example, consider the sampling situation with two survey occasions (one each for the front- and back-seat observers, respectively) and four quadrants within grid cell i, and encounter history H_i = 01 11 00 00 (0 = non-detection and 1 = detection). In this example, LEPC were detected by the back-seat observers in quadrant 1, by the front- and back-seat observers in quadrant 2, and were not detected in quadrants 3 or 4.

Implicit dynamics multi-scale occupancy

We estimated the detection and occupancy probabilities of the LEPC using the implicit dynamics (MacKenzie et al. 2006) version of the multi-scale occupancy model (Nichols et al. 2008, Pavlacky et al. 2012). The multi-scale occupancy model provides inference to the relationship between occupancy patterns and covariates of interest at two spatial scales. Animals select habitat at multiple, hierarchical spatial scales (Hutto 1985), so understanding occupancy patterns at multiple spatial scales is imperative for the successful management of wildlife and their habitats (Chalfoun and Martin 2007). The model allowed estimation of three parameters that corresponded to each level in the hierarchical sampling design: front- and back-seat observers nested within 7.5-km × 7.5-km quadrants to estimate detection, quadrants nested within 15-km × 15-km grid cells to estimate small-scale occupancy of quadrants, and grid cells nested within ecoregions to estimate large-scale occupancy of grid-cells. The parameters of the model were (1) the probability of detection p_{ijkt} for observer k, quadrant j, grid cell i and year t given the quadrant and grid cell were occupied in year t; (2) the probability of small-scale occupancy θ_{ijt} for quadrant j, grid cell i and year t given the grid cell was occupied in year t; and (3) the probability of large-scale occupancy ψ_{it} for grid cell i and year t. The assumptions of the multi-scale occupancy model were no un-modeled heterogeneity in the probabilities of detection and occupancy, closure of each quadrant to changes in occupancy over the observer occasions, independence of the detections of LEPC at each quadrant, and that the target species were never falsely detected (MacKenzie et al. 2006, Nichols et al. 2008, Pavlacky et al. 2012). We fit the models using the RMark interface (Version 2.2.4; Laake 2013, R Core Team 2017) for program MARK (Version 8; White and Burnham 1999). We used the linear model design matrix and logit link function to estimate the β parameters of the covariate model (White and Burnham 1999). We specified each year as a separate group in the parameter index matrix (White and Burnham 1999). Using year as a group effect constrained the parameter space across years, precluding pseudo-replication and under-estimation of variance.

The multi-scale model can be thought of as a within-season robust design (Pollock 1982), whereby quadrants within grid cells were primary occasions for estimating small-scale occupancy (θ), and multiple observers were secondary occasions for estimating detection probability (p) (Pavlacky et al. 2012). From the robust design perspective, the model decomposes the observation process into detection (p) and availability (θ) probabilities, resulting in improved inference on the large-scale occupancy (ψ) of grid cells (Nichols et al. 2008, Mordecai et al. 2011). Because ψ_i corresponds to the occupancy probability of grid cell i and θ_j corresponds to the occupancy probability of quadrant j given that the grid cell i was occupied, the product ψ_i*θ_j represents the unconditional probability of small-scale occupancy at quadrant j (Nichols et al. 2008, Pavlacky et al. 2012).

Annual variation in site occupancy

We used the implicit dynamics (MacKenzie et al. 2006) version of the multi-scale occupancy model (Pavlacky et al. 2012, Hagen et al. 2016) to investigate annual variation in large-scale (ψ) and small-scale (θ) occupancy of the LEPC. The candidate set for large-scale occupancy was composed of five models, including the full model ψ(ecoregion + year + ecoregion * year) and reduced models ψ(ecoregion + year), ψ(ecoregion), ψ(year) and intercept only ψ(.). Likewise, the candidate set for small-scale occupancy was composed of five models, including the full model θ(ecoregion + year + ecoregion * year) and reduced models θ(ecoregion + year), θ(ecoregion), θ(year) and intercept only θ(.). We modeled the detection parameter (p) according to three continuous covariates for ordinal date, time after sunrise, and annual trend; and three factor covariates for ecoregion, observer, and year (Table A1). We excluded detection models containing both the continuous covariate for annual trend and the factor covariate for year. The candidate model set for detection included all subsets of five covariates and the intercept only model p(.), for a total of 61 models. We fit the full models for large-scale and small-scale occupancy using an identity design matrix and sine link function to ensure convergence (White and Burnham 1999), and fit all other models using a linear regression design matrix and logit link function. We fit all subsets of the covariates and parameters (Doherty et al. 2012) for a total of 1,200 models using the RMark interface (Version 2.2.4, Laake 2013, R Core Team 2017) for program MARK (Version 8; White and Burnham 1999).

We ranked the candidate set of models using Akaike's Information Criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002), with sample size defined by the number of surveyed 15-km × 15-km grid cells. We evaluated support for annual variation in large-scale or small-scale occupancy using evidence ratios and cumulative AIC$_c$ weights for balanced model sets ([$w_+(j)$]; Burnham and Anderson 2002). We determined support for detection covariates using variable support for unbalanced model sets according to $\gamma_i = [w_i/(1\text{-}w_i)]/[f_i/(1\text{-}f_i)]$, where w_i is the cumulative AIC$_c$ weight and f_i is the frequency of the covariate i in the model set (Doherty et al. 2012). Values of $\gamma_i >> 1$ indicate support for covariate i, values $\gamma_i \approx 1$ are inconclusive, and values $\gamma_i << 1$ indicate little support for covariate i (Doherty et al. 2012).

We evaluated effect sizes and conditional 90% confidence intervals (CIs) for the year factor from high ranking models using the intercept for year 2012 and β parameters for years 2013–2016 with respect to 0. We model averaged year-specific estimates of large-scale or small-scale occupancy for models with ΔAIC$_c < 4$ in which the year factor occurred (Burnham and Anderson 2002).

Range-wide relationships between covariates and multi-scale occupancy

We used the implicit dynamics (MacKenzie et al. 2006) version of the multi-scale occupancy model (Pavlacky et al. 2012, Hagen et al. 2016) to investigate covariate relationships for large-scale (ψ) and small-scale (θ) occupancy of the LEPC. We used all range-wide data in the four ecoregions from 2012–2016 (McDonald et al. 2016), but did not use the auxiliary data collected within the SGPR and SOPR ecoregions during 2015 (Adachi et al. 2015, Hagen et al. 2016). As above, we fit the models using the RMark interface (Version 2.2.4, Laake 2013, R Core Team 2017) for program MARK (Version 8; White and Burnham 1999).

Prior to model selection, we used a variable screening step to identify potential curvilinear quadratic relationships for continuous covariates, and two-way interactions between covariates for each parameter. To evaluate quadratic covariate relationships, we fit univariate $[\beta_0 + \beta_1 x_i]$ and quadratic $\left[\beta_0 + \beta_1 x_i + \beta_2 x_i^2\right]$ models for each covariate *i*; and to evaluate two-way interactions, we fit additive $\left[\beta_0 + \beta_1 x_i + \beta_2 x_j\right]$ and multiplicative $\left[\beta_0 + \beta_1 x_i + \beta_2 x_j + \beta_3 x_i * x_j\right]$ models for covariates *i* and *j*. We used information-theoretic model selection (Burnham and Anderson 2002) to evaluate support for quadratic covariate relationships, and selected the quadratic relationship for entry into the analysis when AIC_c was lower for the quadratic relationship than the univariate relationship. In a similar fashion, we selected a two-way interaction for entry into the analysis when AIC_c was lower for the multiplicative model than the additive model.

For large-scale occupancy (ψ), we fit the quadratic and interaction models while holding constant small-scale occupancy at θ(Ecoregion) and detection at *p*(Observer + Ecoregion + Year). We evaluated quadratic relationships for 12 covariates and investigated 171 interactions for large-scale occupancy. We found support for eight quadratic relationships and 39 interactions, and we included these in the model selection for large-scale occupancy along with the univariate and additive models.

For small-scale occupancy (θ), we fit the quadratic and interaction models while holding constant large-scale occupancy at ψ(Year) and detection at *p*(Observer + Ecoregion + Year). We investigated quadratic relationships for seven covariates and evaluated 129 interactions for small-scale occupancy. We found support for three quadratic relationships and 11 interactions, and we included these in the model selection for small-scale occupancy along with the univariate and additive models. For detection (*p*), we fit the quadratic and interaction models while holding constant large-scale occupancy at ψ(Year) and small-scale occupancy at θ(Ecoregion). We evaluated quadratic relationships for five covariates, and investigated 14 interactions on detection. We found no evidence of quadratic relationships or interactions and included only the main effects in model selection for the detection parameter.

Range-wide model selection

Model selection procedures increase in complexity when models contain multiple submodels and when research objectives require modeling the effect of multiple, potential predictor variables (Bromaghin et al. 2013). The multi-scale occupancy model we used is composed of three separate submodels: large-scale occupancy (ψ), small-scale occupancy (θ), and detection probability (p) (Nichols et al. 2008, Pavlacky et al. 2012, Hagen et al. 2016). Moreover, our objectives necessitated modelling ψ, θ, and p as functions of multiple predictor variables. We therefore adopted a two-staged model-selection approach to first select plausible structures for each submodel (i.e., the submodel stage), then to consider all possible combinations of plausible submodel structures (i.e., the full-model stage).

We used plausible-combinations model selection (Bromaghin et al. 2013) to determine the most likely drivers of LEPC occupancy at two spatial scales while accounting for incomplete detection. The plausible-combinations approach proceeded in two steps. First we identified plausible covariate relationships for each parameter independently, and second we combined all-model subsets of the submodels across parameters to identify parsimonious full-models (Bromaghin et al. 2013). For each parameter, we selected high-weight submodels with AIC$_c$ weight $w_i > 0.01$ and high-likelihood submodels with $-2\log(\mathcal{L})$ < maximum [$-2\log(\mathcal{L})$ of high-weight models] for entry into the second step of the plausible-combinations model selection analysis (Bromaghin et al. 2013).

In the first step of plausible combinations model selection, we constrained the candidate set of models by omitting submodels with correlated covariates (Pearson's $\rho > 0.6$). We flagged submodels with diminutive (<0.00001) standard errors (SE), and submodels with small (< 0.5) or large (> 5) t-ratios (β/SE) for inspection. In addition, we constrained the candidate set of models by omitting submodels with redundant covariates, irrespective of the magnitude of correlation. Redundant covariates were defined as those representing similar biological hypotheses with non-exhaustive and non-exclusive classification. For example, we did not allow covariates for the landcover of grassland and of native habitat in the same model because they exhibited considerable overlap in areal extent (Table A1). Finally, we expanded the candidate set of models by appending submodels that replaced the main effects by the supported quadratic relationships for covariate i, and two-way interactions for covariates i and j. For example, we evaluated main effects models, such as θ(Ecoregion + CRP + Grass) along with the associated interaction [θ(Ecoregion + CRP + Grass + Ecoregion * CRP + Ecoregion * Grass)] and quadratic [θ(Ecoregion + CRP + CRP^2 + Grass + Grass^2)] models. Following the above example, we also evaluated reduced interaction [θ(Ecoregion + CRP + Grass + Ecoregion * CRP), [θ(Ecoregion + CRP + Grass + Ecoregion * Grass)] and quadratic [θ(Ecoregion + CRP + CRP^2 + Grass), θ(Ecoregion + CRP + Grass + Grass^2)] models.

In the first step of plausible combinations model selection, we ran all subsets of 29 covariates for large-scale occupancy (ψ) with a maximum of three covariates per models while holding constant small-scale occupancy at θ(Ecoregion) and detection at p(Observer + Ecoregion + Year), resulting in a candidate set of 8,249 models. For small-scale occupancy (θ), we ran all subsets of 19 covariates with a maximum of four covariates per model while holding constant large-scale occupancy at ψ(Year) and detection at p(Observer + Ecoregion + Year), resulting in a candidate set of 16,218 models. For the detection (p) parameter, we ran all subsets of six covariates with a maximum of four covariates per model while holding constant large-scale occupancy at ψ(Year) and small-scale occupancy at θ(Ecoregion), resulting in a candidate set of 46 models.

In the second step of the plausible combinations model selection, we combined all subsets of the high-weight and high-likelihood submodels across parameters (Bromaghin et al. 2013), for a total of 40 models. We ranked the candidate set of models using AIC$_c$, and evaluated support for covariate effects on large-scale occupancy, small-scale occupancy, and detection using AIC$_c$, weights (Burnham and Anderson 2002). We illustrated the direction of effects of covariates at the range wide level using model averaged predictions of large-scale occupancy, small-scale occupancy and detection for the candidate set of models and estimated unconditional 90% CIs for the predictions (Burnham and Anderson 2002). We made multi-model inference from the entire candidate set using cumulative AIC$_c$ weights for balanced model sets (Burnham and Anderson 2002) and variable support for unbalanced model sets (Doherty et al. 2012). We evaluated effect sizes from the top-ranking models using β parameters for the covariates and conditional 90% CIs with respect to 0.

We limited the number of all-subset covariate models by allowing a maximum of three covariates in models for large-scale occupancy and four covariates in models for small-scale occupancy. Because of the limits we imposed on the maximum number of covariates allowed for *a priori* model selection, we ran an additional exploratory model selection analysis to determine if the data supported models with greater complexity than the limits imposed by the *a priori* analysis. We added each of the candidate covariates one at a time to the top *a priori* selected models, and we evaluated all subsets of the amended submodels. We fitted a total of 8,526 models, including the base submodels for each parameter. We selected the models using the model selection procedure outlined above. We ranked the candidate set of models using AIC$_c$ and evaluated support for the covariates using cumulative AIC$_c$ weights for balanced model sets (Burnham and Anderson 2002). We evaluated effect sizes and conditional 90% CI for the covariate β coefficients with respect to 0. We model averaged estimates of large-scale or small-scale occupancy for all models within ΔAIC$_c$

< 4 (Burnham and Anderson 2002).

Mapping the range-wide occupancy distribution

We model averaged the predictions of large-scale (ψ) and small-scale (θ) occupancy according to covariate values in the sampling frame for 15-km × 15-km grid cells and 7.5-km × 7.5-km quadrants, respectively. We multiplied the conditional estimates of small-scale occupancy ($\hat{\theta}_j$) for each of the *j* quadrants in grid cell *i* by the corresponding estimate of large-scale occupancy ($\hat{\psi}_i$) to arrive at the unconditional estimates of small-scale occupancy ($\hat{\theta}_j * \hat{\psi}_i$) for all quadrants in the sampling frame (Nichols et al. 2008, Pavlacky et al. 2012). We approximated the SE for the model-averaged unconditional estimate of small-scale occupancy using the delta method (Powell 2007). We estimated the coefficient of variation (CV) for the unconditional estimates of small-scale occupancy to quantify the uncertainty around the predicted occupancy distribution. As some covariates were time-varying, we used covariate values for the year 2016 for the map of predicted occupancy presented herein.

Ecoregional relationships between covariates and multi-scale occupancy

We used the same dataset for the ecoregional modelling effort as previously described for the range-wide modelling effort. Because of the geographic variation in LEPC habitats, distribution, and abundance, we hypothesized that some three-way interactions may exist between covariates in the range-wide models that were not adequately considered in the analysis of the combined data. We included models with two-way interactions when fitting models to ecoregional subsets of the data to obtain additional insight into whether the covariates (or an interaction of two covariates) that were most predictive of occupancy varied within ecoregions; and even if they did not, whether the effect of a given covariate (or an interaction of two covariates) had a consistent relationship with occupancy across ecoregions. We therefore repeated the multi-scale occupancy analysis, analyzing the data from each ecoregion independently.

Ecoregional model selection

We again used the two-staged model-selection procedure of the plausible-combinations approach to model selection (Bromaghin et al. 2013) to determine the most influential covariate drivers of LEPC occupancy at the two spatial scales within each ecoregion, while accounting for incomplete detection. We first selected plausible structures for each submodel of ψ, θ, and p. When fitting the initial models to identify plausible structures for large-scale occupancy (ψ), we fixed the small-scale occupancy submodel to $\theta(.)$ and the detection probability submodel to p(Observer + Year). When fitting initial models for small-scale (θ) occupancy, we fixed the large-scale occupancy submodel to ψ(Year) and the detection probability submodel to p(Observer + Year). When fitting initial models for detection probability (p), we fixed the large-scale occupancy submodel to ψ(Year) and the small-scale occupancy submodel to $\theta(.)$.

The ecoregion-specific datasets required more stringent screening criteria to accommodate poor model stability and spurious results due to over-parameterization given the relatively smaller amounts of data available to the model. In particular, the relatively small number of LEPC detections in three of the four ecoregions with low abundance of the LEPC (McDonald et al. 2014) required special attention. We initially investigated allowing up to six covariates in each submodel, but many models had difficulty converging on stable estimates. To ameliorate overfitting, we reduced the number of covariates we considered in each submodel, depending on the ecoregion (Table 1).

Table 1. Summary of the number of covariates allowed during the plausible-combinations stage of model selection for multi-scale occupancy models fit to ecoregional subsets of the lesser prairie-chicken data from the range-wide monitoring program, 2012–2016. The multi-scale occupancy model included submodels for large-scale occupancy (ψ), small-scale occupancy (θ), and detection probability (*p*). When a quadratic effect was included, the main effect for that covariate was also included, resulting in two covariates in the model for each quadratic term. When an interaction effect was included, the main effect for each interacting covariate was also included, resulting in three covariates in the model for each interaction term. Ecoregion acronyms are defined in Figure 1.

	Submodel		
Ecoregion	**ψ**	**θ**	***p***
1 (SOPR)	≤ 5, with ≤ 3 main effects	≤ 3	≤ 5, with ≤ 3 main effects
2 (SSPR)	≤ 2, with no quadratics or interactions	≤ 2, with no quadratics or interactions	≤ 2, with no quadratics or interactions
3 (MGPR)	≤ 3	≤ 3	≤ 5, with ≤ 3 main effects
4 (SGPR)	≤ 5, with ≤ 3 main effects	≤ 3	≤ 5, with ≤ 3 main effects

We identified the high-weight and high-likelihood submodels (Bromaghin et al. 2013; defined as in the range-wide analysis) for each parameter (i.e., ψ, θ, and *p*), then fitted all possible combinations of plausible submodels. We identified problematic multicollinearity among candidate covariates based on the combination of condition index and the regression coefficient variance-decomposition matrix (Hair, Jr. et al. 2010). We removed models from consideration when the condition index was ≥ 15 and the variance-decomposition proportion was ≥ 0.5. These threshold values were conservative (common values are 30 and 0.9, respectively; Hair Jr. et al. 2010), resulting in the removal of models with severe or even moderate levels of multicollinearity among predictor variables. As in the range-wide modelling effort, we omitted any model that included redundant covariates or covariates with high pairwise correlation (Pearson's $\rho > 0.6$), and we removed models from consideration that had inestimable model coefficients or exhibited instability in the estimated coefficients as evidenced by SE < 0.00001, or *t*-ratios < 0.5 or > 5.0. We then ranked the resulting candidate set of models by AIC_c (Burnham and Anderson 2002). We calculated measures of variable support using the same Doherty et al. (2012) calculations as in the range-wide analysis.

Rather than base our inference on a selected "best" model, we used multi-model inference methods to incorporate model-selection uncertainty into estimates of the effect that individual covariates had on ψ or θ (Burnham and Anderson 2002). We illustrated the direction and magnitude of the effects of covariates by graphing the model-averaged predicted values of ψ or θ (with unconditional 90% CIs) across the observed range of the covariate of interest. We computed model-averaged predictions using all models within the confidence set of models (i.e., models with $\Delta AIC_c < 2$), including models that did not contain the covariate of interest (Burnham and Anderson 2002). As a secondary, exploratory level of inference that did not rely on model averaging, we examined the β coefficient and conditional 90% CI for the covariate of interest in the highest-ranked model that contained the covariate. This secondary level of inference may be less reliable given it ignored model-selection uncertainty; however, we provide these results to allow some insight into the occupancy-covariate relationship for covariates that were in the confidence set of models, but that exhibited no discernable effect in the model-averaged results.

RESULTS

Annual Variation in Range-Wide Site Occupancy

We found little evidence for annual variation in the large-scale occupancy of the LEPC at 15-km × 15-km grid cells (Table B1). According to the evidence ratio, the highest-ranking model for constant large-scale occupancy across years [ψ(.)] was nine times more likely than the highest-ranking model including the year factor [ψ(Year); $\Delta AIC_c = 4.35$; $w_i = 0.008$]. The cumulative AIC_c weight for the effect of year on large-scale occupancy was $w_+(\text{year}) = 0.095$, providing very little support for the year factor. The model-averaged estimate of mean large-scale occupancy across years was $\widehat{\psi} = 0.31$ [SE($\widehat{\psi}$) = 0.03; CI = 0.26, 0.36].

We found limited evidence of annual variation in the small-scale occupancy of the LEPC at 7.5-km × 7.5-km quadrants (Table B1, Figure 2). According to the evidence ratio, the highest ranking model including only the ecoregion effect on small-scale occupancy [θ(Ecoregion)] was three times more likely than the highest ranking model including the additive effects of year and ecoregion [θ(Ecoregion + Year); Table B1]. In addition, the evidence ratio indicated the highest ranking model for the additive effect of year and ecoregion [θ(Ecoregion + Year)] was 45 times more likely than the multiplicative effects of year and ecoregion [θ(Ecoregion * Year); $w_i = 0.001$]. The cumulative AIC$_c$ weight for the effect of year on small-scale occupancy was w_+(Year) = 0.262, providing modest support for the effect of year on small-scale occupancy. However, the cumulative evidence ratio indicated the effect of year on small-scale occupancy was three times more important than the effect of year on large-scale occupancy [w_+(Year) = 0.095]. The additive effect of year in the 9th ranked model (ΔAIC$_c$ = 2.05) indicated small-scale occupancy was lower in year 2013 than in 2012, but was not appreciably different from year 2012 in 2014, 2015 and 2016 (Table B2, Figure 2). In addition, the small-scale occupancy of the LEPC was greater in the SGPR ecoregion than in the MGPR, SSPR and SOPR ecoregions (Table B2, Figure 2).

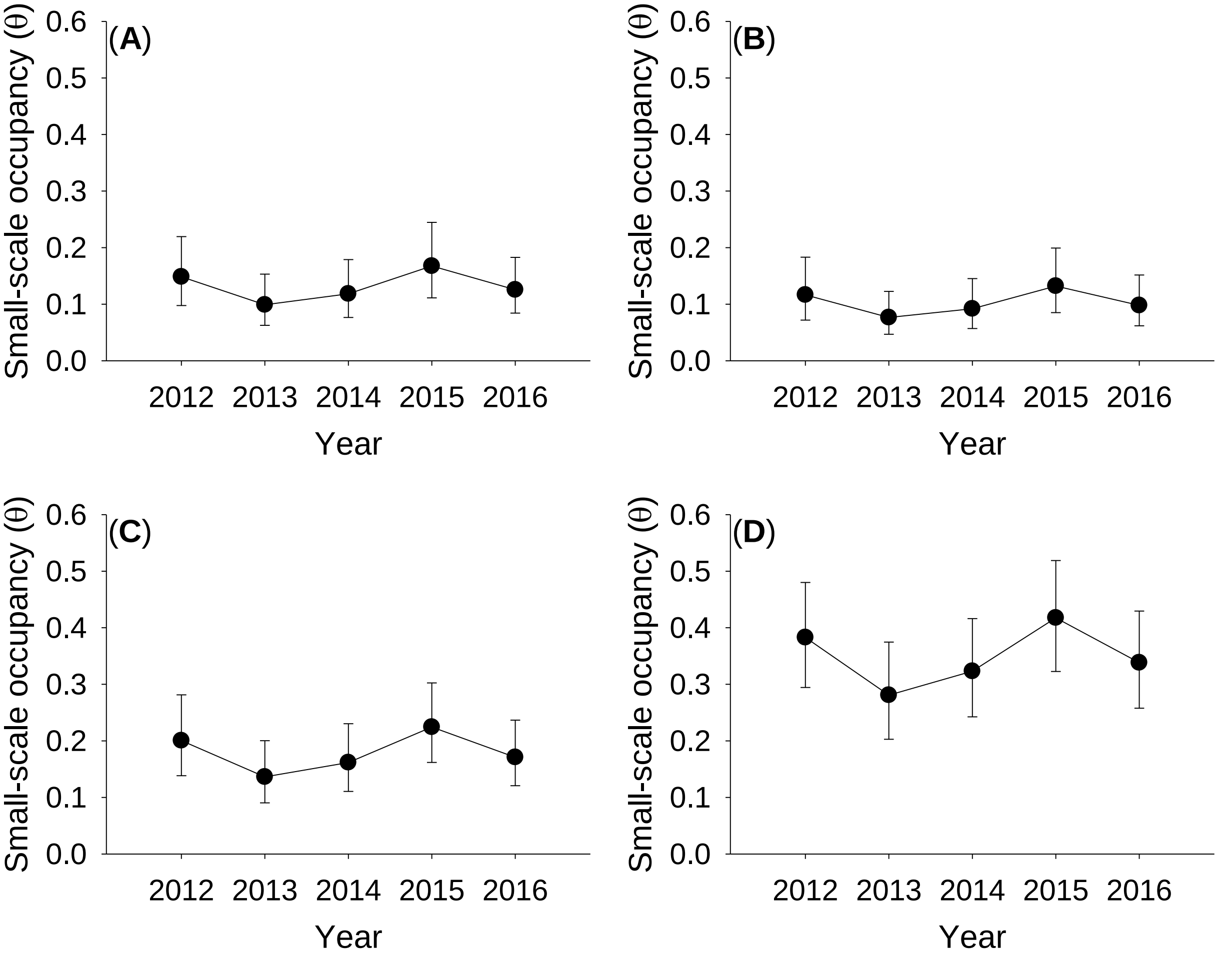

Figure 2. The small-scale occupancy (θ) of the lesser prairie-chicken by ecoregion and year for the (A) Shinnery Oak Prairie, (B) Sand Sagebrush Prairie, (C) Mixed Grass Prairie and (D) Shortgrass CRP/ Mosaic Prairie from the range-wide monitoring program, 2012–2016. The filled symbols are model averaged estimates of small-scale occupancy and the error bars are unconditional 90% confidence intervals.

We found considerable evidence for the effects of observer, annual trend, time after sunrise, and ordinal date on the detection probability of the LEPC (Table B1, Table B3, Figure 3). The support of the detection covariates was greatest for observer ($\gamma_{\text{observer}} = 2.50 \times 10^8$), followed by trend ($\gamma_{\text{trend}} = 3.73$), time after sunrise ($\gamma_{\text{time}} = 2.50$), ordinal date ($\gamma_{\text{date}} = 0.95$), ecoregion ($\gamma_{\text{ecoregion}} = 0.69$) and year ($\gamma_{\text{year}} = 0.18$). The detection of the lesser prairie-chicken was greater for back-seat observers than front-seat observers, and detection increased over survey years, with increasing time after sunrise, and ordinal date (Table B3, Figure 3).

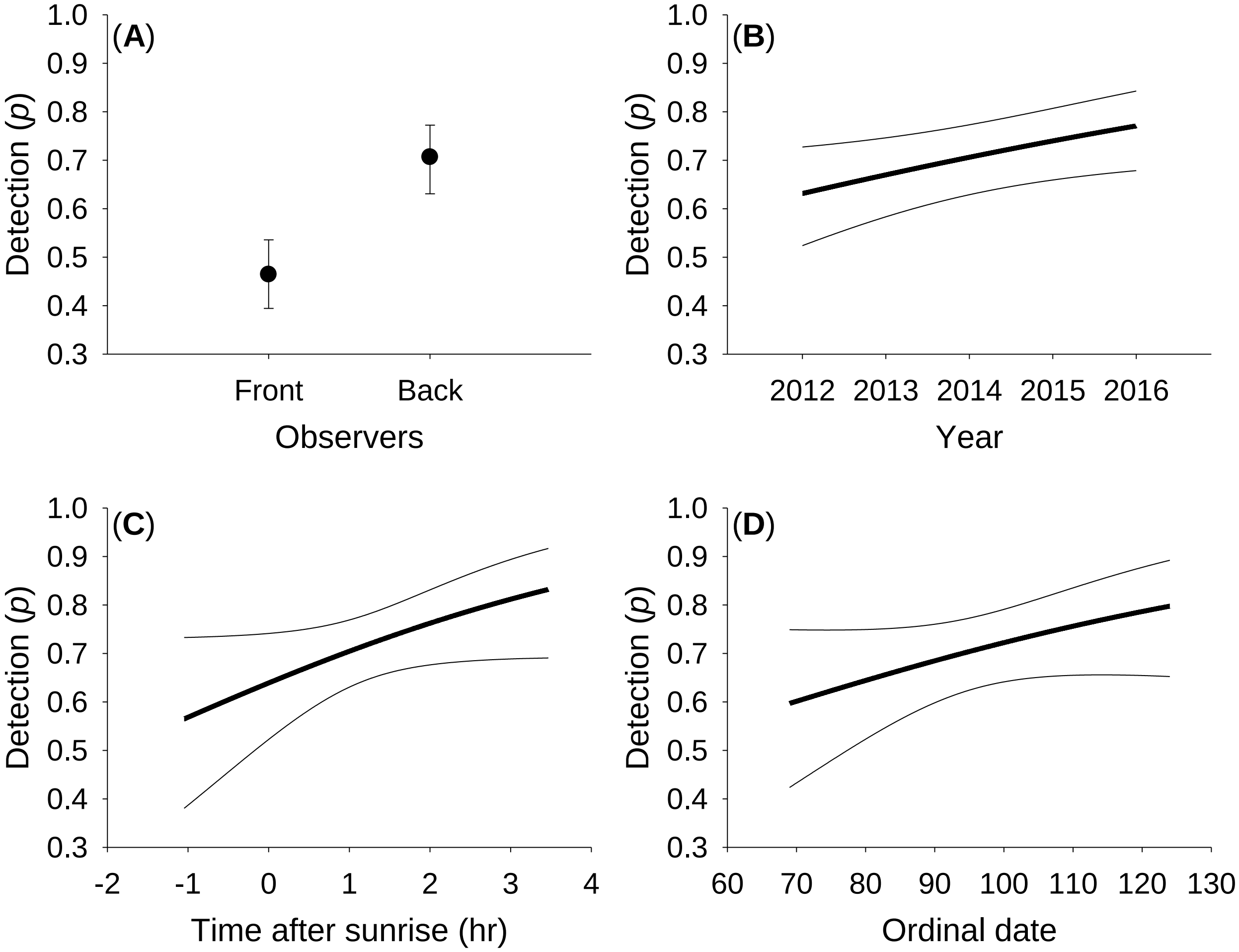

Figure 3. The probability of detection (*p*) of the lesser prairie-chicken by (A) observer, and (B) year, (C) time after sunrise and (D) ordinal date for the back-seat observers from the Shortgrass Prairie CRP/ Mosaic Ecoregion of range-wide monitoring program, 2012–2016. The filled symbols and bold trend lines are model averaged estimates of detection for models including that covariate at mean values of other covariates in the model, and the error bars and bounding lines are unconditional 90% confidence intervals.

Range-wide Multi-scale Covariate Relationships

In the first step of plausible-combinations model selection, we identified two plausible submodels for large-scale occupancy (Table C1). However, we did not consider the second-ranked model containing the quadratic relationship of CRP to be a competing model, because the addition of the quadratic term did not appreciably decrease the -2log($\mathcal{L}$) value for the model (Arnold 2010). For this reason, we considered a single plausible submodel for large-scale occupancy [ψ(CRP + GrassPatch + Shrub)] in the second step of the plausible combinations models selection analysis.

We identified three plausible submodels for small-scale occupancy (Table C2). However, we did not consider the third-ranked model containing the quadratic term for grassland as a competing model (Table C2), because the addition of the quadratic term did not appreciably decrease the -2log($\mathcal{L}$) value relative to the 2^{nd} ranked model (Arnold 2010). For this reason, we considered only the top two models in the second step of the plausible combinations models selection analysis (Table C2). We identified 20 plausible submodels for detection (Table C3), and we considered these models in the second step of the plausible combinations models selection analysis. The support of the detection covariates was greatest for observer ($\gamma_{observer} = 2.53 \times 10^8$), followed by trend ($\gamma_{trend} = 3.24$), and time after sunrise ($\gamma_{time} = 1.11$), and there was less support for ordinal date ($\gamma_{date} = 0.66$), ecoregion ($\gamma_{ecoregion} = 0.51$), and year ($\gamma_{year} = 0.21$).

In the second step of plausible combinations model selection, we ran all subsets of plausible submodels across parameters, resulting in 40 models. The top-ranked model for the multi-scale occupancy relationships of the LEPC contained the effects of shrubland, grassland patch size, and CRP on large-scale occupancy, the interaction between CRP and ecoregion, shrubland, and interaction between the quadratic term for grassland and ecoregion on small-scale occupancy, and the effects of observer, annual trend, and time after sunrise on detection (Table C4). The 2^{nd} ranked model that omitted the quadratic term for grassland and included the interaction between the main effect for grassland and ecoregion for small-scale occupancy showed nearly equal support as the highest ranking model (Table C4). Overall, we found considerable model selection uncertainly and 13 candidate models with $\Delta\text{AIC}_c < 2$ (Table C4).

The large-scale occupancy of the LEPC increased with increasing shrubland landcover, grassland patch size, and amount of CRP-enrolled land (Figure 4). The 90% CIs for these effects did not cover 0, indicating large and precise effect sizes for these covariates (Table C5, Table C6).

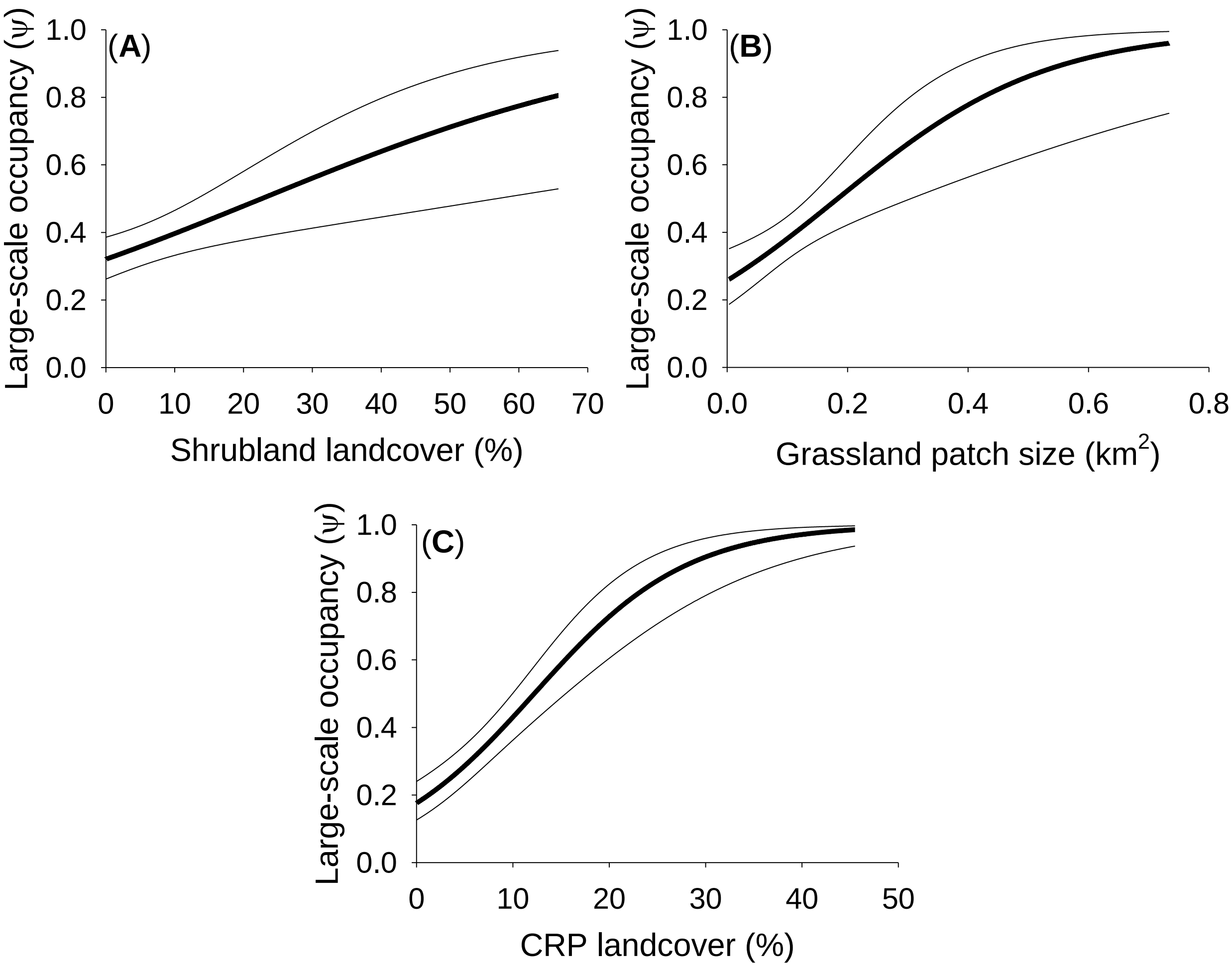

Figure 4. The large-scale occupancy (ψ) of the lesser prairie-chicken at 15 × 15-km grid cells by the (A) percentage (%) of shrubland landcover, (B) mean patch size of grassland landcover (km^2), and (C) percentage of area enrolled in the Conservation Reserve Program (CRP) from the range-wide monitoring program, 2012–2016. The bold trend lines are model averaged estimates of large-scale occupancy at the mean values of other covariates in the model and the bounding lines are 90% CIs.

The small-scale occupancy of the LEPC showed a large increase with increasing amounts of CRP-enrolled land in the SGPR ecoregion, smaller positive effects in the SSPR and MGPR ecoregions, and a much smaller of effect of CRP-enrolled land in the SOPR ecoregion (Figure 5). The interaction between CRP and ecoregion indicated the slope of the CRP effect was much lower in the SOPR, SSPR and MGPR ecoregions than the slope of the CRP effect in the SGPR ecoregion

(Table C5, Table C6). The 90% CIs for the interaction terms did not cover 0, indicating large and precise effect sizes for these multiplicative effects (Table C5, Table C6).

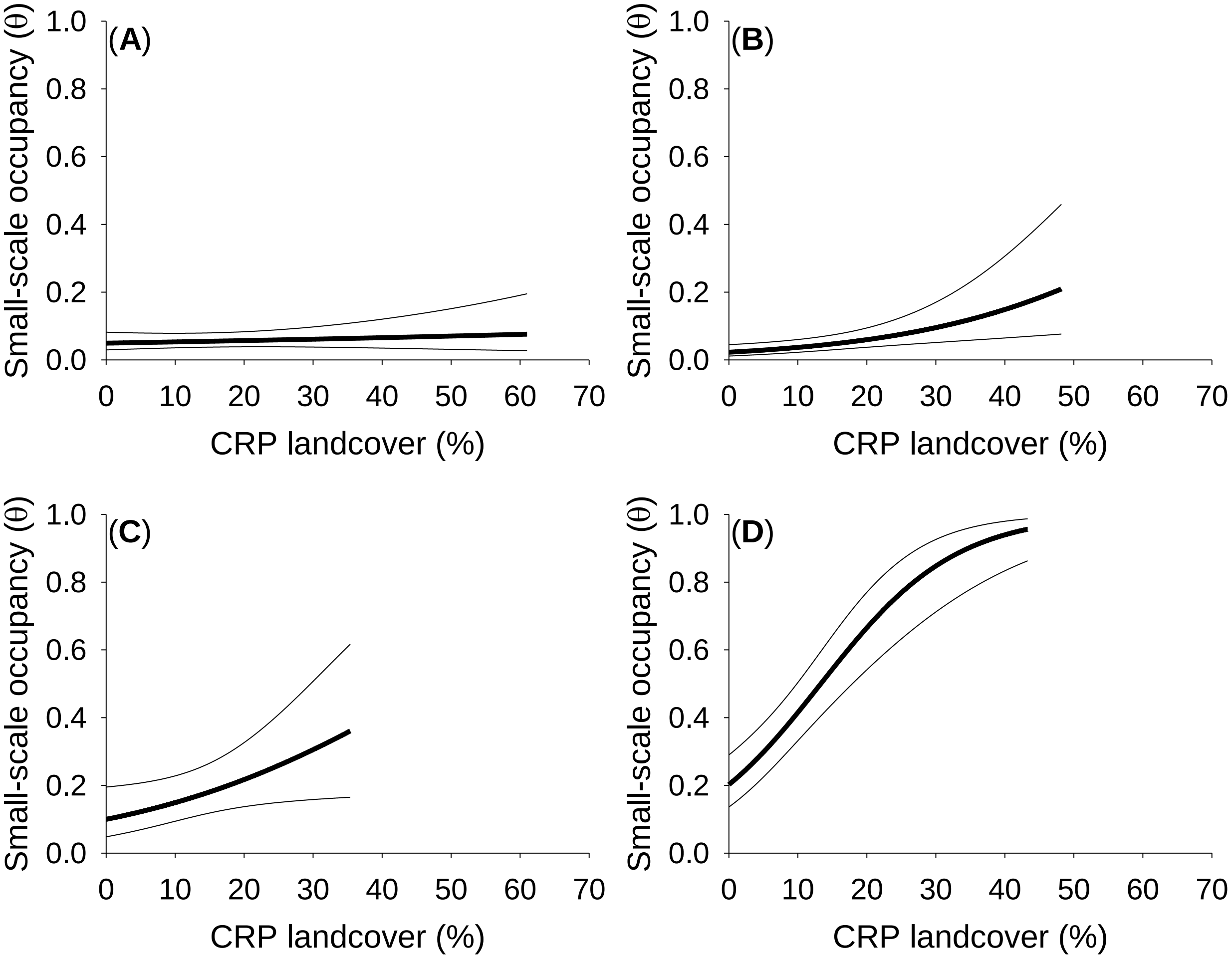

Figure 5. The small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants by the percentage (%) of area enrolled in the Conservation Reserve Program (CRP) in the (A) Shinnery Oak Prairie, (B) Sand Sagebrush Prairie, (C) Mixed Grass Prairie and (D) Shortgrass CRP/ Mosaic Prairie from the range-wide monitoring program, 2012–2016. The bold trend lines are model averaged estimates of small-scale occupancy at the mean values of other covariates in the model and the bounding lines are 90% CIs.

The small-scale occupancy of the LEPC increased with increasing landcover of shrubland (Figure 6). The slope of the positive effect of shrubland was identical in all ecoregions, but the effect was more-pronounced in the SOPR ecoregion because this ecoregion included areas of relatively higher shrubland landcover (Figure 6). The 90% CIs for the effect of shrubland did not cover 0, indicating large and precise effect sizes for this covariate (Table C5, Table C6).

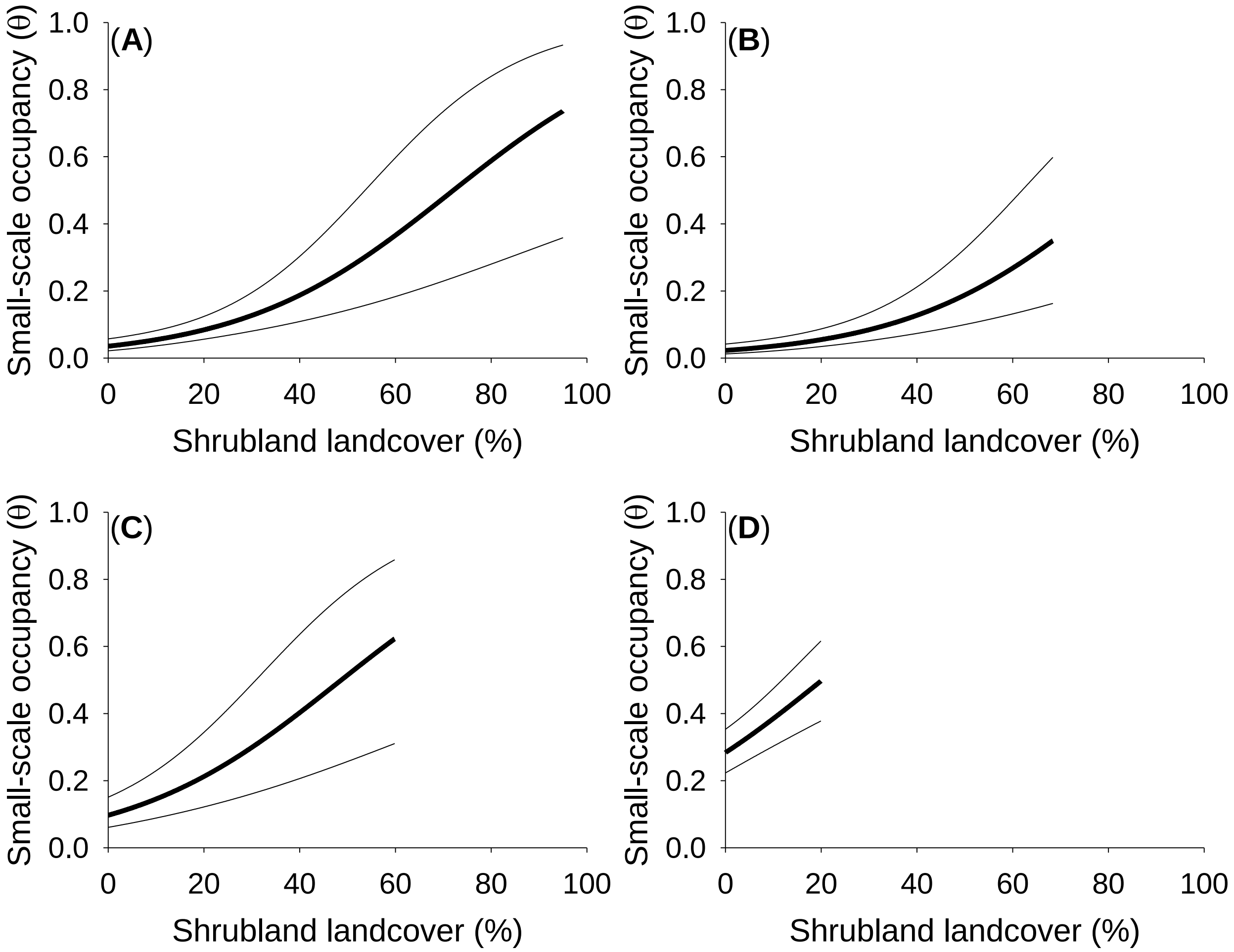

Figure 6. The small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants by the percentage (%) of shrubland landcover in the (A) Shinnery Oak Prairie, (B) Sand Sagebrush Prairie, (C) Mixed Grass Prairie and (D) Shortgrass CRP/ Mosaic Prairie from the range-wide monitoring program, 2012–2016. The bold trend lines are model averaged estimates of small-scale occupancy at the mean values of other covariates in the model and the bounding lines are 90% CIs.

The top-ranked model included the interaction between the quadratic term for grassland and ecoregion for small-scale occupancy (Table C5). The cumulative AIC_c weights indicated the interaction between the quadratic term for grassland and ecoregion [$w_+(j) = 0.48$] and the model with the interaction between linear term for grassland and ecoregion [$w_+(j) = 0.52$] had nearly equal probability of occurring in the best model (Table C4). We found little evidence for the quadratic effects of grassland on the small-scale occupancy of the LEPC in the SGPR and MGPR ecoregions (Table C5). The interaction between the quadratic of grassland and ecoregion showed a large negative quadratic effect of grassland in the SOPR ecoregion and a smaller negative quadratic effect of grassland in the SSPR ecoregion (Figure 7, Table C5). In the SOPR ecoregion, the estimated small-scale occupancy of the LEPC was highest at 34% grassland landcover, and declined thereafter (Figure 7). In the SSPR ecoregion, the estimated small-scale occupancy of the LEPC was highest at 54% grassland landcover, and declined thereafter (Figure 7). The 90% CIs for the quadratic interaction terms of grassland did not cover 0, indicating large and precise effect sizes for these multiplicative effects (Table C5).

The 2nd ranked model exhibited nearly equal support as the top ranked model and included the interaction between the main effect of grassland and ecoregion (Table C6). The small-scale occupancy of the LEPC showed a large linear increase with increasing landcover of grassland in the SGPR ecoregion, a smaller positive effect in the MGPR ecoregion, and diminutive effects of grassland in the SOPR and SSPR ecoregions (Figure 8, Table C6). The interaction between grassland and ecoregion indicated the slope of the grassland effect was much less in the SSPR, SOPR and MGPR ecoregions than the slope of the grassland effect in the SGPR ecoregion (Figure 8, Table C6). The 90% CIs for the interaction terms did not cover 0, indicating large and precise effect sizes for these multiplicative effects (Table C6).

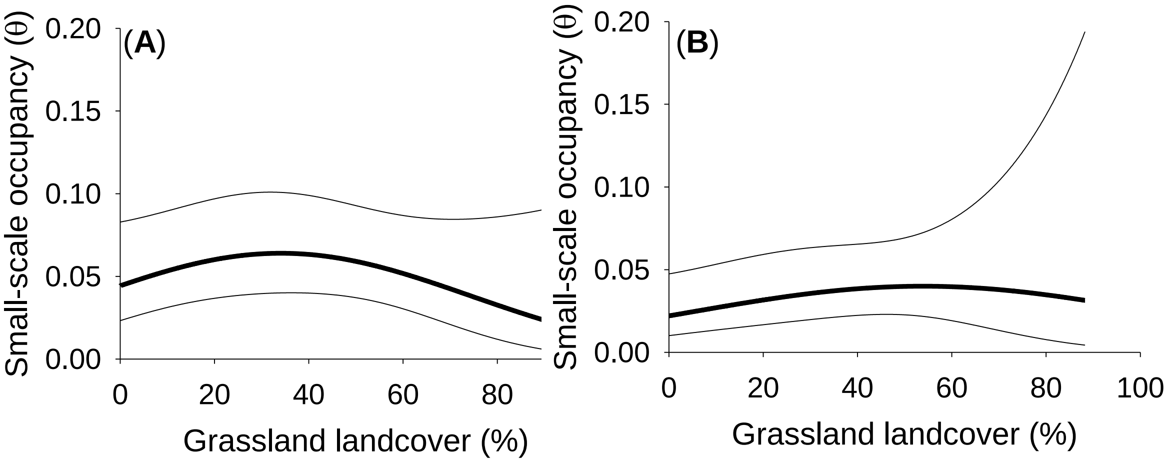

Figure 7. The small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants by the percentage (%) of grassland landcover in the (A) Shinnery Oak Prairie and (B) Sand Sagebrush Prairie from the range-wide monitoring program, 2012–2016. The bold trend lines are model averaged estimates of small-scale occupancy for models containing the quadratic effect of grassland at the mean values of other covariates in the model and the bounding lines are 90% CIs.

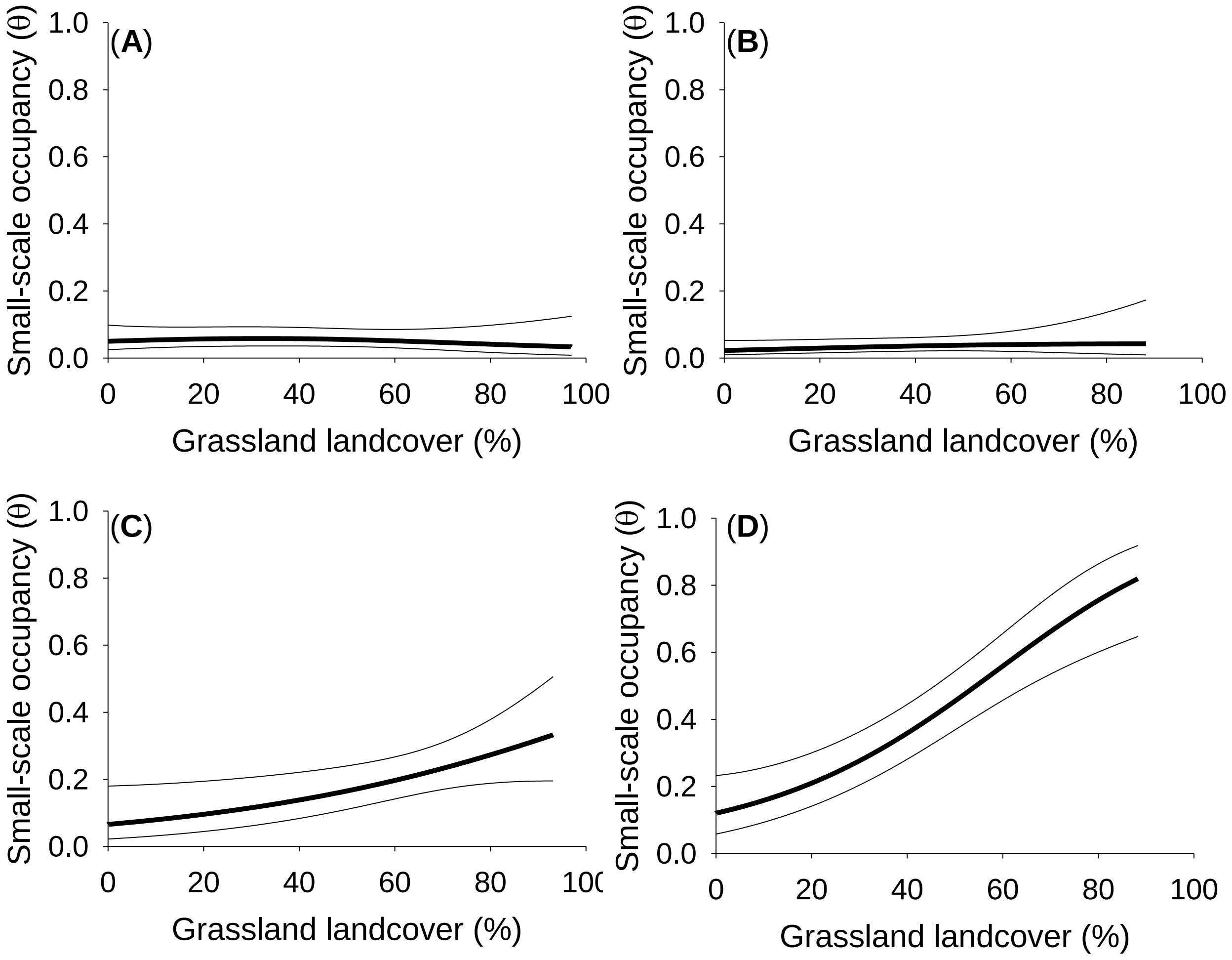

Figure 8. The small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants by the percentage (%) of grassland landcover in the (A) Shinnery Oak Prairie, (B) Sand Sagebrush Prairie, (C) Mixed Grass Prairie and (D) Shortgrass CRP/ Mosaic Prairie from the range-wide monitoring program, 2012–2016. The bold trend lines are model averaged estimates of small-scale occupancy for models containing the main effect and quadratic effect of grassland at the mean values of other covariates in the model and the bounding lines are 90% CIs.

The top-ranked model of detection probability (*p*) included the effects of observer, annual trend, and time after sunrise (Table C4). Observer occurred in every model and was the covariate with the most support for detection, followed by trend ($\gamma_{\text{trend}} = 2.73$), and time after sunrise ($\gamma_{\text{time}} = 1.51$). The ecoregion ($\gamma_{\text{ecoregion}} = 0.87$), ordinal date ($\gamma_{\text{date}} = 0.63$), and year ($\gamma_{\text{year}} = 0.19$) covariates had less support. The detection of LEPC was greater for back-seat observers than front-seat observers, and detection increased over survey years and with increasing time after sunrise (Figure 9, Table C5, Table C6). The covariate effects on *p* are additive to the ecoregion factor; therefore, graphs of *p* for all ecoregions are identical except with different intercepts. For simplicity, we present graphs for only one ecoregion in Figure 9.

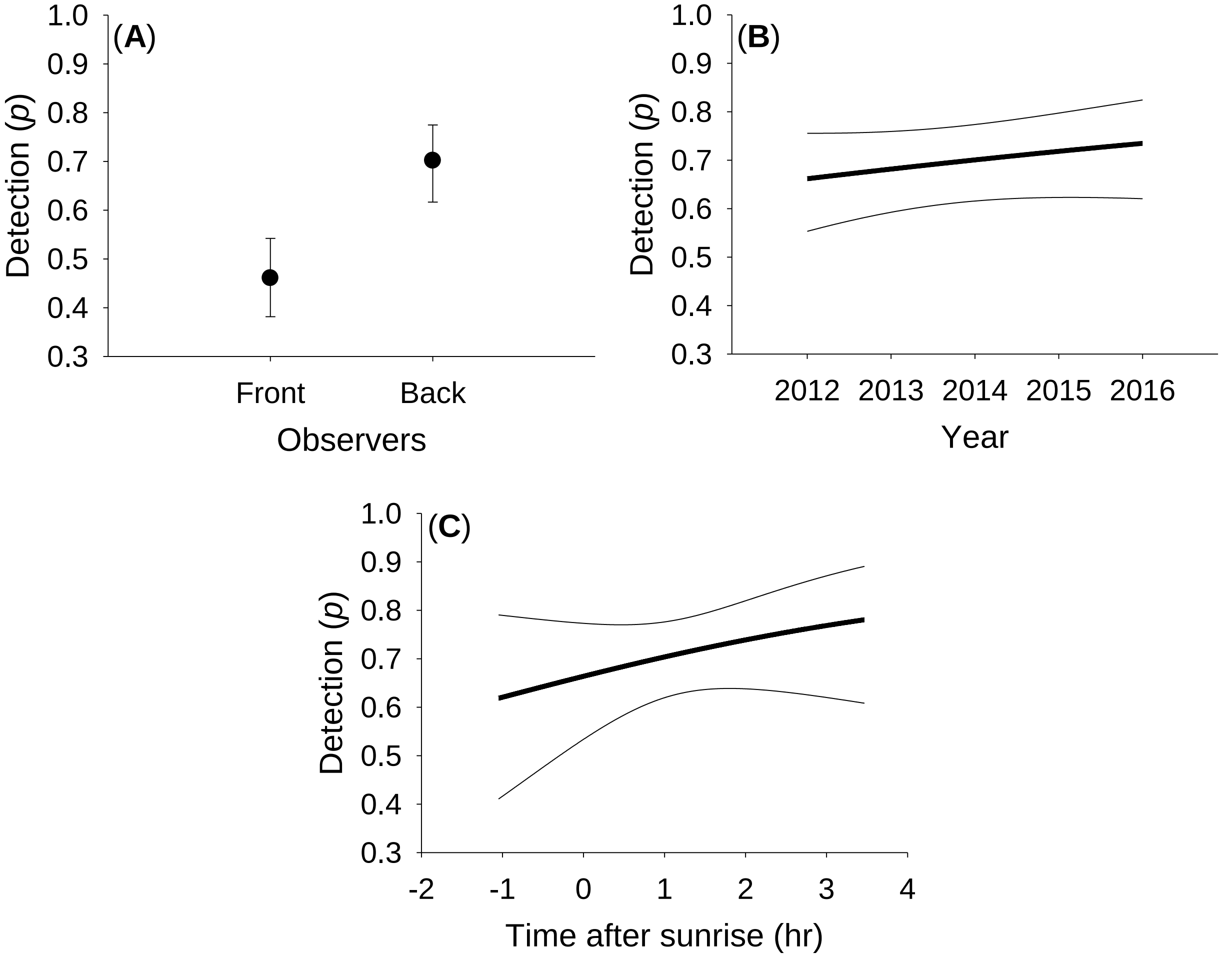

Figure 9. The probability of detection (*p*) of the lesser prairie-chicken by (A) front- and back-seat observers in the Shortgrass Prairie CRP/ Mosaic Ecoregion, and (B) annual trend and (C) time after sunrise for the back-seat observers from range-wide monitoring program, 2012–2016. The additive covariate effects for the other Ecoregion intercepts were the same (not shown). The filled symbols and bold trend lines are model averaged estimates of detection for models including that covariate at mean values of other covariates in the model, and the error bars and bounding lines are unconditional 90% confidence intervals.

Range-wide Exploratory Model Selection

We conducted an exploratory model selection analysis to determine if the data supported models with greater complexity than the limits imposed on the maximum number of covariates allowed during the standard, *a priori* model selection. The top-ranked model for the exploratory analysis of LEPC occupancy contained the effects of woodland landcover with >10% canopy cover on large-scale occupancy, development landcover on small-scale occupancy, and the effects of observer, annual trend, ordinal date, and ecoregion on detection (Table C7). The evidence ratios indicated the effect of woodland landcover with >10% canopy cover on large-scale occupancy [$w_+(j) = 0.88$] was 11 times more likely than the effect of woodland landcover with >5% canopy cover [$w_+(j) = 0.08$], and 108 times more likely than the effect of woodland landcover with >1% canopy cover [$w_+(j) < 0.01$; Table C8]. Large-scale occupancy of the LEPC declined with increasing woodland landcover with >10% canopy cover (Figure 10), and the 90% CIs for the effect did not cover 0, indicating a large and precise effect size for this covariate (Table C9). The cumulative AIC$_c$ weights indicated the effect of development landcover on small-scale occupancy had an 88% probability of being selected in the top model [$w_+(j) = 0.88$], and the evidence ratios showed the effect of primary road density [$w_+(j) = 0.07$] was three times more likely than oil-gas well density [$w_+(j) = 0.02$], 22 times more likely than vertical structures [$w_+(j) < 0.01$], and 132 times more likely than transmission lines [$w_+(j) < 0.01$; Table C10]. Small-scale occupancy of the LEPC declined with increasing development landcover (Figure 11), and the 90% CIs for the effect did not cover 0, indicating a large and precise effect size for this covariate (Table C9).

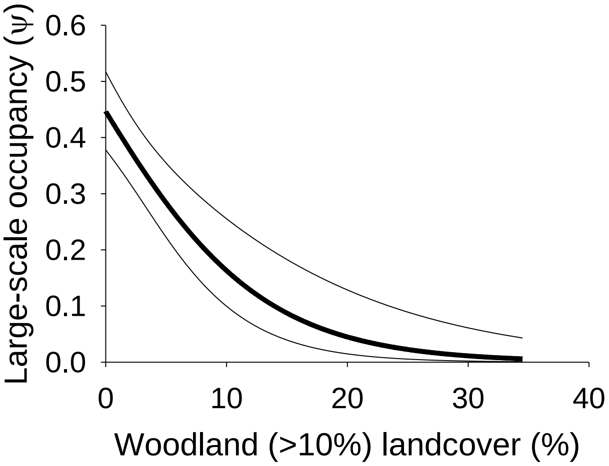

Figure 10. The large-scale occupancy (ψ) of the lesser prairie-chicken at 15 × 15-km grid cells by the percentage (%) of woodland landcover with greater than 10% canopy cover from the range-wide monitoring program, 2012–2016. The bold trend lines are model averaged estimates of large-scale occupancy at the mean values of other covariates in the model and the bounding lines are 90% CIs.

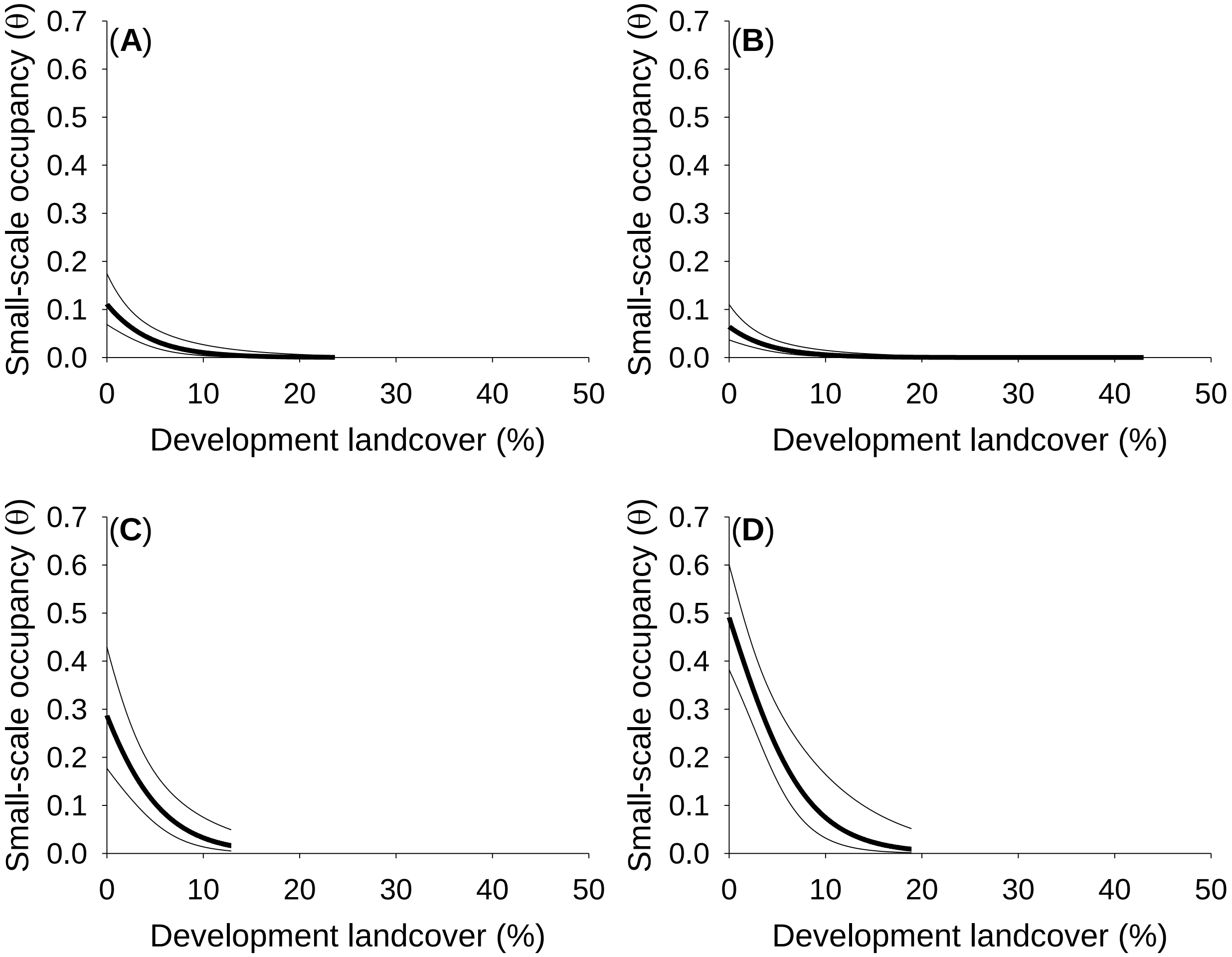

Figure 11. The small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants by the percentage (%) of development landcover in the (A) Shinnery Oak Prairie, (B) Sand Sagebrush Prairie, (C) Mixed Grass Prairie and (D) Shortgrass CRP/ Mosaic Prairie from the range-wide monitoring program, 2012–2016. The bold trend lines are model averaged estimates of small-scale occupancy for models containing the effect of development at the mean values of other covariates in the model and the bounding lines are 90% CIs.

Mapping the Range-wide Occupancy Distribution

We predicted range-wide covariate relationships for large-scale (ψ) and small-scale (θ) occupancy using unconditional estimates of small-scale occupancy (ψ*θ; Figure 12). Because the conditional estimates of small-scale occupancy (θ) are the probability of occupancy of the 7.5-km × 7.5-km quadrants given the 15-km × 15-km grid cells are occupied (Hagen et al. 2016), the product of large-scale (ψ) and small-scale (θ) occupancy is necessary to predict small-scale occupancy at all 7.5-km × 7.5-km quadrants in the region. Mapping unconditional small-scale occupancy provided model-based inference to the occupancy status of the LEPC in a way that accounts for variation in covariate values for grid cells and quadrants in the region (Figure 12). The model-based summaries of unconditional small-scale occupancy from the range-wide predicted distribution were 0.05 (SD = 0.06; CI = 0.00, 0.19) for the Shinnery Oak Prairie, 0.03 (SD = 0.03; CI = 0.00, 0.10) for the Sand Sagebrush Prairie, 0.07 (SD = 0.05; CI = 0.00, 0.17) for the Mixed Grass Prairie, and 0.10 (SD = 0.10; CI = 0.00, 0.32) for the Shortgrass CRP/ Mosaic Prairie (Figure 12). In comparison, the model-averaged point estimates of unconditional small-scale occupancy from the top-ranked $\psi(.)$ θ(Ecoregion) models of the analysis for annual variation were similar to those of the predicted distribution, but the estimated SE of the estimates was considerably smaller than the Standard Deviations (SD) from the predicted distribution, indicating that both design-based and model-based inference on occupancy patterns yielded similar point estimates, but that model-based estimates had greater uncertainty. The point estimates of unconditional small-scale occupancy from the annual variation analysis were 0.04 (SE = 0.01; CI = 0.02, 0.06) for the Shinnery Oak Prairie, 0.03 (SE = 0.01; CI = 0.02, 0.05) for the Sand Sagebrush Prairie, 0.06 (SE = 0.01; CI = 0.04, 0.08) for the Mixed Grass Prairie, and 0.11 (SE = 0.01; CI = 0.08, 0.13) for the Shortgrass CRP/ Mosaic Prairie. The spatially explicit map for the CV of unconditional small-scale occupancy (Figure 13) showed greater uncertainty for multi-scale covariate relationships in the Shinnery Oak Prairie (Mean CV = 0.43; SD = 0.10) and Sand Sagebrush Prairie (Mean CV = 0.43; SD = 0.13) than in the Mixed Grass Prairie (Mean CV = 0.28; SD = 0.07) and Shortgrass CRP/ Mosaic Prairie (Mean CV = 0.22; SD = 0.07).

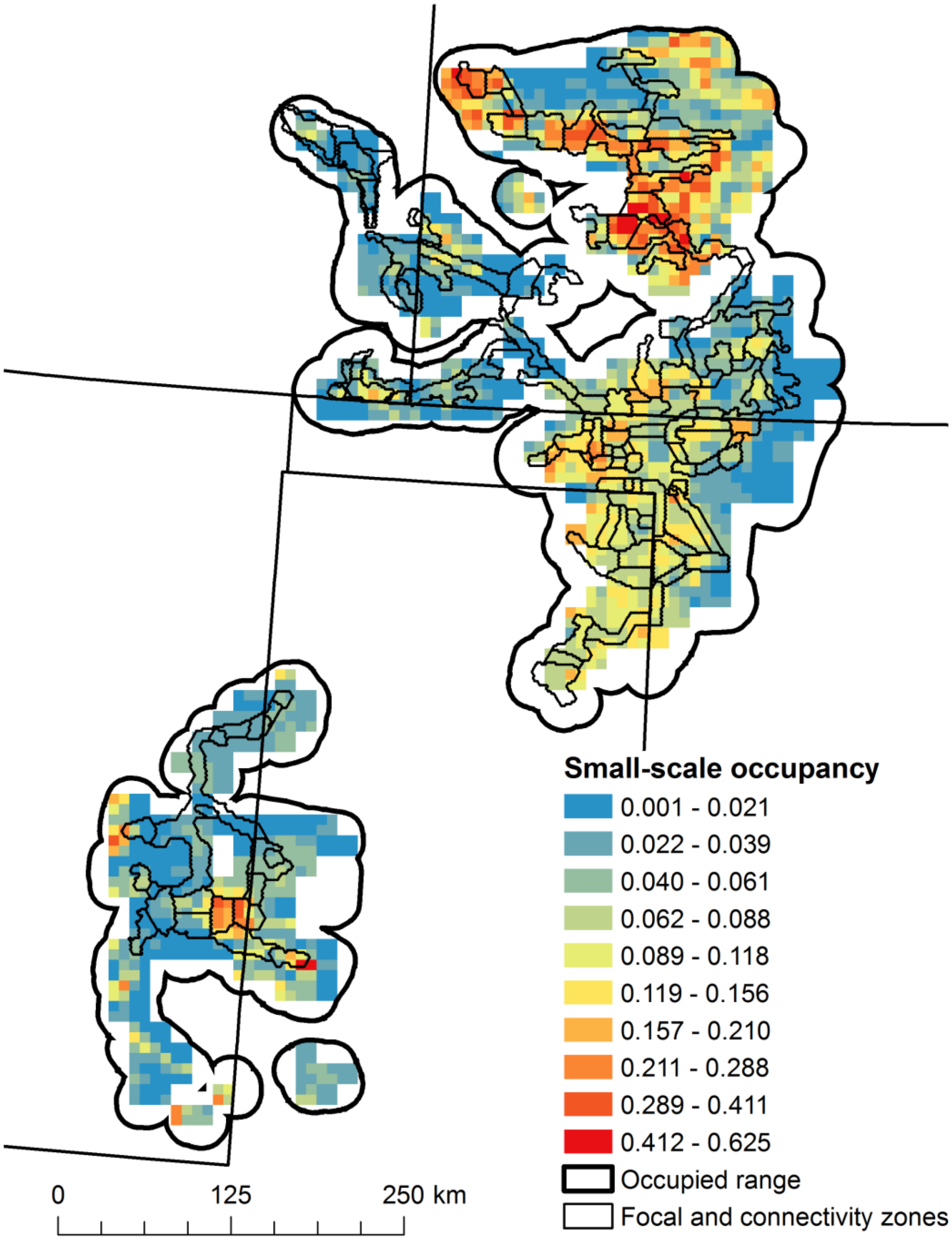

Figure 12. The predicted small-scale occupancy of the lesser prairie-chicken (LEPC) at 7.5-km × 7.5-km quadrants from the *a priori* model selection analysis, range-wide monitoring program, 2016. The values shown by the color ramp are model averaged estimates of unconditional small-scale occupancy ($\psi*\theta$), representing multi-scale covariate relationships for large-scale (ψ) and small-scale (θ) occupancy. The bold bounding lines represent the occupied range of the LEPC plus a 16-km buffer, and the polygons within the occupied range represent the focal and connectivity zones (SGP CHAT 2011).

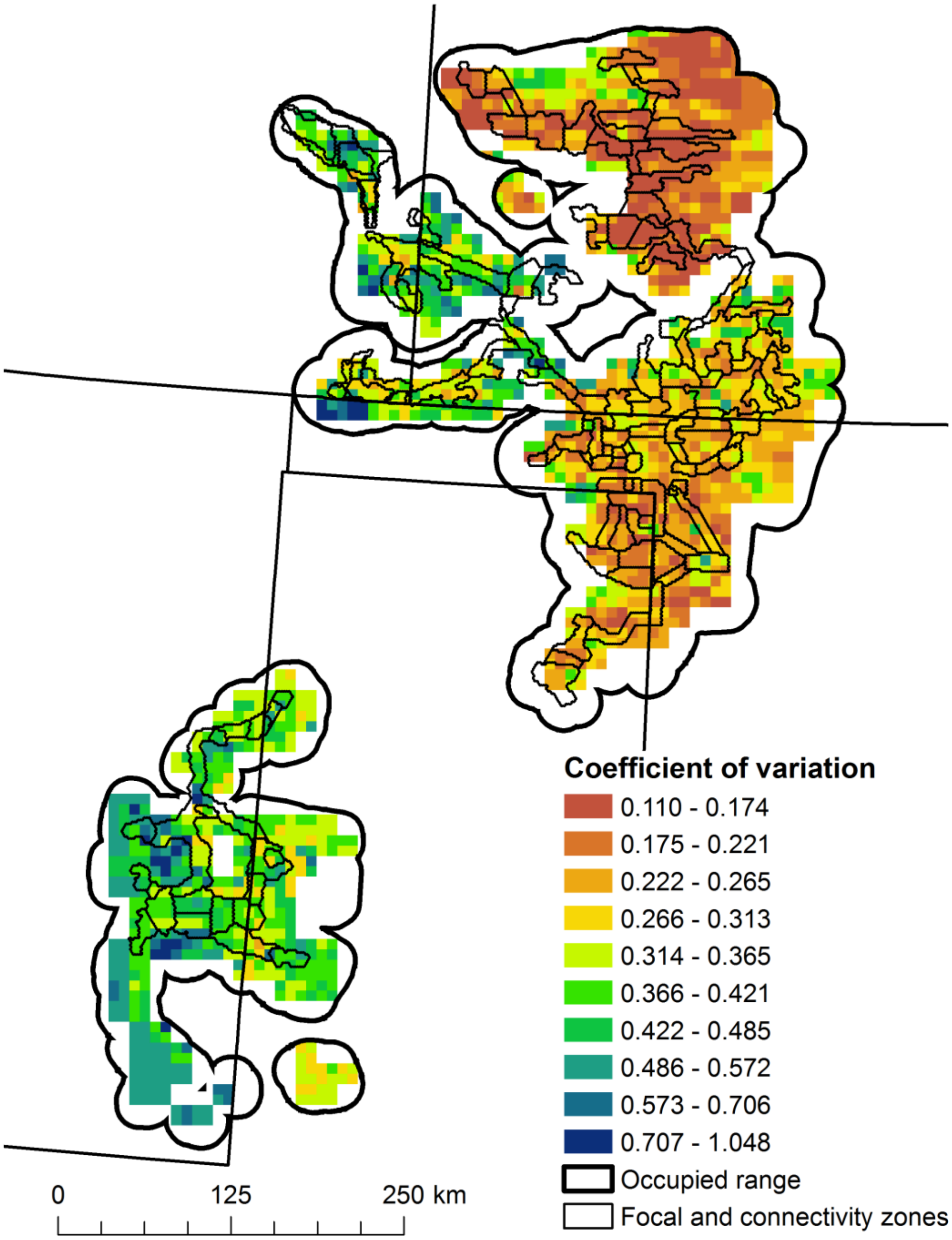

Figure 13. The predicted coefficient of variation (CV) for small-scale occupancy of the lesser prairie-chicken (LEPC) at 7.5-km × 7.5-km quadrants from the *a priori* model selection analysis, range-wide monitoring program, 2016. The values shown by the color ramp are model averaged estimates of the unconditional CV of small-scale occupancy (ψ*θ), representing multi-scale covariate relationships for large-scale (ψ) and small-scale (θ) occupancy. The bold bounding lines represent the occupied range of the LEPC plus a 16-km buffer, and the polygons within the occupied range represent the focal and connectivity zones (SGP CHAT 2011).

Ecoregion-specific Multi-scale Covariate Relationships

Ecoregion 1 – Shinnery Oak Prairie (SOPR)

The combination of plausible submodels resulted in 864 plausible specifications of the full model for the SOPR region, indicating considerably more model-selection uncertainty than in the range-wide modeling effort. We removed 196 models from consideration based on evidence of unreliable convergence of one or more parameter estimates, retaining 668 candidate models for AIC_c ranking. The confidence set of models (i.e., $\Delta AIC_c < 2$) included 13 models, with cumulative AIC_c weight of 0.219 (Appendix D, Table D1).

Four covariates had support scores > 1 for large-scale occupancy (ψ): Quadratic term of CRP patch size, woodland (canopy cover > 5%) landcover, quadratic term of cropland landcover, and woodland (canopy cover > 10%) landcover (Table D2). A quadratic term for shrubland landcover was in all plausible ψ submodels (Table D2). Based on the model-averaged predictions over all models in the confidence set, the average estimated probability of large-scale occupancy was highest at intermediate values of shrubland landcover (Figure 14A) and intermediate values of CRP patch size (Figure 14B). We estimated a negative relationship between two measures of woodland landcover (canopy cover > 5% or > 10%) and large-scale occupancy (Figure 14C, Figure 14D).

There were two covariates for large-scale occupancy that were in the confidence set of models, but for which there was no discernable directionality to the covariate-occupancy relationship in the model-averaged results: grassland landcover and cropland landcover. The highest-ranked model that contained grassland landcover was the 8th ranked model ($\Delta AIC_c = 1.38$). The estimated effect of grassland landcover on ψ was negative in this model, and the CI did not contain 0 ($\beta = -7.19$, CI = –10.91, –3.47). Within the highest-ranked model that contained cropland landcover (the 13th ranked model, $\Delta AIC_c = 1.92$), the estimated effect of the covariate on ψ was curvilinear; but the precision of the estimate for both the main effect (β = 2.18, CI = –12.96, 17.32) and quadratic effect (β = 11.84, CI = –18.10, 41.78) were poor, with 0 contained in the CIs.

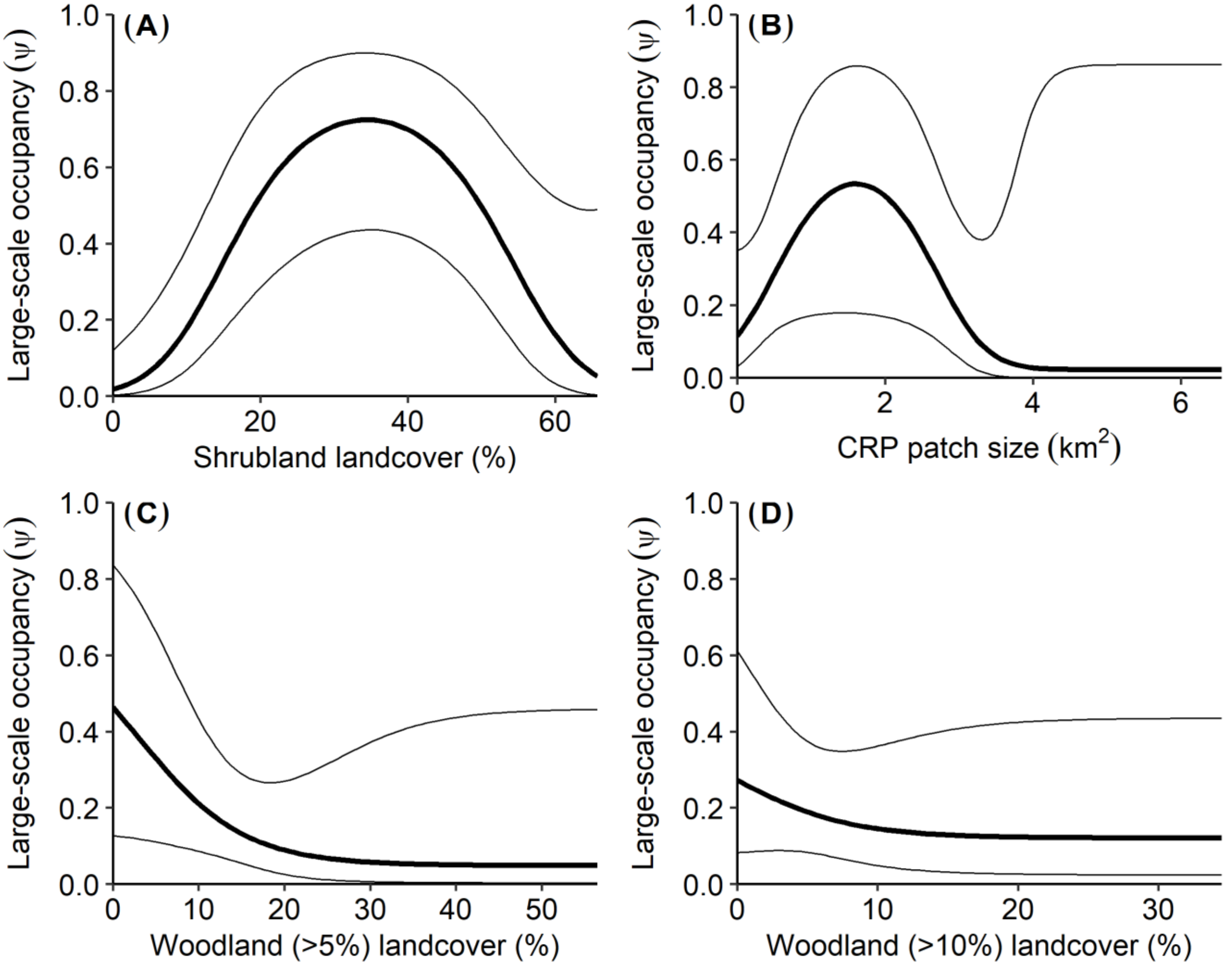

Figure 14. The estimated probability of large-scale occupancy (ψ) of the lesser prairie-chicken at 15 × 15-km grid cells in the Shinnery Oak Prairie ecoregion (SOPR; ecoregion 1) by the (A) shrubland landcover, (B) mean patch size of lands enrolled in the Conservation Reserve Program (CRP; km^2), (C) woodland (canopy cover > 5%) landcover, and (D) woodland (canopy cover > 10%) landcover, 2012–2016. The bold trend lines are model-averaged estimates of large-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

Three covariates had support scores > 1 for small-scale occupancy (θ): cropland landcover, grassland landcover, and woodland (canopy cover > 5%) landcover (Table D3). Based on model-averaged predictions, we estimated a negative relationship between small-scale occupancy and both cropland landcover (Figure 15A) and grassland landcover (Figure 15B).

There were five covariates for small-scale occupancy that were in the confidence set of models, but for which there was no discernable directionality to the covariate-occupancy relationship in the model-averaged results: development landcover, shrubland landcover, woodland landcover with canopy cover >1%, >5%, and >10%. Development landcover occurred in the 8th ranked model ($\Delta AIC_c = 1.3$). The estimated effect of development landcover on θ was negative and the CI did not contain 0 ($\beta = -33.31$, CI = –54.69, –11.93). Within the highest-ranked model that contained shrubland landcover (the 8th ranked model, $\Delta AIC_c = 1.38$), the estimated effect on θ was positive and the CI did not contain 0 ($\beta = 3.19$, CI = 1.09, 5.28). The highest-ranked model contained woodland (canopy cover >1%) landcover. The estimated effect of woodland (canopy cover >1%) landcover on θ in the highest-ranked model was negative; but the precision of the estimate was low, with the CI containing 0 ($\beta = -1.91$, CI = –4.28, 0.46). The 2nd ranked model ($\Delta AIC_c = 0.47$) contained woodland (canopy cover >5%) landcover. Again, its estimated effect on θ in this model was negative, but with the CI of the estimated coefficient containing 0 ($\beta = -2.48$, CI = –6.07, 1.11). The 8th ranked model ($\Delta AIC_c = 1.38$) was the highest ranked model that contained woodland (canopy cover >10%) landcover. Within that model, the estimated effect of woodland (canopy cover >10%) landcover on θ was positive; but the precision of the estimate was low, with the CI containing 0 ($\beta = 2.18$, CI = –3.27, 7.63).

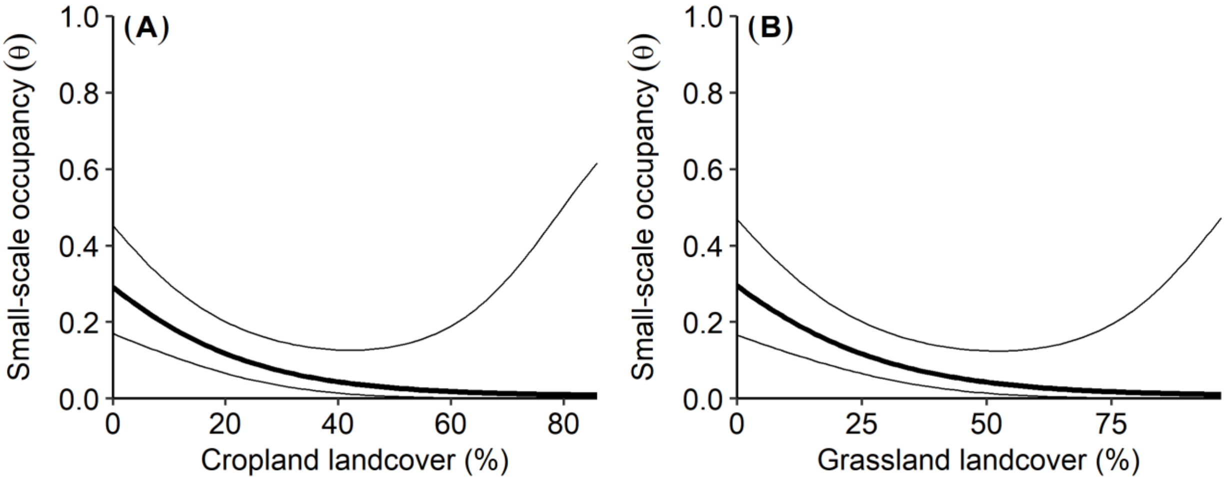

Figure 15. The estimated probability of small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants in the Shinnery Oak Prairie ecoregion (SOPR; ecoregion 1) by the (A) cropland landcover, and (B) grassland landcover, 2012–2016. The bold trend lines are model-averaged estimates of small-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

Ecoregion 2 – Sand Sagebrush Prairie (SSPR)

The combination of plausible submodels resulted in 1386 plausible specifications of the full model for the SSPR region, indicating considerably more model-selection uncertainty than in the range-wide modeling effort. We removed 343 models from consideration based on evidence of unreliable convergence of one or more parameter estimates, retaining 1043 candidate models for AIC_c ranking. The confidence set of models (i.e., those with $\Delta\mathrm{AIC}_c < 2$) included nine models, with cumulative AIC_c weight of 0.181 (Table D4).

Five covariates had support scores >1 for large-scale occupancy (ψ): CRP-enrolled land, wetland landcover, summer drought weeks, CRP patch size, and shrubland landcover (Table D5). Based on the model-averaged predictions over all models in the confidence set, we estimated a positive relationship between shrubland landcover and the probability of large-scale occupancy (Figure 16A) and a positive relationship between the amount of CRP-enrolled land and the probability of large-scale occupancy (Figure 16B).

There were three covariates for large-scale occupancy that were in the confidence set of models, but for which there was no discernable directionality to the covariate-occupancy relationship in the model-averaged results: cropland patch size, wetland landcover, and summer drought weeks. The highest-ranked model that contained cropland patch size (the eighth-ranked model, $\Delta AIC_c = 1.98$), the estimated effect on ψ was positive, and the CI did not contain 0 (β = 6.89; CI = 0.39, 13.40). The highest-ranked model that contained wetland landcover had an estimated negative effect on ψ, and the CI did not contain 0 (β = –185.29; CI = –359.33, –11.24). The ninth-ranked model ($\Delta AIC_c = 1.99$) was the highest-ranked model that contained summer drought weeks. The estimated effect of summer drought weeks on ψ was negative in this model; but the precision of the estimate was poor, with the CI containing 0 (β = –0.23; CI = –0.61, 0.15).

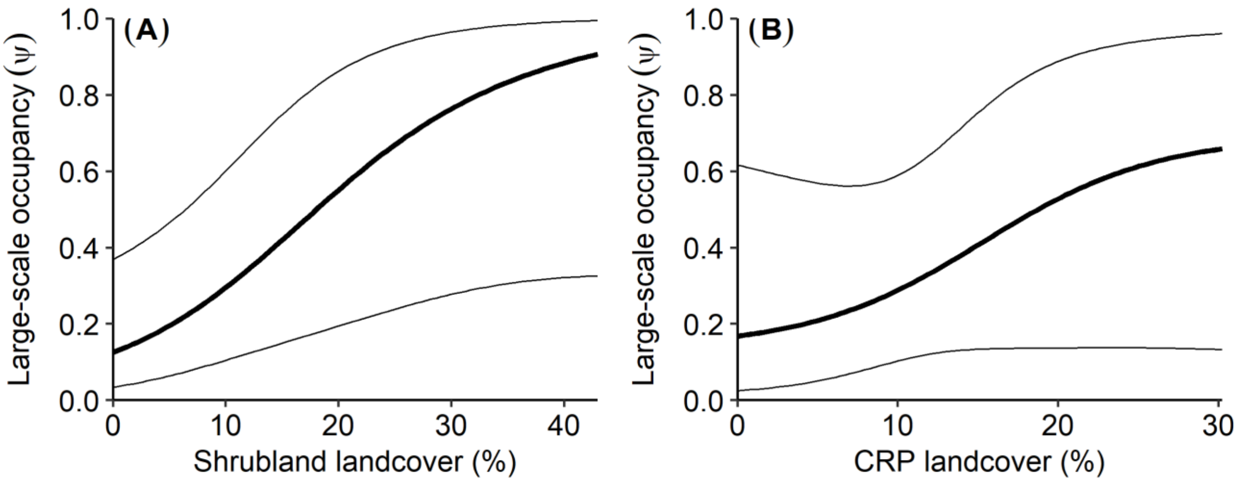

Figure 16. The estimated probability of large-scale occupancy (ψ) of the lesser prairie-chicken at 15 × 15-km blocks in the Sand Sagebrush Prairie ecoregion (SSPR; ecoregion 2) by the (A) shrubland landcover, and (B) percentage of area enrolled in the Conservation Reserve Program (CRP), 2012–2016. The bold trend lines are model-averaged estimates of small-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

Three covariates had support scores >1 for small-scale occupancy (θ): CRP-enrolled land, general habitat landcover, and summer drought weeks (Table D6). Based on the model-averaged predictions over all models in the confidence set, we estimated a positive relationship between the amount of CRP-enrolled land and the probability of small-scale occupancy (Figure 17A) and a negative relationship between cropland landcover and the probability of small-scale occupancy (Figure 17B).

There were three covariates for small-scale occupancy that were in the confidence set of models, but for which there was no discernable directionality to the covariate-occupancy relationship in the model-averaged results: general habitat landcover, summer drought weeks, and wetland landcover. The second-ranked model ($\Delta AIC_c = 1.21$) contained both general habitat landcover and summer drought weeks. Within this model, the estimated effect of general habitat landcover on θ was positive, and the CI did not contain 0 ($\beta = 2.14$; CI = 0.33, 3.95). The estimated effect of summer drought weeks on θ was negative, but the precision of this effect was poor, with 0 contained in the CI ($\beta = -0.09$; CI = –0.19, 0.01). Within the highest-ranked model that contained wetland landcover (the 6th ranked model, $\Delta AIC_c = 1.70$), its estimated effect on θ was negative. However, the precision of this effect was poor, with the CI containing 0 ($\beta = -38.22$; CI = –91.75, 15.31).

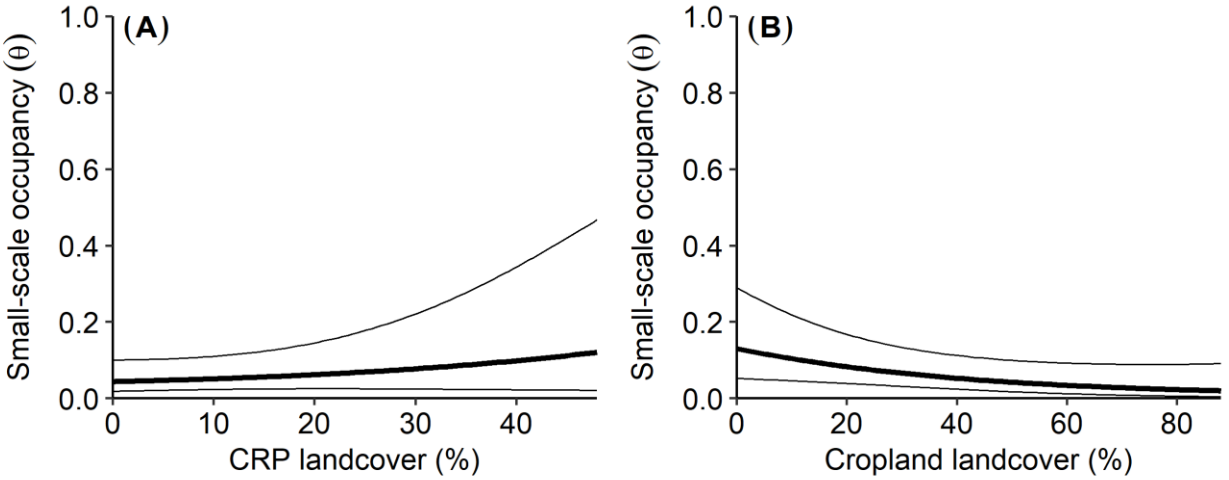

Figure 17. The estimated probability of small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants in the Sand Sagebrush Prairie ecoregion (SSPR; ecoregion 2) by the (A) percentage of area enrolled in the Conservation Reserve Program (CRP), and (B) cropland landcover, 2012–2016. The bold trend lines are model-averaged estimates of small-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

Ecoregion 3 – Mixed Grass Prairie (MGPR)

The combination of plausible submodels resulted in 144 plausible specifications of the full model for the MGPR region, indicating more model-selection uncertainty than in the range-wide modeling effort, but less uncertainty than in the SOPR and SSPR ecoregions. We removed one model from consideration based on evidence of unreliable convergence of one or more parameter estimates, retaining 143 candidate models for AIC_c ranking. The confidence set of models (i.e., those with $\Delta AIC_c < 2$) included 10 models, with cumulative AIC_c weight of 0.292 (Table D7).

There was only one plausible submodel for large-scale occupancy (ψ), thus all models included the same covariates in the ψ submodel, and the variable support calculations gave uninformative, uniform values (Table D8). Based on the model-averaged predictions over all models in the confidence set, we estimated a positive relationship between native habitat patch size and the probability of large-scale occupancy (Figure 18A), and a positive relationship between the amount of CRP-enrolled land and the probability of large-scale occupancy (Figure 18B). Conversely, we estimated a negative relationship between the density of oil-gas wells and large-scale occupancy (Figure 18C).

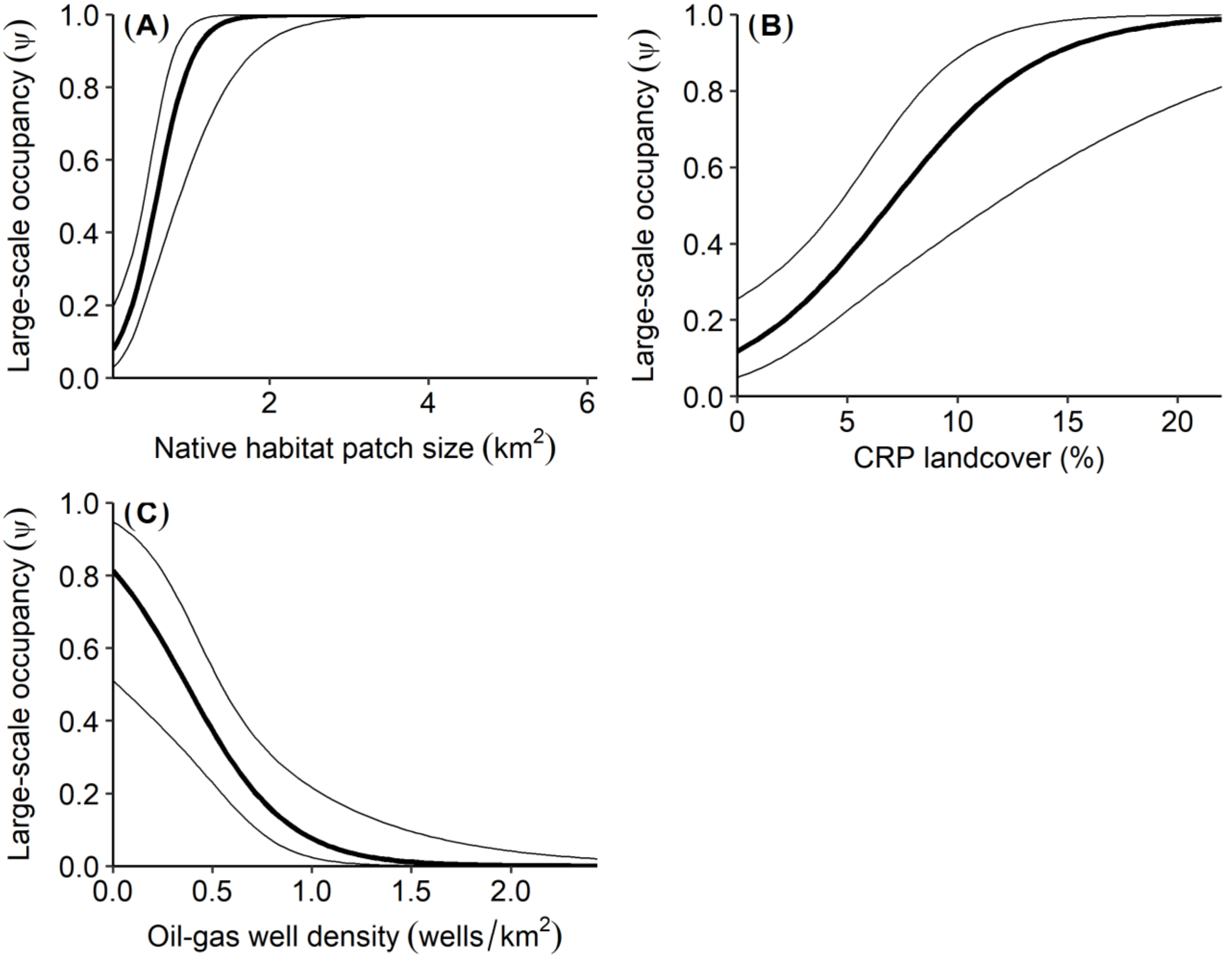

Figure 18. The estimated probability of large-scale occupancy (ψ) of the lesser prairie-chicken at 15 × 15-km blocks in the Mixed Grass Prairie ecoregion (MGPR; ecoregion 3) by the (A) mean patch size of native habitat (shrubland-grassland) landcover (km^2), (B) percentage of area enrolled in the Conservation Reserve Program (CRP), and (C) density of oil-gas wells (wells/km^2), 2012–2016. The bold trend lines are model-averaged estimates of large-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

Five covariates had support scores >1 for small-scale occupancy (θ): development landcover, woodland (canopy cover >10%) landcover, summer drought weeks, grassland landcover, and cropland landcover (Table D9). Based on the model-averaged predictions over all models in the confidence set, we estimated a negative relationship between woodland (canopy cover >10%) landcover and the probability of small-scale occupancy (Figure 19A) and a negative relationship between development landcover and the probability of small-scale occupancy (Figure 19B).

There were eight covariates for small-scale occupancy that were in the confidence set of models, but for which there was no discernable directionality to the covariate-occupancy relationship in the model-averaged results: woodland (canopy cover >1%) landcover, summer drought weeks, grassland landcover, cropland landcover, general habitat landcover, woodland (canopy cover >5%) landcover, prescribed grazing landcover, and shrubland landcover. In our exploratory analysis, the highest-ranked model that contained woodland (canopy cover >1%) landcover was the 2nd ranked model ($\Delta AIC_c = 0.71$), where its estimated effect on θ was negative, and the CI did not contain 0 ($\beta = -6.45$; CI = –11.46, –1.45). Within the highest-ranked model that contained summer drought weeks (the 2nd ranked model, $\Delta AIC_c = 0.71$), its estimated effect on θ was also negative, and the CI did not contain 0 ($\beta = -0.07$; CI = –0.14, –0.01). Within the highest-ranked model that contained woodland (canopy cover >5%) landcover (the sixth-ranked model, $\Delta AIC_c = 1.13$), its estimated effect on θ was negative, and the CI did not contain 0 ($\beta = -11.32$; CI = –19.46, –3.17). Within the highest-ranked model that contained grassland landcover (the third-ranked model, $\Delta AIC_c = 0.92$), its estimated effect on θ was positive, but the CI contained 0 ($\beta = 0.77$; CI = –0.39, 1.93). Within the highest-ranked model that contained cropland landcover (the fourth-ranked model, $\Delta AIC_c = 0.92$), its estimated effect on θ was negative, but the CI contained 0 ($\beta = -0.83$; CI = –2.10, 0.43). Within the highest-ranked model that contained general habitat landcover (the fifth-ranked model, $\Delta AIC_c = 0.97$), its estimated effect on θ was positive, but the CI contained 0 (β = 0.81; CI = –0.44, 2.07). Within the highest-ranked model that contained prescribed grazing landcover (the 7th ranked model, $\Delta AIC_c = 1.18$), its estimated effect on θ was positive, but the CI contained 0 (β = 2.50; CI = –1.69, 6.68). And lastly, within the highest-ranked model that contained shrubland landcover (the ninth-ranked model, $\Delta AIC_c = 1.85$), its estimated effect on θ was negative, but the CI contained 0 (β = –0.96; CI = –4.08, 2.17).

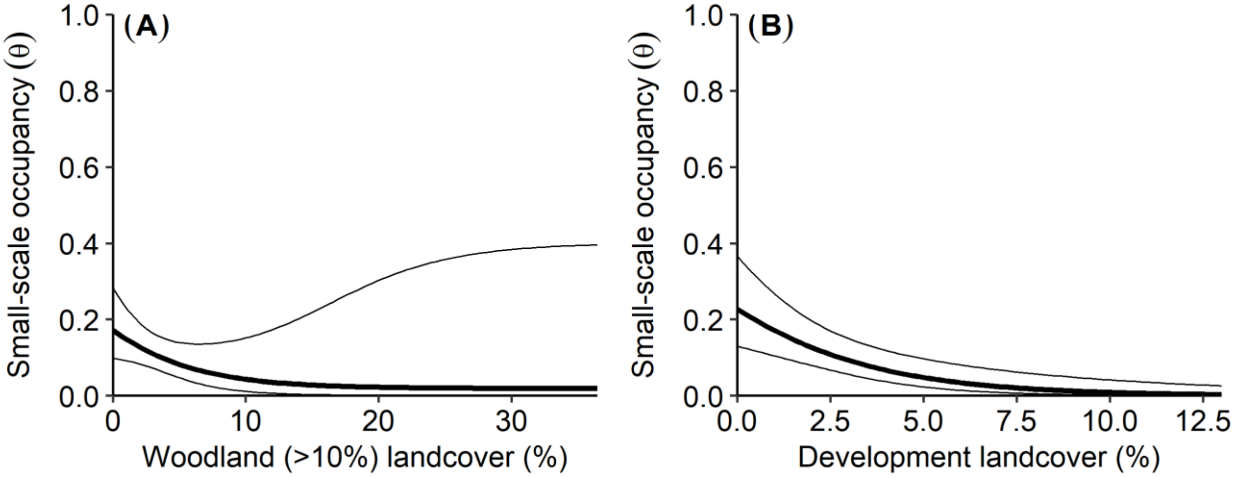

Figure 19. The estimated probability of small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants in the Mixed Grass Prairie ecoregion (MGPR; ecoregion 3) by the (A) woodland (canopy cover >10%) landcover, and (B) development landcover, 2012–2016. The bold trend lines are model-averaged estimates of small-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

Ecoregion 4 – Shortgrass/CRP Mosaic (SGPR)

The combination of plausible submodels resulted in 100 plausible specifications of the full model for the SGPR region, indicating more model-selection uncertainty than in the range-wide modeling effort, but less uncertainty than in the SOPR and SSPR ecoregions. We removed 56 models from consideration based on evidence of unreliable convergence of one or more parameter estimates, retaining 44 candidate models for AIC_c ranking. The confidence set of models (i.e., those with $\Delta AIC_c < 2$) included 11 models, with cumulative AIC_c weight of 0.604 (Table D10).

Grassland patch size was in all plausible submodels for large-scale occupancy (ψ), and two covariates had support scores >1 for large-scale occupancy: CRP-enrolled land and the quadratic effect for cropland patch size (Table D11). Based on the model-averaged predictions over all models in the confidence set, we estimated a curvilinear relationship between cropland patch size and the probability of large-scale occupancy, with highest values of ψ at intermediate patch sizes in the range of 0.3 km^2 to 0.5 km^2 (Figure 20A). We estimated a positive relationship between the amount of CRP-enrolled land and the probability of large-scale occupancy (Figure 20B), and a positive relationship between grassland patch size and the probability of large-scale occupancy (Figure 20C). We estimated a negative relationship between development landcover and the probability of large-scale occupancy (Figure 20D). There were no covariates that appeared in the confidence set of models for which the average estimated probability of large-scale occupancy plotted as a function of the covariates suggested negligible effects on ψ when model-averaged across all models in the confidence set.

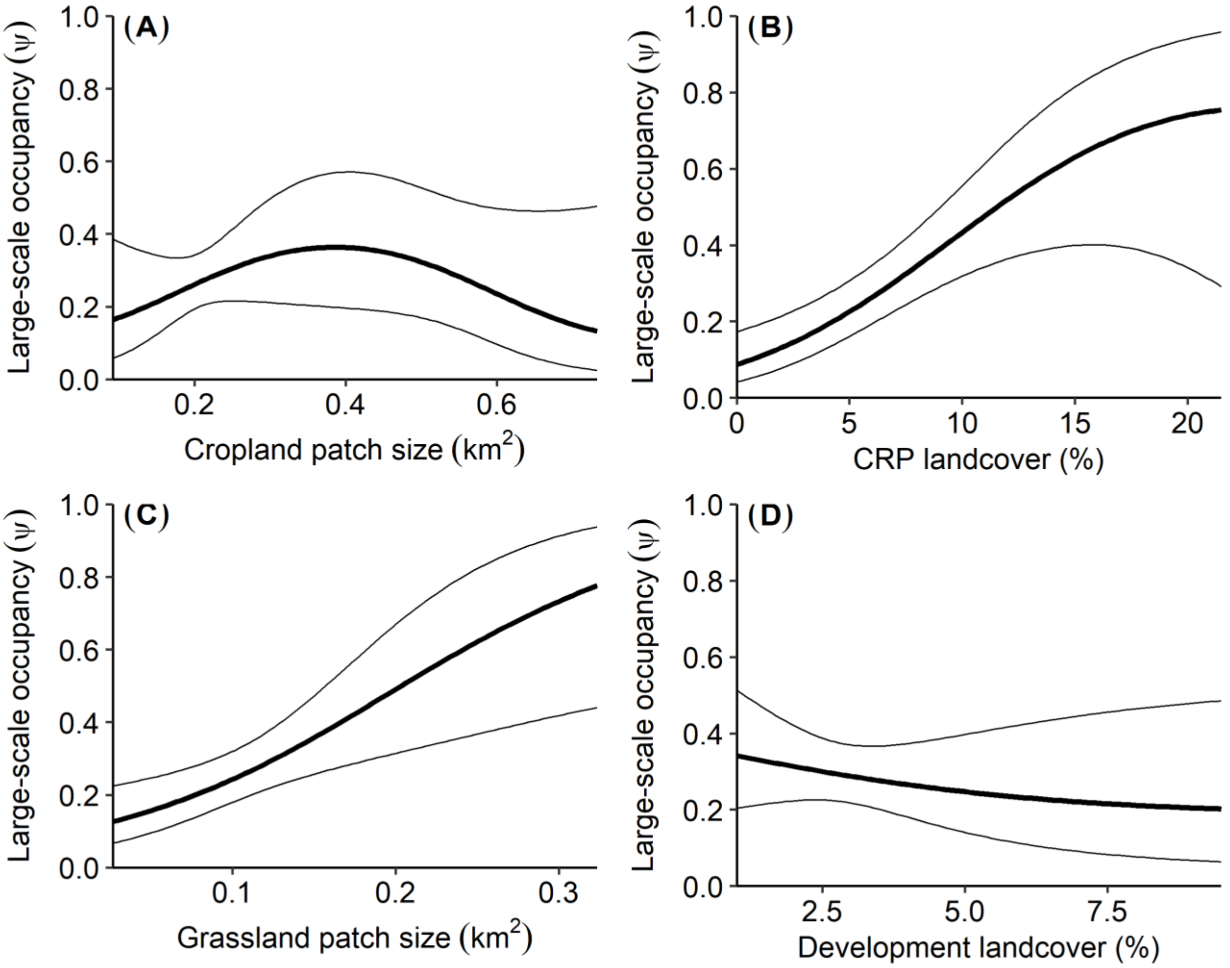

Figure 20. The estimated probability of large-scale occupancy (ψ) of the lesser prairie-chicken at 15 × 15-km blocks in the Shortgrass/CRP Mosaic ecoregion (SGPR; ecoregion 4) by the (A) mean patch size of cropland landcover (km^2), (B) percentage of area enrolled in the Conservation Reserve Program (CRP), (C) mean patch size of grassland landcover (km^2), and (D) development landcover, 2012–2016. The bold trend lines are model-averaged estimates of large-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

Two covariates (i.e., cropland landcover and CRP-enrolled land) were in all plausible submodels for small-scale occupancy (θ), and one covariate (i.e., development landcover) had a support score >1 for small-scale occupancy (Table D12). Based on the model-averaged predictions over all models in the confidence set, we estimated a negative relationship between cropland landcover and the probability of small-scale occupancy (Figure 21A), and a positive relationship between the amount of CRP-enrolled land and the probability of small-scale occupancy (Figure

21B). We estimated a negative relationship between development landcover and the probability of small-scale occupancy (Figure 21C). Native habitat landcover also appeared in the confidence set of models, but with no discernable directionality to the covariate-occupancy relationship in the model-averaged results. Within the highest-ranked model that contained native habitat (4th-ranked model, $\Delta AIC_c = 1.53$), its estimated effect on θ was positive but with 0 contained in the CI (β = 0.23; CI = –10.58, 11.03).

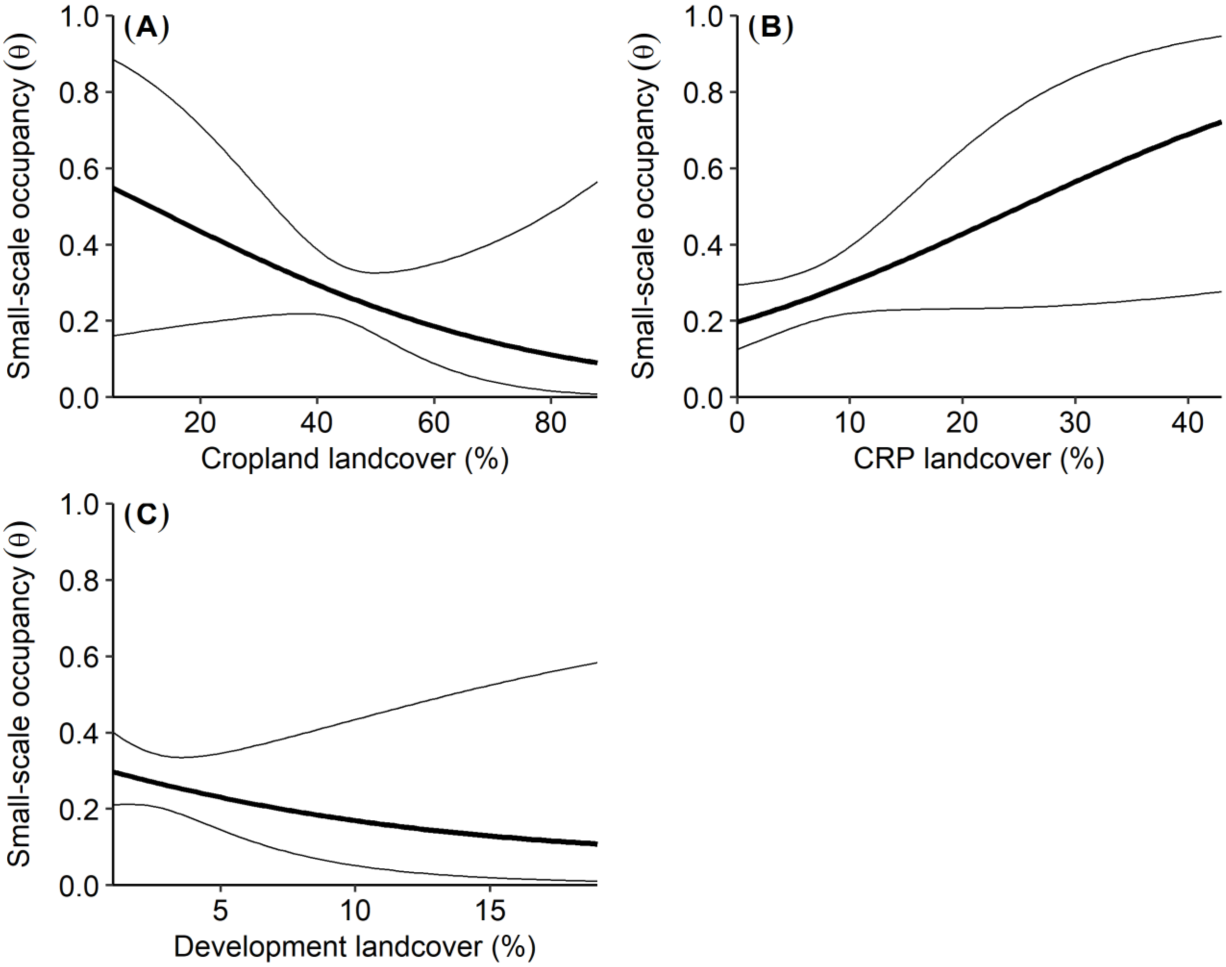

Figure 21. The estimated probability of small-scale occupancy (θ) of the lesser prairie-chicken at 7.5 × 7.5-km quadrants in the Shortgrass/CRP Mosaic ecoregion (SGPR; ecoregion 4) by the (A) cropland landcover, (B) percentage of area enrolled in the Conservation Reserve Program (CRP), and (C), development landcover, 2012–2016. The bold trend lines are model-averaged estimates of small-scale occupancy at the mean values of other covariates in the model, and the bounding lines are 90% CIs.

DISCUSSION

Annual Variation in Site Occupancy

The pattern of implicit dynamics suggested that the geographic range of the LEPC, as indexed by the probability of occupancy, remained stable at the large-scale but fluctuated over time at the small-scale. We found little evidence of annual variation in the large-scale occupancy of the LEPC at 15-km × 15-km grid cells between 2012–2016, but discovered moderate evidence for annual variation in the probability of small-scale occupancy of 7.5-km × 7.5-km quadrants (Figure 2). However, at the scale of 7.5-km × 7.5-km quadrants, the LEPC range dynamics oscillated over time, experiencing an estimated 32% range contraction between 2012 and 2013, 64% range expansion between 2013 and 2015, and 23% range contraction between 2015 and 2016 (Figure 2). The best models for annual variation in small-scale occupancy included the additive effect of ecoregion, suggesting small-scale occupancy was greater in the SGPR ecoregion than in the MGPR, SSPR and SOPR ecoregions, with the same pattern of moderate range contraction and expansion evident in all four ecoregions (Figure 2).

Range-wide Multi-scale Covariate Relationships

Overall, we found strong support for hypotheses that LEPC site occupancy is correlated with landscape composition and configuration, and conservation programs involving CRP at both spatial scales of analysis. We found some support for hypotheses that LEPC site occupancy is correlated with anthropogenic development, perhaps more-so at the finer spatial scale (7.5-km × 7.5-km quadrants). Our results do not support hypotheses for shifts in extent of occurrence in response to drought-related covariates. Therefore, management of landscape mosaics (Haukos and Zavaletta 2016) may be more influential than drought-related climatic patterns (Grisham et al. 2016) at both spatial scales. The lack of drought-related effects may not be surprising, given we observed very low annual variation in site occupancy at 15-km × 15-km grids, and only moderate annual variation in site occupancy at 7.5-km × 7.5-km quadrants. The abundance of LEPC has been shown to correlate with lagged weather/climatic effects (Ross et al. 2016b), and we expect that LEPC abundance may be more sensitive to climatic conditions than LEPC site occupancy is. The exploratory analysis of the range-wide data showed a strong effect of anthropogenic development at the smaller spatial scale, with diminutive probabilities of small-scale occupancy in landscapes with >10% landcover of anthropogenic development.

Landscape composition and configuration, and conservation efforts were the most important predictors of large-scale occupancy of the LEPC at 15-km × 15-km grid cells when modeling the pooled data over all ecoregions. We found little support for the relative effects of anthropogenic disturbance or drought-related patterns at this scale. The landcover of shrubland, mean patch size of grassland, and the linear effect of the amount of CRP-enrolled land were the most important correlates of large-scale occupancy in these pooled data for the range-wide analysis. The most suitable landcover mosaics within 225 km^2 landscapes were composed of large patches of grassland embedded in a matrix with high landcover of shrubland or CRP-enrolled land. These landscape relationships were more important than the overall patch sizes of general habitat (the combination of shrubland, grassland, CRP-enrolled land, and pasture; Table A1) or native habitat (the combination of shrubland and grassland; Table A1), suggesting that CRP-enrolled land and shrubland did not contribute to the patch sizes of native habitat. This pattern of landscape configuration and composition suggested habitat fragmentation is important for grassland, whereas habitat loss is important for CRP-enrolled land. Because patch size is more important than landcover for grassland, landscape management to maintain large patches of grassland may be an important conservation strategy in modified agricultural landscapes (Kareiva and Wennergen

1995). In contrast, the effects of CRP-enrolled land on the large-scale occupancy of the LEPC suggested CRP functioned primarily as between-patch matrix habitat and did not contribute to the patch sizes of grassland vegetation. Nevertheless, because amount (or total area) is more important than patch size for CRP-enrolled land, landscape management of CRP can potentially be implemented in any configuration of patch sizes to offset the effects of habitat loss (Kareiva and Wennergen 1995). Landscape management to implement CRP and maintain high landcover of sand sagebrush and Shinnery oak shrubland may be important conservation strategies, and the loss of these habitat types in any configuration is expected to result in concomitant declines in the large-scale occupancy of the LEPC. The results for large-scale occupancy suggest the amount of CRP-enrolled land or shrubland may increase landscape permeability and facilitate LEPC dispersal between patches of native grassland (Ricketts 2001, Niemuth 2011). Our results do not confirm the preliminary effect of LPCI-prescribed grazing on large-scale occupancy reported by Hagen et al. (2016). The strength of evidence for the effects of landscape composition and configuration appear to have outweighed the smaller effect of prescribed grazing. Hagen et al. (2016) predicted the effect of prescribed grazing would operate at the small-scale, and it is possible that the effects of grazing management operate on third-order habitat use at the home-range scale, rather than second-order habitat use at the landscape scale (Haukos and Zavaletta 2016).

Landscape composition and conservation efforts were the most important predictors for the small-scale occupancy of the LEPC at 7.5-km × 7.5-km quadrants in these pooled data. We found little support for the relative effects of anthropogenic disturbance, drought-related patterns, or temporal variation at this scale. The interaction between ecoregion and CRP-enrolled land, shrubland landcover, the interaction between ecoregion and the quadratic term for grassland landcover, and the interaction between ecoregion and the linear effect of grassland landcover were most important correlates of small-scale occupancy when data were pooled across ecoregions. The positive effect of the amount of CRP-enrolled land on small-scale occupancy of the LEPC was two times greater in the SGPR ecoregion than in the MGPR and SSPR ecoregions, and 15 times greater than in the SOPR ecoregion (Figure 5). The interaction between ecoregion and CRP-enrolled land, suggested the landscape management of CRP in 56.25 km^2 landscapes will be most effective in the SGPR ecoregion, moderately effective in the MGPR and SSPR ecoregions, and least effective in the SOPR ecoregion. The positive slope for the additive effect of shrubland landcover was parallel in all four ecoregions, but because the range of shrubland landcover was low in the SGPR ecoregion (0–20%), shrubland landcover had a greater effect on the extent of LEPC occurrence in the SOPR, SSPR and MGPR ecoregions than in the SGPR ecoregion (Figure 6). The interaction between ecoregion and the quadratic term for grassland landcover in the top-ranked model provided some evidence that in these pooled data, the highest levels of small-scale occupancy occurred at intermediate values of grassland landcover in the SOPR (approximately 30–40% grassland cover) and SSPR (approximately 50–60% grassland cover) ecoregions (Figure 7). The non-linear, quadratic response to grassland landcover in the SOPR and SSPR ecoregions suggested that landscape heterogeneity (Fahrig et al. 2011) of grassland, shrubland, and CRP-enrolled land (as well as their complement, cropland) may be important in these two ecoregions. However, there was nearly equal support for the 2nd ranked model, which included only a linear effect of grassland landcover (Table C4). The positive effect of grassland in the SGPR ecoregion was two times greater than in the MGPR ecoregion, four times greater than in the SSPR ecoregion, and six times greater than in the SOPR ecoregion (Table C6). The interaction effects suggest that managing for greater grassland landcover may be less important in the SOPR and SSPR ecoregion than in the SGPR and MGPR ecoregions. However, the loss of grassland habitat below approximately 30% in the SOPR ecoregion and approximately 50% in the SSPR ecoregion, or loss of shrubland habitat may result in concomitant declines in LEPC occupancy.

Ecoregion-specific Multi-scale Covariate Relationships

Occupancy was modeled separately in each ecoregion to determine if important relationships existed between occupancy and the covariates within ecoregions, and this approach provided greater flexibility to model ecoregional effects beyond the interaction terms included in the range-wide models for the pooled dataset. Additional strong relationships within ecoregions were detected; however, many relationships were weakly supported because data were sparse with few detections of LEPC in ecoregions with low abundance. In all ecoregion-specific modeling, there was more model-selection uncertainty (as evidenced by the number of plausible models) than in the range-wide modeling effort.

Overall, covariates describing the local vegetative landcover, conservation efforts, and anthropogenic land uses were the most important correlates of multi-scale occupancy in the ecoregion-specific analyses (Table 2). We found little support for the relative effects of drought-related covariates on large- or small-scale occupancy. Within vegetation-related covariates, shrubland, woodland, and grassland landcover types were among the most influential; however, the attributes of the vegetative landcover that were most predictive of LEPC occupancy patterns varied somewhat by ecoregion (Table 2). The amount of CRP-enrolled land was the only covariate related to conservation efforts that had clear relationships with LEPC occupancy patterns, and CRP-enrolled land was an influential predictor of occupancy in all ecoregions and at both spatial scales (Table 2). Crop production, the density of oil-gas wells, and anthropogenic development landcover were the covariates related to anthropogenic land uses that were most predictive of LEPC occupancy patterns (Table 2).

Ecoregion 1 – Shinnery Oak Prairie (SOPR)

The most important predictors of large-scale occupancy of 15-km × 15-km grid cells within the SOPR ecoregion data included three covariates describing vegetation (shrubland landcover, woodland [>5%] landcover, and woodland [>10%] landcover) and one covariate describing conservation efforts (CRP patch size). The most suitable areas at the large scale (225 km^2) had intermediate amounts of shrubland landcover (approximately 25–50% shrubland landcover), little-to-no woodland landcover, and intermediately sized patches of CRP (average patch size approximately 1–2.5 km^2). Prediction of the largest values of occupancy at intermediate amounts of shrubland landcover at the large scale (225 km^2) supports the hypothesis that landscape heterogeneity (Fahrig et al. 2011) of shrubland, and CRP-enrolled land may be important. There were few grid cells with average CRP patch sizes > 3 km^2 (mean = 0.11 km^2, 3rd quartile = 0.18 km^2), thus our models provided little clarity about the potential relationship between LEPC occupancy and larger-sized patches of CRP-enrolled land.

Within the SOPR ecoregion, the most important predictors of small-scale occupancy of 7.5-km × 7.5-km quadrants, given occupancy at the 15-km × 15-km scale, included two covariates describing vegetation (cropland landcover and grassland landcover). Small-scale occupancy was generally low within the SOPR ecoregion (< 0.30), but the most suitable areas at the small scale (56.25 km^2) had the lowest amounts of cropland landcover and the lowest amounts of grassland landcover. The negative relationship between grassland landcover and small-scale occupancy was counter to our expectation. We speculate that this effect may, in part, be attributable to the drought that occurred in the region until late 2013, during which time there was relatively little suitable habitat for LEPC in areas with even historically high values of grassland landcover; however, drought itself was not found to be an influential predictor of LEPC occupancy in this analysis, so the interpretation of this finding remains unclear.

Ecoregion 2 – Sand Sagebrush Prairie (SSPR)

The most important predictors of large-scale occupancy of 15-km × 15-km grid cells within the SSPR ecoregion included one covariate describing vegetation (shrubland landcover), and one covariate describing conservation efforts (CRP-enrolled land). The most suitable areas at the large scale (225 km^2) had higher amounts of shrubland landcover and higher amounts of CRP-enrolled land.

Within the SSPR ecoregion, the most important predictors of small-scale occupancy of 7.5-km × 7.5-km quadrants, given occupancy at the 15-km × 15-km scale, included one covariate describing conservation efforts (CRP-enrolled land) and one covariate describing vegetation (cropland landcover). Small-scale occupancy was generally low in the SSPR (< 0.20), but the most suitable areas at the small scale (56.25 km^2) had the highest amounts of CRP-enrolled land and the lowest amounts of cropland landcover. The probability of small-scale occupancy was estimated to approach 0 for quadrants with cropland landcover > approximately 80%.

Ecoregion 3 – Mixed Grass Prairie (MGPR)

The most important predictors of large-scale occupancy of 15-km × 15-km grid cells within the MGPR ecoregion included one covariate describing vegetation (native habitat patch size), one covariate describing conservation efforts (CRP-enrolled land), and one covariate describing anthropogenic land use (oil-gas well density). The most suitable areas at the large scale (225 km^2) had larger-sized patches of native habitat (a composite of shrubland and grassland landcover), higher amounts of CRP-enrolled land, and lower densities of oil-gas wells. The probability of large-scale occupancy was estimated to approach 0 for grid cells with oil-gas well density > approximately 1.25 wells/km^2. There were few grid cells with average patch sizes of native habitat landcover > 1 km^2 (mean = 0.47 km^2, 3rd quartile = 0.48 km^2), so our models provided little clarity about the potential relationship between LEPC occupancy and larger-sized patches of native habitat landcover.

Within the MGPR ecoregion, the most important predictors of small-scale occupancy of 7.5-km × 7.5-km quadrants, given occupancy at the 15-km × 15-km scale, included one covariate describing vegetation (woodland [>10%] landcover) and one covariate describing anthropogenic land use (development landcover). Small-scale occupancy was generally low within the MGPR (< 0.20), but the most suitable areas at the small scale (56.25 km^2) had the lowest amounts of woodland landcover and the lowest amounts of development landcover. The probability of small-scale occupancy was estimated to approach 0 for quadrants with development landcover > approximately 5%, and for quadrants with woodland (>10% canopy cover) landcover > approximately 10%, although the latter estimate was imprecise.

Ecoregion 4 – Shortgrass/CRP Mosaic (SGPR)

The most important predictors of large-scale occupancy of 15-km × 15-km grid cells within the SGPR ecoregion included one covariate describing anthropogenic land use (development landcover), one covariate describing conservation efforts (amount of CRP-enrolled land), and two covariates describing vegetation (cropland patch size and grassland patch size). In these data, the most suitable areas at the large scale (225 km^2) had intermediately sized patches of cropland landcover, higher amounts of CRP-enrolled land, larger-sized patches of grassland landcover, and lower amounts of development landcover. Prediction of the highest occupancy of LEPC at intermediate-sized patches of cropland (approximately 0.3–0.5 km^2) could indicate the importance of habitat mosaics and support the hypothesis that landscape heterogeneity (Fahrig et al. 2011) of cropland, grassland and CRP-enrolled land may be important.

Within the SGPR ecoregion, the most important predictors of small-scale occupancy of 7.5-km × 7.5-km quadrants, given occupancy at the 15-km × 15-km scale, included one covariate describing anthropogenic land use (development landcover), one covariate describing conservation efforts (CRP-enrolled land), and one covariate describing vegetation (cropland landcover). Small-scale occupancy within the SGPR was higher relative to other ecoregions, and the most suitable areas at the small scale (56.25 km^2) had lower amounts of cropland landcover, higher amounts of CRP-enrolled land, and lower amounts of development landcover.

Comparison of Range-wide and Ecoregion-specific Findings

We anticipated that the drivers of LEPC occupancy would vary by ecoregion, suggesting that occupancy models fit to ecoregional subsets of the data would provide additional insight beyond a model fit to the range-wide dataset. There were ecoregional differences in covariate-occupancy relationships; however, the qualitative interpretations of our findings are relatively consistent whether data were analyzed at the range-wide or ecoregional scale (Table 2). In short, we found strong positive relationships in the range-wide dataset between occupancy and shrubland landcover, amount of CRP-enrolled land, and grassland patch size or landcover; and these relationships were generally consistent at both scales of occupancy. Furthermore, the secondary, exploratory analysis of range-wide data suggested negative relationships between occupancy and woodland and development-related landcover. The ecoregion-specific analyses generally agreed with the results of the range-wide analysis, but provided additional insight into the effect of covariates that were found to be ecoregionally important, although not as influential range-wide (e.g., cropland landcover and patch size, development landcover, oil-gas well density, CRP patch size, native habitat patch size, and woodland landcover; Table 2).

The disparity in range-wide and ecoregion-specific responses to cropland may be explained by considering that in many parts of the LEPC range, cropland landcover is the complement of landcover of other vegetation types. In other words, areas that are not cropland are likely to be grassland, shrubland, and/or CRP-enrolled land. Therefore, the positive relationships between small-scale occupancy and the landcover of shrubland, grassland, and CRP-enrolled land from the range-wide analysis are consistent with the negative relationships between small-scale occupancy and cropland landcover from the ecoregion-specific analyses (Table 2). The range-wide analysis showed that grassland patch size was a strong predictor of large-scale occupancy, but the ecoregion-specific analyses showed this covariate was a strong predictor only in the SGPR ecoregion (Table 2). This discrepancy suggests the effect of grassland patch size observed in the range-wide analysis may be largely attributable to a strong relationship between small-scale occupancy and grassland patch size in the SGRP ecoregion and that habitat fragmentation may be a particularly important process in the SGRP ecoregion.

Table 2. Summary of estimated relationships between environmental covariates and large- and small-scale occupancy patterns of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. Range-wide models (RW) were fit to data pooled across all ecoregions, and ecoregional models (Eco) were fit to ecoregional subsets of the data. Asterisks (*) denote relationships from secondary, exploratory analyses, and we provide no indication of the strength of the effect for these due to less confidence in these results. Ecoregion acronyms are defined in Figure 1, and covariates are described in Appendix A, Table A1.

		Ecoregion 1 (SOPR)				**Ecoregion 2 (SSPR)**				**Ecoregion 3 (MGPR)**				**Ecoregion 4 (SGPR)**			
		Large-scale		**Small-scale**		**Large-scale**		**Small-scale**		**Large-scale**		**Small-scale**		**Large-scale**		**Small-scale**	
Group	**Covariate**	**RW**	**Eco**	**RW**	**Eco**	**RW**	**Eco**	**RW**	**Eco**	**RW**	**Eco**	**RW**	**Eco**	**RW**	**Eco**	**RW**	**Eco**
Anthropogenic	Development landcover			*Neg.	*Neg.			*Neg.				*Neg.	Neg.		Weak Neg.	*Neg.	Weak Neg.
	Oil-gas well density										Neg.						
Climate	Summer drought weeks												*Neg.				
Conservation	CRP-enrolled land	Pos.		Weak Pos.		Pos.	Weak Pos.	Pos.	Weak Pos.	Pos.	Pos.	Pos.		Pos.	Pos.	Pos.	Pos.
	Patch size of CRP-enrolled land		Quad.														
Vegetative Landcover	Cropland landcover				Weak Neg.				Weak Neg.								Weak Neg.
	Cropland patch size						*Pos.								Weak Quad.		
	Grassland landcover		*Neg.	Weak Quad.	Weak Neg.			Weak Quad.				Pos.				Pos.	
	Grassland patch size	Pos.				Pos.				Pos.				Pos.	Pos.		
	Shrubland landcover	Pos.	Quad.	Pos.	*Pos.	Pos.	Pos.	Pos.		Pos.		Pos.		Pos.		Pos.	
	Native habitat patch size										Pos.						
	Wetland landcover						*Neg.										
	Woodland (>1%) landcover												*Neg.				
	Woodland (>5%) landcover		Neg.										*Neg.				
	Woodland (>10%) landcover	*Neg.	Weak Neg.			*Neg.				*Neg.			Weak Neg.	*Neg.			
Vegetative Landcover and Conservation	General habitat landcover								*Pos.								

There were only two cases where the direction or form (i.e., positive, negative, or quadratic) of the estimated effect of a covariate differed between the range-wide and ecoregional models and was found to be important (ψ in the SOPR ecoregion, and θ in the SOPR ecoregion). In the first case, the range-wide model based on pooled data indicated the main effect for shrubland was supported over the quadratic effect, and estimated that shrubland landcover had a positive relationship with the probability of large-scale occupancy in all ecoregions, including the SOPR (Figure 4A). However, the ecoregion-specific model fit only to the SOPR data estimated a curvilinear relationship, with higher values of large-scale occupancy at intermediate values of shrubland landcover (Figure 14A). However, this is not a clear conflict between the two modeling attempts, because there are relatively few grid cells with large values of shrubland landcover in the pooled dataset. In addition, low prevalence of shrubland in the SGPR ecoregion prevented the investigation of an interaction between shrubland and ecoregion in the range-wide analysis. The curvilinear relationship resulting in the highest estimates of large-scale occupancy at intermediate values of shrubland landcover in the ecoregion model for SOPR is support for an optimal range of shrubland landcover in environments where there was a broad range of shrubland values.

Second, there was support in range-wide modelling for a weak curvilinear relationship between grassland landcover and small-scale occupancy in the SOPR ecoregion (Figure 7A, Figure 8A) with highest values of small-scale occupancy at intermediate values of grassland landcover, or near-equal support for a weak positive relationship between grassland landcover and small-scale occupancy in the SOPR ecoregion (Table C4, Table C5, Table C6). However, the ecoregion-specific model fit only to the SOPR data estimated a weak negative relationship between small-scale occupancy and grassland landcover (Figure 15B). Given the relatively poor precision of the estimate in the ecoregion-specific model, this disagreement may be inconsequential.

From a practical perspective, fitting models to ecoregional subsets of the data introduced difficulties with model convergence and stability, and model-selection uncertainty was generally high. These difficulties were exacerbated for ecoregions where few birds were observed. We chose to limit the number of covariates we considered and to exclude any quadratic or interaction terms in models for some ecoregions (Table 1). Considering simpler model structures allowed us to circumvent some model instabilities, but also limited our ability to identify and describe more-complex relationships between occupancy and covariates of interest. Interestingly, even for ecoregions where we considered interactive effects between two covariates during the plausible model selection stage, no interaction terms were present in any of the submodels found to be plausible for any ecoregion. This lack of support for interaction terms within the ecoregion models may be further indication that the ecoregional subsets of the survey data could only accommodate simpler model structures.

Fitting occupancy models to the range-wide data represented a trade-off between ecoregional inference and model performance. The range-wide analysis provided a way to share data across ecoregions, and although this reduced the flexibility to investigate ecoregion-specific effects, sharing data improved the performance of the models. The primary problem involved sparse data in the SOPR and SSPR ecoregions, and the low estimates of small-scale occupancy produced estimation problems for logit-link estimates of large-scale occupancy near the boundary of 100% probability of occupancy. Sharing the data across ecoregions allowed additive effects of year, and permitted the investigation of annual variation in occupancy at the two scales that ameliorated the problem of sparse data to some extent. Estimating the parameters across ecoregions may also improve the precision of mapped occupancy estimates throughout the range of the LEPC with potential applications to conservation planning. Finally, the range-wide framework may be useful for investigating annual trends and occupancy distributions, including one-way interactions with ecoregion, whereas the ecoregion framework may be useful for addressing specific conservation objectives for each ecoregions.

We reassert that observational studies such as this warrant caution when interpreting the specificity and causality inferred from the results. Statistical modeling of the type conducted here provides insight into correlative associations between the variables of interest (e.g., occupancy and environmental covariates at the same grid cells or quadrants) in the data (Holland 1986). Understanding explicit causal relationships is imperative to successful wildlife management, but such causal inference is best achieved through manipulative experiments (e.g., before-after-control-impact study designs), or potentially inferred from multiple observational studies with corroborating results (Johnson 2002).

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APPENDICES

Appendix A

Descriptions and sources of covariates used to predict multi-scale occupancy patterns of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016.

Table A1. Descriptions and sources of covariates used to predict multi-scale occupancy patterns of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. The abbreviated name is used to identify variables within model formulas.

Group	Covariate	Abbreviated Name	Description	Source
Anthropogenic	Development landcover	Development	Percentage of area (%) with anthropogenic development. Includes low, medium, and high intensity development categories.	NLCD
Anthropogenic	Oil-gas well density	Well	Density of active oil or gas wells (wells/km^2).	IHS
Anthropogenic	Primary road density	Road	Density of primary roads (km/km^2).	WAFWA
Anthropogenic	Transmission line density	Transmission	Density of electrical transmission lines (km/km^2).	PLATTS
Anthropogenic	Vertical structures	Vertical	Density of vertical structures (structures/km^2) considered obstacles to aviation users.	FAA
Climate	Spring green weeks	Green	Number of weeks during March and April not classified as abnormally dry, moderate, severe, extreme, or exceptional drought.	DM
Climate	Summer drought weeks	Drought	Number of weeks during May and June classified as severe, extreme, or exceptional drought.	DM
Conservation	CRP-enrolled land	CRP	Percentage of area (%) enrolled in the Conservation Reserve Program (CRP).	USDA
Conservation	Patch size of CRP-enrolled land	CRPPatch	Average size (km^2) of patches of CRP-enrolled land.	USDA
Conservation	Prescribed grazing landcover	Grazing	Percentage of area (%) enrolled in prescribed grazing practices.	B&D 2013
Conservation	WAFWA conservation area landcover	Conservation	Percentage of area (%) enrolled in conservation plans administered by WAFWA.	WAFWA
Conservation	WAFWA conservation area-grazing landcover	ConservationGrazing	Percentage of area (%) enrolled in conservation plans administered by WAFWA or enrolled in LPCI prescribed grazing practices.	WAFWA
Detection	Date	Date	Ordinal day of year the survey was conducted.	Field
Detection	Observer	Observer	The observation position (front or back seat) within the aircraft.	Field
Detection	Time	Time	Hours after sunrise the survey was conducted.	Field
Other	Ecoregion	Ecoregion	Ecoregion identifier (1 = SOPR, 2 = SSPR, 3 = MGPR, 4 = SGPR)	Field
Other	Trend	Trend	Year (continuous) the survey was conducted.	Field
Other	Year	Year	Year (categorical) the survey was conducted.	Field
Vegetative Landcover	Cedar landcover	Cedar	Percentage of area (%) with eastern red cedar (*Juniperus virginiana*).	NLCD
Vegetative Landcover	Cropland landcover	Cropland	Percentage of area (%) used for production of annual or woody perennial crops or in active tilling.	NLCD
Vegetative Landcover	Cropland patch size	CroplandPatch	Average size (km^2) of cropland landcover patches.	NLCD

Vegetative Landcover	Grassland landcover	Grass	Percentage of area (%) dominated by gramanoid or herbaceous vegetation not subject to intensive management such as tilling.	NLCD
Vegetative Landcover	Grassland patch size	GrassPatch	Average size (km^2) of grassland landcover patches.	NLCD
Vegetative Landcover	Mesquite landcover	Mesquite	Percentage of area (%) with mesquite (*Prosopis* spp.).	NLCD
Vegetative Landcover	Mesquite-cedar landcover	MesquiteCedar	Percentage of area (%) with eastern red cedar or mesquite.	NLCD
Vegetative Landcover	Native habitat landcover	NativeHabitat	Percentage of area (%) dominated by shrubs, including trees <5 m tall, or gramanoid or herbaceous vegetation not subject to intensive management such as tilling.	NLCD
Vegetative Landcover	Native habitat patch size	NativeHabitatPatch	Average size (km^2) of native habitat landcover patches.	NLCD
Vegetative Landcover	Shrubland landcover	Shrub	Percentage of area (%) dominated by shrubs, including trees <5 m tall.	NLCD
Vegetative Landcover	Wetland landcover	Wetland	Percentage of area (%) dominated by perennial herbaceous vegetation and with soils periodically saturated or covered with water.	NLCD
Vegetative Landcover	Woodland (>1% canopy cover) landcover	Woodland1	Percentage of area (%) with tree canopy cover >1%.	NRCS
Vegetative Landcover	Woodland (>5% canopy cover) landcover	Woodland10	Percentage of area (%) with tree canopy cover >5%.	NRCS
Vegetative Landcover	Woodland (>10% canopy cover) landcover	Woodland5	Percentage of area (%) with tree canopy cover >10%.	NRCS
Vegetative Landcover and Conservation	General habitat landcover	GeneralHabitat	Percentage of area (%) dominated by shrubs, including trees <5 m tall, or gramanoid or herbaceous vegetation not subject to intensive management such as tilling, or enrolled in the Conservation Reserve Program, or planted for livestock grazing or the production of seed or hay crops.	NLCD
Vegetative Landcover and Conservation	General habitat patch size	GeneralHabitatPatch	Average size (km^2) of general habitat landcover patches.	NLCD

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[a] Sources: B&D 2013 (Bartuszevige and Daniels 2013), DM (http://droughtmonitor.unl.edu/),
FAA (https://www.faa.gov/air_traffic/flight_info/aeronav/digital_products/dof/), Field (field-collected data during surveys),
IHS (https://ihsmarkit.com/products/us-oil-gas-spatial-layers.html), NLCD (https://www.mrlc.gov/nlcd2011.php),
NRCS (https://www.nrcs.usda.gov/wps/portal/nrcs/site/national/home/), PLATTS (https://www.platts.com/products/gis-data-electric-power),
USDA (United States Department of Agriculture 2014), WAFWA (WAFWA LPC Geodatabase, unpublished data).

Appendix B

Model selection and parameter estimates for annual variation in large-scale and small-scale occupancy of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016.

Table B1. Model selection for the large-scale occupancy (ψ), small-scale occupancy (θ), and detection (p) of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. The model-selection metrics are the value of the minimized -2 log-likelihood function [$-2\log_e(\mathcal{L})$], parameter number (K), Akaike's Information Criterion adjusted for sample size (AIC$_c$), difference between model and minimum AIC$_c$ value (ΔAIC$_c$) and AIC$_c$ weight (w_i). Models with ΔAIC$_c$ < 4 are shown.

Model	**K**	**-2log($\mathcal{L}$)**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**
ψ(.) θ(Ecoregion) p(Date + Observer + Ecoregion + Trend)	12	2651.69	2675.91	0.00	0.075
ψ(.) θ(Ecoregion) p(Observer + Time + Trend)	9	2657.88	2676.01	0.10	0.071
ψ(.) θ(Ecoregion) p(Date + Observer + Ecoregion + Time + Trend)	13	2649.87	2676.14	0.23	0.067
ψ(.) θ(Ecoregion) p(Observer + Trend)	8	2660.30	2676.40	0.49	0.058
ψ(.) θ(Ecoregion) p(Date + Observer + Time + Trend)	10	2656.42	2676.57	0.66	0.054
ψ(.) θ(Ecoregion) p(Observer + Time)	8	2660.69	2676.79	0.88	0.048
ψ(.) θ(Ecoregion) p(Date + Observer + Trend)	9	2658.92	2677.05	1.14	0.042
ψ(.) θ(Ecoregion) p(Observer + Ecoregion + Trend)	11	2655.67	2677.86	1.95	0.028
ψ(.) θ(Ecoregion + Year) p(Observer + Time + Trend)	13	2651.70	2677.96	2.05	0.027
ψ(.) θ(Ecoregion) p(Observer)	7	2663.96	2678.04	2.13	0.026
ψ(.) θ(Ecoregion) p(Observer + Ecoregion + Time + Trend)	12	2653.85	2678.08	2.17	0.025
ψ(.) θ(Ecoregion + Year) p(Observer + Time)	12	2653.91	2678.14	2.23	0.024
ψ(.) θ(Ecoregion) p(Date + Observer + Time)	9	2660.32	2678.45	2.54	0.021
ψ(.) θ(Ecoregion + Year) p(Observer + Trend)	12	2654.39	2678.61	2.70	0.019
ψ(.) θ(Ecoregion + Year) p(Date + Observer + Ecoregion + Time + Trend)	17	2644.43	2678.87	2.96	0.017
ψ(.) θ(Ecoregion + Year) p(Date + Observer + Time + Trend)	14	2650.60	2678.91	3.00	0.017
ψ(.) θ(Ecoregion + Year) p(Date + Observer + Ecoregion + Trend)	16	2646.59	2678.98	3.08	0.016
ψ(.) θ(Ecoregion) p(Observer + Ecoregion + Time)	11	2656.95	2679.14	3.23	0.015
ψ(.) θ(Ecoregion) p(Observer + Ecoregion)	10	2659.52	2679.68	3.77	0.011
ψ(.) θ(Ecoregion + Year) p(Date + Observer + Trend)	13	2653.43	2679.69	3.78	0.011
ψ(.) θ(Ecoregion + Year) p(Date + Observer + Time)	13	2653.52	2679.78	3.87	0.011
ψ(.) θ(Ecoregion + Year) p(Observer)	11	2657.62	2679.81	3.90	0.011
ψ(.) θ(Ecoregion) p(Date + Observer + Ecoregion + Time)	12	2655.63	2679.85	3.94	0.010
ψ(.) θ(Ecoregion) p(Date + Observer)	8	2663.75	2679.85	3.94	0.010

Table B2. Parameter estimates, Standard Errors (SE), and Lower and Upper 90% Confidence Limits (LCL and UCL, respectively), and for large-scale occupancy (ψ), small-scale occupancy (θ), and detection (*p*) of the lesser prairie-chicken from the highest ranking model for annual variation in small-scale occupancy from the range-wide monitoring program, 2012–2016.

Parameter	Estimate	SE	LCL	UCL
ψ(.)	-0.803	0.132	-1.020	-0.586
θ(intercept)	-0.427	0.245	-0.831	-0.024
θ(Year 2013)	-0.496	0.283	-0.963	-0.030
θ(Year 2014)	-0.305	0.280	-0.766	0.155
θ(Year 2015)	0.105	0.282	-0.359	0.568
θ(Year 2016)	-0.240	0.281	-0.703	0.222
θ(Ecoregion 3)	-0.932	0.215	-1.286	-0.578
θ(Ecoregion 2)	-1.549	0.273	-2.000	-1.099
θ(Ecoregion 1)	-1.318	0.230	-1.697	-0.940
p(intercept)	-0.888	0.332	-1.435	-0.341
p(Time)	0.309	0.189	-0.001	0.620
p(Observer)	1.026	0.171	0.744	1.308
p(Trend)	0.127	0.086	-0.015	0.269

Table B3. Parameter estimates, Standard Errors (SE), and Lower and Upper 90% Confidence Limits (LCL and UCL, respectively) for the detection (*p*) of the lesser prairie-chicken from the best and second best model and range-wide monitoring program, 2012–2016.

Model **Parameter**	**Estimate**	**SE**	**LCL**	**UCL**
Model 1				
p(intercept)	-3.185	1.393	-5.476	-0.893
p(Ecoregion 3)	-0.648	0.330	-1.191	-0.105
p(Ecoregion 2)	0.445	0.452	-0.299	1.189
p(Ecoregion 1)	-0.549	0.363	-1.146	0.048
p(Date)	0.026	0.013	0.004	0.048
p(Observer)	1.017	0.170	0.737	1.298
p(Trend)	0.221	0.085	0.080	0.361
Model 2				
p(intercept)	-0.871	0.315	-1.390	-0.352
p(Time)	0.288	0.185	-0.017	0.593
p(Observer)	1.027	0.171	0.745	1.309
p(Trend)	0.129	0.077	0.002	0.257

Appendix C

Model selection and parameter estimates for covariate relationships on large-scale occupancy, small-scale occupancy and detection of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016.

Table C1. Plausible combinations model selection for large-scale occupancy (ψ) of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. The model-selection metrics are the value of the minimized -2 log-likelihood function $-2\log_e(\mathcal{L})$], parameter number (K), Akaike's Information Criterion adjusted for sample size (AIC_c), difference between model and minimum AIC_c value (ΔAIC_c) and AIC_c weight (w_i). High-weight submodels with $w_i < 0.001$ and high likelihood submodels with $-2\log(\mathcal{L})$ < maximum $-2\log(\mathcal{L})$ of high weight models are shown.

Model[a]	K	$-2\log(L)$	AIC_c	ΔAIC_c	w_i
ψ(CRP + GrassPatch + Shrub)	17	2545.03	2579.48	0.00	0.697
ψ(CRP + CRP^2 + GrassPatch + Shrub)	18	2544.67	2581.17	1.69	0.299

[a] All models include *p*(Ecoregion + Year + Observer) and θ(Ecoregion).

Table C2. Plausible combinations model selection for small-scale occupancy (θ) of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. The model-selection metrics are the value of the minimized -2 log-likelihood function $-2\log_e(\mathcal{L})$], parameter number (K), Akaike's Information Criterion adjusted for sample size (AIC_c), difference between model and minimum AIC_c value (ΔAIC_c) and AIC_c weight (w_i). High-weight submodels with $w_i < 0.001$ and high-likelihood submodels with $-2\log(\mathcal{L})$ < maximum $-2\log(\mathcal{L})$ of high weight models are shown.

Model [a]	***K***	**$-2\log(\mathcal{L})$**	**AIC_c**	**ΔAIC_c**	**w_i**
θ(CRP + Grass + $Grass^2$ + Shrub + Ecoregion + Ecoregion*CRP + Ecoregion*$Grass^2$)	28	2494.53	2551.71	0.00	0.803
θ(CRP + Grass + Shrub + Ecoregion + Ecoregion*CRP + Ecoregion*Grass)	27	2500.13	2555.23	3.52	0.138
θ(CRP + Grass + $Grass^2$ + Shrub + Ecoregion + Ecoregion*CRP + Ecoregion*Grass)	28	2500.13	2557.31	5.60	0.049

[a] All models include *p*(Ecoregion + Year + Observer) and ψ(Year).

Table C3. Plausible combinations model selection for detection (*p*) of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. The model-selection metrics are the value of the minimized -2 log-likelihood function -2log$_e$($\mathcal{L}$)], parameter number (*K*), Akaike's Information Criterion adjusted for sample size (AIC$_c$), difference between model and minimum AIC$_c$ value (ΔAIC$_c$) and AIC$_c$ weight (w_i). High-weight submodels with w_i < 0.001 and high likelihood submodels with -2log($\mathcal{L}$) < maximum -2log($\mathcal{L}$) of high weight models are shown.

Model [a]	***K***	**-2log($\mathcal{L}$)**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**
p(Time + Observer + Trend)	13	2654.00	2680.26	0.00	0.140
p(Observer + Trend)	12	2656.36	2680.59	0.33	0.119
p(Time + Observer)	12	2656.69	2680.91	0.65	0.101
p(Ecoregion + Date + Observer + Trend)	16	2648.70	2681.10	0.84	0.092
p(Date + Time + Observer + Trend)	14	2652.98	2681.29	1.03	0.084
p(Date + Observer + Trend)	13	2655.46	2681.72	1.46	0.068
p(Ecoregion + Observer + Trend)	15	2651.69	2682.03	1.77	0.058
p(Observer)	11	2660.06	2682.25	1.99	0.052
p(Ecoregion + Time + Observer + Trend)	16	2649.94	2682.33	2.07	0.050
p(Date + Time + Observer)	13	2656.44	2682.71	2.45	0.041
p(Ecoregion + Time + Observer)	15	2652.94	2683.28	3.02	0.031
p(Ecoregion + Observer)	14	2655.61	2683.92	3.66	0.023
p(Year + Ecoregion + Date + Observer)	19	2645.61	2684.16	3.90	0.020
p(Date + Observer)	12	2659.95	2684.18	3.92	0.020
p(Ecoregion + Date + Time + Observer)	16	2651.91	2684.30	4.05	0.019
p(Year + Time + Observer)	16	2651.92	2684.31	4.06	0.018
p(Year + Observer)	15	2654.19	2684.54	4.28	0.016
p(Year + Date + Time + Observer)	17	2650.55	2684.99	4.73	0.013
p(Ecoregion + Date + Observer)	15	2654.83	2685.18	4.92	0.012
p(Year + Date + Observer)	16	2653.13	2685.52	5.27	0.010

[a] All models include θ(Ecoregion) and ψ(Year).

Table C4. Model selection for covariate effects on the large-scale occupancy (ψ), small-scale occupancy (θ), and detection (p) of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. The model-selection metrics are the value of the minimized -2 log-likelihood function [$-2\log_e(\mathcal{L})$], parameter number (K), Akaike's Information Criterion adjusted for sample size (AIC_c), difference between model and minimum AIC_c value (ΔAIC_c) and AIC_c weight (w_i). Models with $\Delta AIC_c < 2$ are shown.

Model	***K***	**$-2\log(\mathcal{L})$**	**AIC_c**	**ΔAIC_c**	**w_i**
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Grass^2 + Shrub + Ecoregion + CRP*Ecoregion + Grass^2*Ecoregion) *p*(Time + Observer + Trend)	22	2470.69	2515.43	0.00	0.072
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion + Grass*Ecoregion) *p*(Time + Observer + Trend)	21	2472.78	2515.45	0.02	0.072
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion + Grass*Ecoregion) *p*(Ecoregion + Date + Observer + Trend)	24	2466.77	2515.64	0.22	0.065
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Grass^2 + Shrub + Ecoregion + CRP*Ecoregion + Grass^2*Ecoregion) *p*(Time + Observer)	21	2473.11	2515.78	0.35	0.061
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion + Grass*Ecoregion) *p*(Time + Observer)	20	2475.21	2515.82	0.39	0.059
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Grass^2 + Shrub + Ecoregion + CRP*Ecoregion + Grass^2*Ecoregion) *p*(Ecoregion + Date + Observer + Trend)	25	2464.98	2515.92	0.50	0.056
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion + Grass*Ecoregion) *p*(Observer + Trend)	20	2475.77	2516.37	0.95	0.045
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Grass^2 + Shrub + Ecoregion + CRP*Ecoregion + Grass^2*Ecoregion) *p*(Observer + Trend)	21	2473.87	2516.53	1.11	0.042
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Grass^2 + Shrub + Ecoregion + CRP*Ecoregion + Grass^2*Ecoregion) *p*(Date + Time + Observer + Trend)	23	2469.76	2516.56	1.13	0.041
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion + Grass*Ecoregion) *p*(Date + Time + Observer + Trend)	22	2471.89	2516.62	1.20	0.040
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion + Grass*Ecoregion) *p*(Ecoregion + Time + Observer + Trend)	24	2468.11	2516.98	1.55	0.033

Model	***K***	**-2log($\mathcal{L}$)**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Grass^2 + Shrub + Ecoregion + CRP*Ecoregion + Grass^2*Ecoregion) *p*(Ecoregion + Time + Observer + Trend)	25	2466.22	2517.17	1.74	0.030
ψ(CRP + GrassPatch + Shrub) θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion + Grass*Ecoregion) *p*(Ecoregion + Observer + Trend)	23	2470.50	2517.30	1.87	0.028

Table C5. Parameter estimates, Standard Errors (SE), and Lower and Upper 90% Confidence Limits (LCL and UCL, respectively) for the large-scale occupancy (ψ), small-scale occupancy (θ) and detection (p) of the lesser prairie-chicken from the best model, range-wide monitoring program, 2012–2016.

Parameter	Estimate	SE	LCL	UCL
ψ(intercept)	-2.404	0.412	-3.082	-1.725
ψ(CRP)	12.437	2.397	8.493	16.381
ψ(GrassPatch)	5.699	1.995	2.417	8.980
ψ(Shrub)	3.655	1.599	1.025	6.286
θ(intercept)	-3.100	0.507	-3.936	-2.265
θ(CRP)	10.586	2.182	6.997	14.175
θ(Grass)	2.334	1.745	-0.537	5.205
θ(Grass^2)	1.878	2.152	-1.663	5.419
θ(Shrub)	4.123	1.213	2.127	6.120
θ(Ecoregion 3)	-0.595	0.675	-1.706	0.515
θ(Ecoregion 2)	-1.400	0.733	-2.606	-0.194
θ(Ecoregion 1)	-0.457	0.580	-1.411	0.496
θ(CRP *Ecoregion 3)	-5.552	3.246	-10.893	-0.212
θ(CRP *Ecoregion 2)	-5.983	2.917	-10.783	-1.184
θ(CRP *Ecoregion 1)	-9.861	2.496	-13.968	-5.755
θ(Grass^2*Ecoregion 3)	-1.823	1.367	-4.072	0.425
θ(Grass^2*Ecoregion 2)	-4.119	2.044	-7.483	-0.755
θ(Grass^2*Ecoregion 1)	-5.295	1.513	-7.784	-2.806
p(intercept)	-0.881	0.311	-1.393	-0.369
p(Time)	0.322	0.180	0.025	0.619
p(back-seat Observer)	1.018	0.170	0.737	1.298
p(Trend)	0.117	0.075	-0.007	0.242

Table C6. Parameter estimates, Standard Errors (SE), and Lower and Upper 90% Confidence Limits (LCL and UCL, respectively) for the large-scale occupancy (ψ), small-scale occupancy (θ) and detection (*p*) of the lesser prairie-chicken from the second best model, range-wide monitoring program, 2012–2016.

Parameter	**Estimate**	**SE**	**LCL**	**UCL**
ψ(intercept)	-2.469	0.396	-3.121	-1.818
ψ(CRP)	12.764	2.332	8.927	16.601
ψ(GrassPatch)	5.906	1.965	2.673	9.138
ψ(Shrub)	3.176	1.121	1.331	5.021
θ(intercept)	-3.427	0.513	-4.271	-2.583
θ(CRP)	10.495	2.180	6.908	14.082
θ(Grass)	4.057	0.874	2.618	5.495
θ(Shrub)	4.819	0.982	3.202	6.435
θ(Ecoregion 3)	0.109	0.880	-1.339	1.558
θ(Ecoregion 2)	-1.148	0.876	-2.589	0.294
θ(Ecoregion 1)	0.025	0.713	-1.149	1.198
θ(CRP *Ecoregion 3)	-6.315	3.208	-11.593	-1.036
θ(CRP *Ecoregion 2)	-5.214	2.875	-9.944	-0.485
θ(CRP *Ecoregion 1)	-9.651	2.526	-13.806	-5.495
θ(Grass*Ecoregion 3)	-2.166	1.260	-4.238	-0.093
θ(Grass*Ecoregion 2)	-3.088	1.539	-5.621	-0.556
θ(Grass*Ecoregion 1)	-4.197	1.214	-6.195	-2.198
p(intercept)	-0.873	0.311	-1.386	-0.361
p(Time)	0.312	0.180	0.015	0.608
p(back-seat Observer)	1.017	0.170	0.736	1.298
p(Trend)	0.118	0.076	-0.007	0.243

Table C7. Exploratory model selection for the large-scale occupancy (ψ), small-scale occupancy (θ) and detection (p) of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016. The model-selection metrics are the value of the minimized -2 log-likelihood function $-2\log_e(\mathcal{L})$], parameter number (K), Akaike's Information Criterion adjusted for sample size (AIC_c), difference between model and minimum AIC_c value (ΔAIC_c) and AIC_c weight (w_i). Models with $\Delta AIC_c < 4$ are shown.

Model [a]	K	$-2\log(L)$	AIC_c	ΔAIC_c	w_i
ψ(Woodland10) θ(Grass*Ecoregion + Development) p(Ecoregion + Date + Observer + Trend)	26	2434.90	2487.92	0.00	0.122
ψ(Woodland10) θ(Grass*Ecoregion + Development) p(Time + Observer + Trend)	23	2441.31	2488.11	0.19	0.111
ψ(Woodland10) θ(Grass*Ecoregion + Development) p(Time + Observer)	22	2443.48	2488.21	0.29	0.105
ψ(Woodland10) θ(Grass*Ecoregion + Development) p(Date + Time + Observer + Trend)	24	2440.28	2489.15	1.23	0.066
ψ(Woodland10) θ(Grass*Ecoregion + Development) p(Ecoregion + Time + Observer + Trend)	26	2436.17	2489.19	1.27	0.065
ψ(Woodland10) θ(Grass*Ecoregion + Development) p(Observer + Trend)	22	2444.46	2489.20	1.28	0.064
ψ(Woodland10) θ(Grass*Ecoregion + Development) p(Ecoregion + Observer + Trend)	25	2438.78	2489.72	1.80	0.049
ψ(Woodland10) θ(Grass^2 + Grass^2*Ecoregion + Development) p(Time + Observer + Trend)	24	2441.15	2490.02	2.10	0.043
ψ(Woodland10) θ(Grass^2 + Grass^2*Ecoregion + Development) p(Time + Observer)	23	2443.24	2490.04	2.12	0.042
ψ(Woodland10) θ(Grass^2 + Grass^2*Ecoregion + Development) p(Ecoregion + Date + Observer + Trend)	27	2435.11	2490.21	2.29	0.039
ψ(Woodland10) θ(Grass^2 + Grass^2*Ecoregion + Development) p(Date + Time + Observer + Trend)	25	2440.08	2491.02	3.10	0.026
ψ(Woodland10) θ(Grass^2 + Grass^2*Ecoregion + Development) p(Observer + Trend)	23	2444.39	2491.19	3.27	0.024
ψ(Woodland10) θ(Grass^2 + Grass^2*Ecoregion + Development) p(Ecoregion + Time + Observer + Trend)	27	2436.38	2491.48	3.56	0.021
ψ(Woodland10) θ(Grass^2 + Grass^2*Ecoregion + Development) p(Ecoregion + Observer + Trend)	26	2439.10	2492.12	4.20	0.015
ψ(Woodland5) θ(Grass*Ecoregion + Development) p(Ecoregion + Date + Observer + Trend)	26	2439.82	2492.84	4.92	0.010

[a] All models include ψ(CRP + GrassPatch + Shrub) and θ(CRP + Grass + Shrub + Ecoregion + CRP*Ecoregion).

Table C8. The cumulative AIC$_c$ weights of covariates for large-scale occupancy from the exploratory model selection analysis, range-wide monitoring program, 2012–2016.

Covariate	**Weight**
Woodland10	0.887
Woodland5	0.083
Well	0.008
Woodland1	0.004
MesquiteCedar	0.003
Wetland	0.003
Drought * GrassPatch	0.002
Cedar	0.002
Green * GrassPatch	0.001
Green	0.001
CroplandPatch^2	0.001
Development	0.001
Cropland	0.001
Mesquite	<0.001
CroplandPatch	<0.001
Cropland^2	<0.001
Drought * Shrub	<0.001
Conservation	<0.001
CRP * Drought	<0.001
Vertical	<0.001
ConservationGrazing	<0.001
Trend$^{\mathbf{2}}$	<0.001
Transmission	<0.001
Grazing	<0.001
Drought	<0.001
Road	<0.001
Trend	<0.001
Year	<0.001

Table C9. Parameter estimates, Standard Errors (SE), and Lower and Upper 90% Confidence Limits (LCL and UCL, respectively) for the large-scale occupancy (ψ), small-scale occupancy (θ) and detection (*p*) of the lesser prairie-chicken from the best exploratory model, range-wide monitoring program, 2012–2016.

Parameter	Estimate	SE	LCL	UCL
ψ(intercept)	-1.885	0.399	-2.542	-1.229
ψ(CRP)	11.285	2.461	7.237	15.333
ψ(GrassPatch)	4.103	1.644	1.398	6.808
ψ(Shrub)	3.323	1.109	1.498	5.148
ψ(Woodland10)	-14.263	3.668	-20.297	-8.228
θ(intercept)	-2.646	0.543	-3.540	-1.753
θ(CRP)	8.907	2.004	5.609	12.205
θ(Grass)	3.635	0.824	2.279	4.991
θ(Shrub)	4.002	1.017	2.329	5.676
θ(Ecoregion 3)	0.500	0.885	-0.956	1.957
θ(Ecoregion 2)	-1.071	0.877	-2.515	0.372
θ(Ecoregion 1)	1.395	0.780	0.111	2.680
θ(Development)	-25.059	6.591	-35.901	-14.217
θ(CRP *Ecoregion 3)	-4.960	3.135	-10.117	0.198
θ(CRP *Ecoregion 2)	-4.338	2.762	-8.882	0.207
θ(CRP *Ecoregion 1)	-10.347	2.458	-14.392	-6.302
θ(Grass*Ecoregion 3)	-2.015	1.238	-4.051	0.022
θ(Grass*Ecoregion 2)	-3.144	1.488	-5.593	-0.696
θ(Grass*Ecoregion 1)	-5.973	1.287	-8.091	-3.855
p(intercept)	-2.988	1.334	-5.183	-0.793
p(Ecoregion 3)	-0.728	0.347	-1.300	-0.157
p(Ecoregion 2)	0.425	0.444	-0.37	1.157
p(Ecoregion 1)	-0.697	0.380	-1.321	-0.072
p(Date)	0.025	0.012	0.004	0.045
p(back-seat Observer)	1.001	0.169	0.723	1.280
p(Trend)	0.206	0.084	0.067	0.345

Table C10. The cumulative AIC$_c$ weights of covariates for small-scale occupancy from the exploratory model selection analysis, range-wide monitoring program, 2012–2016.

Covariate	**Weight**
Development	0.879
Road	0.070
Well	0.022
Mesquite	0.007
MesquiteCedar	0.005
Green	0.002
Woodland10	0.002
Year	0.002
Drought * Shrub	0.001
Drought	0.001
Vertical	0.001
Wetland	0.001
Woodland5	0.001
Grazing	0.001
ConservationGrazing	0.001
Woodland1	0.001
Transmission	0.001
Cedar	<0.001
Trend	<0.001
Conservation	<0.001

Appendix D

Ecoregion-specific results describing model selection and variable support for covariate relationships on the probabilities of large-scale occupancy, small-scale occupancy and detection of the lesser prairie-chicken from the range-wide monitoring program, 2012–2016.

Table D1. Model selection for probability of large-scale occupancy (ψ), small-scale occupancy (θ), and detection (p) of the lesser prairie-chicken in the Shinnery Oak Prairie ecoregion (SOPR; ecoregion 1) , 2012–2016. The model-selection metrics are the parameter number (K), value of the minimized -2 log-likelihood function [$-2\log_e(\mathcal{L})$], Akaike's Information Criterion adjusted for sample size (AIC_c), difference between model and minimum AIC_c value (ΔAIC_c), and AIC_c weight (w_i). Models with $\Delta AIC_c < 2$ are shown.

Model	K	**-2log(L)**	**AIC$_c$**	**ΔAIC$_c$**	w_i
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland1 + Cropland + Grass) p(Observer + Year + Date)	14	432.15	461.29	0.00	0.029
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland5 + Cropland + Grass) p(Observer + Trend + Date)	14	432.62	461.76	0.47	0.023
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland1 + Cropland + Grass) p(Observer + Trend)	13	435.08	462.06	0.77	0.020
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland1 + Cropland + Grass) p(Time + Observer + Trend)	14	433.06	462.20	0.90	0.019
ψ(Woodland10 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland1 + Cropland + Grass) p(Observer + Trend + Date)	14	433.14	462.28	0.99	0.018
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland1 + Cropland + Grass) p(Observer)	12	437.55	462.39	1.10	0.017
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland5 + Cropland + Grass) p(Time + Observer + Trend)	14	433.50	462.65	1.35	0.015
ψ(Woodland5 + Grass + Shrub + Shrub^2) θ(Woodland10 + Shrub + Development) p(Observer + Trend)	12	437.83	462.67	1.38	0.015
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland5 + Cropland + Grass) p(Observer + Trend)	13	435.73	462.72	1.42	0.014
ψ(Woodland10 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland1 + Cropland + Grass) p(Observer + Trend)	13	435.94	462.92	1.63	0.013
ψ(Woodland10 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland5 + Cropland + Grass) p(Observer + Trend + Date)	14	433.81	462.95	1.65	0.013
ψ(Woodland5 + CRPPatch + Shrub + CRPPatch^2 + Shrub^2) θ(Woodland5 + Cropland + Grass) p(Observer)	12	438.25	463.09	1.80	0.012
ψ(Woodland5 + Cropland + Shrub + Cropland^2 + Shrub^2) θ(Woodland1 + Cropland + Grass) p(Observer + Trend + Date)	14	434.08	463.22	1.92	0.011

Table D2. The cumulative weight, frequency, and variable support for large-scale occupancy (ψ) of lesser prairie-chickens in the Shinnery Oak Prairie ecoregion (SOPR; ecoregion 1) from the range-wide monitoring program, 2012–2016. “NA” values of support indicate covariates that did not appear in the model set as main effects only, but only in association with their quadratic effect.

Covariate	**Weight**	**Frequency**	**Support**
Shrub^2	1.000	1.000	All models
CRPPatch^2	0.348	0.144	3.175
Woodland5	0.518	0.304	2.457
Cropland^2	0.192	0.144	1.412
Woodland10	0.319	0.254	1.374
Grass	0.053	0.069	0.751
Grass^2	0.076	0.102	0.729
CRP^2	0.084	0.121	0.666
Woodland1	0.090	0.169	0.487
CRP	0.248	0.421	0.453
Mesquite	0.030	0.100	0.281
MesquiteCedar	0.030	0.100	0.281
MesquiteCedar^2	0.012	0.072	0.160
CRPPatch	0.000	0.000	NA
Shrub	0.000	0.000	NA
Cropland	0.000	0.000	NA

Table D3. The cumulative weight, frequency, and variable support for small-scale occupancy (θ) of lesser prairie-chickens in the Shinnery Oak Prairie ecoregion (SOPR; ecoregion 1) from the range-wide monitoring program, 2012–2016.

Covariate	**Weight**	**Frequency**	**Support**
Cropland	0.577	0.323	2.857
Grass	0.608	0.499	1.563
Woodland5	0.370	0.317	1.262
Woodland10	0.182	0.193	0.929
Woodland1	0.448	0.490	0.848
Development	0.392	0.501	0.640
Shrub	0.423	0.677	0.350

Table D4. Model selection for the large-scale occupancy (ψ), small-scale occupancy (θ), and detection (p) of the lesser prairie-chicken in the Sand Sagebrush Prairie ecoregion (SSPR; ecoregion 2) from the range-wide monitoring program, 2012–2016. The model-selection metrics are the parameter number (K), value of the minimized -2 log-likelihood function [$-2\log_e(\mathcal{L})$], Akaike's Information Criterion adjusted for sample size (AIC_c), difference between model and minimum AIC_c value (ΔAIC_c), and AIC_c weight (w_i). Models with $\Delta\text{AIC}_c < 2$ are shown.

Model	***K***	**-2log(*L*)**	**AIC_c**	**ΔAIC_c**	**w_i**
ψ(Wetland + Shrub) θ(Cropland + CRP) p(Observer)	8	270.46	287.06	0.00	0.040
ψ(CRP + Shrub) θ(Drought + GeneralHabitat) p(Observer)	8	271.67	288.27	1.21	0.022
ψ(CRP + Shrub) θ(Drought + Cropland) p(Observer)	8	271.86	288.46	1.40	0.020
ψ(CRP + Shrub) θ(Cropland) p(Observer)	7	274.18	288.64	1.58	0.018
ψ(Wetland + Shrub) θ(Cropland + CRP) p(Time + Observer)	9	269.95	288.70	1.65	0.018
ψ(CRP + Shrub) θ(Wetland + Cropland) p(Observer)	8	272.15	288.75	1.70	0.017
ψ(Wetland + Shrub) θ(Cropland + CRP) p(Observer + Date)	9	270.15	288.91	1.85	0.016
ψ(CroplandPatch + Shrub) θ(Cropland + CRP) p(Observer)	8	272.44	289.04	1.98	0.015
ψ(Drought + Shrub) θ(Cropland + CRP) p(Observer)	8	272.45	289.05	1.99	0.015

Table D5. The cumulative weight, frequency, and variable support for large-scale occupancy (ψ) of lesser prairie-chickens in the Sand Sagebrush Prairie ecoregion (SSPR; ecoregion 2) from the range-wide monitoring program, 2012–2016.

Covariate	Weight	Frequency	Support
CRP	0.261	0.060	5.506
Wetland	0.194	0.060	3.746
Drought	0.085	0.060	1.453
CRPPatch	0.068	0.060	1.133
Shrub	0.902	0.895	1.087
Cropland	0.032	0.035	0.922
GrassPatch	0.138	0.149	0.919
CroplandPatch	0.055	0.060	0.913
MesquiteCedar	0.022	0.031	0.704
ConservationGrazing	0.042	0.060	0.689
Well	0.074	0.114	0.622
Green	0.021	0.060	0.335
GeneralHabitatPatch	0.004	0.013	0.293
Grazing	0.018	0.060	0.281
Transmission	0.016	0.060	0.256
Road	0.016	0.060	0.253
NativeHabitatPatch	0.001	0.004	0.196
Development	0.012	0.060	0.186
Woodland10	0.004	0.035	0.115

Table D6. The cumulative weight, frequency, and variable support for small-scale occupancy (θ) of lesser prairie-chickens in the Sand Sagebrush Prairie ecoregion (SSPR; ecoregion 2) from the range-wide monitoring program, 2012–2016.

Covariate	**Weight**	**Frequency**	**Support**
CRP	0.321	0.123	3.383
GeneralHabitat	0.133	0.107	1.273
Drought	0.338	0.319	1.087
Cropland	0.779	0.792	0.929
Shrub	0.088	0.101	0.859
Wetland	0.103	0.122	0.833
MesquiteCedar	0.047	0.107	0.410
Road	0.046	0.110	0.390
Well	0.040	0.106	0.347

Table D7. Model selection for the large-scale occupancy (ψ), small-scale occupancy (θ), and detection (*p*) of the lesser prairie-chicken in the Mixed Grass Prairie ecoregion (MGPR; ecoregion 3) from the range-wide monitoring program, 2012–2016. The model-selection metrics are the parameter number (*K*), value of the minimized −2 log-likelihood function [$-2\log_e(\mathcal{L})$], Akaike's Information Criterion adjusted for sample size (AIC_c), difference between model and minimum AIC_c value ($\Delta\mathrm{AIC}_c$), and AIC_c weight (w_i). Models with $\Delta\mathrm{AIC}_c < 2$ are shown.

Model	***K***	**-2log(*L*)**	**AIC_c**	**$\Delta\mathrm{AIC}_c$**	**w_i**
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + Development) *p*(Observer)	9	636.14	654.62	0.00	0.049
ψ(NativeHabitatPatch + CRP + Well) θ(Drought + Woodland1 + Development) *p*(Observer)	10	634.74	655.33	0.71	0.034
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + Grass + Development) *p*(Observer)	10	634.95	655.54	0.92	0.031
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + Cropland + Development) *p*(Observer)	10	634.96	655.55	0.92	0.031
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + GeneralHabitat + Development) *p*(Observer)	10	635.00	655.59	0.97	0.030
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland5 + Development) *p*(Observer)	9	637.27	655.76	1.13	0.028
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + Grazing + Development) *p*(Observer)	10	635.21	655.80	1.18	0.027
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + Development) *p*(Time + Observer + Date)	11	633.24	655.95	1.33	0.025
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + Shrub + Development) *p*(Observer)	10	635.89	656.48	1.85	0.019
ψ(NativeHabitatPatch + CRP + Well) θ(Woodland10 + Cropland + Development) *p*(Time + Observer + Date)	12	631.77	656.61	1.99	0.018

Table D8. The cumulative weight, frequency, and variable support for large-scale occupancy (ψ) of lesser prairie-chickens in the Mixed Grass Prairie ecoregion (MGPR; ecoregion 3) from the range-wide monitoring program, 2012–2016.

Covariate	**Weight**	**Frequency**	**Support**
NativeHabitatPatch	1.000	1.000	All models
CRP	1.000	1.000	All models
Well	1.000	1.000	All models

Table D9. The cumulative weight, frequency, and variable support for small-scale occupancy (θ) of lesser prairie-chickens in the Mixed Grass Prairie ecoregion (MGPR; ecoregion 3) from the range-wide monitoring program, 2012–2016.

Covariate	**Weight**	**Frequency**	**Support**
Development	0.987	0.881	9.969
Woodland10	0.500	0.329	2.043
Drought	0.075	0.042	1.856
Grass	0.118	0.084	1.459
Cropland	0.142	0.126	1.150
Grazing	0.125	0.126	0.995
Woodland5	0.284	0.336	0.785
Shrub	0.087	0.126	0.659
Green	0.082	0.126	0.621
GeneralHabitat	0.153	0.245	0.556
Woodland1	0.216	0.336	0.545
Well	0.013	0.119	0.100

Table D10. Model selection for the large-scale occupancy (ψ), small-scale occupancy (θ), and detection (p) of the lesser prairie-chicken in the Shortgrass/CRP Mosaic ecoregion (SGPR; ecoregion 4) from the range-wide monitoring program, 2012–2016. The model-selection metrics are the parameter number (K), value of the minimized -2 log-likelihood function [$-2\log_e(\mathcal{L})$], Akaike's Information Criterion adjusted for sample size (AIC$_c$), difference between model and minimum AIC$_c$ value (ΔAIC$_c$), and AIC$_c$ weight (w_i). Models with ΔAIC$_c$ < 2 are shown.

Model	***K***	**-2log(*L*)**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**
ψ(CroplandPatch + GrassPatch + CRP + CroplandPatch^2) θ(Cropland + CRP + Development) *p*(Time + Observer + Date)	13	1007.53	1034.50	0.00	0.109
ψ(CroplandPatch + GrassPatch + CRP + CroplandPatch^2) θ(Cropland + CRP + Development) *p*(Observer + Date + Year)	16	1002.15	1035.62	1.11	0.063
ψ(CroplandPatch + GrassPatch + CRP + CroplandPatch^2) θ(Cropland + CRP + Development) *p*(Observer + Trend)	12	1010.82	1035.65	1.14	0.062
ψ(CroplandPatch + GrassPatch + CRP + CroplandPatch^2) θ(Cropland + NativeHabitat + CRP) *p*(Time + Observer + Date)	13	1009.06	1036.04	1.53	0.051
ψ(GrassPatch + CRP + Development + CRP^2) θ(Cropland + CRP + Development) *p*(Time + Observer + Date)	13	1009.13	1036.11	1.60	0.049
ψ(GrassPatch + CRP + Development + CRP^2) θ(Cropland + CRP + Development) *p*(Observer + Trend)	12	1011.29	1036.12	1.61	0.049
ψ(CroplandPatch + GrassPatch + CRP + CroplandPatch^2) θ(Cropland + CRP + Development) *p*(Observer)	11	1013.49	1036.19	1.69	0.047
ψ(CroplandPatch + GrassPatch + CRP + CroplandPatch^2) θ(Cropland + CRP + Development) *p*(Observer + Trend + Date)	13	1009.25	1036.22	1.72	0.046
ψ(GrassPatch + CRP + Development + CRP^2) θ(Cropland + NativeHabitat + CRP) *p*(Observer + Trend)	12	1011.47	1036.30	1.80	0.045
ψ(GrassPatch + CRP + Development + CRP^2) θ(Cropland + CRP + Development) *p*(Observer + Date + Year)	16	1002.96	1036.43	1.93	0.042
ψ(GrassPatch + CRP + Development + CRP^2) θ(Cropland + NativeHabitat + CRP) *p*(Time + Observer + Date)	13	1009.48	1036.45	1.95	0.041

Table D11. The cumulative weight, frequency, and variable support for large-scale occupancy (ψ) of lesser prairie-chickens in the Shortgrass/CRP Mosaic ecoregion (SGPR; ecoregion 4) from the range-wide monitoring program, 2012–2016. “NA” values of support indicate covariates that did not appear in the model set as main effects only, but only in association with their quadratic effect.

Covariate	**Weight**	**Frequency**	**Support**
GrassPatch	1.000	1.000	All models
CRP	0.537	0.455	1.392
CroplandPatch^2	0.537	0.455	1.392
Development	0.424	0.455	0.885
CRP^2	0.463	0.545	0.718
Woodland1	0.039	0.091	0.401
CroplandPatch	0.000	0.000	NA

Table D12. The cumulative weight, frequency, and variable support for small-scale occupancy (θ) of lesser prairie-chickens in the Shortgrass/CRP Mosaic ecoregion (SGPR; ecoregion 4) from the range-wide monitoring program, 2012–2016.

Covariate	**Weight**	**Frequency**	**Support**
Cropland	1.000	1.000	All models
CRP	1.000	1.000	All models
Development	0.612	0.500	1.579
NativeHabitat	0.388	0.500	0.633