MULTI-SCALE OCCUPANCY ESTIMATION FOR THE LESSER PRAIRIE-CHICKEN: 2015

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October 17, 2015

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INTRODUCTION

We developed a hierarchical occupancy model (Nichols et al. 2008, Pavlacky et al. 2012) to estimate probability of occupancy and predict habitat relationships at multiple scales for the lesser prairie-chicken (*Tympanuchus pallidicinctus*; LPC). The model was useful for estimating probability of occupancy at two spatial scales and for monitoring rare species of conservation concern (Pavlacky et al. 2012).

We modified the sampling design of the Western Association of Fish and Wildlife Agencies' (WAFWA) LPC monitoring program (McDonald et al. 2015) such that large-scale probability of occupancy corresponds to the presence of the LPC on 15-kilometers (km) × 15-km grid cells and small-scale probability of occupancy corresponds to the presence of the species in four 7.5-km × 7.5-km quadrants nested within the grid cells. The occupancy model also provides a framework for evaluating the ability of different survey methodology to detect the target species (Nichols et al. 2008), including temporal replicates of the survey procedure and/or multiple observers (MacKenzie et al. 2006b). Corresponding to the modified design, the parameters of the model include the large-scale probability of occupancy of grid cells (ψ), the small-scale probability of occupancy of nested quadrants given presence in the grid cells (θ), and probability of detection of LPC among temporal replicates or multiple observers given presence in the quadrants and grid cells (p) (Pavlacky et al. 2012). For brevity, these probabilities were referred to as "occupancy" and "detection."

Because ψ corresponds to the occupancy rate of the grid cells and θ corresponds to the occupancy rate of quadrants given that the grid cell was occupied, the product $\psi*\theta$ represents the probability of small-scale occupancy for all grid cells and quadrants in the sampling frame (Nichols et al. 2008, Pavlacky et al. 2012). The model can be thought of as a within-season robust design (Pollock 1982), where quadrants within grid cells were primary occasions for estimating θ, and temporal replicates or multiple observers were secondary occasions for estimating 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 ψ (Nichols et al. 2009). In this case, θ was thought of as an availability parameter and p was the probability of detection given that the large scale grid cell was occupied (Pavlacky et al. 2012). Finally, the model was useful for predicting multi-scale covariate relationships to inform habitat management at multiple spatial extents (Block et al. 2001; George and Zack 2001). For example, the model can be used to evaluate the relative importance of conservation practices at local and landscape scales and potentially help identify the habitat factors that influence the distribution of a species (Pavlacky et al. 2012).

Objectives

The objectives of the project were to 1) compare the performance of the WAFWA 2015 Range-Wide survey (RW-survey) data with the performance of the RW-survey data when combined with data from repeated temporal replicates of the survey method for estimating multi-scale occupancy rates of the LPC and 2) conduct a pilot analysis to evaluate the potential of the multi-scale occupancy model to predict the effects of habitat and conservation practices on LPC occupancy. We estimated LPC occupancy in two of the four stratums in the RW-survey: Shinnery Oak Prairie Region (SOPR) located in eastern New Mexico-southwest Texas Panhandle and in the Short Grass/Conservation Reserve Program (CRP) mosaic

Prairie Region (SGPR) located in northwestern Kansas (Figure 1). We developed a pilot analysis of the relationships between probability of occupancy and predictor covariates in the SOPR, SGPR, Mixed Grass Prairie Region (MGPR) in the northeast corner of the Texas Panhandle, northwest Oklahoma, and south-central region of Kansas, and the Sand Sage Prairie Region (SSPR) of southeast Colorado, southwest Kansas, and part of the Oklahoma Panhandle (Figure 1).

PART 1: EVALUATION OF SAMPLING DESIGNS

Methods

Study Area

Our study area included the SGPR and SOPR strata (ecoregions) from the WAFWA RW-surveys. Figure 1 illustrates the study area for the RW-survey and indicates the grid cells selected and not selected in 2013, 2014, and 2015 (McDonald et al. 2015). The buffered areas surrounding the sub-areas delineated an approximate 77.7 km (30 miles [mi]) buffer into which the survey may be expanded in the future.

Beginning in 2013 of the RW-survey, we ranked 15-km × 15-km grid cells in the study area from 1 to 536 by an equal probability sampling procedure known as Generalized Random Tessellation Stratified (GRTS) sampling (McDonald et al. 2012, 2014, Stevens and Olsen 2004). We stratified the study area into four strata (Figure 1) and selected GRTS equal probability samples in each stratum. During the RW-surveys, there were 73 of 123 cells surveyed in SOPR and 77 of 165 cells surveyed in SGPR. In 2015, additional funds became available to supplement the RW-survey with temporal replication of the survey methods on a subset of grid-cells in the SOPR and SGPR strata. With the additional funds, 15 grid cells were re-surveyed in the SOPR stratum and 30 grid cells were re-surveyed in the SGPR stratum using the same RW-survey methods. We refer to data from these temporal replications as the 2015 Replicate survey (REP-survey).

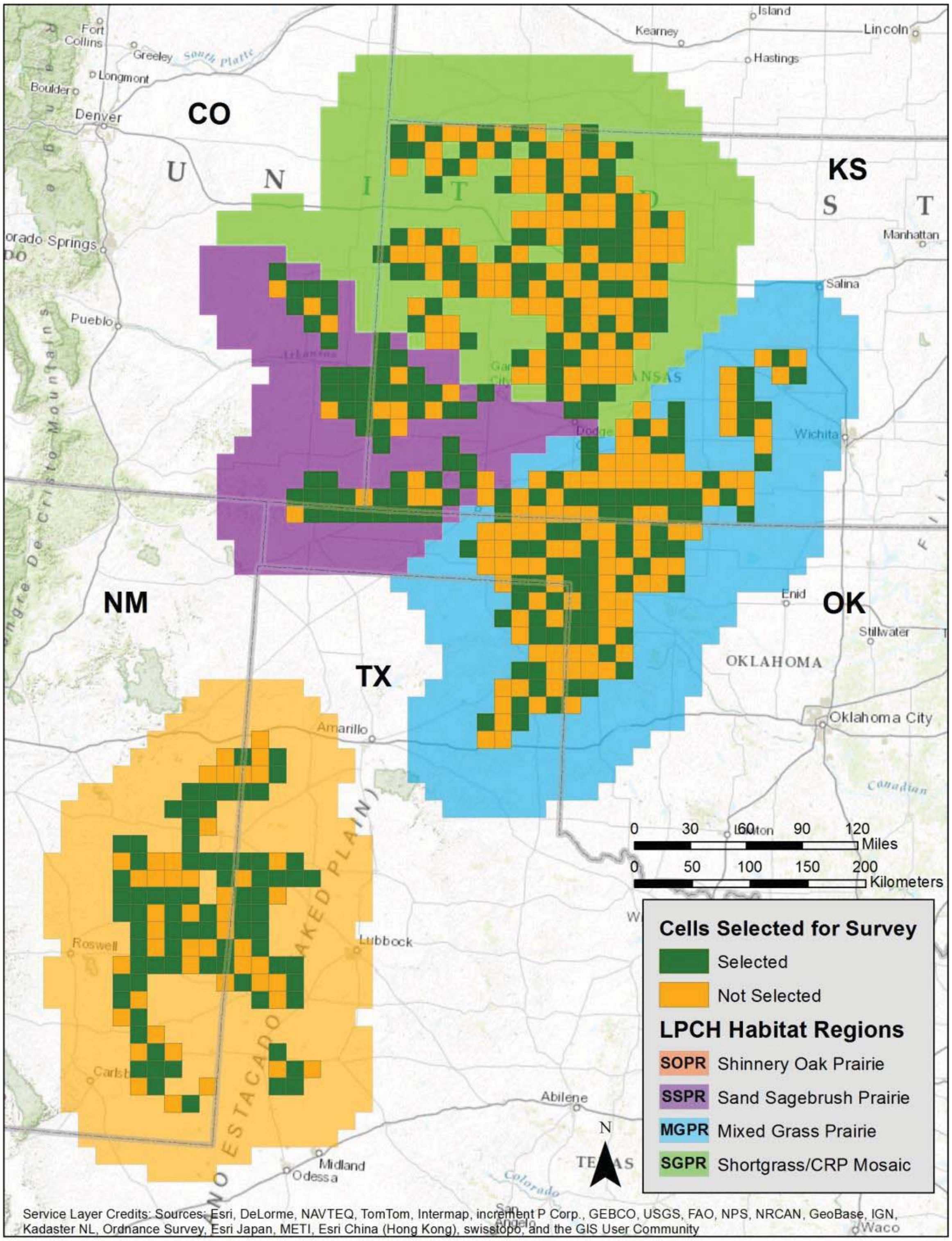

Figure 1. Study area for RW-survey lesser prairie-chicken surveys illustrated with grid cells selected for survey in 2015. The colored areas surrounding the study sub-areas indicated an approximate 77.7 km (30 mi) buffer into which the survey may be expanded in the future.

Aerial Survey Methods

The survey platform used for the surveys was the Raven II (R-44) helicopter from the Robinson Helicopter Company, accommodating two observers in the rear left and right seats, and a third observer in the front left seat. Three helicopters and survey crews operated simultaneously within the study area. Transects were flown north to south or south to north at nominal values of 60 km per hour and 25 m above ground. During the lekking period (March 15 to May 15, 2015), surveys were conducted from sunrise until approximately 2.5 hours after sunrise.

Two 15-km north-south parallel transect were selected in each of the survey grid-cells. The starting point of the first transect was randomly located in the interval (200 meters [m], 7,300 m) on the base of the cell and the second transect was located 7,500 m to the right of the first transect. Survey methods were described in further detail in McDonald et al. (2012).

Estimation of transects on which LPC were detected

The lesser prairie-chicken and greater prairie-chicken species overlap in range in stratum SGPR of northwest Kansas. It was not always possible to ground truth prairie-chicken groups detected in SGPR to determine if a group contained LPC. The Kansas Department of Wildlife, Parks and Tourism conducted extensive ground surveys of LPC. Based on those surveys, estimates were provided for the proportion of LPC in each survey grid cell (Jim Pitman, personal communication, 2014). If a prairie-chicken group could not be ground truthed to determine that LPC were present in the group, we recorded detection of LPC if the estimated proportion of LPC in the grid-cell was greater than 0.5.

Performance of RW-survey and performance of RW-survey combined with REP-survey

We developed two multi-scale occupancy analyses for the SGPR and SOPR strata. The first occupancy analysis used only the RW-survey data and the second analysis used the combination of the RW-survey data and the REP-survey data. We compared the analysis of the RW-survey data to the analysis of the combined RW-survey and REP-survey data to evaluate the performance of the occupancy models, and to determine the extent the additional REP-survey data increased the precision of the occupancy estimates.

The encounter history for the RW-survey analysis used “multiple” observers in the helicopter to estimate the probability of detection. We pooled the encounters of LPC by the observer in the front left seat and pilot in the front right seat (first occasion or search). Similarly, we pooled the encounters of LPC by the observer in the back left seat and observer in 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 for the front and back observers and four quadrants within each grid-cell, and an encounter history H_i = 01 11 00 00 (0 = non-detection and 1 = detection). In this example, LPCs were detected by the back-seat observers in quadrant one, by the front- and back-seat observers in quadrant two, and were not detected in quadrants three and four.

For the combined data from the RW-survey and REP-survey, we developed an encounter history that included the front and back observers for both the RW-survey and REP-survey. For example, consider two survey occasions for the front and back observers nested within the RW-survey and REP-survey and four quadrants within each grid-cell with an encounter history H_i = 0101 1101 0000 0000 (0 = non-detection and 1 = detection). In this example, LPC were detected by the back seat observers in the RW-survey and by the back seat observers in the REP-survey for quadrant one, by the front and back seat observers in the RW-survey and by the back seat observers in the REP-survey for quadrant two, and were not detected in quadrants three and four. A second example illustrates an encounter history with missing data when the REP-survey was not conducted on a grid-cell. As above, consider an encounter history H_i = 01.. 11.. 00.. 00.. (0 = non-detection, 1 = detection and "." = missing data). In this example, LPC were detected by the back-seat observers in the RW-survey for quadrant one, by the front- and back-seat observers in the RW-survey for quadrant two, and were not detected in quadrants three and four. The REP-survey data were set to "missing data" because the grid-cell was not included in the temporal replications.

We estimated the detection and occupancy rates of LPC using the multi-scale occupancy model (Nichols et al. 2008, Pavlacky et al. 2012). The model allowed estimation of three parameters that corresponded to each level in the nested sampling design with front and back 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 strata to estimate large-scale occupancy of grid-cells. The parameters of the model were 1) the probability of detection p_{ijk} for observer k, quadrant j and grid cell i given the quadrant and grid cell were occupied; 2) the probability of small-scale occupancy θ_{ij} for quadrant j and grid cell i given the grid cell was occupied; and 3) the probability of large-scale occupancy ψ_i for grid cell i. The assumptions of the multi-scale occupancy model were 1) no un-modeled heterogeneity in the probabilities of detection and occupancy, 2) each quadrant was closed to changes in occupancy over the observer occasions, 3) the detections of LPC at each quadrant were independent and 4) the target species' were never falsely detected (Nichols et al. 2008, Pavlacky et al. 2012).

We fit the models using the RMark interface (Version 2.1.13; Laake 2013; R Development Core Team 2015) for program MARK (Version 8; White and Burnham 1999). We used the identity design matrix and sine link function to estimate the parameters of the model (White and Burnham 1999). We used the sine link to ensure model convergence and facilitate parameter estimation when parameters were near the boundary of 0 or 1.

We compared the performance of the RW-survey relative to the performance of the combined RW-survey and REP-survey. First, for the RW-survey only we considered three group covariates on detection including a crew factor with three levels [p(crew)], an observer factor with two levels for front and back observers [p(observer)], and a strata factor with two levels for the SOPR and SGPR habitat regions [p(strata)], as well as an intercept only model [p(.)]. In addition, we considered the strata factor for both small-scale [θ(strata)] and large-scale [ψ(strata)] occupancy, as well as the intercept only models [θ(.), ψ(.)]. The set of models for the RW-survey analysis included four models on detection (p), two models on small-scale occupancy (θ) and two models on large-scale occupancy (ψ). We constructed the candidate set of models for the RW-survey analysis using all-subsets of the parameter specifications for a total of 16 models. From the best model of the RW-survey analysis, we estimated the conditional probability of small-scale occupancy ($\hat{\theta}_c = \hat{\theta} * \hat{\psi}$) and calculated the standard error of the estimate using the delta method (Powell 2007).

For the combined data from the RW-survey and REP-survey, we considered all the above group covariates, and included an additional survey factor on detection with two levels for the RW-survey and REP-survey [p(survey)]. The set of models for the combined RW-survey and REP-survey included five models on detection (p), two models on small-scale occupancy (θ) and two models on large-scale occupancy (ψ). We constructed the candidate set of models for the combined RW-survey and REP-survey using all-subsets of the parameter specifications for a total of 20 models.

Results

Performances of the RW-survey and the combined RW-survey and REP-survey

The first occupancy analysis used only the RW-survey data and the second analysis used the combination of RW-survey and REP-survey data (Table 1). A top model was selected using Akaike Information Criterion (Akaike 1973) adjusted for sample size (AIC_c) (Hurvich and Tsai 1989).

Table 1. AICc, Delta AICc, AICc weights and Deviance values for combinations of the model covariates with Delta AICc < 2.0.

RW-survey				
Model	**AICc**	**Δ AICc**	**Weight**	**Deviance**
$\Psi(.)\ \theta(\text{strata})\ p(\text{ observer})$	318.76	0.00	0.25	308.35
$\Psi(.)\theta\ (\text{strata})p(.)$	318.93	0.17	0.23	310.66
$\Psi(\text{ strata})\ \theta\ (\text{strata})p(\text{observer})$	320.42	1.66	0.11	307.85
$\Psi(.)\Theta\ \theta\ (\text{strata})p(\text{strata})$	320.50	1.74	0.10	310.09
$\Psi(\text{strata})\ \theta\ (\text{strata})p(.)$	320.56	1.80	0.10	310.16
RW-survey + REP-survey				
Model	**AICc**	**Δ AICc**	**Weight**	**Deviance**
$\Psi(.)\theta\ (\text{strata})p(\text{ survey})$	402.10	0	0.61	391.70
$\Psi(\text{strata})\ \theta\ (\text{strata})p(\text{ survey})$	403.45	1.35	0.31	390.88

The top model for the first occupancy analysis using only the RW-survey data had an AIC_c value of 318.76. It included an observer factor with two levels for front and back observers for detection [p(observer)], a strata factor with two levels for the SOPR and SGPR habitat regions for small-scale occupancy [θ(strata)], and the intercept only model for large-scale occupancy $\psi(.)$. The top model for the second analysis had an AIC_c value of 402.10 using the combined RW-survey data and REP-survey data. The model included a survey factor on detection with two levels for the RW-survey and REP-survey [p(survey)], a strata factor with two levels for the SOPR and SGPR habitat regions for small-scale occupancy [θ(strata)], and the intercept only model for large-scale occupancy $\psi(.)$.

In evaluating the variation in occupancy estimates of the RW-survey compared to the combined RW-survey and REP-survey, we used the coefficient of variation (CV) which was the ratio of the standard error to the mean. The CV evaluated the extent of variability in relation to the mean. We observed a 3.9% decrease in the CV in the large-scale occupancy (ψ) estimate from the RW-survey analysis to the combined RW-survey and REP-survey (Tables 2 and 3). Additionally we observed a 7.7% and 5.4%

decrease in the CV in the small-scale occupancy (θ) estimate for the SOPR and SGPR strata, respectively from the RW-survey analysis to the combined RW-survey and REP-survey.

Table 2. Estimates for large-scale occupancy (ψ), small-scale occupancy (θ), and probability of detection (*p*) for the top model selected for the RW-survey analysis

Parameter	Estimate (95% Confidence Interval)	CV
ψ(.)	0.35 (0.21, 0.53)	0.23
θ(strata- SGPR)	0.31 (0.18, 0.47)	0.24
θ(strata - SOPR)	0.05 (0.01, 0.13)	0.51
p(observer - front)	0.65 (0.46, 0.80)	0.13
p(observer - back)	0.80 (0.60, 0.92)	0.10

Table 3. Estimates for large-scale occupancy (ψ), small-scale occupancy (θ), and probability of detection (*p*) for the top model selected for the combined RW-survey and REP-survey.

Parameter	Estimate (95% Confidence Interval)	CV
ψ(.)	0.35 (0.21, 0.51)	0.22
θ(strata- SGPR)	0.33 (0.20, 0.49)	0.22
θ(strata - SOPR)	0.06 (0.02, 0.16)	0.48
p(survey - RW)	0.67 (0.52, 0.79)	0.10
p(survey - REP)	0.22 (0.13, 0.35)	0.25

We estimated the conditional small-scale occupancy rate (ψ*θ), i.e., the probability that 7.5-km × 7.5-km quadrant was occupied by LPC given that the 15-km × 15-km grid cell was occupied (Table 4). Given that the grid cell was occupied by LPC, the probability that a quadrant will be occupied ranged from very low (0.017) in the SOPR of eastern New Mexico and western Texas and to relatively high (0.108) in the SGPR of northwestern Kansas (Table 4).

Table 4. Estimates of conditional small-scale occupancy (ψ*θ), standard errors (SE), lower and upper 95% confidence limits (LCL and UCL, respectfully) and coefficients of variation (CV) for the RW-survey and combined RW-survey and REP-survey in the Shinnery Oak Prairie Region (SOPR) and Shortgrass CRP Mosaic Prairie Region (SGPR).

Parameter	Estimate	SE	LCL	UCL	CV
RW-survey					
SOPR	0.017	0.008	0.005	0.037	0.464
SGPR	0.108	0.024	0.066	0.159	0.219
RW and REP-survey					
SOPR	0.021	0.009	0.007	0.043	0.427
SGPR	0.114	0.025	0.070	0.168	0.217

PART 2: PILOT COVARIATE ANALYSES FOR HABITAT AND CONSERVATION PRACTICES

Introduction

We used predictive models and the method of multiple working hypotheses (Chamberlin 1965) to evaluate *a priori* hypotheses for how a preliminary subset of habitat configuration and anthropogenic practices potentially affect site occupancy at multiple spatial scales. We hypothesized that LPC occupancy would decline with increased fragmentation of native landcover and would decline with increasing density of roads in the landscape (Van Pelt et al. 2013). Overall, we predicted the effects of grassland fragmentation and road density would operate at the largest scale, and we predicted the effects of anthropogenic conservation practices would operate on habitat quality and occupancy at the smaller spatial scale. The preliminary subset of habitat configuration and anthropogenic conservation covariates were derived from a set of measurements available on the 15-km × 15-km grid cells and 7.5-km × 7.5-km quadrants (Table 5) and other sources.

Table 5. Descriptions, data sources, and means and ranges of measurements for 15-km × 15-km grid cells in the sampling frame for the 2015 WAFWA range-wide LPC survey. In addition to measurements within 15-km × 15-km grid cells, we obtained the same measures within 7.5-km × 7.5-km quadrants and 7.5-km × 0.6 km transect buffers (not shown).

Covariate	Description	Source	Mean (range)
Cropland	Proportion of cropland land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.35 *P* (0.00 *P* – 0.81 *P*)
CRP	Proportion of Conservation Reserve Program (CRP) land cover within the grid cell	PLJV land cover updated for 2015, SW ReGAP in western NM	0.10 P (0.00 P - 0.40 P)
Mixed grass	Proportion of mixed grass prairie land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.12 *P* (0.00 *P* – 0.80 *P*)
Pasture	Proportion of agricultural pasture land cover within the grid cell	PLJV land cover	0.07 *P* (0.00 *P* – 0.34 *P*)
Shortgrass	Proportion of shortgrass prairie land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.15 *P* (0.00 *P* – 0.90 *P*)
Tall grass	Proportion of tall grass prairie land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	<0.01 *P* (0.00 *P* – 0.05 *P*)
Grassland	Proportion of total grassland land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.34 *P* (0.01 *P* – 0.90 *P*)
Brush management	Percentage of brush management (practice 314) land cover within the grid cell	NRCS spatial database	0.58 % (0.00 % – 11.63 %)
Core practice	Mean percentage of prescribed grazing (practice 528) and upland wildlife habitat management (practice 645) land cover within the grid cell	NRCS spatial database	2.30 % (0.00 % – 85.46 %)
Prescribed burning	Percentage of prescribed burning (practice 338) land cover within the grid cell	NRCS spatial database	0.04 % (0.00 % – 2.24 %)
Prescribed grazing	Percentage of prescribed grazing (practice 528) land cover within the grid cell	NRCS spatial database	2.88 % (0.00 % – 80.63 %)
Upland habitat	Percentage of upland wildlife habitat management (practice 645) land cover within the grid cell	NRCS spatial database	1.72 % (0.00 % – 90.29 %)
General patch size	Mean patch size of general habitat including native landcover, CRP and pasture within the grid cell.	PLJV land cover, SW ReGAP in western NM	0.66 km^2 (0.00 km^2 – 13.75 km^2)
Grassland patch size	Mean patch size of grassland within the grid cell	PLJV land cover, SW ReGAP in western NM	0.40 km^2 (0.01 km^2 – 24.67 km^2)
Native patch size	Mean patch size of native vegetation within the grid cell	PLJV land cover, SW ReGAP in western NM	0.67 km^2 (0.00 km^2 – 9.45 km^2)

Table 5. Descriptions, data sources, and means and ranges of measurements for 15-km × 15-km grid cells in the sampling frame for the 2015 WAFWA range-wide LPC survey. In addition to measurements within 15-km × 15-km grid cells, we obtained the same measures within 7.5-km × 7.5-km quadrants and 7.5-km × 0.6 km transect buffers (not shown).

Covariate	Description	Source	Mean (range)
Major road density	Density of major roads within the grid cell	TIGER/line road layer, US Census Bureau (2014)	1.28 km^{-1} (0.20 km^{-1} – 3.15-km^{-1})
Minor road density	Density of minor roads within the grid cell	TIGER/line road layer, US Census Bureau (2014)	0.10 km^{-1} (0.00 km^{-1} – 0.64 km^{-1})
Total road density	Density of all roads within the grid cell	TIGER/line road layer, US Census Bureau (2014)	1.38 km^{-1} (0.20 km^{-1} – 3.80 km^{-1})
Mesquite shrubland	Proportion of mesquite shrubland (> 25% canopy cover) land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.01 *P* (0.00 *P* – 0.68 *P*)
Mesquite savanna	Proportion of mesquite savanna (< 25% canopy cover) land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.02 *P* (0.00 *P* – 0.62 *P*)
Shinnery oak shrubland	Proportion of shinnery oak shrubland land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.04 *P* (0.00 *P* – 0.69 *P*)
Sand sage shrubland	Proportion of sand sage shrubland land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	0.07 *P* (0.00 *P* – 0.58 *P*)
Total shrubland	Proportion of total shrubland land cover excluding mesquite shrubland within the grid cell	PLJV land cover, SW ReGAP in western NM	0.13 *P* (0.00 *P* – 0.96 *P*)
Pinyon-juniper woodland	Proportion of pinyon-juniper woodland land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	<0.01 *P* (0.00 *P* – 0.07 *P*)
Red cedar woodland	Proportion of red cedar woodland land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	<0.01 *P* (0.00 *P* – 0.03 *P*)
Total woodland	Proportion of total woodland land cover within the grid cell	PLJV land cover, SW ReGAP in western NM	<0.01 *P* (0.00 *P* – 0.08 *P*)

Methods

Derivation of Preliminary Subset of Covariates

We derived four covariates for our preliminary analysis within a Geographic Information System (ArcGIS Version 10.3, ESRI 2014) to quantify the extent of habitat and conservation practices within the grid cells and quadrants of the sampling frame (Table 5). We developed a mean patch size covariate for native landcover (patchsize) using the Playa Lakes Joint Venture (PLJV 2009) and the Southwest Region Gap (Prior-Magee et al. 2007) landcover layers. We used the PLJV dataset for the majority of the LPC range and the Gap dataset for the western most portion of the LPC range outside of the PLJV boundary in New Mexico. With exception of mesquite (*Prosopis* spp.) shrubland with > 25% canopy cover (PLJV 2009), we reclassified all native grassland and shrubland raster values into a single native landcover type and used Spatial Analyst Tools to generalize the raster values into discrete patches of native landcover (ESRI 2014). We intersected the grid-cell and quadrant polygons with the generalized native vegetation layer and estimated the mean patch size of native vegetation (km^2) within each grid-cell and quadrant ($\bar{x}$ = 0.93 km^2, range = 0.00 km^2 - 56.20 km^2).

We developed a major road covariate by overlaying the grid-cell and quadrant polygons with the TIGER/line layer (US Census Bureau 2014) and calculated the length of major roads (km) within each grid-cell and quadrant polygon. We estimated the density of major roads by dividing length of major roads by the area of each grid-cell and quadrant ($\bar{x}$ = 1.28 km^{-1}, range = 0.00 km^{-1} - 7.66 km^{-1}).

We developed a CRP covariate by overlaying the grid-cell and quadrant polygons with the CRP landcover type (excluding CRP tree plantings) within the PLJV (2009) landcover dataset. The CRP data within the landcover data set were updated to reflect lands enrolled in the CRP practice during the 2015 calendar year. We represented the CRP covariate by the proportion of CRP area (*P*) within each grid-cell and quadrant ($\bar{x}$ = 0.10 *P*, range = 0.00 *P* - 0.56 *P*).

Finally, we developed a prescribed grazing covariate (practice 528) using a Natural Resources Conservation Service (NRCS) conservation practice spatial database (National Conservation Practice database, NRCS, US Department of Agriculture, unpublished data). Because the NRCS spatial database was represented by a point feature class, we buffered the point locations by the area enrolled in the prescribed grazing practice during the 2015 calendar year. We overlaid the grid-cell and quadrant polygons with the buffered areas and represented the prescribed grazing covariate by the percentage of area enrolled in the practice within each grid-cell and quadrant ($\bar{x}$ = 2.88 %, range = 0.00 % - 100.00 %).

We derived four predictive covariates for detection (*p*) including a crew factor with four levels for each crew, an observer factor with two levels for front and back observers, a strata factor with four levels for the SGPR, MGPR, SOPR and SSPR habitat regions and a continuous covariate for the starting time of the survey after sunrise.

Pilot Statistical model

We applied the multi-scale occupancy model (Nichols et al. 2008; Pavlacky et al. 2012) to the RW-survey data to evaluate hypotheses for the effects of habitat configuration and conservation practices on LPC occupancy. We fit the models using the RMark interface (Version 2.1.13, Laake 2013; R Core Team 2015) for program MARK (Version 8.0, White and Burnham 1999). We used the intercept - indicator variable design matrix and logit link function to estimate the parameters of the model (White and Burnham 1999).

The model estimated three parameters that corresponded to each level in the nested sampling design with 1) front and back observers nested within 7.5-km × 7.5-km quadrants to estimate detection, 2) quadrants nested within 15-km × 15-km grid cells to estimate small-scale occupancy, and 3) grid cells nested within strata to estimate large-scale occupancy. The parameters of the model were 1) the probability of detection p_{ijk} for observer *k*, quadrant *j* and grid cell *i,* given the quadrant and grid cell were occupied; 2) the probability of small-scale occupancy θ_{ij} for quadrant *j* and grid cell *i* given the grid cell was occupied; and 3) the probability of large-scale occupancy ψ_i for grid cell *i*.

For both small-scale (θ) and large-scale (ψ) occupancy, we evaluated the strength of evidence for four continuous covariates: CRP; prescribed grazing; mean patch size of native landcover (patchsize); major road density; and the categorical habitat region factor. We constructed the candidate set of models using all one and two variable combinations of the covariates, resulting in 10 models for detection (*p*), 15 models for small-scale occupancy (θ) and 15 models for large-scale occupancy (ψ). We ran all subsets of the parameter specifications for a total of 2,250 models.

Preliminary Model selection

We used information-theoretic model selection (Burnham and Anderson 2002) to estimate the relative loss of Kullback-Leibler Information among our candidate models used to approximate relative truth (Burnham and Anderson 2001). We ranked models according to the Akaike Information Criterion (Akaike 1973) adjusted for sample size (AIC_c) (Hurvich and Tsai 1989), evaluated the magnitude of information loss using the change in AIC_c (ΔAIC_c), measured strength of evidence for model *i* using AIC_c weights (w_i), and quantified the plausibility of models *i* and *j* using evidence ratios (w_i / w_j).

We graphed the model averaged predictions and estimated unconditional 95% Confidence Intervals (CI) from candidate sets of models with $\Delta AIC_c < 2$ (Burnham and Anderson 2002). We considered models with $\Delta AIC_c < 2$ to have substantial support and we used these models to make inference from the analyses (Burnham and Anderson 2002). We assessed the strength of evidence for effect sizes by evaluating beta parameter estimates with respect to zero using conditional 90% and 95% CIs (Burnham and Anderson 2002).

Results

A preliminary covariate analysis for effect of habitat and conservation practices on probabilities of occupancy by LPC was conducted using the 2015 RW-survey data. We fit four covariates for probability of detection (*p*): a crew factor with four levels, an observer factor with two levels for front and back observers, a strata factor with four levels for the SGPR, MGPR, SOPR and SSPR habitat regions and a continuous covariate for the starting time of the survey after sunrise. For both small-scale (θ) and large-scale (ψ) occupancy, we fit models using four continuous covariates: CRP; prescribed grazing; mean patch size of native landcover (patchsize); major road density; as well as the habitat region factor. We constructed the candidate set of models using all one and two variable combinations of the covariates resulting in 10 models for detection (p), 15 models for small-scale occupancy (θ) and 15 models for large-scale occupancy (ψ). The top model using the Akaike Information Criterion (Akaike 1973) adjusted for sample size (AIC_c) (Hurvich and Tsai 1989) had an AIC_c value of 603.81 (Table 6).

Table 6. AICc and Delta AICc values for models within two AIC_c values of the top model.

Model	AICc	Delta AICc	Weight	Deviance
ψ (grazing + patchsize), θ (CRP + strata), *p*(observer + strata)	603.81	0.00	0.24	576.48
ψ (CRP + patchsize), θ (CRP + strata), *p*(observer + strata)	605.18	1.38	0.12	577.86
ψ (patchsize), θ (CRP + strata), *p*(observer + strata)	605.60	1.79	0.10	580.47
ψ (grazing + patchsize), θ (CRP+ strata), *p*(observer)	605.73	1.92	0.09	584.93

Illustration of the effects of covariates on probability of detection and probability of occupancy.

We presented results for the top models to illustrate the effect of the covariates on: 1) probability of detection of LPC, 2) probability of occupancy of the 7.5-km × 7.5-km quadrant by LPC, and 3) probability of occupancy of the 7.5-km × 7.5-km quadrants by LPC given occupancy of the grid cells.

Probability of detection given occupancy of quadrants and grid cell

The top model indicated that front and back observers had different probabilities of detection of LPC [*p*(observer); observer factor with two levels]. We illustrated the difference in probability of detection by the front and back observers for the short grass region in northwest Kansas (Figure 2). In northwest Kansas if the 15-km × 15-km grid cell was occupied, we estimated that the probability of detection by the front seat observers was about 0.6 and greater than 0.8 for the back seat observers. The symbols were model-averaged estimates of detection using the models in Table 6. The error bars were unconditional 95% confidence intervals.

The top models also indicated that probability of detection of LPC varied among regions [*p*(strata); strata factor with four levels]. The detection rate of the lesser prairie-chicken was illustrated for the back seat observers given occupancy of the 15-km × 15-km grid cell was plotted for each habitat region (Figure 3). The symbols were model-averaged estimates of detection using the models in Table 6. The error bars were unconditional 95% confidence intervals.

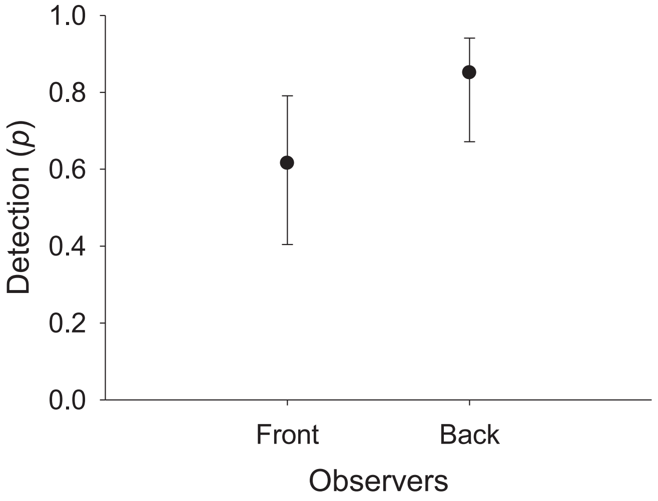

Figure 2. The detection rate of the lesser prairie-chicken by the front and back seat observers given occupancy of the 7.5-km × 7.5-km quadrant was plotted for the short grass habitat region of northwest Kansas. The symbols were model-averaged estimates of detection from the confidence set and the error bars were unconditional 95% confidence intervals.

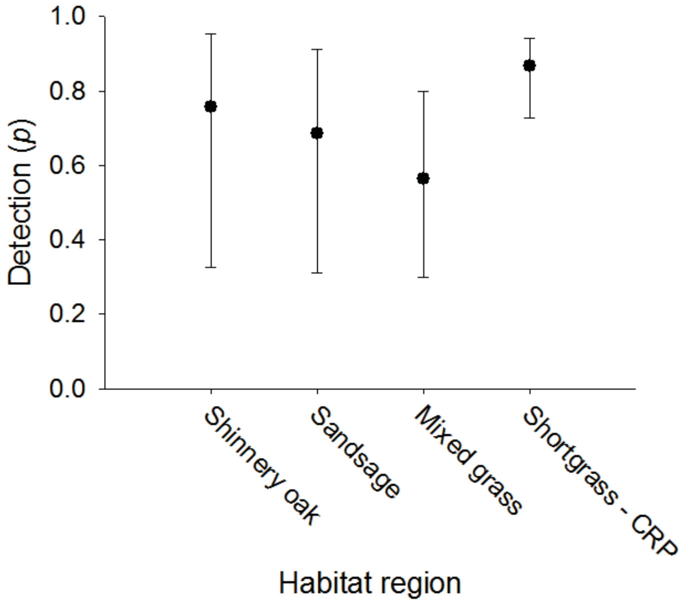

Figure 3. The detection rate of the lesser prairie-chicken for the back seat observers given occupancy of the 7.5-km × 7.5-km quadrant was plotted for each habitat region. The symbols were model-averaged estimates of detection using the models in Table 6 (holding the other covariates at their mean values). The error bars were unconditional 95% confidence interval

Large scale occupancy: Probability of occupancy of 15-km × 15-km grid cells by LPC

All models within two AIC_C values of the top model included the mean patch size of native landcover (patchsize) and had positive relationships to the probability that large scale 15-km × 15-km grid cells were occupied by LPC [ψ(patchsize)] (Tables 6 and 7). The coefficients were positive and statistically significant for all models (Table 7, 95% confidence intervals did not contain 0.0). The large-scale occupancy rate by LPC was plotted as a function of the mean patch size of native landcover (patchsize) holding the other covariates at their mean values (Figure 4). The bold line in Figure 4 was the model-averaged estimate of probability of occupancy of the 15-km × 15-km grid cells by LPC using the models in Table 6, where the bounding lines were unconditional 95% confidence intervals.

There was a statistically significant positive relation between percent prescribed grazing practice and probability of occupancy of the large scale grid cells by LPC at the 90% confidence level (90% confidence intervals were not reported in the tables). There was a strong positive relationship between probability of occupancy of large-scale grid cells by LPC and percentage of CRP; however, the relationship was not quite significant at the 90% confidence level. The evidence ratio based on the AICc selection criterion indicated the top model containing prescribed grazing was two times more plausible than the second and third best model without this covariate. Figure 5 contains the large-scale occupancy rate plotted as a function of the percentage of prescribed grazing land cover (holding the other covariates at their mean values). The bold line was the model-averaged estimate of large-scale occupancy using the models in Table 6. The bounding lines were unconditional 95% confidence intervals.

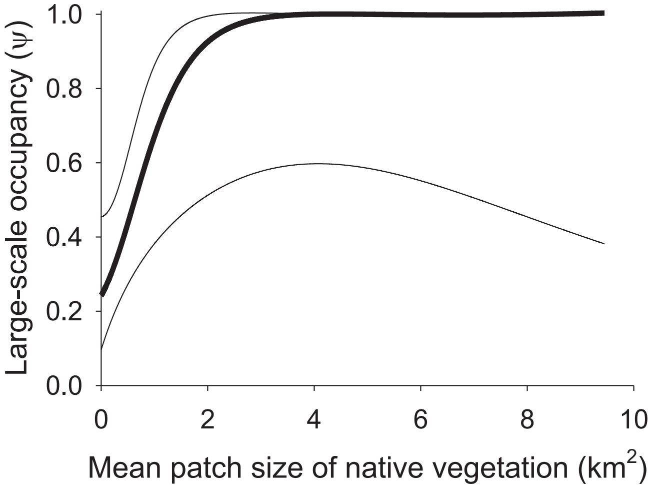

Figure 4. The large-scale occupancy rate, probability of occupancy by lesser prairie-chicken in the 15-km × 15-km grid cells, was plotted as a function of the mean patch size of native landcover (patchsize) (holding the other covariate values at their mean values). The bold line was the model-averaged estimate of large-scale occupancy for the models in Table 6 and the bounding lines were unconditional 95% confidence intervals.

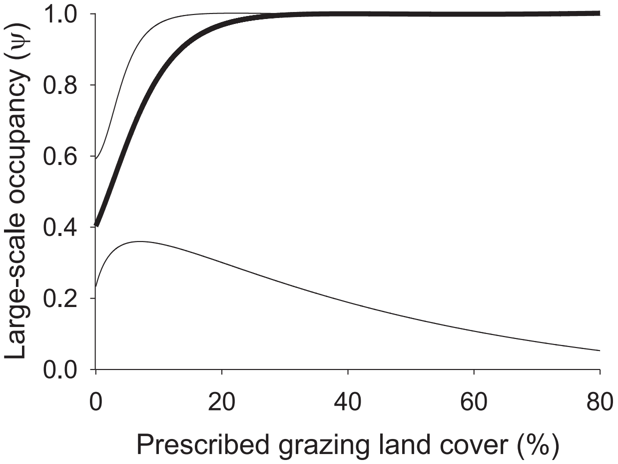

Figure 5. The large-scale occupancy rate, probability of occupancy by lesser prairie-chicken in the 15-km × 15-km grid cells, plotted as a function the percentage of prescribed grazing land cover (holding the other covariates at their mean values). The bold line was the model-averaged estimate of large-scale occupancy using the models in Table 6. The bounding lines were unconditional 95% confidence intervals.

The second of the top four models indicated a positive relationship between percentage of CRP land cover and probability of occupancy by LPC in the large scale grid cells (Table 7). Using this model and holding the other covariates constant at their mean values, we plotted the probability of large scale occupancy as a function percentage of CRP land in the grid cell (Figure 6). The estimates varied from about 0.35 to above 0.7 if more than one-third of the grid cell were to be covered by lands enrolled in the CRP program.

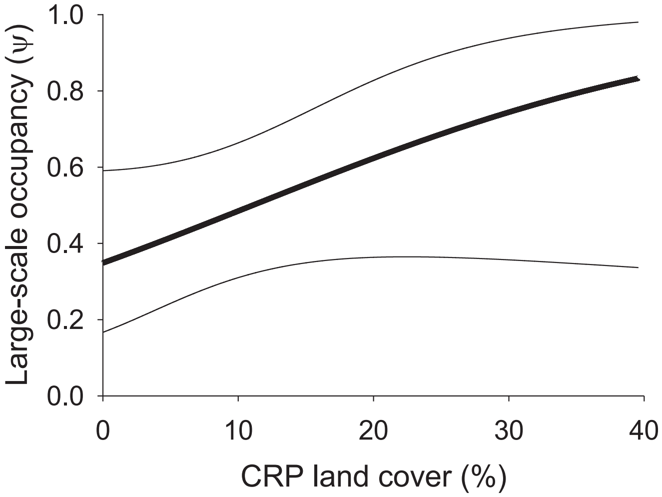

Figure 6. The large-scale occupancy rate, probability of occupancy of 15-km × 15-km grid cells by the lesser prairie-chicken, plotted as a function of Conservation Reserve Program (CRP) land cover (holding the other covariates at their mean values). The bold line was the model-averaged estimate of large-scale occupancy from the models in Table 6. The bounding lines were unconditional 95% confidence intervals.

Small scale occupancy: Probability of occupancy of 7.5-km × 7.5-km quadrants by LPC, given large scale occupancy

The percentage of land enrolled in the CRP practice was in all models within two AIC_C values of the top model indicating positive relationships with probability of occupancy at the small scale 7.5-km × 7.5-km quadrant level, given occupancy in the 15-km × 15-km grid cell [θ(CRP)] (Table 6). The coefficients for θ (CRP) were positive and statistically significant for all models (95% confidence intervals did not contain 0.0, Table 8). The probability of occupancy of small-scale quadrants by lesser prairie-chickens given occupancy of the grid cells was plotted as a function of CRP land cover for the shortgrass habitat region of northwest Kansas (Figure 7). The bold line was the model-averaged estimate of small-scale occupancy from using the models in Table 6. The bounding lines were unconditional 95% confidence intervals.

Given occupancy of the large-scale grid cells, the top models indicated that probability of occupancy at the quadrant level varied among the habitat regions (strata factor with short grass region of northwest Kansas [SGPR] as the reference level). The coefficients for SOPR and SSPR were negative indicating lower probability of occupancy at the quadrant level relative to SGPR in northwest Kansas. The coefficients for MGPR were not statistically significant indicating no significant decrease in occupancy relative to SGPR at the small quadrant scale, given occupancy at the large-scale grid cells.

The small-scale occupancy rate was plotted for each habitat region (holding the other covariates at their mean values) (Figure 8). The symbols were model-averaged estimates of small-scale occupancy using the models in Table 6. The error bars were unconditional 95% confidence intervals.

Table 7. Estimates of coefficients for large-scale occupancy (ψ) for models within two AICc values of the top model. C occupancy (θ) and probability of detection (p) were not reported.

Model	Ψ(Intercept)	Ψ(CRP)	Ψ(grazing
ψ (grazing + patchsize), θ (CRP + strata), p(observer + strata)	-1.57 (-2.33, -0.81)		0.19 (-0.03
ψ (CRP + patchsize), θ (CRP + strata), p(observer + strata)	-2.1 (-3.18, -1.02)	5.640 (-1.5, 12.78)	
ψ (patchsize), θ (CRP + strata), p(observer + strata)	-1.41 (-2.14, -0.67)		
ψ (grazing + patchsize), θ (CRP + strata), p(observer)	-1.57 (-2.33, -0.81)		0.20 (-0.03

Table 8. Estimates of coefficients for small-scale occupancy (θ) for models within two AIC$_c$ values of the top model. Co intercept term for θ were not reported.

Model	θ (CRP)	θ (SOPR)	θ (SSPR)
ψ (grazing + patchsize), θ (CRP + strata), *p*(observer + strata)	7.08 (3.92, 10.23)	-2.72 (-3.93, -1.52)	-1.37 (-2.54, -0.2)
ψ (CRP + patchsize), θ (CRP + strata), *p*(observer + strata)	5.13 (1.70, 8.55)	-2.74 (-3.94, -1.54)	-1.64 (-2.72, -0.56)
ψ (grazing), θ (CRP + strata), *p*(observer + strata)	6.71 (3.62, 9.80)	-2.53 (-3.73, -1.32)	-1.45 (-2.57, -0.33)
ψ (grazing + patchsize), θ (CRP+ strata), *p*(observer)	6.79 (3.76, 9.83)	-2.82 (-3.98, -1.67)	-1.59 (-2.64, -0.54)

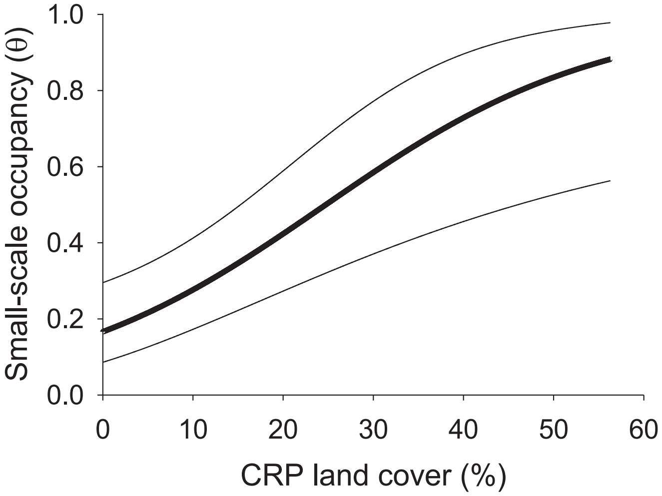

Figure 7. The small-scale occupancy rate, probability of occupancy of 7.5-km × 7.5-km quadrants by lesser prairie-chickens given occupancy of the 15-km × 15-km grid cells, plotted as a function of Conservation Reserve Program (CRP) land cover for the shortgrass habitat region of northwest Kansas. The bold line was the model-averaged estimate of small-scale occupancy from using the models in Table 6. The bounding lines were unconditional 95% confidence intervals.

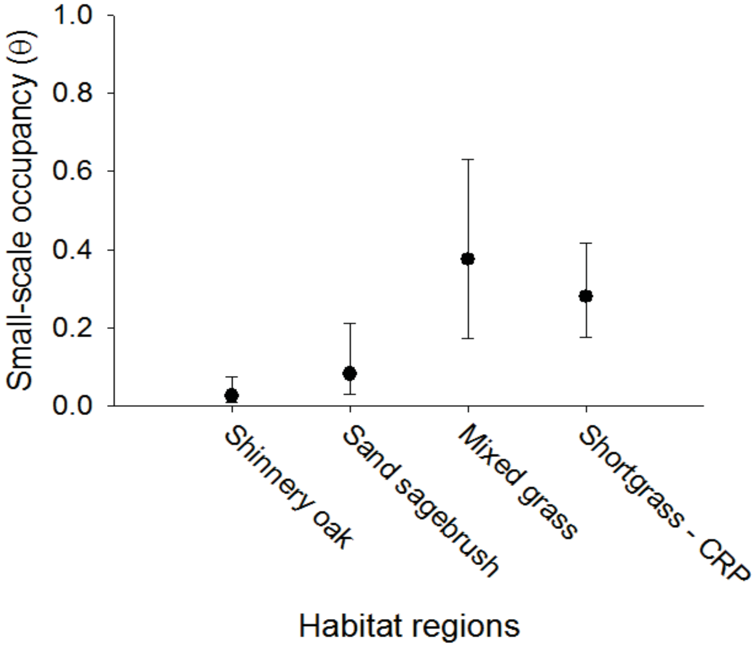

Figure 8. The small-scale occupancy rate, probability of occupancy in 7.5-km × 7.5-km quadrats by lesser prairie-chicken given occupancy of the 15-km × 15-km grid cell was plotted for each habitat regions (holding the other covariates at their mean values). The symbols were model-averaged estimates of small-scale occupancy using the models in Table 6. The error bars were unconditional 95% confidence intervals.

EXECUTIVE SUMMARY

1. We estimated probability of occupancy by lesser prairie-chicken (LPC) using data collected during the range-wide population survey conducted for the Western Association of Fish and Wildlife Agencies (WAFWA) (McDonald et al. 2015). We also collected data in spring 2015 by re-survey of a subset of the grid cells and transects in the WAFWA range-wide survey using the same survey methods. Data from these replicated surveys were pooled with data from the WAFWA survey and the pooled data analyzed for estimation of probability of occupancy by LPC.
2. Forty-five of the 155 grid cells in the Short Grass Prairie Region of northwest Kansas and the Shinnery Oak Prairie Region of eastern New Mexico and western Texas Panhandle of the WAFWA range-wide survey were re-flown by a 3 person crew and pilot in an R44 helicopter, resulting in a 29% increase in the monitoring cost to collect the replicated surveys.
3. We considered two independent searches of spatial sample survey strips within 15-km × 15-km grid cells and 7.5-km × 7.5-km quadrants within grid cells to provide the data necessary for estimate probability of occupancy by LPC. These methods separate probability of detection of LPC from probability of occupancy, using methods developed by MacKenzie et al. (2006a) and expanded by Nichols et al. (2008) and Pavlacky et al. (2012). Observations by the front seat observer and pilot in the R44 helicopter provided the first search of survey strips with either detection or non-detection of LPC. Observations by the rear seat observers provided the second independent search with either detection or non-detection of LPC.
4. We estimated probability of occupancy of the 15-km × 15-km grid cells in the WAFWA range-wide survey for both the original WAFWA 2015 data and the pooled data set. We were able to re-format the WAFWA range-wide survey data to estimate the probability of occupancy of 7.5-km × 7.5-km quadrants by LPC, given occupancy of the 15-km × 15-km grid cell, and 2) probability of detection of LPC given occupancy of the quadrants and grid cell using the recent methods described in Nichols et al. (2008) and Pavlacky et al. (2012).
5. Based on analysis of only the WAFWA range-wide survey data, precision of estimates of occupancy by LPC were in an acceptable range for long term monitoring studies with coefficients of variation (CV) less than 25% (with one exception). These estimates included probability of occupancy by LPC in the large scale 15-km × 15-km grid cells, probability of occupancy by LPC in the small scale 7.5-km × 7.5-km quadrants (given occupancy of the grid cell), and probability of detection of LPC (given occupancy of the grid cell). The exception was a relatively high CV of approximately 50% for estimated probability of occupancy at the small-scale 7.5-km × 7.5-km quadrant level in one of the ecoregions which had very low density of LPC, namely the Shinnery Oak Prairie Region of eastern New Mexico and western Texas Panhandle (McDonald et al. 2015). The same result could be expected in the Sand Sage Prairie Region of southeast Colorado, southwest Kansas and parts of the Panhandle of Oklahoma, which also had very low density.
6. Improvement in precision of occupancy estimates due to the re-survey of a subset of grid cells and transects and pooling the data was very modest for all parameter estimates. For example, the CV for estimated probability of occupancy of the 15-km × 15-km grid cells by LPC decreased from 23% to 22%. The CV for estimated probability of occupancy of 7.5-km × 7.5-km quadrants by LPC when the grid cell was occupied: 1) decreased from 24% to 22% in the Short Grass

Prairie Region of northwest Kansas and 2) decreased from 51% to 48% in the Shinnery Oak Prairie Region of eastern New Mexico and western Texas Panhandle.

7. We developed Geographical Information System (GIS) data layers with values for 26 measurements on the grid cells and quadrants in the sampling frame for the WAFWA range-wide population surveys. These values were measures of habitat configuration and anthropogenic land management practices which potentially affected occupancy of grid cells and quadrants by LPC.
8. We selected a subset of the 26 measures and derived a preliminary set of covariates (predictor variables) to include in a pilot modeling exercise. Full analysis and modeling of effects of habitat configuration and anthropogenic land management practices on occupancy by LPC requires additional research and was beyond the scope of this study.
9. The objective of the pilot modeling exercise was to evaluate whether there was enough precision in the WAFWA range-wide survey data to discover statistically significant relationships between the derived covariates and probability of occupancy by LPC without using data from the replicated grid cells. This preliminary set of covariates included: 1) mean patch size of native grass and shrubland landcover (excluding mesquite shrubland > 25%), 2) percentage of Conservation Reserve Program (CRP) land during 2015, 3) percentage of prescribed grazing practice during 2015, and 4) density of major roads (length/area).
10. We conducted a pilot analysis modeling the effects of the preliminary set of covariates on probability of occupancy by LPC in large scale 15-km × 15-km grid cells surveyed. We were also able to re-format the data to expand the pilot analysis to model the effects of the subset of covariates on: 1) probability of occupancy of 7.5-km × 7.5-km quadrants by LPC given occupancy of the grid cell and 2) probability of detection of LPC given occupancy of the quadrants and grid cell.
11. We found statistically significant positive relationships between mean patch size of native vegetation and probability of occupancy by LPC in the large scale grid cells at the 95% confidence level.
12. There was a strong statistically significant positive relation between percent prescribed grazing practice and probability of occupancy by LPC in the large scale grid cells at the 90% confidence level ($\beta = 0.193$; 90% CI = 0.005, 0.382). The evidence ratio based on the AICc selection criterion indicated the top model containing prescribed grazing was two times more plausible than the second and third best model without this covariate.
13. There was a positive relationship between probability of occupancy of large scale grid cells by LPC and proportion of CRP land cover. The analysis provided some evidence for the effect of CRP cover in addition to native habitat patch size, however the relationship was not quite significant at the 90% confidence lever.
14. We found a statistically significant positive relationship between the proportion of CRP managed lands and probability of occupancy by LPC in the small scale 7.5-km × 7.5-km quadrants given that the large scale grid cell was occupied. This relationship was statistically significant at the 95% confidence level. This effect suggested that the addition of CRP land cover increased the occupancy rate of LPC beyond the effect of native patch size alone.
15. We observed large differences among small-scale occupancy rates of 7.5-km × 7.5-km quadrants by LPC (given occupancy of the large scale grid cell) in the four ecoregions. However, we found little support for differences among large-scale occupancy rates of 15-km × 15-km grid cells among the four ecoregions. We offer three explanations for the absence of habitat region effects

at the large scale. First, small-scale occupancy of quarter grids can be interpreted as prevalence within 15-km × 15-km grids and thus would better represent abundance than large-scale occupancy of the 15-km × 15-km grids. Second, because occupancy rates increase with increasing area of the sampling unit (MacKenzie et al. 2006), the occupancy rate of 225 km^2 grid cells was expected to be high even in habitat regions with low density of the LPC. Third, small-scale occupancy measures the probability of availability given the grid cell was occupied and p measures the probability of detection given that the small-scale quadrants and grid cell were occupied. In habitat regions with low density of the LPC, the estimates of large-scale occupancy were adjusted upward to account for situations where the LPC was largely unavailable for sampling (Pavlacky et al. 2012). Finally, the conditional estimate of small-scale occupancy indicated the occupancy rate of 7.5-km × 7.5-km quadrants was six times greater in the Short Grass Prairie Region of northwest Kansas than in the Shinnery Oak Prairie Region of eastern New Mexico and western Texas Panhandle. These values corresponded closely to population size estimates from the monitoring program (McDonald et al. 2015).

RECOMMENDATION

If funds are available in spring 2016 to supplement the WAFWA range-wide survey effort, our recommendation is that the funds be used to increase the sample size and spatial replication of grid-cells surveyed in the two ecoregions that had low density of LPC in 2015; namely, the Shinnery Oak Prairie Region of eastern New Mexico and western Texas Panhandle and in the Sand Sage Prairie Region of southeastern Colorado, southwest Kansas, and parts of the Oklahoma Panhandle.

We justify this recommendation by noting that:

1. Precision of estimates of probability of occupancy in the ecoregions with relatively high density of LPC were in an acceptable range with coefficients of variation less than 25%.
2. Statistically significant relationships were found in a pilot study exploring relationships between important natural habitat configuration and anthropogenic land management practices and probability of occupancy by LPC. This pilot modeling study used only data available from the 2015 WAFWA range-wide survey.
3. Precision of estimates of probability of occupancy in ecoregions with relatively low density of LPC were improved, but modestly by re-survey of a subset of the same grid cells in the WAFWA range-wide survey. Increasing the sample size and spatial replication of grid cells in the low LPC density ecoregions of the WAFWA range-wide survey will also improve the precision of the same estimates.
4. Increasing the sample size and spatial replication of grid cells will improve precision of estimates of population sizes in the WAFWA range-wide survey of those low density ecoregions.
5. Finally, the literature supports our recommendation. When considering sampling design tradeoffs between the sample sizes for temporal and spatial replicates, increasing the sample size of spatial replicates was often more efficient than increasing the number of repeat visits

for estimating occupancy rates of rare species (Mackenzie and Royle 2005). Accordingly, adding spatial replicates to the Shinnery Oak Prairie Region and in the Sand Sage Prairie Region where the LPC were rare is expected to be more effective in improving the precision of the occupancy estimates than increasing temporal replicates.

ACKNOWLEDGEMENTS

Financial support for the 2013, 2014, and 2015 range-wide surveys and this report were provided by grants to the Western Association of Fish and Wildlife Agencies from the wildlife agencies of the states of Colorado, Kansas, New Mexico, Oklahoma, and Texas, the Bureau of Land Management, the National Fish and Wildlife Foundation, and various oil and gas companies and associations. We wish to acknowledge our use of the ground survey data collected by the Kansas Department of Wildlife, Parks and Tourism and the initial analysis of these data provided by Michael Houts, GIS/Remote Sensing Specialist, Kansas Biological Survey. We also wish to acknowledge the assistance of the aerial survey crew members and pilots.

Financial support for part of the supplemental temporal replications of the survey was provided by Pheasants Forever and funded by Grant Agreement #68-3A75-14-120 between the Natural Resources Conservation Service (NRCS) and Pheasants Forever.

We thank Alex Daniels from the Playa Lakes Joint Venture, and Rob Sparks and Brittany Woiderski, Bird Conservancy of the Rockies, for Geographic Information Systems work to develop spatial covariates for the project. We thank Christian Hagen for his input and discussions on lesser prairie-chicken ecology and development of hypotheses for the covariate analyses.

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