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RESEARCH ARTICLE

Multiscale occupancy modeling provides insights into range-wide conservation needs of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*)

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ABSTRACT

The range-wide monitoring program for the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) plays an important role in landscape conservation initiatives for the recovery of this species. Methodologies to evaluate the species' responses to habitat conditions and conservation practices are necessary to evaluate the success of these initiatives. We adapted the design of the range-wide monitoring program and applied a multiscale occupancy model. The objectives were to (1) estimate occupancy at multiple spatial scales and (2) conduct an exploratory evaluation of responses to habitat condition and conservation practices at multiple spatial scales. The application of the model to a single year of data from the range-wide monitoring program yielded a coefficient of variation (CV) of large-scale occupancy of 17%. The CVs of small-scale occupancy for the 4 ecoregions ranged between 21% and 52% and were acceptable for detecting differences between strata. We used the method of multiple working hypotheses and predictions from fitted models to evaluate a priori how a subset of habitat configuration and anthropogenic practices potentially affect site occupancy at multiple spatial scales. We derived a subset of habitat configuration and anthropogenic conservation covariates based on the 15 × 15 km grid cells and 7.5 × 7.5 km quadrants. Our results show that Lesser Prairie-Chicken occupancy was positively affected by increased mean patch size of native land cover in the landscape, and by the percentage of land enrolled in prescribed grazing at the large scale (225 km^2) and in the Conservation Reserve Program at the small scale (56 km^2).

Keywords: conservation practices, Lesser Prairie-Chicken, monitoring, multiscale occupancy, *Tympanuchus pallidicinctus*

Los modelos de ocupación a múltiples escalas brindan información sobre las necesidades de conservación de todo el rango de *Tympanuchus pallidicinctus*

RESUMEN

El programa de monitoreo de todo el rango de *Tympanuchus pallidicinctus* juega un papel importante en las iniciativas de conservación del paisaje para la recuperación de la especie. Las metodologías para evaluar las respuestas de *T. pallidicinctus* a las condiciones del hábitat y a las prácticas de conservación son necesarias para estimar el éxito de estas iniciativas. Adaptamos el diseño del programa de monitoreo de todo el rango y aplicamos un modelo de ocupación de múltiples escalas. Los objeticos fueron 1) estimar la ocupación de *T. pallidicinctus* a múltiples escalas espaciales y 2) conducir una evaluación exploratoria de las respuestas de *T. pallidicinctus* a las condiciones de hábitat y a las prácticas de conservación a múltiples escalas espaciales. La aplicación del modelo a un único año de datos del programa de monitoreo de todo el rango generó un coeficiente de variación (CV) de la ocupación a gran escala = 17%. El CV de la ocupación a pequeña escala para las cuatro ecorregiones varió entre 21% y 52% y fue aceptable para detectar diferencias entre los estratos. Usamos predicciones de modelos ajustados y el método de múltiples hipótesis de trabajo para evaluar a priori como un subconjunto de configuraciones del hábitat y de prácticas antropogénicas afecta potencialmente la ocupación del sitio a múltiples escalas espaciales. Derivamos un subconjunto de covariables de la configuración del hábitat y de la conservación antropogénica tomado como base una grilla de celdas de 15 km × 15 km y de cuadrantes de 7.5 km × 7.5 km. Mostramos que la ocupación de *T. pallidicinctus* estuvo afectada positivamente por un aumento del tamaño promedio del parche con cobertura nativa en el paisaje y por el porcentaje de tierra involucrada en prácticas de pastoreo prescripto a gran escala (225 km^2), y por el Programa de Conservación de Reservas en el paisaje a pequeña escala (56 km^2).

Palabras clave: monitoreo, ocupación a múltiples escalas, prácticas de conservación, *Tympanuchus pallidicinctus*

INTRODUCTION

The Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) is a species of conservation concern (Van Pelt et al 2013, U.S. Fish and Wildlife Service [USFWS] 2014). The primary threats to the species are habitat loss and fragmentation (Fischer and Lindenmayer 2007) that result from land uses incompatible with the species' biology. Modifications to Lesser Prairie-Chicken habitat include conversion of native habitat for tillage agriculture, eastern redcedar (*Juniperus virginiana*) encroachment, and energy development (Woodward et al. 2001, Pruett et al. 2009, 2011, Hagen et al. 2011). The current distribution is ~16% of the estimated historical range at the time of European settlement (Hagen and Giesen 2005, Van Pelt et al. 2013). However, in one portion of the species' range, recent responses to changes in habitat quantity and configuration provide reason for optimism (Spencer 2013). Lesser Prairie-Chickens recently reoccupied portions of their historical range in Kansas, USA. In fact, the current distribution extends beyond the known historical range (Hagen and Giesen 2005, Van Pelt et al. 2013; Figure 1). The range shifts have coincided with the establishment and maintenance of Conservation Reserve Program (CRP) fields that provide the necessary vegetation structure for Lesser Prairie-Chickens throughout the shortgrass prairies (Rodgers and Hoffman 2005, Ripper et al. 2008). Population trends in this ecoregion have increased with changes in distribution, despite declines in other ecoregions (Garton et al. 2016).

Although the Lesser Prairie-Chicken was recently vacated from protection under the Endangered Species Act, a broad partnership (for a detailed list, see http://www.lpcinitiative.org) has coalesced to conserve and restore populations where necessary (Van Pelt et al. 2013). Landscape-scale initiatives are underway that are designed to yield population-level responses to conservation practices, including improved grazing systems, tree removal, and restoring native grasslands (Van Pelt et al. 2013, U.S. Department of Agriculture 2014). Monitoring of biological responses to these conservation actions is of paramount importance for maintaining Lesser Prairie-Chicken populations into the future.

Statistically rigorous monitoring techniques are needed to assess population status and responses to anthropogenic impacts and conservation efforts (Jones 2011). Historically, Lesser Prairie-Chicken populations have been monitored using counts of males at leks (communal breeding grounds) from point-based or route-based surveys (Garton et al. 2016). Although these data provide an invaluable index and historical record of population abundance, the survey methods are unable to correct for species or individuals that are present but not detected, and the sampled leks are not drawn from a random sample (Garton et al. 2011, 2016). These shortcomings led to the development of a range-wide aerial survey to provide a robust annual estimate of abundance as the basis for a long-term monitoring program (McDonald et al. 2014). Since 2012, abundance has been estimated annually across 4 ecoregions that encompass the Lesser Prairie-Chicken distribution (Figure 1; McDonald et al. 2015). Briefly, the method entails double-observer counts along 2 aerial (i.e. helicopter) transects that are nested within a 15 × 15 km grid cell. Each grid cell was randomly selected from a spatially balanced sampling scheme (McDonald et al. 2014). The approach enables robust estimation of the abundance of Lesser Prairie-Chickens and their leks using distance-sampling methods (Buckland et al. 2004, McDonald et al. 2014).

Monitoring both abundance and occupancy is important for a comprehensive understanding of the status of wildlife populations, including population size and geographic distribution (Jones 2011). Site occupancy, or the proportion of sites occupied, is primarily related to the aspect of a population involving the distribution or geographic range of a species (MacKenzie and Nichols 2004). Although it is important to note that changes in abundance may occur with or without changes to range size, occupancy is a complementary and viable state variable for monitoring trends and assessing population status for species of conservation concern (MacKenzie and Nichols 2004, Noon et al. 2012). In some cases, occupancy may be preferable to abundance for rare species with sparse data, considering trade-offs between bias and precision, and the simplicity or complexity of an estimator (MacKenzie et al. 2006). For example, abundance often demonstrates greater annual and local variation than site occupancy (Joseph et al. 2006), and covariate relationship models for abundance often exhibit greater complexity (e.g., Oedekoven et al. 2014). Abundance estimation is often problematic for monitoring rare species, particularly at large spatial scales, because abundance requires greater sample sizes and numbers of detections than occupancy to achieve a comparable level of precision (MacKenzie and Nichols 2004, MacKenzie et al. 2006). Although methods to estimate abundance from overdispersed lek counts are well developed (Royle et al. 2004, Miller et al. 2013), highly clustered counts with excess zeros often translate into low precision of the abundance estimates. In comparison, occupancy modeling provides a relatively parsimonious and straightforward approach for evaluating species–habitat relationships and responses to conservation practices (Tyre et al. 2003, Gu and Swihart 2004, MacKenzie 2006).

Evaluations of the abundance and occupancy responses of the Lesser Prairie-Chicken are needed to assess the outcomes of the landscape initiatives designed to conserve

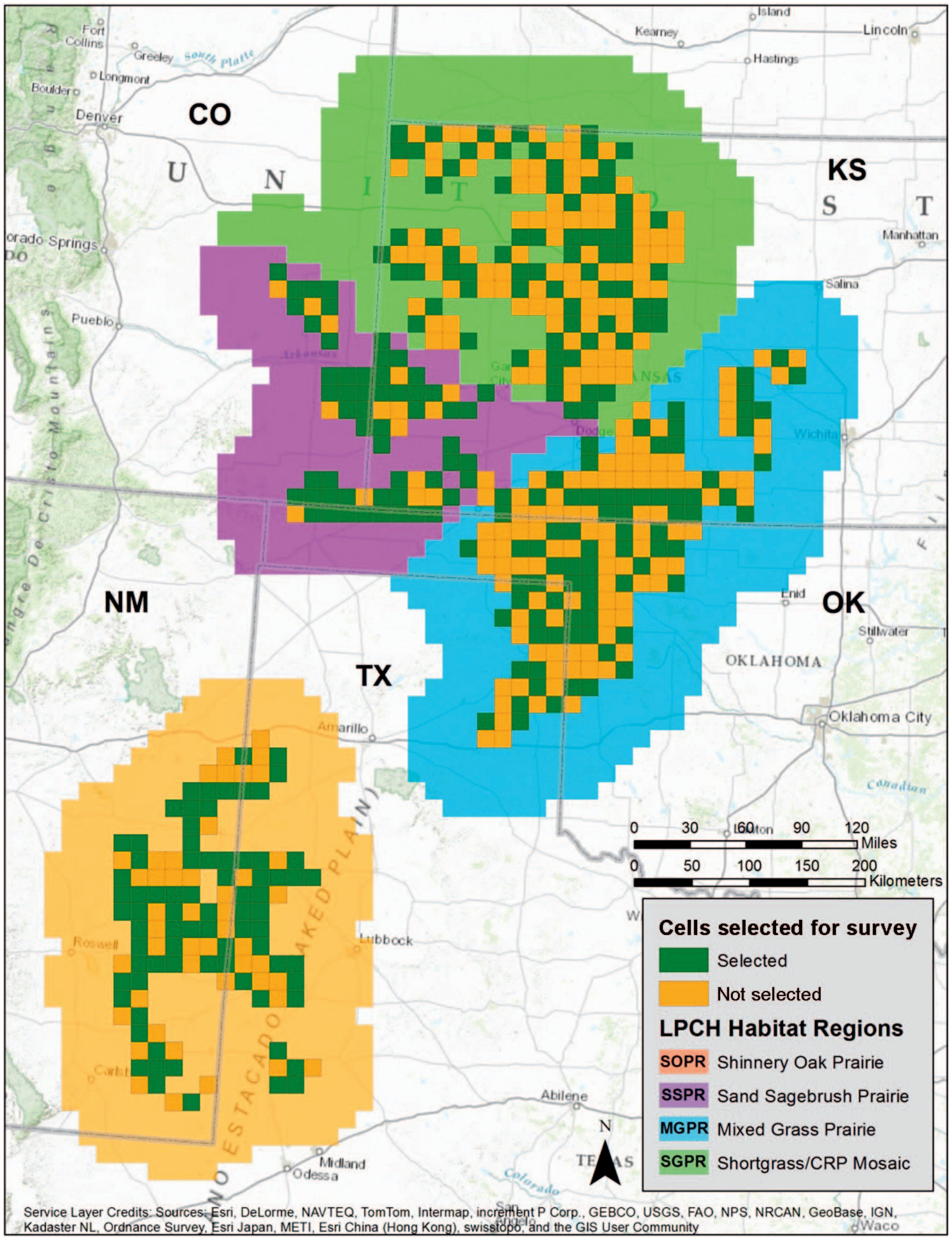

FIGURE 1. Study area for Lesser Prairie-Chicken surveys (i.e. RW-survey) illustrated with grid cells selected for survey in 2015. The colored areas surrounding the study subareas indicated ~77.7 km (30 miles) buffer into which the survey may be expanded in the future (after McDonald et al. 2014).

or enhance populations locally, regionally, and nationally (Van Pelt et al. 2013, U.S. Department of Agriculture 2014). In 2012, the Western Association of Fish and Wildlife Agencies (WAFWA) began a Lesser Prairie-Chicken population monitoring program (McDonald et al. 2014, 2015) that is well suited for estimating both abundance and site occupancy. Here, we present an occupancy approach to determine the status and habitat responses in the range-wide distribution of the Lesser Prairie-Chicken population. We partitioned the detection–nondetection data collected under the monitoring program (McDonald et al. 2015) into 7.5 × 7.5 km quadrants and estimated Lesser Prairie-Chicken occupancy at large and small scales using the models presented in Pavlacky et al. (2012), Mordecai et al. (2011), and Nichols et al. (2008). This type of model can predict multiscale covariate relationships to inform habitat management at multiple spatial extents at which species may respond differently (Block et al. 2001, George and Zack 2001, Mutter et al. 2015). For example, the model can be used to evaluate the

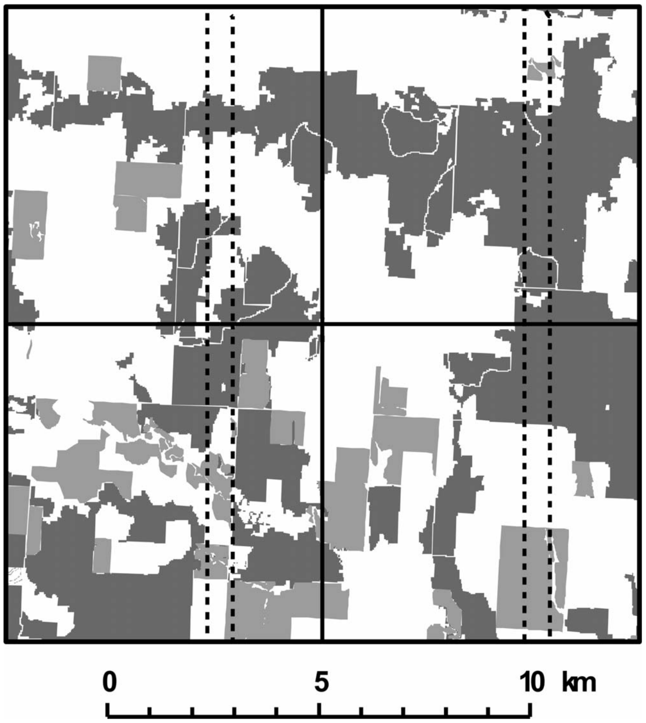

FIGURE 2. An example 15 × 15 km grid cell illustrating the 7.5 × 7.5 km quadrants and segmented flight transects within each quadrant. The flight transects are depicted in dashed bounding lines, native land cover is shown in dark gray, and CRP land cover is shown in light gray. The mean patch size of native vegetation for the 15 × 15 km grid cell is 0.55 km^2, and the percentage of CRP is 6% in the northwest quadrant, $<$1% in the northeast quadrant, 20% in the southeast quadrant, and 22% in the southwest quadrant.

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, Mutter et al. 2015).

Corresponding to the modified design, the parameters of the model include the large-scale probability of occupancy (ψ) of grid cells (15 × 15 km), the small-scale probability of occupancy (θ) of nested quadrants (7.5 × 7.5 km) given presence in the grid cells (Figure 2), and the probability of detection (p) of Lesser Prairie-Chickens given presence in a quadrant (Pavlacky et al. 2012). For brevity, these probabilities were referred to as "occupancy" and "detection." Each of these scales corresponds to landscapes found to be relevant to Lesser Prairie-Chicken ecology. At a minimum, the species appears to be sensitive to different types of fragmentation at the quadrant scale (56.25 km^2; Fuhlendorf et al. 2002), with similar patterns at the 225 km^2 scale (grid cell) and beyond (Bartuszevige and Daniels 2016). These sampling frames represent a balance in ecological relevance and sampling coverage of a wide-ranging but rare species.

Our goal was to examine the adaptability of the current range-wide aerial survey (hereafter "RW-survey") to estimate Lesser Prairie-Chicken occupancy. Prior to this study, the efficacy of multiple observers to estimate detection probabilities from a single visit to the sampling unit was unknown. Thus, we evaluated 2 datasets—from the original design of the RW-survey and from an adaptation in sampling design with repeated temporal replicates to estimate occupancy. Our objectives were to (1) estimate occupancy at multiple spatial scales from the range-wide monitoring program, (2) compare the performances of the original RW-survey data to the RW-survey data when supplemented with repeated temporal replicates for estimating multiscale occupancy, and (3) conduct an exploratory evaluation of the multiscale occupancy model's potential to predict the effects of habitat and conservation practices on Lesser Prairie-Chicken occupancy.

Our a priori set of models was devised to evaluate various factors that could contribute to occupancy at 2 spatial scales. Our hypotheses predicted that large-scale occupancy would increase with available native prairie and decrease as a function of vegetation fragmentation and road development. We hypothesized that CRP land cover would augment the patch size of native vegetation, and that evidence for additive effects of patch size and CRP beyond those of patch size alone would provide support for this hypothesis. Because prescribed grazing is implemented on individual ranches, we hypothesized that grazing heterogeneity would affect occupancy at the smaller 56 km^2 scale (McNew et al. 2012, Bartuszevige and Daniels 2013). A prescribed grazing plan as implemented through the Natural Resources Conservation Service (NRCS) Lesser Prairie-Chicken Initiative (LPCI), and as reported here, must include grazing management that is designed to address limiting vegetation factors for the species (USFWS 2011). Combined, these hypotheses provide insights into the habitat and conservation needs of Lesser Prairie-Chickens at multiple scales.

METHODS

Study Area

The monitoring program (McDonald et al. 2015) spanned the entire occupied range (8 million ha) of the study species, including parts of Colorado, Kansas, New Mexico, Oklahoma, and Texas, USA (Figure 1). The distribution of the species was divided into 4 ecoregions: Shinnery Oak Prairie Region (SOPR), located in eastern New Mexico–southwest Texas Panhandle; Shortgrass–CRP Mosaic Prairie Region (SGPR), located in northwestern Kansas; Mixed Grass Prairie Region (MGPR) in the northeast corner of the Texas Panhandle, northwest Oklahoma, and south-central Kansas; and Sand Sagebrush Prairie Region

(SSPR) of southeast Colorado, southwest Kansas, and part of the Oklahoma Panhandle (Figure 1).

Sampling Design

We used the existing 4 ecoregions (hereafter "strata") of the study area (Figure 1) and generalized random tessellation stratified (GRTS) sampling that provides equal probability samples in each stratum (Stevens and Olsen 2004). During the 2013–2015 RW-surveys, there were 77 of 123 cells surveyed in SOPR, 73 of 165 cells surveyed in SGPR, 78 of 176 cells surveyed in MGPR, and 55 of 71 cells surveyed in SSPR, totaling 6.4 million ha of the 8 million ha in the range (McDonald et al. 2014, 2015). In 2015, 15 and 30 grid cells were resurveyed in the SOPR and SGPR strata, respectively, using the same RW-survey methods. These 45 temporal replicates were randomly selected to evaluate the effectiveness of repeated surveys in improving the precision of the occupancy estimates. We refer to data from these temporal replications as the 2015 replicate survey (hereafter "REP-survey").

Aerial Survey Methods

The Raven II (R-44) helicopter was the survey platform used in the surveys (McDonald et al. 2014). This helicopter accommodated 2 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 hr^{-1} and 25 m above ground. During the lekking period (March 15–May 15, 2015), surveys were conducted from sunrise until ~2.5 hr after sunrise. Two 15 km north–south parallel transects were selected in each of the survey grid cells (Figure 2). The starting point of the first transect was randomly located in the interval (200–7,300 m) on the base of the cell, and the second transect was located 7,500 m to the east of the first transect. The survey methods are described in further detail in McDonald et al. (2014).

Estimation of transects on which prairie-chickens were detected. The Lesser Prairie-Chicken and Greater Prairie-Chicken (*T. cupido*) species overlap in distribution in the SGPR stratum of northwest Kansas, and it was not possible to distinguish between species from the helicopter. All groups detected in the SGPR aerial survey ($n = 115$) were ground-truthed to determine whether Lesser Prairie-Chickens were present. Among the 115 detections, 10 Lesser Prairie-Chicken leks, 21 Greater Prairie-Chicken leks, 2 mixed-species leks, and 82 nonlekking groups were verified on the ground. The Kansas Department of Wildlife, Parks and Tourism (KDWPT) conducts extensive ground surveys of prairie-chicken leks each year and provided estimates for the proportion of Lesser Prairie-Chickens in each survey grid cell (McDonald et al. 2015). If a prairie-chicken group could not be ground-truthed to determine that at least one Lesser Prairie-Chicken was present, we recorded detection of Lesser Prairie-Chickens if KDWPT's estimated proportion of Lesser Prairie-Chickens in the grid cell was >0.5 (McDonald et al. 2014).

Multiscale Occupancy Framework for the Range-wide Monitoring Program

The encounter history for the RW-survey data used "multiple" observers in the helicopter to estimate the probability of detection. We pooled the encounters of prairie-chickens by the observer in the front left seat and the pilot in the front right seat (first occasion or search). Similarly, we pooled the encounters of prairie-chickens by the observer in the back left seat and the observer in the back right seat (second occasion or search). This yielded an encounter history with 2 occasions or searches of a quadrant for the RW-survey. In addition to multiple observers on the same visit, the approach can accommodate repeat visits in time to the sampling grid. For the REP-survey, we developed an encounter history that included the front and back observers for both the RW-survey and the REP-survey that was repeated in time.

Statistical Model for Multiscale Occupancy

The multiscale model can be thought of as a within-season robust design (Pollock 1982), whereby 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. 2008, Mordecai et al. 2011). The modeling approach allows the estimation of occupancy at the scale of grid cells and quadrants. Because ψ corresponds to the occupancy probability of the grid cells and θ corresponds to the occupancy probability of quadrants given that the grid cell was occupied, the product $\hat{\theta}_c = \hat{\psi} * \hat{\theta}$ represents the conditional probability of small-scale occupancy for all grid cells and quadrants in the sampling frame (Nichols et al. 2008, Pavlacky et al. 2012).

We fitted the multiscale occupancy models using RMark 2.1.13 (Laake 2013, R Development Core Team 2015), an interface for MARK 8 (White and Burnham 1999). The parameters of the model are (1) the probability of detection p_{ijk} for grid cell i, quadrant j, and observer k given that the quadrant and grid cell were occupied; (2) the probability of small-scale occupancy θ_{ij} for grid cell i and quadrant j given that the grid cell was occupied; and (3) the probability of large-scale occupancy ψ_i for grid cell i. The assumptions of the multiscale occupancy model (Nichols et al. 2008, Pavlacky et al. 2012) are that (1) there was no unmodeled 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 prairie-chickens at each quadrant were independent, and (4) the target species were never falsely detected.

Model selection. We used information-theoretic model selection (Burnham and Anderson 2002) to estimate the relative loss of Kullback-Leibler information among candidate models used to approximate relative truth (Burnham and Anderson 2002). We ranked models according to Akaike's 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 the 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 assessed the precision of the effect sizes for models with $\Delta AIC_c < 2$ by evaluating regression coefficient estimates (β) with respect to zero using conditional 90% confidence intervals (CIs). We used 90% CIs to better reflect expectations from confirmatory AIC model selection (Arnold 2010) and to be consistent with confidence levels used in WAFWA status reports of Lesser Prairie-Chicken abundance. We graphed model-averaged predictions and estimated unconditional 90% CIs 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 inferences on effect sizes of the covariates (regression coefficients).

Occupancy Estimation at Multiple Spatial Scales

Using only data from the range-wide monitoring program, we considered 3 group covariates on detection, including a crew factor with 3 levels [p(crew)]; an observer factor with 2 levels for front and back observers [p(observer)]; and a strata factor with 4 levels for the SGPR, MGPR, SOPR, and SSPR strata [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 [ψ(.), θ(.)]. A total of 7 variations in modeling detection probability included all subsets of 1- and 2-variable combinations of the detection covariates. The candidate set also included 2 variations in modeling small-scale occupancy (θ) and 2 variations in modeling large-scale occupancy (ψ). We constructed the candidate set of models using all subsets of the parameter specifications for a total of 28 models. From the best model, we estimated the conditional probability of small-scale occupancy ($\hat{\theta}_c = \hat{\psi} * \hat{\theta}$) and calculated the standard error and 90% CI of the estimate using the delta method (Powell 2007).

Temporal replication. We compared the RW-survey to the REP-survey analysis to evaluate the performance of the occupancy models, and to determine the extent to which the additional REP-survey data increased the precision of the occupancy estimates. We developed 2 multiscale 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 and the REP-survey data. For the 2 analyses, we considered all the above group covariates, but for the combined RW-survey and REP-survey analysis, we included an additional survey factor on detection with 2 levels for the RW-survey and REP-survey [p(survey)]. We constructed the candidate set of models using all subsets of univariate parameter specifications, for a total of 16 models for the RW-survey analysis and 20 models for the combined RW-survey and REP-survey analysis. We calculated the coefficient of variation (CV) for all estimators by $SE(\hat{\mu}) / \hat{\mu}$, where $\hat{\mu}$ is the parameter estimate and $SE(\hat{\mu})$ is its standard error. The CV served as a measure of relative precision for the comparison of parameter estimates between RW-survey and REP-survey.

Occupancy as a Function of Habitat and Conservation

Covariates. We applied the multiscale occupancy model to the RW-survey data to evaluate hypotheses for the effects of habitat configuration and conservation practices on Lesser Prairie-Chicken occupancy. For both small-scale (θ) and large-scale (ψ) occupancy, we evaluated the strength of evidence for 4 continuous covariates—CRP, prescribed grazing, mean patch size of native land cover (patchsize), and major road density—and the categorical factor, stratum. We constructed the candidate set of models using all 1- and 2-variable combinations of the covariates, resulting in 10 variations in modeling detection (p), 15 variations in modeling for small-scale occupancy (θ), and 15 variations in modeling large-scale occupancy (ψ). We ran all subsets of the parameter specifications for a total of 2,250 models.

We derived 4 covariates from GIS analyses (Appendix Table 4) to evaluate our a priori hypotheses (ArcGIS 10.3; ESRI, Redlands, California, USA). We developed the covariate patchsize using the Playa Lakes Joint Venture (2009) and the Southwest Region Gap (Prior-Magee et al. 2007) land-cover layers. 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 ($\bar{x} = 0.93$; range: 0.00–56.20 km^2). A major road covariate was created by overlaying the grid-cell and quadrant polygons with the TIGER/Line layer (U.S. Census Bureau 2014), and the length of major roads (km) within each grid cell and quadrant polygon was calculated. We estimated the density of major roads by dividing the length of major roads by the area of each grid cell and quadrant ($\bar{x} = 1.28$; range: 0.00–7.66 km^{-1}). We developed a CRP covariate by overlaying the grid-cell and quadrant polygons with the CRP land-

TABLE 1. Model selection for large-scale occupancy (ψ), small-scale occupancy (θ), and detection (*p*) of Lesser Prairie-Chicken. Model-selection metrics are the value of the minimized –2 log-likelihood function, –2log(*L*); number of parameters, *K*; Akaike's Information Criterion adjusted for sample size, AIC_c; difference between model and minimum AIC_c values, ΔAIC_c; and AIC_c weight, w_i. Models with $\Delta AIC_c < 4$ are shown.

Model	−2log(*L*)	*K*	AIC_c	ΔAIC_c	w_i
ψ(.) θ(strata) *p*(observer + strata)	611.37	10	632.16	0.00	0.438
ψ(.) θ(strata) *p*(observer)	618.96	7	633.36	1.20	0.241
ψ(.) θ(strata) *p*(observer + crew)	615.80	9	634.45	2.29	0.139
ψ(.) θ(.) *p*(observer + strata)	621.08	7	635.48	3.32	0.083

cover type (excluding CRP tree plantings) within the land-cover dataset during the 2014 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: 0.00–0.56 *P*). Finally, we developed a prescribed grazing covariate (conservation practice 528) using a NRCS conservation practice spatial database (Bartuszevige and Daniels 2013). We buffered the point locations of NRCS projects by the area enrolled in the prescribed grazing practice during the 2014 calendar year and overlaid the grid-cell and quadrant polygons with the buffered areas to represent 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 4 predictive covariates for detection (*p*), including a crew factor with 4 levels for each crew; an observer factor with 2 levels for front and back observers; a strata factor with 4 levels for the SGPR, MGPR, SOPR, and SSPR strata; and a continuous covariate for the starting time of the survey after sunrise.

RESULTS

Occupancy Estimation at Multiple Spatial Scales

Adaptation of the RW-survey count data yielded reasonable estimates of Lesser Prairie-Chicken occupancy. First, we describe outcomes of fitting occupancy estimation models to RW-survey detection–nondetection data. Second, we evaluate the effectiveness of repeated temporal surveys for increasing precision in our occupancy estimates. Lastly, we expand the set of categorical estimation models to include a set of 4 covariates to explain patterns on the landscape that may be driving occupancy at multiple scales.

The best approximating model for Lesser Prairie-Chicken detection (*p*) included the effects of observer and stratum (Table 1). The evidence ratio indicated that the top model containing the effects of observer and stratum was ~2 times more plausible than the second-best model containing only the observer effect (Table 1). The probabilities of detection in the top model were greater for the back-seat observer than for the front-seat observer (Appendix Table 5; β = 1.30; 90% CI: 0.68–1.92), and were lower in the MGPR stratum than in the SGPR and SSPR stratum (Appendix Table 5; β = –1.53; 90% CI: –2.51 to –0.55). The 90% CIs for differences in detection between the SOPR and SSPR (β = –0.73; 90% CI: –2.35 to 0.89) and SGPR strata (β = –1.02; 90% CI: –2.33 to 0.30) included zero, indicating low precision and no measurable differences between the detection probabilities of these regions.

The best model for the small-scale occupancy (θ) of the Lesser Prairie-Chicken included the effects of stratum. The evidence ratio indicated that the top model containing the effect of stratum was ~5 times more plausible than the fourth-best model with a constant probability of small-scale occupancy (Table 1). Small-scale occupancy in the top model was lower in the SSPR (β = –0.96; 90% CI: –1.86 to –0.06) and SOPR (β = –2.03; 90% CI: –3.01 to –1.05) strata than in the SGPR stratum (Table 2), but the CI for the difference between the MGPR and SGPR strata included zero (Appendix Table 5; β = 0.29; 90% CI: –0.59 to 1.17).

The best approximating model for the large-scale occupancy (ψ) of the Lesser Prairie-Chicken included a constant probability of occupancy across the strata (Table 1). The evidence ratio indicated that the top model containing the constant probability of occupancy was ~15 times ($w_i = 0.43$) more plausible than the fifth-best model containing the stratum strata effect ($w_i = 0.03$).

The estimates of conditional small-scale occupancy ($\hat{\theta}_c = \hat{\psi} * \hat{\theta}$) indicated that the Lesser Prairie-Chicken occupied 0.13 (90% CI: 0.08–0.20) of the MGPR stratum, 0.10 (90% CI: 0.15–0.21) of the SGPR stratum, 0.05 (90% CI: 0.03–0.09) of the SSPR stratum, and 0.02 (90% CI: 0.01–0.04) of the SOPR stratum. The CVs of the conditional occupancy estimates were reasonable for making inference for the MGPR (0.29) and SGPR (0.21) strata but were more uncertain for the SSPR (0.40) and SOPR (0.49) strata.

Performances of the RW-survey vs. REP-survey. The best approximating model for the RW-survey data indicated that the detection probabilities for the back-seat observers were greater than those for the front-seat observers (Table 2). The best model for the combined RW- and REP-survey indicated that the detection probabilities were greater for the RW survey than for the REP survey (Table 2). The best model for both analyses indicated that small-scale occu-

TABLE 2. Model selection for the comparison between the RW-survey and combined RW-survey and REP-survey for the Shinnery Oak Prairie Region and Shortgrass–CRP Mosaic Prairie Region. Model-selection metrics are the value of the minimized –2 log-likelihood function, –2log(*L*); number of parameters, *K*; Akaike's Information Criterion adjusted for sample size, AIC_c; difference between model and minimum AIC_c values, ΔAIC_c; and AIC_c weight, w_i. Models with $\Delta AIC_c < 4$ are shown.

Survey model	−2log(*L*)	*K*	AIC_c	ΔAIC_c	w_i
RW-survey					
ψ(.) θ(strata) *p*(observer)	308.35	5	318.76	0.00	0.249
ψ(.) θ(strata) *p*(.)	310.66	4	318.93	0.17	0.228
ψ(strata) θ(strata) *p*(observer)	307.85	6	320.42	1.66	0.108
ψ(.) θ(strata) *p*(strata)	310.09	5	320.50	1.74	0.104
ψ(strata) θ(strata) *p*(.)	310.16	5	320.56	1.80	0.101
ψ(strata) θ(strata) *p*(strata)	309.59	6	322.16	3.40	0.045
ψ(.) θ(strata) *p*(crew)	310.04	6	322.60	3.85	0.036
RW-survey and REP-survey					
ψ(.) θ(strata) *p*(survey)	391.70	5	402.10	0.00	0.610
ψ(strata) θ(strata) *p*(survey)	390.88	6	403.45	1.35	0.311

pancy was greater in the SGPR stratum than in the SOPR stratum (Table 2). The best model for both analyses indicated that large-scale occupancy was constant across the 2 strata (Table 2).

Point estimates of large-scale occupancy (ψ) and small-scale occupancy (θ) did not vary appreciably among the methods (Appendix Table 6). We used the CV to evaluate the relative precision in occupancy estimates of the RW-survey compared to the combined RW- and REP-survey. The CV for estimated probability of occupancy at the large scale (ψ) decreased from 23% to 22% when data from the 2 surveys were combined (Appendix Table 6). The CV for estimated probability of occupancy at the small scale (1) decreased from 24% to 22% in the SGPR of northwest Kansas and (2) decreased from 51% to 48% in the SOPR of eastern New Mexico and the western Texas Panhandle (Appendix Table 6).

Probability of detection as a function of conservation. The best approximating model for Lesser Prairie-Chicken detection included the effects of observer and stratum (Table 3). The evidence ratio indicated that the top model containing the effects of observer and stratum was ~3 times more plausible than the fourth-best model containing only the observer effect (Table 3). The top models indicated that front and back observers had different probabilities of detecting Lesser Prairie-Chickens [*p*(observer); observer factor with 2 levels] (Table 3). In northwest Kansas, if the grid cell and quadrant were occupied, the estimated probability of detection was 0.62 (90% CI: 0.40–0.80) for the front-seat observers and 0.85 (90% CI: 0.67–0.95) for the back-seat observers. The top models also indicated that detection varied among 4 strata [*p*(strata)] and were comparable to estimates of *p* from the RW-survey analysis (Appendix Table 5).

Large-scale Occupancy as a Function of Conservation

The best model for the large-scale occupancy of the Lesser Prairie-Chicken as a function of habitat contained the effects of patch size of native land cover and prescribed grazing (Table 3). The evidence ratio indicated that the top model was 2 times more plausible than the second-best model containing patch size of native land cover and CRP, and ~2 times more plausible than the third-best model with only the patch-size effect (Table 3). There was nearly equal support for the second-best model, including the patch size of native land cover and CRP and the third-best model containing only the patch size of native land cover.

TABLE 3. Exploratory model selection for covariate effects on large-scale occupancy (ψ), small-scale occupancy (θ), and detection (*p*) of Lesser Prairie-Chicken. Model-selection metrics are the value of the minimized –2 log-likelihood function, –2log(*L*); number of parameters, *K*; Akaike's Information Criterion adjusted for sample size, AIC_c; difference between model and minimum AIC_c values, ΔAIC_c; and AIC_c weight, w_i. Models with $\Delta AIC_c < 4$ are shown.

Model	−2log(*L*)	*K*	AIC_c	ΔAIC_c	w_i
ψ(patchsize + grazing) θ(CRP + strata) *p*(observer + strata)	576.48	13	603.81	0.00	0.238
ψ(patchsize + CRP) θ(CRP + strata) *p*(observer + strata)	577.86	13	605.18	1.38	0.120
ψ(patchsize) θ(CRP + strata) *p*(observer + strata)	580.47	12	605.60	1.79	0.097
ψ(patchsize + grazing) θ(CRP + strata) *p*(observer)	584.93	10	605.73	1.92	0.091
ψ(patchsize + grazing) θ(CRP + strata) *p*(observer + crew)	581.46	12	606.59	2.79	0.059
ψ(patchsize + grazing) θ(CRP + strata) *p*(observer + hour)	583.81	11	606.77	2.96	0.054
ψ(patchsize + CRP) θ(CRP + strata) *p*(observer)	586.28	10	607.08	3.27	0.046
ψ(patchsize + road) θ(CRP + strata) *p*(observer + strata)	580.37	13	607.70	3.89	0.034
ψ(patchsize) θ(CRP + strata) *p*(observer)	589.06	9	607.71	3.90	0.034

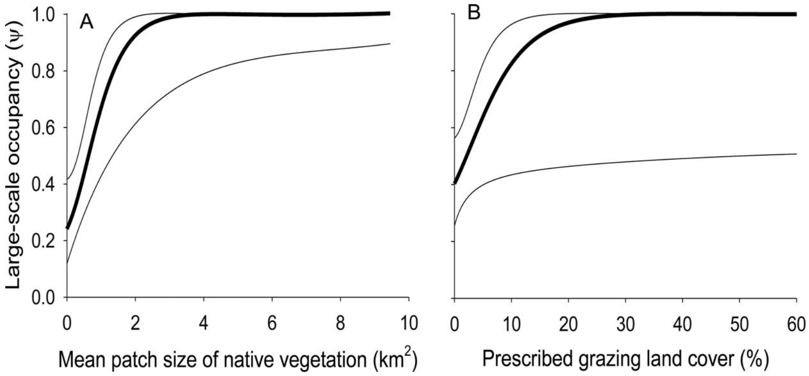

FIGURE 3. Large-scale occupancy rate (ψ) of Lesser Prairie-Chicken in 15 × 15 km grid cells by (**A**) mean patch size of native land cover (patchsize) and (**B**) prescribed-grazing land cover (holding the other covariates at their mean values) in the exploratory analysis. The bold line indicates the model-averaged estimate of large-scale occupancy for the models in Table 5, and the bounding lines are unconditional 90% confidence intervals.

All models with $\Delta\mathrm{AIC_c}$ values <4 included the covariate mean patch size of native land cover (patchsize; Table 3). The large-scale occupancy of the Lesser Prairie-Chicken increased with increasing patch size of native vegetation (Figure 3A) and increasing land cover of prescribed grazing (Figure 3B and Appendix Table 7). The 90% CI for these parameter estimates excluded zero, indicating measurable effect sizes for patch size of native vegetation and prescribed grazing (Appendix Table 7). The large-scale occupancy probability of the Lesser Prairie-Chicken was >0.5 when mean patch size of native land cover was >0.66 km^2 (i.e. holding the other covariates at their mean values; Figure 3A). The 90% CI for the effect of CRP narrowly covered zero, indicating marginal precision in relation to the effect size for this covariate (Appendix Table 7).

Small-scale Occupancy as a Function of Conservation

The best approximating model for small-scale occupancy included the effects of CRP and stratum. The percentage of land enrolled in the CRP practice was in all models with $\Delta\mathrm{AIC_c}$ values <4 (Table 3). The evidence ratio indicated that the top model including the effects of CRP and stratum was 54 times more plausible than the next-best model containing only the effect of stratum ($w_i < 0.01$). Small-scale occupancy increased with increasing land cover of CRP (Figure 4A). The 90% CI for the effects of CRP on small-scale occupancy excluded zero, indicating measurable effect sizes for this covariate (Appendix Table 8). The small-scale occupancy of the Lesser Prairie-Chicken was >0.5 when CRP land cover exceeded 20% of a quadrant in the shortgrass stratum of northwest Kansas (Figure 4A). In addition, small-scale occupancy was greater in the MGPR and SGPR than in the SOPR and SSPR strata, but the MGPR and SGPR strata were not measurably different (Figure 4B). The 90% CIs for the effects of the SOPR and SSPR strata excluded zero, indicating measurable differences in the small-scale occupancy between these strata and the SGPR stratum in

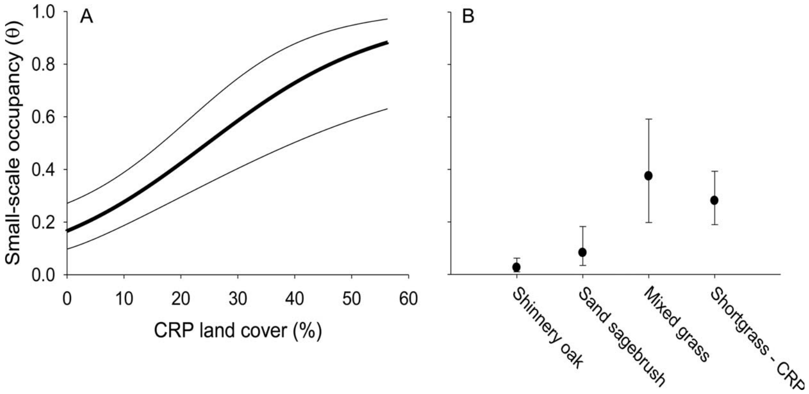

FIGURE 4. Small-scale occupancy rate (θ) of 7.5 × 7.5 km quadrants of Lesser Prairie-Chicken, given occupancy of the 15 × 15 km grid cells by (**A**) Conservation Reserve Program (CRP) land cover within the shortgrass stratum of northwest Kansas and (**B**) stratum at the mean value of CRP land cover in the exploratory analysis. The bold symbols and line indicate the model-averaged estimates of small-scale occupancy from the models in Table 5. The error bars and bounding lines are unconditional 90% confidence intervals.

northwest Kansas (Appendix Table 8). The 90% CIs for the positive effect of MGPR included zero, providing little evidence for a difference in small-scale occupancy in relation to the SGPR stratum in northwest Kansas (Appendix Table 8).

DISCUSSION

Our work provides initial insights into the effectiveness of utilizing established aerial surveys for estimating Lesser Prairie-Chicken occupancy at multiple scales. Our primary findings are threefold: (1) with minor adjustments to how the data are recorded and by subdividing the grid, occupancy could be estimated at multiple scales with reasonable levels of precision; (2) temporal replicates were not cost effective; and (3) an exploratory set of a priori hypotheses were modeled and covariates were identified that helped explain large- and small-scale occupancy. These findings support the conservation concept that broad landscapes and management practices may be effective in maintaining or improving the condition of the landscape (Fuhlendorf et al. 2002).

The multiscale occupancy model assumed that the Lesser Prairie-Chicken was never falsely detected in the course of sampling (MacKenzie et al. 2006, Pavlacky et al. 2012), and this assumption may have been violated in the Shortgrass Prairie–CRP Mosaic stratum of northern Kansas (Figure 1). The ranges of Lesser and Greater prairie-chickens overlapped in the Shortgrass Prairie–CRP Mosaic stratum, and because it was not possible to identify the species from the helicopter, the Lesser Prairie-Chicken may have been falsely detected in this stratum. Falsely detecting Lesser Prairie-Chickens may have resulted in overestimating detection and occupancy in the Shortgrass Prairie–CRP Mosaic stratum. However, ground-truth surveys of Lesser Prairie-Chicken leks were used to adjust the encounter histories using the proportion of Lesser Prairie-Chickens in each survey grid cell (McDonald et al. 2015), and this likely reduced the prevalence of false detections in the stratum. An existing occupancy framework similar to the Nichols et al. (2008) model provides a way to directly account for incomplete detection and misidentification (Miller et al. 2011). This approach is expected to be an improvement over ad hoc approaches to address identification issues but would require model development to add an additional parameter for misidentification (see also Schaefer et al. 2015).

Monitoring both abundance and occupancy provides a comprehensive understanding of the status of the Lesser Prairie-Chicken, including both population size and geographic distribution. The ability to evaluate range contraction and expansion in relation to population size is an important consideration for managing rare species of conservation concern (MacKenzie and Nichols 2004, Noon et al. 2012). In some cases, occupancy estimation may be better suited than abundance estimation for monitoring rare species at large spatial scales, because greater precision of the estimates is expected from a given sample size (MacKenzie and Nichols 2004). For example, an increase in geographic range size with no appreciable change in population density may represent considerable conservation progress for the species. In addition, habitat–occupancy relationships are useful for evaluating the effectiveness of conservation practices and identifying habitat features responsible for range expansion and contraction (Gu and Swihart 2004, MacKenzie 2006).

Spatial or temporal replication can be an important design component when examining relationships of occupancy to landscape variables (MacKenzie and Royle 2005, Guillera-Arroita et al. 2010). We empirically tested whether temporal replicates improved precision in the occupancy estimates. If precision was improved by temporal replication, repeated visits in time would likely need to be added as a design component to future surveys. Forty-five grid cells in the SGPR of northwest Kansas and the SOPR of eastern New Mexico and the western Texas Panhandle of the WAFWA range-wide survey were reflown by a 3-person crew and pilot in an R44 helicopter. The precision of occupancy estimates did not improve appreciably, resulting from temporal replicate surveys of a subset of grid cells. For example, the CV for estimated probability of large-scale occupancy by Lesser Prairie-Chickens decreased by 4%. The CV for estimated probability of small-scale occupancy of quadrants by Lesser Prairie-Chickens when the grid cell was occupied decreased by 8% in the SGPR and by 5% in the SOPR. This subset alone resulted in a 29% increase in monitoring costs to collect the replicated surveys. Thus, we proceeded to examine habitat and conservation relationships to occupancy without further considering temporal replicates.

Our analyses were used to evaluate whether there were adequate detections from the RW-survey to discover ecologically relevant relationships between the derived covariates and the probability of occupancy by Lesser Prairie-Chickens. The covariates were chosen to address biological questions of patch size, the potential role of conservation activity, and anthropogenic disturbance. We are encouraged by the levels of precision and predictability detected in our exploratory modeling; however, exploration of potential interactions between the strata and each natural and anthropogenic covariate was beyond the scope of this analysis. Now that we have demonstrated that our approach is reasonable, a more detailed analysis (i.e. multiyear and larger set of covariates) is underway. For example, we fully expect that the magnitude of effects of patch size of native vegetation and the amount of CRP may differ among the 4 strata. Inclusion of additional covariates

(Appendix Table 4) and their interactions in the candidate models may indicate other correlations with occupancy.

There were measurable and positive effect sizes between mean patch size of native vegetation and probability of occupancy by Lesser Prairie-Chickens in the large-scale grid cells. Ecologically, we recognize that the Lesser Prairie-Chicken is a landscape-scale species (Fuhlendorf et al. 2002, Winder et al. 2015). Our findings suggest that in landscapes with a mean CRP value of 10% and a mean prescribed-grazing value of 3%, and with mean patch size >1.5 km^2, the proportion of occupied grid cells is >0.83. Although minimum patch-size requirements for viability still elude our understanding of Lesser Prairie-Chicken ecology, our results provide an indication of what minimum patch sizes in the landscape may be for a site to at least be occupied.

The strong positive relationship between percent prescribed grazing and probability of occupancy in our modeling is also encouraging, though unexpected at the large scale. This relationship indicates that current conservation investments may be targeted correctly (Bartuszevige and Daniels 2013) and that occupancy is positively related to ongoing conservation practices. Under NRCS's Lesser Prairie-Chicken Initiative (LPCI; USFWS 2011), prescribed grazing is implemented with specific habitat objectives designed to address limiting factors in vegetation structure or heterogeneity for the species. As suggested in the LPCI Conference Report (USFWS 2011), prescribed grazing may play an important, albeit indirect, role in preventing the fragmentation of native vegetation at the landscape scale. The predictions suggested that, at the mean value of patch size (0.67 km^2) and CRP (10%), and with $>15\%$ of a grid under prescribed grazing, the proportion of grid cells occupied by the Lesser Prairie-Chicken was >0.92. At this broad of a scale (225 km^2), these are correlative (albeit strong) relations, not causal, and inference should be tempered accordingly.

CRP is known to provide local and landscape benefits to Lesser Prairie-Chickens (Fields et al 2006, Bartusevige and Daniels 2013). At the scale of 15 × 15 km grid cells, we found large-scale occupancy to be weakly related to proportion of CRP land cover. Thus, our analysis provides some evidence for the additive effect of CRP cover on native-habitat patch size. It appears that native prairie is important and CRP is beneficial at broad scales, but to a lesser degree than CRP is beneficial at the smaller scale. Determining the landscape thresholds and mosaics of these habitats is a critical component of the future conservation of Lesser Prairie-Chickens.

Alternatively, CRP managed land within 7.5 × 7.5 km quadrants was highly related to small-scale probability of occupancy, given that the large-scale grid cell was occupied. The odds ratio for the effect of CRP in the best model indicated that small-scale occupancy by Lesser Prairie-Chickens increased by 12% for every 1% increase in CRP land cover. However, future research is needed to determine the relative effects of CRP in the different strata. Nevertheless, this effect suggests that the addition of CRP land cover increased the proportion of quarter-grids occupied by Lesser Prairie-Chickens beyond the effect of native patch size alone. Locally, CRP fields appear to provide suitable nesting cover and are often juxtaposed to native vegetation that may offer higher-quality brood habitat (Fields et al. 2006). It has been hypothesized that heterogeneity in vegetation structure is of paramount importance for maintaining or improving Lesser Prairie-Chicken population growth rates (Hagen et al. 2009, 2013, Hovick et al. 2014).

We observed large differences among small-scale occupancy probabilities of 7.5 × 7.5 km quadrants by Lesser Prairie-Chickens (given occupancy of the large scale grid cell) in the 4 strata. However, we found little support for differences in large-scale occupancy among the 4 strata. We offer 3 explanations for the absence of stratum effects at the large scale. First, although abundance in the 15 × 15 km grid cells varied by stratum (McDonald et al. 2015), occupancy was expected to correspond more closely with abundance at smaller spatial scales (Noon et al. 2012). As suggested by Noon et al. (2012), the conditional small-scale occupancy of 7.5 × 7.5 km grid cells for the strata corresponded closely to density estimates from the monitoring program (McDonald et al. 2015). Second, because the probability of occupancy increases with increasing area of the sampling unit (MacKenzie et al. 2006), the occupancy of 225 km^2 grid cells was expected to be high even in strata with low density of Lesser Prairie-Chickens. Third, small-scale occupancy measures the probability of availability given that the grid cell was occupied, and p measures the probability of detection given that the small-scale quadrant was occupied. In strata with low density of Lesser Prairie-Chickens, the estimates of large-scale occupancy were adjusted upward to account for situations where Lesser Prairie-Chickens were rare and largely unavailable for sampling on the line transects (Pavlacky et al. 2012).

Conservation Implications

Occupancy models can provide precise estimates for monitoring conservation outcomes from the WAFWA range-wide survey effort. To ensure adequate precision across the species' distribution, our recommendation is to increase the sample size for the number of grid cells surveyed in the 2 low-density strata, the SOPR and SSPR. We make this recommendation on the basis of the following findings. The CV of large-scale occupancy (ψ) was 17%, and estimates of small-scale occupancy (θ) in high-density strata were in an acceptable range, with CVs $\leq 31\%$. The precision of occupancy estimates in low-density strata was marginally improved by resurvey of a subset of the same grid cells in the WAFWA range-wide survey. Increasing the sample size and spatial replication of grid cells will improve the precision of estimates of occupancy and population sizes in the WAFWA range-wide survey of those low-density strata. Finally, there is a body of evidence in the literature, based on simulations, that supports our recommendation. When considering sampling-design trade-offs between sample sizes for temporal and spatial replicates, increasing the sample size of spatial replicates is often more efficient than increasing the number of repeated visits for estimating the probability of occupancy of rare species (Mackenzie and Royle 2005, Guillera-Arroita et al. 2010). Accordingly, an analytic-numeric approximation (Bailey et al. 2007) showed that adding spatial replicates to the Shinnery Oak Prairie and Sand Sage Prairie Region where Lesser Prairie-Chickens were rare was more effective in improving the precision of the occupancy estimates than increasing temporal replicates (D. C. Pavlacky personal observation).

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APPENDIX TABLE 4. Descriptions, data sources, and means and ranges of measurements for 15 × 15 km grid cells in the sampling frame for the 2015 WAFWA range-wide Lesser Prairie-Chicken survey. In addition to measurements within 15 × 15 km grid cells, we obtained the same measures within 7.5 × 7.5 km quadrants and 7.5 × 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 New Mexico	0.35 (0.00–0.81 *P*)
CRP	Proportion of Conservation Reserve Program (CRP) land cover within the grid cell	PLJV land cover updated for 2015, SW ReGAP in western New Mexico	0.10 (0.00–0.40 *P*)
Mixed grass	Proportion of mixed-grass prairie land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.12 (0.00–0.80 *P*)
Pasture	Proportion of agricultural pasture land cover within the grid cell	PLJV land cover	0.07 (0.00–0.34 *P*)
Shortgrass	Proportion of shortgrass-prairie land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.15 (0.00–0.90 *P*)
Tallgrass	Proportion of tallgrass-prairie land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	$<$0.01 (0.00–0.05 *P*)
Grassland	Proportion of total grassland land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.34 (0.01–0.90 *P*)
Brush management	Percentage of brush management (practice 314) land cover within the grid cell	NRCS spatial database	0.58 (0.00–11.6%)
Core practice	Mean percentage of prescribed grazing (practice 528) and upland wildlife habitat management (practice 645) land cover within the grid cell	NRCS spatial database	2.30 (0.00–85.5%)
Prescribed burning	Percentage of prescribed burning (practice 338) land cover within the grid cell	NRCS spatial database	0.04 (0.00–2.2%)
Prescribed grazing	Percentage of prescribed grazing (practice 528) land cover within the grid cell	NRCS spatial database	2.88 (0.00–80.6%)
Upland habitat	Percentage of upland wildlife habitat management (practice 645) land cover within the grid cell	NRCS spatial database	1.72 (0.00–90.3%)
General patch size	Mean patch size of general habitat, including native land cover, CRP, and pasture, within the grid cell.	PLJV land cover, SW ReGAP in western New Mexico	0.66 (0.00–13.7 km^2)
Grassland patch size	Mean patch size of grassland within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.40 (0.01–24.6 km^2)
Native patch size	Mean patch size of native vegetation within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.67 (0.00–9.4 km^2)
Major road density	Density of major roads within the grid cell	TIGER/Line road layer, U.S. Census Bureau (2014)	1.28 (0.20–3.1 km^{-1})
Minor road density	Density of minor roads within the grid cell	TIGER/Line road layer, U.S. Census Bureau (2014)	0.10 (0.00–0.6 km^{-1})
Total road density	Density of all roads within the grid cell	TIGER/Line road layer, U.S. Census Bureau (2014)	1.38 (0.20–3.8 km^{-1})
Mesquite shrubland	Proportion of mesquite shrubland ($>$25% canopy cover) land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.01 (0.00–0.68 *P*)
Mesquite savanna	Proportion of mesquite savanna ($<$25% canopy cover) land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.02 (0.00–0.62 *P*)
Shinnery oak shrubland	Proportion of shinnery oak shrubland land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.04 (0.00–0.69 *P*)
Sand sage shrubland	Proportion of sand sage shrubland land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.07 (0.00–0.58 *P*)
Total shrubland	Proportion of total shrubland land cover excluding mesquite shrubland within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	0.13 (0.00–0.96 *P*)
Pinyon–juniper woodland	Proportion of pinyon–juniper woodland land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	$<$0.01 (0.00–0.07 *P*)
Redcedar woodland	Proportion of redcedar woodland land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	$<$0.01 (0.00–0.03 *P*)
Total woodland	Proportion of total woodland land cover within the grid cell	PLJV land cover, SW ReGAP in western New Mexico	$<$0.01 (0.00–0.08 *P*)

APPENDIX TABLE 5. Parameter estimates, standard error (SE), lower and upper 90% confidence limits (LCL and UCL, respectively), and coefficients of variation (CV) for large-scale occupancy (ψ), small-scale occupancy (θ), and detection (p) from the top model of the RW-survey analysis.

Parameter	Estimate	SE	LCL	UCL	CV
ψ(.)	0.336	0.056	0.250	0.434	0.167
θ(SGPR)	0.307	0.064	0.212	0.422	0.210
θ(MGPR)	0.371	0.114	0.209	0.569	0.307
θ(SSPR)	0.145	0.062	0.069	0.279	0.426
θ(SOPR)	0.055	0.029	0.023	0.127	0.520
p(SGPR—front)	0.638	0.086	0.488	0.765	0.135
p(SGPR—back)	0.866	0.054	0.749	0.934	0.063
p(MGPR—front)	0.276	0.094	0.149	0.454	0.342
p(MGPR—back)	0.583	0.134	0.361	0.777	0.230
p(SSPR—front)	0.389	0.169	0.164	0.673	0.435
p(SSPR—back)	0.700	0.161	0.398	0.892	0.230
p(SOPR—front)	0.459	0.228	0.158	0.794	0.496
p(SOPR—back)	0.757	0.177	0.390	0.938	0.233

APPENDIX TABLE 6. Parameter estimates, standard error (SE), lower and upper 90% confidence limits (LCL and UCL, respectively), and coefficients of variation (CV) for large-scale occupancy (ψ), small-scale occupancy (θ), and detection (p) from the top model of the RW-survey analysis and the combined RW-survey and REP-survey analysis.

Parameter	Estimate	SE	LCL	UCL	CV
RW-survey					
ψ(.)	0.353	0.081	0.233	0.494	0.229
θ(SGPR)	0.306	0.072	0.201	0.436	0.235
θ(SOPR)	0.049	0.025	0.020	0.112	0.515
p(observer—front)	0.645	0.086	0.495	0.772	0.133
p(observer—back)	0.800	0.080	0.637	0.902	0.100
RW-survey and REP-survey					
ψ(.)	0.346	0.076	0.233	0.479	0.220
θ(SGPR)	0.331	0.074	0.222	0.461	0.222
θ(SOPR)	0.061	0.029	0.027	0.131	0.475
p(survey—RW)	0.670	0.067	0.552	0.770	0.100
p(survey—REP)	0.223	0.055	0.145	0.327	0.248

APPENDIX TABLE 7. Beta parameter estimates, standard error (SE), and lower and upper 90% confidence limits (LCL and UCL, respectively) for large-scale occupancy (ψ) for models within <2 ΔAIC_c values of the top model in this exploratory analysis. Coefficients for small-scale occupancy (θ) and detection (p) are not shown. The covariates are the mean patch size of native land cover (patchsize), land cover of the prescribed grazing practice (grazing), and land cover of the Conservation Reserve Program (CRP).

Model parameter	Estimate	SE	LCL	UCL
ψ(patchsize + grazing) θ(CRP + strata) p(observer + strata)				
Intercept	−1.57	0.39	−2.21	−0.93
Patchsize	1.73	0.73	0.53	2.93
Grazing	0.19	0.11	0.00	0.39
ψ(patchsize + CRP) θ(CRP + strata) p(observer + strata)				
Intercept	−2.10	0.55	−3.01	−1.19
Patchsize	2.19	0.77	0.92	3.46
CRP	5.64	3.64	−0.36	11.64
ψ(patchsize) θ(CRP + strata) p(observer + strata)				
Intercept	−1.41	0.37	−2.03	−0.79
Patchsize	2.03	0.78	0.75	3.32
ψ(patchsize + grazing) θ(CRP + strata) p(observer)				
Intercept	−1.57	0.39	−2.21	−0.93
Patchsize	1.73	0.73	0.53	2.94
Grazing	0.20	0.12	0.00	0.40

APPENDIX TABLE 8. Beta parameter estimates, standard error (SE), and lower and upper 90% confidence limits (LCL and UCL, respectively) for small-scale occupancy (θ) for models within <2 ΔAIC_c values of the top model in this exploratory analysis. Coefficients for large-scale occupancy (ψ) and detection (p) are not shown. The covariates are the land cover of the Conservation Reserve Program (CRP), and the levels of the strata factor are Shinnery Oak Prairie Region (SOPR), Sand Sagebrush Prairie Region (SSPR), Mixed Grass Prairie Region (MGPR), and Shortgrass–CRP Mosaic Prairie Region (SGPR).

Model parameter	Estimate	SE	LCL	UCL
ψ(patchsize + grazing) θ(CRP + strata) p(observer + strata)				
Intercept	−1.68	0.35	−2.27	−1.10
CRP	7.08	1.61	4.42	9.73
Strata—MGPR	0.40	0.54	−0.49	1.29
Strata—SSPR	−1.37	0.60	−2.36	−0.39
Strata—SOPR	−2.72	0.62	−3.74	−1.70
ψ(patchsize + CRP) θ(CRP + strata) p(observer + strata)				
Intercept	−1.46	0.38	−2.08	−0.83
CRP	5.13	1.75	2.25	8.00
Strata—MGPR	0.69	0.60	−0.30	1.67
Strata—SSPR	−1.64	0.55	−2.55	−0.72
Strata—SOPR	−2.74	0.61	−3.75	−1.72
ψ(patchsize) θ(CRP + strata) p(observer + strata)				
Intercept	−1.72	0.36	−2.31	−1.13
CRP	6.71	1.58	4.11	9.31
Strata—MGPR	0.66	0.57	−0.28	1.60
Strata—SSPR	−1.45	0.57	−2.39	−0.50
Strata—SOPR	−2.53	0.61	−3.54	−1.51
ψ(patchsize + grazing) θ(CRP + strata) p(observer)				
Intercept	−1.54	0.36	−2.14	−0.94
CRP	6.79	1.55	4.24	9.35
Strata—MGPR	−0.11	0.41	−0.79	0.57
Strata—SSPR	−1.59	0.54	−2.48	−0.70
Strata—SOPR	−2.82	0.59	−3.80	−1.85