Impacts of Mesquite Distribution on Seasonal Space Use of Lesser Prairie-Chickens ☆

Authors: Boggie, Matthew A., Strong, Cody R., Lusk, Daniel, Carleton, Scott A., Gould, William R., et al.

Impacts of Mesquite Distribution on Seasonal Space Use of Lesser Prairie-Chickens ☆

Matthew A. Boggie [a,*], Cody R. Strong [b], Daniel Lusk [b], Scott A. Carleton [c], William R. Gould [d], Randy L. Howard [e], Clay Nichols [f], Michael Falkowski [g], Christian Hagen [h]

[a] Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA
[b] Fish, Wildlife, and Conservation Ecology, New Mexico State University, Las Cruces, NM 88003, USA
[c] US Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces, NM 88003, USA
[d] College of Business, New Mexico State University, Las Cruces, NM 88003, USA
[e] Bureau of Land Management, Roswell, NM 88201, USA
[f] US Fish and Wildlife Service, Arlington, TX 76006, USA
[g] Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80523, USA
[h] Oregon State University, Bend, OR 97702, USA.

ARTICLE INFO

ABSTRACT

Loss of native grasslands by anthropogenic disturbances has reduced availability and connectivity of habitat for many grassland species. A primary threat to contiguous grasslands is the encroachment of woody vegetation, which is spurred by disturbances that take on many forms from energy development, fire suppression, and grazing. These disturbances are exacerbated by natural- and human-driven cycles of changes in climate punctuated by drought and desertification conditions. Encroachment of honey mesquite (Prosopis glandulosa) into the prairies of southeastern New Mexico has potentially limited habitat for numerous grassland species, including lesser prairie-chickens (Tympanuchus pallidicinctus). To determine the magnitude of impacts of distribution of mesquite and how lesser prairie-chickens respond to mesquite presence on the landscape in southeastern New Mexico, we evaluated seasonal space use of lesser prairie-chickens in the breeding and nonbreeding seasons. We derived several remotely sensed spatial metrics to characterize the distribution of mesquite. We then used these data to create population-level resource utilization functions and predict intensity of use of lesser prairie-chickens across our study area. Home ranges were smaller in the breeding season compared with the nonbreeding season; however, habitat use was similar across seasons. During both seasons, lesser prairie-chickens used areas closer to leks and largely avoided areas with mesquite. Relative to the breeding season, during the nonbreeding season habitat use suggested a marginal increase in mesquite within areas of low intensity of use, yet aversion to mesquite was strong in areas of medium to high intensity of use. To our knowledge, our study is the first to demonstrate a negative behavioral response by lesser prairie-chickens to woody encroachment in native grasslands. To mitigate one of the possible limiting factors for lesser prairie-chickens, we suggest future conservation strategies be employed by land managers to reduce mesquite abundance in the southern portion of their current range.

Introduction

Before European settlement, the central Great Plains were largely unbroken prairies. Since that time, the contemporary Great Plains have been heavily fragmented and the natural processes that once maintained their structure have been disrupted by encroachment of woody shrubs, anthropogenic disturbances, and changes in climate (Brown, 1989; Engle et al., 2008). These impacts, which are manifested in habitat fragmentation and degradation, are key threats to species that rely on prairie ecosystems (Heimlich and Kula, 1991; Vickery et al., 1999). Furthermore, interactions between natural and anthropogenic disturbances can exacerbate the encroachment of woody shrubs and differences in soil and site fertility make some environments more vulnerable to shrub encroachment than others (Fuhlendorf et al., 2008).

Several woody shrub species that exhibit high rates of encroachment on grasslands are honey mesquite (Prosopis glandulosa, hereafter mesquite) and eastern redcedar (Juniperus virginiana). Across the Great Plains, eastern redcedar encroachment appears to be the greatest species of concern in northern and eastern regions, whereas mesquite is the

greatest species of concern in southern regions (Falkowski et al., 2017-this issue). The dynamics of historic and current encroachment of mesquite in the southern Great Plains, particularly New Mexico, are poorly described and understood. Potential factors contributing to contemporary mesquite expansion in New Mexico include fire suppression, livestock grazing, and changes in climate (Hastings and Turner, 1965; Neilson, 1986; Brown, 1989; Fredrickson et al., 1998; Fredrickson et al., 2005).

Mesquite has expanded into or contracted from the grasslands of New Mexico in response to drought and desertification interceded by periods of cooling (Fredrickson et al., 1998). At the time of European settlement, New Mexico was characterized primarily by a grassland prairie ecosystem but has been slowly encroached by woody shrubs since (Humphrey, 1958; Fredrickson et al., 1998). The widespread dispersal of mesquite in New Mexico following European settlement is believed to have occurred primarily via seed dispersal by livestock (Fredrickson et al., 1998, 2005). Mesquite seeds are resilient to digestion and are actively dispersed by domesticated animals such as cattle, sheep, and goats (Kneuper et al., 2003). The Camino Real, a primary road for European settlers to cross the Jornada del Muerto of New Mexico, is still visible in satellite imagery due to the high density and prominence of mesquite on the historical route. The thick mesquite cover is a legacy of European settlers and their livestock (Fredrickson et al., 2005). Dispersal of seeds by livestock, lack of fire, and changing climate patterns that promote mesquite prevalence has resulted in widespread distribution of mesquite in New Mexico (Brown, 1989).

Previous work has documented the abiotic and biotic impacts that mesquite encroachment has on ecosystem processes. Mesquite alters carbon and nitrogen dynamics of the environments it invades and fundamentally changes soil bacteria and fungi, thereby altering patterns of litter decomposition (Throop and Archer, 2007; Creamer et al., 2011; Hollister et al., 2010). Mesquite presence decreases near-surface temperatures relative to native grasslands (Beltran-Przekurat et al., 2008), increases evapotranspiration (Nie et al., 2012), outcompetes other desert plants with its comparatively deep root structure, and increases spatial heterogeneity in respiration (Cable et al., 2012). Moreover, mesquite decreases both perennial grass and herbaceous biomass and reduces forage for both wildlife and livestock (Teague et al., 2008; Mohamed et al., 2011).

The impacts of mesquite encroachment are far encompassing and complex, and the full magnitude of these effects is still unclear. As encroachment of woody plants increases across grasslands, birds that depend on grasslands can suffer a steady decline in available habitat (Lloyd et al., 1998; Peterjohn and Sauer, 1999; Herkert et al., 2003). Encroachment of woody plants also fragments habitat, resulting in the decline of many grassland-obligate birds (Coppedge et al., 2001). Lesser prairie-chickens *(Tympanuchus pallidicinctus),* for example, are a species of conservation concern that require large contiguous blocks of grassland environments (Woodward et al., 2001).

Mesquite encroachment has been identified as degrading or potentially limiting habitat availability for lesser prairie-chickens across their contemporary range (Van Pelt et al., 2013; USDA, 2014). Few studies, however, have attempted to quantify these effects, even though the impact of mesquite is of special importance to management and conservation of lesser prairie-chickens in New Mexico (Hunt and Best, 2010; Behney et al., 2012). Conversion to a mesquite-dominated landscape is thought to ultimately be unsuitable for lesser prairie-chickens. Moreover, once established, the vertical vegetation structure of mesquite may provide predator perches (Fuhlendorf et al., 2002; Hagen et al., 2004). Predator avoidance may impact use of an environment by avian species, and individuals may modulate their use on the basis of the perception of predation risk (Thomson et al., 2006). Predatory birds, for example, are more abundant in areas containing mesquite than areas lacking mesquite within environments occupied by lesser prairie-chickens (Behney et al., 2012). It is speculated that lesser prairie-chickens may avoid areas because of perceived higher predation risk due to the presence of predatory birds (Behney et al., 2012). Despite active research into many impacts of mesquite encroachment, the relationship between mesquite presence and patterns of seasonal use of habitat by lesser prairie-chickens is unknown.

Understanding the relationship between distribution of mesquite and habitat used by lesser prairie-chickens is important for conservation strategies that consider the negative effects of mesquite presence and/or aim to minimize further loss of habitat. Our goals were to use resource utilization functions (Marzluff et al., 2004; Kertson et al., 2011) to evaluate how mesquite distribution and the seasonal abscission of the foliage of mesquite mediated the use of habitat by lesser prairie-chickens in the breeding and nonbreeding season.

Methods

Study Area

Our study area encompasses 1,147 km^2 and is composed of two properties administered by the Bureau of Land Management and a complex of private and state holdings surrounding these properties in Chaves and Lea counties (Fig. 1). The Sand Ranch and Mescalero Sands Area of Critical Environmental Concern are located north and south of Highway 380 near Caprock, New Mexico. Both areas have a history of disturbance in the form of herbicidal treatments, wildfire, grazing, and low levels of energy development. Broadly, the study area is composed of two diverse mosaics of primarily shinnery oak *(Quercus havardii)* prairie-dominated sandhills and sandy plains (Pettit, 1979; Doerr and Guthery, 1983; Smythe, 2006).

Capture and Radiotelemetry

We captured male and female lesser prairie-chickens during the breeding season from March through May of 2013 and 2014. During morning hours, we used 12 x 12 m pulley-operated or magnet-operated drop nets (Wildlife Capture Services LLC, Flagstaff, AZ), whoosh nets (Hawkseye Nets, Virginia Beach, VA), and walk-in funnel traps (Haukos and Smith, 1989) to capture birds on leks (i.e., communal breeding grounds). Whoosh nets were composed of 13.7 × 4.6 m mesh nets propelled from a ground-level position by bungie cords. Walk-in traps were a series of chicken wire enclosures connected by fencing, where birds are funneled toward a conical wire doorway (Haukos and Smith, 1989).

Once captured, we aged, sexed, weighed, and fitted birds with very high frequency (VHF) or satellite transmitters. We used barring on their 9th and 10th primaries to age birds and pinnae feather length and eye comb color to determine sex (Copelin, 1963; Toole, 2005). We used a necklace-style harness with a durable string looped to attach VHF transmitters to captured birds (American Wildlife Enterprises, Monticello, FL). We used a backpack harness design to attach satellite transmitters (22-g, solar-powered PTT-100 models Microwave Telemetry, Columbia, MD) composed of Teflon ribbon and crimps fashioned from copper pipe to secure the ligature. GPS fixes from satellite transmitters were transmitted every 2 h, for a total of 12 transmissions per day.

We used triangulation to locate radio-tagged birds with azimuths taken <60 min apart to limit error due to movement (Kenward, 2001). We used receivers (Model R1000 Communications Specialists Telemetry Receivers, Orange, CA) and dipole yagis to assist in preliminary location of birds and then three-element yagis to estimate the precise location of birds. We used Global Positioning System (GPS) units (Garmin eTrex30 GPS, Olathe, KS) to obtain Universal Transverse Mercator (UTM) coordinates for observer locations of birds. Any bird whose location was unchanged for ≥2 days was walked-up on and visually verified if it was alive or dead. We collected locations for females daily during the breeding season and males at least two to three times a week. Following the breeding season, we located males and females two to three times per week. We used Location of a Signal (LOAS, Ecological Software Solutions LLC, Hegymagas, Hungary) to process telemetry azimuths and triangulations. We censored any triangulated locations with error
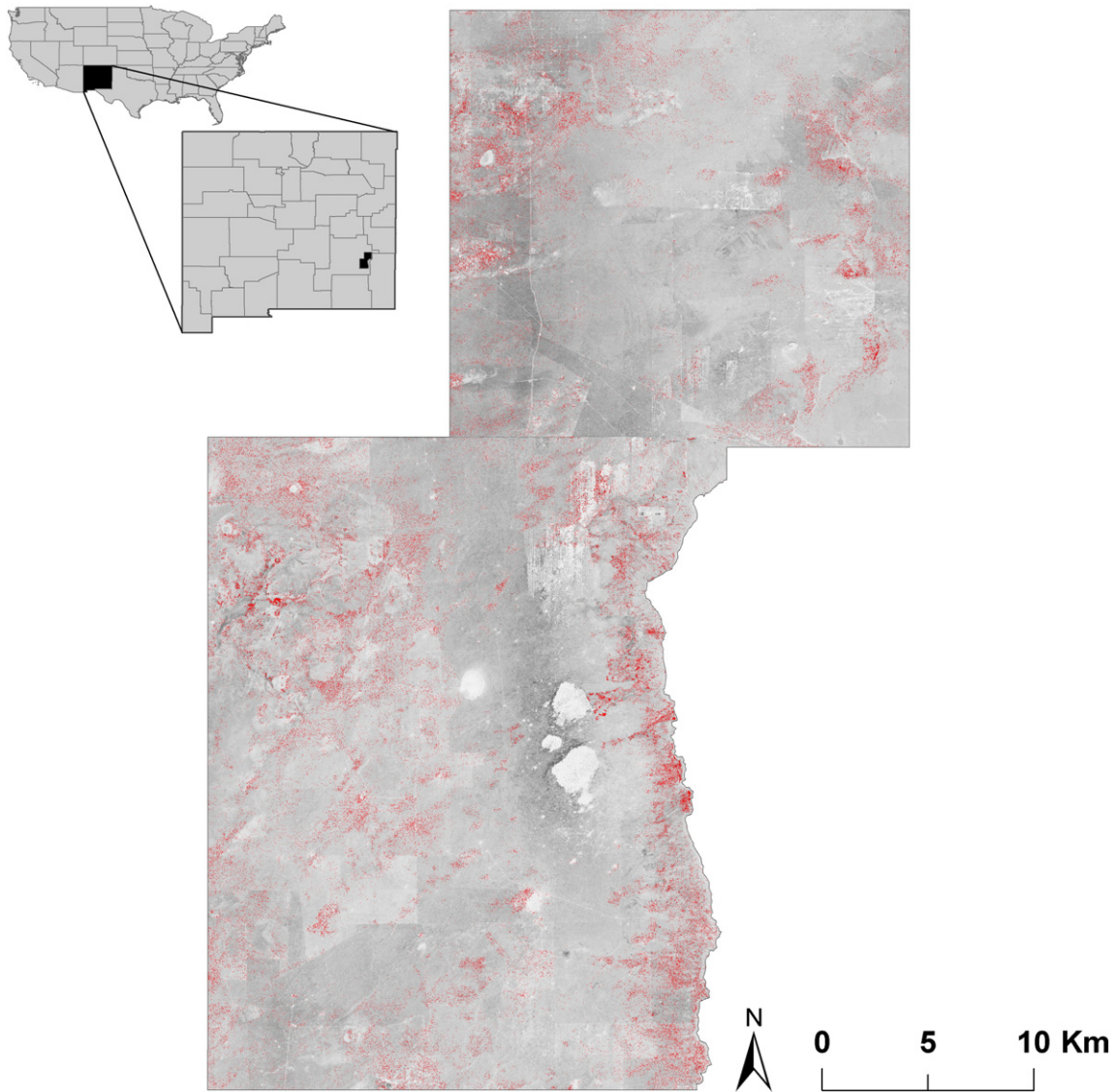
Figure 1. Study area in southeastern New Mexico, located in Chaves and Lea Counties, with mesquite plant distribution digitized in red.

ellipses ≥ 10 000 m². We stored georeferenced locations in a geodatabase in ArcGIS v10.2 (ESRI, Redlands, CA). During the lekking season, locations for males were determined in the late morning or afternoon after lekking activity had ceased. Locations for nesting hens included both repeated nest site locations and locations when she was away from the nest. Because hen movements typically occurred at sunrise and near sunset, tracking schedules did not always allow for locating hens at those times (Winder et al., 2014).

Estimating Utilization Distributions

To evaluate seasonal space use, we estimated utilization distributions for each bird during the breeding (March – August) and nonbreeding (September – February) season. The utilization distribution (i.e., home range) is a probability density function representing differential space use or probability of occurrence (Marzluff et al., 2004; Sandercock et al., 2015). To estimate seasonal home ranges of birds, we used the 95% fixed kernel method. We used likelihood cross-validation as the smoothing parameter because it generally outperforms and is less biased than other frequently used smoothing parameters such as least-squares cross-validation (Horne and Garton, 2006). We created home ranges in the Geospatial Modelling Environment (Beyer, 2012). Each home range had a spatial resolution of 30 m. We used two sample *t*-tests to

determine if sizes of home ranges differed between the breeding and nonbreeding seasons.

Derivation of Spatial Layers

To characterize landscape conditions within utilization distributions, we created several spatial metrics that we hypothesized would likely describe how lesser prairie-chickens used the landscape. We derived a spatial layer for mesquite canopy that represented the extent of mesquite canopy within the study area. We used multiband (blue, green, red, and near infrared) 1-m resolution digital ortho-photographs acquired from the National Agriculture Imagery Program (NAIP) to map the locations of crown diameters of mesquite bushes in the study area. NAIP imagery is flown during the agriculture growing season. The NAIP imagery we used was captured in May and June of 2011. From the imagery we calculated the normalized difference vegetation index (NDVI; a normalized ratio between the red and near infrared image bands), which enhances image sensitivity to photosynthetically active vegetation (Tucker, 1979). We used image segmentation and classification procedures in eCognition (Trimble, 2013) to extract individual mesquite locations and derive a binary mesquite canopy cover map of NDVI images. We performed multiresolution segmentation at multiple scales and used a combination of texture, geometry, layer values, and

NDVI thresholds to classify image objects. Errors of misclassification were edited manually within the software environment. We then used the cover map for binary mesquite canopy to estimate canopy cover. We applied a moving window that was 0.404 ha (1 acre) in size and classified canopy cover of mesquite into seven classes (0 = < 1%, 1 = 1 − 5%, 2 = 5 − 10%, 3 = 10 − 15%, 4 = 15 − 30%, 5 = 30 − 50%, 6 = > 50%). To validate and assess accuracy of the derived canopy layer, we systematically sampled 32 locations of mesquite encroachment in the study area approximately 5 yr following acquisition of the NAIP imagery. We established plots in the 32 locations that were 404 m^2 and measured the diameter at breast height, as well as crown diameters of all mesquite bushes within each plot. We recorded the plot centers with a high-precision GPS unit and measured distance and azimuth of each mesquite bush from each plot center. We used these data to create a set of field validation data represented by a stem map of each plot and calculated plot-level canopy cover. We then compared the derived mesquite canopy cover layer to the field validation data and used a confusion matrix and standard accuracy statistics. Overall accuracy for derived mesquite canopy cover was 63% (Falkowski et al., 2017-this issue).

We also created a spatial layer that represented the distance to mesquite present within the study area by converting the binary mesquite canopy layer to a Euclidean distance layer with each pixel within the raster representing the distance to the nearest mesquite bush. Similarly, we created a Euclidean distance layer for distance to nearest leks within the study area. Previous studies have shown a strong association between space use and habitat use by lesser prairie-chickens and proximity to leks (Winder et al., 2014, 2015). We used ArcGIS v10.2 (ESRI, Redlands, CA) to derive Euclidean distance layers. The resolution of all spatial layers matched the 30-m resolution of utilization distributions.

Resource Utilization Functions

We used resource utilization functions to evaluate resource use of lesser prairie-chickens within utilization distributions (corresponds to third-order scale, sensu Johnson, 1980) and to identify how mesquite presence and other important landscape features contribute to patterns of habitat use (Marzluff et al., 2004; Millspaugh et al., 2006; Kertson et al., 2011). In contrast to conventional resource selection functions, resource utilization functions consider the utilization distribution of an animal as the sampling unit rather than individual locations (Kertson et al., 2011). Furthermore, resource utilization functions offer the ability to quantify interanimal variation, have high power to detect use of resources, and reduce potential sources of error associated with evaluating habitat use only on location points (Marzluff et al., 2004). In resource utilization functions, the selected isopleth level of the home range defines the area available to the animal (Marzluff et al., 2004; Sandercock et al., 2015). Our methods to generate the data needed for the analysis of resource utilization functions were consistent with previous studies (Marzluff et al., 2004; Kertson and Marzluff, 2011; Kertson et al., 2011; Winder et al., 2014). We defined the area used by birds as the 95% isopleth of the home ranges. For each bird we generated a 95% volume polygon, which is the spatially explicit area that contains 95% of the volume of the probability density represented by the utilization distribution. We then generated raster grids of utilization distributions with rescaled utilization distribution values between 1 (lowest intensity of use) and 95 (highest intensity of use), which corresponded to the height of the utilization distribution at a given pixel. To assess the influence of mesquite on seasonal habitat use and the presence of leks at each pixel within the utilization distribution, we generated a uniform sampling grid for each utilization distribution such that each pixel received a sample point. We then extracted values of the utilization distribution and the three spatial layers we derived (mesquite canopy, distance to mesquite, distance to lek) for each pixel within the utilization distribution of each bird. Derived spatial layers were limited to those previously listed because the study area has only one gravel road, <5 two-track roads, no energy development, and no powerline distribution poles or lines, and most fences had been

removed. Thus, we included the landscape-level structures that might be influencing patterns of seasonal space use.

Although the mesquite canopy layer was created during the growing period of mesquite that coincides with the breeding season, we were interested to see what effect mesquite presence had on habitat use in the nonbreeding season. With mesquite bushes being partially defoliated during later periods in the nonbreeding season, the mesquite canopy layer potentially overestimates the canopy cover of mesquite in the nonbreeding season. This provides a unique opportunity to investigate if seasonal habitat use by lesser prairie-chickens is influenced by only mesquite presence or if the canopy cover of mesquite is influencing seasonal habitat use. If lesser prairie-chickens avoid mesquite in both seasons, we would expect to see a negative relationship between habitat use and mesquite canopy and distance to mesquite in both seasons. If lesser prairie-chickens are avoiding areas with high canopy cover of mesquite, but not mesquite presence per se, we would expect to see a stronger negative relationship between habitat use and distance to mesquite in the breeding season compared with the nonbreeding season and a positive relationship between habitat use and mesquite canopy in the nonbreeding season as birds would likely use areas avoided in the breeding season because of the absence of mesquite canopy. Moreover, in the nonbreeding season the relationship between distance to mesquite and habitat use would be less negative as birds are incorporating areas with mesquite within areas of habitat use because use is not obviated by canopy cover of mesquite bushes.

We used the RUF package in Program R (version 3.2.0, R Foundation for Statistical Computing, Vienna, Austria) to estimate individual and population-level resource utilization functions. The multiple regression function in the RUF package uses a maximum likelihood approach to estimate regression coefficients and uses a Matern covariance structure to account for spatial autocorrelation among pixel values. The response variable in the models was the rescaled pixel values of the utilization distribution (values ranging between 1 and 95), and the explanatory variables or covariates were the pixel values for the three spatial layers representing mesquite canopy cover, distances to mesquite, and distance to leks. We log transformed the rescaled utilization distribution values to meet assumptions of normality and homogeneity of variance (Hooten et al., 2013). To make population-level inferences for each covariate in the resource utilization functions, we averaged standardized coefficients across all individuals and computed variance estimates for the averaged standardized coefficients that accounted for interanimal variability (Marzluff et al., 2004). Because two of the covariates in our model were proximity measures, the interpretation of a positive coefficient for proximity measures suggested an increase in use with greater distance from the landscape metric (i.e., avoidance) and a negative coefficient for proximity measures suggested a decrease in use with greater distance from the landscape metric (i.e., selection).

Males and females were represented in our sample in the breeding and nonbreeding seasons, but our sample was skewed toward males, particularly in the nonbreeding season (males = 20, females = 6), but also in the breeding season (males = 14, females = 10). Consequently, because of our small sample size of females, we did not attempt to make comparisons between sexes in our resource utilization functions. Thus, we pooled standardized coefficients across sexes for the breeding and nonbreeding season to make population-level inferences. We did, however, evaluate the effect of season on the resource utilization functions.

We averaged unstandardized coefficients across all individual resource utilization functions to derive a map of predicted intensity of use by lesser prairie-chickens within our study area. We used the predicted equation for the averaged, unstandardized coefficients representing the population-level resource utilization functions to predict intensity of use for each pixel of the study area that accounted for mesquite canopy cover, distance to mesquite, and distance to lek. To evaluate the predictive performance of our population-level resource utilization function, we used k-fold cross-validation (Boyce et al., 2002). We used five folds, and for each iteration, we randomly selected 75% of

the individuals as a training set, estimated their resource utilization functions and averaged their unstandardized coefficients, predicted their intensity of use, and binned the predicted values into 10 bins. We then used the remaining 25% of individuals as our validation set and used Spearman's rank correlation (r_s) to compare the frequencies of observed values of intensity of use in our validation set that fell within the 10 bins of predicted intensity of use. If our model was a good predictor of intensity of use, we would expect a strong positive correlation as the frequencies of predicted values from the validation set would closely correspond to those of observed frequencies of intensity of use.

To complement the resource utilization functions, we estimated a proximity metric for mesquite and lek. We measured the distance to nearest lek and mesquite from the centroid of the 1% isopleth of utilization distributions for each bird. The 1% isopleth represents the volume of the utilization distribution with the highest intensity of use and an area where birds concentrate their use. We used two sample *t*-tests to determine if distances to lek and mesquite from centroid of 1% isopleth differed by season.

Results

Sizes of Home Range

We captured and radio-tagged 40 birds during the breeding season and nonbreeding season in 2013 (males = 8, females = 7) and 2014 (males = 18, females = 7). We only used birds with ≥ 15 relocations during a season. In 2014, four birds were fitted with satellite transmitters
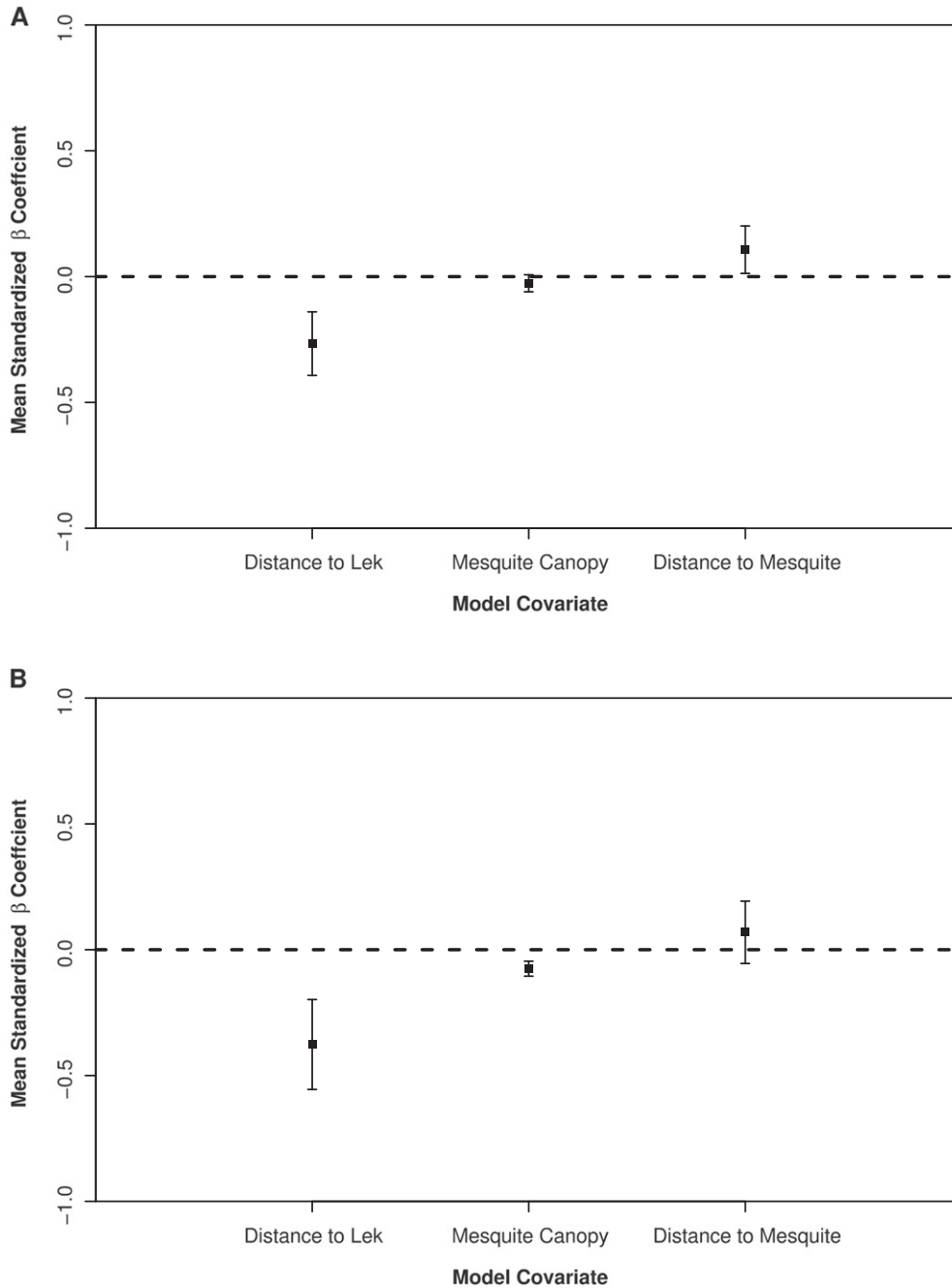
Figure 2. Mean standardized coefficients and 95% confidence intervals for the population-level resource utilization function for lesser prairie-chickens in the (A) breeding and (B) nonbreeding season in southeastern New Mexico reveal that birds are closely associated with lek locations (negative mean standardized β coefficients) and avoid areas with mesquite (positive mean standardized β coefficients) and high mesquite canopy cover (negative mean standardized β coefficients).

and their data were subsampled across both seasons and within week and time of day to match the average number of relocations for birds tagged with VHF transmitters. Size of home ranges were different between seasons ($t_{48} = 3.31$, $P = 0.001$), smaller in the breeding season (8.3 ± 1.4 km^2, mean $\pm$ SE) compared with the nonbreeding season (15.9 ± 1.8 km^2).

Resource Utilization Functions

We developed resource utilization functions for 24 birds in the breeding season (males = 14, females = 10) and 26 birds in the nonbreeding season (males = 20, females = 6). The number of pixels in each utilization distribution used in the resource utilization functions ranged from 668 to 35,536 in the breeding season and 5,083 to 42,399 in the nonbreeding season. The population-level resource utilization functions for both the breeding and nonbreeding seasons were similar. On average, birds in both seasons had a higher probability of using areas closer to leks, farther away from mesquite, and areas with lower mesquite canopy cover (Fig. 2). The averaged unstandardized coefficients for distance to

leks were similar for both seasons, and 95% confidence intervals did not overlap zero. The 95% confidence intervals for distance to mesquite for the breeding season did not overlap zero but slightly overlapped zero in the nonbreeding season. Similarly, in the nonbreeding season the 95% confidence interval for mesquite canopy did not overlap zero but slightly overlapped zero in the breeding season (see Fig. 2). The averaged, unstandardized coefficients, however, for mesquite canopy and distance to mesquite in both seasons were negative and positive, respectively, indicating general seasonal avoidance of areas with mesquite.

We created a single population-level resource utilization function that represented both seasons because of the similarity between the averaged standardized coefficients between seasons. We used this resource utilization function to predict intensity of use within the study area (Fig. 3). Our results from the k-fold cross-validation indicated that the predictive performance of our population-level resource utilization function was high and observed use was highly correlated with predicted use within the study area ($r_s = 0.95$, $P = < 0.0001$).

Average distance to nearest lek site from the centroid of the 1% isopleth in the breeding season (973.5 ± 140.9 m) and nonbreeding
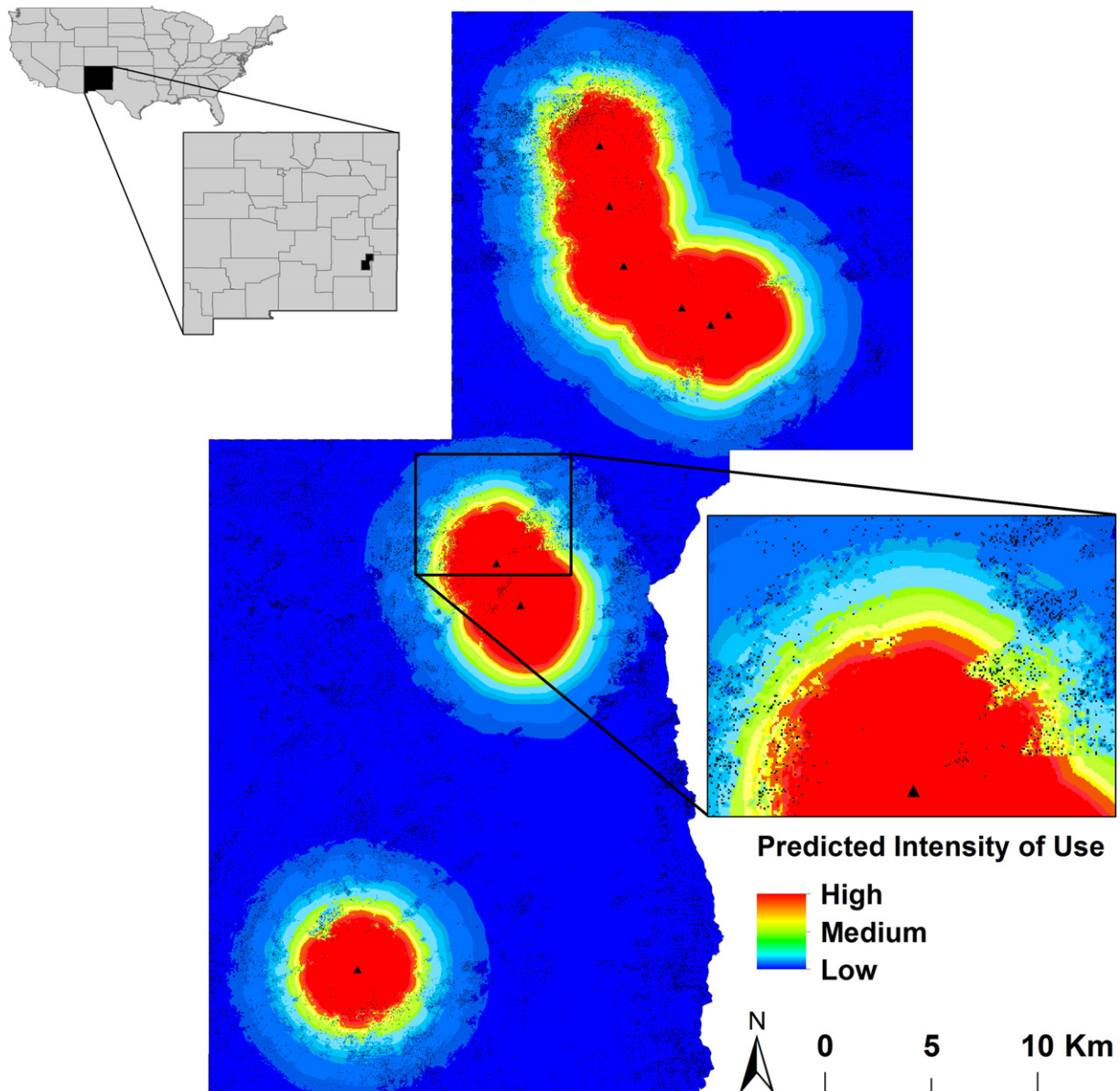

Figure 3. Predicted intensity of use of lesser prairie-chickens throughout their annual cycle in southeastern New Mexico is heavily influenced by mesquite distribution (inset; *black dots*) and centered around lek sites (*closed triangles*).

season (1389.5 ± 245.9 m) was similar ($t_{48} = 1.45$, $P = 0.16$). Likewise, average distance to nearest mesquite bush from the centroid of the 1% isopleth in the breeding season (360.8 ± 69.3 m) and nonbreeding season (420.9 ± 71.3 m) was similar ($t_{48} = 0.60$, $P = 0.55$).

Discussion

Encroachment of woody vegetation has emerged as a primary concern for the persistence and recovery of many grouse species (McNew et al., 2012; Baruch-Mordo et al., 2013; Lautenbach, 2015). Only a few studies have suggested that abundance of woody vegetation (e.g., eastern redcedar) is lower in areas used or suspected to be used by lesser prairie-chickens in Texas and Oklahoma (Jones, 1963; Fuhlendorf et al., 2002; Lautenbach, 2015; Lautenbach, 2017-this issue). To our knowledge, our study is the first to quantify avoidance of mesquite across both breeding and nonbreeding seasons by lesser prairie-chickens. The estimated resource utilization function for the breeding season from this study revealed a clear avoidance of mesquite (see Fig. 2A). During the nonbreeding season, the estimated resource utilization function suggested a slight decrease in avoidance of mesquite; however, on average it suggested that individuals were selecting areas where mesquite was absent (see Fig. 2B) despite a twofold increase in average size of home ranges during the nonbreeding season. Moreover, our estimates of average distance to nearest mesquite to centroid of 1% isopleths of utilization distributions were similar in the breeding and nonbreeding seasons. Our results suggest that mesquite presence is a primary ecological driver of space use and limits available habitat for lesser prairie-chickens, a pattern that has been documented in other studies and similar species. In environments where eastern redcedar is the dominant woody plant, lesser prairie-chickens only select nest and brood sites in areas where densities of eastern redcedar were <2 ha^{-1} or 2% canopy at the 89-ha scale (Lautenbach, 2015). Furthermore, the probability of colonization for greater prairie-chickens *(Tympanuchus cupido),* an ecologically similar species, decreases when woody plant cover exceeds 5% (McNew et al., 2012).

To combat the encroachment of mesquite on grasslands in southern New Mexico and increase available habitat to lesser prairie-chickens, state, federal, and private agencies are aggressively waging a war on woody plant invasion by chemically treating mesquite. These treatment efforts have raised questions concerning what lesser prairie-chickens are avoiding. Specifically, are they avoiding the fully foliated canopy of a mesquite bush or the mesquite bush itself, with or without leaves? Following chemical treatment, mesquite bushes are defoliated and left for 2 − 3 yr before investing in efforts to remove standing dead structure. Removal of above-ground biomass and sometimes below-ground root systems is a time-intensive and expensive process often requiring archaeological clearances and environmental impact statements. If lesser prairie-chickens are avoiding fully foliated canopies and not defoliated plant skeletons, efforts to remove above-ground biomass may not be necessary. Letting mesquite decomposition occur naturally could be an alternative and less expensive option in low-density stands.

The mesquite canopy layer represented the bulkier fully foliated canopy during the breeding season. We used the mesquite canopy layer, however, in both the breeding and nonbreeding season, allowing us to evaluate if birds were avoiding mesquite regardless of season and foliar condition or if avoidance was more influenced by foliated mesquite. If birds were avoiding mesquite regardless of season, we would expect negative standardized coefficients for mesquite canopy and positive standardized coefficients for distance to mesquite in both seasons. Conversely, if there was differential avoidance by birds as a function of season, the magnitude and direction of the parameter estimates for these covariates would change. We observed comparable values in the average standardized coefficients for mesquite canopy regardless of season; however, the influence of distance to mesquite was less during the nonbreeding season compared with breeding season (see Fig. 2A − 2B). The relationship between mesquite canopy

and distance to mesquite is intertwined, and the small seasonal differences are likely attributed to home ranges being on average twice as large during the nonbreeding season compared with the breeding season. Larger home ranges during the nonbreeding season likely contributed to a marginal increase in some of the lower canopy classes and a slightly higher occurrence of mesquite in areas of low intensity of use, spatially represented by the outer portions of the utilization distributions (Fig. 4). In both seasons, however, classes of mesquite canopy within utilization distributions were relatively low and decreased precipitously from outer to inner areas of utilization distributions, suggesting avoidance of areas with mesquite present (see Fig. 4A − 4B). The class of mesquite canopy that accounted for the largest percent within utilization distributions of all birds was the lowest class (<1% mesquite canopy), which contained many values where percent mesquite canopy was zero, and the highest class of mesquite canopy (>50% mesquite canopy) was not found in the utilization distributions of any birds in either season (see Fig. 4A − 4B). Moreover, the 1 − 5% canopy class comprised <15% of all utilization distributions regardless of season, suggesting low tolerance of mesquite. The pattern of general mesquite avoidance seasonally, however, is supported by low prevalence of mesquite at any location in the utilization distribution (<0.05% for any rescaled value of the utilization distributions) and the steep decline in percent of mesquite in areas of low to high intensity of use (Fig. 4C − 4D). Seasonal habitat use suggests that mesquite-encroached prairies in our study area have characteristics that are avoided by lesser prairie-chickens throughout their life-history stages.

In this study, locations of leks also exerted a strong influence on space use by lesser prairie-chickens (see Fig. 2A − 2B and Fig. 3). It is widely accepted that leks, predominantly attended by males, are anchored by females selecting for preferred nesting and brood-rearing habitat in close proximity to leks (Schroeder and White, 1992; Gibson, 1996; Winder et al., 2014). Furthermore, movements of male lesser prairie-chickens have been shown to be more closely linked to lek sites than females during the nonbreeding season (Robinson, 2015). Females, however, also select locations near lek sites during the nonbreeding and breeding season because of the need to reproduce and the relationship between location of lek and proximity to preferred breeding habitat (Giesen, 1994; Winder et al., 2015). Because we had a higher percentage of males ($n = 34$; 58%) than females ($n = 16$; 32%) during this study, there is a possibility that a male sex bias in relation to proximity of leks could be driving our population-level patterns of space use and the results of our predictions derived from our resource utilization function. Although this may be a factor, our acknowledged disparity of female lesser prairie-chickens compared with males precluded an opportunity to investigate the exertion of the males influence on distance to lek in the resource utilization functions. We therefore must caution that the effects of distance to leks on space use and the resource utilization function may be influenced more by males than females. Across seasons, however, average distance between nearest lek and centroid of 1% isopleth of utilization distributions were similar. Moreover, the effects of mesquite avoidance were detected in both seasons, even with distance to lek being a dominating influence.

Interestingly, the results of this study indirectly indicate that lek locations are also established in locations away from mesquite presence, a relationship that should be explored by research in the future. Distinguishing characteristics, for example, between active and abandoned lek sites in southeastern New Mexico are the absence and presence of mesquite, respectively (Hunt and Best, 2010). Patterns of space use by lesser prairie-chickens in this study suggest both a strong affinity for areas near leks and an avoidance of mesquite, implying that the two are not necessarily mutually exclusive. Our results are especially important as they emphasize the importance of maintaining current areas with low prevalence of mesquite, removing mesquite to increase habitat availability, and also increase the potential of colonization of new nesting areas and establishment of new lek sites (McNew et al., 2012).
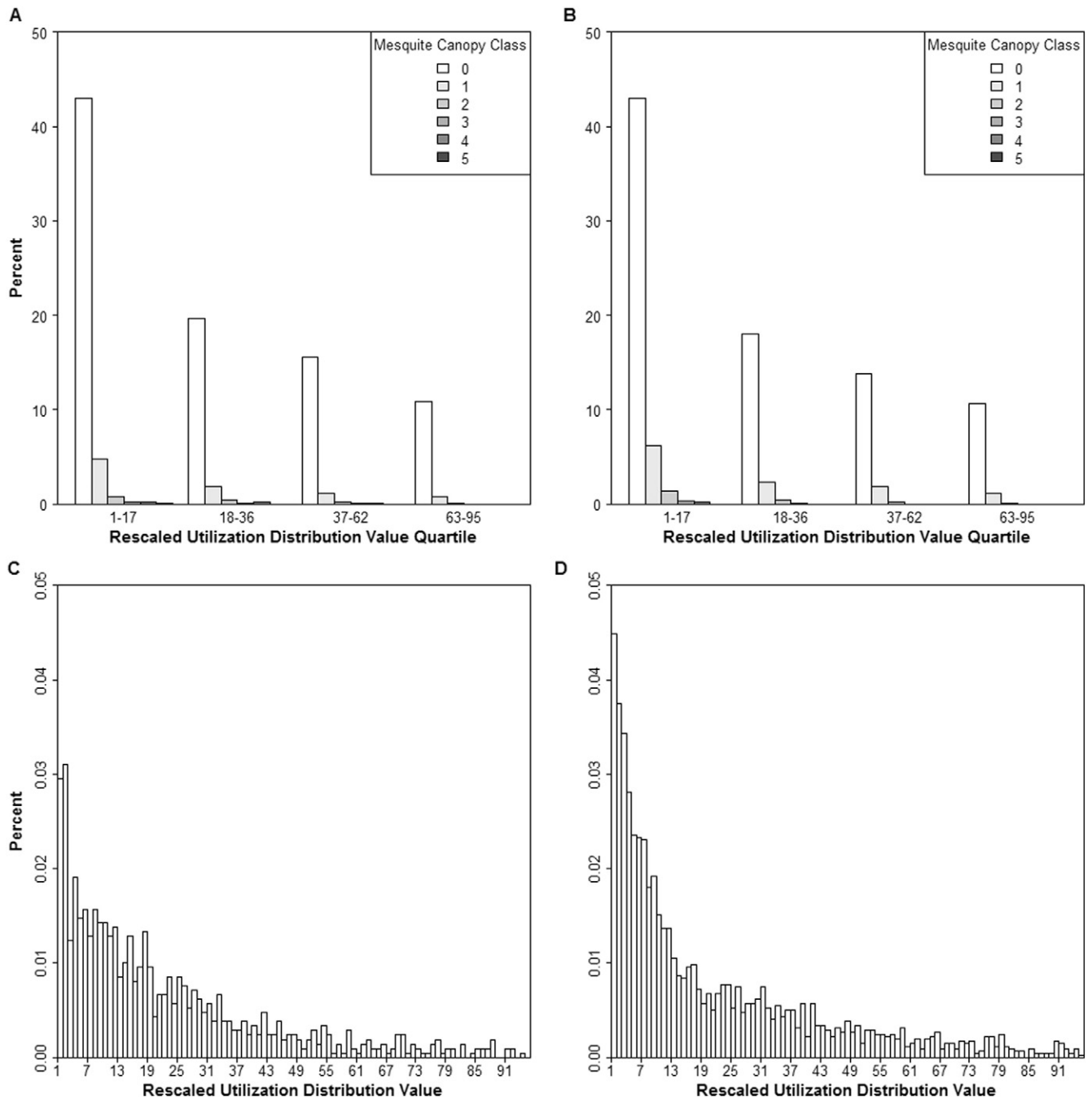
Figure 4. Prevalence of classes of mesquite canopy and mesquite plants within utilization distributions of lesser prairie-chickens during the breeding and nonbreeding season in southeastern New Mexico in 2013−2014. Percent of classes of mesquite canopy (0 = < 1%, 1 = 1−5%, 2 = 5−10%, 3 = 10−15%, 4 = 15−30%, 5 = 30−50%) within quartiles of rescaled utilization distribution values (1 lowest intensity of use to 95 highest intensity of use) during the breeding season (A) and nonbreeding season (B) is largely composed of the lowest class of mesquite canopy (<1% canopy cover) and overall, classes of mesquite canopy decrease from low to high values of intensity of use. Percent of mesquite plants present within rescaled utilization distribution values during the breeding season (C) and nonbreeding season (D) is marginal (<0.05 for any value of intensity of use) and decreases from low to high values of intensity of use.

Implications

Mesquite appears to limit habitat regardless of canopy cover extent. Furthermore, when mesquite is present in areas of use by lesser prairie-chickens, it is represented by the lowest canopy cover classes (1–15%). Medium to high canopy cover classes (16–50%) were rarely present in areas used by lesser prairie-chickens. These patterns suggest that low canopy stands of mesquite represent habitat selected by lesser prairie-chicken that is "at risk" of being lost. Thus, we can organize canopy cover into conservation (1–15%) and restoration categories (16–50%), given the absence of any occurrence of the latter in the utilization distributions. Actively treating and removing lower canopy cover mesquite from currently occupied prairie may increase available habitat for lesser prairie-chickens and reduce the threat of habitat loss. To restore habitat, targeting areas with higher canopy cover of mesquite in the occupied range should increase connectivity and availability of habitat. Arguably, efforts of habitat restoration can be more costly in terms of time and resources than habitat conservation. Thus, prioritizing the removal of low canopy cover mesquite may be a more cost-effective way to increase suitable environments for prairie chickens during both breeding and nonbreeding seasons.

Acknowledgments

References

Baruch-Mordo, S., Evans, J.S., Severson, J.P., Naugle, D.E., Maestas, J.D., Kiesecker, J.M., Falkowski, M.J., Hagen, C.A., Reese, K.P., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biology Conservation 167, 233–241.

Behney, A.C., Boal, C.W., Whitlaw, H.A., Lucia, D.R., 2012. Raptor community composition in the Texas Southern High Plains Lesser Prairie-Chicken Range. Wildlife Society Bulletin 36, 291–296.

Beltran-Przekurat, A., Pielke, R.A., Peters, D.P.C., Snyder, K.A., Rango, A., 2008. Modeling the effects of historical vegetation change on near-surface atmosphere in the northern Chihuahuan Desert. Journal of Arid Environment 72, 1897–1910.

Beyer, H.L., 2012. Geospatial Modelling Environment (version 0.7.3.0).Available at: http://www.spatialecology.com/gme (accessed 9.25.15).

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecology Modeling 157, 281–300.

Brown, D.A., 1989. Physiological and morphological problems for dispersal and survival of grasses in a changing environment. In: Malanson, G.P. (Ed.)Natural areas facing climate change. Academic Publishing, The Hague, The Netherlands.

Cable, J.M., Barron-Gafford, G.A., Ogle, K., Pavao-Zuckerman, M., Scott, R.L., Williams, D.G., Huxman, T.E., 2012. Shrub encroachment alters sensitivity of soil respiration to temperature and moisture. Journal of Geophysical Research 117, G01001.

Copelin, F.F., 1963. The Lesser Prairie-Chicken in Oklahoma. Technical Bulletin 6. Oklahoma Department of Wildlife Conservation, Jenks, OK, USA.

Coppedge, B.R., Engle, D.M., Masters, R.E., Gregory, M.S., 2001. Avian response to landscape change in fragmented southern Great Plains grasslands. Ecology Applications 11, 47–59.

Creamer, C.A., Filley, T.R., Boutton, T.W., Oleynik, S., Kantola, I.B., 2011. Controls on soil carbon accumulation during woody plant encroachment: evidence from physical fractionation, soil respiration, and $\delta^{13}C$ of respired CO_2. Soil Biology and Biochemistry 43, 1678–1687.

Doerr, T.B., Guthery, F.S., 1983. Effects of tebuthiuron on Lesser Prairie-Chicken habitat and foods. Journal of Wildlife Management 47, 1138–1142.

Engle, D.M., Coppedge, B.R., Fuhlendorf, S.D., 2008. From the Dust Bowl to the Green Glacier: human activity and environmental change in Great Plains grasslands. In: Van Auken, O.W. (Ed.), Western North American juniperus communities: a dynamic vegetation type.

ESRI, 2014. ArcGIS v10.2 Desktop: Release 10.2. Environmental Systems Research Institute, Redlands, CA, USA.

Falkowski, M.J, Evans, J.S., Naugle, D.E., Hagen, C.A., Carleton, S.A., Maestas, J.D., Khalyani, A.H., Poznanovic, A.J., Lawrence, A.J., 2017. Mapping Tree Canopy Cover in Support of Proactive Prairie Grouse Conservation inWestern North America. Rangeland Ecology & Management Conifer Special Edition. 70, 15–24.

Fredrickson, E.L., Estell, R.E., Laliberte, A., Anderson, D.M., 2005. Mesquite recruitment in the Chihuahuan Desert: historic and prehistoric patterns with long-term impacts. Journal of Arid Environments 65, 285–295.

Fredrickson, E., Havstad, K.M., Estell, R., Hyder, P., 1998. Perspectives on desertification: southwestern United States. Journal of Arid Environments 39, 191–207.

Fuhlendorf, S.D., Woodward, A.J.W., Leslie Jr., D.M., Shackford, J.S., 2002. Multi-scale effects of habitat loss and fragmentation on Lesser Prairie-Chicken populations. Landscape Ecology 17, 617–628.

Fuhlendorf, S.D., Archer, S.A., Smeins, F.E., Engle, D.M., Taylor, C.A., 2008. The combined influence of grazing, fire, and herbaceous productivity on tree-grass interactions. In: Van Auken, O.W. (Ed.), Western North American *Juniperus* communities: a dynamic vegetation type. Springer, New York, NY, USA.

Gibson, R.M., 1996. A re-evaluation of hotspot settlement in lekking sage grouse. Animal Behavior 52, 993–1005.

Giesen, K.M., 1994. Movements and nesting habitat of lesser prairie-chicken hens in Colorado. Southwestern Nature 39, 96–98.

Hagen, C.A., Jamison, B.E., Giesen, K.M., Riley, T.Z., 2004. Guidelines for managing Lesser Prairie-Chicken populations and their habitats. Journal of Wildlife Management 32, 69–82.

Hastings, J.R., Turner, R.M., 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semiarid region. University of Arizona Press, Tucson, AZ, USA.

Haukos, D.A., Smith, L.M., 1989. Lesser prairie-chicken nest site selection and vegetation characteristics in tebuthiuron-treated and untreated sand shinnery oak in Texas. Great Basin Nature 49, 624–626.

Heimlich, R.E., Kula, O.E., 1991. Economics of livestock and crop production on post-CRP lands. In: Joyce, L.A., Mitchell, J.E., Skold, M.D. (Eds.), The conservation reserve: yesterday, today and tomorrow. General technical report RM-203. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA, pp. 11–23.

Herkert, J.R., Reinking, D.L., Wiedenfeld, D.A., Winter, M., Zimmerman, J.L., Jensen, W.E., Finck, E.J., Koford, R.R., Wolfe, D.H., Sherrod, S.K., Jenkins, M.A., Faaborg, J., Robinson, S.K., 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conservation Biology 17, 587–594.

Hollister, E.B., Schadt, C.W., Palumbo, A.V., Ansley, R.J., Boutton, T.W., 2010. Structural and functional diversity of soil bacterial and fungal communities following woody plant encroachment in the southern Great Plains. Soil Biology and Biochemistry 42, 1816–1824.

Hooten, M.B., Hanks, E.M., Johnson, D.S., Alldredge, M.W., 2013. Reconciling resource utilization and resource selection functions. Journal of Animal Ecology 82, 1146–1154.

Horne, J.S., Garton, E.G., 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70, 641–648.

Humphrey, R.R., 1958. The desert grassland: a history of vegetational change and an analysis of causes. Botanical Review 24, 193–252.

Hunt, J.L., Best, T.L., 2010. Vegetative characteristics of active and abandoned leks of lesser prairie-chickens (Tympanuchus pallidicinctus) in southeastern New Mexico. Southwest Nature 55, 477–487.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Jones, R.E., 1963. Identification and analysis of lesser and Greater Prairie-Chicken habitat. Journal of Wildlife Management 27, 757–778.

Kenward, R.E., 2001. A manual of wildlife radio tagging. Academic Press, London, UK 311 p.

Kertson, B.N., Marzluff, J.M., 2011. Improving studies of resource selection by understanding resource use. Environmental Conservation 38, 18–27.

Kertson, B.N., Spencer, R.D., Marzluff, J.M., Hepinstall-Cymerman, J., Grue, C.E., 2011. Cougar space use and movements in the wildland-urban landscape of western Washington. Ecological Applications 21, 2866–2881.

Kneuper, C.L., Scott, C.B., Pinchak, W.E., 2003. Consumption and dispersion of mesquite seeds by ruminants. Journal of Range Management 56, 255–259.

Lautenbach, J.M., 2015. Lesser prairie-chicken reproductive success, habitat selection, and response to trees [thesis]. Kansas State University, Manhattan, KS, USA.

Lautenbach, J.M., Plumb, R.T., Robinson, S.G., Hagen, C.A., Haukos, D.A., Pitman, J.C., 2017. Lesser Prairie-Chicken Avoidance of Trees in a Grassland Landscape. Rangeland Ecology & Management Conifer Special Edition. 70, 78–86.

Lloyd, J., Mannan, R.W., Destefano, S., Kirkpatrick, C., 1998. The effects of mesquite invasion on southeastern Arizona grassland bird community. Wilson Bulletin 110, 403–408.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P., Handcock, M.S., 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85, 1411–1427.

McNew, L.B., Prebyl, T.J., Sandercock, B.J., 2012. Effects of rangeland management on the site occupancy dynamics of prairie-chickens in a protected prairie preserve. Journal of Wildlife Management 76, 38–47.

Millspaugh, J.J., Nielsen, R.M., McDonald, L., Marzluff, J.M., Gitzen, R.A., Rittenhouse, C.D., Hubbard, M.W., Sheriff, S.L., 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70, 384–395.

Mohamed, A.H., Holechek, J.L., Bailey, D.W., Campbell, C.L., DeMers, M.N., 2011. Mesquite encroachment impact on southern New Mexico rangelands: remote sensing and geographic information systems approach. Journal of Applied Remote Sensing 5, 053514.

Nie, W., Yuan, Y., Kepner, W., Erickson, C., Jackson, M., 2012. Hydrological impacts of mesquite encroachment in the upper San Pedro watershed. Journal of Arid Environments 82, 147–155.

Neilson, R.P., 1986. High resolution climatic analysis and southwest biogeography. Science 232, 27–34.

Peterjohn, B.G., Sauer, J.R., 1999. Population status of North American grassland birds. Studies of Avian Biology 19, 27–44.

Pettit, R.D., 1979. Effects of picloram and tebuthiuron pellets on sand shinnery oak communities. Journal of Range Management 32, 196–200.

Robinson, S., 2015. Landscape ecology, survival and space use of lesser prairie-chickens [thesis]. Kansas State University, Manhattan, KS, USA.

Sandercock, B.K., Alfaro-Barrios, M., Casey, A.E., Johnson, T.N., Mong, T.W., Odom, K.J., Strum, K.M., Winder, V.L., 2015. Effects of grazing and prescribed fire on resource selection and nest survival of Upland Sandpipers in an experimental landscape. Landscape Ecology 30, 325–337.

Schroeder, M.A., White, G.C., 1992. Dispersion of Greater Prairie-Chicken nests in relation to lek location: evaluation of the hot-spot hypothesis of lek evolution. Behavioral Ecology 4, 266–270.

Smythe, L.A., 2006. Response of nesting grassland birds to sand shinnery oak communities treated with tebuthiuron and grazing in eastern New Mexico [thesis]. Texas Tech, Lubbock, TX, USA.

Teague, W.R., Ansley, R.J., Pinchak, W.E., Dowhower, S.L., Gerrard, S.A., Waggoner, A., 2008. Interannual herbaceous biomass response to increasing honey mesquite cover on two soils. Rangeland Ecology & Management 61, 496–508.

Thomson, R.L., Forsman, J.T., Sarda-Palomera, F., Monkkonen, M., 2006. Fear factor: prey habitat selection and its consequences in a predation risk landscape. Ecography 29, 507–514.

Throop, H.L., Archer, S.R., 2007. Interrelationships among shrub encroachment, land management, and litter decomposition in a semidesert grassland. Ecological Applications 17, 1809–1823.

Toole, B.E., 2005. Survival, seasonal movements, and cover use by lesser prairie chickens in the Texan Panhandle [thesis]. Texas A&M University, College Station, TX, USA.

Trimble, 2013. eCognition Developer, 8.9.0 ed. Munich, Germany: Trimble Geospatial Imaging, Arnulfstrasse 126, 80636.

Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing Environment 8, 127–150.

US Department of Agriculture, 2014. Natural Resources Conservation Service: Conservation beyond boundaries LPCI 2014 Progress ReportAvailable at: http://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/programs/initiatives/?cid=nrcsdev11_023912 (accessed 11.27.15).

Van Pelt, W.E.V., Kyle, S., Pitman, J., Klute, D., Beauprez, G., Schoeling, D., Janus, A., Haufler, J.B., 2013. The Lesser Prairie-Chicken Range-wide Conservation Plan. Interstate Working Group. Western Association of Fish and Wildlife Agencies, Cheyenne, WY, USA.

Vickery, P.D., Tubaro, P.L., Cardoso da Silva, J.M., Peterjohn, B., Herkert, J.R., Cavalcanti, R.B., 1999. Conservation of grassland birds in the western hemisphere. In: Vickery, P.D., Herkert, J.R. (Eds.), Ecology and conservation of grassland birds of the western hemisphere.

Winder, V.L., McNew, L.B., Gregory, A.J., Hunt, L.M., Wisely, S.M., Sandercock, B.K., 2014. Space use by female greater prairie-chickens in response to wind energy development. Ecosphere 5, 3.

Winder, V.L., Gregory, A.J., McNew, L.B., Sandercock, B.K., 2015. Responses of male greater prairie-chickens to wind energy development. Condor 117, 284–296.

Woodward, A.J., Fuhlendorf, S.D., Leslie Jr., D.M., Shackford, J., 2001. Influence of landscape composition and change on lesser prairie-chicken (Tympanuchus pallidicinctus) populations. American Midland Naturalist 145, 261–274.