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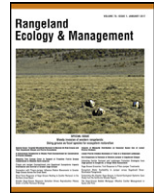
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Lesser Prairie-Chicken Avoidance of Trees in a Grassland Landscape[☆]



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ABSTRACT

Grasslands are among the most imperiled ecosystems in North America. Reasons that grasslands are threatened include conversion to row-crop agriculture, fragmentation, and changes in fire regimes. The reduction of fire processes in remaining prairies has resulted in tree encroachment and establishment in grasslands, further reducing grassland quantity and quality. Grassland birds have been experiencing precipitous population declines in recent decades, commensurate with landscape changes to grasslands. The lesser prairie-chicken (*Tympanuchus pallidicinctus* Ridgway) is a declining species of prairie grouse of conservation concern. We used second- and third-order habitat selection metrics to test if female lesser prairie-chickens avoid grasslands where trees were present. Our results indicated that female lesser prairie-chickens selected habitats avoiding the nearest trees by 283 m on average, nearly twice as far as would be expected at random. Lesser prairie-chickens were 40 times more likely to use habitats with tree densities of 0 trees · ha⁻¹ than habitats with 5 trees · ha⁻¹. Probability of use indicated that lesser prairie-chickens were 19 times more likely to use habitats 1000 m from the nearest tree when compared with using habitats 0 m from the nearest tree. Nest survival was not affected at densities < 2 trees · ha⁻¹; however, we could not test if nest survival was affected at greater tree densities as no nests were detected at densities > 2 trees · ha⁻¹. Avoidance of trees could be due to perceived increased predation risk, reduced habitat quality, or a combination of these potentially confounding factors. Preventing further establishment and expansion of trees in landscapes occupied by lesser prairie-chickens could contribute to the continued persistence of the species. Additionally, restoring grasslands through tree removal may facilitate conservation efforts for grassland species such as the lesser prairie-chicken by improving habitat quality and promoting expansion of occupied range.

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Introduction

Grasslands have experienced the greatest reduction of occurrence for any North American ecosystem (Samson and Knopf, 1994). Great Plains grasslands are one of the most threatened ecosystems in North America (Cully et al., 2003; Samson et al., 2004). Historically, conversion of grasslands to row-crop agriculture was the major cause of grassland loss

(White et al., 2000). However, loss of ecological drivers, including periodic fire and large native herbivore grazing, has further degraded grassland quality by facilitating tree encroachment (Samson et al., 2004; Engle et al., 2008). Encroachment by trees in the Southern Great Plains has replaced conversion of grassland to row-crop agriculture as the major cause of contemporary grassland fragmentation and degradation (Bragg and Hulbert, 1976; Coppedge et al., 2001a, 2001b; Engle et al., 2008).

Invading trees in grasslands reduces species richness and alters plant and animal communities (Coppedge et al., 2001a; Chapman et al., 2004; Engle et al., 2008; Ratajczak et al., 2012). In the presence of woody plants, especially trees, herbaceous biomass and species richness decreases with an increase in woody canopy cover (Smith and Stubbendieck, 1990; Briggs et al., 2002; Limb et al., 2010), with dominant plant communities shifting from C4 grasses to C3 grasses (Gehring and Bragg, 1992; but see Limb et al., 2010). Transformation of grassland into woodland can occur rapidly, as aerial photographs indicate that tall-grass prairie can convert to a closed-canopy forest in as little as 40 yr (Briggs et al., 2002).

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The shift from grassland to woodland as a result of tree encroachment has negative consequences on grassland wildlife species (Coppedge et al., 2001a; Engle et al., 2008; Alford et al., 2012). Grassland bird communities are of particular interest due to recent declines and their role as indicators of grassland health (Peterjohn and Sauer, 1999; Brennan and Kuvlesky, 2005). Prairie grouse have specifically been identified as species to focus grassland conservation efforts because they require large blocks of diverse habitat (Svedarsky et al., 2000; Poiani et al., 2001; Hagen et al., 2004; Silvy and Hagen, 2004; Brennan and Kuvlesky, 2005; Pruett et al., 2009).

Prairie grouse have been reported to have negative associations with trees and forest cover. Greater sage-grouse (*Centrocercus urophasianus* Bonaparte) lek (i.e., breeding site) activity was found to decline as juniper (*Juniperus* sp.) canopy cover increases and the probability of greater sage-grouse lek persistence is near zero at 5% juniper canopy cover (Baruch-Mordo et al., 2013). The probability of colonization of unoccupied lek sites by greater prairie-chickens (*Tympanuchus cupido* L.) decreased to < 2% as the proportion of woodland increased > 20% (McNew et al., 2012). Lek sites of greater prairie-chickens in Minnesota, Wisconsin, and Kansas were negatively associated with forest landcover (Merrill et al., 1999; Niemuth, 2003; Gregory et al., 2011). Forest cover was cited as a strong predictor of greater prairie-chicken lek presence with mean percent forest cover two to three times greater at random points than at lek sites (Merrill et al., 1999; Niemuth, 2003); only 9% forest cover renders prairie unsuitable for greater prairie-chicken leks (Gregory et al., 2011). Additionally, greater prairie-chickens select prairie for nesting where tree cover is minimal and nest survival increases as distance to nearest tree increases (McKee et al. 1998; Matthews et al., 2013; Hovick et al., 2015).

Tree encroachment was identified as a primary threat leading to fragmentation and loss of habitat for the lesser prairie-chicken (*Tympanuchus pallidicinctus* Ridgway) in the decision to list the species as federally threatened in May 2014 (USFWS, 2014). Despite the September 2015 judicial decision to vacate the listing rule on procedural grounds, the threat of woody encroachment has not diminished. Increasing woodland encroachment has been implicated as a source of habitat loss and cause of population decline for lesser prairie-chickens (Fuhlendorf et al., 2002). However, lesser prairie-chicken response to tree encroachment has not been quantified. Understanding the role of tree encroachment in habitat selection by lesser prairie-chickens is important for the conservation of the species and grasslands they occupy (Pruett et al., 2009a).

Our goal was to assess responses of lesser prairie-chickens within grasslands that are being invaded by eastern redcedar (*Juniperus virginiana* L.) and other tree species. Our objectives were threefold: 1) to measure lesser prairie-chicken response to trees at different spatial scales using second-order (i.e., selection of home range within a geographic region) and third-order (i.e., selection of habitat within a home range) habitat selection frameworks (Johnson, 1980); 2) to investigate possible effects of trees on nest site selection and nest survival, and 3) to investigate relationship between tree density and tree canopy coverage. We predicted that lesser prairie-chickens would 1) select seasonal and nesting habitats farther from trees than available, 2) exhibit an avoidance threshold of seasonal use and nesting to tree density, and 3) experience reduced nest survival as a function of tree density and proximity.

Methods

Study Site

The study site was located in south-central Kansas on 14 000 ha of private land within Kiowa and Comanche counties (Fig. 1). The study site was primarily mixed-grass prairie within the Red Hills region of Kansas with livestock grazing, prescribed fire, and interspersed with row-crop agriculture. Grasslands were grazed by cattle (*Bos taurus* L.), typically in

cow/calf pairs for yearlong grazing periods or yearling stocker steers/heifers for a 180-day grazing season (April–September). Fire return intervals in the system range from 4 to 6 yr, which are comparable with the estimated regional historic fire return interval of 5–10 yr (Joern and Keeler, 1995). Herd size and stocking rates varied by producer and management strategy. Soils included limy and loamy uplands, sandy and loamy lowlands, and subirrigated bottomlands. The study site was categorized within the Central Rolling Red Plains major land resource area (Natural Resources Conservation Service; <http://apps.cei.psu.edu/mlra/>; accessed 24 February 2016). Tree removal, primarily eastern redcedar, has been ongoing for ~30 yr in portions of the study site. However, tree encroachment into grasslands continues across the study site, with eastern redcedar, a native species, being the dominant invading species. Other native invading tree species included American elm (*Ulmus americana* L.) and hackberry (*Celtis occidentalis* L.). Non-native invading trees include Siberian elm (*Ulmus pumila* L.), Chinaberry (*Melia azedarach* L.), and tamarisk (*Tamarix* sp.).

Dominant grasses at the study site included little bluestem (*Schizachyrium scoparium* [Michx.] Nash), blue grama (*Bouteloua gracilis* [Hbk.] Lag.), hairy grama (*B. hirsuta* Lag.), side oats grama (*B. curtipendula* [Michx.] Torr.), and tall dropseed (*Sporobolus compositus* [Poir] Merr.). Other dominant vegetation across the study site included sand sagebrush (*Artemisia filifolia* Torr.), purple poppy mallow (*Callirhoe involucrata* [Torr. & Gray] Gray), heath aster (*Aster ericoides* L.), evening primrose (*Oenothera macrocarpa* Nutt.), broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby), sand plum (*Prunus angustifolia* Marshall), and smooth sumac (*Rhus glabra* L.). Common tree species on the study site included eastern redcedar, eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall), and elm (*Ulmus* sp.).

Field Methods

We captured female lesser prairie-chickens at leks during spring 2013 and 2014 using walk-in traps (Haukos et al., 1990; Schroeder and Braun, 1991) and drop nets (Silvy et al., 1990). We classified captured lesser prairie-chickens as male or female and yearling or adult on the basis of plumage characteristics (Copelin, 1963). Captured females were fitted with either a very-high-frequency (VHF) radio transmitter (Model A3900, Advanced Telemetry System, Isanti, MN) or satellite transmitter with Global Positioning System (GPS) capability (platform transmitting terminals [PTT]; Model PTT-100 22-g Argos/GPS PTT, Microwave Telemetry, Columbia, MD). Captured individuals were released at the capture site following attachment of transmitters. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee under protocol 3241 and the Kansas Department of Wildlife, Parks, and Tourism scientific collection permits SC-042-2013 and SC-079-2014.

We monitored female lesser prairie-chickens fitted with VHF radio transmitters regularly (i.e., > 3 times · week⁻¹) via triangulation to record telemetry locations (Cochran and Lord, 1963). Location of a Signal (Ecological Software Solutions, Naples, FL) software was used to estimate Universal Transverse Mercator coordinates from VHF data collected in the field. We tracked females from March 2013 to March 2015. The PTTs recorded GPS points approximately every 2 hours from 0600 to 2400. The GPS points were transmitted using the Argos System and then made available to researchers.

We assumed that females were incubating nests if telemetry locations and PTT GPS fixes were relatively consistent for ≥ 3 days without a mortality signal. We used homing to locate nests of VHF-marked females (Pitman et al., 2005; Grisham et al., 2013). Nests of PTT-marked females were found by searching within the error radius (18 m) of the consistent GPS point. Nests were visited once during the incubation period and remotely monitored until the female was determined to be off the nest using telemetry or PTT GPS locations, after which nest fate was identified (Pitman et al., 2005). We located 3 nests of unmarked females

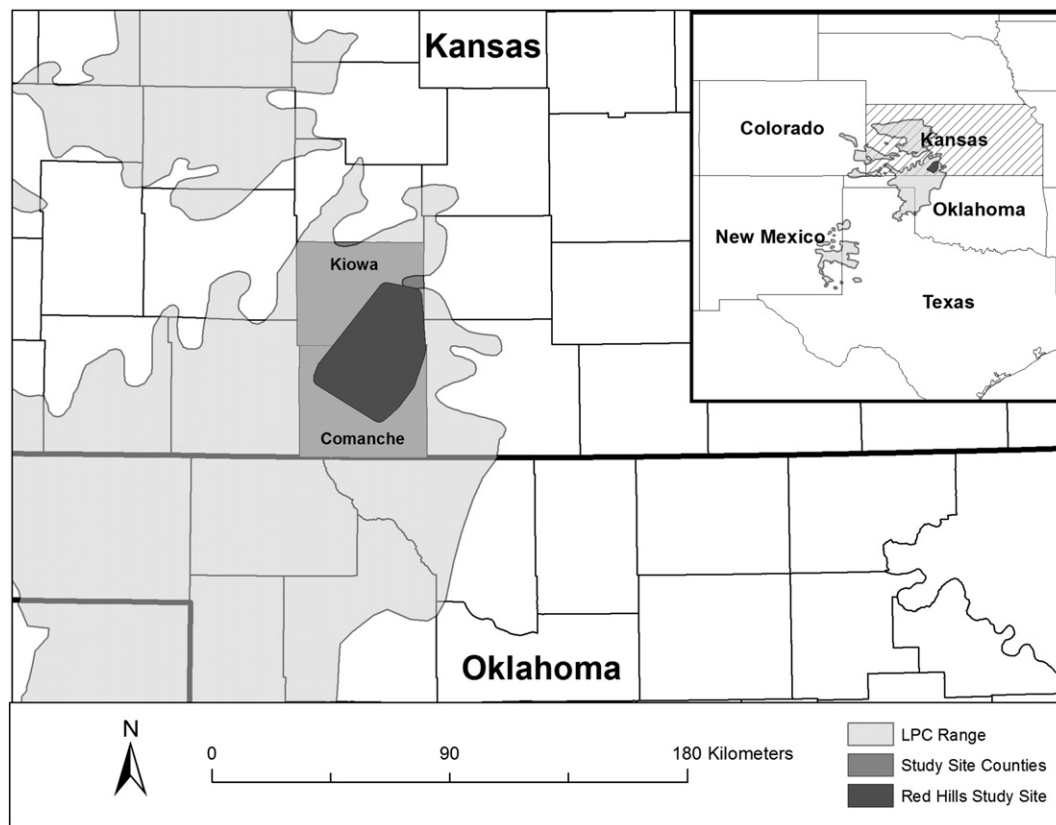


Figure 1. Study site location for evaluating the response of female lesser prairie-chickens to the occurrence of trees in Kiowa and Comanche counties within the Red Hills region of south-central Kansas during 2013 and 2014.

that had been destroyed. We included these in our habitat selection analysis only. Because of the lack of information on exposure days, we did not incorporate them with our nest survival analysis.

Spatial Analysis

Individual trees within the study site were digitized and mapped by hand using the 2012 National Agricultural Imagery Program (NAIP; retrieved from the Kansas Data Access and Support Center, 15 July 2014, <http://www.kansasgis.org/>) 1-m resolution imagery in ArcGIS 10 (ESRI 2011, ArcGIS 10, Environmental Systems Research Institute, Redlands, CA). We verified these data by visiting areas across the study area, ground-truthing, and using local expertise. We hypothesized that lesser prairie-chickens would behave similarly to the presence of any tree, regardless of species. Thus, all trees were classified the same. The proportion of trees encroaching into grasslands on the study site was ~0.77 eastern redcedar and ~0.23 deciduous trees. Digitized trees ranged in height from 1 m to 25 m. The only trees detected from imagery that were 1 m in height were eastern redcedar, because of their conspicuous appearance on the landscape.

We used lesser prairie-chicken locations collected through VHF telemetry ($n = 9\,757$) and PTT GPS data points ($n = 20\,434$) to assess habitat use relative to the presence and density of trees. We imported all lesser prairie-chicken used points into ArcGIS 10 and then measured the Euclidean distance from each point to the nearest tree (m). We then extracted the value of tree density (trees \cdot ha $^{-1}$) from each spatial grid (see later) for each point. The elevation (m) and slope (%) for each used point were extracted from a Digital Elevation Model (DEM) accessed from the Kansas Data Access and Service Center (retrieved 15 July 2014). In addition, the same information was collected at nest locations to identify trends in nest placement in relation to distance to tree, tree densities, elevation, and slope. Elevation and slope were included as

potentially important variables due to the association among trees, drainages, and slopes. These data were used to identify whether lesser prairie-chickens were avoiding areas based on trees or differently selecting areas with relatively higher elevations and more level slopes.

To avoid selecting an arbitrary spatial scale, we established 10 landscape grids ranging from 1 ha to 100 ha and investigated the effect of tree density on the pattern of use by lesser prairie-chickens as recommended by Boyce (2006). We then used ArcGIS to count the number of individual trees within each grid cell and then calculated densities (trees \cdot ha $^{-1}$) for each cell at each scale. We used an information theoretic approach (e.g., Akaike's Information Criterion [AIC_c] corrected for a small sample size) to determine the spatial scale (i.e., grid size) most relevant to lesser prairie-chicken habitat selection (Boyce, 2006; Albanese et al., 2012). We then used tree densities from the respective grid size to examine its influence on lesser prairie-chicken habitat selection in an information-theoretic approach identifying the best approximating model by the lowest AIC_c value and greatest model weight (Burnham and Anderson, 2002). We then examined the effect of each covariate by its beta value and 95% CIs. If the 95% CIs did not include zero, the effect was determined to be measurable. This approach prevented use of an arbitrary spatial scale and instead provided a scale driven biologically by lesser prairie-chickens (Albanese et al., 2012). We evaluated used locations and nest sites separately, as ecological factors driving nest placement were likely operating at a different spatial scale than used locations. Used locations were defined as a place where a female lesser prairie-chicken was estimated to be by the PTT or by telemetry. Spatial scale analyses were conducted in Program R (R core development team, version 3.0.1, 2013, Vienna, Austria).

The Lesser Prairie-Chicken Range-wide Conservation Plan and Natural Resources Conservation Service used canopy coverage instead of tree density as a measure of tree encroachment (Van Pelt et al., 2013; USDA, 2014). To increase the practical application of our work, we examined

the ability of our tree density coverage to predict tree canopy coverage. We randomly selected a subset of the study site and digitized canopy cover using ArcGIS 10 and the 2012 NAIP imagery to relate tree density to canopy cover. We then used linear regression in Program R to predict canopy coverage as function of tree densities (R core development team, version 3.0.1, 2013, Vienna, Austria).

Statistical Analyses

Third-Order Selection

Space-use data were analyzed for all PTT-marked females during 6-mo seasonal periods (breeding [March 15–September 15] and non-breeding [September 16–March 14]). If individual female lesser prairie-chickens were monitored in multiple seasons or years, we considered each 6-mo breeding or nonbreeding season to be independent and accepted limited pseudoreplication to maximize use of our data set (Winder et al., 2014). We used utilization distributions (UDs) to quantify space use of females as a continuous, probabilistic variable using the Brownian Bridge Movement Model (BBMM; Horne et al., 2007) with the BBMM function in a BBMM package (Nielson et al., 2012) of the statistical program R (R core development team, version 3.1.2, 2014, Vienna, Austria). The BBMM is a continuous-time stochastic model of movement in which the probability of being in a specific space at a given time is conditioned on the starting and ending locations, time elapsed between those two locations, error associated with the transmitter, and mobility of the organism (Horne et al., 2007). This methodology explicitly makes use of autocorrelated telemetry data and is well suited for GPS data (Bullard, 1999; Walter et al., 2011). Only UD's that were based on > 90 locations within a 6-mo season were included in the analysis. The Brownian motion variance (σ_m^2), which is related to the animal's mobility, was estimated for each female separately, and ranged between 87.5 m² and 2654.8 m² with a mean of 494.8 m² (SE = 80.9 m²).

The spatial extent of space use and availability of variables of interest were defined by the 99% isopleth of the BBMM UD boundary for each female's home range (Kertson and Marzluff, 2011; Winder et al., 2014). A raster surface with 30-m² cells was created within the UD. Use values, bounded from 1 to 99, were assigned to each cell on the basis of the relative volume (height) of the utilization distributions of that cell and then space-use data were log_e transformed to meet assumptions of linear multiple regression models (Kertson and Marzluff, 2011). Resource Utilization Functions (RUFs; Marzluff et al., 2004) in the RUF.fit package (Handcock, 2007) for Program R were used to relate the effect that distance to tree (m), tree density (trees · ha⁻¹), elevation (m), and slope (%) have on female lesser prairie-chicken space use. RUFs are based on relative space use where the unit of study is the individual utilization distribution. An RUF relates the intensity of use to the resources available within the 99% isopleth on a cell-by-cell basis in a multiple linear regression framework to obtain standardized β coefficients. These coefficients indicate the relative importance or influence of each variable to the variation in the utilization distribution of each female (Marzluff et al., 2004; Kertson and Marzluff, 2011). Population inferences were developed by calculating the standardized $\bar{\beta}$ coefficient for each predictor pooling across years for each 6-mo seasonal period (Winder et al., 2014). If the influence of a specific variable differed from zero based on 95% confidence intervals [CI], we inferred that the influence of that variable was greater (+) or less (–) than expected compared with the availability of that variable within the home range (Marzluff et al., 2004; Winder et al., 2014).

Second-Order Selection

We used a resource selection framework (i.e., used/available study design) to examine habitat selection at the population level and potential displacement of space use by trees across home range scale for all individuals (e.g., Manly et al., 1992; Boyce et al., 2002). This scale of analysis enabled us to quantify the effects of tree encroachment across

a broader landscape. We considered the study site as available, and the study site contained all female lesser prairie-chicken home ranges and 3 000 m buffer around all female home ranges due to potential movements of female lesser prairie-chickens (Plumb, 2015). For second-order selection, we excluded all locations collected while a female was incubating on the nest from our analysis of second-order habitat selection as a separate analysis was conducted using nest locations. We also removed redundant locations (e.g., roost locations) from second-order selection to avoid biasing to points used multiple times. In addition, we removed the points for 1 wk postcapture to allow for acclimation to transmitters. After data reduction, we randomly selected 1-point · day⁻¹ for females equipped with PTTs to minimize spatial autocorrelation. We then used ArcGIS 10 to generate three times as many telemetry and GPS locations ($n = 16\,758$ points) and randomly distributed them across the study site to serve as a reference for what was available (Allred et al., 2011).

We used models developed a priori, which included single and multiple variable models for the covariates of distance to trees (m) and tree density (trees · ha⁻¹). Although our focus was the effect of trees, we surmised that topography and tree presence could be confounded (i.e., steep slopes with or without trees may not be selected) and thus included the covariates elevation (m) and slope (%) to the model set. We also tested a global model that included all of the covariates of interest and a null model where no covariates were tested. We included quadratic form of distance to tree to test for threshold effects. We modeled the other three covariates only as linear functions because of either the limited range of values (i.e., elevation, slope) or skewed distribution (i.e., tree density). We did not evaluate distances to other structures and microhabitat characteristics because we were primarily interested in exploring lesser prairie-chicken habitat selection in relation to trees and tree densities.

We then used logistic regression to compare used points to available points (Manly et al., 2002; Allred et al., 2011). To avoid any potential correlation issues among distance to nearest tree, tree density, elevation, and slope, we standardized all points by taking the z-score for each variable of interest (Allred et al., 2011; Hovick et al., 2015). Models were ranked using AIC_c, and we selected the model with the lowest AIC_c value and greatest model weight (Burnham and Anderson, 2002). Models with $\Delta AIC_c \leq 2$ were considered equally parsimonious. All statistical analyses were conducted using Program R (R core development team, version 3.0.1, 2013, Vienna, Austria).

To identify the threshold of use, we used the following logistic regression function to estimate relative probability of use (Keating and Cherry, 2004):

$$f(x) = \frac{\exp(\beta_1(x_1) + \beta_2(x_2) + \beta_i(x_i))}{1 + \exp(\beta_1(x_1) + \beta_2(x_2) + \beta_i(x_i))} \quad (1)$$

Where the probability of use was approximately equal to zero, we assigned that as the threshold where use ceased for tree density and distance to nearest tree. We used the same function for nesting and use points.

Nest Survival

We used the nest survival model within Program MARK to estimate daily nest survival and determine if any of the covariates affected nest survival (White and Burnham, 1999; Dinsmore et al., 2002). We used a 35-day exposure period to incorporate a mean incubation and laying period for lesser prairie-chickens. We used tree density, distance to tree, slope, and elevation as individual covariates in the nest survival model. We selected 15 models a priori to estimate daily nest survival. Models were ranked using AIC_c, and we selected the model with the lowest AIC_c value and greatest model weight (Burnham and Anderson, 2002). We did not evaluate other vegetation covariates affecting nest

survival as we were primarily interested in examining the relationship of nest survival to trees.

Results

We captured 58 female lesser prairie-chickens in the Red Hills of Kansas during 2013 and 2014. The removal of redundant points and random selection of one GPS point · day⁻¹ for PTTs resulted in 9 757 points for analysis. Combined with VHF (*n* = 5 970), this resulted in 15 727 unique locations. The 16-ha grid (400 × 400 m) was the best approximating scale for tree density in relation to lesser prairie-chicken locations, with the next best model being 16, and 860 AIC_c value was for both second- and third-order selection. Used points were located twice as far from trees than random points (used: 282.5 m ± 0.96 SE, random: 128.9 m ± 0.77 SE).

We located and monitored 63 nests over the 2 yr of the study. In contrast to the lesser prairie-chicken seasonal use points, factors influencing nest sites were best analyzed at a scale using 600 m × 600 m grid cells (36 ha). Nests were placed nearly twice as far from trees than randomly generated points (nest: 292.7 m ± 19.7 SE; random: 172.0 m ± 20.9 SE).

Second-Order Selection

We used 14 models to test our hypotheses using tree density, distance to nearest tree, elevation, and slope to test for habitat selection across home ranges. Using the 16-ha grid, we found the highest ranked model that best fit the location data was the global model for used points (Table 1). The global model included distance to nearest tree, tree density, elevation, and slope. The magnitude of the coefficients from the global model for used points indicated that tree density and distance to the nearest tree were important factors in lesser prairie-chicken habitat selection at this scale.

The β estimates for coefficients of the global model indicate relative influence of probability of habitat use. Lesser prairie-chicken use patterns showed a strong negative relationship with tree density (β = -4.23, 95% CI = -4.52, -3.98), indicating that females used areas with lower tree densities than were available in the study site (Fig. 2A). Lesser prairie-chickens were 40 times more likely to use habitats with tree densities of 0 trees · ha⁻¹ than habitats with 4 trees · ha⁻¹ (Fig. 3A). Lesser prairie-chickens had a greater

Table 1

Rankings of models testing the relative influence of tree density (Density; trees · ha⁻¹), distance to nearest tree (Dist. Tree; m), elevation above sea level (Elevation; m), and slope (%) in determining female lesser prairie-chickens habitat selection at the 16-ha scale, in Kiowa and Comanche counties, Kansas, 2013–2014

Model	ΔAIC _c ¹	K ²	w _i ³	Dev. ⁴
Global ⁵	0 ⁶	5	1	18651
Density + Dist. Tree	540.1	3	< 0.001	19195
Density + Slope + Elevation	1490.9	4	< 0.001	20144
Density + Elevation	1503.3	3	< 0.001	20158
Density + Slope	2407.4	3	< 0.001	21063
Density	2410.7	2	< 0.001	21068
Dist. Tree + Slope + Elevation	2896.0	4	< 0.001	21549
Dist. Tree + Elevation	2995.3	3	< 0.001	21650
Dist. Tree + Slope	3455.6	3	< 0.001	22111
Dist. Tree	3489.3	2	< 0.001	22147
Elevation	5358.4	2	< 0.001	24016
Slope + Elevation	5358.8	3	< 0.001	24014
Slope	6448.2	2	< 0.001	25105
Null ⁷	6467.7	1	< 0.001	25127

¹ Deviance differences in Akaike's information criterion, corrected for a small sample size.
² Number of parameters.
³ Akaike weights.
⁴ Deviance.
⁵ Global model included Density, Dist. Tree, slope, and elevation.
⁶ Minimum AIC_c = 18 661.
⁷ Null model compared used and random locations with no covariates.

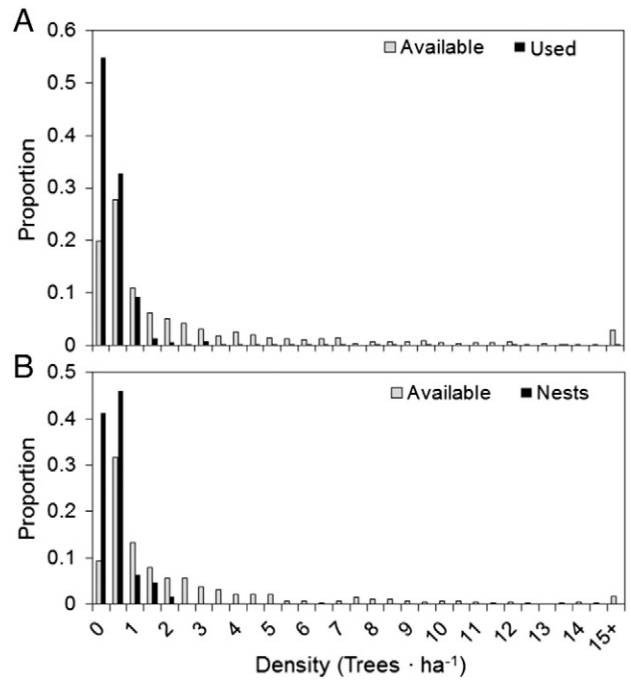


Figure 2. Comparison of the proportion of seasonal-use points of lesser prairie-chicken females against the proportion of available tree densities at the scale of 16 ha (A) and the proportion of nest sites of lesser prairie-chicken against the proportion of available tree densities at the scale of 36 ha (B) in Kiowa and Comanche counties Kansas, 2013–2014.

probability of use as distance to nearest tree increased (β = 0.68, 95% CI = 0.64, 0.72). Probability of use indicated that lesser prairie-chickens were nine times more likely to use habitats 1000 m from the nearest tree when compared with using habitats 0 m from the nearest

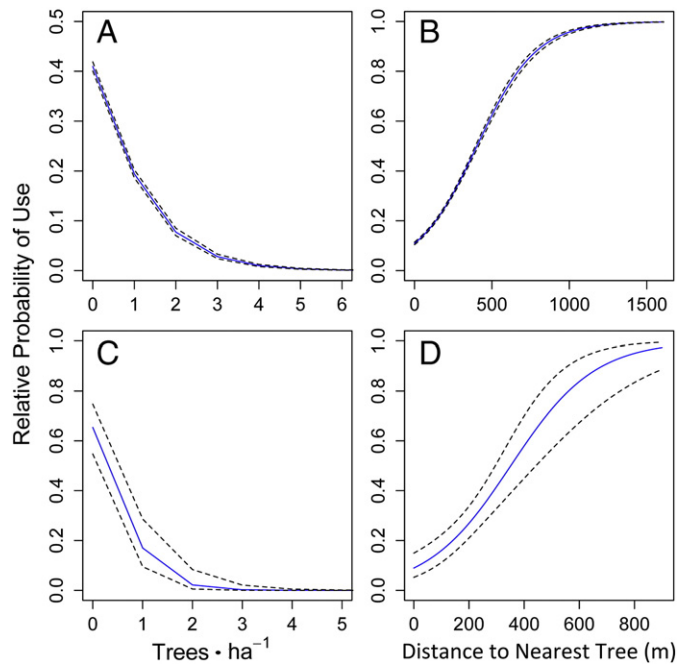


Figure 3. Relative probability of female lesser prairie-chickens' use (95% CI) in relation to distance to the nearest tree (m; A). Relative probability of female lesser prairie-chicken habitat use (95% CI) in relation to distance to tree density (trees · ha⁻¹) at the 16-ha scale (B), probability of nest site (95% CI) in relation to distance to the nearest tree (m; C), and relative probability of female lesser prairie-chicken nest site selection (95% CI) in relation to tree densities (trees · ha⁻¹) at the 36-ha scale (D) in Kiowa and Comanche counties, Kansas, 2013–2014.

tree (Fig. 3B). Coefficients for elevation and slope suggest that lesser prairie-chickens were more likely to select areas with higher elevations ($\beta = 0.49$, 95% CI = 0.45, 0.54) and habitats with shallower slopes ($\beta = 0.20$, 95% CI = 0.16, 0.23).

Third-Order Habitat Selection

We estimated 23 and 14 utilization distributions for the 6-mo breeding and nonbreeding seasons, respectively, pooled across both years. On average, females used breeding season habitat at greater distances from trees and with lower tree densities than available within the home range ($\beta_{distance} = 0.12$, 95% CI = 0.05, 0.19; $\beta_{density} = -0.10$, 95% CI = -0.14, -0.05). Elevation and slope were not significant predictors of space use during the breeding season.

Tree density was the only predictor of space use during the nonbreeding season; females avoided areas as tree density increased ($\beta_{density} = -0.19$, 95% CI = -0.27, -0.11). Space use relative to nearest tree was similar to the breeding season in magnitude and direction; however, it was not measurable ($\beta_{distance} = 0.11$, 95% CI = -0.06, 0.29). Consistent with the breeding season, slope and elevation were not predictors of nonbreeding season space use.

Nest Site Selection

Lesser prairie-chicken nest placement had a negative relationship ($\beta = -1.12$, 95% CI = -1.18, -1.06) to tree density, and no nests were placed in habitats with > 2 trees · ha⁻¹ (see Fig. 2B). Of the models tested, distance to nearest tree combined with tree density best predicted nest placement (Table 2). The probability of a lesser prairie-chicken placing a nest in habitat with 0 trees · ha⁻¹ was 30 times greater than placing a nest in habitats with two trees · ha⁻¹ (see Fig. 3C). Female lesser prairie-chickens were more likely to select nest sites at greater distances ($\beta = 1.40$, 95% CI = 1.36, 1.44) from trees than would be available at random. The probability of lesser prairie-chickens placing nests 1000 m away from the nearest tree was 10 times greater than that of a nest being placed 0 m from the nearest tree (see Fig. 3B). Nests were placed at higher elevations ($\beta = 0.55$, 95% CI = 0.52, 0.58) on average; however, slope ($\beta = 0.13$, 95% CI = 0.10, 0.15) was not an important predictor of nest site selection.

Table 2

Rankings of models to test relative influence of tree density (Density; trees · ha⁻¹), distance to nearest tree (Dist. Tree; m), elevation above sea level (Elevation; m), and slope (%) in determining lesser prairie-chicken nest site selection at the 36-ha scale in Kiowa and Comanche counties, Kansas, 2013–2014

Model	ΔAIC_c^1	K ²	w _i ³	Dev. ⁴
Density + Dist. Tree	0.0 ⁵	3	0.817	137.4
Global ⁶	3.6	5	0.138	137.0
Density	7.3	2	0.022	146.7
Density + Slope	8.8	3	0.010	146.3
Density + Elevation	8.9	3	0.010	146.3
Density + Slope + Elevation	10.6	4	0.004	146.1
Dist. Tree	65.4	2	<0.001	204.9
Dist. Tree + Elevation	66.6	3	<0.001	204.0
Dist. Tree + Slope	67.0	3	<0.001	204.4
Dist. Tree + Slope + Elevation	67.6	4	<0.001	203.3
Null ⁷	102.4	1	<0.001	243.8
Elevation	104.2	2	<0.001	243.6
Slope	104.3	2	<0.001	243.7
Elevation + Slope	106.1	3	<0.001	243.6

¹ Deviance.
² Number of parameters.
³ Differences in Akaike's information criterion, corrected for a small sample size.
⁴ Akaike weights.
⁵ Global model included density, a quadratic function of Density, Dist. Tree, slope, and elevation.
⁶ Minimum AIC_c = 143.3.
⁷ Null model compared used and random locations with no covariates.

Table 3

Model ranking for lesser prairie-chicken nest survival using the covariates of elevation (m), slope (%), distance to nearest tree (m), and tree density (trees · ha⁻¹) in Kiowa and Comanche counties, Kansas, 2013–2014

Model	ΔAIC_c^1	K ²	w _i ³	Dev. ⁴
Elevation	0.0	2	0.18	401.1
Slope	0.88	2	0.12	399.5
Distance to Tree	1.42	2	0.09	401.0
Density	1.54	2	0.08	401.1
Elevation + Slope	1.68	3	0.08	399.2
Distance to Tree + Elevation	1.77	3	0.08	399.3
Density + Elevation	1.88	3	0.07	399.4
Distance to Tree + Quadratic Distance to Tree	2.16	3	0.06	399.7
Distance to Tree + Slope	2.85	3	0.04	400.3
Density + Slope	2.85	3	0.04	400.4
Density + Quadratic Density	2.96	3	0.04	400.5
Distance to Tree + Density	3.40	3	0.03	400.9
Elevation + Slope + Distance to Tree	3.58	4	0.03	399.1
Elevation + Slope + Density	3.60	4	0.03	399.1
Elevation + Slope + Distance to Tree + Density	5.52	5	0.01	399.0

¹ Differences in Akaike's information criterion, corrected for a small sample size.
² Number of parameters.
³ Akaike weights. 4 Deviance.

There was no single best predictor of daily nest survival among the investigated seven competing models (Table 3). The top predictor of nest survival of the covariates tested was elevation, followed by slope (see Table 3). However, neither elevation nor slope was a significant predictor of nest survival ($\beta_{Elevation} = -0.020$, 95% CI = -0.053, 0.012; $\beta_{Slope} = 0.067$, 95% CI = -0.091, 0.225). Distance to tree did not have an effect on nest survival ($\beta_{Distance} = -0.413E-3$, 95% CI = -0.002, 0.002). Nest survival does not appear to be affected by tree density ($\beta_{Density} = 0.096$, 95% CI = -0.790, 0.983); however, we did not observe any nests located in areas ≥ 2 trees · ha⁻¹.

Not surprising, tree densities varied across the study site and canopy coverage was related to tree density. Tree densities on the study site ranged from 0.0 to 59.0 trees · ha⁻¹. Tree density was a satisfactory predictor of percent canopy coverage ($R^2 = 0.60$, $\beta_{Density} = 0.389$; SE = 0.032, $P < 0.001$; Fig. 4).

Discussion

Our study is the first to investigate the effect of trees on female lesser prairie-chicken space use, nest site selection, and nest survival. Our work confirms that lesser prairie-chicken space use can be driven by low levels of tree encroachment. Previous work on prairie grouse has

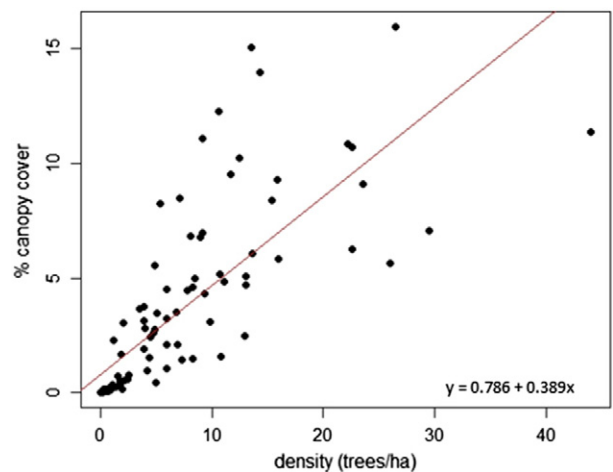


Figure 4. The relationship of tree density to canopy coverage of eastern redcedar for management of lesser prairie-chicken habitat in Kiowa and Comanche counties, Kansas 2013–2014.

primarily focused on lek location, drivers of lek site selection relative to the occurrence of trees, and nest survival relative to forest cover. Our results indicated that female lesser prairie-chickens 1) selected areas at greater distances from trees and lower tree densities than would be expected at random at two different orders of selection; 2) placed nests in habitats with tree densities $< 2 \text{ trees} \cdot \text{ha}^{-1}$ and at distances $\geq \sim 300 \text{ m}$ from nearest tree; 3) nest survival was not affected by tree densities up to two trees $\cdot \text{ha}^{-1}$ or distance to nearest tree; and 4) use and nest placement effectively cease at tree density thresholds of 8 trees $\cdot \text{ha}^{-1}$ and 2 trees $\cdot \text{ha}^{-1}$, respectively. Nest sites were selected at a larger scale (36 ha) than used points (16 ha); a potential result of different life history needs and ecological drivers commensurate with each scale. Lastly, our results indicated that tree density was an adequate predictor of canopy coverage. Counting individual trees from aerial imagery using remote sensing can be easier at times than estimating canopy coverage, especially over large expanses of land.

Because tree encroachment has been implicated as a source of habitat loss and fragmentation for lesser prairie-chickens (Fuhlendorf et al., 2002), we predicted that female lesser prairie-chickens would select habitats relative to density and distance to trees. It is evident that female lesser prairie-chickens avoid trees, as probability of use increased as tree densities decreased and distance from the nearest tree increased; however, lesser prairie-chickens avoided trees by $\sim 300 \text{ m}$ on average when selecting habitat and nest sites. Topographic habitat selection indicated that female lesser prairie-chickens selected areas of higher elevations, but selection was not related to the steepness of slope, indicating trees in uplands and hilltops may influence female lesser prairie-chickens more than trees in drainages, creating a larger functional habitat loss in upland areas.

Our prediction of a tolerance threshold for nest placement as a function of tree density was substantiated. We did not detect female lesser prairie-chickens nesting in areas with $\geq 2 \text{ trees} \cdot \text{ha}^{-1}$ ($\sim 1.56\%$ canopy cover) at the 36-ha ($\sim 89 \text{ ac}$) spatial scale. Our findings are consistent with greater prairie-chicken response to trees, where minimal tree cover and distance from woodlands (a 20% increase in relative probability of selection for each 100 m) were primary factors in nest site selection (Matthews et al., 2013; Hovick et al., 2015). Surprisingly, our data did not detect reduced nest success as a function of tree density or distance to nearest tree. This finding may be explained in part by the definitive hierarchical pattern of avoidance of trees. That is, lesser prairie-chickens have enough options in this contemporary landscape in which they can select nest sites away from trees and not succumb to the habitat sink (Lautenbach, 2015). Similarly, waterfowl, which have a nesting strategy similar to prairie grouse, exhibited no negative responses in nest survival to eight variables with respect to woody vegetation in Minnesota grasslands (Thompson et al., 2012).

Prairie grouse habitat selection is a balancing act of predator avoidance, thermoregulation, and forage availability (Gratson, 1988). The marked threshold effects observed in our study suggest that predator avoidance may outweigh thermoregulation and foraging needs. High-density tree areas still retain elements of potential habitat (D. Haukos, unpublished data), yet these areas were highly avoided during selection of seasonal use and nest sites. Raptors are major predators of lesser prairie-chickens (Hagen et al., 2007; Wolfe et al., 2007; Pirijs, 2011; Plumb, 2015) and tree encroachment into grasslands may provide additional perches for raptors (Reinert, 1984; Widén, 1994; Manzer and Hannon, 2005). Additionally, mammalian predators are more likely to occupy grassland sites with edge habitat and woodland (Litvaitis and Shaw, 1980; Gese et al., 1988; Kuehl and Clark, 2002; Manzer and Hannon, 2005). Other prairie grouse select habitat to avoid predators (Gratson, 1988). Avoidance of trees as a functional response to a perceived predation risk has been hypothesized to be the source of this behavior in prairie-grouse and other bird species (e.g., Gratson, 1988; Thompson et al., 2014, 2016).

Restoration of grasslands through removal of trees would allow for testing of some of these hypotheses related to avoidance. We predict

that grasslands with trees removed would become available habitat for lesser prairie-chickens within 1–2 yr postremoval. Greater sage-grouse readily used habitats 1 yr post juniper removal (Frey et al., 2013). Models indicate that colonization of potential habitat by greater prairie-chickens is hindered by woodlands (McNew et al., 2012). After initial population declines, grassland passerines increased in abundance 4–6 yr after broad-scale tree removal (Thompson et al., 2016). The next step in understanding lesser prairie-chicken conservation involves an experimental harvest of trees to restore grasslands. This would provide valuable information to grassland managers and ensure that conservation practices enhance lesser prairie-chicken populations.

Implications

Trees, like the eastern redcedar, can encroach into prairie uplands at rates of 2.3% forest cover $\cdot \text{yr}^{-1}$ (Briggs et al., 2002). Thus, preventing trees from establishing in grassland habitat occupied by lesser prairie-chickens would reduce functional habitat loss potentially contributing to conservation of lesser prairie-chicken populations. Regular use of prescribed fire is a cost-effective way to prevent trees from establishing in grasslands (Ortmann et al., 1998; Fuhlendorf et al., 2008).

Grassland restoration for the lesser prairie-chicken may be most effective if tree removal efforts are initially targeted in regions occupied by lesser prairie-chickens. Targeting occupied areas will improve habitat quality, increase habitat occupancy over time, and allow populations to disperse into unoccupied habitats. Mechanical removal, chemical applications, and prescribed fire are all methods that could be employed to remove already established trees from grasslands (Ortmann et al., 1998; Fuhlendorf et al., 2008). Following tree removal, design of a regular prescribed fire program may prevent new trees from establishing from the soil seed bank.

Conservation efforts for lesser prairie-chicken may be most effective when targeting areas with $> 2 \text{ trees} \cdot \text{ha}^{-1}$ ($> 1.56\%$ canopy cover) to enhance nesting habitat in areas currently occupied by lesser prairie-chickens. Beginning tree-removal efforts in areas with lower tree densities and moving into areas with greater tree densities will open up potential habitat more quickly, similar to suggestions to prioritize management for greater sage-grouse (Baruch-Mordo et al., 2013). Once areas occupied by lesser prairie-chickens have been cleared of trees, moving into unoccupied areas could provide additional habitat and these areas may be colonized.

Focusing management initially on areas with low tree densities also has financial benefits because costs of tree removal in grasslands vary depending on the level of infestation. Using estimates from 2015, removing trees from grasslands with light infestations (1–5% canopy cover) had a cost of $\$158.62 \cdot \text{ha}^{-1}$ (C. Hagen, Lesser Prairie-Chicken Initiative), making light infestations the most cost-effective to treat. As the level of infestation increases to medium (6–15% canopy cover) and heavy ($> 15\%$ canopy cover), cost increases to $\$400.46$ and $\$1035.72 \cdot \text{ha}^{-1}$, respectively (C. Hagen, Lesser Prairie-Chicken Initiative). Thus, it may be more cost-effective for current government cost-share conservation programs to prioritize areas with low canopy cover in an effort to rapidly restore grasslands. Establishing a prescribed fire program after tree removal will increase the effectiveness of current cost-share programs.

Historically, periodic fire prevented trees from becoming established in grasslands. With the loss of periodic fire in Southern Great Plains grasslands, trees have since become established and reduced grassland habitats. Removing trees, although costly, would be an excellent opportunity to create and maintain habitat for a species of conservation concern while also improving conditions for a suite of species dependent on grasslands in the Southern Great Plains.

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