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Research Article

Factors Influencing Nesting Ecology of Lesser Prairie-Chickens

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ABSTRACT Lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations have declined since the 1980s. Understanding factors influencing nest-site selection and nest survival are important for conservation and management of lesser prairie-chicken populations. However, >75% of the extant population is in the northern extent of the range where data on breeding season ecology are lacking. We tested factors influencing fine-scale and regional nest-site selection and nest survival across the northern portion of the lesser prairie-chicken range. We trapped and affixed satellite global positioning system and very high frequency transmitters to female lesser prairie-chickens ($n = 307$) in south-central and western Kansas and eastern Colorado, USA. We located and monitored 257 lesser prairie-chicken nests from 2013 to 2016. We evaluated nest-site selection and nest survival in comparison to vegetation composition and structure. Overall, nest-site selection in relation to vegetation characteristics was similar across our study area. Lesser prairie-chickens selected nest microsites with 75% visual obstruction 2.0–3.5 dm tall and 95.7% of all nests were in habitat with ≥1 dm and ≤4 dm visual obstruction. Nests were located in areas with 6–8% bare ground, on average, avoiding areas with greater percent cover of bare ground. The type of vegetation present was less important than cover of adequate height. Nest survival was maximized when 75% visual obstruction was 2.0–4.0 dm. Nest survival did not vary spatially or among years and generally increased as intensity of drought decreased throughout the study although not significantly. To provide nesting cover considering yearly variation in drought conditions, it is important to maintain residual cover by managing for structural heterogeneity of vegetation. Managing for structural heterogeneity could be accomplished by maintaining or strategically applying practices of the Conservation Reserve Program, using appropriate fire and grazing disturbances in native working grasslands, and establishing site-specific monitoring of vegetation composition and structure.

KEY WORDS habitat selection, Kansas, lesser prairie-chicken, nest-site selection, nest survival, *Tympanuchus pallidicinctus*.

Recruitment has been identified as the most influential vital rate for growth of gamebird populations (Wisdom and Mills 1997, Clark et al. 2008, Hagen et al. 2009, Taylor et al. 2012, Ross et al. 2018). Sensitivity analyses consistently rank nest survival and brood survival as leading factors contributing to population growth for prairie-chickens (*Tympanuchus* spp.; Wisdom and Mills 1997, Hagen et al. 2009, McNew et al. 2012). Variation in regional nest and brood survival can lead to different spatial population projections, indicating the importance of local conditions and management to prairie-chicken populations (McNew et al. 2012). Understanding regional differences in nest-site selection and nest survival can allow managers to develop focused conservation plans at

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fine spatial scales for species of conservation concern to improve population performance.

The lesser prairie-chicken (*T. pallidicinctus*) is segregated among 4 distinct ecoregions, forming disjunct populations across the species' range based upon unique land cover types and climate: Sand Shinnery Oak (*Quercus havardii*) Prairie, Sand Sagebrush (*Artemisia filiafolia*) Prairie, Mixed-Grass Prairie, and Short-Grass Prairie-Conservation Reserve Program (CRP) Mosaic ecoregions (McDonald et al. 2014, Boal and Haukos 2016). This species has experienced population declines and range contraction since the 1980s (Hagen et al. 2004, Boal and Haukos 2016, Rodgers 2016). In addition to variable land cover and land use threats to population growth, precipitation varies across the range of the lesser prairie-chicken, with the Sand Shinnery Oak Prairie Ecoregion in the southwest portion of the species range receiving approximately 50% of the average annual precipitation received by the northern and eastern portions of the range (Grisham et al. 2016*b*). Lesser prairie-chicken reproduction varies with precipitation. In years of drought, lesser prairie-chickens may not initiate nests or abandon nests (Grisham et al. 2014).

Variation in climate and habitat across the range of the lesser prairie-chicken results in regional differences in nest-site selection and nest survival. Nest sites in the Sand Shinnery Oak Prairie and Sand Sagebrush Prairie ecoregions generally have greater cover of shrubs at nest-sites (16.2–50.9% and 7.1–15.3%, respectively; Hagen et al. 2013) because generally these regions have less reliable precipitation, resulting in shrubs providing more reliable vegetation structure for nesting (Grisham et al. 2016*b*). Comparatively, in the Mixed-Grass Prairie ecoregion, lesser prairie-chickens select nest sites with greater amounts of grass cover with percent shrub cover consisting of 2.7% (Hagen et al. 2013). Visual obstruction readings at nest sites are consistent across the range of lesser prairie-chickens, ranging from 1.8–4.7 dm (Hagen et al. 2013). Bare ground was avoided in all regions (Hagen et al. 2013, Fritts et al. 2016).

The northern portion of the lesser prairie-chicken range, located in Kansas and eastern Colorado, USA, includes the entirety of the Sand Sagebrush Prairie and Short-Grass Prairie-CRP Mosaic ecoregions, and the northern portion of Mixed-Grass Prairie Ecoregion (McDonald et al. 2014, Haukos and Boal 2016). In contrast to other ecoregions, lesser prairie-chickens have experienced range expansion and mild population growth within the Short-Grass Prairie-CRP Mosaic Ecoregion since the mid-1990s (Dahlgren et al. 2016, Rodgers 2016). Lesser prairie-chicken range expansion into the Shortgrass Prairie-CRP Mosaic Ecoregion has been attributed primarily to the conversion of row-crop agricultural lands to CRP grasslands, many of which were planted to mixed and tallgrass prairie species, which were historically absent in the ecoregion (Dahlgren et al. 2016, Rodgers 2016, Sullins et al. 2018*b*). The majority of the remaining range and much of the remaining population of the lesser prairie-chicken lies within the northern extent of its occupied range (McDonald et al. 2014, Boal and Haukos 2016). Of the extant 33,269 lesser prairie-chickens estimated in 2017, 64% resided in the Short-Grass Prairie-CRP Mosaic Ecoregion, 4% resided in the Sand Sagebrush Prairie Ecoregion, and approximately 12% in the Kansas portion of the Mixed-Grass Prairie Ecoregion (McDonald et al. 2017).

Within the southern portions of the lesser prairie-chicken range, residual grass cover and shrub cover are important nest habitat; additionally, drought can limit reproduction in this region, creating a boom-bust pattern in population demography (Haukos and Smith 1989; Hagen et al. 2013; Grisham et al. 2014, 2016*b*). Residual grass cover remains important in the northern lesser prairie-chicken range, but environmental conditions and threats differ from the southern populations. For instance, there is an increased importance of fire and more precipitation on average in the northern extent of lesser prairie-chicken range (Grisham et al. 2016*a*, Lautenbach 2017). Understanding habitat and environmental factors influencing reproductive success in the northern portion of the lesser prairie-chicken range will contribute to conservation planning and development of local and regional management strategies to increase lesser prairie-chicken abundance and occupied range. Testing potential factors influencing nest-site selection and nest survival of lesser prairie-chickens will increase ecoregion-specific information available to managers for sound management decisions.

Our primary goal was to assess nest-site selection and nest survival relative to regional and vegetation characteristics among ecoregions across the northern extent of lesser prairie-chicken range. Our objectives were 3-fold: investigate the influence of vegetative characteristics on nest-site selection by lesser prairie-chickens at the scale of the study regions throughout the northern range of the species and across all study areas, compare nest-site selection between the Short Grass Prairie-CRP Mosaic and Mixed-Grass Prairie ecoregions, and estimate nest survival and regional and vegetation variables affecting survival concurrently among different ecoregions in Kansas and Colorado. We hypothesized that there would be a greater selection of grass cover in south-central Kansas because of greater average annual precipitation compared to northwest Kansas (30-yr average annual precipitation in south-central Kansas and northwest Kansas was 59–69 cm and 47–52 cm, respectively [Sullins et al. 2018*a*]); nest survival would be greater in northwest Kansas than south-central Kansas, based on recent population increases and range expansion (Dahlgren et al. 2016); and nest survival would relate more to fine-scale habitat variables than region.

STUDY AREA

We conducted our study from 15 March 2013 to 15 July 2016 on 7 study sites located within Kansas and Colorado that represented 3 of the 4 defined ecoregions occupied by lesser prairie-chickens: 3 in south-central Kansas, 2 in northwest Kansas, and 2 in eastern Colorado (Fig. 1; McDonald et al. 2014). The south-central Kansas sites were located on private lands in Clark, Comanche, and Kiowa counties and all occurred within the Mixed-Grass Prairie Ecoregion. The

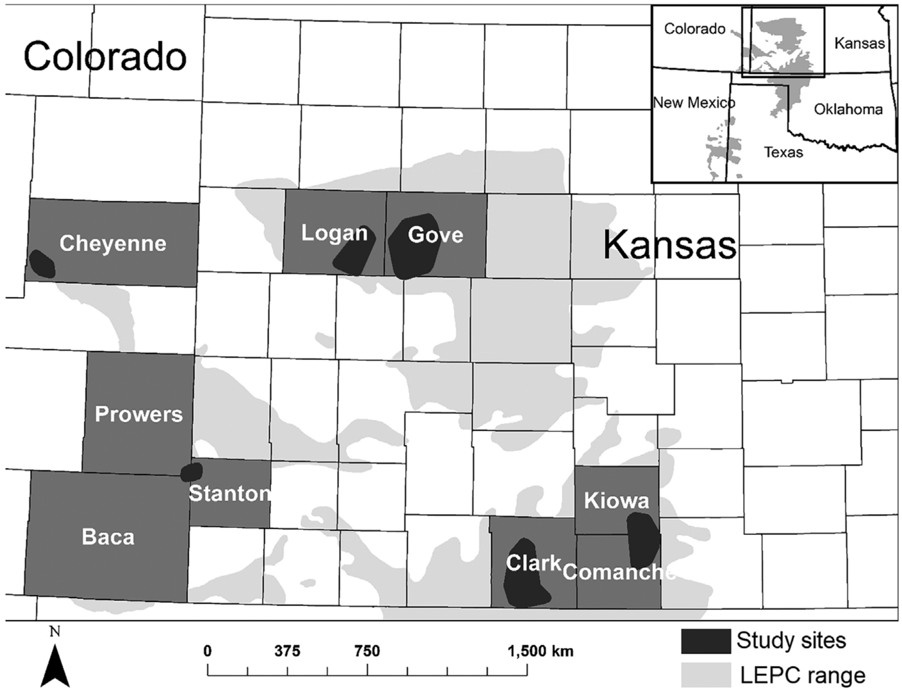

Figure 1. Study sites for lesser prairie-chicken (LEPC) nesting ecology during 2013–2016 across Kansas and Colorado, USA.

region primarily consisted of mixed-grass prairie on loamy and sandy soils. Land use was dominated by livestock grazing and row-crop agriculture, with primary crops consisting of wheat, corn, and sorghum. The Clark site was 77% grassland, 14% cropland, and 5.5% CRP, whereas the Kiowa and Comanche site was 87% grassland, 8.9% cropland, and 2.2% CRP (Robinson 2015). Dominant vegetation within the region included little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), sideoats grama (*B. curtipendula*), buffalograss (*B. dactyloides*), sand dropseed (*Sporobolus cryptandrus*), alkali sacaton (*S. airoides*), Louisiana sagewort (*Artemisia ludiviciana*), western ragweed (*Ambrosia psilostachya*), Russian thistle (*Salsola* sp.), kochia (*Kochia scoparium*), annual sunflower (*Helianthus annuus*), sand sagebrush, and eastern red cedar (*Juniperus virginiana*). Common species of mammals and birds within the region included coyote (*Canis latrans*), thirteen-lined ground-squirrels (*Ictidomys tridecemlineatus*), black-tailed prairie-dog (*Cynomys ludovicianus*), white-tailed deer (*Odocoileus virginianus*), eastern meadowlark (*Sturnella magna*), western meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), and dickcissel (*Spiza americana*).

In northwest Kansas, study sites were located on private lands within Gove and Logan counties within the Short-Grass Prairie-CRP Mosaic Ecoregion (Fig. 1). The Smoky Valley Ranch in Logan County, owned and managed by The Nature Conservancy, was included in the study. These study sites were a mosaic of short-grass and mixed-grass prairies, CRP grasslands, and row-crop agriculture on silt loam soils. Dominant land uses included livestock grazing, row-crop agriculture, and CRP. The landscape surrounding the Gove study site was composed of 8.0% CRP, 34% cropland, and 54% native working grasslands; the landscape surrounding the Logan study site was 8.0% CRP, 32% cropland, and 56% native working grassland (Robinson 2015). Dominant vegetation included blue grama, hairy grama, buffalograss, little bluestem, side oats grama, big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed. Some of the species planted within the CRP fields included little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, Indiangrass (*Sorghastrum nutans*), white sweet clover (*Melilotus alba*), yellow sweet clover (*M. officinalis*), Maximillian sunflower (*Helianthus maximiliani*), Illinois bundleflower, purple prairie clover (*Dalea purpurea*), and prairie coneflower (*Ratibida columnifera*). Wheat, sorghum, and corn were major crops in the region. Common mammals and birds at the site included coyote, black-tailed prairie-dog, thirteen-lined ground-squirrel, white-tailed deer, western meadowlark, grasshopper sparrow, and horned lark (*Eremophila alpestris*).

Within eastern Colorado, the study sites were located on private lands in Baca, Cheyenne, and Prowers counties. All study sites were within the Sand Sagebrush Prairie Ecoregion (Fig. 1). Land use within the study site included ranching-pastureland, row-crop agriculture, and CRP grasslands. Dominate vegetation in the region included blue grama, hairy grama, sideoats grama, little bluestem, sand sagebrush, kochia, and Russian thistle. Major crops within the region included wheat, sorghum, and corn. Common mammals and birds at the site included coyote, swift fox (*Vulpes velox*), black-tailed prairie-dog, thirteen-lined ground-squirrel, western meadowlark, grasshopper sparrow, and horned lark. We combined nests in the northwest Kansas and Colorado sites because of similarities between study areas (both were dominated by a landscape mosaic) and the small sample size of nests in Colorado.

Temperatures ranged from −26 to 43°C, with average daily minimum and maximum temperatures of 6.0°C and 21.2°C, respectively, during the period of data collection (15 Mar 2013 to 31 Aug 2016; National Oceanic and Atmospheric Administration [NOAA] 2017*a*). Drought severity varied throughout the study and was characterized using the Palmer Drought Severity Index (PDSI), an index of relative dryness derived from temperature and precipitation data. The standardized index is centered at zero; ≤−4 indicates severe drought and anything above 0 indicates wetter than average (Palmer 1965). Values of PDSI during the previous summer have been linked to fluctuations in lesser prairie-chicken population abundance during spring lek attendance (Ross et al. 2016). During breeding seasons of 2013, 2014, 2015, and 2016, PDSI values were −2.56, −0.96, 0.87, and 1.91, respectively. During the nonbreeding seasons, average PDSI values were −1.15, −0.27, and 1.60 in 2013, 2014, and 2015, respectively (NOAA 2017*b*). Overall, drought intensity decreased from March 2013 to August 2016 when the study ended. For more information on weather conditions during the study see Sullins et al. (2018*a*, *b*) and Lautenbach (2017).

METHODS

Capture and Monitoring

We captured lesser prairie-chicken females at leks using walk-in traps and drop nets, which do not negatively affect survival (Haukos et al. 1990, Silvy et al. 1990, Schroeder and Braun 1991, Grisham et al. 2015). We trapped leks from 10 March–15 May during 2013–2016. We sexed and aged captured lesser prairie-chickens using plumage characteristics (Copelin 1963). We fitted captured females with either a 22-g global positioning system (GPS) satellite transmitter (platform transmitting terminals [PTT]; Microwave Telemetry, Columbia, MD, USA, and North Star Science and Technology, Oakton, VA, USA) or a 12-g very high frequency (VHF) radio-transmitter (Advanced Telemetry System, Isanti, MN, USA). Each PTT contained sensors to transmit calibrated indices for unit temperature and motion, which we used to determine if individuals were alive. We mounted PTTs on the rump using leg harnesses made of Teflon ribbon (Dzialak et al. 2011). The VHF radio-transmitters were equipped with a 12-hour mortality switch. We released captured individuals at the site of capture. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocol numbers 3241 and 3703), Kansas Department of Wildlife, Parks, and Tourism (scientific collection permit numbers SC-042-2013, SC-079-2014, SC-001-2015, and SC-014-2016), and Colorado Parks and Wildlife (scientific collection license numbers 13TRb2053, 14TRb2053, and 15TRb2053).

We located female lesser prairie-chickens fitted with VHF transmitters via triangulation (≥3 times/week) using a 3-element, hand-held Yagi antenna, along with a radio receiver (Advanced Telemetry Systems, Isanti, MN, USA, and Communication Specialists, Orange, CA, USA) to record telemetry locations via triangulation based on a minimum of 3 bearings (Cochran and Lord 1963). We used a maximum 20-minute time interval between bearings to minimize error from lesser prairie-chicken movement (Pitman et al. 2005). We used a hand-held GPS unit to record Universal Transverse Mercator (UTM) coordinates (Garmin eTrex 30, Garmin International, Olathe, KS, USA) and Location of a Signal software (Ecological Software Solutions, Hegymagas, Hungary) to estimate UTM coordinates from VHF data collected in the field. For lesser prairie-chickens fitted with PTTs, the duty cycle for GPS fixes was 1 data point taken every 2 hours from 0400–2200 (∼8–10 points/day) with a data transmission cycle via the Argos system of 8 hours on and 50 hours off. Potential location error using PTTs was ≤18 m.

We identified nest locations by approaching females marked with VHF transmitters using homing once a female had been recorded in the same location for ≥3 consecutive days (White and Garrott 1990, Pitman et al. 2005). For females with PTTs, we used GPS locations to indicate when each female had begun incubation using the constant GPS location over an approximate 3-day period to initially locate each nest. We also checked locations for nests when females visited the same locations each day from 1200–1400 over a 3-day period and when females displayed unique movement patterns relative to non-nesting females (Boal et al. 2013). We recorded the UTM coordinates of nest locations using a hand-held GPS unit. When we approached nests, we wore rubber boots and latex gloves to reduce scent and scent trails around the nests. At each nest, we recorded the number of eggs present. We floated 3–4 eggs per clutch to estimate nest initiation date, nest incubation date, and predicted hatch date (Coats 1955, Pitman et al. 2006, McNew et al. 2009, Grisham et al. 2013). We attempted to spend as little time as possible at the nest (<5 min; Grisham 2012). Thereafter, we monitored nests remotely using radio signal and GPS location of females. If telemetry or GPS fixes indicated the female was off the nest for an unusual amount of time (generally 2–3 days), we approached to assess nest fate (Pitman et al. 2005). We categorized nests as successful (≥1 egg hatching) or unsuccessful (depredated, destroyed, or abandoned). We considered a nest abandoned if the nest was left unattended for ≥3 consecutive days. We considered a nest successful if we found pipped egg shells in the nest or egg shells with intact membranes. We recorded the number of hatched eggs in the clutch.

Nest Vegetation

We conducted a standardized vegetation survey at each nest bowl and each nest site within 3 days after we identified the fate of the nest using protocols adopted by the Natural Resources Conservation Service Lesser Prairie-Chicken Initiative and Lesser Prairie-Chicken Interstate Working Group as sampling strategies for standardization among field studies (Pitman et al. 2005, Grisham et al. 2013). We recorded the dominant plant surrounding the nest and management type of the pasture or field. We estimated percent canopy cover of shrubs, forbs, grasses, bare ground, and litter using a modified Daubenmire frame at the nest bowl and 4 m from the point center in each cardinal direction (Daubenmire 1959). We measured litter depth every 0.5 m in each cardinal direction out to 4 m. We estimated height (dm) of a 75% visual obstruction reading using a Robel pole at the point center from a distance of 4 m and a height of 1 m (Robel et al. 1970). We measured vegetation following the same techniques used at the nest at a paired random point at a random distance within 360 m from the nest in a random direction (Grisham 2012).

Additionally, we measured vegetation characteristics at random points distributed throughout each study site using the same techniques to investigate nest site selection. We generated random points throughout the study sites at a rate of 1 per 4 ha with a maximum of 10 points per patch as a way to distribute points across the landscape. We delineated and digitized user-defined habitat patches in ArcGIS 10.2 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA) using aerial imagery available in the basemap layer (product of ESRI, i-cubed, USDA FSA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGP). We identified patches as areas of homogenous vegetation >2 ha in size and placed them in categories (e.g., grassland, grassland lowland, CRP) and confirmed category via ground truthing (Sullins et al. 2018*b*). We measured vegetation at points within all delineated patches during spring and summer.

Statistical Analyses

We compared nest vegetation characteristics (visual obstruction; percent cover of litter, grass, forbs, bare ground, and shrubs) between used and paired random sites using a factorial analysis of variance. Main effects included region and vegetation characteristics. Factors included in the analysis of variance were region and nest site versus random point.

We used logistic regression to assess nest-site selection, where we compared nest sites (used) separately to random points distributed across each study site (available; Design III, Manly et al. 2002). We assessed second-order selection of nests sites by female lesser prairie-chickens (Johnson 1980). We included percent cover of litter, grass, forbs, bare ground, and shrubs, and visual obstruction and a quadratic visual obstruction term because we hypothesized that there was likely a structural threshold for nest-site selection by female lesser prairie-chickens. We used 5,406 random points, with 1,411 and 3,995 in northwest Kansas and south-central Kansas, respectively. We weighted models to account for disparity between the number of nests and random points across both ecoregions and within ecoregion. We evaluated beta coefficients from the model to estimate selection within the logistic regression function. If the 95% confidence interval of the betas did not overlap zero, we considered those betas significant. We used Program R (R Core Development Team, version 3.2.2, 2015, Vienna, Austria) for all statistical analyses. We used $\alpha = 0.05$ for statistical significance.

To assess nest survival, we used the nest survival procedure within the package RMark in Program R (White and Burnham 1999, Dinsmore et al. 2002, Laake 2013). We used a 38-day exposure period composed of a 10-day laying period (average clutch size) and a 28-day incubation period to estimate nest survival across the laying and incubation period (Grisham et al. 2014, Blomberg et al. 2015). Nests were active from 3 April–18 July for a 105-day nesting period. We used the delta method to estimate variance when extrapolating daily nest survival to overall nest survival (Powell 2007). We used the estimated initiation date of the nest (i; Blomberg et al. 2015), the day before the nest hatched or failed as the last day the nest was checked alive (j), and the date of hatch or failure as the last day the nest was checked (k; Dinsmore et al. 2002) to estimate exposure days for each nest.

We tested 20 *a priori* potential models to determine factors influencing daily nest survival. These models included additive and interactive combinations of region, year, nest vegetation variables, and nest initiation date. Visual obstruction, grass cover, and litter cover are important to nest survival and nest-site selection in other ecoregions and forb cover has been identified as important for brood rearing habitat; therefore, we tested these variables in our models (Pitman et al. 2005, Fields et al. 2006, Grisham et al. 2013, Hagen et al. 2013). We hypothesized that nest survival would be different between the 2 ecoregions; thus, we included ecoregion in the analyses. We combined habitat and ecoregion variables because we anticipated there may be a difference in habitat conditions between the 2 ecoregions. Furthermore, during the course of the study, there were very different environmental conditions each year, which may have influenced habitat conditions. We used the mean value for any missing data values for nests (Grisham et al. 2014). We used Akaike's Information Criterion, corrected for a small sample size (AIC_c), ΔAIC_c, and Akaike weights to select models (Burnham and Anderson 2002). If models had $\Delta AIC_c < 2$ we considered them to be competitive.

RESULTS

Nest Characteristics

From 2013–2016, we captured 307 females and located and monitored 257 nests (60 in 2013, 120 in 2014, 62 in 2015, and 15 in 2016) in Kansas and Colorado. Of all the nests found, 204 of the nests were first attempts and 53 were renests. Within south-central Kansas, we found and monitored 22, 68, 42, and 15 nests in 2013, 2014, 2015, and 2016, respectively. Within northwest Kansas, we monitored 41, 53, and 20 nests in 2013, 2014, and 2015, respectively. We located 65.3% of nests in grazed pastures, 20.4% in ungrazed pastures, 13.6% in CRP fields, and 0.8% in row-crop agricultural fields. Nest fates across all years and regions were 32.8% hatched, 55.7% depredated, 1.5% trampled, 1.9% lost because the female was killed off the nest, and 6.9% abandoned; we were unable to identify the cause of failure for 1.1% of nests.

Table 1. Dominant plant surrounding nests of lesser prairie-chickens within northwest Kansas and eastern Colorado (NW; $n = 118$) and south-central Kansas (SC; $n = 141$), USA, and across all regions (total) during 2013–2016.

	NW		SC		Total	
Species	**Nests**	**%**	**Nests**	**%**	**Nests**	**%**
Alkali sacaton	0	0.0	4	2.8	4	1.5
Big bluestem	0	0.0	3	2.1	3	1.1
Blue grama	11	9.1	3	2.1	14	5.3
Broom snakeweed (*Gutierrezia sarothrae*)	0	0.0	1	0.7	1	0.4
Buffalograss	0	0.0	1	0.7	1	0.4
Cheat grass (*Bromus tectorum*)	6	5.0	12	8.5	18	6.9
Domestic wheat	2	1.7	0	0.0	2	0.8
Grama sp.	0	0.0	0	0.0	0	0.0
Indiangrass	2	1.7	0	0.0	2	0.8
Kochia	1	0.8	0	0.0	1	0.4
Little bluestem	17	14.0	45	31.9	62	23.7
Louisiana sagewort	0	0.0	6	4.3	6	2.3
Purple threeawn (*Aristida purpurea*)	1	0.8	3	2.1	4	1.5
Russian thistle	1	0.8	0	0.0	1	0.4
Sand dropseed	9	7.4	13	9.2	22	8.4
Sand lovegrass (*Eragrostis trichodes*)	0	0.0	1	0.7	1	0.4
Sand sagebrush	2	1.7	2	1.4	4	1.5
Sideoatsgrama	50	41.3	9	6.4	59	22.5
Soapweed yucca (*Yucca glauca*)	2	1.7	0	0.0	2	0.8
Switchgrass	3	2.5	1	0.7	4	1.5
Tall dropseed (*Sporobolus compositus*)	0	0.0	31	22.0	31	11.8
Vine mesquite (*Panicum obtusum*)	0	0.0	1	0.7	1	0.4
Western ragweed	0	0.0	2	1.4	2	0.8
Western wheatgrass (*Pascopyrum smithii*)	6	5.0	0	0.0	6	2.3
Unidentified grass sp.	3	2.5	0	0.0	3	1.1
Not recorded	5	4.1	3	2.1	8	3.1

The dominant vegetation type surrounding nests was grass (Table 1). In northwest Kansas, the most common species surrounding a nest was sideoats grama (41.3%), whereas little bluestem was the most common species in south-central Kansas (31.9%; Table 1). Nests were also commonly placed in dropseed and sacaton grasses (*Sporobolus* spp.) in both regions (Table 1). On average, grasses made up 54% and 64% of vegetation surrounding nests in south-central Kansas and northwest Kansas, respectively (Table 2). Forbs were more readily used in south-central Kansas, likely because of a greater proportion of forb availability on the south-central Kansas study sites (Tables 1,2). Shrubs were rarely used in both regions (Tables 1,2).

There were regional differences in vegetation between nest sites and paired random within-patch points. Within south-central Kansas, visual obstruction was 75% greater and percent bare ground was 35% less at nests than paired random points (Table 2). Percent covers of grass, forbs, litter, and shrubs were used in proportion to paired sites within grasslands in south-central Kansas. Within northwest Kansas, female lesser prairie-chickens selected nest sites with 70% greater visual obstruction, 40% greater litter cover, and 43% less cover of bare ground than at paired sites (Table 2).

A quadratic relationship for visual obstruction was present for nest-site selection; both regions exhibited a convex quadratic pattern of visual obstruction with a maximum probability of use at 75% visual obstruction of 3 dm (Table 3; Fig. 2). Female lesser prairie-chickens selected nest sites with more litter and fewer shrubs than available

Table 2. Comparison of average and standard errors (SE) of vegetation composition and structure at nest sites and paired random points of lesser prairie-chicken nests in south-central Kansas (SC) and northwest Kansas and eastern Colorado (NW), USA, 2013–2016.

	Nests	**SE**	**Paired**	**SE**	**DF**	***F***	***P***
SC							
75% visual obstruction (dm)	2.53	0.12	1.45	0.19	1, 279	92.77	0.001
Litter (%)	15.65	2.28	14.54	2.07	1, 279	0.51	0.477
Grass (%)	53.99	3.53	50.35	3.77	1, 279	1.94	0.164
Forbs (%)	21.01	2.12	19.86	2.11	1, 279	0.58	0.448
Bare ground (%)	8.28	1.40	12.85	2.05	1, 279	13.35	0.001
Shrubs (%)	1.31	0.72	2.22	1.13	1, 279	1.81	0.180
NW							
75% visual obstruction (dm)	1.88	0.13	1.10	0.19	1, 195	50.49	0.001
Litter (%)	23.73	2.70	17.01	2.48	1, 195	12.35	0.001
Grass (%)	63.93	3.14	62.80	4.67	1, 195	0.13	0.721
Forbs (%)	7.53	1.62	8.31	1.88	1, 195	0.42	0.516
Bare ground (%)	6.88	1.26	12.07	3.99	1, 195	8.35	0.004
Shrubs (%)	1.96	1.06	1.02	0.92	1, 195	2.14	0.145

Table 3. Resource selection functions, standard errors, and 95% confidence intervals (lower [LCI] and upper [UCI]) of lesser prairie-chicken nest-site selection in relation to vegetative features in Kansas and Colorado, USA, during 2013–2016. Variables included percent cover of litter (litter), grass (grass), forbs (forbs), bare ground (bare), and shrubs (shrub); visual obstruction reading (VOR, dm); and a quadratic function of VOR (VOR^2) for all study sites (all), study sites in northwest Kansas and Colorado (NW), and sites in south-central Kansas (SC).

	Estimate	SE	95% LCI	95% UCI
All sites				
Intercept	−2.925	1.290	−5.486	−0.407
*Litter	0.035	0.013	0.009	0.062
Grass	−0.007	0.012	−0.031	0.017
*Forbs	−0.031	0.015	−0.060	−0.001
*Bare	−0.032	0.015	−0.062	−0.002
Shrub	−0.014	0.023	−0.061	0.031
*VOR	3.312	0.412	2.549	4.167
*VOR^2	−0.577	0.091	−0.765	−0.409
NW				
Intercept	1.205	2.235	−3.167	5.653
*Litter	−0.032	0.022	−0.076	−0.010
Grass	−0.046	0.024	−0.093	0.000
Forbs	−0.037	0.026	−0.089	0.014
*Bare	−0.072	0.027	−0.127	−0.021
Shrub	0.013	0.043	−0.068	0.100
*VOR	3.715	0.669	2.503	5.133
*VOR^2	−0.781	0.171	−1.143	−0.473
SC				
Intercept	−6.420	2.247	−11.400	−3.591
*Litter	0.076	0.026	0.036	0.123
Grass	−0.007	0.019	−0.037	0.026
Forbs	−0.024	0.023	−0.056	0.022
Bare	−0.020	0.024	−0.056	0.024
*Shrub	−0.054	0.041	−0.128	−0.014
*VOR	5.225	0.919	3.787	7.138
*VOR^2	−0.832	0.176	−1.197	−0.558

*Significant coefficients.

within south-central Kansas (Table 3). In northwest Kansas, both litter and bare ground were avoided (Table 3).

Nest Survival

Nest survival for all sites in all years averaged 0.390 ± 0.028 (SE; 95% CI = 0.336–0.444). When averaged across all years, nest survival ($\hat{S}$) varied little between regions ($\hat{S}_{SC} = 0.367 \pm 0.043$, 95% CI = 0.296–0.438; $\hat{S}_{NW} = 0.420 \pm 0.043$, 95% CI = 0.336–0.502). Among years when we monitored nests in both regions, point estimates of nest survival were greater in 2015 than 2013 and 2014 ($\hat{S}_{2013} = 0.384 \pm 0.055$, 95% CI = 0.277–0.491; $\hat{S}_{2014} = 0.347 \pm 0.040$, 95% CI = 0.269–0.426; $\hat{S}_{2015} = 0.508 \pm 0.058$, 95% CI = 0.389–0.615); however, confidence intervals overlapped, indicating no significant difference among years. During 2016, we monitored nests only in south-central Kansas and considerable uncertainty was present in the nest survival estimate because of relatively low sample size ($\hat{S}_{2016} = 0.262 \pm 0.101$, 95% CI = 0.095–0.468). Nest survival reflected annual environmental conditions within each region, with nest survival lowest in the drought years of 2013 and 2014 and greatest in 2015 (Table 4). Nest survival was greater in first nest attempts than renest attempts, although the difference was minor ($\hat{S}_{First} = 0.398 \pm 0.031$, 95% CI = 0.377–0.458; $\hat{S}_{Renest} = 0.357 \pm 0.063$, 95% CI = 0.237–0.479).

Variation in nest survival was best explained by region and visual obstruction (Table 5). The habitat variable that best explained variation in nest survival was a quadratic model of 75% visual obstruction of vegetation structure (Table 5). Daily nest survival peaked at 3.6 dm in both northwest Kansas and south-central Kansas (Fig. 3). The relationships

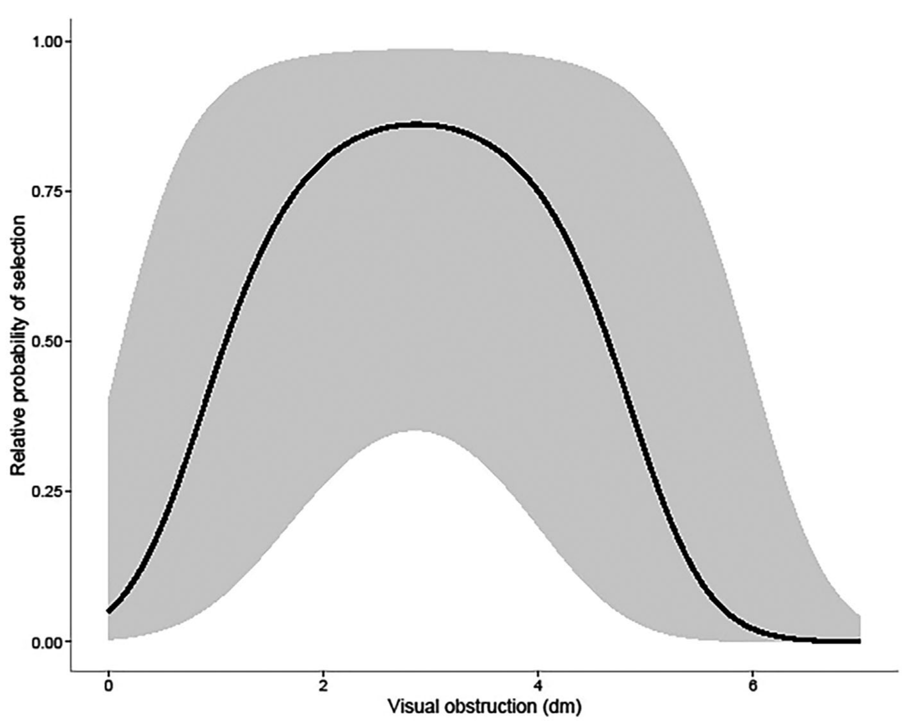

Figure 2. Probability of lesser prairie-chicken nest placement for 75% visual obstruction for all regions of Kansas and Colorado, USA, for 2013–2016, shown with 95% confidence intervals.

Table 4. Daily survival rates (DSR), nest survival estimates for the 38-day exposure period (S), and 95% confidence intervals (lower [LCI] and upper [UCI]) for lesser prairie-chickens within south-central Kansas (SC) and northwest Kansas and eastern Colorado (NW), USA, during 2013–2016. We calculated estimates using the model region × year.

Year	Region	DSR	SE (DSR)	DSR LCI	DSR UCI	S	SE (S)	S LCI	S UCI
2013	NW	0.972	0.005	0.961	0.980	0.339	0.065	0.217	0.466
	SC	0.981	0.005	0.967	0.989	0.480	0.102	0.276	0.660
2014	NW	0.979	0.004	0.970	0.985	0.442	0.065	0.314	0.564
	SC	0.967	0.005	0.957	0.975	0.277	0.049	0.186	0.375
2015	NW	0.984	0.005	0.971	0.991	0.544	0.105	0.324	0.721
	SC	0.981	0.004	0.973	0.987	0.491	0.070	0.349	0.619
2016	SC	0.965	0.007	0.950	0.999	0.262	0.101	0.095	0.468

between daily nest survival and visual obstruction were consistent among years but differed by region, with south-central Kansas having slightly lower survival than northwest Kansas (Fig. 3). Models using variables of percent cover of vegetation at the nest performed poorly (Table 5). Nest initiation date had little influence on the survival of nests (Table 5).

DISCUSSION

Our study represents the most comprehensive investigation of lesser prairie-chicken nest-site selection and survival within the northern portion of the species range. Our findings indicate that peak nest-site selection occurred when vegetation structure included 2.0–3.5 dm of 75% visual obstruction. This relationship was consistent across all of our study sites. We observed that nest survival was greatest when 75% visual obstruction was between 20–40 cm, similar to peak nest-site selection. For instance, nest survival increased by 24% and 73% when 75% visual obstruction increased from 0 to 1 dm in northwest Kansas and south-central Kansas, respectively. Nest survival again increased by 3% and 11% between 1 and 2 dm for northwest Kansas and south-central Kansas, respectively. Lastly, we found differences in nest survival between region and year; however, nest survival estimates did not vary significantly and nest survival generally increased as drought conditions lessened.

Nest-site selection by female lesser prairie-chickens indicated visual obstruction was more important than vegetative composition, regardless of the study site. Percent cover of litter was consistently selected at nest sites, suggesting residual cover was important for nest-site selection in south-central Kansas and across both regions. However, litter was avoided in northwest Kansas, perhaps because of grazing pressure during drought conditions reducing available litter. Consistent with other studies, we found avoidance of bare ground at nest sites selected by female lesser prairie-chickens across our 2 study regions (Hagen et al 2013, Grisham et al 2014). We observed 7–8%

Table 5. Model ranking for lesser prairie-chicken daily survival. Models compared included variable combinations of region (south-central Kansas vs. eastern Colorado and northwest Kansas, USA), year (2013, 2014, 2015, 2016), visual obstruction reading (VOR), a quadratic function of VOR (VOR^2), percent cover of litter (litter), percent cover of grass (grass), percent cover of forbs (forbs), nest initiation date (initiation), a quadratic function of nest initiation date ($initiation^2$), and a constant model (constant).

Model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	Deviance[e]
Region + VOR + VOR^2	4	1,426.5	0.0	0.38	1,418.5
Region + VOR	3	1,428.0	1.5	0.18	1,422.0
VOR + VOR^2	3	1,428.2	1.7	0.16	1,410.2
Region + year + VOR + VOR^2	9	1,429.2	2.7	0.10	1,423.2
Year + VOR + VOR^2	6	1,429.9	3.5	0.07	1,417.9
Region + year + VOR	8	1,430.9	4.4	0.04	1,414.8
VOR	2	1,431.2	4.7	0.04	1,427.2
Year + VOR	5	1,433.1	6.6	0.01	1,423.1
Initiation	2	1,435.5	9.0	0.00	1,431.5
Year	4	1,435.5	9.1	0.00	1,427.5
Region × year	7	1,435.8	9.3	0.00	1,421.8
Null	1	1,435.9	9.4	0.00	1,425.9
Initiation + $initiation^2$	3	1,437.0	10.5	0.00	1,435.0
Forbs	2	1,437.3	10.8	0.00	1,433.3
VOR + litter + grass + forbs	5	1,437.4	10.9	0.00	1,431.4
Litter	2	1,437.4	10.9	0.00	1,433.4
Region	2	1,438.7	12.2	0.00	1,434.7
Grass	2	1,438.7	12.2	0.00	1,434.7
Litter + grass + forbs	4	1,439.2	12.7	0.00	1,431.2
Region + year + grass + forbs + litter	10	1,439.7	13.2	0.00	1,419.6

[a] Number of parameters.
[b] Akaike's Information Criterion, corrected for a small sample size.
[c] Difference in Akaike's Information Criterion, corrected for a small sample size.
[d] Akaike weights.
[e] Deviance.

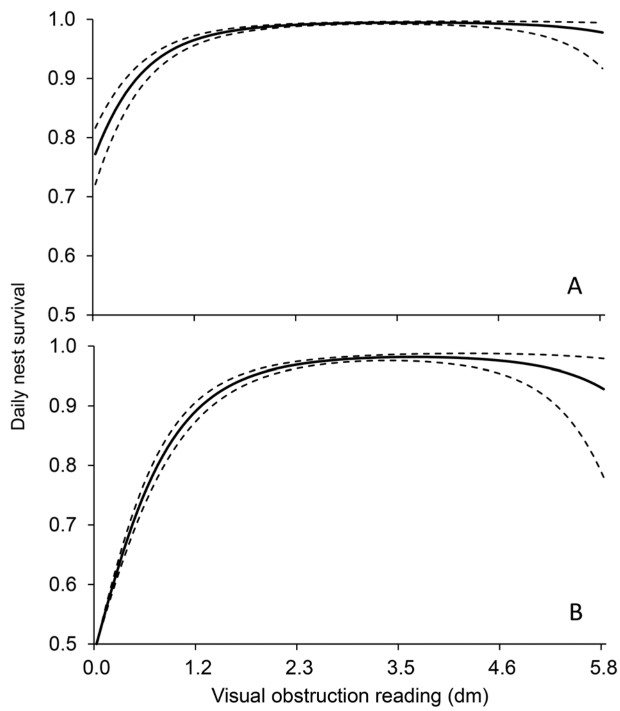

Figure 3. Daily nest survival rates of lesser prairie-chickens over the extent of observed 75% visual obstruction readings in northwest Kansas and eastern Colorado (A) and south-central Kansas (B), USA, during 2013–2016.

cover of bare ground at nest sites, on average. Within the Sand Shinnery Oak Prairie Ecoregion, Fritts et al. (2016) reported approximately 35% bare ground surrounding nests. The importance of vertical visual obstruction for nest establishment was consistent between study regions and consistent with other studies across the range of the lesser prairie-chicken (Pitman et al. 2005, Hagen et al. 2013, Grisham et al. 2014). The quadratic pattern we observed between nest-site selection and visual obstruction, however, has not been previously documented for lesser prairie-chickens.

Differences in annual average precipitation throughout the lesser prairie-chicken range drive differences in vegetation composition and structure, which in turn alters lesser prairie-chicken nest-site selection across their range (Grisham et al. 2016*b*). For instance, within the Sand Sagebrush Prairie and Sand Shinnery Oak ecoregions, lesser prairie-chicken selection of percent shrub cover increases at nest sites during drought years and as grazing intensity increases (Wilson 1982, Haukos and Smith 1989, Davis 2009, Grisham et al. 2013, Hagen et al. 2013). This shift in selection indicates that lesser prairie-chickens alter habitat use by region to optimize visual obstruction at nest sites. As precipitation becomes more reliable in the eastern portion of their range, lesser prairie-chickens increase use of grass and residual herbaceous cover for nest cover even in areas where shrubs (sand sagebrush, wild plum [*Prunus* spp.], and sumac [*Rhus* spp.]) may be readily available. Although selection for vegetation structure at nest sites was similar among the ecoregions we evaluated, management practices that provide quality nesting cover (e.g., 2.0–4.0 dm visual obstruction) may vary greatly by ecoregion and a singular rangewide management prescription will not be effective (Plumb 2015, Kraft 2016, Sullins et al. 2018*b*). Unlike in the Sand Shinnery Oak Prairie, we did not find selection for shrub cover (Grisham et al. 2016*b*). There was a greater selection for litter across all ecoregions.

Most other studies use 100% visual obstruction to measure vegetation structure. We used 75% visual obstruction based on the results from Lautenbach (2015). Our results indicated that lesser prairie-chickens are selecting nest sites under a quadratic relationships peaking at 2.0–3.5 dm of 75% visual obstruction. This range also maximized nest survival rates in comparison to other vegetation measurements. Although no other lesser prairie-chicken study has reported this threshold relationship, it is consistent with other grouse studies (Wiebe and Martin 1998, McNew et al. 2014). Similarly, nest survival was maximized between 2.0 and 4.0 dm in a quadratic relationship with 75% visual obstruction where visual obstruction was a better predictor of nest survival than vegetation composition; however, this relationship may be biased high because we sampled nest vegetation within 3 days of assessing nest fate, allowing vegetation to grow taller surrounding successful nests (Gibson et al. 2016, Smith et al. 2018). Our findings are consistent with those from greater prairie-chicken (*T. cupido*) research; however, greater prairie-chicken peak nest survival occurred at a greater visual obstruction, likely because of greater vegetation growth resulting from increased precipitation relative to lesser prairie-chicken range (McNew et al. 2014). Our findings indicate a tradeoff between cover and predation risk. For example, if a nest was placed in habitat that has >40 cm of 75% visual obstruction, the ability of the incubating female to detect and successfully escape a predation attempt may be hindered. On the contrary, vegetation with <20 cm of 75% visual obstruction may not adequately complement the female's cryptic plumage, exposing her and her clutch (Wiebe and Martin 1998). In addition to possibly providing vegetative cover, increased visual obstruction has also been linked with cooler microclimates, which could lead to increased nest survival (Wiebe and Martin 1998, Hovick et al. 2014, Grisham et al. 2016*a*, Lautenbach 2017). Cooler microclimates will also have greater relative humidity, which can also be influential in nest survival (Grisham et al. 2016*a*, Lautenbach 2017).

Annual and regional variation of lesser prairie-chicken nest survival can be influenced by weather. Our study began during one of most severe recorded droughts and drought conditions lessened as the study concluded (Heim 2017). Our results are consistent with other findings across the lesser prairie-chicken range where nest survival was negatively influenced by intensive drought conditions (Lyons et al. 2011, Grisham et al. 2014). Nest survival can decrease by 10% for every half hour when temperatures exceed 34°C (Grisham et al. 2016*a*). Additionally, long-term population trends show a decrease in years following drought and increase following years with normal or above-average precipitation (Ross et al. 2016). Our study sites were located primarily on large, intact grasslands, which have a greater potential for quick recovery following periods of drought.

Populations recovered relatively quickly on our study sites following one of the worst recorded droughts (Hagen et al. 2017, McDonald et al. 2017). Habitat within the Sand Shinnery Oak Ecoregion is much more fragmented and populations are slower to recover from extreme droughts (McDonald et al. 2017). Despite temporal effects and stochastic factors that are challenging or nearly impossible for managers to control, management that creates cover within the 2–4 dm range of heights available to lesser prairie-chickens will likely elicit the greatest increase in nest survival and nest densities.

MANAGEMENT IMPLICATIONS

Ensuring available nesting habitat across the range of environmental variation would help to reduce annual reproductive variability. Implementation of management strategies that create vegetation structure with 2.0–4.0 dm of 75% visual obstruction to increase predator and thermal refugia should increase the availability of selected nest habitats and likely improve nest survival. Strategies to improve vegetation structure on the landscape include patch-burn grazing, maximizing pasture size (>400 ha), reduced stocking rates (<0.4 animal units/ha), low-moderate grazing deferments (60–100 days), resting pastures, and placement of CRP grasslands in close proximity to leks.

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