



Research Article

Using Grazing to Manage Herbaceous Structure for a Heterogeneity-Dependent Bird

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ABSTRACT Grazing management recommendations often sacrifice the intrinsic heterogeneity of grasslands by prescribing uniform grazing distributions through smaller pastures, increased stocking densities, and reduced grazing periods. The lack of patch-burn grazing in semi-arid landscapes of the western Great Plains in North America requires alternative grazing management strategies to create and maintain heterogeneity of habitat structure (e.g., animal unit distribution, pasture configuration), but knowledge of their effects on grassland fauna is limited. The lesser prairie-chicken (*Tympanuchus pallidicinctus*), an imperiled, grassland-obligate, native to the southern Great Plains, is an excellent candidate for investigating effects of heterogeneity-based grazing management strategies because it requires diverse microhabitats among life-history stages in a semi-arid landscape. We evaluated influences of heterogeneity-based grazing management strategies on vegetation structure, habitat selection, and nest and adult survival of lesser prairie-chickens in western Kansas, USA. We captured and monitored 116 female lesser prairie-chickens marked with very high frequency (VHF) or global positioning system (GPS) transmitters and collected landscape-scale vegetation and grazing data during 2013–2015. Vegetation structure heterogeneity increased at stocking densities ≤ 0.26 animal units/ha, where use by nonbreeding female lesser prairie-chickens also increased. Probability of use for nonbreeding lesser prairie-chickens peaked at values of cattle forage use values near 37% and steadily decreased with use $\geq 40\%$. Probability of use was positively affected by increasing pasture area. A quadratic relationship existed between growing season deferment and probability of use. We found that 70% of nests were located in grazing units in which grazing pressure was < 0.8 animal unit months/ha. Daily nest survival was negatively correlated with grazing pressure. We found no relationship between adult survival and grazing management strategies. Conservation in grasslands expressing flora community composition appropriate for lesser prairie-chickens can maintain appropriate habitat structure heterogeneity through the use of low to moderate stocking densities (< 0.26 animal units/ha), greater pasture areas, and site-appropriate deferment periods. Alternative grazing management

Received: 21 April 2020; Accepted: 2 October 2020

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strategies (e.g., rest-rotation, season-long rest) may be appropriate in grasslands requiring greater heterogeneity or during intensive drought. Grazing management favoring habitat heterogeneity instead of uniform grazing distributions will likely be more conducive for preserving lesser prairie-chicken populations and grassland biodiversity. © 2021 The Wildlife Society.

KEY WORDS Andersen-Gill, deferment, forage use, grassland heterogeneity, lesser prairie-chicken, pasture area, resource selection function, stocking density, *Tympanuchus pallidicinctus*.

Grasslands are among the most imperiled ecosystems across the globe (Samson et al. 2004, Hoekstra et al. 2005), and extant grasslands are highly susceptible to anthropogenic disturbance with >3.5 million ha managed as pastureland for grazing (Goldewijk 2001). Grazing and periodic fire are the principal keystone drivers in maintenance and enhancement of grassland biodiversity in the Great Plains in North America. Mistargeted grazing practices, however, can negatively affect grassland species diversity, composition, function, and structure (Milchunas et al. 1988, Fleischner 1994, Knapp et al. 1999, Samson et al. 2004). Grazing intensity (i.e., forage use, grazing pressure, stocking rate), classification of grazers (i.e., sex, age, species), and spatiotemporal patterns of grazing are the primary determinants of grazing-associated effects (Fuhlendorf and Engle 2001). Grazing management designed to maximize annual livestock performance (e.g., management for vegetation homogeneity) is potentially harmful to grassland ecosystem function (Fleischner 1994; Hovick et al. 2014, 2015). Although a few wildlife species may benefit from habitat created by homogenous grazing disturbance, it is detrimental to most species, such as grassland birds, reliant on variable vegetation structure at a landscape scale (Knopf 1994). A shift in management strategy towards creating and maintaining landscape heterogeneity (i.e., variation in plant composition and structure) has been proposed to remedy these effects (Fuhlendorf et al. 2006).

The recoupling of fire and grazing (i.e., pyric herbivory) is commonly suggested and implemented as a means of creating landscape heterogeneity (Fuhlendorf et al. 2009), but a cultural pattern of fire suppression has limited the implementation of pyric-herbivory as a management tool in certain geographies (Taylor 2005). Moreover, in semi-arid systems such as the short-grass steppe of northeastern Colorado, USA, patch-burn grazing strategies alone fail to produce adequate nesting habitat for grassland bird species requiring relatively robust herbaceous microhabitat (Augustine and Derner 2015). In the absence of pyric-herbivory, alternative methods for creating structural heterogeneity across spatiotemporal scales, particularly in semi-arid landscapes, may be valuable. Traditional grazing systems tend to create uniform grazing disturbances by increasing stocking density (i.e., number of animal units per unit area), reducing pasture area, and increasing deferment during the growing season (i.e., proportion of growing season [Apr to 1 Oct] in which livestock were absent from a pasture). Thus, reversing these management actions should promote variation in spatiotemporal grazing disturbance and,

subsequently, a heterogeneity-based vegetation response to grazing (Fuhlendorf and Engle 2001). A growing body of evidence describes how domestic grazers perceive, interact with, and affect their environment on the Great Plains (Launchbach and Howerly 2005, Derner et al. 2009, Allred et al. 2011). Additional insights from experimental design focused on the effects of grazing disturbances on vegetation structure metrics empirically related to a wildlife species resource selection and fitness would also be valuable (Fritts et al. 2018; Smith et al. 2018; Milligan et al. 2020a, b).

In the Great Plains, prairie grouse are grassland-obligate species that require vegetation heterogeneity across broad landscapes to complete their life cycle (Haukos and Zavaleta 2016, Milligan et al. 2020a). Livestock grazing on extant grasslands has the potential to affect habitat quality for prairie grouse through changes in vegetation composition and structure. Previous investigations have assessed prairie grouse response to grazing strategies intended to promote landscape heterogeneity (e.g., patch-burn grazing, rest-rotation grazing) in vegetation relative to traditional grazing strategies (e.g., continuous grazing, annual burning and high intensity grazing) that create vegetation homogeneity across pastures. Milligan et al. (2020a, b, c) reported that rest-rotational grazing did not influence nest success or female survival of sharp-tailed grouse (*Tympanuchus phasianellus*) but found a weak positive relationship with placement of home range during the breeding season. Female greater prairie-chickens (*T. cupido*) monitored on lands managed with patch-burn grazing had annual survival estimates 35% greater than those managed with annual burning and intensive early cattle stocking (Winder et al. 2018). Female greater prairie-chickens monitored at properties managed with patch-burn grazing selected areas with low stocking rates and high fire frequencies but avoided recently burned areas (Winder et al. 2016). Smith et al. (2018) reported equivocal effects of livestock presence and indices of local livestock use on nest-site selection and survival of greater sage-grouse (*Centrocercus urophasianus*). No published studies relate space use, resource selection, and demographics of prairie grouse populations to specific grazing metrics such as intensity, deferment, forage use, and pasture size.

The lesser prairie-chicken (*T. pallidicinctus*) occupies semi-arid grasslands and shrublands of the southwestern Great Plains and requires heterogeneous environments to fulfill all life-stage needs (Fig. 1; Haukos and Zavaleta 2016). In particular, as primary factors influencing population demography, female lesser prairie-chickens transition among

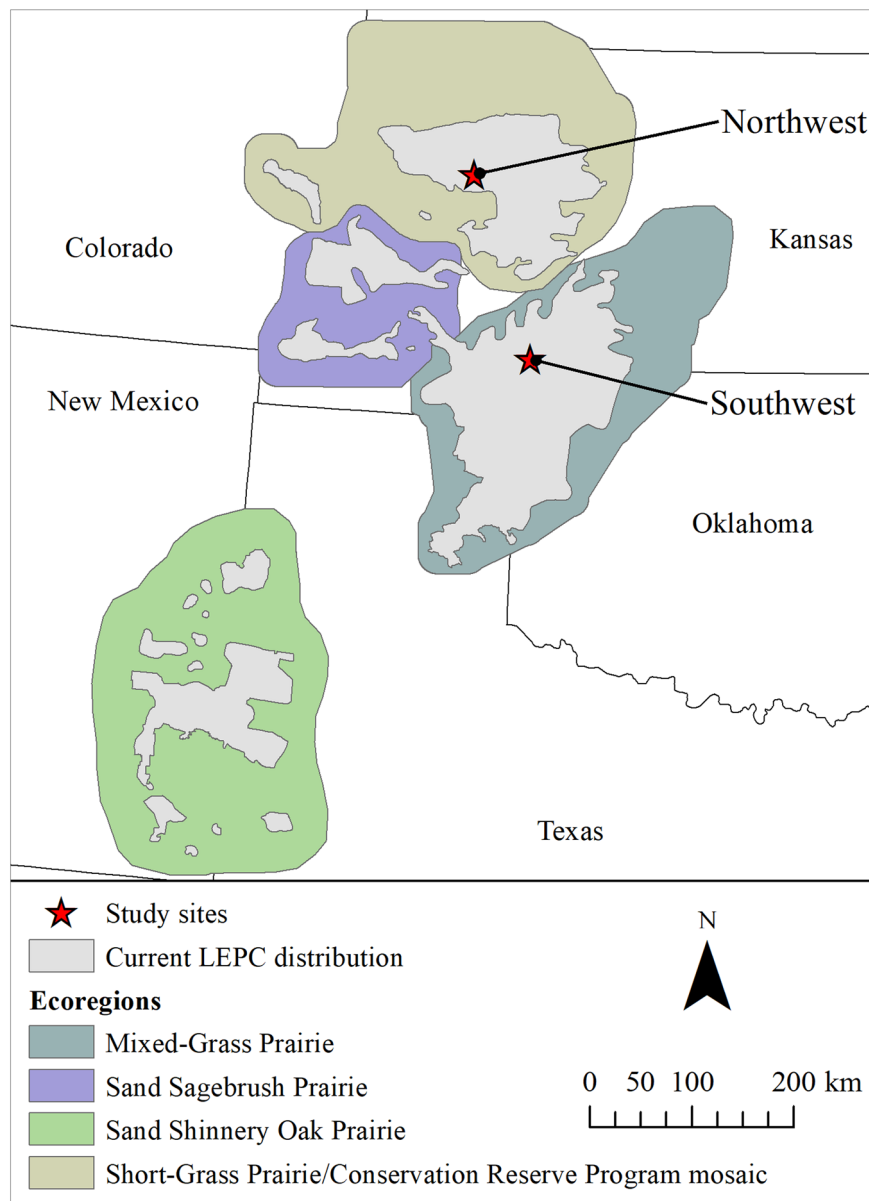


Figure 1. Study area locations where we assessed lesser prairie-chicken (LEPC) population response to livestock grazing from 2013–2015 in relation to lesser prairie-chicken distribution and ecoregions in the Southern Great Plains, USA (McDonald et al. 2014). The Northwest study area was located within Logan and Gove counties, Kansas, USA, and the Southwest study area was located within Clark County, Kansas.

a wide range of vegetation composition and structure types across all reproductive states (Hagen et al. 2009, 2013; Lautenbach 2015; Haukos and Zavaleta 2016; Lautenbach et al. 2019). When grazing management objectives are conceptualized with a goal of creating lesser prairie-chicken microhabitat, recommendations often include creation of habitat heterogeneity to accommodate nesting and brooding habitat needs by referencing a range of structural vegetation metrics (e.g., visual obstruction, height, and canopy cover; Fritts et al. 2016, Haukos and Zavaleta 2016, Lautenbach et al. 2019). Typically, a negative relationship between lesser prairie-chicken habitat quality and grazing disturbance is assumed, with recommendations generally including a light to moderate stocking rate or forage use (e.g., 33–50%; Hagen et al. 2004, Kansas Natural Resources Conservation Service

2014). Short-duration grazing at moderate grazing intensity (~50% forage use) was benign or beneficial to lesser prairie-chicken nesting ecology and adult survival, respectively, in sand shinnery oak (*Quercus havardii*) ecosystems of southeastern New Mexico, USA (Fritts et al. 2016, 2018). The effectiveness of managed grazing to create landscape heterogeneity, conditional on regional variation in precipitation, soils, and vegetation productivity, for conservation of lesser prairie-chickens on private lands is poorly understood (Giesen 1994, Hagen and Elmore 2016, Hagen et al. 2017).

Grazing management prescriptions developed to enhance lesser prairie-chicken habitat may influence management of livestock operations. Landowner incentive programs such as the Lesser Prairie-Chicken Initiative through the United States Department of Agriculture Natural Resources

Conservation Service and Western Association of Fish and Wildlife Agencies Range-wide Conservation Plan targeted potential monetary gaps between livestock production and grazing management to improve lesser prairie-chicken habitat (Van Pelt et al. 2013). Assessing the ability for heterogeneity-based grazing management to balance lesser prairie-chicken habitat and livestock production goals would be useful to optimize cost-effectiveness of future conservation efforts on private working lands.

Our objectives were to evaluate how heterogeneity-based grazing influenced vegetation structure in semi-arid environments, and could be used to manage habitat for female lesser prairie-chickens. We predicted that larger pastures, exhibiting reduced stocking densities and deferment periods, would contain the greatest habitat heterogeneity at the pasture scale. We hypothesized that lesser prairie-chickens would respond differentially to variation in grazing disturbance. We predicted a nonlinear relationship between probability of use and increasing grazing pressure. We predicted a positive relationship between female lesser prairie-chicken resource use (nonbreeding space use and nest-site selection) and larger pastures, decreased stocking density, and shorter deferment period. Third, we predicted that nest survival and adult female survival would mirror relationships between habitat use and grazing management.

STUDY AREA

Our research was concentrated on portions of 3 large ranches located in 2 distinct areas of the Short-Grass Prairie/Conservation Reserve Program (CRP) Mosaic Ecoregion (i.e., Northwest) and confluence of the Sand Sagebrush Prairie and Mid-Grass Prairie (i.e., Southwest) ecoregions where densities of lesser prairie-chickens were relatively high in western Kansas, USA, during 2013–2015 (Fig. 1; McDonald et al. 2014). The Northwest study area was focused on 2 study sites dominated by private land within Logan and Gove counties in northwest Kansas (~785 m elevation). Topography included numerous draws, ravines, and wooded riparian areas intersecting a relatively level landscape. The Southwest study area was located on private lands south of Ashland, Kansas, within Clark County (~615 m elevation). Topography was primarily flat with little change in elevation, and included the Cimarron river on the southern edge of the study area. The ranches comprised 25,259 ha, of which we included 13,398 ha in 33 pastures in this study. Primary land uses for both study areas were livestock grazing, energy exploration and extraction, and both dryland and irrigated row-crop agriculture. Conservation Reserve Program grasslands and row-crop agriculture were more abundant in Northwest than Southwest (Robinson et al. 2018). In the Northwest study area, mean annual precipitation was 48.7 cm with an overall average annual temperature of 11.1°C. Average annual maximum temperature was 20.0°C and average annual minimum temperature was 2.1°C (United States Climate Data, <http://usclimatedata.com>, accessed 15 Jan 2018). Annual precipitation during the 2013–2015 study period was similar to the long-term

average: 45.0, 55.1, and 49.4 cm, respectively. The Southwest study area had a mean annual precipitation of 61.8 cm with an overall average annual temperature of 13.3°C. Average annual maximum temperature was 21.3°C and average annual minimum temperature was 5.2°C (United States Climate Data, <http://usclimatedata.com>, accessed 15 Jan 2018). Annual precipitation during the 2013–2015 study period was slightly less than the long-term average in 2013 (41.0 cm), similar to the long-term average in 2014 (59.7 cm), and slightly greater than the long-term average in 2015 (78.7 cm). Primary occurrence of precipitation was from April to August as thunderstorms, with occasional precipitation as frontal events during fall (Sep–Dec). Winter was usually dry and windy with occasional snow events.

Predominant soil and community types (ecological sites) in the Northwest study area included limy upland, loamy upland, chalk flats, and loamy lowland. The Southwest study area was dominated by saline subirrigated, subirrigated, sandy, and sands sites. Dominant grasses in the Northwest study area included blue grama (*Bouteloua gracilis*), buffalograss (*B. dactyloides*), and western wheatgrass (*Pascopyrum smithii*). In addition to blue grama, dominant grasses in the Southwest study area were alkali sacaton (*Sporobolus airoides*) and sand dropseed (*S. cryptandrus*). Dominant fauna in the Northwest study site consisted of coyote (*Canis latrans*), swift fox (*Vulpes velox*), striped skunk (*Mephitis mephitis*), northern harrier (*Circus cyaneus*), Swainson's hawk (*Buteo swainsoni*), red-tailed hawk (*Buteo jamaicensis*), ring-necked pheasant (*Phasianus colchicus*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Dominant fauna in the Southwest study site consisted of coyote, striped skunk, American badger (*Taxidea taxus*), northern harrier, red-tailed hawk, ring-necked pheasant, and white-tailed deer.

METHODS

Capture and Bird Locations

We used walk-in funnel traps and drop nets to capture female lesser prairie-chickens on leks during spring (mid-Mar through mid-May) of 2013–2015 (Haukos et al. 1990, Silvy et al. 1990). We fitted captured females with either a very high frequency (VHF) radio-transmitter or global positioning system (GPS) satellite-transmitter (platform transmitting terminals [PTT]). We attached VHF transmitters (12 g or 15 g) with an estimated battery life of 790 days using a bib-style harness to individuals >500 g (Advanced Telemetry Systems, Isanti, MN, USA). We fitted solar-powered GPS-PTT (22 g, PTT-100, Microwave Telemetry, Columbia, MD, USA) transmitters to females weighing >700 g using a rump-style harness method (Dzialak et al. 2011). We released marked lesser prairie-chickens at the lek of capture. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocol 3241) and Kansas Department of Wildlife, Parks and

Tourism scientific wildlife permits (SC-042-2013, SC-079-2014, SC-001-2015).

We monitored radio-tagged birds from March 2013 through February 2016. We located VHF-fitted females using fixed-location triangulation 3–4 times/week throughout the lifespan of the bird or transmitter (Cochran and Lord 1963). We used handheld receivers and 3-element Yagi antennae to collect ≥ 3 bearings/location. We entered telemetry bearings into Location of a Signal software (Ecological Software Solutions, Hegymagas, Hungary) to obtain Universal Transverse Mercator coordinates of the estimated location. We generally limited error polygons of each estimated bird location to 0.1 ha. We monitored status of each VHF-tagged female via an 8-hour mortality switch installed in the transmitter. We obtained fixes of GPS-PTT locations every 2 hours during 0600–2400 (depending on sunlight and battery charge). Recorded GPS fixes uploaded to ARGOS satellites every 3 days. Potential error of these points was < 18 m. If we obtained a mortality signal, we used either homing (VHF) or previous GPS locations to locate the transmitter and identify cause-specific mortality or another reason for transmitter loss.

Grazing Management Information

Fifty-five pastures across the 3 ranches represented a gradient of grazing intensities and management strategies available to relatively high densities of lesser prairie-chickens. For functionality and efficiency, ranch managers within our study sites generally rotated cattle through pastures while keeping animal units (i.e., herd size) and forage consumption goals constant (e.g., 50% forage use for all pastures). Producers provided grazing management records of animal class (e.g., female and calf, male) herd size, average mass, and grazing duration in each pasture. We delineated pasture boundaries and calculated area (ha) for each pasture using the calculate geometry tool in ArcGIS 10.2 (Esri, Redlands, CA, USA).

We categorized 3 metrics in grazing management as indicators of potential increased within-pasture microhabitat heterogeneity: increased pasture size, decreased stocking density, and shorter period of livestock deferment during the growing season. Collectively, we defined implementation of these patterns as heterogeneity-based grazing management. We used recorded grazing data and pasture area calculations to determine grazing pressure (animal unit months/ha [AUM/ha]), stocking density (animal unit/ha [AU/ha]), and deferment (proportion of growing season in which cattle were absent [Apr–Sep]). We calculated grazing pressure at weekly intervals during each grazing period for each year.

In conjunction with pasture boundaries, we created ecological site maps using ArcGIS 10.2 (U.S. Department of Agriculture [USDA] 2013). We estimated the area (ha) within each pasture occupied by unique ecological sites (USDA 2013). We obtained expected average annual forage production estimates from state and transition models unique to each defined ecological site (USDA 2013). We estimated the expected forage available in each pasture by multiplying

the area (ha) of each unique ecological site by the average predicted annual forage production (kg/ha). We summed each unique ecological site present within a given pasture to obtain an estimate for available forage expected during average precipitation conditions. This would be the likely approach to estimate available forage by producers with large ranches and multiple grazing units. Using grazing pressure calculations, we determined forage consumption estimates for each pasture based on an expected forage efficiency of 50% and a consumption rate of 363 kg/month/1.0 AU (454-kg female; Holechek et al. 1989). To estimate forage use for each pasture, we multiplied the forage consumption estimate by 2 (to account for the destruction of forage via trampling, urinating, and defecating) and divided by the expected available forage. We estimated forage use values at weekly intervals during grazing periods to provide a cumulative measure of disturbance as grazing events progressed. Summary of the spatial and temporal scale for grazing variables are available online in Supporting Information (Table S1).

Vegetation Heterogeneity

To determine effects of vegetation heterogeneity on selection by lesser prairie-chickens, we conducted standardized vegetation surveys at each ranching operation using 33 existing pastures as experimental units with an average area of 406 ha (Table S2, available online in Supporting Information). We completed surveys during October to March 2014–2015. We either randomly generated vegetation survey points within monitored pasture units (i.e., available) using the create random points tool in ArcGIS 10.2 or randomly selected points from a pool of locations obtained from marked female lesser prairie-chickens. All survey points were limited to grassland pastures in which we collected grazing management data.

At each survey point, we recorded a 100% visual obstruction reading (VOR; the maximum height in cm completely visually obscured by vegetation) in each cardinal direction using a Robel pole at plot center from a distance of 4 m and height of 1 m (Robel et al. 1970). We recorded the tallest vegetation present within a 60 × 60-cm quadrat located at plot center, and 4 m out from plot center in each cardinal direction (Daubenmire 1959).

We then binned averaged readings for each survey point with others of identical sampling period and pasture. Secondly, we calculated the mean, coefficient of variation, and standard deviation of 100% VOR (cm) and vegetation height (cm) across each bin of survey points (binned by pasture). We also calculated grazing management components (grazing pressure, forage use, stocking density, pasture area, deferment) for each pasture and paired components with the appropriate vegetation calculations. We did not perform vegetation surveys in a given pasture until grazing was completed for the year. For each grazing management component, we divided survey points into 2 groups: above the median and below the median. We used 2-sample *t*-tests to compare vegetation values above and below the median for each grazing management component. We set $\alpha = 0.05$.

Nonbreeding Habitat and Nest-Site Selection

We evaluated habitat selection during 2013–2016 using mixed-effect resource selection functions (RSF; Boyce et al. 2002, Manly et al. 2002, Gillies et al. 2006). We employed RSFs to evaluate nonbreeding habitat (Oct–Mar) and nest-site selection by female lesser prairie-chickens. Each RSF incorporated a used versus available study design limited to contiguous portions of each ranch with available grazing data (Boyce et al. 2002, Manly et al. 2002).

For each nonbreeding RSF, we distributed 1 random location for each time- and date-stamped lesser prairie-chicken location using the create random points tool in ArcGIS 10.2. We constrained random locations to pastures within each study site to facilitate comparison among used and available pastures. Within study sites, pastures were well within the average dispersal distance of lesser prairie-chickens (~16 km) and therefore available (Earl et al. 2016). The development of RSF model sets was a 2-fold process. First, we developed a nonbreeding RSF model set to establish baseline habitat selection response of nonbreeding females to the intensity of grazing observed within our study sites. Second, we evaluated effects of heterogeneity-based grazing management strategies in the context of increasing grazing intensity. The grazing intensity model set included linear and nonlinear (quadratic) predictors of grazing pressure (AUM/ha) and forage use (%). We included the grazing intensity variable found to be the most influential in nonbreeding habitat selection in all secondary model sets as important context to interpreting the multifaceted response of female lesser prairie-chickens to grazing. Additionally, we suspected the inclusion of an objective grazing intensity metric in secondary model sets would be essential for applicable interpretation of results. We developed 3 secondary model sets (1 for each heterogeneity-based management strategy) to investigate our questions and hypotheses regarding linear and nonlinear predictors of deferment, stocking density, and pasture area. These will be referred to individually as the deferment, stocking density, and pasture area models.

Our nest dataset for testing included nest locations from successful (≥ 1 egg hatched/nest) and unsuccessful (failed nest or no recorded nest attempt) breeders. Because of our limited sample of nests due to the lag effect of grazing factors affecting nest-site selection (e.g., 2015 nest-site selection in response to grazing practices in 2014), we developed 1 set of models to evaluate nest-site selection. Nests require residual vegetation cover and at the time of nest-site selection, current year grazing disturbance generally has little influence on available nest sites (Hagen et al. 2004). Thus, we assigned grazing management components from the previous year to used and available nest sites. For example, a covariate associated with a nest in May of 2015 describes grazing during the 2014 grazing year (Apr 2014–Mar 2015). The nest-site RSF model set included 17 *a priori* models that evaluated our predictions for grazing disturbance and heterogeneity-based grazing management strategies.

In nonbreeding and nest-site-selection RSFs, we did not include explanatory variables exhibiting a correlation of

$|r| > 0.7$ in the same model. We included bird and nest identification as a random effect (random intercept) in nonbreeding RSFs and nest-site selection models, respectively (Gillies et al. 2006). Additionally, we included a random intercept of ranch in all RSF model sets. We z-transformed all continuous variables to address scaling issues among predictors and back-transformed variables for plotting response curves. We included a null (constant) model in each model set. We excluded year and site variables from our model set because the range of grazing intensities represented would have been reduced. We conducted all RSF analyses in Program R (version 3.0.1, R Foundation for Statistical Computing, Vienna, Austria) using the `glmer()` function within the `lme4` package (Bates et al. 2015).

Nest Location and Survival

We identified nest locations by homing in on VHF-marked females after females were in the same relative location for 3 consecutive days (Pitman et al. 2005, Lautenbach et al. 2019). We monitored females marked with GPS-PTTs remotely until GPS locations indicated nest initiation or early incubation. We approached nests wearing rubber boots and latex gloves to reduce possible scent trails. At first nest visit, we flushed the female and floated her eggs to estimate date of incubation (McNew et al. 2009). We monitored each nesting female daily during 2013–2015 until locations indicated that the female had left the nest. We considered nests successful if we found ≥ 1 egg exhibiting pipping, intact egg membranes, or chicks with females following hatching; otherwise, we classified the nest as unsuccessful.

We used the nest survival model in Program MARK to determine if grazing disturbance influenced nest survival of lesser prairie-chickens (White and Burnham 1999). We tested linear effects of grazing pressure, forage use, stocking intensity, deferment, pasture area, and date of the nesting season on nest survival. We examined correlations of covariates and did not include correlated ($|r| > 0.7$) covariates in the same model. We developed 24 models in an *a priori* model set that tested hypotheses related to grazing management components and daily survival rate, and estimated overall nest survival for an average exposure period of 38 days (Lautenbach et al. 2019).

Adult Survival

We used an Anderson-Gill model to evaluate how continuous, encounter-specific grazing management covariates affect hazard rates for female lesser prairie-chickens throughout the study period (Dinkins et al. 2014). We used Cox proportional hazard models to evaluate the influence of our grazing management strategies (Andersen and Gill 1982). We used all available locations for encounters of VHF-marked lesser prairie-chickens. We randomly selected PTT-marked bird locations at the rate of 1 point per bird per day from 8–10 points available per day. The frequency of locations allowed for modeling of daily survival using a daily encounter history. We randomly selected available locations for each day using the `r.sample` command in Geospatial Modeling Environment

(Beyer 2012). We used only points and mortalities located within monitored cattle operations. We created an *a priori* model set using predictors of grazing intensity and heterogeneity-based grazing management tools. We limited models to single variables because we recorded few mortalities. We tested model diagnostics with the *cox.zph* function to determine if these data met assumptions for proportional hazard functions (Fox and Weisberg 2011). Additionally, we used Kaplan-Meier methodology to estimate annual survival (Kaplan and Meier 1958).

For all analyses, we used an information-theoretic approach, Akaike's Information Criterion adjusted for small sample sizes (AIC_c), to rank and select individual models for inference within each model suite (Anderson and Burnham 2002). We considered models with $\Delta AIC_c \leq 2$ to be equally parsimonious. If beta estimates from top models differed from zero (i.e., 95% CIs did not overlap zero), then we determined the variable to be influential and plotted the relative probability of use curve (effects package; Ihaka and Gentleman 1996).

RESULTS

We captured 116 female lesser prairie-chickens during spring 2013–2015. Our pooled nonbreeding VHF and GPS-PTT location dataset included 7,018 nonbreeding lesser prairie-chicken locations and an equal number of random points. Grazing pressure ranged from 0–2.31 AUM/ha ($\bar{x} = 0.47 \pm 0.37$ [SD] AUM/ha). Estimated forage use values ranged from 0–77% ($\bar{x} = 15.0 \pm 12.2\%$). Stocking

density ranged from 0–0.96 AU/ha ($\bar{x} = 0.31 \pm 0.25$ AU/ha). Pasture area ranged from 33–736 ha ($\bar{x} = 464.29 \pm 166.69$ ha). Growing season deferment across all locations ranged from 0–100% of the growing season ($\bar{x} = 73.32 \pm 18.41\%$). Density distributions varied between used and available locations for forage use, pasture area, deferment, and stocking density (Fig. 2).

Vegetation Heterogeneity

We sampled 914 random points in 33 pastures ($\bar{x} = 27.7$ points/pasture) to assess effect of grazing management on vegetation heterogeneity. We calculated means, coefficients of variation, and corresponding standard deviations of visual obstruction (100% cm) and vegetation height (cm) for 2 grazing intensity predictors (grazing pressure and forage use) and 3 heterogeneity-based grazing management tools (stocking density, pasture area, deferment) across 33 pastures; we used 26 pastures for stocking density models during 2 sampling years (Table S2, available online in Supporting Information). As stocking density decreased, vegetation density was more variable (i.e., heterogeneous). Pastures subjected to relatively lower values of stocking density (<0.26 AU/ha) had more heterogeneous vegetation density, exhibiting roughly 40% greater values of standard deviation ($t_{21.067} = 2.79$, $P = 0.01$) and coefficient of variation ($t_{18.89} = 3.17$, $P = 0.005$) for 100% VOR than pastures subjected to relatively greater values of stocking density (>0.26 AU/ha; Fig. 3; Table S3, available online in Supporting Information). We did not detect any other significant relationships during vegetation response analyses.

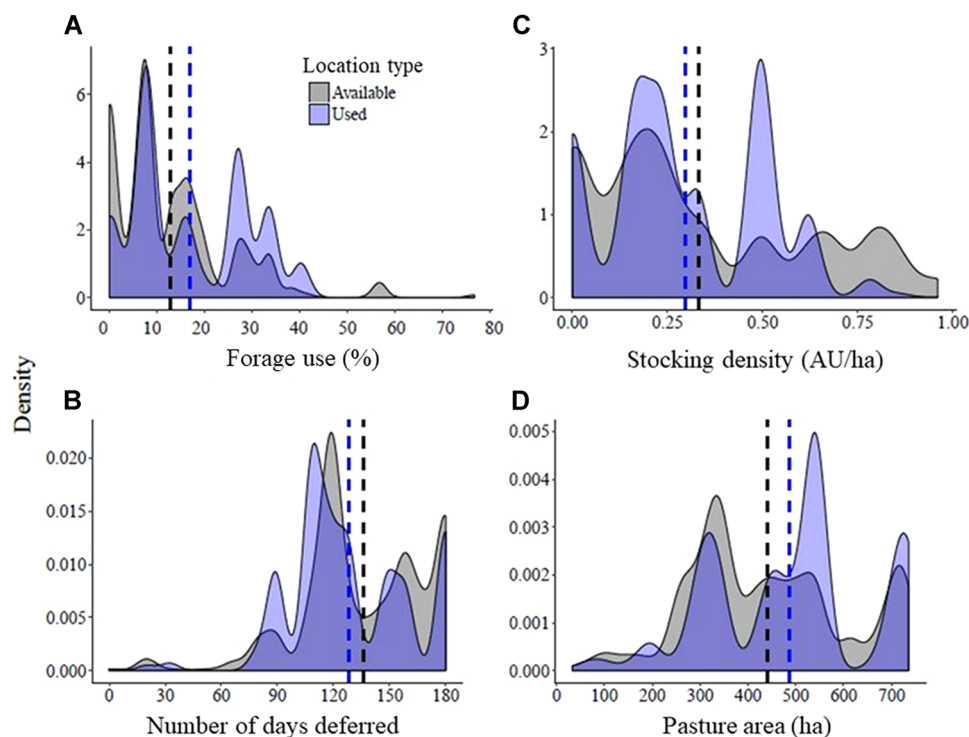


Figure 2. Density distributions of available and used locations obtained for resource selection functions evaluating the influence of grazing management components A) forage use, B) number of growing season days deferred, C) stocking density (animal units [AU]/ha), and D) pasture area on nonbreeding habitat selection by female lesser prairie-chickens in monitored grasslands, western Kansas, USA, 2013–2016. Vertical dashed lines represent the means associated with each set of available (black) and used (blue) locations.

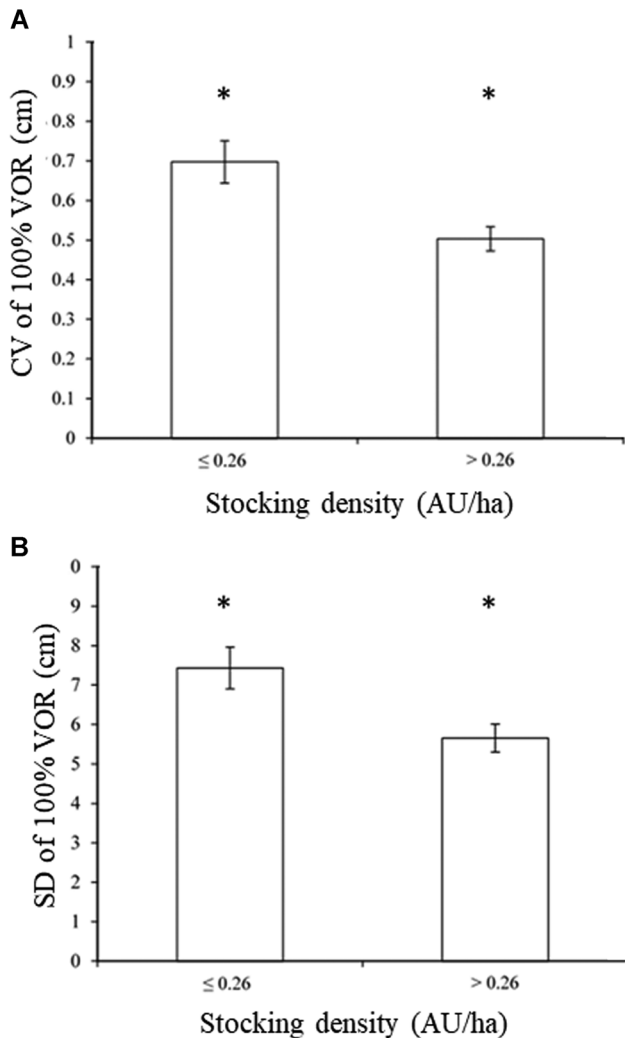


Figure 3. Mean estimates and standard errors of A) coefficient of variation (CV) of 100% visual obstruction (VOR; cm) and B) standard deviation (SD) of 100% VOR (cm) associated with 2 categories of stocking density (≤ 0.26 and > 0.26 animal units/ha [AU/ha]) applied to pastures in western Kansas, USA, 2013–2015. An asterisk (*) denotes that means differed as determined by a 2-sample *t*-test ($P < 0.05$).

Nonbreeding Habitat and Nest-Site Selection

For nonbreeding habitat selection, the results of the grazing intensity model set identified a quadratic relationship with forage use with 100% of model weight (Table 1). The variance associated with the random effects of bird and ranch were 0.025 (SD = 0.159) and 0.088 (SD = 0.029), respectively. Relative probability of use exhibited a quadratic relationship with forage use and lesser prairie-chicken habitat selection, with selection being the greatest close to 40% (Fig. 4). The quadratic effect of forage use was included in all secondary nonbreeding RSF model sets because it was the best predictor of the baseline response of lesser prairie-chickens to increasing grazing disturbance.

The top-ranked RSF model in the pasture area model set included additive influences of forage use, forage use², and pasture area (Table 1). The variance associated with the random effects of bird and ranch were 0.026 (SD = 0.160) and 0.059 (SD = 0.243), respectively. The positive beta

associated with pasture area and our model output indicated a positive linear relationship between pasture size and habitat selection by female lesser prairie-chickens (Table 2; Fig. 4).

The top-ranked model in our deferment model set was an interaction between forage use² and deferment² (Table 1). The variance associated with the random effects of bird and ranch were 0.048 (SD = 0.229) and 0.139 (SD = 0.374), respectively. Probability of use was lowest when pastures were deferred for approximately 40% of the growing season (Fig. 4). The second-ranked model of the additive version forage use² and deferment² was equally parsimonious ($\Delta AIC_c = 0.92$; Table 1).

The top-ranked model in the stocking density model set included additive effects of forage use, forage use², and stocking density and an interaction between stocking density and forage use² (Table 1). The variance associated with the random effects of bird and ranch were 0.052 (SD = 0.229) and 0.444 (SD = 0.666), respectively. Beta estimates indicated a negative relationship between stocking density and probability of lesser prairie-chicken use (Table 2). At mean values of forage use, the stocking density response curve indicated a 75% drop in relative probability of use when stocking densities were near zero AU/ha and a relative probability of use of approximately 15% as stocking density approached 1.0 AU/ha. The relationship between stocking density and forage use yields an increase in probability of use as stocking density decreases at forage use values from 0–80% (Fig. 4).

Five models of nest-site selection were equally parsimonious with values $\leq 2 \Delta AIC_c$, all of which included the quadratic relationship of grazing pressure (Table 3). The top model reported variances of 0.000 (SD = 0.000) and 1.703 (SD = 1.305) for unique nest and ranch, respectively. Our results indicated that only the quadratic relationship of grazing pressure was an influential predictor of nest-site placement being a variable in 7 of the 8 top-ranked models (Tables 2, 3). The quadratic relationship of grazing pressure illustrated that the relative probability of nest-site placement was maximized near 1.2 AUM/ha (Fig. 5).

Nest-Site Location and Survival

We located and monitored 37 nests within grazed pastures in our study sites. All nests were located in pastures exhibiting forage use values below 40%. Twenty-six of 37 (70%) nests were located where grazing pressure was < 0.8 AUM/ha.

We modeled daily nest survival for 34 nests; we censored 3 nests because they failed before we located them. Of the 34 nests, 28 were first attempts and 6 were renests. Drawing inference from our constant model, the daily survival rate of monitored nests was 0.983 (95% CI = 0.972–0.989). Nest success for the 38-day exposure incubation period was 50.1%. Seven of our 24 *a priori* nest survival models had a $\Delta AIC_c \leq 2$, but all of these models included a quadratic trend of day over the nesting season (date + date²; Table 4). The top-ranked model excluded all grazing metrics but supported a quadratic trend of day over the nesting season (date + date²), indicating that all other variables in the

Table 1. Model ranking for resource selection functions, based on Akaike's Information Criterion corrected for small sample size (AIC_c), evaluating habitat selection by female lesser prairie-chickens within monitored working grasslands in Kansas, USA, 2013–2015. We developed model sets to investigate grazing intensity (1), and heterogeneity-based grazing management (2, 3, 4) influences on nonbreeding habitat selection. Model sets include the following variables: forage use (% of forage consumed or destroyed), grazing pressure (index of grazing units per area over time; animal unit month [AUM]/ha), pasture area (size of pasture unit; ha), deferment (number of days during the grazing season [Apr–Sep] a pasture unit is void of cattle), and stocking density (number of grazing units per unit area; animal unit [AU]/ha). We include number of parameters (*K*), deviance (Dev), and Akaike weight (*w_i*) for each model.

Model set	Model structure	<i>K</i>	Dev	ΔAIC _c	<i>w_i</i>
1) Grazing intensity	Forage use	4	18,756.86	0.00	1.00
	Forage use	3	18,894.92	136.06	<0.001
	Grazing pressure ²	4	19,289.18	532.31	<0.001
	Grazing pressure	3	19,295.28	536.41	<0.001
	Null	2	19,459.42	698.55	<0.001
2) Pasture area	Forage use ² + pasture area	5	18,692.18	0.00	0.54
	Forage use ² × pasture area	6	18,690.50	0.32	0.46
	Forage use ²	4	18,756.86	62.68	<0.001
	Pasture area	3	19,200.62	504.45	<0.001
	Null	2	19,459.42	761.23	<0.001
3) Deferment	Forage use ² × deferment ²	7	17,648.46	0.00	0.44
	Forage use ² + deferment ²	6	17,647.38	0.92	0.28
	Forage use ² + deferment	5	17,650.52	2.06	0.16
	Forage use ² × deferment	6	17,652.88	2.42	0.13
	Deferment ²	4	18,061.26	408.79	<0.001
	Deferment	3	18,143.36	488.88	<0.001
	Forage use ²	4	18,756.86	1,104.39	<0.001
	Null	2	19,459.42	1,802.94	<0.001
4) Stocking density	Forage use ² × stocking density	6	18,183.54	0.00	0.81
	Forage use ² + stocking density	5	18,188.46	2.92	0.19
	Forage use ²	4	18,756.86	569.32	<0.001
	Stocking density	3	19,271.14	1,081.61	<0.001
	Null	2	19,459.42	1,267.88	<0.001

potentially competitive models were spurious. Grazing pressure occurred in the second- and third-best supported models (Table 4). Stocking density also occurred in the second-ranked model but was an uninformative parameter. Daily nest survival estimates were lowest (0.968–0.970) between days 25 and 32 of the exposure period for each nest. The top-ranked model with grazing effects predicted a negative relationship between grazing pressure and daily survival, but it was not measurably different from zero ($\beta_{\text{grazing pressure}} = -1.53$, 95% CI = -3.36 – 0.29 ; Fig. 6). Although a positive relationship was indicated by the stocking density beta estimate ($\beta_{\text{stocking density}} = 2.49$, 95% CI = -1.06 – 6.04), it was not measurably different from zero.

Adult Survival

We used 14 mortality events and 39 bird years to model the effect of grazing management components on hazard rates. Our model selection indicated the null model was the best predictor of survival within our model set, but there was considerable model uncertainty ($\Delta\text{AIC}_c \leq 2$; Table 5). The overall annual survival rate of female lesser prairie-chickens across all study sites was 0.317 (SE = 0.107, 95% CI = 0.16–0.62).

DISCUSSION

Overall, our results suggest that lesser prairie-chickens respond positively to light to moderate grazing disturbances (e.g., forage use <50% and stocking densities <0.26 AU/ha) in semi-arid environments based on expected production for the ecological sites defined by soil

types and precipitation. Heterogeneity-based grazing strategies also promoted habitat quality for an increased number of grassland species compared to grazing strategies prioritizing standardized, uniform grazing distributions (Pavlacky et al. 2019). Our research concentrated on ranching operations that had a relatively long history of implementing light to moderate grazing intensities that supported high densities of lesser prairie-chickens. Ranches within our study areas that implemented heavy grazing (>60% forage use) intensities did not support lesser prairie-chickens in sufficient numbers to be included in the study, but each of our study ranches contained pastures that sustained heavy grazing intensities and emulated what was occurring on adjacent properties but at larger scales. Our results support the conclusion of Fritts et al. (2016) that increasing levels of grazing disturbance, past critical thresholds (i.e., 40% forage use, grazing pressure >1.2 AUM/ha), negatively affected female habitat selection and potentially nest success. We concur with Milligan et al. (2020a) that a wider range of forage use rates may have revealed stronger effects on selection and possibly demographic rates, but our findings were consistent with the conclusion that greater than moderate grazing intensity negatively influence use by lesser prairie-chickens.

In continuous grazing systems, the creation of heterogeneity is contingent on the awareness of forage quality, subsequent competition among grazers for quality forage, and realized distribution of grazing pressure across a pasture (Hart et al. 1988, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). The forage quality-grazing

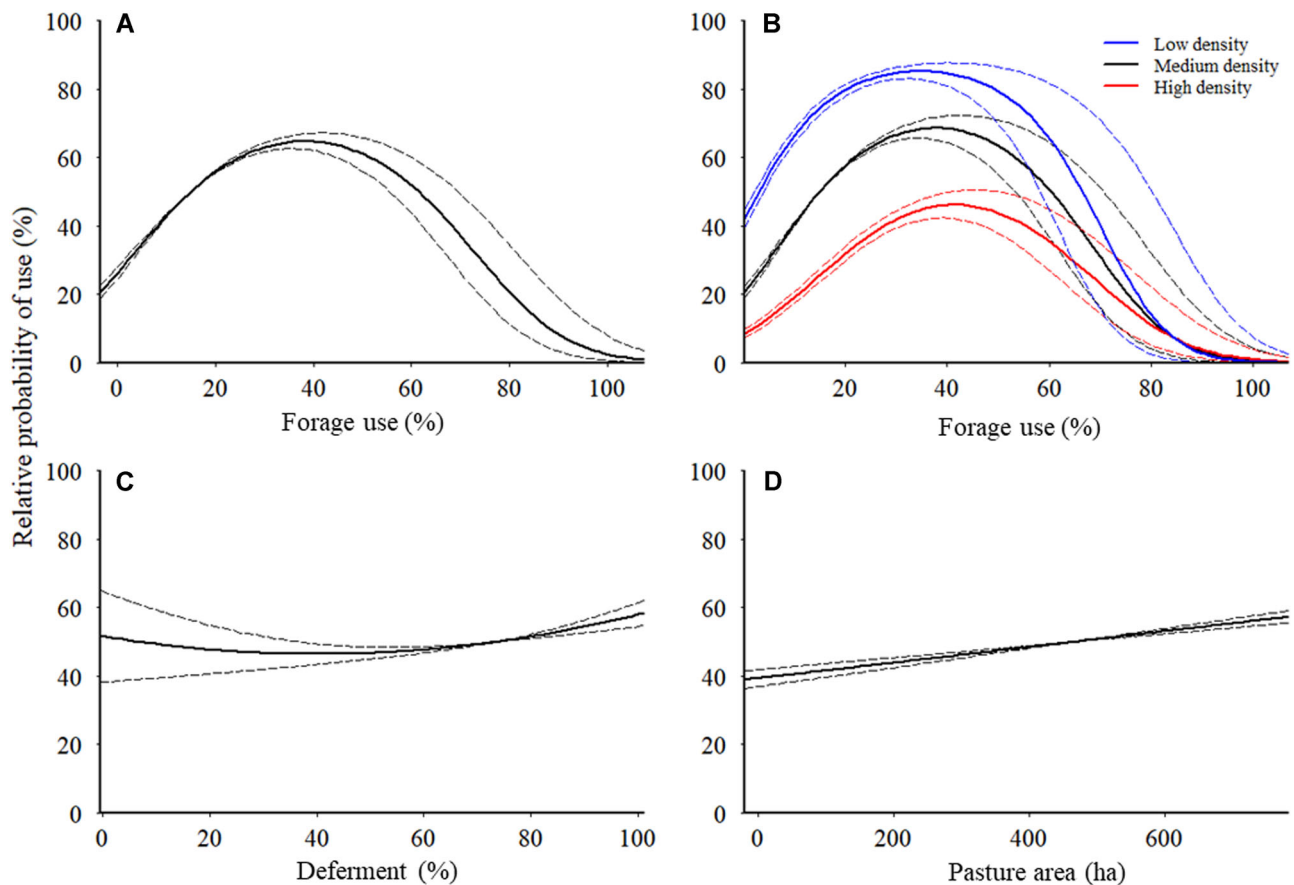


Figure 4. Relative probability of use response curves illustrating nonbreeding habitat selection by female lesser prairie-chickens in relation to A) forage use (%), B) forage use at 3 levels of stocking density ($\bar{x} \pm 1$ SD; animal units/ha [AU/ha]; low [0.06 AU/ha], medium [0.13 AU/ha], and high [0.56 AU/ha]), C) deferment (proportion of growing season), and D) pasture area (ha) within monitored grasslands grazed by cattle in western Kansas, USA, 2013–2015. We developed response curves using output from resource selection functions. We calculated forage use assuming a 50% grazing efficiency (proportion of the allocated forage consumed by livestock). The prediction curves are bounded by 95% confidence intervals (dashed lines).

distribution process is primarily influenced by stocking density. Cattle perceive variation in forage quality across a pasture and selectively graze accordingly. At high levels of stocking density, competition for high quality forage increases and cattle are forced to graze in lower quality areas

(Barnes et al. 2008). Increased competition for high quality forage associated with high stocking densities leads to greater uniformity of grazing pressure (use of the entire gradient of forage quality), resulting in uniformity in microhabitat structure across a pasture (Fuhlendorf et al. 2006). When

Table 2. Summary of beta coefficients (β) and 95% upper (UCI) and lower (LCI) confidence intervals from top-ranked resource selection functions identified using Akaike's Information Criterion for nonbreeding habitat selection (2013–2016) and nest-site selection (2013–2015) by female lesser prairie-chickens within monitored working grasslands in western Kansas, USA, 2013–2016.

Model set	Variables	β	95% LCI	95% UCI
1) Grazing intensity	Forage use	0.6397	0.5908	0.6885
	Forage use ²	−0.1681	−0.1959	−0.1404
2) Pasture area	Forage use	0.5739	0.5226	0.6252
	Forage use ²	−0.1504	−0.1790	−0.1218
	Pasture area	0.1546	0.1169	0.1923
3) Deferment	Forage use	0.7825	0.7049	0.8600
	Forage use ²	−0.1878	−0.2215	−0.1542
	Deferment ²	0.0442	0.0055	0.0830
	Deferment	0.1594	0.1002	0.2186
	Forage use ² : deferment ²	−0.0301	−0.0650	0.0048
4) Stocking density	Forage use	0.8440	0.7909	0.8971
	Forage use ²	−0.2274	−0.2719	−0.1828
	Stocking density	−1.0697	−1.1698	−0.9696
	Forage use ² : stocking density	0.0331	0.0049	0.0612
5) Nest-site selection	Grazing pressure	1.0067	0.2557	1.7577
	Grazing pressure ²	−0.3285	−0.6787	0.0216
	Pasture area	0.3154	−0.0701	0.7009

Table 3. Model ranking of resource selection functions, based on Akaike's Information Criterion corrected for small sample size (AIC_c), evaluating nest-site selection by lesser prairie-chickens within monitored working grasslands in western Kansas, USA, 2014–2015. We developed model sets to investigate influences of grazing intensity and heterogeneity-based grazing management. Variables in models sets include forage utilization (% of forage consumed or destroyed), grazing pressure (index of grazing units per area over time; animal unit month [AUM]/ha), pasture area (size of pasture unit; ha), deferment (number of days during the grazing season [Apr–Sep] a pasture unit is void of cattle), and stocking density (number of grazing units per unit area; AU/ha). We include number of parameters (K), deviance (Dev), and Akaike weight (w_i) for each model.

Model structure	K	Dev	ΔAIC_c	w_i
Grazing pressure ² + pasture area	5	181.28	0.00	0.18
Grazing pressure ²	4	183.86	0.45	0.14
Grazing pressure ² × stocking density	6	179.64	0.48	0.14
Grazing pressure ² + deferment	5	182.06	0.77	0.12
Grazing pressure ² × pasture area	6	180.88	1.72	0.08
Forage use ² + pasture area	5	183.50	2.21	0.06
Grazing pressure ² × deferment	6	181.54	2.39	0.05
Grazing pressure ² + stocking density	5	183.84	2.56	0.05
Forage use ²	4	185.96	2.56	0.05
Pasture area	3	189.58	4.08	0.02
Forage use ² × pasture area	6	183.50	4.35	0.02
Forage use ² + stocking density	5	185.78	4.49	0.02
Forage use ² + deferment	5	185.84	4.55	0.02
Forage use ² × deferment	6	185.36	6.21	0.01
Deferment	3	191.78	6.28	0.01
Null	2	193.88	6.33	0.01
Forage use ² × stocking density	6	185.76	6.61	0.01
Stocking density	3	193.72	8.23	0.00

stocking densities are held at low to moderate values, the pattern of grazing disturbance across a pasture mimics the pattern of forage quality (Chapman et al. 2007). Subsequently, a gradient of light to heavy grazing disturbance develops as pasture size increases. The gradient in grazing disturbance creates a corresponding gradient of vegetation structure and thus microhabitat heterogeneity. As predicted, results indicated that female lesser prairie-chickens select habitat based on the microhabitat heterogeneity created at lower values of stocking density.

Table 4. Model ranking based on Akaike's Information Criterion corrected for small sample size (AIC_c) of lesser prairie-chicken nest survival estimation for nests in working grasslands monitored in western Kansas, USA, during 2015. *A priori* models included variable combinations of date during the nesting season (date), a quadratic function of date (date²), grazing pressure (animal unit month [AUM]/ha), stocking density (animal unit [AU]/ha), pasture area (ha), forage use (proportion of forage consumed or destroyed), deferment (number of days deferred during the grazing season), and a constant model. We include number of parameters (K), deviance (Dev), and Akaike weight (w_i) for each model.

Model structure	K	Dev	ΔAIC_c	w_i
Date + date ²	3	164.62	0.00	0.16
Date + date ² + grazing pressure + stocking density	5	161.38	0.79	0.11
Date + date ² + grazing pressure	4	163.62	1.02	0.10
Date + date ² + pasture area	4	163.83	1.22	0.09
Date + date ² + stocking density	4	164.14	1.54	0.07
Date + date ² + forage use	4	164.52	1.92	0.06
Date + date ² + deferment	4	164.55	1.94	0.06
Date + date ² + grazing pressure + pasture area	5	162.66	2.08	0.06
Date + date ² + grazing pressure + deferment	5	163.30	2.72	0.04
Null	1	171.76	3.12	0.03
Date + date ² + forage use + pasture area	5	163.77	3.19	0.03
Date + date ² + forage use + stocking density	5	163.90	3.31	0.03
Date + date ² + forage use + deferment	5	164.34	3.75	0.02
Grazing pressure	2	170.74	4.11	0.02
Grazing pressure + stocking density	3	168.84	4.22	0.02
Pasture area	2	171.00	4.37	0.02
Stocking density	2	171.43	4.80	0.01
Forage use	2	171.61	4.98	0.01
Deferment	2	171.70	5.06	0.01
Grazing pressure + pasture area	3	169.78	5.16	0.01
Grazing pressure + deferment	3	170.43	5.81	0.01
Forage use + pasture area	3	170.88	6.26	0.01
Forage use + stocking density	3	171.13	6.51	0.01
Forage use + deferment	3	171.42	6.80	0.01

Previous researchers have assumed that increases in grazing disturbance (i.e., forage use, grazing pressure) result in negative effects on microhabitat quality for lesser prairie-chickens (Hagen et al. 2004, Dahlgren et al. 2016,

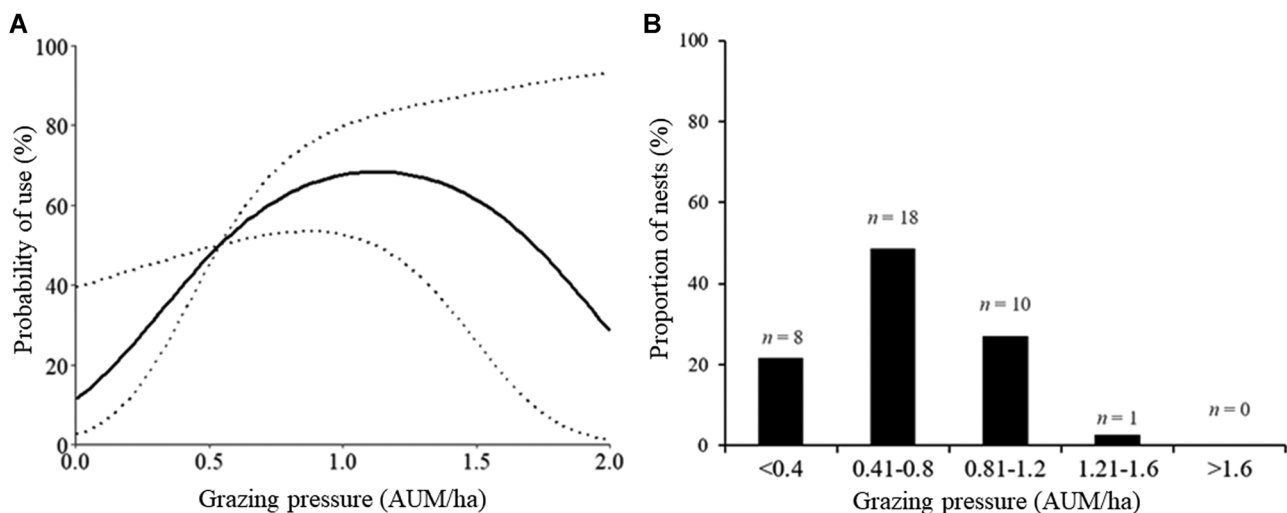


Figure 5. A) Relative probability of use curve (bounded by 95% CIs) describing nest-site selection by female lesser prairie-chickens in relation to grazing pressure (animal units/ha [AU/ha]) during the 2015 nesting season in monitored grasslands in western Kansas, USA. B) Proportions of nest-site locations used to estimate nest-site selection observed within 0.4 animal unit months (AUM)/ha interval bins of grazing pressure estimates.

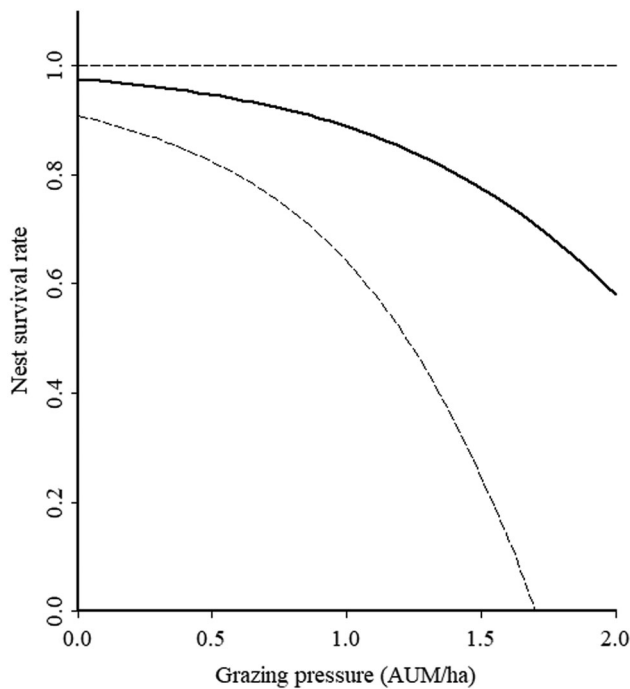


Figure 6. Daily nest survival response curve (bounded by 95% CIs) of lesser prairie-chickens in relation to grazing pressure (animal unit months [AUM]/ha) in monitored grasslands of western Kansas, USA, 2014–2015. We held stocking density and date² at their mean during modeling. Response curves are enveloped within 95% confidence intervals (dashed lines).

Hagen and Elmore 2016). We observed a threshold effect on lesser prairie-chicken habitat use in the northern portion of the species' distribution where relative probability of use was maximized near 40% forage use and steadily decreased at forage use beyond this threshold. These values corroborate prescriptions of forage use values between 30–50% recommended by Western Association of Fish and Wildlife Agencies in the Lesser Prairie-Chicken Range-Wide Conservation Plan and Natural Resources Conservation Service Lesser Prairie-Chicken Initiative (Van Pelt et al. 2013, Kansas Natural Resources Conservation Service 2014). Effects of forage use likely fluctuate as plant community composition, precipitation, and forage production vary. Thus, average expected forage production within monitored grasslands in our study was 2,639 kg/ha. Consideration for site-specific conditions (i.e., precipitation,

Table 5. Model ranking for Anderson-Gill models, based on Akaike's Information Criterion corrected for small sample size (AIC_c), for 5 models identifying the effects of grazing strategies on annual survival of female lesser prairie-chickens within working grasslands monitored in western Kansas, USA, during 2013–2016. *A priori* models included single-variable models of forage use (proportion of forage consumed or destroyed), grazing pressure (animal unit month [AUM]/ha), stocking density (animal unit [AU]/ha), and pasture area (ha). We include number of parameters (*K*), deviance (Dev), and Akaike weight (*w_i*) for each model.

Model structure	<i>K</i>	Dev	ΔAIC _c	<i>w_i</i>
Null	1	73.37	0.00	0.36
Stocking density	2	74.77	1.40	0.18
Grazing pressure	2	74.79	1.42	0.15
Forage use	2	75.18	1.81	0.15
Pasture area	2	75.37	2.00	0.13

plant community composition, forage production potential, historical management) will be essential for prescribing forage use values to achieve desired vegetation structural goals.

Previous research indicates that lesser prairie-chicken nest-site placement is characterized by the tendency of females to place nests in areas of greater grass cover, litter cover, and visual obstruction with relatively lower area of bare ground (Davis 2009, Hagen et al. 2013, Grisham et al. 2014, Haukos and Zavaleta 2016, Lautenbach et al. 2019). Nest-site selection had the greatest relative probability of occurrence at forage use values of 15–20% and declined rapidly as forage use increased past 20%. This result concurred with previously established patterns of nest-site selection by lesser prairie-chickens and importance of lightly disturbed habitat (Fritts et al. 2016, Haukos and Zavaleta 2016).

Baseline responses of habitat selection by lesser prairie-chickens to grazing disturbance provided insights into effects of heterogeneity-based grazing management. Variation of environmental characteristics such as soils, plant communities, and microhabitat structure is positively correlated with spatial scale (Wiens 1989, 2000). Thus, there is likely an inherent positive relationship between habitat heterogeneity and increasing pasture size within our study sites. Intuitively, an increase in pasture size also increased the probability of a required lesser prairie-chicken female resource (i.e., leks, nest habitat, brood habitat, winter cover) being present. Despite the increased probability of lesser prairie-chicken microhabitat presence at larger scales, it is unlikely that the relationship between pasture area and presence of quality habitat is independently creating the increased probability of use by female lesser prairie-chickens as pasture area increases. Our results combined with established concepts of grazing ecology indicate that grazing management strategies associated with larger pasture areas, such as stocking density, may be a more significant influence on microhabitat heterogeneity and lesser prairie-chicken occurrence than pasture size alone.

There was a threshold effect of deferment where probability of use increased at low and high values of deferment. We hypothesize that site-specific variation is influencing this pattern. For example, long periods of rest or deferment are likely beneficial for grasslands that exhibit relatively low potential for the production of nesting habitat. Alternatively, in grasslands exhibiting high potential for biomass production, longer grazing periods may be required to achieve desired habitat outcomes. Additional investigations focusing on the influence of deferment with consideration for regional variation is required to understand this pattern.

We did not observe a definitive pattern of lesser prairie-chicken adult survival and nest success in response to heterogeneity-based grazing strategies as we did with patterns of habitat selection. Our data suggested, however, that increasing grazing disturbance during the year previous to nest initiation may have negative influence on lesser prairie-chicken nest success. This pattern was contrary to grazing studies on other prairie grouse that reported equivocal effects

(Fritts et al. 2016, Smith et al. 2018, Milligan et al. 2020a). Although in some cases, grazing indirectly affected nesting success by providing (or removing) adequate vegetation visual obstruction. Increasing female survival during the breeding season, combined with improving recruitment is often a priority for lesser prairie-chicken population management (Hagen et al. 2009, 2013). Development of ranch-scale heterogeneity (among pastures) may mitigate effects of grazing disturbance by providing pastures with quality nesting or brood-rearing microhabitat (Fritts et al. 2018). For example, a manager could prioritize nest success within certain pastures by applying specific grazing prescriptions. In our study systems, models suggest pastures with an annual grazing pressure of 0.5 AUM/ha would result in nest success of approximately 61% based on expected available forage. Nest success at this level would be above average and representative of a stable or growing population (Hagen et al. 2013). Additionally, areas managed for greater nest success may also provide habitat that favors adult female survival during the breeding season because significant portions of adult female mortality occurs during nesting and survival is positively correlated with greater values of overhead cover (Hagen et al. 2007). Other pastures could then be grazed at levels convenient for livestock production or brood habitat. Adaptive grazing may promote heterogeneity among pastures following a deferred-rotation grazing strategy (Merrill 1954) and ensure the presence of quality habitat as weather and climate amplify the negative effects of forage use on vegetation structure (Ross et al. 2016a, b; Fritts et al. 2018). At finer scales (i.e., within pasture), success of heterogeneity-based grazing prescriptions may hinge on the development of interspersed nesting, brooding, and nonbreeding habitats (Hagen et al. 2009, Gehrt et al. 2020).

Applying site-specific grazing prescription may also be beneficial for overall participation in lesser prairie-chicken conservation strategies by private landowners. If recommendations for grazing management inhibit profitability, they will not be relevant in providing certainty for this imperiled species. Long-term grazing extension research in the region of our study suggests that moderate stocking rates (i.e., 45–50% forage use) optimize forage production and livestock gains (Launchbaugh 1957). Recent market data applied to the same long-term research suggest that moderate stocking rates also maximize profitability (K. R. Harmony, Kansas State University, personal communication).

Although effective grazing prescriptions are site-specific, our results indicate that some grazing is beneficial for lesser prairie-chickens, whereas intensive grazing can be harmful or cause avoidance of potential habitat. Our results offer an alternative for creating heterogeneous habitat for female lesser prairie-chickens through grazing management when prescribed fire may not be feasible. Heterogeneity-based grazing management strategies may not be optimum for some working grasslands where plant community composition and relatively low precipitation may not promote lesser prairie-chicken nest microhabitat under the influence of even light grazing disturbances. The prevalence of short-grass prairie dominated by buffalo grass and blue grama in

the Short-Grass Prairie/CRP Mosaic Ecoregion may require a rest-rotation grazing management scheme including season-long rest of pastures to create beneficial microhabitat for nesting (e.g., 100% visual obstruction >20 cm; Lautenbach et al. 2019). Only with the addition of mid- and tall grasses through the CRP were populations of lesser prairie-chickens sustainable in this ecoregion (Sullins et al. 2018). Therefore, a moderate grazing disturbance at the landscape scale is likely within the range of forage use goals adequate for maintaining lesser prairie-chicken habitat throughout much of the species' range.

MANAGEMENT IMPLICATIONS

Some of the largest contemporary recorded lesser prairie-chicken population densities were recorded within our study sites on landscapes characterized by long-term grazing management. Therefore, our findings are primarily in the context of maintaining and improving existing occupied habitat. Although other factors (e.g., energy development, habitat fragmentation) may be involved, lesser prairie-chickens were not present in detectable densities on neighboring sites that used more intensive grazing strategies. In regions with similar plant species composition and environmental characteristics to our study sites, heterogeneity-based grazing management may benefit lesser prairie-chickens by establishing strategies that include large pastures, low stock densities, and relatively long grazing periods. Grazing disturbance would best be targeted at 10–25% forage use in areas capable of producing nesting structure, but we encourage variation in forage use (15–50%) to meet heterogeneity needs among pastures. If the potential for nesting vegetation structure is limited or inconsistent because of the plant community or precipitation, maintenance of available nesting habitat may be possible through targeted deferment or forage use <15%. Management considerations to increase quality of lesser prairie-chicken habitat might not be as applicable to sites exhibiting less-favorable conditions resulting from the deleterious effects of long-term, heavy, continuous grazing or recent intensive drought events. More likely, our findings are better suited to sites exhibiting site potential and soil qualities conducive for supporting quality lesser prairie-chicken habitat.

ACKNOWLEDGMENTS

The contents and opinions herein do not necessarily reflect the views or policies of the United States Fish and Wildlife Service or the Kansas Department of Wildlife, Parks and Tourism. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank K. E. Sexson, J. L. Kramer, M. W. Mitchener, D. K. Dahlgren, J. A. Prendergast, K. A. Fricke, D. J. Kraft, R. W. Tacha, P. G. Kramos, A. A. Flanders, and B. S. T. Hyberg for their assistance with the project. We thank 2 anonymous reviewers for reviewing earlier versions of this manuscript. Research was funded by the USDA, Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative;

Kansas Department of Wildlife, Parks, and Tourism (Federal Assistance Grant KS W-73-R-3); The Kingsbury Family Foundation; and USDA Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA7, KSCFWRU RWO 62).

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Associate Editor: Anthony Roberts.

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