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RESEARCH ARTICLE

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Availability of lesser prairie-chicken nesting habitat impairs restoration success

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Abstract

Regional populations of lesser prairie-chickens (*Tympanuchus pallidicinctus*) have been declining irregularly since the early 1900s (Jensen et al. 2000). Populations in the Sand Sagebrush Prairie Ecoregion of Kansas and Colorado, USA, have been experiencing declines during the last 2 decades. Ecoregion-wide declines included the Cimarron and Comanche National Grasslands in southwestern Kansas and southeastern Colorado, respectively, from which lesser prairie-chickens were nearly extirpated by 2016. In 2014, the United States Department of Agriculture (USDA)–Forest Service created a vegetation management plan to restore lesser prairie-chicken nesting habitat on the National Grasslands. We used management plan recommendations to evaluate available nesting habitat on National Grasslands and surrounding areas for 394 transmitter-marked lesser prairie-chickens translocated to the Sand Sagebrush Prairie Ecoregion during 2016–2019. We found that a small proportion of vegetation measurements met the USDA–Forest Service's 100% visual obstruction guidelines of 25.4 to 38.1 cm (Cimarron: 5.3–21.8% of observations among cover types; Comanche: 1.5–3.0%), and grass species with a high value for nesting were rare (Cimarron: 0.5–20.1% of observations within each cover type; Comanche: 1.5–3.0%). Lesser prairie-chickens selected for 2 of the

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10 National Grasslands' cover types (shrubland state and warm season shortgrass state) during breeding season movements, but only shrubland state was selected for during nesting. Our results indicate that nesting habitat for lesser prairie-chickens is limited on Cimarron and Comanche National Grasslands. As private grassland was also avoided during nesting, lesser prairie-chickens in Baca and Morton counties are currently primarily relying on Conservation Reserve Program (CRP) grasslands to meet nesting habitat thresholds (Morton, KS: 17.7% CRP; Baca, CO: 16.6% CRP), which may be insufficient to sustain a viable population. Due to the impermanence of CRP, efforts to sustain local populations are likely to depend on increased improved lesser prairie-chicken nesting habitat on National Grasslands. Grazing strategies such as rest-rotation and year-long deferments may provide opportunities to restore lesser prairie-chicken habitat on sand sagebrush prairie.

KEYWORDS

Colorado, grasslands, Kansas, National Grasslands, public land, sand sagebrush prairie, *Tympanuchus pallidicinctus*, USDA–Forest Service

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations are undergoing declines in abundance and no longer occupy core areas of their range (Hagen et al. 2017). Declines are especially evident in the Sand Sagebrush (*Artemisia filifolia)* Prairie Ecoregion (McDonald et al. 2014), which once supported the highest density of lesser prairie-chickens within the species range (Haukos et al. 2016). During the 1980s, when populations in the Sand Sagebrush Prairie Ecoregion were at a contemporary high, most individuals were concentrated in large tracts of sand sagebrush prairie, which was co-dominated by sand sagebrush and mid- and tall-grasses (Haukos et al. 2016). Two of the largest intact landscapes were on the Cimarron and Comanche National Grasslands, which are managed by the United States Department of Agriculture (USDA)–Forest Service in southwestern Kansas and southeastern Colorado, USA, respectively (Figure 1). The National Grasslands were largely restored to sand sagebrush prairie from eroded crop and grazing lands following the drought of the 1930s. Combined, the National Grasslands are the predominant public lands supporting lesser prairie-chickens throughout their range and were considered strongholds for lesser prairie-chicken populations in the Sand Sagebrush Prairie Ecoregion (Elmore and Dahlgren 2016).

Lesser prairie-chickens on the National Grasslands have been declining since the late 1980s in concert with declines throughout the Sand Sagebrush Prairie Ecoregion (Figure 2; Hagen et al. 2017, Nasman et al. 2021). Starting in the early 2000s, multi-season habitat use shifted from tracts of sand sagebrush prairie to U.S. Department of Agriculture Conservation Reserve Program (CRP) grasslands in the region (Giesen 2000, Haukos et al. 2016). In the past 2 decades, lesser prairie-chicken populations on both National Grasslands experienced declines as birds consistently increased use of CRP tracts adjacent to boundaries of the National Grasslands (Kansas Department of Wildlife and Parks, unpublished data). Subsequently, use of sand sagebrush prairie on the National Grasslands declined until effective extirpation of lesser prairie-chickens from the National Grasslands by 2016, following a multi-year drought. The Sand Sagebrush Prairie Ecoregion now has the lowest lesser prairie-chicken population density of any ecoregion based on aerial surveys, with a 2021 population estimate of 440 birds (90% confidence interval = 55–963; Nasman et al. 2021). Population viability analysis indicates that the ecoregion's lesser prairie-chicken population has a high likelihood of extirpation by 2046 unless immediate action is taken to reverse the decline (Hagen et al. 2017).

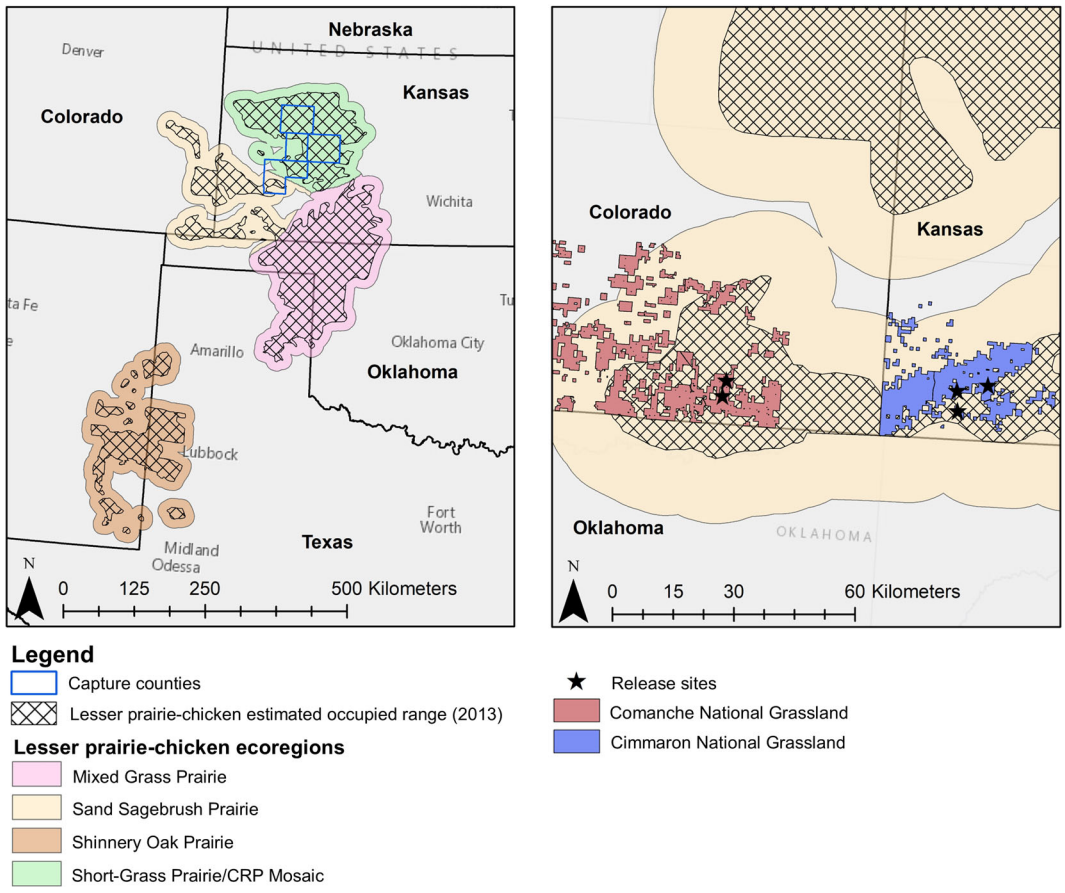

FIGURE 1 Lesser prairie-chicken ecoregions of estimated occupied range in Texas, New Mexico, Oklahoma, Colorado, and Kansas, USA, and locations of the USDA–Forest Service Cimarron and Comanche National Grasslands in Kansas and Colorado, respectively. Lesser prairie-chickens were captured in Gove, Finney, Lane, and Ness counties in Kansas and released at one of 5 sites on the Cimarron and Comanche National Grasslands.

The USDA–Forest Service has been attempting to restore lesser prairie-chicken populations on the National Grasslands since their declines became apparent. Restoration efforts were formalized in a lesser prairie-chicken habitat management plan in 2014, which states that lesser prairie-chicken habitat requirements will be considered when planning grazing, fire regimes, energy development, road construction, and fence placement on the National Grasslands (USDA–Forest Service 2014). The plan includes a set of habitat guidelines, based on recommendations in Van Pelt et al. (2013), which include 25.4–38.1 cm of visual obstruction (Robel et al. 1970), 15–20% coverage of sand sagebrush, 40–50% cover of native grasses, and 15–25% cover of native forbs. The habitat guidelines are intended to ensure that areas within 3.21 km of historic or existing leks on National Grasslands are managed to promote both nesting and brooding habitat for lesser prairie-chickens (USDA–Forest Service 2014). Grazing in lesser prairie-chicken areas is currently managed on an allotment scale, with stocking rates adjusted annually based on precipitation during the previous year. Other efforts by the USDA–Forest Service to conserve lesser prairie-chickens and their habitats include fence marking, road reclamation, and periodic prescribed fire (USDA–Forest Service 2014, Teige et al. 2021).

Several studies have attempted to determine whether vegetation on National Grasslands meets requirements for lesser prairie-chicken habitat. Two studies, which compared canopy cover of grasses, forbs,

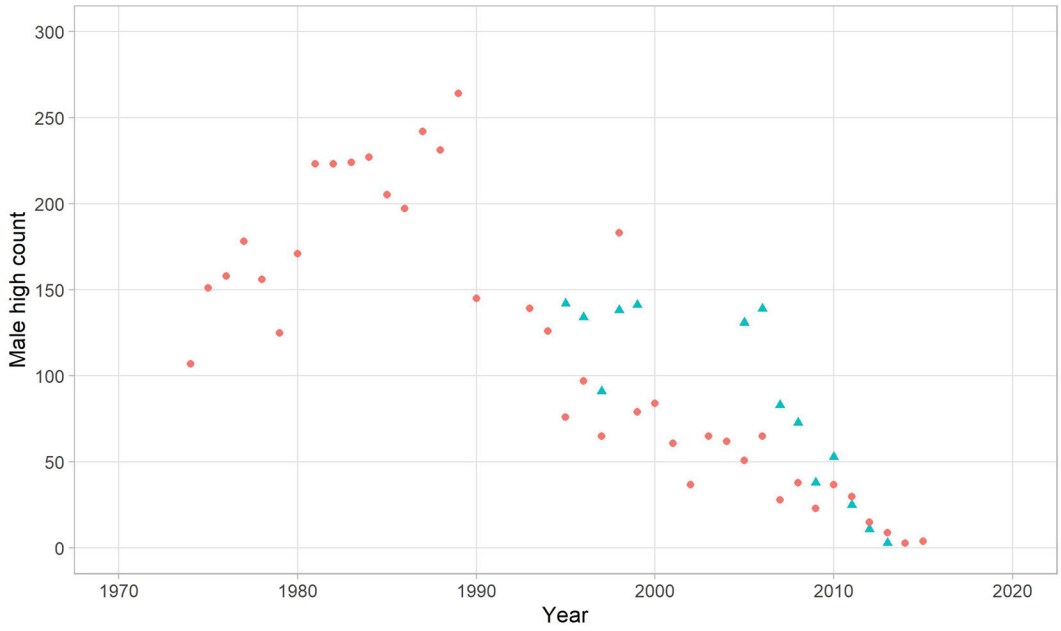

FIGURE 2 Male high count of lesser prairie-chickens counted lekking in Baca County, Colorado (red points), and Morton County, Kansas, USA (blue triangles), including leks on the Comanche and Cimarron National Grasslands, respectively. Data from Colorado were collected by Colorado Parks and Wildlife from 1962 to 2016, and data from Kansas were collected by Kansas Department of Wildlife and Parks from 1995 to 2016. Data are only included for years with a thorough lek survey effort.

and shrubs on National Grasslands to historic measurements (Giesen 1994), found that grass cover has increased and bare ground cover has decreased on Comanche National Grassland since lesser prairie-chicken populations were at their peak in the 1980s (Rondeau and Decker 2010, Rondeau et al. 2013). Work by Wuenschel (2016) reported that some vegetation cover measurements taken in 2015 fell within USDA–Forest Service guidelines in the 2014 management plan, although vegetation structure was lacking. Based principally on vegetation cover measurements, both studies concluded that National Grasslands had the capacity for supporting nesting habitat for lesser prairie-chickens; however, neither study considered how vegetation structure and grass species used for nesting might affect use by lesser prairie-chickens. Past studies indicate that both components are essential to lesser prairie-chicken nesting habitat and could affect resource selection decisions by lesser prairie-chickens (Haukos and Zavaleta 2016).

We conducted our study in conjunction with a translocation of lesser prairie-chickens to the National Grasslands during 2016–2019, in conjunction with the Kansas Department of Wildlife, Parks and Tourism and Colorado Parks and Wildlife. Although the primary goals of the translocation included reestablishing a self-sustaining population of lesser prairie-chickens on the National Grasslands and augmenting populations in the Sand Sagebrush Prairie Ecoregion, the translocation effort also provided an opportunity to assess vegetation surrounding release sites and quantify habitat selection by translocated birds on the National Grasslands and in the Sand Sagebrush Prairie Ecoregion. Our objectives were to 1) measure availability of nesting habitat in cover types on the National Grasslands and throughout release counties based on definitions in the 2014 Management Plan, 2) determine selection of cover types and vegetation structure by translocated lesser prairie-chickens, and 3) assess use of National Grasslands for nesting by translocated lesser prairie-chickens.

STUDY AREA

Capture site

We captured lesser prairie-chickens during fall 2016 and spring 2017–2019 in the Short-Grass Prairie/CRP Mosaic Ecoregion. With permission of private landowners, we captured lesser prairie-chickens on leks in short- and mid-grass prairie and crop cover types in Gove, Lane, Ness, and Finney counties, Kansas (1,357,189 ha). Land use in the counties was a mixture of row-crop agriculture, energy extraction, CRP grassland, and grazing on native short- and mixed-grass prairie (McDonald et al. 2014, Dahlgren et al. 2016, Robinson et al. 2018). Historical (1960 to 2015) mean monthly temperatures ranged from −8.9 to 28.8°C, and annual precipitation ranged from 29.4 to 83.3 cm ($\bar{x}$ = 53.3 cm) in Healy, Kansas. During the study period (2016 to 2019) mean monthly temperatures ranged from −4.1 to 26.6°C, and annual precipitation ranged from 51.3 to 65.0 cm (Healy, Kansas; data from High Plains Regional Climate Center 2021).

Vegetation in the source population area primarily reflected native short-grass prairie composition, but also contained species of mixed-grass prairie (Sullins 2017). Common grass species included little (*Schizachyrium scoparium*) and big bluestem (*Andropogon gerardii*), sideoats (*Bouteloua curtipendula*), blue (*B. gracilis*) and hairy grama (*B. hirsuta*), buffalograss (*B. dactyloides*), switchgrass (*Panicum virgatum*), composite (*Sporobolus compositus*) and sand dropseed (*S. cryptandrus*), western wheatgrass (*Pascopyrum smithii*), and inland saltgrass (*Distichlis spicata*). Forb species included slimflower scurfpea (*Psoralidium tenuiflorum*), winterfat (*Krascheninnikovia lanata*), western ragweed (*Ambrosia psilostachya*), broom snakeweed (*Gutierrezia sarothrae*), white heath aster (*Symphyotrichum ericoides*), and field sagewort (*Artemisia campestris*; McGregor and Barkley 1986). The dominant succulent species was plains prickly pear (*Opuntia macrorhiza*). Shrub species included sand sagebrush and 4-wing saltbush (*Atriplex canescens*; Fields et al. 2006). Grass species in CRP included little and big bluestem, sideoats and blue grama, buffalograss, switchgrass, western wheatgrass, and indiangrass (*Sorghastrum nutans*). Forb species included alfalfa (*Medicago sativa*), white (*Melilotus alba*) and yellow sweet clover (*M. officinalis*), Maximillian sunflower (*Helianthus maximiliani*), prairie bundleflower (*Desmanthus illinoensis*), purple prairie-clover (*Dalea purpurea*), and upright prairie coneflower (*Ratibida columnifera*; Fields et al. 2006).

Release sites

The 2 counties containing release sites (Baca County, Colorado [662,260 ha], and Morton County, Kansas [189,069 ha]) were composed of row-crop agriculture (31.8% Baca, 47.7% Morton), CRP grasslands (16.6% Baca, 17.7% Morton), and a combination of sand sagebrush and short-grass prairies (49.8% Baca, 33.9% Morton). The USDA–Forest Service managed 65,437 ha of these counties (12.2% Baca, 23.0% Morton) as a part of the Comanche and Cimarron National Grasslands, with a focus on providing multi-use opportunities for grazing, energy exploitation, and wildlife recreation. The Cimarron National Grassland has a long history of oil and gas extraction, with 1,014 completed wells on record (Kansas Geological Survey 2020). The Comanche National Grassland has significantly fewer wells (72 completed; Colorado Oil and Gas Conservation Commission 2020).

Vegetation composition and structure on National Grasslands varied based on soil type and grazing intensity and included both short-grass and sand sagebrush prairie. Short-grass prairie species matched those found at the capture site, with high occurrence of blue grama and buffalograss. In the sand sagebrush prairie, grass species included sand dropseed, blue grama, needle and thread (*Hesperostipa comata*), threeawn (*Aristida* spp.), cheatgrass (*Bromus tectorum*), and sand bluestem (*Andropogon hallii*). Forb species included annual buckwheat (*Eriogonum annuum*), blazing star (*Liatris* spp.), western ragweed, prairie (*Helianthus petiolaris*) and annual sunflower (*H. annuus*), camphorweed (*Heterotheca subaxillaris*), fumewort (*Corydalis aurea*), Indian blanket flower (*Gaillardia pulchella*), Russian thistle (*Salsola tragus*), pigweed (*Amaranthus hybridus*), tansy aster (*Machaeranthera tanacetifolia*), bush

morning glory (*Ipomoea leptophylla*), evening primrose (*Calylophus serrulatus*), buffalo bur (*Solanum rostratum*), buffalo gourd (*Cucurbita foetidissima*), wax goldenweed (*Grindelia papposa*), prickly lettuce (*Lactuca serriola*), Texas croton (*Croton texensis*), marestail (*Conyza canadensis*), cutleaf ironplant (*Haplopappus spinulous*), and toothed spurge (*Euphorbia dentata*). Succulent species included yucca (*Yucca glauca*) and plains prickly pear. The shrub community was dominated by sand sagebrush.

Vegetation in CRP tracts in Baca and Morton counties included similar species to those observed at the capture site. Historical (1960 to 2015) mean monthly temperatures ranged from −4.6 to 29.7°C, and annual precipitation ranged from 28.4 to 74.1 cm ($\bar{x}$ = 46.0 cm) in Elkhart, Kansas. During the study period (2016 to 2019) mean monthly temperatures ranged from 0.3 to 27.3°C, and annual precipitation was above average and ranged from 40.9 to 67.0 cm (Elkhart, Kansas; data from High Plains Regional Climate Center 2021).

METHODS

Translocation

From fall 2016 to spring 2019, we captured and translocated lesser prairie-chickens from northwestern Kansas to the Cimarron and Comanche National Grasslands. We captured lesser prairie-chickens on leks using walk-in funnel traps (Haukos et al. 1990) as well as tension and magnetic drop nets (Silvy et al. 1990). We transported birds to a central location for processing and transmitter attachment before they were driven to a release site on either the Cimarron or Comanche National Grasslands (188 and 220 km from the processing site, respectively). Only males were caught during the initial fall 2016 release; all subsequent releases were in spring and included both males and females. From 2016 through 2019, we deployed necklace-style very-high-frequency (VHF) 15-g transmitters (RI-2B Holohil Systems Ltd., Carp, Ontario, Canada; Series A3900, Advanced Telemetry Systems, Isanti, MN, USA) on 279 translocated birds (144 males, 135 females). In 2018 and 2019, we deployed 22-g Satellite Platform Transmitting Terminal (SAT-PTT) GPS transmitters (PTT-100, Microwave Telemetry, Columbia, MD, USA) on 115 translocated birds (43 males, 72 females). We used Teflon straps and elastic ribbon to secure these transmitters above the rump of each bird (Dzialak et al. 2011). Transmitter mass, including the mass of the 6-g satellite transmitter harness, never exceeded 5% of the bird's mass (Fair et al. 2010). We monitored VHF-tagged birds ≥3 times per week via radiotelemetry, with locations estimated via triangulation using the program LOAS (Ecological Software Solutions, Hegymagas, Hungary). We monitored satellite-tagged birds remotely. Transmitters recorded GPS locations every 2 hours between 1100 and 0500 UTC (0600 and 0000 Central Daylight Time) and uploaded into the Argos satellite system every 3 days. We released birds within 11 hours of capture on either the Cimarron or the Comanche National Grasslands in areas chosen for their proximity to presumed high quality nesting habitat and historical leks. Starting in spring 2018, we adjusted release sites to ensure birds were released near active lekking sites.

Cover type delineation

To assess habitat selection at release sites, we delineated cover types within the counties of release (Baca County, CO, and Morton County, KS). As vegetation communities were fairly uniform on private land, cover types on private land were categorized based solely on land use. The National Grasslands, however, had considerable variation in extant vegetation composition and structure due to differing grazing practices and soil types, and so were divided into subclasses.

For private land, we classified land under contract as Conservation Reserve Program grassland as the CRP cover type (as determined by a 2014 shapefile provided by the USDA Farm Service Agency). We classified all other land under private ownership as either row crop, private rangeland, or developed based on the U.S. Department of

Agriculture's Cropland Data Layer (USDA–NASS 2019). Private rangeland was defined as areas of shrubland or grassland that were privately owned and not under contract as CRP grassland. For public land, we assigned cover types based on the ecological site and the plant communities present. Ecological sites categorize areas based on their physiographic characteristics and tendency to support similar plant communities (Caudle et al. 2013). Each ecological site also includes a set of transition states (Stringham et al. 2003), which describe the set of vegetation communities arising from certain disturbances and management practices. Each transition state was used as a potential cover type on public land (Table S1, available online in Supporting Information).

We assigned public land cover types to each of the National Grasslands' 425 grazing allotments (mean area = 296 ha) in Baca and Morton counties. To determine the transition state cover type for each allotment, we sampled vegetation communities by conducting 2 step-point plant identification transects in each allotment (details in the Vegetation Measurements section). We then matched the vegetation community present (specifically, the most frequently observed species) to the most similar transition state for that allotment's Ecological Site. On the occasion that there were 2 ecological sites in an allotment, we divided the allotment into 2 units that were sampled and sorted into cover types separately. If an allotment could not be sampled due to personnel limitations, we assigned that allotment to the public land (no measurements) cover type (29% of the Cimarron, 86% of the Comanche). This cover type was predominantly in areas with no historic use by lesser prairie-chickens or documented use by translocated lesser prairie-chickens (Figure 3). Finally, we renamed one of the transition states (reference state on the Comanche) to grass/shrubland state to prevent confusion with a common scientific term and better describe the observed plant community.

Vegetation measurements

To assign cover types to National Grasslands allotments and evaluate whether National Grasslands and surrounding areas were meeting nesting habitat guidelines for lesser prairie-chickens, we sampled vegetation in each cover type except crop and developed during June 1–October 1 of 2018 and 2019. We sampled vegetation using 2 types of randomly distributed surveys: step-point plant identification transects and point vegetation surveys. We conducted 2 step-point plant identification transects at randomly sampled locations within each patch of a given cover type (Evans and Love 1957). Each technician kept a 1-m pace along a straight 250-m transect and recorded the plant species that occurred at a given point at each ~1 m increment. Each transect resulted in 250 separate points of plant observations representative of the plant community present. We used the community metrics to delineate cover types on the National Grasslands and evaluate grass species available for lesser prairie-chicken nesting cover. We classified the value of grass species for nesting based on the USDA–Forest Service's Lesser Prairie-Chicken Management Plan (USDA–Forest Service 2014), which provides lists of high and moderate value grass species for creating lesser prairie-chicken nesting habitat. We categorized remaining non-listed grass species as low value. We then aggregated the percent of plant observations from step-point transects in each cover type based on percent of observations that were of high, moderate, and low value grass species, as well as percent of observations that were of forbs, shrubs, or succulents.

We conducted 10 point-vegetation surveys at randomly sampled locations within each patch of a given cover type, measuring the vegetation structure and canopy cover present at each site. We measured vegetation structure using visual obstruction readings, obtained by estimating the amount of a Robel pole visible from 4 m away and 1 m above the ground in each of the 4 cardinal directions. Robel pole readings provide an index of vegetation height and density at the given point (Robel et al. 1970). We recorded the highest centimeter value at which the pole was completely obstructed by vegetation (100% visual obstruction). We averaged together measurements from the 4 cardinal directions by obstruction level to obtain a single measurement for each location. We measured canopy cover present at each point vegetation survey site using a 60 × 60 cm Daubenmire frame (Daubenmire 1959). We placed the frame in the center of each randomly sampled point, as well as 4 m away in each

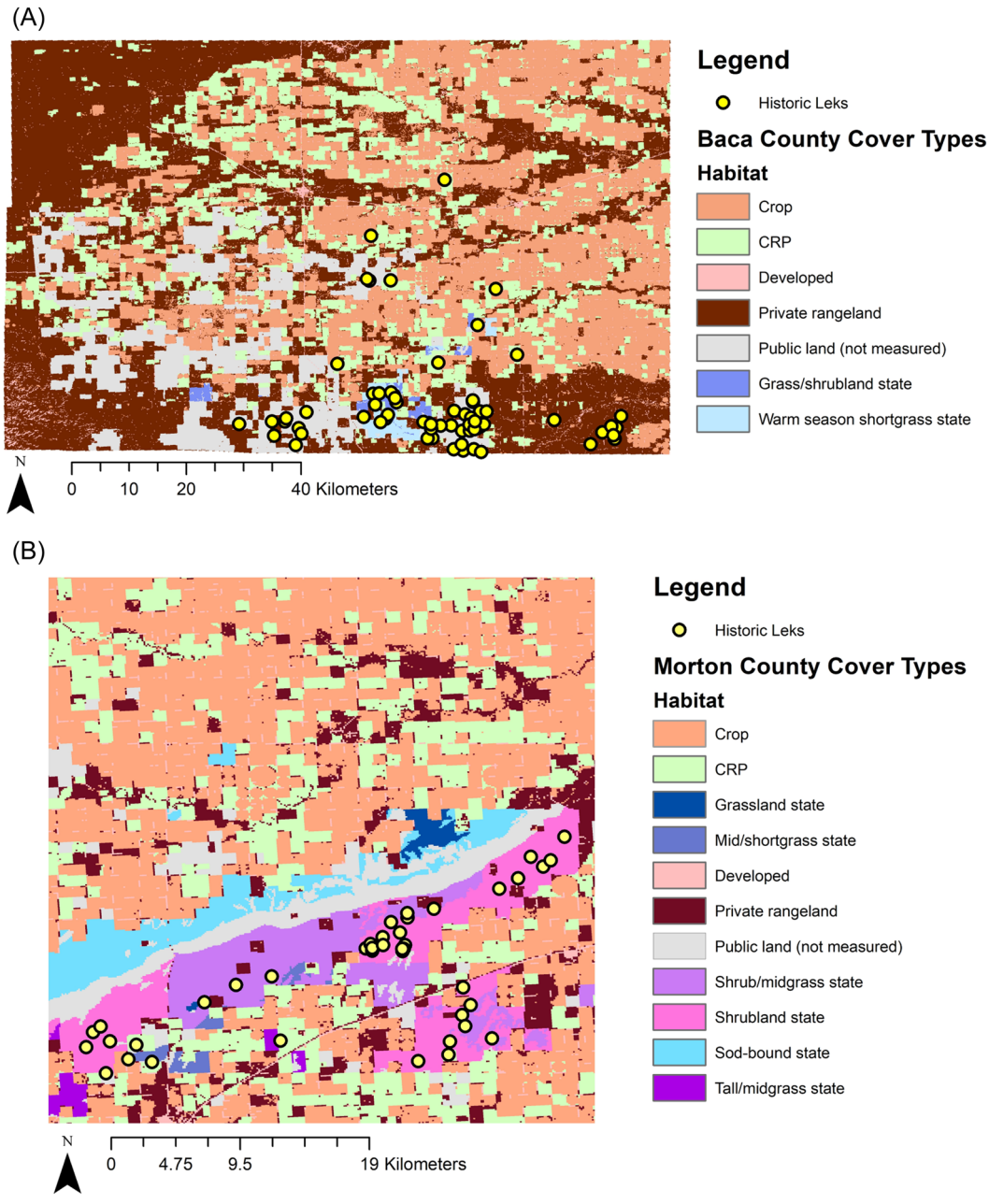

FIGURE 3 Cover types in Baca (A) and Morton (B) counties in southeastern Colorado and southwestern Kansas, USA, as determined by comparing vegetation community measurements the USDA-NRCS's Ecological Site Description Transition States. Historic leks (1979–2019) are marked with yellow points to illustrate cover types historically occupied by lesser prairie-chickens. Only one of these historic leks was still active when the translocation began in Fall 2016.

cardinal direction, to quantify the percent canopy cover for grasses, forbs, shrubs, litter, and bare ground. The canopy cover measurement for each vegetation type was assigned to a range (0%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, 96–100%; Daubenmire 1959). Midpoints of these ranges were used in all analyses of canopy cover measurements.

Habitat selection

We used locations of satellite-tagged birds to examine habitat selection by translocated lesser prairie-chickens following release. After release, 99% of birds underwent a 1–2 month dispersal period, traveling 15–474 km prior to localization (female $\bar{x}$ = 175 km, male $\bar{x}$ = 103 km; Berigan 2019). Because of the distance and duration of dispersal movements, we were unable to locate most VHF birds until the movement had concluded. We therefore excluded VHF-tagged birds from the habitat selection analysis.

Characteristics of dispersal movements presented obstacles for defining availability of habitat for translocated birds; not all birds were exposed to the same cover types, and differences in speed during their movements suggested that not all areas visited should be considered equally available. We accounted for these issues by using a step-selection function to measure their 2nd order (Johnson 1980) selection of cover types (Fortin et al. 2005), while adjusting for individual differences in selection and availability following Muff et al. (2020). We fit a step-selection function to each bird's individual breeding season trajectory from release through 15 September. The end date for our trajectories follows Lautenbach et al. (2017) delineation of the lesser prairie-chicken breeding season, which falls between 15 March and 15 September. Steps were much longer between 0600 and 0800, when birds were more likely to disperse or move between patches of grassland, than they were during the rest of the diurnal hours, when birds made shorter foraging steps within the areas that they had flown to in the morning. As selection at a cover type scale was primarily of interest, we resampled each of the trajectories to a single location per day. We used the location, velocity, and turn-angle of each of a bird's daily steps to generate 9 available steps using package amt in R (Signer et al. 2019, R Core Team 2020). Some individuals did not survive long enough after release to allow an adequate comparison of selection between cover types. We therefore censored individuals that did not survive at least 2 weeks after release. Our cut-off point of 2 weeks was based on the time frame that is frequently used to reduce capture effect in survival studies (Winterstein et al. 2001), including studies on lesser prairie-chickens (Hagen et al. 2007). As cover types were only delineated for Baca and Morton counties, we removed any steps that did not fall within these 2 counties. We then used the R package glmmTMB (Brooks et al. 2017) to assess how each cover type predicted used or available sites. Although step-selection functions are traditionally fit using a conditional logistic regression model (Fortin et al. 2005), we used a likelihood-equivalent Poisson model following Muff et al. (2020). The Poisson model allowed us to include individual slopes and intercepts for each tagged bird as random effects, compensating for bias introduced by individually-varying availability and selection preferences. Selection for each cover type was compared to selection for a reference cover type, crop, which was chosen due to its prevalence and the lack of resources for lesser prairie-chicken occupancy. We evaluated selection of each cover type using beta estimates from the Poisson model and 95% confidence intervals to determine if selection for or against a cover type was statistically significant.

Nesting

To evaluate nesting habitat within cover types, we recorded nest locations of translocated birds in Baca County, Colorado, and Morton County, Kansas, from 2017–2019. We identified 42 nests from satellite-tagged females and 84 nests from females equipped with VHF transmitters. We determined nest locations for satellite-tagged individuals based on weekly GPS updates, which were checked in-person after nest fate was established (Lautenbach et al. 2019). We determined nest locations for VHF-tagged birds using daily checks of localized birds using radiotelemetry, followed by visual confirmation or flush to determine the exact location of the nest. We used nest locations in a design II resource selection function to determine selection of cover types at a 2nd order scale (Manly et al. 2002). Nest locations were employed as used points for the nest site selection analysis. To generate available points, we created a simple line trajectory of each bird's movements throughout the breeding season and randomly generated points along each trajectory. We then subsampled randomly generated points so that there

were an equal number of used and available locations. We tested for selection of certain cover types during nesting using a binomial-family generalized linear model. Because of low sample size in the reference state (crop), we elected to combine Morton County and Baca County cropland into a single cover type for the nest site selection analysis.

RESULTS

From 2016 to 2019, we translocated 394 birds to the National Grasslands. Of the 115 birds that were equipped with satellite transmitters since 2018, 94 survived at least 2 weeks and were included in the step-selection function. Satellite-tagged birds provided a total of 8,041 steps in the 2018 and 2019 breeding seasons that could be used to analyze habitat selection during their movements. We collected 2,115 visual obstruction points and 598 step-point transects quantifying the vegetation structure and communities of CRP and public land in Baca County, Colorado, and Morton County, Kansas. We used the transect data to classify private and public land into cover types based on land ownership and vegetation communities (Figure 3; Table S1).

Vegetation measurements

Kansas

High value grass species were present in Kansas CRP (24.0% of observations) and Cimarron National Grassland's tall/midgrass state (20.1%), but less frequently observed in private rangeland or any of the 5 other Cimarron cover types (0.5–3.3%; Figure 4). The USDA–Forest Service's guidelines of 25.4 to 38.1 cm visual obstruction guidelines were met for 5.3–21.8% of observations on public land and 7–14.4% of observations on private land (Figure 5). Cover types on the Cimarron National Grassland met USDA–Forest Service canopy cover guidelines for grass cover (6.1–36.4%), forb cover (16.7–36.4%), and shrub cover (0–8.1%) more frequently than private land cover types (grass cover: 6.9–9.3%; forb cover: 16.3–16.9%; shrub cover: 0%).

Colorado

High value grass species in Colorado were more frequently observed on private land (11.0–11.2% of observations) than on public land (1.5–3.0%; Figure 4). The USDA–Forest Service's guidelines of 25.4 to 38.1 cm visual obstruction guidelines were rarely met on either public (1.5–3.0%) or private land (2.3–3.1%; Figure 5). The USDA–Forest Service's canopy cover guidelines were met at similar frequency for grass and forb cover on public (grass cover: 12.4–16.1%; forb cover: 22.1–31.9%) and private land (grass cover: 10.8–21.9%; forb cover: 15.8–29.2%). Shrub cover guidelines were met more frequently on public (8.1–9.6%) than private land (1.2–3.1%). Summary tables of all vegetation measurements, including comparisons to historic measurements, are available in Supporting Information (Tables S2–S8).

Habitat selection

In Kansas, only CRP and the shrubland state cover type were selected at a statistically greater rate than crop (Figure 6). In Colorado, only the warm season shortgrass state cover type was selected at a greater rate than crop (Figure 7). Other cover types were either avoided in comparison to crop (Kansas: one private and one public cover

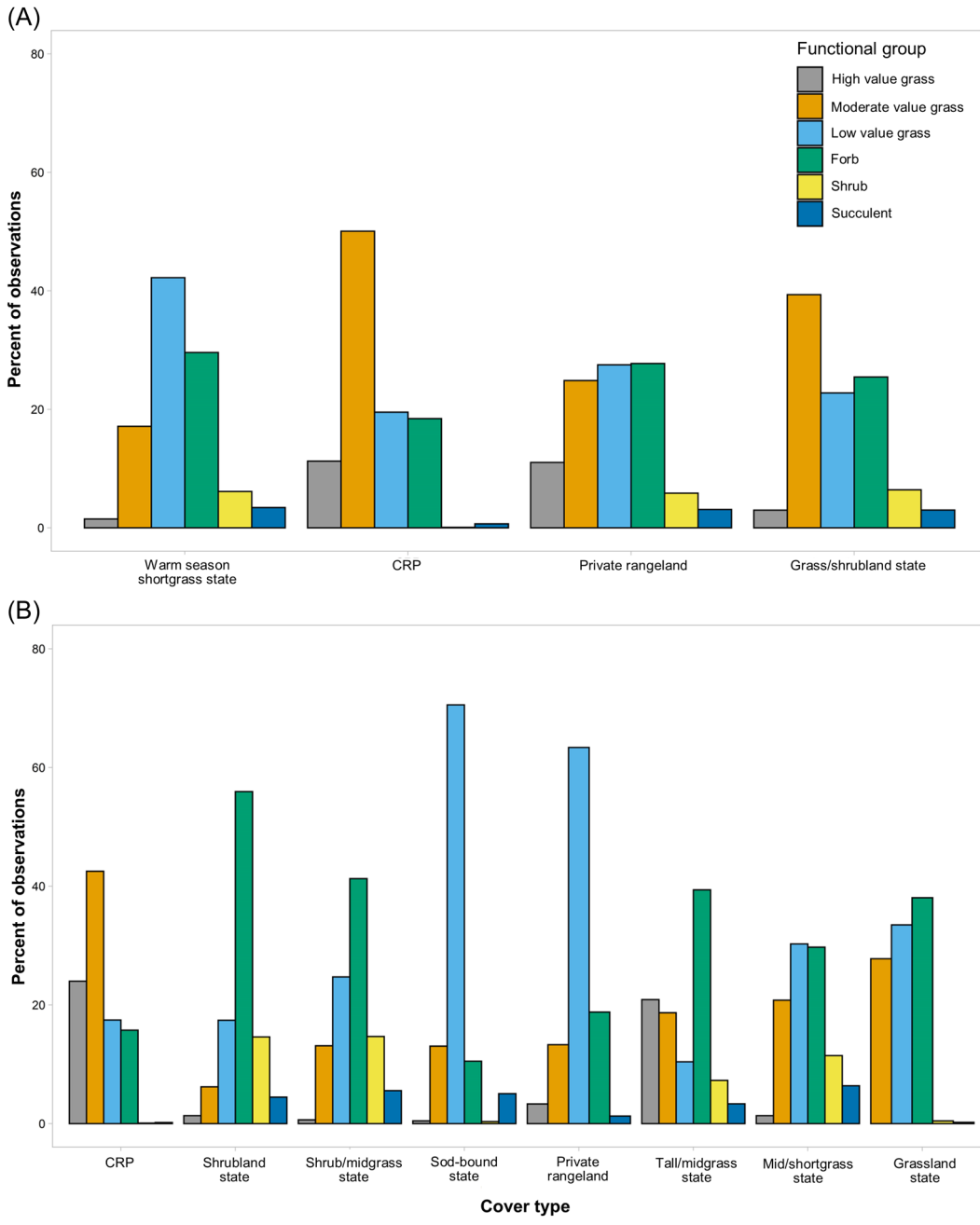

FIGURE 4 Vegetation composition of each cover type in Baca (A) and Morton (B) counties in southeastern Colorado and southwestern Kansas, USA. Cover types are based on USDA-NRCS Ecological Site Descriptions, further classified into site-specific transition states using the results of step-point plant identification transects. Grass species were ranked using categories published in the Lesser Prairie-Chicken Management Plan for the Cimarron and Comanche National Grasslands (2014). The crop, developed, and public land (no measurements) cover types were excluded due to a lack of representative vegetation measurements.

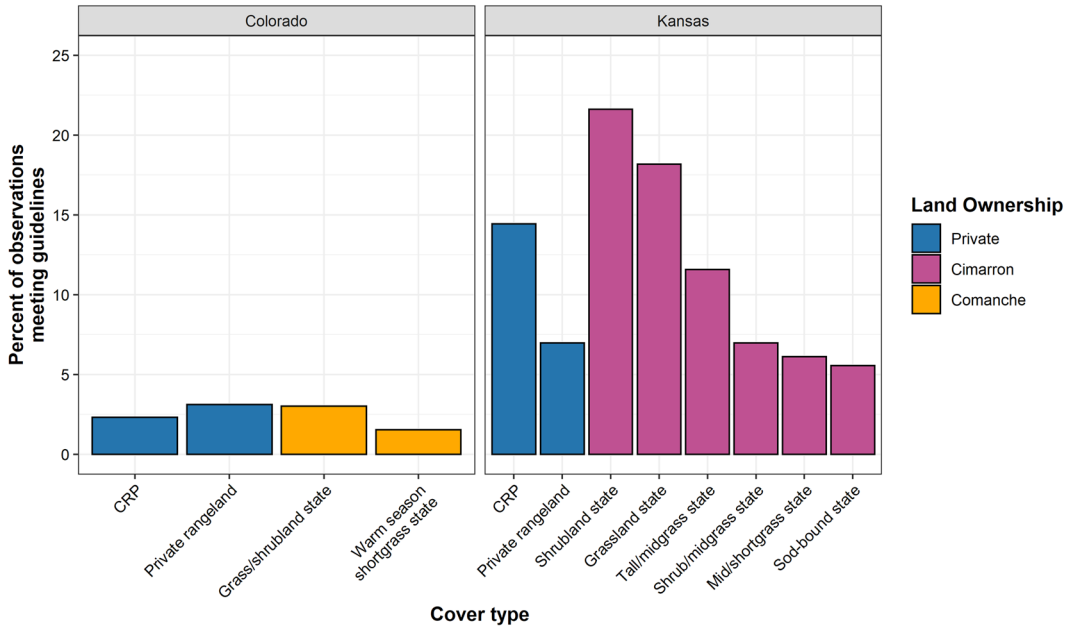

FIGURE 5 Percent of visual obstruction readings meeting guidelines in each cover type on Cimarron and Comanche National Grasslands and on surrounding private land in Morton County, Kansas, and Baca County, Colorado, USA, during 2018 and 2019. Guidelines used in the comparison (25.4–38.1 cm) are published in the Lesser Prairie-Chicken Management Plan for the Cimarron and Comanche National Grasslands (2014). Cover types are based on USDA-NRCS Ecological Site Descriptions, further classified into site-specific transition states using the results of step-point plant identification transects. The crop, developed, and public land (no measurements) cover types were excluded due to a lack of representative vegetation measurements.

type; Colorado: no cover types) or were not selected at a statistically different rate than crop (Kansas: 1 private and 5 public cover types; Colorado: 3 private and 2 public cover types).

Nesting

We assessed selection of cover type for nesting for 69 nests in Morton County, Kansas, and 57 nests in Baca County, Colorado. Most translocated bird nests in each state occurred in CRP (Colorado CRP: 69.2% of nests; Kansas CRP, 59.4% of nests), and translocated birds selected heavily for CRP during nesting in both states (Figure 8). The Cimarron and Comanche National Grasslands hosted a comparatively small proportion of nests (Comanche: 26.9% of Colorado nests; Cimarron: 30.4% of Kansas nests). Only 2 of the 10 cover types on the National Grasslands were selected over Crop for nesting (Comanche: grass/shrubland state, Cimarron: shrubland state). Private rangeland was rarely used for nesting in either state (Kansas: 0%; Colorado: 1.9% of nests).

DISCUSSION

Lesser prairie-chicken space use and population stability rely on the presence of nesting habitat. Nesting habitat dictates space use by both male and female lesser prairie-chickens, with males predominantly choosing lek sites near nesting habitat as indicated by presence of females (Aulicky 2020). Nesting habitat also improves lesser

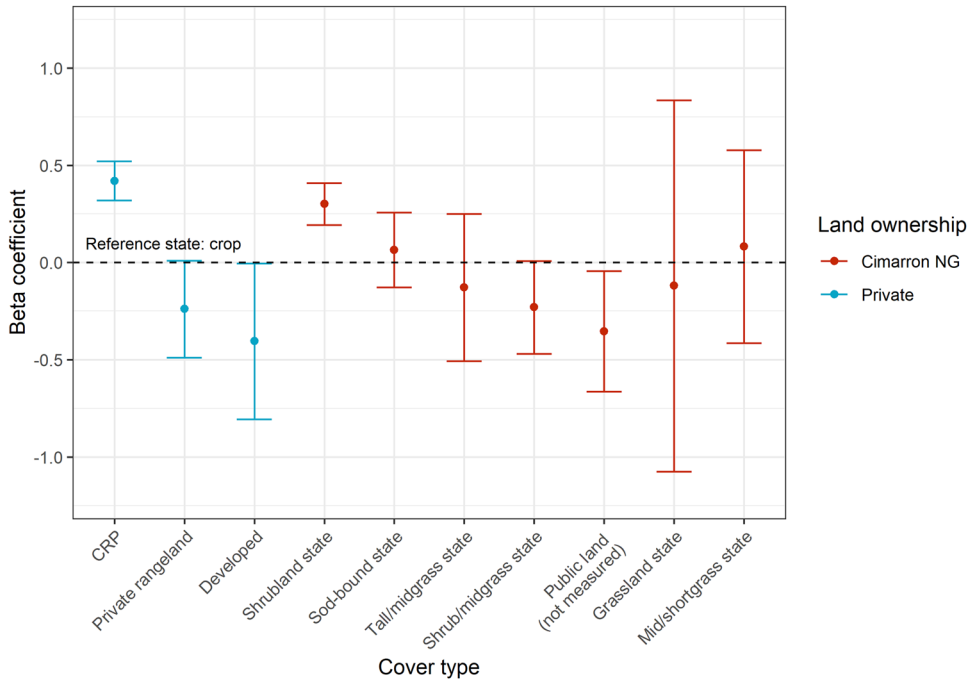

FIGURE 6 Breeding season selection β coefficient (+95% CI) for each cover type on Cimarron National Grassland and surrounding private land in Morton County, Kansas, USA, during 2018 and 2019. Selection was determined using a step selection function modified following Muff et al. (2020). Cover types are based on USDA-NRCS Ecological Site Descriptions, further classified into site-specific transition states using results of step-point plant identification transects.

prairie-chicken population stability by providing a buffer against reductions in juvenile survival during droughts (Ross et al. 2018). Tracts of nesting habitat, especially when adjacent to sufficient brooding habitat, can create refugia allowing lesser prairie-chickens to persist through extended droughts (Ross et al. 2016, Sullins et al. 2018). Maintaining appropriate levels of nesting habitat, managed to meet ecoregion-specific guidelines, is therefore essential to the long-term persistence of lesser prairie-chicken populations.

Unfortunately, nesting habitat is currently not well distributed throughout cover types in the Sand Sagebrush Prairie Ecoregion. While cropland provides some foraging opportunities for lesser prairie-chickens, it provides none of the nesting habitat requirements necessary for lesser prairie-chickens. Our results suggest that private rangeland is also providing limited visual obstruction or grass species that lesser prairie-chickens could use for nesting. The only cover type that reliably provided nesting habitat was Kansas CRP, which had both high visual obstruction and high value grass species. Colorado CRP also had high value grass species, but the lack of visual obstruction limited the amount of nesting habitat that this cover type provided. The potential of CRP to increase lesser prairie-chicken population abundance and occupied range in the Sand Sagebrush Prairie Ecoregion is also constrained by limited enrollment periods and its relatively low proportion on the landscape (Baca, CO: 16.5%; Morton, KS: 16.7%). The National Grasslands have the advantage of permanence, and their large contiguous tracts of grassland have historically made them ideal nesting refugia for the Sand Sagebrush Prairie Ecoregion, especially during periods of intensive drought. However, the National Grasslands are not currently providing nesting habitat, which impedes their ability to act as refugia on the landscape. Lack of nesting habitat seems to be primarily due to inappropriate vegetation conditions on the National Grasslands; specifically, a lack of visual obstruction and appropriate nesting grass species.

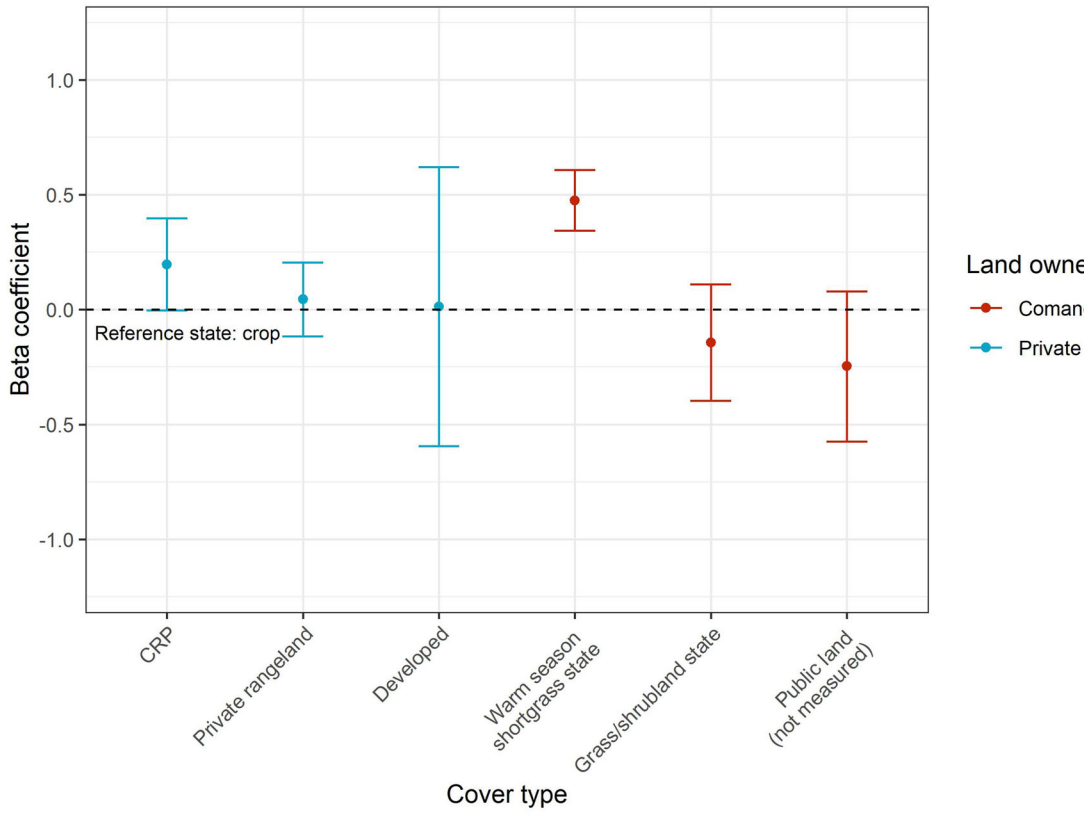

FIGURE 7 Breeding season selection β coefficient (+95% CI) for each cover type on Comanche National Grassland and surrounding private land in Baca County, Colorado, USA, during 2018 and 2019. Selection was determined using a step selection function modified following Muff et al. (2020). Cover types are based on USDA-NRCS Ecological Site Descriptions, further classified into site-specific transition states using results of step-point plant identification transects.

Visual obstruction and nesting grass species are both critical to providing lesser prairie-chicken habitat. Visual obstruction of vegetation is a central component of nesting cover and has a large role in predicting lesser prairie-chicken lek attendance (Lautenbach et al. 2019, Gehrt et al. 2020). Lesser prairie-chicken leks are usually surrounded by vegetation with visual obstruction selected for nesting (mean 36.3% of observations within 5 km, range 11.4–42.5%; Gehrt et al. 2020). Landscapes, like the National Grasslands and the surrounding Sand Sagebrush Prairie Ecoregion, without habitat meeting visual obstruction recommendations are less likely to have long-term lek persistence (Aulicky 2020). A lack of desired grass species is also of concern, as lesser prairie-chickens rely on mid- and tall bunchgrasses for nesting cover (Haukos and Zavaleta 2016). Although lesser prairie-chickens have been recorded using sand sagebrush for nesting cover when bunchgrasses are not available (Haukos and Zavaleta 2016), translocated birds rarely nested in cover types without high or moderate quality grass species (Berigan 2019, Teige 2021). A lack of either visual obstruction or high value grass species is likely a significant impediment to lesser prairie-chicken habitat use or nesting throughout much of the Cimarron and Comanche National Grasslands.

Accordingly, we found a pattern of avoidance of most cover types on National Grasslands by translocated lesser prairie-chickens following release. During breeding season movements, 8 of 10 National Grasslands cover types were not selected at a statistically greater rate than crop, a cover type that provides few resources for

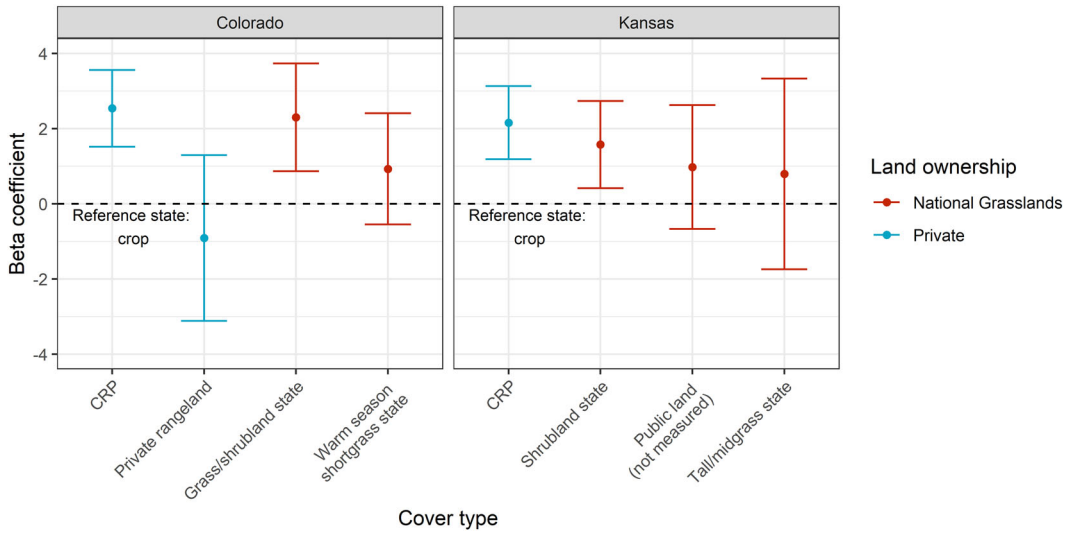

FIGURE 8 Nesting site selection β coefficient (+95% CI) for each cover type on Cimarron and Comanche National Grasslands and surrounding private land in Morton County, Kansas and Baca County, Colorado, USA, during 2018 and 2019. Selection was determined using a design II resource selection function following Manly et al. (2002). Cover types are based on USDA-NRCS Ecological Site Descriptions, further classified into site-specific transition states using results of step-point plant identification transects. Seven cover types had *P*-values >0.99 due to low sample sizes and are not displayed here.

lesser prairie-chickens. Of the 2 exceptions, shrubland state and warm season shortgrass state, only the shrubland state also attracted nesting birds. In the absence of vegetation data, there might be alternative explanations for this avoidance of the National Grasslands. One alternative explanation would be natal habitat preference induction (Stamps and Swaisgood 2007), which is selection for a cover type that an animal was hatched or raised in. As our translocated birds were raised in landscapes with CRP grasslands (Sullins et al. 2018), birds experiencing natal habitat preference induction would theoretically select CRP grasslands surrounding the release site over sand sagebrush prairie of comparable habitat quality. However, our vegetation sampling results showed that there was less nesting habitat in sand sagebrush prairie than was provided in comparable CRP grasslands in the study area. In their selection for CRP grasslands, translocated birds are making decisions that we would expect non-translocated birds to make given these vegetation results. From 2011–2013, satellite transmitters were deployed on several native birds on the Cimarron National Grassland and these birds displayed similar selection patterns to what we describe here (D. Haukos, unpublished data). Therefore, habitat selection patterns are likely influenced more by limited nesting habitat availability than natal habitat preference induction.

The current lack of nesting habitat on the National Grasslands is particularly perplexing given the historic record of high lesser prairie-chicken use of these areas (Haukos et al. 2016). The areas we classified as shrubland state and shrub/midgrass state on the Cimarron National Grassland historically supported at least 42 leks; due to the lesser prairie-chicken's tendency to nest within 3.2 km of a lek (Boal and Haukos 2016), these areas should have contained considerable quality nesting habitat. The Cimarron National Grassland was also originally seeded with several high value grass species, including little bluestem and sand lovegrass (Guest 1968), which are no longer present on most of the National Grasslands. It is unclear why nesting habitat is no longer present at historical levels. Drought has caused declines in visual obstruction on the National Grasslands in the past, but our study was conducted during a period of above-average precipitation for the region (High Plains Regional Climate Center 2021). Another potential driver may have been changes in grazing practices over the past 5 decades. On the Cimarron

National Grassland, for example, grazing pressure was kept comparatively light from the 1940s through the 1960s. Cattle use was carefully rationed to avoid causing damage during a severe drought during the 1950s, with cattle grazing an average of 16,025 animal unit months (AUMs) per year in 1953–1962 on the Cimarron (Guest 1968). Grazing pressure on the Cimarron has nearly doubled since then, with an average of 29,389 AUMs grazed per year in 2016–2018 (N. Brewer, USDA–Forest Service, personal communication). It is probable that a sustained increase in grazing pressure over the course of several decades was sufficient to reduce visual obstruction and change the vegetation community composition of the National Grasslands, resulting in high value grass species from the original seeding being outcompeted by species that provide little nesting habitat for lesser prairie-chickens (Holechek et al. 1989).

Declines in nesting habitat availability on the National Grasslands may indicate larger issues throughout the Sand Sagebrush Prairie Ecoregion. Most of the sand sagebrush prairie in the ecoregion also undergoes significant grazing pressure, and our nesting results showed that private rangelands provide limited nesting habitat (Kansas: zero nests, Colorado: one nest). The shift in habitat use from sand sagebrush prairies to CRP grasslands starting in the early 2000s occurred not just on the National Grasslands but throughout the ecoregion. It is likely that the same drivers that reduced nesting habitat availability on the National Grasslands are also reducing nesting habitat availability on sand sagebrush prairies throughout the ecoregion.

A lack of nesting habitat on sand sagebrush prairies could bring lesser prairie-chicken populations below landscape-scale habitat thresholds for population stability. Several studies have found that lesser prairie-chickens require large proportions of the landscape to be composed of grassland for populations to be successful. Crawford and Bolen (1976) estimated that at least 63% of a 2,331 ha area would have to be grassland to sustain a lesser prairie-chicken population. Sullins et al. (2019) found that lesser prairie-chicken occupancy of a site was maximized when 77% of land within a 5 km radius of that site is grassland, and Ross et al. (2016) determined that lesser prairie-chicken recovery from drought is most effective when 90.4% of land within 3 km of a survey route was grassland. While these studies assume that all grassland areas (including both CRP and public/private sand sagebrush prairie) equally increase the probability of use by lesser prairie-chickens, our results indicate that only CRP is currently reliably providing the resources required for lesser prairie-chickens to nest throughout much of the Sand Sagebrush Prairie Ecoregion despite CRP grasslands comprising a small proportion of the landscape (Morton, KS: 17.7%; Baca, CO: 16.6%) in comparison to sand sagebrush prairies (Morton, KS: 34.1%; Baca, CO: 49%). For the counties to meet the landscape grassland threshold for occupancy to support lesser prairie-chickens and provide quality nesting habitat, CRP in much of Baca and Morton counties would have to be retained, enhanced (i.e., improved visual obstruction), and expanded while also restoring sand sagebrush habitat on the National Grasslands and private rangeland.

MANAGEMENT IMPLICATIONS

Contemporary populations of lesser prairie-chickens in the Sand Sagebrush Prairie Ecoregion will need to rely on a combination of CRP and sand sagebrush prairies to persist. In the short term, continued maximum enrollment and retention of CRP remains the most straightforward way to avoid extirpation of lesser prairie-chicken populations in this ecoregion. In the long term, changes in grazing management, including reductions in grazing intensity and distribution through strategies such as growing season deferment, rest-rotation periods of at least a year, and increasing pasture size will likely be necessary to restore nesting habitat to private and public tracts of sand sagebrush prairie (Kraft et al. 2021). Multi-year grazing deferments would also allow the regrowth of nesting cover and protect it from grazing and trampling between growing seasons. Conservation strategies that increase the overall grassland on the landscape would contribute to meeting grassland thresholds for lesser prairie-chickens throughout the Sand Sagebrush Prairie Ecoregion.

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CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

All capture and handling was completed under Kansas State University Institutional Animal Care and Use Committee Permit No. 3703, Kansas Scientific Wildlife Permits SC-024-2018 and SC-015-2019, and Colorado Scientific Wildlife Permits SC-128-2016, SC-079-2017, SC-076-2018, and SC-077-2019.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website. These include additional details about the cover types used in this study, additional results from our vegetation surveys of Baca and Morton counties, and comparisons to historical data from the Cimarron and Comanche National Grasslands.

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