Research Article

Demographic Consequences of Conservation Reserve Program Grasslands for Lesser Prairie-Chickens

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ABSTRACT Knowledge of landscape and regional circumstances where conservation programs are successful on working lands in agricultural production are needed. Converting marginal croplands to grasslands using conservation programs such as the United States Department of Agriculture Conservation Reserve Program (CRP) should be beneficial for many grassland-obligate wildlife species; however, addition of CRP grasslands may result in different population effects based on regional climate, characteristics of the surrounding landscape, or species planted or established. Within landscapes occupied by lesser prairie-chickens (*Tympanuchus pallidicinctus*), CRP may provide habitat only for specific life stages and habitat selection for CRP may vary between wet and dry years. Among all study sites, we captured and fitted 280 female lesser prairie-chickens with very high frequency (VHF)- and global positioning system (GPS) transmitters during the spring lekking seasons of 2013–2015 to monitor habitat selection for CRP in regions of varying climate. We also estimated vital rates and habitat selection for 148 individuals, using sites in northwest Kansas, USA. The greatest ecological services of CRP became apparent when examining habitat selection and densities. Nest densities were approximately 3 times greater in CRP grasslands than native working grasslands (i.e., grazed), demonstrating a population-level benefit (CRP = 6.0 nests/10 km^2 ± 1.29 [SE], native working grassland = 1.7 nests/10 km^2 ± 0.62). However, CRP supporting high nest density did not provide brood habitat; 85% of females with broods surviving to 7 days moved their young to other cover types. Regression analyses indicated lesser prairie-chickens were approximately 8 times more likely to use CRP when 5,000-ha landscapes were 70% rather than 20% grassland, indicating variation in the level of ecological services provided by CRP was dependent upon composition of the larger landscape. Further, CRP grasslands were 1.7 times more likely to be used by lesser prairie-chickens in regions receiving 40 cm compared to 70 cm of average annual precipitation and during years of greater drought intensity. Demographic and resource selection analyses revealed that establishing CRP grasslands in northwest Kansas can increase the amount nesting habitat in a region where it may have previously been limited, thereby providing refugia to sustain populations through periods of extreme drought. Nest survival, adult survival during breeding, and nonbreeding season survival did not vary between lesser prairie-chickens that used and did not use CRP grasslands. The finite rate of population growth was also similar for birds using CRP and using only native working grasslands, suggesting that CRP provides habitat similar to that of native working grassland in this region. Overall, lesser prairie-chickens may thrive in landscapes that are a mosaic of native working grassland, CRP grassland, with a minimal amount of cropland, particularly when nesting and brood habitat are in close proximity. © 2018 The Wildlife Society

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Populations of lesser prairie-chickens (*Tympanuchus pallidicinctus*) have decreased in occupied range and density since the 1980s, leading to a temporary listing as threatened under the Endangered Species Act of 1973, as amended, from May 2014 to July 2016 (Taylor and Guthery 1980, Haukos and Boal 2016, Ross et al. 2016*a*). The lesser prairie-chicken was removed from the list of threatened species in response to a judicial decision in September 2015 (U.S. Fish and Wildlife Service 2016). However, environmental conditions such as grassland conversion to other uses or cover types and periodic drought continue to affect the lesser prairie-chicken across its range (Fuhlendorf et al. 2002, Silvy et al. 2004, Wolfe et al. 2007, Haukos and Boal 2016, Robinson et al. 2016*a*). Lesser prairie-chickens require large areas of grassland with specific vegetation structure (Haukos and Zaveleta 2016). Large grasslands may allow lesser prairie-chickens to persist among episodic periods of drought and above-average precipitation that influence population fluctuations (Grisham et al. 2013, Haukos and Zaveleta 2016, Ross et al. 2016*a*).

In contrast to the range-wide declining population trajectory and broad-scale habitat loss throughout much of their distribution, the lesser prairie-chicken has expanded its range and significantly increased in abundance in the Shortgrass/CRP Mosaic Ecoregion of northwest Kansas, USA (SGPR; north of the Arkansas River; Fig. 1) since the mid-1990s (Rodgers 1999, Jensen et al. 2000, Dahlgren et al. 2016). Although survey efforts were minimal prior to becoming a candidate for the Endangered Species Act in 1998, there is limited indication of lesser prairie-chicken occurrence in this ecoregion prior to the late 1990s (Hagen 2003, Rodgers 2016). A possible factor contributing to population expansion in the SGPR Ecoregion is a response to the maturation of United States Department of Agriculture Conservation Reserve Program (CRP) grasslands (Rodgers 1999, 2016; Dahlgren et al. 2016; Spencer et al. 2017). Hagen (2003) summarized reports of lesser prairie-chickens throughout Kansas and noted records of a harvested lesser prairie-chicken in Logan County in 1921, the occurrence of 2 small populations farther south near the southwest border of Lane County and near the northeast corner of Finney County in 1955, and records of unknown prairie-chicken species farther east in Ellis and Rush counties from 1962 to 1976 (Baker 1953, Schwilling 1955, Waddell 1977). In contrast to the isolated historical sightings, the SGPR Ecoregion may currently support approximately 55% of the estimated lesser prairie-chicken range-wide population (McDonald et al. 2014, 2016).

Throughout the northern distribution of the lesser prairie-chicken's range that encompasses the SGPR Ecoregion, a precipitation gradient results in a distinct east-to-west transition from mixed-grass to short-grass prairie (McDonald et al. 2014, Grisham et al. 2016). In the short-grass prairie, frequent drought and lack of adequate vegetation structure may have limited lesser prairie-chicken occupancy and abundance to low, apparently undetectable, levels prior to the advent of CRP (Rodgers and Hoffman 2005, Dahlgren et al. 2016, Rodgers 2016). Experts suggest that lesser prairie-chickens in the short-grass prairie, and other areas west of the 100th meridian, were formerly confined to relatively small patches of mixed-grass, sand sagebrush (*Artemisia filifolia*), and sand shinnery oak (*Quercus havardii*; Giesen 1994, Haukos and Zaveleta 2016, Rodgers 2016). The addition of CRP grasslands to landscapes of short-grass prairie in northwest Kansas may mimic natural patches of taller vegetation, which formerly occurred only on sandy soils, in somewhat moister microclimates, on north facing slopes, or in drainages.

Adding taller vegetation in the form of CRP grasslands to a short-grass prairie landscape would increase the amount of cover and increase heterogeneity at the landscape scale. Spatial heterogeneity can be particularly important for generating habitat stability and maintaining habitat for multiple life stages of grassland birds (Knopf 1996, Fuhlendorf et al. 2006, McNew et al. 2015, Sandercock et al. 2015). Heterogeneity established by the taller vegetation and thick litter layer of CRP in a matrix of short-grass prairie with more open canopy may create a landscape capable of supporting nesting and brood-rearing life stages for lesser prairie-chickens (Hagen et al. 2013). For example, a previous study in the SGPR Ecoregion detected 70% (41/59) of lesser prairie-chicken nests in CRP; however, only 37% (10/27) of broods spent most of their time in CRP (Fields et al. 2006).

Additionally, a lack of grazing and the native tall-grass species composition of CRP may ensure the presence of habitat during drought, when short-grass prairie growth is limited and contributes little to available lesser prairie-chicken habitat. Spatial heterogeneity is important in ensuring available habitat in the southern Great Plains, which exhibit strong temporal and spatial variation in net primary productivity (Sala et al. 1988, Grisham et al. 2016). Nesting
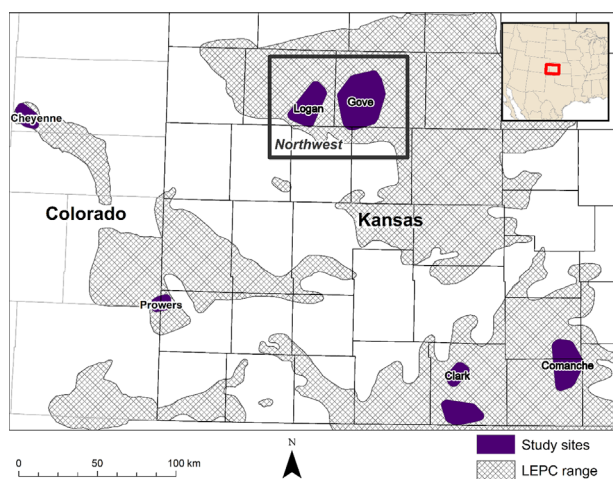

Figure 1. Locations of the 5 study sites where we marked, captured, and monitored lesser prairie-chickens (LEPC) in 2013–2016 to estimate regional use of Conservation Reserve Program grasslands in Kansas and Colorado, USA. The northwest Kansas study sites are highlighted with a black box to identify the spatial extent of landscape-scale resource selection functions and demographic estimates herein. The estimated contemporary lesser prairie-chicken range is identified by black crosshatches.

cover may be readily available throughout native working grasslands (i.e., grazed) during wet years and nearly absent during drought (Grisham et al. 2013, Haukos and Zaveleta 2016). During drought in short-grass dominated landscapes, the added refugia and stability of CRP grasslands would likely increase the resistance and resiliency of populations to intensive drought.

Last, the ecological response of lesser prairie-chickens to CRP grasslands is likely influenced by a general increase in grassland abundance at the landscape scale. Grasslands in northwest Kansas are comparatively more fragmented than the occupied mixed grass prairie portions of the state (Spencer et al. 2017). In landscapes that consist of <60% grassland, general availability of grasslands may be the most limiting for lesser prairie-chickens (Crawford and Bolen 1976, Ross et al. 2016b). Conversion of marginal croplands back into grasslands through CRP could allow landscapes to surpass a critical threshold. Further, the increased grassland abundance provides an additional mechanism to stabilize populations. For example, the amount of available grassland within a 3-km landscape surrounding leks can influence the resilience of lesser prairie-chicken populations to drought (Ross et al. 2016b).

Although increased grassland abundance at the landscape scale can be beneficial, not all grasslands provide habitat equal in quality (Hagen et al. 2009, Lautenbach 2015, Robinson 2015). Conservation Reserve Program grasslands are often smaller in size than native working grasslands (grazed grasslands) and occur in landscapes where grassland has been fragmented through conversion to row crop agriculture (Dahlgren et al. 2016, Rodgers 2016). The potential for more concentrated small patches of habitat in CRP may increase risk of predation and create ecological traps, particularly if predators conduct area-concentrated searches (Gates and Gysel 1978, Ringelman 2014). Based on results from a previous 2-year study in the SGPR Ecoregion, it appears that CRP grasslands do not function as ecological traps for lesser prairie-chickens; demographic performance was similar in CRP grasslands compared to other cover types (Fields et al 2006). Alternatively, the use of CRP grasslands by lesser prairie-chickens may follow an ideal free distribution model if individuals select habitat that maximize individual fitness (Fretwell and Lukas 1970, Whitman 1980). In an ideal free distribution, when densities within a patch increase, the fitness of individuals within the patch decrease. Individuals move into marginal habitats only after a density is surpassed in more optimal habitat (Fretwell and Lucas 1970). In such a distribution, estimates of individual demographic performance would only be beneficial when linked with inference from resource selection, densities, and carrying capacity, which are needed to discern habitat quality at the population level (Van Horne 1983, Rodewald 2015).

Overall, it remains unclear if CRP grasslands merely increase the amount of available habitat above an extinction threshold, increase the spatial heterogeneity of certain grassland landscapes, provide high-quality habitat for lesser prairie-chickens by increasing the fitness of individuals, or provide for a limiting life-stage-specific habitat at a landscape scale. In sum, this information can be used to target conservation efforts and develop management strategies. To fill knowledge gaps, our objectives included identifying landscape and regional climatic constraints in which CRP becomes usable by lesser prairie-chickens. We then assessed the individual-level habitat quality of CRP and other grassland cover types based on the finite rate of population growth (λ) and vital rates among individuals using CRP and native working grasslands (Rodewald 2015). Last, we estimated nesting densities to provide inference of population-level habitat quality. Overall, this study describes the circumstances in which CRP provides habitat for lesser prairie-chickens and demographic performance of birds using CRP.

STUDY AREA

The study area encompassed the mixed- to short-grass portions of the lesser prairie-chicken range in Kansas and Colorado, USA (Fig. 1). A longitudinal precipitation gradient spanned from east (69 cm) to west (37 cm) across the extent of Kansas into eastern Colorado with a concomitant transition from mixed- to short-grass prairie (Grisham et al. 2016, PRISM 2016). Pockets of sand sagebrush prairie were interspersed on sandy soils, especially in the southwest portion of the study area. Mosaics of CRP and row-crop agriculture were associated in areas with arable soils. Most of the large grasslands that remain were restricted to areas of sandy or rocky soils or areas with rough terrain (Spencer et al. 2017). Within the study area, we collected resource selection and vital rate data at 5 study sites including 2 in Colorado and 3 in Kansas (Fig. 1). Temperatures ranged from −26°C to 43°C (extreme min. and max. temp), with average daily minimum and maximum temperatures of 5°C and 21°C, respectively, during the period of data collection (15 Mar 2013 to 15 Mar 2016; National Oceanic and Atmospheric Administration [NOAA] 2016a).

The Red Hills and Clark study sites were in the Mixed-Grass Prairie Ecoregion, whereas the Logan and Gove Study sites were in the SGPR Ecoregion (McDonald et al. 2014). The Cheyenne County and Prowers County study sites each represent isolated portions of the current lesser prairie-chicken range in Colorado and occurred within the Sand Sagebrush Prairie (Hagen and Giesen 2005, McDonald et al. 2014).

At the northwest Kansas study site, annual average long-term (30-year) precipitation varied between 47 cm and 52 cm in Gove and Logan counties, respectively (PRISM 2016). The portion of the study site occurring in Logan County (41,940 ha) was comprised of relatively more short-grass prairie and less precipitation than the Gove County (87,822 ha) portion to the east. The transition between semi-arid and temperate precipitation levels divided the counties (Plumb 2015, Robinson 2015). Dominant plant species on the northwest Kansas study site included sideoats grama (*Bouteloua curtipendula*), blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), western wheatgrass (*Pascapyron smithii*), little bluestem (*Schizachyrim scoparium*), broomed snakeweed (*Gutierrezia sarothrae*),

purple threeawn (*Aristida purpurea*), and annual bromes (*Bromus* spp.; Lauver et al. 1999). The northwest study site was a mosaic of CRP (7.4%), cropland (36%), and native short-grass or mixed-grass prairie (54%; Robinson 2015). The Gove County portion was composed of 8.0% CRP, 34% cropland, and 54% native working grassland and the Logan County portion was composed of 8.0% CRP, 32% cropland, and 56% native working grassland. Soils were predominantly silt loams (80% and 75% of soil type by site, respectively), but clay loams and fine sandy loams were also present (Soil Survey Staff 2015). Research was mostly conducted on private working grasslands but also included the Smoky Valley Ranch (6,600 ha) in Logan County, owned and operated by The Nature Conservancy. Historical ecological factors that maintained grasslands at the northwest study site included periods of drought, bison (*Bison bison*) grazing, and fire. However, fire is largely absent from the current landscape and grazing by cattle is controlled within fenced pastures. Full season or rotational grazing operations for cow-calf and yearling herds were the dominant system used among local ranchers. A significant portion of CRP was hayed prior to and during the study because of drought conditions, a few tracts were inter-seeded and disked, and others were undisturbed and idle. Mammalian and avian fauna at the site included coyote (*Canis latrans*), swift fox (*Vulpes velox*), black-tailed prairie-dog (*Cynomys ludovicianus*), thirteen-lined ground-squirrel (*Ictidomys tridecemlineatus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), western meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), and horned lark (*Eremophila alpestris*).

Precipitation varied during the study. Data collection began during an exceptional drought in the spring and summer of 2013 with a shift to more normal conditions in 2014 and 2015 (NOAA 2016*a*, *b*). Palmer Drought Severity Indices (PDSI; smaller number = more severe drought) were −3.4, −0.67, and 0.39 during the breeding season (Mar–Aug) and −1.85, −0.16, and 0.38 during the nonbreeding season (Sep–Feb) of 2013, 2014, and 2015, respectively (Augustine 2010, NOAA 2016*b*). During the nesting period (Apr–Jul), PDSI were estimated at −3.44, −1.58, and 0.57 in 2013, 2014, and 2015, respectively (NOAA 2016*b*). Annual precipitation was 39 cm, 48 cm, and 49 cm in 2013, 2014, and 2015, respectively (NOAA 2016*a*). These data indicated the occurrence of a drought during the first spring and summer of the study.

The Clark study site was primarily located in western Clark County, Kansas, on the transition between of the mixed-grass prairie and sand sagebrush prairie. On average, the site received 59 cm of rain annually and was dominated by sand dropseed, western ragweed (*Ambrosia psilostachya*), blue grama, Russian thistle (*Salsola tragus*), little bluestem (*Schizacyrim scoparium*), alkali sacaton (*Sporobolus airoides*), and sand sagebrush (PRISM 2016). The Clark site was 77% grassland, 14% cropland, and 5.5% CRP (Robinson 2015) and was was largely comprised of 2 privately owned ranches: 1 in the Cimarron River floodplain (32,656 ha) dominated by loamy fine sands, fine sandy loams, and fine sands with the other in rolling hills (14,810 ha) 20 km north on mostly silty clay, clay loam, and silt loam (Soil Survey Staff 2015). Rotational grazing systems for cow-calf and yearling herds were used in this area.

The Red Hills study site (49,111 ha) was in the mixed-grass prairie of Comanche and Kiowa counties and represented the eastern boundary of the current lesser prairie-chicken range. The Red Hills study site received the greatest annual precipitation, where average annual precipitation was 69 cm (PRISM 2016). Dominant plant species included little bluestem, Louisiana sagewort (*Artemisia ludiviciana*), side-oats grama, western ragweed, sand dropseed, annual bromes, and blue grama. The Red Hills study site was 87% grassland, 8.9% cropland, and 2.2% CRP (Robinson 2015). The site was comprised of large contiguous grasslands with many drainages and cow-calf and yearling (season-long) grazing systems. Research efforts focused on a large ranch that implemented a patch-burn grazing system wherein large pastures were divided into thirds or fourths and a portion was sequentially burned annually. Dominant soils included sandy loam, clay loam, and clay (Soil Survey Staff 2015).

Two study sites in Colorado were dominated by sideoats grama, blue grama, sand dropseed, sand sagebrush, field bindweed (*Convolvulus arvensis*), Russian thistle, and kochia (*Kochia scoparia*; J. Reitz, Colorado Parks and Wildlife, unpublished data). The Prowers County study site (1,146 ha) was comprised of relict patches of grassland (largely CRP) within a landscape mosaic of dryland and irrigated row-crop agriculture. The study site was composed of 43% cropland, 28% native working grassland, and 25% CRP (Homer et al. 2015). Prowers County dominantly comprised of loamy soils (Soil Survey Staff 2015) and received 43 cm of precipitation annually (PRISM 2016). Most CRP fields were enrolled into the program in the mid-1980s. Many tracts had recently undergone mid-contract management to increase forb abundance and diversity of the grassland tract. To meet the management requirements, typically a third of the CRP fields were disked, creating linear strips of disturbed and undisturbed grass (J. Reitz, personal communication). The study site in Cheyenne County (16,968 ha) was comprised of large expanses of lightly and heavily grazed sand sagebrush prairie where 30-year precipitation averages were lowest of all study sites (37 cm; PRISM 2016). The Cheyenne County study site was composed of 99% native working grassland, 1% cropland, and no CRP grassland; the site largely occurred on sandy soils (Homer et al. 2015, Soil Survey Staff 2015). Although there was no CRP within the minimum convex polygon used to delineate the Cheyenne County study site, CRP grasslands were present <4 km to the north and south of the study site, within the mean dispersal distance of lesser prairie-chickens (16.18 km; Earl et al. 2016).

METHODS

We captured lesser prairie-chickens at leks between early March and mid-May using walk-in funnel traps and drop nets (Haukos et al. 1990, Silvy et al. 1990). Upon capture, we sexed lesser prairie-chickens based on plumage coloration, pinnae length, and tail pattern (Copelin 1963). We aged each

individual as yearling (second-year; SY) or adult (after-second-year; ASY) depending on the color patterns, shape, and wear of the outermost flight feathers (P9 and P10), which are retained from juvenal plumage in SY birds (Ammann 1944). We prepared protocols and obtained collection permits to capture and handle birds through the Kansas State University Institutional Animal Care and Use Committee (protocols 3241 and 3703); Kansas Department of Wildlife, Parks, and Tourism scientific collection permits (SC-042-2013, SC-079-2014, SC-001-2015); and the Colorado Parks and Wildlife scientific collection license numbers 13TRb2053, 14TRb2053, and 15TRb2053.

We captured females and marked them with 4 plastic leg bands corresponding to region, year, and lek to identify and resight individuals in the field. We tagged birds with a 15-g very-high-frequency transmitter (VHF; A3960, Advanced Telemetry System, Isanti, MN, USA), or 22-g global positioning system (GPS) satellite Platform Transmitter Terminal (SAT-PTT) transmitter (PTT-100, Microwave Technology, Columbia, MD, USA and North Star Science and Technology, King George, VA, USA). We attached VHF transmitters as a necklace with whip antennae down the middle of the back and GPS transmitters were rump mounted using straps that were fastened around each thigh. We released all birds immediately at the site of capture. We obtained diurnal locations for each VHF-marked female 4 times/week using triangulation and Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary). We typically downloaded 8–10 GPS locations/day from each satellite-marked female using the ARGOS system, contingent on available daily solar charge. We recorded GPS locations every 2 hours during the day with a 6-hour gap between 2300 and 0500 when birds were assumed to be roosting.

Selection of CRP

We investigated lesser prairie-chicken use of CRP grasslands from 3 perspectives: the influence of spatial variability of precipitation, the influence of temporal variability of precipitation, and the influence of the surrounding matrix. We evaluated the influence of average annual precipitation on the use of CRP grasslands among lesser prairie-chicken populations in Kansas and Colorado (all study sites; Fig. 1). We investigated the influence of PDSI on selection of land cover types within the northwest Kansas site (Gove and Logan counties). Last, we assessed the influence of the surrounding matrix on use of CRP fields within the SGPR Ecoregion, which encompassed the northwest Kansas site (McDonald et al. 2014).

Influence of spatial variability of precipitation on use.—Use of CRP grasslands by lesser prairie-chickens may vary regionally because of changes in average annual precipitation, which is a primary factor influencing cover and food production. To examine the relationship of average annual precipitation on use of CRP by lesser prairie-chickens in Kansas and Colorado, we first subsampled 2 locations per bird per week from all sites. We then generated 5 random locations within a 4-km radius of each subsampled location

used by a marked lesser prairie-chickens. The 4-km-radius scale outcompeted other models incorporating landscapes within a 2-km radius based on Akaike's Information Criterion corrected for small sample sizes (AIC$_c$) and was also used to assess landscapes surrounding CRP described below (J. D. Kraft, Kansas State University, unpublished data). We assigned a value of 1 to all locations used by lesser prairie-chickens and a 0 to all random locations. We used a logistic regression to describe the combined influence of CRP and precipitation on point use among lesser prairie-chickens among all study sites. Random locations and associated designation as CRP or non-CRP controlled for variation in CRP availability among sites. We assigned average annual precipitation to each location using the 30-year normal precipitation values made available by the PRISM Climate Group (PRISM 2016). Candidate models included single-variable models of CRP presence (0 or 1), annual average precipitation, and additive and interactive models including effects of CRP and average annual precipitation on the probability of use of a location.

Influence of temporal variability of precipitation on selection.—After we examined how the long-term spatial variability of precipitation influenced the use of CRP among individual lesser prairie-chickens throughout the study area, we investigated how selection of CRP grasslands varied temporally with short-term changes in precipitation (drought severity) at the northwest Kansas site. We assigned used locations from marked birds a value of 1 for the response variable. We sub-sampled our pool of bird locations using the sample() command in Program R to 1 location per bird per day to limit potential temporal and spatial autocorrelation associated with SAT-PTT locations. We generated 1 random location for each bird location to define resources available to the population. We constrained random paired locations within the northwest study site boundary (Fig. 1) and assigned the same date to the random location as the corresponding used location. We assigned all random locations a response variable value of 0. For all locations (used and random), we identified a cover type category following Spencer et al. (2017). We assigned 3 different PDSI values to each location. Lag PDSI described the average PDSI value calculated during the previous 12-month period from April to March. Thus, a location recorded during July of 2014 would be assigned the mean PDSI value calculated from April 2013 to March 2014. Monthly PDSI described the PDSI value associated with the same month during which a location was recorded. Average growing season PDSI was the mean value of PDSI calculated during the growing season (Apr–Sep) of the current year. For example, the PDSI value associated with a location recorded in October 2014 was the mean PDSI calculated during April–September 2014. We developed single-variable models for each covariate (landcover type, lag PDSI, monthly PDSI, and average growing season PDSI) and ranked them using the model ranking protocol described below.

Influence of the surrounding matrix.—Efforts to assess the influence of the surrounding matrix on lesser prairie-chicken

selection of CRP grasslands were focused on the northwest Kansas study site. We compared all landscapes associated with CRP tracts used by lesser prairie-chickens to random landscapes that also had a CRP component. Similar to habitat use analyses described previously, we employed logistic regression in the form of a resource selection function to investigate the influence of the matrix surrounding CRP grasslands on selection (Boyce et al. 2002, Manly et al. 2002). With the used versus available framework, we identified CRP fields used by lesser prairie-chickens based on the presence of bird locations from April 2013 to March 2016. We then distributed the same number of random locations in CRP lands located throughout the SGPR Ecoregion encompassing the northwest Kansas study site (McDonald et al. 2014). We delineated landscapes by buffering each location by 4 km using the buffer tool in ArcGIS (Environmental Systems Research Institute [ESRI], Redlands, CA, USA) and using landcover maps created through concurrent research (Spencer et al. 2017). In northwest Kansas, the surrounding matrix for CRP grasslands was largely restricted to cropland or working native grassland cover types. Thus, what was not working native grassland was typically cropland. We evaluated the influence of total area of grassland on lesser prairie-chicken selection of CRP grasslands. We measured total area of working native grassland in the 4-km-radius landscapes using FRAGSTATS (McGarigal et al. 2012). We limited landscape metrics to total area grassland for the main text of the manuscript in hopes to provide a simple relationship that would be implemented by wildlife managers, and because the patterns of habitat fragmentation are rarely as influential as total habitat loss, particularly for focal species that are sensitive to habitat loss (Andren 1994, Villard and Metzger 2014). However, fragmentation can exert broader scale influence among metapopulations and results from a more detailed landscape analysis are included in Supporting Information (Hanski 2015).

Model selection and evaluation.—We examined correlations between pairs of covariates and did not allow correlated variables ($r > 0.70$) within the same model. After model fitting, we ranked and selected the most parsimonious model based AIC_c and informative beta coefficients (Burnham and Anderson 2002). We considered models with $\Delta AIC_c \leq 2$ to be equal to the top-ranked model. Untransformed beta estimates from the top-ranking model were informative when coefficients did not overlap zero at the 95% confidence interval. We plotted predicted probability of use curves for top models in each model set. We conducted all resource selection functions in Program R (R Development Core Team 2016) using the glm package for generalized linear models.

Use of CRP in Northwest Kansas
We measured the proportion of locations from GPS-marked individuals that occurred in cropland, native working grassland, and CRP grassland during the breeding (15 Mar–15 Sep) and nonbreeding seasons (16 Sep–14 Mar)

from 2013 to 2016. Such an approach can complement inference from resource selection functions that are imperfect because of constitutive relationships with the resource composition of study areas evaluated (Garshelis 2000). We used GIS layers from the National Landcover Database (NLCD) 2011 and a CRP layer provided under agreement by the United States Department of Agriculture Farm Services Agency to delineate cropland, native working grassland, and CRP grassland land cover types (Homer et al. 2015). We then overlaid all locations from GPS-marked individuals and estimated the proportion of locations occurring in each cover type during each season and all seasons combined. The GPS transmitters generally have a spatial error of ± 5 m; well within the 30-m × 30-m resolution pixels used in our analyses (Davis et al. 2013).

Vegetation Characteristics of CRP and Native Working Grasslands
We assessed the fine-scale vegetative characteristics of CRP and native working grasslands to provide inference on the potential for each cover type to provide quality microhabitat for lesser prairie-chickens. We collected measurements of grassland variables at random point locations distributed among CRP and native working grasslands available to lesser prairie-chickens within the northwest Kansas study site. We randomly generated available points throughout the study sites at a rate of 1 per 4 ha with a maximum of 10 points per patch. We delineated user-defined habitat patches and digitized them in ArcGIS 10.2 using aerial imagery available in the basemap layer (product of ESRI, i-cubed, U.S. Department of Agriculture Farm Service Agency, U.S. Geological Survey, Automating Equipment Information Exchange, GeoEye, Getmapping, Aerogrid, Instituto Geográfico Português). We identified patches as areas of homogenous vegetation >2 ha and placed them in categories (i.e., native working grassland and CRP) and confirmed categories using ground truthing. We refer to grasslands that were typically managed for cattle production, privately owned, and composed of native grass species as native working grassland throughout the text. We measured vegetation at points within all delineated patches during summer and within a stratified random sample of 20% of patches during fall and winter. We captured vegetation data at more points during the spring breeding season to provide a robust estimate of available reproductive habitat.

At all random locations, we estimated a point-center measurement of percent canopy cover of forbs, bare ground, grass, shrub, and annual bromes within a 60 × 60-cm modified Daubenmire frame (Daubenmire 1959). We estimated 4 additional estimates of canopy cover 4 m from point center at all cardinal directions (5 estimates/point). We obtained visual obstruction readings 4 m from point center at all cardinal directions and we recorded height in dm at which we estimated 100%, 75%, 50%, 25%, and 0% visual obstruction (4 estimates/point; Robel et al. 1970). We measured litter depth (cm) at 0.5-m increments stretching 4 m north, east, south, and west of point center (32 estimates/

point; Davis et al. 1979). We visually estimated the 3 most abundant species within a 4-m radius of each point.

From the top 3 most abundant plant species, we estimated the frequency of tall-grass species occurrence at locations within CRP and native working grasslands. Dominant tall-grass species included little bluestem, big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*). The occurrence of these tall-grass species is suggested to be a reasonable indicator of quality nesting cover for lesser prairie-chickens (Hagen et al. 2013). We also directly estimated the proportion of random points that met characteristics of available nesting habitat following Lautenbach (2015). Available nesting locations had a 75% visual obstruction in the range of 1.5–3.5 dm and bare ground cover estimates <20% when averaged among measurements taken at each random point (e.g., 4-m radius microhabitat; Lautenbach 2015). We used a Hotelling T^2 test to examine a multivariate difference among vegetation measured in CRP and native working grasslands (Johnson and Wichern 1988). Once we identified a significant variation in multivariate space ($P < 0.05$), we then used an unequal variances Welch 2-sample *t*-test to examine differences in all vegetative measurements among CRP and native working grasslands.

Demographic Rates

Vital rate data collection.—We estimated vital rates and population growth for lesser prairie-chickens that used and did not use CRP grasslands at the northwest Kansas study site to assess the demographic influence of CRP in the region. We classified a lesser prairie-chicken as using CRP if it had ≥1 location in CRP during a season. We collected fecundity and survival data during the breeding seasons (15 Mar–15 Sep) and nonbreeding seasons (16 Mar–14 Sep) of 2013–2016. During the breeding season, searches for nest locations occurred when females localized for >3 days or appeared to be nesting based on satellite data. Upon discovery of a nest, we recorded the location of the nest and counted and floated eggs to predict hatch date. We monitored nests remotely by telemetry for VHF-transmitted lesser prairie-chickens and by examining satellite locations for GPS-transmitted birds. Once a female left a nest location, we visited the area to identify nest success or failure based on eggshell appearance and presence or absence of predator sign at the nest site. If a nest was successful, we monitored brood and chick survival by conducting brood flush counts at lesser prairie-chicken female locations within 1 hour of sunrise at weekly intervals from 14 to 60 days after hatch. We thoroughly searched the area surrounding each transmittered female to maximize chick detection. If we did not detect chicks, we flushed the female once more to make sure the brood was no longer present. Between flushes, we located VHF-marked brooding females, and chicks when possible, daily until chicks were 14 days old then 4 times a week after reaching the 14-day-old mark.

Fecundity parameters.—We estimated nesting propensity (NEST; probability a female decides to nest) using a Horvitz–Thomson estimator that accounted for bias from nests that failed before being detected (Dinsmore et al. 2002). We estimated nesting propensity only for GPS-marked females because of the greater resolution location data (8–10 locations/day) and typically verified nest establishment within 3 days of a nest being attempted. Prior to incubation, female lesser prairie-chickens typically visited nests each day from 1200 to 1400 to establish a nest and lay eggs while displaying unique movement patterns relative to non-nesting females (Sullins 2017). To account for undetected nests, we divided 1 by the 3-day nest survival rate estimated from the daily survival rate, then multiplied this number by the total number of detected nests to provide an adjusted estimate of the total number of nests (Dinsmore et al. 2002). We divided the adjusted number of nests by the number of females that were captured presumably before losing a first nest (before 22 Apr) and survived long enough to attempt a nest (survived to 10 May). We estimated propensity to re-nest (RENEST) following a similar protocol but estimated the proportion of females that attempted to re-nest after losing their first nest but not dying during the nest predation events.

We counted clutch size for all first (CLUTCH1) and known second (CLUTCH2) nest attempts and tested for differences in average clutch size between birds that nested in CRP and native working grasslands (i.e., grazed) using a 2-sample *t*-test assuming equal variance. We estimated hatchability following Hagen et al. (2009) as the proportion of chicks hatched per egg laid (HATCH). We estimated daily nest survival rates over a 35-day exposure period with a 10-day laying period and a 25-day incubation period for yearlings and adults. Small sample sizes precluded our ability to estimate nest survival separately for first and re-nest attempts in CRP and native working grassland. We estimated nest survival among attempts for CRP and native working grassland (NSURV) with the nest survival procedure within Program MARK (White and Burnham 1999, Dinsmore et al. 2002). We ranked models based on AIC_c and evaluated models based on model weight (w_i; Burnham and Anderson 2002). Ultimately, we used the model including CRP as a covariate estimated in the R package RMark interface to estimate nest survival throughout the laying and incubation period because we were interested in differences between birds nesting in and out of CRP (Laake 2013, R Development Core Team 2016). We used the delta method to calculate standard errors for each nest survival rate (Powell 2007). We estimated chick survival (CHICK) to 35 days post hatch using models of Lukacs et al. (2004). We did not estimate chick survival separately for CRP and native working grasslands because only 1 brood that survived >7 days used CRP. However, we did estimate the proportion of broods that had ≥1 chick survive to >7 days post-hatch from nests that were in CRP versus native working grasslands. We estimated 35-day survival as the product of weekly survival rates over 5 week-long intervals and estimated the standard error for chick survival using the delta method assuming independence. We estimated fecundity (*F*) for the 2 nesting

attempts (*a*) using the equation below based on Hagen et al. (2009).

$$Fa = [(NEST \times CLUTCH1 \times NSURV) + (1 - NSURV)$$
$$\times (RENEST \times CLUTCH2 \times NSURV)]$$
$$\times (HATCH \times 0.5 \times CHICK)$$

Nest densities.—Even if nest survival was not higher in CRP grasslands compared to native working grasslands, the addition of CRP grasslands could benefit lesser prairie-chickens by increasing the landscape-scale carrying capacity for lesser prairie-chickens nests (Pidgeon et al. 2006, Chalfoun and Martin 2007). We estimated cover type-specific nest densities within 5-km-radius landscapes surrounding each lek to compare the nesting capacity between CRP and native working grasslands in northwest Kansas. We estimated nest densities of transmittered lesser prairie-chickens within a 5-km radius of each lek trapped during spring 2013–2016. We then averaged nest densities in CRP and native working grassland among all leks and estimated the standard deviation of nest densities among landscapes associated with leks. The 5-km-radius buffer around leks represented an estimate of the perceptual range of habitat selection for female lesser prairie-chickens. Greater than 85% of females established nests within this distance from lek of capture in our study, which is comparable to the typical use of nesting habitat within 3 km of leks (Hagen and Giesen 2005, Sullins 2017).

Landscape-scale reproduction.—We estimated the proportions of female lesser prairie-chickens with 7-day-old broods using CRP, native working grassland, or croplands that also nested in CRP. We used the nest location (e.g., CRP or native working grassland) and location occurring closest to the 7-day mark, which encompassed the critical brood survival period. Most lesser prairie-chicken broods die in the first week of life (Lautenbach 2015). The percentage of females using CRP to nest and native working grasslands to brood will identify how lesser prairie-chickens use the CRP or native working grassland mosaic for reproduction.

Female survival parameters.—We used Kaplan–Meier models to estimate breeding season survival for adult and yearling lesser prairie-chickens during 2013–2016 breeding seasons (*Sb*; 15 Mar–15 Sep) in Program MARK. We used the same Kaplan–Meier models to estimate nonbreeding season (16 Sep–14 Mar) survival (*Snb*) for adults and yearlings combined (White and Burnham 1999). We used a juvenile survival (35 days post-hatch to first breeding season; *Sjuv*) estimate from a previous study on lesser prairie-chickens in western Kansas: 0.539 ± 0.089 (SE; Hagen et al. 2009). We did not obtain a sufficient sample size to estimate this demographic parameter for our study population in northwest Kansas. We estimated nonbreeding and breeding season survival separately because of differences in habitat use during these 6-month seasons (Haukos and Zaveleta 2016). We then estimated annual survival (*S*) for each age class (*c*) as:

$$Sc = Sb \times Snb$$

Population matrix.—We integrated fecundity and survival parameters for female lesser prairie-chickens using CRP and native working grasslands into a matrix population model (**A**) wherein *Fy* represented yearling fecundity, *Fa* was adult fecundity, *Sjuv* was juvenile survival, *Sy* was yearling annual survival, and *Sa* was adult annual survival.

$$A = \begin{bmatrix} Fy \times Sjuv & Fa \times Sjuv \\ Sy & Sa \end{bmatrix}$$

We used 1,000 bootstrap iterations of the R package popbio (Stubben and Milligan 2007) to generate estimates and standard deviations of the finite rate of population change (λ), generation time in years (T), and net reproductive rate (R_0) for birds using CRP and not using CRP. To explore parameter space, we used uniform distributions encompassing the range of nesting propensity and renesting propensity for matrix model calculations. We also conducted a retrospective analysis to estimate vital rates that contributed the most to difference in population growth rates among female lesser prairie-chickens that used native working grassland and CRP grasslands. Vital rates estimated separately among CRP and native working grasslands included nest survival, clutch size, breeding season survival, and nonbreeding season survival. We grouped individuals as CRP or native working grassland based on the location of the nest for nest survival and clutch size and based on the use or complete avoidance of CRP for adult survival estimates. We estimated contributions to λ for each treatment using a fixed-effects life-table response experiment and used 1,000 bootstrap iterations to estimate standard deviations for the contribution values (Caswell 1989).

RESULTS

We captured, marked, and monitored 280 female lesser prairie-chickens from 2013 to 2016 among all sites. Overall, we marked 156 individuals with GPS-transmitters and 124 individuals with VHF-transmitters. At the northwest Kansas site, we marked 146 female lesser prairie-chickens with GPS- or VHF-transmitters and used these birds to estimate the demographic response to CRP. Of the females monitored in northwest Kansas, 10% were of unknown age, 28% were ASY, and 63% were SY.

Selection of CRP

Influence of spatial variability of precipitation on selection.—Using 7,462 locations from 96 female lesser prairie-chickens marked with GPS-transmitters and 37,310 random locations, we examined the influence of average annual precipitation and CRP on the probability of use by lesser prairie-chickens among all study sites. At a regional scale, CRP grasslands were 1.7 times more likely to be used by lesser prairie-chickens in regions receiving 40 cm compared to 70 cm of average annual precipitation ($\delta 1 = -0.0314 \pm 0.0048$, marginal effect of annual average precipitation on predicted probability of using CRP; Fig. 2). The model including the interactive effect of CRP presence
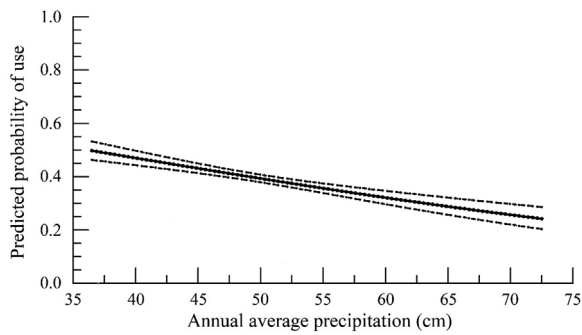
Figure 2. Predicted probability of use of Conservation Reserve Program (CRP) grasslands by lesser prairie-chickens in Kansas and Colorado, USA, 2013–2016 as a function of average annual precipitation estimated in 800-m × 800-m pixels (PRISM 2016). The displayed relationship of annual average precipitation and probability of use is only for CRP grasslands based on the interaction model that included presence of CRP and average annual precipitation. Dashed lines indicate 95% confidence intervals.

Figure 4. Predicted probability of use of Conservation Reserve Program (CRP) grasslands by lesser prairie-chickens in northwest Kansas, USA, 2013–2016 as a function of the amount of native working grassland in a 5,026-ha (4-km radius) landscape. Dashed lines indicate 95% confidence intervals.

and annual average precipitation outcompeted all other candidate models and had an AIC_c model weight of 1.0.

Influence of temporal variability of precipitation on selection.—Within the northwest Kansas study site, probability of use of CRP increased with increased drought severity as indicated by the lag PDSI value. The predicted probability of using CRP was positively related to PDSI and was 1.89 times greater when the lag PDSI value equaled −4 (more severe drought) compared to a value of 4 (less severe drought; $\delta_1 = -0.1963 \pm 0.0322$, marginal effect of PDSI lag on predicted probability of using CRP; Fig. 3). In contrast, the predicted probability of using native working grassland was negatively related to PDSI and was 1.18 times less when the lag PDSI value was −4 compared to 4 and overlapped zero at the 95% confidence interval ($\delta_1 = -0.0278 \pm 0.0272$, marginal effect of PDSI lag on predicted probability of using native working grassland; Fig. 3).

Influence of the surrounding matrix.—We sampled 62 used and 62 random CRP fields and their surrounding 4-km landscapes in the SGPR Ecoregion within the estimated distribution of lesser prairie-chickens. The matrix surround-
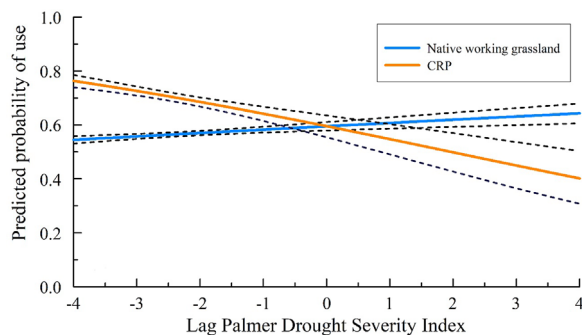
ing each CRP field varied in the amount (716–4,209 ha) and percent of grassland (14–84%) and clumpiness of grasslands (0.7230.961; see Fig. A1, available online in Supporting Information). In northwest Kansas, CRP grasslands were 8.6 times more likely to be used by lesser prairie-chickens when local landscapes (∼5,027 ha) were comprised of approximately 70% (∼3,500 ha) native grassland compared to approximately 20% (1,000 ha) native grassland ($\beta_{area} = 0.00155 \pm 0.000331$, $P < 0.001$; Fig. 4).

Use of CRP

Lesser prairie-chickens ($n = 79$) used native working grasslands more frequently than CRP in northwest Kansas during the breeding and nonbreeding seasons of 2013–2016 (Table 1). Of the locations from GPS-marked birds, 70% of locations were in native working grasslands with 20% in CRP grasslands (Table 1).

Vegetation Differences Between CRP and Native Working Grasslands

Overall, CRP grasslands supported taller vegetation with a greater litter depth, had less shrub cover, less bare ground,

Figure 3. Predicted probability of lesser prairie-chickens in Kansas and Colorado, USA, 2013–2016 using Conservation Reserve Program (CRP) or native working grassland as a function of drought severity (Palmer Drought Severity Index) during the previous year (low numbers = greater drought severity). Dashed lines indicate 95% confidence intervals.
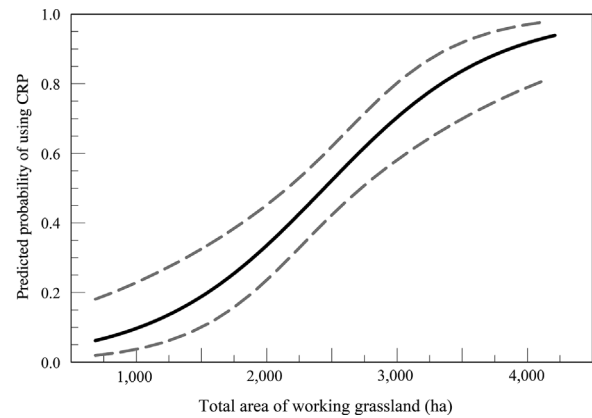
Table 1. Locations used by, and available to, lesser prairie-chickens in northwest Kansas, USA. We present proportion of locations ($n = 89,297$) of lesser prairie-chickens ($n = 148$) marked with GPS-transmitters occurring in cropland, Conservation Reserve Program (CRP) grasslands, and native working grasslands during the breeding (15 Mar–14 Sep), nonbreeding (16 Sep–14 Mar), and all seasons combined in northwest Kansas during 2013–2016. Proportional availability of cover types is based on minimum convex polygons drawn around all points at the northwest Kansas study sites (Plumb 2015, Robinson 2015).

Season	Cropland	CRP	Native working grassland
Used			
Breeding	0.07	0.20	0.73
Nonbreeding	0.20	0.19	0.61
All seasons	0.10	0.20	0.70
Available			
All seasons[a]	0.35	0.08	0.57

[a] Availability of landcover types remained the same among seasons.

Table 2. Sample sizes, means, and standard deviation of microsite (4-m radius) vegetation measurements collected at random locations distributed within the northwest Kansas, USA study site in 2013–2016.

Vegetation measurements[a]	Native working grasslands			CRP grasslands					
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	t	Df	P
Visual obstruction readings (VOR)									
25% VOR (dm)	1.95	1.64	6,918	3.34	2.04	3,372	−33.7	5,475	0.001
75% VOR (dm)	0.98	1.29	6,918	2.06	1.64	3,372	−34.4	5,550	0.001
Horizontal cover estimates									
Litter (%)	19.37	18.07	8,674	23.14	20.05	4,229	−10.3	7,387	0.001
Grass (%)	59.17	26.77	8,674	64.54	26.63	4,229	−11.1	8,289	0.001
Shrub (%)	1.83	8.95	8,674	0.01	0.31	4,228	18.2	8,707	0.001
Bare (%)	15.35	20.23	8,674	7.98	14.79	4,229	22.7	11,367	0.001
Forb (%)	8.11	13.05	8,674	7.02	18.11	4,230	0.8	5,727	0.410
Litter depth (cm)	1.20	1.57	55,520	2.72	3.26	27,072	−72.7	33,345	0.001
Grass height (cm)	17.07	15.75	1,720	32.34	19.81	841	−19.5	1,375	0.001
Frequency of tall-grass occurrence[b]	0.13	0.33	1,735	0.63	0.48	846			
Proportion suitable nesting locations	0.20		1,713	0.46		834			

[a] Vegetation measurements include visual obstruction readings collected using a 2-m-tall Robel pole marked at alternating decimeters. We measured horizontal cover estimates using a 60-cm^2 Daubenmire frame, and litter depth and grass height using a ruler. The frequency of tall-grass occurrence is an estimate of the number or locations having a tall-grass species as 1 of the 3 most abundant plants. Proportion suitable nesting locations is the proportion of location having suitable nesting habitat as described in Lautenbach (2015; 75% VOR:1.5–3.5 dm, bare [%]: 0–20).

[b] Tall-grass species included little bluestem, big bluestem, switchgrass, and indiangrass.

more tall-grass species, and provided a greater number of suitable nesting microhabitats (Hotelling's $T^2 = 69.73$, $P < 0.001$; Table 2).

Demographic Rates

Nests.—We monitored 109 lesser prairie-chicken nests during 2013, 2014, and 2015 in northwest Kansas. Total clutch size did not vary among females that nested in CRP (9.70 ± 3.17 [SE]) and native working grassland (9.61 ± 2.56; $t_{99} = 0.13$, $P = 0.90$; Table 3). Females on average laid 10.33 ± 0.25 eggs for their first nest and 7.23 ± 0.58 eggs for their second clutch ($t_{99} = 5.35$, $P \leq 0.001$). Re-nesting attempts in CRP and native working grasslands were limited and too few to provide estimates of re-nesting survival ($n = 4$ and 15 respectively; Table 3).

Nesting propensity varied among years and was estimated at 82.0%, 88.0%, and 100% in 2013, 2014, and 2015, respectively. Low nesting propensity corresponded with index of drought severity (PDSI) during the nesting season. The probability of a marked female re-nesting following the loss of a first nest was estimated at 15.3%, 53.7%, and 35.7% in 2013, 2014, and 2015, respectively.

The highest-ranked nest survival model based on AIC_c was the null model ($w_i = 0.25$), followed by a year ($w_i = 0.21$), CRP ($w_i = 0.17$), age class ($w_i = 0.11$), and nesting attempt model ($w_i = 0.09$), all of which had a $\Delta AIC_c < 2$. Support for the null model suggested that daily survival rates of lesser prairie-chicken nests was similar among land cover types, years of the study, age classes, and nesting attempts. Lesser prairie-chickens that nested in CRP had an estimated nest survival rate of 0.505 ± 0.079, whereas those that used native working grasslands had an estimated nest survival of 0.405 ± 0.053 (Table 3). The top-ranking model with a covariate included year and nest survival was estimated at 0.365 ± 0.068, 0.422 ± 0.066, and 0.604 ± 0.101 in 2013, 2014, and 2015, respectively. Because our goal was to determine cumulative effects of CRP on lesser prairie-chicken population demography, we used the CRP model to estimate nest survival.

Of the nests monitored in northwest Kansas, 34% produced young, 52% were depredated, and 11% abandoned. Only 3% of nests were trampled by cattle, all within native working grassland pastures. The proportion of eggs that successfully

Table 3. Fecundity and survival variables estimated for female lesser prairie-chickens that used Conservation Reserve Program (CRP) grasslands at some point in their life cycle and those that never used CRP (Non-CRP) cover types in northwest Kansas, USA, during the breeding season (15 Mar–15 Sep) and nonbreeding season (15 Sep–15 Mar) during 2013–2016. We estimated chick survival and hatchability among all cover types.

Variable	CRP				Non-CRP			
	Estimate	SE	95% CI	n	Estimate	SE	95% CI	n
Nest survival	0.51	0.079	0.35–0.66	34	0.41	0.05	0.30–0.51	75
Clutch size of first nest	10.5	0.45	9.6–11.4	30	10.3	0.31	9.7–10.8	56
Clutch size of second nest	4.5	1.04	2.5–6.5	4	7.8	0.62	6.7–9.0	19
Nest density (nests/10 km^2)[a]	6.0	1.29	3.5–8.6	20	1.7	0.62	0.41–3.03	18
Percentage of broods[b]	14.3			1	86.0			6
Breeding season survival	0.42	0.064	0.30–0.55	65	0.44	0.07	0.31–0.57	63
Nonbreeding season survival	0.71	0.100	0.52–0.91	22	0.57	0.1	0.35–0.76	31

[a] We estimated nest density within the 5-km-radius area surrounding each lek and sample sizes reflect the number of leks.

[b] Estimate of the percentage of 7-day-old broods occurring in CRP or Non-CRP grasslands from nests that hatched in CRP.

hatched within a successful nest (hatchability) was estimated as 75% ± 0.048 from 35 successful nests in northwest Kansas. Among nests, hatchability varied from 10% to 100% of eggs successfully hatching.

Nest densities.—Approximately 40% of nests occurred in CRP grassland in 2013 and 2014, whereas only 10% of nests were in CRP in 2015. Across the 5-km lek buffers, CRP made up 17.3% of the available grassland. Overall, nest density point estimates of marked lesser prairie-chickens were ~3 times greater in CRP grasslands than in native working grassland (CRP = 6.0/10 km^2 ± 1.29, native working grassland = 1.7/10 km^2 ± 0.62). Nest densities were greater in CRP grasslands compared to native working grassland in 85% (17/20) of 5-km-radius landscapes surrounding each lek.

Landscape-scale reproduction.—In northwest Kansas, 1 out of 7 female lesser prairie-chickens successfully used CRP as nesting and brooding habitat to rear chicks to 7 days. The remaining females (85%) used CRP grasslands as nesting substrate, and successfully raised chicks to 7 days old, moved broods to other cover types within the first 7 days of life. Of these females, half moved their broods to native working grasslands and the other half were moved to cropland. All successful broods that hatched in native working grassland nests, excluding 1 brood that used CRP for a half day, remained in native working grassland for the first 7 days of life.

Chick survival.—The strong selection of non-CRP cover types for brood rearing did not allow for the estimation of chick survival in CRP and non-CRP cover types. Pooling across strata, we estimated an overall 35-day chick survival from 34 broods for northwest Kansas at 0.261 ± 0.071. Although our sample sizes precluded estimating chick survival for individuals using CRP and native working grassland as brooding habitat, we estimated the proportion of broods that successfully survived >7 days post-hatch from nests in CRP and native working grasslands. Of broods from successful nests in CRP, 7 of 11 survived and 9 of 20 broods from nests in native working grassland survived to >7 days post-hatch.

Survival.—We estimated survival for 128 adult females during the breeding season and 53 during the nonbreeding season in 2013, 2014, and 2015 combined. For birds that did not use CRP grasslands during the breeding season, survival was estimated as 0.440 (95% CI = 0.289–0.591) and 0.565 (95% CI = 0.371–0.755) for nonbreeding season. For female lesser prairie-chickens that used CRP, survival was 0.421 (95% CI = 0.290–0.552) for the breeding season and 0.711 (95% CI = 0.515–0.907) for the nonbreeding season.

Population matrix.—Population growth rate point estimates for birds that used CRP (λ = 0.601, SD = 0.135) compared to those that only used native working grasslands (λ = 0.491, SD = 0.114) overlapped at 95% confidence intervals (95% CI; CRP = 0.336–0.866, Non-CRP = 0.268–0.714). Female lesser prairie-chickens had a net reproductive rate of R0 = 0.094 ± 0.0695 (estimate ± SD; female chicks/female/generation) when using CRP at a landscape scale and a net reproductive rate of R0 = 0.0547 ± 0.0396 when not
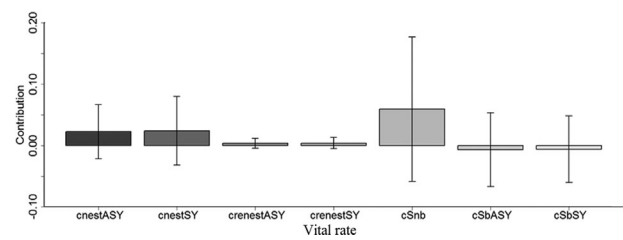

Figure 5. Life-stage contributions for after-second-year (ASY) and second-year (SY) female lesser prairie-chickens to greater population growth rate estimates of birds using Conservation Reserve Program grasslands compared to birds using only native working grasslands (reference) in northwest Kansas, USA, 2013, 2014, and 2015. Life-stage contributions included nest survival (cnestASY, cnestSY), survival of subsequent nesting attempts (crenestASY, cnestSY), nonbreeding adult survival (cSnb), and breeding season survival of adults (cSbASY) and yearlings (cSbSY). We calculated contributions following Caswell (1989) and errors bars represent 95% confidence intervals.

using CRP, suggesting that breeding females are not replacing themselves. However, generation times were similar for lesser prairie-chickens using CRP (3.340, SD = 0.303 years) and those that never used CRP (3.183 SD = 0.254 years). The larger point estimate for generation time for lesser prairie-chickens using CRP likely resulted from the greater adult survival rates (slightly longer lifespans) and did not indicate lesser prairie-chickens using CRP had lower fecundity.

The fixed-effects life-table response experiment decomposed the difference in λ (difference = +0.110 for CRP) among birds using CRP and native prairie. The life-table response experiment revealed that nonbreeding survival contributed most to the difference in population growth rates between lesser prairie-chickens using CRP at a landscape scale and those not using CRP (contribution [c] = 0.0592, SD = 0.0600, 53.0% of difference; Fig. 5). Contributions from nest survival for SY (c = 0.0240, SD = 0.0284, 21.8% of difference) and ASY (c = 0.0224, SD = 0.0224, 20.4% of difference) contributed the second- and third-most to the difference in population growth rates between female lesser prairie-chickens using and not using CRP.

DISCUSSION

We provide evidence of landscape-scale mechanisms that may have allowed lesser prairie-chickens to expand their range and increase regionally in abundance during the past 3 decades in northwest Kansas despite ongoing population declines elsewhere throughout much of its 5-state range (Van Pelt et al. 2013). Understanding mechanisms that have allowed lesser prairie-chickens to expand in this region may be key to the foreseeable persistence of this species on privately owned working lands, especially considering current climate change predictions (Rodgers and Hoffman 2005, Cook et al. 2015, Grisham et al. 2016, Haukos and Zaveleta 2016, Rodgers 2016). Our combined habitat use and demographic results provide a holistic estimation of individual and population-level effects of CRP on lesser prairie-chickens based on long-term evolved behavioral cues (resource selection) and realized fitness over the 3-year

window of data collection. The results herein should be interpreted, in context of the current population status (Garshelis 2000), at a landscape spatial scale and within the temporal scale of the study to understand true population response. In summary, CRP grasslands provide habitat during the nesting and nonbreeding period and are of importance during drought years in northwest Kansas, and in drier portions of the lesser prairie-chicken's range (e.g., Colorado). Last, under the current regulatory guidelines and successional state, CRP benefits lesser prairie-chickens where lands occur in areas of appropriate climate and where the surrounding matrix is predominantly grassland. Therefore, the most beneficial strategic conservation efforts would be those that spatially prioritize CRP to areas within grassland-dominated landscapes of favorable regional climate in which CRP grasslands achieve optimal structure for use by lesser prairie-chickens and increase spatial heterogeneity. In Kansas, this is already being partially implemented through the establishment of conservation priority areas (Rodgers 2016). Other research and management experiments in this system suggest that the use of grazing, burning, and disking also appear promising to extend the utility of CRP grasslands for lesser prairie-chickens outside of the nesting and nonbreeding periods (J. Reitz, personal communication) and in the eastern extent of the species range where average annual precipitation is >65 cm and supports mixed grass prairie (Hagen et al. 2004).

Selection of High-Quality Habitat

Lesser prairie-chickens were distributed among cover types of similar demographic consequence, supporting an ideal free distribution and providing no evidence of one cover type functioning as higher quality habitat among all life stages and when not accounting for densities (Van Horne 1983). Although it could be suggested that CRP fields function as ecological traps, for which avian species are attracted to suitable cover in small grassland patches, our results indicated that lesser prairie-chickens had similar fitness in CRP and native working grasslands (Gates and Gyel 1978). If exhibiting an ideal free distribution, lesser prairie-chickens would be able to discern habitat quality and their distribution would provide a reasonable long-term estimate of habitat quality when habitat is not saturated and recent changes to the environment are minimal (Fretwell and Lucas 1970, Whitman 1980, Rodewald 2015).

During spring 2013, estimates of the lesser prairie-chicken population size in Kansas were lower than any estimate since large-scale monitoring began in 1978 (Ross et al. 2016b). Therefore, any locations still occupied by lesser prairie-chickens may represent a core area of optimal habitat quality (Guthery et al. 2005) or, alternatively, a location that provided refugia during drought events as reported in our study. In either case, demographic assessments during a population low will likely not encompass the full spectrum of habitat quality. Assessing the full spectrum of habitat quality may require a significantly longer study for a boom or bust species such as the lesser prairie-chicken, or an analytical framework linking changes in densities with individual fitness.

The ideal free distribution model provides insight into how densities can be related to the fitness of individuals using certain habitats (habitat quality; Fretwell and Lucas 1970). In an ideal free distribution when densities within a patch increase, fitness of individuals within the patch decrease. Individuals move into marginal habitats only after a density is surpassed in more optimal habitat (Fretwell and Lucas 1970). Therefore, in circumstances where the ideal free distribution exists, individuals should have similar fitness among differing habitat patches and densities must be considered when evaluating habitat quality (Fretwell and Lucas 1970, Van Horne 1983). The similar nest survival estimates for lesser prairie-chickens using CRP and native working grasslands in comparison to contrasting nest densities among cover types supports patterns predicted in the ideal free distribution. Congruent with our results, Fields et al. (2006) estimated that nest survival was not different between CRP and native working grasslands of northwest Kansas. Although we provided densities of marked lesser prairie-chickens only during the nesting period, estimates indicated greater nest densities (3×) in CRP compared to native working grassland and agreed with vegetation data that indicated CRP provided over twice the number of suitable nesting locations.

Nesting microhabitats appear to be more readily available in CRP grasslands in this region as indicated primarily by the greater nesting densities by marked female lesser prairie-chickens and secondarily by the greater proportion of suitable nesting locations based on vegetative characteristics (Table 2). By incorporating nesting densities (estimated from marked individuals), we have provided evidence of population-level demographic effects on reproduction that would benefit lesser prairie-chickens occurring in landscapes with CRP (Van Horne 1983, Rodewald 2015). Higher densities may translate into increased lesser prairie-chicken reproductive output in landscapes with more CRP in northwest Kansas. Such increased reproductive output may offset higher mortality for lesser prairie-chickens in northwest Kansas where adult survival estimates are lowest among populations in Kansas (Plumb 2015, Robinson 2015).

Regional and Life-Stage Variation in Benefits of CRP

Conservation Reserve Program grasslands in northwest Kansas benefited lesser prairie-chickens by increasing habitat equal in quality to native working grasslands for adults and by increasing reproductive output. The contribution of non-breeding season survival to changes in population growth has not been previously documented. However, nonbreeding survival of adults ranked first and second in importance at 2 study sites based on elasticity values for a population of lesser prairie-chickens inhabiting sand sagebrush prairie (Hagen et al. 2009). The positive influence of CRP during this period, albeit the estimated λ was still <1, may be related to the provision of denser cover that is more likely to remain following winter snow storms or may be related to the proximity of CRP to waste grain in adjacent crop fields. Some experts suggest that prairie-chicken populations achieve peak abundance in landscapes having 10–15% of the area in grain production and lesser prairie-chickens may

have boomed in the presence of small-scale farming in the early 1900s (Baker 1953, Jackson and DeArment 1963, Rodgers 2016). A nearly 3-fold increase in use of croplands during the nonbreeding season may indicate the use of grain fields when foods become limited outside of the growing season. Although confidence intervals overlapped, we provide some evidence that birds using CRP may have greater survival during the nonbreeding season, but benefits of CRP in this region were largely realized during the nesting period.

The documented utility of CRP as nest habitat and the purported regional population increase following the addition of CRP suggests that nest habitat may have been previously limiting in northwest Kansas. In northwest Kansas, juxtaposition of patches of native mixed-grass prairie plant species (CRP grasslands), which are not grazed, throughout short-grass prairie has increased the amount of grassland cover and structural heterogeneity of grasslands in the region (Table 2). The same effects may not be realized farther to the east where nesting habitat is likely not limiting and CRP may become too dense and tall even for use as nesting habitat (>30–50 cm tall; Rodgers and Hoffman 2005). In addition to being too tall or thick, CRP in the eastern portion of the lesser prairie-chicken range is more likely to be adjacent to woodlands; these conditions are an underlying result of increased average annual precipitation (Bond 2008, Grisham et al. 2016). Although we were not able to control for availability of CRP grasslands among all our sites, our results indicated a greater use of CRP among all life stages in areas of lower annual average precipitation (Fig. 2).

Making CRP useable for lesser prairie-chickens outside of broad-scale climatic and fine-scale life-stage constraints will rely on the proper application of disturbance. The lack of disturbance (e.g., grazing and burning) outside of mid-contract management (Negus et al. 2010) for CRP grasslands in areas receiving >65 cm of precipitation may make them unavailable for nesting lesser prairie-chickens. Alternatively, the lack of disturbance throughout the northern distribution of lesser prairie-chickens may make CRP unavailable as brood-rearing habitat. In northwest Kansas, CRP grasslands were not used by lesser prairie-chicken broods likely because the ground layer was too dense and thick for a small chick (<15 g) to move around and because a lack of forbs limited accessibility to food resources (Bergerud and Gratson 1988, Hagen et al. 2013). The CRP grasslands in northwest Kansas provided nesting habitat adjacent to more disturbed native working grassland (~20% forb cover; Lautenbach 2015) and cropland used by broods in the first 7 days of life. In contrast, adding ungrazed CRP to landscapes in the mixed-grass eastern extent of the lesser prairie-chicken range would be less likely to achieve this pairing of nest and brood habitat. Further, the addition of CRP is less likely to address a limiting factor in the eastern extent of the lesser prairie-chicken range where mean annual net primary productivity is approximately $200 \, g/m^2$ greater than at our western most study site (Sala et al. 1988). Conservation Reserve Program grassland establishment may improve habitat quality in landscapes for lesser prairie-chickens only when increasing the spatial heterogeneity of those landscapes or the amount of grassland past an extinction threshold.

Role of CRP in Surpassing Habitat-Based Thresholds

Lesser prairie-chickens were most likely to use CRP grasslands when local landscapes ($\sim$50 km^2 ha) were >70% ($\sim$35 km^2) native working grasslands, and when CRP fields were established in areas where patches of native grasslands were clumped together or contiguous (Figs. A1 and A2, available online in Supporting Information). Our estimates of habitat selection document the influence of factors at scales larger than the typical home range of lesser and greater prairie-chickens (*Tympanuchus cupido*) and are comparable to previous research that estimated support for stable populations when >25-km^2 areas were comprised of greater than 63% native prairie (Crawford and Bolen 1976, Plumb 2015, Robinson 2015, Winder et al. 2015). To maintain a genetically healthy lesser prairie-chicken population, the minimum amount of contiguous habitat has been estimated at 85 km^2 and is based on the presence of 6 leks that are on average 1.6 km away from each other (Applegate and Riley 1998, Westemeier et al. 1998, Van Pelt et al. 2013, DeYoung and Williford 2016). However, estimates have ranged from 49 km^2 to approximately 20 km^2 of contiguous native prairie based on providing habitat for a single lek or at the population level (Haukos and Zaveleta 2016). Ultimately, the conservation of lesser prairie-chickens will require the maintenance of a geographic range large enough and of sufficient quality to rebound from detrimental stochastic processes (demographic and genetic rescue) and unpredictable environmental conditions prevalent within the extant distribution (Sala et al. 1988, Simberloff 1994, Grisham et al. 2016, Ross et al. 2016a).

The loss of grassland through conversion to cropland in the early 1900s in the SGPR Ecoregion may have reduced the amount of available grassland cover below a threshold to overcome stochastically driven extinction by lesser prairie-chickens (Simberloff 1994, Spencer et al. 2017). Larger areas of intact grasslands are more likely to provide heterogeneity-sourced refugia during drought and generate population momentum to resist negative stochastic events (Simberloff 1994, Ross et al. 2016b). It is much less likely for a small patch of grassland to predictably provide microhabitats capable of supporting nesting, brooding, and winter habitat in comparison to larger grasslands. Additionally, landscapes having a greater grassland abundance would also result in greater reproductive output during periods of favorable weather (Garton et al. 2016, Ross et al. 2016a). Maximizing reproductive output during periodic favorable periods may be a particularly important population strategy in the semi-arid portion of the southwestern Great Plains, where precipitation-driven net primary productivity varies greatly on an annual basis (Sala et al. 1988). Amid such climatic and photosynthetic variability, population resilience of lesser prairie-chickens to drought periods has been empirically related to greater grassland area within 3 km of leks with an optimum value of 90% grassland (Ross et al. 2016b).

The population resilience to drought may stem from the decision to nest or forego nesting during a season. Our results and past reports from a study in west Texas have documented the decreased propensity to nest during intensive drought (Grisham et al. 2014). In west Texas, only 20% of marked female lesser prairie-chickens nested during a record extreme drought (Grisham et al. 2014, Su and Dickinson 2014). In our study, nesting propensity was lowest in 2013 (82%) and greatest in 2015 (100%), which were the years of the most and least severe PDSI, respectively (NOAA 2016b). Further, we documented that female lesser prairie-chickens were more likely to select CRP grasslands as drought severity increased. Given our observations, it is plausible that lesser prairie-chickens reduce nesting effort when environmental conditions are not favorable for nest survival. This behavior may differentiate lesser prairie-chickens from greater prairie-chickens, which appear to exhibit high nest propensity even during drought (McNew et al. 2012). Alternatively, drought may not restrict the availability of nesting habitat, and therefore the propensity to nest, in wetter portions of the greater prairie-chicken distribution. The decision to nest or not could be controlled by the availability of nesting habitat that should increase with CRP on the landscape in northwest Kansas, or, alternatively, by water availability (Robinson et al. 2016b), both of which are likely main factors in the boom-bust population fluctuation.

MANAGEMENT IMPLICATIONS

Managers interested in maximizing ecological benefits of CRP to lesser prairie-chicken populations could concentrate CRP incentives in areas receiving <55 cm of average annual precipitation and in 50-km^2 landscapes that would surpass a 65% grassland threshold with the addition of CRP grasslands. Within these landscapes, a management strategy for CRP signup could include further incentives for areas adjacent to large tracts of remnant prairie. Continued planting of native mixed- and tall-grass species when seeding CRP grassland in Kansas and Colorado would provide maximum benefits for lesser prairie-chickens. Management practices (e.g., grazing, burning, haying, or disking) to achieve the optimal structure for nesting and increase the amount of brood habitat within CRP grasslands in the eastern portion of the lesser prairie-chicken range could be examined in an adaptive management framework.

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