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# Factors affecting female space use in ten populations of prairie chickens

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**Abstract.** Conservation of wildlife depends on an understanding of the interactions between animal movements and key landscape factors. Habitat requirements of wide-ranging species often vary spatially, but quantitative assessment of variation among replicated studies at multiple sites is rare. We investigated patterns of space use for 10 populations of two closely related species of prairie grouse: Greater Prairie-Chickens (*Tympanuchus cupido*) and Lesser Prairie-Chickens (*T. pallidicinctus*). Prairie chickens require large, intact tracts of native grasslands, and are umbrella species for conservation of prairie ecosystems in North America. We used resource utilization functions to investigate space use by female prairie chickens during the 6-month breeding season from March through August in relation to lek sites, habitat conditions, and anthropogenic development. Our analysis included data from 382 radio-marked individuals across a major portion of the extant range. Our project is a unique opportunity to study comparative space use of prairie chickens, and we employed standardized methods that facilitated direct comparisons across an ecological gradient of study sites. Median home range size of females varied ~10-fold across 10 sites (3.6–36.7 $km^2$), and home ranges tended to be larger at sites with higher annual precipitation. Proximity to lek sites was a strong and consistent predictor of space use for female prairie chickens at all 10 sites. The relative importance of other predictors of space use varied among sites, indicating that generalized habitat management guidelines may not be appropriate for these two species. Prairie chickens actively selected for prairie habitats, even at sites where ~90% of the land cover within the study area was prairie. A majority of the females monitored in our study (>95%) had activity centers within 5 km of leks, suggesting that conservation efforts can be effectively concentrated near active lek sites. Our data on female space use suggest that lek surveys of male prairie chickens can indirectly assess habitat suitability for females during the breeding season. Lek monitoring and surveys for new leks provide information on population trends, but can also guide management actions aimed at improving nesting and brood-rearing habitats.

**Key words:** fragmentation; grassland; grouse; home range; land cover; landscape metrics; lek; prairie; prairie grouse; resource utilization function; spatial ecology; *Tympanuchus*.

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## Introduction

Effective management of wildlife populations relies on understanding key relationships among ecological resources, critical habitats, and species occurrence (Boyce and McDonald 1999, Nielsen et al. 2006, Aldridge and Boyce 2007, Aarts et al. 2008). Species with broad geographic ranges may experience diverse ecological conditions across natural gradients of climate and primary productivity or across anthropogenic gradients of landscape configuration and composition. Thus, the spatial ecology of wildlife populations is driven by environmental factors that interact across space and time (Krebs 1985, Garshelis 2000, Miller and Hanham 2011). Relationships between resource use and availability are often assumed to be stationary across a species distribution (Meyer et al. 1998, Boyce and McDonald 1999), but growing evidence indicates that demography and habitat requirements of wildlife populations vary spatially (Wiens and Milne 1989, Mitchell et al. 2001, Hagen et al. 2009, McNew et al. 2011, 2013, Allen et al. 2014). Effective conservation of a species with a broad geographic range requires a detailed understanding of resource use and links to landscape features (Garshelis 2000).

Here, we investigate geographic variation in the spatial ecology of two closely related species: Greater Prairie-Chicken (*Tympanuchus cupido*) and Lesser Prairie-Chicken (*T. pallidicinctus*; Fig. 1). Prairie chickens were widely distributed upland gamebirds that have undergone major range contractions following conversion of native prairie habitats to rowcrop agriculture. Current populations are highly fragmented, and population numbers continue to decline within the core of their extant range (Hagen and Giesen 2005, Johnson et al. 2011). Greater and Lesser Prairie-Chickens are state-listed in different parts of their ranges and are listed as Vulnerable by the International Union for Conservation of Nature (Hagen and Giesen 2005, Johnson et al. 2011, BirdLife International 2013*a*, *b*). Declines among Greater Prairie-Chickens have left relict populations in portions of their historic range (Illinois, Iowa, Missouri, and Wisconsin), and small populations are prone to deleterious effects of inbreeding depression and loss of evolutionary potential (Westemeier et al. 1998, Bellinger et al. 2003). In core areas of their current range, populations of Greater Prairie-Chickens remain large enough to support harvest in fall or winter (Colorado, Kansas, Minnesota, Nebraska, North and South Dakota).

Greater and Lesser Prairie-Chickens are a closely related pair of sibling species (Drovetski 2002). Distributions are parapatric because the two species are segregated by habitat for much of their range, but they form mixed-species leks and occasionally hybridize in a narrow contact zone in northwestern Kansas (Bain and Farley 2002; Fig. 1). Greater Prairie-Chickens occupy mesic prairie habitats including tallgrass prairie, whereas Lesser Prairie-Chickens occur in more xeric habitats including prairies dominated by mixed-grass, sand sagebrush (*Artemisia filifolia*), or sand shinnery oak (*Quercus havardii*; Hagen and Giesen 2005, Johnson et al. 2011). Both species of prairie chickens are considered umbrella species for native grasslands because they have large space use requirements (Svedarsky et al. 2000, Poiani et al. 2001, Hagen and Giesen

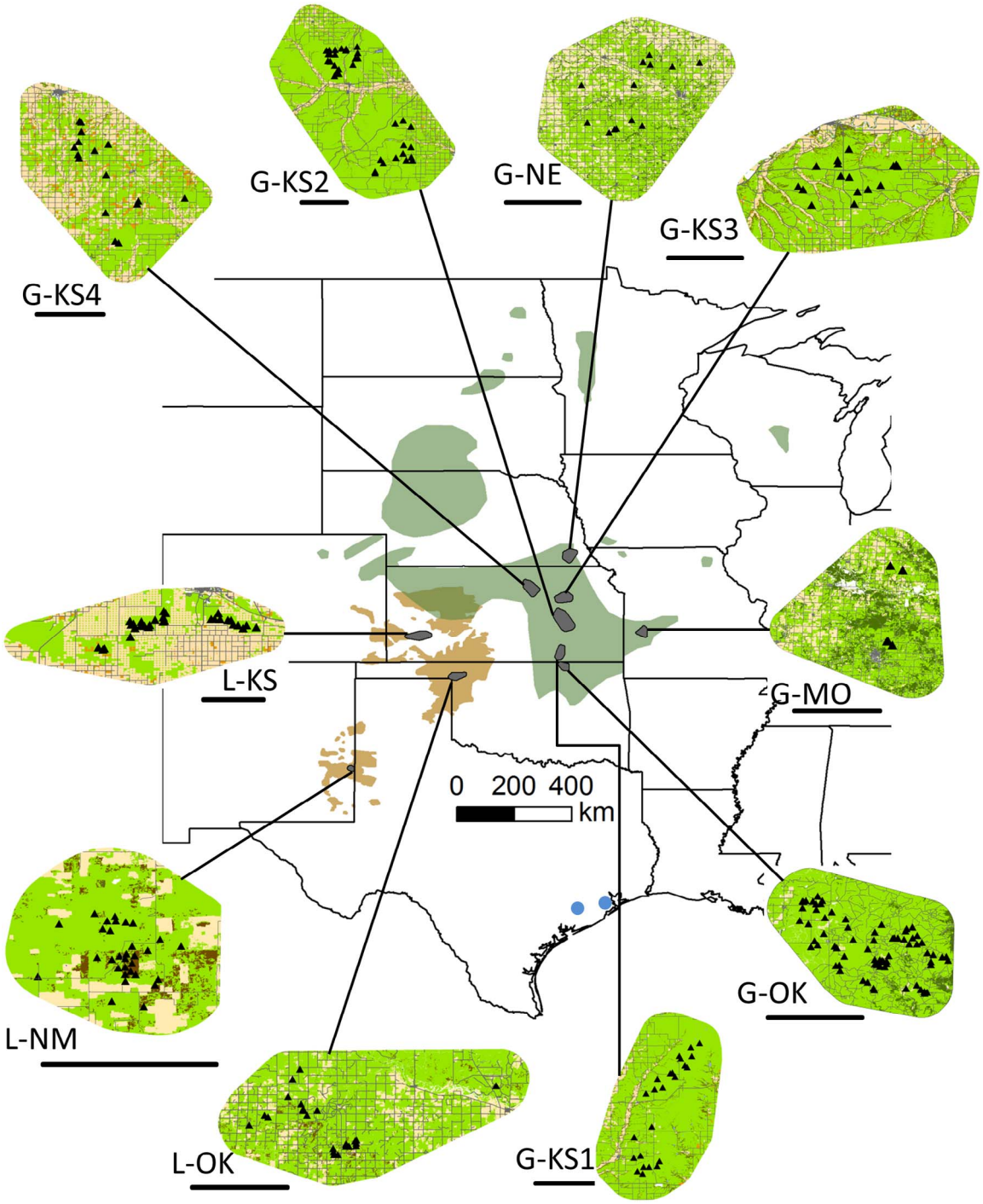


Fig. 1. Map of study sites for interpopulation analyses of space use by female prairie chickens. Greater Prairie-Chicken extant range is green; Lesser Prairie-Chicken extant range is tan; Attwater's Prairie-Chicken extant range is blue; and individual study sites are gray polygons. For expanded site polygons, black triangles are lek locations, and dark gray lines are roads. Land cover classes include: light green = prairie; dark green = woodland; tan = cropland, dark brown = shrubland; orange = Conservation Reserve Program (CRP) land. Black bars with each site are 20-km scale bars.

2005, Johnson et al. 2011). Prairie chickens require a mosaic of habitats for successful reproduction and survival, including open sites for leks, dense vegetative cover for concealment during nesting, and areas of intermediate vegetative structure that are rich in forbs for brood-rearing (Gregory et al. 2011, Johnson et al. 2011, Hagen et al. 2013, Matthews et al. 2013). Prairie chickens have a promiscuous mating system, and males display for females at communal lek sites (Hagen and Giesen 2005, Nooker and Sandercock 2008, Johnson et al. 2011). Females attempt at least one nest each year, lay large clutches of 8–14 eggs, regularly renest after clutch loss, and provide sole parental care to offspring (McNew et al. 2011). Demographic models indicate that reproductive success and female survival drive population dynamics of prairie chickens (Patten et al. 2005, Hagen et al. 2009, Pruett et al. 2011, Behney et al. 2012, McNew et al. 2012*a*).

Given conservation concern for the two species, prairie chickens have been the focus of a series of intensive demographic studies investigating population responses to grassland management (McNew et al. 2012*b*, 2015), energy development (Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011, McNew et al. 2014, Winder et al. 2014*a*, 2015), and translocations for population recovery (Kemink and Kesler 2013, Carrlson et al. 2014). Previous studies have been site-based, with conservation and management recommendations aimed at demographic responses to local environmental conditions. Quantitative data on the spatial ecology of prairie chickens are limited, but several previous studies have investigated spatial ecology and demography at multiple sites. McNew et al. (2011, 2012*a*, 2013) found that fragmentation, grassland management, and other site-specific landscape characteristics determined local variation in nest site selection and nest and adult female survival rates for Greater Prairie-Chickens breeding at three sites in eastern Kansas. For Lesser Prairie-Chickens, high adult mortality was linked to a larger clutch size and higher renesting rates in Oklahoma versus populations in New Mexico (Patten et al. 2005, Pruett et al. 2011). Hagen et al. (2009) found that sensitivity of the rate of population change ($\lambda$) to nest success and chick survival differed for two populations of Lesser Prairie-Chickens separated by ~20 km in western Kansas. Together, these past studies raise the possibility that ecological relationships between prairie chickens and landscape features vary spatially and at relatively short distances.

Replicated population studies of vertebrate species at multiple sites are rare but can provide important insights into local adaptation and evolution of life histories (Sandercock et al. 2005, Salgado-Ortiz et al. 2008, Bears et al. 2009, Jansen et al. 2014). Our collaborative analysis is a unique opportunity for a large-scale analysis of the spatial ecology of prairie chickens. Comparisons among published estimates are often hampered by differences in methodology, which requires use of meta-analytic tools to calculate effect sizes (Hagen et al. 2007, 2013). Here, we perform post hoc analyses of data collected with a standardized set of field protocols at 10 field sites in the Great Plains. We used kernel density methods to estimate home range size and compositional analysis to examine habitat selection by females at each study site. Moreover, we used resource utilization functions (RUFs) to investigate landscape-level drivers of space use by female prairie chickens among different populations. RUFs relate differential space use within an animal's home range to potential landscape features driving space use decisions in a multiple regression framework that accounts for spatial autocorrelation among multiple locations from the same individual (Marzluff et al. 2004, Kertson et al. 2011).

The primary objective of our collaborative analysis was to investigate variation in spatial ecology and habitat requirements of female prairie chickens across an ecological gradient of different landscapes (Niemuth 2011). We addressed this objective by examining the effects of anthropogenic and ecological features on habitat selection and home range size. Prairie grouse have negative responses to many types of anthropogenic development, including increased chick mortality and lek abandonment near oil and gas development, and avoidance of wind energy development, roads, and power lines (Pitman et al. 2005, Aldridge and Boyce 2007, Pruett et al. 2009, Hagen et al. 2011, Winder et al. 2014*b*). Thus, we investigated space use of female prairie chickens in response to roads and edges of habitat patches. Lek sites are integral to the behavioral ecology of prairie chickens and are

usually located on hilltops adjacent to suitable nesting habitat for females (Emlen and Oring 1977, Schroeder 1991, Merrill et al. 1999, Niemuth 2000, Gregory et al. 2011). Thus, we investigated female prairie chicken space use with respect to elevation and proximity to lek sites. State wildlife agencies monitor prairie-chicken populations by spring counts of males at lek sites using aerial and ground-based surveys (McDonald et al. 2014). However, lek surveys usually lack detailed information on female movements and demography. If female space use is associated with locations of male lek sites, an ecological link between the sexes would establish that lek surveys can serve the dual purpose of monitoring prairie chicken population trends and identifying habitats required by breeding females (McDonald et al. 2014).

## Methods

### *Study sites*

Data were collected at 10 field sites, including three populations of Lesser Prairie-Chickens in New Mexico, Oklahoma, and Kansas (L-NM, L-OK, and L-KS), and seven populations of Greater Prairie-Chickens in Oklahoma, Kansas, Nebraska, and Missouri (G-OK, G-KS1-4, G-NE, and G-MO; Fig. 1; Appendix A: Table A1). Monitoring efforts ranged from 2 to 12 years at each field site, within the 16-year period from 1997 to 2012. Field sites spanned multiple ecoregions and contained different levels of anthropogenic alteration of the landscape. Mean annual precipitation during the years of monitoring at each study site varied ~3-fold among our sites along a west-to-east gradient, with three xeric sites receiving <60 cm per year, four intermediate sites receiving between 70 and 95 cm per year, and three mesic sites receiving >100 cm of precipitation per year (Appendix A: Table A1). Annual precipitation is closely linked to primary productivity of herbaceous plants, and our 10 sites followed an ecological gradient of ecosystem productivity (Knapp and Smith 2001). We use the term "prairie" with regional descriptors to designate differences in ecosystems across our study sites. Tallgrass prairie and mixed-grass prairie habitats in eastern Kansas, Missouri, Nebraska, and Oklahoma were dominated by grasses and forbs (G-KS1–4, G-MO, G-NE, G-OK, and L-OK), whereas prairie grasses co-dominated with sand sagebrush in western Kansas (L-KS) and shinnery oak in eastern New Mexico (L-NM). Six of our 10 sites were managed rangelands used for cattle production (G-MO, G-KS1–4, and L-OK); two sites were small patches of prairie interspersed in a matrix of row-crop agriculture (G-NE and L-KS), one site was sand shinnery oak prairie (L-NM), and one site was a large prairie preserve (G-OK; Fig. 1, Table A1). Density of paved and unpaved roads varied >5-fold across our study sites, ranging from 0.4 km of road per $km^2$ in eastern New Mexico to 2.2 km of road per $km^2$ in northcentral Kansas (Fig. 1; Appendix A: Table A1).

### *Capture and monitoring of prairie chickens*

For the purposes of our study, we define a lek as a traditional display site with ≥2 males recorded during the monitoring period (Connelly et al. 2000, Garton et al. 2011). Leks were located by searching for displaying prairie chickens at sunrise on days with low winds during early spring. We also located leks with assistance from local landowners and wildlife conservation officers. Lek sites were mapped using portable global positioning systems (GPS) with accuracy of about ±5 m. We made every effort to search our entire study sites for lekking activity, and all known leks were included in our analyses, but we cannot discount the possibility that some leks remained undetected in our field projects. We captured prairie chickens at lek sites with walk-in traps and drop-nets between January and May (Haukos et al. 1990, Schroeder and Braun 1991). Captured birds were marked with a uniquely numbered metal leg band and colored leg bands, and were sexed and aged by plumage. Each female was tagged with a 10–15 g VHF radio transmitter attached with an elastic or wire necklace harness (~1.0–1.5% of body weight; model A3950, ATS, Isanti, Minnesota, USA; or model RI-2B, Holohil, Carp, Ontario, Canada). VHF radios had an expected battery life of 12–24 months and were equipped with mortality switches that changed pulse rate when the transmitter was stationary for 6–12 hours. Radio-marked females were located by triangulation or homing with portable radio receivers and handheld antennas (model R2000, ATS, Isanti, Minnesota, USA) or by triangulation with vehi-

cle-mounted null peak systems (Cox et al. 2002). We relocated birds 3–7 times per week during the 6-month breeding season (March–August). Coordinates for triangulated locations were estimated with Program Locate (ver. 3.34, Pacer Computing, Tatamagouche, Nova Scotia, Canada), or Location of a Signal software (ver. 4.0, Ecological Software Solutions, Hegymagas, Hungary).

### *Space use*

We analyzed space use data during a 6-month breeding season (1 March–31 August). A few female prairie chickens were monitored in multiple years (30 of 382 individuals, ~8%), but we considered movements in different years to be independent bird-seasons and accepted a small amount of pseudoreplication to use our complete dataset. Female home ranges during the 6-month breeding season (hereafter, home ranges) encompassed the space requirements of an individual female for foraging, reproduction, and survival during the period from 1 March to 31 August (Powell 2000). We restricted our analysis to females with at least 30 locations, and more than 20 locations which were not associated with a nest or a brood. We included multiple locations associated with nest or brood attendance because reproductive activities correspond to the periods of greatest mortality risk for female prairie chickens (Wolfe et al. 2007, Winder et al. 2014*a*). The data requirements for spatial modeling introduce a potential bias because home ranges can only be estimated for females that survive long enough to accumulate an adequate number of locations. On the other hand, females that die early in the breeding season contribute little to population growth, and factors that affect performance of successful birds should be more important for conservation. We accepted the tradeoff between number of locations and survival to investigate space use and associated habitat choices of successful female prairie chickens during the breeding season.

We estimated 95% and 50% volume contour home ranges using the fixed kernel density estimator and percent volume contour options in Hawth's Tools for ArcMap 9.3 (spatialecology.com/htools; ESRI, Redlands, California, USA; Seaman et al. 1999, Powell 2000, Beyer 2004, Laver and Kelly 2008). Spatial distributions of bird locations differed among individuals, and we used least squares cross-validation to calculate a unique bandwidth value or smoothing parameter ($h$) for each female (Worton 1989, Powell 2000). We assessed breeding season habitat selection by female prairie chickens at two of three hierarchical scales (Johnson 1980). *First-order selection*, or the geographical distribution of a species, was not included in our analyses because range maps have been reported elsewhere (Hagen and Giesen 2005, Gregory et al. 2011, Johnson et al. 2011; A. J. Gregory, *unpublished manuscript*). *Second-order selection* is the placement of an individual's home range within the larger geographical range of the species, whereas *third-order selection* is the differential space use patterns within the home range. We addressed habitat selection of prairie chickens at the second- and third-order levels of selection.

For *second-order analyses* of habitat selection, we used the adehabitat package in Program R (ver. 2.15.1, R Foundation for Statistical Computing, Vienna, Austria) and conducted compositional analysis of used versus available prairie habitat at each study site (Johnson 1980, Aebischer et al. 1993, Garshelis 2000, Calenge 2006). To avoid arbitrary delineation of the boundaries at each study site, we used least squares cross-validation to calculate a site-specific $h$ value and used kernel density estimation to create a 99% volume contour that defined the *available space* in the landscape composition at a given site. A single volume contour of available space was created from all locations of all females used in space use analyses at each site. We then used each female's 95% home range to represent the *used space* at an individual level. We used landscape data from publicly available GIS layers for land cover classes, roads, and elevation from the Kansas Data Access & Support Center (2005; www.kansasgis.org), Missouri Spatial Data Information Service (2005; msdis.missouri.edu), New Mexico Resource Geographic Information System Program (2000; rgis.unm.edu), Oklahoma Center for Geospatial Information (2000–2003; www.ocgi.okstate.edu), and the National Land Cover Database (2006; www.mrlc.gov/nlcd2006.php). Layers were available for all sites at a 30-m resolution with $30 \times 30$ m pixel size. We used the

Intersect tool in ArcMap 9.3 to quantify the percent prairie within each individual 95% home range and each study site.

We used linear models to test for the effects of precipitation, available prairie area, road density, lek density (active leks per $km^2$ across the study site), and lek spacing on variation in the size of female home ranges. We used the average nearest neighbor (ANN) index tool in ArcMap 9.3 to examine patterns of lek spacing. The ANN tool tested whether lek sites were clustered (ANN $<$ 1), randomly distributed (ANN $\approx$ 1), or dispersed (ANN $>$ 1; Appendix A: Table A2). The nearest neighbor index is a ratio of the observed mean distance among leks to the expected mean distance in a hypothetical random distribution.

We combined our data on female proximity to leks and female home range size to calculate a boundary distance that would capture most of the space use by females around leks. First, we located the center, or centroid, of each female's home range by identifying the 1% volume contour with Hawth's Tools (Beyer 2004). Second, we determined the geographic center of the 1% contour and used this location as the centroid for each female's home range. The centroid represented the smallest core of the most heavily used area within the utilization distribution. We measured distances (km) from the centroid of each female home range to the nearest lek, road, and land cover patch edge. Third, we examined the distribution of distances between the centroid of female home ranges to the nearest lek. We used the 95th percentile as the maximum distance that the centroid of a female's home range might be from the nearest lek. Fourth, we examined the size distribution of female home ranges based on 95% contours. We found the median home range size and used the radius for a circle of the same area as the dimensions of a typical home range. Last, we calculated the boundary distance as the sum of the maximum distance to the home range centroid plus the radius of a typical home range. Our estimates of boundary distance should capture about 95% of the space use of a population of females at a given site and could be used to set goals for habitat management.

### *Resource utilization functions*

We used resource utilization functions (RUFs) to analyze *third-order selection* or selection of habitat components within the home range (Johnson 1980, Aebischer et al. 1993, Marzluff et al. 2004). The outline of a home range provides information on *where* an animal is estimated to have been located, but intensity of space use across the home range is rarely uniform. Individuals often exhibit differential space use where some areas are frequently used while others are rarely used (Marzluff et al. 1997). Linking differential space use to landscape features provides information on *why* an animal selected areas of frequent use (Powell 2000). We used utilization distributions to quantify the probability of space use within the home range and then related space use to landscape metrics with multiple regression models in an RUF framework (Marzluff et al. 2004, Hepinstall et al. 2005, Millspaugh et al. 2006, Kertson et al. 2011). Beta coefficients from RUFs can be used to draw inferences about the direction and magnitude of relationships between intensity of space use and values of selected resources at either an individual or a population level (Marzluff et al. 2004, Kertson et al. 2011). We followed methods of Kertson and Marzluff (2009) to model space use, build utilization distributions, extract landscape metric values, and develop RUF models using the ruf package in Program R (version 2.13.11; R Foundation for Statistical Computing, Vienna, Austria).

The first step in the RUF process was to generate 99% volume contour polygons for the home range of each female prairie chicken. The second step was to create a raster of the utilization distribution within the 99% volume contour for each female's home range. We assigned a use value bounded from 1 to 99 for each $30 \times 30$ m cell within the home range, based on the relative volume (height) of the utilization distribution in each cell (Marzluff et al. 2004, Kertson and Marzluff 2010). The third step was to determine landscape conditions at each grid cell within the home range for key resources hypothesized to predict space use. We identified four landscape metrics that were hypothesized a priori to be predictors of space use by female prairie chickens. Prairie chickens are open country birds and may avoid habitats fragmented by

small forest patches or row-crop agriculture. Distance to edge of a land cover patch was an index of patchiness of land cover, regardless of cover type (Patten et al. 2011). Prairie grouse may be sensitive to anthropogenic disturbance, and we used distance to nearest road as an index of proximity to traffic and vehicle noise (Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011, Winder et al. 2014*b*). Gregory et al. (2011) showed that lek sites are often on hilltops and other high points on the landscape. We modeled absolute elevation and distance to nearest monitored lek as two landscape features that might affect female space use. To assess effects of land use and land cover, we used GIS layers for land cover classes, roads, and elevation. Distance to patch edge was estimated using land cover class grids, the extract raster edge function in Hawth's Tools, and the spatial analyst Euclidian distance tool in ArcMap 9.3. We derived raster grids for distance to nearest road, lek, and patch edge using the spatial analyst Euclidian distance tool. We then used the spatial analyst extraction tool to create spatially explicit data files as input for RUF models (Kertson and Marzluff 2010).

The last step in our RUF analyses was to relate the height of each utilization distribution to resource values on a cell-by-cell basis to obtain coefficients of relative resource use. Data on relative space use were scored from 1 for a low probability of use to 99 for a high probability of use, and we $\log_e$-transformed the scores to meet the assumption of linearity for multiple regression models. We used ruf package for Program R to estimate RUFs with both standardized and unstandardized β coefficients. To develop population level inferences, we calculated mean standardized β coefficients ($\bar{\beta}$) for each landscape metric at each site with a variance that incorporated inter-individual variation (Marzluff et al. 2004). For inferences at individual and population levels, standardized coefficients with 95% confidence intervals that did not overlap zero were considered significant predictors of space use (Marzluff et al. 2004). For distance metrics, negative coefficients indicated selection for proximity to a landscape feature, whereas for elevation, positive coefficients indicated selection for hilltops. We ranked the relative importance of significant landscape metrics using the magnitude of the absolute value of the mean standardized β coefficients. To assess heterogeneity among individuals, we used individual standardized β coefficients and associated 95% confidence intervals to quantify the number of female prairie chickens with significant positive or negative relationships between space use and each of the four explanatory factors.

## Results

### *Seasonal range estimation*

We estimated seasonal ranges and population level resource utilization functions for female Greater and Lesser Prairie-Chickens at 10 separate field sites in five states. We monitored 5–74 leks per site and analyzed space use data for a total of 382 radio-marked females over 412 bird-seasons. Sample sizes per site ranged from 9 to 107 bird-seasons with an average sample of 33–122 locations per bird during the 6-month season (Appendix A: Table A2). Home range size was estimated without bias with respect to sampling effort because the 99% home range size was not related to number of individual locations at any of the 10 sites (linear models, $F_{1,7–105} < 2.0$, $P > 0.17$). Median home range size (95%) varied ~10-fold among sites, from 3.6 $km^2$ for Greater Prairie-Chickens in Nebraska (G-NE) to 36.7 $km^2$ for Greater Prairie-Chickens in Oklahoma (G-OK; Table 1, Fig. 2). We observed a nonsignificant trend between 95% home range area and mean annual precipitation where home ranges of female prairie chickens were larger in areas that received greater amounts of precipitation ($F_{1,8} = 3.95$, $P = 0.08$, adjusted $r^2 = 0.25$; Fig. 3). Area of 95% home range was not related to road density, lek density, lek spacing, or landcover in prairie habitats at any of our study sites ($F_{1,8} = 0.21–2.1$, $P = 0.19–0.66$, adjusted $r^2 = 0.05–0.10$).

Our study site boundaries were delineated using bird locations. Landcover in prairie habitat ranged from 45% to 89% across study sites, whereas use of prairie habitat in home ranges (95% contours) averaged from 70% to 97% (Table 2). Compositional analysis of habitat selection indicated that prairie chickens selected prairie areas more often than expected by chance based on availability at 9 of 10 sites (Wilks' $\Lambda = 0.21$ to 0.84, $P < 0.005$; Table 2). The only study site at which use of prairie habitat did not differ from availability was G-OK where our sample size

Table 1. Characteristics of the breeding home range (± SE) for 10 populations of radio-monitored female prairie chickens in the Great Plains.

| Study site | Mean no. locations/bird | Bandwidth (km) | 50% area ($km^2$) | 95% area ($km^2$) | 99% area ($km^2$) | Distance to lek (km) | Distance to road (km) | Distance to edge (km) |
|---|---|---|---|---|---|---|---|---|
| L-NM | 39 ± 2 | 0.52 ± 0.05 | 1.2 | 4.8 | 6.8 | 0.67 ± 0.07 | 1.63 ± 0.19 | 0.27 ± 0.06 |
| L-KS | 99 ± 3 | 1.02 ± 0.15 | 1.8 | 8.5 | 14.1 | 0.74 ± 0.04 | 1.76 ± 0.07 | 1.06 ± 0.04 |
| L-OK | 35 ± 1 | 0.68 ± 0.16 | 1.7 | 7.2 | 10.3 | 0.69 ± 0.11 | 0.30 ± 0.04 | 0.22 ± 0.04 |
| G-KS4 | 49 ± 2 | 1.10 ± 0.13 | 4.1 | 20.9 | 33.3 | 1.36 ± 0.20 | 0.31 ± 0.03 | 0.21 ± 0.03 |
| G-KS2 | 57 ± 2 | 1.19 ± 0.10 | 4.8 | 19.5 | 28.6 | 1.32 ± 0.17 | 1.49 ± 0.14 | 0.46 ± 0.03 |
| G-NE | 94 ± 4 | 0.57 ± 0.11 | 0.8 | 3.6 | 5.4 | 1.62 ± 0.17 | 0.33 ± 0.02 | 0.40 ± 0.04 |
| G-KS3 | 47 ± 2 | 0.80 ± 0.09 | 2.0 | 10.6 | 15.1 | 1.60 ± 0.24 | 0.39 ± 0.07 | 0.35 ± 0.04 |
| G-KS1 | 46 ± 2 | 1.15 ± 0.11 | 5.8 | 24.6 | 34.9 | 1.09 ± 0.12 | 0.89 ± 0.13 | 0.36 ± 0.03 |
| G-MO | 122 ± 8 | 0.65 ± 0.10 | 1.7 | 8.0 | 12.7 | 0.68 ± 0.09 | 0.44 ± 0.06 | 0.19 ± 0.03 |
| G-OK | 33 ± 2 | 1.31 ± 0.28 | 5.3 | 36.7 | 57.3 | 0.47 ± 0.13 | 0.53 ± 0.11 | 0.06 ± 0.03 |

*Notes:* Study site abbreviations indicate Greater Prairie-Chickens (G) or Lesser Prairie-Chickens (L) and state (Fig. 1). Bandwidth = smoothing parameter ($h$) used in kernel density estimation, individually determined for each bird using least squares cross validation. Median estimates of area are given for 50%, 95%, and 99% volume contours of female breeding home ranges. Distance metrics include mean distance from the centroid of the breeding home range to nearest lek, road, or edge of land cover patch.

was small ($n = 9$ birds). Non-prairie habitat averaged 16% of total home range area for females at our 10 study sites (Table 2; range: 3% at G-KS2 and G-KS1 to 30% at G-KS4 and G-OK). Mean distance between the centroid of the home range and the nearest lek ranged from 0.5 to 1.6 km (Table 1). Only a few female Greater Prairie-Chickens (~3%, 7 of 260) had home range centroids located ≥5 km from the nearest known lek site (Table 3).

### *Predictors of space use*

Our resource utilization function models included four landscape factors and found that distance to lek was the strongest and most consistent predictor of space use within their home ranges for female prairie chickens at all 10 field sites (= −0.61 to −0.18). Negative coefficients indicated that females selected areas close to leks within their home ranges (Fig. 4a). Not all individual females exhibited this pattern, but across our 10 study sites, an average of 80% (± 4) of females selected for habitats close to leks

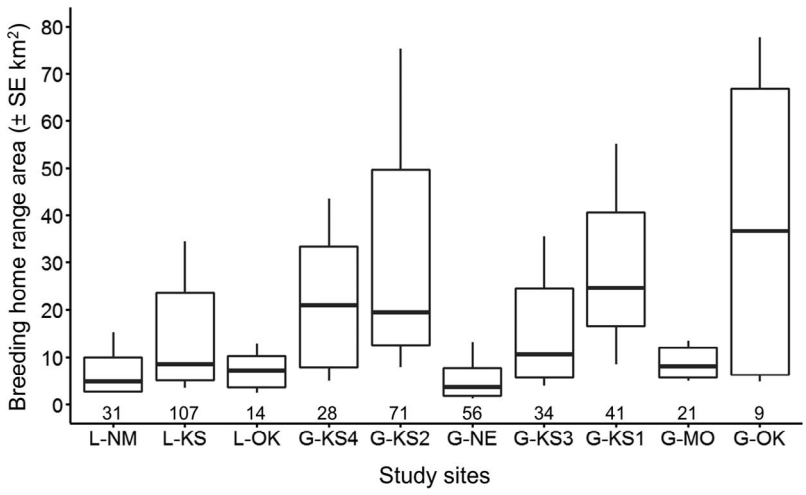


Fig. 2. Box plots of 95% volume contour breeding home range area for female Greater and Lesser Prairie-Chickens at 10 sites in the Great Plains. The thick horizontal bar is the median, boxes span first and third quartiles (25–75%), and whiskers are the 85% CIs. Sites are ranked left to right from low to high mean annual precipitation (38–129 cm/year). Numbers below bars indicate sample size of home ranges for breeding females.

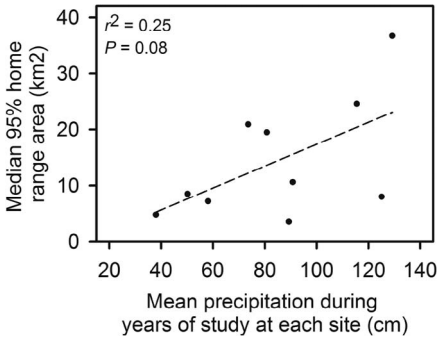


Fig. 3. Relationship between median 95% home range size and mean annual precipitation for female Greater and Lesser Prairie-Chickens at 10 study sites.

(range: 50–100%, $n = 10$ study sites).

Topography varied among our study sites, and western sites in New Mexico and Oklahoma were relatively flat (CV elevation $< 3\%$; Appendix A: Table A1). Topography was a significant predictor of space use by female prairie chickens at four eastern sites with greater variation in elevation (CV $\geq 7\%$), with greater space use in areas of relatively high elevation (G-MO, G-KS1, G-KS2, and G-KS3; Fig. 4d). Mean standardized beta coefficients for these sites ranged from $\bar{\beta} = +0.12$ to $+0.15$, indicating that elevation had a moderate effect on female space use within their home ranges.

Female Lesser Prairie-Chickens in New Mexico avoided areas near roads within their home ranges ($\bar{\beta} = +0.27$; Fig. 4b), and averaged 1.6 km between home range centroid and the nearest road (Table 1). In contrast, female prairie chickens selected areas close to roads within their ranges at four other sites (G-KS1, G-KS3, G-KS4, and L-KS; $\bar{\beta} = -0.18$ to $-0.07$; Fig. 4b). Mean distance between home range centroid and the nearest road varied from 0.3 to 1.8 km among these four sites (Table 1). Road density varied among sites (0.4–2.2 km of road per km$^2$; Appendix A: Table A1), but population-level β coefficients for distance to road were not related to site-specific road density ($F_{1,8} = 0.17$, $P = 0.69$, adjusted $r^2 = 0.11$; Appendix B: Fig. B1).

We observed differences among sites in the relationship between space use within home ranges and distance to patch edge. Negative coefficients for distance to patch edge indicated females selected areas near patch edges at two sites ($\bar{\beta} = -0.19$ at G-OK and $-0.15$ at L-NM), whereas positive coefficients indicated avoidance of patch edges at two sites ($\bar{\beta} = +0.06$ at G-KS2

Table 2. Percent of prairie as available space within the study site and mean percent prairie as used space within the 95% breeding home ranges (± SE) of radio-monitored female prairie-chickens at 10 study sites across five states in the Great Plains.

| Study site | % study site in prairie land cover | % prairie in 95% breeding home range | Compositional analysis | |
|---|---|---|---|---|
| | | | Wilks' Λ | $P \leq$ |
| L-NM | 71 | 78 ± 4 | 0.72 | 0.0014 |
| L-KS | 45 | 85 ± 2 | 0.43 | 0.0001 |
| L-OK | 75 | 82 ± 2 | 0.54 | 0.0035 |
| G-KS4 | 62 | 70 ± 3 | 0.75 | 0.0046 |
| G-KS2 | 89 | 97 ± 1 | 0.25 | 0.0001 |
| G-NE | 67 | 80 ± 1 | 0.41 | 0.0001 |
| G-KS3 | 89 | 95 ± 1 | 0.51 | 0.0001 |
| G-KS1 | 89 | 97 ± 1 | 0.21 | 0.0001 |
| G-MO | 57 | 87 ± 2 | 0.16 | 0.0001 |
| G-OK | 80 | 70 ± 6 | 0.84 | 0.2105 |

*Note:* Study site abbreviations indicate Greater Prairie-Chickens (G) or Lesser Prairie-Chickens (L) and state (Fig. 1).

Table 3. Distance from the centroid of the breeding home range to nearest lek (95th percentile) for radio-monitored female prairie chickens at 10 study sites across five states in the Great Plains.

| Study site | 95th percentile distance to lek (km) | Radius of circle of equal area to median 95% breeding home range (km) | Recommended boundary distance around leks (km) |
|---|---|---|---|
| L-NM | 1.25 | 1.24 | 2.49 |
| L-KS | 1.45 | 1.65 | 3.10 |
| L-OK | 1.30 | 1.51 | 2.81 |
| G-KS4 | 3.22 | 2.58 | 5.80 |
| G-KS2 | 3.01 | 2.49 | 5.50 |
| G-NE | 4.88 | 1.07 | 5.95 |
| G-KS3 | 4.51 | 1.84 | 6.35 |
| G-KS1 | 2.23 | 2.80 | 5.03 |
| G-MO | 1.15 | 1.60 | 2.75 |
| G-OK | 1.41 | 3.42 | 4.83 |

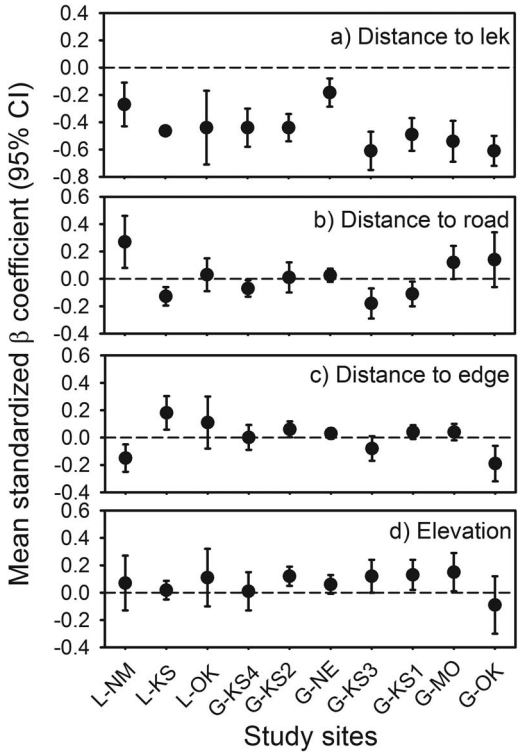


Fig. 4. Mean standardized resource utilization function coefficients ($\bar{\beta} \pm 95\%$ CI) for four landscape metrics. Resource utilization functions were calculated for 99% volume contours of the breeding home ranges of radio-marked female Greater and Lesser Prairie-Chickens at 10 sites in the Great Plains. Sites are ranked left to right from low to high mean annual precipitation (range = 38–129 cm/year).

and +0.18 at L-KS; Fig. 4c), with no evidence of selection at the remaining six sites. Home range centroids averaged <300 m from patch edges at the two sites with positive coefficients, and >450 m from patch edges at the two sites with negative coefficients (Table 1).

## Discussion

A growing number of field studies have demonstrated that space use and resource selection are dynamic features of wildlife populations. Conservation and management actions must consider spatial and individual variation in behavior and demography, in addition to environmental and anthropogenic factors (Coates et al. 2013, Godsall et al. 2013, Tarjuelo et al. 2013, Winder et al. 2014*b*). Our study provides new insights into the spatial ecology of Greater and Lesser Prairie-Chickens across their geographic ranges, which will aid management efforts for these species of conservation concern. First, home range size varied substantially among species, populations, and individuals. Larger home ranges were related to higher amounts of annual precipitation, but home range size was not related to availability of prairie habitats, road density, lek density, or lek spacing across the ecological gradient of our study. Second, our compositional analysis of home ranges indicated that prairie chickens actively selected for prairie habitats, even if ~90% of the land cover in a study site was prairie habitat. Last, our resource utilization analysis of landscape factors driving differential space use within home ranges showed that distance to lek was the primary driver of female space use across all 10 populations of prairie chickens. Past studies of lekking grouse have reported habitat use by female grouse is linked to areas near lek sites (Bradbury et al. 1989, Schroeder 1991, Gibson 1996, Dzialak et al. 2011, Coates et al. 2013). Nevertheless, the standardized methods of our study provide new quantitative data for widespread use of habitats close to leks by females across the extant range of two species of conservation concern. Last, we found unexpected variation in the relative importance of all other landscape level predictors of space use across sites, suggesting that generalized habitat management guidelines are inappropriate for prairie grouse.

Home range size is not a fixed species-specific trait, but a behavioral trait with a strong facultative component related to resource availability (Garshelis 2000). We employed standardized methods to examine home ranges of prairie chickens, which facilitated direct comparisons among study sites and provided range-wide insights into the factors influencing space use (Laver and Kelly 2008). Home range size varied ~10-fold among seven populations of Greater Prairie-Chickens, implying that site-specific variation in ecology can strongly influence space use requirements. We detected a trend for larger female home range size at sites with higher amounts of annual precipitation. Major rainfall and storm events can result in direct loss of nests due to flooding or hail, or indirect losses of nests

if wet plumage reduces concealment from scent-based predators (Flanders-Wanner et al. 2004, Fields et al. 2006, Webb et al. 2012, McNew et al. 2014). Nest losses frequently lead to dispersal movements by females and a subsequent increase in home range size (V. L. Winder, *unpublished data*). We hypothesize that increased rates of nest loss via rainfall events and depredation might be drivers of the observed relationship between large home range size and precipitation.

The 95% home range estimates from our collaborative analysis exceeded most published estimates for prairie chickens (Augustine and Sandercock 2011, Patten et al. 2011, Kemink and Kesler 2013). Our results further indicate that female home range size during the breeding season could be as large as ~9 $km^2$ for Lesser Prairie-Chickens and ~37 $km^2$ for Greater Prairie-Chickens. Although maximum size estimates could be used as generous estimates of space requirements at unstudied sites, we observed large intra-specific differences in space requirements. Thus, we caution against generalization within and among species.

Prairie chickens are obligate prairie birds, and females actively selected for prairie habitats within their home ranges at 9 of 10 study sites. Nonetheless, the strong level of selection we observed in our compositional analysis of habitat selection was surprising. At three of our study sites, the study areas were comprised of ~90% prairie (G-KS1, G-KS2, and G-KS3). Even in prairie-dominated landscapes, female prairie chickens selected for prairie habitat above and beyond its availability so that prairie comprised ≥95% of their home ranges. Elsewhere, Merrill et al. (1999) found that stable Greater Prairie-Chicken leks were associated with less forest and cropland and larger patches of prairie than temporary leks.

Habitats selected by female Greater and Lesser Prairie-Chickens were consistently close to leks. The relationship between space use and proximity to leks was ubiquitous among our 10 study populations and consistently had the largest effect on space use. In our study, habitats selected by female prairie chickens coincided with lek locations, which was consistent with previous studies of nest placement in other lekking grouse (Bradbury et al. 1989, Schroeder 1991, Gibson 1996, Dzialak et al. 2011, Coates et al. 2013). Links between female space use and lek placement are consistent with the hotspot hypothesis, which predicts that males should establish lek sites where female home ranges are relatively dense or at the intersection of dispersed female home ranges (Bradbury et al. 1986). Lek density was correlated with lek stability and number of attending males in populations of Greater Prairie-Chickens in northeastern Colorado (Schroeder and Braun 1992), and Greater Sage-Grouse in California (*Centrocercus urophasianus*; Bradbury et al. 1989). Thus, lek persistence and local population viability rely on the availability and relative quality of nesting habitats for females in proximity to leks. Our study lacked consistent data on number of males attending leks, and we were unable to test for links between female space use and male numbers. Interactions among male numbers at leks, habitat features around leks, and female space use remain poorly studied aspects of the ecology of prairie chickens and should be assessed in future studies. Movement data for our study were collected by monitoring females marked with VHF radio-collars, but field logistics of radio-telemetry limited locations to a few points per individual per week. More frequent sampling would be needed to address hypotheses about resources driving stage-specific habitat selection such as space use during nesting vs. brood-rearing stages of the breeding season. Recent improvements in GPS and satellite collars have made it possible to collect multiple locations per individual per day, enabling future studies to address questions about stage-specific habitat selection.

### *Conservation implications*

Our study was a quantitative examination of landscape level drivers of space use by female prairie chickens at 10 sites in five states in the Great Plains. Standardized lek surveys are often used by wildlife managers to monitor trends in grouse populations. Lek surveys have been criticized because bird counts are often treated as population indices, but probability of detection is imperfect and could be affected by sex, age, day of season, and weather conditions (Walsh et al. 2004, Clifton and Krementz 2006, Blomberg et al. 2013). At each study site, we found a consistent pattern of female selection for

areas near leks, which suggests that lek surveys of prairie chickens can monitor male lekking activity and population numbers, but also habitat features important to females during the breeding season. Such evidence emphasizes the need to develop robust, easy-to-use survey methods to assess population trends of prairie chickens. Aerial lek surveys have been used to monitor range-wide populations of Lesser Prairie-Chickens at the ecoregion scale (McDonald et al. 2014). Survey effort was stratified based on the quality of available nesting habitat, recognizing the need to provide quality habitat adjacent to leks to maintain sustainable populations. Implementing a similar protocol to inform conservation decisions about Greater Prairie-Chicken habitat could be a first step toward avoiding a federal listing for this species.

Greater than 95% of the females monitored in our study had centers of activity within 5 km of leks. Proximity to leks suggests that landscape-level changes that remove substantial amounts of prairie from breeding areas have the potential to cause landscape-level shifts in prairie chicken space use. In Nebraska, Greater Prairie-Chickens show preferred use of lands enrolled in the Conservation Reserve Program (CRP; Matthews et al. 2011, 2013). Our results reaffirm that conservation efforts that retain prairie at a landscape scale are critical to support prairie chicken populations. Habitat loss of prairie used by prairie chickens is currently a concern, either through conversion to agricultural production or fragmentation by energy development. Our compositional analysis suggests that habitat loss may have negative consequences if remaining prairie patches are not large enough to provide necessary resources. Our resource utilization function analysis provided strong evidence that the area within 5 km of a lek receives preferential use by female prairie chickens. Accordingly, we expect that effects of energy development and other anthropogenic disturbance should be deleterious in the zone $\leq$5 km from lek sites. Lesser Prairie-Chickens avoid oil development at $\leq$5 km (Pitman et al. 2005, Hagen et al. 2011), whereas Greater Prairie-Chickens exhibit behavioral avoidance but have limited demographic responses to wind energy development (Pruett et al. 2009, McNew et al. 2014, Winder et al. 2014*a*, *b*, 2015).

Our results provide mixed evidence for behavioral avoidance of roads and patch edges by breeding female prairie chickens. Lesser Prairie-Chickens in New Mexico avoided areas near roads and selected for areas near land cover patch edges, but the same species selected for areas near roads and avoided areas near patch edges in western Kansas. Road densities at these two sites were similar, but overall land cover patterns were different. At the New Mexico site, shinnery oak prairie was the dominant land cover class, with some shrubland and cropland interspersed. At the western Kansas site, cropland was the dominant land cover class, with some prairie and CRP interspersed in this more intensively managed landscape. Thus, the same landscape feature may be selected for or avoided in different populations of the same species, highlighting the potential value of site-specific management and conservation of prairie chicken populations. Our work exemplifies the complexities of working to conserve populations with varied responses to landscape characteristics in different ecological contexts. Prairie chicken populations would likely benefit from management to maintain suitable prairie cover, with a heterogeneous mosaic of prairie habitats, including open sites for leks, dense vegetative cover for concealment during nesting, and areas of intermediate vegetative structure for brood-rearing. Future research needs to include comparisons of female survival, hazard rates, and causes of mortality among study populations, and linkages of demographic rates to space use to determine population viability (Boyce and McDonald 1999, Garshelis 2000, Aldridge and Boyce 2007, Dzialak et al. 2011).

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## Supplemental Material

## Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/ES14-00536.1.sm