



Space Use of Female Greater Prairie-Chickens in Response to Fire and Grazing Interactions[☆]



Virginia L. Winder^{a,*}, Lance B. McNew^b, Jim C. Pitman^{c,1}, Brett K. Sandercock^d

^a Department of Biology, Benedictine College, Atchison, KS 66002, USA

^b Department of Animal and Range Sciences, Montana State University, Bozeman, MT 59717, USA

^c Kansas Department of Wildlife, Parks and Tourism, Emporia, KS 66801, USA

^d Division of Biology, Kansas State University, Manhattan, KS 66506, USA

ARTICLE INFO

Article history:

Received 23 January 2016

Received in revised form 16 June 2016

Accepted 9 August 2016

Keywords:

home range

intensive early stocking

patch-burn grazing

prescribed fire

resource utilization function

Tympanuchus cupido

ABSTRACT

Ecological interactions between fire and grazing have shaped the evolutionary history of grassland ecosystems. Currently, grassland birds have experienced ongoing population declines, following widespread implementation of intensive rangeland management practices that reduce habitat heterogeneity. Patch-burn grazing is an alternative rangeland management strategy that promotes habitat heterogeneity and biodiversity. We conducted a 3-yr. field study in the central Flint Hills of Kansas to compare the spatial ecology of female Greater Prairie-Chickens (*Tympanuchus cupido*) in rangelands managed with intensive rangeland management versus patch-burn grazing. This is the first study on the effects of patch-burn grazing on the space use decisions of Greater Prairie-Chickens at the home range scale. We used seasonal estimates of home range for 6-mo breeding and nonbreeding periods, as well as resource utilization functions to investigate the response of female prairie chickens to landscape metrics describing fire, grazing, and proximity to anthropogenic structures or lek sites. In our analysis of all radio-marked females, distance to lek was consistently the strongest predictor of space use during both breeding and nonbreeding seasons. Females captured at properties managed with patch-burn grazing selected areas with low stocking rates and high fire frequencies, and they avoided recently burned areas. Our study provides new evidence that patch-burn grazing can improve grassland habitat for Greater Prairie-Chickens, an umbrella species in the tallgrass prairie ecosystem. Patch-burn grazing created preferred habitats for female Greater Prairie-Chickens, with a relatively frequent fire return interval, a mosaic of burned and unburned patches, and a reduced stocking rate in unburned areas avoided by grazers. Widespread implementation of patch-burn grazing could result in significant improvements in habitat quality for wildlife in the tallgrass prairie ecosystem.

© 2017 The Society for Range Management. Published by Elsevier Inc. All rights reserved.

Introduction

Grasslands are among the most threatened ecosystems in the world, primarily because of extensive conversion to croplands (Vitousek et al., 1997; White et al., 2000; With et al., 2008; Fuhlendorf et al., 2012). In North America, > 95% of the historical extent of tallgrass prairie has been lost to rowcrop agriculture, oil and gas extraction, and urban development during the past century (Samson et al., 2004; Hoekstra et al., 2005). The ~2 million - ha Flint Hills ecoregion of Kansas and Oklahoma represents ~80% of the remaining tallgrass prairie in North

America (Samson and Knopf, 1994; With et al., 2008; Rahmig et al., 2009). The shallow, rocky soils of the Flint Hills make the ecoregion unsuitable for rowcrop cultivation, but >90% of the grasslands in the Flint Hills are used to support an economically valuable cattle industry (With et al., 2008). In the 1970s, many rangeland managers in the Flint Hills shifted from year-round grazing at moderate stocking rates with periodic prescribed burning to a rangeland management practice based on intensive early stocking combined with annual burning (hereafter, “intensive early stocking”; Smith and Owensby, 1978). Ranchers implementing intensive early stocking use prescribed fire annually in the spring to promote growth of high-quality forage plants that support intensive stocking of pastures with steers for ~100 days, during April to July. Intensive early stocking aims to maximize livestock production by generating uniform forage conditions that promote even grazing across the landscape (Hart, 1978; Fuhlendorf and Engle, 2001; Holecheck et al., 2004; Allred et al., 2014).

Historically, grazing and fire were natural processes, and the ecological interaction of these factors has shaped the development of grassland ecosystems (Milchunas et al., 1988; Knapp et al., 1999; Askins,

[☆] Funding and equipment were provided by the Kansas Department of Wildlife, Parks & Tourism, Kansas State University, the National Park Service, and U.S. Fish and Wildlife Service Sportfish and Wildlife Restoration Program.

* Correspondence: Virginia L. Winder, Dept of Biology, Benedictine College, Atchison, KS 66002, USA.

E-mail address: vwinder@benedictine.edu (V.L. Winder).

¹ Current address: Jim C. Pitman, Western Association of Fish & Wildlife Agencies, Emporia, KS 83202, USA.

2000; Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2006). Fire influences ungulate grazing patterns because grazers prefer recently burned areas with high-quality forage (Coppedge and Shaw, 1998; Allred et al., 2011). In turn, reduced grazing in unburned areas leads to accumulation of standing plant litter, which affects the timing, extent, and intensity of subsequent fires (Fuhlendorf and Engle, 2001). The historic interaction between fire and grazing created a shifting mosaic of vegetation that fulfilled habitat requirements for the dynamic life cycles of species in the grassland ecosystem (Fuhlendorf and Engle, 2001; Brennan and Kuvlesky, 2005; Fuhlendorf et al., 2006; Sandercock et al., 2015). Rangeland management in the Flint Hills currently generates a homogenous pattern of disturbance and reduces structural and spatial heterogeneity of grassland habitats. The ecological effects of a departure from natural pattern and process are a concern, and implementation of intensive early stocking coincided with population declines in grassland wildlife species (Zimmerman, 1997; Knapp et al., 1998; Brennan and Kuvlesky, 2005; Reinking, 2005; With et al., 2008). Overall, grassland birds have declined continent wide at a greater rate than any other guild of terrestrial birds in North America over the past 70 years (Knopf, 1994; Fuhlendorf et al., 2006).

Patch-burn grazing is an alternative rangeland management strategy that promotes biodiversity and agricultural productivity and could meet the management goals of conservation biologists and rangeland managers (Christensen, 1997; Ostfeld et al., 1997; Wiens, 1997; Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2006). In the Flint Hills ecoregion, ranchers implementing patch-burn grazing divide pastures into ~3–5 patches using fire breaks, without cross-fencing. Typically, one patch in each pasture is burned on a rotational basis each year, and cattle are allowed to move freely among patches within a pasture, but due to selective grazing, the most recently burned patch receives the heaviest grazing pressure. Patch-burn grazing treatments can be modified on the basis of ecosystem-specific rainfall patterns and vegetation recovery rates. For example, a rancher in a shortgrass prairie ecosystem might subdivide a pasture into 8–10 patches and burn 1–2 patches each year, with a longer recovery time between disturbance. Patch-burn grazing creates a temporally and spatially shifting mosaic that includes patches in different stages of successional recovery (Coppedge and Shaw, 1998; Fuhlendorf and Engle, 2001). Patch-burn grazing mimics historical fire-grazing interactions, which could benefit declining species of grassland animals by promoting structural, compositional, and spatial heterogeneity of vegetation, while still providing viable revenue from cattle production (Fuhlendorf and Engle, 2001, 2004; Churchwell et al., 2008; Coppedge et al., 2008; Powell, 2008; Rensink, 2009; Limb et al., 2011).

Greater Prairie-Chickens (*Tympanuchus cupido*, hereafter “prairie chickens”) are endemic to native grasslands of North America. Population numbers have decreased by ~50% over the past 30 years in the Flint Hills ecoregion, following habitat loss and changes in rangeland management that affect habitat quality (Johnson et al., 2011; Pitman et al., 2012). Prairie chickens have large seasonal home ranges (~10–25 km²) and require a mosaic of habitats for successful reproduction and survival, including open sites for leks, tall 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; Winder et al., 2014b, 2015a, b). Prairie chickens have a promiscuous mating system, and males display for females at communal lek sites (Nooker and Sandercock, 2008; Johnson et al., 2011). Females attempt at least one nest each year, lay large clutches of 8–14 eggs, regularly re-nest after clutch loss, and provide sole parental care to offspring (McNew et al., 2011).

Quantitative information on the spatial ecology of prairie chickens is limited, especially with respect to potential responses to rangeland management and seasonal differences in habitat use (Niemuth, 2011). For some lekking grouse, individuals attend leks during the fall non-breeding period when the photoperiod is similar to the spring lekking period. Lek attendance during the fall can play a critical role in settlement decisions and reproductive success for the following spring

(Rintamäki et al., 1999). Decisions about habitat selection by female prairie chickens can influence population viability because differential habitat selection is often linked to variation in demographic rates (Boyce and McDonald, 1999; Garshelis, 2000; Aldridge and Boyce, 2007; Dzialak et al., 2011; McNew et al., 2013). Habitat selection by females influences nest success (McNew et al., 2015), and reproductive success and female survival in turn drive population dynamics (Hagen et al., 2009; McNew et al., 2012a). To investigate the effects of rangeland management on habitat use, we collected year-round movement data on radio-marked females captured on properties managed with intensive early stocking or patch-burn grazing in East Central Kansas. We used kernel density estimation of seasonal home ranges and resource utilization functions (RUFs) to investigate the seasonal responses of female prairie chickens to landscape metrics describing fire, grazing, patchiness, anthropogenic structures, and lek sites (Marzluff et al., 2004; Kertson et al., 2011). The interaction between fire and grazing influences the long-term site occupancy by prairie chickens (McNew et al., 2012b), and patch-burn grazing creates a mosaic of heterogeneous habitats, providing prairie chickens with a greater diversity of habitat types from which to choose (Fuhlendorf et al., 2006). If patch-burn grazing creates the diverse habitat types required by prairie chickens, we predicted that prairie chickens would have smaller seasonal home ranges at properties managed with patch-burn grazing than properties managed with intensive early stocking. Additionally, we predicted that female prairie chickens would avoid recently burned and heavily grazed areas, as well as areas with infrequent fire return intervals within their seasonal home ranges.

More than 95% of the Flint Hills ecoregion is privately owned, and the vast majority of the ecoregion is managed for cattle production (With et al., 2008). Given the economic and cultural importance of the cattle industry in the Flint Hills, information on the effects of patch-burn grazing on grassland vertebrates will be integral to building effective conservation strategies for tallgrass prairie in the ecoregion. The results of our field study provide new insights into the quantitative spatial ecology of prairie chickens in response to rangeland management and can be used to improve management and conservation efforts for prairie grouse.

Methods

Study Site

Our field study was conducted during 2011–2013 in an ~3000-km² region in portions of Butler, Chase, Greenwood, Lyon, and Morris Counties, five of the most intensively burned counties in the Flint Hills ecoregion (Fig. 1; Mohler and Goodin, 2012). Native grassland was the dominant land cover type in the region (~90%). Road density was relatively low at ~0.58 km of road per km² within the region, compared with other areas in the Flint and Smoky Hills (Winder et al., 2015a). Mean precipitation from 1980 to 2010 in the region was 92.4 cm per yr. (National Oceanic and Atmospheric Administration, National Centers for Environmental Information).

Within the region, we had permission to access ~1100 km² of private lands (see Fig. 1, hereafter “study site”). A majority of the study site was privately owned land (1050 km², 95%), and the remaining sites were managed by the National Park Service at the Tallgrass Prairie National Preserve (50 km², 5%). The National Preserve and two privately owned properties (Browning Ranch ~30 km² and Koger Ranch ~15 km²; cumulatively ~10%) were managed with patch-burn grazing while the remaining private lands at our study site were primarily managed with intensive early stocking (~1000 km²; ~90%; see Fig. 1).

Management strategies on intensive early stocking properties were dependent upon annual weather conditions. In years with typical rainfall, intensive early stocking properties were managed with an annual spring prescribed burn and stocking rates of 1 head per 0.8 ha for ~90 days during April–July (~3 animal unit months, or AUM·ha⁻¹). However, drought conditions during our field study resulted in many intensive early stocking property managers reducing or postponing

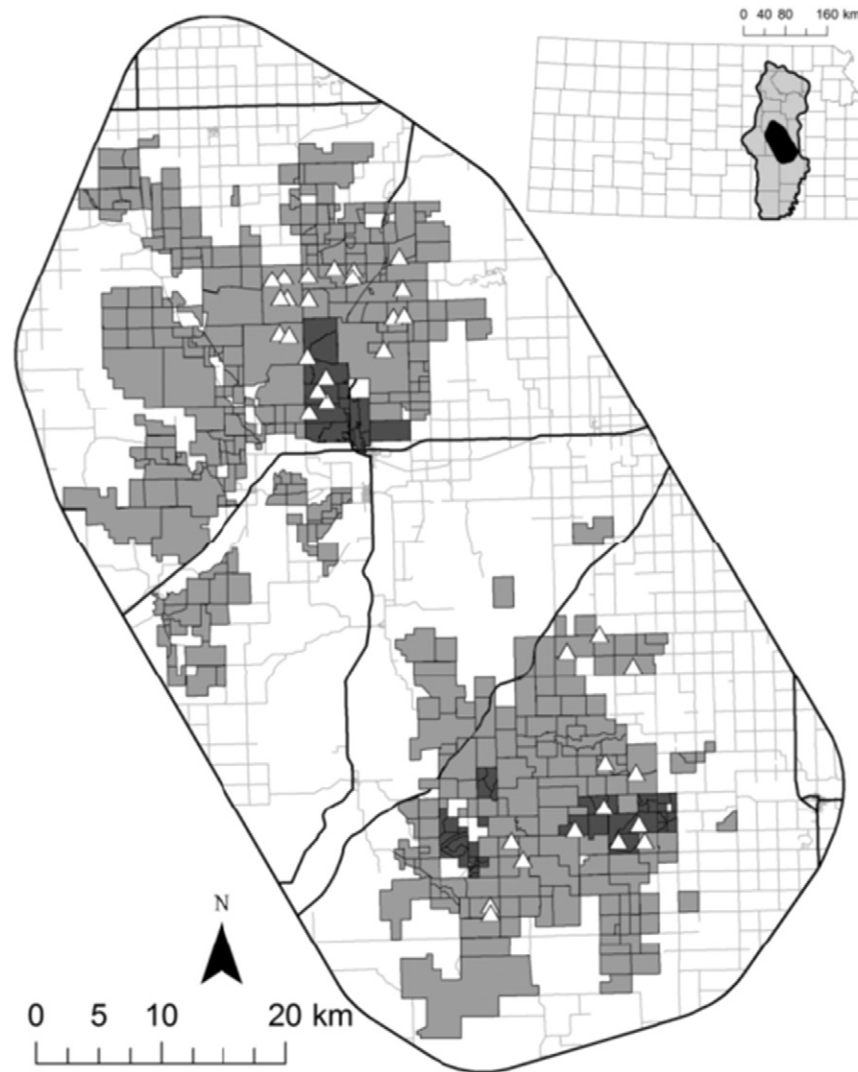


Figure 1. Map of field study site for analyses of space use by female Greater Prairie-Chickens in the central Flint Hills of Kansas, 2011–2013. Dark black lines are state highways; gray lines are ranch, county, or city roads. Pastures in light gray were managed with intensive early stocking and annual burning. Pastures in dark gray were managed with patch-burn grazing. Greater Prairie-Chicken leks are represented by white triangles. Inset: light gray polygon = Flint Hills ecoregion.

prescribed burns in 2012 and 2013, or stocking cattle at lower rates. Average stocking rate during the study at intensive early stocking properties was 2.33 ± 1.03 SD AUM per ha^{-1} . More than 90% of rangelands managed with intensive early stocking were burned in the spring of 2011, ~10% was burned in 2012, but only ~1% of the study area managed with intensive early stocking was burned in the spring of 2013 because of drought conditions. Even after stocking adjustments, drought created habitat conditions similar to intensive grazing without adequate residual fuel needed to carry a spring fire. Management strategies for patch-burn grazing properties were consistent over the 3-yr. field effort, and our project spanned one complete fire and grazing rotation. Pastures managed with patch-burn grazing were divided into thirds, and each third was burned once every 3 yr. Cattle were free to move among patches within a pasture but tended to concentrate grazing on the most recently burned patches (Fuhlendorf and Engle, 2004). Patch-burn grazing properties were stocked with cattle at $1.5\text{--}2$ AUM $\cdot \text{ha}^{-1}$, or with bison at 0.45 AUM $\cdot \text{ha}^{-1}$.

Capture and Monitoring of Prairie Chickens

We mapped lek sites using handheld Global Positioning System (GPS) units with an accuracy of ~5 m. We made every effort to search our entire study site for lekking activity when prairie chickens were

conspicuous, and all known leks were included in our analyses. We captured prairie chickens with walk-in traps or drop-nets at 34 leks during March–May, including 25 leks at intensive early stocking properties and 9 leks at patch-burn grazing properties. Captured birds were uniquely marked with a numbered metal leg band and colored leg bands and were sexed and aged by plumage (Henderson et al., 1967). Females were marked with 11-g VHF radio transmitters attached with a wire necklace harness (Model A3950, Advanced Telemetry Systems [ATS], Isanti, MN). VHF radios had an expected battery life of ~18 mo and were equipped with mortality switches that changed pulse rate when the transmitter was stationary for >6 h. Radio-marked females were located by triangulation or homing with portable radio receivers and handheld Yagi antennas (Model R2000, ATS). We relocated birds ≥ 3 times per wk. during the 6-mo *breeding* season (1 March–31 August), and ≥ 2 times per wk. during the 6-mo *nonbreeding* season (1 September–28 or 29 February). Observers rotated their check schedules among monitored females within each week to relocate birds at different times of the day. We double-checked the area of triangulated locations in the field to ensure that all sides of the triangle were <200 m in length (~1 ha), minimizing error in our location estimates. We estimated coordinates for all locations in Program Locate III with UTM's projected in NAD 1983, Zone 14 N (v. 3.34, Tatamagouche, Nova Scotia, Canada).

Statistical Analyses

We analyzed location and space use data separately for the 6-mo breeding and nonbreeding seasons. A subset of female prairie chickens was monitored in multiple years (19 of 93 individuals, ~20%), but we accepted a limited amount of pseudoreplication to use our complete dataset. For the purposes of our study, we considered the seasonal home range to be the amount of space an individual female required to forage, reproduce (breeding season only), and survive during the 6-mo breeding or nonbreeding seasons. We restricted our analysis to females with 30 or more locations, and with at least 20 locations not associated with a nest or a brood (Seaman et al., 1999). 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., 2014a). The data requirements for spatial modeling introduced a potential bias because home ranges can only be estimated for females that survive long enough to accumulate an adequate number of locations. We accepted the tradeoff between number of locations and survival to investigate space use and associated habitat choices of successful female prairie chickens, since the performance of successful birds is of greatest importance for conservation.

Seasonal Range Estimation

We estimated 50%, 95%, and 99% volume contours for the seasonal home ranges of female prairie chickens using the Fixed Kernel Density Estimator and Percent Volume Contour options in Hawth's Tools for ArcMap 9.3 (spatial ecology.com/htools; ESRI, Redlands, CA; 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 seasonal home range (Worton, 1989; Powell, 2000). We used separate main effects linear models to test for the effects of season; year; nest outcome; individual β coefficients from RUF models; distance from home range centroid to nearest lek, road, or landcover patch edge; and fire and grazing conditions at the home range centroid on seasonal home range size. We monitored nests for radio-collared females daily during egg-laying and incubation (McNew et al., 2015). We classified nest outcome as successful (≥ 1 chick hatched) or failed on the basis of evidence at the nest bowl (McNew et al., 2013, 2015).

We combined our data on female proximity to leks and female seasonal home range size to calculate a threshold distance that would capture most of the space use by females around leks (after Winder et al., 2015a). First, we identified the 1% volume contour of each home range with Hawth's Tools (Beyer, 2004). Second, we determined the geographic center of the 1% contour and used this location as the centroid, representing the smallest core of the most heavily used area within the utilization distribution. We measured distances (km) from the centroid of each seasonal home range to the nearest lek, road, and land cover patch edge. Third, we examined the distribution of distances between the centroid of a seasonal home range and the nearest lek. We used the 95th percentile as the maximum distance that the centroid of a female's seasonal home range might be from the nearest lek. Fourth, we examined the size distribution of female seasonal home ranges on the basis of 95% contours. We calculated the median area of the seasonal home ranges and used the radius for a circle of the same area as the median seasonal home range because most home ranges are roughly circular in shape. Lastly, we calculated the boundary distance as the sum of the maximum distance from the seasonal home range centroid to the nearest lek plus the radius of the median seasonal home range. Our estimates of threshold distance should capture ~95% of the space use of a population of females at a given site, and the threshold could be used to set goals for habitat management.

Resource Utilization Functions

We used resource utilization functions (RUFs) to analyze selection of habitat components within the seasonal home range, sometimes called third-order habitat selection (Johnson, 1980; Aebischer et al., 1993; Marzluff et al., 2004). The outline of a seasonal home range provides information on *where* an animal is estimated to have been located, and linking differential space use to landscape features provides information on *why* an animal selected areas of frequent use (Marzluff et al., 1997; Powell, 2000). We used utilization distributions to quantify the probability of space use within the seasonal 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; Millsbaugh et al., 2006; Kertson et al., 2011). We used beta coefficients from RUFs to draw individual and population level inferences about the direction and magnitude of relationships between intensity of space use and values of selected resources (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 (Marzluff et al., 2004; ver. 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 seasonal home ranges of each female prairie chicken. The second step was to create a raster of the utilization distribution within the 99% volume contour for each seasonal home range. We assigned a use value bounded from 1 to 99 for each 30×30 m cell within the seasonal home range on the basis of the relative volume or 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 seasonal home range for key resources hypothesized to predict space use. We identified seven landscape metrics that we hypothesized a priori to be predictors of space use by female prairie chickens. Three variables were related to rangeland management: cumulative fire frequency as an indicator of potential legacy effects of prescribed fire (number of years burned from 2000 to 2011 based on satellite imagery and a Geographic Information Systems (GIS) layer prepared by Mohler and Goodin, 2012), years since last prescribed fire, and stocking rate of cattle or bison ($\text{AUM} \cdot \text{ha}^{-1}$). Each year of our study, we surveyed landowners to obtain stocking and burning data specific to each of the ~500 pastures in our study site. We used the spatial data to create rasters with 30-m resolution for stocking rates and fire histories to assess the effects of rangeland management practices on space use by female prairie chickens. When a female's seasonal home range included areas for which we could not obtain stocking and prescribed fire data (typically <5% of home range area), we used mean stocking rates and prescribed fire values for that year. Our approach allowed us to retain all individuals in our analyses of space use and analyze other landscape-level drivers of space use at their full spatial scale within the seasonal home range.

Prairie chickens are open-country birds and may avoid grassland habitats fragmented by small forest patches or row-crop agriculture (Patten et al., 2011). We used distance to land cover patch edge as an index of the patchiness of land cover. 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; Pruet et al., 2009; Hagen et al., 2011; Winder et al., 2014b, 2015a, b). Gregory et al. (2011) showed that lek sites are often located at 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.

We used landscape data from publicly available GIS layers from the Kansas Data Access & Support Center to model land cover classes, roads, and elevation at a 30-m resolution with a 30×30 m pixel size (2005; www.kansasgis.org). We estimated distance to patch edge

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 with 30-m resolution for distance to nearest road, lek, and land cover 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.fit 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. We used data on relative space use from the utilization distribution and scored values from 1 for a low probability of use to 99 for a high probability of use. We log_e-transformed relative space use scores to meet the assumption of linearity for multiple regression models. We used the ruf package for Program R to estimate RUFs with both standardized and unstandardized β coefficients (Marzluff et al., 2004; Kertson and Marzluff, 2010). To develop population level inferences, we calculated mean standardized β coefficients (β̄) for each landscape metric, with variance calculations that controlled for interindividual 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 our landscape metrics.

Our first RUF analysis of female prairie chicken space use included additive effects of all seven of our predictor landscape metrics, our complete dataset for all radio-marked females with enough locations for kernel density estimation, and data from both 6-month breeding and nonbreeding seasons. Only ~10% of our study area was managed with patch-burn grazing, and some leks were located up to 12 km from pastures managed with patch-burn grazing (see Fig. 1). Female prairie chickens typically nest <5 km from the lek where they were captured (Winder et al., 2015a). Individuals captured at leks far from properties managed with patch-burn grazing had little chance to select landscape characteristics created by patch-burn grazing if they were not likely to encounter a patch-burn grazing pasture in their movements. Therefore, we used a second set of RUF models to examine space use of females captured at properties managed with patch-burn grazing. Our second set of models included additive effects of the three predictor variables directly related to rangeland management activities: stocking rate, cumulative fire frequency (2000–2011), and years since prescribed fire. It was limited to breeding season movement data because our sample size of individuals during the nonbreeding season was small (n = 23).

Results

Seasonal Home Range Size Estimation

We analyzed movement data for 93 females over 157 bird-seasons (6-mo breeding or nonbreeding seasons), including 112 breeding bird-seasons and 45 nonbreeding bird-seasons. Females had an average of 58 ± 2 SE locations per bird during the breeding season and 46 ± 1 locations during the nonbreeding season (Table 1). Typically, concerns about bias in estimates of home range size center on a positive relationship between seasonal home range size and sampling effort (Seaman et al., 1999). We observed a nonsignificant negative trend between seasonal home range size and number of individual locations (linear model, t = -1.926, df = 155, adjusted r² = 0.02, P = 0.06) and moved forward under the assumption that our threshold of 30 individual locations was

Table 1
Seasonal home ranges (central tendency ± SE [range]) of female Greater Prairie-Chickens monitored with radiotelemetry in Kansas, 2011–2013.

Season ¹	Mean no. of locations	Mean bandwidth ² (km)	Mean landscape metric values at home range centroid								
			Median 50% area (km ²)	Median 95% area (km ²)	Median 99% area (km ²)	Distance to lek (km)	Distance to road (km)	Distance to edge (km)	Stocking rate ³ (AUM·ha ⁻¹ ·ha)	Yr since burn	Fire frequency ⁴ (2000–2011)
Breeding n = 112	58 ± 2 [30, 109]	1.30 ± 0.09 [0.26, 4.50]	5.0 [0.3, 89.0]	20.9 [2.2, 352.6]	32.9 [3.5, 508.4]	1.3 ± 0.1 [0.1, 9.3]	1.7 ± 0.1 [0.03, 5.0]	0.5 ± 0.03 [0.04, 1.7]	0.9 ± 0.03 [0.2, 2.3]	1 ± 0.1 [0, 5]	8.3 ± 0.2 [0, 12]
Nonbreeding n = 45	46 ± 1 [30, 70]	1.41 ± 0.12 [0.41, 3.78]	7.7 [1.0, 56.3]	34.1 [5.0, 241.4]	56.9 [7.4, 350.5]	2.5 ± 0.3 [0.5, 7.6]	1.7 ± 0.2 [0.2, 4.9]	0.4 ± 0.05 [0.0, 1.58]	0.9 ± 0.04 [0.1, 1.5]	0.6 ± 0.1 [0, 4]	8.7 ± 0.3 [0, 12]

¹ Breeding season (6 mo) = 1 March through 31 August; nonbreeding season (6 mo) = 1 September through 28 or 29 February.
² Bandwidth = smoothing parameter (h) used in kernel density estimation, individually determined for each bird using least squares cross validation.
³ AUM = animal unit months; a measure of stocking intensity.
⁴ Number of years burned in the 12-yr. period from 2000 to 2011 based on satellite imagery, Mohler and Goodin, 2012.

adequate to estimate seasonal home range size without bias. Home range size (99% contour) did not differ among years ($F_{1, 155} = 2.88$, $P = 0.09$) or between seasons ($F_{1, 155} = 1.22$, $P = 0.27$), but median home range size tended to be ~40% smaller during the breeding season than the nonbreeding season (see Table 1).

Breeding Season

Size of breeding home ranges (95% contour) ranged from 2 to 353 km², with a median area of 21 km² (see Table 1). Breeding home ranges were larger when the centroid of the home range was farther from the nearest lek ($F_{1, 110} = 9.80$, $P = 0.002$; Appendix A). Nest failure also resulted in larger home range sizes (logistic regression, $z = -2.15$, $df = 88$, $P = 0.03$). Female prairie chickens with a successful first nest had a median 95% breeding home range size of 15 km² ($n = 34$), whereas females whose first nest attempt failed had a median home range of 35 km² ($n = 56$).

Centroids of breeding home ranges tended to be ~1 km from a lek, 1.7 km from the nearest road, 0.5 km from a patch edge, in areas of moderate stocking intensity, 1 yr. postfire, and in areas that had been burned ~2 out of 3 yr. (see Table 1). More than 97% of monitored females had home range centroids <5 km from the nearest lek (Appendix B). We calculated a radius to serve as a focal distance for management of habitat around leks. The value for the 95th percentile of distance from home range centroid to nearest lek was 3.01 km. The median 95% breeding home range size was 20.9 km², and a circle of equal area has a radius of 2.6 km. Adding the 95th percentile of distance from home range centroid to nearest lek and the radius of a circle of the same size as the median home range resulted in a focal buffer distance around leks of 5.6 km.

Nonbreeding Season

Size of nonbreeding home ranges (95% contour) ranged ~50-fold among individual females, from 5 to 241 km², with a median area of 34 km² (see Table 1). Centroids of nonbreeding home ranges tended to be ~2.5 km from a lek, 1.7 km from a road, 0.4 km from a patch edge, in areas of moderate stocking intensity, < 1 yr. postfire, and in areas that had been burned approximately 3 out of 4 yr (see Table 1).

Predictors of Space Use

All Females

Our first RUF analysis of space use included all females regardless of rangeland management at lek of capture, incorporated movement data during both 6-mo breeding and nonbreeding seasons, and considered seven landscape predictors related to rangeland management strategies, anthropogenic influence, and lek sites. During the 6-mo breeding season, distance to lek was consistently the strongest predictor of space use ($\bar{\beta} = -0.59$ to -0.35 ; Fig. 2A–C). Negative coefficients indicated that females selected areas close to leks within their breeding ranges, and 83% of individual females (93 of 112) followed this pattern. In 2011, a year of normal rainfall, females avoided heavily stocked areas ($\bar{\beta} = -0.10$; 65% of individuals, 24 of 37) and selected areas with a high cumulative fire frequency within their breeding home ranges ($\bar{\beta} = +0.09$, 57% of individuals, 21 of 37; see Fig. 2A). In 2012, a drought year, females selected heavily stocked areas ($\bar{\beta} = +0.08$, 53% of individuals, 18 of 34) and areas on ridges and hilltops ($\bar{\beta} = +0.13$, 59% of individuals, 20 of 34; Fig. 2B).

RUF models for 6-mo nonbreeding home ranges indicated that distance to lek remained an important driver of space use during 2 of the 3 yr. of our study ($\bar{\beta} = -0.32$ in 2011 and -0.53 in 2012; Fig. 2D–F). Across all years, 64% of individuals (29 of 45) selected space close to leks within their nonbreeding home ranges. Females also selected for frequently burned areas within nonbreeding home ranges ($\bar{\beta} = +0.19$ in 2012 and $+0.08$ in 2013; see Fig. 2E–F).

Females from Patch-Burn Grazing Leks

Our second resource utilization analysis of space use included movement data during the 6-mo breeding season for the subset of female

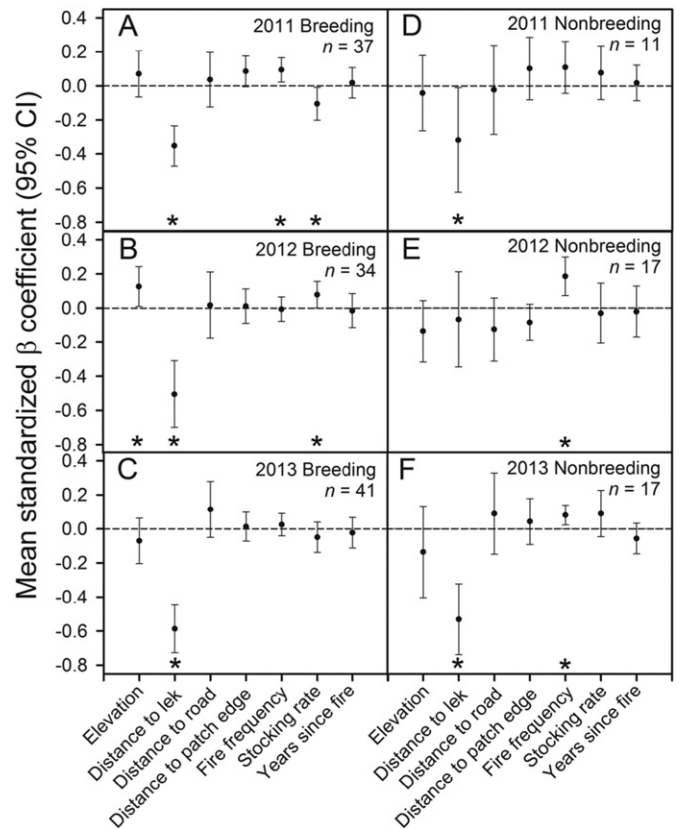


Figure 2. Mean standardized resource utilization function (RUF) coefficients ($\bar{\beta}$) and 95% confidence intervals for seven landscape metrics. We used resource utilization functions to analyze space use within 99% home ranges during breeding (A–C) and nonbreeding seasons (D–F) for radio-marked female Greater Prairie-Chickens in Kansas, 2011–2013.

prairie chickens captured at leks on patch-burn grazing properties. Here, we considered three landscape metrics related to rangeland management strategies. Females selected areas with low stocking rates ($\bar{\beta} = -0.11$, 55% of individuals, 29 of 53) and high fire frequencies ($\bar{\beta} = +0.09$, 55% of individuals, 29 of 53; Fig. 3). We also observed a weak tendency for females to select unburned areas ($\bar{\beta} = +0.05$, 53% of

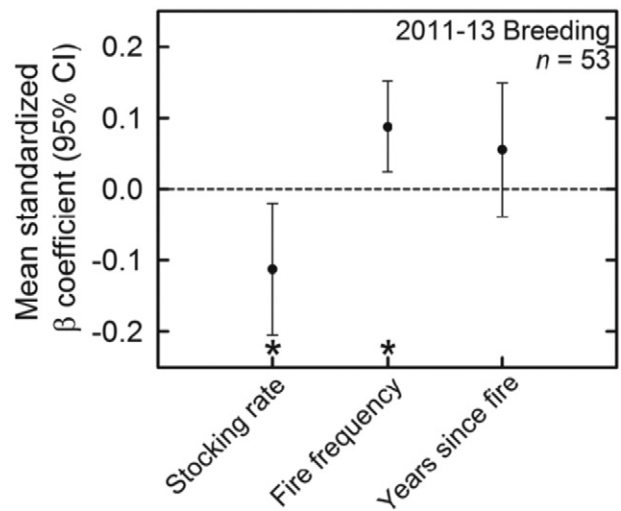


Figure 3. Mean standardized resource utilization function coefficients ($\bar{\beta}$) and 95% confidence intervals for three landscape metrics related to rangeland management. We used resource utilization functions to analyze space use within the breeding 99% home ranges of radio-marked female Greater Prairie-Chickens captured at leks on properties managed with patch-burn grazing in Kansas, 2011–2013.

individuals, 28 of 53), but the magnitude of the coefficient for this relationship suggests it was not as important to space use decisions as stocking rate and long-term fire frequency.

Drivers of Space Use as Predictors of Home Range Size

Breeding Season

Size of breeding home range was not related to individual β coefficients from RUF models ($F_{1, 110} < 0.001$ – 2.70 , $P = 0.10$ – 0.99), fire and grazing metrics at the home range centroid ($F_{1, 110} = 0.44$ – 1.09 , $P = 0.30$ – 0.51), distance from home range centroid to nearest road ($F_{1, 110} = 0.21$, $P = 0.65$) or nearest patch edge ($F_{1, 110} = 1.19$, $P = 0.27$), or rangeland management treatment at the lek of capture (patch-burn grazing vs. intensive early stocking; $F_{1, 110} = 0.72$, $P = 0.40$).

Nonbreeding Season

Area of 95% nonbreeding home ranges was related to individual β coefficients for distance to lek ($F_{1, 43} = 7.80$, $P = 0.008$, adjusted $r^2 = 0.13$), distance to road ($F_{1, 43} = 9.67$, $P = 0.003$, adjusted $r^2 = 0.16$), and cumulative fire frequency ($F_{1, 43} = 19.05$, $P < 0.0001$, adjusted $r^2 = 0.29$), with larger home ranges when females selected for areas near leks, avoided roads, and when cumulative fire frequency was low (Appendix C). Females also had larger nonbreeding home ranges when the centroid of their home range was close to leks ($F_{1, 43} = 5.56$, $P = 0.02$, adjusted $r^2 = 0.10$), farther from roads ($F_{1, 43} = 13.10$, $P = 0.001$, adjusted $r^2 = 0.22$), and in unburned pasture ($F_{1, 42} = 7.04$, $P = 0.01$, adjusted $r^2 = 0.12$; see Appendix C). An additive model including these six significant predictors explained ~50% of the variation in home range size within our dataset ($F_{6, 37} = 8.12$, $P < 0.0001$, adjusted $r^2 = 0.50$). Size of 95% nonbreeding home ranges was not related to individual β coefficients for elevation ($F_{1, 43} = 0.84$, $P = 0.36$), stocking intensity at the home range centroid ($F_{1, 42} = 0.10$, $P = 0.76$), cumulative fire frequency at the home range centroid ($F_{1, 43} = 3.61$, $P = 0.06$), distance from home range centroid to nearest patch edge ($F_{1, 43} = 0.02$, $P = 0.89$), or rangeland management treatment at the lek of capture (patch-burn grazing versus intensive early stocking; $F_{1, 43} = 0.17$, $P = 0.68$).

Discussion

Our 3-yr. field study provides evidence that rangeland management practices influence space use by female Greater Prairie-Chickens during the breeding and nonbreeding seasons in the Flint Hills ecoregion of eastern Kansas. Patch-burn grazing created preferred habitats for female Greater Prairie-Chickens, with a relatively frequent fire return interval, a mosaic of burned and unburned patches, and an effectively reduced stocking rate in unburned areas (Coppedge and Shaw, 1998; Fuhlendorf et al., 2006; Allred et al., 2011). Females captured at leks on properties managed with patch-burn grazing selected areas with low stocking rates, patches that were frequently burned, and areas that were not recently burned. Simultaneous selection for areas managed with relatively frequent fire and areas that were not recently burned provides support that patch-burn grazing generates the types of habitat and resources required by female prairie chickens. A typical patch-burn grazing management strategy uses a 3-yr. fire rotation across three patches. Every year, two-thirds of every pasture is relatively undisturbed, at least 1 yr. post fire, and therefore receives less grazing pressure. Rotational burning provided the diversity of habitats selected for by birds at our study sites. Thus, our field study provides new data that patch-burn grazing has the potential to improve grassland habitat for an umbrella species in the tallgrass prairie ecosystem (Wiens, 1974; Poiani et al., 2001; Fuhlendorf et al., 2006; Rahmig et al., 2009).

Resource selection by female prairie chickens in our study varied among years. In 2011, when >90% of the landscape in our study area was burned, females avoided heavily stocked areas. In 2012, when only ~10% of the study area was burned and ranchers reduced stocking

rates because of drought conditions, female prairie chickens selected for heavily stocked areas. Annual variation in selection coefficients suggests that prairie chickens may respond quickly to changes in rangeland management. Our results provide evidence that managing rangelands with patch-burn grazing generates annually shifting fire and grazing patterns at a scale that is ecologically relevant to prairie chickens and should also benefit other grassland vertebrates, such as herpetofauna, songbirds, and mammals, by providing a heterogeneous mosaic of grassland habitats (Fuhlendorf et al., 2006; Rahmig et al., 2009; Fuhlendorf et al., 2012; Holcomb et al., 2014; McNew et al., 2015; Sandercock et al., 2015).

Proximity to lek was the primary driver of female prairie chicken space use during both breeding and nonbreeding seasons, consistent with our previous work (Winder et al., 2015a). Links between female space use and lek placement are consistent with the hotspot hypothesis, which predicts that males should establish lek sites where home ranges of breeding females are relatively dense or at the intersection of dispersed female home ranges (Bradbury et al., 1986). Selection for areas near leks during the nonbreeding season was unexpected because females were not mating or seeking out nesting habitat during the nonbreeding period. However, male prairie chickens undergo a fall lekking season, and both sexes may remain close to display areas, possibly prospecting for lek territories or mates for the following spring (Rintamäki et al., 1999; Salter and Robel, 2000). Distance from 95% home range centroid to the nearest lek was ~1 km during the breeding season and ~2.5 km during the nonbreeding season. Standardized lek surveys are often used by wildlife managers to monitor trends in grouse populations (Winder et al., 2015b). Lek surveys have been criticized because bird counts are often treated as population indices, but detection probabilities are imperfect and fail to account for day of season, sex, age, and weather conditions (Walsh et al., 2004; Clifton and Kremetz, 2006; Blomberg et al., 2013). Nonetheless, consistent preference for areas near leks suggests that lek surveys of prairie chickens may be sampling habitat features important to females year-round.

Home range size can affect individual survival and productivity through interactions with predators and energy costs. Larger home ranges might incur higher costs, including energy requirements to fuel long movements and increased mortality risk due to an animal's relative unfamiliarity with its environment (Burger, 1988; Patten et al., 2011). We identified two drivers of breeding home range size at our study site. Breeding season home range size increased ~twofold if the home range centroid was 3 km versus 1 km from the nearest lek, and for females with a failed first nest compared with birds with a successful first nest. Elsewhere, we reported that patch-burn grazing increased vegetative cover at nest sites, which improved nest survival rates for prairie chickens (McNew et al., 2015). Here, we found no evidence that patch-burn grazing reduced seasonal home range size of female prairie chickens. Overall nest survival rates were low during the drought conditions of our study (~15%), but patch-burn grazing buffered the negative effects of drought on nest survival of prairie chickens (McNew et al., 2015). Long-term monitoring in normal or above-average rainfall conditions would be helpful to understand the interactions among rangeland management, habitat conditions, nest success, and space use.

Nonbreeding home ranges were ~60% larger than home ranges during the breeding season. Previous studies have had limited success at identifying landscape-level predictors of home range size (Winder et al., 2015a), but we constructed a model with six predictor variables that explained ~50% of the variation in nonbreeding home range size. The most influential predictor of nonbreeding home range size was individual response to fire frequency. Nonbreeding home ranges were larger if females selected for frequently burned areas within their home ranges, and selection for frequently burned areas was a significant driver of space use at a population level during 2 of the 3 yr. of our study. Frequent fire prevents encroachment by woody plants in tallgrass prairie, which reduces availability of perch sites for raptors and the edge habitats used by mesocarnivores (Briggs et al., 2002). Our results

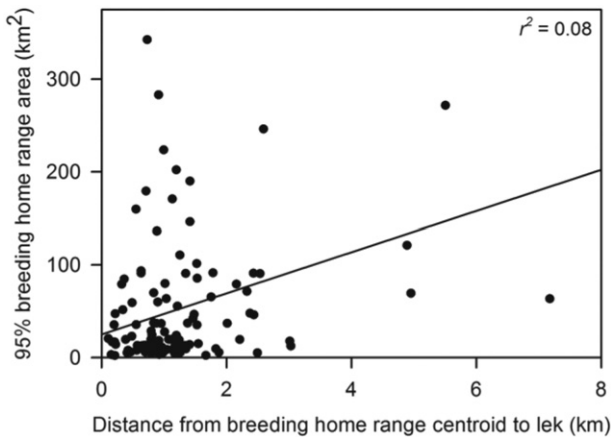
indicate that female prairie chickens may have accepted the potential costs associated with increasing their nonbreeding home ranges in favor of the benefits of escaping high predation pressure in infrequently burned areas.

Conservation Implications

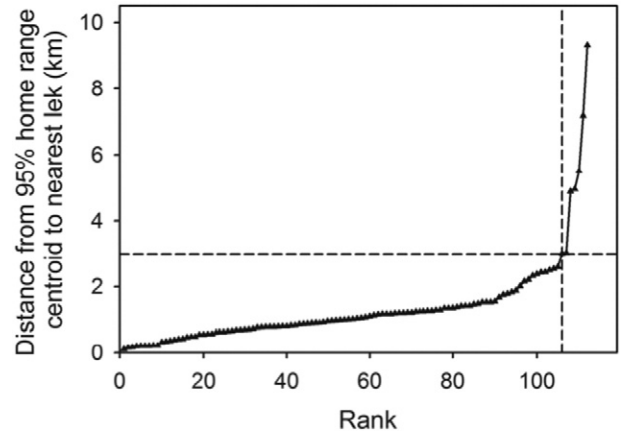
More than 90% of the extant distribution of Greater Prairie-Chickens occurs on private lands managed for cattle production. Therefore, the fate of this sensitive grassland species will be linked to decisions about rangeland management practices in the hands of private landowners and managers (Johnson et al., 2011). The Flint Hills is one of the remaining strongholds for Greater Prairie-Chicken populations and is vital to the long-term persistence of many obligate grassland birds (Reinking, 2005; With et al., 2008). The diverse habitat types and large amounts of space required by female prairie chickens indicate that large tracts of heterogeneous grasslands are necessary for populations to persist (Fuhlendorf and Engle, 2001; Winder et al., 2014b, 2015a, b). We found that Greater Prairie-Chickens selected for habitats created by patch-burn grazing management practices. Our study joins mounting evidence that populations and communities of grassland birds are affected by the interaction between fire and grazing (Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2006; Coppedge et al., 2008; Hovick et al., 2014; McNew et al., 2015; Sandercock et al., 2015). Widespread implementation of patch-burn grazing could result in significant improvements in the quality of habitats for grassland wildlife in tallgrass prairie ecosystems (Fuhlendorf et al., 2006; Swinton et al., 2007; Churchwell et al., 2008; Coppedge et al., 2008; Black et al., 2011; Fuhlendorf et al., 2012). Patch-burn grazing also has benefits for cattle producers, including livestock weight gains equal to or exceeding intensive early stocking, ability to manipulate grazing to limit erosion and control water access, and control of noxious plant species, horn flies, and ticks (Steuter, 1986; Coppedge et al., 1998; Vermeire et al., 2004; Cummings et al., 2007; Limb et al., 2011; Fuhlendorf et al., 2012; Scasta et al., 2012; Polito et al., 2013).

Ranching is steeped in tradition, and shifts in rangeland management practices do not come quickly or easily. One major logistical constraint for many private landowners is the investment of time and equipment to create the fire breaks necessary to implement patch-burn grazing. Conservation strategies should focus on education, logistical assistance, and cost-share programs to support patch-burn grazing and other comparable management strategies that treat fire and grazing not as tools, but as ecosystem processes for generating heterogeneous grassland habitats (Fuhlendorf and Engle, 2004; Fuhlendorf et al., 2012).

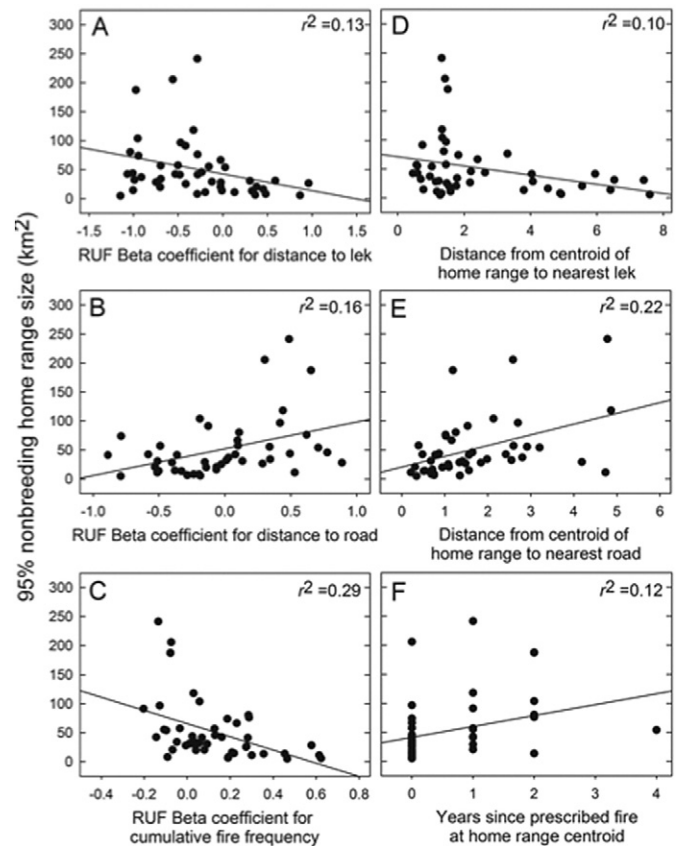
Appendix A. Relationship between distance from 95% breeding home range centroid to nearest lek and 95% breeding home range size for radio-monitored female Greater Prairie-Chickens in Kansas, 2011–2013. Circles represent breeding home range characteristics for individual females; black line was the best fit from a linear regression model. Untransformed values are shown, but analyses were conducted on natural log transformed data ($F_{1, 110} = 9.80, P = 0.002$).



Appendix B. Ranks for distance from 95% breeding home range centroid to nearest lek for female Greater Prairie-Chickens monitored by radio-telemetry in Kansas, 2011–2013. Triangles represent ranked distances for individual female prairie chickens ($n = 112$ bird-seasons); dashed lines indicate the 95th percentile at 3.0 km.



Appendix C. Predictors of 95% nonbreeding home range size for radio-monitored female Greater Prairie-Chickens in Kansas, 2011–2013. Circles represent nonbreeding home range characteristics for individual females; black line is the best fit from a linear regression model. Untransformed values are shown, but analyses were conducted on natural log transformed data. Values for r^2 are from single-factor linear models. Full multifactor model: 95% home range size ~ distance to lek + distance to road + cumulative fire frequency + distance from centroid to nearest lek + distance from centroid to nearest road + years since prescribed fire at centroid; $F_{6, 37} = 8.12, P < 0.0001$, adjusted $r^2 = 0.50$.



Acknowledgements

Our study was made possible by the generous cooperation of private landowners who allowed access to their lands, the Tallgrass Prairie National Preserve, and many dedicated field technicians who collected field data. We extend special thanks to Dr. William Browning and Jane Koger for allowing access to their private ranches and for their dedication to prairie chicken research and conservation. Kristen Hase and Brian Obermeyer provided advice and logistical support.

References

- Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from radiotracking data. *Ecology* 61, 65–71.
- Aldridge, C.L., Boyce, M.S., 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater Sage-Grouse. *Ecological Applications* 17, 508–526.
- Allred, B.W., Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution* 1, 132–144.
- Allred, B.W., Scasta, J.D., Hovick, T.J., Fuhlendorf, S.D., Hamilton, R.G., 2014. Spatial heterogeneity stabilizes livestock productivity in a challenging climate. *Agriculture, Ecosystems and Environment* 193, 37–41.
- Askins, R.A., 2000. Restoring North America's birds: lessons from landscape ecology. Yale University Press, New Haven, CT, USA 352 p.
- Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. Available at: <http://www.spatial ecology.com/htools> Accessed 1 January 2016.
- Black, S.H., Shepherd, M., Vaughan, M., 2011. Rangeland management for pollinators. *Rangelands* 33, 9–13.
- Blomberg, E.J., Sedinger, J.S., Nonne, D.V., Atamian, M.T., 2013. Annual male lek attendance influences count-based population indices of Greater Sage-Grouse. *Journal of Wildlife Management* 77, 1583–1592.
- Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14, 268–272.
- Bradbury, J.W., Gibson, R.M., Tsai, I.M., 1986. Hotspots and the dispersion of leks. *Animal Behaviour* 34, 1694–1709.
- Brennan, L.A., Kuvlesky Jr., W.P., 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69, 1–13.
- Briggs, J.M., Knapp, A.K., Brock, B.L., 2002. Invasion of woody plants in tallgrass prairie: a fifteen-year study of fire and grazing interactions. *American Midland Naturalist* 147, 287–294.
- Burger Jr., L.W., 1988. Movements, home range, and survival of female Greater Prairie-Chickens in relation to habitat pattern [thesis]. University of Missouri, Columbia, MO, USA.
- Christensen, N.L., 1997. Managing for heterogeneity and complexity on dynamic landscapes. In: Pickett, S.T.A., Ostfeld, R.S., Shachak, M., Likens, G.E. (Eds.), *The ecological basis for conservation: heterogeneity, ecosystems, and biodiversity*. Chapman and Hall, New York, NY, USA, pp. 167–186.
- Churchwell, R.T., Davis, C.A., Fuhlendorf, S.D., Engle, D.M., 2008. Effects of patch burn management on Dickcissel nest success in a tallgrass prairie. *Journal of Wildlife Management* 72, 1596–1604.
- Clifton, A.M., Kremetz, D.G., 2006. Estimating numbers of Greater Prairie-Chickens using mark-resight techniques. *Journal of Wildlife Management* 70, 479–484.
- Coppedge, B.R., Shaw, J.H., 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management* 51, 258–264.
- Coppedge, R.T., Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., 2008. Avian community response to vegetation and structural features in grassland managed with fire and grazing. *Biological Conservation* 141, 1196–1203.
- Coppedge, B.R., Leslie Jr., D.M., Shaw, J.H., 1998. Botanical composition of bison diets on tallgrass prairie in Oklahoma. *Journal of Range Management* 51, 379–382.
- Cummings, D.C., Fuhlendorf, S.D., Engle, D.M., 2007. Is altering grazing selectivity of invasive forage species with patch burning more effective than herbicide treatments? *Rangeland Ecology & Management* 60, 253–260.
- Dzialak, M.R., Olson, C.V., Harju, S.M., Webb, S.L., Mudd, J.P., Winstead, J.B., Hayden-Wing, L.D., 2011. Identifying and prioritizing Greater Sage-Grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. *PLoS One* 6, e26273.
- Fuhlendorf, S.D., Engle, D.M., 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51, 625–632.
- Fuhlendorf, S.D., Engle, D.M., 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* 41, 604–614.
- Fuhlendorf, S.D., Engle, D.M., Elmore, R.D., Limb, R.F., Bidwell, T.G., 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecology & Management* 65, 579–589.
- Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., Leslie Jr., D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* 16, 1706–1716.
- Garshelis, D.L., 2000. Delusions in habitat evaluation: measuring use, selection, and importance. In: Boitani, L., Fuller, T.K. (Eds.), *Research techniques in animal ecology*. Columbia University Press, New York, NY, USA, pp. 111–164.
- Gregory, A.J., McNew, L.B., Prebyl, T.J., Sandercock, B.K., Wisely, S.M., 2011. Hierarchical modeling of lek habitats of Greater Prairie-Chickens. *Studies in Avian Biology* 39, 21–32.
- Hagen, C.A., Grisham, B.A., Boal, C.W., Haukos, D.A., 2013. A meta-analysis of Lesser Prairie-Chicken nesting and brood-rearing habitats: implications for habitat management. *Wildlife Society Bulletin* 37, 750–758.
- Hagen, C.A., Pitman, J.C., Loughin, T.M., Sandercock, B.K., Robel, R.J., Applegate, R.D., 2011. Impacts of anthropogenic features on habitat use by Lesser Prairie-Chickens. *Studies in Avian Biology* 39, 63–75.
- Hagen, C.A., Sandercock, B.K., Pitman, J.C., Robel, R.J., Applegate, R.D., 2009. Spatial variation in Lesser Prairie-Chicken demography: a sensitivity analysis of population dynamics and management alternatives. *Journal of Wildlife Management* 73, 1325–1332.
- Hart, R.H., 1978. Stocking rate theory and its application to grazing on rangelands. In: Hyder, D.N. (Ed.), *Proceedings of the First International Rangeland Congress, Society for Range Management*. SRM, Denver, CO, USA, pp. 547–550.
- Henderson, F.R., Brooks, F.W., Wood, R.E., Dahlgren, R.B., 1967. Sexing of prairie grouse by crown feather patterning. *Journal of Wildlife Management* 31, 764–769.
- Hepinstall, J.A., Marzluff, J.M., Handcock, M.S., Hurvitz, P., 2005. Incorporating utilization distributions into the study of resource selection. In: Huzurbazar, S. (Ed.), *Resource selection methods and applications*. Omnipress, Madison, WI, USA, pp. 2–19.
- Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Robers, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8, 23–29.
- Holcomb, E.D., Davis, C.A., Fuhlendorf, S.D., 2014. Patch-burn management: implications for conservation of avian communities in fire-dependent sagebrush ecosystems. *Journal of Wildlife Management* 78, 848–856.
- Holecheck, J., Pieper, R.D., Herbel, C.H., 2004. *Range management: principles and practices*. Prentice Hall, Upper Saddle River, NJ, USA, pp. 1–607.
- Hovick, T.J., Elmore, R.D., Allred, B.W., Fuhlendorf, S.D., Dahlgren, D.K., 2014. Landscapes as a moderator of thermal extremes: a case study from an imperiled grouse. *Ecosphere* 5, art35.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Johnson, J.A., Schroeder, M.A., Robb, L.A., 2011. Greater Prairie-Chicken (*Tympanuchus cupido*). In: Poole, A. (Ed.), *The Birds of North America Online: Cornell Laboratory of Ornithology*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
- Kertson, B.N., Marzluff, J.M., 2009. Animal movement, home range, and resource utilization (RUF) analysis in ArcMap 9.3. School of Forest Resources, University of Washington, Seattle, WA, USA.
- Kertson, B.N., Marzluff, J.M., 2010. Improving studies of resource selection by a greater understanding of resource use. *Environmental Conservation* 38, 391–396.
- Kertson, B.N., Spencer, R.D., Marzluff, J.M., Hepinstall-Cymerman, J., Grue, C.E., 2011. Cougar space use and movements in the wildland-urban landscape of western Washington. *Ecological Applications* 21, 2866–2881.
- Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., Towne, E.G., 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience* 49, 39–50.
- Knapp, A.K., Briggs, J.M., Hamett, D.C., Collins, S.L., 1998. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, Oxford, England, pp. 1–364.
- Knopf, F.L., 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15, 247–257.
- Laver, P.N., Kelly, M.J., 2008. A critical review of home range studies. *Journal of Wildlife Management* 72, 290–298.
- Limb, R.F., Fuhlendorf, S.D., Engle, D.M., Weir, J.R., Elmore, R.D., Bidwell, T.G., 2011. Pyric-herbivory and cattle performance in grassland ecosystems. *Rangeland Ecology & Management* 64, 659–663.
- Marzluff, J.M., Knick, S.T., Vekasy, M.S., Schueck, L.S., Zariello, T.J., 1997. Spatial use patterns and habitat selection of Golden Eagles in southwestern Idaho. *Auk* 114, 673–687.
- Marzluff, J.M., Millsbaugh, J.J., Hurvitz, P., Handcock, M.S., 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85, 1411–1427.
- Matthews, T.W., Tyre, A.J., Taylor, J.S., Lusk, J.J., Powell, L.A., 2013. Greater Prairie-Chicken nest success and habitat selection in southeastern Nebraska. *Journal of Wildlife Management* 77, 1202–1212.
- McNew, L.B., Gregory, A.J., Wisely, S.M., Sandercock, B.K., 2012a. Demography of Greater Prairie-Chickens: regional variation in vital rates, sensitivity values, and population dynamics. *Journal of Wildlife Management* 76, 987–1000.
- McNew, L.B., Prebyl, T.J., Sandercock, B.K., 2012b. Effects of rangeland management on the site occupancy dynamics of prairie chickens in a protected prairie preserve. *Journal of Wildlife Management* 76, 38–47.
- McNew, L.B., Gregory, A.J., Sandercock, B.K., 2013. Spatial heterogeneity in habitat selection: nest site selection by Greater Prairie-Chickens. *Journal of Wildlife Management* 77, 791–801.
- McNew, L.B., Gregory, A.J., Wisely, S.M., Sandercock, B.K., 2011. Reproductive biology of a southern population of Greater Prairie-Chickens. *Studies in Avian Biology* 39, 209–221.
- McNew, L.B., Winder, V.L., Pitman, J.C., Sandercock, B.K., 2015. Alternative rangeland management strategies and the nesting ecology of Greater Prairie-Chickens. *Rangeland Ecology & Management* 68, 298–304.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132, 87–106.
- Millsbaugh, J.J., Nielson, R.M., McDonald, L., Marzluff, J.M., Gitzen, R.A., Rittenhouse, C.D., Hubbard, M.W., Sheriff, S.L., 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70, 384–395.
- Mohler, R.L., Goodin, D.G., 2012. Mapping burned areas in the Flint Hills of Kansas and Oklahoma, 2000–2010. *Great Plains Research* 22, 15–25.
- National Oceanic and Atmospheric Administration, National Centers for Environmental Information. Station No. 147305. Available at: ncdc.noaa.gov. Accessed 1 January 2016.

- Niemuth, N.D., 2011. Spatially explicit habitat models for prairie grouse. *Studies in Avian Biology* 39, 3–20.
- Nooker, J.K., Sandercock, B.K., 2008. Phenotypic correlates and survival consequences of male mating success in lek-mating Greater Prairie-Chickens (*Tympanuchus cupido*). *Behavioral Ecology and Sociobiology* 62, 377–1388.
- Ostfeld, R.S., Pickett, S.T.A., Shachak, M., Likens, G.E., 1997. Defining scientific issues. In: Pickett, S.T.A., Ostfeld, R.S., Shachak, M., Likens, G.E. (Eds.), *The ecological basis for conservation: heterogeneity, ecosystems, and biodiversity*. Chapman and Hall, New York, NY, USA, pp. 3–10.
- Patten, M.A., Pruett, C.L., Wolfe, D.H., 2011. Home range size and movements of Greater Prairie-Chickens. *Studies in Avian Biology* 39, 51–62.
- Pitman, J.C., Hagen, C.A., Robel, R.J., Loughin, T.M., Applegate, R.D., 2005. Location and success of Lesser Prairie-Chicken nests in relation to vegetation and human disturbance. *Journal of Wildlife Management* 69, 1259–1269.
- Pitman, J.C., Kramer, J., Michener, M., 2012. Prairie-chicken lek survey - 2012. Kansas Department of Wildlife, Parks, and Tourism, Pratt, KS, USA.
- Poiani, K.A., Merrill, M.D., Chapman, K.A., 2001. Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. *Conservation Biology* 15, 513–522.
- Polito, V.J., Baum, K.A., Payton, M.E., Little, S.E., Fuhlendorf, S.D., Reichard, M.V., 2013. Tick abundance and levels of infestation on cattle in response to patch burning. *Rangeland Ecology & Management* 66, 545–552.
- Powell, R.A., 2000. Animal home ranges and territories and home range estimator. In: Boitani, L., Fuller, T.K. (Eds.), *Research techniques in animal ecology*. Columbia University Press, New York, NY, USA, pp. 65–110.
- Powell, A.F.L.A., 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. *Journal of Field Ornithology* 79, 41–52.
- Pruett, C.L., Patten, M.A., Wolfe, D.H., 2009. Avoidance behavior by prairie grouse: implications for wind energy development. *Conservation Biology* 23, 1253–1259.
- Rahmig, C.J., Jensen, W.E., With, K.A., 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. *Conservation Biology* 23, 420–432.
- Reinking, D.L., 2005. Fire regimes and avian responses in the central tallgrass prairie. *Studies in Avian Biology* 30, 116–126.
- Rensink, C.B., 2009. Impacts of patch-burn grazing on livestock and vegetation in the tallgrass prairie [thesis]. Kansas State University, Manhattan, KS, USA, pp. 1–44.
- Rintamäki, P.T., Karvonen, E., Alatalo, R.V., Lundberg, A., 1999. Why do Black Grouse males perform on lek sites outside the breeding season? *Journal of Avian Biology* 30, 359–366.
- Salter, G.C., Robel, R.J., 2000. Capturing Lesser Prairie-Chickens on leks during fall. *Transactions of the Kansas Academy of Science* 103, 46–47.
- Samson, F.B., Knopf, F.L., 1994. Prairie conservation in North America. *Bioscience* 44, 418–421.
- Samson, F.B., Knopf, F.L., Ostlie, W.R., 2004. Great plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32, 6–15.
- Sandercock, B.K., Alfaro-Barrios, M., Casey, A.E., Johnson, T.N., Mong, T.W., Odom, K., Strum, K.M., Winder, V.L., 2015. Effects of grazing and prescribed fire on resource selection and nest survival of Upland Sandpipers in an experimental landscape. *Landscape Ecology* 30, 325–337.
- Scasta, J.D., Engle, D.M., Talley, J.L., Weir, J.R., Stansberry, J.C., Fuhlendorf, S.D., Harr, R.N., 2012. Pyric-herbivory to manage horn flies (Diptera: Muscidae) on cattle. *Southwestern Entomologist* 37, 325–334.
- Seaman, D.E., Millsap, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R., 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63, 739–747.
- Smith, E.F., Owensby, C.E., 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills range. *Journal of Range Management* 31, 14–17.
- Steuter, A.A., 1986. Fire behavior and standing crop characteristics on repeated seasonal burns: northern mixed prairie. In: Koonce, A.L. (Ed.), *Prescribed burning in the Midwest: state of the art*. University of Wisconsin, College of Natural Resources, Fire Science Center, Stevens Point, WI, USA, pp. 54–59.
- Swinton, S.M., Lupi, F., Robertson, G.P., Hamilton, S.K., 2007. Ecosystem services and agriculture: cultivating agricultural ecosystems for diverse benefits. *Ecological Economics* 64, 245–252.
- Vermeire, L.T., Mitchell, R.B., Fuhlendorf, S.D., Gillen, R.L., 2004. Patch burning effects on grazing distribution. *Rangeland Ecology & Management* 57, 248–252.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499.
- Walsh, D.P., White, G.C., Remington, T.E., Bowden, D.C., 2004. Evaluation of the lek-count index for Greater Sage-Grouse. *Wildlife Society Bulletin* 32, 56–68.
- White, R.P., Murray, S., Rohweder, M., 2000. Pilot analysis of global ecosystems: grassland ecosystems. World Resources Institute, Washington, DC Available at: pdf.wri.org.
- Wiens, J.A., 1974. Habitat heterogeneity and avian community structure in North American grassland birds. *American Midland Naturalist* 91, 195–213.
- Wiens, J.A., 1997. The emerging role of patchiness in conservation biology. In: Pickett, S.T.A., Ostfeld, R.S., Shachak, M., Likens, G.E. (Eds.), *The ecological basis for conservation: heterogeneity, ecosystems, and biodiversity*. Chapman and Hall, New York, NY, USA, pp. 93–107.
- Winder, V.L., Carrlson, K.M., Gregory, A.J., Hagen, C.A., Haukos, D.A., Kesler, D.C., Larsson, L.C., Matthews, T.W., McNew, L.B., Patten, M.A., Pitman, J.C., Powell, L.A., Smith, J.A., Thompson, T., Wolfe, D.H., Sandercock, B.K., 2015a. Factors affecting female space use in ten populations of prairie chickens. *Ecosphere* 6, art166.
- Winder, V.L., Gregory, A.J., McNew, L.B., Sandercock, B.K., 2015b. Responses of male Greater Prairie-Chickens to wind energy development. *Condor* 117, 284–296.
- Winder, V.L., McNew, L.B., Gregory, A.J., Hunt, L.M., Wisely, S.M., Sandercock, B.K., 2014a. Effects of wind energy development on the survival of Greater Prairie-Chickens. *Journal of Applied Ecology* 51, 395–405.
- Winder, V.L., McNew, L.B., Gregory, A.J., Hunt, L.M., Wisely, S.M., Sandercock, B.K., 2014b. Space use by female Greater Prairie-Chickens in response to wind energy development. *Ecosphere* 5, art3.
- With, K.A., King, A.W., Jensen, W.E., 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 141, 3152–3167.
- Wolfe, D.H., Patten, M.A., Shochat, E., Pruett, C.L., Sherrod, S.K., 2007. Causes and patterns of mortality in Lesser Prairie-Chickens *Tympanuchus pallidicinctus* and implications for management. *Wildlife Biology* 13, 95–104.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70, 164–168.
- Zimmerman, J.L., 1997. Avian community responses to fire, grazing, and drought in the tallgrass prairie. In: Knopf, F.L., Samson, F.B. (Eds.), *Ecology and conservation of Great Plains vertebrates*. Springer-Verlag, New York, NY, USA, pp. 167–180.