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Effects of Landscape Characteristics on Annual Survival of Lesser Prairie-Chickens

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ABSTRACT.—Agriculture and development have caused landscape change throughout the southwestern Great Plains in the range of the lesser prairie-chicken (*Tympanuchus pallidicinctus*). Landscape alteration within the lesser prairie-chicken range may contribute to range contraction and population losses through decreases in survival rates. Our objectives were to determine if (1) landscape configuration (*i.e.*, the spatial arrangement of habitat) or composition (*i.e.*, the amount of habitat), at the study-site scale, affected annual survival of females, (2) relationships exist between landscape context (*i.e.*, landscape configuration and composition) and weekly survival to assess effects of landscape composition and configuration on lesser prairie-chicken populations, and (3) anthropogenic features influenced daily mortality risk. We captured 170 female lesser prairie-chickens and used very-high-frequency and GPS (Global Positioning System) transmitters to track their movement and survival for 2 y. We used known-fate survival models to test if landscape configuration or composition within three sites in Kansas were related to differences in female survival among sites. In addition, we tested for relationships between weekly survival and landscape configuration or composition within home ranges. Finally, we used Andersen-Gill models to test the influence of distance to anthropogenic features on daily mortality risk. Differences in survival were evident between sites with differing landscape compositions as annual survival in Northwestern Kansas ($\hat{S}$ = 0.27) was half that of Clark County, Kansas ($\hat{S}$ = 0.56), which corresponded with 41.9% more grassland on the landscape in Clark County; landscape configuration did not measurably differ among sites. Survival was greater for prairie-chickens with home-ranges that had greater patch richness, and in areas with 30% crop

and 57% grassland. Female lesser prairie-chickens also experienced greater mortality risk closer to fences at patch edges. Further conversion of grassland landscapes occupied by lesser prairie-chickens should be avoided to reduce habitat loss and fragmentation thresholds that could affect survival. We suggest continued encouragement of Conservation Reserve Program enrollment in western areas of the lesser prairie-chicken range to maintain or increase the amount of grassland to increase annual survival.

INTRODUCTION

Settlement of the Southern Great Plains starting in the latter part of the 19th century caused wide-spread alteration of grassland landscapes, which was accelerated following discovery and large-scale utilization of the Ogallala aquifer by the mid-20th century (Lewis, 1990; Coppedge *et al.*, 2001). Landscape fragmentation and habitat loss in the Great Plains, namely loss of grasslands with increasing isolation and reduction in size of grassland patches (Fahrig, 2003), resulted from direct conversion of land from native prairie to agricultural production, including row-cropping or grazing by domestic livestock (Haukos and Boal, 2016; Rodgers, 2016). Quality of remaining grasslands has also declined across time with the alteration of ecological drivers, such as the removal of fire resulting in tree encroachment (Fuhlendorf *et al.*, 2002, 2017; Lautenbach *et al.*, 2016; Spencer *et al.*, 2017). Anthropogenic features on the landscape have further fragmented and isolated grassland patches. Power lines, fences, roads, energy infrastructure, and other types of urbanization can affect distribution and space use of prairie birds, creating barriers to movement, reducing habitat availability due to avoidance, and by enhancing conditions for predators to traverse and perceive the landscape, increasing the risk of predation (Pruett *et al.*, 2009; Hagen *et al.*, 2011). With a growing demand for domestic

energy, food, and infrastructure, an increase in anthropogenic structures and other landscape changes are persistent, thereby increasing potential negative effects on grassland species (Coppedge *et al.*, 2001; Hovick *et al.*, 2014).

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is considered an umbrella species of the western portion of the Southern Great Plains (Miller *et al.*, 2016), and its conservation could provide ecological benefits to many other species (Hagen and Giesen, 2005). Lesser prairie-chickens traverse large areas, requiring a heterogeneous landscape configuration for all life-history stages (Fuhlendorf and Engle, 2001; Haukos and Zavaleta, 2016; Robinson et al. 2017). Population declines of lesser prairie-chickens have been commensurate with aforementioned losses of prairie habitat (Haukos and Zavaleta, 2016). Quantifying demographic responses to variation in available habitat area, habitat configuration, and anthropogenic features on the landscape are necessary to identify factors contributing to population dynamics.

The theoretical foundation underpinning landscape ecology predicts the existence of a threshold of habitat loss, due to both reduction in both quantity and quality, that when exceeded is detrimental to demographic rates (Fahrig and Merriam, 1985; Fahrig, 2001, 2003). Population resilience to habitat loss needs to be considered on a species-specific basis, as a species' life-history dictates responses to landscape fragmentation (Dooley and Bowers, 1998). Alternatively, there may be an optimum landscape context that maximizes species-specific population growth and therefore persistence. However, if an area supports potential habitat and is colonized by a population, but adult survival or reproductive output of the extant population is not sufficient to offset mortality, long-term persistence is unlikely without corresponding immigration (Pulliam, 1988). Relationships between population dynamics and landscape features need to be quantified at multiple scales, from individuals to populations, to assess habitat quality (Fahrig and Merriam,

1985; Dooley and Bowers, 1998; Chalfoun and Martin, 2007). If relationships exist between lesser prairie-chicken adult survival and landscape configuration (*i.e.*, the spatial arrangement of habitat) or composition (*i.e.*, the amount of habitat and patch types), understanding both direct and indirect drivers of these relationships can also assist to target areas on the landscape for conservation planning, development of management strategies, and assure long-term population persistence (Fahrig, 2002; Mills, 2007; Johnson *et al.*, 2010).

Past studies on lesser prairie-chickens have determined patterns of avoidance of power lines, buildings, and, to a lesser extent, paved roads and oil wells (Hagen *et al.*, 2011; Bartuszevige and Daniels, 2016; Grisham *et al.*, 2016b). Further, increasing landscape fragmentation decreases the probability of lek persistence (Woodward *et al.*, 2001). However, few studies have investigated relationships between landscape context (*i.e.*, landscape configuration and composition) and lesser prairie-chicken survival. At a fine scale, some lesser prairie-chicken populations have increased survival with increased shrub cover and vegetation density (Patten *et al.*, 2005). Habitat loss, increased patch isolation, and anthropogenic development also have the potential to negatively affect female lesser prairie-chickens through several mechanisms including both direct mortality (*i.e.*, collision with anthropogenic structures) and indirect mortality (*i.e.*, predator subsidization). Research designed to relate effects of landscape features, composition, and configuration on survival is needed for lesser prairie-chickens. Results of such research will inform future management and conservation actions by identifying whether differences in landscape characteristics are contributing to declines of lesser prairie-chicken populations through effects on annual survival.

Lesser prairie-chickens in Kansas occupy three ecoregions with distinct soil and vegetative characteristics and varying degrees of structural fragmentation (McDonald *et al.*,

2014; Spencer *et al.*, 2017). The existence of populations of lesser prairie-chickens across the Southern Great Plains in differing landscape configurations and compositions allows for a robust assessment of adult survival as a function of landscape characteristics. Our objectives were to (1) estimate and compare annual lesser prairie-chicken survival among three sites with different landscape contexts, (2) determine relationships between landscape metrics and weekly survival to understand how landscape composition, and configuration, affect lesser prairie-chicken populations, and (3) estimate the effect of distance to anthropogenic features and landcover type on daily lesser prairie-chicken mortality risk. We hypothesized annual survival would be lower for sites with less available grassland, individuals with less grassland in their home range, and populations with a greater fragmented landcover configuration. We also expected to find anthropogenic features that can act as perches or habitat for predators (power lines, fences, oil wells) would increase the mortality risk for female lesser prairie-chickens.

METHODS

STUDY AREA

We selected study sites for areas known to have populations of lesser prairie-chickens. Three study sites were located in three ecoregions across the range of lesser prairie-chickens in Kansas (Fig. 1). Ecoregions were characterized by different landscape configuration, soil types, plant assemblages, management regimes, and vegetation conditions (McDonald *et al*., 2014; Dahlgren *et al*., 2016; Haukos *et al*., 2016; Wolfe *et al*., 2016).

Our study site in Northwestern Kansas, was in the Short-Grass Prairie/Conservation Reserve Program (CRP) Mosaic Ecoregion (McDonald *et al*., 2014). The Northwestern population of lesser prairie-chickens may have recently expanded north of the Arkansas River (Bain, 2002; Fields *et al*., 2006; Oyler-McCance *et al*., 2016; Rodgers, 2016). The Northwestern

150 study area (38˚50’15.624’’N, 100˚46’8.546’’W) was 1714 km^2 and located in Gove and Logan
151 counties. The primary land uses in this area were livestock grazing, energy extraction, CRP, and
152 both dryland and row-crop agriculture on silt-loam soils (Table 1).

153 In southern Kansas, lesser prairie-chickens are found in the Mixed-Grass Prairie
154 Ecoregion, with some areas exhibiting vegetation characteristics similar to the Sand Sagebrush
155 Prairie Ecoregion (McDonald *et al.*, 2014). We had two sites in south-central Kansas. The Red
156 Hills study site (37˚21’17.102’’N, 99˚7’13.45’’W) was 491 km^2, primarily on private lands in
157 Kiowa and Comanche counties within the Mixed-Grass Prairie Ecoregion. Primary land uses for
158 this area included livestock grazing, oil and gas extraction and exploration, and interspersed row-
159 crop agriculture. The Clark County study site (37˚9’34.155’’N, 99˚52’45.61’’W) within south-
160 central Kansas was 712 km^2 and located on the boundary of the Mixed-Grass Prairie and Sand
161 Sagebrush Prairie Ecoregions. Land use was dominated by livestock grazing, oil and gas
162 extraction, and row-crop agriculture (Table 1).

163 CAPTURE

164 We trapped lesser prairie-chickens at leks in spring (March–May) during 2013 and 2014
165 using walk-in drift traps and dropnets (Haukos *et al.*, 1990; Silvy *et al.*, 1990; Schroeder and
166 Braun, 1991). Lesser prairie-chickens were identified to sex using the presence of air-sacs,
167 greater pinnae length in males, and tail color patterns (Copelin, 1963).

168 We fitted female lesser prairie-chickens with either a 12- to 15-g bib-style very-high-
169 frequency (VHF) transmitter (A3960, Advanced Telemetry System, Isanti, MN, U.S.A.) or a
170 rump-mounted 22-g Satellite Platform Transmitting Terminal GPS transmitter (PTT-100,
171 Microwave Telemetry, Columbia, MD, U.S.A.). We attached SAT-PTT transmitters on the rump
172 using leg harnesses made of Teflon® ribbon with elastic at the front of the harness for flexibility

(Dzialak *et al.*, 2011). All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocol 3241). Field work was conducted under Kansas Department of Wildlife, Parks and Tourism scientific collection permits (SC-042-2013 and SC-079-2014).

TRACKING

We located female prairie-chickens outfitted with VHF transmitters via triangulation 3–4 times per weeks from March 2013–March 2015. Upon detection, individuals were triangulated from three to five points to their estimate location. A three-element hand-held Yagi antenna and receiver were used to take compass bearings on individuals. Bearings were ≥15 degrees apart and taken within 20 min to decrease error from bird movement. Bearings and Universal Transverse Mercator (UTM) positions were entered into the program Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate the UTM location of the bird and calculate an error polygon around the point. Error around VHF locations ranged from zero to 1 ha. Fixed-wing aircraft were used to locate individuals with VHF radios that had dispersed from the study site.

Birds outfitted with a Satellite-PTT transmitter had up to ten locations recorded per day between 0600 and 2200 with 18 m accuracy. Points were uploaded to the Argos satellite system every three days and downloaded weekly for mortality assessments.

SURVIVAL ANALYSIS

We delineated study site boundaries by creating Minimum Convex Polygons (MCP) using the Minimum Bounding Geometry tool in ArcGIS 10.2 (ESRI Inc., 2013, Redlands, CA, U.S.A.) around all recorded bird points for each field site for the first year of study. We also buffered the study areas at two distances from the centroid of the study area to determine if our

study sites were representative of the surrounding landscape and if female survival at the study sites reflected our delineated study sites or the surrounding landscape. We used a 25 km buffer to standardize study site shape to a circle for a direct comparison among study sites, as 25 km was the greatest distance from the centroid of any one study area to the outside of the study area MCP; and a 50 km buffer to represent the overall landscape that lesser prairie-chickens may encounter during dispersal (Earl *et al*., 2016). Buffers were limited to the current estimated range of the lesser prairie-chicken, as this was the extent of the landcover layer used.

For landscape metrics, we used a 2013 landcover layer of the lesser prairie-chicken range developed by Spencer et al. (2017) from 30 m x 30 m resolution Landsat imagery. The landcover layer included five landcover classes (patch types: grassland, crop, CRP, urban, and water) but grassland and CRP did not distinguish grassland type or structure. Although the 50 km buffer was limited to the extent of the lesser prairie-chicken range landcover layer, comparison with aerial imagery confirmed that the landscape outside of the range was similar to that where the presumed occupied range stops. We merged the landcover layer with the 2014 CRP layer from the U.S. Department of Agriculture, Farm Services Agency, and clipped the landcover layer using the Clip tool in ArcGIS 10.2 to the shape of each study site. We then used program FRAGSTATS to describe landscape configuration within each study site (McGarigal *et al.*, 2012). The contagion metric, interspersion and juxtaposition index (IJI), mean patch size, and standard error of mean patch size were calculated within each study site polygon, and for 25 km and 50 km buffers around the centroid of the study site as measures of landscape configuration. We used the contagion and IJI metrics as a way to describe the fragmentation within each study site. Contagion is scaled 0 to 100, where a value of zero equates to a landscape in which there are no like adjacencies and a value of 100 is a single patch type. Alternatively, the IJI uses the

proportion of like adjacencies on a cell-basis, with a high IJI representing an increasingly fragmented landscape. We also calculated landscape composition of grassland, cropland, and CRP as the percent occurrence of each within the landscape of each study site and 25 and 50 km buffers around the centroid of each study site (Fig. 2).

To calculate individual covariates for the model testing the effect of landscape characteristics on survival, we created MCPs for all individuals that had ≥3 unique points with error polygons ≤1 ha around each point as an estimate of home range (Table 2). Each bird-year (March 15th–March 14th) was treated as an independent period due to variation in weather and land management across years (*e.g.*, precipitation, application of prescribed fire, haying, crop types, and grazing density). Use of MCPs allow for determination of a single, contiguous landscape potentially available for each individual, as kernel density estimates and Brownian Bridge Movement Models generated for these birds from space-use analyses were composed of disjointed polygons (Plumb, 2015; Robinson *et al.*, 2017). We used the same landcover data as for the study site analysis, except clipped to the MCP of each bird. Landscape metrics were calculated using FRAGSTATS to measure landscape composition and configuration within the home range of each bird. Patches were truncated at the edge of the MCP, as we were unable to determine a bird's perception of the landscape past where we had location information. Landscape configuration metrics calculated within home ranges were total area, mean patch size, contagion, IJI, and patch richness (McGarigal and Marks, 1995). Patch richness was the number of different patch types within each home range. For landscape composition metrics, we calculated the percentage of each home range that was grassland, cropland, or CRP. We tested for correlation among the configuration metrics using Pearson's correlation coefficient; if a metric pair was correlated at greater than $|r| = 0.5$, we did not include both in the same model.

We used FRAGSTATS metrics of configuration as individual covariates in one model set and FRAGSTATS metrics of composition as individual covariates in a second model set to derive functional relationships (White and Burnham, 1999). We created 14 *a priori* models using individual FRAGSTATS configuration metrics, additive site and FRAGSTATS metrics, and interactive site and FRAGSTATS metrics, followed by ranking of the models using AIC_c. We also created 19 *a priori* models using composition metrics, including study site and quadratic terms.

We used known-fate models in Program MARK to estimate cumulative annual survival for female lesser prairie-chickens at each study site for two bird-years (March 15, 2013–March 14, 2014 and March 15, 2014–March 14, 2015: White and Burnham 1999). We tested five models, including a null model, a site model, a year model, a site and year additive model and a site and year interactive model. Models were ranked using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson, 2002). Models with a $\Delta AIC_c \leq 2$ were considered competing models. We also modeled weekly survival using the known-fate model in Program MARK to evaluate the effect of landscape characteristics on the survival of individuals (White and Burnham, 1999; Winder *et al.*, 2014b). Encounter histories for both models were compiled using weekly encounters across the 52 wk annual period, although sample sizes varied due to the need for enough points to create MCPs.

ANDERSEN-GILL MODELING

We used an Andersen-Gill modeling framework to identify how continuous, encounter specific covariates affects mortality risk for lesser prairie-chickens (Dinkins et al., 2014; Winder *et al*., 2017). The mortality risk from Andersen-Gill models is the change in the survival rate with each change in a given covariate (Johnson *et al*., 2004a). Andersen-Gill models use Cox

proportional hazard models, but instead of having an entry date, exit date, and event for each individual, this approach models entry, exit, and event for each encounter per individual (Andersen and Gill, 1982). Use of Andersen-Gill models allows for time periods that individuals were not present in the study, such as dispersal from the study site, transmitter malfunctions, or lack of daily monitoring, such as with VHF individuals. The Andersen-Gill framework also allows for left-censoring of individuals with staggered entry into the data set (Johnson *et al.*, 2004b).

We only used birds that had ≥2 locations, one of which being the mortality location, to model the effect of distance to anthropogenic features on mortality risk. To obtain a covariate for the encounters of each individual bird, we created separate distance rasters of each study site for distance to road, fence, distribution power line, oil well and known leks using the Euclidean Distance tool in ArcGIS 10.2, with 30 m x 30 m grid cells. Oil well and road layers were obtained from the Kansas GIS and Data Support Center (http://www.kansasgis.org/). We hand-delineated fences based on field inspection. Distribution power line layers were from the Kansas Corporation Commission (http://www.kcc.state.ks.us/). Each cell of a distance raster layer has a value that identifies the distance that cell is from the nearest structure. For each use-point bird location, we extracted the distance from the starting point of an encounter to each structure using the Extract Multi Values tool in ArcGIS, as well as the landcover type from the landcover and CRP layer. We centered and scaled all input variables (Schielzeth, 2010).

For VHF birds, all available points were used for encounters, as birds were not located more than once on any given day. We randomly selected one point per bird per day for satellite birds as the SAT-PTT birds had as many as 10 points available/day. We chose a point for each day using the r.sample command in Geospatial Modeling Environment to simplify to a daily

encounter history and make use of both the SAT-PTT and VHF transmitter points (Beyer, 2015). Only points and mortalities within the delineated study sites were used.

Using the 'coxph' function in the 'survival' package, we identified the relative effect of covariates on mortality risk and annual survival from regression coefficients (Therneau, 2014). We built 26 *a priori* models, which represented each variable alone, additive models of site and variable combinations, and additive models of each combination of two variables. Model diagnostics were tested with the 'cox.zph' function to determine if these data met assumptions of proportional hazards (Fox and Weisberg, 2011). All models with $\Delta AIC_c \leq 2$ were considered competing models. If the mortality risk from the top models differed from zero (*i.e.*, 95% confidence intervals of the beta estimate did not overlap zero), then we judged the variable to be biologically important and plotted the predicted risk curve.

RESULTS

STUDY SITE COMPOSITION AND CONFIGURATION

A total of 170 individuals, representing 193 bird years and 108 mortality events were included in the overall model for annual known-fate survival of female lesser prairie-chickens, 81 individuals in 2013–2014 and 112 in 2014–2015. There were two top models in the model set with $\Delta AIC_c \leq 2$, one representing differences among study sites ($w_i = 0.59$) and another representing differences among study sites and years ($w_i = 0.22$, Table 3). We made inference based on the top-ranked model representing differences among sites, as adding year did not improve the model fit and was considered spurious. Northwest Kansas had a lower annual survival estimate than any of the other sites, at 0.27 (n = 110, 95% CI = 0.20–0.38). Survival in Northwestern Kansas was 50% lower than in Clark County, ($\hat{S} = 0.56$, n = 25, 95% CI = 0.38–0.81). The annual survival of lesser prairie-chickens within the Red Hills was similar to the Clark

311 County site ($\hat{S}$= 0.48, n = 58, 95% CI = 0.36–0.64). The overall annual survival of female lesser
312 prairie-chickens across all study sites was 0.37 (95% CI = 0.30–0.45).

313 Sites differed in landscape configuration and composition metrics (Table 1). Calculated
314 FRAGSTATS contagion metrics within the study sites indicated Northwest Kansas was
315 fragmented relative to the Clark County and Red Hills sites (Table 1). Fragmentation was
316 evident, as contagion values were lower and IJI values were greater for the Northwest site
317 relative to the other study sites. Although high variation among patches resulted in no statistical
318 difference, point estimates of mean patch size were 34 and 47.6% smaller for the Northwestern
319 site relative to the Clark County and Red Hills sites, respectively. All study sites were less
320 fragmented than their corresponding 25 and 50 km buffered areas, with larger mean patch sizes
321 and larger contagion values (Table 1).

322 The Northwest site was composed of less grassland and more cropland than the other
323 study sites (Table 1). It has been hypothesized CRP compensates for the loss of native grassland
324 in the northern portion of the lesser prairie-chicken range, but including CRP as grassland still
325 resulted in the Northwest site supporting 15.2 and 25.3% less grassland than Clark County or the
326 Red Hills. Additionally, all study sites had more grassland and less cropland in the delineated
327 study areas than the 25 km or 50 km buffers (Table 1).

328 HOME RANGE COMPOSITION AND CONFIGURATION

329 We used 170 total bird-years to estimate relationships among weekly survival of lesser
330 prairie-chickens and home-range scale habitat configuration and composition. Home range size
331 was not correlated with the total number of points used to calculate the MCP (r = 0.27) and
332 neither home range size nor the number of points used to calculate the MCPs were correlated
333 with configuration metrics within home ranges. The average annual MCP home range size was

3749.43 ha (SE = 780.02). The IJI was negatively correlated with patch richness within home ranges (r = –0.52); therefore, we only included patch richness as an individual covariate in survival models, as contagion could still be used to assess patch isolation. The sample of individuals for which survival was calculated included 96 mortality events. Only two models had a $w_i > 0$, Site × Patch Richness ($w_i = 0.85$, $AIC_c = 917.54$) and Site + Patch Richness ($w_i = 0.15$, $AIC_c = 920.96$). The configuration metric model supported by the data was Site × Patch Richness, as Site + Patch Richness had a $\Delta AICc > 2$. For all sites there was a significant trend of increasing survival as patch richness within home ranges increased ($\beta = 1.17$, 95% CI = 0.64–1.69; Fig. 3).

The composition metrics (% crop, % grassland, and % CRP) were all correlated, and therefore were not combined in models. There were two top-ranked models in the home-range composition model set (Table 4). Top-ranked models were Site + % $Crop^2$ and Site + % $Grassland^2$ models. Slope estimates for both models were significant for the linear terms ($\beta_{crop} = 0.079$, 95% CI = 0.034–0.13 and $\beta_{grass} = 0.085$, 95% CI = 0.041–0.13, respectively) and the quadratic terms ($\beta_{crop\text{^}2} = -0.0013$, 95% CI = -0.002–-0.00025 and $\beta_{grass\text{^}2} = -0.00074$, 95% CI = -0.0011–-0.00039, respectively) indicated a peak in weekly survival when proportion of crop within a lesser prairie-chicken's home range was 31.3% and proportion of grassland within a lesser prairie-chicken's home range was 57% (Fig. 4).

ANDERSEN-GILL

Using one encounter per day for each bird resulted in 18,063 encounters from 189 total bird years with 96 total mortality events. The model best supported by these data was Site + Distance to fence (Table 5). Across all Kansas study sites, mortality risk for female lesser prairie-chickens increased as distance to fence decreased (Fig. 5). Regression coefficients in our

357 model indicate a greater magnitude of risk relative to decreased distance from fences for birds in
358 Northwest Kansas (mortality risk = 1.15, SE = 0.38) compared to Red Hills and Clark County
359 (Fig. 5).

360 ## DISCUSSION

361 We investigated effects of landscape composition and configuration on annual survival of female
362 lesser prairie-chickens in Kansas. We were able to identify habitat composition (crop = 31%,
363 grassland = 57%) amounts within home ranges to maximize weekly survival and determined that
364 home ranges with greater patch richness had a positive effect on survival. Annual survival varied
365 distinctly among our study sites, and we note the three sites also differed markedly in their
366 landscape composition, suggesting that landscape composition influences survival. Increased
367 survival for sites with more grassland cover indicates that a minimum threshold grassland area is
368 needed to support a lesser prairie-chicken population, between the levels seen in Northwest,
369 Kansas and Clark County (grassland composition 54 to 76%, respectively). Finally, we found
370 that mortality risk for lesser prairie-chickens were greatest in Northwest Kansas and increased as
371 distance to fences decreased for all sites.

372 Results from the individual-level (*i.e.*, home range) analysis were inconclusive in
373 showing that configuration of home ranges have an effect on survival rates. It is possible that
374 lesser prairie-chickens are already selecting areas for their home range within the range of
375 tolerable fragmentation, which we would be unable to detect with survival models, suggesting
376 lesser prairie-chickens perceive landscape factors outside of their home range. Alternatively, we
377 found that proportion of cropland (30%) and grassland (50–70%) within home ranges maximizes
378 weekly survival. These results add a survival-based mechanism to past studies that identified
379 occupied lesser prairie-chicken habitat occurred below a threshold of 37% cultivation and a more

recent study indicating that abundance and resiliency of lesser prairie-chickens decreased after reaching a threshold of 9.6% cropland (Crawford and Bolen, 1976; Ross *et al.*, 2016a).

We also found a positive significant relationship with an increase in survival corresponding with an increase in patch richness within home ranges. Increasing survival relative to the number of patch types does not necessarily mean increased fragmentation increases survival, as contagion metrics did not explain survival. The patch types themselves could exist in small patches within the grassland matrix, providing additional cover and forage types; therefore, not significantly increasing the breakup of grassland (Campbell, 1972). Instead, this may indicate lesser prairie-chickens experience increased survival when they have a variety of available landcover options within their home range. This relationship is intuitive, as spatial heterogeneity benefits lesser prairie-chickens and other grassland birds, because they require different landscape types throughout different life stages (Fuhlendorf and Engle, 2001; Sandercock *et al.*, 2014). Selection for heterogeneity also extends to finer scales, as lesser prairie-chickens select for larger livestock pastures that exhibit greater structural heterogeneity (Kraft, 2016). Effects of habitat loss have been shown to be greater than effects of fragmentation for species abundance, species persistence, and reproduction (Andrén, 1994; Fahrig, 2003). A single female lesser prairie-chicken can require thousands of hectares of space during her annual cycle, most of which should be grasslands (Robinson *et al.*, 2017). Therefore, our data suggests lesser prairie-chickens may exhibit enough mobility to navigate among the various patches to find the requisite types of grassland for distinct life stages (*i.e.*, nesting, brooding, foraging, Hagen *et al.*, 2009).

Our survival estimates in Northwest Kansas were lower than any other published estimates of annual lesser prairie-chicken survival, which range from 0.31 to 0.59, although estimates from Red Hills and Clark County sites fall within the published range (Jamison, 2000;

Hagen *et al.*, 2007; Lyons *et al.*, 2009; Haukos and Zavaleta, 2016). Differences among the study sites, with the Northwest site being more fragmented at the patch and cell level and also comprised of less grassland, were evident at the study-site scale and within 25 km and 50 km buffered landscapes. While differences among sites in proportion of landcover type may not necessarily mean habitat loss in all landscapes, the Southern Great Plains region was nearly all grass or shrub-dominated prairie before the arrival of European settlers and onset of agriculture (Samson and Knopf, 1994). One of our most pronounced findings was that all of the study sites, which were chosen due to their recognized densities of lesser prairie-chickens, were less fragmented and comprised of more grassland than the surrounding landscape out to a 50 km buffer. This suggests aggressive restoration efforts may be necessary to restore grassland at broader scales and reduce fragmentation to increase the probability of lesser prairie-chicken survival within their occupied range.

The effect of distance to anthropogenic features on annual survival indicated the closer an individual was to a fence, the greater risk of mortality, and the risk varied regionally. Fence collision risk has been shown to be significant in Oklahoma (Wolfe *et al.*, 2007). However, increased mortality risk relative to fences in our study was unlikely to be attributed to collision mortality as in a concurrent study Robinson *et al.* (2016) reported evidence for only 1 collision/187 km of fence surveyed despite walking >2800 km of fences and documenting 1 mortality for 12,706 documented fence crossings by transmittered lesser prairie-chickens. Instead of collision risk, the increased mortality risk in relation to fences in Kansas could be due to a relationship with increasing predator densities at patch edges. Fences are frequently used as perches by raptors, one of the most common lesser prairie-chicken predators (Hagen *et al.*, 2007; Behney *et al.*, 2012; Boal, 2016). Fences also serve as corridors for mammalian predators, such

as coyotes (*Canis latrans*) or red fox (*Vulpes vulpes*), that are known predators of grassland birds. Increase of predation risk is especially relevant in working grasslands where two-track roads tend to coincide with fences, which can act as mammalian movement corridors (Bradley and Fagre, 1988). Our analysis indicated distance to powerline, oil well, or road had little influence on lesser prairie-chicken mortality risk, contrary to Hovick *et al*. (2014) reporting these anthropogenic features negatively affected survival and lek persistence for other grouse species. Lesser and greater prairie-chickens (*Tympanuchus cupido*) have already been shown to exhibit avoidance behavior of anthropogenic features such as power lines (Hagen *et al*., 2011), and wind turbines (Winder *et al.*, 2014a), so if avoidance has already occurred, detection of an effect on survival may be difficult.

Combining evidence from all three sets of survival estimation, lesser prairie-chickens in Northwestern Kansas are likely to experience lower survival in the long-term relative to the other study sites in Kansas, due to greater mortality risk. The percentage of grassland in Northwest Kansas (54%) may be near the threshold for persistence of lesser prairie-chickens. Prior to the establishment of the CRP in Kansas, lesser prairie-chickens were not detected in Northwestern Kansas (Rodgers, 2016). Properties enrolled in the CRP generally replaced cropland, as prior to CRP many landscapes exceeded the cropland threshold for persistence of lesser prairie-chickens. Grasses in CRP grasslands also contribute structural heterogeneity to the short-grass prairie landscape (Kraft, 2016; Spencer *et al.*, 2017). Without continued support and enrollment of land into CRP, the landscape currently supporting lesser prairie-chickens in Northwestern Kansas could easily dip below the threshold level of grassland and negatively affect annual survival and population growth rates.

Although we were able to identify a home range landcover composition that increased annual survival, the optimum cropland composition was exceeded within the Northwest study site and 25 km and 50 km buffers. Therefore, it is less likely for birds to have the ability to place their home ranges in areas to reach this optimum composition in the Northwest population, which could have contributed to the relatively low annual survival. Furthermore, our conclusions are based on a landcover layer that does not distinguish grassland structure appropriate for lesser prairie-chickens (*i.e.*, mixed-grass prairie compared to short-grass prairie: Spencer *et al.*, 2017). We may have overestimated the amount of grassland available for lesser prairie-chickens in the western, more arid, portion of the species range by including short-grass prairie, where grassland management can leave grassland unsuitable for lesser prairie-chickens (Hagen *et al.*, 2004). Consideration of available grassland structure and reduced grassland area at buffers surrounding our study areas could lead to less available habitat within these ecoregions than we presumed, such that if birds disperse from the immediate study area, they would have little chance of finding available habitat resulting in an increased likelihood of succumbing to mortality (Earl *et al.*, 2016, D. Haukos, unpubl. Data).

Our study was partially conducted during and following a period of severe drought (2012 and 2013), which has been linked to lesser prairie-chicken declines (Ross *et al.*, 2016b). The drought could have depressed survival rates if structure of residual vegetation was insufficient to provide concealment from predators (Ross *et al.*, 2016b). Across all sites and years, the majority of mortality events occurred during the nesting season, before the growing season for warm-season grasses (Plumb, 2015; Robinson, 2015). The lack of residual vegetation during drought could have left female lesser prairie-chickens at all sites more exposed on their nests (Hagen and Giesen, 2005; Grisham *et al.*, 2016a), but the northwest portion of the lesser prairie-chicken

range in Kansas is more arid than the south-central sites, so the effect of drought could have exacerbated mortality and further explain lower survival in this region during our study (Robinson *et al.*, 2017). Additionally, the increase of survival with an increasing number of patch types could link to drought, as lesser prairie-chickens may seek out CRP for the increased cover (Spencer *et al.*, 2017) and cropland for foraging opportunities (Campbell, 1972).

Given our results, managers interested in benefiting lesser prairie-chicken populations and increasing their resiliency to intensive drought could maintain grassland within the core occupied lesser prairie-chicken range and restore croplands adjacent to grasslands. Spatial heterogeneity of conserved grassland would increase occupancy and available habitat for required life stages (Hagen *et al.*, 2009, 2016). Additionally, to increase occupied range of the lesser prairie-chicken, the amount of grassland in landscapes outside of the areas where lesser prairie-chickens currently persist needs to be increased to surpass the 50–70% threshold, within an average lesser prairie-chicken home range, to improve survival. Dispersal may be facilitated by restoring grassland close to existing lesser prairie-chicken populations to increase the probability of range expansion (Earl *et al.*, 2016). If grasslands are reduced below the threshold of landscape composition required for lesser prairie-chickens, we could see declines in adult female survivorship. Increased CRP enrollment may supplement native grassland, especially within the short-grass prairie (Hagen *et al.*, 2016), and targeted enrollment should occur close to existing lesser prairie-chicken populations and in close proximity to grassland to increase the likelihood of population persistence. Future research would benefit by investigating landscape connectivity and the ability of birds to disperse though different landscape configurations to prioritize areas for grassland conservation and management.

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TABLE 1.–Composition of grassland, cropland, and Conservation Reserve Program (CRP) and FRAGSTATS metrics calculated within sites for comparison of annual survival of female lesser prairie-chickens in Kansas at spatial scale of study sites, study site and surrounding 25 km radius, and study site and surrounding 50-km radius during 2013–2015

		Composition			Configuration		
Site	Landscape	%Grassland	%Crop	%CRP	Mean Patch Size (SE; ha)	Contagion	IJI[1]
Northwest	Study Site	54.0	36.0	7.4	33.29 (8.84)	61.5	66.5
	25 km Buffer	51.8	38.8	6.7	32.27 (8.66)	61.4	65.7
	50 km Buffer	40.7	51.4	4.8	27.22 (4.26)	61.6	61.7
Clark	Study Site	76.6	14.2	5.5	50.39 (23.34)	69.5	58.2
	25 km Buffer	74.2	16.4	6.0	42.99 (16.56)	68.0	61.8
	50 km Buffer	62.5	27.3	7.1	34.75 (9.50)	62.9	66.8
Red Hills	Study Site	86.7	8.9	2.2	63.49 (45.45)	79.3	52.4
	25 km Buffer	73.8	18.3	5.6	44.22 (22.33)	69.3	66.5
	50 km Buffer	60.4	31.4	5.7	35.12 (10.03)	63.9	66.1

[1]Interspersion/Juxtaposition Index

TABLE 2.– Total available lesser prairie-chicken locations from three Kansas study sites collected using satellite transmitters (SAT-PTT) and very-high-frequency (VHF) transmitters used to calculate minimum convex polygons during 2013–2015. Reported means are the mean of number of points per bird used to calculate the MCP.

Site	SAT-PTT			VHF		
	Number of Birds	Total Number of Points	Mean Points Per Bird (SE)	Number of Birds	Total Number of Points	Mean Points Per Bird (SE)
Clark County	17	30,497	1,793 (246)	7	503	71 (20)
Northwest	58	78,379	1,351 (149)	36	1,251	34 (5)
Red Hills	31	37,740	1,217 (165)	21	1,228	58 (10)

TABLE 3.–Comparison of models in Program MARK used to explain variation in annual survival of female lesser prairie-chickens in Kansas for 2013–2014 and 2014–2015. Data from three sites were included in these models; Clark County, Red Hills, and Northwest

Model	K*	Deviance	ΔAIC_c	w_i*
Site	3	1029.09	0.00	0.59
Site + Year	4	1029.08	2.00	0.22
Site * Year	6	1027.70	2.62	0.16
Constant	1	96.89	6.12	0.03
Year	2	1036.59	7.50	0.01

*K = Number of parameters, w_i = Model weight,

AICc of top-ranked model = 1033.09

TABLE 4.–Comparison of models in Program MARK used to explain variation in landscape composition on survival of female lesser prairie-chickens in Kansas during 2013–2014 and 2014–2015. Model ranking based on Akaike Information Criterion corrected for small sample size (AIC_c) for 19 models, including a null model. Site models considered three study sites – Northwest, Kansas, Red Hills, and Clark County, Kansas. Models with no support ($w_i = 0$) were not included in these results

Model	K*	Deviance	ΔAIC_c	w_i*
Site + %Crop^2	5	920.64	0	0.36
Site + %Grass^2	5	920.80	0.15	0.33
Site * %Crop^2	9	915.56	2.95	0.08
Site * %Grass^2	9	917.61	2.99	0.08
Site * %Crop	6	921.76	3.12	0.08
Site + %Crop	4	925.96	3.32	0.07

*K = Number of parameters, w_i = Akaike model weight, AIC_c = 960.36 for the best fit model

737 TABLE 5.–Model ranking for Andersen-Gill models, based on Akaike Information Criterion
738 corrected for small sample size (AIC_c) for 26 models, including a null model, determining the
739 effect of distance to anthropogenic features and landcover type (grassland, cropland, and CRP)
740 on survival of lesser prairie-chickens in Kansas during 2013–2015. Models with no support (w_i =
741 0) were not included in these results.

Model	K*	Deviance	ΔAICc	w_i*
Site + Fence	3	784.44	0	0.71
Site * Fence	5	782.52	2.07	0.25
Site + Lek	3	792.44	7.99	0.01
Site + Oil	3	794.16	9.72	0.01

*K = Number of parameters; AICc = 790.45 for the best fit model; w_i = Akaike model weight

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FIG. 1.–Study sites in Kansas used to test the effect of landscape fragmentation on survival of female lesser prairie-chickens during 2013–2015. The underlying gray region represents the current estimated lesser prairie-chicken range within Kansas. Polygons indicate our Northwest Kansas study sites in Gove and Logan counties, our Red Hills study site in Kiowa and Comanche counties, and our Clark site in Clark County, Kansas

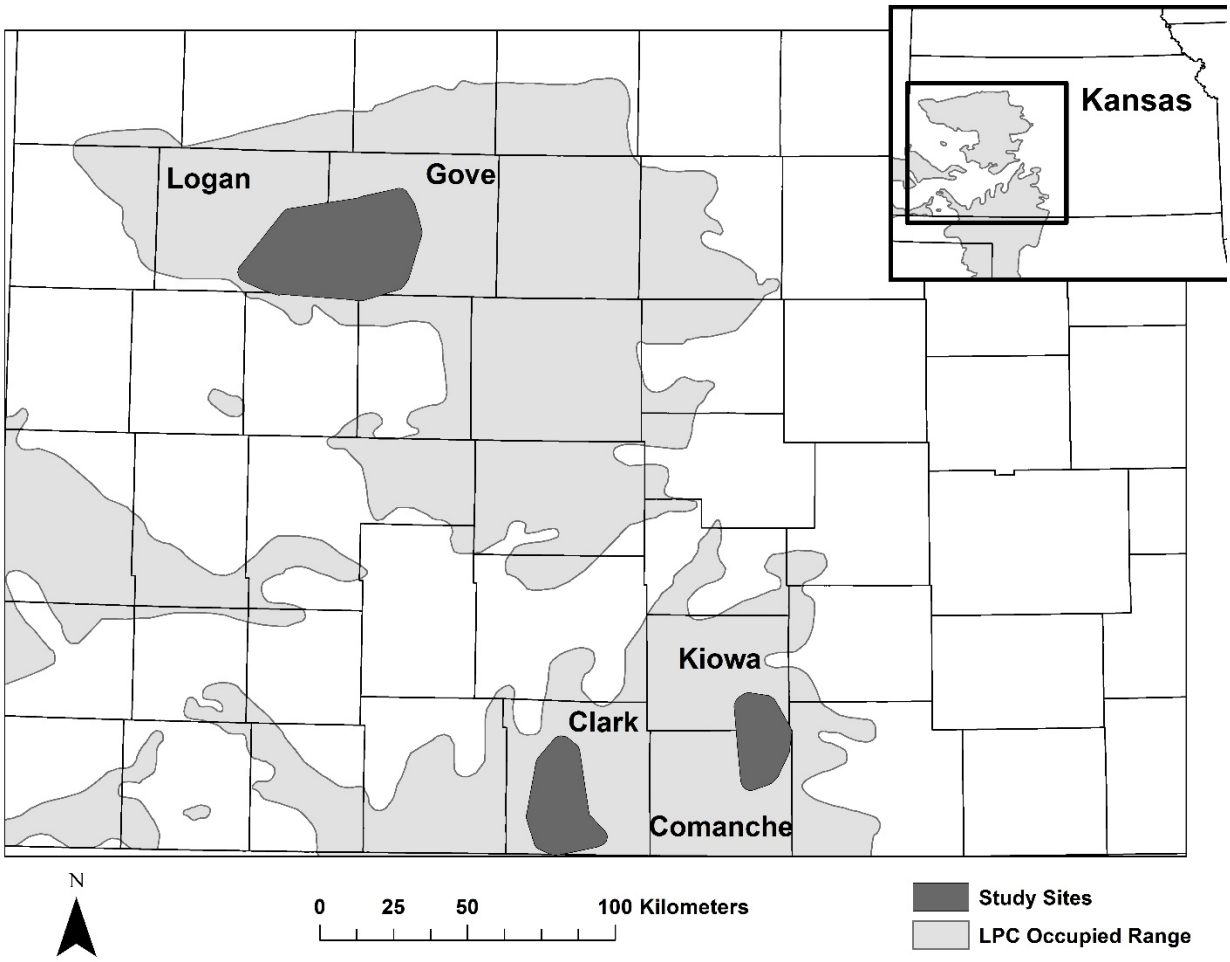
FIG. 2.–Landscape composition of study sites from Northwestern Kansas (Gove and Logan counties; top), Clark (Clark County, Kansas; center), and Red Hills (Kiowa and Comanche counties; bottom), illustrating that study sites have different proportions of landcover types, which differed from the surrounding landscape and represented as a 50 km buffer from the centroid of the study site

FIG. 3–Functional relationships from Program MARK for weekly survival of lesser prairie-chickens versus patch richness within individual home ranges in Kansas during 2013–2015. Patch richness is the number of patch types that occurred in each individual home range

FIG. 4–Functional relationships from Program MARK for weekly survival of lesser prairie-chickens versus percent crop (**A**) and percent grassland (**B**) within individual home ranges during 2013-2015 for three sites in Kansas

FIG. 5–Predicted mortality risk of female lesser prairie-chickens for distance to fence from Andersen-Gill models for continuous encounter covariates during 2013–2015. Site + distance to fence (m) predicted curve, with three different study sites in Kansas (Clark County, Red Hills,

and Northwest). Predicted curves only represent mortality risk for distance to fence that we located mortalities. Mortality risk from this model indicate that lesser prairie-chickens in Northwest Kansas experience greater risk (mortality risk at distance 0 = 2.49, 95% CI = 1.88–3.09) in relation to fences than lesser prairie-chicken in the Red Hills (mortality risk at distance 0 = 1.32, 95% CI = 0.78–1.86) and Clark County (mortality risk at distance 0 = 0.79, 95% CI = 0.20–1.37) study sites



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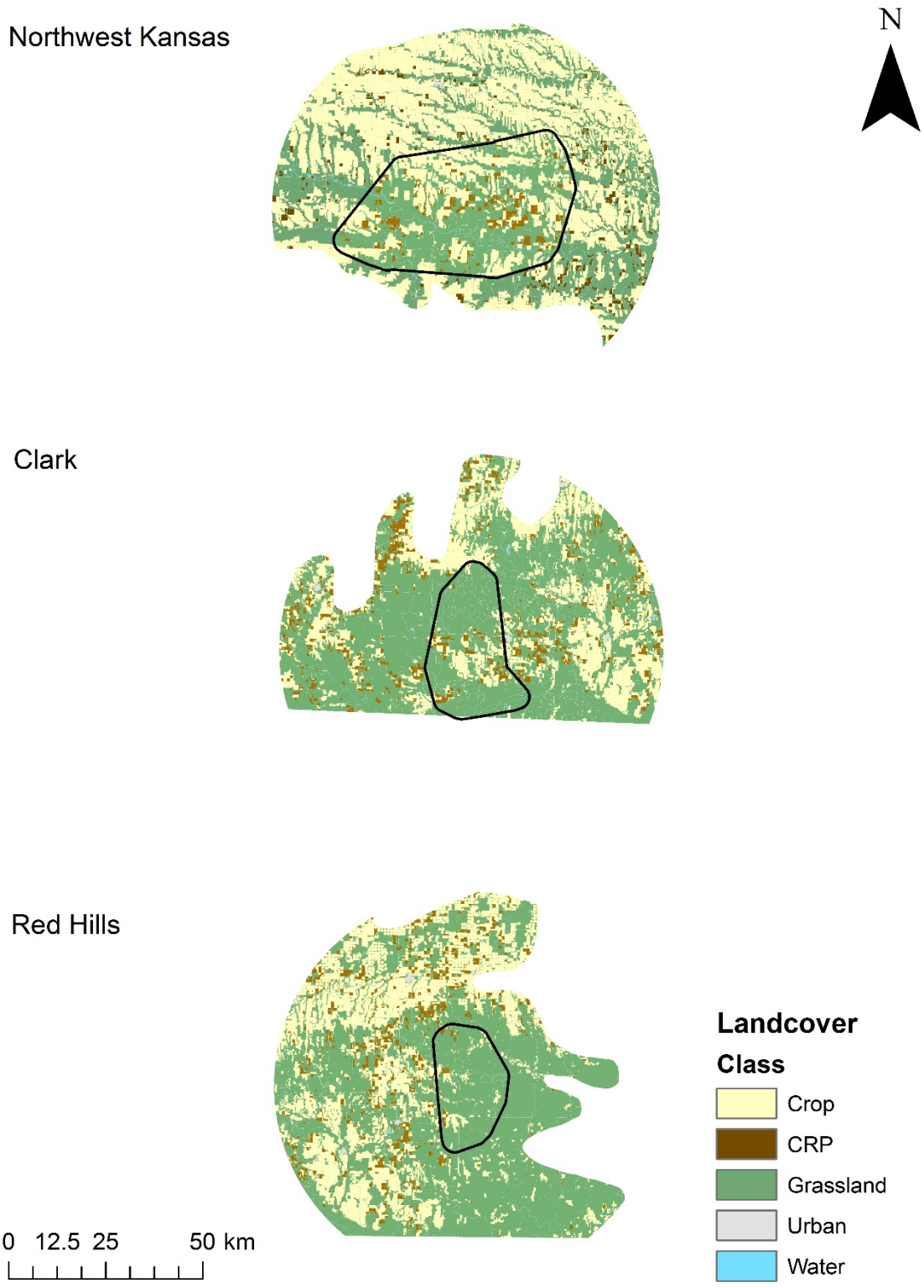
777 Fig. 1


Northwest Kansas
N
Clark
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0 12.5 25 50 km
Landcover
Class
Crop
CRP
Grassland
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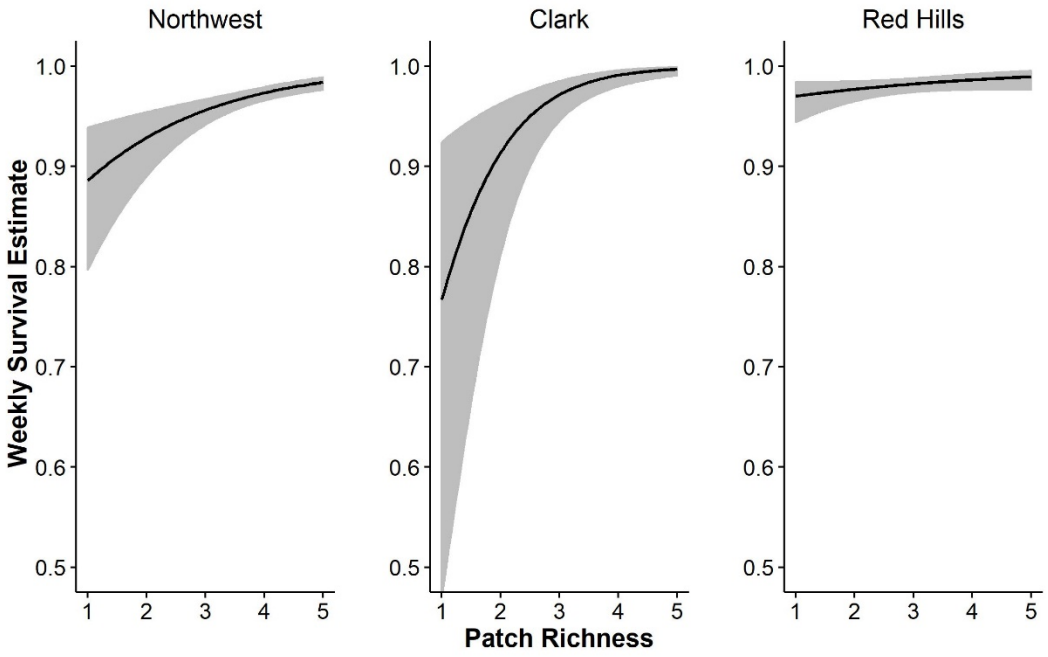
779 Fig. 2



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782 Fig. 3

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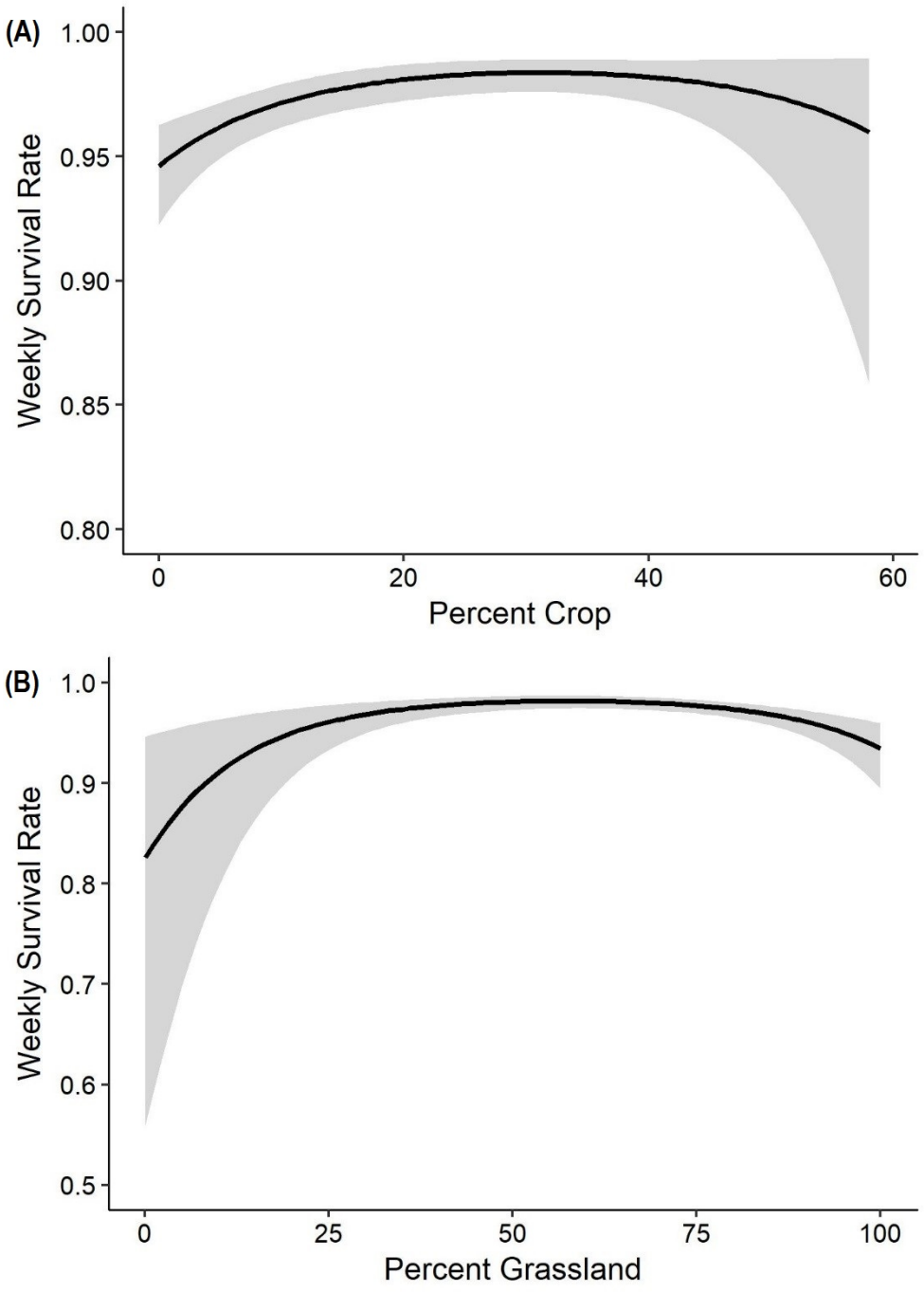

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786 Fig. 4

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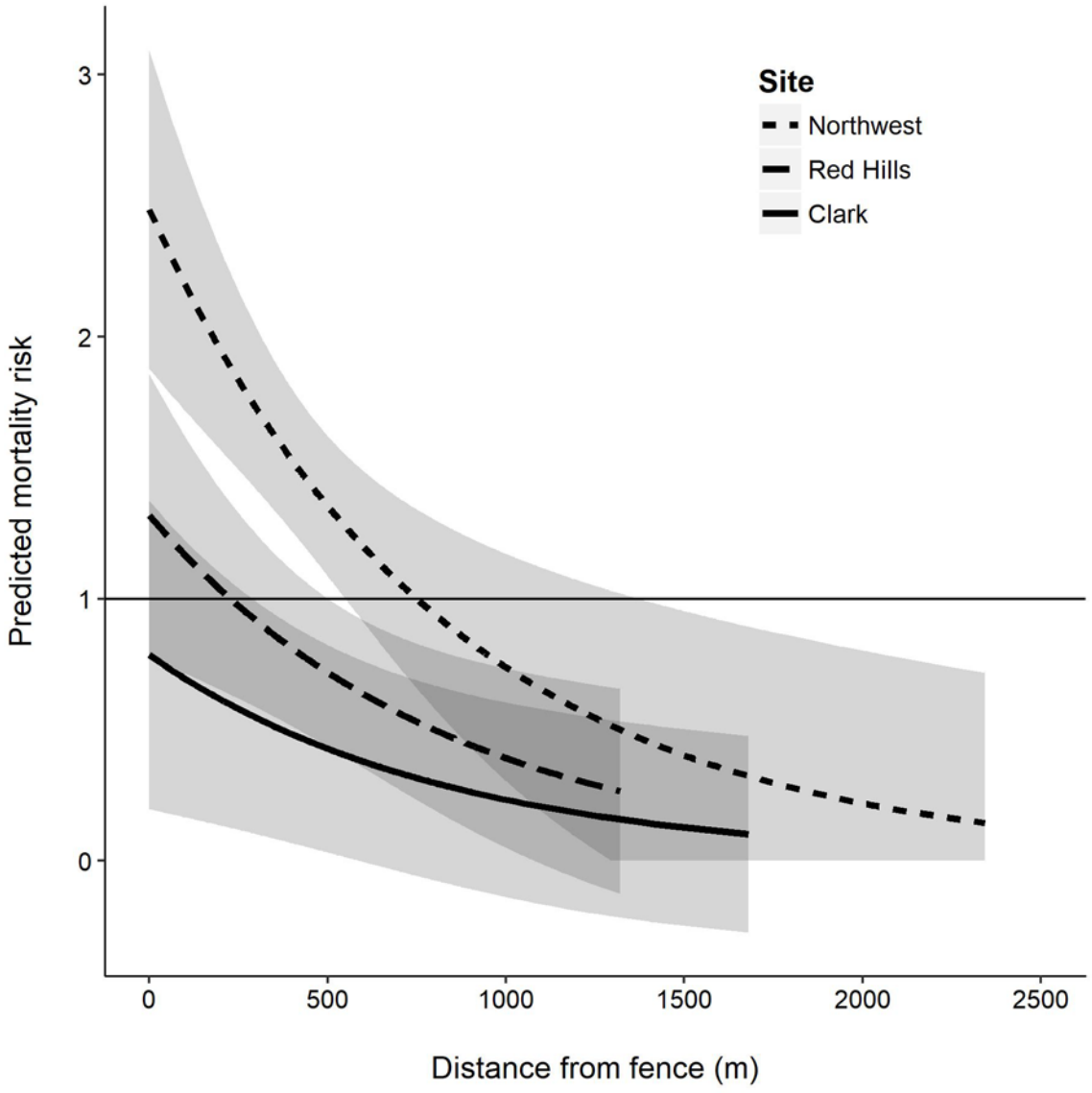

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790 Fig. 5

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