

LANDSCAPE ECOLOGY, SURVIVAL AND SPACE USE OF
LESSER PRAIRIE-CHICKENS

by

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Abstract

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) has experienced range-wide population declines and range contraction since European settlement. Due to ongoing declines, lesser prairie-chickens were listed as threatened under the Endangered Species Act in 2014; however, uncertainty regarding the legal status of the species has developed following a judicial decision to vacate the listing in September 2015. Regardless, new research is required for conservation planning, especially for understudied portions and temporal periods of the occupied range. I evaluated nonbreeding lesser prairie-chicken survival using known-fate models, and tested for the influence of environmental, landscape and predator effects on weekly survival. I estimated nonbreeding home-range size using fixed kernel density estimators and Brownian Bridge movement models for VHF and Satellite tagged lesser prairie-chickens, and measured habitat use during the 6-month nonbreeding period (16 September – 14 March). I also determined the influence of lek location on space use intensity within home ranges using resource utilization functions. Female survival was high (0.75, SE = 0.05) and consistent across nonbreeding seasons, but not explainable by selected variables. Mean home range size for birds with GPS transmitters (955 ha, SE = 128.5) was 215% larger than for individuals with VHF transmitters (303 ha, SE = 24.1) and 136% greater during the 2014-2015 nonbreeding season than the 2013-2014 season. Males and females were tied to leks throughout the nonbreeding season, and this relationship was not variable across the months of the nonbreeding season. Proportions of habitat used differed among study sites, but temporal trends were not evident. Lesser prairie-chickens exhibited consistency among ecoregions for home-range, space use, and survival; however, with differing habitat use among regions, management should be on the regional scale.

Agriculture and energy development have caused fragmentation of the landscape where lesser prairie-chickens evolved. I used known fate survival models to test if landscape composition or configuration within sites caused survival to differ by site, as well as within home ranges to determine if functional relationships exist between weekly survival and landscape configuration or composition. I used Andersen-Gill models to test whether distance to anthropogenic features affected hazard rates. Differences in survival rates between sites, with survival rates 50% greater in Clark County, Kansas compared to Northwestern, Kansas, corresponded to differences in the amount of grassland habitat on the landscape, but study-site configuration was not measurably different. Increasing the number of patch types within home ranges increased survival, indicating positive effects of heterogeneity. In addition, as distance to fences decreased, lesser prairie-chickens experienced greater risk. Overall, further breakup of grassland landscapes that lesser prairie-chickens occupy should be avoided, to avoid habitat loss and fragmentation thresholds that could further affect survival rates. Additionally, fences should be removed or avoided around active leks.

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Chapter 1 - Nonbreeding Survival of Female Lesser Prairie-Chickens

Introduction

Demographic rates are a crucial piece of a larger puzzle required to target and prioritize management decisions for wildlife populations (Sandercock 2006). Although it is important to estimate population survival, fecundity, and size, these values can be used to develop more complex models that identify specific limiting vital rates to determine those life stages most critical for the increase in population numbers (Sandercock 2006). Identifying influential vital rates is especially important in the case of declining and spatially-limited species, such as the lesser prairie-chicken (*Tympanuchus pallidicinctus*). As an indicator species within a declining grassland ecosystem, conservation of lesser prairie-chicken populations will not only improve the status of the species, but also provide management tools to conserve western Great Plains grasslands for all dependent species.

Due to long-term declines of >90% from historical high counts, occupied range contractions (Taylor and Guthery 1980, Hagen et al. 2004) and a recent decline of >50% from 2012 to 2013 (McDonald et al. 2014), the lesser prairie-chicken was listed as a threatened species across its entire range in May 2014 (U.S. Fish and Wildlife Service 2014). However, the listing was vacated by a Texas federal judge in September of 2015, leaving the status of the lesser prairie-chicken uncertain (*Permian Basin Petroleum Association et al. v. Department of Interior, U.S. Fish and Wildlife Service*, [Case 7:14-cv-00050-RAJ, U.S. District Court, Western District of Texas, Midland-Odessa Division]). The species range is confined to the Southern Great Plains, including portions of Kansas, Colorado, Texas, New Mexico, and Oklahoma. Lesser prairie-chickens currently inhabit a fraction of their pre-settlement range (Taylor and Guthery 1980). The exact area of the pre-settlement range is unclear (Rodgers 2016), but

conversion and fragmentation of landscapes within their current estimated range is not (Samson and Knopf 1994, Coppedge et al. 2001). Due to extensive landscape fragmentation, lesser prairie-chicken populations occur as a metapopulation with isolated sub-populations delineated within defined spatially-distinct ecoregions among the five states. Kansas contains portions of three of the four ecoregions in which lesser prairie-chickens occur, supporting >60% of the range-wide population (VanPelt et al. 2013, McDonald et al. 2014). Ecoregions are defined by different spatial location, soil types, species composition, and vegetation structure. These differences beg the question, are there differences in survival between the ecoregions and how do we properly recommend management prescriptions for such a system?

Breeding season demographics have generally been the focus of past studies on lesser prairie-chickens, but few studies have specifically targeted the estimation of survival rates and other aspects of nonbreeding season ecology (see citations in Table 1.1). The lack of information about nonbreeding lesser prairie-chickens is especially true for the northern extent of the range. With a species that goes through distinct population boom and bust fluctuations in numbers, putatively due to drought periods and other large-scale environmental events, survival rates need to be measured across space and time to determine and predict the impacts of varying environmental conditions on population survival rates (Hagen et al. 2009, Grisham et al. 2013). Further, separating the influence of environmental conditions and habitat quality on survival rates is critically important for conservation planning.

Conditions experienced during the nonbreeding season may impact future reproductive potential of lesser prairie-chickens, as individuals in poor body condition entering the breeding season may be less physically fit to mate, incubate eggs and tend to chicks, leading to intermittent breeding. A low survival rate during the nonbreeding season would also impact the

overall number of individuals who are able to reproduce. Historically, unfortunately, having an adequate sample size for nonbreeding season studies has been problematic. Small nonbreeding sample size is primarily due to the main capture period being during the spring lekking season, requiring individuals to both survive, and transmitters to function for up to six months prior to data collection during the nonbreeding season. It is difficult to capture female lesser prairie-chickens during fall and winter due to their cryptic nature and secretive nature while not at leks. However, the nonbreeding season is possibly an important factor in their overall life-cycle.

Available estimates of female survival in nonbreeding season are consistently greater than breeding season survival rates. Of the five studies that have provided an estimate of nonbreeding survival, the lowest rate was 0.63 for six-months (Kukal 2010) and the highest rate was 0.83 for six-months (Pirius et al. 2013). There was a lack of consistency for the defined temporal duration of survival estimates among studies, which is important when extrapolating a daily or weekly survival estimate out to a larger period, so I standardized past estimates to 6-months (Table 1.1). Nonbreeding estimates for other species of prairie-grouse, namely greater prairie-chickens (*Tympanuchus cupido*) and greater-sage grouse (*Centrocercus urophasianus*), are equally understudied, with the few finding comparable survival rates to lesser prairie-chicken studies (Connely et. al 2004, Winder et al. 2014). Additionally, the drivers of nonbreeding season survival have not been investigated, but overwinter survival could possibly be related to vegetative conditions, predator abundance, and extreme weather conditions such as extreme low temperatures. To determine whether nonbreeding survival is influential for lesser prairie-chickens, relative to breeding season survival, a study between ecoregions with a consistent temporal extent and method is necessary.

Contemporary wildlife research allows for a variety of approaches to estimate survival rates using individually-marked animals. Known fate models are used when the encounter probability of an individual is 1.0 and timing of mortality can be determined, such as with telemetry data. The Kaplan-Meier model is one of the most frequently used known fate approaches (Kaplan and Meier 1958), which can be implemented in Program MARK (White and Burnham 1999) and Program R (R Core Team 2014). This method allows for right-censoring of individuals that are no longer able to be documented during defined encounter periods, as well as left-censoring when individuals are added to the sample in a staggered manner. The Kaplan-Meier model does not allow for the explicit use of covariates; thus, it is frequently paired with Cox Proportional Hazard models to determine the effect of covariates on survival and hazard rates (Pollock et al. 1989). Several assumptions must be met to proceed with a known-fate analysis. The sample of individuals, observational periods, and censoring occurrences need to be random, and marking methods cannot have adverse effects on survival rates (Winterstein et al. 2001). I used Very High-Frequency (VHF) bib-style radios and rump-mounted satellite platform transmitting terminal GPS (SAT-PTT) transmitters to monitor survival of individuals in this study. Hagen et al. (2006) determined that VHF radio-transmitters do not affect survival rates of male lesser prairie-chickens. The breeding season complement to this study found that overall survival rates were similar between individuals with VHF transmitters and those with SAT-PTT transmitters (Plumb 2015), but there is the potential for the nonbreeding season to exhibit different results due to vegetation, weather changes, and changes in bird behavior between the two periods.

As a portion of the lesser prairie-chicken life-cycle that is understudied, my objectives were 1) to identify whether nonbreeding survival is influential for lesser prairie-chickens,

relative to breeding season survival rates, 2) to assess temporal patterns of mortality across the nonbreeding season, and determine 3) if nonbreeding survival can be explained by environmental, landscape or predator effects, and 4) if there is a difference in survival rates between individuals marked with bib-style VHF transmitters and individuals marked with SAT-PTT transmitters. I estimated the six-month survival rates of female lesser prairie-chickens for two nonbreeding seasons (16th of September – 8th of March; 2013-2014 and 2014-2015), at three sites in Kansas. Additionally, I documented the pattern for mortality events of lesser prairie-chickens during the nonbreeding season. I hypothesized that survival would be greater for birds in the southern study sites versus the northern study site due to greater shrub availability and a milder climate. I hypothesized that lesser prairie-chicken survival will be lower during times of high raptor abundance, low temperatures will coincide with high mortality events, and lesser prairie-chickens that spent more of their time in areas with greater grass and forb cover, or in taller vegetation, will have higher survival rates. I hypothesized that the majority of predation will be by avian predators and periods of increased raptor abundance will have greater influence on lesser prairie-chicken mortality than temperature or vegetation characteristics. Last, I hypothesized that during both years of this study, nonbreeding season survival rates will be greater than the breeding season survival rates for the preceding season in all study sites.

Study Area

In northwestern Kansas, lesser prairie-chickens are found in the Short-Grass Prairie/Conservation Reserve Program (CRP) Mosaic Ecoregion (Van Pelt et al. 2013, McDonald et al. 2014). Presence of lesser prairie-chickens in this ecoregion are the result of a recent documentation north of the Arkansas River, which has been studied once prior (Bain 2002, Fields et al. 2006, Rodgers 2016). In south-central Kansas, lesser prairie-chickens are

found in the Mixed -Grass Prairie and Sand Sagebrush Prairie Ecoregions (Van Pelt et al. 2013, McDonald et al. 2014). Three study sites were located in these three ecoregions across the lesser prairie-chicken range in Kansas (Figure 1.1). The northwestern Kansas study site consisted of private lands in Gove and Logan counties; whereas, in south-central Kansas, there were two study sites on private lands in Kiowa, Comanche and Clark counties.

In northwest Kansas, the study site was 171,437 ha and located in Gove and Logan counties on private lands and the Smoky Valley Ranch, owned and managed by The Nature Conservancy. The primary land uses in this area were livestock grazing, energy extraction and both dryland and irrigated row-crop agriculture. This study area was in the Shortgrass Prairie/CRP Mosaic Ecoregion (Van Pelt et al. 2013, McDonald et al. 2014), with CRP grasslands and row-crop agriculture on silt-loam soils. Mixed-grass prairie plants and structure occurred with certain soils. Dominant vegetation in the region included blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsute*), buffalograss (*B. dactyloides*), little bluestem (*Schizachyrium scoparium*), sideoats grama (*B. curtipendula*), big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annuum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed (*Ambrosia psilostachya*; Lauer et al. 1999). Native grass species planted in CRP fields included little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indian grass (*Sorghastrum nutans*) (Fields 2004). The CRP fields were interseeded with forbs in the 1990s; and the seed mixture included white sweet clover (*Melilotus alba*), yellow sweet clover (*Melilotus officinalis*), Maximilian sunflower (*Helianthus maximiliani*), Illinois bundleflower, purple prairie clover (*Dalea*

purpurea), and prairie coneflower (*Ratibida columnifera*; Fields 2004). Wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), and corn (*Zea mays*) were the major crops in the region.

In south-central Kansas, the Red Hills study site was 49,111 ha and centered on private lands in Kiowa and Comanche counties within the Mixed-Grass Prairie Ecoregion (Van Pelt et al. 2013, McDonald et al. 2014). The Red Hills site consisted of mixed-grass prairie on loamy soils. Primary land uses for this area included livestock grazing and oil and gas extraction and exploration, with row-crop and dryland agriculture interspersed throughout the region. Dominant vegetation in south-central Kansas included little bluestem, blue grama, hairy grama, sideoats grama, buffalograss, sand dropseed (*Sporobolus cryptandrus*), Louisiana sagewort (*Artemisia ludoviciana*), western ragweed (*Ambrosia psilostachya*), sand sagebrush (*Artemisia filiafolia*), and eastern red cedar (*Juniperus virginiana*; Lauver et al. 1999).

The Clark County site within south-central Kansas was 71,209 ha and located at the Mixed-Grass Prairie Ecoregion and Sand Sagebrush Prairie Ecoregion boundary (McDonald et al. 2014). Land use was dominated by livestock grazing, oil and gas extraction, and row-crop agriculture. Dominant vegetation in the area included: little bluestem, sideoats grama, blue grama, hairy grama, big bluestem, alkali sacaton (*Sporobolous airoides*), invasive Russian thistle (*Salsola kali*), kochia (*Kochia scoparia*), annual sunflower (*Helianthus annuus*), and sand sagebrush. This study site also had large areas of alkali flats along drainages.

Methods

Capture

Lesser prairie-chickens were captured at leks in spring (March – May) during 2013 and 2014. Birds were trapped using walk-in drift traps, magnetic dropnets, and rope-trigger dropnets (Haukos et al. 1990, Silvy et al. 1990, Schroeder and Braun 1991). These capture methods do not decrease survival probabilities of individuals (Grisham et al. 2015). Captured individuals were

aged using the degree of spotting on the 9th and 10th primaries; second-year birds had spotting within 3.8 cm from the feather tip and after-second-year birds had spotting ≥ 3.8 cm from the tip (Copelin 1963). I also used the amount of wear of the feather tips as juvenile grouse do not molt those primaries until their second year, and thus, have more frayed feather tips (Copelin 1963). The sex of individuals was determined using tail feather color; females had barred tail feathers and male prairie-chickens had mainly black tail feathers (Copelin 1963).

Each individual was marked with individual color band combinations using size-4 color bands (Avinet, Dryden, New York, USA) and individually numbered butt-end aluminum bands (National Band and Tag Company, Newport, USA). Female lesser prairie-chickens were outfitted with either 12-15-g bib-style VHF transmitters (A3960, Advanced Telemetry System, Isanti, USA) or a rump-mounted 22-g Satellite Platform Transmitting Terminal (PTT) GPS transmitter (PTT-100, Microwave Telemetry, Columbia, USA). SAT-PTT transmitters were attached on the rump using leg harnesses made of Teflon[®] ribbon, and elastic at the front of the harness for flexibility (Bedrosian and Craighead 2010, Dzialak et al. 2011). All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee protocol (3241) and Kansas Department of Wildlife, Parks and Tourism scientific wildlife permits (SC-042-2013 and SC-079-2014).

Monitoring

Female lesser prairie-chickens outfitted with VHF transmitters were located via triangulation 3-4 times per week during the nonbreeding season (16 September – 14 March). Individuals were located using an Advanced Telemetry Systems Receiver (R4000 or R4500, Advanced Telemetry Systems, Isanti, USA) or a Communications Specialists Receiver (R-1000, Communications Specialists, Orange, USA). If individuals could no longer be located due to dispersal from the study site, attempts were made to locate birds using a fixed-wing Cessna

aircraft. If a mortality signal was obtained, homing was used to locate the bird and an attempt was made to determine fate.

Birds that were outfitted with a Satellite-PTT transmitter recorded up to eight GPS positions a day, with ± 18 m accuracy, during the nonbreeding season between the hours of 06:00 and 22:00. Points were uploaded to the Argos satellite system, and downloaded weekly for locations and mortality assessments. As soon as a bird was determined to have died based on the satellite data, I searched within a 50 m radius surrounding the point of mortality until the transmitter and carcass were located.

The specific cause of mortality was evaluated, if possible. If there were bite marks on the carcass or transmitter, or if the carcass was cached, the predator was identified as mammalian (Hagen et al. 2007). Potential mammalian predators include American badger (*Taxidea taxus*), coyote (*Canis latrans*), swift fox (*Vulpes velox*) and bobcat (*Lynx rufus*). If the carcass was decapitated, the breast muscle is removed, raptorial scat or pellets were found around the carcass, or there was evidence of feather plucking, the predator was identified as avian (Hagen et al. 2007). Raptor species observed during the nonbreeding season are swainson's hawk (*Buteo swainsoni*), northern harrier (*Circus cyaneus*), prairie falcon (*Falco mexicanus*), red-tailed hawk (*B. jamaicensis*), rough-legged hawk (*B. lagopus*), bald eagle (*Haliaeetus leucocephalus*), broad-winged hawk (*B. platypterus*), great-horned owl (*Bubo virginianus*), short-eared owl (*Asio flammeus*), and golden eagle (*Aquila chrysaetos*). Other evidence, such as feces, dens or burrows were used as evidence to identify cause of mortality. If cause of mortality was not identifiable by information at the carcass site, I classified it as unknown fate. If there was no evidence of mortality, such as with a possible dropped collar, I right-censored that individual.

Point Vegetation Surveys

Vegetation surveys were conducted at two randomly selected female lesser prairie-chicken point locations per week during the nonbreeding seasons of 2013-2014 and 2014-2015. I estimated the percent cover of litter, grass, forbs, and bare ground within percentile ranges using a 60 x 60 cm modified Daubenmire frame (Daubenmire 1959). Within the Daubenmire frame, I also measured tallest vegetation height (cm). Percent grass cover, percent forb cover, and tallest vegetation were averaged for each bird across the 6-month study period and each measure was used as a single individual covariate in Program MARK to represent the average vegetation that an individual was selecting throughout the season. If data were not collected for an individual for a season, such as if a bird left the study site or permission could not be obtained to access locations (7% of individuals), I used the average vegetation data for all of the birds within that study site as the individual covariate for that season (Mark Manual Citation).

Raptor Surveys

Weekly raptor surveys were conducted across all study sites starting in March of 2014 for an index of raptor abundance patterns, due to a concurrent research objective beginning the second year of this study (# raptors/transect). During the nonbreeding season, surveys were conducted 1-2 times a week. If two surveys were conducted in a given week, then the average value was used. Occasionally a raptor survey was missed entirely for a week, in which case I used the average for the weeks on either side of the missed week for the missing data.

Raptor surveys were conducted on a 16-km route, passing through portions of cropland, grassland, and CRP tracts. Routes were chosen systematically, to assure inclusion of all three landcover types on the transect. Three-minute point counts were conducted at 0.8-km intervals. Surveys were restricted to between 09:00 and 13:00 to standardize across study sites. Surveys were not conducted during days with rainfall. Detection of all raptors was recorded with the

number of individuals, estimated distance from the survey route, and whether the raptor was flying or perched. For the purposes of this analysis, I only used raptors likely to prey on lesser prairie-chickens based on size and past observations. These raptors included bald eagle, northern harrier, prairie falcon, rough legged-hawk, red-tailed hawk and ferruginous hawk.

Survival Analysis

Known-fate models were used in Program MARK (White and Burnham 1999) to test the factors of site, year, low temperatures, and raptor abundance as predictors for nonbreeding season survival of female lesser prairie-chickens. Survival was modeled on a weekly time-step for the six month nonbreeding season (September 16th – March 8th). Factors examined for this analysis were year, transmitter type, percent grass and forb cover, average vegetation height, differences among study sites and differences between years. Starting date of weeks were held consistent between the two nonbreeding seasons.

As raptor abundance was not collected the first year of the study, I tested this effect in a separate model set for the 2014-2015 nonbreeding season. Temperature data were retrieved from the Kansas State University Weather Data Library (KState Research and Extension 2014). As covariates in survival models, I used the average temperature lows within a week and the minimum low temperature within each week. Weather stations were in Quinter (146637), Coldwater (141704), and Ashland (140365), Kansas, for the northwestern, Red Hills and Clark County field sites, respectively. I developed 12 potential models for both years combined, and 11 potential models for just the second year of the study (2014-2015). Models were ranked using the Akaike Information Criterion for small sample sizes (AICc; Burnham and Anderson 2002). Models with a $\Delta AICc \leq 2$ were considered competing models (Burnham and Anderson 2002). The average weekly survival rate was raised to the 25th power to extrapolate over the 25-week

nonbreeding season, and the delta method was used to determine the standard error for S_{week} ²⁵ (Powell 2007).

Kaplan-Meier functions were analyzed with the survival package (Therneau 2014) in Program R version 3.1.1 (R Core Team 2014). Cox proportional hazard functions were used to test for differences between transmitter types, age at capture, and/or among sites to determine if these effects had a significant impact on nonbreeding survival. Model diagnostics were tested with the `cox.zph` function to determine if the data met the assumptions of proportional hazards (Fox 2002). Log-rank tests were used to determine if there was a significant difference between transmitter type, site, year or age. Models were ranked using AICc, and models with $\Delta\text{AICc} \leq 2$ were considered competing models. Survival estimates with overlapping confidence intervals were considered not statistically different. I examined weekly patterns of mortality using hazard functions in Program R with the `gss` package. These functions fit smoothing splines to weekly survival data, to identify weeks in which there is a greater instantaneous risk to female lesser prairie-chickens (DelGiudice et al. 2006, Gu 2014). A smoothing factor of 1.2 was used to display the hazard functions.

Results

A total of 88 individual female lesser prairie-chicken bird-years survived the 2013 and 2014 breeding seasons prior to being included as part of the nonbreeding season; 6 individuals survived both breeding seasons ($n = 94$ bird-years; Table 1.2). Of these, 52 individuals were outfitted with Satellite-PTT transmitters, and 42 individuals were outfitted with VHF transmitters (Table 1.2). A total of 22 mortalities were recorded during the nonbreeding season, across both years of the study. Of these 22 mortalities, four were due to avian predation (18%), eight to mammalian predation (36%) and 10 (46%) were unknown events. Mortality events were

relatively evenly spaced across the nonbreeding season (0-2 mortalities/week) except for a single week in 2014 (November 17 – 23) with three mortality events (Figure 1.2).

There was no single dominant model for the Program MARK analysis testing the influence of temporal and vegetative covariates on survival across the nonbreeding season (Table 1.3). Instead, there were eight competing models with a ΔAICc of ≤ 2 . Top models included linear trends in percent grass ($\beta = -0.03, \text{SE} = 0.22, 95\% \text{ CI} = -0.073, 0.012$), minimum low temperature ($\beta = 1.97, \text{SE} = 1.39, 95\% \text{ CI} = -0.76, 4.70$), mean low temperatures ($\beta = 1.91, \text{SE} = 1.51, 95\% \text{ CI} = -1.05, 4.88$), and percent forb ($\beta = 0.15, \text{SE} = 0.26, 95\% \text{ CI} = -0.35, 0.066$). Other top models included quadratic trends in minimum ($\beta = -3.86, \text{SE} = 7.33, 95\% \text{ CI} = -18.23, 10.51$) and mean low temperatures ($\beta = -6.43, \text{SE} = 8.57, 95\% \text{ CI} = -23.23, 10.36$), as well as the constant model. Based on model weight, percent grass, minimum low temperature, mean low temperature and the null model all had almost double the weight of the other four top models (Table 1.3). None of the regression coefficients differed from zero, as the 95% confidence intervals of all beta estimates overlap zero. Thus, hypothesized functional relationships among vegetation covariates and survival did not explain variation in survival. Year was not included in a top ranking model for this set, and confidence intervals of estimates overlapped zero, so I did not separate out survival rates by year.

A model for differences in survival among the three sites was one of the top ranked models, but confidence intervals of survival rates overlapped among all study sites (Figure 1.3). Mean survival rates in the southern Kansas study sites (Red Hills: 0.83 and Clark County: 0.80) were 22.1% and 17.7% greater than northwestern Kansas (0.68) with both years combined (Figure 1.3).

The null model was used instead of model averaging to estimate nonbreeding survival because none of the tested variables in the models that ranked higher in this set were significant. This model represents the overall survival rate, for all years and sites, without taking into account any of the covariates, as none were significant. The null model resulted in an overall nonbreeding, 25-week survival estimate of 0.75 (95% CI = 0.66-0.84). This estimate represents the overall nonbreeding survival rate among the three field sites in Kansas.

Relative raptor abundance increased across the 25-week nonbreeding season from mid-September to mid-March (Figure 1.4). The most abundant species observed in all study sites were northern harriers (31%, 15% and 26% of observations for northwestern, Clark County and Red Hills, respectively), with red-tailed hawk being common in the south-central study sites (78% and 44% of observations for Clark County and Red Hills respectively), and rough-legged hawk being common in the northwestern site (12% of observations). Adding the results of raptor surveys to the 2014-2015 model set did not change model ranking or fit of the models; the slope of the linear trend did not differ from zero ($\beta = 0.52$, $SE = 1.72$; Table 1.4).

Model selection from the Kaplan-Meier survival analysis, used to test differences in survival between SAT-PTT and VHF marked individuals, indicated that there was a lack of support for a single model in this set (Table 1.5). The top three models (Transmitter, Transmitter + Year, Transmitter * Year) all had a $\Delta AICc \leq 2$ with a transmitter effect included, which was the only variable with a significant term in the model set ($Z = -2.31$, $P = 0.021$). The difference in survival rates between the two transmitters was only evident in the first year of the study, with a significantly higher survival rate for VHF individuals relative to SAT-PTT individuals (2013-2014; Figure 1.5). The second year of the study shows confidence intervals that overlapped

(Figure 1.5). Combining both years, confidence intervals for the transmitter type overlap for the cumulative survival function (Figure 1.6) and overall survival rates (Figure 1.5).

Estimated hazard rates were low (0.025 per week) across the 25-week nonbreeding season (Figure 1.7). However, there was a peak in instantaneous risk of mortality corresponding to week 10 in 2014 in which three mortalities were recorded. This week also corresponds to the first peak in relative raptor abundance from raptor surveys in 2014. I did not separate hazard rates by year, as this was not a significant term in the Kaplan-Meier survival model.

Discussion

Yearly variation in weather and subsequent vegetative response are hypothesized to be the main drivers of prairie-grouse vital rates (Flanders-Wanner et al. 2004). I used seasonal survival rates and individual average vegetation characteristics to test this hypothesis for the nonbreeding season. From this analysis, there were no clear trends or factors in nonbreeding season survival of female lesser prairie-chickens for any of the variables that I selected, including year, weather, vegetation characteristics, or relative predator abundance. In addition, there was no temporal trend across the nonbreeding season survival for female lesser prairie-chickens, suggesting that mortality was a random event during the nonbreeding season. With mortality during the nonbreeding season acting as a random event, it is likely not additively contributing to population declines, and conservation goals cannot be set to increase this rate and subsequently effect population growth.

My overall estimate of nonbreeding survival was within the range of past studies of nonbreeding lesser prairie-chickens. The study most comparable to mine is Hagen et al. (2007), because his sample was comprised of females and conducted in Kansas in a region west and south of my study sites. Their estimate of survival was 0.77 for November to February, and

converted to a six-month rate, the estimate is 0.68, which is lower than my nonbreeding estimate of 0.75, but within the range of survival estimates spanned by my three sites. My estimate was also in a similar range to the remainder of nonbreeding lesser prairie-chicken survival studies where the range of survival estimates was from 0.63 to 0.77 (Jamison 2000, Lyons et al. 2009, Kukul 2010, Pirius et al. 2013; Table 1.1). The evidence for a consistent overwinter survival across the lesser prairie-chicken range suggests that this period is not contributing to the long-term population decline or differences in persistence among populations across the species range.

The 6-month survival estimates did not differ between the two years across all study sites. I hypothesized an increase in survival from the first year of the study (2013-2014) to the second year of the study (2014-2015) because of the alleviation of extreme drought that occurred across much of the Southern Great Plains from 2011-2013, including the 2013 breeding season. Decreased precipitation, coupled with increased grazing pressure, should have left less residual vegetation for lesser prairie-chicken cover during the 2013-2014 nonbreeding season compared to 2014-2015 season. During 2014, breeding season rain started in late May in all study sites and continued consistently across the remainder of the growing season, resulting in an increase in residual vegetation for the 2014-2015 nonbreeding season across all study sites in Kansas (S. Robinson unpubl. data). However, with differences not evident in survival between these years, nonbreeding survival does not appear to be related to precipitation characteristics of the preceding breeding season.

Additionally, survival rates did not statistically differ among study sites. However, a lower mean survival was evident for northwestern Kansas compared to the south-central sites. Several differences exist between these sites that have the possibility of explaining this difference. The southern study sites had a mixed-grass vegetation community, which includes an

increased shrub cover relative to the northwest Kansas study site. Shrubs provide increased cover for improved thermoregulation and predator avoidance during the nonbreeding period (Patten et al. 2005a). The southern study sites were also centered on more intact grasslands. Intact grasslands with low fence, road, and power-line density should correspond to less potential hazards for prairie-chickens. Power lines, fences, and roads act as areas for avian perching and predator corridors; an absence of these could correspond to a decrease in mortality (Patten et al. 2005b). I would expect lesser prairie-chicken survival to be greater in areas with higher habitat quality and lower population density, but this research was conducted on some of the best remaining lesser prairie-chicken habitat in Kansas, which could explain why survival rates were not significantly different among populations.

My prediction that survival during the nonbreeding season would be greater than that for the breeding season for the preceding year was supported. The seasonal survival rates estimated for the breeding season (March 15-September 15) in 2013 and 2014 were 0.42 (95% CI = 0.31 – 0.52) and 0.48 (95% CI = 0.38 – 0.58), respectively (Plumb 2015). The estimates were 39 to 44% lower than the corresponding nonbreeding survival rate from this study. Reduced survival in the breeding season relative to the nonbreeding season is intuitive as female lesser prairie-chickens should have reduced predation risk during the nonbreeding season because they do not have to exert extra energy or risk exposure to visit leks, locate nesting sites, incubate eggs, or protect broods. Additionally, over the years of this study, no extreme weather events (blizzards or ice storms) occurred at my study sites, which could have additively increased mortality risk to lesser prairie-chickens.

The observed increase in hazard rate for the single week in the 2014-2015 nonbreeding season corresponded with the arrival of fall migrants in counts of raptors. However, I was unable

to determine whether avian mortality represented an overall greater proportion of mortality during any time period due to the difficulty of assigning cause-specific mortality resulting in assigning 46% of mortalities to unknown causes. One study within the lesser prairie-chicken range has documented an increased abundance of raptors during the nonbreeding season as well, concluding that the nonbreeding season had the greatest risk of predation from avian predators (Behney et al. 2012). However, the Behney et al. (2012) study occurred in the southern portion of the lesser prairie-chicken range. My study may not have detected this same trend, as in the northern portion of the range, some populations of raptors are only migratory. Additional years of raptor surveys should add more information to this analysis, as the raptors surveys did not begin until the second year of the study.

Hagen et al. (2006) found that a similar number of VHF transmitted and banded male lesser prairie-chickens returned to leks the next year, indicating that VHF transmitters do not have an effect survival of male lesser prairie-chickens. My analysis indicates that SAT-PTT individuals had a lower survival rate than VHF marked individuals in the 2013-2014 nonbreeding season. Plumb (2015) also found SAT-PTT individuals with a decreased survival rate relative to VHF individuals during a single breeding season, but there was no difference between transmitter types during other seasons or for his entire study. However, the estimated survival rates for SAT-PTT transmitted birds were within the bounds of past lesser prairie-chicken nonbreeding studies. The VHF survival rate from the first year of this study was 20% higher than past studies. This inflated survival rate was likely due to the censoring of many of the VHF marked individuals from the study due to transmitter failure or bird dispersal, although mortalities likely occurred. It is possible that the birds dispersing outside of tracking range are succumbing to greater mortality than the birds who remain in the study area. We can record

mortalities with the SAT-PTT tags, but not with the VHF transmitters during long distance mortalities. Potentially missing mortalities of censored birds would have increased the survival rate for VHF lesser prairie-chickens, as those individuals would have been censored at time of dispersal or transmitter failure. It is likely that some of these individuals died, but they are recorded as alive within the data set. With SAT-PTT individuals, I was able to document all mortalities, so this survival rate is likely to be more representative than the high VHF estimate. Further, the same attachment method, with transmitters of proportional weight, survival estimates of SAT-PTT and VHF transmitters were tested on greater sage-grouse and no difference was detected between survival rates of the two transmitters (Bedrosian and Craighead 2010). Thus, although I found differences in survival rates for SAT-PTT marked individuals and VHF marked between years, over the course of the study, survival estimates were similar between transmitter types and to previous studies.

Survival rates during the nonbreeding season are also understudied in other prairie-grouse species relative to the proportion of breeding season studies. Nonbreeding season estimates of survival of greater prairie-chickens are nearly double that of the breeding season (Augustine and Sandercock 2011, Winder et al. 2014). Populations of greater sage-grouse generally have high survival rates during the winter, but can be greatly reduced by harsh and extreme winters (Wik 2002, Connely et. al 2004, Moynahan et al. 2006). Severe weather events affecting overwinter mortality is also likely the case for lesser prairie-chickens, as a severe blizzard in Colorado in 2011 greatly reduced populations of lesser prairie-chickens (J. Reitz, Colorado Parks and Wildlife, pers. comm). Many species of grouse are experiencing population declines (Storch 2007), but for prairie-grouse, survival rates for the nonbreeding season do not seem to be influential on population growth relative to breeding survival and recruitment. My conclusion

regarding nonbreeding survival is additionally corroborated by a sensitivity analysis for lesser prairie-chickens in south-west Kansas, where breeding season survival, nest survival and chick survival were the most influential vital rates contributing to lesser prairie-chicken population growth rates (Hagen et al. 2009). Future research should examine lag effects of weather conditions and the potential impact cross-seasonal effects have on the survival, fitness and condition of females to determine if nonbreeding season conditions affect breeding conditions and success differently among years. My results do not suggest that nonbreeding season survival rates are greatly reducing population numbers for future reproductive potential of populations, with relatively high and consistent survival rates. Management should focus on improving survival rates of adults, nests and broods during the breeding season over concerns with nonbreeding season survival.

Management Implications

My results indicate that mortality during the six month nonbreeding season is an unpredictable, random occurrence. Lesser prairie-chicken survival was constant at all levels of used grass cover, forb cover and vegetation height. Maintaining quality grasslands, with high amounts of grass and forb cover during the year should provide adequate habitat for lesser prairie-chickens during the nonbreeding season. As nonbreeding mortality was similar among three sites within Kansas, between years and across studies, future management to enhance population growth rates should focus on management that can improve vital rates of lesser prairie-chickens that are variable and influential, such as nesting and brooding.

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Figure 1.1 Study site locations for female lesser prairie-chicken survival research in 2013 to 2015 in Kansas. The northwestern study site was in Logan and Gove Counties. The Red Hills study site was in Kiowa and Comanche counties, and the Clark County study site was in Clark County. Study sites were delineated using a Minimum Convex Polygon around locations of lesser prairie-chickens that did not exhibit dispersal.

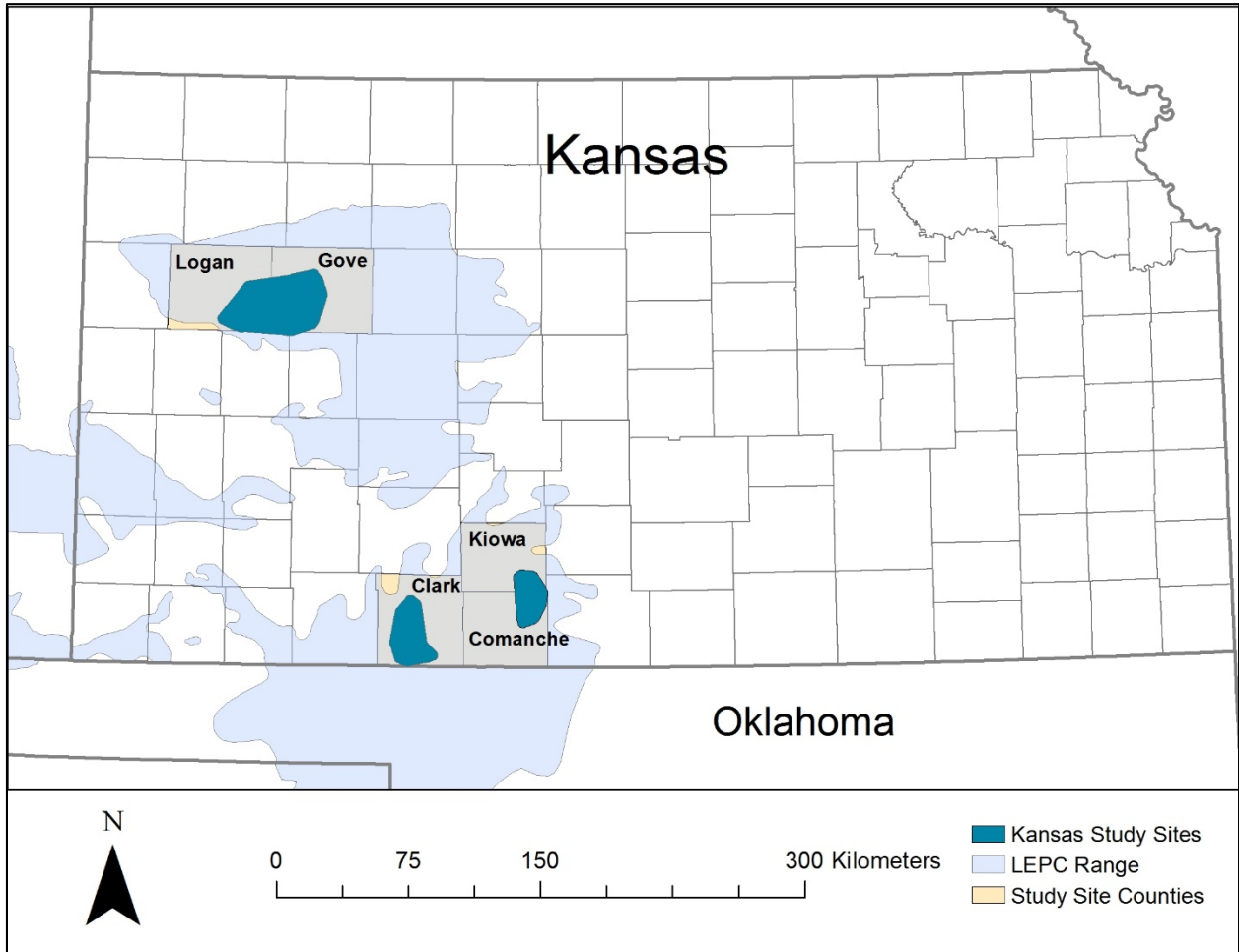


Figure 1.2 Mortality distribution by week across the 25-week nonbreeding season for three sites in Kansas (Northwest, Clark County and Red Hills). With all sites combined, there was no evident trend in when mortalities occurred across the nonbreeding season.

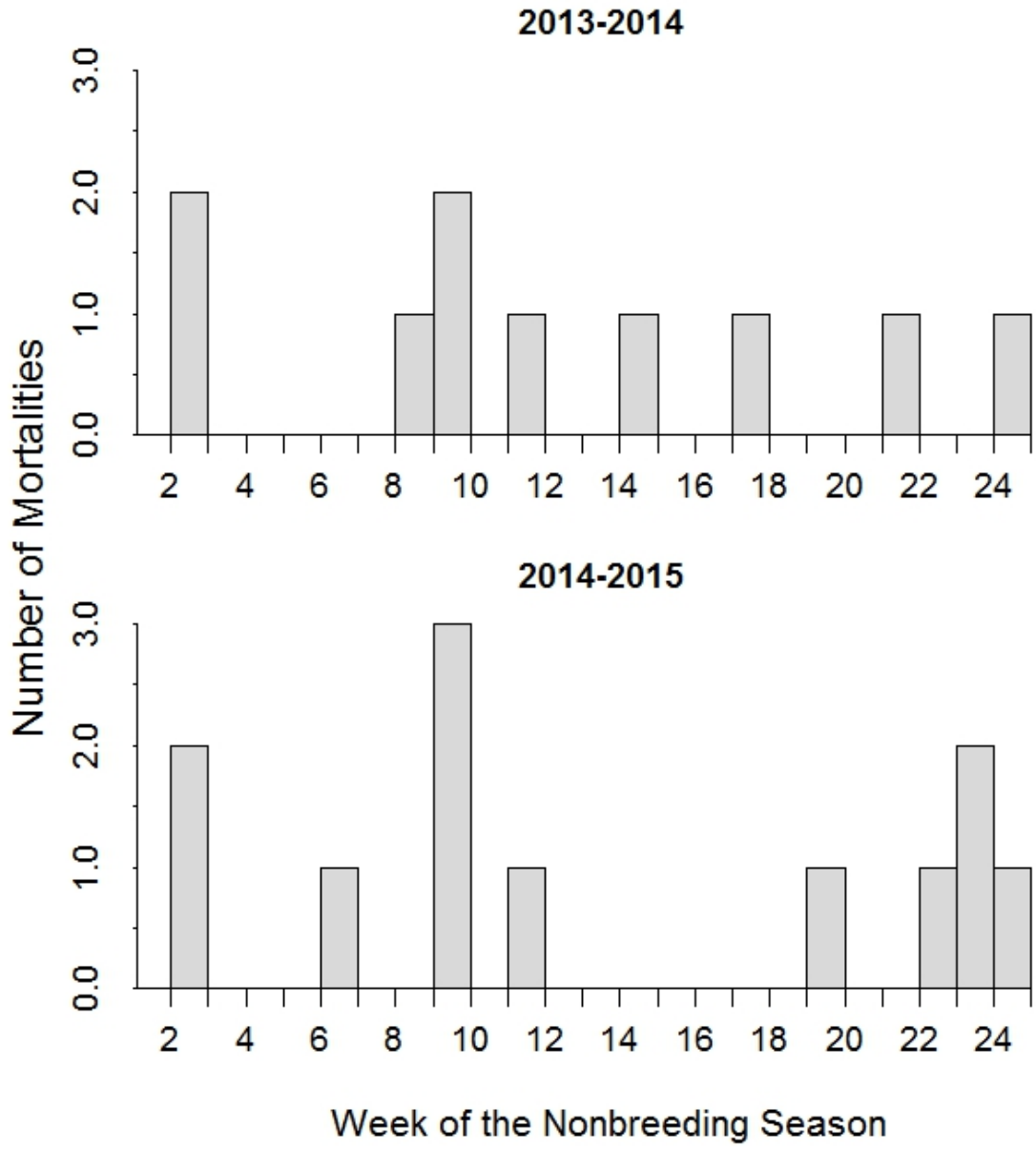


Figure 1.3 Survival rates (with 95% CI) by study site in Kansas for female lesser prairie-chickens during the 6-month nonbreeding season (16 September-8 March; 25 weeks), pooled across years (2013-2014 and 2014-2015). Study sites are defined as NW for northwestern Kansas, RH for the Red Hills, Kansas, and Clark for the Clark County, Kansas. Weekly estimates were generated in Program MARK, and the delta method was used to generate standard error for the entire 25-week nonbreeding season.

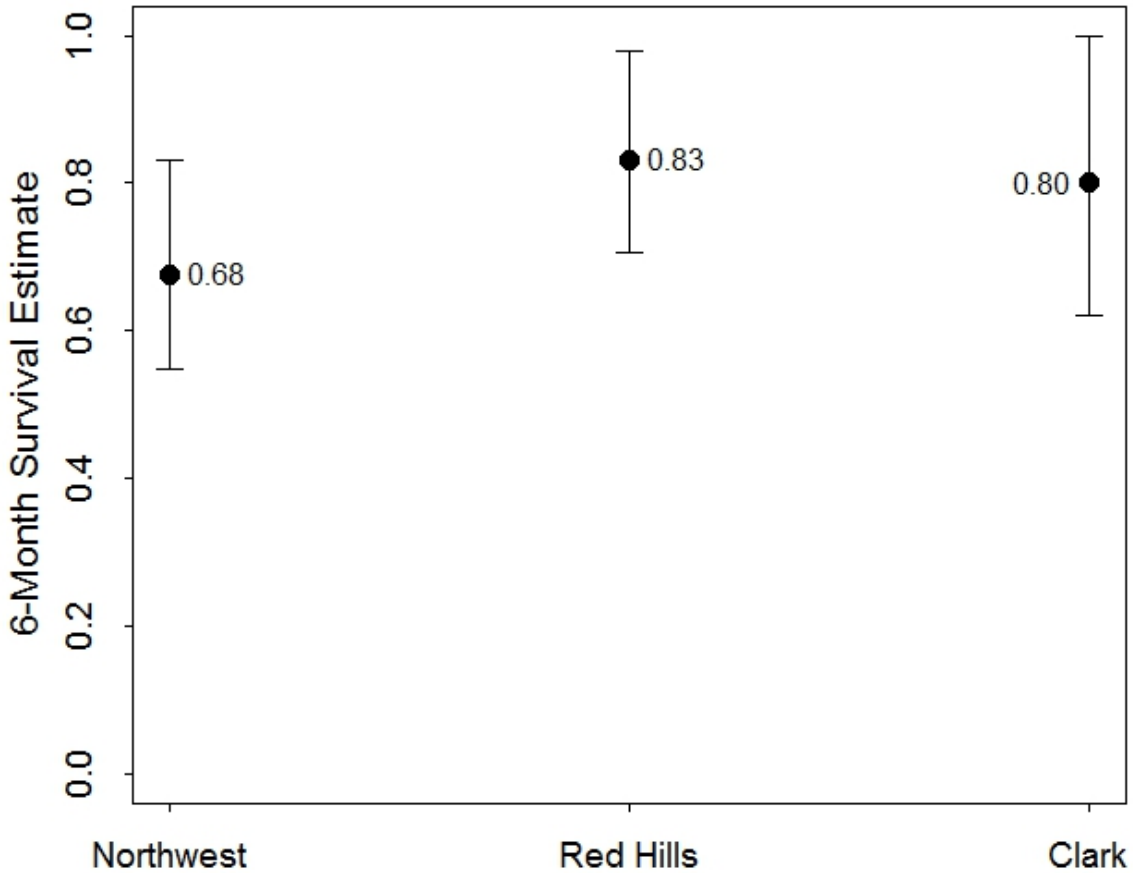


Figure 1.4 Counts of raptors (number of birds/16 km) during weekly surveys conducted at each of the three Kansas study sites (Northwest, Red Hills, Clark Co.) for the 6-month nonbreeding season across 2014-2015. Vertical line at week-10 representing the week with the highest hazard instantaneous hazard rate corresponding to the first high counts of raptors. Counts were for the entire 16-km survey, where 3-minute point counts were conducted every 0.8 km.

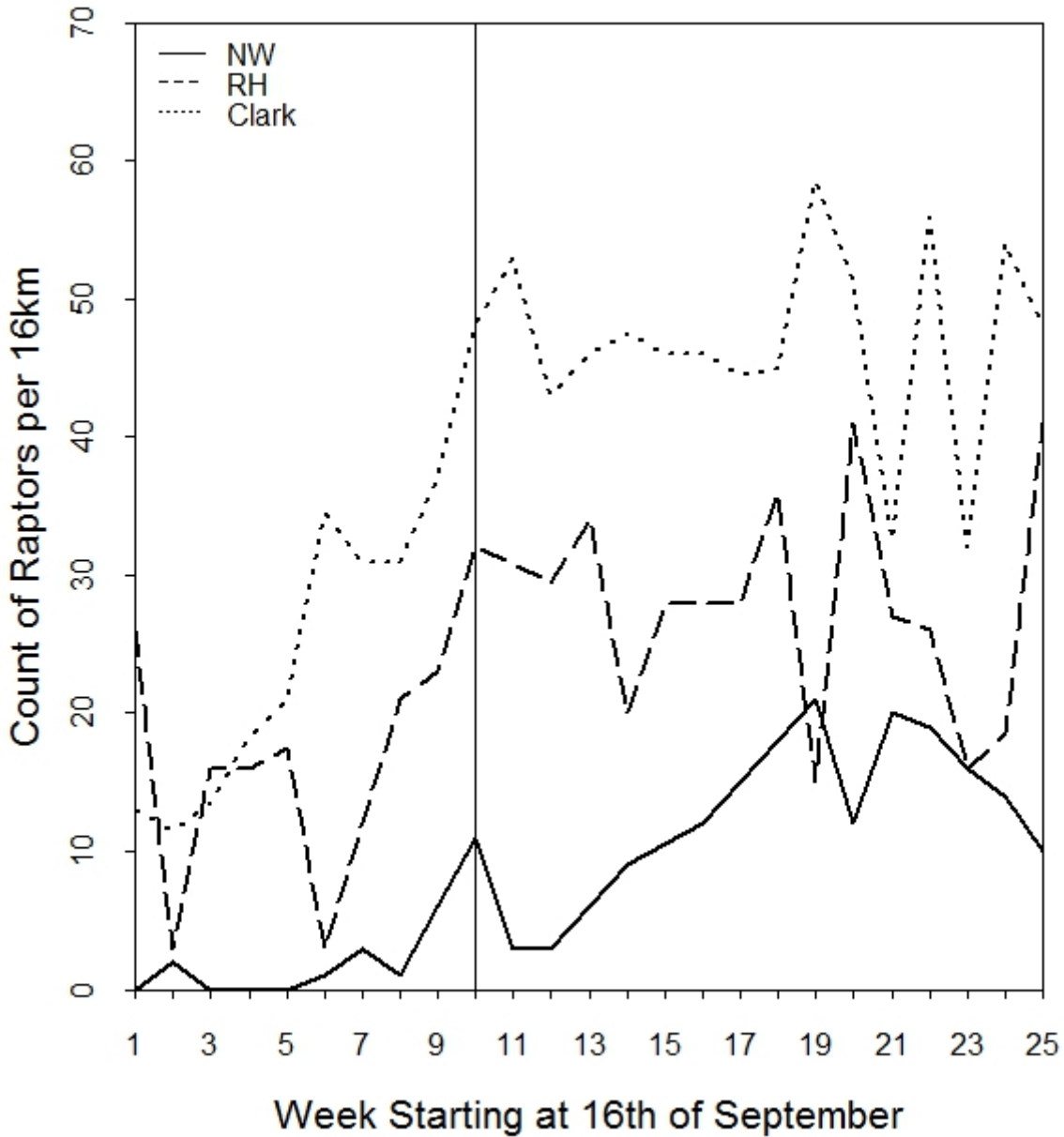


Figure 1.5 Estimates of survival from a Kaplan-Meier survival analysis (with 95% CI), showing differences between female lesser prairie-chickens marked with SAT-PTT and VHF transmitters in Kansas separated by the two seasons of data collection for 2013-2014, 2014-2015, and both years combined. The 95% confidence intervals around the estimates do not overlap for 2013-2014 but do for 2014-2015 and combined years.

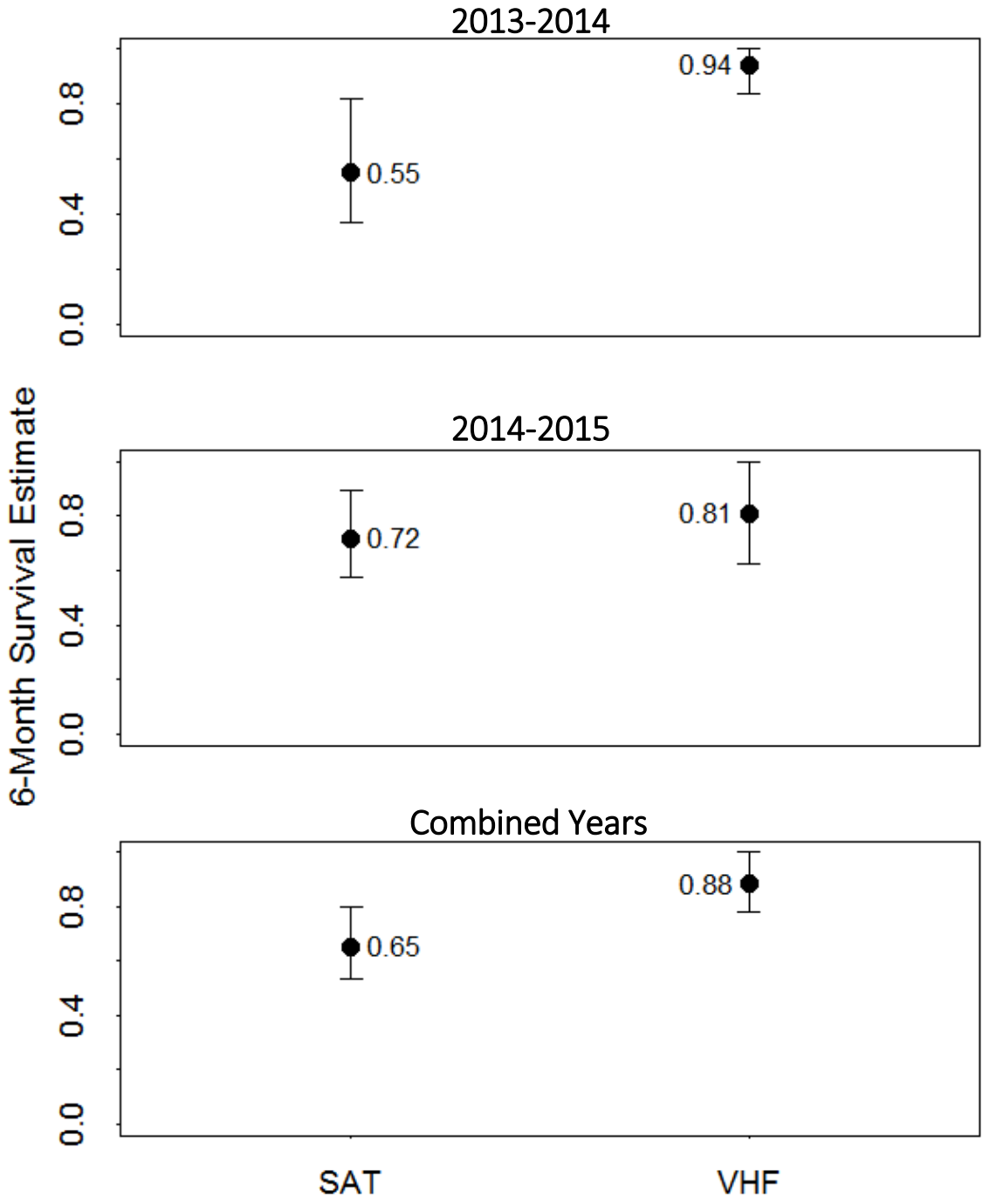


Figure 1.6 Kaplan-Meier survival curve (with 95% CI as dashes) illustrating cumulative survival curves as solid lines for female lesser prairie-chickens in Kansas outfitted with VHF (n = 42) transmitters and SAT-PTT transmitters (n = 52) over the 25-week nonbreeding season (16 September – 8 March), combining nonbreeding seasons from 2013-2014 and 2014-2015.

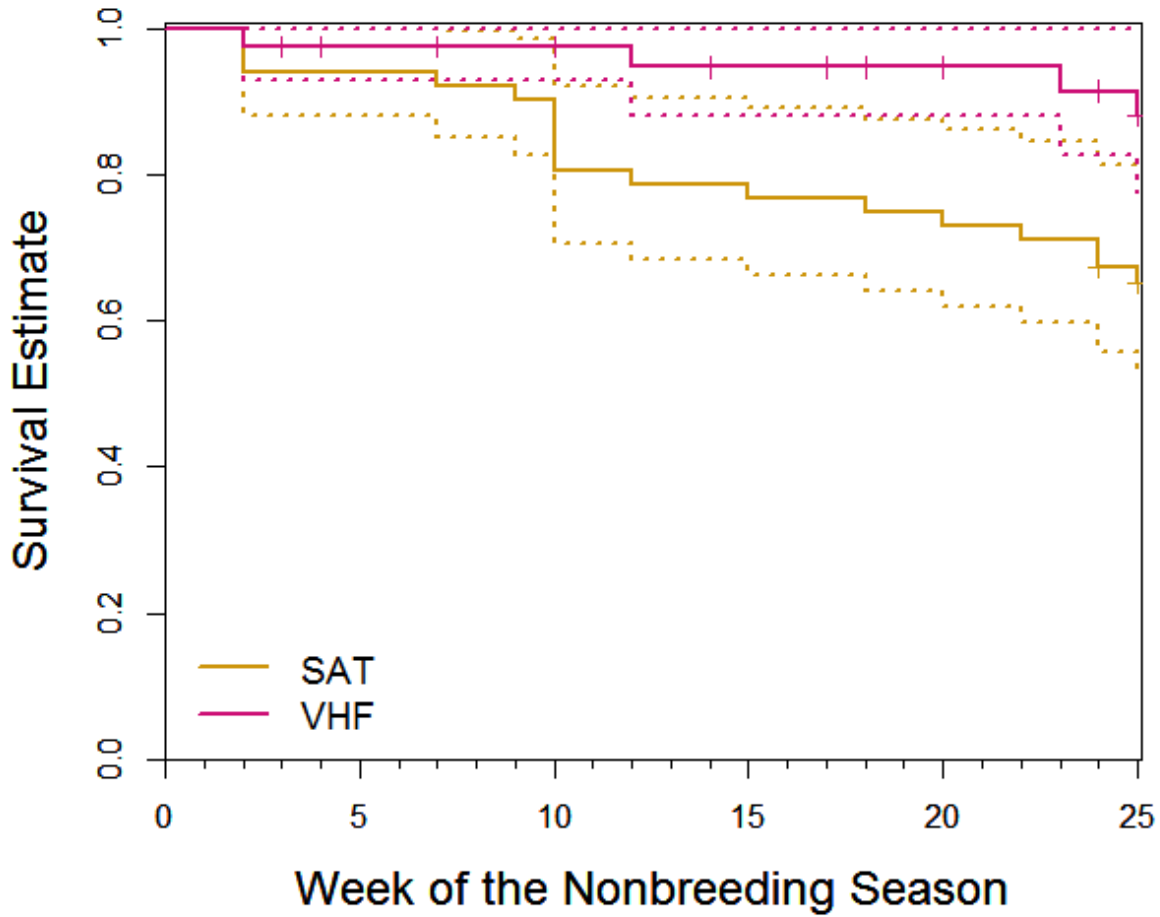


Figure 1.7 Hazard rate for female lesser prairie-chickens across the 6-month 2013-2014 and 2014-2015 nonbreeding seasons in Kansas. Week 1 corresponds to the 16-22 of September. Hazard rates indicate the instantaneous hazard rate for each week. A constant smoothing factor of 1.2 was used. The peak at the end of the curve is due to increased censoring of individuals during the final months of the nonbreeding season in that year.

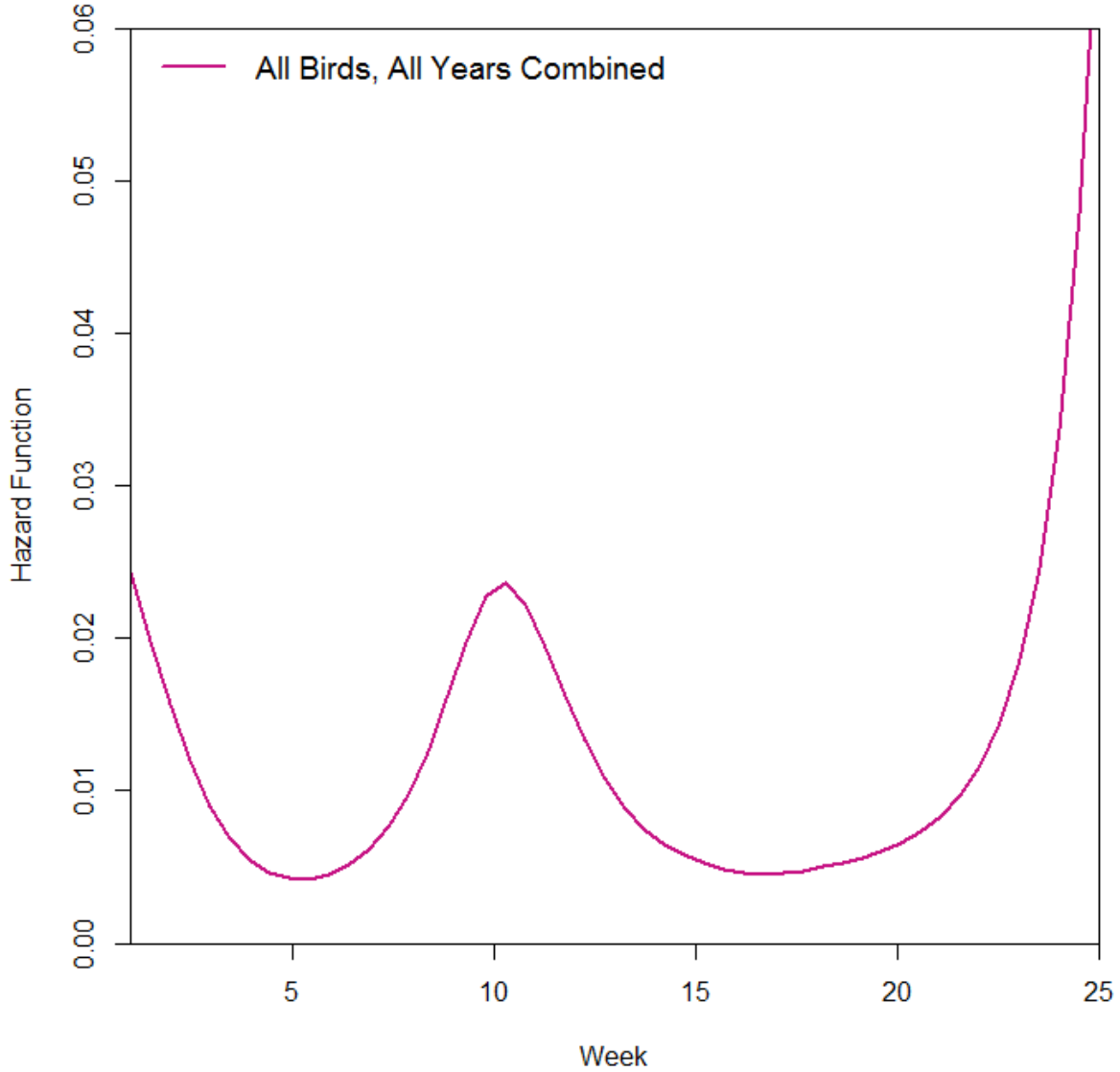


Table 1.1 Studies reporting 6-month survival estimates of lesser prairie-chickens during the nonbreeding season. Estimates are converted from reported estimates to 6-month rates for comparisons.

Author and Year	Study Area	Survival Rate	Sample Size
Hagen et al. 2007	Kansas	0.68	220 females
Jamison 2000	Kansas	0.74	160 both sexes
Kukal 2010	Texas	0.63	41 both sexes
Pirius et al. 2013	Texas	0.72	53 both sexes
Hagen et al. 2006	Kansas	0.65	216 males
Lyons et al. 2009	Texas	0.72	187 both sexes
Robinson 2015	Kansas	0.75	88 females

Table 1.2 Total number of female lesser prairie-chickens that survived the breeding season to be included in the nonbreeding survival study in Kansas. Number of individuals were separated by year, study site, and transmitter type. Six individuals survived the 2013 and 2014 breeding seasons and 2013-2014 nonbreeding season to be included in the 2014-2015 nonbreeding season.

Year	Site	Total #	#VHF	#SAT
2013	Northwest	25	13	12
	Red Hills	17	9	8
2014	Northwest	22	9	13
	Red Hills	15	7	8
	Clark	15	4	11
Total		94	42	52

Table 1.3 Model selection table based on AICc rankings for Program MARK analysis of lesser prairie-chicken survival data, combining encounter histories from 2013-2014 and 2014-2015 nonbreeding seasons in Kansas. Models included effects of mean percent cover (%) of grass and forbs, and mean vegetation height (cm) as individual covariates, linear trends with minimum low and mean low weekly temperatures, study site, year and transmitter type as well as *a priori* combinations of site and year

Model Name	Model Statistic				
	K	Deviance	AICc	Δ AICc	w_i
S % grass	2	246.98	250.99		0.16
S min temp	2	247.04	251.05	0.06	0.16
S constant	1	249.16	251.16	0.17	0.15
S mean low temp	2	247.47	251.48	0.49	0.13
S % forb	2	248.77	252.77	1.79	0.07
S min low temp ²	3	246.78	252.79	1.80	0.07
S site	3	246.80	252.81	1.82	0.06
S mean low temp ²	3	246.94	252.96	1.97	0.06
S vegetation height	2	249.11	253.12	2.13	0.06
S year	2	249.13	253.14	2.15	0.06
S site + year	4	246.54	254.56	3.58	0.03
S site x year	5	246.00	256.03	5.04	0.01

K = Number of parameters
 w_i = Model weight

Table 1.4 Model selection table based on AICc rankings for Program MARK analysis of lesser prairie-chicken survival data from the 2014-2015 nonbreeding season in Kansas. Models included effects of mean percent cover (%) of grass and forbs, and mean vegetation height (cm) as individual covariates, linear trends with minimum low and mean low weekly temperatures, weekly raptor survey counts, study site, year, and transmitter type as well as *a priori* combinations of site and year, temperature, and raptor abundance.

Model Name	Model Statistic				
	K	Deviance	AICc	Δ AICc	w_i
S % grass	2	137.22	141.24		0.20
S mean low temp	2	137.91	141.92	0.69	0.14
S constant	1	140.09	142.10	0.86	0.13
S mean low temp	2	138.27	142.28	1.05	0.12
S % forb	2	139.13	143.14	1.90	0.08
S # raptor + mean low temp	3	137.19	143.21	1.98	0.08
S site	3	137.20	143.23	1.99	0.07
S # raptor + min low temp	3	137.62	143.64	2.41	0.06
S # raptor	2	140.00	144.01	2.78	0.05
S veg height	2	140.09	144.10	2.86	0.05
S #raptor ²	3	139.90	145.93	4.69	0.02

K = Number of parameters

w_i = Model weight

Table 1.5 Model selection table based on AICc rankings for Kaplan-Meier analysis of nonbreeding adult female lesser prairie-chicken survival data in Kansas during 2013-2014 and 2014-2015. Models included effects of age at capture (SY vs ASY), study site (Northwest, Red Hills, Clark County), season (2013-2014 and 2014-2015), and transmitter type (VHF vs SAT-PTT) as well as *a priori* combinations of factors.

Model Name	Model Statistics			
	K	AICc	Δ AICc	Deviance
Transmitter	1	186.12		184.08
Transmitter x Season	3	186.67	0.55	180.4
Transmitter + Season	2	187.81	1.69	183.68
Null	1	190.8	4.68	190.8
Year	1	192.84	6.72	190.8
Site	2	193.05	6.93	188.92
Age	2	193.29	7.17	189.16
Site + Year	3	195.12	9	188.86
Site x Year	5	199.2	13.08	188.52

K = Number of parameters

Chapter 2 - Home-range and Space Use of Nonbreeding Lesser Prairie-Chickens in Southern Great Plains

Introduction

Understanding how wildlife species move and use space is crucial to developing meaningful conservation strategies. A home-range can be defined as the cumulative depiction of space used based on decisions an individual makes during stages of their life cycle to maximize fitness (Powell 2000). The home range should contain all of the necessary resources to meet the ecological needs of an individual including reproductive opportunities, forage, and cover (Mitchell and Powell 2004, Powell and Mitchell 2012). To both survive and reproduce, an individual needs to be able to minimize energy expenditure and mortality risk. Thus, measuring variation in and individual's home range size and placement across time and space can be a useful representation of how a species perception of the landscape influences space use within the constraints of resource availability. The ability to understand and predict the cumulative space that specific populations of species will use can also be useful in the implementation of management and conservation strategies to determine size and location of management actions.

Grasslands have experienced one of the greatest declines of all ecosystems within the United States, with some areas having lost as much as 99% of the pre-European settlement area (Samson and Knopf 1994). The loss of grassland has been attributed to conversion of crops, suppression of natural fire, and climate change, which is affecting the timing and intensity of drought across the Great Plains (Samson and Knopf 1994, Askins et al. 2007, Trenberth et al. 2014). The conversion of prairie to cropland has fragmented existing prairie into smaller blocks of less contiguous land. Additionally, remaining prairie is often managed for livestock production and may represent a lack of quality for species that need robust vegetative structure for central life stages. Incumbent with the loss and degradation of grassland is the decline of bird

species that rely entirely upon large, relatively intact tracts of prairie (Brennan and Kuvlesky 2005). Specifically, within the southern Great Plains, the lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a representative umbrella species that has experienced long-term declines (Hagen and Giesen 2005, Pruett et al. 2009).

Lesser prairie-chickens are a species of prairie-grouse found in the southern Great Plains of Kansas, Colorado, New Mexico, Oklahoma and Texas. Lesser prairie-chickens have been a species of conservation concern for many years, as both their abundance and occupied range have declined since pre-European settlement (Hagen et al. 2004). The population decline has been attributed to extensive land conversion from native prairie to cropland, unmanaged livestock grazing, invasive species, and increasing energy infrastructure (Woodward et al. 2001, Hagen and Giesen 2005). Due to ongoing declines, lesser prairie-chickens were listed as threatened in May, 2014 under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2014). Although the listing was vacated by a federal judge in September of 2015 (*Permian Basin Petroleum Association et al. v. Department of Interior, U.S. Fish and Wildlife Service*, [Case 7:14-cv-00050-RAJ, U.S. District Court, Western District of Texas, Midland-Odessa Division]), populations remain low, and require a conservation strategy to restore lesser prairie-chickens back to a sustainable population level. Despite knowledge that decline and degradation of grasslands have reduced habitat quality for lesser prairie-chickens, a better understanding of each portion of their life-cycle, including those that may have been previously overlooked, such as their nonbreeding ecology, is needed to develop successful conservation strategies. Current management prescriptions are being advised range wide, but lesser prairie-chickens occupy four distinct ecoregions across their range (Sand Shinnery Oak Prairie, Sand Sagebrush Prairie, Mixed-Grass Prairie and Short-Grass Prairie/CRP Mosaic), which differ in vegetation

composition, structure and soil types (Van Pelt et al. 2013, McDonald et al. 2014). An increased understanding of the differences and similarities among the four ecoregions, and across the lesser prairie-chicken annual life-cycle, is required to reverse the decline of lesser prairie-chickens.

As an obligate grassland bird, placement of home ranges by lesser prairie-chickens depends partially on the configuration of the grassland landscape, such as the size and connectedness of grassland patches (Taylor and Guthery 1980). Lesser prairie-chickens require a habitat matrix in which grassland habitat patches are connected to facilitate movement, dispersal, and access to forage and cover (Pruett et al. 2009). However, due to landscape changes in the southern Great Plains, available habitat for the lesser prairie-chicken has decreased from pre-settlement availability (Rodgers 2016). The amount of habitat does not appear to be decreasing rapidly in many areas, but lesser prairie-chicken populations remain low relative to long-term averages and are continuing to decline in some regions (McDonald et al. 2014, Spencer 2014).

Overall grassland loss has not drastically changed throughout the northern portion of their range since at least the 1950s and drivers of the recent declines of lesser prairie-chickens remain unclear (Spencer 2014). Ecological studies of a declining species need to determine the target areas for conservation, and whether those areas remain consistent spatially and temporally across inhabited ecoregions (Sanderson et al. 2002, Pressey et al. 2007). The time of year when prairie-chickens are the least studied is the nonbreeding season. The nonbreeding period has been defined for lesser prairie-chickens as the portion of the year when females are not attending leks, nests or broods. If nonbreeding season habitat requirements are not included in conservation plans and strategies, then central life-stages may be overlooked. Nonbreeding season ecology can have an effect on breeding ecology by cross-seasonal effects, such as providing quality habitat to maintain body quality; thus, improving individual survival and fitness rates (Norris and Marra

2007). Additionally, additive mortality during the nonbreeding season can effectively reduce the reproductive potential of an entire population during the breeding season (Norris and Marra 2007). Cross-seasonal interactions are not well understood and their potential importance have been overlooked in resident species such as lesser prairie-chickens. A better understanding of nonbreeding lesser prairie-chicken ecology is required to determine if management objectives are addressing all of the habitat needs for their annual cycle, as opposed to just the needs of nesting and brooding females.

One of the gaps in nonbreeding season ecology is home range and space use (Table 2.1). Addressing this gap in knowledge is necessary, as the possibility exists that use of the landscape in the non-breeding season is fundamentally different than the breeding season due to differences in how time is spent, and the lack of limitations in space use that are implicit during the breeding season. The central difference between the two seasons is that females do not constrain their space use by attending nests, leks, and broods (Plumb 2015). Individual breeding season home ranges can be driven by sex, as females attend nests and broods and both sexes attend leks, but information is lacking as to whether males and females use space differentially during the nonbreeding season. Home range size can also be driven by time, as different weather conditions alter the landscape to be more or less favorable to lesser prairie-chickens and by ecoregion, as each region is defined by different characteristics that affect lesser prairie-chicken use. Nonbreeding season studies, which are limited to the southern portions of the lesser prairie-chicken range, reported larger home ranges and greater movements than during the breeding season (Candelaria 1979, Jones 2009, Lyons et al. 2009, Kukul 2010, Pirius 2011). Estimates of average nonbreeding home range size vary between 62 and 1946 ha; however, most estimates are hampered by low sample size of radio-marked birds (Haukos and Zavaleta 2016). Constraints on

home range size for the nonbreeding season are largely unknown during this time period. One hypothesis is that despite the time of year, female prairie-chickens are tied to leks and will use space in areas close to leks, as the location of these central display areas are due to placement in the best available habitat (Schroeder and White 1992, Gibson 1996).

The lek is a feature on the landscape that all prairie-chickens need to attend at some point in their life-cycle; thus, it is included in their overall home range. During the breeding season, females need to be in some proximity of leks for reproduction but typically remain close to leks throughout their life cycle (Giesen 1994, Winder et al. 2015). This could be due to lek placement in high quality lesser prairie-chicken habitat, which supports the recommendation that areas around lekking sites need to be conserved (Woodward et al. 2001). The area around leks must also consist of nesting and brooding habitat, as well as adequate habitat for concealment and forage (Ahlborn 1980, Applegate and Riley 1998). Male lesser prairie-chickens are known to lek during the months that the photoperiod is similar to that of the spring lekking period (Jones 1964), but influence leks having on nonbreeding female lesser prairie-chicken space use is not well understood. To further understand whether leks remain important to lesser prairie-chickens during the nonbreeding season, intensity of use within the home range can be used.

In addition to the lek being a potential driver of intensity of space use during the nonbreeding season, finer scale habitat use may also vary across the nonbreeding season as grassland structure and composition are altered by grazing and weather, decreasing the ability of vegetation to act as cover or food for lesser prairie-chickens. When this degradation of habitat occurs, it may be necessary for lesser prairie-chickens to find alternate sources of food and cover. One possible place to access increased cover is in fields enrolled in the Conservation Reserve Program (CRP), which are former croplands planted to perennial vegetation cover that is

generally not grazed or burned within the northern range of lesser prairie-chickens. Overall lack of management of CRP fields creates areas with denser cover than grazed grasslands (Delisle and Savidge 1997). Last, lesser prairie-chickens could spend an increased amount of time in crop fields foraging for waste grain. Changes in habitat use through time could also drive broad-scale changes in home range size and space use, as prairie-chickens need to increase the overall space used to incorporate sufficient habitat to meet resource needs. Furthermore, with lesser prairie-chickens located in four ecoregions across the Southern Great Plains, understanding differential habitat use across the nonbreeding season can assist in the identification of differences among ecoregions and whether or not these differences must be accounted in population management range-wide.

A study of lesser prairie-chicken space use and habitat use on the landscape requires the use of radio-transmitters to track these secretive birds with large space requirements through space and time. Past studies have mainly used Very High Frequency (VHF) transmitters to locate lesser prairie-chickens on the landscape. However, this method is limited by the amount of effort put into finding individual birds and variation in transmitter range, due to transmitters and topography. Recent technological advances have made GPS Satellite Platform Transmitting Terminal (SAT-PTT) tags that are small enough ($\leq 5\%$ of mass) to attach to birds such as lesser prairie-chickens. The transmitters provide a finer scale of data, both spatially and temporally, and can be used to ask and answer fine-scale space and habitat use questions. However, the standard method of estimating home range with these two transmitter types are different, with data from VHF transmitters analyzed using fixed kernel density estimators, and GPS data analyzed using models that account for temporal autocorrelation, such as Brownian Bridge movement models (Bullard 1999, Horne et al. 2007, Walter et al. 2015). My project is the first study to utilize these

transmitters on nonbreeding lesser prairie-chickens, a comparison of space use resulting from these two transmitter types, and the techniques to analyze these data should be done.

My objectives were to 1) compare estimates of home range size among sexes, ecoregions and seasons, 2) evaluate nonbreeding lesser prairie-chicken space use relative to lek locations, and 3) document temporal changes in habitat use across the nonbreeding season. A secondary objective of this research was to 4) compare home range size between VHF individuals with fixed-kernel density estimators and SAT-PTT home individuals calculated with Brownian Bridge movement models. I predict that females have larger home ranges than males, and that males will use space closer to leks within home ranges relative to females, because male lek-mating grouse visit leks in the fall. I predict that if lek locations influence lesser prairie-chickens home range placement during the nonbreeding season, relative influence will decrease during the central months of the nonbreeding season (November, December and January) compared to October and February, as breeding season space use will have less influence during these months. I also hypothesized an increasing trend in use of CRP and cropland over the nonbreeding season, as birds move to areas with increased cover such as CRP fields and areas with increased food such as waste grain.

Study Area

Within the current five-state range that lesser prairie-chickens occupy there are four different ecoregions. In Kansas, there are sections of the Sand Sagebrush Prairie Ecoregion, the Mixed-Grass Prairie Ecoregion and the Short-Grass Prairie/CRP mosaic Ecoregion, Colorado contains portions of the Sand Sagebrush and the Short-Grass/CRP ecoregions, and New Mexico is in of the Sand Shinnery Oak Prairie Ecoregion (SSO; Figure 2.1). The different ecoregions support different densities of lesser prairie-chickens, with the greatest densities of birds

occurring in the SCRP and MGR of Kansas (McDonald et al. 2014). Lower densities were found in the SSB and SSO ecoregions.

Study sites were delineated by creating a Minimum Convex Polygon using the Minimum Bounding Geometry tool in ArcGIS 10.2 (ESRI Inc., 2013, Redlands, USA) around all of the bird points for each site, excluding dispersal events. The study sites were located in three areas of Kansas, eastern Colorado, and eastern New Mexico (Figure 2.2). The study area in Kansas included two sites within the Short-Grass Prairie/CRP Mosaic Ecoregion dominated by CRP grasslands and row-crop agriculture on silt-loam soils (McDonald et al. 2014). The study site in Northwestern Kansas was 171,437 ha, and located in Gove and Logan counties, on private land and the Smoky Valley Ranch, owned and managed by The Nature Conservancy. The primary land uses in this area were livestock grazing, energy extraction and both center-pivot and row-crop agriculture. Mixed-grass prairie species occurrence increased from west to east in this region. Dominant vegetation in the region included: blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsute*), buffalograss (*B. dactyloides*), little bluestem (*Schizachyrium scoparium*), sideoats grama (*B. curtipendula*), big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annuum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed (*Ambrosia psilostachya*; Lauver et al. 1999). Grass species planted in CRP fields included little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indian grass (*Sorghastrum nutans*, Fields 2004). The CRP fields were interseeded with forbs in the 1990s; those planted included white sweet clover (*Melilotus alba*), yellow sweet clover (*Melilotus officinalis*), Maximilian sunflower (*Helianthus maximiliani*), Illinois bundleflower, purple prairie clover (*Dalea purpurea*), and prairie

coneflower (*Ratibida columnifera*; Fields 2004). Wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), and corn (*Zea mays*) were the major crops in the region.

The Red Hills Kansas study site was 49,111 ha and centered on private lands in Kiowa and Comanche counties within the Mixed-Grass Prairie Ecoregion (McDonald et al. 2014). The south-central Kansas site consisted of mixed-grass prairie on loamy soils. Primarily land uses for the Red Hills included livestock grazing, oil and gas extraction, and row-crop agriculture.

Dominant vegetation in south-central Kansas included little bluestem, blue grama, hairy grama, sideoats grama, buffalograss, sand dropseed (*Sporobolus cryptandrus*), Louisiana sagewort (*Artemisia ludoviciana*), western ragweed (*Ambrosia psilostachya*), sand sagebrush (*Artemisia filiafolia*), and eastern red cedar (*Juniperus virginiana*; Lauver et al. 1999).

The Clark County study site within south-central Kansas was 71,209 ha and located at the Mixed-Grass Prairie Ecoregion and Sand Sagebrush Prairie Ecoregion boundary (McDonald et al. 2014). Land use was dominated by livestock grazing, oil and gas extraction, and row-crop agriculture. Dominant vegetation in the area included: little bluestem, sideoats grama, blue grama, hairy grama, big bluestem, alkali sacaton (*Sporobolous airoides*), Russian thistle (*Salsola kali*), kochia (*Kochia scoparia*), annual sunflower (*Helianthus annuus*), and sand sagebrush. This study site also had considerable alkali flats along drainages.

Within eastern Colorado, the study site was located on private lands in Cheyenne, Baca, and Prowers counties totaling 28,388 ha. Two disjointed study areas were combined into a single area due to low sample size. All study sites were within the Sand Sagebrush Prairie Ecoregion (McDonald et al. 2014; Figure 2.1). Land use within the study site included livestock grazing, row-crop agriculture, and CRP grasslands. Dominant vegetation in the region included: blue grama, hairy grama, sideoats grama, buffalograss, little bluestem, big bluestem, sand sagebrush,

kochia, and Russian thistle. Major crops within the region included wheat, sorghum, and corn. Oil and gas development was infrequent in this site.

The New Mexico study site was 63,756 ha located in Lea and Roosevelt counties of the Southern High Plains within the Sand Shinnery Oak Prairie Ecoregion. Birds were trapped on the Milnesand Prairie and North Bluit Prairie Chicken Areas owned by the New Mexico Department of Game and Fish. Plants that dominate this ecoregion include sand dropseed, hairy grama, little bluestem, big bluestem, silver bluestem, yellow bluestem and sideoats grama. Common forbs include silverleaf nightshade (*Solanum elaeagnifolium*), spectacled pod (*Dimorphocarpa wislizenii*), Indian blanket (*Gaillardia pulchella*), woolly locoweed (*Astragalus ollissimus*), annual sunflower scarlet gaura (*Gaura coccinea*), and halfshrub sundrop (*Calylophus serrulatus*, Grisham 2012). Shrubs in this region include sand shinnery oak (*Quercus havardii*) and sand sagebrush. Land use was dominated by livestock grazing, oil and gas production, and center-pivot agriculture (Grisham 2012).

Methods

Capture

Lesser prairie-chickens were captured at leks in spring (March – May) during 2013 and 2014 in Northwest and Red Hills, Kansas as well as Colorado. Lesser prairie-chickens were only captured at leks in the spring of 2014 in Clark County, Kansas and New Mexico. Birds were trapped using walk-in drift traps, magnetic droppnets, and rope-trigger droppnets (Haukos et al. 1990, Silvy et al. 1990, Schroeder and Braun 1991). Captured individuals were aged using the degree of spotting on the 9th and 10th primaries; second-year birds had spotting within 3.8 cm from the feather tip, and after-second-year birds had spotting ≥ 3.8 cm from the feather tip. I also used the amount of wear of the feather tips as juvenile grouse do not molt those primaries until their second year; thus, have frayed feather tips (Copelin 1963). I sexed individuals using tail

feather color; females had barred tail feathers and male prairie-chickens had mainly black tail feathers (Copelin 1963).

Female lesser prairie-chickens were outfitted with either 12-15-g bib-style VHF transmitters (A3960, Advanced Telemetry System, Isanti, USA), or a rump-mounted 22-g Satellite Platform Transmitting Terminal GPS transmitter (PTT-100, Microwave Telemetry, Columbia, Maryland, USA). SAT-PTT transmitters were attached on the rump using leg harnesses made of Teflon[®] ribbon, with elastic at the front of the harness for flexibility (Bedrosian and Craighead 2010, Dzialak et al. 2011). Male lesser prairie-chickens were opportunistically fit with the remaining SAT-PTT transmitters after females stopped attending leks in May.

Female lesser prairie-chickens are difficult to capture during the nonbreeding season, and the sample size for my study was comprised of individuals that survived from the previous spring trapping season. For this study, the nonbreeding season was defined as the six-month period between the 16th of September and the 14th of March. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee under protocol #3241, the Kansas Department of Wildlife, Parks and Tourism scientific collection permits (SC-042-2013 and SC-079-2014), and the Colorado Parks and Wildlife scientific collection licenses (13TRb2053 and 14TRb2053). New Mexico birds were captured by researchers from New Mexico State University under permits from New Mexico Game and Fish.

Tracking

Female prairie-chickens outfitted with VHF transmitters were located three to four times per week during the nonbreeding season. We triangulated individuals from three to five locations using a three-piece hand-held Yagi antenna and either an Advanced Telemetry Systems Receiver (R4000, R4500, Advanced Telemetry Systems, Isanti, USA) or a Communications Systems

Receiver (R1000, Communications Specialists, Orange, USA). Bearings of locations were ≥ 15 degrees apart and taken within 20 minutes to decrease error from bird movement. Bearings and Universal Transverse Mercator (UTM) positions for birds with VHF radios were entered into the program Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary) to determine the estimated UTM location of the individual and estimate an error polygon around the point. I attempted to limit error polygons to 0.1 ha, but used locations with error polygons up to 1ha for birds with a limited number of locations (~22%).

Birds outfitted with a Satellite-PTT transmitter recorded up to eight positions a day, with ± 18 m accuracy, every two hours between 06:00 – 22:00 during the nonbreeding season. Locations were uploaded to the Argos satellite, downloaded every three days into the Argos System, and compiled weekly.

Home Range

A utilization distribution is a probability distribution of an animal's locations throughout the time period of monitoring (Van Winkle 1975). Home ranges for Satellite-PTT marked individuals were estimated by calculating a utilization distribution using Brownian Bridge Movement Models (Horne et al. 2007). The program adehabitatHR, and function kernelbb was used to calculate the utilization distributions (Calenge 2006). Utilization distributions (UD) for SAT-PTT individuals were estimated for the entire nonbreeding season, as well as monthly estimates from October - February. Brownian Bridge Movement Models take into account the time lag between successive locations, the path between the two locations, and temporal autocorrelation, which represents a refinement over the use of fixed kernel density estimators for these type of data (Bullard 1991, Walter et al. 2011). Home ranges for the entire nonbreeding season (September 16-March 14) were estimated for SAT-PTT individuals that had at least 100

points (alive about 13 days) within the season. Monthly home ranges were calculated for SAT-PTT individuals that had at least one point per day throughout an entire month.

Home ranges for VHF-marked individuals were estimated using a fixed kernel density estimator and least squares cross validation (LSCV) for smoothing with the function kernelUD (Calenge 2006). Home ranges were estimated for birds that had ≥ 30 locations for one nonbreeding season (Seaman et al. 1999). Due to the tendency for about half of the individuals during the nonbreeding season to disperse from the area we captured them (S. Robinson unpubl. data), LSCV could not converge across the gap between where they were last detected and where individuals were located again using aircraft. I used the average smoothing parameter from all individuals for which LSCV was able to converge for, to calculate the kernel density estimate of individuals with a gap in tracking times. These home ranges ended up as two main areas with a gap in-between as no information was known about the movement between the time of dispersal and the time of relocation. As a maximum of four points per week were obtained for VHF birds, there were no birds that had enough points to estimate monthly home ranges.

Variation in Home Range

Welch's two-sample *t*-tests using Program R were used to test for differences in average home-range size between transmitter types (VHF and SAT-PTT), sexes, and seasons. If a difference existed between VHF and SAT-PTT home range sizes, they were separated and differences between site and season were tested separately. I used one-way Analysis of Variance (ANOVA) to compare home range size among study sites. Analysis among study sites were separated by season because the New Mexico and Clark County study sites were not present for comparisons for the first season. If site was a significant main effect in the model ($P < 0.05$), I used a post-hoc Tukey's HSD test to determine differences in mean home range sizes among study sites. I used a one-way ANOVA to test for differences in mean home range size among

months. I used simple linear regression to test for a temporal trend in proportion of locations in crop, CRP or grassland habitat types by site across the seven months of the nonbreeding season.

Resource Utilization Functions

The probability distribution of use within the utilization distribution can be used to relate space use to features on the landscape. Home ranges were used from both nonbreeding male and female lesser prairie-chickens to test us by lesser prairie-chicken of space in relation to leks during the nonbreeding season with resource utilization functions in the package `ruf.fit` in Program R (Handcock 2007, R Core Team 2014). Resource utilization functions use a multiple regression framework. The intensity of use from the utilization distribution serves as the dependent variable (Marzluff et al. 2004). The 99% isopleth defined the extent of the available habitat within each individual's home range (Kertson and Marzluff 2011). I related intensity of use to distance from all known leks. Lek locations used were located by surveys within each study site. I also used Kansas leks from the Kansas Department of Wildlife, Parks, and Tourism from lek surveys across the study sites and aerial surveys performed by WEST Inc. (McDonald et al. 2014). Distance rasters for lek locations at each site were created using the Euclidean Distance tool in ArcGIS 10.2 (ESRI Inc., 2013, Redlands, USA). Resource utilization functions produce standardized beta estimates for each individual, which are then averaged across all individuals for a population level estimate of space use (Marzluff et al. 2004). A negative beta estimate for distance to lek would indicate an increase in space use closer to leks, because as distance to lek increases, use would decrease. Resource utilization functions were analyzed for the entire nonbreeding season and separately for the months of October, November, December, January and February to determine if space was being used closer to leks than expected by chance and if space use in relation to known leks varied across the nonbreeding season, between males and females, and among sites.

Habitat Use

The landscape of study sites within the ecoregions was characterized using the 2009 Playa Lakes Joint Venture land cover layer and a 2014 layer of all properties enrolled in CRP across the range of lesser prairie-chicken provided under agreement with the U.S. Department of Agriculture, Farm Service Agency (Playa Lakes Joint Venture 2009). The Playa Lakes Joint Venture layer and the CRP layer each had a resolution of 30 m x 30 m. An accuracy assessment was conducted on these landcover layers, and found that grassland was overall classified correctly, but confusion could arise as to what type of grassland (McLachlan 2012). For habitat use analysis, all native grassland and shrubland classes were grouped into a single grassland habitat type to avoid any misclassification. In New Mexico, agricultural land (i.e., wheat) was often confused with short-grass prairie, so it may be overrepresented (McLachlan 2012). All bird points from the nonbreeding season were imported into ArcGIS version 10.2, and I used the Identity tool to determine the habitat type for each bird point. The majority of locations (97.8%) were from SAT-PTT locations, which had an error of 18 m, allowing for accurate habitat type identification from the landcover layers. Categories used for reporting habitat use were grouped into Grassland, CRP, Cropland, and Other. Grassland habitat types were short-grass, mixed-grass, sand sagebrush and sand shinnery oak prairie. Crop types included wheat, sorghum, corn, alfalfa, and fallow. Classes that comprised the “Other” group were riverine systems, river, channel, wet meadow, secondary roads, 4-lane roads, saline, stock pond, emergent marsh, and playas.

Results

Nonbreeding home ranges were estimated for 87 individual lesser prairie-chickens (Table 2.2). During the 2014-2015 nonbreeding season, six SAT-PTT transmitters malfunctioned. The six individuals did not have enough consecutive points to calculate utilization distributions with

Brownian Bridge movement models correctly and were censored. Additionally, over the course of the study, five individuals dispersed outside of my defined study areas. The 95% home ranges for these individuals were not included in the home range size comparison, as these movements were considered natal dispersal and not within-season home ranges.

Average home range size for lesser prairie-chickens outfitted with SAT-PTT transmitters ($\bar{x} = 954.7$ ha, SE = 128.5) were 215% larger than home ranges for lesser prairie-chickens fitted with VHF transmitters ($\bar{x} = 303.5$ ha, SE = 24.1; $t_{71} = -4.98$, $P < 0.001$). Mean home range size did not differ among sites ($F_{2,14} = 0.45$, $P = 0.65$) or seasons ($F_{1,14} = 0.03$, $P = 0.87$, Table 2.3) for VHF marked lesser prairie-chickens. Male prairie-chickens were only outfitted with SAT-PTT transmitters (Table 2.2), so I tested for home range size between sexes just for SAT-PTT individuals. Average home range sizes did not differ between female ($\bar{x} = 986$ ha, SE = 185.4) and male lesser prairie-chickens ($\bar{x} = 904.7$ ha, SE = 112.4; $t_{65} = -0.37$, $P = 0.72$). Average home range size was about three times smaller during the 2013-2014 nonbreeding season ($\bar{x} = 536.1$ ha, SE = 67.4) than the 2014-2015 nonbreeding season ($\bar{x} = 1264.9$ ha, SE = 205.7; $t_{46} = -3.66$, $P < 0.001$). During the 2013-2014 nonbreeding season, average home range size was ~50% smaller in the northwestern study site compared to the Red Hills and Colorado study sites ($F_{2,34} = 3.68$, $P = 0.017$; Table 2.4). Tukey's HSD test indicated that the difference was between northwestern Kansas ($\bar{x} = 336.9$ ha, SE = 69.7) and Colorado ($\bar{x} = 694.7$ ha, SE = 149.4). In the 2014-2015 nonbreeding season, with two additional sites (Clark County and New Mexico), there was no difference in home range size among study sites for SAT-PTT marked lesser prairie-chickens ($F_{4,34} = 0.90$, $P = 0.47$).

I had a total of 285 bird-months, from 69 individuals that had at least 100 points within a month, across October-February, with sexes combined, for comparing average monthly home

range size of SAT-PTT birds (Table 2.5). There were no differences in home range size among months ($F_{4,280} = 0.81$, $P = 0.52$). The overall mean monthly home range across all sites was 600.8 ha (SE = 50.0).

The resource utilization function using distance to lek as a variable indicated that lesser prairie-chickens used space closer to leks ($\beta = -0.15$, SE = 0.028, 95% CI = -0.2055, -0.0958) within their home range than expected by chance (Figure 2.3). The mean beta between sexes showed that males spent more time closer to leks ($\beta = -0.37$, 95% CI = -0.50, -0.25) than female lesser prairie-chickens ($\beta = -0.074$, 95% CI = -0.12, -0.026).

Across the entire nonbreeding season, birds in northwestern and Red Hills Kansas, Colorado and New Mexico sites used space within their home ranges closer to leks than expected (Figure 2.4). Lesser prairie-chickens in Clark County, Kansas, displayed a pattern of avoidance of space in relation to lek locations, but confidence intervals of population beta estimates overlapped zero. With all sites combined, monthly space use in relation to leks did not change among the months of the nonbreeding season, as beta estimates of all months overlapped, and space was used closer to leks in all months except November (Figure 2.5). Space use in relation to leks by month varied by site, with no consistent pattern among sites (Figure 2.6). Birds in the Red Hills study site used space close to leks in all months whereas all other sites had some overlap with zero (Figure 2.6e). In October, lesser prairie-chickens in Colorado and New Mexico also used space closer to leks, but in November only New Mexico lesser prairie-chickens used space close to leks (Figure 2.6a,b). In December and January, birds in northwest Kansas and Colorado used space close to leks, but in February this relationship was only seen in northwest Kansas (Figure 2.6b,c).

Components of habitat use varied overall and monthly among study sites during the nonbreeding season (Figure 2.7). Grassland comprised the majority of habitat use at all sites except Colorado, for which CRP consisted of the majority of habitat use. In the Clark County study site, there was an increase in use of both CRP and Cropland with a decrease in Grassland use across the nonbreeding season (Figure 2.7). At the Red Hills study site, there was a decreasing trend in CRP use over the nonbreeding season (Figure 2.7). This decrease was from about 2% to zero. However, this was likely not a biologically relevant change in habitat use, as it represented the use of a CRP field by a single bird and ceased when she died. Lesser prairie-chickens in northwestern Kansas exhibited a pattern of increasing Cropland and CRP use as the nonbreeding season progressed, but this trend was not statistically significant (Table 2.6). I observed a relatively large proportion of the “other” habitat type used by birds in the Clark County and Red Hills study sites (Figure 2.7). I classified wet meadow and lowlands as “Other” for these study sites, representing the variable nature of habitat use among the study sites.

Discussion

Nonbreeding season ecology of lesser prairie-chickens is a necessary portion of the life-cycle to study for understanding the relative importance of habitat areas, required spatial extents, cross-seasonal effects, and informing conservation planning for this species of conservation concern. Unfortunately, due to sample size constraints from difficulty of catching females after the spring lekking season and lack of interest by assuming that this period is not affecting population growth, the nonbreeding season is an understudied portion of lesser prairie-chicken space use. The lack of information regarding nonbreeding season space use is especially true in the northern extent of the lesser prairie-chicken range, north of the Arkansas River in Kansas and Colorado. A better understanding of the full life-cycle of species is necessary to determine

whether nonbreeding lesser prairie-chickens are using space differently than breeding lesser prairie-chickens. I found 1) the mean home range size estimated for VHF transmitters is much less than those estimated from SAT-PTT transmitters. I also found that, 2) home range size is variable between nonbreeding seasons, 3) male and female lesser prairie-chickens remain close in space to leks throughout the nonbreeding season, and 4) although proportions of habitat components used among ecoregions is different, there is little change in use across the nonbreeding season for most sites.

Home range size of lesser prairie-chickens with SAT-PTT transmitters was three times greater than for lesser prairie-chickens with VHF transmitters. Methods for home range estimation of lesser prairie-chickens in the past have typically used either minimum convex polygons or fixed kernel density estimators with location data from VHF transmitters. VHF transmitters provide a coarser temporal scale of data compared to the SAT-PTT transmitters used (3-4 points/week vs. 50+ points/week). Lesser prairie-chickens outfitted with VHF transmitters often cannot be located during movement events away from the area birds were captured in until relocated by aircraft or from extensive ground-based searching. Conversely, the SAT-PTT individuals were tracked throughout their entire movement process even when dispersing from core study sites, which allowed for location of individuals when they are out of range from convenient receiver locations. The possibility also exists that the differences observed between the transmitter types are because of low sample size from VHF transmitted individuals, coupled with the large variation in home ranges of SAT-PTT individuals. This difference in home range size between transmitter types does not allow for comparison between my estimates of home range size for SAT-PTT transmitted lesser prairie-chickens to past studies, which only used VHF technology.

The estimated home range size of nonbreeding lesser prairie-chickens estimated with kernel density estimators in this study ($\bar{x} = 303.5$ ha) is within the range of estimates from past studies estimated from both kernels and minimum convex polygons. The single study that reported nonbreeding home range size in Kansas reported a range of 229 to 409 ha for October (Jamison 2000). Pirius (2011) reported nonbreeding home range estimates for VHF birds in Texas that were greater than my study by about 200 ha. Taylor (1978), using minimum convex polygons, found a wide array of home range sizes across months, with a peak in December (1946 ha) and a large decrease by February (62 ha). With estimates for VHF individuals similar to past studies, but much larger estimates for SAT-PTT individuals, it is likely that previous VHF studies underestimated the spatial extent of lesser prairie-chicken use during the nonbreeding season. As SAT-PTT transmitters are constantly decreasing in cost and size, with a 17-g transmitter already available at the time of writing this, future studies interested in space use should use these transmitters to better understand species that have the propensity to use space on the landscape scale, such as lesser prairie-chickens.

For SAT-PTT home range estimates, nonbreeding season home ranges were 181% larger than the breeding season home ranges for the counterpart to this study. Plumb (2015) found an average home range size of breeding female lesser prairie-chickens in Kansas and Colorado to be $340 \text{ ha} \pm 53$, using the same methods with SAT-PTT individuals and Brownian Bridge Movement Models. The increased size of home ranges during the nonbreeding season indicates that estimates obtained for the breeding season do not accurately represent the amount of space required for lesser prairie-chickens on an annual basis. With the capability to triple their home range size without dispersing out of the study site, coupled with increased survival rates during the nonbreeding season (Chapter I), it is likely that during the breeding season home range size is

not limited by available habitat, as lesser prairie-chickens can use a greater amount of space without impacting survival rates. Home range size limitations during the breeding season are more likely explained by reproductive activities that limit the extent of movement from a central location, such as tending nests and broods (Plumb 2015). Combining the breeding and nonbreeding locations for these birds to calculate annual home ranges will indicate whether the amount of annual space used increases or remains consistent in comparison to the nonbreeding season.

Home range size varied by site only in the first nonbreeding season, with the mean home range estimate in northwestern Kansas site being 50% smaller than that for Colorado and the Red Hills. Home range sizes were not statistically different among sites for the 2014-2015 nonbreeding season, but the same pattern was observed; northwestern Kansas had a smaller home range size than all other sites. However, overall, home range size did not differ among sites or ecoregions between the two seasons of this study. One of the likely reasons for the lack of difference in home range size among study sites was the large amount of variability in home range size among individuals within study sites, which can be observed in large standard errors for home ranges, especially in the Red Hills and Clark County. The variation in home range size is due to individual variation, with some individuals moving a great deal over the course of the year and others remaining in a comparatively small area. That a difference in home range size was not observed among study sites in different ecoregions, such as New Mexico in the Sand Shinnery Oak Prairie Ecoregion and the Red Hills in the Mixed-Grass Prairie Ecoregion, or between areas with different lesser prairie-chicken densities, indicates that lesser prairie-chickens have similar nonbreeding space requirements across their range. The next step to understanding this relationship could be to separate birds that exhibit different life-cycle strategies, such as

extensive versus limited movement, and try to understand why birds are behaving in different ways, such as genetic differentiation.

Mean home range size during the 2013-2014 nonbreeding season was 136% greater than that for the 2014-2015 nonbreeding season. During the 2013 growing season, the entire Southern Great Plains region remained in a severe drought, but the 2014 growing season brought more rain across all study sites (KState Research and Extension 2014, Figure 2.8). Increased precipitation during the growing season alters the landscape to increase habitat quality for lesser prairie-chickens, relative to drought years. This increase in habitat quality could increase the perspective of available habitat on the landscape by lesser prairie-chickens, as well as increase functional connectivity (Hodgson et al. 2011). Additional years of data for the nonbreeding season may determine whether this pattern of increasing home range size with increasing habitat quality remains consistent. While home range size may be different in years with different amounts of precipitation, yearly differences in home range size did not have an effect on survival of nonbreeding lesser prairie-chickens (Chapter I). As increased home range size during the nonbreeding season does not decrease survival or coincide with differences among ecoregions, seasons with more movement could allow for the potential colonization of new habitat; thus, increasing the probability of population persistence.

Nonbreeding season space use is understudied in other species of prairie-grouse, with only a single study that explicitly estimated nonbreeding home range size (Winder et al. 2014). The estimated nonbreeding season home ranges using VHF transmitters for greater prairie-chickens (*Tympanuchus cupido*) in eastern Kansas were 7.1-7.8 km² (710-780 ha; Winder et al. 2014). These home range estimates are 148% larger than my VHF estimates of home range size; however, a direct comparison cannot be made between the studies, due to the lack of SAT-PTT

individuals in Winder et al. (2014). They reported that home range size increased with increasing levels of fragmentation: however, I did not find mean home range differences between study sites with differing levels of relative fragmentation (Chapter III).

Contrary to my prediction, home range size did not differ between males and females for the nonbreeding season. Lesser prairie-chickens congregate into mixed sex wintering flocks after the breeding season (Riley et al. 1993), which could lead to males and females moving in a similar fashion. However, despite the similarity in home range size, intensity of space use within home ranges in relation to leks differed between males and females. Differential space use between sexes was likely due to the tendency of males to use leks more often throughout the year. For example, males visited leks during the months of September and October, when the photoperiod was similar to that of the photoperiod in the spring lekking season, and will move back to leks in late February (Applegate and Riley 1998).

Overall, lesser prairie-chickens used space in their home range closer to leks than areas within their home range that were further away from leks throughout the nonbreeding season. A relationship with leks would be expected for the breeding season, when lesser prairie-chickens are all visiting leks for reproductive purposes. Nonbreeding season use of space around leks could be explained by leks forming in areas where females are already most likely to be located, due to higher quality nesting and brooding habitat (Schroeder and White 1992, Gibson 1996). If leks are already placed in the highest quality available habitat for lesser prairie-chickens, then there would be little reason for males or females to leave the vicinity of the lek during the nonbreeding season. Such a relationship for the nonbreeding season was unexpected, adding increasing evidence that landscapes around existing leks should be prioritized for conservation and mitigation. The notion of lek importance is already well understood for breeding lesser

prairie-chickens, so maintaining breeding season habitat, but with increased buffering around those areas to account for nonbreeding space use is likely adequate for annual lesser prairie-chicken habitat needs.

With similar life history strategies, it appears that regardless of the species, prairie-chickens are tied to the lek throughout the year. Distance to lek was the strongest predictor of space use for female greater prairie-chickens in Kansas, with a negative relationship for both breeding and nonbreeding seasons (Winder et al. 2014). The breeding season counterpart to my study found that distance to lek was also a significant predictor for space use in female prairie-chickens, but as expected, the relationship was stronger ($\beta = -0.11$, $SE = 0.03$; Plumb 2015). Identification of lek importance during the nonbreeding season could have positive impacts for the future of lesser prairie-chicken conservation, as it provides a target on the landscape to prioritize land conservation and acquisition initiatives.

With consistent relationship between leks and home range size across the four lesser prairie-chicken ecoregions, my next step was examining nonbreeding habitat use to test whether habitat needs changed throughout the season, or differed among ecoregions. Although lesser prairie-chickens used different proportions of grassland, cropland and CRP among study sites, the proportion of use did not change over time within each study site, with one exception, in Clark County Kansas. It appears that the differences of habitat use in these ecoregions correspond to the apparent availability of habitat, such as the nearly explicit use of grassland in the Red Hills and the predominant use of habitat in Colorado being CRP. These findings necessitate the study of resource selection specific to each ecoregion or at finer spatial scales to determine habitat areas important and possibly limiting for lesser prairie-chickens. Only birds in the Clark County study site varied components of habitat used across the nonbreeding season.

The Clark County study site also exhibited increased mean weekly movement relative to the other study sites (Table A.1). However, home range size in Clark County was not significantly different from other sites, and despite not using space close to leks within their home range. If bird density is greater in this region, it could explain the use of space away from leks and the change in habitat use, as a spillover effect from the prime habitat surrounding leks, but this possibility would need to be tested by estimating lesser prairie-chicken density among study sites. Alternatively, the trend with decreased habitat use of grassland may correspond to a decrease of habitat quality around the leks, which would lead birds to require cropland and CRP to meet their cover and food requirements. I only had one year of data from this site for the purpose of this analysis, and an additional year of data could determine that differences are not as apparent as these initial results suggest.

If the Clark County, Kansas, study site is considered an outlier in regards to nonbreeding lesser prairie-chicken space and habitat use, we see consistency among lesser prairie-chickens in all ecoregions. My data fill knowledge gaps in relation to habitat use and space use for nonbreeding lesser prairie-chickens, which can be used in the future to inform managers how to assimilate nonbreeding ecology into overall management objectives. Future researchers need to consider availability in relation to use to determine how important habitat types across the different ecoregions.

Management Implications

Management should be taking into account nonbreeding or annual home range size estimates, not just breeding season, when trying to determine the proper amount of space required for a sustainable lesser prairie-chicken population. Future habitat management should focus on preserving habitat around leks to maintaining habitat quality sufficient for lek placement. Past recommendations of area around leks required for lek persistence were ≥ 2000 ha

tracts of grassland (Hagen et al. 2004); this area recommendation fits with my results to conserve existing habitat around leks. If these areas are already conserved, acquiring and improving habitat outward from lek locations will aid in the functional connectivity of the landscape and aid in future population persistence. Specific habitat requirements need to be developed by ecoregion to realistically and more beneficially manage for lesser prairie-chicken habitat in the future, such as keeping CRP available to birds in the Shortgrass/CRP Prairie, Sand Sagebrush and Shinnery Oak Prairies, but contiguous grassland patches in the Mixed-Grass prairie.

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Figure 2.1 Defined ecoregions across the lesser prairie-chicken range (McDonald et al. 2014). States represented in this study were Kansas, Colorado and New Mexico. Kansas contains portions of the Mixed-Grass, Sand Sagebrush and Shortgrass/CRP Mosaic Prairie. Colorado contains the Sand Sagebrush Prairie and New Mexico contains the Sand Shinnery Oak Prairie.

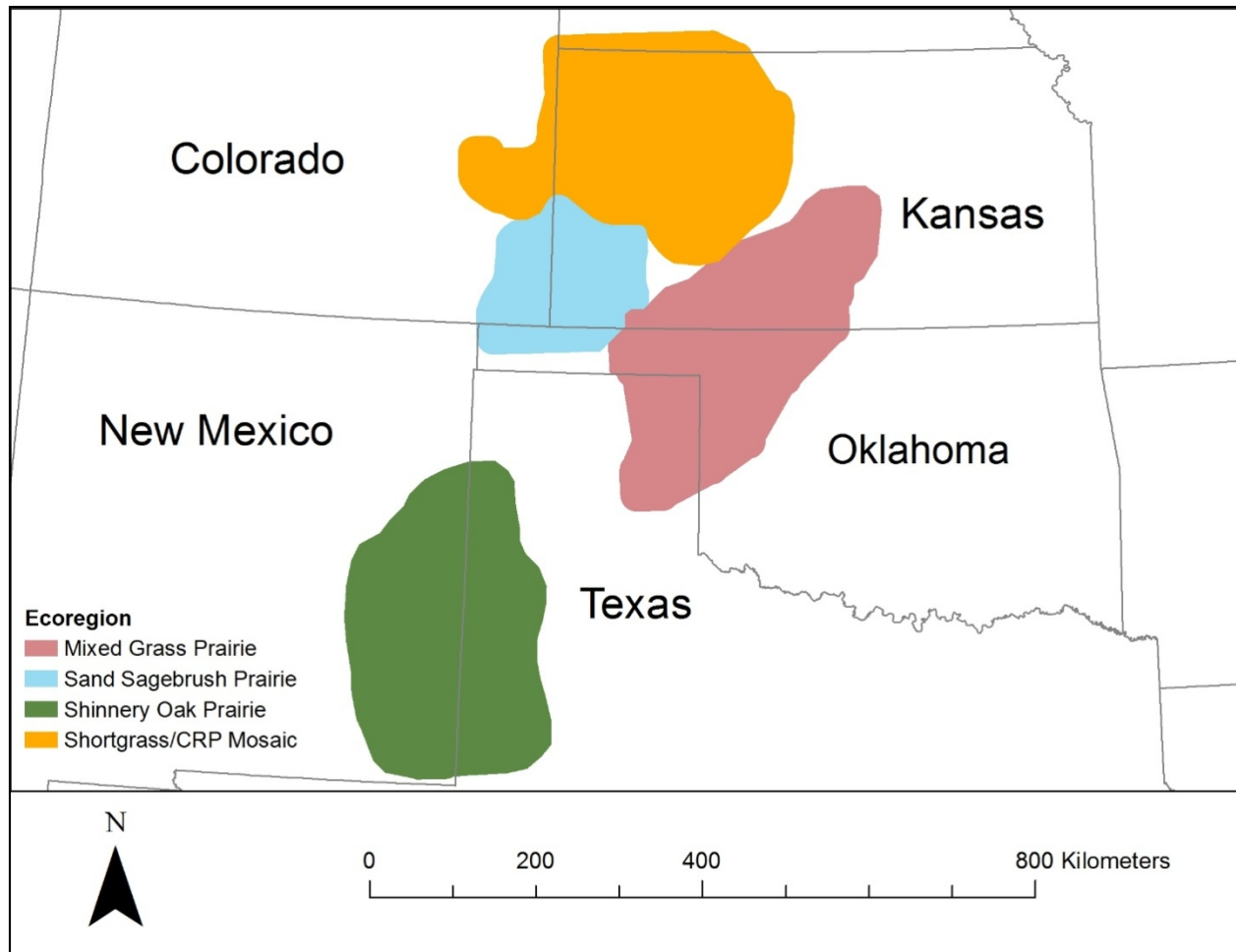


Figure 2.2 Map of study sites across the current lesser prairie-chicken range (shown in light blue). The Kansas study sites (Northwest, Clark, Red Hills; shown in blue) were located in Logan, Gove, Kiowa, Comanche and Clark counties. The Colorado study sites were primarily located in Prowers and Baca counties (shown in purple) and the New Mexico study site was located in Lea and Roosevelt counties (shown in orange).

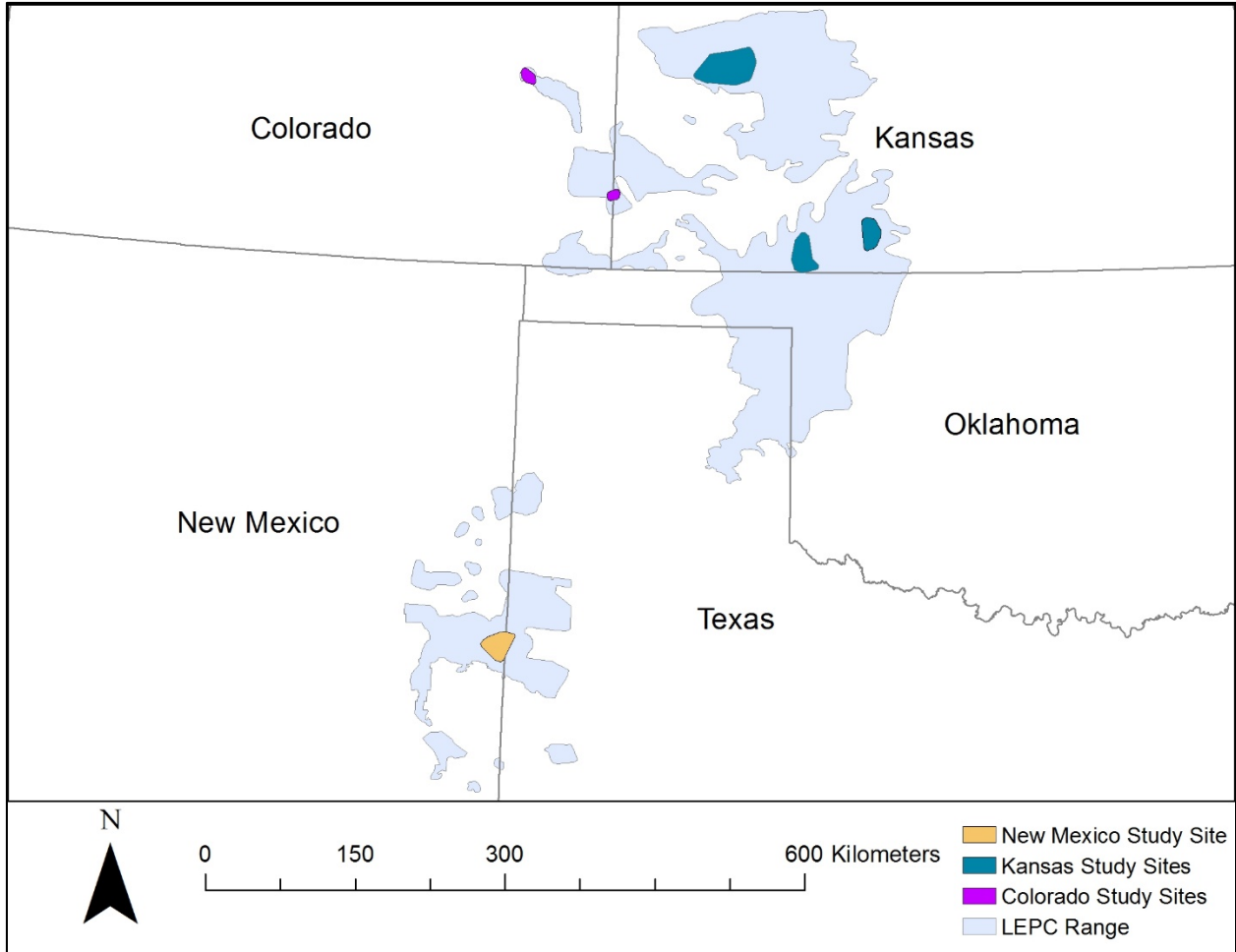


Figure 2.3 Examples of home ranges of two lesser prairie-chickens representing differential space use within their home ranges relative to lek locations. Darker areas indicate areas with greater intensity of space use, with the white area indicating the 99% isopleth, or “available” space.

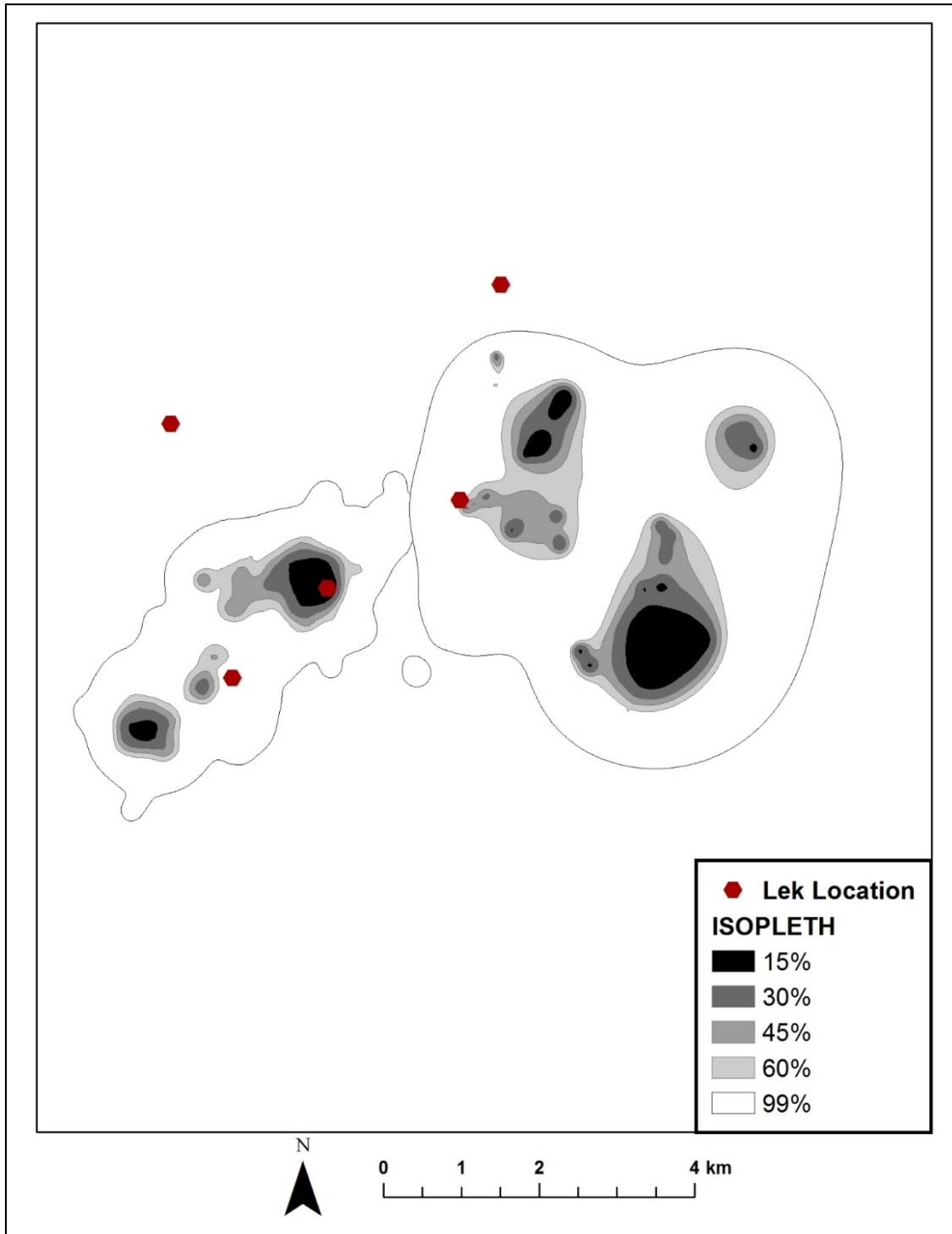


Figure 2.4 Beta estimates (with 95% CI) for each study site of distance to lek for nonbreeding lesser prairie-chickens during 2013-2015 based on Resource Utilization Functions. Distance to lek was a consistent predictor of space use for Colorado, New Mexico, Northwestern Kansas, Red Hills, Kansas, but was not a consistent predictor of space use for Clark County, Kansas. Samples for Kansas and Colorado sites were composed of more females than males (Clark; 94%, Northwest; 86% and Red Hills; 83%, Colorado; 56%), compared to New Mexico (13%).

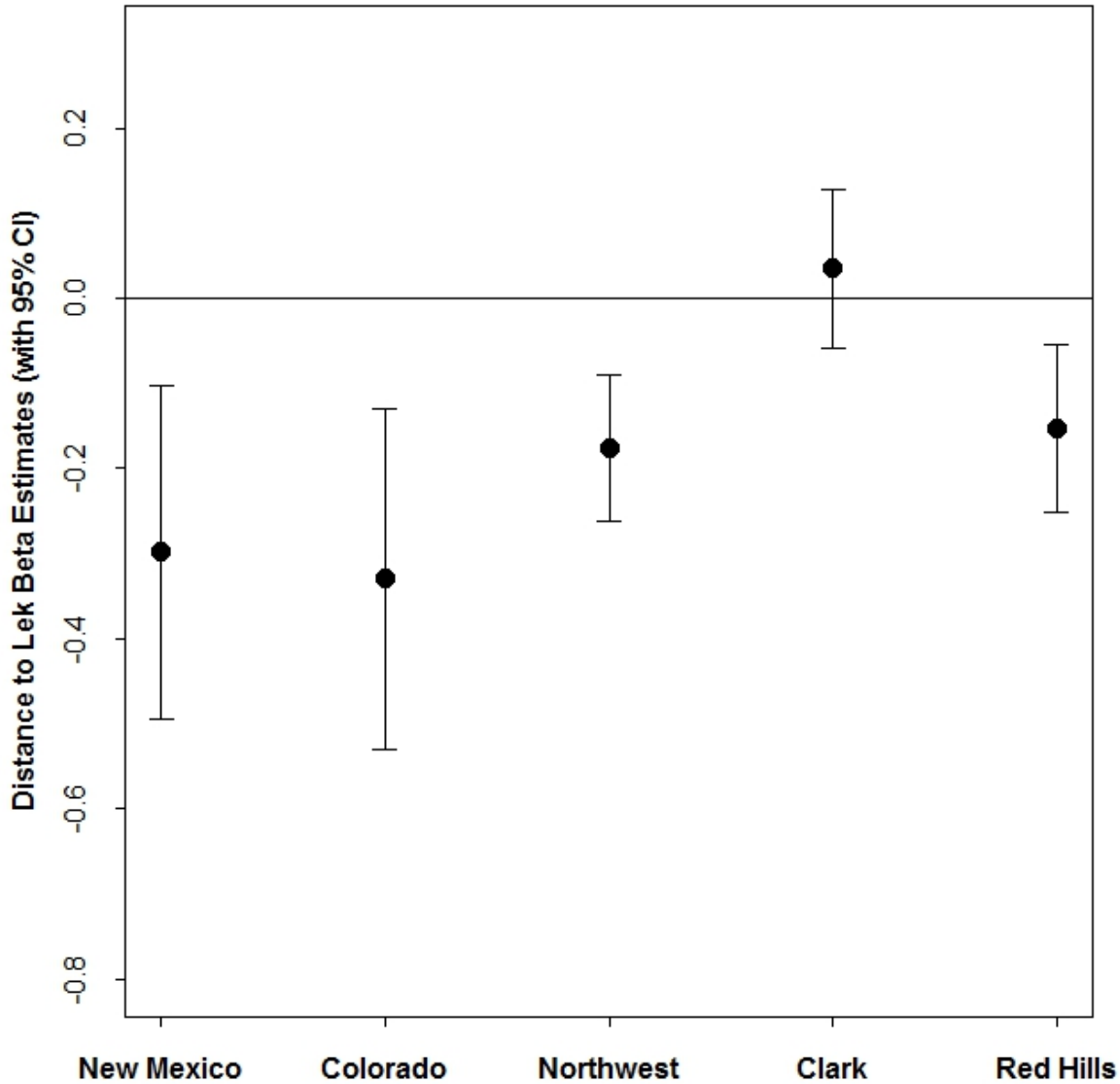


Figure 2.5 Monthly beta estimates (with 95% CI) for distance to lek for all nonbreeding lesser prairie-chicken in Kansas, Colorado and New Mexico during 2013-2015. Distance to lek was a significant predictor of space use in the months of October, December, January and February, but November had a confidence interval overlapping zero, indicating it was not a significant predictor of space use during that month. Sample sizes are primarily (77%) composed of female lesser prairie-chickens.

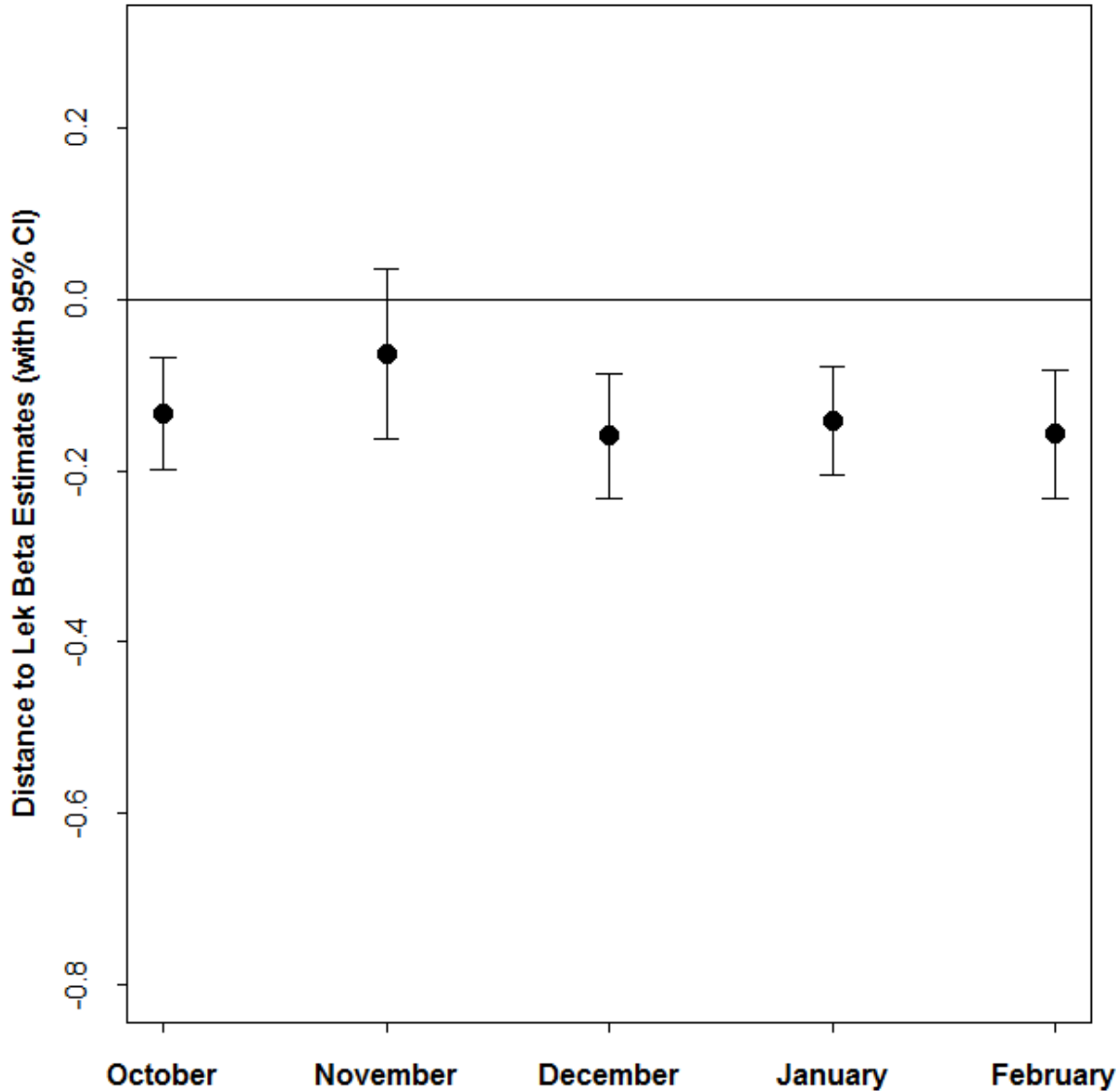


Figure 2.6 Monthly beta estimates for all sites for distance to lek as a predictor of lesser prairie-chicken space use during 2013-2015 for a) New Mexico, b) Colorado, c) Northwest, Kansas, d) Clark County, Kansas, and e) Red Hills, Kansas. Beta estimates were considered significant predictors of space use if their CI did not overlap zero. No differences were observed among months, within study sites. Samples for Kansas and Colorado sites were composed of more females than males (Clark; 94%, Northwest; 86% and Red Hills; 83%, Colorado; 56%), compared to New Mexico (13%).

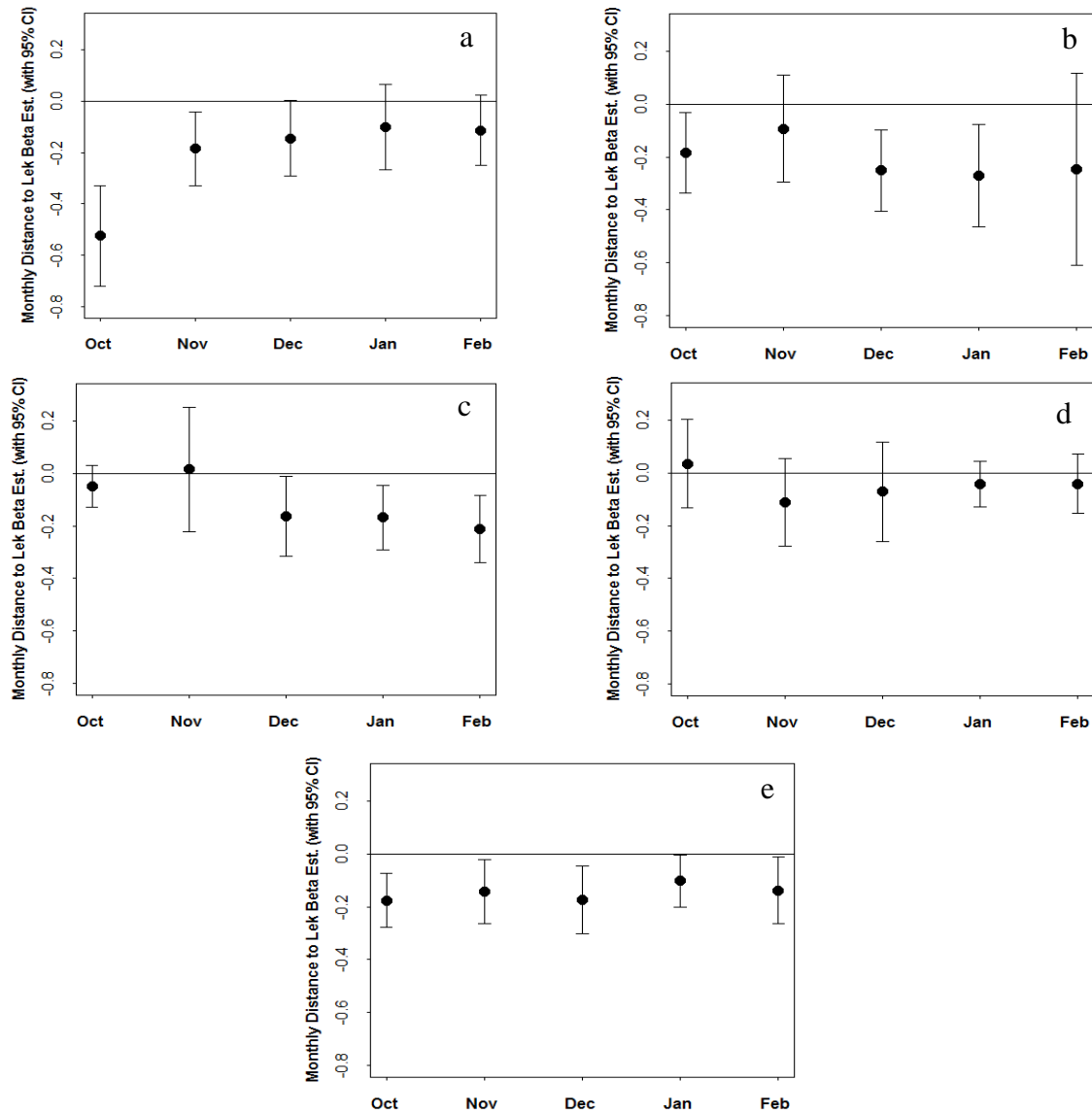


Figure 2.7 Proportion of habitat composition used by lesser prairie-chickens across months for all sites during the nonbreeding seasons of 2013-2014 and 2014-2015 for Colorado, Northwest and Red Hills, and just for the nonbreeding season of 2014-2015 for New Mexico and Clark. Trends indicate a decrease in use of grassland, corresponding to an increase in use of crop and Conservation Reserve Program (CRP) fields for Clark County, but not any other site.

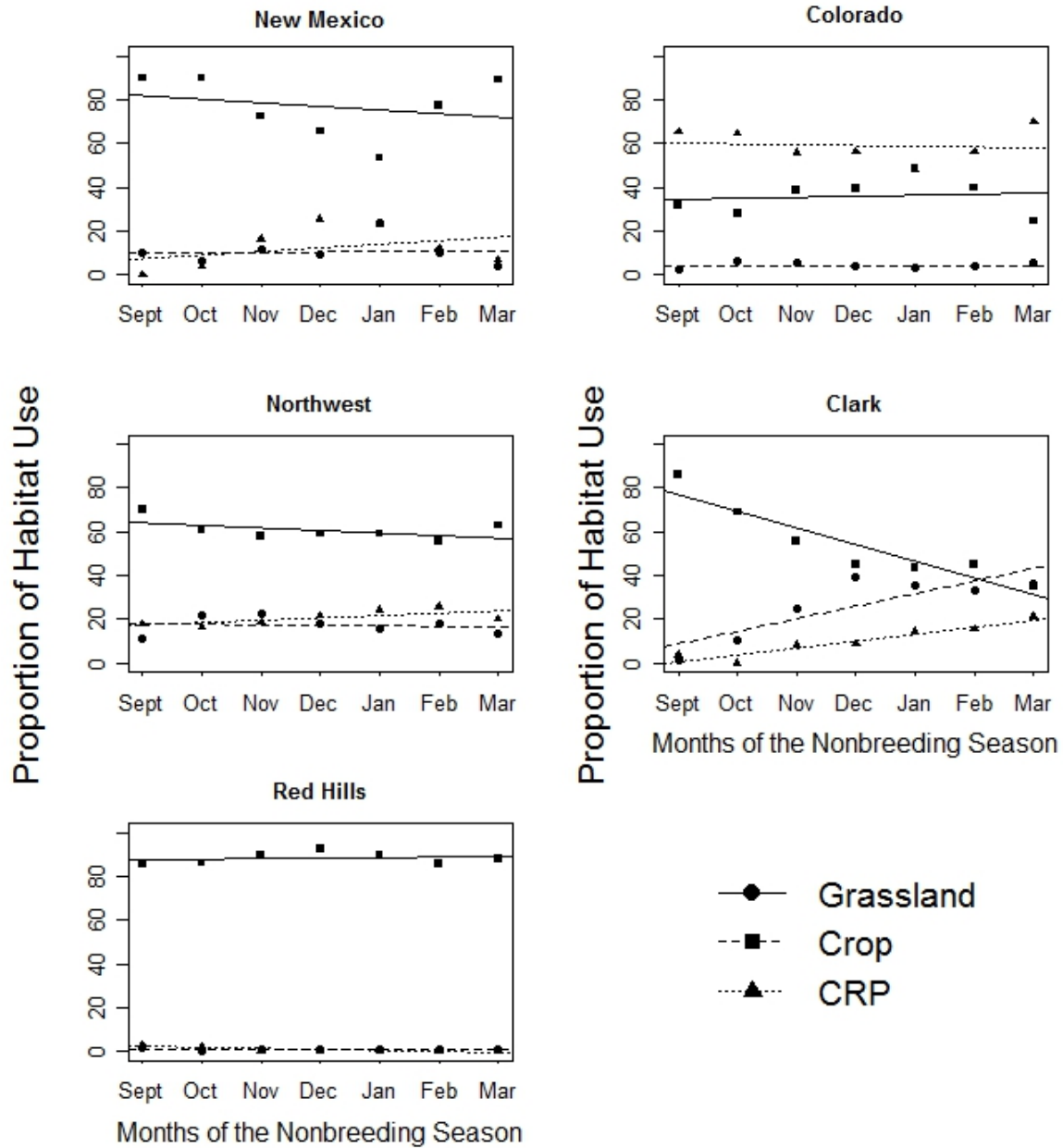


Figure 2.8 Total precipitation levels in during the growing season (April through September) for 2013 and 2014 across 5 study sites in Kansas, Colorado and New Mexico.

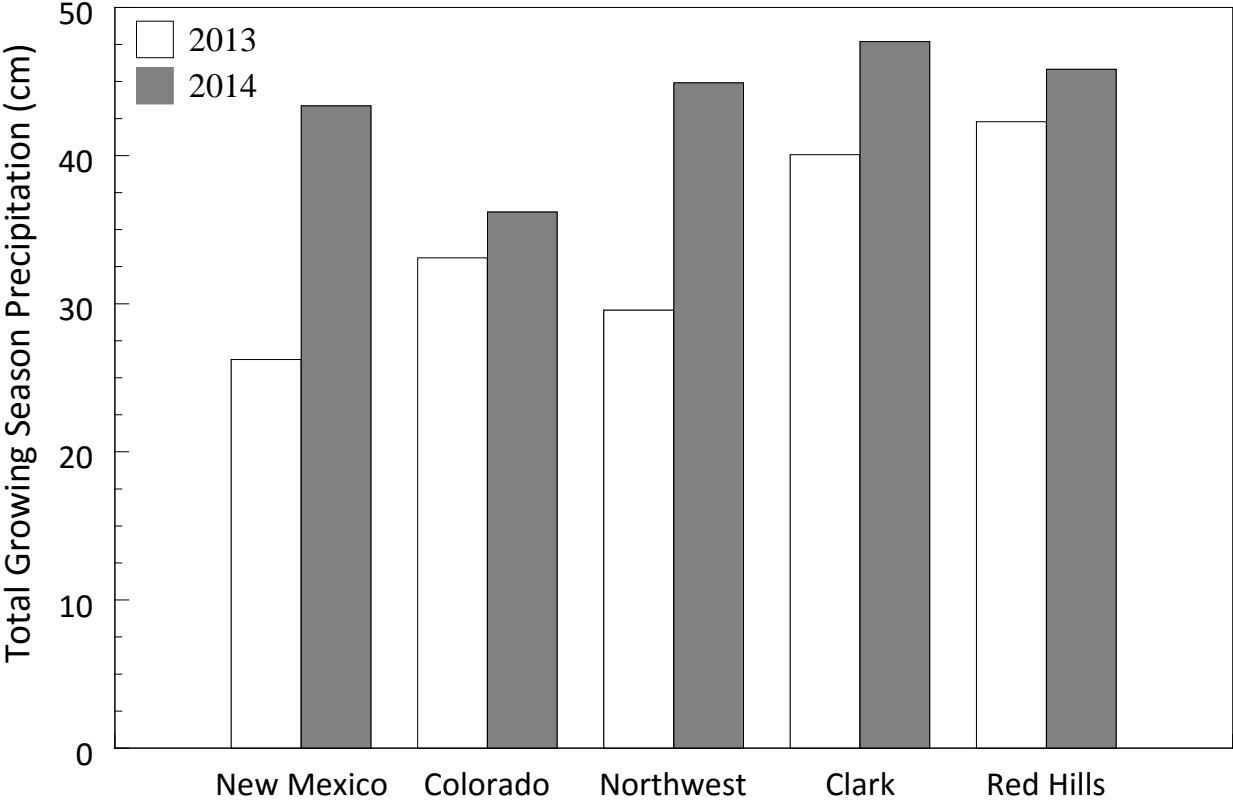


Table 2.1 Studies of nonbreeding lesser prairie-chicken home range size, displaying state, season, home range estimate and method of estimation.

Source	State	Sample Size	Season	Home Range (ha)	Method ¹
Candelaria 1979	New Mexico	2 males	Fall and Winter	298.19, both sexes	Grid maps
		2 females			
Jamison 2000	Kansas	23 males	October	229-409, males	KDE
Pirius 2011	Texas	6 female	Nonbreeding	503.5, female	KDE
		17 male		489.1, male	
Taylor 1978	Texas	12 male 7 female	November	160-789, both sexes	MCP
			December	1946, both sexes	
			January	331, both sexes	
Toole 2005	Texas	7 individuals	Seasonal	207, both sexes	MCP
		19 females		303.5, females	KDE
Robinson 2015	Kansas	46 females 22 males	Nonbreeding	954.7, both sexes	BBMM

¹ KDE = Kernel Density Estimate, MCP = Minimum Convex Polygon; BBMM = Brownian Bridge Movement Model

Table 2.2 Total number of Males (M) and Females (F), as well as SAT-PTT (SAT) and VHF marked lesser prairie-chickens during each year, used to estimate home range size for five sites in Kansas, Colorado and New Mexico, and two nonbreeding seasons (2013-2014, 2014-2015) Kansas study sites include Northwest, Red Hills and Clark County, with one site each in Colorado and New Mexico. Individuals were included in the overall home range estimation if they did not disperse outside of the delineated study site and survived at least 2 weeks into the nonbreeding season.

Study Site	2013-2014					2014-2015				
	M	F	SAT	VHF	Total	M	F	SAT	VHF	Total
Northwest	2	15	12	5	17	3	11	10	4	14
Red Hills	3	11	11	3	14	2	9	8	3	11
Clark Co.	-	-	-	-	-	1	13	10	4	14
Colorado	2	4	6	-	6	2	1	3	-	3
New Mexico	-	-	-	-	-	7	1	8	-	8
Total					37					50

Table 2.3 95% Kernel Density Estimates (ha) of 95% volume contour home range for VHF marked, nonbreeding female lesser prairie-chickens in Kansas. The nonbreeding season was the six-month period between 16 September and 14 March. Home range size was estimated for individuals that had ≥ 30 points throughout the entire nonbreeding season.

Study Site	2013-2014				2014-2015			
	N	\bar{x}	SE	Range	N	\bar{x}	SE	Range
Northwest	5	293.2	25.36	234.6-387.5	4	371.52	63.66	249.4-548.5
Red Hills	3	323.55	47.2	267.9-417.4	3	231.42	91.57	57.2-367.3
Clark County	-	-	-	-	4	287.37	55.65	130.9-369.1

Table 2.4: Average 95% isopleth home range (ha) of Satellite-marked lesser prairie-chickens in Kansas, Colorado and New Mexico during the nonbreeding seasons of 2013-2014 and 2014-2015. Estimates include both male and female lesser prairie-chickens. All satellite marked individuals had ≥ 100 points with which to estimate home ranges with.

Site	2013-2014				2014-2015			
	N	\bar{x}	SE	Range	N	\bar{x}	SE	Range
Northwest	12	336.88 ^A	69.74	62.1-706.4	10	683.73	103.58	227.3-1168.3
Red Hills	11	666.80	119.27	211.1-1391.7	8	1498.04	866.70	260.2-7473.5
Colorado	6	694.71 ^A	149.38	302.4-1180.9	3	1178.97	736.28	305.5-2642.4
Clark	-	-	-	-	10	1730.12	311.30	539.8-3412.4
New Mexico	-	-	-	-	8	1208.91	173.05	608.2-2071.6

^A Means differed in 2013-2014 ($P < 0.05$)

Table 2.5 Monthly home range estimates for satellite marked male and female lesser prairie-chickens in Kansas, Colorado and New Mexico, that had ≥ 100 points available within a whole months. Home ranges were estimated using Brownian Bridge movement models.

Month	Number of Bird-Months	Mean	SE
October	63	703.0	174.4
November	61	674.4	108.2
December	58	596.0	77.6
January	52	449.6	51.8
February	51	546.2	68.4
Total	285	600.8	50.1

Table 2.6 Results from simple linear regression assessing trends of habitat use for nonbreeding lesser prairie-chickens in three study site in Kansas (Northwest, Red Hills, and Clark County), Colorado, and New Mexico during 2013 – 2015.

Site	Habitat Type	$r^2 \leq$	$F_{1,5} \leq$	$P \leq$
Northwest	Grassland	0.26	1.78	0.24
	CRP	0.48	4.67	0.083
	Crop	0.02	0.1	0.76
Red Hills	Grassland	0.038	0.2	0.68
	CRP	0.64	8.74	0.032*
	Crop	0.001	0.001	0.98
Clark County	Grassland	0.86	31.45	0.0025**
	CRP	0.9	46.16	0.0011**
	Crop	0.72	12.92	0.016*
Colorado	Grassland	0.012	0.063	0.81
	CRP	0.012	0.062	0.81
	Crop	0.001	0.001	0.99
New Mexico	Grassland	0.064	0.34	0.58
	CRP	0.12	0.69	0.45
	Crop	0.0012	0.006	0.94

Chapter 3 - Effects of landscape characteristics on survival of female lesser prairie-chickens

Introduction

Settlement of the Southern Great Plains by early pioneers caused wide-spread change of grassland landscapes (Coppedge et al. 2001). Landscape fragmentation in the plains, namely loss of grasslands with an increase in grassland patch isolation (Fahrig 2003), has resulted from direct conversion of land from native prairie to agriculture uses, such as row-cropping or livestock grazing, but has also been caused by the addition of anthropogenic objects on the landscape. Power lines, fences and infrastructure of oil and gas can affect species distribution and space use by creating barriers to movement, discrete area of species avoidance, and creating new places for predators to traverse and perceive the landscape (Robel et al. 2004, Pruett et al. 2009). With a growing demand for energy, food, and infrastructure as the human population grows, impacts on grassland species are going to increase through the addition of anthropogenic features and changes in landscape structure.

Lesser prairie-chickens (*Tympanuchus pallidicinctus*) are an umbrella species in grasslands for which conservation could be beneficial to many species on the landscape. This species is able to traverse large areas of the landscape, and requires a heterogeneous landscape configuration with varying habitat characteristics for nesting, brooding, cover, and foraging (Fuhlendorf and Engle 2001). Lesser prairie-chickens have experienced population declines since the settlement of the Southern Great Plains in the late 1800s, with the most recent population peak in the 1980s, and additional sharp declines documented since 2012 (McDonald et al. 2014, Garton et al. 2016). Declines of lesser prairie-chickens have been attributed to large-scale conversion of grassland to crops, drought, and increase in energy infrastructure across the landscape (Hagen and Giesen 2005). Quantifying the effect of variations in habitat amount,

habitat configuration, and anthropogenic features on the landscape is necessary to further understand factors driving population declines. Lesser prairie-chickens in Kansas and Colorado persist in three ecoregions with distinct soil and vegetative characteristics and varying degrees of perceptual fragmentation (McDonald et al. 2014). The existence of populations of birds in landscapes with different patterns of configuration, and variable amounts of habitat loss, can allow for an assessment of population vital rates as a function of landscape fragmentation and configuration.

Studies in landscape ecology predict the existence of a threshold at which habitat loss is too great for populations to persist (Fahrig and Marriam 1985, Fahrig 2001, Fahrig 2003). The response of population persistence to habitat loss needs to be considered on a species-basis, as the specific mechanisms of a species life-history that would dictate responses to fragmentation (Dooley and Bowers 1998). As populations begin to reach this threshold, it would be expected that vital rates of populations would begin to decline as a warning sign of the approaching population decline and eventual extinction. For example, if mortality outweighs reproduction due to lack of available habitat, populations will inevitably decline (Fahrig 2002). Changes in population dynamics can be driven by the configuration of the landscape, composition of the landscape, and heterogeneity of the impacts of anthropogenic features on the landscape. However, to understand the influence on these processes, habitat loss and habitat fragmentation need to be measured and interpreted separately, as fragmentation impacts may be less influential relative to habitat loss (Fahrig 2003). We need to understand the processes that affect this threshold and potential localized extinction that can occur once it is reached. Additionally, the relationships among population dynamics and landscape effects need to be identified at multiple scales, from the effect on individuals to effects on populations (Fahrig and Marriam 1985,

Dooley and Bowers 1998). If relationships exist among lesser prairie-chicken vital rates and landscape structure, understanding the direct and indirect drivers of these relationships can also assist mitigation to target areas on the landscape for habitat mitigation (Fahrig 2002).

Habitat loss, increased patch isolation and anthropogenic development, have the potential to negatively affect lesser prairie-chicken females through several mechanisms, such as an increase in edge habitat between habitat types increasing predator occupancy and increased barriers to movement away from areas lacking key survival requirements (Patten et al. 2005). Energy development also has the potential to increase stress and reduce body condition in upland game birds; thus, reducing survival and future reproductive output (Lima 1986, Blickley et al. 2012). Past studies have determined patterns of avoidance of power lines, buildings, and, to a lesser extent, paved roads and oil wells by lesser prairie-chickens (Hagen et al. 2011). Thresholds have also been identified for habitat selection around anthropogenic landscape features (Plumb 2015). The effect of landscape change on the persistence of leks and overall population growth has been addressed indicating that increasing landscape fragmentation decreases the probability of lek persistence (Woodward et al. 2001). To my knowledge, studies have not yet investigated the relationship between landscape change and lesser prairie-chicken survival.

Survival rates of female lesser prairie-chickens have been identified as having one of the greatest effects on the finite rate of population change in Kansas (Hagen et al. 2009). A study of greater sage-grouse (*Centrocercus urophasianus*) found that there was a negative association between female survival and powerline density (Dinkins et al. 2014). Fences and powerlines could also decrease lesser prairie-chickens survival through their availability as perches for avian predators. Although seasonal variation in raptor abundance from a one year study did not directly

affect nonbreeding survival of female lesser prairie-chickens (Chapter I), the effect on survival may be indirect, such as through increased abundance of raptor perches (Ellis 1984, Dinkins et al. 2014). Noise from oil wells and roads could influence mortality due to increased sound affecting body condition and foraging rates (Ware et al. 2015); roads could influence hazards through direct mortality from car strikes (Case 1978). These relationships need to be investigated for lesser prairie-chickens; thus, research designed to determine the effect of landscape features, habitat composition and configuration on survival can help inform future management and conservation actions. Using survival across the annual cycle of lesser prairie-chickens, from the lekking through the nonbreeding seasons, will allow for a better understanding of the overall effect that landscape characteristics can have on lesser prairie-chicken survival. This information will be the first step in the design of an optimal landscape to maximize the lesser prairie-chickens probability of population persistence.

My objectives were to 1) estimate annual lesser prairie-chicken survival and assess differences in landscape composition and configuration among study sites in Kansas and Colorado, 2) determine if landscape composition and configuration within home ranges have an effect on lesser prairie-chicken survival rates, and 3) determine if distance to anthropogenic features and landcover type influence lesser prairie-chicken hazard rates. I hypothesized that annual survival rates will be lower for sites, and individuals with less grassland habitat, and a more fragmented landcover configuration. I also expected to find that anthropogenic features that can act as perches for predators (powerlines, fences, oil wells) will increase hazard rates for female lesser prairie-chickens.

Study Area

Four study sites were located in three ecoregions across the range of lesser prairie-chickens in Kansas and Colorado (Figure 3.1). In northwestern Kansas, lesser prairie-chickens are found in the Short-Grass Prairie/Conservation Reserve Program (CRP) Mosaic Ecoregion (Van Pelt et al. 2013, McDonald et al. 2014). This population of lesser prairie-chickens may have recently expanded north of the Arkansas River (Bain 2002, Fields et al. 2006, Rodgers 2016). In south-central Kansas, lesser prairie-chickens are found in the Mixed-Grass Prairie and Sand Sagebrush Prairie Ecoregions (Van Pelt et al. 2013, McDonald et al. 2014). The Short-Grass/CRP, Mixed-Grass and Sand Sagebrush ecoregions were characterized by different soil types, plant assemblages, management regimes, and vegetation conditions. The northwestern Kansas study site consisted of private lands in Gove and Logan counties. Whereas, in south-central Kansas, I had two study sites, which consisted of private lands in Kiowa, Comanche, and Clark counties. The Colorado study site was primarily located in Cheyenne and Prowers counties.

The northwestern Kansas study site was 171,437 ha, and located in Logan and Gove Counties. The primary land uses in this area were livestock grazing, energy extraction, and both dryland and row-crop agriculture. The northwestern study site was located in the Shortgrass Prairie/Conservation Reserve Program (CRP) Mosaic Ecoregion (Van Pelt et al. 2013, McDonald et al. 2014), with CRP grasslands and row-crop agriculture on silt-loam soils. Dominant vegetation in the region included blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsute*), buffalograss (*B. dactyloides*), little bluestem (*Schizachyrium scoparium*), sideoats grama (*B. curtipendula*), big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat

(*Eriogonum annuum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed (*Ambrosia psilostachya*; Lauver et al. 1999). Mixed-grass prairie species occurred on certain soil types. Grass species planted in CRP fields included little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indian grass (*Sorghastrum nutans*) (Fields 2004). The CRP fields were interseeded with forbs in the 1990s; forbs included white sweet clover (*Melilotus alba*), yellow sweet clover (*Melilotus officinalis*), Maximillian sunflower (*Helianthus maximiliani*), Illinois bundleflower, purple prairie clover (*Dalea purpurea*), and prairie coneflower (*Ratibida columnifera*; Fields 2004). Wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), and corn (*Zea mays*) were the major crops in the region.

In south-central Kansas, I had two study sites in mixed-grass prairie on loamy soils. The Red Hills, Kansas study site was 49,111 ha and centered on private lands in Kiowa and Comanche counties within the Mixed-Grass Prairie Ecoregion (Van Pelt et al. 2013, McDonald et al. 2014). Primary land uses for this area included livestock grazing, oil and gas extraction and exploration, with row-crop agriculture interspersed throughout the region. Dominant vegetation in south-central Kansas included little bluestem, blue grama, hairy grama, sideoats grama, buffalograss, sand dropseed (*Sporobolus cryptandrus*), Louisiana sagewort (*Artemisia ludoviciana*), western ragweed (*Ambrosia psilostachya*), sand sagebrush (*Artemisia filiafolia*), and eastern red cedar (*Juniperus virginiana*; Lauver et al. 1999). The Clark County study site within south-central Kansas was 71,209 ha and located at the boundary of the Mixed-Grass Prairie and Sand Sagebrush Prairie Ecoregions (Van Pelt et al. 2013, McDonald et al. 2014). Land use was dominated by livestock grazing, oil and gas extraction, and row-crop agriculture. Dominant vegetation in the area included: little bluestem, sideoats grama, blue grama, hairy

grama, big bluestem, alkali sacaton (*Sporobolous airoides*), Russian thistle (*Salsola kali*), kochia (*Kochia scoparia*), annual sunflower (*Helianthus annuus*), and sand sagebrush. The Clark County site also had considerable alkali flats along drainages.

Within eastern Colorado, study sites were located on private lands in Cheyenne and Prowers counties totaling 28,388 ha. All study sites were within the Sand Sagebrush Prairie Ecoregion (Van Pelt et al. 2013, McDonald et al. 2014; Figure 1.1). Land use within the study site was livestock grazing, row-crop agriculture, and CRP grasslands. Dominant vegetation in the region included blue grama, hairy grama, sideoats grama, buffalograss, little bluestem, big bluestem, sand sagebrush, kochia, and Russian thistle. Major crops within the region were wheat, sorghum, and corn.

Methods

Capture

Lesser prairie-chickens were captured at leks in spring (March – May) during 2013 and 2014. Birds were trapped using walk-in drift traps, magnetic dropnets, and rope-trigger dropnets (Haukos et al. 1990, Silvy et al. 1990, Schroeder and Braun 1991). Captured individuals were aged using the degree of spotting on the 9th and 10th primaries; second-year birds had spotting within 3.8 cm from the feather tip and after-second-year birds had spotting \geq 3.8 cm from the tip (Copelin 1963). I also used the amount of wear of the feather tips as juvenile grouse do not molt those primaries until their second year, and thus, have more frayed feather tips (Copelin 1963). The sex of individuals was determined using tail feather color; females had barred tail feathers and male lesser prairie-chickens had mainly black tail feathers (Copelin 1963).

Female lesser prairie-chickens were outfitted with either 12-15-g bib-style VHF transmitters (A3960, Advanced Telemetry System, Isanti, USA) or a rump-mounted 22-g Satellite Platform Transmitting Terminal GPS transmitter (PTT-100, Microwave Telemetry,

Columbia, USA). SAT-PTT transmitters were attached on the rump using leg harnesses made of Teflon[®] ribbon with elastic at the front of the harness for flexibility (Bedrosian and Craighead 2010, Dzialak et al. 2011). All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocol 3241), Kansas Department of Wildlife, Parks and Tourism scientific collection permits (SC-042-2013 and SC-079-2014), and Colorado Parks and Wildlife scientific collection licenses (13TRb2053 and 14TRb205).

Tracking

Female prairie-chickens outfitted with VHF transmitters were located via triangulation 3-4 times per week. Once individuals were detected they were triangulated from 3-5 locations to estimate location. A three-piece hand-held Yagi antenna and either an Advanced Telemetry Systems Receiver (R4000, R4500, Advanced Telemetry Systems, Isanti, USA) or a Communications Systems Receiver (R-1000, Communications Specialists, Orange, USA) were used to take bearings on individuals. Bearings were ≥ 15 degrees apart and taken within 20 minutes 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 determine the estimated UTM location of the individual and calculate an error polygon around the point. I attempted to limit error polygons to 0.1ha, but used locations up to one ha (~21%). If individuals could no longer be located due to dispersal from the study site, fixed wing aircraft was used locate them.

Birds outfitted with a Satellite-PTT transmitter had up to ten locations recorded per day, with ± 18 m accuracy, between the hours of 06:00 and 22:00. Points were uploaded to the Argos satellite and downloaded weekly for mortality assessments.

Survival Analysis

Study sites were delineated by creating a Minimum Convex Polygon (MCP) using the Minimum Bounding Geometry tool in ArcGIS 10.2 (ESRI Inc., 2013, Redlands, USA) around all of the bird points for each site, excluding dispersal events of greater than five km in less than one week. To describe fragmentation levels in each study site, I used the program FRAGSTATS (McGarigal et al. 2012). The contagion metric, mean patch size and the standard deviation of mean patch size were calculated within each study site as a measures of landscape configuration. The contagion metric uses the proportional abundance of a landcover class, and the proportion of like adjacencies, and unlike adjacencies for a patch type. A greater contagion value represents a less fragmented landscape, such that a value of zero equates to a landscape in which there are no like adjacencies, and a value of 100 is a landscape of a single patch type. This metric is inversely related to edge density, such that a greater edge density will result in a lower contagion value (McGarigal and Marks 1995). I also calculated habitat composition within each study site, and within a 50-km buffer around the centroid of each study site, to determine whether or not study sites were representative of the overall landscape, or if survival rates were representative of the overall landscape rather than the study site.

I used Kaplan-Meier models in the survival package (Therneau 2014) in Program R (R Core Team 2014) to estimate cumulative annual survival for female lesser prairie-chickens at each study site for two years (March 15 – March 14, 2013-2014 and 2014-2015). Kaplan-Meier models tested the annual survival rate between sites and years using all birds following a one-week censoring period. I tested four models, including a null model, a site model, a site and year additive model as well as a site and year interactive model. Cox proportional hazard models were ranked using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). Models with a $\Delta AICc \leq 2$ were considered competing models.

I calculated MCPs for all individuals that had ≥ 3 points available as an estimate of home range (Table 3.1). Each bird-year (March 15th – March 14th) was treated as an independent period due to variation between years in weather and land use. MCPs were used to have a single, contiguous landscape potentially available for each individual, as kernel density estimates and Brownian Bridge Movement Models used for some birds in the past had several disjointed core areas that were not attached (Chapter II, Plumb 2015).

Using the Playa Lakes Joint Venture landcover class layer joined with a CRP layer from the Farm Service Agency within the lesser prairie-chicken range (Playa Lakes Joint Venture 2009), I clipped the landcover layer including six landcover classes (Grassland, Crop, CRP, Urban, Water/Wet, and Other), using the Clip tool in ArcGIS 10.2, within the MCP of each bird. Landscape metrics were calculated using FRAGSTATS to measure habitat composition and configuration within the home range of each bird. Landscape metrics calculated within home ranges were Total Area, Mean Patch Size, Contagion, Interspersion/Juxtaposition, and Patch Richness (Table 3.2; McGarigal and Marks 1995) I also calculated the percentage of each home range that was Grassland, Crop or CRP. I tested for correlation among the configuration metrics using Pearson's correlation coefficient.

I modeled survival, using the LD format, known-fate model in Program Mark. Encounter histories were compiled using weekly encounter histories across the 52-week annual cycle. FRAGSTATS metrics of configuration were used as individual covariates in one model set, and FRATSTATS metrics of composition were used as individual covariates in a second model set to derive functional relationships (White and Burnham 1999). I created 12 *a priori* models using individual FRAGSTATS configuration metrics, and additive site by FRAGSTATS metrics, and

ranked the models using AICc (Table 3.3). I also created 19 *a priori* models using composition metrics, including site and quadratic terms (Table 3.4).

Andersen-Gill Modeling

I used an Andersen-Gill modeling framework to determine how continuous, encounter specific covariates affect hazard rates for lesser prairie-chickens (Dinkins et al. 2014).

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. 2004).

To obtain a covariate for the encounters of each individual bird, separate distance rasters were created of each study site for distance to road, fence, distribution power line, oil well and lek using the Euclidean Distance tool in ArcGIS 10.2 and 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/>). I delineated 2-, 3-, 4-, 5-, and 6-strand, permanent livestock fences by hand, and distribution power line layers were from Kansas distribution lines were from the Kansas Corporation Commission (<http://www.kcc.state.ks.us/>). Each cell of these rasters has a value that identifies the distance that cell is from the nearest feature. For each use point bird location, I extracted the distance to each feature using the Extract Multi Values tool. The landcover type for each point was extracted using a spatial join in ArcGIS 10.2 from the Playa Lakes Joint Venture/Farm Service Agency CRP layer. I used Pearson's correlation coefficient to determine if any of the variables were correlated.

For VHF birds, all available points were used for encounters. For satellite birds I randomly selected one point per bird per day, as I modeled survival on a daily encounter history, and the SAT-PTT birds had as many as 10 points a day available. I chose the point for the day using the `r.sample` command in Geospatial Modeling Environment for a random selection of one of the points within a day (Beyer 2012). Only points and mortalities within the delineated study sites were used. I did not include Colorado lesser prairie-chickens due to lack of anthropogenic layer availability.

I 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 the data met the assumptions of proportional hazards (Fox 2002). Using the `coxph` function in the survival package (Therneau 2014), I determined the relative effect of covariates on annual survival from regression coefficients. All models with $\Delta\text{AICc} \leq 2$ were considered competing models. If the hazard ratio from the top models was different from zero (coefficient values $\neq 0$; 95% confidence intervals of the beta estimate did not overlap zero), then I determined that the variable was significant and plotted the predicted risk curve.

Results

Study Site Composition and Configuration

A total of 200 bird years and 111 mortality events were included in the overall annual survival model. There were two top models in the model set with $\Delta\text{AICc} \leq 2$ (Table 3.5). The top model represented differences among study sites. Northwest Kansas exhibited a lower survival estimate than any of the other sites (Figure 3.2). The only significant trend in annual survival rates was between Clark County and Northwest Kansas. The northwestern Kansas survival rate was 50% lower than in Clark County, Kansas (Figure 3.2). The second top model was a constant

survival rate over all of the study sites. The overall annual survival rate of female lesser prairie-chickens across all study sites was 0.369 (SE = 0.038, 95% CI = 0.30-0.45).

FRAGSTATS contagion metrics calculated within each of the study sites indicated that there was not a difference in contagion among Clark County and Northwestern Kansas (Table 3.6). Mean patch size was greatest in northwestern Kansas, and lowest in Colorado but the standard deviation of mean patch size of all sites was much larger than the mean, indicating no clear difference in mean patch size among sites (Table 3.6). For habitat composition, differences were evident between Clark County and Northwestern Kansas in terms of both the study site and the 50-km buffer around the centroid of the study site (Figure 3.3). The Clark County study site, and the surrounding landscape around the Clark County site had more grassland than the Northwest study site, by 15.9% and 41.8% respectively. Additionally, the Clark County site was more representative of the overall landscape, compared to the Northwestern study site, which had 74.4% more grassland than the surrounding landscape (Table 3.7).

Home Range Composition and Configuration

To estimate functional relationships among weekly survival of lesser prairie-chickens and home-range scale habitat configuration and composition, 177 total bird-years were used, as I only used individuals for which there were ≥ 3 locations and an error of one ha. Home range size was not correlated with the total number of points used to calculate the MCP, nor were either correlated with the configuration metrics within home ranges. There were no correlated metrics among the FRAGSTATS configuration metrics, thus all were used to relate landscape configuration to weekly survival. The sample of individuals for which survival was calculated included 98 mortality events. There was a single top model in the configuration metric model set with $\Delta AICc \leq 2$, which was Site + Patch Richness ($\beta = 0.51$, 95% CI = 0.32, 0.69; Table 3.3).

For all sites, there was a significant trend of increasing survival as the number of patch types within home ranges increased (Figure 3.4).

There were two equally parsimonious models in the home-range composition model set, and the top models were the Site + %Crop² model, and the Site + %Grassland² model. Slope estimates for both models were significant ($\beta = -0.0013$, $SE = 0.00053$) and ($\beta = -0.00074$, $SE = 0.00018$), and indicate a peak in weekly survival when proportion of crop within a lesser prairie-chicken's home range is about 30%, and when proportion of grassland within a lesser prairie-chickens home range is about 40-70% (Figure 3.5).

Andersen-Gill

To model the effect of distance to anthropogenic features on hazard rates, 189 total bird years were used, with 96 total mortality events, as I only used Kansas birds that had ≥ 2 locations, one of which being the mortality location. Sample size for these models included 79 and 110 individuals in the 2013-2014 and 2014-2015 seasons, respectively. There was a single top model in the model set with a $\Delta AICc \leq 2$, which was site + distance to fence (Table 3.8). This model accounted for 71% of the weight of the model set. The regression coefficients in this model show an increased risk relative to decreased distance from fences for birds in northwestern Kansas (hazard rate = 1.15, $SE = 0.38$) compared to the Red Hills and Clark County, Kansas. Across all Kansas study sites, hazard rates for female lesser prairie-chickens increased as distance to fence decreased (Figure 3.6).

To determine whether this relationship was caused by mortality due to collision with fences, I calculated the average distance to fence for mortalities among the study sites. The average distance to fence for mortalities overall was 321.64 m ($SE = 29.24$). By site, average distance to fence for mortalities for Clark, Northwest, and Red Hills was 207.99 m ($SE = 72.66$), 315.57 m ($SE = 39.72$) and 378.31 m ($SE = 38.76$), respectively. Additionally, the fence

densities for the three Kansas sites were 1.69 km/km², 1.76 km/km², and 1.53 km/km² for Northwest, Red Hills and Clark, respectively.

Discussion

I investigated the effect of landscape fragmentation on annual survival of female lesser prairie-chickens in Kansas and Colorado through three different frameworks and four scales. I found that differences in survival rates were evident between two study sites in Kansas, and that this difference can be explained by differences in study site habitat composition, with greater survival corresponding to a greater proportion of grassland habitat both within the study site and across the greater landscape area. However, I found that landscape configuration, measured with the contagion metric in FRAGSTATS was not different between these regions. Additionally, I was able to identify optimum habitat composition amounts within home ranges to maximize weekly survival, but found that a more fragmented landscape composition does not negatively affect weekly survival rates. Results alternatively indicated that a landscape with more landscape types had a positive effect on survival. Finally I found that hazard rates for lesser prairie-chickens increased as distance to fences decreased.

From four study sites in Kansas and Colorado, I was able to document significant differences in annual survival between two of the study sites. Survival rates were lowest in northwestern Kansas, with 95% confidence intervals that did not overlap with Clark County, Kansas, which had nearly double the survival estimate. I was not able to find differences between these sites in terms of landscape configuration with the contagion metric, but there were differences in the proportion of grassland habitat between these two sites. This difference in habitat proportions was evident at both the study site scale, as well as within the larger, 50 km buffered landscape. As landscape fragmentation results from the combination of habitat loss, and

the resulting changes in landscape configuration from grassland patch isolation, it may be possible to attribute these differences in survival to the differences in habitat loss alone. While differences in habitat proportions may not necessarily mean habitat loss in all landscapes, the Southern Great Plains were entirely grassland before the arrival of European settlers and the onset of agriculture in this region. Additionally, differences in landscape configuration between these two study sites may not have been detectable due to the way contagion is calculated. Contagion uses the proportion of like adjacencies, among cells, for all cover classes, and the northwestern study site has sizable areas that are unfragmented grassland, as well as areas that are unfragmented cropland, which contributes to the overall metric.

Similarly, the results of the individual-level (i.e., home range) analysis were inconclusive in returning results for the actual configuration of the landscape, based on the metrics chosen to represent fragmentation. However, I did find a positive, significant relationship with an increase in survival corresponding with an increase in the number of patch types within home ranges. This relationship does not necessarily mean that increased fragmentation increases survival, as contagion and interspersion/juxtaposition metrics did not explain survival. Instead, this may indicate that lesser prairie-chickens experience increased survival when they have a variety of habitat options available. This relationship is intuitive, as habitat heterogeneity benefits lesser prairie-chickens, and other grassland birds, because they require different habitat types throughout different life stages (Fuhlendorf and Engle 2001, Sandercock et al. 2015). The composition analysis within home ranges was also able to identify that there is an ideal amount of crop within a home range (30%), and an ideal amount of grassland within home ranges (40-70%). These results are congruent with past studies that identified that occupied lesser prairie-chicken habitat was in areas with up to 37% cultivation, with the remainder of landcover in

grassland (Crawford and Bolen 1976). It is likely CRP makes up the majority of any gaps between grassland and cropland within these landscapes, but future analyses will be required to determine the true importance of this landcover class on the landscape.

The effect of distance to anthropogenic features on annual survival of lesser prairie-chickens indicated that the closer an individual was to a fence, the greater risk of mortality. A past study on lesser prairie-chickens in Oklahoma found that fence collision was a primary and influential source of mortality (Patten et al. 2005, Wolfe et al. 2007). However, other studies that investigated cause-specific mortality of lesser prairie-chickens did not find fence collision to occur or be an influential cause of mortality (Merchant 1982, Haukos 1988, Jamison 2000, Fields 2004, Hagen et al. 2007, Kukul 2010, Pirius 2011, Grisham 2012, Holt 2012). Studies on other grouse species, such as red grouse (*Lagopus lagopus scoticus*) and greater sage-grouse have also found that collision is an important source of mortality (Baines and Andrew 2003, Beck et al. 2006, Stevens et al. 2012). However, similarly to lesser prairie-chickens, many greater sage-grouse studies did not find fences to be an important source of mortality (e.g., Blomberg 2013, Davis et al. 2014). From this study, the increased hazard rate relative to fences is unlikely to be attributed to collision mortality, as average distance to fence for mortalities was greater than 200 m at each site. Additionally, a concurrent study investigated whether fence collision was a significant cause of mortality for lesser prairie-chickens in Kansas and Colorado. Greater than 2800 km of fences were walked across all of the study sites, and only 12 traces of collision mortality were documented. Additionally, from all of the mortalities of transmittered birds during this study, there was only evidence found of a single collision as a cause of mortality (D. Haukos, unpublished data). The increased rate of fence collisions found in Oklahoma may be due to a higher fence density relative to Kansas, with fence densities of 1.53-1.76 km/km² in Kansas,

compared to 3.8 linear km/km² in Oklahoma (Wolfe et al. 2009). Instead of collision risk, the increased hazard rate in relation to fences could be a relationship with predator density. 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), and it may be that the closer a lesser prairie-chicken comes to a fence, there is an increased likelihood of an encounter with an avian predator. There was not support in these models for an effect on survival of distance to distribution line, oil well or road on lesser prairie-chicken mortality rates, despite a past study finding that these anthropogenic features negatively affected both survival rates and lek persistence for greater prairie-chickens (Hovick et al. 2014). Lesser prairie-chickens have already been shown to exhibit avoidance behavior of anthropogenic features such as power lines (Hagen et al. 2011, Plumb 2015), so if avoidance is already occurring, that may preclude an effect on survival rates.

It is possible that survival is not the proper vital rate from which to analyze the effects of fragmentation through differences in landscape configuration. It has been proposed that the response to fragmentation may be on the overall finite growth rate rather than annual survival or reproductive potential alone (Henle et al. 2004). Effects from fragmentation are also likely a function of dispersal power, individual area requirements, and interaction with environmental changes that come about from fragmentation (Henle et al. 2004). In the future, it would benefit this analysis to calculate these metrics for different classifications of the landscapes, especially a landscape layer that was classified from on-the-ground collected data. These analyses are sensitive to both the grain and extent of landcover data, as well as how the landscape is represented, in terms of patch delineation and classification (O'Neill et al. 1996, Hargis et al. 1998, Wu 2004). My results indicate that survival rates are instead representative of the overall quantity of habitat, which has been the case in past studies investigating the effect of

fragmentation on biodiversity (Fahrig 2003). It is also possible that the landscape configuration of my study sites is not yet fragmented enough to significantly alter lesser prairie-chicken annual survival, as these data were collected on some of the best lesser prairie-chicken remaining available habitat across the range of the species. Each study site was comprised of more grassland and less cropland than the overall landscape, indicating that lesser prairie-chickens can occupy these areas that represent the prime habitat for them in Kansas and Colorado, rather than the surrounding area. Instead, this depressed survival rate documented in Northwestern Kansas may be from decreased functional connectivity, rather than structural connectivity (Taylor et al. 1993). Without the ability to disperse out of the core study area and locate habitat that is both large enough and of adequate quality, birds who attempt to disperse will either die, or return to the study area unsuccessful and possibly in reduced body condition. A depressed survival rate, which is related to a lack in overall grassland habitat indicates that it is crucial to preserve the grassland habitat in the areas represented by our study sites, especially in northwestern Kansas where survival rates are lowest. Further loss of habitat within the areas occupied by lesser prairie-chickens could cause further reduction in survival rates, and eventually result in population extirpation.

Chick and nest survival have been shown to have the greatest impact on lesser prairie-chicken growth rates (Hagen et al. 2009), so the next step for this analysis is to determine the effect of landscape configuration and composition on these vital rates. Past studies of lesser prairie-chickens have documented an effect of anthropogenic features on the placement of nests, but little effect on nest survival (Pitman et al. 2005). Future analyses could also use vegetation characteristics within home ranges to determine if vegetation height or different varieties of cover have an effect on survival rates of lesser prairie-chickens. This study will also need to

include resource selection and comparing fragmentation within actual home ranges to random home ranges within the study sites. Pairing results from the Andersen-Gill model with a full analysis of resource selection will allow for the creation of a predicted map that indicates where lesser prairie-chickens will select habitat and where their hazards will be reduced. The resulting map could identify areas on the landscape to focus management for lesser prairie-chickens.

Management Implications

Lesser prairie-chicken are exposed to a greater predation risk closer to fences. This risk begins to level out at > 1 km. Past studies have also identified that both male and female lesser prairie-chickens are using space close to leks throughout the annual cycle. I would recommend that fences be removed within 1 km of leks or perch prevention devices be installed to reduce the presence of raptors on fences close to leks. Caution should also be employed before adding new fences to areas of the lesser prairie-chicken range. Additionally, maintaining landscape heterogeneity within the lesser prairie-chicken range will be beneficial to lesser prairie-chicken survival as was evidenced by the increase in survival rates as patch richness increased. Current landscape configurations do not yet seem to be fragmented enough to negatively affect lesser prairie-chicken survival; however, continued land conversion should be avoided to maintain landscapes persist to allow at least 40-70% grassland on the landscape.

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Figure 3.1 Study sites in Kansas and Colorado evaluating the effect of landscape fragmentation on lesser prairie-chicken survival during 2013-2015. The light blue region represents the current estimated lesser prairie-chicken range within Kansas and Colorado. Purple represents the Colorado study sites in Prowers, Baca and Cheyenne counties. Dark blue represents the Kansas study sites in Gove, Logan, Kiowa, Comanche and Clark counties.

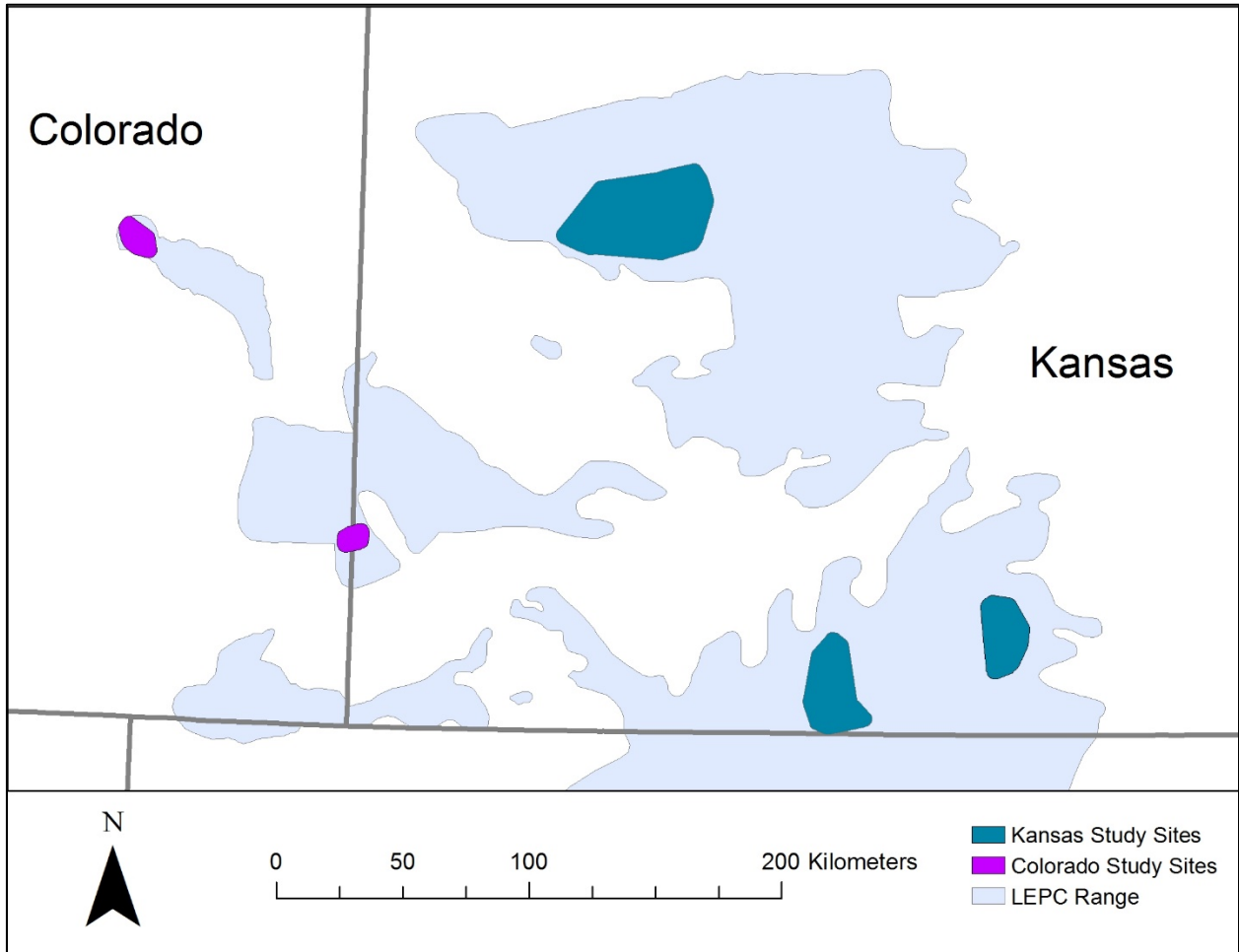


Figure 3.2 Annual survival estimates and 95% confidence intervals of female lesser prairie-chickens for three study sites in Kansas (Clark County, Red Hills, Northwest) and Colorado. Survival rates were estimated using known-fate models in Program Mark, and estimates represent the cumulative annual survival rate. A year was defined as March 15th-March 14th. Years of the study were grouped (2013-2014 and 2014-2015). Differences among study site survival rates were considered statistically significant if confidence intervals do not overlap.

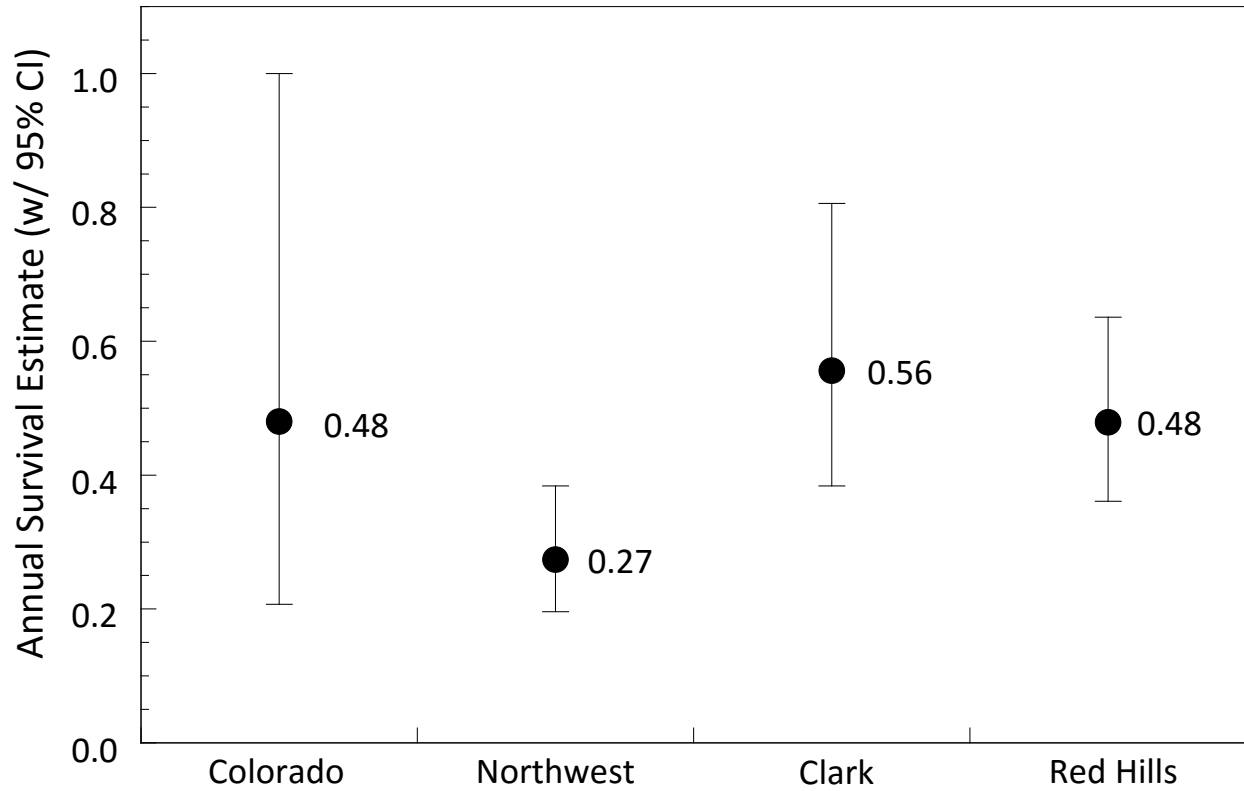


Figure 3.3 Landscape composition of study sites from Clark County Kansas (top), and northwestern Kansas (Gove and Logan Counties; bottom) illustrating that study sites have different proportions of landcover types within them, and also different from the surrounding landscape, which is buffered 50-km from the centroid of the study site.

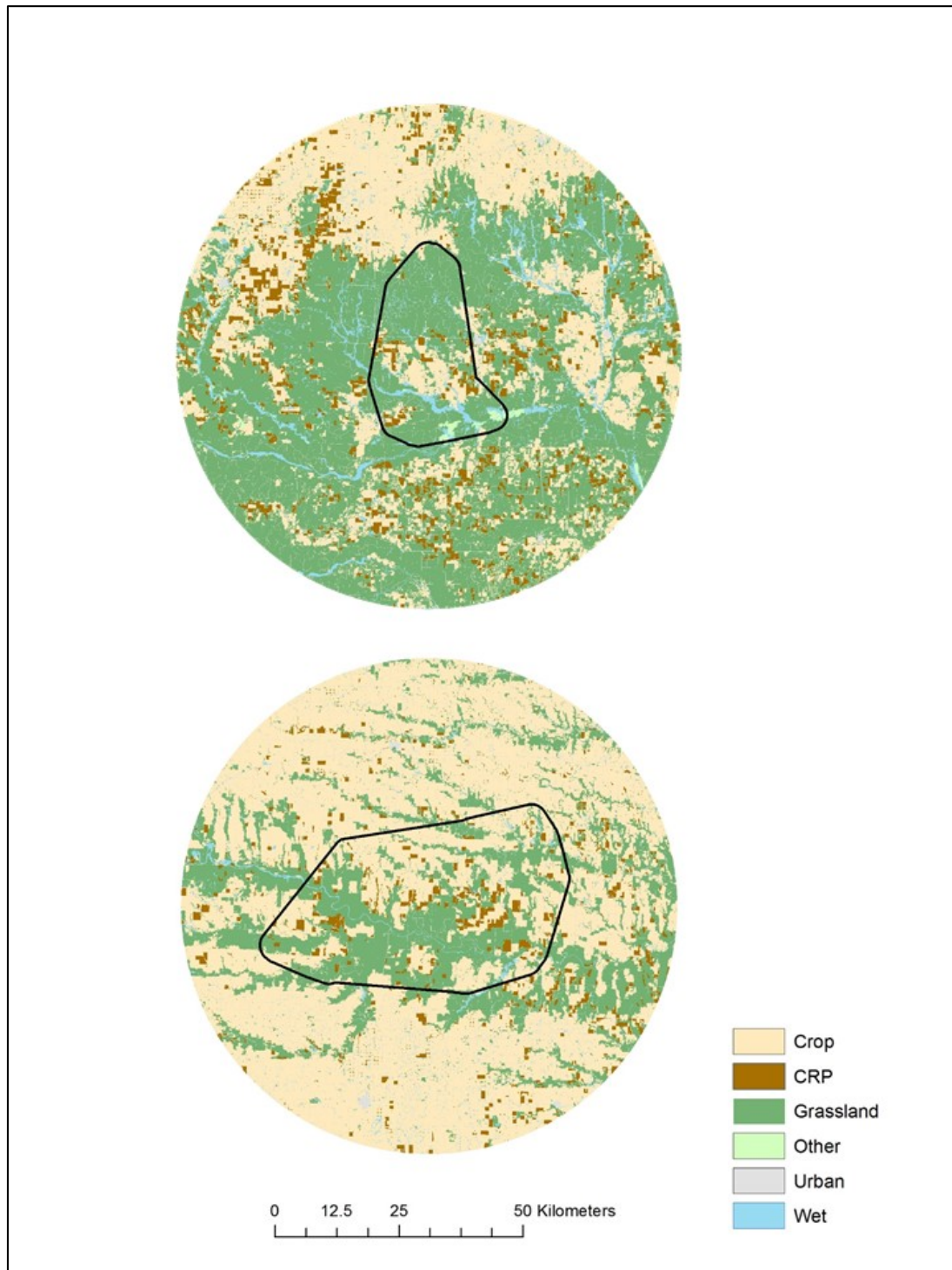


Figure 3.4 Functional relationship from Program Mark of weekly survival of lesser prairie-chickens and patch richness within individual home ranges during 2013-2015. Patch richness for this study indicates the number of patch types (1-6) that occurs in each individual home range.

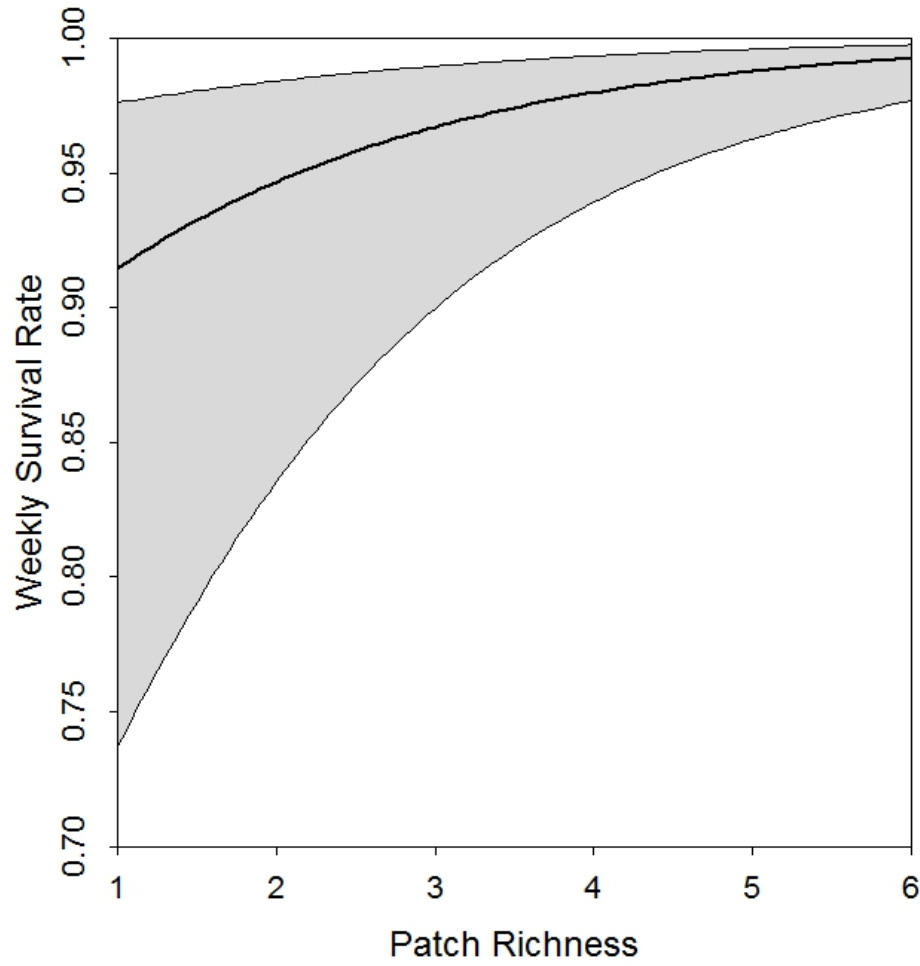


Figure 3.5 Functional relationship from Program Mark of weekly survival of lesser prairie-chickens and percent crop (a) and percent grassland (b) within individual home ranges during 2013-2015, for three sites in Kansas.

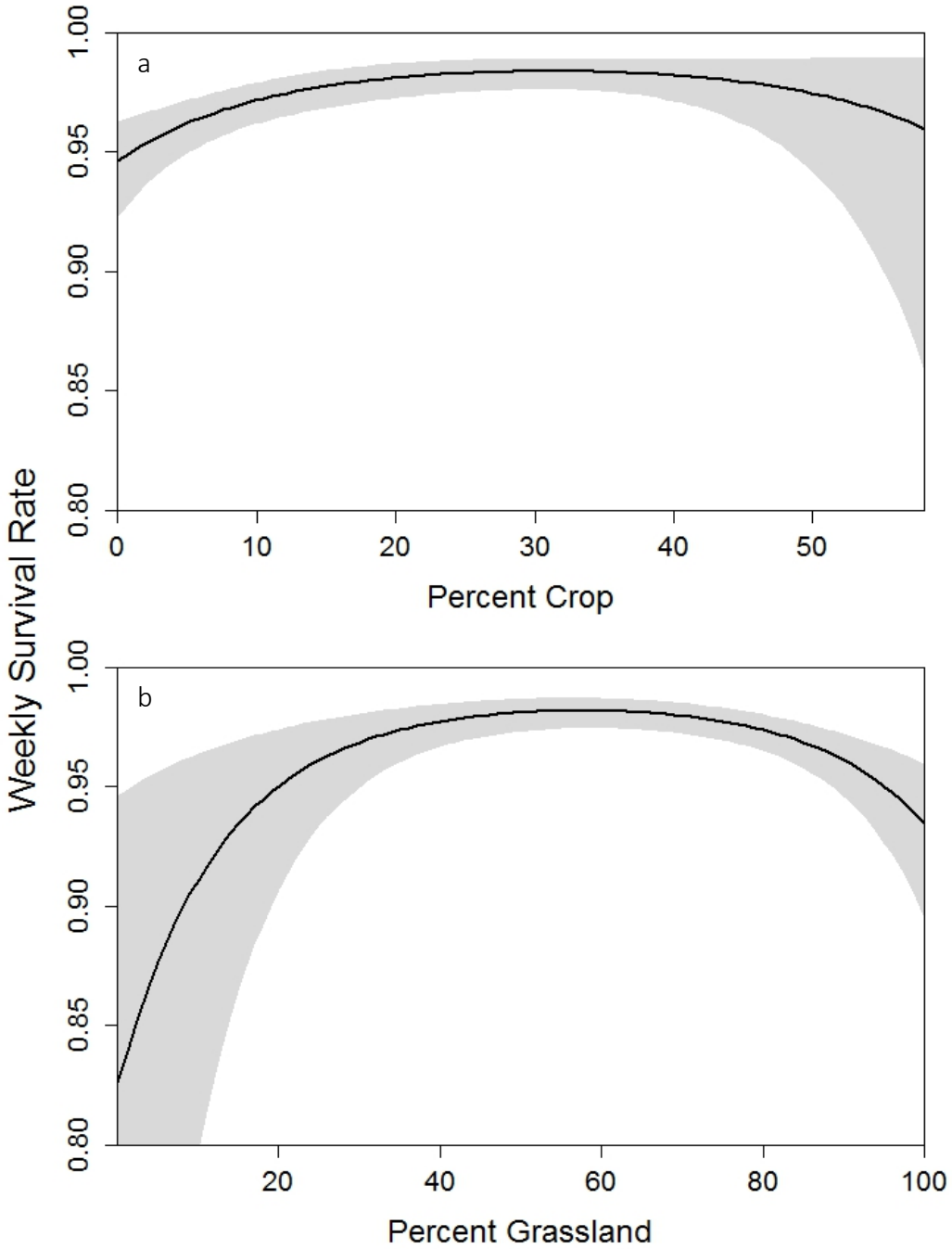


Figure 3.6 Predicted hazard rate of female lesser prairie-chickens for distance to fence from Andersen-Gill models for continuous encounter covariates during 2013-2015. Site + distance to fence (m) predicted curve, with three different study sites in Kansas (Clark County, Red Hills, and Northwest). Predicted curves only represent hazard rates for distance to fence that I located mortalities. Hazard rates from this model indicate that lesser prairie-chickens in northwestern Kansas experience greater risk in relation to fences than lesser prairie-chicken in the Red Hills and Clark County study sites ($H_z = 1.15 \pm 0.37$).

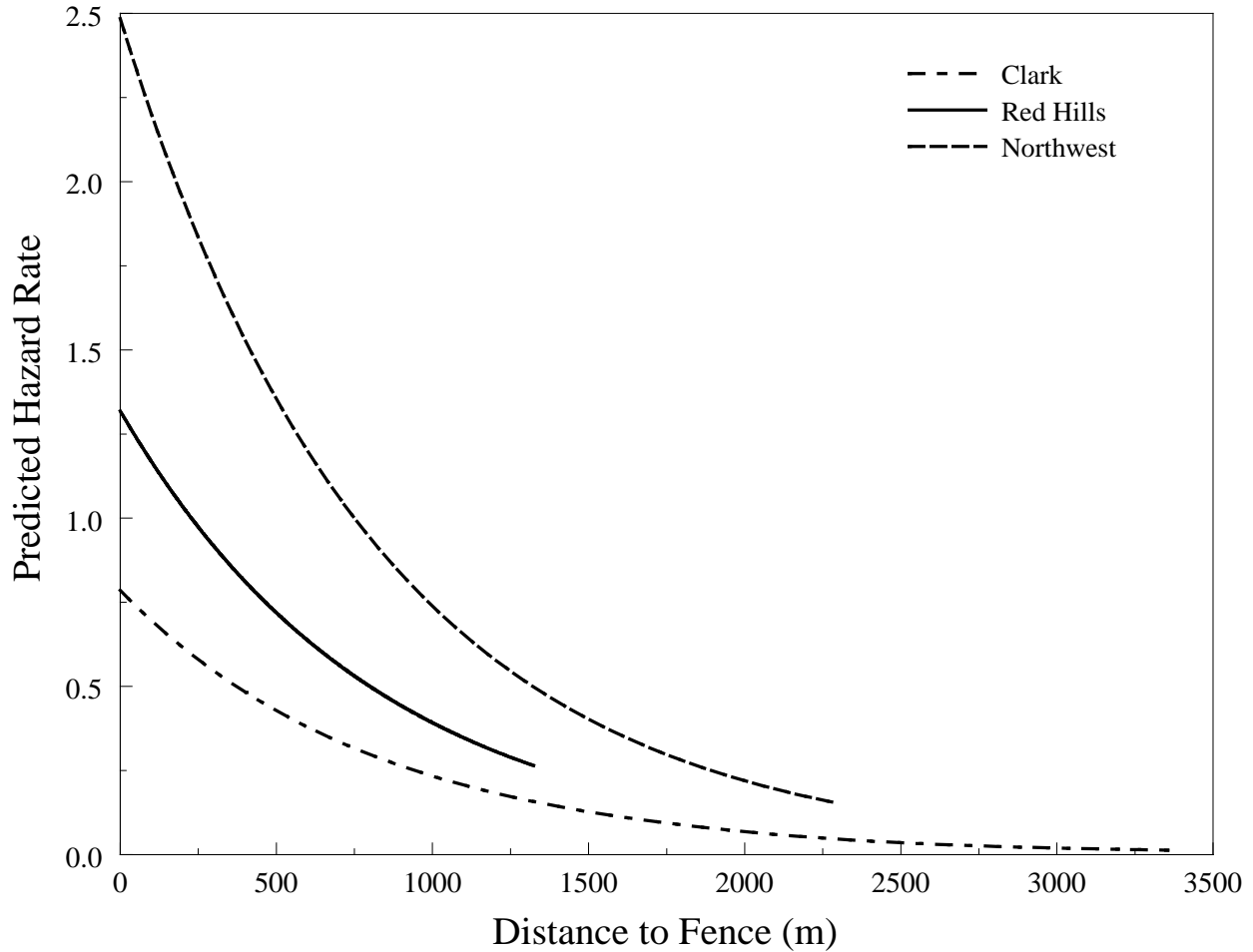


Table 3.1 Total available points for lesser prairie-chickens in Kansas and Colorado with SAT-PTT and VHF transmitters used to calculate minimum convex polygons during 2013-2015. Mean values are the mean value per site and overall for each bird used to calculate the polygons.

SAT-PTT				VHF			
Site	Total Number of Points	Mean	SE	Site	Total Number of Points	Mean	SE
Clark	30497	1794	6	Clark	503	72	2
Northwest	69693	1223	4	Northwest	1464	38	1
Red Hills	40536	1308	4	Red Hills	1252	57	1
Colorado	13954	1993	11	Colorado	-	-	-
All	154680	1381	27	All	3219	47	1

Table 3.2 FRAGSTATS metrics calculated within individual home ranges, to use as individual covariates in known-fate models within Program Mark. Definitions of metrics are adapted from McGarigal and Marks 1995.

FRAGSTATS Metric	Definition
Total Area (ha)	The total area of the landscape
Mean Patch Size (ha)	The total area of the landscape, divided by the total number of patches
Contagion (%)	The degree of clumping of patches on the landscape, based on cell adjacencies, inversely related to edge density.
Interspersion/Juxtaposition Index (%)	The degree to which patches are intermixed, based on patch adjacencies
Patch Richness	The number of different patch types represented within the landscape.
PLAND (%)	The total area of a patch type, divided by the total area of the landscape

Table 3.3 Model ranking based on Akaike Information Criterion corrected for small sample size (AICc) for 12 models testing the effect of landscape configuration on survival of female lesser prairie-chickens in Kansas and Colorado during 2013-2014 and 2014-2015. Site models considered the four study sites - Northwestern, Red Hills and Clark County, Kansas, and Colorado.

Model	K	Deviance	ΔAIC_c	w_i
Site + Patch Richness	5	952.44	0	0.92
Patch Richness	2	965.20	6.76	0.03
Interspersion/Juxtaposition	2	966.36	7.92	0.02
Site + Interspersion/Juxtaposition	5	960.55	8.11	0.02
Total Area	2	968.39	9.94	0.01
Site + Total Area	5	963.66	11.23	0
Site	4	977.55	23.11	0
Site + Mean Patch Size	5	976.69	24.25	0
Site + Contagion	5	977.19	24.76	0
Constant	1	985.60	25.16	0
Mean Patch Size	2	985.02	26.58	0
Contagion	2	985.59	27.15	0

K = Number of parameters

w_i = Akaike model weight

$AIC_c = 962.45$ for the best fit model

Table 3.4 Model ranking based on Akaike Information Criterion corrected for small sample size (AICc) for 19 models testing the effect of landscape composition on survival of female lesser prairie-chickens in Kansas and Colorado during 2013-2014 and 2014-2015. Site models considered the four study sites - Northwestern, Red Hills and Clark County, Kansas, and Colorado.

Model	K	Deviance	Δ AICc	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
Site + %Grass	4	934.22	11.58	0.00
Site + %CRP	4	934.37	11.73	0.00
Site * %CRP	6	930.90	12.26	0.00
%Grass ²	3	936.93	12.28	0.00
Site + %CRP ²	5	933.03	12.39	0.00
%CRP	2	939.05	12.40	0.00
Site	3	937.14	12.49	0.00
Site * %CRP ²	9	926.23	13.61	0.00
%CRP ²	3	938.48	13.83	0.00
%Crop ²	3	938.52	13.87	0.00
%Crop	2	941.76	15.11	0.00
Constant	1	944.97	16.32	0.00
%Grass	2	944.97	18.32	0.00

K = Number of parameters

w_i = Akaike model weight

AICc = 960.36 for the best fit model

Table 3.5 Model selection table Kaplan-Meier survival analysis, for cumulative annual survival rates of female lesser prairie-chickens in Kansas and Colorado for 2013-2014 and 2014-2015. Data from four sites were included in these models, three in Kansas (Clark County, Red Hills and Northwest) and one in Colorado.

Model Name	K	Deviance	$\Delta AICc$	w_i
Site	3	1053.1	0	0.48
Constant	1	1060.68	1.45	0.23
Site + Year	4	1053.04	2.02	0.17
Year	1	1060.07	2.77	0.11

K = Number of parameters

w_i = Akaike model weight

AICc = 1059.23 for the best fit model

Table 3.6 FRAGSTATS metrics calculated within sites for comparison of annual survival of female lesser prairie-chickens among study sites during 2013-2015. Clark, Northwest and Red Hills were Kansas study sites, and the Colorado study site consisted of two distinct areas in eastern Colorado.

Site	Total Area (ha)	Contagion (%)	Mean Patch Size (ha)	St. Dev of Mean Patch Size (ha)
Clark	71209	60.25	34.94	231.74
Northwest	129762	59.67	39.52	288.42
Red Hills	49111	66.28	32.05	387.32
Colorado	28428	64.09	29.44	231.74

Table 3.7 Comparison of composition of grassland, cropland and CRP between study areas, and the 50 km radius landscape surrounding these study areas. The 50km buffer represents a circle with a 50-km radius from the centroid of the study area. Composition metrics were calculated in the program FRAGSTATS.

Study Site		% Grass	% Crop	% CRP
Clark	50 km buffer	52.34	32.27	7.43
	Study Area	64.05	17.35	5.53
	Difference	18.28	-86.02	-34.26
Northwest	50 km buffer	25.90	65.17	4.28
	Study Area	45.16	43.90	7.44
	Difference	74.35	-32.63	73.73
Red Hills	50 km buffer	50.98	33.74	4.78
	Study Area	76.51	8.47	2.19
	Difference	50.09	-74.91	-54.25
Colorado	50 km buffer	43.97	38.87	13.59
	Study Area	60.27	26.51	9.75
	Difference	37.06	-31.81	-28.25

Table 3.8 Model ranking for Andersen-Gill models, based on Akaike Information Criterion corrected for small sample size (AICc) for 26 models determining the effect of distance to anthropogenic features and landcover type on survival of lesser prairie-chickens in Kansas during 2013-2015.

Model Name	Model Statistics			
	K	Deviance	Δ AICc	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
site * lek	5	790.58	10.14	0
site + powerline	3	795.2	10.75	0
site + road	3	795.34	10.9	0
site + landcover	3	795.5	11.05	0
fence	1	800.22	11.77	0
fence + road	2	800.04	13.6	0
site * oil	5	794.12	13.68	0
site * landcover	5	794.42	13.98	0
site * powerline	5	794.46	14.02	0
site * road	5	794.58	14.14	0
lek	5	794.68	14.25	0
fence * road	3	799	14.56	0
lek	1	805.4	16.95	0
powerline	1	806.5	18.05	0
constant	1	809.94	19.5	0
road + powerline	2	806.5	20.05	0
road	1	809.02	20.57	0
oil	1	809.44	21	0
landcover	1	809.48	21.03	0
road * powerline	3	805.9	21.46	0
road + oil	2	808.86	22.42	0
road * oil	3	808.34	23.91	0

K = Number of parameters

w_i = Akaike model weight

AICc = 790.45 for the best fit model

Appendix A - Weekly Movements of Nonbreeding Lesser Prairie-Chickens

Table A.1 Mean cumulative weekly movements (m) of satellite platform transmitting terminal marked nonbreeding lesser prairie-chickens in three sites in Kansas (Northwest, Red Hills, Clark County), Colorado and New Mexico. Nonbreeding season was considered the 6-month period between 16 September and 14 March, for 2013-2014 and 2014-2015.

	2013			2014		
	n	\bar{x}	SE	n	\bar{x}	SE
Northwest	271	9.16	0.3	296	9.46	0.4
Red Hills	187	7.61	0.4	169	8.32	0.36
Clark	-	-	-	254	13.54	0.58
Colorado	103	8.16	0.48	75	9.17	0.58
New Mexico	-	-	-	165	9.99	0.38