Lek dynamics and range-wide morphometric patterns of lesser prairie-chickens

by

Carly S. Hildebrant Aulicky

B.S., Rutgers University, 2011
M.S., University of Glasgow, 2014

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2020

Abstract

The lesser prairie-chicken (*Tympanuchus pallidicinctus)* is a lek-breeding prairie-grouse of the Southern Great Plains. The lesser prairie-chicken range spans four ecoregions with an east-west precipitation gradient and is subject to severe droughts on a 5-10 year cycle. The influence of the range-wide precipitation gradient and severe drought cycle on lesser prairie-chicken morphology is unknown and a range-wide morphometric compilation has never been assembled. The lesser prairie-chicken population booms and busts in response to drought and estimates of population trends are made from counts of displaying males on leks. Despite the conservation importance of leks, there are many untested assumptions about how leks form on the landscape and what factors determine their persistence into subsequent breeding seasons. My dissertation seeks to fill these knowledge gaps, by (1) assembling a range-wide synthesis of lesser prairie-chicken morphometrics data, (2) determining severe weather influences on morphometric traits, (3) test the hotspot hypothesis as an explanation for lek formation, (4) determine factors that influence lek persistence and (5) evaluate lek formation and persistence findings in translocated population that has no existing lek complex. I assembled a range-wide data set of (n = 2,048) lesser prairie-chicken morphometrics from the period of 1986 to 2019 and compared among ecoregions and weather conditions based on the Palmer Drought Severity Index. Lesser prairie-chicken morphometric traits are largest in the Short-Grass and Sand Shinnery Oak Prairies and smaller in in the Mixed-Grass and Sand Sagebrush Prairies. Morphometric changes following years of extreme weather are universal across ecoregions, where adult female traits remain unaffected and male sexually selected traits increase in size after extreme weather. Incredibly, lesser prairie-chicken body fat during spring lekking is tightly constrained by sex with males exhibiting 2-3% body fat, whereas females exhibited 4-8% across all weather conditions. I tested the hotspot hypothesis, which posits that leks should form in areas where males are most likely to encounter females, and anthropogenic and female movement data as determinants of lek persistence in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie ecoregions of Kansas with 143 GSP-backpacked females from 2013-2016 and 53 individual leks. As a lek-breeding species, lesser prairie-chicken females are solely responsible for incubating their nest and raising broods, which creates a sexually driven difference in space and habitat use that is reflected in both the formation and persistence of leks on the landscape. I found that lesser prairie-chicken lek dynamics are driven by female habitat constraints, where increased female space use and number of nest sites starting at a 5 km scale ($F_{5,\,78} = 2.50$, $P = 0.04$) determines the number of males displaying at leks and concentrations of female spatial use determines where new leks form on the landscape. I then compared patterns of established lek complexes to the dynamics of lek formation and persistence in the translocation of lesser prairie-chickens ($n = 411$) to the Sand Sagebrush Prairie Ecoregion in 2016-2019. The formation and persistence of leks by translocated birds is also driven by female space utilization, where the location of newly formed leks comprised of translocated birds can be explained by female nesting attempts and space use and the persistence and stability of translocation leks can be explained by multiyear nesting efforts by females starting at a 5 km buffer ($F_{4,\,21} = 6.57$, $P = 0.01$). My research offers an explanation for the spatial-temporal dynamics of lek formation and persistence on the landscape and provides means to use morphometrics to evaluate weather stressors and resource allocation in lesser prairie-chickens.

Lek dynamics and range-wide morphometric patterns of lesser prairie-chickens

by

Carly S. Hildebrant Aulicky

B.S., Rutgers University, 2011
M.S., University of Glasgow, 2014

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2020

Approved by:

Major Professor
David A. Haukos

Copyright

Abstract

The lesser prairie-chicken (*Tympanuchus pallidicinctus)* is a lek-breeding prairie-grouse of the Southern Great Plains. The lesser prairie-chicken range spans four ecoregions with an east-west precipitation gradient and is subject to severe droughts on a 5-10 year cycle. The influence of the range-wide precipitation gradient and severe drought cycle on lesser prairie-chicken morphology is unknown and a range-wide morphometric compilation has never been assembled. The lesser prairie-chicken population booms and busts in response to drought and estimates of population trends are made from counts of displaying males on leks. Despite the conservation importance of leks, there are many untested assumptions about how leks form on the landscape and what factors determine their persistence into subsequent breeding seasons. My dissertation seeks to fill these knowledge gaps, by (1) assembling a range-wide synthesis of lesser prairie-chicken morphometrics data, (2) determining severe weather influences on morphometric traits, (3) test the hotspot hypothesis as an explanation for lek formation, (4) determine factors that influence lek persistence and (5) evaluate lek formation and persistence findings in translocated population that has no existing lek complex. I assembled a range-wide data set of (n = 2,048) lesser prairie-chicken morphometrics from the period of 1986 to 2019 and compared among ecoregions and weather conditions based on the Palmer Drought Severity Index. Lesser prairie-chicken morphometric traits are largest in the Short-Grass and Sand Shinnery Oak Prairies and smaller in in the Mixed-Grass and Sand Sagebrush Prairies. Morphometric changes following years of extreme weather are universal across ecoregions, where adult female traits remain unaffected and male sexually selected traits increase in size after extreme weather. Incredibly, lesser prairie-chicken body fat during spring lekking is tightly constrained by sex with males exhibiting 2-3% body fat, whereas females exhibited 4-8% across all weather conditions. I tested the hotspot hypothesis, which posits that leks should form in areas where males are most likely to encounter females, and anthropogenic and female movement data as determinants of lek persistence in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie ecoregions of Kansas with 143 GSP-backpacked females from 2013-2016 and 53 individual leks. As a lek-breeding species, lesser prairie-chicken females are solely responsible for incubating their nest and raising broods, which creates a sexually driven difference in space and habitat use that is reflected in both the formation and persistence of leks on the landscape. I found that lesser prairie-chicken lek dynamics are driven by female habitat constraints, where increased female space use and number of nest sites starting at a 5 km scale ($F_{5, 78} = 2.50$, $P = 0.04$) determines the number of males displaying at leks and concentrations of female spatial use determines where new leks form on the landscape. I then compared patterns of established lek complexes to the dynamics of lek formation and persistence in the translocation of lesser prairie-chickens ($n = 411$) to the Sand Sagebrush Prairie Ecoregion in 2016-2019. The formation and persistence of leks by translocated birds is also driven by female space utilization, where the location of newly formed leks comprised of translocated birds can be explained by female nesting attempts and space use and the persistence and stability of translocation leks can be explained by multiyear nesting efforts by females starting at a 5 km buffer ($F_{4, 21} = 6.57$, $P = 0.01$). My research offers an explanation for the spatial-temporal dynamics of lek formation and persistence on the landscape and provides means to use morphometrics to evaluate weather stressors and resource allocation in lesser prairie-chickens.

Table of Contents

List of Figures

List of Tables

Acknowledgements

There are many people who allowed this dissertation to come to fruition and for this research to be completed. First and foremost, thank you Dave. Your kindness and unwavering support have meant the world to me. You gave me a fresh start when I thought that there was no place left for me in wildlife biology. I will forever be grateful for your mentorship and belief in me. My time working with you allowed me to learn to love science again.

Thank you to the all the wonderful people who comprise the Kansas Cooperative Fish and Wildlife Research unit. Research is an effort of many parts, and I would like to thank Maiah and Tara for ensuring and everyone at the Division of Biology Main Office (Becki, Crystal, Sara, and Terri) that everything ran smoothly behind the scenes. Thank you to Dan and John for teaching Liam and me how to trap lesser prairie-chickens and getting our first field season off the ground.

The collaborative and close-knit community of lesser prairie-chicken researchers has been an incredible experience. I would like to express my gratitude to everyone who provided morphometrics data for my first chapter. Thank you to Dr. Christian Hagen, Jim Pitman, Dr. Blake Grisham, Michael Patten, Don Wolfe, Craig Olawksy, and Dr. Clint Boal for sharing morphometric data for this work.

I also have the deepest appreciation for everyone involved in coordinating and executing the translocation project at the Kansas Department of Wildlife, Parks, and Tourism, Colorado Parks and Wildlife, and at the U.S. Forest Service. Thank you to especially to Kent Fricke, Kraig Schultz, Jonathan Reitz, and Liza Rossi, for leading the way on this effort. Your dedication to the lesser prairie-chicken is truly admirable. I would also like to extend thanks to Matt Bain from The Nature Conservancy, who offered us housing and storage space at the Smoky Valley Ranch. I would like to extend my deepest gratitude to all the landowners who allowed us access on this project, without your willingness there would be no research.

I would like to thank all the of the research technicians that made sure that birds were moved, tracked, and admired. Thank you, Zach, Ariana, Wayne, Trent, Ben, Seth, Nicole, JoJo, Anna, Kimberly, and Allison, for your hard work on this project. To Elli, Nick, and Megan, it has been a privilege and honor to watch your transition from field techs to graduate students. I look forward to seeing where your careers take you next.

My time at Kansas State would not have been the same without the friendships I developed along the way. Thank you, Emily, for the depth and sincerity of your friendship, your thoughtfulness, and all the laughs. Thank you, Elise, for being the HLM to my rainbow sprinkles, for the adventures, the deep (heavily caffeinated) chats, and for your unwavering support even as my journey took me in unexpected directions. Thank you to the Flying Squirrel Posse, Alix and Liam, who made my time in the Coop Unit an absolute blast and who have proven to be lifelong friends. Liam, I wish to express my deepest appreciation for everything you've done for the translocation project from being an ace coder to keeping an eye on the big picture goals. While no research project can ever claim to be a well-oiled machine, I knew I could count on you to act as my balance. Alix, I knew we were going to be friends ever since you interrogated me about my cubicle tea collection. Your friendship is fierce and has been a light in uncertain times. Thank you, Missy, for your uncanny ability to point out my inner strength. This dissertation would have never been completed without you and I am forever grateful to you for every minute of conversation to get me here.

I owe the deepest thanks to my family, who's love and encouragement got me through the rollercoaster ride of my graduate experience at Kansas State. Thank you, Dad and Autumn, for listening to me practice talks and random tangents about birds along the way. Thank you, Katie, for being a voice of reason and for being quick to point out the humor in my life. Mom, I am so grateful to have you in my life and there will never be a way to truly express how much your love helped make this dream become reality. You've been my best friend, my adventure buddy, and biggest cheerleader. I'm lucky to have you in my corner every step of the way.

Chapter 1 - Analysis of Range-Wide Morphometric Traits in Lesser Prairie-Chickens: Ecoregional Differences, Influence of Drought, and Breeding Implications of Nutrient Reserves

Introduction

Morphology measurements are ubiquitous in avian studies. Collecting morphometric measurements is both inexpensive and standardized, offering unique opportunities to apply morphometric records to questions about evolutionary pressures on a species across space and time. From morphometrics data, it is possible to discern changes to body size over time and determine if these differences are due to localized variation, sexual selection, or nuances in evolutionary pressures upon specific populations within the species' range. Physiological measures such as body tissue composition and measures of external morphology reflect the availability of resources and ability of an individual to acquire them, which can then be applied to questions about habitat quality (Stevenson and Woods Jr. 2006, Milenkaya et al. 2013). Allocation of resources to different morphometric traits and metrics of condition such as nutrient reserves can also be used to indicate reproductive costs (Höglund and Sheldon 1998, Lebigre et al. 2013, Elliott et al. 2014). Morphometrics can serve as a useful tool informing management questions for species of conservation concern because of the far reach of these data through space and time in avian studies.

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a non-migratory prairie-grouse found in the southern Great Plains of North America. The lesser prairie-chicken has declined in abundance and occupies only an estimated 17% of the species' presumed historical range (Haukos and Boal 2016). Consequently, the lesser prairie-chicken was federally listed as threatened in 2014, and while the listing decision was vacated in 2015 after litigation and the species delisted in 2016, it remains a species of conservation concern throughout the range (Haukos and Boal 2016, U.S. Fish and Wildlife Service 2016).

As with other species of grassland birds, much of this decline has been attributed to conversion of native grasslands to row-crop agriculture and declining habitat quality (Haukos and Boal 2016, Rosenberg et al. 2019). This decline is exacerbated by the amount of contiguous and dynamic grassland required to sustain lesser prairie-chickens on the landscape (Taylor and Guthery 1980, Applegate and Riley 1998, Bidwell et al. 2002, Haukos and Boal 2016). Lesser prairie-chicken populations require an estimated 486-20,234 ha of grassland to persist, with both short vegetation structure for male lek displays and sufficient vegetation height and visual obstruction for nesting, brooding, and overwintering (Anderson 1969, Davis 2009, Hunt and Best 2010, Hagen et al. 2013, Grisham et al. 2014, Haukos and Boal 2016). Because lesser prairie-chickens require a large dynamic grassland landscape, they serve as an umbrella species for other grassland birds (Sandercock et al. 2011, Haukos and Zavaleta 2016).

Precipitation strongly influences availability of resources throughout much of the semi-arid lesser prairie-chicken range and is a determinant of lesser prairie-chicken population density and occupied range, which boom-bust in response to weather (Giesen 2000, McDaniel and Williamson 2016, Ross et al. 2016*b*, Hagen et al. 2017). The lesser prairie-chicken range encompasses an ~40 cm east-west precipitation gradient with a greater average annual precipitation in the eastern (70 cm) extent compared to the western extent (43 cm; Figure 1.1; Grisham et al. 2016, Haukos and Zavaleta 2016). The lesser prairie-chicken range also spans a growing season averaging from 220 days in the southern extent and 160 days in the northern extent of the range (Figure 1.1; Grisham et al. 2016, Haukos and Zavaleta 2016).

Drought is prevalent in the study area and large-scale intensive droughts occur almost every 20 years (Grisham et al. 2016*a*). Intensive localized droughts occur every 5-10 years on the High Plains and drive a boom-bust pattern in lesser prairie-chicken population demography (Fields et al. 2006, Grisham et al. 2013, Ross et al. 2016*b*). The effect of weather on lesser prairie-chickens is most noticeable during nesting, brood rearing, and fall dispersal, when eggs and young are vulnerable to temperature and precipitation extremes and yearlings move to establish in new territories (Fields et al. 2006, Grisham et al. 2013, Ross et al. 2016*b*).

The contemporary lesser prairie-chicken range is divided among four ecoregions, the Short-Grass Prairie/CRP Mosaic, Sand Sagebrush Prairie, Mixed-Grass Prairie, and Sand Shinnery Oak Prairie across Colorado, Oklahoma, Texas, New Mexico, and Kansas (Figure 1.2; McDonald et al. 2014, Grisham et al. 2016). Among the four ecoregions, habitat fragmentation has left Sand Shinnery Oak Prairie and Sand Sagebrush Prairie ecoregions isolated from the remaining range (Hagen et al. 2010, DeYoung and Williford 2016). While being potentially vulnerable to genetic drift, only Sand Shinnery Oak Prairie Ecoregion lesser prairie-chicken populations were found to be genetically distinct (Hagen et al. 2010, DeYoung and Williford 2016, Oyler-McCance et al. 2016).

Within the four ecoregions, the population located in the Kansas Short-Grass Prairie/CRP Mosaic Ecoregion is currently the most abundant (McDonald et al. 2013, Hagen et al. 2016, 2017, Nasman et al. 2018). Lesser prairie-chickens in Short-Grass Prairie/CRP Mosaic are also the most recently established lesser prairie-chicken population within the range (mid-1990s; Rodgers and Hoffman 2005, Dahlgren et al. 2016). Comparatively, until the late 1980s, the Sand Sagebrush Prairie Ecoregion of southwestern Kansas and southeastern Colorado, had the greatest density of lesser prairie-chickens until multiple years of extreme drought and a series of intense winter storms precipitated an estimated >98% decline from peak bird numbers in the late 1980s by 2014 (Jensen et al. 2000, Garton et al. 2016, Hagen et al. 2017).

Lesser prairie-chickens may adapt and react differently to weather and resource stress among ecoregions. Because the lesser prairie-chicken is a boom-bust species largely affected by precipitation, the number of surviving individuals and past periods of drought may strongly influence current morphological phenotypes across the species' range (Merchant 1982, Grisham et al. 2013, 2014). Morphometric characteristics can reflect available resources (i.e., habitat quality) during periods of growth, and patterns in morphometric traits may reflect morphological phenotypes better suited to times of food stress (Bell et al. 2007, Janssen et al. 2011, Killpack and Karasov 2012, Brown et al. 2013, Björklund et al. 2015).

Grouse molt primary wing feathers and retrice feathers between August and October and lesser prairie-chicken males have been documented with molting pinnae feathers in the fall (unpublished data), allowing feather lengths to mirror resources available prior to and during their growth (Bendell 1955, Davis 1968, Johnsgard 2008). Taken across the precipitation gradient of the lesser prairie-chicken range, morphology can indicate influences of weather and habitat quality by examining differences in attributes among ecoregions and within ecoregions across time. Morphological patterns offer insight to phenotype and fitness influences on population structure, which can aid in predicting changes to morphometric traits and nutrient reserves under the increasing drought duration and frequency projected for prairie ecosystems (Grisham et al. 2013, 2016*a*, Godar 2016).

By assembling a range-wide morphometrics record, I sought to address questions about spatial-temporal differences such as weather effects on morphometric traits across the lesser prairie-chicken range. My first objective was to compile a range-wide record of lesser prairie-chicken morphology. Prior to this work, there were four published studies regarding lesser prairie-chicken morphology, which can only account for morphological attributes of birds during limited periods within the Sand Sagebrush Prairie Ecoregion of Kansas or in the Sand Shinnery Oak Prairie Ecoregion of Texas or New Mexico, two of which focused on the growth and development of chicks (Hagen et al. 2004, Pitman et al. 2004, Bell et al. 2007, Behney et al. 2012).

My second objective was to determine what aspects of lesser prairie-chicken morphology are fixed or variable across ecoregions. I hypothesized that some morphometric attributes will vary across ecoregions in correspondence with the temperature and precipitation gradient across the lesser prairie-chicken range. I predicted that lesser prairie-chickens in the northern portion of the range would have larger attributes than individuals in the southern portions due to differences severity in summer temperature and drought, despite the increased growing season. I hypothesized that variation among ecoregions and within an ecoregion is driven by temperature and precipitation of the year prior to capture, when climatic influences would be strongest on the growth of new feathers and tarsus lengths for juvenile birds. I predicted that changes in morphometric traits closely follow extreme temperature and precipitation events, principally drought due to its importance in the boom-bust cycle of lesser prairie-chicken populations. I further predicted that following extreme weather events, structural size of the cohorts of second-year (i.e., juvenile) birds measured in the following year will decrease.

My third objective was to ascertain the relationship between lesser prairie-chicken morphology and habitat quality using precipitation as a proxy for availability of resources (e.g., food). I tested the hypothesis that temperature and precipitation influence lesser prairie-chicken nutrient reserves, body fat and protein, in association with the temperature and precipitation gradient. I predicted that birds in northern ecoregions of lesser prairie-chicken range will have a greater proportion of body fat compared to birds of the southern ecoregions and the proportion of body fat is related to weather conditions in the prior year. I tested the prediction that drought will produce a cohort effect in subsequent generations, where lesser prairie-chickens reared in food-limited environments will have a smaller body size.

My final objective was to apply morphometrics to understanding reproductive costs and outcomes for lesser prairie-chickens. There is evidence that lek displays are energetically demanding for males, due in part to the loss of mass over the duration of a breeding season and reduced male survival rates in May-June after breeding season ends, especially when potential display costs are compounded with drought, high temperatures, or changes in predator communities (e.g., raptor migration; Wolfe et al. 2007, Grisham 2012, McDaniel and Williamson 2016). I predicted that for recaptured males throughout the lesser prairie-chicken range, male mass loss is primarily comprised of stored body fat. Similarly, I tested the prediction that because of sexual selective pressures on male lesser prairie-chickens, when resources are scarce, males will allocate resources selectively to sexually selected traits, such as pinnae and tail feathers. In accordance with this prediction, during periods of extreme weather events, I anticipated that sexually selected traits are less variable than other morphological traits that are not under sexual selection.

Female lesser prairie-chickens provide sole parental care to their offspring, carrying a significant reproductive cost in nesting efforts and rearing broods (Arnold et al. 1995, Milonoff et al. 2004). Female nesting timing and success are influenced by weather conditions as a determinant of spring vegetation growth, with earlier periods of growth corresponding to earlier nesting attempts (Boal et al. 2010, Grisham et al. 2013, 2014, McDaniel and Williamson 2016).

The role of female morphometrics and physical condition, reflected in nutrient reserves such as body fat and protein, is an unknown factor in nesting outcome. I hypothesized that female morphometric traits influence nesting success and predicted that females with greater mass and nutrient reserves have greater nest success rates than those with fewer nutrient reserves.

Study Area

Short-Grass Prairie/CRP Mosaic

The Short-Grass Prairie/CRP Mosaic (hereafter Short-Grass Prairie) Ecoregion is a landscape of short-grass and mixed-grass prairies combined with Conservation Reserve Program (CRP) tracts located in northwestern Kansas (Dahlgren et al. 2016). The Short-Grass Prairie is comprised of silt loam soils with dominant vegetation inclusive of blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsute*), buffalograss (*B. dactyloides*), sideoats grama (*B. curtipendula*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed (*Ambrosia psilostacha*; Robinson 2015, 2018, Sullins 2017, Sullins et al. 2018). Conservation Reserve Program tracts in Kansas were initially seeded with native grasses, primarily consisting of little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indian grass (*Sorghastrum nutans*; Fields et al. 2006, Robinson 2018, Sullins et al. 2018). Annual average long-term (30 year) precipitation varies between 40 and 50 cm (Dahlgren et al. 2016).

Sand Sagebrush Prairie

The Sand Sagebrush Prairie Ecoregion is comprised of sandy soil types in southwestern Kansas and southeastern Colorado. Plant composition typically includes sand sagebrush

(*Artemisa filifolia*), yucca (*Yucca* spp.), little bluestem, sideoats grama, sand lovegrass (*Eragrostis trichodes*), sand dropseed (*Sporobolus cryptandrus*), blue grama, sand bluestem (*Andropogon hallii*), annual buckwheat, western ragweed, prairie sunflower, annual sunflower (*Helianthus annuus*), Indian blanket flower (*Gaillardia pulchella*), tansy aster (*Machaeranthera tanacetifolia*), bush morning glory (*Ipomoea leptophylla*), evening primrose (*Oenothera* spp.), buffalo bur (*Solanum rostratum*), and buffalo gourd (*Cucurbita foetidissima*; Hagen et al. 2005, Haukos et al. 2016). Average annual precipitation for the Sand Sagebrush Ecoregion ranges from 40.6 to 51.7cm (Haukos et al. 2016).

Mixed-Grass Prairie

The Mixed-Grass Prairie Ecoregion is an extensive area of loamy soils that spans from south-central Kansas through Oklahoma into the northeastern edge of the Texas panhandle (Bidwell et al. 2002, Lautenbach 2015, Wolfe et al. 2016, Lautenbach 2017). Dominant vegetation within the range includes little bluestem, blue grama, hairy grama, sideoats grama, buffalograss, sand dropseed, big bluestem, invasive Russian thistle (*Salsola kali*), kochia (*Kochia scoparia*), annual sunflower (*Helianthus annuus*), Louisiana sagewort (*Artemisia ludiviciana*), western ragweed, sand sagebrush, and eastern red cedar (*Juniperus virginiana*; Lautenbach 2015, Wolfe et al. 2016, Lautenbach 2017). Average annual precipitation varies by longitude for the Mixed-Grass Prairie Ecoregion, with eastern areas of the ecoregion receiving 63.9-76.3 cm of rain, while the core of the ecoregion receives 51.8-63.8 cm, and western areas receive 40.6-51.7 cm (Grisham et al. 2016*a*). Mixed-Grass Prairie is the only ecoregion to fall in three different precipitation belts from east to west and it receives more rainfall than the other ecoregions within the lesser prairie-chicken range, averaging ~60 cm, with diminished fluctuations in annual precipitation values than other ecoregions of the lesser prairie-chicken range (Grisham et al. 2016*a*).

Sand Shinnery Oak Prairie

The Sand Shinnery Oak Prairie Ecoregion is comprised entirely of sand soils and extends from the Texas panhandle into the eastern New Mexico (Grisham et al. 2016*a*). Sand Shinnery Oak prairie plant composition typically includes sand shinnery oak (*Quercus havardii*), sand sagebrush, sand bluestem, big bluestem, little bluestem, sand dropseed, purple three-awn (*Aristida purpurea*), sand paspalum (*Paspalum setaceum*), silverleaf nightshade (*Solanum elaeagnifolium*), spectacled pod (*Dimorphocarpa wislizeni*), Indian blanket flower, wooly locoweed (*Astragalus mollissimus*), annual sunflower, scarlet gaura (*Gaura coccinea*), and halfshrub sundrop (*Oenothera serrulate*: Woodward et al. 2001, Grisham 2012, Grisham et al. 2016). Sand Shinnery Oak Prairie within the lesser prairie-chicken range spans two distinct bands of the east-west precipitation gradient, with annual precipitation in eastern Sand Shinnery Oak Prairie averaging 40.6-51.7 cm and the western extent 27.8-40.5 cm (Grisham et al. 2016*a*, *b*). Most of the precipitation in the Sand Shinnery Oak Prairie comes from localized severe thunderstorms (Grisham 2012, Grisham et al. 2016*b*). In addition to receiving the least precipitation in the lesser prairie-chicken range, Sand Shinnery Oak Prairie also experiences the highest temperatures, greater annual fluctuations in annual precipitation, and more frequent and intense drought conditions (Grisham 2012, Grisham et al. 2016*b*).

Methods

Lesser Prairie-Chicken Capture and Morphometrics Collection

Researchers trapped lesser prairie-chickens on leks using funnel traps, drop nets, and rocket nets during spring 1986-2019 (Table 1.1). Birds were sexed by dimorphic characteristics such as differences in tail color patterns and aged using patterns of spotting, wear, and molt of the outermost 9th and 10th primary feathers (Copelin 1963, Pyle 2008). In the assembled data set, I differentiated individual birds by metal bands with a unique identification number, combinations of color bands, or by a telemetry/signal identifier dependent upon project. Morphometric measurements were recorded for all sex and age classes (adult and juvenile; Figure 1.3).

When noted, bird mass (g) was measured using a spring balance; pinnae feather (mm) and tail length (mm) were measured from the base of the longest feather to tip with a ruler; wing length was measured as the length from the wrist to the end of the longest flattened primary (mm); and diagonal tarsus diagonal tarsus (mm) was measured with calipers from the bottom of the joint to the end of the metatarsus bone, determined by gently bending the foot. All morphometric measurements are reported in grams for body mass and estimated nutrient reserves, and millimeters for associated lengths.

Morphology as an Index of Habitat Quality

I used body mass as a proxy for energy reserves and estimated fat and protein composition based on the mathematical relationship between bird mass and fat and protein composition for lesser prairie-chickens (Haukos et al. 1989). Using predictive regression equations and raw data generated by Haukos et al. (1989), I first estimated bird body lengths. Then, I used the predictive relationship of the combination of body length, body mass, and wing chord to estimate grams of fat and protein for male and female birds.

Statistical Analysis

I accounted for discrepancies introduced from combining multiple data sources by testing each data set with a Shapiro-Wilks test and used the Interquartile Rule to remove outliers. This was followed by a series of analysis of variance (ANOVA) models of each morphometric trait comparing data source within the same ecoregion to account for potential observer bias. Pseudoreplication within the data set was accounted for by averaging morphometric measurements for individuals captured multiple times within the same year. Lesser prairie-chickens exhibit both sexual size dimorphism and differences in morphometric traits size between juvenile and adult birds (Hagen et al. 2004, Lislevand et al. 2009). Due to the morphological differences among age and sex classes, all models were separated by sex with differences between adult and juvenile birds accounted for as either separate models or through the inclusion of age as a model term.

To account for correlation between morphological traits, I generated a correlation matrix using Pearson Correlation to determine correlation between lesser prairie-chicken traits. Pearson Correlation of the morphometric suite indicates that lesser prairie-chicken mass, wing and pinnae have a weak correlation ($r > |0.26|$) for both sexes in all ecoregions. To account for correlation among traits, I tested a series of multivariate analysis of variance (MANOVA) models in addition to exploring influences using ANOVA models. After significant ANOVA ($P < 0.05$), I used least significant difference post-hoc test to separate ecoregions and age/sex classes. Together, I applied multivariate and single variable models to determine significant differences among ecoregions and underlying patterns for age and sex classes. I explored spatial and temporal range-wide morphology patterns using principal component analysis (PCA) models by age and sex class. The resulting principal components accounted for sources of variation within the morphological data, indicating where the greatest source of variation was across ecoregions. I used the predicted nutrient reserve values in ANOVA to compare nutrient reserves among ecoregions and determine the influence of weather on nutrient reserves of lesser prairie-chickens throughout time across the range. I tested separate models sets for males and females, due to the differences of behavior and reproductive costs between sexes. To account for variation across ecoregions, I tested models for both sexes within an ecoregion as well as comparing among ecoregions.

Applying Morphometrics to Costs of Reproduction

I examined the relationship between female morphometrics and nest fate for females captured in Short-Grass and Mixed-Grass Prairie ecoregions of Kansas during 2013-2016. Only first nesting attempts were considered in the analysis to keep the time between capture morphometric measurements and nesting attempt as short as possible. I tested nest survival in Program MARK for 72 first nesting attempts for adult and juvenile females. Nest survival models were selected for best fit with corrected Akaike information criterion (AIC_c).

I examined differences between first recorded male mass and last recorded male mass for 127 male records over the duration of the breeding season (mid-March through mid-April). This data set was comprised of 125 unique individuals from 1987-2018 in Mixed-Grass Prairie, Sand Shinnery Oak Prairie, and Short-Grass Prairie ecoregions. There were two unique individuals recorded in Mixed-Grass Prairie in Oklahoma multiple times in two distinct breeding seasons, where each breeding season was considered separately. I used paired *t*-tests between first and last capture mass, fat, and protein to determine if significant change in male mass was detectable.

Weather Variables

I incorporated the Palmer Drought Severity Index (PDSI) to explore the relationship between weather events and lesser prairie-chicken morphology. The PDSI is a measurement of meteorological drought that accounts for the correlated influence of temperature and physical water. Drier periods are depicted with negative values and wetter conditions with positive values

(Palmer 1965, Ross et al. 2016*b*, Dai and National Center for Atmospheric Research Staff 2019). I averaged Palmer Drought Severity Index values based for two significantly different periods of the year, determined by first splitting the year into biologically significant periods of prebreeding, breeding, nesting, brooding, and nonbreeding as well as yearly averaged PDSI value and reducing redundancy via Pearson Correlation Coefficient.

Prebreeding, breeding, and nonbreeding PDSI values were correlated ($r > |0.73|$), whereas nesting and brooding periods were positively related ($r = 0.84$) as well as the average yearly PDSI value ($r > |0.90|$). I simplified PDSI values into two biologically significant categories of average PDSI values for late spring and summer months during the nesting and brooding period here after referred to as lag summer and the average PDSI values for the nonbreeding and early spring months, here after referred to as lag non-summer. I employed the PDSI values in the MANOVA and ANOVA models to determine differences among ecoregions and the influence of meteorological drought on morphometric traits within ecoregions.

Results

Range-Wide Record of Lesser Prairie-chicken Morphology

I assembled a range-wide data set of lesser prairie-chicken morphometrics with 556 in Short-Grass, 877 Mixed-Grass, 88 Sand Sagebrush, and 960 Sand Shinnery Oak records of birds measured in each ecoregion (Table 1.1). This data set includes 1709 and 772records for males and females, respectively, from the period of 1986 to 2019. Highly correlated model terms were removed prior to model selection (Table 1.2; Table 1.3). I determined morphometric patterns for mass, flattened wing chord, pinnae feather length, tail feather length, and tarsus length across the range (Table 1.4).

Variation in Range-Wide Morphometric Suite

For all age and sex categories, PCA results indicated that the first principal component explained 95-91% of variance in the range-wide morphometric suite (Table 1.5). The first principal component primarily loaded on lesser prairie-chicken body mass, with positive loading for adult birds and negative loadings for juvenile birds (Table 1.6). With inclusion of the second principal component, the cumulative proportion of variation explained in the morphometric suite ranged from 96-97%; although the contribution from the second principal component to explaining morphometric variation across the range is minimal (Table 1.5). The second principal component rested primarily on tail lengths, with negative loadings in adult males and juvenile female tail lengths and positive loadings in adult females and juvenile males (Table 1.6).

Differences in Morphometrics Among Ecoregions

There are differences among ecoregions for morphometric traits of adult male ($F_{10, 494} = 9.06$, $P < 0.001$), juvenile male ($F_{10, 434} = 6.74$, $P < 0.001$), adult female ($F_{5, 72} = 5.276$ $P < 0.001$), and juvenile female ($F_{10, 440} = 6.87$, $P < 0.001$) lesser prairie-chickens. Morphometric differences among ecoregions vary by age and sex category. Notably, Mixed-Grass and Sand Sagebrush prairies typically have smaller morphometrics compared to Sand Shinnery Oak and Short-Grass prairies that typically have larger morphometrics. The size contrast is greatest between Mixed-Grass and Sand Shinnery Oak prairies.

The smaller morphometrics of Mixed-Grass Prairie birds is most noticeable in body mass. Although body mass explained the majority of morphometric variation across the range in the PCA, this pattern is driven by lesser prairie-chickens of the Mixed-Grass Prairie Ecoregion (Figure 1.5). Adult female ($F_{3, 249} = 3.72$, $P = 0.01$), adult males ($F_{3, 993} = 8.31$, $P < 0.001$), juvenile males ($F_{3, 667} = 13.89$, $P < 0.001$) and juvenile females ($F_{3, 496} = 4.25$, $P < 0.001$) have lower mean masses in Mixed-Grass Prairie compared to birds in the three other ecoregions (Table 1.5).

Pinnae lengths for adult ($F_{3,\,873} = 11.76$, $P < 0.001$) and juvenile males ($F_{3,\,585} = 9.13$, $P < 0.001$) are greatest in Short-Grass and Sand Shinnery Oak Prairies and shortest in Sand Sagebrush and Mixed-Grass Prairies (Figure 1.6). Juvenile female pinnae length is the most varied among ecoregions ($F_{3,\,396} = 7.79$, $P < 0.001$), however, this may be due to limited sample size in the Sand Sagebrush Ecoregion ($n = 10$; Table 1.4). Adult female pinnae lengths are longest in Sand Shinnery Oak Prairie ($F_{2,\,187} = 5.98$, $P < 0.001$) and shortest in Mixed-Grass Prairie. Tail length for adult ($F_{3,\,781} = 25.3$, $P < 0.001$) and juvenile males ($F_{3,\,536} = 14.59$, $P < 0.001$) are longer in Sand Sagebrush Prairie while Mixed-Grass Prairie birds have the smallest tails (Figure 1.8). For adult ($F_{3,\,208} = 15.08$, $P < 0.001$) and juvenile females ($F_{3,\,434} = 17.6$, $P < 0.001$), tail lengths are longer in Short-Grass and Sand Shinnery Oak and smaller in Mixed-Grass and Sand Sagebrush prairies (Figure 1.7). Wing lengths are the longest for all age and sex categories in Sand Shinnery Oak Prairie (Figure 1.8). Sand Sagebrush Prairie birds have a smaller mean wing length than the other ecoregions for adult females ($F_{3,\,232} = 7.49$, $P < 0.001$) and juvenile males ($F_{3,\,648} = 7.58$, $P < 0.001$), whereas juvenile females ($F_{3,\,485} = 12.55$, $P < 0.001$) and adult males ($F_{3,\,960} = 36.34$, $P < 0.001$) are similar between Sand Sagebrush and Mixed-Grass prairies.

Tarsus lengths were distinctively larger in Sand Shinnery Oak Prairie than other ecoregions (Table 1.4; Figure 1.9). Unlike with mass or feather lengths, the mean tarsus lengths of adult male lesser prairie-chickens ($F_{3,\,401} = 76.54$, $P < 0.001$) are significantly different in all ecoregions. Interestingly, Short-Grass Prairie birds of all sex and age categories have the shortest tarsus lengths, but also a much wider range of tarsus lengths (Table 1.4; Figure 1.9). For adult female ($F_{3,127} = 8.15$, $P < 0.001$), juvenile male ($F_{3,327} = 44.61$, $P < 0.001$), and juvenile female ($F_{3,335} = 25.38$, $P < 0.001$), Sand Sagebrush tarsus lengths fall between Sand Shinnery Oak and Mixed-Grass prairies and is not different as it is for adult males (Figure 1.9).

The Relationship Between Weather Events and Morphometric Traits

Changes in morphometric traits are tied closely to the cyclic drought cycle in the Great Plains. Morphometric attributes of lesser prairie-chickens respond to precipitation and temperature changes in the summer months when the majority of precipitation occurs across the range, but there is little influence comparatively from Palmer Drought Severity Index values from the remainder of the year. Furthermore, Palmer Drought Severity Index was a significant factor in MANOVA models of lag summer months for adult males ($F_{20,988}=5.78$, $P < 0.001$), juvenile males ($F_{20,868} = 5.67$, $P < 0.001$), and juvenile females ($F_{10,440} = 4.14$, $P < 0.001$), but not for adult females ($F_{15,216} = 0.69$, $P = 0.79$). Models of lag non-summer month Palmer Drought Severity Index were not influential for adult males ($F_{10,494} = 1.38$, $P = 0.18$), adult female ($F_{5,72} = 0.65$, $P = 0.66$), and juvenile males ($F_{10,434} = 1.73$, $P=0.07$). There were insufficient data for a juvenile female model.

Not all morphometric traits in the range-wide lesser prairie-chicken suite were influenced by lag summer weather conditions. For adult male, juvenile male, and juvenile female lesser prairie-chickens, mass and wing chord were insignificant model terms for all multivariate models (Figures 1.10, 1.11). However, for adult females, no morphometric trait was affected by the lag summer precipitation, suggestive of constraints on morphometric traits for females.

Pinnae length was the only common significant multivariate model term for adult male ($F_{4,248} = 10.57$, $P < 0.001$), juvenile male ($F_{4,218} = 3.61$, $P <0.01$) and juvenile female ($F_{2,223} = 10.55$, $P < 0.001$) lesser prairie-chickens (Figure 1.12). Incredibly, male pinnae lengths were longer after summer periods of severe to moderate drought than some of the moister PDSI categories in Sand Shinnery Oak and Short-Grass prairies (Figure 1.12).

Shortened pinnae lengths for male lesser prairie-chickens were observed after summer months with extreme moisture or drought in Sand Shinnery Oak Prairie ($F_{4, 390} = 5.37$, $P < 0.001$). Greater pinnae lengths for male lesser prairie-chickens were observed after periods of normal precipitation or moderate drought in Short-Grass Prairie ($F_{2, 144} = 11.08$, $P < 0.001$). Juvenile female pinnae lengths in Short-Grass ($F_{2, 133} = 5.72$, $P < 0.01$) were greater after summers of severe drought, and Sand Shinnery Oak ($F_{3, 112} = 8.38$, $P < 0.001$) prairies were longer after summers of normal precipitation to moderate drought (Figure 1.12).

Tail length was a significant multivariate model term for both adult ($F_{4, 248} = 4.56$, $P < 0.01$) and juvenile ($F_{4, 218} = 13.83$, $P < 0.001$) male lesser prairie-chickens. For Mixed-Grass, Short-Grass, and Sand Shinnery Oak prairie birds, longer male tail lengths were associated with high moisture in the proceeding summer months and shorter tail lengths with prior summer moderate moisture or drought (Figure 1.13). In Sand Shinnery Oak, adult and juvenile males both exhibited longer tail lengths in periods of drought as well as in periods of extreme summer moisture (Figure 1.13).

For juvenile males ($F_{4, 218} = 13.45$, $P < 0.001$) and females ($F_{2, 223} = 11.40$, $P < 0.001$), tarsus lengths were affected by lag summer weather. Juvenile female lesser prairie-chicken tarsus lengths were longer in periods of normal moisture than after summers of moderate or severe drought in Short-Grass ($F_{2, 164} = 8.56$, $P < 0.001$) and Sand Shinnery Oak ($F_{4, 32} = 2.71$, $P = 0.05$) prairies (Figure 1.14). In Short-Grass Prairie, juvenile male ($F_{2, 149} = 11.74$, $P < 0.001$) tarsus lengths followed female patterns with increased length following summers within a normal PDSI category and decreases after summers with periods of severe or moderate meteorological drought (Figure 1.14).

Relationship Between Lesser Prairie-Chicken Morphology and Habitat Quality

Nutrient reserves were calculated using the sex-specific equations derived in Haukos et al. (1989) for 969 adult male, 648 juvenile male, 243 adult female, and 477 juvenile records (Tables 1.7, 1.8). Following trends in lesser prairie-chicken body mass, calculated nutrient reserves exhibited low variation among ecoregions within individual sex and age categories. Only adult ($F_{3,\,965} = 12.68$, $P < 0.001$) male lesser prairie-chickens have variation in mean body fat among ecoregions. Mean body fat for both adult ($F_{3,\,239} = 1.71$, $P = 0.17$) and juvenile ($F_{3,\,473} = 2.04$, $P = 0.12$) female lesser prairie-chickens did not differ among ecoregions.

However, there is a striking sexually dimorphic difference in body fat between sexes (Figure 1.15). When grams of fat are considered as a proportion of an individual's overall body mass, male lesser prairie-chickens exhibited 2-3% body fat. Whereas, females exhibited 4-8% body fat, and the individuals with less body fat were typically juvenile females primarily in Short Grass or Sand Shinnery Oak prairie ecoregions (Table 1.8).

In contrast to the sexually dimorphic differences in estimated body fat, estimated grams of protein did not exhibit a sexually dimorphic trend (Figure 1.16). Grams of protein were consistent across adult and juvenile age categories, with a difference in grams protein between ecoregions for adult males ($F_{3,\,965} = 18.49$, $P < 0.001$), juvenile males ($F_{3,\,644} = 18.33$, $P < 0.001$), adult females ($F_{3,\,239} = 3.38$, $P = 0.02$), and juvenile females ($F_{3,\,473} = 3.59$, $P = 0.01$). Across age and sex classes, lesser prairie-chicken protein was constrained around ~20% body protein regardless of ecoregion. Adult and juvenile male mean protein was greatest in Sand Shinnery Oak Prairie, which was similar to mean protein levels of Short-Grass Prairie, and lowest in

Mixed-Grass Prairie, which was similar to Sand Sagebrush Prairie (Figure 1.16). Female protein was less varied, with the greatest mean protein similar in Sand Shinnery Oak, Short-Grass, and Sand Sagebrush prairie and lowest mean protein in Mixed-Grass Prairie for both adult and juvenile females (Figure 1.16).

While there was a stark sexual dimorphism to lesser prairie-chicken body fat, lesser prairie-chicken nutrient reserves followed the same significance trends for age and class models for lag weather affects as the analysis of the morphometric suite. Considering the relative stability of female mass prior to the nesting and brooding season, adult female body mass and nutrient reserves appear unaffected by weather events with minimal effects on juvenile female lesser prairie-chicken (Figures 1.17, 1.18). Among these results, juvenile female nutrient reserves were significant only once in Mixed-Grass Prairie for body fat ($F_{4,203} = 2.85$, $P = 0.02$).

Male lesser prairie-chicken nutrient reserves followed the pattern where birds of Sand Shinnery Oak and Mixed-Grass prairies have the most significantly affected nutrient reserve traits by summer lag PDSI (Figure 1.19). Male body fat was greatest after moist summer months for adult ($F_{5,514} = 13.16$, $P = 0.02$) and juvenile ($F_{5,287} = 10.38$, $P < 0.001$) males in Mixed-Grass Prairie. Whereas adult ($F_{4,250} = 15.8$, $P < 0.001$) and juvenile ($F_{4,182} = 10.37$, $P < 0.001$) males had less body fat following normal PDSI values or in moderate to extreme meteorological drought in Sand Shinnery Oak Prairie (Figure 1.19). Only adult male body fat ($F_{2,150} = 3.12$, $P = 0.05$) in Short-Grass Prairie was affected by lag PDSI. Similarly, body protein of adult ($F_{5,514} = 6.31$, $P < 0.001$) and juvenile males ($F_{5,287} = 11.27$, $P < 0.001$) in Mixed-Grass Prairie, and adult male body protein in Sand Shinnery Oak Prairie ($F_{4,250} = 3.47$, $P < 0.01$) was greatest after years with normal or extreme moisture, with the least protein following years with moderate to extreme drought (Figure 1.20).

Application of Morphometrics to Reproductive Costs and Outcomes

Morphometric attributes of Kansas Short-Grass and Mixed-Grass prairie females did not have a significant influence on nest survival for 72 first nesting attempts (Table 1.9). The highest ranked model based on AIC_c was the constant model for daily survival, followed by equivalent AIC_c constant survival models for fat, protein, and minimum and maximum fat (Table 1.9). For both failed and successful nests, female morphometric traits bear no notable differences, suggesting that morphometrics are likely constrained by nesting and brooding requirements and there is no variation in morphometric attributes that contribute to nesting outcome (Figure 1.21).

Within the range-wide data set, I examined differences between first recorded male mass and last recorded male mass for 127 male records over the duration of the breeding season (mid-March through mid-April). This data set was comprised of 125 unique individuals from 1987-2018 in Mixed Grass Prairie, Sand Shinnery Oak Prairie, and Short-Grass Prairie (Tables 1.10-1.13). There are two unique individuals that were recorded in Mixed Grass Prairie in Oklahoma multiple times in two distinct breeding seasons, where each breeding season was considered separately. Changes in male mass with each subsequent recapture event were used to determine changes in male lesser prairie-chicken fat and protein composition.

The overall trend is for males to lose mass over the duration of a field season (Figure 1.22). Paired *t*-tests yielded differences between first and last recorded mass, grams of body fat, and grams of protein. Mean grams ($t_{126} = 5.85$, $P < 0.001$), body fat ($t_{126} = 5.80$, $P < 0.001$) and protein ($t_{126} = 5.86$, $P < 0.001$) of lesser prairie-chicken males significantly decreased between first and last recapture events.

While there was a significant difference between first and last recorded mass, fat, and protein this does not fully account for the wide range of observed changes in nutrient reserves in male lesser prairie-chickens. When recaptured males from across the lesser prairie-chicken range considered as a whole, individual male mass may increase or decrease up to ~100g within the three weeks of their first weeks of capture (Figure 1.23). This examination of the scope of change in nutrient reserve data for male lesser prairie-chickens indicates that a loss of nutrient reserves is not a universal pattern (Figure 1.23).

Minimum values for all nutrient reserves slowly increased over the duration of the breeding season, while maximum values decreased (Tables 1.11-1.13). The median and average recorded values for male nutrient reserves, respectively, decrease, with a brief late breeding season increase followed by a second decline in average grams of mass, fat, and protein.

The majority of this spread in changes in mass over a single breeding season are noticeable in Mixed-Grass Prairie birds, which may be partially reflective of the sample sizes of recaptured males within the three ecoregions considered. However, as overall changes in mass are shared characteristics across Mixed-Grass, Sand Shinnery Oak, and Short-Grass prairies it is likely that the smaller representative sample sizes of the other two ecoregions simply do not characterize this pattern.

Discussion

Ecoregion-specific and age and sex morphometric differences for lesser prairie-chickens appear to be tied to the Southern Great Plains drought cycle, which is largely driven by temperature and precipitation over the summer months. Within the morphometric suite of body mass, wing chord, pinnae length, tail length, and tarsus length, body mass explains up to 95% of morphometric variation among ecoregions. This variation in mass is driven by the lower masses of lesser prairie-chickens in the Mixed-Grass Prairie Ecoregion, which typically have smaller morphometric characteristics than birds of the other three ecoregions within the range.

Lesser prairie-chickens in the Mixed-Grass Prairie Ecoregion exhibited consistently smaller morphometric traits despite having the greatest annual precipitation and relatively less severe droughts compared to the rest of the range. The comparatively smaller body size of Mixed-Grass Prairie lesser prairie-chickens may not be a reflection of ecoregion specific pressures, as the Sand Sagebrush Prairie lesser prairie-chickens often exhibited similar size despite differences in productivity. Instead it is more likely that there are underlying pressures at work in the Short-Grass and Sand Shinnery Oak Prairies driving lesser prairie-chicken morphometrics to increased size compared to the Mixed-Grass Ecoregion.

The largest lesser prairie-chickens in the range are often Short-Grass and Sand Shinnery Oak prairie birds, with Sand Shinnery Oak Prairie birds exhibiting larger tarsus lengths than birds in other ecoregions. The increased size of morphometric traits for Sand Shinnery Oak Prairie birds may be due to the relatively high average annual temperature, where increased tarsus lengths might act to assist in heat dispersion (Meiri and Dayan 2003, Kirchman and Schneider 2014, Grisham et al. 2016*a*, *b*). Alternatively, tarsus length differences in Sand Shinnery Oak prairie birds may be attributable to the genetic differences of the Sand Shinnery Oak Ecoregion from the other three ecoregions within the lesser prairie-chicken range (Hagen et al. 2010, Oyler-McCance et al. 2016). Comparatively, the Short-Grass Prairie lesser prairie-chicken population is the most recently established population and located in a wetter portion of the species' range than Sand Shinnery Oak prairie (Oyler-McCance et al. 2016, Rodgers 2016).

Unlike Sand Shinnery Oak Prairie birds, female lesser prairie-chickens typically exhibit larger morphometric traits in Short-Grass Prairie. This suggests a selective pressure acting on female attributes in the Short-Grass Prairie that may be distinct from climatic pressures of the Sand Shinnery Oak Prairie birds. While lesser prairie-chickens in the Short-Grass Prairie do overlap in range with greater prairie-chickens, and the two species are known to produce viable hybrid offspring, the likelihood of pervasive hybridization resulting in a population shift to larger overall morphometric traits is small (Bain and Farley 2002, Dahlgren et al. 2016). Birds of the Short-Grass Prairie also show greater range of morphometric traits than birds of Sand Shinnery Oak Prairie but are not consistently among the largest for all traits considered.

Previous summer precipitation has a lag effect on morphometric traits throughout all four ecoregions regardless of where they fall within the east-west precipitation gradient. Mixed-Grass and Sand Shinnery Oak Prairies share morphometric patterns following periods of summer drought, despite occurring at opposite ends of the temperature and precipitation gradient within the lesser prairie-chicken range. The similarities in morphometric response between the ecoregions suggests that allocation of resources during periods of limited access is universal across the lesser prairie-chicken range. Based on ecoregion-specific differences in size, it is likely the climatic differences exert a selective pressure on maximum size for morphometric traits while resource allocation based on precipitation is held common across the range.

Across all four ecoregions, it is especially notable that adult female lesser prairie-chicken morphometric traits are relatively fixed and unresponsive to changes to temperature or precipitation across all four ecoregions across the time periods considered (A 1.1-1.6). However, the proceeding summer's weather does affect traits of juvenile females. This age-specific difference in influence of weather effects may be related to differences in resource allocation between juvenile and adult birds. Juvenile development necessitates allocation of resources to both fixed and annually replaced morphometric traits, while adult birds allocate resources to maintenance of feathers during molt or body mass.

Feather lengths are especially reflective of restricted access to resources and the allocation of those resources to morphometric traits. Feather traits are subject to annual development, reflecting the access to resources prior and during the periods of their growth and for lesser prairie-chickens they also reflect differences in allocation of sexually selected traits. Lesser prairie-chicken feather lengths for tail and pinnae decrease after periods of extreme drought. However, male lesser prairie-chickens exhibit longer pinnae lengths after proceeding summers of moderate to severe drought.

As a sexually selected characteristic, pinnae length may be an important indication of male quality and having longer pinnae after drought may act as an important signal to distinguish healthy males from others on a lek. Further support of this explanation is the consistency of wing feather lengths with other non-sexually selected morphometric traits. Greater lesser prairie-chicken wing lengths after moderate or normal precipitation values and decreases after high precipitation or severe drought, also suggests a preferential allocation to sexually selected traits rather than all feathers at molt.

The sexually selected feather lengths of male lesser prairie-chickens can also be juxtaposed with juvenile tarsus lengths. Tarsus lengths are a fixed feature mirroring the available resources at the time of development. Juvenile male and female lesser prairie-chickens that develop during years of drought are smaller than birds that develop in periods of normal or greater precipitation. Unlike feather characteristics, which appear to have a universal pattern observed in all ecoregions, the influence of precipitation on tarsus length during growth is seen almost exclusively in birds of Short-Grass Prairie. Only juvenile females exhibit reduced tarsus lengths for Sand Shinnery Oak Prairie after summer drought, implicating the greater tarsus lengths observed in Sand Shinnery Oak Prairie serve a functional purpose at the greater lengths observed in the ecoregion.

Out of all the morphometric characteristics considered, mass is the most subject to rapid change. This is why the tight constraint of female mass across ecoregions and lag PDSI conditions is striking in comparison to the fluctuation within male mass in Mixed-Grass and Sand Shinnery Oak prairies. As with the allocation of resources to sexually selected feather traits in males, the constraint in female mass is likely associated with the breeding season and the strong division of reproductive effort in lesser prairie-chickens as a lek breeding species. All birds used in analyses were caught during the breeding season in March and April, when morphological measurements are reflective of breeding condition and allocation of resources to traits prior to the breeding season. The sexually dimorphic constraint in mass is reflected in the differences in nutrient reserves, where percent body fat that is tightly constrained across lag PDSI conditions and ecoregion with ~8% fat for females and 2-3% in males. It is also worth noting, that female lesser prairie-chickens have been shown to modulate reproductive costs in intensive droughts by either forgoing or reducing nesting attempts and limitations posed by nutrient reserves may be mediated by behavior (Boal et al. 2010, Grisham 2012, Grisham et al. 2014).

The low percent of male body fat at the beginning of the breeding season would seem to support that observed mass loss over the duration of the breeding season is indicative of courtship displays being conditionally expensive. The hypothesis of courtship cost in lek breeding birds is common and this is an underlying assumption that links lesser prairie-chicken mass over the duration of the breeding season to courtship displays (Boal et al. 2010, Grisham et al. 2013, Hagen et al. 2013). However, determining the extent of reproductive cost of lek displays is far more nebulous and, based on recapture data, cannot be reduced simply to a metabolic expense because of decreased mass.

When recaptured males from across the lesser prairie-chicken range are considered as a whole, individual male mass may increase or decrease up to ~100g within the three weeks of their first weeks of capture. The large variation around change in individual mass is likely tied to differences in reproductive effort, which can act to modulate physiological costs of displays (Patricelli and Krakauer 2010). Even for individuals where there is a sustained loss of mass throughout the breeding season, this difference in mass is likely negligible for most males. The average difference between first and last recorded mass is ~22g, spread across mass gains and losses with few individuals reaching a change in mass as great as ~100 g. However, there is the remaining question about what comprises the majority of male mass loss from first measurement to last measurement.

Within the overall difference of mass, only ~30% of total mass can be accounted for with differences in male body fat and protein. Water mass may explain a portion of this loss that is not currently accounted for in the presented analyses, but it is unlikely to explain the totality of the remaining difference. Similar to the modification of digestive systems like many other avian species, grouse can modulate the size of their digestive systems (Moss 1983, Olawsky 1987, McCloskey et al. 2009). Modification of digestive tissue mass, metabolic cost of display, and modulation of potential courtship costs through behavior are viable lines for future lines of inquiry about mass loss in lesser prairie-chickens (Olawsky 1987).

The most striking result is the tight constraint on breeding season body fat in females across drought and wet years, which alludes to a biological constraint on fat required to successfully breed. Nesting success for lesser prairie-chickens is estimated at 40%, but my analyses found that no morphometric trait had an impact on nesting success (Hagen et al. 2007, Haukos and Boal 2016). This tight constraint on fat may contribute to the lack of significant signal for morphometric or nutrient reserve influences on nest success of Short-Grass or Mixed-Grass prairie females in Kansas. Since fat is constrained across conditions, it therefore does not vary among successful or unsuccessful first nesting attempts. Without subsequent recapture of nesting females on second or third nesting attempts, we cannot determine if nesting outcome for subsequent attempts is determined by the ability or inability to maintain 8% body fat.

With increasingly dramatic climatic swings in a species range that is prone to drought every 5-10 years it is unclear what this will mean for the ability of females to maintain ~8% body fat prior to nesting across the precipitation gradient. As a boom-bust species, lesser prairie-chicken populations are especially vulnerable to the projected changing precipitation and temperature patterns under climate change (Ross et al. 2016*b*). The projected shift of precipitation events outside of the growing season along with fewer, severe storms providing an increasing amount of moisture is especially concerning due to the implications that has for both plant communities on the prairie (Grisham et al. 2013, 2016*a*). Increasing woody encroachment as well as a shift in understory plant communities are likely and, when considered with implications for overall ecosystem productivity with less precipitation during the growing season, the ability to maintain optimal body fat for breeding may become increasingly difficult. Females nesting under extreme conditions have lower nesting propensity and success; with the projected increased drought and unpredictable, concentrated rain throughout the Great Plains, it is likely that females will have increasing difficulty meeting biological constraints for nesting (Grisham et al. 2014).

As the easternmost ecoregion within the lesser prairie-chicken range, Mixed-Grass Prairie has the most consistent and greatest amount of precipitation. Despite the increased precipitation, the influences of lag summer PDSI values on Mixed-Grass Prairie lesser prairie-chicken morphometric traits follows the much more dynamic drought cycles of the Sand Shinnery Oak and Short-Grass prairies. Morphometric response to drought is essentially uniform across the lesser prairie-chicken range, regardless of the potential buffering effects of a more consistent annual average precipitation or greater annual rainfall than the other three ecoregions in the range. Even within the Mixed-Grass Prairie Ecoregion it is uncertain if lesser prairie-chickens will be able to maintain nutrient reserves to breeding constraints with increasing propensity for drought and erratic precipitation events across the Great Plains.

Management Implications

Management of lesser prairie-chickens should continue to collect an extensive set of morphometric measurements when individual birds are captured or recovered. Morphometrics offer a time capsule of selective influences on birds throughout the range that is irreplaceable. Morphometrics, as exemplified in this work, can be utilized to monitor shifts in selective pressures. Against the baseline of morphometric patterns outlined in this work, managers can make inferences about resource access available during growth based on the size of tarsus lengths, seasonal influences in wing lengths, and rapid response in changes in bird mass. Furthermore, changes to the constrained ranges of adult female morphometric traits could act as important signal of massive underlying change in future management that would be overlooked without collecting and examining morphometric traits.

Conclusion

Lesser prairie-chicken morphometric traits are largest in Short-Grass and Sand Shinnery Oak prairies with smaller traits in Mixed-Grass and Sand Sagebrush prairies. The increased morphometric size for lesser prairie-chickens in Short-Grass and Sand Shinnery Oak Prairies is likely due to different selective pressures. The Sand Shinnery Oak Prairie is the most genetically distinct ecoregion in addition to being subject to greater extreme weather events compared to the other ecoregions in the range. The larger size of morphometric traits in Short-Grass Prairie is likely driven by female measurements, suggesting that there may be reproductive constraints driving this selection. The stability of adult female morphometrics throughout the range regardless of lag-PDSI values is also suggestive of strong selective constraints on female size.

For males and juvenile females, mass, wing, and tarsus lengths follow an anticipated pattern of decrease after extreme summer moisture or drought. Despite the effect of weather on morphometric traits, changes to morphology appear to be in response to precipitation and temperature prior to growth rather than substantiated changes in morphometric traits over time. Interestingly, following moderate to severe summer drought, pinnae feather lengths increase for male birds, implicating the possibility of honest signaling following periods of limited resources.

Sexually selected constraints are also exhibited in lesser prairie-chicken body fat, which is tightly constrained by sex regardless of weather or ecoregion when birds are measured in the breeding season. Perhaps because of how tightly body fat is constrained at the beginning of the breeding season, there was no significant relationship between the outcome of female’s first nesting attempt based on nutrient reserves or wing lengths. The relationship between nutrient reserves and nesting success may be more important in subsequent nesting attempts for females that fail their first nesting attempt. For displaying males, mass loss sustained over the duration of a breeding season is highly varied with individuals recorded as losing or gaining as much as 100g between recapture events. Courtship behavior is likely used to modulate any potential metabolic cost of displaying and effort likely varies by alpha males and those of subdominant status. Together, patterns of male morphological plasticity and relatively fixed female morphology is indicative of sexual selection and breeding constraints by sex acting to shape morphological traits in the lesser prairie-chicken across the range despite some differences in size among ecoregions.

Literature Cited

Anderson, R. K. 1969. Prairie chicken responses to changing booming-ground cover type and height. Journal of Wildlife Management 33:636–643.

Applegate, R. D., and T. Z. Riley. 1998. Lesser prairie-chicken management. Rangelands 20:13–15.

Arnold, T. W., M. G. Anderson, R. B. Emery, M. D. Sorenson, and C. N. de Sobrino. 1995. The effects of late-incubation body mass on reproductive success and survival of canvasbacks and redheads. Condor 97:953–962.

Bain, M. R., and G. H. Farley. 2002. Display by apparent hybrid prairie-chickens in a zone of geographic overlap. Condor 104:683–687.

Behney, A. C., B. A. Grisham, C. W. Boal, H. A. Whitlaw, and D. A. Haukos. 2012. Sexual selection and mating chronology of lesser prairie-chickens. Wilson Journal of Ornithology 124:96–105.

Bell, L. A., J. C. Pitman, M. A. Patten, D. H. Wolfe, S. K. Sherrod, and S. D. Fuhlendorf. 2007. Juvenile lesser prairie-chicken growth and development In southeastern New Mexico. Wilson Journal of Ornithology 119:386–391.

Bendell, J. F. 1955. Age, molt and weight characteristics of blue grouse. Condor 57:354–361.

Bidwell, T., S. Fuhlendorf, B. Gillen, S. Harmon, R. Horton, R. Manes, R. Rodgrs, S. Sherrod, and D. Wolfe. 2002. Ecology and management of the lesser prairie-chicken E-970. Oklahoma Cooperative Extension Service Division of Agricultural Sciences and Natural Resources Oklahoma State University.

Björklund, M., A. Borras, J. Cabrera, and J. C. Senar. 2015. Increase in body size is correlated to warmer winters in a passerine bird as inferred from time series data. Ecology and Evolution 5:59–72.

Boal, C., D. Haukos, and B. Grisham. 2010. FINAL REPORT – PHASE I: understanding the ecology, habitat use, phenology and thermal tolerance of nesting lesser prairie-chickens to predict population level influences of climate change.

Brown, C. R., M. B. Brown, and E. A. Roche. 2013. Fluctuating viability selection on morphology of cliff swallows is driven by climate. Journal of Evolutionary Biology 26:1129–1142.

Copelin, F. 1963. The lesser prairie chicken in Oklahoma. Oklahoma Wildlife Conservation Department, Oklahoma City, OK.

Dahlgren, D. K., R. D. Rodgers, R. D. Elmore, and M. R. Bain. 2016. Grasslands of western Kansas, north of the Arkansas River. Pages 259–280 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Dai, A., and National Center for Atmospheric Research Staff. 2019. The climate data guide: Palmer Drought Severity Index (PDSI). Palmer Drought Severity Index. <https://climatedataguide.ucar.edu/climate-data/palmer-drought-severity-index-pdsi>. Accessed 15 May 2020.

Davis, D. M. 2009. Nesting ecology and reproductive success of lesser prairie-chickens in shinnery oak-dominated rangelands. Wilson Journal of Ornithology 121:322–327.

Davis, J. A. 1968. The postjuvenal wing and tail molt of the ruffed grouse (Bonasa Umbellus Monticola) in Ohio. Ohio Journal of Science 68:8.

DeYoung, R. W., and D. L. Williford. 2016. Genetic variation and population structure in the prairie grouse implications for conservation in the lesser prairie-chicken. Pages 77–97 *in* D. A. Haukos and C. W. Boal, editors. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Elliott, K. H., M. Le Vaillant, A. Kato, A. J. Gaston, Y. Ropert-Coudert, J. F. Hare, J. R. Speakman, and D. Croll. 2014. Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. Journal of Animal Ecology 83:136–146.

Fields, T. L., G. C. White, W. C. Gilgert, and R. D. Rodgers. 2006. Nest and brood survival of lesser prairie-chickens in west central Kansas. Journal of Wildlife Management 70:931–938.

Garton, E. O., C. A. Hagen, G. M. Beauprez, S. C. Kyle, J. C. Pitman, D. D. Schoeling, and W. E. V. Pelt. 2016. Population dynamics of the lesser prairie-chicken. Pages 49–76 *in*. Ecology and conservation of lesser prairie-chicken. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Giesen, K. M. 2000. Population status and management of lesser prairie-chicken in Colorado. Prairie Naturalist 32:137–148.

Godar, A. J. 2016. Influence of climate change and land use on lesser prairie-chicken (Tympanuchus Pallidicinctus) population persistence in the Sand Sagebrush and Short-Grass Prairies. Thesis, Texas Tech University, Lubbock, Texas.

Graham, B. A., and C. W. Boal. 2015. Causes of mortality and temporal patterns in breeding season survival of lesser prairie-chickens in Shinnery Oak Prairies. Wildlife Society Bulletin 39:536–542.

Grisham, B. A. 2012. The ecology of lesser prairie-chickens in Shinnery Oak-Grassland communities in New Mexico and Texas with implications toward habitat management and future climate change. Dissertation, Texas Tech University, Lubbock, Texas.

Grisham, B. A., C. W. Boal, D. A. Haukos, D. M. Davis, K. K. Boydston, C. Dixon, and W. R. Heck. 2013. The predicted influence of climate change on lesser prairie-chicken reproductive parameters. F. Seebacher, editor. PLoS ONE 8:e68225.

Grisham, B. A., P. K. Borsdorf, C. W. Boal, and K. K. Boydston. 2014. Nesting ecology and nest survival of lesser prairie-chickens on the southern high plains of Texas. Journal of Wildlife Management 78:857–866.

Grisham, B. A., A. J. Godar, and C. P. Griffin. 2016*a*. Climate change. Pages 221–242 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Grisham, B. A., J. C. Zavaleta, A. C. Behney, P. K. Borsdorf, D. R. Lucia, C. W. Boal, and D. A. Haukos. 2016*b*. Ecology and conservation of lesser prairie-chickens in Sand Shinnery Oak Prairie. Pages 315–344 *in*. Ecology and Conservation of Lesser Praire-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Hagen, C. A., E. O. Garton, G. Beauprez, B. S. Cooper, K. A. Fricke, and B. Simpson. 2017. Lesser prairie-chicken population forecasts and extinction risks: an evaluation 5 years post-catastrophic drought. Wildlife Society Bulletin 41:624–638.

Hagen, C. A., B. A. Grisham, C. W. Boal, and D. A. Haukos. 2013. A meta-analysis of lesser prairie-chicken nesting and brood-rearing habitats: implications for habitat management. Wildlife Society Bulletin 37:750–758.

Hagen, C. A., D. C. Pavlacky, K. Adachi, F. E. Hornsby, T. J. Rintz, and L. L. McDonald. 2016. Multiscale occupancy modeling provides insights into range-wide conservation needs of lesser prairie-chicken (Tympanuchus pallidicinctus). Condor 118:597–612.

Hagen, C. A., J. C. Pitman, R. J. Robel, and R. D. Applegate. 2004. Morphology of lesser prairie-chickens in Kansas. Prairie Naturalist 36:95–102.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2007. Age-specific survival and probable causes of mortality in female lesser prairie-chickens. Journal of Wildlife Management 71:518–525.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, D. H. Wolfe, R. J. Robel, R. D. Applegate, and S. J. Oyler-McCance. 2010. Regional variation in mtDNA of the lesser prairie-chicken. Condor 112:29–37.

Hagen, C. A., G. C. Salter, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2005. Lesser prairie-chicken brood habitat in sand sagebrush: invertebrate biomass and vegetation. Wildlife Society Bulletin 33:1080–1091.

Haukos, D. A., and C. W. Boal, editors. 2016. Ecology and conservation of lesser prairie-chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Haukos, D. A., A. A. Flanders, C. A. Hagen, and J. C. Pitman. 2016. Lesser prairie-chickens of the Sand Sagebrush Prairie. Pages 281–298 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Haukos, D. A., L. M. Smith, and C. D. Olawsky. 1989. Nutrient Reserve models for post-breeding lesser prairie-chicken. Pages 268–274 *in*. Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies. Volume 43.

Haukos, D. A., and J. C. Zavaleta. 2016. Habitat. Pages 99–132 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Höglund, J., and B. C. Sheldon. 1998. The Cost of Reproduction and Sexual Selection. Oikos 83:478–483.

Hunt, J. L., and T. L. Best. 2010. Vegetative characteristics of active and abandoned leks of lesser prairie-chickens (Tympanuchus pallidicinctus) in southeastern New Mexico. Southwestern Naturalist 55:477–487.

Janssen, M. H., P. Arcese, T. K. Kyser, D. F. Bertram, and D. R. Norris. 2011. Stable isotopes reveal strategic allocation of resources during juvenile development in a cryptic and threatened seabird, the marbled murrelet (Brachyramphus marmoratus). Canadian Journal of Zoology 89:859–868.

Jensen, W. E., D. A. Robinson, and R. D. Applegate. 2000. Distribution and population trend of lesser prairie-chicken in Kansas. Prairie Naturalist 32:169–175.

Johnsgard, P. A. 2008. Molts and plumages. Pages 37–50 *in*. Grouse and quails of North America. 2nd edition. University of Nebraska Press.

Killpack, T. L., and W. H. Karasov. 2012. Growth and development of house sparrows (Passer domesticus) in response to chronic food restriction throughout the nestling period. Journal of Experimental Biology 215:1806–1815.

Kirchman, J. J., and K. J. Schneider. 2014. Range expansion and the breakdown of Bergmann’s Rule in red-bellied woodpeckers (Melanerpes carolinus). Wilson Journal of Ornithology 126:236–248.

Lautenbach, J. D. 2017. The role of fire, microclimate, and vegetation in lesser prairie-chicken habitat selection. Thesis, Kansas State University, Manhattan, KS.

Lautenbach, J. M. 2015. Lesser prairie-chicken reproductive success, habitat selection, and response to trees. Thesis, Kansas State University, Manhattan, KS.

Lebigre, C., R. V. Alatalo, and H. Siitari. 2013. Physiological costs enforce the honesty of lek display in the black grouse (Tetrao tetrix). Oecologia 172:983–993.

Lislevand, T., J. Figuerola, and T. Székely. 2009. Evolution of sexual size dimorphism in grouse and allies (Aves: Phasianidae) in relation to mating competition, fecundity demands and resource division. Journal of Evolutionary Biology 22:1895–1905.

McCloskey, J. T., J. E. Thompson, A. D. Tjelmeland, and B. M. Ballard. 2009. Body composition and gut morphology of migrating and wintering Wilson’s snipe. Waterbirds 32:96–105.

McDaniel, P., and B. Williamson. 2016. Conservation of lesser prairie-chickens: a case study. Pages 243–255 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

McDonald, L., J. Griswold, T. Rintz, and G. Gardner. 2013. Range-wide population size of the lesser prairie-chicken: 2012 and 2013. West EcoSystems Technology, Inc., Laramie, Wyoming. <http://doi.wiley.com/10.1002/wsb.417>. Accessed 6 May 2020.

Meiri, S., and T. Dayan. 2003. On the validity of Bergmann's Rule. Journal of Biogeography 30:331–351.

Merchant, S. S. 1982. Habitat-use, reproductive success, and survival of female lesser prairie chickens in two years of contrasting weather.

Milenkaya, O., N. Weinstein, S. Legge, and J. R. Walters. 2013. Variation in body condition indices of crimson finches by sex, breeding stage, age, time of day, and year. Conservation Physiology 1:1–14.

Milonoff, M., H. Pöysä, P. Runko, and V. Ruusila. 2004. Brood rearing costs affect future reproduction in the precocial common goldeneye Bucephala clangula. Journal of Avian Biology 35:344–351.

Moss, R. 1983. Gut size, body weight, and digestion of winter foods by grouse and ptarmigan. Condor 85:185–193.

Nasman, K., T. Rintz, R. Clark, G. Gardner, and L. McDonald. 2018. Range-wide population size of the lesser prairie-chicken: 2012 to 2018. West EcoSystems Technology, Inc., Laramie, Wyoming.

Olawsky, C. D. 1987. Effects of shinnery oak control with tebuthiuron on lesser prairie-chicken populations. Thesis, Texas Tech University, Lubbock, Texas.

Oyler-McCance, S. J., R. W. DeYoung, J. A. Fike, C. A. Hagen, J. A. Johnson, L. C. Larsson, and M. A. Patten. 2016. Rangewide genetic analysis of lesser prairie-chicken reveals population structure, range expansion, and possible introgression. Conservation Genetics 17:643–660.

Palmer, W. C. 1965. Meteorological drought. U.S. Department of Commerce Weather Bureau, Washington, D.C.

Patricelli, G. L., and A. H. Krakauer. 2010. Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. Behavioral Ecology 21:97–106.

Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2004. Gender identification and growth of juvenile lesser prairie-chickens. Condor 107:87–96.

Pyle, P. 2008. Lesser Prairie-Chicken Tympanuchus pallidicinctus. Pages 195–197 *in*. Identification Guide to North American Birds Part II. Slate Creek Press, Point Reyes Station.

Robinson, S. 2015. Landscape ecology, survival, and space use of lesser prairie-chickens. Thesis, Kansas State University, Manhattan, KS.

Robinson, S. G., D. A. Haukos, R. T. Plumb, J. D. Kraft, D. S. Sullins, J. M. Lautenbach, J. D. Lautenbach, B. K. Sandercock, C. A. Hagen, A. Bartuszevige, and M. A. Rice. 2018. Effects of landscape characteristics on annual survival of lesser prairie-chickens. American Midland Naturalist 180:66–86.

Rodgers, R. D. 2016. A history of lesser prairie-chickens. Pages 15–38 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Rodgers, R. D., and R. W. Hoffman. 2005. Prairie grouse population response to conservation reserve program grasslands: an overview. Pages 120–128 *in* A. W. Allen and M. W. Vandever, editors. The Conservation Reserve Program- Planting for the Future: Proceedings of a National Conference. U.S. Geological Survey, Biological Resources Division, Fort Collins, Colorado.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366:120–124.

Ross, B. E., D. Haukos, C. Hagen, and J. Pitman. 2016. The relative contribution of climate to changes in lesser prairie-chicken abundance. Ecosphere 7. <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1323>. Accessed 6 May 2020.

Sandercock, B. K., K. Martin, and G. Segelbacher, editors. 2011. Ecology, conservation, and management of grouse. Studies in Avian Biology No. 39, Cooper Ornithological Society University of California Press, Berkeley.

Stevenson, R. D., and W. A. Woods Jr. 2006. Condition indices for conservation: new uses for evolving tools. Integrative and Comparative Biology 46:1169–1190.

Sullins, D. S. 2017. Regional variation in demography, distribution, foraging, and strategic conservation of lesser prairie-chickens in Kansas and Colorado. Dissertation, Kansas State University, Manhattan, KS.

Sullins, D. S., J. D. Kraft, D. A. Haukos, S. G. Robinson, J. H. Reitz, R. T. Plumb, J. M. Lautenbach, J. D. Lautenbach, B. K. Sandercock, and C. A. Hagen. 2018. Demographic consequences of conservation reserve program grasslands for lesser prairie-chickens. Journal of Wildlife Management 82:1617–1632.

Taylor, M. A., and F. S. Guthery. 1980. Fall-winter movements, ranges, and habitat use of lesser prairie chickens. Journal of Wildlife Management 44:521–524.

U.S. Fish and Wildlife Service. 2016. Endangered and threatened wildlife and plants; lesser prairie-chicken removed from list of endangered and threatened Wildlife. Federal Register. Volume 81.

Wolfe, D. H., L. C. Larsson, and M. A. Pattern. 2016. The lesser prairie-chicken in the Mixed-Grass Prairie Ecoregion of Oklahoma, Kansas, and Texas. Pages 299–314 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Wolfe, D. H., M. A. Patten, E. Shochat, C. L. Pruett, and S. K. Sherrod. 2007. Causes and patterns of mortality in lesser prairie-chickens Tympanuchus pallidicinctus and implications for management. Wildlife Biology 13:95–104.

Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie, and J. Shackford. 2001. Influence of landscape composition and change on lesser prairie-chicken (Tympanuchus pallidicinctus) populations. American Midland Naturalist 145:261–274.

Figures

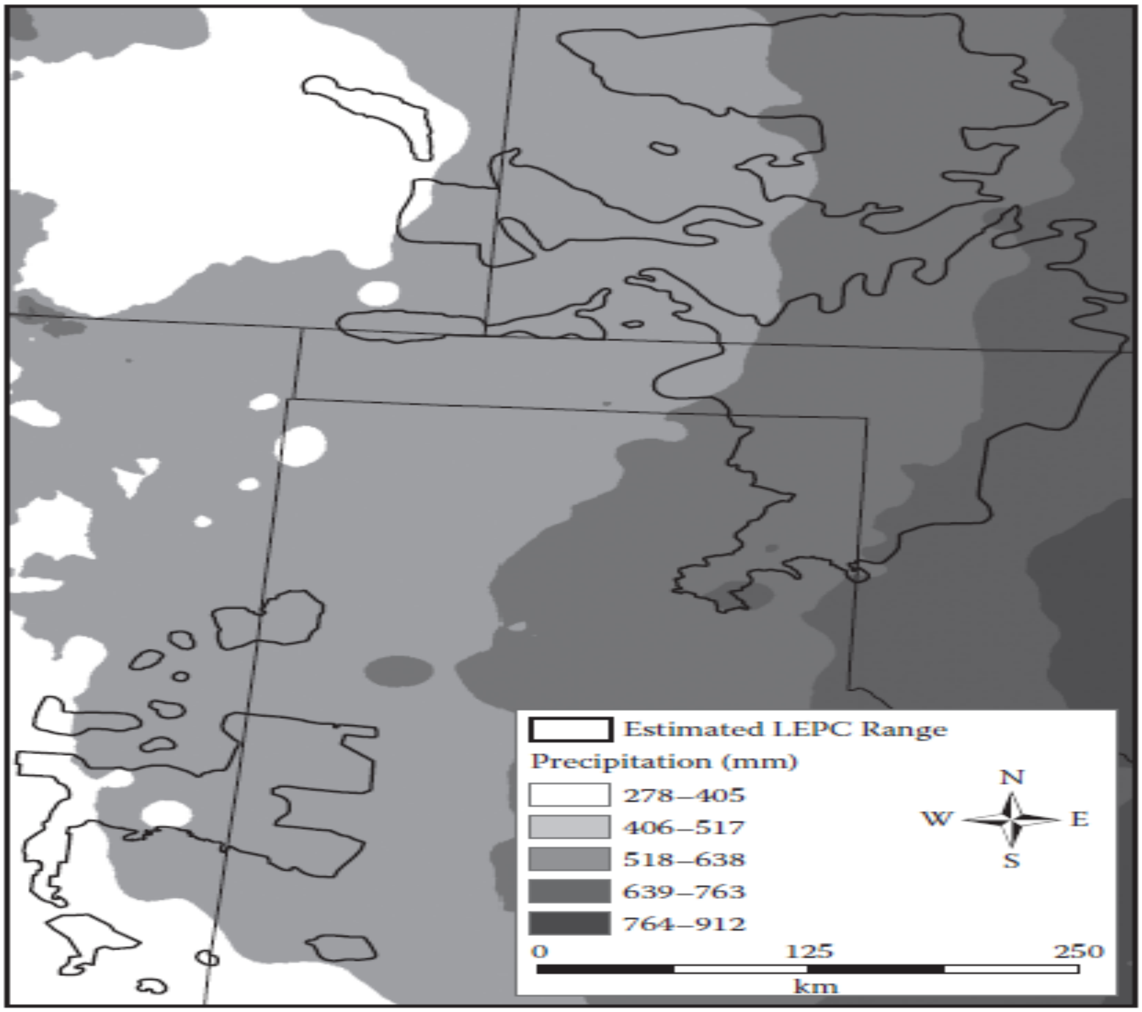

Figure 1.1 Precipitation Gradient in the Southern Great Plains

The lesser prairie-chicken range has an east-west precipitation gradient, with decreasing precipitation moving west, and a growing season gradient that runs north-south with a longer season in the southern extent. Figure adapted from Haukos and Boal (2016).

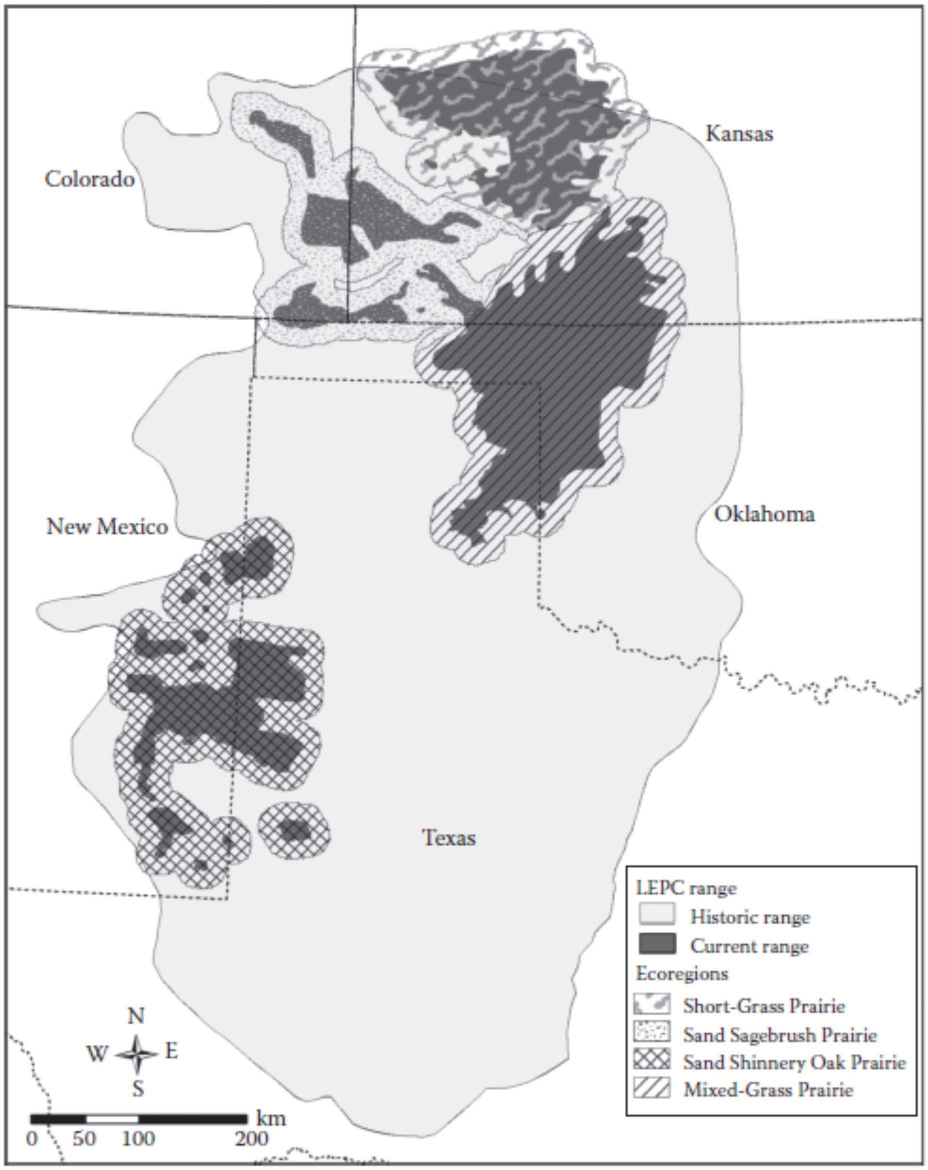

Figure 1.2 Presumed historical and contemporary range of lesser prairie-chickens (LEPC) in the Southern Great Plains

The range is comprised of four ecoregions, the Short-Grass Prairie/CRP Mosaic, Sand Sagebrush Prairie, Mixed-Grass Prairie, and Sand Shinnery Oak Prairie. Lesser prairie-chickens are presumed to currently occupy ~17% of their original range remaining across all four ecoregions. Figure adapted Haukos and Boal (2016).

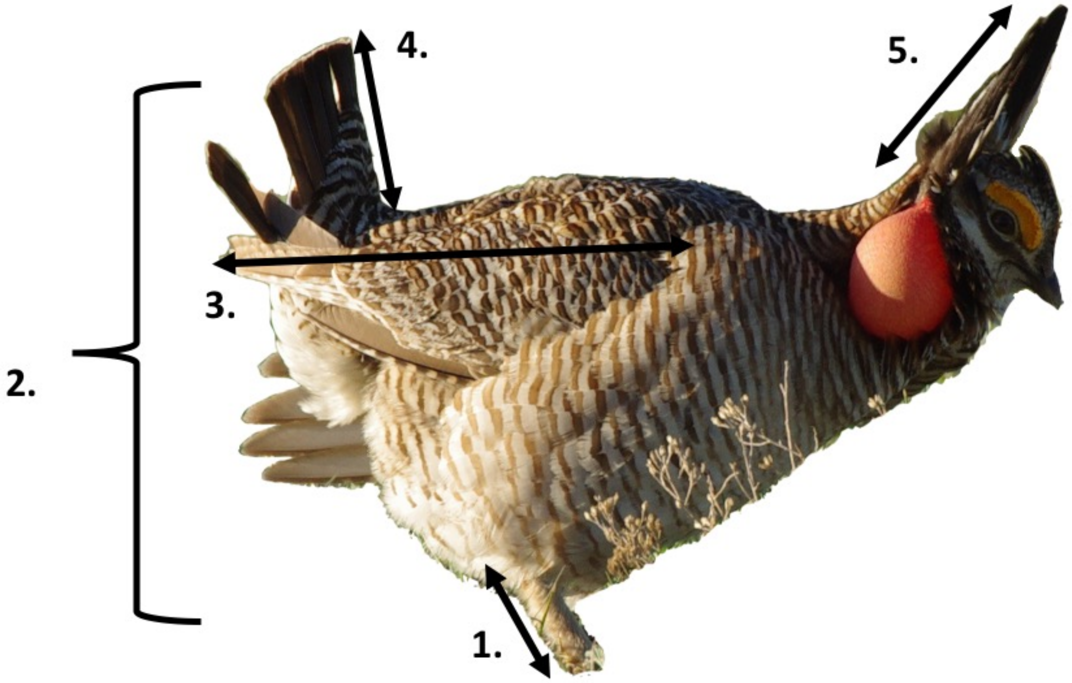

Figure 1.3 The five morphometric attributes commonly measured across the species range (NM, TX, OK, CO, KS) from 1986-2019.

Measurements taken include 1. Tarsus, 2. mass, 3. flattened wing length, 4. Tail or retrice feather length and, 5. pinnae feather length.

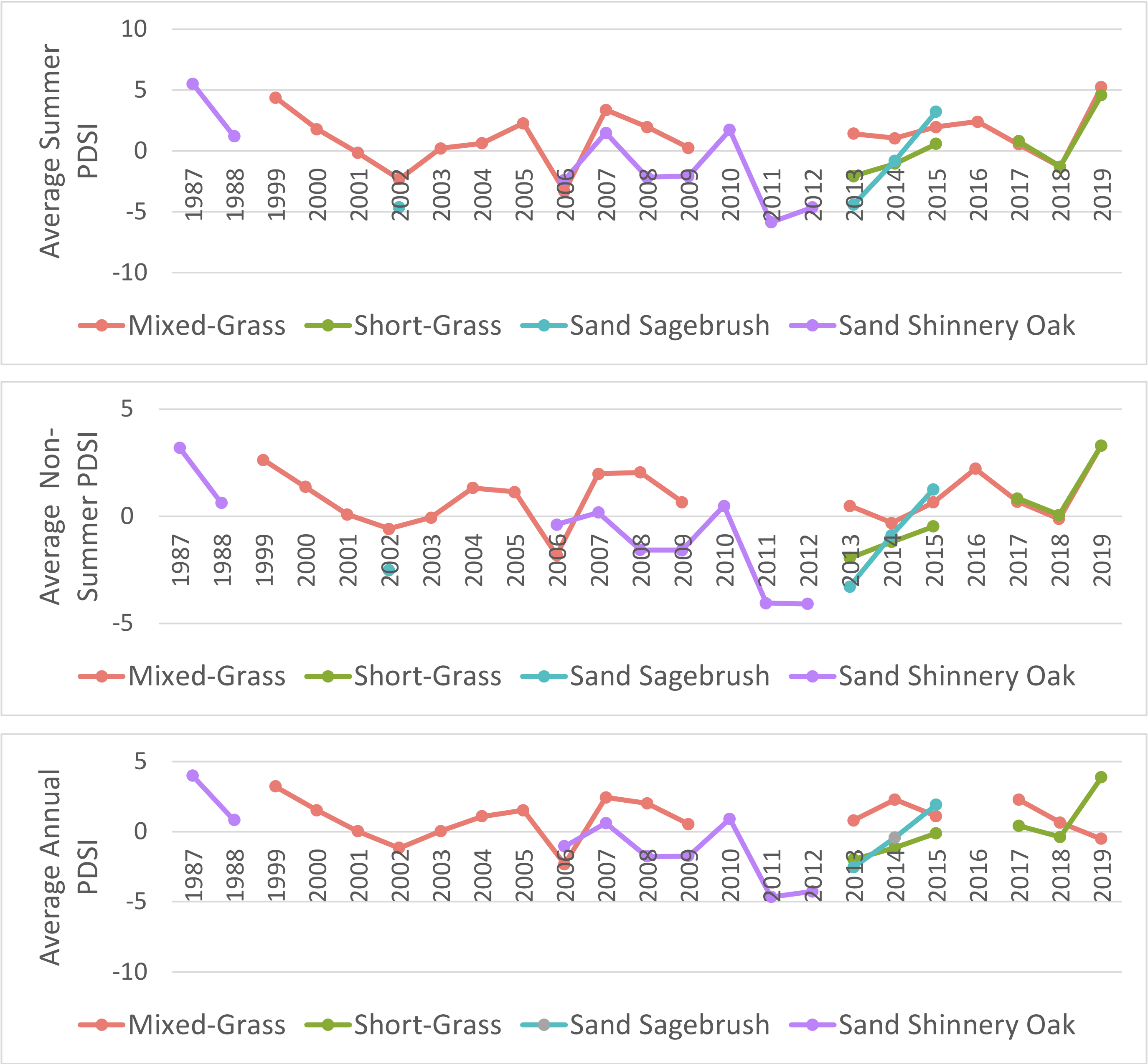

Figure 1.4 Average annual Palmer Drought Severity Index (PDSI) across the four ecoregions of the lesser prairie-chicken range in the Southern Great Plains from 1987-2019.

Average PDSI in the Southern Great Plains is driven primarily by summer precipitation and temperature and is subject to severe droughts on a 5-10 year cycle. The Mixed-Grass Ecoregion receives the greatest precipitation while the Sand Shinnery Oak Ecoregion in the southern extent of the lesser prairie-chicken range hits extreme lows.

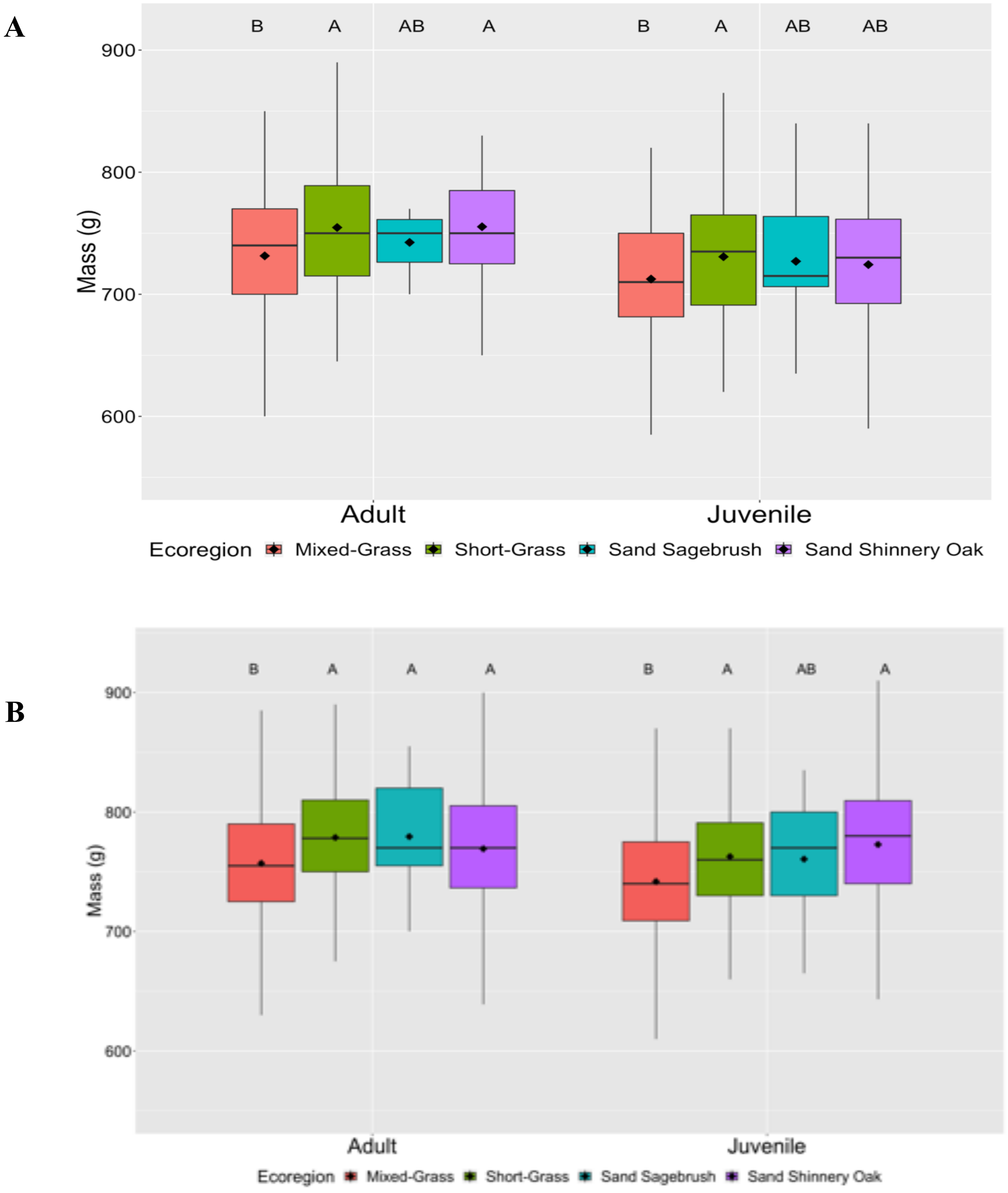

Figure 1.5 Ecoregion-specific body mass by age and sex category for lesser prairie-chickens measured from 1986-2019 in the Southern Great Plains.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean mass values. Female mass (A) and adult male mass (B) relatively consistent across ecoregions. Juvenile male (B) mass exhibits the largest difference between Mixed-Grass and Sand Shinnery Oak Prairie.

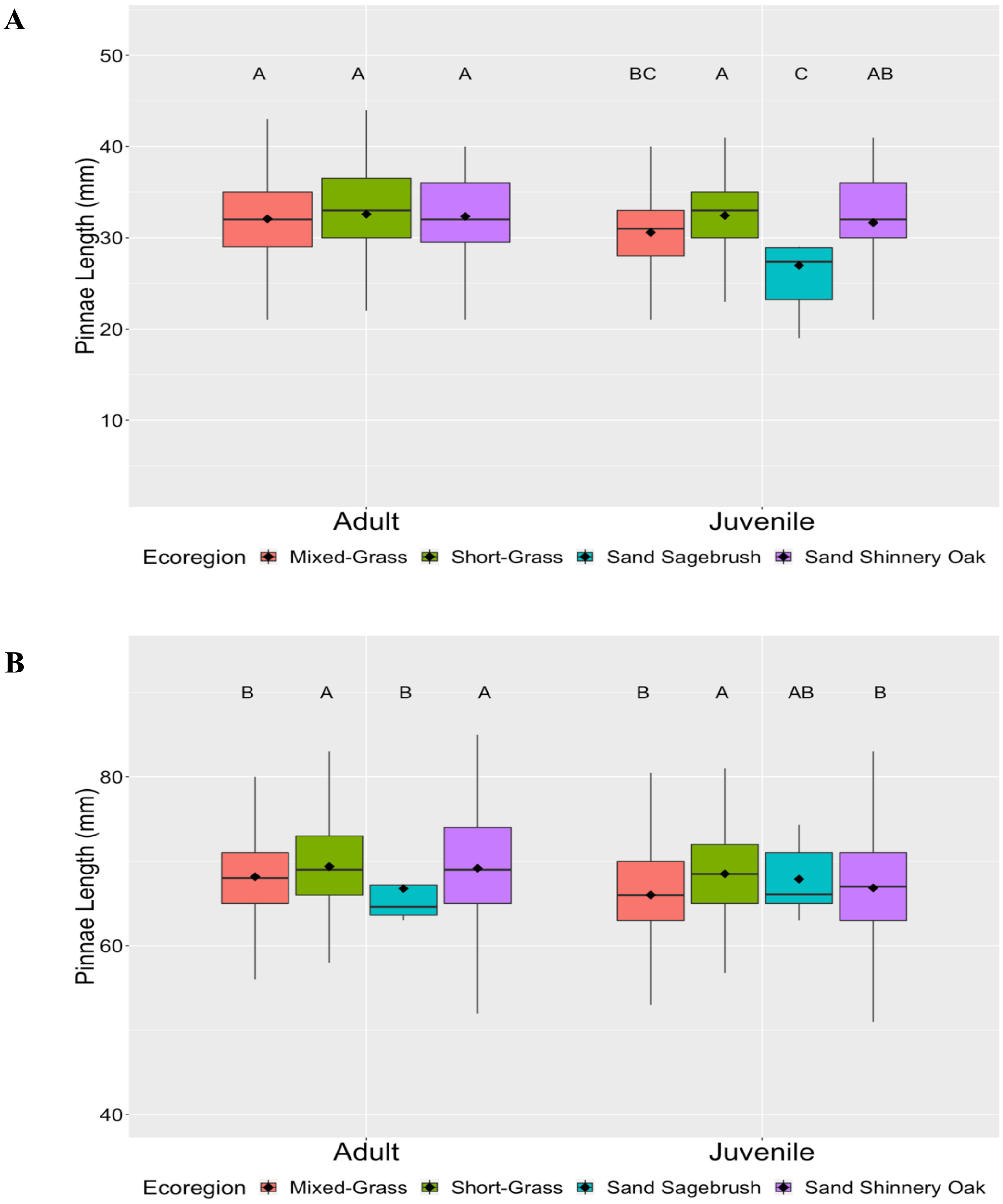

Figure 1.6 Ecoregion-specific pinnae feather lengths for female (A) and male (B) lesser prairie-chickens by age from measurements of birds across the Southern Great Plains from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean pinnae values. Adult male lesser prairie-chicken pinnae lengths are longer in Short-Grass and Sand Shinnery Oak Prairie and shorter pinnae in Sand Sagebrush and Mixed-Grass Prairie while juvenile males exhibit the opposite pattern. Juvenile female pinnae (B) exhibit the greatest difference between ecoregions, although this may be a reflection of the sample size (n=10) for Sand Sagebrush females.

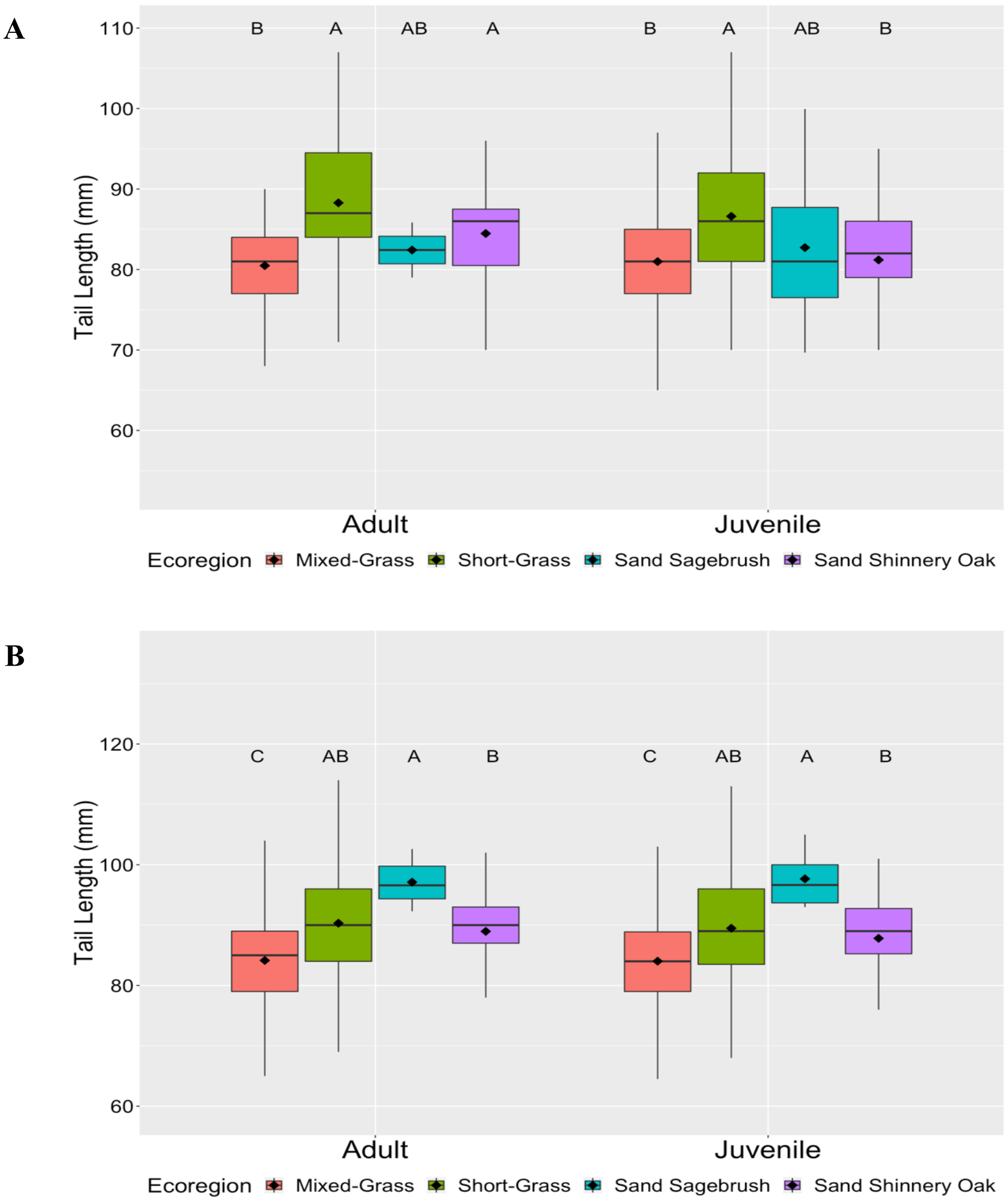

Figure 1.7 Ecoregion-specific tail measurements by age and sex class from lesser prairie-chickens measured from 1986-2019 across the Southern Great Plains.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean tail values. Female tail lengths (A) are largest in Short-Grass and Sand Shinnery Oak Prairie and shortest in Sand Sagebrush Prairie. Male tail lengths (B) cluster in three different groupings with longest tail lengths in Sand Sagebrush and shortest in Mixed-Grass Prairie. Short-Grass Prairie birds exhibit a wide range of tail lengths, which may have contributed to lack of signal for ecoregion-specific variation.

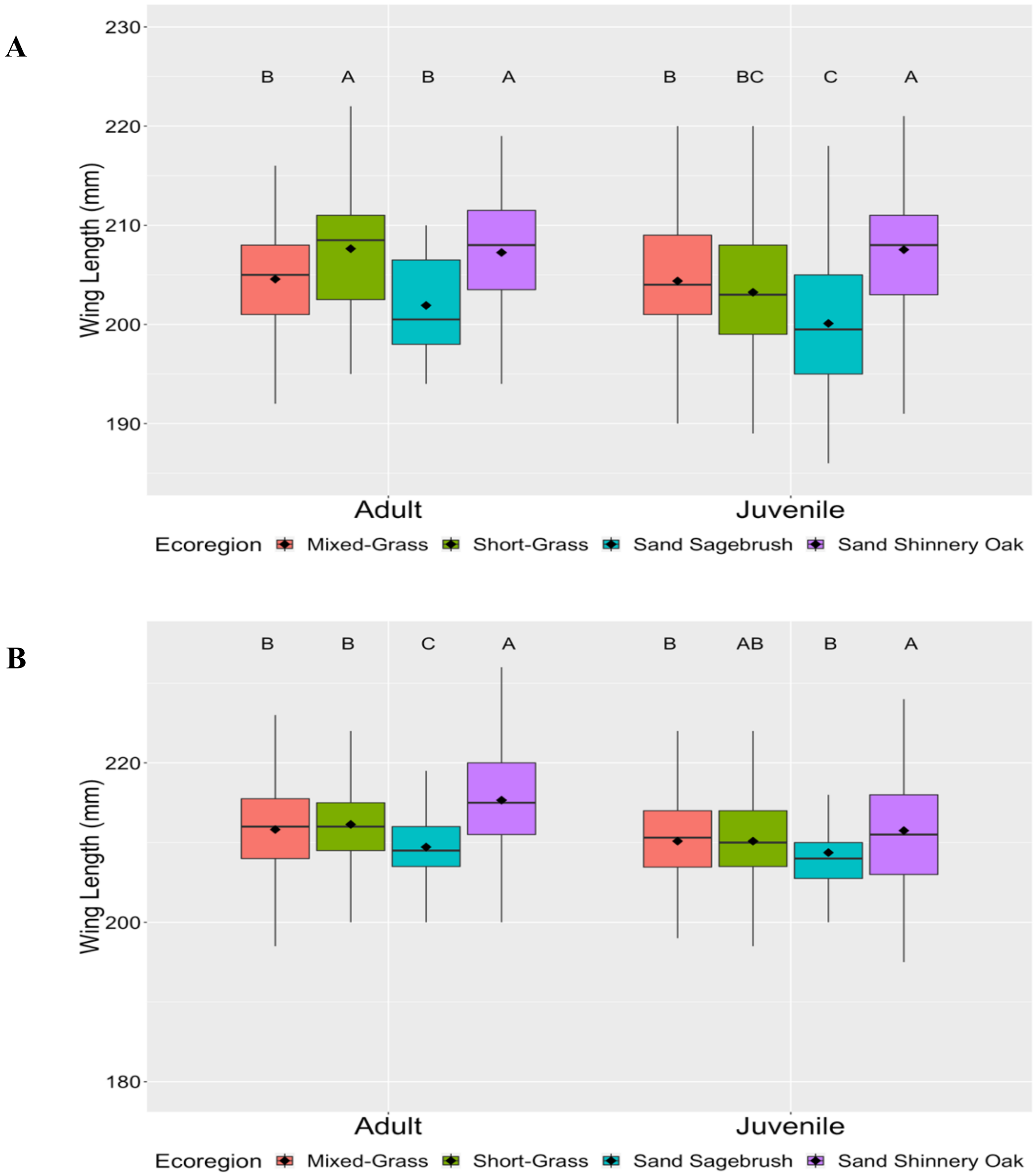

Figure 1.8 Ecoregion-specific lesser prairie-chicken wing lengths by age and sex categories from birds measured from 1986-2019 in the Southern Great Plains.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean wing values. For both female (A) and male (B) lesser prairie-chickens, Sand Shinnery Oak birds have the largest wing lengths, followed closely by Short-Grass Prairie birds, while Sand Sagebrush and Mixed-Grass Prairie birds have the smallest wing lengths.

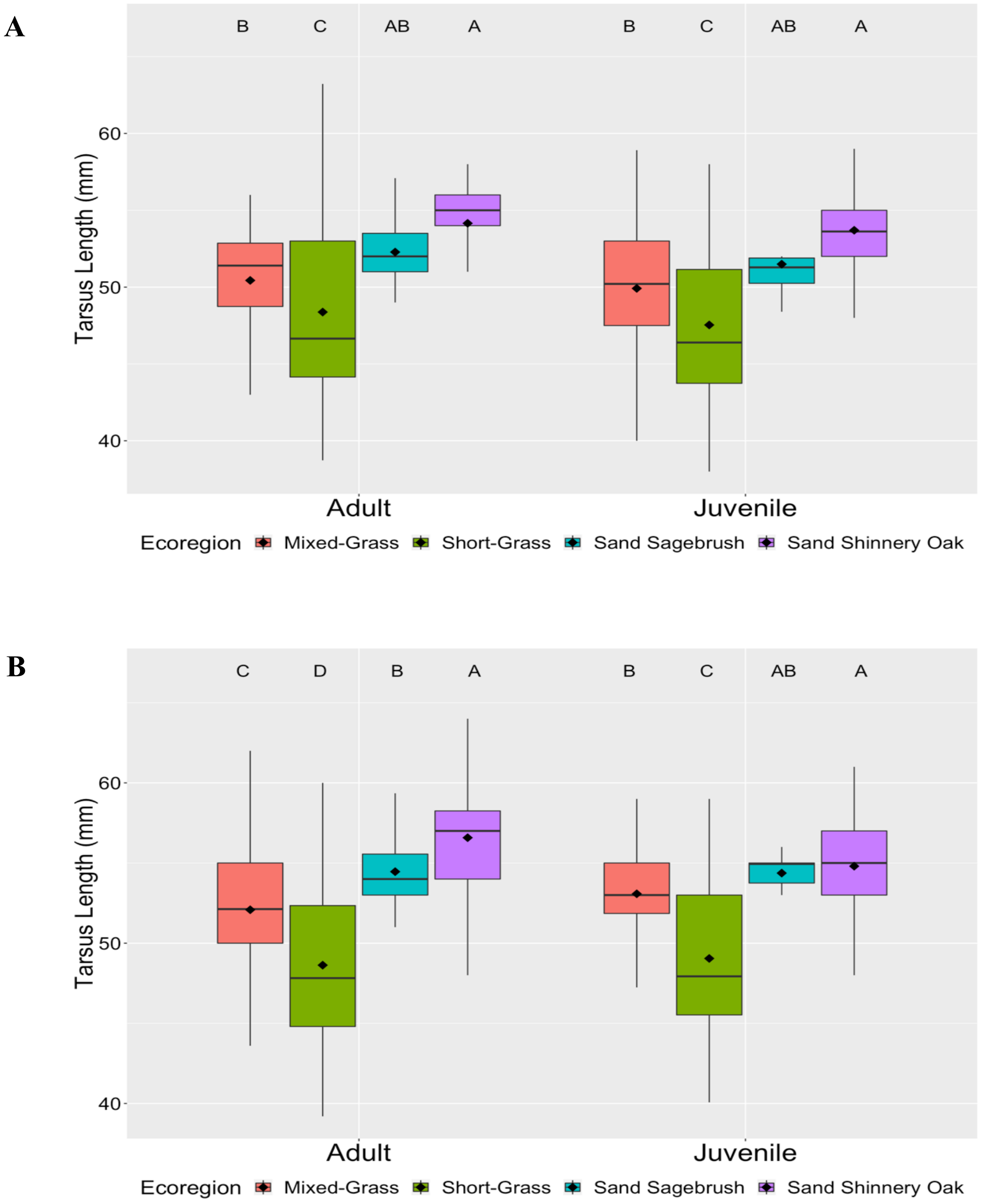

Figure 1.9 Ecoregion-specific lesser prairie-chicken tarsus lengths by age and sex category from birds measured from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean tarsus values. Adult male (B) tarsus lengths are significantly different among all four ecoregions within the lesser prairie-chicken range. For all age and sex categories, Sand Shinnery Oak Prairie birds have the longest tarsus lengths and Short-Grass Prairie birds have the shortest tarsus lengths.

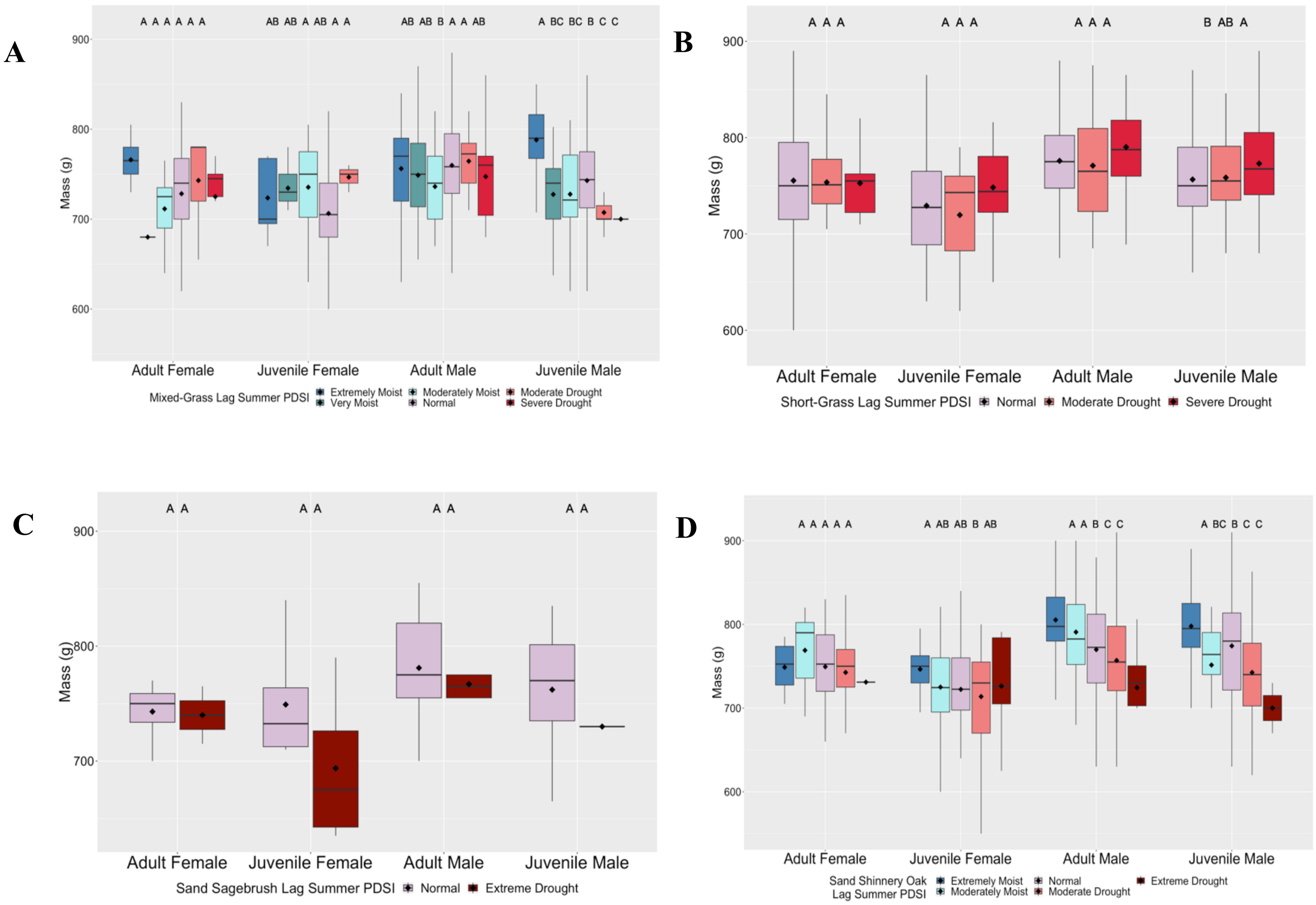

Figure 1.10 Lesser prairie-chicken mass depicted by age/sex category in all four South Great Plains ecoregions by lag-summer Palmer Drought Severity Index (PDSI) value from birds measured from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean mass values. There are no significant differences in mass due to lag-summer PDSI for any age or sex group across all ecoregions. Sand Shinnery Oak (D) and Mixed-Grass Prairie (A) mass increased after greater moisture and decreased following moderate or extreme drought for adult and juvenile males.

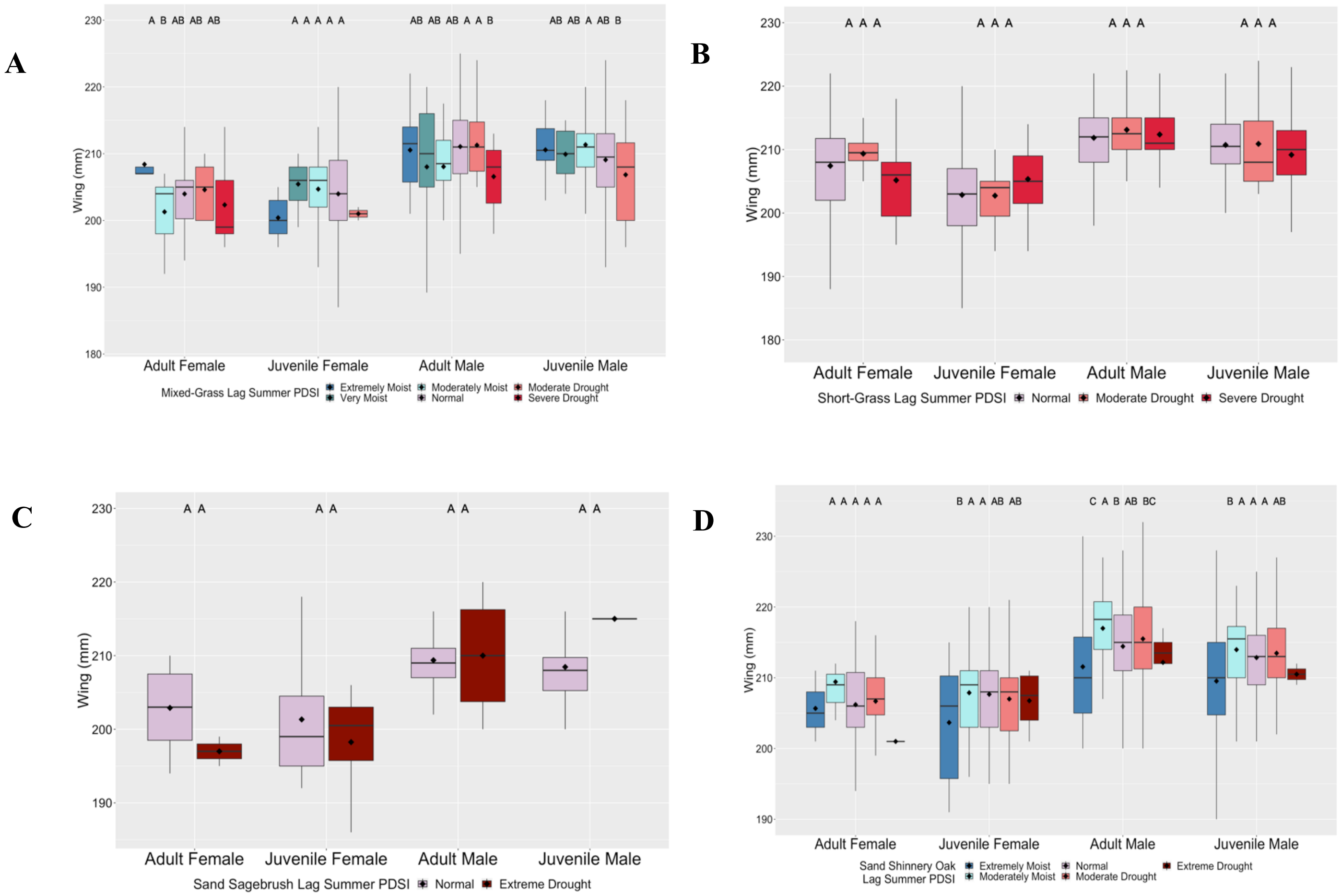

Figure 1.11 Lesser prairie-chicken wing lengths by all four ecoregions and age/sex categorization by lag-summer Palmer Drought Severity Index (PDSI).

All birds were measured in the South Great Plains from 1986-2019. Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean wing values. Wing lengths remain relatively consistent regardless of changes to precipitation and temperature within an ecoregion. Male wing lengths do increase after moderate or normal PDSI summers and decrease after drought or extremely moist summers in Mixed-Grass (A) and Sand Shinnery Oak Prairies (D).

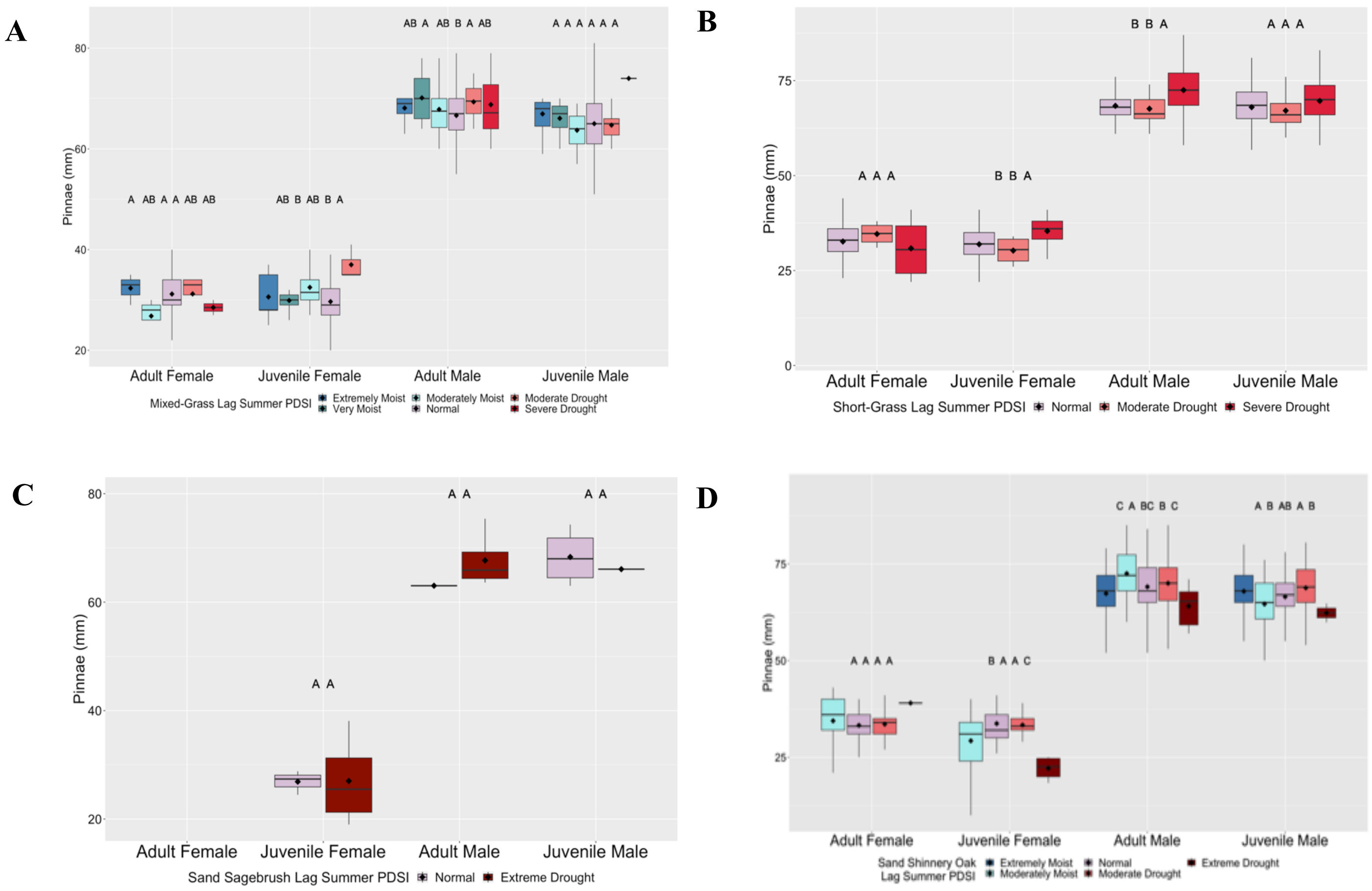

Figure 1.12 Lesser prairie-chicken pinnae length by age/sex category, ecoregion, and lag summer Palmer Drought Severity Index.

All birds were measured in the South Great Plains from 1986-2019. Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean pinnae values. Notably in Sand Shinnery Oak (D) and (B) Short-Grass Prairies, male pinnae lengths increase after summers of moderate to severe drought.

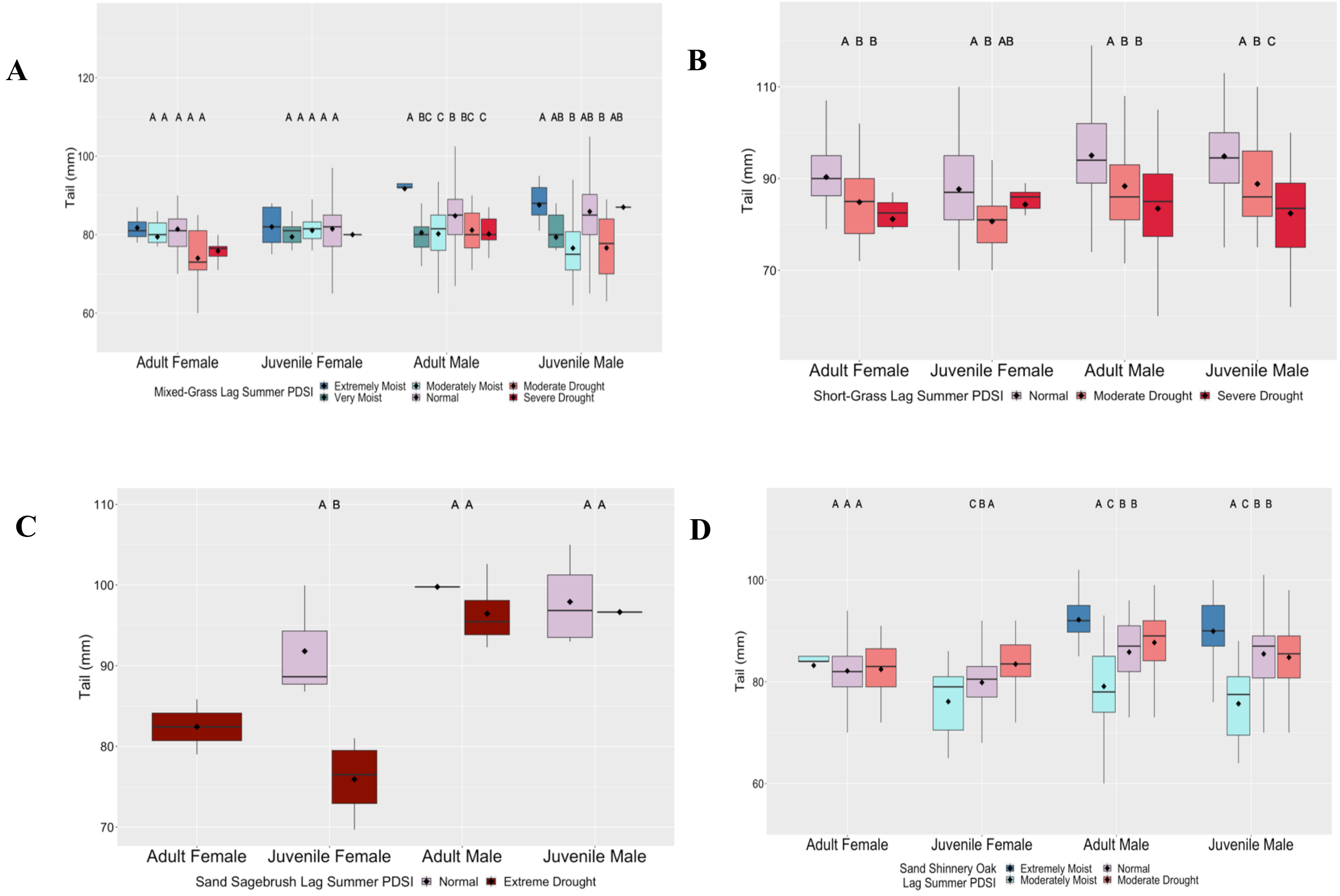

Figure 1.13 Lesser prairie-chicken tail lengths by age/sex category, ecoregion and lag summer Palmer Drought Severity Index category.

All birds were measured in the South Great Plains from 1986-2019. Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean tail values. Longer tail lengths are observed after high moisture in Mixed-Grass (A), Short-Grass (B), and Sand Shinnery Oak (D) Prairies and shorter tail lengths after summers of moderate moisture or drought.

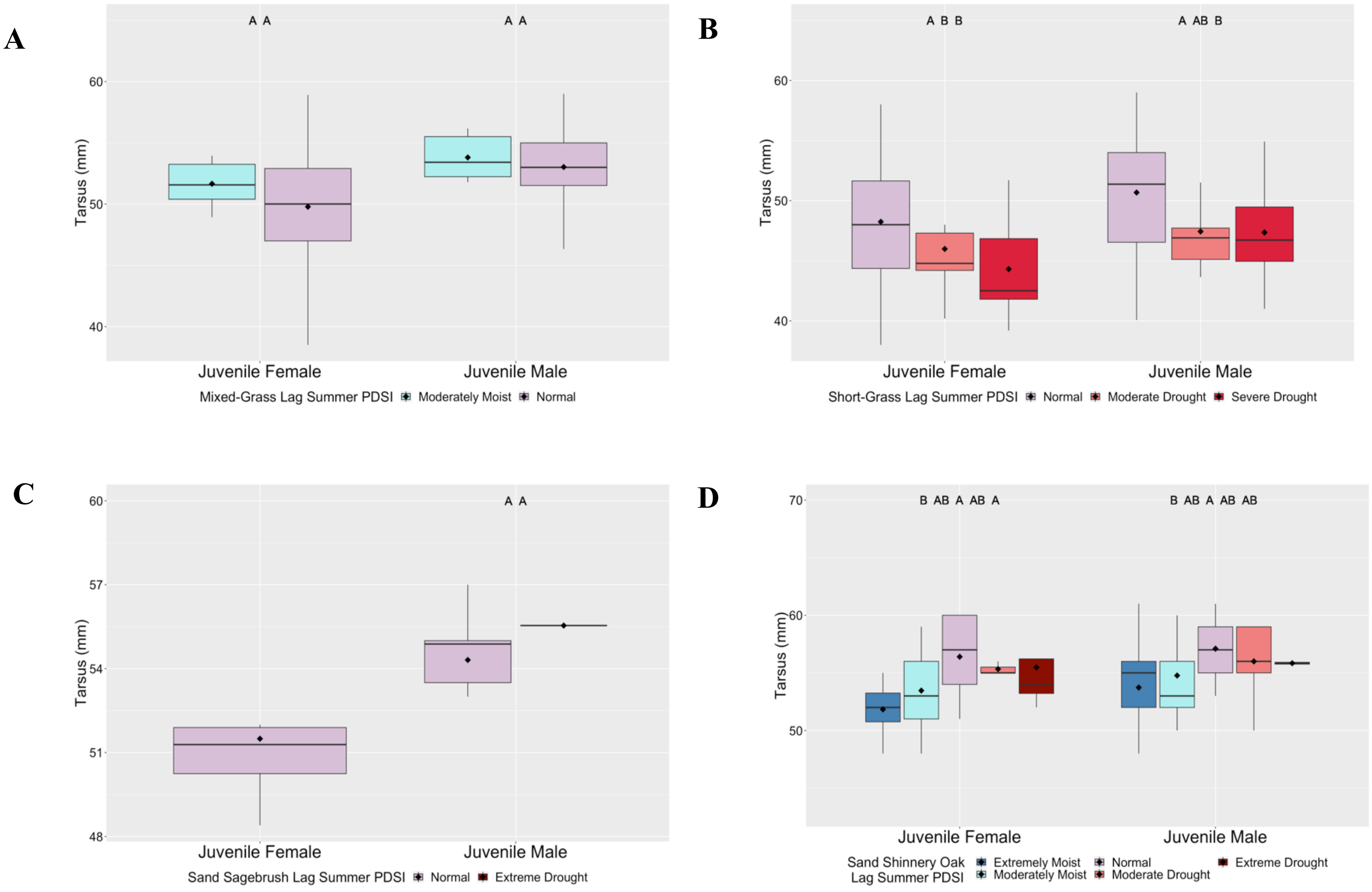

Figure 1.14 Juvenile lesser prairie-chicken tarsus lengths by ecoregion and lag summer Palmer Drought Severity Index.

All birds were measured in the South Great Plains from 1986-2019. Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean tarsus values. Tarsus lengths increased following normal precipitation in Short-Grass Prairie (B) and Sand Shinnery Oak Prairie (D) and decreased after moderate and severity drought for juvenile male and female birds.

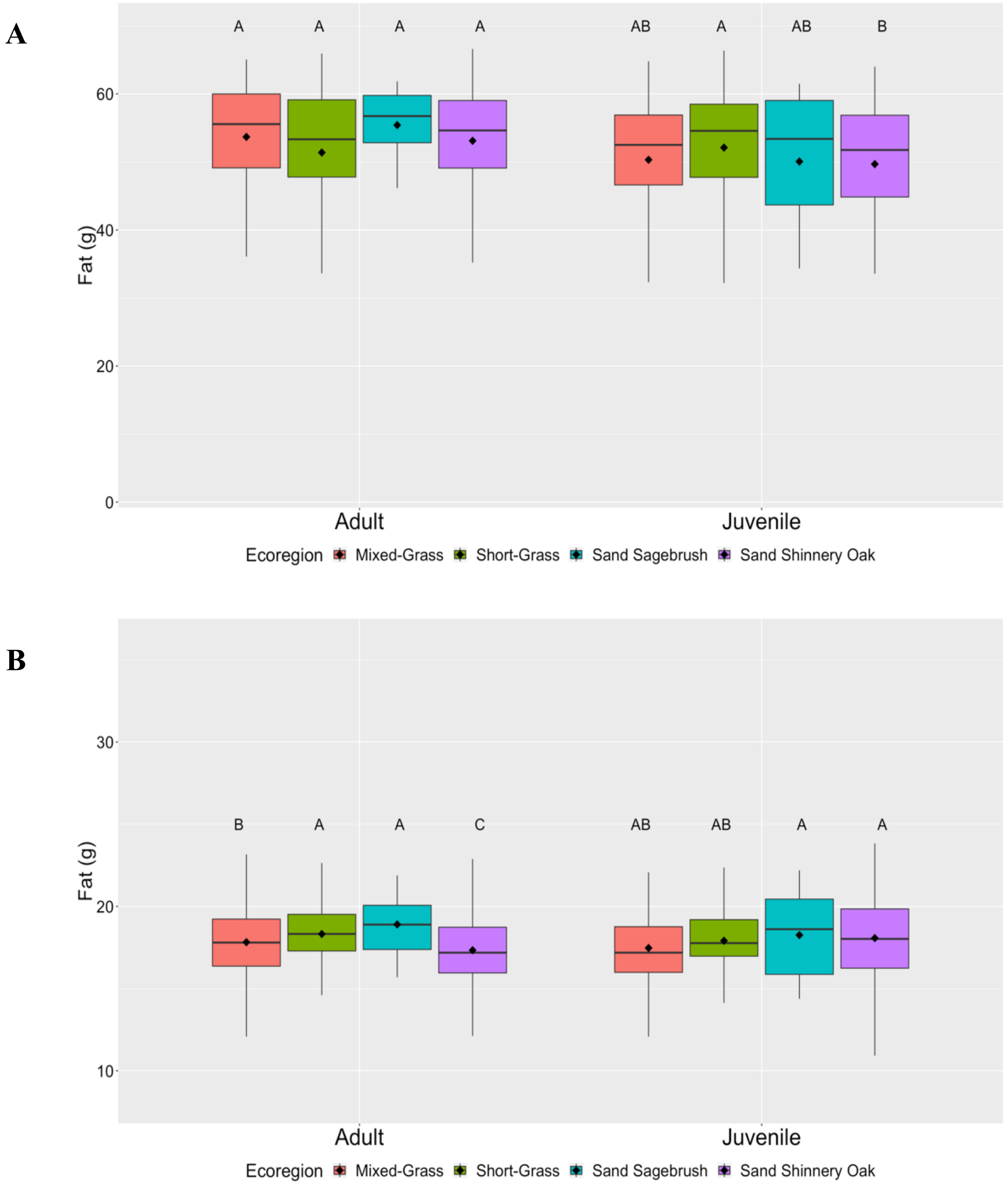

Figure 1.15 Lesser prairie-chicken body fat by age and sex classification. Birds were measured in all four ecoregions the South Great Plains from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean fat values. Female body fat (A) for juvenile birds in Sand Shinnery Oak Prairie differs from other ecoregions, while male body fat (B) trends for adult males shows greater differences among ecoregions than juvenile males.

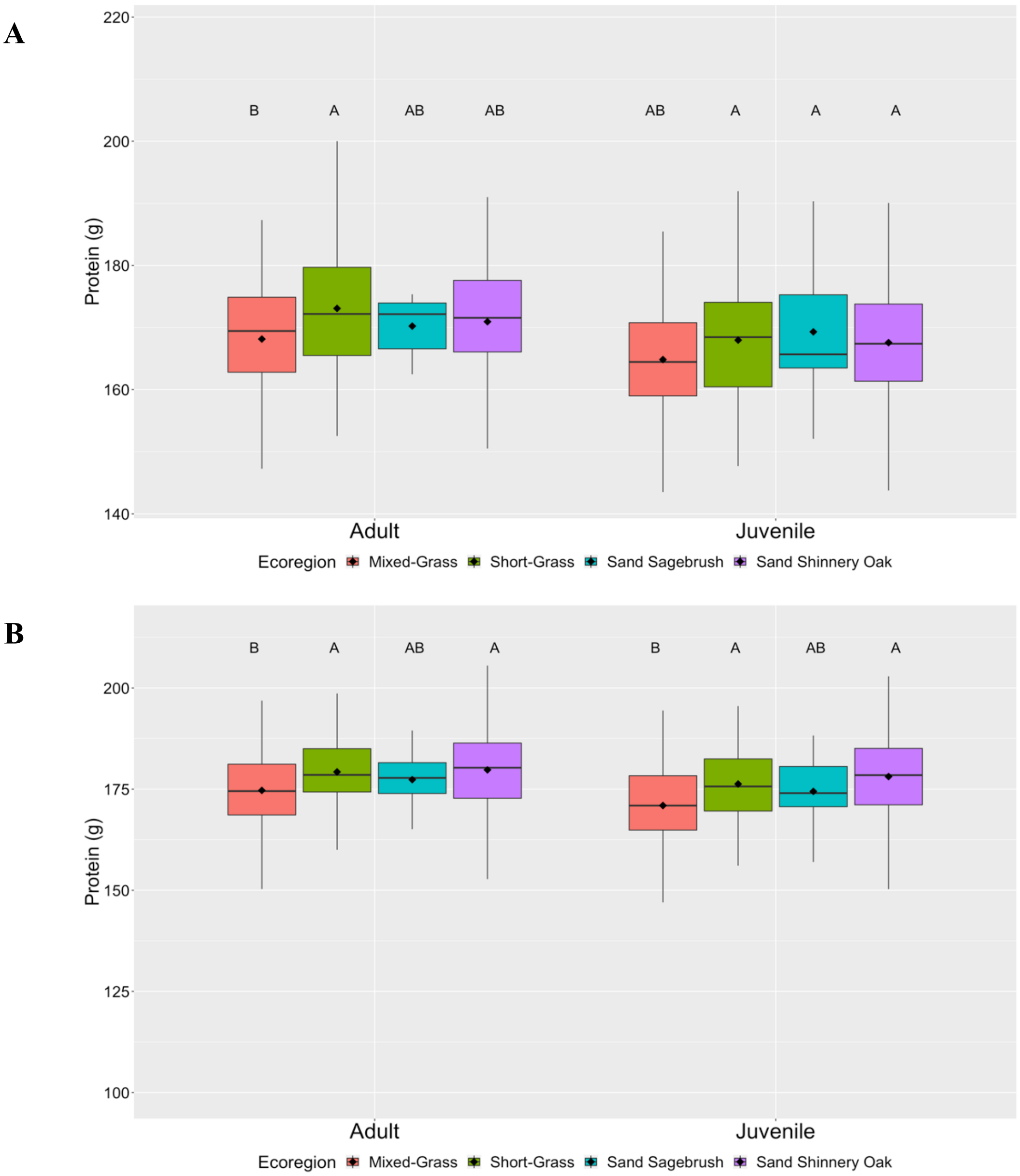

Figure 1.16 Lesser prairie-chicken body protein by age and sex classification. Birds were measured in all four ecoregions the South Great Plains from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean protein values. There were significant differences in grams protein between ecoregions for both sexes, but no sexual size dimorphism between females (A) and males (B) for proportion of body protein. Sand Shinnery Oak Prairie and Short-Grass Prairie birds had the greatest body protein. Mixed-Grass Prairie birds had the least amount of body protein.

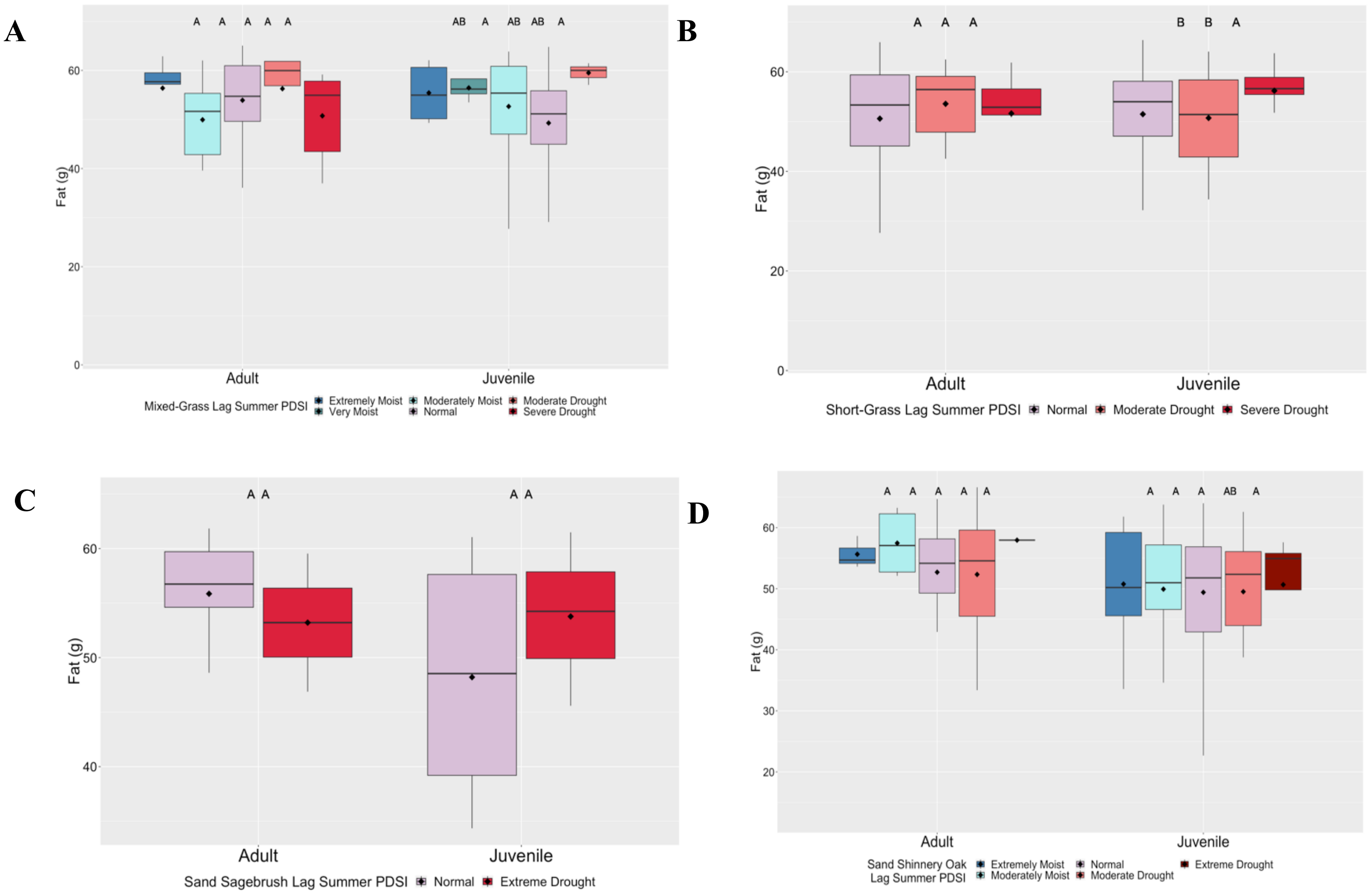

Figure 1.17 Female lesser prairie-chicken fat by age class, ecoregion, and lag summer Palmer Drought Severity Index for all four ecoregions in the Southern Great Plains from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean protein values. There is no significant difference in grams of body fat by Palmer Drought Severity Index for adult females for any ecoregion and one significant difference in body fat for juvenile females in Short-Grass prairie (B).

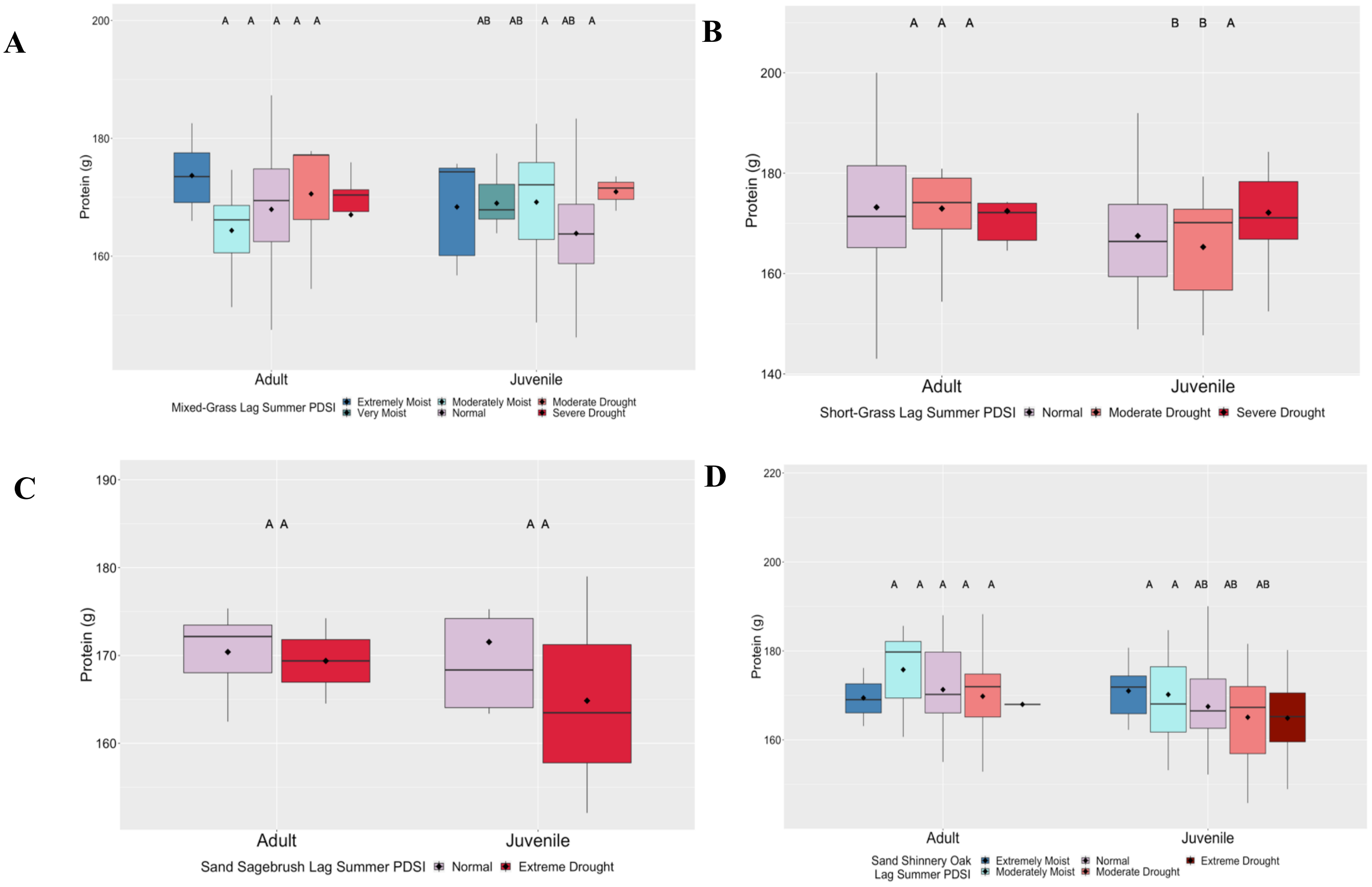

Figure 1.18 Female body protein by age category, ecoregion, and lag summer Palmer Drought Severity Index for birds measured in the Southern Great Plains from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean protein values. Only Short-Grass juveniles (B) exhibited differences in female body protein.

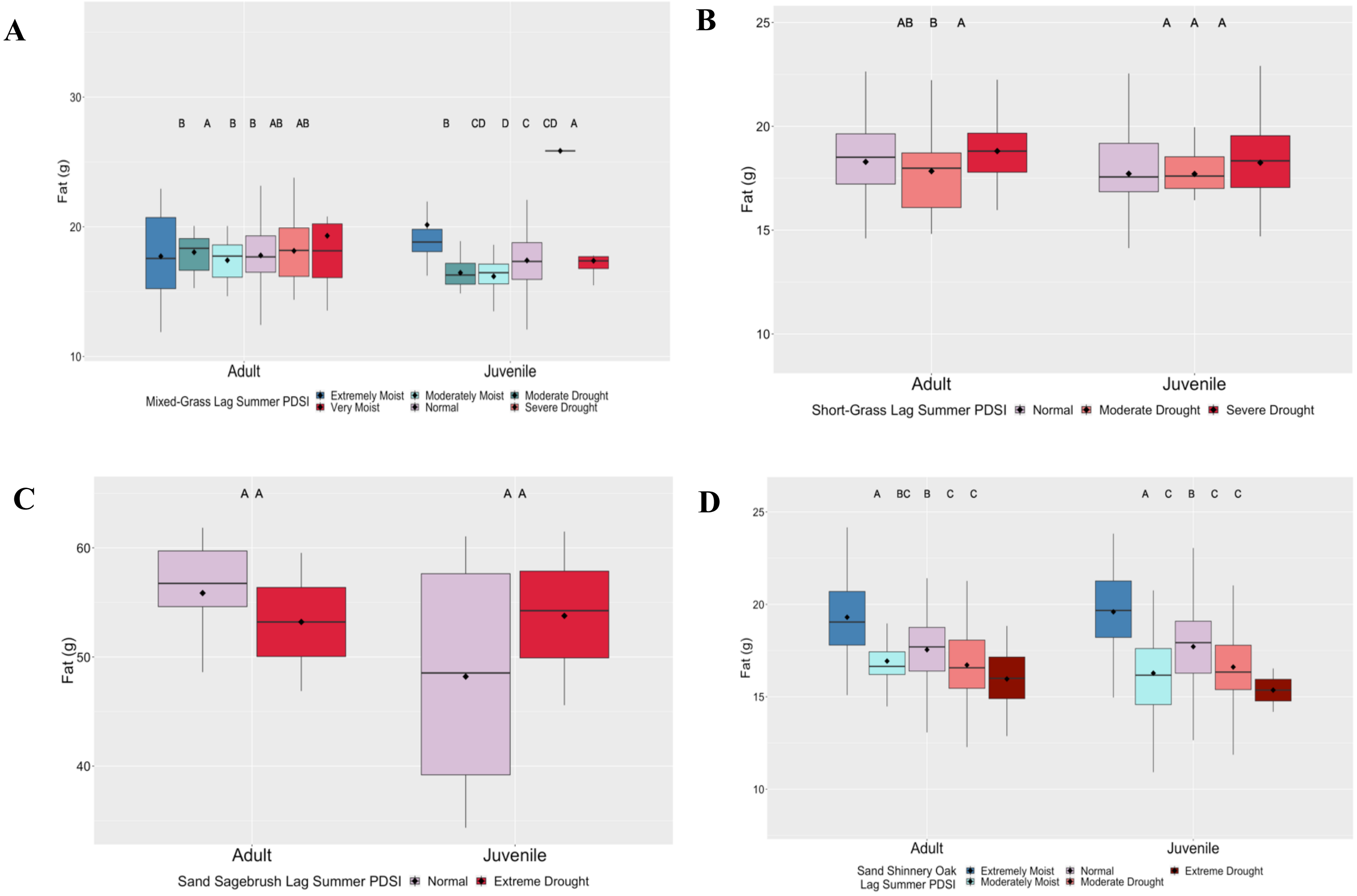

Figure 1.19 Male lesser prairie-chicken body fat by age class, ecoregion, and lag summer Palmer Drought Severity Index for birds measured in the Southern Great Plains from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean fat values. The amount of male body fat in Mixed-Grass (A) and Sand Shinnery Oak (D) Prairies was significantly affected by lag summer PDSI, with greater amounts of body fat after extremely wet years.

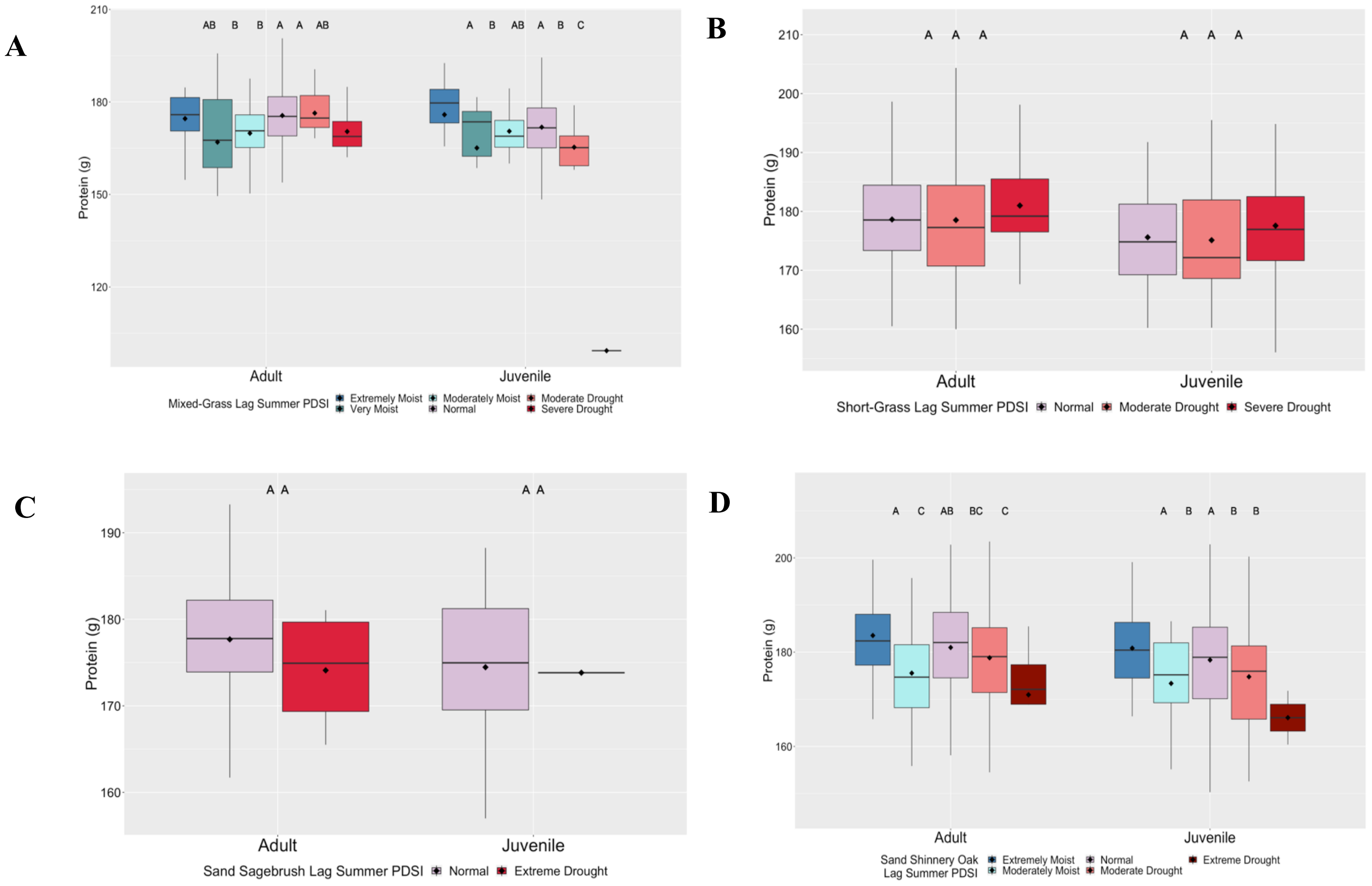

Figure 1.20 Male lesser prairie-chicken body protein by age class, ecoregion, and lag summer Palmer Drought Severity Index in the Southern Great Plains from 1986-2019.

Assigned letters indicate differences among ecoregions from Least Significant Difference tests and points indicate mean protein values. Male body protein of Mixed-Grass (A) and Sand Shinnery Oak (D) Prairies increase with greater lag summer moisture and decrease after drought.

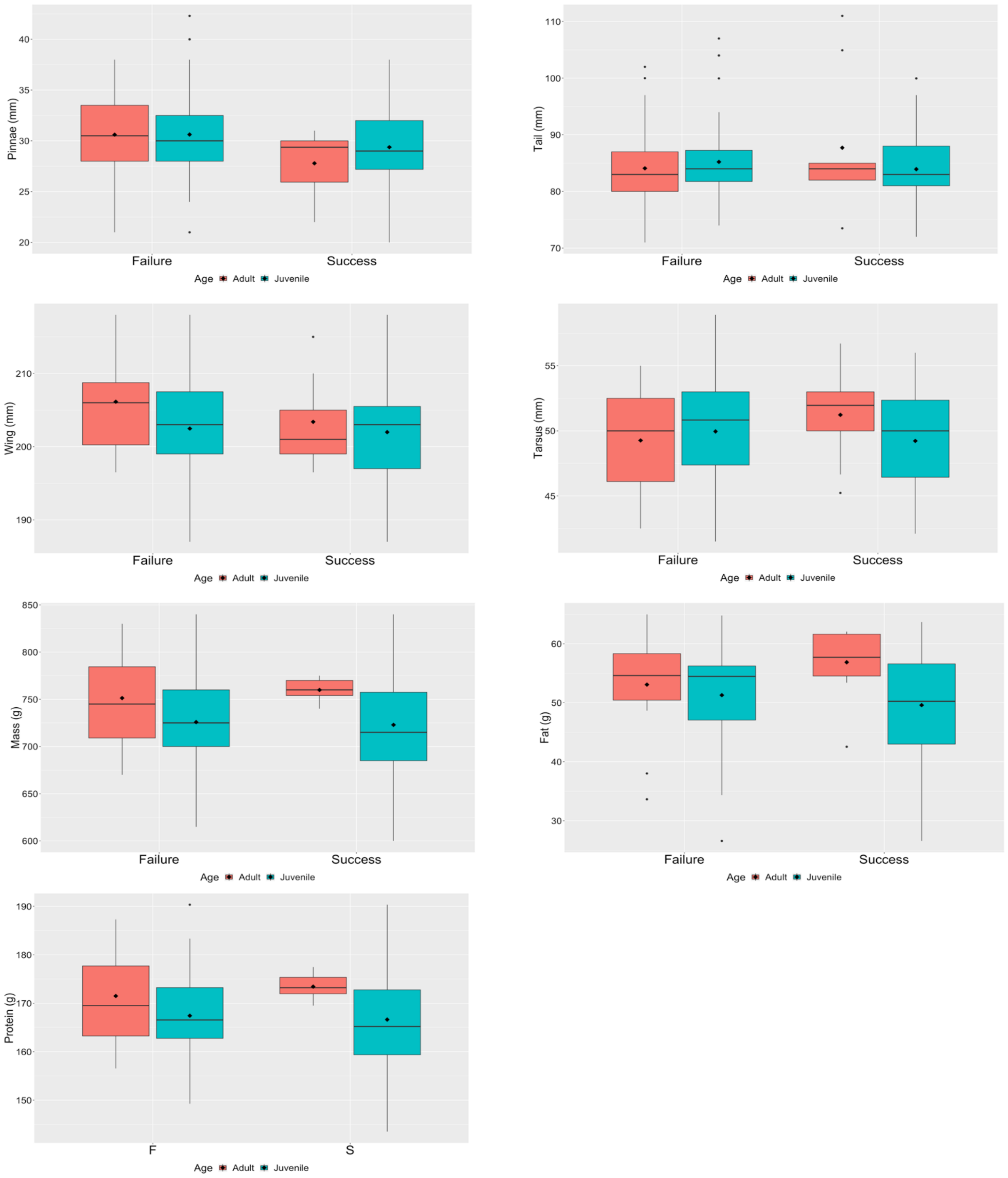

Figure 1.21 Female morphometrics for birds that nested in Mixed-Grass and Short-Grass Prairies in Kansas from 2013-2017 by the nest outcome for their first nest attempt.

Neither nutrient reserves nor morphometric traits influence nest success.

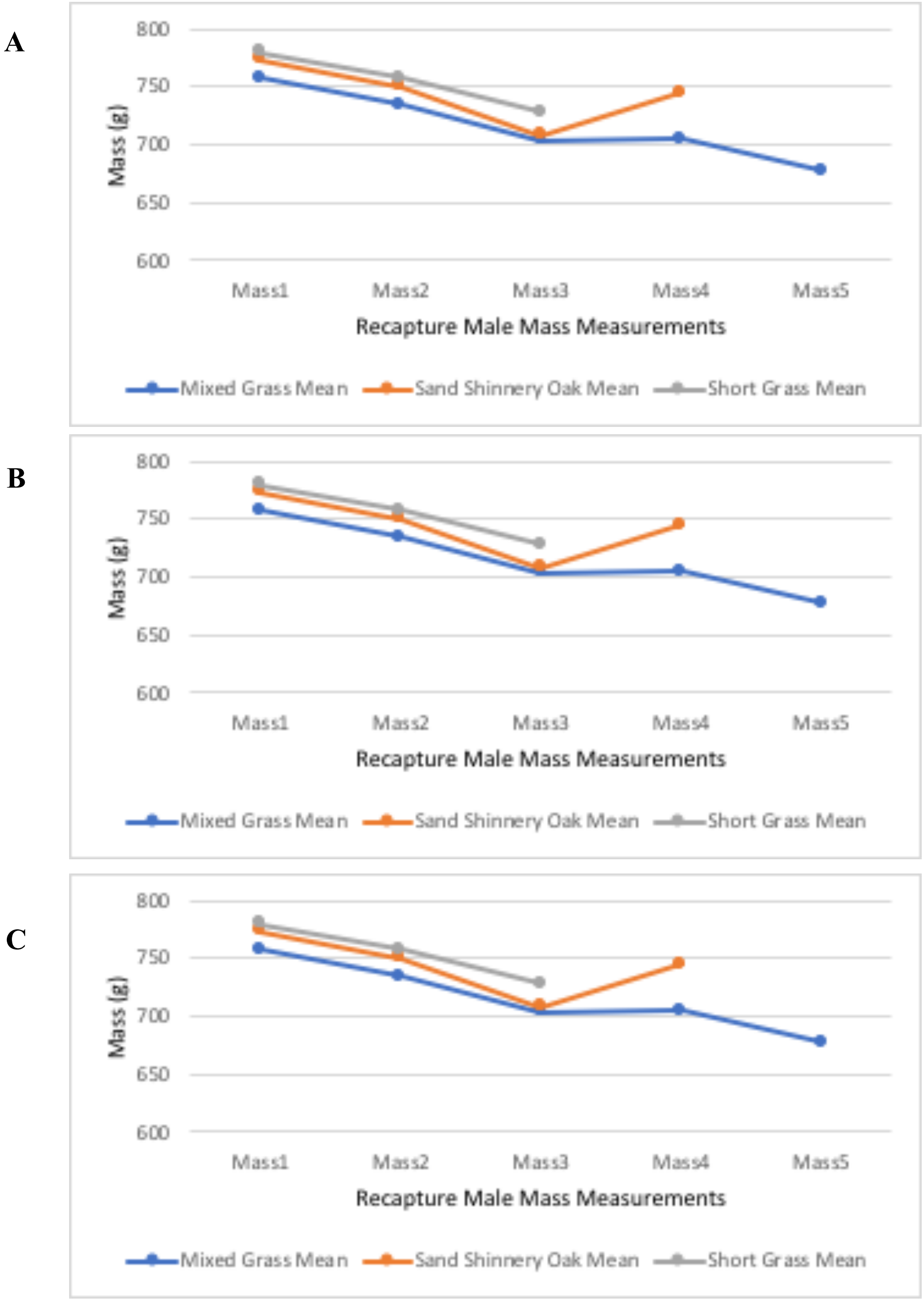

Figure 1.22 Change in mean lesser prairie-chicken male nutrient reserves over a single breeding season in Mixed-Grass, Short-Grass, and Sand Shinnery Oak Ecoregions (n=125) from 1987-2018.

Individual males were captured up to five times within a single season, showing changes within male nutrient reserves by ecoregion. Mean male mass (A) and protein (C) for Sand Shinnery Oak Prairie birds, increases for individuals captured a third time, while Mixed-Grass and Short-Grass Prairie males show a continued decline.

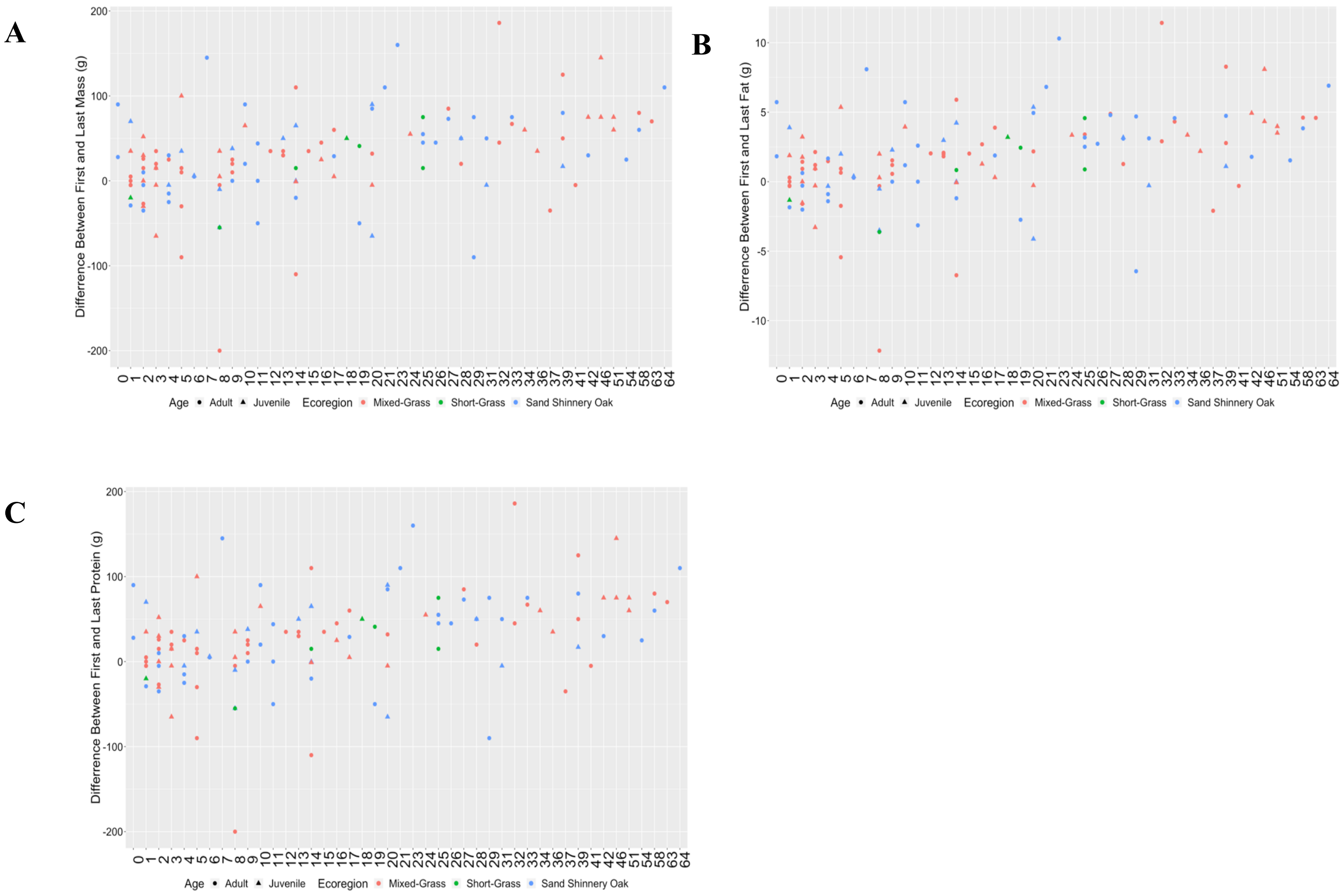

Figure 1.23 Difference between first and last nutrient reserve measurements for male lesser prairie-chickens within a single breeding season.

Male lesser prairie-chickens were captured in Mixed-Grass, Short-Grass, and Sand Shinnery Oak Ecoregions (n=125) from 1987-2018. Male nutrient reserves can increase or decrease as much as 100g of mass (A) over the days between first and last capture, which is reflected in grams of fat (B) and protein (C).

Tables

Table 1.1 Range-wide lesser prairie-chicken morphometrics data were compiled from 12 of contributed datasets from across the Southern Great Plains.

These data were collected from 1986-2019 from lesser prairie-chickens trapped using funnel traps, drop nets, and rocket nets during spring breeding.

Ecoregion	State	Years	Source
Mixed-Grass	OK	1999-2009	Michael Patten & Don Wolfe
Mixed-Grass	KS	2013-2019	Kansas Cooperative Fish and Wildlife Research Unit
Sand Sagebrush	KS	2002	Christian Hagen & Jim Pitman
Sand Sagebrush	CO	2013-2016	Kansas Cooperative Fish and Wildlife Research Unit
Sand Shinnery Oak	TX	1987-1988	David Haukos
Sand Shinnery Oak	TX & NM	1984-1985	Craig Olawsky
Sand Shinnery Oak	TX	2008-2012	Blake Grisham
Sand Shinnery Oak	NM	2006-2010	Blake Grisham
Sand Shinnery Oak	NM	2001-2005	Michael Pattern
Short-Grass	KS	2000-2002	Christian Hagen, Jim Pitman, Matthew Bain
Short-Grass	KS	2013-2015	Kansas Cooperative Fish and Wildlife Research Unit
Short-Grass	KS	2017-2019	Kansas Cooperative Fish and Wildlife Research Unit

Table 1.2 Pearson Correlation of the commonly measured morphometric suite for lesser prairie-chickens measured in the Southern Great Plains from 1986-2019.

Sand Sagebrush Prairie has a small sample size and the high correlation between traits likely reflects sample size rather than a strong correlation between morphometric traits.

Short-Grass/CRP Mosaic Ecoregion											
	Male						Female				
	Mass	Wing	Pinnae	Tail	Tarsus		Mass	Wing	Pinnae	Tail	Tarsus
Mass	1	0.29	0.2	0.05	0.07	Mass	1	0.39	0.21	0.16	0.24
Wing	0.29	1	0.18	0.13	-0.04	Wing	0.39	1	0.23	0.08	0.16
Pinnae	0.2	0.18	1	0.04	-0.05	Pinnae	0.21	0.23	1	0.16	-0.08
Tail	0.05	0.13	0.04	1	0.14	Tail	0.16	0.08	0.16	1	0.18
Tarsus	0.07	-0.04	-0.05	0.14	1	Tarsus	0.24	0.16	-0.08	0.18	1
Mixed-Grass Prairie Ecoregion											
	Male						Female				
	Mass	Wing	Pinnae	Tail	Tarsus		Mass	Wing	Pinnae	Tail	Tarsus
Mass	1	0.28	0.21	0.17	0.06	Mass	1	0.14	0.17	0.12	0.27
Wing	0.28	1	0.27	0.19	-0.03	Wing	0.14	1	0.23	0.11	-0.13
Pinnae	0.21	0.27	1	0	0.05	Pinnae	0.17	0.23	1	-0.05	0
Tail	0.17	0.19	0	1	0.09	Tail	0.12	0.11	-0.05	1	0.2
Tarsus	0.06	-0.03	0.05	0.09	1	Tarsus	0.27	-0.13	0	0.2	1
Sand Sagebrush Prairie Ecoregion											
	Male						Female				
	Mass	Wing	Pinnae	Tail	Tarsus		Mass	Wing	Pinnae	Tail	Tarsus
Mass	1	0.16	0.29	0.18	0.24	Mass	1	0.49	0.54	0.41	-0.49
Wing	0.16	1	0.7	0.57	0.18	Wing	0.49	1	0.11	0.53	-0.2
Pinnae	0.29	0.7	1	0.36	0.22	Pinnae	0.54	0.11	1	-0.25	0.87
Tail	0.18	0.57	0.36	1	-0.29	Tail	0.41	0.53	-0.25	1	-0.74
Tarsus	0.24	0.18	0.22	-0.29	1	Tarsus	-0.49	-0.2	0.87	-0.74	1
Sand Shinnery Oak Prairie Ecoregion											
	Male						Female				
	Mass	Wing	Pinnae	Tail	Tarsus		Mass	Wing	Pinnae	Tail	Tarsus
Mass	1	0.06	0.12	0.1	-0.01	Mass	1	0.01	-0.04	0.32	0.01
Wing	0.06	1	0.26	-0.12	0.07	Wing	0.01	1	0.21	0.04	0.14
Pinnae	0.12	0.26	1	-0.1	0.26	Pinnae	-0.04	0.21	1	-0.04	0.34
Tail	0.1	-0.12	-0.1	1	NA	Tail	0.32	0.04	-0.04	1	NA
Tarsus	-0.01	0.07	0.26	NA	1	Tarsus	0.01	0.14	0.34	NA	1

Table 1.3 Pearson correlation of Palmer Drought Severity index values by biologically significant periods for lesser prairie-chickens.

The year is divided starting from the nesting, brooding, and fall and winter months prior to the prebreeding and breeding season of the following year. Summer month PDSI was correlated with the values of the previous year, while non-summer months inclusive of spring breeding season are also correlated. Based on these results, PDSI was split into a summer and winter category for the study period of 1986-2019 for each ecoregion.

	Prebreeding	Breeding	Lag Nesting	Lag Brooding	Lag Nonbreeding	Lag Annual
Prebreeding	1	0.93	0.06	0.33	0.85	0.4
Breeding	0.93	1	-0.01	0.24	0.73	0.31
Lag Nesting	0.06	-0.01	1	0.84	0.28	0.9
Lag Brooding	0.33	0.24	0.84	1	0.6	0.92
Lag Nonbreeding	0.85	0.73	0.28	0.6	1	0.64
Lag Annual	0.4	0.31	0.9	0.92	0.64	1

Table 1.4 Age/sex class range-wide lesser prairie-chicken morphometrics by ecoregion.

Mixed-Grass prairie birds have the smallest morphometric traits on average, while Short-Grass and Sand Shinnery Oak Prairie have larger morphometric traits on average. All birds were measured between 1986-2019.

Ecoregion		Adult Male					Juvenile Male					Adult Female					Juvenile Female				
		n	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**
Short-Grass	Mass (g)	153	778.64	3.71	675	890	157	762.69	3.68	580	890	69	754.71	6.78	600	890	170	730.75	4.06	620	890
	Wing (mm)	150	212.28	0.49	194	230	146	210.18	0.5	179	227	66	207.64	0.77	188	222	165	203.24	0.51	185	230
	Pinnae (mm)	147	69.38	0.45	55	87	145	68.51	0.54	40	83	49	32.58	0.93	3	44	136	32.43	0.41	18	46
	Tail (mm)	145	90.32	0.96	60	125	151	89.48	0.84	62	113	67	88.28	0.92	71	107	166	86.61	0.67	54	110
	Tarsus (mm)	147	48.63	0.39	39.2	60	152	49.05	0.36	40.07	59	65	48.38	0.66	38.73	63.2	166	47.54	0.36	38	58
		n	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**
Mixed-Grass	Mass (g)	369	757.04	2.21	625	885	219	741.81	3.5	596.5	890	93	729.07	5.12	560	830	175	711.29	3.61	575	820
	Wing (mm)	358	210.57	0.27	186	229	213	209.21	0.44	182	224	85	203.94	0.57	192	216	168	203.96	0.5	187	230
	Pinnae (mm)	330	67.13	0.25	53.5	85	198	65.09	0.40	40	84	76	30.87	0.51	21	45	141	29.96	0.38	20	50
	Tail (mm)	336	84.05	0.39	59	135	207	84.43	0.72	61	126	87	80.45	1.03	54	111	170	81.34	0.55	56	104
	Tarsus (mm)	122	52.08	0.38	40	62	92	53.08	0.34	44	63	42	50.5	0.49	43	56	129	49.92	0.34	38.51	58.91
		n	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**
Sand Sagebrush	Mass (g)	43	779.42	6.39	700	855	21	760.57	11.28	665	835	12	742.5	7	700	770	10	727	19.78	635	840
	Wing (mm)	41	209.44	0.67	200	220	23	208.74	1.26	200	225	12	201.92	1.59	194	210	10	200.1	2.79	186	218
	Pinnae (mm)	5	66.77	2.27	63.03	75.38	5	67.88	2.07	63.02	74.3	0					7	26.97	2.32	19	38.09
	Tail (mm)	5	97.12	1.85	92.29	102.6	5	97.66	2.21	92.99	105	2	82.42	3.42	79	85.8	7	82.72	3.82	69.68	99.96
	Tarsus (mm)	36	54.46	0.32	51	59.35	20	54.37	0.34	50	57	11	52.28	0.68	49	57.1	6	51.49	1.04	48.4	56
		n	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**	**n**	$\bar{x}$	**SE**	**Min**	**Max**
Sand Shinnery Oak	Mass (g)	432	769.22	2.69	565	935	274	772.8	3.52	550	910	79	747.42	5.7	600	850	144	722.72	4.48	550	840
	Wing (mm)	414	214.86	0.3	195	234	270	211.9	0.42	190	234	73	206.63	0.69	191	219	145	207.18	0.51	191	221
	Pinnae (mm)	395	69.64	0.33	49	94	241	67.35	0.43	46	92	65	33.57	0.58	21	46	116	32.06	0.58	10	53
	Tail (mm)	297	86.58	0.44	60	105	117	85.73	0.56	64	101	57	82.39	0.74	68	96	95	80.47	0.71	53	95
	Tarsus (mm)	100	56.58	0.37	45	67	67	54.8	0.46	43	65	13	54.15	0.95	47	58	37	53.7	0.54	48	62

Table 1.5 Principal components of lesser prairie-chicken morphometric traits by age and sex class indicate that 95-91% of variance is explained in the first principal component PC1 for all age/sex classifications.

All birds were measured from 1986-2019 in the Southern Great Plains.

	Adult Male				
	PC1	PC2	PC3	PC4	PC5
Standard Deviation	46.73	11.17	6.09	5.26	4.76
Proportion of Variance	0.91	0.05	0.02	0.01	0.01
Cumulative Proportion	0.91	0.96	0.98	0.99	1.00
	Juvenile Male				
	PC1	PC2	PC3	PC4	PC5
Standard Deviation	46.68	10.35	6.81	5.82	4.22
Proportion of Variance	0.91	0.05	0.02	0.01	0.01
Cumulative Proportion	0.91	0.96	0.98	0.99	1.00
	Adult Female				
	PC1	PC2	PC3	PC4	PC5
Standard Deviation	54.58	8.82	6.55	4.49	4.23
Proportion of Variance	0.95	0.02	0.01	0.01	0.01
Cumulative Proportion	0.95	0.97	0.99	0.99	1.00
	Juvenile Female				
	PC1	PC2	PC3	PC4	PC5
Standard Deviation	50.58	8.49	6.34	4.87	4.00
Proportion of Variance	0.94	0.03	0.01	0.01	0.01
Cumulative Proportion	0.94	0.97	0.99	0.99	1.00

Table 1.6 Principal component loadings by morphometric variable for each age/sex classification.

Influence of individual variables in determining variance explained by individual of principal components. All birds were measured from 1986-2019 in the Southern Great Plains

			Adult Male		
	PC1	PC2	PC3	PC4	PC5
Wing (mm)	0.036	-0.026	0.678	-0.720	-0.142
Mass (g)	0.998	0.042	-0.039	0.009	0.017
Pinnae (mm)	0.023	0.006	0.704	0.693	-0.152
Tail (mm)	0.041	-0.998	-0.006	0.023	0.046
Tarsus (mm)	0.01	-0.044	-0.209	-0.001	-0.977
			Juvenile Male		
	PC1	PC2	PC3	PC4	PC5
Wing (mm)	-0.034	0.169	-0.281	0.944	0.0002
Mass (g)	-0.998	-0.019	0.058	-0.015	0.007
Pinnae (mm)	-0.053	0.112	-0.915	-0.295	-0.245
Tail (mm)	-0.008	0.977	0.139	-0.134	0.089
Tarsus (mm)	0.006	0.062	0.246	0.063	-0.965
			Adult Female		
	PC1	PC2	PC3	PC4	PC5
Wing (mm)	0.045	-0.150	0.588	0.717	0.340
Mass (g)	0.998	0.037	-0.020	-0.017	-0.047
Pinnae (mm)	0.003	-0.240	0.760	-0.549	-0.257
Tail (mm)	0.031	-0.958	-0.282	0.023	0.012
Tarsus (mm)	0.036	0.002	-0.03	-0.428	0.902
			Juvenile Female		
	PC1	PC2	PC3	PC4	PC5
Wing (mm)	-0.024	0.099	0.971	0.211	0.038
Mass (g)	-0.999	0.022	-0.031	0.014	0.022
Pinnae (mm)	-0.033	-0.108	0.194	-0.729	-0.647
Tail (mm)	-0.021	-0.989	0.076	0.099	0.077
Tarsus (mm)	-0.004	-0.003	-0.110	0.644	-0.757

Table 1.7 Male lesser prairie-chicken nutrient reserves by age class and ecoregion. Nutrient reserves calculated using sex specific equations derived in Haukos et al. (1989).

All birds captured in the Southern Great Plains between 1986-2019.

		Adult Male					Juvenile Male				
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Short-Grass	Wing (mm)	153	212.08	0.47	194	230	147	211.17	0.63	194	250
	Mass (g)	153	778.39	3.59	675	890	147	762.9	3.59	660	890
	Fat (g)	153	18.32	0.14	12.62	22.64	147	17.91	0.18	8.91	22.91
	Proportion Fat	153	0.02	0	0.02	0.03	147	0.02	0	0.01	0.03
	Protein (g)	153	179.25	0.72	155.71	204.36	147	176.27	0.75	156.07	211.56
	Proportion Protein	153	0.23	0	0.22	0.25	147	0.23	0	0.22	0.27
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Mixed-Grass	Wing (mm)	354	210.23	0.41	124	229	211	208.24	0.6	112	224
	Mass (g)	354	756.76	2.60	625	885	211	741.28	2.98	610	890
	Fat (g)	354	17.82	0.12	10.91	33.98	211	17.47	0.14	11.24	36.1
	Proportion Fat	354	0.02	0	0.02	0.04	211	0.02	0	0.02	0.04
	Protein (g)	354	174.67	0.52	123.35	200.64	211	2.87	0.67	99.32	201.9
	Proportion Protein	354	0.23	0	0.15	0.25	211	0.23	0	0.14	0.25
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Sand Sagebrush	Wing (mm)	41	209.44	0.67	200	220	21	209	1.32	200	225
	Mass (g)	41	777.44	6.55	700	855	21	760.57	11.28	665	835
	Fat (g)	41	18.9	0.27	15.69	21.88	21	18.25	0.54	14.38	22.19
	Proportion Fat	41	0.02	0	0.02	0.03	21	0.02	0	0.02	0.03
	Protein (g)	41	177.33	1.19	161.71	193.27	21	174.43	2.02	156.99	188.25
	Proportion Protein	41	0.23	0	0.22	0.24	21	0.23	0	0.22	0.24
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Sand Shinnery Oak	Wing (mm)	421	214.82	0.3	195	244	269	211.81	0.43	190	241
	Mass (g)	421	769.75	2.71	603	935	269	772.19	3.48	601	910
	Fat (g)	421	17.33	0.11	10.44	25.18	269	18.07	0.16	8.19	23.83
	Proportion Fat	421	0.02	0.01	0.01	0.03	269	0.02	0	0.01	0.03
	Protein (g)	421	179.75	0.51	147.92	209.53	269	178.10	0.01	146.01	214.67
	Proportion Protein	491	0.23	0	0.21	0.26	269	0.23	0	0.21	0.27

Table 1.8 Female lesser prairie-chicken nutrient reserves by age class and ecoregion. Nutrient reserves calculated using sex specific equations derived in Haukos et al. 1989.

All birds captured in the Southern Great Plains between 1986-2019.

		Adult Female					Juvenile Female				
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Short-Grass	Wing (mm)	68	207.71	0.75	188	222	164	202.92	0.47	185	220
	Mass (g)	68	754.63	6.8	600	890	164	729.69	4.03	620	890
	Fat (g)	68	51.38	1.35	2.88	65.94	164	52.11	0.74	4.02	66.37
	Proportion Fat	68	0.07	0	0	0.08	164	0.07	0	0.01	0.08
	Protein (g)	68	173.08	1.32	143.03	200.01	164	167.96	0.77	147.7	199.91
	Proportion Protein	68	0.23	0	0.22	0.24	164	0.23	0	0.22	0.24
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Mixed-Grass	Wing (mm)	85	204.49	0.45	192	216	163	204.09	0.4	187	220
	Mass (g)	85	732.68	4.42	620	830	163	712.71	3.49	600	820
	Fat (g)	85	53.9	0.7	36.08	65.61	163	50.49	0.66	2.54	64.79
	Proportion Fat	85	0.07	0	0.05	0.08	163	0.07	0	0	0.08
	Protein (g)	85	168.64	0.84	147.26	187.30	163	165.84	0.66	143.51	185.45
	Proportion Protein	85	0.23	0	0.23	0.13	163	0.23	0	0.22	0.24
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Sand Sagebrush	Wing (mm)	12	201.92	1.59	194	210	9	201.67	2.58	192	218
	Mass (g)	12	742.5	7	700	770	9	737.22	18.93	645	840
	Fat (g)	12	55.41	1.57	46.16	61.84	9	50.06	3.38	34.35	61.49
	Proportion Fat	12	0.07	0	0.06	0.08	9	0.07	0	0.04	0.08
	Protein (g)	12	170.23	1.31	162.47	175.35	9	169.31	3.7	152.08	190.34
	Proportion Protein	12	0.23	0	0.23	0.23	9	0.23	0	0.23	0.24
		n	**$\bar{x}$**	**SE**	**Min**	**Max**	**n**	**$\bar{x}$**	**SE**	**Min**	**Max**
Sand Shinnery Oak	Wing (mm)	78	206.91	1.15	191	218	141	206.89	0.51	191	221
	Mass (g)	78	752.49	7.42	600	830	141	725.98	4.5	600	840
	Fat (g)	78	51.62	1.54	25.23	62.76	141	49.69	0.89	12.75	64
	Proportion Fat	78	0.07	0	0.04	0.08	141	0.07	0.04	0.02	0.08
	Protein (g)	78	172.56	1.44	143.75	188.02	141	0.07	0	143.75	190.06
	Proportion Protein	78	0.23	0	0.22	0.24	141	0.23	0	0.22	0.24

Table 1.9 First nest survival models for Kansas Mixed-Grass and Short-Grass prairies. The constant daily nest survival model was the best performing, suggesting that female nutrient reserves and morphometrics do not influence survival of their first nest attempt.

Inclusion of female age. All nests were monitored between 2013-2017.

Model	AIC_c	ΔAIC_c	AIC_c Weights	Model Likelihood	Num. Par	Deviance
Constant DSR	438.34	0	0.16	1	1	436.34
Constant by site: fat	439.97	1.63	0.07	0.44	4	431.95
Constant by site: protein	439.97	1.63	0.07	0.44	4	431.95
Constant by site: min fat	439.97	1.63	0.07	0.44	4	431.95
Constant by site: max fat	439.97	1.63	0.07	0.44	4	431.95
Constant DSR juvenile	440.00	1.66	0.07	0.44	2	436.00
Constant DSR adult	440.00	1.66	0.07	0.44	2	436.00
Constant by site	440.66	2.32	0.05	0.31	3	434.65
Constant by site wing	441.27	2.92	0.04	0.23	4	433.25

Table 1.10 Change in male lesser prairie-chicken mass from first capture and last capture event within a breeding season in the Mixed-Grass Prairie Ecoregion, Sand Shinnery Oak Prairie Ecoregion, and Short-Grass Prairie/CRP Mosaic Ecoregion.

Males were captured up to five times within a season between 1987 and 2018, though the majority of birds were captured only one additional time, where there is the greatest range of recapture male mass.

Mixed-Grass Prairie Ecoregion

	Mass1	Mass2	Mass3	Mass4	Mass5	Days Between Capture
n	67	67	16	4	2	67
$\bar{x}$	756.98	734.52	703.83	705	677.5	17.48
SE	7.06	6.16	13.05	25.82	2.5	2.01
Min	600	620	615	645	675	0
Max	890	860	785	765	680	63

Sand Shinnery Oak Prairie Ecoregion

	Mass1	Mass2	Mass3	Mass4	Mass5	Days Between Capture
n	53	52	8	1	0	53
$\bar{x}$	773.25	749.54	708.12	745		17.96
SE	7.75	8.24	20.85			2.07
Min	640	625	640			0
Max	885	940	800	745		64

Short-Grass Prairie/CRP Mosaic Ecoregion

	Mass1	Mass2	Mass3	Mass4	Mass5	Days Between Capture
n	7	7	2	0	0	7
$\bar{x}$	779.43	757.14	727.5			15.71
SE	16.4	25	2.5			3.34
Min	705	690	725			1
Max	825	850	730			25

Table 1.11 Changes in observed male body fat for birds in Mixed Grass, Sand Shinnery Oak, and Short Grass ecoregions within a breeding season within a breeding season in the Mixed-Grass Prairie Ecoregion, Sand Shinnery Oak Prairie Ecoregion, and Short-Grass Prairie/CRP Mosaic Ecoregion.

Males were captured up to five times within a season between 1987 and 2018.Nutrient reserves were estimated with the equations derived in Haukos et al. (1989). Unlike male mass, the maximum observed grams body fat decreases with each subsequent recapture events.

Mixed-Grass Prairie Ecoregion

	Fat1	Fat2	Fat3	Fat4	Fat5	Days Between Capture
n	67	67	16	4	2	67
$\bar{x}$	18.14	16.83	15.31	15.42	14.07	17
SE	0.33	0.26	0.7	1.38	0.36	2.01
Min	10.84	12.87	10.67	12.13	13.72	1
Max	25.51	25.65	21.52	18.75	14.43	63

Sand Shinnery Oak Prairie Ecoregion

	Fat1	Fat2	Fat3	Fat4	Fat5	Days Between Capture
n	53	52	8	1	0	53
$\bar{x}$	18.18	16.71	14.43	14.69		17.96
SE	0.37	0.41	0.6			2.07
Min	12.11	11.74	12.11	14.59		64
Max	25.13	25.35	16.77	14.59		64

Short-Grass Prairie/CRP Mosaic Ecoregion

	Fat1	Fat2	Fat3	Fat4	Fat5	Days Between Capture
n	7	7	2	0	0	7
$\bar{x}$	17.15	15.87	16.38			15.71
SE	1.37	1.24	0.93			3.34
Min	9.89	11.22	15.46			1
Max	20.37	22.06	17.31			25

Table 1.12 Changes in observed lesser prairie-chicken male body protein for birds in Mixed-Grass, Sand Shinnery Oak, and Short-Grass ecoregions within a breeding season.

Males were captured up to five times within a season between 1987 and 2018. Nutrient reserves were estimated with the equations derived in Haukos et al. 1989. Male body protein changes follow closely with changes in overall male mass, with some increase in grams protein at the second capture event.

Mixed-Grass Prairie Ecoregion

	Protein1	Protein2	Protein3	Protein4	Protein5	Days Between Capture
n	67	67	16	4	1	67
$\bar{x}$	173.65	170.04	165.92	165.41	160.94	17
SE	1.37	1.26	2.14	4.15	0.16	2.01
Min	135.61	130.79	151.09	156.1	160.78	1
Max	195.56	192.59	178.48	175.09	161.11	63

Sand Shinnery Oak Prairie Ecoregion

	Protein1	Protein2	Protein3	Protein4	Protein5	Days Between Capture
n	53	52	8	1	0	53
$\bar{x}$	177.51	173.52	166.87	175.29		17.96
SE	1.35	1.41	3.9	175.29		2.07
Min	152.69	151.1	154.39	175.29		0
Max	195.58	205.86	184.61	175.29		64

Short-Grass Prairie/CRP Mosaic Ecoregion

	Protein1	Protein2	Protein3	Protein4	Protein5	Days Between Capture
n	7	7	2	0	0	7
$\bar{x}$	180.05	176.28	169.39			15.71
SE	3.77	5.25	0.8			3.34
Min	166.49	162.67	168.59			1
Max	196.67	199.67	170.19			25

Appendix A - Supplemental Figures

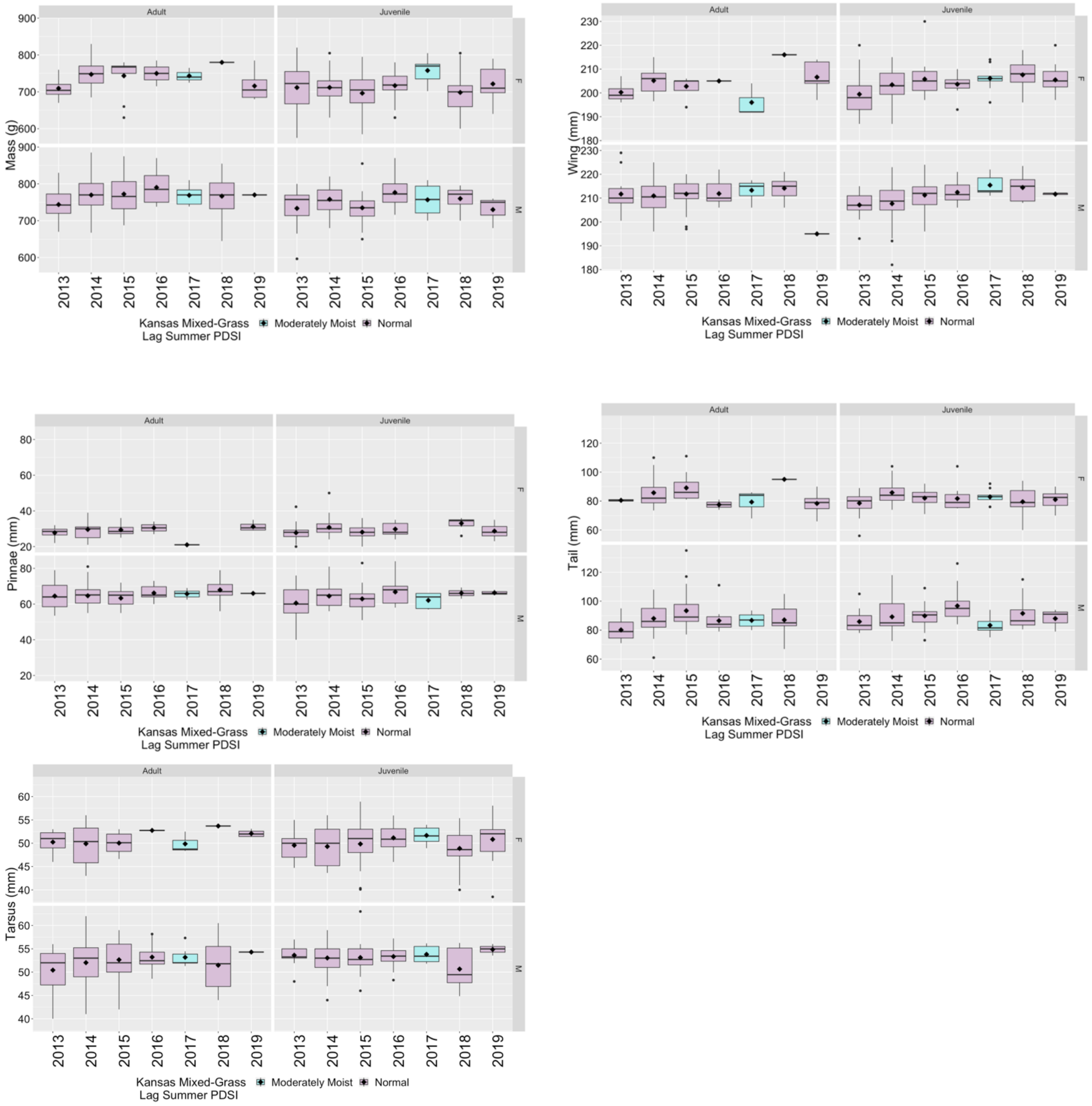

Figure A.1 Lesser prairie-chicken morphometric attributes by age and sex category in Mixed-Grass Prairie of Kansas.

Lesser prairie-chicken morphometric attributes by age and sex category in Mixed-Grass Prairie of Kansas. While morphometric traits are influenced by weather conditions of the prior year, there does not appear to be a directional shift in lesser prairie-chicken morphometrics over the period monitored (2013-2019). Points indicate mean values.

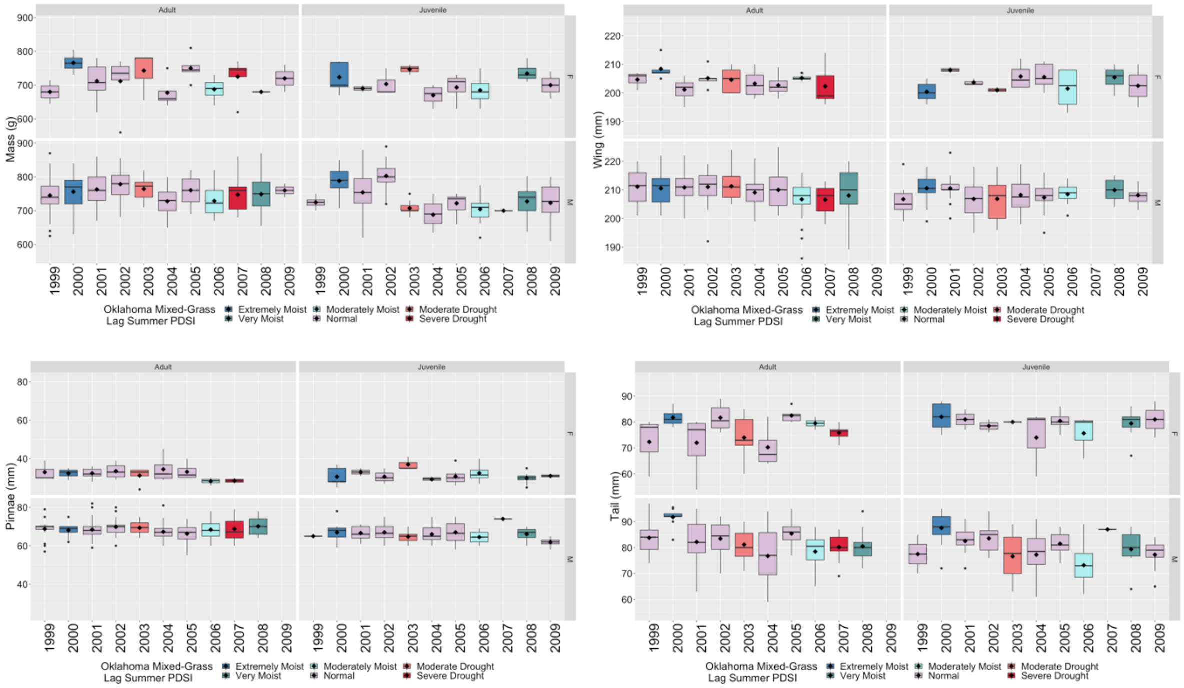

Figure A.2 Lesser prairie-chicken morphometric attributes by age and sex category in Mixed-Grass Prairie of Oklahoma from 1999-2009.

While morphometric traits are influenced with a predictable pattern based on the prior summer's precipitation, there does not appear to be a directional shift in lesser prairie-chicken morphometrics over time. Points indicate mean values

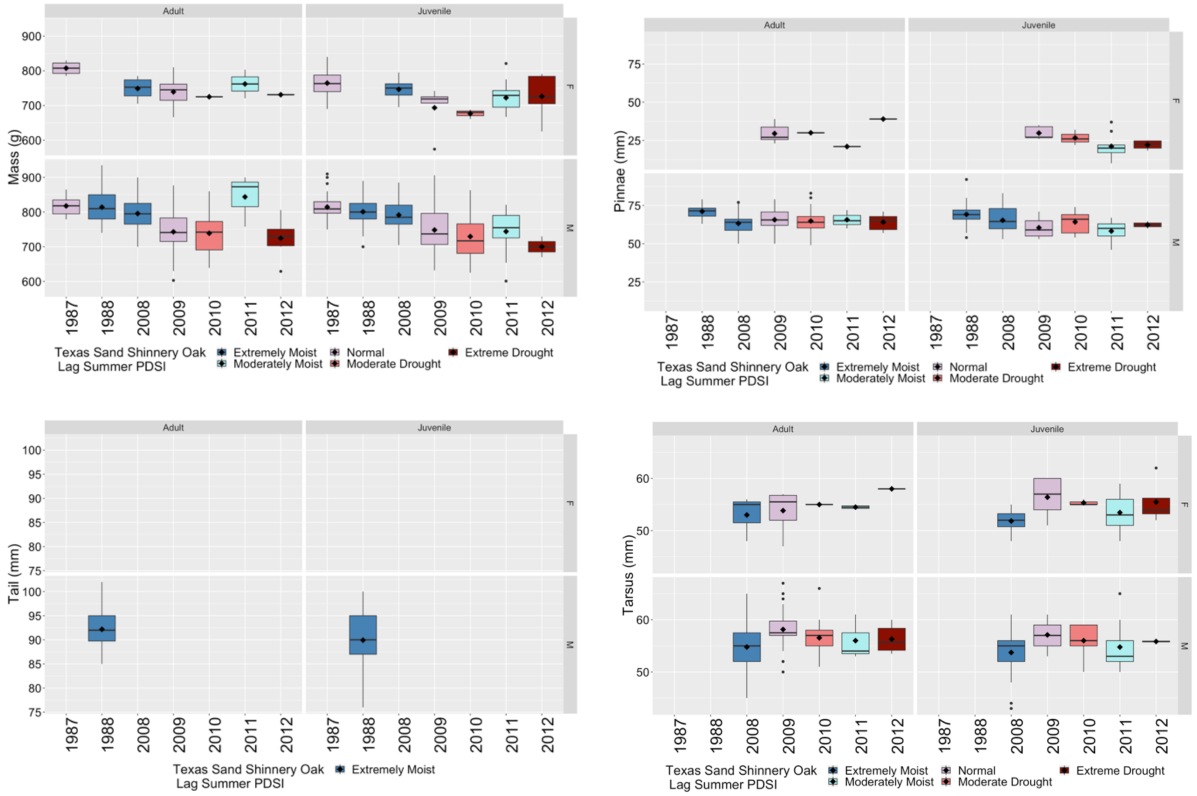

Figure A.3 Lesser prairie-chicken morphometric attributes by age and sex category in Sand Shinnery Oak Prairie of Texas from 1987-2012.

While morphometric traits are influenced with a predictable pattern based on the lag summer's precipitation, especially between drought and high moisture years, there does not appear to be a directional shift in lesser prairie-chicken morphometrics over time. Points indicate mean values.

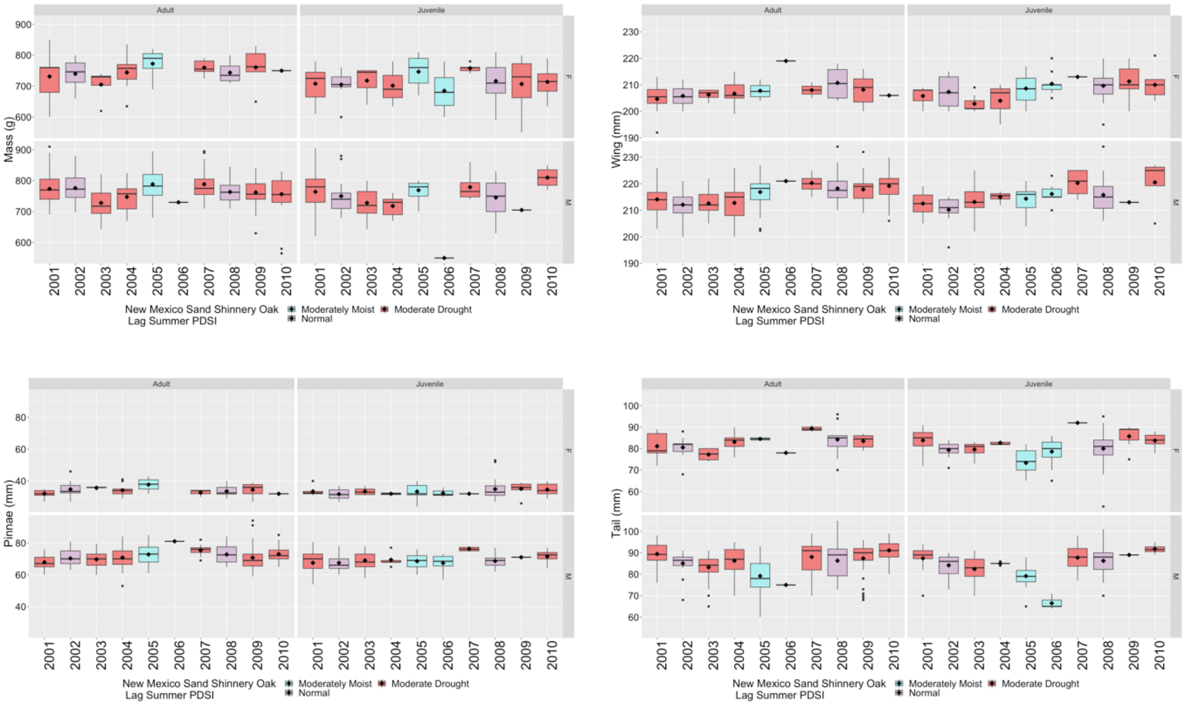

Figure A.4 Lesser prairie-chicken morphometric attributes by age and sex category in Sand Shinnery Oak Prairie of New Mexico from 2001-2010.

While morphometric traits are influenced by lag summer's precipitation, especially between drought and high moisture years, there does not appear to be a directional shift in lesser prairie-chicken morphometrics over time. Points indicate mean values.

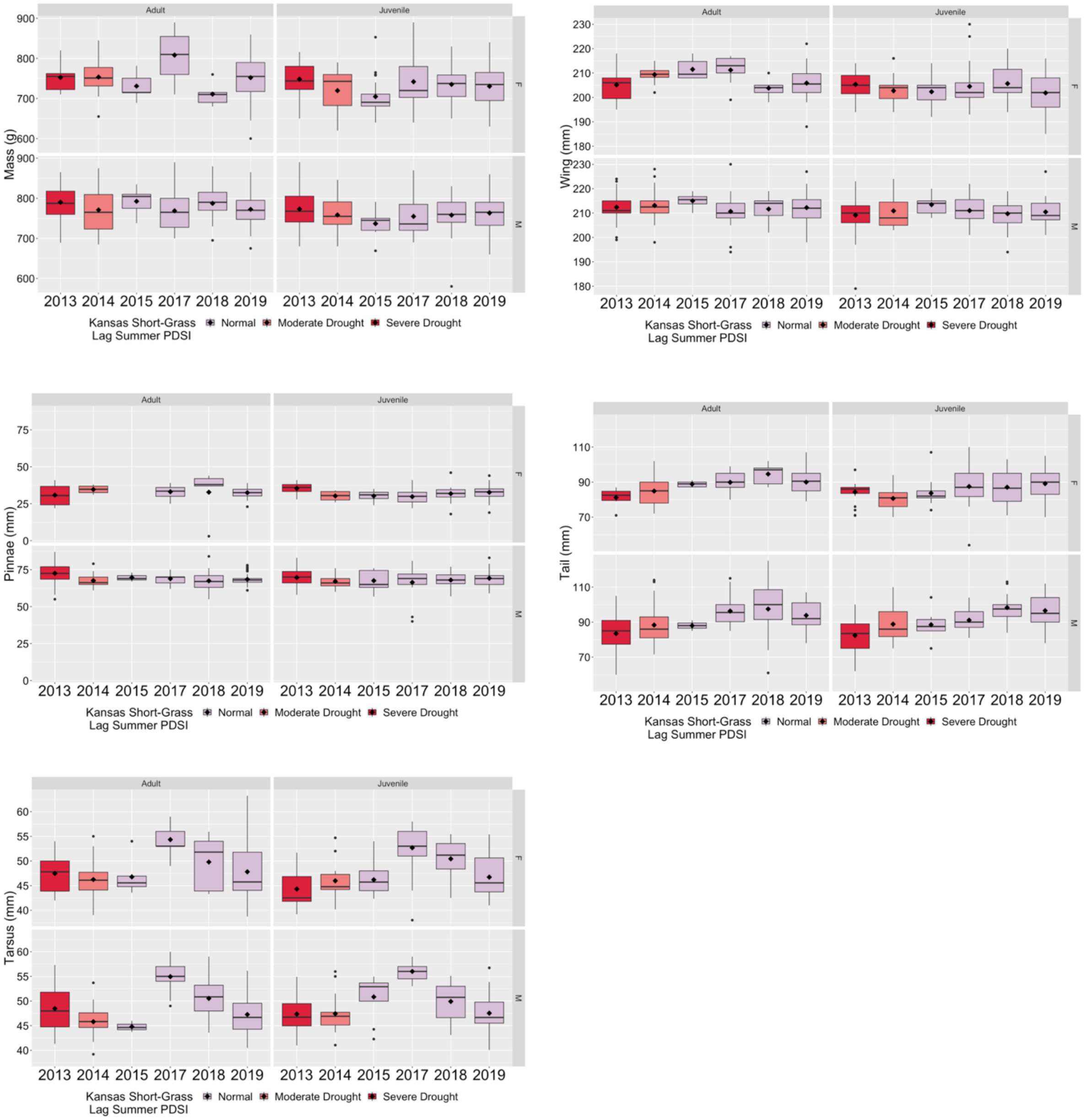

Figure A.5 Lesser prairie-chicken morphometric attributes by age and sex category in Short-Grass Prairie of Kansas from 2013-2019.

While lesser prairie-chicken morphometric traits are influenced by lag summer's precipitation, there does not appear to be a directional shift in lesser prairie-chicken morphometrics over time. Points indicate mean values.

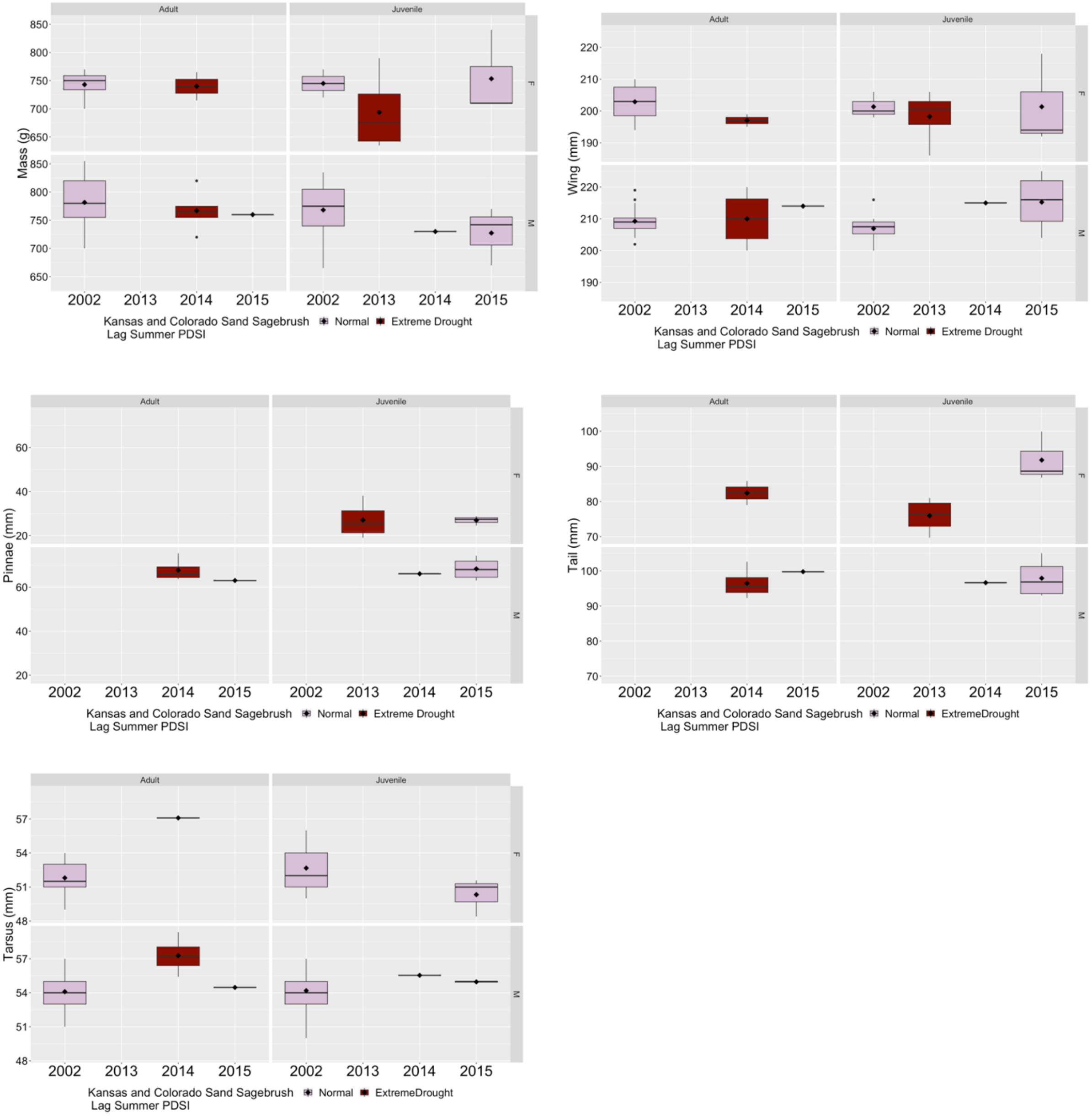

Figure A.6 Lesser prairie-chicken morphometric attributes by age and sex category in Sand Sagebrush Prairie of southeastern Colorado and southeastern Kansas from 2002-2015.

While lesser prairie-chicken morphometric traits are influenced by lag summer's precipitation and continued normal precipitation years, there does not appear to be a directional shift in lesser prairie-chicken morphometrics over time. Points indicate mean values.

Chapter 2 - Lesser Prairie-Chicken Lek Dynamics and Female Space Utilization

Introduction

The term lek defines both a unique place on the landscape and a sexually selected behavior. There are three common components for the numerous taxa where a lek breeding strategy has independently evolved. The first is that a lek is formed where a combination of vegetation and structural features accentuate characteristics of male breeding displays. The second is that male displays are performed in groups of three or more individuals, either sharing the same area or within audible distance of one another. The third characteristic is what makes a lek different from other grouped male courtship displays, as males on leks have various levels of social interactions that range from aggressive territorial disputes and disruption of copulation attempts to fully cooperative and complicated multi-male displays depending on species. An ubiquitous aspect of lek breeding is that only a few of males that display together on a lek successfully reproduce and no male provides resources or paternal care (Hoglund and Alatalo 1995, Fiske et al. 1998, Alonso et al. 2010, Behney et al. 2012*b*).

With so few males on a lek contributing to reproduction, the question arises: why would selective pressure cause males to form leks, compete directly with other males for female selection, and put energy into display if they are unlikely to reproduce? There are several hypotheses for the underlying mechanisms that led to the evolution of leks. Many hypotheses were generated starting in the 1960s through studying lek breeding grouse species such as sage grouse (*Centrocercus urophasianus*) and other prairie grouse (*Tympanuchus* spp.; Bergerud and Gratson 1988, Hoglund and Alatalo 1995).

While some hypotheses have been rejected in field manipulations or observations of grouse leks, several hypotheses remain viable for the mechanisms of lek evolution. Adequately addressing these remaining hypotheses is difficult, as it requires following the movements of both sexes to determine the influence of home ranges, habitat quality, and female distributions on the formation of lek displays (Bergerud and Gratson 1988).

Several hypotheses have already been rejected as the underlying mechanism for the formation of leks due to little supporting evidence. The predation hypothesis, which posits that males benefit from displaying together as a means of reducing predation risk was disproven due to insufficient predation of grouse on leks (Bradbury and Gibson 1983, Wolfe et al. 2007, Behney et al. 2011). The information-sharing hypothesis states that individuals form leks to share information about food resources, which has largely been dismissed due to the unlikeliness of food resources being limiting (Bergerud and Gratson 1988). The habitat limitation hypothesis argues that the habitat used by males for leks is limiting and patchily distributed, forcing males to display together, but display habitat is rarely limiting (Westcott 1994). The remaining hypotheses about underlying mechanisms of lek formation assume that males display in groups due to female selection or constraints of female parental care.

As the sole caregiver to their offspring, females are constrained to habitat that can provide the resources to raise offspring (Bradbury and Gibson 1983, Ekblom et al. 2005, Durães 2009, Isvaran and Ponkshe 2013). Under the hotspot hypothesis, leks form in areas where female home ranges touch or overlap (Bradbury and Gibson 1983, Gibson and Bradbury 1985, Beehler and Foster 1988, Bradbury et al. 1989*c*, Westcott 1994, Widemo and Owens 1995). Males who congregate in hotspots increase the likelihood of reproductive success by being in areas where females are more likely to occur. The hotspot hypothesis rests on the assumption that males have capacity to assess habitat quality or female density; it is believed that the brief fall lek display period for grouse serves as a way for males to assess leks and females to search for nesting habitat (Bergerud and Gratson 1988). Despite competing for mating opportunities with other males aggregating in the hotspot, the greater likelihood of female encounter is worth competing with other males for reproductive opportunities (Bergerud and Gratson 1988). There is some evidence that locations where grouse form leks are correlated to the relative greater abundance of quality nesting cover (Hamerstrom and Hamerstrom 1973, Gehrt et al. 2020). The hotspot hypothesis is the working hypothesis that underlies most management plans for lekking grouse species.

The ability to test the hotspot hypothesis has been historically limited by the ability to assess movements of individuals, due to the limitations of mass and the prohibitive cost of radio transmitters and personnel to track marked birds. Birds are only capable of safely carrying <3% of their body mass, which previously limited fine-scale telemetry to larger bodied species (Hansbauer and Pimentel 2008). Technological advances in telemetry have reduced the cost for very-high-frequency (VHF) radio transmitters, battery life, signal strength, and mass of transmitters (Bridge et al. 2011). Furthermore, the advent of satellite telemetry tags has enabled biologists to follow individual animals more efficiently and for longer periods of time (Cagnacci et al. 2010). Due to technological advances in animal tracking, it is now possible to test the hotspot hypothesis in lekking prairie grouse (Silva et al. 2017).

All species of prairie grouse exhibit classic leks, where males cluster into a common display area and each male defends a territory (Wittenberger 1978, Johnsgard 1994). Males form leks in areas with short vegetation and relatively higher elevation, distinguished by different vegetation composition and structure from both nesting and brood habitats (Johnsgard 2002). As prairie-grouse are nonmigratory grassland obligates, both sexes spend their annual cycle closely associated with lek locations (Johnsgard 2002, Timmer 2012, Haukos and Boal 2016). Males show strong lek-site fidelity, displaying at the same territory within a lek year after year (Dunn and Braun 1985, Woodward et al. 2001, Riley 2004, Pitman et al. 2006). Annual lek surveys is the principle method that agencies use to determine population trends of the prairie grouse, relying on the fidelity of males to display territories (Applegate 2000, McRoberts et al. 2011, McDonald et al. 2013, Timmer et al. 2013, Sadoti et al. 2016).

Addressing dispersal is inherent to addressing the hotspot hypothesis. For lek breeding species the question of whether leks or females lead dispersal into novel habitat underlies the mechanics of where and when leks appear on the landscape. The leading hypothesis for prairie grouse that dispersal is female driven, with young females venturing out in search of nesting and brood habitats (Bergerud and Gratson 1988). Under the female-driven dispersal hypothesis, males would evaluate existing leks in the fall prior to their first breeding season, and if there are few interactions with females, they are likely to form new leks in areas with greater female interaction (Bergerud and Gratson 1988). When juvenile males make larger dispersals in the spring, they likely move from lek to lek and evaluate potential reproductive success in the number of female visitations to the lek (Bergerud and Gratson 1988, Pitman et al. 2006). Female-driven dispersal would support the predictions of the hotspot hypothesis, where prairie grouse leks are formed in relationship to female densities (Bradbury et al. 1989*a*, Jiguet and Bretagnolle 2006).

There is increasing support for female-driven dispersal in prairie grouse, where females have moved large distances (Pitman et al. 2006, Weil and Jensen 2015, Earl et al. 2016, Berigan 2019). This suggests that prairie grouse move across their landscape in a step-wise fashion where females lead and leks follow (Bergerud and Gratson 1988, Bradbury et al. 1989*a*). Despite the increasing evidence of female-driven colonization, there is no conclusive evidence indicating that where leks form is due to female densities.

Lek habitats occur on areas with elevated topography and relatively shorter vegetation structure, likely to increase efficiency of males to signal quality to females. There is more habitat available to form leks than males can use (Bergerud and Gratson 1988, Westcott 1994, Hovick et al. 2015). Despite being a grassland obligate, lesser prairie-chicken males frequently form leks in cropland with suitably short vegetation in certain landscapes (Aulicky unpublished data). Therefore, where leks are placed on the landscape will likely correspond strongly to female habitat constraints (hotspot hypothesis) and changes in the surrounding landscape may determine the persistence of a lek. Female habitat utilization follows their reproductive needs and differs significantly from male display arenas (Hagen et al. 2013). Female lesser prairie-chickens require vegetation to hide nests from predators and an adjacent different habitat type rich with insects and forb seeds for their broods (Fields et al. 2006, Pitman et al. 2006, Hagen et al. 2013).

Developing an understanding of how leks form and what aspects determine their continued existence on the landscape is a critical aspect of lesser prairie-chicken management and conservation. Estimates of population abundance and trends are made from lek counts of males and the majority of lesser prairie-chicken activity during their life cycle occurs within 4-5 km from a lek (Haukos and Boal 2016). Furthermore, all banding and tracking efforts come from trapping birds of both sexes when they visit lek locations (Haukos et al. 1990, Grisham et al. 2015). An understanding of the mechanisms of lek breeding will, therefore, influence the success of management and conservation plans.

Lesser prairie-chicken leks are dynamic; the density of leks in an area changes between breeding seasons and even within a breeding season in response to population changes. Satellite leks typically form late in a breeding season as off-shoots from larger established leks and are less stable than established (≥2 years) leks (Haukos and Smith 1999). Interestingly, the persistence and disappearance of leks from the landscape occurs even with the high site fidelity adult males show to leks, returning year after year to breed at the same lek (Hagen et al. 2005). Some leks persist into multiple breeding seasons, while others do not last longer than a single season. As with the underlying assumption that leks form following the hotspot hypothesis, why some leks persist into subsequent breeding years while others vanish has not been formally addressed.

Factors contributing to lek declines of prairie grouse occur at multiple scales. The land cover surrounding leks has been found to have a significant influence on the number of attending males at leks and the conversion of grassland to cropland has been attributed to lek declines (Niemuth 2000, Smith et al. 2005). Increasing anthropogenic structures on the landscape can also lead to lek abandonment (Hess and Beck 2012, Winder et al. 2015). Changes in vegetation characteristics at the lek level, including increasing grass height, can cause lek abandonment (Anderson 1969, Hunt and Best 2010).

While factors contributing to lek declines have been identified, examination of lek dynamics from the perspective of formation and persistence is uncommon. If the hot spot hypothesis explains why leks form, it is likely that changes to female density in response to alterations of landcover and land use underlies the declines of leks. If nesting habitat or brood habitat around a lek were insufficient for a female's breeding requirements, it is likely that females will disperse to an area where their offspring are more likely to survive (Gehrt et al.

2020). Under the assumptions of the hotspot hypothesis, if females leave for an area of higher quality nesting or brood habitat, then juvenile males will follow. If female habitat requirements shift, moving the density of females away from an established lek, juvenile males will follow female densities as they disperse. Without recruitment of juvenile males, existing leks will vanish over time as adult males die out.

My first objective is to test the hotspot hypothesis as a determinant of lek formation. While it is likely that there are many underlying mechanisms for the formation of leks and hypotheses regarding lek formation are not mutually exclusive, the spatial behavior of males and females should implicate what hypothesis or hypotheses contribute to the formation of lesser prairie-chicken leks. The hotspot hypothesis states that leks form in areas with the greatest potential to encounter females. I tested the prediction that leks will occur in areas with the greatest concentration of female spatial locations.

My second objective was to identify attributes that influence persistence of leks on the landscape by examining changes in the number of displaying males. I focused my research on the spatial and temporal influences on the persistence of a lek display area over time, including female space use, changes to the surrounding lek complex, anthropogenic features, landcover, and lek vegetation. It is likely that there are multiple, interactive factors that determine if a lek persists into the following breeding season and these factors are likely related closely to the underlying mechanisms that cause the formation of lek displays. Therefore, I considered many of the same environmental and social influences in this line of inquiry as I did in my examination of the lek formation hypotheses. I predict that female habitat constraints will be the strongest predicting factor for lek persistence, leading to a quick collapse of a lek.

Study Area

The lesser prairie-chicken range is subdivided into four ecoregions: the Short-Grass Prairie/CRP Mosaic, Sand Sagebrush Prairie, Mixed-Grass Prairie, and Sand Shinnery Oak Prairie (McDonald et al. 2013). The contemporary range falls across Colorado, Oklahoma, Texas, New Mexico, and Kansas. Short-Grass, Mixed-Grass, and Sand Sagebrush Prairie all fall within the state of Kansas, including the entirety of the Short-Grass Prairie Ecoregion in the lesser prairie-chicken range. The Kansas Short-Grass Prairie Ecoregion has the most abundant lesser prairie-chicken population (Hagen et al. 2016, 2017, McDonald et al. 2016, Nasman et al. 2018).

The Southern Great Plains is subject to localized droughts on a 5-10 year cycle and large-scale intensive droughts almost every 20 years (Grisham et al. 2016*a*). The drought cycle drives the lesser prairie-chicken boom-bust population demography, especially during vulnerable periods such as nesting, brood rearing, and fall dispersal (Fields et al. 2006, Grisham et al. 2013, Ross et al. 2016*b*). In the years prior to and in the first year this study, the Southern Great Plains was subject to wide-spread and intensive drought from 2011-2013 (NOAA National Centers for Environmental Information 2011, Hagen et al. 2017). Also notably, in 2015 the Southern Great Plains was subject to extensive flooding (NOAA National Centers for Environmental Information 2015).

Short-Grass Prairie/CRP Mosaic

The Short-Grass Prairie/CRP Mosaic (hereafter Short-Grass Prairie) Ecoregion is a landscape of short-grass and mixed-grass prairies combined with U.S. Department of Agriculture Conservation Reserve Program (CRP) tracts intermixed with cropland located in northwestern Kansas (Dahlgren et al. 2016). The Short-Grass Prairie is comprised of silt loam soils with dominant vegetation inclusive of blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsute*), buffalograss (*B. dactyloides*), sideoats grama (*B. curtipendula*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed (*Ambrosia psilostacha*; Robinson 2015, Sullins 2017, Robinson et al. 2018, Sullins et al. 2018). Conservation Reserve Program tracts in Kansas were initially seeded with native grasses, primarily consisting of little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indian grass (*Sorghastrum nutans*; Fields et al. 2006, Robinson et al. 2018, Sullins et al. 2018). Annual average long-term (30 year) precipitation varies between 40 and 50 cm (Dahlgren et al. 2016).

Mixed-Grass Prairie

The Mixed-Grass Prairie Ecoregion is an extensive area of loamy soils that spans from south-central Kansas through Oklahoma into the northeastern edge of the Texas panhandle. Dominant vegetation within the range includes little bluestem, blue grama, hairy grama, sideoats grama, buffalograss, sand dropseed, big bluestem, invasive Russian thistle (*Salsola kali*), kochia (*Kochia scoparia*), annual sunflower (*Helianthus annuus*), Louisiana sagewort (*Artemisia ludiviciana*), western ragweed, sand sagebrush, and eastern red cedar (*Juniperus virginiana*; Lautenbach 2015, Wolfe et al. 2016, Lautenbach 2017). Average annual precipitation varies by longitude for the Mixed-Grass Prairie Ecoregion, with eastern areas of the ecoregion receiving 63.9-76.3 cm of rain, while the core of the ecoregion receives 51.8-63.8 cm, and western areas receive 40.6-51.7 cm (Grisham et al. 2016*a*). Mixed-Grass Prairie is the only ecoregion to fall in three different precipitation belts from east to west and it receives more rainfall than the other ecoregions within the lesser prairie-chicken range, averaging ~60 cm, with diminished fluctuations in annual precipitation values than other ecoregions of the lesser prairie-chicken range (Grisham et al. 2016*a*).

Methods

Lesser Prairie-Chicken Capture and GPS Telemetry

Researchers trapped lesser prairie-chickens on leks using funnel traps and drop nets during spring 2013-2017 in Kansas Short-Grass and Mixed-Grass prairies (Table 2.1). Birds were sexed by dimorphic characteristics such as differences in tail color patterns and aged using patterns of spotting, wear, and molt of the outermost 9th and 10th primary feathers (Copelin 1963, Pyle 2008). In the assembled data set, I differentiated individual birds by metal bands with a unique identification number, combinations of color bands, and by a telemetry/signal identifier. Birds were outfitted with a rump-mounted Satellite Platform Transmitting Terminal (PTT) GPS transmitter (Model PTT-100, Microwave Telemetry, Columbia, Maryland, USA) using leg harnesses made of Teflon® ribbon, and elastic at the front of the harness for flexibility (Bedrosian and Craighead 2007, Dzialak et al. 2011, Farve 2012*a*). GPS transmitters provided individual locations approximately every two hours between 0500 and 2300, which were downloaded from the ARGOS satellite system every three days, dependent on solar energy available to the tag.

Lek Observations and Vegetation Surveys

Lek surveys were conducted in conjunction with Kansas Department of Wildlife, Parks, and Tourism, which maintains a long-term road survey effort for lesser prairie-chickens (Ross et al. 2016*a*, *b*). Lek observation data used in these analyses were collected by the U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit as part of a multi-year lesser prairie-chicken research effort, where birds were captured at leks and equipped with GPS tags. As part of the capture effort, daily counts of male and female lesser prairie-chickens are recorded from late-March to mid-April.

After mid-April, lek vegetation composition and structure were measured along four 100 m transects radiating out from the center of each lek in each cardinal direction. Lek center was determined from observation of male locations and edges of feathers and fecal sign. Starting from 0 m, Daubenmire horizontal cover, plant composition (by species or functional group), and visual obstruction (%) using a Robel pole at 0, 25, 50, 75, and 100% cover measurements were recorded at every 10 m interval (Gehrt et al. 2020). Tallest grass height and litter depth were also recorded in millimeters. I averaged readings from each cardinal direction for each unit of distance of the vegetation survey to create an average composition from the central point of the lek outward past the lek edge (typically points from 0-40 m represented the active area of the lek and 50-100 m represented the adjacent vegetation).

Incorporating Female Movements to Test the Hotspot Hypothesis

I used published and unpublished spatial and movement data from three study sites in the Short-Grass Prairie and Mixed-Grass Prairie ecoregions (Robinson 2015, Robinson et al. 2016, 2018, Sullins 2017, Sullins et al. 2018, Plumb et al. 2019). The optimized hotspot tool in ArcGIS was used to determine clustered patterns within female GPS location points from female movements recorded at each field site. The optimized hotspot tool determines statistically significant hot or cold clusters based on the number of points and the surrounding number of points based on given locations using the Getis-Ord Gi* statistic, where a hot spot is determined as statistically significant when surrounded by other high sum values of points (ESRI n.d.).

When the sum of points and neighbors are different from an expected sum, indicating the cluster cannot be explained by random chance, then the hot spot is statistically significant (ESRI n.d.). Getis-Ord Gi* is a frequently used methodology in determining spatial clustering in wildlife studies (Kuletz et al. 2015, Shilling and Waetjen 2015, Cleasby et al. 2020). The relationship between concentrated areas of female location points prior to lek observation was used to test the validity of the hot spot hypothesis. Lek locations with maximum male counts were compared to lag female locations, determining if leks form and shift in relationship to the female use of space.

Lek Dynamics At 10 km, 5 km, 2 km, and 1 km Spatial Scales

I created 10 km, 5 km, 2 km, and 1 km buffers around lek sites using ArcGIS and applied the zonal statics tool to individual leks to determine surrounding percent grassland and cropland land cover. Land cover data were determined using 2013 Landsat 8 satellite imagery assembled by Spencer et al. (2017). Counts of point features from female movements, nest sites, and anthropogenic features were determined using QGIS count points in polygon tool at each buffer scale. Lengths of roadways, inclusive of county roads and state highways, and electric distribution lines were determined for each spatial scale using the sum line lengths tool in QGIS.

Counts of female spatial points were determined by year as a total number of recorded locations as well as the number of unique individual females who had points within each buffer scale. The number of nests within each buffer scale was determined and used in analyses as same year nesting efforts and as previous year nesting efforts. The number of neighboring lek locations was also determined at each buffer scale.

Anthropogenic data were provided from State of Kansas GIS Data Access and Support Center (DASC) repository, with the wind turbine database from U.S. Geological Survey, oil well data from Kansas Geological Survey, electric lines from Kansas Corporation Commission, cell towers from Federal Communications Commission Antenna Structure Registry, and roadways from Kansas Department of Transportation: Bureau of Transportation Planning. Wind turbine data were considered but excluded from analyses as the nearest wind turbines were constructed after lek observations ended for the only leks within the data set that would have been influenced.

Weather

I incorporated average annual Palmer Drought Severity Index (PDSI) values to explore the relationship between weather events and maximum male lek attendance. The PDSI is a measurement of meteorological drought that accounts for the correlated influence of temperature and precipitation as a measure of soil moisture. Drier periods are depicted with negative values and wetter conditions with positive values (Palmer 1965, Ross et al. 2016*b*, Dai and National Center for Atmospheric Research Staff 2019).

Analyses of Lek Dynamics

A series of linear regressions were tested by buffer scale (10, 5, 2, 1 km) with maximum observed male counts or maximum female counts as the dependent variable. Each scale and sex model suite included anthropogenic features, counts of nests of tracked females, female locations and leks, percent grassland land cover, and year as independent variables. Anthropogenic features considered included oil wells active in the year prior to observation, length of roadway, length of electric distribution lines, number of cell towers. Female spatial locations used in the models were lag locations from the year prior to lek observation of maximum male or female numbers. Year was included to account for annual changes in maximum male counts, female locations, nest-site selection, and changes to anthropogenic features within buffers. At the lek level, linear regression models were tested for each 10 m distance of lek vegetation measured from (0-100 m) for a total of 11 models. Each lek vegetation model included grass height, visual obstruction reading, litter depth, percent grass, percent forb, percent litter, year, and site. As with the landscape scale model suite, each distance was tested separately for maximum observed male and maximum observed female numbers. Each measured distance of lek vegetation was tested separately to assess where, if at any distance moving away from lek center, lek vegetation acts as a driver of maximum male or female numbers.

All independent variables were tested for correlation with a Pearson test prior to inclusion in the models. For variables with ($r > |0.80|$) correlation, the least biologically significant variables were excluded from the global model. All models were selected with combined forward and backward selection based on Akaike Information Criterion (AIC) from the global model. Top ranked models were determined by comparative AIC_c. Top AIC_c models were reduced by backward selection of individual variables to determine importance of model terms. The importance of individual variables within best fit models was determined by beta significance ($\alpha = 0.05$) and effect size.

Results

My results are based on 53 individual leks across three field sites in two ecoregions, with a total of 107 observation records during 2013-2017. Vegetation surveys were recorded on 43 leks from 2014-2015. A total of 143 individual females equipped with GPS transmitters across all three sites were used in spatial analyses and linear models (Table 2.1).

Spatial Patterns of Lek Formation and Factors in Lek Persistence at Large Scale

Optimized hot spot maps show a pattern consistent with the hotspot hypothesis. Where female spatial locations concentrate into hot spots, significant clustering of points denoted by warm colors in the figures, new leks appear and existing leks remain stable or increase in number of attending males (Figures 2.1-2.3). This pattern is established based on lag female locations from the year prior to the breeding season where leks were observed or found. The examination of female spatial locations within the same year as lek observations implicates that once female space use shifts away from established leks, there is a continued decline of number of attending males (Figure 2.4). Changes in male numbers at leks from year to year follows lag female space use prior to the breeding season of observation more closely than changes in female space use within the same year (Figure B.1-B.3).

Together, this lends support to the underlying assumption that female space use prior to breeding season (March-April) influence where leks form and the stability of male attendance at existing leks. Consistent with the hotspot hypothesis, it appears that female movements influence lek stability and formation over time. As concentrated areas of female GPS locations shift away from existing lek locations, in subsequent breeding seasons numbers of maximum observed males shrink in response. The pattern of lek formation and changes in the number of attending males in relationship to female space use is universal across field sites and years (Figures 2.1-2.3). Female movements are likely a reflection of habitat constraints for nest-site selection, implicated by the strong relationship between the number of female points and percent grassland land cover (Figure 2.4).

Maximum male numbers at leks at the 5 km to 2 km scales are influenced primarily by female movements and land cover (Table B.1). However, the 10 km ($F_{3,\,84} = 2.21$, $P = 0.09$) and 1 km scale ($F_{3,\,84} = 2.10$, $P = 0.12$) models were insignificant (Table B.1). When considered together, female spatial use follows increasing percent grassland at 5 km and 2 km scales, where maximum male observations follow increasing number of female spatial points (Figure 2.4). At the 5 km scale ($F_{6,\,81} = 2.65$, $P = 0.02$), the most parsimonious model includes non-significant anthropogenic factors (Table B.1). However, a reduction of the 5 km model to significant terms ($F_{1, 105} = 14.93$, $P < 0.001$) shows that maximum observed males at a lek increases as the number of nests from tracked females increase that year ($\beta = 0.43$, SE = 0.11, $P < 0.001$).

As with the 5 km model, the most parsimonious fit for the 2 km scale had non-significant model anthropogenic terms and reduction to significant terms (Table B.1). With reduction to significant terms ($F_{2, 104} = 8.76$, $P < 0.001$), the maximum number of males observed at a lek increases with an increasing number of nests from tracked females ($\beta = 0.64$, SE = 0.19, $P < 0.01$) that breeding season. While proportion of grassland is included in the 2 km model, the individual term is not significant cover ($\beta = 6.50$, SE = 3.87, $P = 0.09$). The relationship between tracked female movements and number of nest-sites within a 2 km buffer indicate that this spatial relationship is due to female habitat constraints due to breeding (Figure 2.5). Leks with the greatest number of displaying males, with maximum numbers of males >15, occur in 2 km locations with greater than 70% grassland and with ~8 tracked female nest sites (Figure 2.5). For these large leks, 7 tracked female nest-sites can account for up to 64% of all tracked female nesting efforts in a breeding season (Table 2.2).

In contrast, maximum female numbers at leks are influenced at the 10 km, 5 km scale, while the 2 km ($F_{4, 79} = 2.29$, $P = 0.07$) model was insignificant (Table B.2). The most parsimonious 1 km ($F_{2, 80} = 3.20$, $P = 0.05$) model had no individually significant terms, despite model significance (Table B.2). Maximum observed female numbers exhibit site-specific differences at the 10 km and 5 km scale. For 10 km ($F_{6, 77} = 2.49$, $P = 0.03$), the Mixed-Grass prairie sites in the Red Hills ($\beta = 2.12$, SE = 0.07, $P < 0.01$) and Ashland ($\beta = 2.46$, SE = 0.05, $P < 0.001$) were different from the Short-Grass Prairie site.

Following trends observed with male numbers, the maximum number of females at leks at the 5 km scale ($F_{5, 78} = 2.50$, $P = 0.04$) increases with tracked female nesting effort. Unlike male numbers, however, an increase in female numbers is determined not by same year nesting efforts but the numbers of nests attempted by tracked females in the prior year at the 5 km distance ($\beta = 0.34$, SE = 0.16, $P = 0.03$). At this scale, maximum female numbers decrease with increasing PDSI ($\beta = -0.86$, SE = 0.43, $P = 0.05$) and lag points ($\beta = -0.0003$, SE = 0.0001, $P = 0.04$), although the beta coefficient value for lag points is very low. The decrease of observed females with increasing moisture associated with increasing PDSI values may be tied to the difference in number of females observed by site, such as Ashland ($\beta = 3.11$, SE = 0.54, $P < 0.001$). Between sites, there were less observed females in the Short-Grass prairie at the Northwest site ($\beta = -2.33$, SE = 1.14, $P = 0.04$) compared to maximum observed females in two Mixed-Grass Prairie sites (Figure 2.6).

Lek Vegetation Factors in Persistence

All models of maximum male numbers and measured distances of lek vegetation are influenced by the year 2015, which reflects the wide-spread and extensive flooding in the Southern Great Plains at that time. Similarly, the effect of the higher precipitation is observed in almost all distance models of female maximum numbers (Figure 2.7). Mean grass height measured appears to increase at the majority of distances between 2014 and 2015, particularly for the Ashland and the Red Hills sites in the Mixed-Grass Prairie (Figure 2.8). The increasing grass height between 2014 and 2015 matches changes in annual PDSI, where the increased moisture in 2014 facilitated increased plant growth in the Mixed-Grass Prairie before measurements in 2015 (Figure 2.8).

Mean male maximums also differed by ecoregion. The Red Hills site in the Mixed-Grass Prairie had both the greatest and lowest average for lek male counts for the years in which lek vegetation was measured (2014-2015; Figure 2.6). Ashland, the second Mixed-Grass Prairie site, had the greatest average number of males observed at leks in 2014 (Figure 2.6). Together with the increased grass heights observed in the Mixed-Grass prairie, both site and year differences reoccur in the vegetation models as significant (Table B.3). For the 60 m ($F_{3, 39} = 3$, $P=0.04$) and 70 m ($F_{3, 39} = 3$, $P = 0.04$), significant model terms are identical with differences found only in ecoregion and year (Red Hills $\beta = -5.16$, SE = 1.95, $P = 0.01$; Ashland 2014 $\beta = 12.1$, SE = 1.35, $P<0.001$). For the 90 m model ($F_{4, 39} = 2.77$, $P = 0.04$) only Ashland 2014 ($\beta = 10.65$, SE = 2.14, $P < 0.001$).

Maximum Male Numbers at Lek Center (0-30 m)

At lek center ($F_{5, 37} = 2.73$, $P = 0.03$), maximum male numbers are primarily affected by site, with the Mixed-Grass Prairie sites differing from the Short-Grass Prairie site (Red Hills, $\beta = -6.78$, SE = 2.06, $P < 0.01$) and Ashland in 2014 ($\beta = 12.98$, SE = 1.94, $P < 0.001$). At 10 m ($F_{6, 36}= 3.39$, $P = 0.01$) the Mixed-Grass Prairie sites in the Red Hills ($\beta = -5.2$, SE = 1.82, $P < 0.01$), and Ashland ($\beta = 14.05$, SE = 1.8, $P <0.001$) again differ from Short Grass-Prairie. The year 2015 ($\beta = 3.75$, SE = 1.49, $P = 0.02$) was also different from 2014 measurements.

There is a slight decrease in maximum male numbers ($\beta = -0.01$, SE = 0.005, $P = 0.02$) with increasing grass height at 10 m. For the 20 m model ($F_{5, 37} = 4.04$, $P = 0.01$), increasing grass height also slightly decreases male numbers ($\beta = -0.02$, SE = 0.005, $P < 0.01$) and 2015 measurements are significant ($\beta = 4.27$, SE = 1.55, $P < 0.01$). However, increasing visual obstruction ($\beta = 1.11$, SE = 0.42, $P = 0.01$) and percent shrub cover ($\beta = 0.37$, SE = 0.16, $P = 0.02$) increases male numbers. At 30 m ($F_{3, 39} = 3$, $P = 0.04$) Maximum male numbers differ again by year and ecoregion (Red Hills $\beta = -5.16$, SE = 1.95, $P = 0.01$; Ashland 2014 $\beta = 12.96$, SE = 1.35, $P < 0.001$), but no vegetation factor was included in the top ranked model.

The lek center is where male lesser prairie-chickens display and increasing grass height decreasing maximum male numbers is likely related to the stomping aspect of lesser prairie-chicken courtship displays. At 20 m, the relationship between increased 100% visual obstruction and shrub cover and increased male numbers is mirrored in female lek vegetation models and may be related to female use of visual obstruction as observational cover. Maximum male numbers differ between the Short-Grass Prairie and Mixed-Grass Prairie, which is also reflected in annual differences in vegetation heights at lek center.

Maximum Male Numbers at Lek Edge (40-100 m)

At the edge of where males would actively display, 40 m ($F_{3, 39} = 3.63$, $P = 0.02$), increasing visual obstruction ($\beta = 0.93$, SE = 0.33, $P < 0.01$) increases maximum male numbers at leks. At this distance, mean visual obstruction is different in 2014 ($\beta = 13.42$, SE = 2.95, $P < 0.001$). Moving towards lek edge, at 80 m ($F_{3, 39} = 2.12$, $P = 0.11$), increasing visual obstruction ($\beta = 0.67$, SE = 0.33, $P = 0.05$) increases maximum males observed at leks and, as with other models, 2014 is significant ($\beta = 9.17$, SE = 1.28, $P<0.001$). At 100 m ($F_{7, 24} = 3.11$, $P = 0.02$), decreasing grass height increases maximum male numbers ($\beta = -0.01$, SE = 0.005, $P = 0.02$) while Ashland 2014 ($\beta = 16.75$, SE = 2.67, $P < 0.001$) and 2015 ($\beta = 5.70$, SE = 1.75, $P < 0.01$) are also significant.

Moving away from lek center and areas where males display, increasing visual obstruction increases maximum male numbers observed. This mirrors results for maximum female models at lek edge, implicating the importance of cover at lek sites. Furthermore, males rarely venture far from leks during the breeding season, and increased cover at the edges would offer protective roost sites adjacent to lek center.

Female Lek Vegetation Models

The same reoccurring year and site-specific differences observed in maximum male models also reoccur in the maximum observed female models. Additionally, for models 20 to 100 m, with the exception of 80 m where it was not a significant term, increasing visual obstruction increases maximum female attendance (Table B.4). While increasing visual obstruction seems at odds with the visibility required for male displays, when females visit leks, they will typically stay to the edges of the lek center in thicker vegetation for extended lengths of time before engaging with displaying males in the short vegetation. Having increased visual obstruction at the periphery of the lek center likely provides females with protective cover, potentially from both audacious males vying for a mate and any predators attracted to male displays.

Maximum Female Numbers at Lek Center (0-30 m)

For lek vegetation models of maximum female numbers, the 10 m ($F_{3,39} = 2.10$, $P = 0.12$) model was not significant (Table B.4). At the 0 m ($F_{4,38} = 3.42$, $P = 0.02$) scale, increasing percent litter ($\beta = 0.05$, SE = 0.02, $P = 0.02$) increases maximum female counts. At lek center Ashland in 2014 ($\beta = 3.23$, SE = 0.52, $P < 0.001$) is significant and the Short-Grass Prairie site is significant ($\beta = -2.07$, SE = 0.67, $P < 0.01$). At 20 m ($F_{3,39} = 3.16$, $P = 0.04$), 2014 is significant ($\beta = 2.27$, SE = 0.42, $P < 0.001$), while increasing visual obstruction ($\beta = 0.27$, SE = 0.15, $P = 0.09$) and percent forb ($\beta = 0.05$, SE = 0.02, $P = 0.05$) increase maximum observed females at leks. In the 30 m ($F_{2,40} = 5.26$, $P = 0.01$) model, increasing visual obstruction ($\beta = 0.32$, SE =

0.14, $P = 0.03$) increased females observed while increasing percent of litter horizontal cover ($\beta = -0.04$, SE = 0.02, $P = 0.05$) slightly decreased female numbers.

At lek center, maximum female numbers observed at leks increase with visual obstruction. Females spend most of their time visiting leks observing males and increased visual obstruction offers protection and may serve as a behavioral cue for female interest. Female lesser prairie-chickens slowly approach displaying males, often stopping in thick vegetation stands along the way for extended periods of time before coming onto lek center and mingling with males. It is likely that departure from vegetation cover acts as a signal of female interest and may mediate male attention and the aggression of display efforts.

Maximum Female Numbers and Lek Edge (40-100 m)

Moving away from lek center, the 40 m ($F_{6, 36} = 2.17$, $P = 0.07$) was not significant (B 2.7). In the 50 m ($F_{5, 37} = 3.27$, $P = 0.02$) model, Ashland 2014 ($\beta = 2.20$, SE = 1.02, $P = 0.04$) along with the year 2015 ($\beta = 1.24$, SE = 0.58, $P = 0.04$) are significant and increasing visual obstruction continues to increase maximum female numbers ($\beta = 0.35$, SE = 0.15, $P = 0.02$). At 60 m ($F_{3, 39} = 3.32$, $P = 0.03$), both 2014 ($\beta = 2.81$, SE = 0.37, $P < 0.001$) and 2015 ($\beta = 1.18$, SE = 0.59, $P = 0.05$) are significant. As with prior models, increasing visual obstruction ($\beta = 0.14$, SE = 0.07, $P = 0.04$) increases maximum female numbers and increasing shrub cover decreases female numbers ($\beta = -0.15$, SE = 0.06, $P = 0.01$). For 70 m ($F_{6, 36} = 4.46$, $P < 0.01$), Ashland 2014 ($\beta = 5.03$, SE = 1.25, $P < 0.001$), 2015 ($\beta = 1.83$, SE = 0.59, $P < 0.01$) and the Red Hills ($\beta = 1.99$, SE = 0.14, $P < 0.01$) site are all significant, again separating Mixed-Grass Prairie sites from the Short-Grass Prairie. As with prior models, increasing visual obstruction increases female maximum numbers ($\beta = 0.46$, SE = 0.14, $P < 0.01$) while increasing horizontal cover of grass ($\beta = -0.05$, SE = 0.02, $P < 0.01$) and forb ($\beta = -0.08$, SE = 0.03, $P < 0.01$) decrease female numbers. Moving towards the edge of the lek vegetation measurements, at 80 m ($F_{7, 35} = 2.33$, $P = 0.05$), Ashland intercept ($\beta = 6.86$, SE = 2.11, $P < 0.001$) is significant. Increased percent cover for grass ($\beta = -0.05$, SE = 0.02, $P = 0.05$), forb ($\beta = -0.011$, SE = 0.04, $P = 0.01$), and litter ($\beta = -0.11$, SE = 0.04, $P = 0.02$) results in decreasing female maximum numbers. At 90 m ($F_{8. 34} = 3.54$, $P < 0.001$), Ashland 2014 ($\beta = 5.18$, SE = 1.10, $P < 0.001$) and 2015 ($\beta = 1.29$, SE = 0.60, $P = 0.04$) and the Red Hills ($\beta = 1.64$, SE = 0.89, $P = 0.07$) are significant, with the continued trend of increasing visual obstruction increasing maximum number of females observed at leks ($\beta = 0.32$, SE = 0.10, $P < 0.01$). As with the 80 m model, increasing grass ($\beta = -0.03$, SE = 0.01, $P = 0.02$), forb ($\beta = -0.08$, SE = 0.03, $P < 0.01$), and shrub ($\beta = -0.09$, SE = 0.05, $P = 0.10$) cover. At the furthest distance considered 100 m ($F_{2, 29} = 5.11$, $P = 0.01$), 2014 ($\beta = 2.48$, SE = 0.43; $P < 0.001$) was significant while increasing visual obstruction increased female maximum numbers ($\beta = 0.33$, SE = 0.11, $P < 0.01$).

While many of the lek vegetation models of maximum female number indicate that females decrease with horizontal cover, effect sizes are small. In instances of forb and shrub horizontal cover, it may reflect the limited visual obstruction offered by most forbs and cacti. Visual obstruction for both Mixed-Grass and Short Grass Prairie at lek sites is provided by grass and increasing 100% visual obstruction drives maximum female numbers at lek sites.

Discussion

Like other grassland obligates, lesser prairie-chickens are imperiled by loss of prairies contributing to declining population abundance and occupied range (Jarnevich and Laubhan 2011, Sandercock et al. 2011, Spencer et al. 2017*a*). While the species is under state protection throughout its range, the lesser prairie-chicken was federally listed as threatened in 2014, the decision was vacated in 2015 and species delisted in 2016 (Haukos and Boal 2016). Currently, the lesser prairie-chicken occupies only 17% of the species' historical range and remains a conservation concern (Haukos and Boal 2016). With lek counts informing population estimates, leks are crucial to the conservation and management of lesser prairie-chickens. With this work, underlying determinants of where leks form on the landscape and what factors influence their persistence can be applied to lesser prairie-chicken lek dynamics.

Lesser prairie-chicken lek formation follows the predictions for the hotspot hypothesis, with new leks forming in areas of greatest female use. This relationship between female spatial locations is further supported by the largest leks occurring where there is the greatest concentration of female activity prior to breeding season. Furthermore, maximum female numbers observed at leks are influenced by prior nesting efforts at the 5 km scale, implicating that that lek dynamics are driven by behavior and space use prior to the breeding season of observation. The number of males observed at leks decrease with shifts in female locations in the prior breeding season. In my analysis of behavioral, land cover, and anthropogenic factors as potential influences of lek persistence, it is evident that male numbers and lek dynamics are driven by female constraints at both landscape and lek scales.

At 5 km to 2 km scales, grassland land cover, active or prior nest sites of tracked females, and female space use are significant determinants of male numbers at a lek year over year. Female spatial use and habitat constraints for nesting and brooding are more influential in determining maximum male numbers at leks than anthropogenic features such as oil wells. Avoidance of anthropogenic features by lesser prairie-chickens is well established (Pitman et al. 2005, Hagen et al. 2011, Hovick et al. 2014, Bartuszevige and Daniels 2016, Sullins 2017, Plumb et al. 2019). While this work did not find anthropogenic features as significant model factors in lek dynamics at the scales considered, it is likely not due to their influence on how lesser prairie-chickens use habitat. Instead, it is likely that the influence anthropogenic features have on lek formation and persistence is reflected in female spatial locations and avoidance of those features by females.

It is worth also considering the implications of female constraints as future determinants of lek formation and persistence. Increasing anthropogenic features on the landscape increase fragmentation of grassland habitat and decrease available habitat for lesser prairie-chicken. Under projections of climate change for the Great Plains, conditions are favorable for an expansion of woody foliage and a decrease of grasslands (Grisham et al. 2013, 2016*a*). As with anthropogenic features, lesser prairie-chickens abandon and avoid woody encroachment (Fuhlendorf et al. 2002, Behney et al. 2012*a*, Lautenbach et al. 2017). When managing for female constraints, it is necessary to determine if the plan accounts for necessary thermal refuge and robust, drought resistant forbs to allow females to nest under increasingly severe drought regimes and higher temperatures (Grisham et al. 2016*a*, Lautenbach 2017).

The importance of female constraints driving lek dynamics for male lesser prairie-chickens also implicates several other important conservation and management considerations. For lek breeding birds, there is an underlying question of how dispersal works within this extreme sexually selected system: what moves first, females or the lek? With female habitat constraints driving both formation and persistence of leks on the landscape, it is evident that females must drive dispersal into novel habitat for lesser prairie-chickens. There is evidence for female driven lesser prairie-chicken dispersal in translocation, which shows that females are capable of moving incredible distances (Figure 2.11; Chapter 3). As the determinant of lek dynamics, connectivity among populations is also determined by female lesser prairie-chickens (Gulick 2019).

At the lek scale, maximum male numbers are influenced by grass height at lek center, where increasing grass height could impede their ability to display. Moving away from lek center to the lek edge, increasing visual obstruction increases both male and female max counts. Female lesser prairie-chickens will observe displays from thicker vegetation stands at lek edges to avoid being harried by overeager males and increased visual obstruction likely encourages their attendance at leks. For males, increased maximum numbers with visual obstruction at the outer edges of the lek site is likely a reflection of both encouraging female visitation and providing male roost sites (personal observation ~60-70 m from lek center). Male lesser prairie-chickens rarely go far from leks during the breeding season, and the ability to roost close to display areas may serve an important role in lek site selection due to the role of time spent at display sites in determining male status (Castellano 2009). Lesser prairie-chicken females visit in greatest numbers in the first two weeks of April and establishing both dominance and increasing time spent on lek could ultimately determine if a male reproduces within his lifetime (average ~2 years; Boal and Haukos 2016, Rodgers 2016). The amount and uniformity of visual obstruction around leks is likely malleable in lek site selection, as not all lesser prairie-chicken lek sites are located in grasslands.

Unlike tropical lek breeding birds, such as manakins (Pipridae spp.), which are unyielding in the vegetation composition and structure of a lek site, lesser prairie-chickens will form sizable leks in cropland as well as native grassland (unpublished data; Chapter 3). It is worth noting that cropland lek sites are typically grassland adjacent, providing visual obstruction for female access and observation (personal observation). This phenomenon can be explained by the hotspot hypothesis, as female habitat constraints and increasing the likelihood of encountering mates determines optimal lek placement. Short structured cropland fits within the limited visual obstruction observed on grassland leks and because lesser prairie-chickens do not use vegetation structure as part of their displays, this explains the malleability of lesser prairie-chicken lek sites on the landscape.

While tropical and grassland lek breeding species have starkly different displays, with highly complicated and cooperative displays found in the tropics and simplified and competitive displays found in prairie-grouse, the hotspot hypothesis offers the best explanation for lek placement upon the landscape. For prairie-grouse, nest site selection is the driving influence of female constraints (Gibson 1996, Gehrt et al. 2020). In tropical species, leks are formed based on availability of fruit, such to the point that even multiple lek breeding species with unique lek site requirements can be found clustered around the same fruit resources (Ryder et al. 2006, Loiselle et al. 2007, Dahlgren et al. 2016).

This work solidifies the hotspot hypothesis as the best explanation for lek formation on the landscape for lesser prairie-chickens. With the increased spatial resolution offered by GPS locations, it was possible to explore the underlying assumptions for the hotspot hypothesis including female driven dispersal and the relationship of time in female space use to lek placement (Bergerud and Gratson 1988, Gibson 1996). Furthermore, questions regarding lek formation and placement upon the landscape do not often intersect with determining factors of lek persistence once those leks have been established. As this work shows, the underlying determinants of formation influence persistence and the collapse or persistence of leks can be explained by the hotspot hypothesis as well.

Linking the evolutionary mechanisms of lek formation and persistence to conservation management could prove to be an invaluable tool. While there has been some evidence of lek abandonment due to extensive grazing regimes, it is evident that lesser prairie-chicken males will adjust lek placement or use unconventional lek sites if the surrounding habitat can fit within female constraints (unpublished data; Niemuth 2000, Hunt and Best 2010). This determination is important, because it provides greater freedom for managers to focus efforts on nesting and brood habitat upon the landscape.

Management Implications

Lek counts provide lesser prairie-chicken population estimates and serve as the focal point for any research question as the means to capture and track birds throughout the year. With female habitat constraints driving lek dynamics and persistence of leks, this suggests that the best way to maintain leks on a landscape is to increase habitat suitable for nests and broods (Gehrt et al. 2020). Male lesser prairie-chickens will form leks in areas of short, sparse vegetation adjacent only to areas with high female traffic and managing for nesting habitat will increase persistence of leks. Increasing nesting habitat is therefore imperative, and is substantially lacking around Kansas leks (Gehrt et al. 2020). Working with private landowners and stakeholders to find solutions such as grazing rotations to allow thick bunch grasses to remain in the system to increase visual obstruction for nest sites should prioritized. Increasing surrounding visual obstruction at the edges of short-vegetation stands will also increase the attendance of females at lek sites, which will also increase the likelihood of lek persistence.

Conclusion

Lesser prairie-chicken lek dynamics are driven by female habitat constraints, with both formation and persistence of leks on the landscape determined by spatial utilization by females. Maximum observed male lesser prairie-chicken numbers at leks are determined by the ability of females to find quality nesting habitat, as active and prior nesting sites determines lek dynamics starting at a 5 km scale. Grassland managed for visual obstruction required for nesting habitat is, therefore, the best way for managers to secure existing leks and foster formation of new leks. Male lesser prairie-chickens will find lek habitat based on female use, even if that vegetation does not fit within a classic grassland framework. In a landscape where most remaining grasslands are working lands, management of vegetation structure through grazing and burning regimes for visual obstruction will act to maintain and create new leks.

Literature Cited

Alonso, J. C., M. Magaña, C. Palacín, and C. A. Martín. 2010. Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort. Behavioral Ecology and Sociobiology 64:1589–1600.

Anderson, R. K. 1969. Prairie chicken responses to changing booming-ground cover type and height. Journal of Wildlife Management 33:636–643.

Applegate, R. D. 2000. Use and misuse of prairie chicken lek surveys. Wildlife Society Bulletin 28:457–459.

Bartuszevige, A. M., and A. Daniels. 2016. Impacts of energy development, anthropogenic structures, and land use change on lesser prairie-chickens. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Bedrosian, B., and D. Craighead. 2007. Evaluation of techniques for attaching transmitters to common raven nestlings. Northwestern Naturalist 88:1–6.

Beehler, B. M., and M. S. Foster. 1988. Hotshots, hotspots, and female preference in the organization of lek mating systems. American Naturalist 131:203–219.

Behney, A. C., C. W. Boal, H. A. Whitlaw, and D. R. Lucia. 2011. Interactions of raptors and lesser prairie-chickens at leks in the Texas Southern High Plains. Wilson Journal of Ornithology 123:332–338.

Behney, A. C., C. W. Boal, H. A. Whitlaw, and D. R. Lucia. 2012*a*. Raptor community composition in the Texas Southern High Plains lesser prairie-chicken range. Wildlife Society Bulletin 36:291–296.

Behney, A. C., B. A. Grisham, C. W. Boal, H. A. Whitlaw, and D. A. Haukos. 2012*b*. Sexual selection and mating chronology of lesser prairie-chickens. Wilson Journal of Ornithology 124:96–105.

Bergerud, A. T., and M. W. Gratson, editors. 1988. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis.

Berigan, L. A. 2019. Dispersal, reproductive success, and habitat use by translocated lesser prairie-chickens. Thesis, Kansas State University, Manhattan, KS.

Boal, C. W., and D. A. Haukos. 2016. The lesser prairie-chicken a brief introduction the grouse of the Southern Great Plains. Pages 1–11 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, Boca Raton, FL.

Bradbury, J. W., and R. M. Gibson. 1983. Leks and mate choice. Pages 109–138 *in* P. Bateson, editor. Mate Choice. Cambridge University Press, New York.

Bradbury, J. W., R. M. Gibson, C. E. McCarthy, and S. L. Vehrencamp. 1989*a*. Dispersion of displaying male sage grouse: II. The role of female dispersion. Behavioral Ecology and Sociobiology 24:15–24.

Bradbury, J. W., S. L. Vehrencamp, and R. M. Gibson. 1989*b*. Dispersion of displaying male sage grouse: I. Patterns of temporal variation. Behavioral Ecology and Sociobiology 24:1–14.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, W. D. Robinson, and M. Wikelski. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. BioScience 61:689–698.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2157–2162.

Castellano, S. 2009. Unreliable preferences, reliable choice and sexual selection in leks. Animal Behaviour 77:225–232.

Cleasby, I. R., E. Owen, L. Wilson, E. D. Wakefield, P. O'Connell, and M. Bolton. 2020. Identifying important at-sea areas for seabirds using species distribution models and hotspot mapping. Biological Conservation 241:108375.

Copelin, F. 1963. The lesser prairie chicken in Oklahoma. Oklahoma Wildlife Conservation Department, Oklahoma City, OK.

Dahlgren, D. K., R. D. Rodgers, R. D. Elmore, and M. R. Bain. 2016. Grasslands of western Kansas, north of the Arkansas River. Pages 259–280 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Dai, A., and National Center for Atmospheric Research Staff. 2019. The climate data guide: Palmer Drought Severity Index (PDSI). Palmer Drought Severity Index. <https://climatedataguide.ucar.edu/climate-data/palmer-drought-severity-index-pdsi>. Accessed 15 May 2020.

Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. Auk 102:621–627.

Durães, R. 2009. Lek structure and male display repertoire of blue-crowned manakins in eastern Ecuador. Condor 111:453–461.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6.

Earl, J. E., S. D. Fuhlendorf, D. Haukos, A. M. Tanner, D. Elmore, and S. A. Carleton. 2016. Characteristics of lesser prairie-chicken (Tympanuchus pallidicinctus) long-distance movements across their distribution. Ecosphere 7:1–13.

Ekblom, R., S. A. Sæther, D. Hasselquist, D. Hannersjö, P. Fiske, J. A. Kålås, and J. Höglund. 2005. Female choice and male humoral immune response in the lekking great snipe (Gallinago media). Behavioral Ecology 16:346–351.

ESRI. n.d. How hot spot analysis (Getis-Ord Gi) works. ArcGIS Pro. <https://pro.arcgis.com/en/pro-app/tool-reference/spatial-statistics/h-how-hot-spot-analysis-getis-ord-gi-spatial-stati.htm>.

Farve, R. 2012. Demonstration of satellite / GPS telemetry for monitoring fine- scale movements of lesser prairie-chickens.

Fields, T. L., G. C. White, W. C. Gilgert, and R. D. Rodgers. 2006. Nest and brood survival of lesser prairie-chickens in west central Kansas. Journal of Wildlife Management 70:931–938.

Fiske, P., P. T. Rintamäki, and E. Karvonen. 1998. Mating success in lekking males: a meta-analysis. Behavioral Ecology 9:328–338.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie, and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landscape Ecology 17:617–628.

Gehrt, J. M., D. S. Sullins, and D. A. Haukos. 2020. Looking at the bigger picture: how abundance of nesting and brooding habitat influences lek-site selection by lesser prairie-chickens. American Midland Naturalist 183:52–77.

Gibson, R. M. 1996. A re-evaluation of hotspot settlement in lekking sage grouse. Animal Behaviour 52:993–1005.

Gibson, R. M., and J. W. Bradbury. 1985. Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. Behavioral Ecology and Sociobiology 18:117–123.

Grisham, B. A., C. W. Boal, D. A. Haukos, D. M. Davis, K. K. Boydston, C. Dixon, and W. R. Heck. 2013. The predicted influence of climate change on lesser prairie-chicken reproductive parameters. F. Seebacher, editor. PLoS ONE 8:e68225.

Grisham, B. A., C. W. Boal, N. R. Mitchell, T. S. Gicklhorn, P. K. Borsdorf, D. A. Haukos, and C. E. Dixon. 2015. Evaluation of capture techniques on lesser prairie-chicken trap injury and survival. Journal of Fish and Wildlife Management 6:318–326.

Grisham, B. A., A. J. Godar, and C. P. Griffin. 2016. Climate change. Pages 221–242 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Gulick, C. K. 2019. Effects of working grassland management on lesser prairie-chicken resource selection within home ranges and during dispersal events. Thesis, Kansas State University, Manhattan, KS.

Hagen, C. A., E. O. Garton, G. Beauprez, B. S. Cooper, K. A. Fricke, and B. Simpson. 2017. Lesser prairie-chicken population forecasts and extinction risks: an evaluation 5 years post-catastrophic drought. Wildlife Society Bulletin 41:624–638.

Hagen, C. A., B. A. Grisham, C. W. Boal, and D. A. Haukos. 2013. A meta-analysis of lesser prairie-chicken nesting and brood-rearing habitats: implications for habitat management. Wildlife Society Bulletin 37:750–758.

Hagen, C. A., D. C. Pavlacky, K. Adachi, F. E. Hornsby, T. J. Rintz, and L. L. McDonald. 2016. Multiscale occupancy modeling provides insights into range-wide conservation needs of lesser prairie-chicken (Tympanuchus pallidicinctus). Condor 118:597–612.

Hagen, C. A., J. C. Pitman, T. M. Loughin, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2011. Impacts of anthropogenic features on habitat use by lesser prairie-chickens. Pages 63–75 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, Conservation, and Management of Grouse. Volume 39. Studies in Avian Biology, Cooper Ornithological Society, University of California Press, Berkeley and Los Angeles.

Hagen, C. A., G. C. Salter, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2005. Lesser prairie-chicken brood habitat in sand sagebrush: invertebrate biomass and vegetation. Wildlife Society Bulletin 33:1080–1091.

Hamerstrom, F., and F. Hamerstrom. 1973. The prairie chicken in Wisconsin highlights of a 22-year study of counts, behavior, movements, turnover and habitat. Technical Bulletin, Department of Natural Resources, Madison, Wisconsin.

Hansbauer, M. M., and R. G. Pimentel. 2008. A comparison of five techniques for attaching radio-transmitters to tropical passerine birds. Revista Brasileira de Ornitologia 6.

Haukos, D. A., and C. W. Boal, editors. 2016. Ecology and conservation of lesser prairie-chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Haukos, D. A., and L. M. Smith. 1999. Effects of lek age on age structure and attendance of lesser prairie-chickens (Tympanuchus pallidicinctus). American Midland Naturalist 142:415–420.

Haukos, D. A., L. M. Smith, and G. S. Broda. 1990. Spring trapping of lesser prairie-chickens. Journal of Field Ornithology 61:20–25.

Hess, J. E., and J. L. Beck. 2012. Disturbance factors influencing greater sage-grouse lek abandonment in north-central Wyoming. Journal of Wildlife Management 76:1625–1634.

Hoglund, J., and R. V. Alatalo. 1995. Leks. Princeton University Press.

Hovick, T. J., B. W. Allred, R. D. Elmore, S. D. Fuhlendorf, R. G. Hamilton, and A. Breland. 2015. Dynamic disturbance processes create dynamic lek site selection in a prairie grouse. C. A. Hagen, editor. PLOS ONE 10:e0137882.

Hovick, T. J., R. D. Elmore, D. K. Dahlgren, S. D. Fuhlendorf, and D. M. Engle. 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. C. Elphick, editor. Journal of Applied Ecology 51:1680–1689.

Hunt, J. L., and T. L. Best. 2010. Vegetative characteristics of active and abandoned leks of lesser prairie-chickens (Tympanuchus pallidicinctus) in southeastern New Mexico. Southwestern Naturalist 55:477–487.

Isvaran, K., and A. Ponkshe. 2013. How general is a female mating preference for clustered males in lekking species? A meta-analysis. Animal Behaviour 86:417–425.

Jarnevich, C. S., and M. K. Laubhan. 2011. Balancing energy development and conservation: a method utilizing species distribution models. Environmental Management 47:926–936.

Jiguet, F., and V. Bretagnolle. 2006. Manipulating lek size and composition using decoys: an experimental investigation of lek evolution models. American Naturalist 168:758–768.

Johnsgard, P. A. 1994. Arena birds sexual selection and behavior. Smithsonian Institution Press, Washington.

Johnsgard, P. A. 2002. Grassland grouse and their conservation. The Smithsonian Institution, Washington.

Kuletz, K. J., M. C. Ferguson, B. Hurley, A. E. Gall, E. A. Labunski, and T. C. Morgan. 2015. Seasonal spatial patterns in seabird and marine mammal distribution in the eastern Chukchi and western Beaufort seas: Identifying biologically important pelagic areas. Progress in Oceanography 136:175–200.

Lautenbach, J. D. 2017. The role of fire, microclimate, and vegetation in lesser prairie-chicken habitat selection. Thesis, Kansas State University, Manhattan, KS.

Lautenbach, J. M., R. T. Plumb, S. G. Robinson, C. A. Hagen, D. A. Haukos, and J. C. Pitman. 2017. Lesser prairie-chicken avoidance of trees in a grassland landscape. Rangeland Ecology & Management 70:78–86.

Loiselle, B. A., J. G. Blake, R. Durães, T. B. Ryder, W. Tori, and J. H. V. Rivera. 2007. Environmental and spatial segregation of leks among six co-occurring species of manakins (Pipridae) in eastern Ecuador. Auk 124:420–431.

McDonald, L., J. Griswold, T. Rintz, and G. Gardner. 2013. Range-wide population size of the lesser prairie-chicken: 2012 and 2013. West EcoSystems Technology, Inc., Laramie, Wyoming. <http://doi.wiley.com/10.1002/wsb.417>. Accessed 6 May 2020.

McDonald, L., K. Nasman, T. Rintz, F. Hornsby, and G. Gardner. 2016. Range-wide population size of the lesser prairie-chicken: 2012, 2013, 2014, 2015, 2016. West EcoSystems Technology, Inc., Laramie, Wyoming.

McRoberts, J. T., M. J. Butler, W. B. Ballard, H. A. Whitlaw, D. A. Haukos, and M. C. Wallace. 2011. Detectability of lesser prairie-chicken leks: A comparison of surveys from aircraft. Journal of Wildlife Management 75:771–778.

Nasman, K., T. Rintz, R. Clark, G. Gardner, and L. McDonald. 2018. Range-wide population size of the lesser prairie-chicken: 2012 to 2018. West EcoSystems Technology, Inc., Laramie, Wyoming.

Niemuth, N. D. 2000. Land use and vegetation associated with greater prairie-chicken leks in an agricultural landscape. Journal of Wildlife Management 64:278.

NOAA National Centers for Environmental Information. 2011. State of the climate: drought for May 2011. NOAA. <https://www.ncdc.noaa.gov/sotc/drought/201105>. Accessed 30 Jul 2020.

NOAA National Centers for Environmental Information. 2015. State of the climate: national climate report for May 2015. NOAA. <https://www.ncdc.noaa.gov/sotc/national/201505>. Accessed 30 Jul 2020.

Palmer, W. C. 1965. Meteorological drought. U.S. Department of Commerce Weather Bureau, Washington, D.C.

Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. Journal of Wildlife Management 63:1259–1269.

Pitman, J. C., B. E. Jamison, C. A. Hagen, R. J. Robel, and R. D. Applegate. 2006. Brood break-up and juvenile dispersal of lesser prairie-chicken in Kansas. Prairie Naturalist 38:85–99.

Plumb, R. T., J. M. Lautenbach, S. G. Robinson, D. A. Haukos, V. L. Winder, C. A. Hagen, D. S. Sullins, J. C. Pitman, and D. K. Dahlgren. 2019. Lesser prairie-chicken space use in relation to anthropogenic structures. Journal of Wildlife Management 83:216–230.

Pyle, P. 2008. Lesser Prairie-Chicken Tympanuchus pallidicinctus. Pages 195–197 *in*. Identification Guide to North American Birds Part II. Slate Creek Press, Point Reyes Station.

Riley, T. Z. 2004. Private-land habitat opportunities for prairie grouse through federal conservation programs. Wildlife Society Bulletin 32:83–91.

Robinson, S. 2015. Landscape ecology, survival, and space use of lesser prairie-chickens. Thesis, Kansas State University, Manhattan, KS.

Robinson, S. G., D. A. Haukos, R. T. Plumb, C. A. Hagen, J. C. Pitman, J. M. Lautenbach, D. S. Sullins, J. D. Kraft, and J. D. Lautenbach. 2016. Lesser prairie-chicken fence collision risk across its northern distribution. Journal of Wildlife Management 80:906–915.

Robinson, S. G., D. A. Haukos, R. T. Plumb, J. D. Kraft, D. S. Sullins, J. M. Lautenbach, J. D. Lautenbach, B. K. Sandercock, C. A. Hagen, A. Bartuszevige, and M. A. Rice. 2018. Effects of landscape characteristics on annual survival of lesser prairie-chickens. American Midland Naturalist 180:66–86.

Rodgers, R. D. 2016. A history of lesser prairie-chickens. Pages 15–38 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Ross, B. E., D. A. Haukos, C. A. Hagen, and J. C. Pitman. 2016*a*. Landscape composition creates a threshold influencing lesser prairie-chicken population resilience to extreme drought. Global Ecology and Conservation 6:179–188.

Ross, B. E., D. Haukos, C. Hagen, and J. Pitman. 2016*b*. The relative contribution of climate to changes in lesser prairie-chicken abundance. Ecosphere 7. <https://onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1323>. Accessed 6 May 2020.

Ryder, T. B., J. G. Blake, and B. A. Loiselle. 2006. A test of the environmental hotspot hypothesis for lek placement in three species of manakins (Pipridae) in Ecuador. Auk 123:247–258.

Sadoti, G., K. Johnson, and T. P. Albright. 2016. Modelling environmental and survey influences on lek attendance using long-term lek survey data. E. Roskaft, editor. Ibis 158:821–833.

Sandercock, B. K., K. Martin, and G. Segelbacher, editors. 2011. Ecology, conservation, and management of grouse. Studies in Avian Biology No. 39, Cooper Ornithological Society University of California Press, Berkeley.

Shilling, F. M., and D. P. Waetjen. 2015. Wildlife-vehicle collision hotspots at US highway extents: scale and data source effects. Nature Conservation 11:41–60.

Silva, J. P., F. Moreira, and J. M. Palmeirim. 2017. Spatial and temporal dynamics of lekking behaviour revealed by high-resolution GPS tracking. Animal Behaviour 129:197–204.

Smith, J. T., L. D. Flake, K. F. Higgins, G. D. Kobriger, and C. G. Homer. 2005. Evaluating lek occupancy of greater sage-grouse in relation to landscape cultivation in the Dakotas. Western North American Naturalist 65:310–320.

Spencer, D., D. Haukos, C. Hagen, M. Daniels, and D. Goodin. 2017. Conservation reserve program mitigates grassland loss in the lesser prairie-chicken range of Kansas. Global Ecology and Conservation 9:21–38.

Sullins, D. S. 2017. Regional variation in demography, distribution, foraging, and strategic conservation of lesser prairie-chickens in Kansas and Colorado. Dissertation, Kansas State University, Manhattan, KS.

Sullins, D. S., J. D. Kraft, D. A. Haukos, S. G. Robinson, J. H. Reitz, R. T. Plumb, J. M. Lautenbach, J. D. Lautenbach, B. K. Sandercock, and C. A. Hagen. 2018. Demographic consequences of conservation reserve program grasslands for lesser prairie-chickens. Journal of Wildlife Management 82:1617–1632.

Timmer, J. M. 2012. Relationship of lesser prairie-chicken density to landscape characteristics in Texas. Thesis, Texas Tech University, Lubbock, Texas.

Timmer, J. M., M. J. Butler, W. B. Ballard, C. W. Boal, and H. A. Whitlaw. 2013. Abundance and density of lesser prairie-chickens and leks in Texas. Wildlife Society Bulletin 37:741–749.

Weil, B., and B. Jensen. 2015. An unexpected journey: Greater prairie-chicken travels nearly 4000km after translocation to Iowa. American Midland Naturalist 174:343–349.

Westcott, D. A. 1994. Leks of Leks: A Role for Hotspots in Lek Evolution? Proceedings: Biological Sciences 258:281–286.

Widemo, F., and I. P. F. Owens. 1995. Lek size, male mating skew and the evolution of lekking. Nature 373:148–151.

Winder, V. L., A. J. Gregory, L. B. McNew, and B. K. Sandercock. 2015. Responses of male greater prairie-chickens to wind energy development. Condor 117:284–296.

Wittenberger, J. F. 1978. The evolution of mating systems in grouse. Condor 80:126.

Wolfe, D. H., M. A. Patten, E. Shochat, C. L. Pruett, and S. K. Sherrod. 2007. Causes and patterns of mortality in lesser prairie-chickens Tympanuchus pallidicinctus and implications for management. Wildlife Biology 13:95–104.

Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie, and J. Shackford. 2001. Influence of landscape composition and change on lesser prairie-chicken (Tympanuchus pallidicinctus) populations. American Midland Naturalist 145:261–274.

Figures

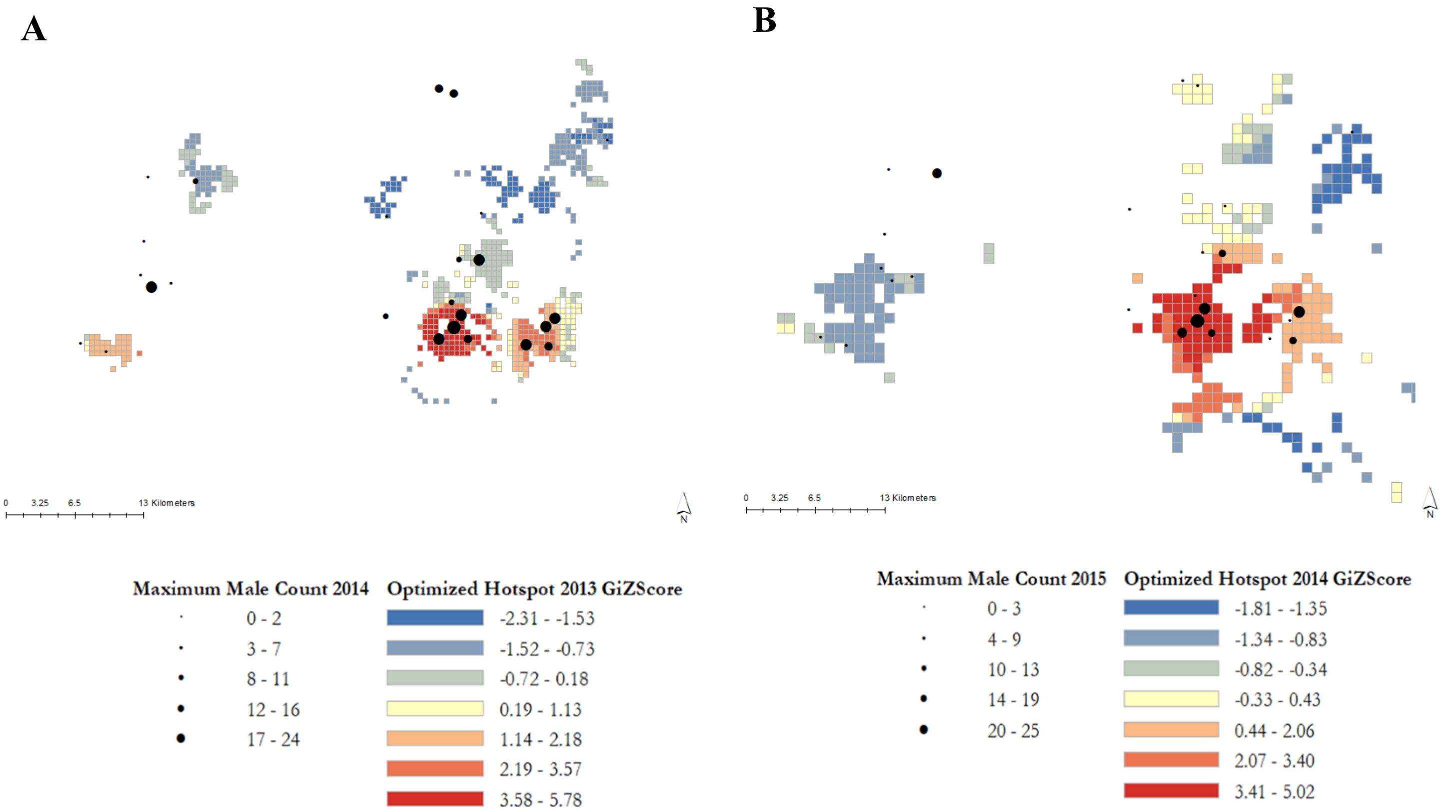

Figure 2.1 Female lesser prairie-chicken spatial location concentrations from the optimized hotspot tool for the Northwest field site, located in Kansas Short-Grass Prairie/CRP Mosaic Ecoregion.

Fishnet polygon cell size for 2013 (A) was 933 m, with an optimal fixed distance of 7664.91 m, and 376 weighted polygons ($\bar{x} = 93.05$, SD = 297.93). Fishnet polygon cell size for 2014 (B) was 500 m, with an optimal fixed distance of 3741.76 m, and 608 weighted polygons ($\bar{x} = 41.16$, SD = 97.03). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. Points indicate maximum male observed numbers at leks from 2014 (A) and 2015 (B), with increasing size indicative of increasing numbers of observed males displaying at that site. To examine the influence of female space use prior to the season, leks are plotted over lag points from the year prior to the observation data. Large leks are primarily located in areas of greatest female spatial locations and as female movements concentrate in previously warm areas, those leks are maintained while those in previously cool areas disappear or shrink in size.

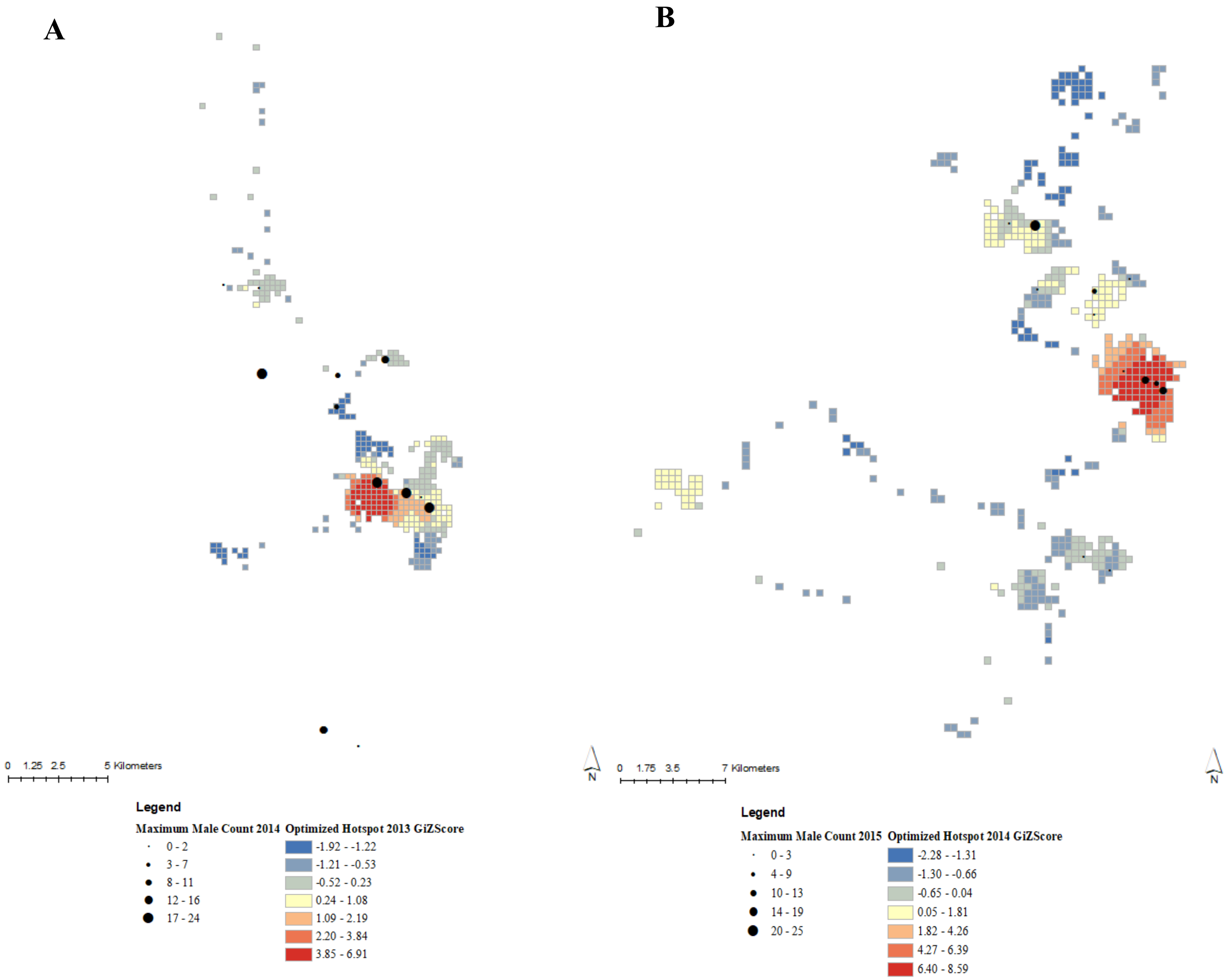

Figure 2.2 Female lesser prairie-chicken spatial location concentrations from the optimized hotspot tool for the Red Hills field site, in the Mixed-Grass Prairie Ecoregion of Kansas.

Fishnet polygon cell size for 2013 (A) was 269 m, with an optimal fixed distance of 1139.32 m, and 340 weighted polygons ($\bar{x} = 41.17$, SD = 82.96). Fishnet polygon cell size for 2014 (B) was 449 m, with an optimal fixed distance of 2743.0 m, and 471 weighted polygons ($\bar{x} = 43.41$, SD = 96.49). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. Points indicate maximum male observed numbers at leks from 2014 (A) and 2015 (B), with increasing size indicative of increasing numbers of observed males displaying at that site. To examine the influence of female space use prior to the season, leks are plotted over lag points from the year prior to the observation data. Large leks are primarily located in areas of greatest female spatial locations and as female movements concentrate in previously warm areas, those leks are maintained while those in previously cool areas disappear or shrink in size.

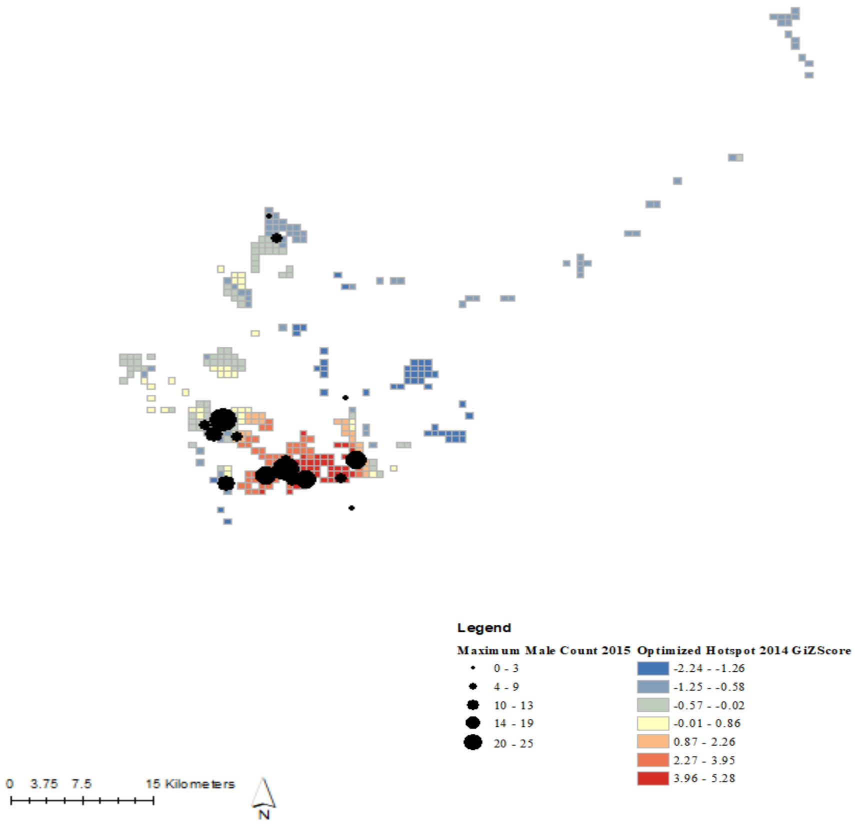

Figure 2.3 Female lesser prairie-chicken spatial location concentrations from the optimized hotspot tool for the Ashland field site, the second of two sites in the Mixed-Grass Prairie Ecoregion of Kansas.

Fishnet polygon cell size for 2014 was 729 m, with an optimal fixed distance of 7068.20 m, and 363 weighted polygons ($\bar{x}$ = 69.08, SD = 169.09). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. Points indicate maximum male observed numbers at leks from 2014, with increasing size indicative of increasing numbers of observed males displaying at that site. To examine the influence of female space use prior to the season, leks are plotted over lag points from the year prior to the observation data. Large leks are primarily located in areas of greatest female spatial locations and as female movements concentrate in previously warm areas, those leks are maintained while those in previously cool areas disappear or shrink in size.

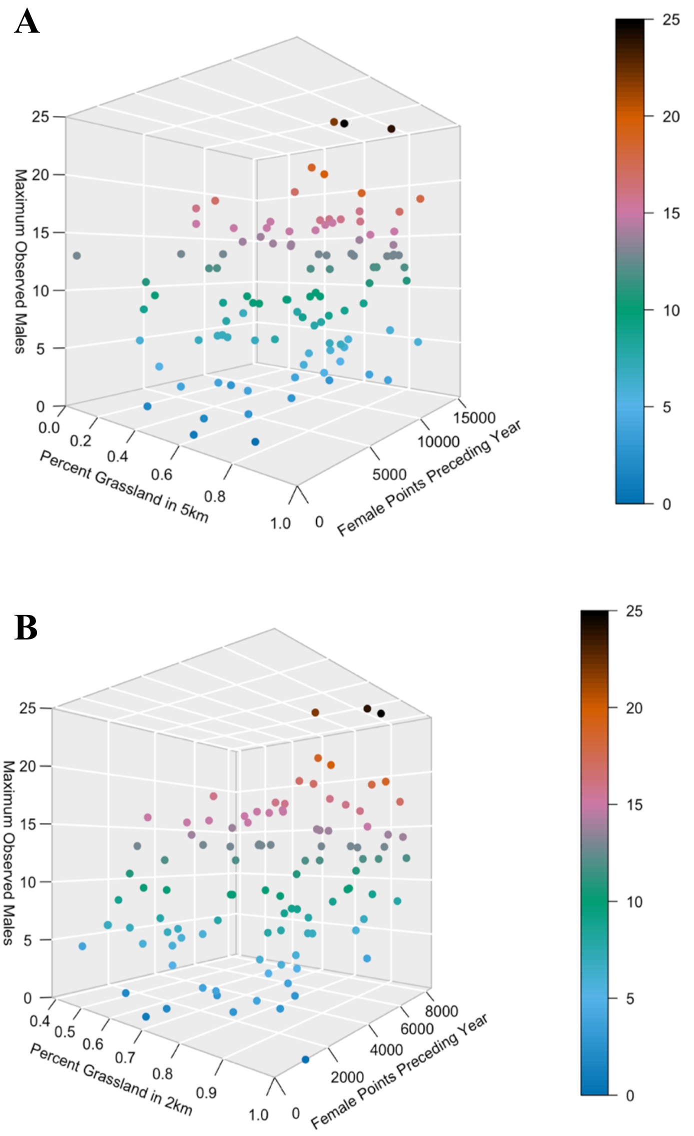

Figure 2.4 For lesser prairie-chickens monitored in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie Ecoregions of Kansas from 2013-2016, there is a three-way relationship between the number of female points, the amount of grassland, and the maximum number of males observed.

This relationship is evident starting at 5 km (A) and persists closer to the lek at 2 km (B). It is also notable that even when the amount of grassland within that distance is small, increasing male numbers still closely follow increasing female points from the prior year.

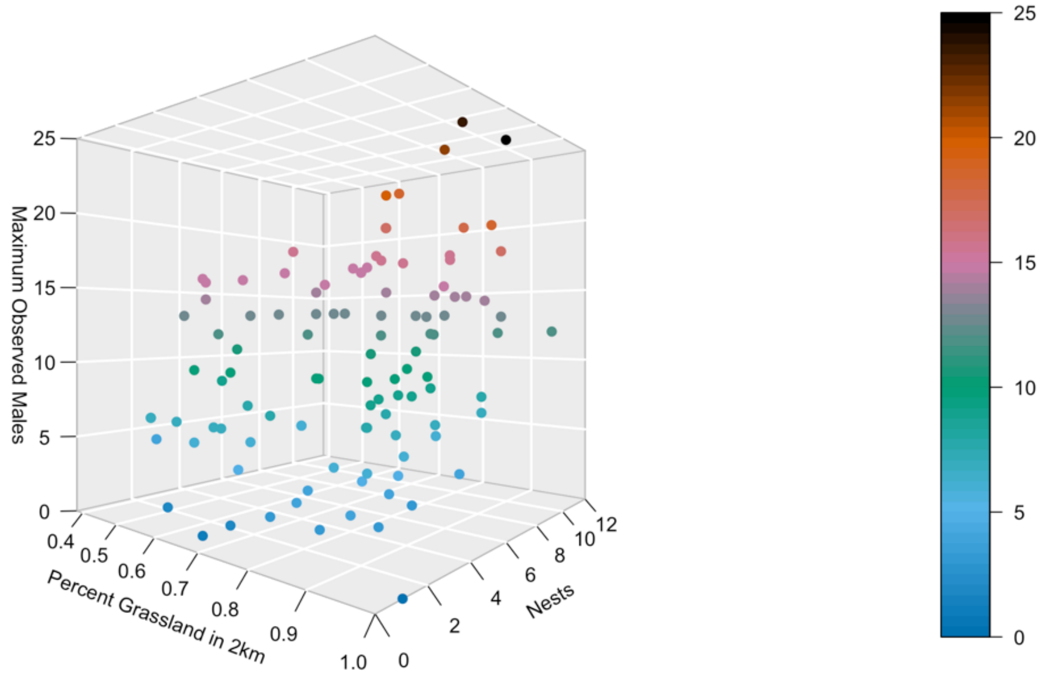

Figure 2.5 For lesser prairie-chickens monitored in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie Ecoregions of Kansas from 2013-2016, there is a three-way relationship between the percent of grassland, maximum observed male numbers, and the number of nesting attempts within a 2 km buffer.

Even with decreasing grassland, maximum males track closely with the number of previous nesting attempts. This suggests that it is likely not the quantity of grassland that matters as much as the quality of nesting habitat.

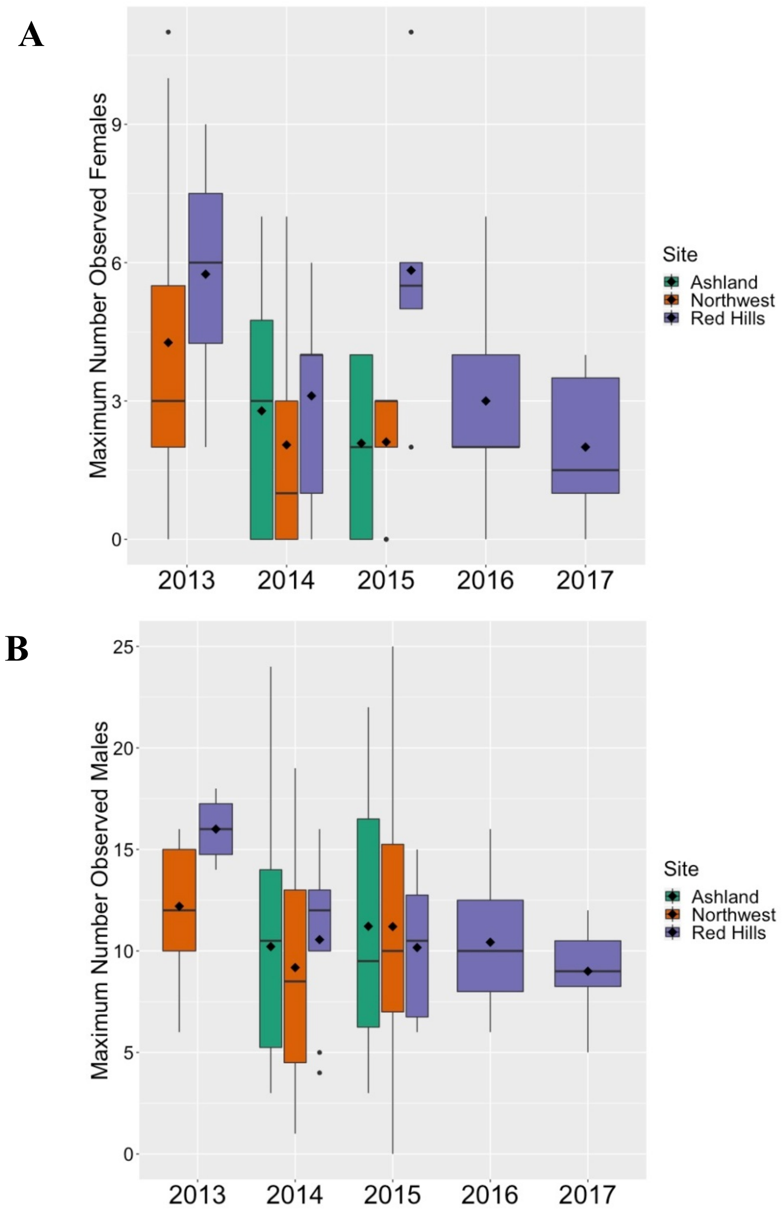

Figure 2.6 Maximum observed lesser prairie-chicken females (A) and males (B) by year (2013-2017) and Kansas field site.

Averages indicated by points, median by the boxplot line. Maximum observed numbers are greatest in the Mixed-Grass Prairie Red Hills field site for females, while the second Mixed-Grass Prairie site, Ashland, and the Short-Grass Prairie Northwest field site has the greatest range of maximum observed males. While maximum observed numbers decline at the Red Hills study area, it is unclear if this reflects a significant population decline.

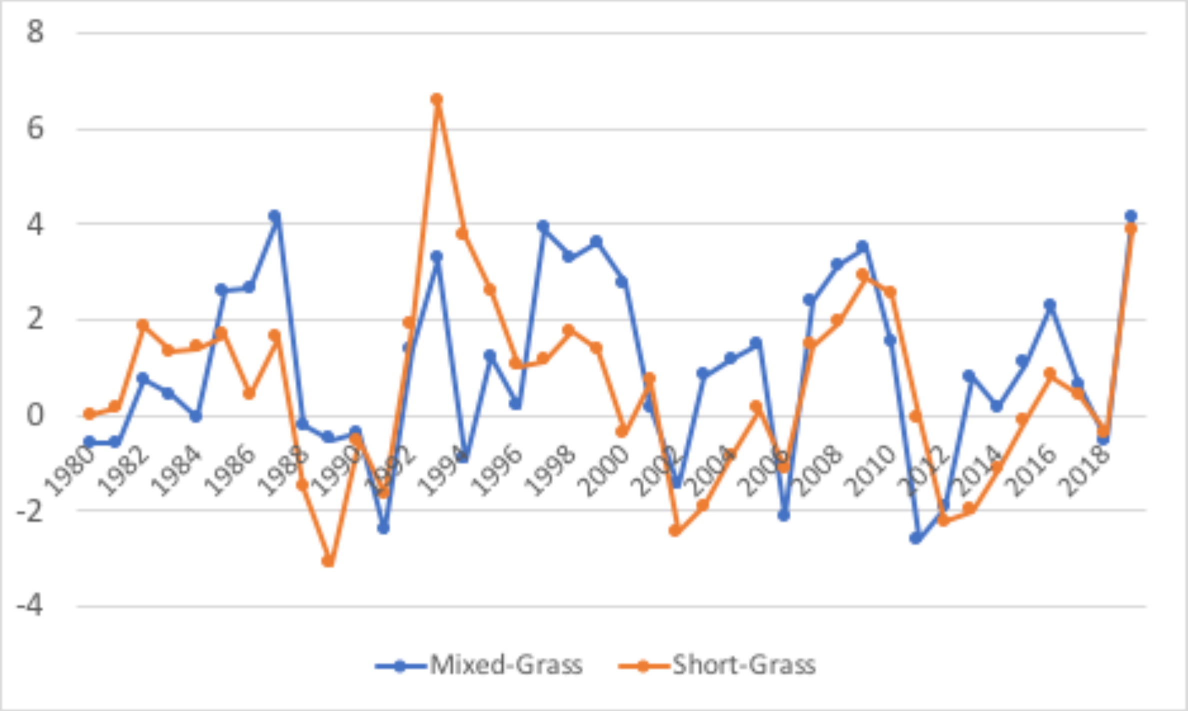

Figure 2.7 Average annual Palmer Drought Severity Index (PDSI) by lesser prairie-chicken ecoregion.

Mixed-Grass Prairie and Short-Grass Prairie/CRP Mosaic ecoregions, as part of the Great Plains are subject to drought on 5-year cycles. Mixed-Grass Prairie had a greater annual PDSI in 2014 than Short-Grass Prairie, which received more precipitation in 2015.

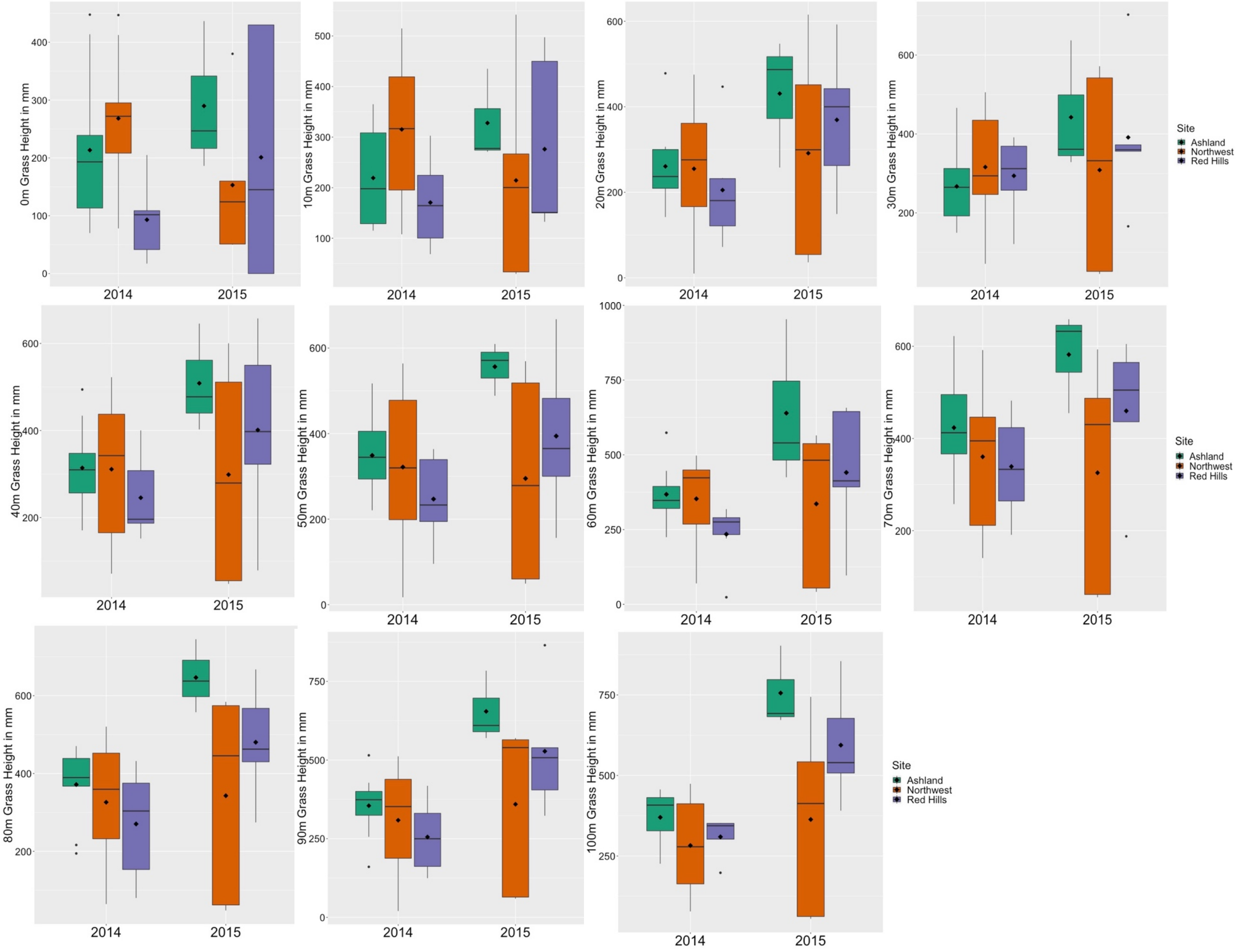

Figure 2.8 Grass height (mm) by year (2014-2015) and field site across all 11 recorded distances (0 m-100 m) of lesser prairie-chicken lek vegetation measurement in Kansas. The Mixed-Grass Prairie Ecoregion sites, Ashland and Red Hills, both have notably greater grass heights in 2015 following the increased Palmer Drought Severity Index values of 2014 compared to the Short-Grass Prairie/CRP Mosaic Ecoregion site.

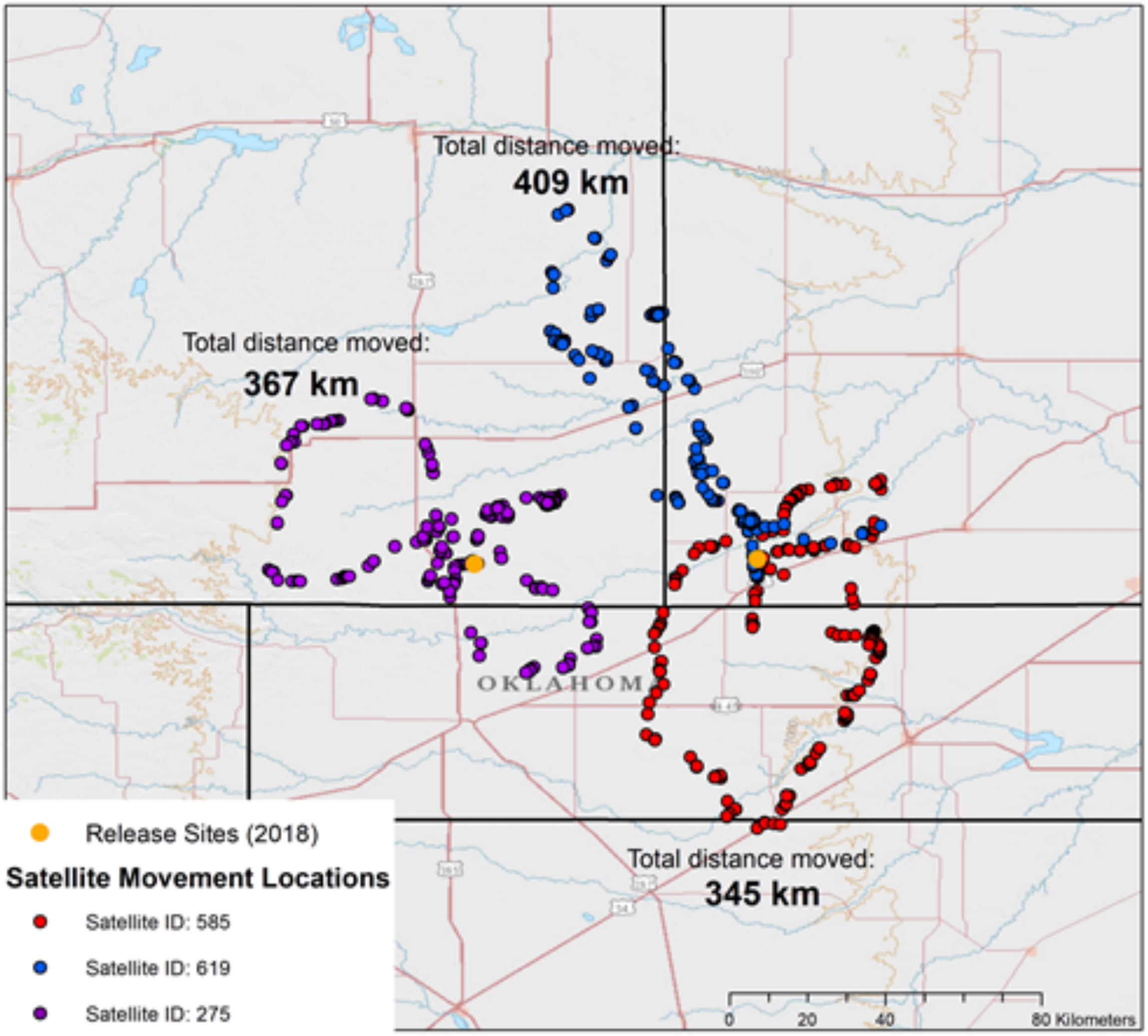

Figure 2.9 Examples of long-distance movements by female lesser prairie-chickens after translocation from the Short-Grass Prairie/CRP Mosaic Ecoregion to the Sand Sagebrush Ecoregion of southwestern Kansas in 2018.

Lesser prairie-chicken females are capable of dispersing long distances, implicating that females are the colonizing sex in lesser prairie-chickens and this drives the formation and persistence of leks on the landscape. Figure produced by Berigan (2019).

Tables

Table 2.1 The number of lesser prairie-chicken data records collected at three field sites in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Ecoregions of Kansas from 2013-2017.

Number of data records by field site for each portion of the analyses. Lek vegetation survey data was collected from 2014-2015 during the study. Data from the Ashland site was acquired from 2014-2015, giving Ashland fewer overall data points compared to the Northwest and Red Hills sites.

	Northwest (Short-Grass)	Red Hills (Mixed-Grass)	Ashland (Mixed-Grass)	Total
Number leks	24	12	17	53
GPS-tagged females	69	42	32	143
Lek counts	47	32	28	107
Lek vegetation surveys	19	11	13	43

Table 2.2 Number of lesser prairie-chicken nesting attempts for females tracked in Short-Grass Prairie/CRP Mosaic and Mixed-Grass Ecoregions of Kansas from 2013-2017.

All nest attempts were located by tracking GPS movements and only represent females equipped with rump-mounted SAT-PTT tags.

Site	2013	2014	2015	2016	2017
Ashland		18	14		
Northwest	15	30	17		
Red Hills	11	26	13	16	7

Appendix B - Supplemental Figures and Tables

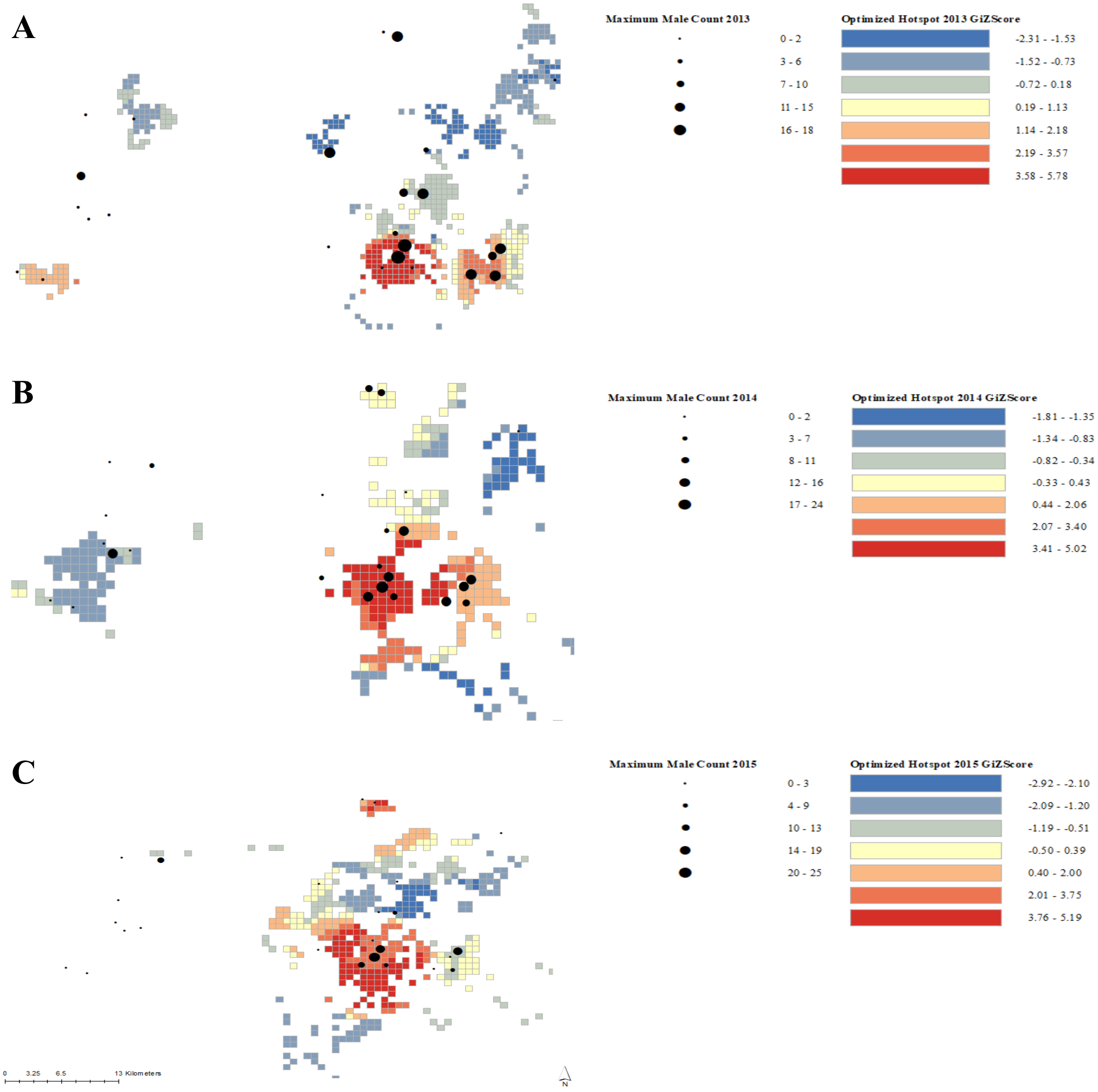

Figure B.1 Optimized hot sport maps of female spatial locations and changes in number of attending males at leks within the same year for the North Western field site in Short-Grass prairie from 2013-2015.

Fishnet polygon cell size for 2013 (A) was 269 m, with an optimal fixed distance of 1139.32 m, and 340 weighted polygons ($\overline{x}$ = 41.17, SD = 82.96). Fishnet polygon cell size for 2014 (B) was 449 m, with an optimal fixed distance of 2743.0 m, and 471 weighted polygons ($\overline{x}$ = 43.4,1 SD = 96.49). Fishnet polygon cell size for 2015 (C) was 802 m, with an optimal fixed distance of 6927.22 m, and 511 weighted polygons ($\overline{x}$ = 51.55, SD = 141.81). In 2013 (A) female space use begins to concentrate towards the center of the study site, causing expansion of existing leks and formation of new ones in 2014 (B) and in 2015 (C), the only large leks remaining on the landscape are those with concentrated points in the year prior. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering.

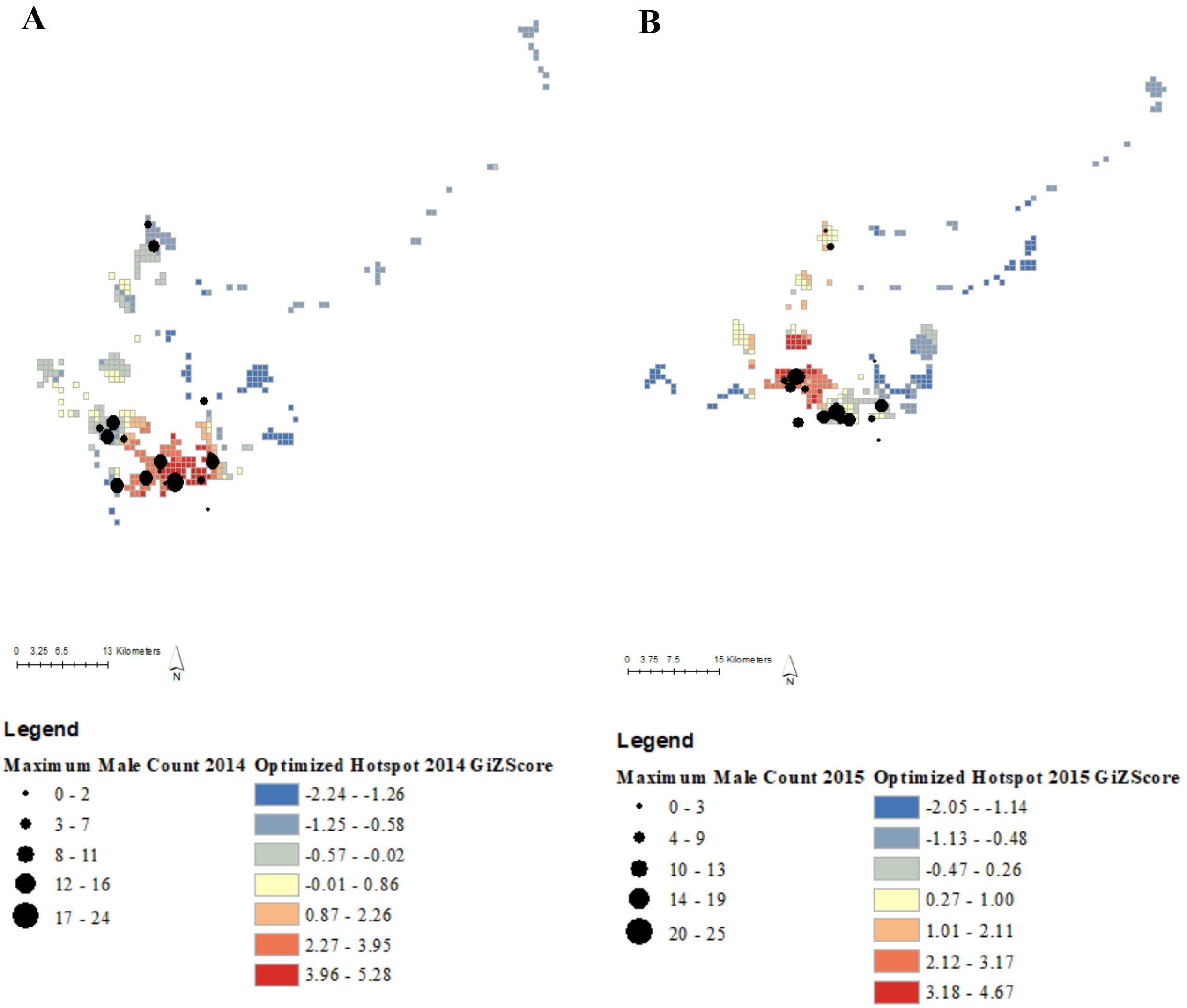

Figure B.2 Optimized hot sport maps of female spatial locations and changes in number of attending males at leks within the same year for the Ashland field site in Kansas Mixed-Grass Prairie from 2014-2015.

Between 2014 (A) female space use shifted, resulting in new lek formation in 2015 (B). Large leks are primarily located in areas of greatest female spatial locations. Fishnet polygon cell size for 2014 (A) was 729 m, with an optimal fixed distance of 7068.20 m, and 363 weighted polygons ($\bar{x}$ = 69.08, SD = 169.09). Fishnet polygon cell size for 2015 (B) was 857 m, with an optimal fixed distance of 7250.48 m, and 320 weighted polygons ($\bar{x}$ = 85.45, SD=187.74). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering.

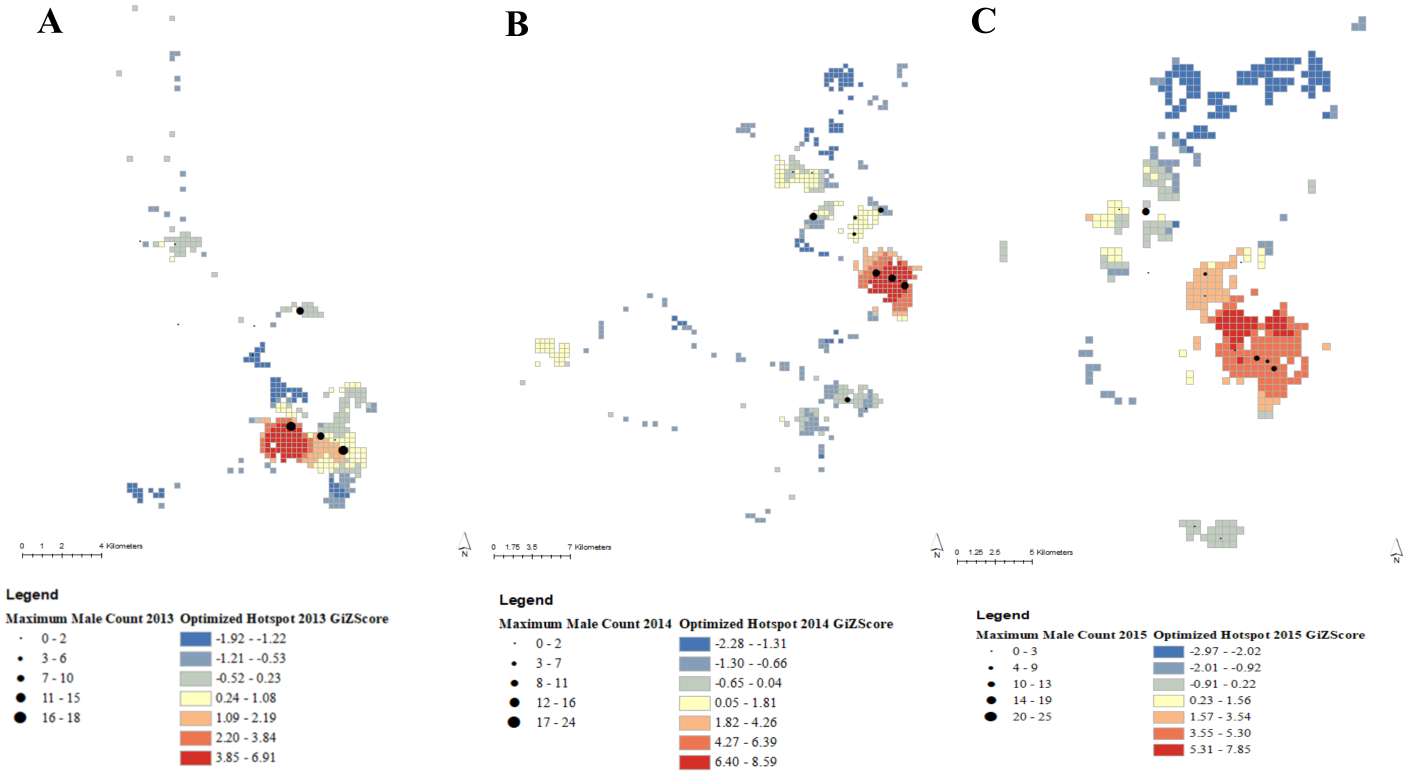

Figure B.3 Optimized hot sport maps of female spatial locations and changes in number of attending males at leks within the same year for the Red Hill field site in Kansas Mixed-Grass Prairie from 2013-2015.

Fishnet polygon cell size for 2013 (A) was 269 m, with an optimal fixed distance of 1139.32 m, and 340 weighted polygons ($\bar{x}$ = 41.17, SD=82.96). Fishnet polygon cell size for 2014 (B) was 449 m, with an optimal fixed distance of 2743.0 m, and 471 weighted polygons ($\bar{x}$ = 43.41, SD=96.49). Fishnet polygon cell size for 2015 (C) was 479 m, with an optimal fixed distance of 3872.46 m, and 420 weighted polygons ($\bar{x}$ = 46.08, SD=92.98). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. Female space use concentrated around central leks in 2013 (A) and 2014 (B). By 2015 (C) smaller leks in areas with female locations that were not statistically significant had collapsed.

Table B.1 Linear model selection of maximum number of lesser prairie-chicken males observed displaying at leks by spatial scale for lek data collected from 2013-2017 in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie Ecoregions of Kansas.

Anthropogenic features drop from top models, leaving land cover and female spatial use as model terms.

			10 km					
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Percent Grassland + Lag Female Points + Prior Nest	0.07	0.04	2.21	3, 84	544.46	0	0.61	0.09
Percent Grassland + Lek + Lag Female Points + Prior Nest	0.08	0.04	1.86	4, 83	545.92	1.47	0.29	0.13
Percent Grassland + Lek + Lag Female Points + Prior Nest + PDSI	0.08	0.03	1.49	5, 82	548.17	3.71	0.09	0.20
Percent Grassland + Lek + Lag Female Points + Prior Nest +PDSI + Year	0.11	0.02	1.18	8, 79	553.38	8.92	0.01	0.32
Percent Grassland + Lek + Lag Female Points + Prior Nest + PDSI + Site + Year	0.13	0.02	1.18	10, 77	555.40	13.77	0	0.32
Percent Grassland + Lek + Lag Female Points + Prior Nest + PDSI + Oil Wells + Site + Year	0.14	0.01	1.11	11, 76	557.46	11.63	0	0.36
Percent Grassland + Lek + Lag Female Points + Prior Nest + Road Length + PDSI + Oil Wells + Site + Year	0.14	0.01	1.05	12, 75	559.68	16.06	0	0.41
Percent Grassland + Lek + Lag Female Points + Cell Tower + Prior Nest + Road Length + PDSI + Oil Wells + Site + Year	0.16	0.001	1.04	13, 74	561.35	17.81	0	0.42
Percent Grassland + Lek + Lag Female Points + Cell Tower+ Prior Nest + Road Length + Electric Length + PDSI + Oil Wells + Site + Year	0.16	-0.01	0.96	14, 73	564.25	20.79	0	0.50
Percent Grassland +Lek +Lag Female Points +Cell Tower+ Nest+ Prior Nest + Road Length+ Electric Length+ PDSI+ Oil Wells+ Site+ Year	0.16	-0.02	0.88	15, 72	568.32	23.86	0	0.59

Table B.1 Continued

				5 km				
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Percent Grassland + Cell Tower + Nest + Prior Nest + Road Length + Oil Wells	0.16	0.10	2.65	6, 81	542.49	0	0.70	0.02
Percent Grassland + Cell Tower + Nest + Prior Nest + Road Length + Electric Length + Prior Wells	0.16	0.09	2.25	7, 80	544.90	2.40	0.21	0.04
Percent Grassland + Lek + Cell Tower + Nest + Prior Nest + Road Length + Electric Length + Oil Wells	0.17	0.08	1.96	8, 79	547.33	4.84	0.06	0.06
Percent Grassland + Lek + Lag Female Points + Cell Tower +Nest + Prior Nest + Road Length + Electric Length + Oil Wells	0.17	0.07	1.72	9, 78	549.94	7.45	0.02	0.10
Percent Grassland + Lek+ Lag Female Points + Cell Tower+ Nest + Prior Nest + Road Length + Electric Length + PDSI + Oil Wells	0.17	0.06	1.53	10, 77	552.63	10.13	0	0.14
Percent Grassland + Lek + Lag Female Points + Cell Tower + Nest + Prior Nest + Road Length + Electric Length + PDSI + Oil Wells + Site	0.17	0.04	1.28	12, 75	557.81	15.32	0	0.25
Percent Grassland +Lek +Lag Female Points+ Cell Tower+ Nest+ Prior Nest+ Road Length+ Electric Length+ PDSI+ Oil Wells+ Site +Year	0.18	0.01	1.05	15, 72	565.69	23.30	1.0	0.41
Nest	0.12	0.12	14.93	1, 105	641.90	99.40	0	P<0.001
Nest + Prior Wells	0.13	0.11	7.61	2, 104	643.67	101.18	0	P<0.001
Nest + Road Length + Oil Wells	0.13	0.11	5.19	3, 103	645.43	102.93	0	P<0.001
Cell Tower + Nest + Road Length + Oil Wells	0.14	0.10	4.00	4, 102	647.15	104.66	0	P<0.001
Percent Grassland + Cell Tower + Nest + Road Length + Oil Wells	0.14	0.09	3.19	5, 101	649.35	106.86	0	0.01

Table B.1 Continued

2 km								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Percent Grassland + Nest + Prior Nest + PDSI + Oil Wells	0.18	0.13	3.64	5, 82	538.18	0	0.67	0.01
Percent Grassland + Lek + Nest + Prior Nest + PDSI + Oil Wells	0.18	0.12	3.04	6, 81	540.35	2.17	0.23	0.01
Percent Grassland + Lek + Nest + Prior Nest +Electric Length + PDSI + Oil Wells	0.19	0.12	2.62	7, 80	542.57	4.39	0.07	0.02
Percent Grassland + Lek + Nest + Prior Nest +Road Length + Electric Length + PDSI + Oil Wells	0.19	0.11	2.29	8, 79	544.95	6.77	0.02	0.03
Percent Grassland + Lek + Lag Female Points + Nest + Prior Nest + Road Length +Electric Length + PDSI + Oil Wells	0.19	0.10	2.02	9, 78	547.44	9.27	0.01	0.05
Percent Grassland + Lek + Lag Female Points + Nest + Prior Nest + Road Length + Electric Length + PDSI + Oil Wells + Site	0.20	0.09	1.76	11, 76	551.39	13.21	0	0.08
Percent Grassland+ Lek+ Lag Female Points+ Nest+ Prior Nest+ Road Length+ Electric Length+ PDSI+ Oil Wells+ Site+ Year	0.21	0.06	1.36	14, 73	559.65	21.47	0	0.19
Percent Grassland + Nest + PDSI	0.18	0.16	7.62	3, 103	639.03	100.85	0	P<0.001
Percent Grassland + Nest + PDSI + Oil Wells	0.19	0.16	5.98	4, 102	640.18	102.01	0	P<0.001
Percent Grassland + Nest	0.14	0.13	8.76	2, 104	641.63	103.45	0	P<0.001

Table B.1 Continued

				1 km				
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Percent Grassland + Lek + Lag Female Points	0.07	0.04	2.10	3, 84	544.79	0	0.60	0.11
Percent Grassland + Lek + Lag Female Points + Nest	0.08	0.03	1.72	4, 83	546.45	1.67	0.26	0.15
Percent Grassland + Lek + Lag Female Points + Nest + Oil Wells	0.08	0.02	1.44	5, 82	548.44	3.65	0.03	0.22
Percent Grassland + Lek + Lag Female Points + Nest + PDSI + Oil Wells	0.08	0.01	1.22	6, 81	550.64	5.85	0.03	0.31
Percent Grassland + Lek + Lag Female Points+ Nest + Prior Nest + PDSI +Oil Wells + Site	0.09	-0.01	0.86	9, 77	552.27	7.49	0.01	0.56
Percent Grassland + Lek + Lag Female Points+ Nest + Prior Nest + PDSI + Oil Wells + Site + Year	0.10	-0.05	0.68	12, 74	559.85	15.06	0	0.77
Percent Grassland + Lek + Lag Female Points+ Nest + Prior Nest +Road Length + PDSI + Oil Wells + Site + Year	0.10	-0.06	0.62	13, 73	561.83	17.97	0	0.83

Table B.2 Linear model selection of maximum number of lesser prairie-chicken females observed at leks by spatial scale for lek data collected from 2013-2017 in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie Ecoregions of Kansas.

Linear model selection of maximum number of lesser prairie-chicken females observed at leks by spatial scale for lek data collected from 2013-2017 in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie Ecoregions of Kansas. Anthropogenic features drop from best fit models, leaving land cover and female spatial use as model terms. Female lesser prairie-chickens have been shown to avoid anthropogenic features, so it may be that these attributes are represented in female movements.

			10 km					
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Lag Female Points + Site + Year	0.16	0.10	2.49	6, 77	378.85	0	0.57	0.03
Lag Female Points +Cell Tower + Site + Year	0.17	0.10	2.25	7, 76	380.44	1.58	0.26	0.04
Lag Female Points+ Cell Tower+ Oil Wells + Site + Year	0.18	0.09	2.05	8, 75	382.17	3.32	0.11	0.05
Lag Female Points + Cell Tower+ Electric Length + Oil Wells + Site + Year	0.19	0.09	1.90	9, 74	383.97	5.12	0.04	0.06
Lag Female Points + Cell Tower + Road Length + Electric Length + Oil Wells + Site + Year	0.19	0.08	1.74	10, 73	386.22	7.36	0.01	0.09
Lag Female Points +Cell Tower+ Nest+ Road Length+ Electric Length+ Oil Wells+ Site+ Year	0.20	0.07	1.59	11, 72	388.70	9.84	0	0.12
Lag Female Points+ Cell Tower + Nest + Road Length + Electric Length + PDSI + Oil Wells + Site + Year	0.20	0.06	1.44	12, 71	391.55	12.70	0	0.17
Percent Grassland + Lag Female Points + Cell Tower+ Nest + Road Length + Electric Length + PDSI + Oil Wells + Site + Year	0.20	0.05	1.32	13, 70	394.49	15.63	0	0.22
Percent Grassland + Lag Female Points + Cell Tower + Nest + Prior Nest + Road Length + Electric Length + PDSI + Oil Wells + Site + Year	0.20	0.03	1.21	14, 69	397.52	18.67	0	0.29
Percent Grassland+ Lek +Lag Female Points+ Cell Tower+ Nest+ Prior Nest+ Road Length+ Electric Length+ PDSI+ Oil Wells+ Site+ Year	0.20	0.02	1.11	15, 68	400.66	21.80	0	0.36

Table B.2 Continued

			5 km					
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Lag Female Points + Prior Nest + PDSI + Site	0.14	0.08	2.50	5, 78	378.77	0	0.42	0.04
Lag Female Points + Cell Tower + Prior Nest + PDSI + Site	0.16	0.09	2.36	6,77	379.54	0.76	0.29	0.04
Lag Female Points + Cell Tower + Nest + Prior Nest + PDSI + Site	0.17	0.09	2.21	7, 76	380.68	1.91	0.16	0.04
Lek + Lag Female Points + Cell Tower + Nest + Prior Nest + PDSI + Site	0.18	0.09	2.07	8, 75	382.05	3.28	0.08	0.05
Lek + Lag Female Points + Cell Tower + Nest + Prior Nest + Road Length + PDSI + Site	0.19	0.09	1.89	9, 74	384.06	5.28	0.03	0.07
Percent Grassland + Lek + Lag Female Points + Cell Tower+ Nest + Prior Nest + Road Length + PDSI + Site	0.19	0.08	1.72	10, 73	386.40	7.62	0.01	0.09
Percent Grassland + Lek + Lag Female Points + Cell Tower + Nest + Prior Nest + Road Length + Electric Length + PDSI + Site	0.19	0.07	1.58	11, 72	388.85	10.08	0	0.12
Percent Grassland + Lek + Lag Female Points + Cell Tower+ Nest + Prior Nest + Road Length + Electric Length + PDSI + Prior Wells + Site	0.20	0.06	1.45	12, 71	391.50	12.73	0	0.17
Percent Grassland + Lek + Lag Female Points + Cell Tower+ Nest + Prior Nest + Road Length + Electric Length + PDSI + Prior Wells + Site + Year	0.21	0.04	1.22	15, 68	398.96	20.19	0	0.27

Table B.2 Continued

2 km

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
PDSI + Site	0.10	0.06	2.29	4, 79	379.67	0	0.45	0.07
Prior Nest + PDSI + Site	0.12	0.06	2.08	5, 78	380.78	1.10	0.26	0.08
Lag Female Points + Prior Nest + PDSI + Site	0.13	0.07	1.97	6, 77	381.75	2.07	0.16	0.08
Lag Female Points + Nest + Prior Nest + PDSI + Site	0.14	0.07	1.83	7, 76	383.18	3.50	0.08	0.09
Percent Grassland + Lag Female Points + Nest + Prior Nest + PDSI + Site	0.15	0.06	1.71	8, 75	384.78	5.10	0.04	0.11
Percent Grassland + Lag Female Points + Nest + Prior Nest + PDSI + Oil Wells + Site	0.16	0.06	1.57	9, 74	386.80	7.13	0.01	0.14
Percent Grassland + Lag Female Points +Nest + Prior Nest + Electric Length + PDSI + Oil Wells + Site	0.16	0.05	1.42	10, 73	389.27	9.59	0	0.19
Percent Grassland + Lek + Lag Female Points + Nest + Prior Nest + Road Length + Electric Length + PDSI + Oil Wells + Site + Year	0.18	0.01	1.05	14, 69	399.70	20.03	0	0.42
Site	0.04	0.02	2.01	2, 100	489.21	109.53	0	0.14

1 km

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Prior Nest + Percent Grassland	0.07	0.05	3.20	2, 80	374.37	0	0.46	0.05
Prior Nest	0.04	0.03	3.50	1, 81	375.04	0.67	0.33	0.07
Prior Nest+ PDSI +Oil Wells+ Site	0.12	0.06	2.10	5,77	377.11	2.74	0.12	0.07
Percent Grassland+ Prior Nest +PDSI +Oil Wells+ Site	0.13	0.06	1.85	6, 76	378.89	4.52	0.05	0.10
Percent Grassland+ Lag Female Points + Prior Nest + PDSI +Oil Wells+ Site	0.13	0.05	1.64	7, 75	380.90	6.53	0.02	0.14
Percent Grassland+ Lag Female Points + Prior Nest +Road Length+ PDSI +Oil Wells+ Site	0.13	0.04	1.44	8, 74	383.32	8.95	0.01	0.20
Percent Grassland +Lag Female Points+ Nest+ Prior Nest+ Road Length+ PDSI +Oil Wells+ Site+	0.14	0.03	1.27	9, 73	385.90	11.53	0	0.27
Percent Grassland+ Lag Female Points+ Nest+ Prior Nest+ Road Length+ PDSI+ Oil Wells+ Site+ Year	0.17	0.02	1.17	12, 70	391.28	16.91	0	0.32
PDSI + Site	0.10	0.07	3.74	3, 99	484.43	110.06	0	0.01
PDSI+ Oil Well+ Site	0.10	0.07	2.78	4, 98	486.68	112.31	0	0.03

Table B.3 Linear model selection of maximum number of lesser prairie-chicken males displaying at leks from 2014-2015 by lek vegetation characteristics by 10 m distance of measurement in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie Ecoregions of Kansas.

Grass height and visual obstruction are reoccurring significant model terms.

0 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site + Grass Height + Percent Grass	0.27	0.17	2.73	5, 37	263.25	0	0.72	0.03
Year + Site + Grass Height + Percent Grass + Percent Forb	0.28	0.16	2.30	6, 36	265.81	2.56	0.20	0.06
Year + Site + Grass Height + Percent Grass + Percent Forb + Percent Litter	0.29	0.15	2.08	7, 35	268.06	4.81	0.06	0.07
Year + Site + Grass Height + Litter Depth + Percent Grass + Percent Forb + Percent Litter	0.30	0.13	1.79	8, 34	271.27	8.02	0.01	0.11
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.30	0.11	1.58	9, 33	274.67	11.43	0	0.16
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.30	0.09	1.40	10, 32	278.32	15.07	0	0.22

10 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site + Grass Height + Litter Depth + Percent Shrub	0.36	0.25	3.39	6, 36	260.53	0	0.70	0.01
Year + Site + Grass Height + Litter Depth + Percent Grass + Percent Shrub	0.38	0.25	3.00	7, 35	262.76	2.24	0.23	0.01
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Shrub	0.38	0.24	2.63	8, 34	265.68	5.15	0.05	0.02
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Shrub	0.39	0.23	2.39	9, 33	268.50	7.98	0.01	0.03
Year+ Site+ Grass Height+ Litter Depth+ Robel+ Percent Grass+ Percent Forb+ Percent Litter+ Percent Shrub	0.39	0.21	2.09	10, 32	272.33	11.81	0.0	0.06

Table B.3 Continued

20 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Grass Height + Litter Depth + Robel+ Percent Shrub	0.35	0.27	4.04	5, 37	258.01	0	0.65	0.01
Year + Grass Height + Litter Depth + Robel + Percent Forb + Percent Shrub	0.37	0.27	3.56	6, 36	259.73	1.72	0.27	0.01
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Shrub	0.38	0.25	3.03	7, 35	262.62	4.61	0.06	0.01
Year + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.38	0.24	2.62	8, 34	265.76	7.75	0.01	0.02
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.41	0.22	2.21	10, 32	271.36	13.35	0	0.04

30 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**Δ AIC_c**	**w_i**	**P**
Year + Site + Robel	0.19	0.12	3.00	3, 39	262.23	0	0.64	0.04
Year + Site + Robel + Percent Forb	0.20	0.12	2.43	4, 38	264.08	1.84	0.25	0.06
Year + Site + Litter Depth + Robel + Percent Forb	0.21	0.11	2.01	5, 37	266.40	4.17	0.08	0.10
Year + Site + Grass Height + Litter Depth + Robel + Percent Forb	0.22	0.09	1.71	6, 36	269.00	6.77	0.02	0.15
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb	0.23	0.08	1.51	7, 35	271.64	9.41	0.01	0.20
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Shrub	0.24	0.06	1.32	8, 34	274.81	12.57	0	274.81
Year+ Site+ Grass Height+ Litter Depth+ Robel+ Percent Grass+ Percent Forb+ Percent Litter+ Percent Shrub	0.24	0.00	0.24	10,32	282.24	20.01	0	0.46

Table B.3 Continued

40 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Robel + Percent Grass	0.22	0.16	3.63	3, 39	260.57	0	0.76	0.02
Year + Site + Robel + Percent Grass	0.26	0.17	2.66	5, 37	263.53	2.96	0.17	0.04
Year + Site + Robel + Percent Grass + Percent Shrub	0.27	0.15	2.26	6, 36	266.01	5.44	0.05	0.06
Year + Site + Litter Depth + Robel + Percent Grass + Percent Shrub	0.28	0.14	1.94	7, 35	268.89	8.32	0.01	0.09
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Shrub	0.28	0.12	1.69	8, 34	272.01	11.44	0.0	0.14
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Litter + Percent Shrub	0.29	0.09	1.46	9, 33	275.60	15.03	0.0	0.20
Year + Site + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.29	0.06	1.29	10, 32	279.40	18.83	0	0.28

50 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site + Litter Depth	0.23	0.15	2.86	4, 38	262.56	0	0.61	0.04
Year + Site + Grass Height + Litter Depth	0.25	0.15	2.43	5, 37	264.54	1.98	0.23	0.05
Year + Site + Grass Height + Litter Depth + Percent Shrub	0.27	0.15	2.24	6, 36	266.14	3.58	0.10	0.06
Year + Site + Grass Height + Litter Depth + Percent Forb + Percent Shrub	0.30	0.16	2.13	7, 35	267.70	5.14	0.05	0.07
Year + Site + Grass Height + Litter Depth + Robel + Percent Forb + Percent Shrub	0.31	0.15	1.94	8, 34	270.26	7.70	0.01	0.09
Year + Site + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Shrub	0.32	0.13	1.69	9, 33	273.73	11.16	0	0.13
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.32	0.10	1.48	10, 32	277.57	15.01	0	0.19

Table B.3 Continued

60 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site	0.19	0.12	3.00	3, 39	262.23	0	0.53	0.04
Year + Site + Grass Height	0.22	0.14	2.66	4, 38	263.24	1.0	0.32	0.05
Year + Site + Grass Height + Robel	0.23	0.13	2.24	5, 37	265.38	3.15	0.11	0.07
Year + Site + Grass Height + Robel+ Percent Grass	0.24	0.12	1.93	6, 36	267.75	5.52	0.03	0.10
Year + Site + Grass Height + Robel + Percent Grass + Percent Forb	0.25	0.10	1.66	7, 35	270.66	8.43	0.01	0.15
Year + Site + Grass Height + Robel+ Percent Grass +Percent Forb + Percent Shrub	0.25	0.07	1.41	8, 34	274.08	11.85	0	0.23
Year + Site + Grass Height + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.25	0.04	1.22	9, 33	277.72	15.49	0	0.32

70 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site	0.19	0.12	3.00	3, 39	262.23	0	0.56	0.04
Year + Site + Grass Height	0.21	0.13	2.57	4, 38	263.56	1.33	0.29	0.05
Year + Site + Grass Height + Robel	0.23	0.12	2.20	5, 37	265.55	3.31	0.11	0.08
Year + Site + Grass Height + Robel+ Percent Shrub	0.24	0.11	1.86	6, 36	268.17	5.93	0.03	0.12
Year + Site + Grass Height + Litter Depth + Robel + Percent Shrub	0.25	0.10	1.63	7, 35	270.85	8.61	0.01	0.16
Year + Site + Grass Height + Litter Depth + Robel + Percent Litter + Percent Shrub	0.25	0.08	1.45	8, 34	273.82	11.58	0	0.21
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Litter + Percent Shrub	0.25	0.05	1.25	9, 33	277.41	15.18	0	0.30
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.26	0.02	1.10	10, 32	281.26	19.03	0	0.39

Table B.3 Continued

80 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Robel+ Percent Shrub	0.14	0.07	2.12	3, 39	263.05	0	0.58	0.11
Year + Robel + Percent Forb + Percent Shrub	0.17	0.08	1.88	4, 38	266.10	1.43	0.29	0.13
Year + Robel + Percent Grass + Percent Forb + Percent Shrub	0.18	0.06	1.58	5, 37	268.42	3.75	0.09	0.19
Year + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.19	0.06	1.44	6, 36	270.49	5.82	0.03	0.23
Year + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.20	0.04	1.26	7, 35	273.34	8.67	0.01	0.30
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.22	0.03	1.17	8, 34	275.99	11.32	0	0.35
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.24	0.01	1.03	10, 32	281.95	17.28	0	0.44

Table B.3 Continued

90 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site + Robel	0.23	0.14	2.77	4, 39	262.86	0	0.66	0.04
Year + Site + Litter Depth + Robel	0.24	0.14	2.32	5, 37	265.00	2.15	0.23	0.06
Year + Site + Grass Height + Litter Depth + Robel	0.26	0.13	2.07	6, 36	267.04	4.19	0.08	0.08
Year + Site + Grass Height + Litter Depth + Robel + Percent Forb	0.27	0.12	1.85	7, 35	269.47	6.61	0.02	0.11
Year + Site + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb	0.27	0.10	1.60	8, 34	272.69	9.83	0	0.16
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Shrub	0.27	0.08	1.39	9, 33	276.22	13.37	0	0.23
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.28	0.05	1.22	10, 32	280.09	17.23	0	0.32

100 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site + Grass Height + Litter Depth + Percent Forb + Percent Shrub	0.48	0.32	3.11	7, 24	195.39	0	0.86	0.02
Year + Site + Grass Height + Litter Depth + Robel + Percent Forb + Percent Shrub	0.48	0.30	2.69	8, 23	199.22	3.83	0.13	0.03
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Shrub	0.49	0.28	2.34	9, 22	203.58	8.19	0.01	0.05
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.49	0.25	2.01	10, 21	208.80	13.41	0	0.09

Table B.4 Linear model selection of maximum number of lesser prairie-chicken females observed at leks from 2014-2015 by lek vegetation characteristics by 10 m distance of measurement in the Short-Grass Prairie/CRP Mosaic and Mixed-Grass Prairie Ecoregions of Kansas.

Grass height and visual obstruction are reoccurring significant model terms moving away from lek center (0-30 m).

0 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Site + Percent Litter	0.26	0.19	3.42	4, 38	175.75	0	0.56	0.02
Year + Site + Percent Forb + Percent Litter	0.29	0.19	3.03	5, 37	177.09	1.35	0.28	0.02
Year + Site + Percent Grass + Percent Forb + Percent Litter	0.31	0.20	2.73	6, 36	178.78	3.03	0.12	0.03
Year + Site + Litter Depth + Percent Grass + Percent Forb + Percent Litter	0.32	0.18	2.33	7, 35	181.67	5.92	0.03	0.05
Year + Site + Litter Depth + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.32	0.16	2.01	8, 34	184.86	9.12	0.01	0.07
Year + Site + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.32	0.14	1.74	9, 33	188.49	12.74	0	0.12
Year+ Site+ Grass Height+ Litter Depth+ Robel+ Percent Grass+ Percent Forb+ Percent Litter+ Percent Shrub	0.32	0.11	1.52	10, 32	192.37	16.62	0.0	0.18

10 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Site	0.14	0.07	2.10	3, 39	179.84	0	0.60	0.12
Year + Site + Percent Shrub	0.17	0.08	1.89	4, 38	181.19	1.35	0.31	0.13
Year + Site + Grass Height + Percent Shrub	0.17	0.06	1.53	5, 37	183.75	3.91	0.09	0.20
Year + Site + Grass Height + Litter Depth + Percent Shrub	0.18	0.05	1.34	6, 36	186.21	6.37	0.02	0.27
Year + Site + Grass Height + Litter Depth + Percent Litter + Percent Shrub	0.19	0.02	1.14	7, 35	189.28	9.44	0.01	0.36
Year + Site + Grass Height + Litter Depth + Percent Forb + Percent Litter + Percent Shrub	0.19	0.00	0.98	8,34	192.64	12.80	0	0.47
Year + Site + Grass Height + Litter Depth + Robel + Percent Forb + Percent Litter + Percent Shrub	0.19	-0.03	0.85	9. 33	196.18	16.35	0	0.58
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.19	-0.07	0.74	10, 32	200.07	20.23	0	0.68

Table B.4 Continued

20 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Robel + Percent Forb	0.20	0.13	3.16	3, 39	176.90	0	0.52	0.04
Year + Grass Height + Robel + Percent Forb	0.23	0.15	2.86	4, 38	177.66	0.75	0.36	0.04
Year + Grass Height + Robel + Percent Grass + Percent Forb	0.23	0.13	2.25	5, 37	180.46	3.55	0.09	0.07
Year + Site + Grass Height + Robel DM + Percent Grass + Percent Forb	0.27	0.13	1.90	7, 35	184.29	7.38	0.01	0.10
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb	0.28	0.11	1.63	8, 34	187.59	10.69	0	0.15
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.28	0.08	1.41	9, 33	191.19	14.29	0	0.22
Year + Site + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.28	0.05	1.23	10, 32	195.07	18.17	0	0.31

30 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Robel + Percent Litter	0.21	0.17	5.26	2, 40	173.66	0	0.53	0.01
Robel + Percent Litter + Percent Shrub	0.23	0.17	3.88	3, 39	175.05	1.39	0.27	0.02
Robel + Percent Forb + Percent Litter + Percent Shrub	0.25	0.17	3.20	4, 38	176.49	2.83	0.13	0.02
Year + Robel+ Percent Forb + Percent Litter + Percent Shrub	0.27	0.18	2.80	5, 37	178.05	4.39	0.06	0.03
Year + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.27	0.15	2.27	6, 36	181.08	7.42	0.06	0.06
Year + Site + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.32	0.16	1.97	8, 34	185.17	11.51	0	0.08
Year + Site + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.32	0.14	1.76	9, 33	188.30	14.64	0	0.11
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.32	0.11	1.54	10, 32	192.17	18.51	0	0.17

Table B.4 Continued

40 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Site + Robel + Percent Grass + Percent Forb + Percent Litter	0.27	0.14	2.17	6, 36	181.62	0	0.63	0.07
Year + Site + Robel + Percent Grass + Percent Forb + Percent Litter	0.29	0.15	2.06	7, 35	183.24	1.62	0.28	0.07
Year + Site + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.30	0.14	1.85	8, 34	185.97	4.35	0.07	0.10
Year + Site + Grass Height + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.31	0.13	1.68	9, 33	188.92	7.30	0.02	0.13
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.31	0.10	1.47	10, 32	275.60	11.17	0	0.20

50 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Site + Robel+ Percent Forb	0.31	0.21	3.27	5, 37	176.13	0	0.77	0.02
Year + Site + Litter Depth + Robel+ Percent Forb	0.31	0.19	2.67	6, 36	179.03	2.90	0.18	0.03
Year + Site + Grass Height + Litter Depth + Robel + Percent Forb	0.31	0.17	2.25	7, 35	182.12	5.99	0.04	0.05
Year + Site + Grass Height + Litter Depth + Robel + Percent Forb + Percent Litter	0.31	0.15	1.93	8, 34	185.44	9.31	0.01	0.09
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.31	0.12	1.66	9, 33	189.07	12.94	0	0.14
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.31	0.10	1.45	10, 32	192.95	16.82	0	0.20

Table B.4 Continued

60 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Robel + Percent Shrub	0.20	0.14	3.32	3, 39	176.50	0	0.62	0.03
Year + Robel + Percent Forb + Percent Shrub	0.22	0.14	2.75	4, 38	178.04	1.55	0.29	0.04
Year + Robel + Percent Forb + Percent Litter + Percent Shrub	0.23	0.12	2.16	5, 37	180.83	4.33	0.07	0.08
Year + Grass Height + Robel+ Percent Forb + Percent Litter + Percent Shrub	0.23	0.10	1.76	6, 36	183.81	7.32	0.02	0.14
Year + Grass Height + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.23	0.07	1.48	7, 35	186.96	10.46	0	0.21
Year + Site + Grass Height + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.26	0.06	1.31	9, 33	192.02	15.52	0	0.27

70 m

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site + Robel + Percent Grass + Percent Forb	0.43	0.33	4.46	6, 36	170.99	0	0.76	<0.01
Year + Site + Litter Depth + Robel + Percent Grass + Percent Forb	0.43	0.32	3.79	7, 35	173.85	2.87	0.18	<0.01
Year + Site + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.44	0.31	3.33	8, 34	176.65	5.67	0.04	0.01
Year + Site + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.45	0.30	2.96	9, 33	179.70	8.71	0.01	0.01
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.46	0.29	2.69	10, 32	182.78	11.80	0	0.02

Table B.4 Continued

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
80 m								
Site + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.32	0.18	2.33	7, 35	181.68	0	0.80	0.05
Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.32	0.16	2.02	8, 34	184.82	3.13	0.17	0.07
Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.33	0.14	1.79	9, 33	188.10	6.42	0.03	0.11
Year + Site + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.33	0.12	1.57	10, 32	191.87	10.19	0	0.16
90 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Site + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.45	0.33	3.54	8, 34	175.48	0	0.81	<0.01
Year + Site + Grass Height +Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.46	0.31	3.13	9, 33	178.65	3.17	0.17	0.01
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.46	0.29	2.73	10, 32	182.51	7.03	0.02	0.02
100 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Robel	0.26	0.21	5.11	2, 29	129.47	0	0.55	0.01
Year + Robel+ Percent Grass	0.30	0.23	4.03	3, 28	130.47	1.0	0.34	0.02
Year + Grass Height + Litter Depth + Robel + Percent Grass	0.32	0.19	2.48	5, 26	135.86	6.39	0.02	0.06
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb	0.33	0.17	2.07	6, 25	139.01	9.54	0	0.09
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.34	0.14	1.73	7, 24	142.76	13.29	0	0.15
Year + Site + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.36	0.10	1.40	9, 22	150.37	20.89	0	0.25

Chapter 3 - Implications of Lek Formation and Persistence on Translocation Outcomes: Lesser Prairie-Chicken Lek Dynamics Without an Existing Lek Complex

Introduction

Until the late 1980s, the Sand Sagebrush Prairie Ecoregion of southwestern Kansas and southeastern Colorado had the greatest density of lesser prairie-chickens within the contemporary occupied range of the species (Jensen et al. 2000, Garton et al. 2016, Hagen et al. 2017). The lesser prairie-chicken population in Sand Sagebrush Prairie declined an estimated >98% by 2016 (Jensen et al. 2000, McDonald et al. 2016). The contemporary decline began with a peak estimate of approximately >86,000 birds in the late 1970s, and was exacerbated by years of extreme drought and a series of intense winter storms during the past two decades (Jensen et al. 2000, McDonald et al. 2016).

Despite having sufficient land cover and associated habitat to support lesser prairie-chickens, the Sand Sagebrush Prairie Ecoregion is sufficiently isolated from the other three ecoregions within the lesser prairie-chicken range, preventing successful reestablishment of populations through dispersal. By 2014, the estimated population size was 513 (95% CI 432-633) and in 2016 the population trend was ~57 (90% CI 0-137.52; McDonald et al. 2016 Nasman et al. 2018). With so few native Sand Sagebrush birds remaining, it is unlikely that a population could be reestablished without increasing the number of lesser prairie-chickens from an outside source. Even with the population declines, much of the original land cover in the Sand Sagebrush Prairie Ecoregion is available for colonization and expansion of a lesser prairie-chicken population (Haukos and Boal 2016, Spencer et al. 2017*b*). To bolster the rapidly diminishing

Sand Sagebrush Prairie Ecoregion population, a multiagency effort was formed to translocate lesser prairie-chickens from areas of high densities in the Kansas Short-Grass Prairie/CRP Mosaic Ecoregion.

Currently, the Kansas Short-Grass Prairie/CRP Mosaic Ecoregion (hereafter Short-Grass Prairie) supports the most abundant lesser prairie-chicken population (Nasman et al. 2018). Despite its abundance, success of the Short-Grass Prairie population is tied to USDA Conservation Reserve Program (CRP) grasses during nesting and nonbreeding seasons, which birds select over other available habitat, especially during drought (Sullins et al. 2018). Availability of CRP grass is dependent on the voluntary enrollment of farmers, funding for government incentives, agricultural productivity, and weather of a given year (Agriculture 2012, Dahlgren et al. 2016, Haukos and Boal 2016, Spencer et al. 2017*b*). If availability of CRP was to decline in the Short-Grass Prairie/CRP Mosaic Ecoregion, the largest remaining lesser prairie-chicken population will likely decline in abundance and occupied range. The uncertainty around the continuance of the Short-Grass Prairie population due to the reliance of this population on CRP necessitates that management efforts focus on maintaining viable populations in the other three ecoregions.

Among the other three ecoregions within the lesser prairie-chicken range, the Sand Sagebrush Prairie Ecoregion holds a unique importance for lesser prairie-chicken management. Unlike the majority of the species range, which is almost exclusively private lands, the Sand Sagebrush Prairie Ecoregion includes the U.S. Forest Service Cimarron and Comanche National Grasslands in southwestern Kansas and southeastern Colorado, respectively. Translocation of birds from the Kansas Short-Grass Prairie Ecoregion to the National Grasslands has the potential to reestablish lesser prairie-chickens on predominantly public lands, in addition to contributing to the viability of what was historically believed to be the most prevalent lesser prairie-chicken population.

Translocation has been successfully employed for many bird species of conservation concern, but most translocation efforts of grouse have failed or been largely unsuccessful due the inability to retain birds at release sites (Snyder et al. 1999). Success of translocation projects partially rests on the number of birds and methodology of release, but it also depends on the ability of managers to retain birds in the targeted area after release (Coates and Delehanty 2006, Baxter et al. 2013, Gruber-Hadden et al. 2016). Retaining birds in the release area requires an understanding of habitat requirements and behavior, particularly an understanding of how the species disperses and uses space following release.

Data from Earl et al. (2016) supports the hypothesis that females are the major long-distance dispersers, which suggests that lekking species like prairie-grouse move across their landscape in a step-wise fashion where females lead and lek formation follows (Bergerud and Gratson 1988, Bradbury et al. 1989*b*, *d*). A prior translocation study of greater prairie-chickens (*Tympanuchus cupido*) found that translocated birds are capable of moving incredibly large distances and have low survival (Weil and Jensen 2015). Analyses of bird movements from this translocation effort by Berigan (2019) also support the role of females as the drivers of lesser prairie-chicken dispersal, where total dispersal movements have exceeded 470 km and average 145 km (Figure 3.1). However, it remains unclear what criteria females use to assess landscapes to establish home ranges, and what factors influence the directionality of their dispersal.

The leading hypothesis is that females drive prairie-grouse dispersal, with young females venturing out into new landscapes in search of quality nesting and brood-rearing habitats (Bergerud and Gratson 1988). In contrast, young males are believed to evaluate existing leks in the fall prior to their first breeding season in the spring (Bergerud and Gratson 1988). During this period, females are evaluating potential nesting habitat for the following breeding season. If mating prospects are perceived to be slim (i.e., few interactions with females) young males likely move on to join other existing leks or form new leks. This hypothesis relies on the assumption that prairie grouse leks are formed in relationship to female densities, meeting the predictions of the hotspot hypothesis (Bradbury et al. 1989*a*, Jiguet and Bretagnolle 2006; Chapter 2).

With females increasingly shown to be the drivers of lesser prairie-chicken dispersal, the question remains of how the existence and formation of leks relates to where and how individuals will disperse or what role leks play in stabilizing populations in a particular space (Rodgers 1992). Prairie grouse offer unique translocation challenges in retaining birds at the release site because they are a lek breeding species. Prior translocation efforts have been considered unsuccessful if birds fail to form leks and there is preliminary evidence that lek formation and presence matters in the success of translocation of lekking grouse (Snyder et al. 1999). The role of leks that form after translocation in shaping either dispersal or the stabilization of populations for prairie-grouse remains largely unknown, due to the limited understanding of how prairie-grouse disperse.

Past translocation efforts of prairie-grouse have rested on untested assumptions about how lek breeding species disperse and navigate new landscapes. While management of prairie-grouse largely focuses on females as the limiting sex, it is assumed that because leks are a dominant fixture dictating where birds spend most of their time, lek location and attendance drive dispersal with males leading females into novel habitat. Despite evidence of long-distance movement by females, management and translocations in the past have assumed that establishing males and leks on a landscape will be the greatest determinant of whether or not a translocation effort succeeds (Snyder et al. 1999). Prairie-grouse translocations, including the translocation of lesser prairie-chickens described in this work, assume that males are the dispersing sex and establishing males on a landscape will assist in retaining birds of both sexes at the release site.

My research evaluates the validity of this assumption and compares the patterns of lek formation and persistence from native birds in the Short-Grass Prairie Ecoregion to the birds translocated to the Sand Sagebrush Prairie Ecoregion. In previous work, I have illustrated that non-translocated populations in the Short-Grass Prairie and Mixed-Grass Prairie ecoregions of Kansas form leks in areas of highest female spatial use and in close proximity to nesting sites, as expected under the hotspot hypothesis (Chapter 2). Prior to this work, there was no conclusive evidence to indicate that leks are formed in response to female densities in accordance of the female-driven hypothesis about the relationship of leks to dispersal.

Translocation of lesser prairie-chickens is a unique opportunity to test the hotspot hypothesis in essentially unoccupied habitat. Without a preexisting lek complex to influence bird behavior, translocated bird movements provide a close approximation to how juvenile birds likely navigate the landscape after brood break up and the process of colonizing unoccupied habitats. Through translocated birds, it is possible to study lek dynamics within the lens of dispersal and determine if management assumptions of establishing male birds first or releasing at historical lek locations are viable approaches to translocation strategies.

My first objective was to determine if translocated males form leks in accordance with the hotspot hypothesis. I predict that leks formed by translocated Short-Grass Prairie males will be driven by female space use and nest-site selection, forming adjacent to areas that have sufficient visual obstruction for nesting. Similarly, I predict that males will not selectively seek vegetation structure similar to leks where they were captured in Short-Grass Prairie over existing leks of Sand Sagebrush Prairie males or establishing new leks in Sand Sagebrush Prairie.

The second objective of my investigation was to determine those factors, such as anthropogenic features or female space use, which influence the persistence of a lek into a subsequent year. Over the duration of the translocation effort, male lesser prairie-chickens have grouped in many different areas to display. Often these groupings are too small to be classified as a lek (<3 males) and formed immediately after males are translocated. Typically, smaller groupings of newly formed smaller leks (<4 males) are ephemeral, lasting no longer than the end of the breeding season before collapsing. Unlike satellite leks, which are also comprised of a small number of males, young, and unstable compared to older and bigger leks, ephemeral leks form and collapse rapidly without the presence of an existing lek complex (Haukos and Smith 1999). The question arises from observing ephemeral leks turnover within a single breeding season of whether (1) this phenomenon follows the observed patterns of non-translocated birds in the Short-Grass Prairie source population and (2) if persistence of leks can be attributed to female space use.

Assessing potential factors influencing the persistence of newly forming leks will allow managers to decide if the population is likely to continue and, furthermore, if future translocation efforts are a viable management strategy. Continuity of leks and year-over-year counts of males will be used to assess if the translocation effort can be considered successful. Determining what factors influence lek stability will provide an area of focus for future management and translocation efforts. My prior work has illustrated that in established lek complexes of the Short-Grass Prairie and Mixed-Grass Prairie ecoregions of Kansas, female space utilization and nest site selection not only determines where leks are formed, but also acts a substantive determinant of male numbers from year to year (Chapter 2). I predict that leks formed after translocation will follow the same pattern, where female habitat use is the strongest determinant of male numbers into subsequent breeding seasons.

Study Area

Capture Site: Short-Grass Prairie Ecoregion

The capture site encompassed Gove and Logan counties of northwestern Kansas, with all capture locations on private land. Northwest Kansas is a mosaic of short-grass and mixed-grass prairies, land enrolled in the Conservation Reserve Program (CRP) of the U.S. Department of Agriculture, and agriculture on silt loam soils. The Short-Grass Prairie Ecoregion is comprised of silt loam soils with dominant vegetation inclusive of blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsute*), buffalograss (*B. dactyloides*), sideoats grama (*B. curtipendula*), little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed (*Ambrosia psilostacha*; Robinson 2015, 2018; Sullins 2017; Sullins et al. 2018). Conservation Reserve Program tracts in Kansas were initially seeded with native grasses, primarily consisting of little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indian grass (*Sorghastrum nutans*; Fields et al. 2006, Robinson et al. 2018, Sullins et al. 2018). Annual average long-term (30 year) precipitation varies between 40 and 50 cm (Dahlgren et al. 2016).

Release site: Sand Sagebrush Prairie Ecoregion

The release sites were located on Cimarron and Comanche National Grasslands administered by the U.S. Forest Service in the Sand Sagebrush Prairie Ecoregion of southwestern Kansas and southeastern Colorado (Haukos et al. 2016). Release sites were located at historic lek locations or in areas with the highest quality nesting habitat on the National Grasslands (Figure 3.2). The National Grasslands comprise approximately 224,000 ha of area in the ecoregion; the Cimarron (Morton and Stevens counties, Kansas; nearly 44,000 ha) and Comanche (Baca, Otero, and Las Animas counties, Colorado; nearly 180,000 ha). This area represents the bulk of public land in the lesser prairie-chicken range and includes a 142 km band of sand sagebrush, primarily associated with the Cimarron River in Colorado and Kansas (Dahlgren et al. 2016, Haukos and Boal 2016).

Release sites located on the Cimarron National Ecological sites are primarily sand, sandy, or choppy sand soils. Plant composition typically includes sand sagebrush (*Artemisa filifolia*), yucca (*Yucca* spp.), little bluestem, sideoats grama, sand lovegrass (*Eragrostis trichodes*), sand dropseed (*Sporobolus cryptandrus*), blue grama, sand bluestem (*Andropogon hallii*), annual buckwheat, western ragweed, prairie sunflower, annual sunflower (*Helianthus annuus*), Indian blanket flower (*Gaillardia pulchella*), tansy aster (*Machaeranthera tanacetifolia*), bush morning glory (*Ipomoea leptophylla*), evening primrose (*Oenothera* spp.), buffalo bur (*Solanum rostratum*), and buffalo gourd (*Cucurbita foetidissima*; Hagen et al. 2005, Haukos et al. 2016). Average annual precipitation for the Sand Sagebrush Ecoregion ranges from 40.6 to 51.7 cm (Haukos et al. 2016).

Methods

A joint effort between the U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Colorado Parks and Wildlife, and Kansas Department of Wildlife, Parks, and Tourism trapped lesser prairie-chickens in Kansas Short-Grass Prairie Ecoregion using funnel traps and drop nets during fall 2016 and spring (2017-2019; Table 3.1). Captured birds were sexed by dimorphic characteristics such as differences in tail color patterns and aged using patterns of spotting, wear, and molt of the outermost 9th and 10th primary feathers (Copelin 1963, Pyle 2008). In the assembled data set, I differentiated individual birds by metal bands with a unique identification number, combinations of color bands, and by a telemetry/signal identifier. All capture and handling of lesser prairie-chickens during 2018 and 2019 was completed under Institutional Animal Care and Use Committee Permit #3703 and Kansas Scientific Wildlife Permits SC-024-2018 and SC-015-2019 and in compliance with state and federal regulations by state agencies during 2016 and 2017.

Birds were fitted or a very-high-frequency (VHF) bib-mounted radio transmitter in fall 2016 and spring 2017 (RI-2B Holohil Systems Ltd., Carp, Ontario, Canada). In 2018-2019 birds were equipped with a different brand VHF collar Model #A3950 or A3960; Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) or a rump-mounted Satellite Platform Transmitting Terminal (PTT) GPS transmitter (Model PTT-100, Microwave Telemetry, Columbia, Maryland, USA). GPS transmitters were attached using leg harnesses made of Teflon® ribbon with sewn-in elastic for flexibility (Bedrosian and Craighead 2007, Dzialak et al. 2011, Farve 2012*b*).

GPS transmitters provided individual locations approximately every two hours between 0500 and 2300, which were downloaded from the ARGOS satellite system every three days, dependent on solar energy available to the tag. Locations for individuals equipped with VHF transmitters were collected three times per week following attachment of the transmitter until death or radio failure. Individuals equipped with VHF transmitters were located using located using truck-mounted, null-peak antenna systems or with 2-4-element Yagi antennas.

Bird locations were estimated using triangulation with a minimum of three bearings taken within a 20-minute period to minimize biases and error associated with bird movement. Aircraft was used up to four times per year to locate birds that dispersed beyond the release area. All birds were captured, processed, and released at either the Comanche or Cimarron National Grasslands within the same day. For all years of the translocation effort, birds were hard released at a location determined by site biologists, with two release locations used in Comanche National Grassland and three release locations in the Cimarron National Grassland were used over the duration of the project (Figure 3.2). For the purpose of this work, only birds released on Cimarron National Grasslands are considered.

Lek Observations and Vegetation Surveys

Lek observation data used in these analyses were collected by with Colorado Parks and Wildlife, Kansas Department of Wildlife, Parks, and Tourism, and the Kansas Cooperative Fish and Wildlife Research Unit as part of a multi-year lesser prairie-chicken research effort. As part of the capture process, daily counts of male and female lesser prairie-chickens are collected from late-March- mid April. Lek surveys were also conducted spring during 2017-2020 at release locations and after the translocation of birds for the year had concluded, surveys for new formations of leks were also conducted. Lek surveys sites were determined primarily from radio or GPS telemetry data, using the spatial locations of male lesser prairie-chickens to determine if individuals could be repeatedly found at the same area. If there were at least two males, the area would be surveyed at first light to determine if males were engaging in display behaviors, such as cackling. While a lek is defined as having three or more males engaged in interactive grouped display, for the purposes of studying the formation of leks after birds have been translocated to a novel landscape, areas where less than males displayed are considered ephemeral leks. Ephemeral leks formed rapidly after translocation within the ~2-3-week period after male birds were released in the Sand Sagebrush Prairie and rarely lasted past the end of the breeding season.

During mid- to late April, lek vegetation composition and structure were measured along four 100 m transects radiating out from the center each lek in each cardinal direction for both capture site and release site leks. Lek center was determined from observation of male display activity and the concentration of lost feathers and fecal sign. The edges of heavy activity were determined by flagging the outermost locations of feather and fecal sign and the center assessed from the heaviest use area within the perimeter. Starting from 0 m, Daubenmire horizontal cover, plant composition (by species or functional group), and visual obstruction (%) using a Robel pole at 0, 25, 50, 75, and 100% cover measurements were recorded at each 10 m interval out to 100 m. Tallest grass height and litter depth were also recorded in centimeters. Lek vegetation height and structure influences lek abandonment in greater prairie-chickens (Anderson 1969, Niemuth 2000).

Lek Dynamics At 10 km, 5 km, 2 km, and 1 km Spatial Scales

I created 10 km, 5 km, 2 km, and 1 km buffers around lek sites using ArcGIS and applied the zonal statistics tool to individual leks to estimate surrounding percent grassland and cropland land cover. Land cover data were determined using the 2016 National Land Cover Database from the Multi-Resolution Land Characteristics Consortium (Homer et al. 2020). Counts of point features from hen movements, nest sites, and anthropogenic features were determined using QGIS count points in polygon tool at each buffer scale. Lengths of roadways, inclusive of county roads and state highways, and electric distribution lines were determined for each spatial scale using the sum line lengths tool in QGIS.

Counts of female spatial points were determined by year as a total number of recorded locations and the number of unique individual females with points within each buffer scale. Separate counts were made for female locations within the same year as lek observations and female locations from the prior year. The number of nests by transmittered birds within each buffer scale was determined and used in analyses as same year nesting efforts and previous year nesting efforts. The number of neighboring lek locations was also determined at each buffer scale.

Anthropogenic data were provided from State of Kansas GIS Data Access and Support Center (DASC) repository, oil well data from Kansas Geological Survey, electric lines from Kansas Corporation Commission, cell towers from Federal Communications Commission Antenna Structure Registry, and roadways from Kansas Department of Transportation: Bureau of Transportation Planning. The nearest wind turbines were constructed after lek observations ended.

Analyses of Lek Dynamics

To determine if the hotspot hypothesis explains the formation of lesser prairie-chicken leks upon the landscape, female locations were mapped using the optimized hotspot and kernel density tools in ArcGIS. The optimized hotspot tool determines significant hot or cold clusters based on given locations using the Getis-Ord Gi* statistic (ESRI n.d.). Significant hot spots are filled with relatively greater numbers of locations, which have high weighted values, and also surrounded by other high valued features (ESRI n.d.). When the sum of these features is different from an expected sum of points than what could be attributed to random chance, it is reported as significant (ESRI n.d.). Getis-Ord Gi* is a frequently used methodology in determining spatial clustering in wildlife studies (Kuletz et al. 2015, Shilling and Waetjen 2015, Cleasby et al. 2020).

To account for the wide distribution of female spatial locations, kernel density estimates were used to map the same inputs to indicate areas of clustered locations too small to be picked out as significant by the optimized hotspot analyses. Kernel density surfaces were calculated in addition to the optimized hotspot outputs to assess clustering patterns of female space use compared to lek sites. Kernel density also relates input features to the surrounding neighborhood, fitting a surface layer to each input female location where the highest value is at the point location and the value decreases moving away from that point (ESRI n.d.). The final output is the additive values of each calculated surface.

As translocated birds are actively navigating a novel landscape and males were found displaying shortly after release, both same year and lag year female movements were examined to determine the extent of influence of female space use and lek formation. The spatial outputs of the optimized hot spot and kernel density tools indicate where female locations are the most concentrated. Under the hotspot hypothesis, leks should appear where they have the greatest likelihood of encountering females. A comparison of where leks form with the depicted areas of concentrated female locations will indicate if there is a pattern of lek formation in areas of high female space use.

Analyses of Lek Persistence

A series of linear regressions were tested by buffer scale (10, 5, 2, 1 km) with maximum observed male counts as the dependent variable. Three model suites were considered for each distance: the first with anthropogenic features, the second with same year female space use and land cover as independent variables, and the third with lag locations and individual records from the year prior to lek observation. Anthropogenic features model suite considered included oil wells active in the year prior to observation, length of roadway, length of electric distribution lines, number of cell towers, length of rail, and year. Female space use model suites tested same year and lag locations, number of unique individual females, number of current and previous nests, number of neighboring leks, percent grassland land cover, and year of observation. Year was included to account for annual variation in maximum male counts, female locations, nest site selection, and anthropogenic features within buffers. At the lek level, linear regression models were tested for each 10 m distance of lek vegetation measured from (0-100 m) for a total of 11 models. Lek vegetation model suite included grass height, visual obstruction reading, litter depth, percent grass, percent forb, percent litter, year, and site. Each measured distance of lek vegetation was tested separately to assess where, if at any distance moving away from lek center, lek vegetation acts as a driver of maximum male or female numbers.

Prior to inclusion in the models, all variables were tested for correlation with a Pearson test. Variables with ($r > |0.80|$) correlation were excluded from the global model prior to model selection. All models were selected with combined forward and backward selection based on Akaike Information Criterion (AIC) from the global model. Top ranked models were determined by comparative AIC_c. The importance of individual variables within best fit models was determined by beta significance ($\alpha = 0.05$) and 95% confidence intervals surrounding the beta coefficient.

Comparing Capture and Release Site Leks

To capture birds for translocation, all lesser prairie-chickens were removed from leks the Short-Grass Prairie Ecoregion. To determine if released males favor similar vegetation structure when they form leks in the Sand Sagebrush Prairie Ecoregion, visual obstruction and horizontal cover were compared between grassland leks where birds were captured and those that formed after release. Lek vegetation measurements were compared at each 10 m distance, starting from lek center (0 m), in 11 multivariate analysis of variance (MANOVA) models. Individual significant terms ($P < 0.05$) were subsequently tested with analysis of variance (ANOVA).

Results

Kansas Sand Sagebrush Prairie Lek Turnover

A total of 13 VHF equipped males were initially released in fall of 2016 to augment remaining native Sand Sagebrush Prairie leks and potentially form new leks in the release area (Table 3.1). The intention of the fall release was to solidify persistence of the remaining three native leks in Kansas and Colorado by releasing males on National Grasslands prior to the release of females in the following spring. At the time of the first bird release, only one of the three remaining native leks was located on the Cimarron National Grassland in Kansas with (2-3 displaying males in 2016). Male lesser prairie-chickens were released at the lek site in hopes of bolstering the existing numbers at the lek.

Between the fall 2016 release and the subsequent release of 35 birds in spring of 2017, a total of five leks were populated with a mixture of native Sand Sagebrush Prairie Ecoregion males and translocated Short-Grass Prairie Ecoregion males (Table 3.1). Out of the five leks active in spring 2017, three were located in grassland (3, 6, and 7 displaying males) and two in cropland (2-3 and 5 displaying males; Figure 3.3). Three of the five leks were adjacent to, but not on National Grassland property. The leks were spread to the north or south of the Cimarron National Grassland boundary, with the furthest established lek ~28km north from the release site.

Despite the fall translocation of males intended to augment the last active native Sand Sagebrush Prairie lek, the native bird lek collapsed in spring 2017. Prior to collapse, the lek shifted from National Grassland property to adjacent CRP, but many of the males that had been displaying at the native lek abandoned for a CRP lek within a half mile of original site that was comprised of a mix of native and translocated males. The loss of the last Cimarron native lek was likely due to the lack of associated nesting attempts by attending females while the lek was active (Berigan 2019). With males abandoning the Cimarron National Grassland prior to lek collapse, all the 2017 leks were on private property. It is noteworthy that the only leks to persist until the end of the translocation effort in 2020 formed in 2017 (Figure 3.3). Both of these leks were National Grassland adjacent and serve as focal points for lesser prairie-chicken distribution on the landscape.

After the first spring release in 2017, there was a dynamic lek formation and collapse in response to the injection of additional translocated birds in subsequent springs. This dynamic becomes especially evident after spring 2018, when only three of the leks active in 2017 persisted (Figure 3.3). Two of these leks were the north and southern locations adjacent to the National Grasslands, while the third formed as a smaller grassland lek to the north of the National Grasslands. While three new leks formed after the 2018 release, two were ephemeral and collapsed by the end of the 2018 breeding season in May. Both ephemeral leks were formed on private grasslands with a maximum count of 3 males (Figure 3.3).

Before the last translocation in spring 2019, males were only actively displaying at the northern (12 males) and southern lek (6 males) sites adjacent to the National Grasslands (1km to 500 m). A small satellite lek collapsed in 2019 while three new leks appeared, including the first Cimarron National Grassland leks since 2017 (7 displaying males; Figure 3.3). Two leks formed on the Cimarron, one small lek at the release site for that year and another just inside the northern edges of the National Forest Service property. Entering into the 2020 breeding season, there were four active leks that had persisted from spring 2019. In 2020, nine newly formed leks were detected, but the majority of new discoveries were small groupings of two males and thus unlikely to persist (Figure 3.3). Without the dual effort of translocating birds and monitoring leks, considerably greater hours were devoted to lek searching and observation in 2020. It is possible that a portion of these leks formed in prior years but were not discovered due to their locations on the periphery of the study area.

The two leks that have persisted since 2017 straddled the northern and southern bounds of the Cimarron National Grassland and are on private land adjacent to National Grassland. The northern-most lek, Broken Windmill, was located in short-grass prairie 1 km from an isolated patch of National Grassland property. In the south, Circus lek was located in crop stubble ~470m from an isolated patch of contiguous National Grassland property. Despite differences in cover types, both leks persisted until 2020 and served as important focal areas for translocated lesser prairie-chickens. However, it is unlikely that lek proximity to National Grasslands property determined the persistence or formation of these leks as both were isolated patches. Females primarily selected surrounding CRP or privately managed grasslands for nesting, with the exception of two nesting attempts in the Circus adjacent National Grassland property following the termination of the CRP contract in the bordering property.

Differences Between Capture and Release Site Leks

My results are based on 31 capture leks in the Short-Grass Prairie Ecoregion and 8 leks formed by translocated birds in the Sand Sagebrush Prairie Ecoregion. For spatial movements of hens, only females who lived longer than 3 months were included. Spatial locations from 32 GPS and 24 VHF hens were utilized in this work.

Lek center (0-30 m) and edge (40-100 m) vegetation was, on average, greater for grass height and visual obstruction at release sites than capture sites (Table 3.2). When comparing lek vegetation measured at capture and release sites from 2018 to 2020, there was a difference in grass height and visual obstruction among sites and years by distance (Figure 3.4). These differences are concentrated at lek center (0-30 m), 40 m, and the outer edge (70-100 m). Similarly, there was a greater average visual obstruction at leks attended by translocated males than at capture leks. This difference was likely driven by the vegetation measurements of leks at the release site in 2020, due to high precipitation in the 2019 growing season and the increased number of discovered grassland leks and the lack of capture lek measurements in 2020. Some vegetation variables were correlated among the distances considered, but none were sufficiently correlated as to implicate multicollinearity (Table C.1). Horizontal shrub cover was excluded from the lek center (0 m) model due to absence of any shrubs in those samples.

At lek center, the vegetation suite differed by site (Wilks lambda = 0.61, $F_{7,35} = 3.23$, $P < 0.001$) and year (Wilks lambda = 0.43, $F_{14,70} = 2.65$, $P < 0.001$) with an interaction between site and year (Wilks lambda = 0.57, $F_{7,35} = 3.82$, $P < 0.001$). Grass height ($F_{1,41} = 5.29$, $P = 0.02$) differed between sites (capture $\bar{x} = 13.82$ cm, SD = 6.19; translocation $\bar{x} = 27.8$ cm, SD = 14.45) and among years with 2020 different ($\bar{x} = 29.0$ cm, SD = 15.43) from 2019 ($\bar{x} = 15.29$ cm, SD = 5.65) and 2018 ($\bar{x} = 14.6$ cm, SD = 10.71). Visual obstruction ($F_{1,41} = 4.71$, $P = 0.04$) differed between release ($\bar{x} = 0.025$ dm, SD = 0.08) and capture ($\bar{x} = 0.0$, SD = 0) by year, with 2020 differing from 2018-2019.

Visual obstruction is low at lek center and the capture leks had on average 0 decimeters completely obstructed. Lek center had different horizontal cover of grass by year ($F_{2,41} = 4.17$, $P = 0.02$) where 2019 ($\bar{x} = 72.47\%$, SD = 20.87) differed from 2018 ($\bar{x} = 57.12\%$, SD = 17.65).

Percent bare ground horizontal cover also differed by year ($F_{2, 41} = 4.17$, $P = 0.02$) where 2018 differed ($\bar{x} = 21.5\%$, SD = 18.37) from 2019 ($\bar{x} = 10.74\%$, SD = 12.77) and 2020 ($\bar{x} = 4.67\%$, SD = 5.68). Percent litter horizontal cover differed by site ($F_{1, 41} = 5.46$, $P = 0.02$) where the release site ($\bar{x} = 26.83\%$, SD = 23.76) had higher percentage of litter from the capture site ($\bar{x} = 15.12\%$, SD = 23.76).

At 10 m, lek vegetation differed between sites (Wilks lambda = 0.62, $F_{8,34} = 2.61$, $P = 0.02$), with grass height ($F_{1, 41} = 16.61$, $P < 0.0001$) at the release site ($\bar{x} = 32.21$ cm, SD = 13.51) greater than capture site leks ($\bar{x} = 19.08$ cm SD = 71.53). Horizontal cover of litter ($F_{1, 41} = 7.71$, $P < 0.001$) different between 2020 ($\bar{x} = 26.25\%$, SD = 25.37) and 2019 ($\bar{x} = 14.12\%$, SD = 10.31). At 20 m, there are differences among release sites (Wilks lambda = 0.59, $F_{8, 35} = 3.06$, $P < 0.01$) and years (Wilks lambda = 0.46, $F_{16, 70} = 2.10$, $P < 0.02$), where grass height ($F_{1, 42} = 18.0$, $P < 0.0001$) differed between release ($\bar{x} = 41.46$ cm, SD = 12.96) and capture ($\bar{x} = 25.21$ cm, SD = 9.74) sites. Grass height in 2020 ($\bar{x} = 40.88$ cm, SD=11.39) differed from 2019 ($\bar{x} = 25.59$ cm, SD=9.18) and 2018 ($\bar{x} = 28.74$ cm, SD=14.33).

At 30 m, typically the furthest extent of where males actively display on a lek, there was a difference between release and capture sites (Wilks lambda = 0.62, $F_{8, 37} = 2.88$, $P = 0.01$). Grass height ($F_{1, 44} = 10.36$, $P < 0.001$) and visual obstruction ($F_{1, 44} = 8.74$, $P < 0.01$) differed between sites, with translocation leks having greater grass heights and obstruction. There is a greater average grass height ($\bar{x} = 42.03$ cm, SD =14.93) and visual obstruction ($\bar{x} = 0.18$ dm, SD = 0.26) for the release site than capture site ($\bar{x} = 29.86$ cm, SD = 9.11; $\bar{x} = 0.03$ dm, SD = 0.26, respectively).

At lek center (0-30 m) translocation grassland leks had greater visual obstruction grass heights compared to capture leks in the Short-Grass Prairie Ecoregion. This is likely a reflection of differences in land use as much as the inclusion of 2020 translocation leks. Grassland translocation leks are primarily in private areas that are not being grazed. However, Short-Grass Prairie capture lek sites are located on working lands that are worked in a rotation system that produces shorter vegetation at lek center.

Lek Edge (40-100 m)

Moving away from lek center at 40 m, lek vegetation differed by site (Wilks lambda = 0.662, $F_{8, 37} = 2.35$, $P = 0.04$), with grass height ($F_{1, 44} = 6.24$ cm, $P = 0.02$) and visual obstruction ($F_{1, 44} = 5.672$, $P = 0.02$) greater in the release site ($\bar{x} = 40.29$ cm, SD = 14.51; $\bar{x}$ = 0.15 dm, SD = 0.21, respectively) than the capture site ($\bar{x}$ = 30.15 cm, SD = 1 0.39; $\bar{x}$ = 0.04 dm, SD = 0.09, respectively). Between lek center and the edge of the lek at 50 m and 60 m, neither site nor year different for the vegetation suite considered. Both the 70 m (Wilks lambda = 0.42, $F_{16, 74} = 2.44$, $P < 0.01$) and 80 m distance (Wilks lambda = 0.38, $F_{16, 72} = 2.75$, $P < 0.01$) differed by year, but not by site. At 70 m, mean grass height ($F_{2, 43} = 4.17$, $P = 0.02$) was greater in 2020 ($\bar{x} = 48.67$ cm, SD = 13.65) and visual obstruction ($F_{2, 43} = 4.05$ dm, $P = 0.02$) differed in 2020 ($\bar{x} = 0.38$ dm, SD = 0.34) from 2019 ($\bar{x} = 0.04$ dm, SD = 0.12). At 80 m, visual obstruction also differed ($F_{2, 43} = 3.73$, $P = 0.03$) in 2020 ($\bar{x}$ = 0.29 dm, SD = 0.40) from 2019 ($\bar{x}$ = 0.02 dm, SD = 0.07).

At the very outer edges of the lek, year and location both differed for the vegetation suite. At 90 m, there were differences in vegetation by year (Wilks lambda = 0.36, $F_{8, 35} = 2.95$, $P < 0.001$) for grass height ($F_{2,42} = 7.49$, $P < 0.01$), visual obstruction ($F_{2,42} = 6.25$, $P < 0.01$) and percent shrub cover ($F_{2,42} = 6.17$, $P < 0.01$). For grass height ($\bar{x} = 52.38$ cm, SD = 15.23), visual obstruction ($\bar{x}$ = 0.37 dm, SD = 0.34) and percent shrub cover ($\bar{x}$ = 3.54%, SD = 6.63), 2020 differed from both 2018 ($\bar{x}$ = 0%, SD = 0) and 2019 ($\bar{x}$ = 0.03%, SD = 0.16). At the furthest distance of 100 m, 2020 differed from 2018 and 2019 (Wilks lambda = 0.39, $F_{16, 68} = 2.57$, $P < 0.01$) for grass cover ($F_{2, 41} = 4.25$ $P = 0.02$) and shrub cover ($F_{2, 41} = 6.80$, $P < 0.01$).

As with measurement of lek center, the prevalent influences of lek edges are also the differences in land use for the grasslands used by lesser prairie-chickens in this study. It is worth noting that despite increased vegetation heights and obstruction from lek edge, that lesser prairie-chickens from dynamic working lands will use these locations. It is likely that increasing visual obstruction at 60-70 m distance from center can act as a protective barrier for visiting females (Chapter 2).

Lek Vegetation and Maximum Male Numbers

Maximum male numbers at Sand Sagebrush Prairie Ecoregion leks were influenced by grassland vegetation characteristics from lek center (0 m) to the outermost edge at 100 m. Notably, all distance models were significant and share several commonalities. Lek vegetation heights for translocation leks measured in 2020 had a negative influence on maximum male numbers. Increasing grass height was positively associated with male numbers for all distance models except for 90 m (Table C.2). The reduction in maximum male numbers may be partially driven by the discovery of 9 leks in 2020, of which the majority were two males at the time of their discovery, and the survival rate for translocated birds (~40% Berigan 2019).

In the 0 m model ($F_{4, 31} = 56.22$, $P < 0.001$), as grass height increased ($\beta = 0.05$, SE = 0.01, $P < 0.001$), the number of observed males increased. Both 2018 ($\beta = 3.93$, SE = 0.61, $P < 0.001$) and 2019 ($\beta = 7.72$, SE = 0.69, $P < 0.001$) differed in maximum male numbers. For 10 m ($F_{3, 32} = 55.03$, $P < 0.001$), as grass height increased ($\beta = 0.03$, SE = 0.01, $P = 0.03$) the number of males observed at translocation leks increased. At 20 m ($F_{4, 31} = 58.9$, $P < 0.001$), increasing grass height ($\beta = 0.05$, SE = 0.01, $P < 0.001$) also increased maximum male numbers and all years were significant (2018 β = 3.1, SE = 0.57, $P < 0.001$; 2019 β = 7.38, SE = 0.62, $P < 0.001$; 2020 β = -0.90, SE = 0.38, $P = 0.03$). At 30 m ($F_{4, 31} = 86.92$, $P < 0.001$), increasing visual obstruction (β = -0.92, SE = 0.42, $P = 0.04$) decreased maximum male observation numbers while increasing grass height (β = 0.06, SE = 0.01, $P < 0.001$) increased maximum male numbers. All years were also significant at 30 m (2018 β = 2.5, SE = 0.42, $P < 0.001$; 2019 β = 6.11, SE = 0.54, $P < 0.001$; 2020 β = -1.44, SE = 0.33, $P < 0.001$).

Lek Edge (40-100 m)

At 40 m ($F_{8, 27} = 28.8$, $P < 0.001$), increasing grass height (β = 0.03, SE = 0.01, $P = 0.02$) increased maximum male numbers while increasing percent grass (β = -0.03, SE = 0.01, $P = 0.03$) and shrub (β = -0.05, SE = 0.02, $P = 0.02$) decreased maximum male numbers. The years 2018 (β = 6.75, SE = 1.31) and 2019 (β = 7.31, SE = 0.65) were also significant at 40 m. Moving toward the edge of the lek at 50 m ($F_{6, 29} = 69.93$, $P < 0.001$), with increasing percent cover of grass (β = -0.06, SE = 0.01, $P < 0.001$) and litter (β = -0.07, SE = 0.01, $P < 0.001$), the maximum male numbers at a lek decrease. Increasing grass height at 50 m (β = 0.03, SE = 0.01, $P <0.001$) increased maximum male numbers. As with prior distances, 2018 (β = 7.62, SE = 0.97, $P <0.001$) and 2019 (β = 7.69, SE = 0.54, $P <0.001$) were significant.

At 60 m ($F_{5, 30} = 50.41$, $P < 0.001$), increasing percent litter cover (β = -0.02, SE = 0.01, $P = 0.05$) and visual obstruction (β = -1.03, SE = 0.45, $P = 0.03$) decreased maximum male numbers. Increasing grass height at 60 m (β = 0.06, SE = 0.01, $P <0.001$) increased maximum male numbers and all years were also significant (2018 β =2.5, SE = 0.58, $P <0.001$; 2019 β =6.94, SE = 0.59, $P <0.001$; 2020 β = -0.98, SE = 0.38, $P=0.02$). At 70 m ($F_{3, 32} = 58.97$, $P < 0.001$), increasing grass height ($\beta = 0.03$, SE = 0.01, $P < 0.01$) increases the maximum number of males observed at leks and all years were significant.

For 80 m ($F_{6, 29} = 32.88$, $P < 0.001$), increased grass height ($\beta = 0.04$, SE = 0.01, $P < 0.01$) increased maximum male numbers and all years were significant (2018 $\beta = 5.3$, SE = 1.05, $P < 0.001$; 2019 $\beta = 7.03$, SE = 0.72, $P < 0.001$; 2020 $\beta = -1.17$, SE = 0.44, $P < 0.01$). At 90 m ($F_{3, 32} = 50.54$, $P < 0.001$) only the years of measurement were significant (2018 $\beta = 3.8$, SE = 0.62, $P < 0.001$; 2019 $\beta = 7.16$, SE = 0.73, $P < 0.001$; 2020 $\beta = -1.10$, SE = 0.46, $P = 0.02$). At the furthest distance measured, 100 m ($F_{5, 30} = 40.89$, $P < 0.001$), increased grass height ($\beta = 0.03$, SE = 0.01, $P < 0.01$) increased maximum male numbers and all years were significant (2018 $\beta = 3.16$, SE = 0.62, $P < 0.001$; 2019 $\beta = 7.91$, SE = 0.67, $P < 0.001$; 2020 $\beta = -0.86$, SE = 0.42, $P = 0.05$).

Lek Formation and Testing the Hotspot Hypothesis in Novel Habitat

Examination of all female VHF and GPS locations with the optimized hot spot maps show clusters of female locations by Broken Windmill and Circus leks, which straddle the northern and southern boundaries of the Cimarron National Grassland (Figure 3.5). Females that remain nearby to the release sites appear to avoid the Cimarron National Grassland, allocating their space utilization to the northern or southern CRP or private working lands (Figure 3.5). There was a cool spot north of this population center, which reflected a concentrated area of cropland and female locations as well as the formed leks tracked to the surrounding grasslands (Figure 3.5). Many of the leks to the north of the Cimarron National Grassland were located on either young green wheat or stubble from previous corn or grain sorghum crops, which were likely on the edges of the female home ranges in the area.

Female space use within the same breeding season exhibited a closer tie between where females are concentrated and where new leks formed than maps depicting lag points. The movements of newly released hens drive the formation of leks by males immediately after their release, rather than newly released males cuing to existing hen locations. However, leks that had high concentrations of lag points are those that have the greatest persistence on the landscape (Figures 3.8-3.9, 3.12-3.13).

Ephemeral leks (<4 males), which were short-lived leks that formed immediately after release and only lasted until the end of that breeding season, shared formation characteristics with leks that grow in size or maintain stability between years. New leks were typically ephemeral and their collapse within a single season can be attributed to female abandonment of nearby grassland habitat. As with lesser prairie-chicken leks in an established lek-complex in Short-Grass Prairie Ecoregion, leks that persisted into subsequent breeding seasons or increased in size between breeding seasons are those with greater female space use in the surrounding areas (Figures 3.6-3.7, 3.10-3.11, 3.14-3.15). As female locations shifted away from existing lek locations, newly formed leks quickly disappeared.

The number of nests around smaller, new leks was a good predictor of whether the lek will be ephemeral or persist into the next breeding season (Figure 3.16). With decreasing numbers of active nesting attempts from year to year, smaller leks ultimately disappeared within a season (Figure 3.16). Together with broader patterns of female locations and lek formation, this implicates that translocated male lesser prairie-chickens cue not necessarily to female movements, but to female habitat constraints. As with non-translocated birds in Short-Grass Prairie Ecoregion, the response by males to female space use was consistent with predictions of the hotspot hypothesis (Chapter 2).

Lek Dynamics At 10 km, 5 km, 2 km, and 1 km Spatial Scales

Maximum male numbers at leks decreased with increasing lengths of railroad at the 10 km scale ($F_{3,22} = 3.94$, $P = 0.02$; Table C.3), but the effect sizes are too small to hold biological relevance. The models based on female movements the same year they were released ($F_{1, 24} = 4.05$, $P = 0.06$; Table C.5) and prior movements ($F_{2, 18} = 2.07$, $P = 0.16$; Table C.4) were not significant at the 10 km scale. Starting at the 5 km scale, anthropogenic features no longer significantly influenced observed male maximum numbers ($F_{3, 22} = 2.35$, $P = 0.10$; Table C.3).

However, at the 5 km scale, both the same-year ($F_{4, 16} = 5.04$, $P = 0.01$; Table C.5) and lag points models ($F_{4, 21} = 6.57$, $P = 0.01$; Table C.4) are significant, with increasing number of same year nesting efforts ($\beta = 0.59$, SE = 0.22, $P = 0.01$; $\beta = 0.65$, SE = 0.22, $P = 0.01$) increasing maximum male numbers at leks. The number of active nests at 5 km appears to be a cue for male lesser prairie-chickens independent of percentage of grassland land cover, suggesting that males cue to females rather than habitat (Figure 3.17). This was also reflected in the substantial number of translocation leks ($n = 6$) that established in crop fields rather than grassland habitats (Figure 3.2).

Within a 2 km scale, both the prior and same year female movement models were significant ($F_{2, 15} = 16.33$, $P < 0.001$, Table C.4; $F_{2, 20} = 27.16$, $P < 0.001$, Table C.5), with the same model terms with minor variations on significance For the 2 km within-year female movement model, with an increasing number of female points ($\beta = 0.001$, SE = 0.0004, $P = 0.03$) and active nests ($\beta = 0.93$, SE = 0.23, $P < 0.001$) there is increasing observed maximum male numbers at leks. For the lag model, only increasing active nests increases maximum male numbers ($\beta = 1.17$, SE = 0.22, $P < 0.001$). The significance of same year female movements as well as prior year movements reflects the nature of translocation. With each introduction of birds in the spring, released males prioritize finding a site to display and were likely cuing off of female space use from hens released with them.

For established leks that have persisted into another breeding season, space use by females that have been translocated previously becomes an important determinant of male numbers. The pattern of female space use and nest-site selection driving lek dynamics continued within 1 km of leks. For the lag female movements model ($F_{4, 13} = 11.78$, $P < 0.001$; Table C.4) and increasing number of female movements ($\beta = 0.001$, SE = 0.0006, $P < 0.001$) and nests ($\beta = 1.32$, SE = 0.37, $P < 0.001$) increases maximum male numbers at leks. In the same year, female movements model ($F_{2, 20} = 10.79$, $P < 0.001$; Table C.5), increased nesting effort also increased observed male numbers ($\beta = 1.31$, SE = 0.35, $P < 0.001$).

Discussion

Previous translocation attempts moving lesser prairie-chickens from Kansas onto the Sand Sagebrush Prairie Ecoregion in Colorado from 1988-1996 failed (Snyder et al. 1999). The outcome of the current translocation effort is yet to be determined, but success will be measured through the ability of females to successfully nest and produce a viable population through successful recruitment. The ability of hens to differentiate the novel landscape of Sand Sagebrush Prairie Ecoregion is reflected in the persistence and dynamics of leks. Three of eighteen leks formed in the 4 years of monitored bird release in Kansas were ephemeral, suggesting that released hens failed to find habitat that fit their needs for nesting for multiple seasons and birds of both sexes abandoned the area.

For leks formed by translocated males on grassland, there were some significant differences between the leks formed in the Sand Sagebrush Prairie Ecoregion compared to those in the Short-Grass Prairie Ecoregion. Interestingly, grass height and visual obstruction were greater at translocation leks, although this is likely because the vast majority of leks formed after translocation were not on the Cimarron National Grassland (Figure 3.18). While the Cimarron National Grassland properties are extensively grazed, translocation leks that formed on private grassland properties have formed in areas that are not grazed. Capture lek sites in grassland of the Short-Grass Prairie Ecoregion were private working lands used for cattle production and in various stages of grazing rotation. Increasing grass height from lek center to 100 m at translocation leks increases maximum male numbers, which is distinct from increasing visual obstruction from other vegetation, which decreases maximum male numbers.

Despite the ecoregion-specific differences in plant communities between the Sand Sagebrush Prairie and Short-Grass Prairie ecoregions, dominant plant composition overlaps largely between the capture leks and leks formed after translocation. Common plant species for both translocation leks and capture sites were typically blue grama, side oats grama, or buffalo grass (Figure 3.19). These grass species are associated with grazing and would offer little visual obstruction. Increased grass height and visual obstruction at the Sand Sagebrush Prairie Ecoregion lek sites are likely due to the propensity of release site leks to form in grasslands that are not actively grazed. As with established lek complexes observed in Short-Grass Prairie and Mixed-Grass Prairie ecoregions (Chapter 2), formation and persistence of lek dynamics in the Sand Sagebrush Prairie Ecoregion translocated system were driven primarily by female space utilization. As expected under the hotspot hypothesis, the number of nesting attempts were a significant determinant of male numbers at leks from year to year. Additionally, the rapid formation and collapse of ephemeral leks within the same breeding season as release can be explained by female nesting attempts and space use.

The two most persistent translocated leks, a grassland and crop stubble lek, can be explained by the hotspot hypothesis, despite the differences in landcover. Female habitat constraints drive lek placement, and ultimately, the stability of that lek into subsequent breeding seasons. Their location and continuity indicate where hens have had the greatest and continued success in finding habitat with sufficient cover to nest within 5 to 2 km of the lek site, despite what seems on the surface to be an unconventional choice for a lek site.

While both leks have continued into the last year of active monitoring for the study, it appears that Circus lek, despite the 4-year persistence, is in a steady state of decline (Figure 3.20). The average number of displaying males have decreased each year, which matches a trend of decreasing numbers of nests in the surrounding habitat in each subsequent year (Figure 3.20). This is likely due in part to the loss of a nearby Conservation Reserve Program grassland and development of nearby oil infrastructure during the last 2 years of monitoring. Abandonment of Circus lek appears to be eminent, as newly discovered leks in the surrounding areas indicate that female nesting sites have shifted in response to changes in habitat quality. It is likely that some males will abandon, but the majority of males will remain and display at Circus until death, resulting in a slow but steady decline of this lek until its complete disappearance from this landscape. There is hope remaining in the development and discovery of leks to the south of Circus, suggesting female space use has shifted rather than females completely abandoning the area in long-distance dispersal (unpublished data).

In contrast, Broken Windmill remains in a location of relatively high nesting efforts within 5 km during each year of the study and is far more likely to persist into the near future (Figure 3.20). As the vegetation height increases from year to year at the lek site, it may eventually cause the lek to shift. However, as long as viable nesting habitat is available and there are females to nest, this lek is the most likely to persist.

Female spatial behaviors after release are also reflected in the existence of ephemeral leks and offer an explanation for the early breeding season movements of translocated males between leks. Typically in established lek complexes, lesser prairie-chicken males show high lek site fidelity (Woodward et al. 2001, Fuhlendorf et al. 2002, Pitman et al. 2006). However, translocated males were recorded making multiple movements among lek sites, although net dispersal is <20 km from the release site (Berigan 2019). Additionally, after breeding seasons have concluded, males have been observed moving extensively in patches with nesting sites, with spatial locations very close to individual nesting hens (personal observation).

It is also notable that during the course of the intensive monitoring of VHF and GPS locations from 2018-2020, leks formed by translocated males have predominantly been to the north and south of the Cimarron National Grasslands. This space use likely reflects the pursuit of visual obstruction creating quality nesting habitat. Only 31 of 134 nests (23%) documented from 2017-2020 were located on the Cimarron National Grasslands (unpublished data). Two translocation leks formed on National Grassland property, one nearby the 2019 release site which was one of the few locations to have several nesting hens on the Cimarron National Grasslands, and the other located on the northern edge adjacent to private land with nesting activity.

Despite the focus on fecundity and female habitat constraints within lesser prairie-chicken research, when and how females select their nest sites is shrouded in mystery. The ability of males to track female movements and nest-site selection within the span of weeks after being released in a novel environment is nothing short of remarkable. While 69% of lesser prairie-chicken females returned after long-distance dispersals (>300 km; Figure 3.1), it is unclear what factors determine why females stop dispersing and attempt nesting after translocation, as neither leks nearby the release site or quality of habitat causes them to stop their dispersal movements (Berigan 2019).

However, there is some evidence that the relationship between female space use and lek formation and presence matters in the success of translocation of lekking grouse. Released male, hand-reared greater prairie-chickens in Wisconsin stayed near captive females to establish a lek (Toepfer 1976). Translocation studies of sage grouse (*Centrocercus urophasianus*) failed when individuals returned to familiar leks near nesting females (Toepfer et al. 1990). While recruitment of males to leks determines lek continuity, increasing female nest site-selection and space use nearby is best determinant of whether juvenile males will join an existing lek.

Now that translocation of birds from the Short-Grass prairie has ended, persistence of monitored leks will depend predominately on the ability to maintain quality nesting habitat in core use areas. Managing for lek sites is unnecessary, as evident by the longest persisting lek being located in crop stubble and a total of 6 translocation leks forming in cultivated fields. Keeping leks active and lesser prairie-chickens on the landscape will rest on female habitat constraints. Shifting and unstable lek dynamics are a signal of a lack of nesting habitat and continued dispersal of females.

Management Implications

Translocation is a potential management strategy for lesser prairie-chickens, but relocation of a lek-breeding species comes with unique considerations and complications. While translocation has been employed in lek-breeding prairie-grouse many times before, almost all of these efforts have failed, including a prior effort in Colorado Sand Sagebrush Prairie Ecoregion (Snyder et al. 1999). Some commonalities include the utilization of hard release techniques and failure to optimize the likelihood of translocated females nesting after release (Snyder et al. 1999). It is possible to use calls and decoys as artificial cues for males to form leks in a desired location, but these translocation efforts also ultimately fail when the leks do not persist. These prior efforts and the design of this translocation rest on the assumption that the formation of leks drive prairie-grouse dispersal into novel habitats and, by establishing males and leks on the landscape first, birds would be less predisposed to disperse from the release site. Interestingly, this assumption is in odds with the core of lesser prairie-chicken management, which prioritizes female habitat constraints and habitat needs as both the limiting sex and sole parent for offspring. Even after leks were established at the Kansas release site, translocated female lesser prairie-chickens often nested (<3.2 km) from known leks (Berigan 2019).

Instead, managers should consider how to work within female reproductive and habitat constrains for the purpose of translocation. In established Kansas lek complexes, ~25% of the landscape within 5 km is quality nesting habitat (Gehrt et al. 2020). Prior to future translocation efforts, the availability and quality of nesting habitat at the desired release site should be determined. The ~25% nesting habitat in established lek complexes is under management goals and it is likely for any effort involving prairie-chickens that establishing a greater percentage of nesting habitat within 5 km of the desired location for leks would assist greatly in maintaining leks that form immediately after release (Gehrt et al. 2020).

For long-term viability of translocated lesser prairie-chickens on the landscape, it is also necessary to anticipate vegetation community changes and structural needs under climate change projections for the Great Plains. Ability to mitigate woody encroachment and maintain thermal refuge and robust forbs should ideally also be considered prior to translocation. Anticipating and planning for female habitat constraints will determine the outcome of lesser prairie-chicken translocation efforts.

Conclusion

As with established lek complexes observed in Short-Grass Prairie and Mixed-Grass Prairie Ecoregions, formation and persistence of lek dynamics in the Sand Sagebrush Prairie Ecoregion translocated system are driven primarily by female space utilization. As expected under the hotspot hypothesis, the number of nesting attempts were a significant determinant of male numbers at leks. Even the rapid formation and collapse of ephemeral leks within the same breeding season as release can be explained by female nesting attempts and space use. Most translocated leks collapsed within 2 years, with the exception of 2, which implicates that there are few areas capable of sustaining continued nesting efforts by hens. Future translocation efforts should address the available nesting habitat prior to the release of birds and determine if there is sufficient cover to sustain long-term nest site selection. Alternative translocation methods such as translocated birds outside of the breeding season or using a soft rather than hard release may also prove more fruitful for keeping females in desired locations on the landscape.

Stable leks will form in response to female space utilization, as short grassland is rarely limiting, and lesser prairie-chickens have shown a propensity to use any short vegetation to establish a lek when female habitat needs are met in the surrounding landscape. As the dispersing and limiting sex, females ultimately determine if birds will stay at a targeted release site and if translocation can reestablish a viable population. Lek dynamics can be used to assess if these needs are met in future monitoring of the translocated birds in the Sand Sagebrush Prairie Ecoregion, as maximum male numbers are a reflection of female habitat needs and whether or not hens can find quality habitat for nesting on the landscape.

Literature Cited

Agriculture, U. S. D. of. 2012. Conservation Programs. 2:83–91.

Anderson, R. K. 1969. Prairie chicken responses to changing booming-ground cover type and height. Journal of Wildlife Management 33:636–643.

Baxter, R. J., R. T. Larsen, and J. T. Flinders. 2013. Survival of resident and translocated greater sage-grouse in Strawberry Valley, Utah: A 13-year study. Journal of Wildlife Management 77:802–811.

Bedrosian, B., and D. Craighead. 2007. Evaluation of techniques for attaching transmitters to common raven nestlings. Northwestern Naturalist 88:1–6.

Bergerud, A. T., and M. W. Gratson, editors. 1988. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis.

Berigan, L. A. 2019. Dispersal, reproductive success, and habitat use by translocated lesser prairie-chickens. Thesis, Kansas State University, Manhattan, KS.

Bradbury, J. W., R. M. Gibson, C. E. McCarthy, and S. L. Vehrencamp. 1989*a*. Dispersion of displaying male sage grouse - II. The role of female dispersion. Behavioral Ecology and Sociobiology 24:15–24.

Bradbury, J. W., S. L. Vehrencamp, and R. M. Gibson. 1989*b*. Dispersion of displaying male sage grouse - I. Patterns of temporal variation. Behavioral Ecology and Sociobiology 24:1–14.

Cleasby, I. R., E. Owen, L. Wilson, E. D. Wakefield, P. O’Connell, and M. Bolton. 2020. Identifying important at-sea areas for seabirds using species distribution models and hotspot mapping. Biological Conservation 241:108375.

Coates, P. S., and D. J. Delehanty. 2006. Effect of capture date on nest-attempt rate of translocated sharp-tailed grouse Tympanuchus phasianellus. Wildlife Biology 12:277–283.

Copelin, F. 1963. The lesser prairie chicken in Oklahoma. Oklahoma Wildlife Conservation Department, Oklahoma City, OK.

Dahlgren, D. K., R. D. Rodgers, R. D. Elmore, and M. R. Bain. 2016. Grasslands of western Kansas, north of the Arkansas River. Pages 259–280 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. D. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6.

ESRI. n.d. How hot spot analysis (Getis-Ord Gi) works. ArcGIS Pro. <https://pro.arcgis.com/en/pro-app/tool-reference/spatial-statistics/h-how-hot-spot-analysis-getis-ord-gi-spatial-stati.htm>.

ESRI. n.d. Optimized Hot Spot Analysis. ArcGIS Pro. <https://pro.arcgis.com/en/pro-app/tool-reference/spatial-statistics/optimized-hot-spot-analysis.htm#:~:text=Given>.

ESRI. n.d. How optimized hot spot analysis works. ArcGIS Pro. <https://pro.arcgis.com/en/pro-app/tool-reference/spatial-statistics/how-optimized-hot-spot-analysis-works.htm>.

ESRI. n.d. How Kernel Density works. ArcGIS Pro. <https://pro.arcgis.com/en/pro-app/tool-reference/spatial-analyst/how-kernel-density-works.htm>.

Farve, R. 2012. Demonstration of satellite/GPS telemetry for monitoring fine-scale movements of lesser prairie-chickens. United States Department of Agriculture Forest Service National Technology & Development Program Inventory and Monitoring, San Dimas Technology and Development Center, California.

Fields, T. L., G. C. White, W. C. Gilgert, and R. D. Rodgers. 2006. Nest and brood survival of lesser prairie-chickens in west central Kansas. Journal of Wildlife Management 70:931–938.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie, and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landscape Ecology 17:617–628.

Garton, E. O., C. A. Hagen, G. M. Beauprez, S. C. Kyle, J. C. Pitman, D. D. Schoeling, and W. E. V. Pelt. 2016. Population dynamics of the lesser prairie-chicken. Pages 49–76 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Gehrt, J. M., D. S. Sullins, and D. A. Haukos. 2020. Looking at the bigger picture: how abundance of nesting and brooding habitat influences lek-site selection by lesser prairie-chickens. American Midland Naturalist 183:52–77.

Gruber-Hadden, N. W., T. A. Messmer, B. D. Maxfield, D. N. Koons, and M. R. Guttery. 2016. Population vital rates of resident and translocated female greater sage-grouse. Journal of Wildlife Management 80:753–760.

Hagen, C. A., E. O. Garton, G. Beauprez, B. S. Cooper, K. A. Fricke, and B. Simpson. 2017. Lesser prairie-chicken population forecasts and extinction risks: an evaluation 5 years post-catastrophic drought. Wildlife Society Bulletin 41:624–638.

Hagen, C. A., G. C. Salter, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2005. Lesser prairie-chicken brood habitat in sand sagebrush: invertebrate biomass and vegetation. Wildlife Society Bulletin 33:1080–1091.

Haukos, D. A., and C. W. Boal, editors. 2016. Ecology and conservation of lesser prairie-chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Haukos, D. A., A. A. Flanders, C. A. Hagen, and J. C. Pitman. 2016. Lesser prairie-chickens of the Sand Sagebrush Prairie. Pages 281–298 *in*. Ecology and Conservation of Lesser Prairie-Chickens. Volume 48. Studies in Avian Biology, Cooper Ornithological Society, CRC Press, Boca Raton, FL.

Haukos, D. A., and L. M. Smith. 1999. Effects of lek age on age structure and attendance of lesser prairie-chickens (Tympanuchus pallidicinctus). American Midland Naturalist 142:415–420.

Homer, C., J. Dewitz, S. Jin, G. Xian, C. Costello, P. Danielson, L. Gass, M. Funk, J. Wickham, S. Stehman, R. Auch, and K. Riitters. 2020. Conterminous United States land cover change patterns 2001–2016 from the 2016 National Land Cover Database. ISPRS Journal of Photogrammetry and Remote Sensing 162:184–199.

Jensen, W. E., D. A. Robinson, and R. D. Applegate. 2000. Distribution and population trend of lesser prairie-chicken in Kansas. Prairie Naturalist 32:169–175.

Jiguet, F., and V. Bretagnolle. 2006. Manipulating lek size and composition using decoys: an experimental investigation of lek evolution models. American Naturalist 168:758–768.

Kuletz, K. J., M. C. Ferguson, B. Hurley, A. E. Gall, E. A. Labunski, and T. C. Morgan. 2015. Seasonal spatial patterns in seabird and marine mammal distribution in the eastern Chukchi and western Beaufort seas: Identifying biologically important pelagic areas. Progress in Oceanography 136:175–200.

McDonald, L., K. Nasman, T. Rintz, F. Hornsby, and G. Gardner. 2016. Range-wide population size of the lesser prairie-chicken: 2012, 2013, 2014, 2015, 2016. West EcoSystems Technology, Inc., Laramie, Wyoming.

Nasman, K., T. Rintz, R. Clark, G. Gardner, and L. McDonald. 2018. Range-wide population size of the lesser prairie-chicken: 2012 to 2018. West EcoSystems Technology, Inc., Laramie, Wyoming.

Niemuth, N. D. 2000. Land use and vegetation associated with greater prairie-chicken leks in an agricultural landscape. Journal of Wildlife Management 64:278.

Pitman, J. C., B. E. Jamison, C. A. Hagen, R. J. Robel, and R. D. Applegate. 2006. Brood break-up and juvenile dispersal of lesser prairie-chicken in Kansas. Prairie Naturalist 38:85–99.

Pyle, P. 2008. Lesser Prairie-Chicken Tympanuchus pallidicinctus. Pages 195–197 *in*. Identification Guide to North American Birds Part II. Slate Creek Press, Point Reyes Station.

Robinson, S. 2015. Landscape ecology, survival, and space use of lesser prairie-chickens. Thesis, Kansas State University, Manhattan, KS.

Robinson, S. G., D. A. Haukos, R. T. Plumb, J. D. Kraft, D. S. Sullins, J. M. Lautenbach, J. D. Lautenbach, B. K. Sandercock, C. A. Hagen, A. Bartuszevige, and M. A. Rice. 2018. Effects of landscape characteristics on annual survival of lesser prairie-chickens. American Midland Naturalist 180:66–86.

Rodgers, R. D. 1992. A technique for establishing sharp-tailed grouse in unoccupied range. Wildlife Society Bulletin (1973-2006) 20:101–105.

Shilling, F. M., and D. P. Waetjen. 2015. Wildlife-vehicle collision hotspots at US highway extents: scale and data source effects. Nature Conservation 11:41–60.

Snyder, J. W., E. C. Pelren, and J. A. Crawford. 1999. Translocation histories of prairie grouse in the United States. Wildlife Society Bulletin (1973-2006) 27:428–432.

Spencer, D., D. Haukos, C. Hagen, M. Daniels, and D. Goodin. 2017. Conservation Reserve Program mitigates grassland loss in the lesser prairie-chicken range of Kansas. Global Ecology and Conservation 9:21–38.

Sullins, D. S. 2017. Regional variation in demography, distribution, foraging, and strategic conservation of lesser prairie-chickens in Kansas and Colorado. Dissertation, Kansas State University, Manhattan, KS.

Sullins, D. S., J. D. Kraft, D. A. Haukos, S. G. Robinson, J. H. Reitz, R. T. Plumb, J. M. Lautenbach, J. D. Lautenbach, B. K. Sandercock, and C. A. Hagen. 2018. Demographic consequences of conservation reserve program grasslands for lesser prairie-chickens. Journal of Wildlife Management 82:1617–1632.

Toepfer, J. E. 1976. Movements and behavior of transplanted radio-tagged prairie chickens in Wiisconsin. Thesis, University of Wisconsin Stevens Point, Stevens Point, Wisconsin.

Toepfer, J. E., R. L. Eng, and R. K. Anderson. 1990. Translocating Prairie Grouse: What Have We Learned? Pages 569–579 *in*. Transactions of the North American Natural Resources Conference.

Weil, B., and B. Jensen. 2015. An unexpected journey: Greater prairie-chicken travels nearly 4000km after translocation to Iowa. American Midland Naturalist 174:343–349.

Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie, and J. Shackford. 2001. Influence of landscape composition and change on lesser prairie-chicken (Tympanuchus pallidicinctus) populations. American Midland Naturalist 145:261–274.

Figures

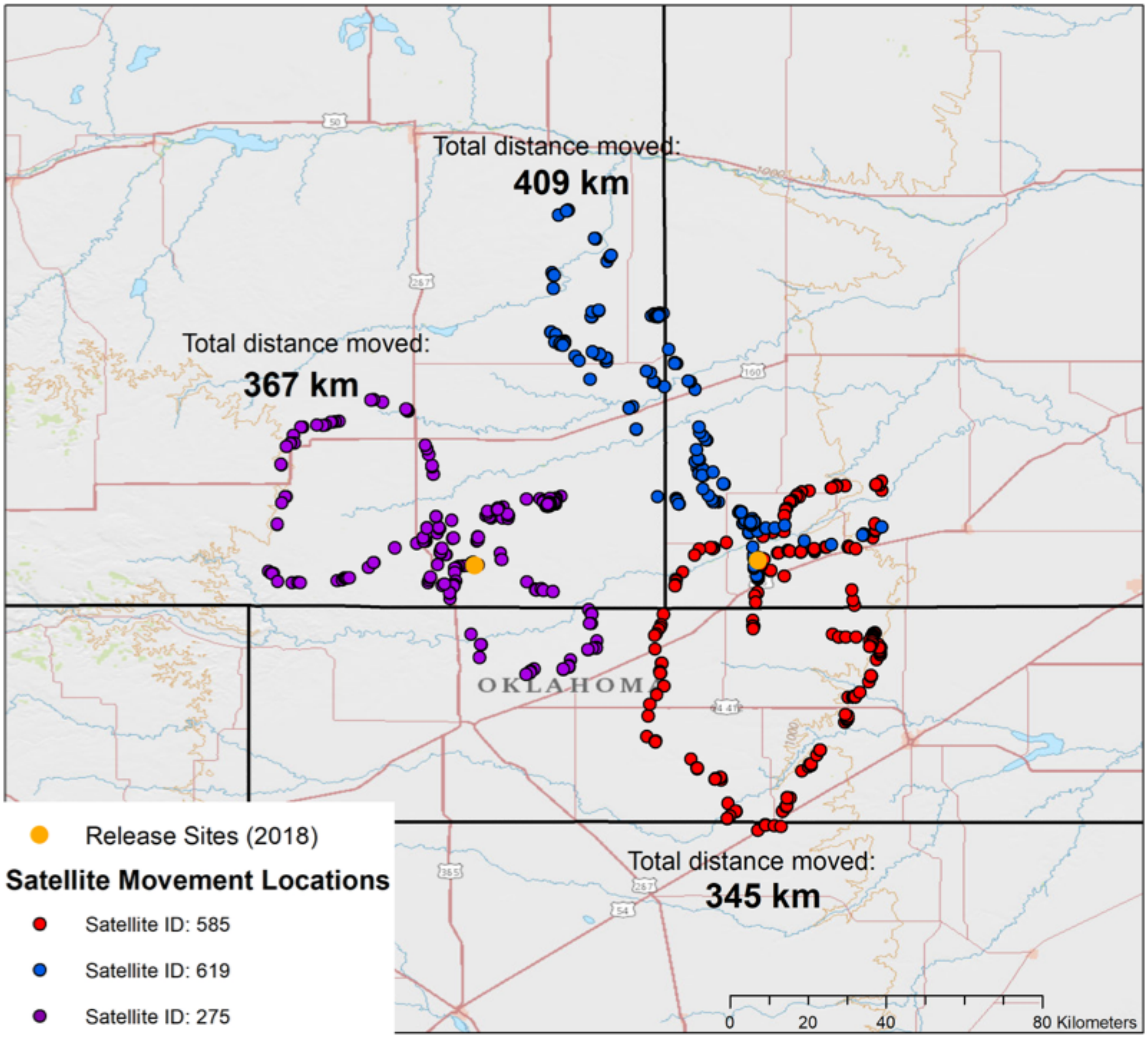

Figure 3.1 Females translocated to the Sand Sagebrush Prairie of southwestern Kansas regularly exceeded 300 km dispersal movements, with patterns that resembled exploratory loops (with home range establishment near the release site) rather than permanent dispersal.

Figure from Berigan (2019).

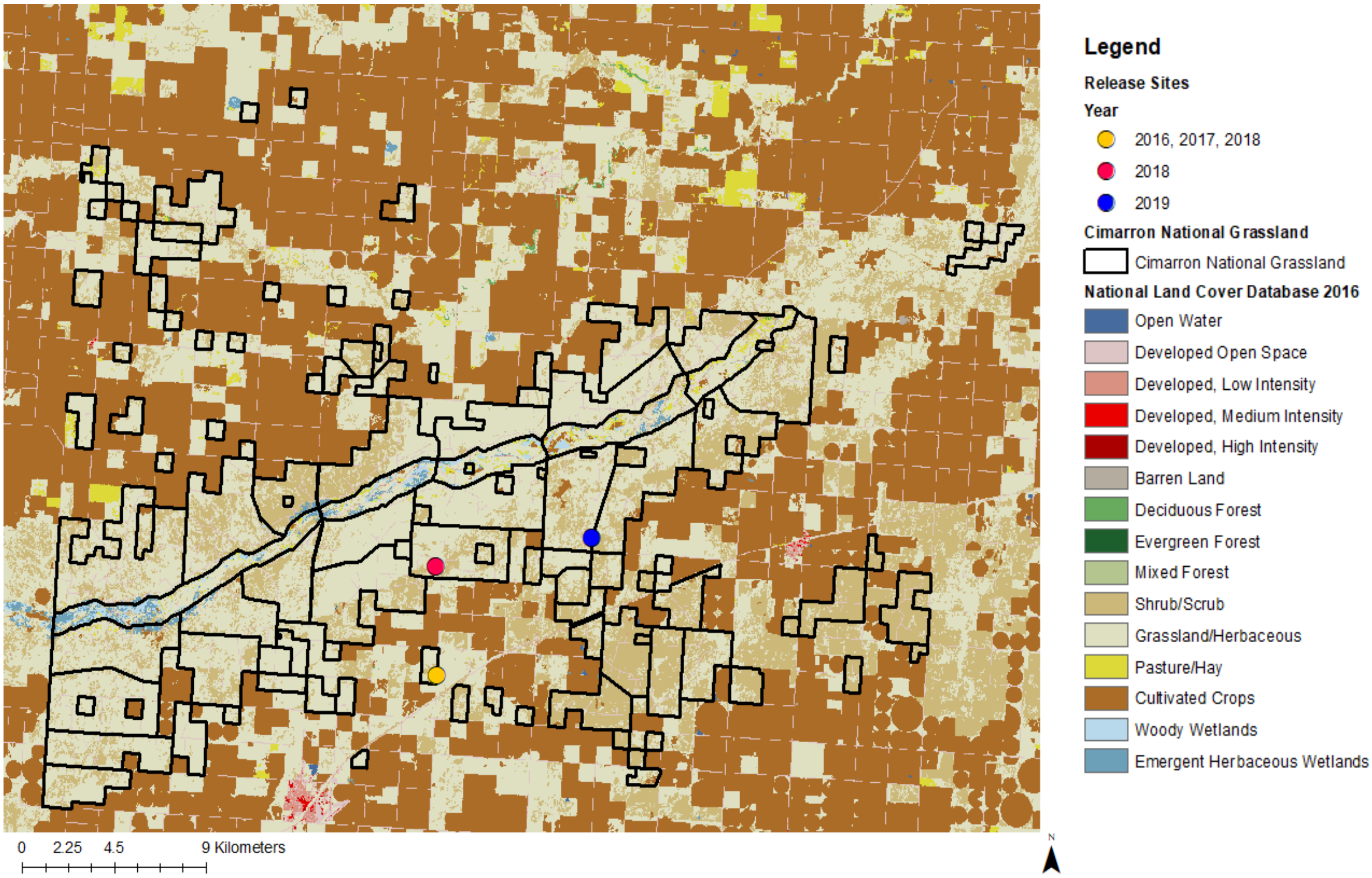

Figure 3.2 Location of the 3 release sites (indicated by colored point) on the Cimarron National Grasslands in southwestern Kansas from 2016-2019 for lesser prairie-chickens translocated from northwest Kansas.

Release sites were predetermined based on lesser prairie-chicken space use, focusing on releasing birds close to active leks.

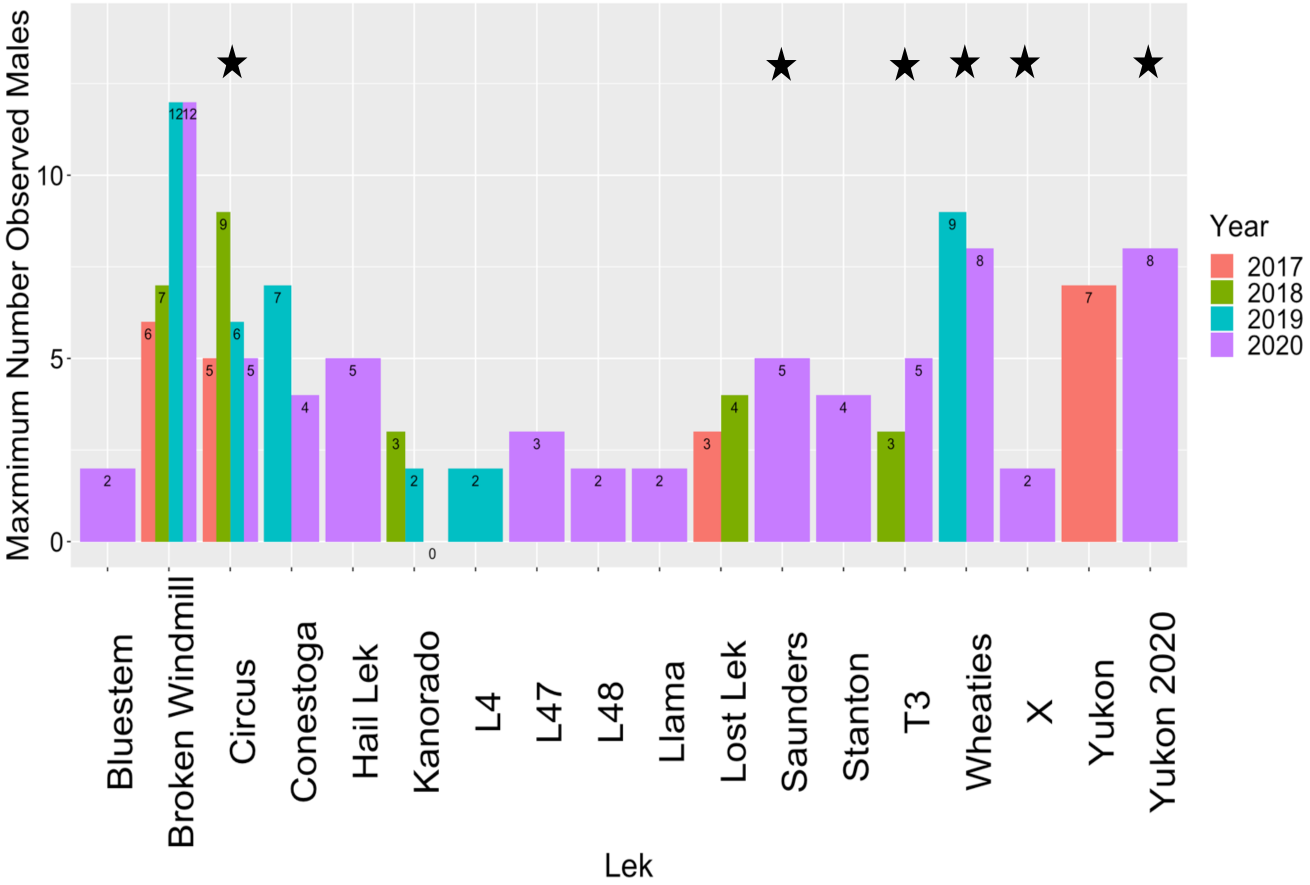

Figure 3.3 Maximum male counts on 17 leks formed after translocation of lesser prairie-chickens to the Kansas Sand Sagebrush Prairie Ecoregion from 2016-2019.

Notably many leks are ephemeral, collapsing within weeks of formation before the end of the breeding season. While groups of 2 males are insufficient to be classified as a lek (≥3 males), with the rapid turnover of lek sites it is worth noting the grouping as a potential location for a full lek in the subsequent year. Stars indicate crop leks.

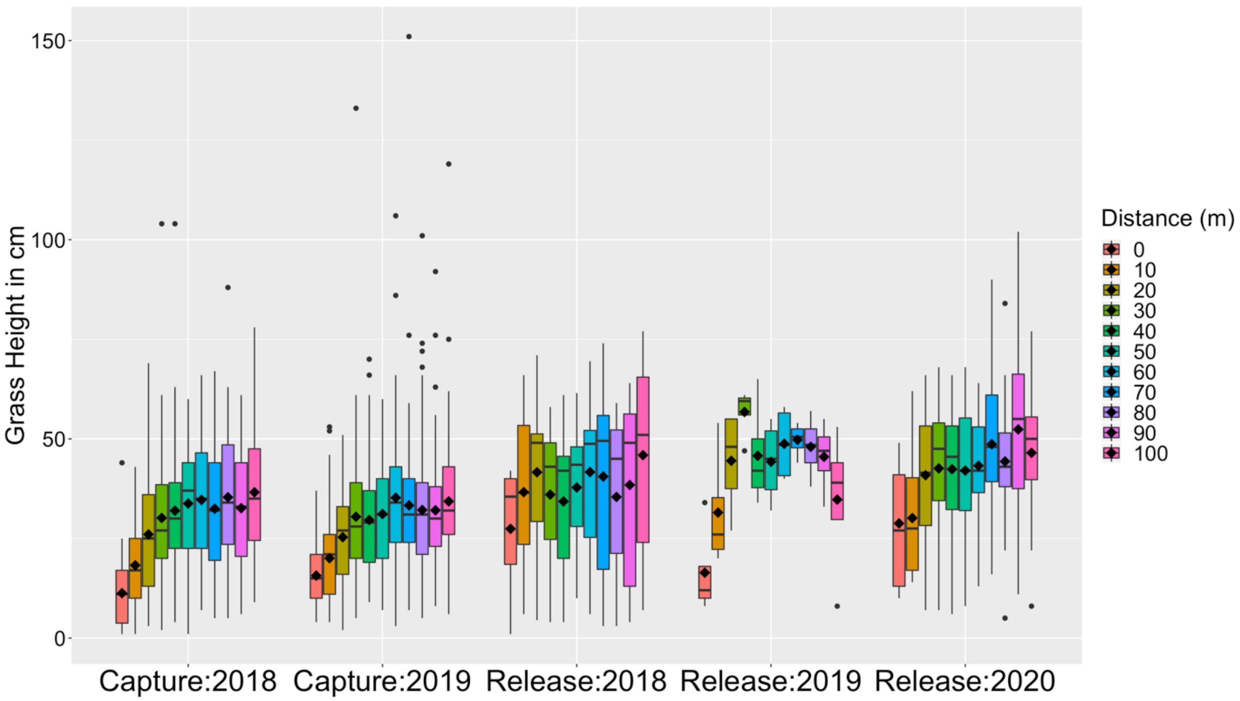

Figure 3.4 Lek grass height by distance measured from lek center at capture leks in Short Grass Prairie and translocation leks in Sand Sagebrush Prairie Kansas from 2018-2020.

While there is a greater range of tall grasses at Short-Grass capture leks, most measured grass on translocated leks were greater than that of the capture site. Additionally, overall grass height for translocated leks increased in 2020, especially notable in the lek center (0-30 m).

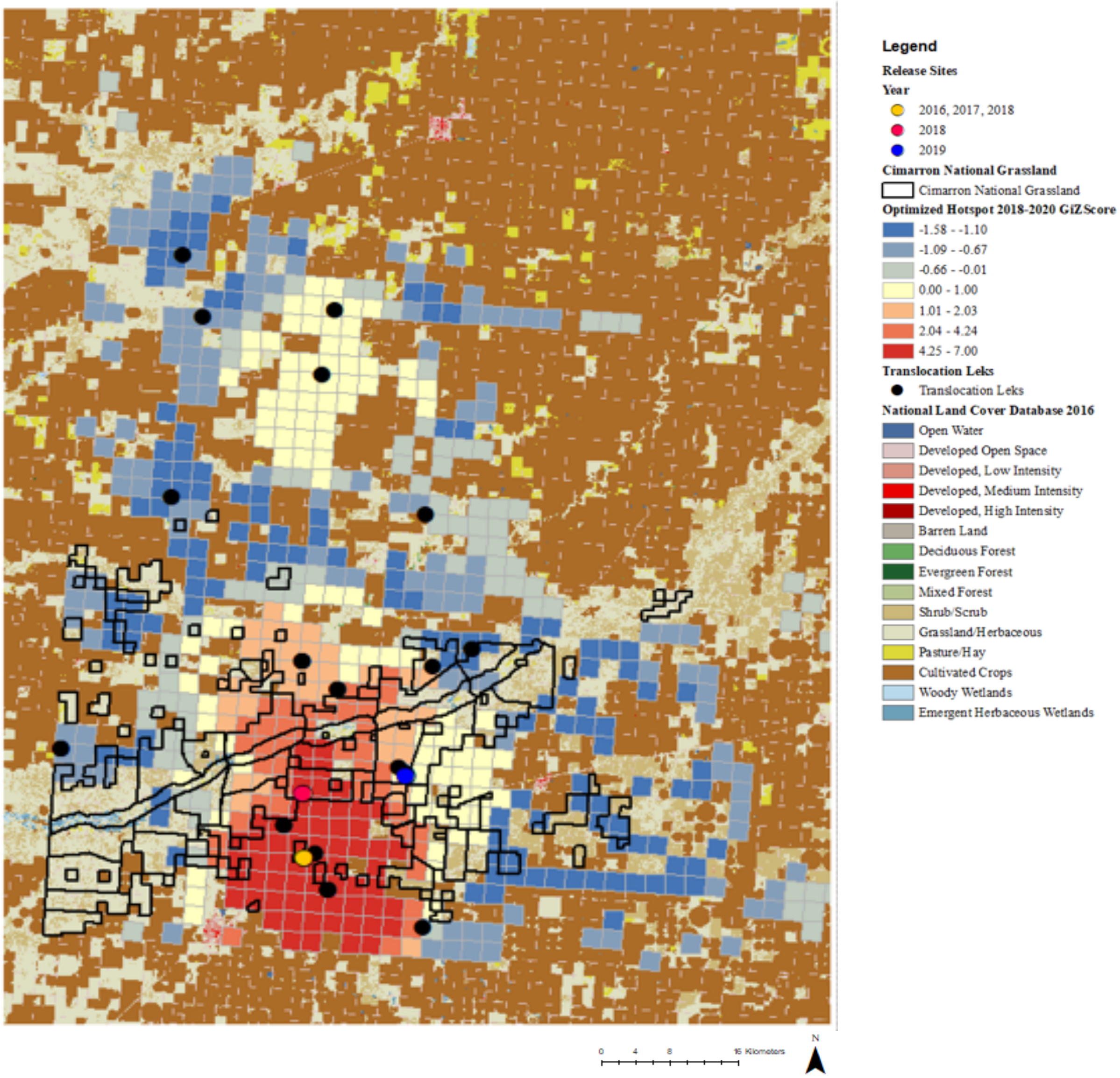

Figure 3.5 Optimized hotspot map of all VHF and GPS female locations from 2018-2020 for all released female lesser prairie-chickens that lived for more than three months after translocation to the Sand Sagebrush Prairie in southwestern Kansas.

Fishnet polygon cell size 1868 m, with an optimal fixed distance of 7963 m, and 594 weighted polygons ($\bar{x}$ = 63.68, SD = 257.41). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. Female spatial use straddles the Cimarron National Grassland, depicted as an outline, and the north and southern boundaries held the two most persistent leks. In 2020, more leks were discovered further north of the grasslands, where the tighter soils encourage more of short-grass plant community.

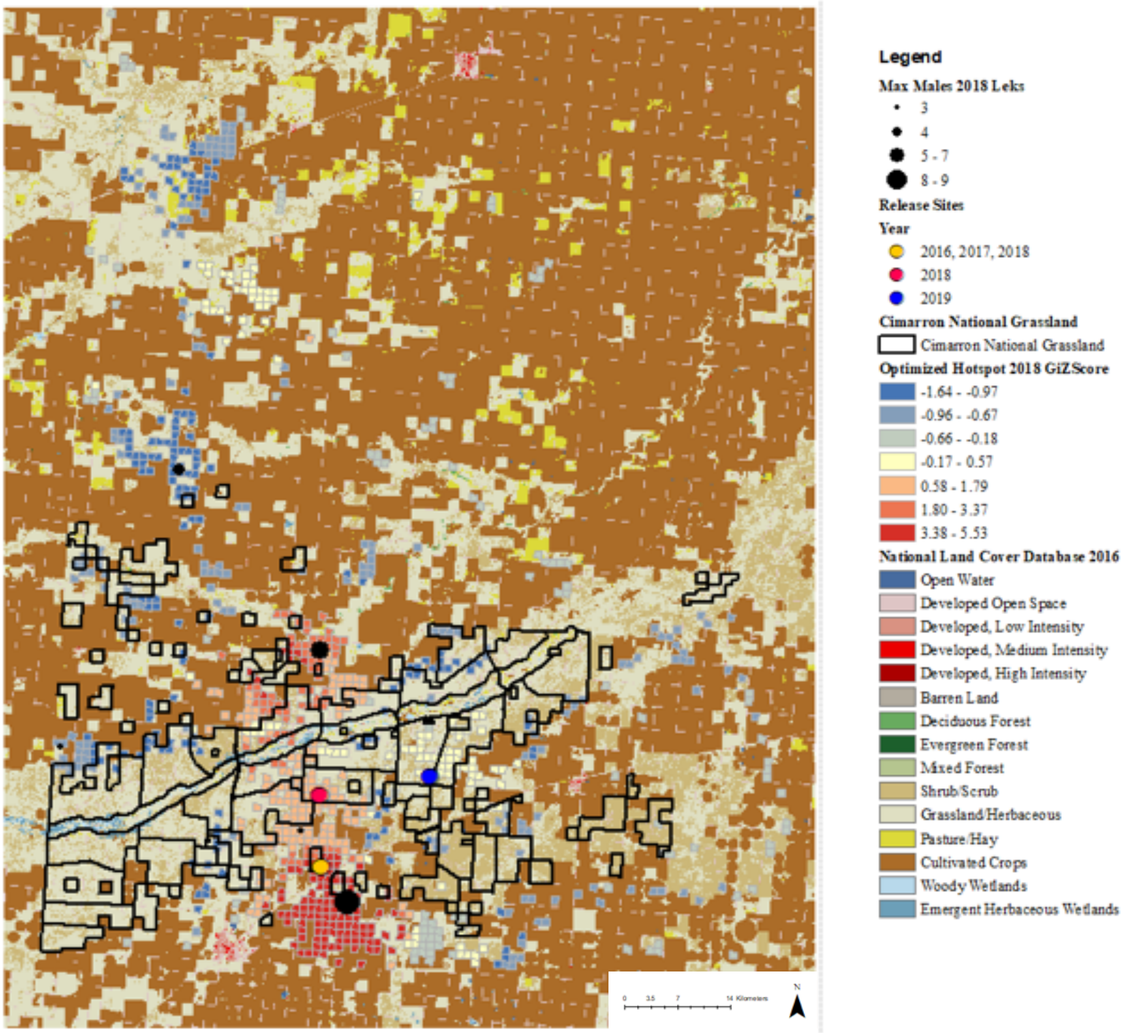

Figure 3.6 Optimized hot spot map of same year female locations in 2018 and maximum male numbers at leks sites in the Sand Sagebrush Prairie of southwestern Kansas.

Fishnet polygon cell size for 2018 was 660 m, with an optimal fixed distance of 4964.46 m, and 923 weighted polygons ($\bar{x}$ = 15.42, SD = 62.88). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. The two leks with the greatest concentrated locations are Broken Windmill to the north and Circus to the south. Smaller ephemeral leks formed in areas of female space use between Broken Windmill to the north and Circus to the south, but these leks did not persist past the end of the 2018 breeding season.

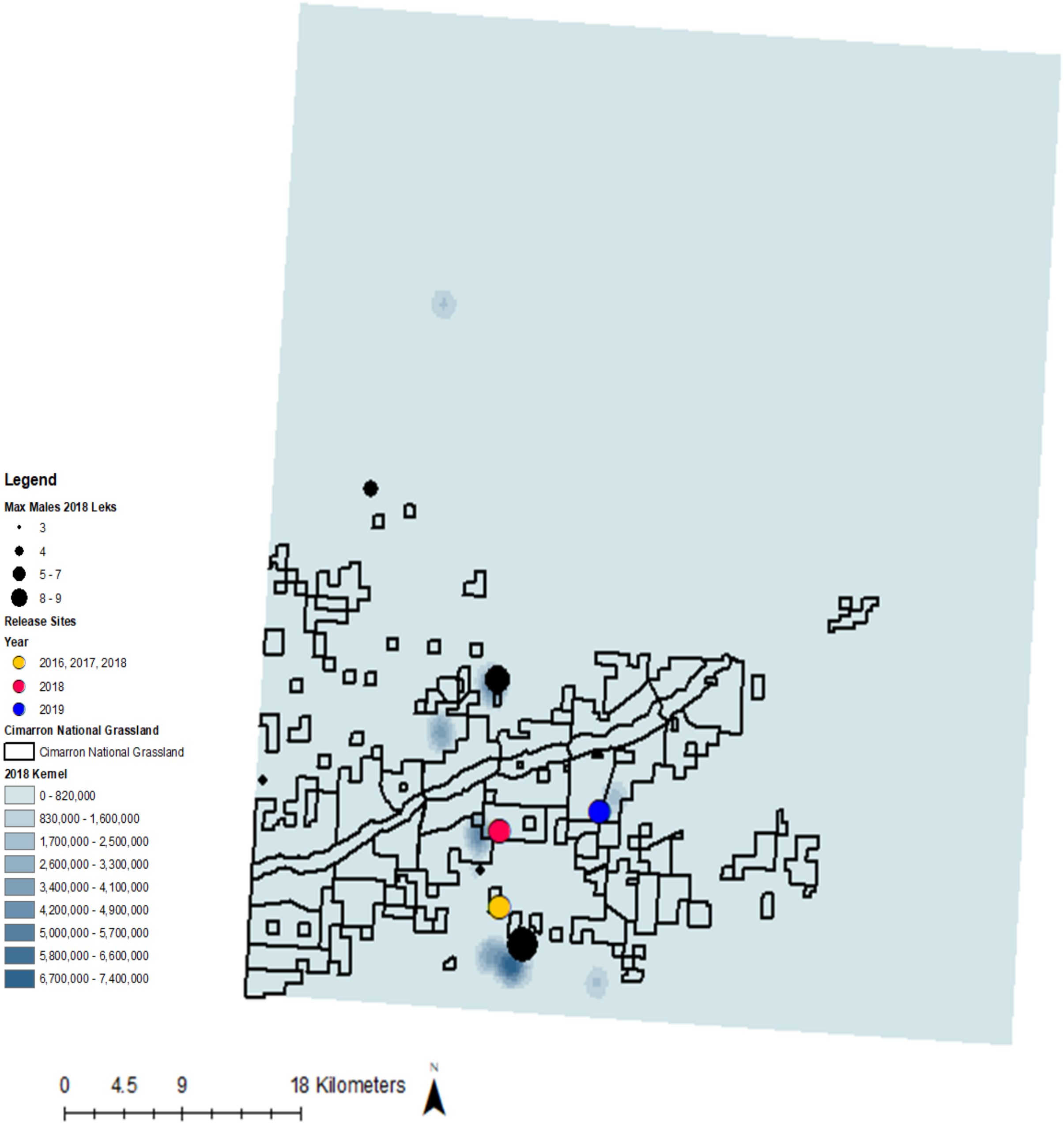

Figure 3.7 Kernel density map of same year VHF and GPS locations as 2018 lek male high counts of leks formed by translocated males in the Sand Sagebrush Prairie of southwestern Kansas.

Density of female location points can be observed by the central ephemeral lek, but despite having concentrated female use nearby, the lek collapses like the other two lek points sans female locations.

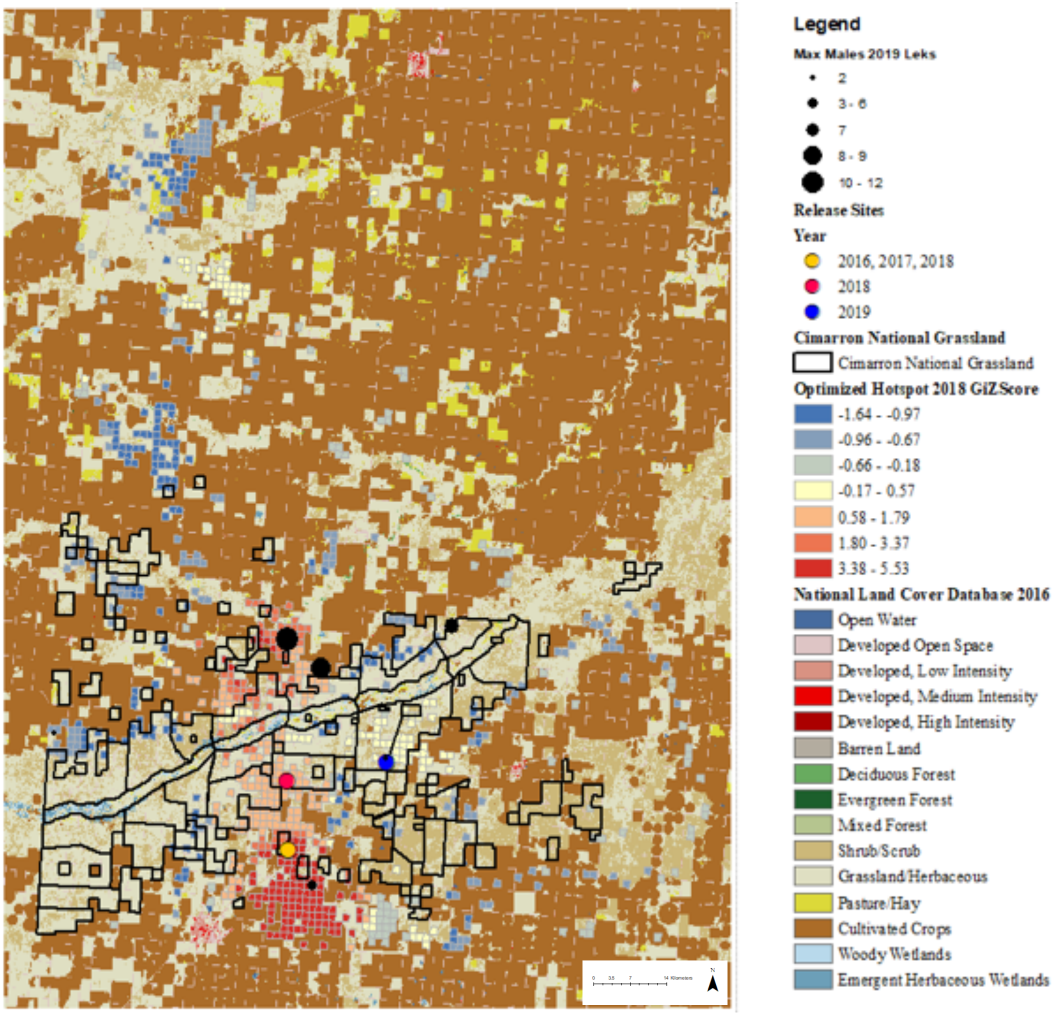

Figure 3.8 Optimized hot spot map of female lag points from 2018 in the year prior to male counts at Kansas Sand Sagebrush prairie translocation leks in 2019.

Fishnet polygon cell size for 2018 was 660 m, with an optimal fixed distance of 4964.46 m, and 923 weighted polygons ($\bar{x} = 15.42$, SD = 62.88). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. While there were female lag-points by newly formed leks, there were no significant concentrations of female points, suggesting that males were cuing closely to released females shortly after release.

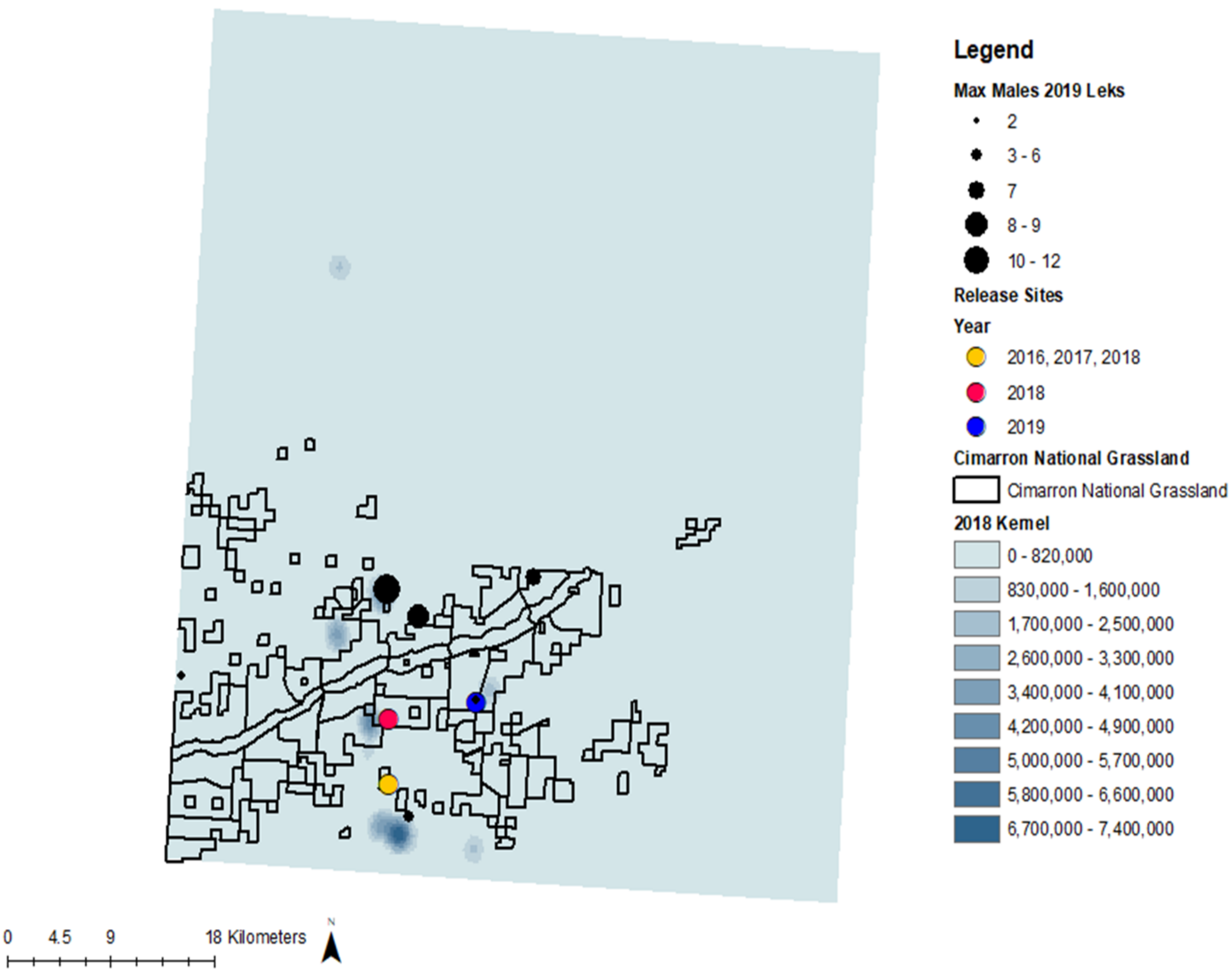

Figure 3.9 Kernel density map of female lag points from 2018 prior to 2019 male counts at translocation leks in Sand Sagebrush Prairie of southwestern Kansas.

The concentrations of female lag points are primarily observed at the northern and southern edges of the Cimarron National Grassland by Broken Windmill and Circus leks. It is worth noting that the concentrated areas of female spatial locations from 2018 that do not have leks associated with them in 2019 were confirmed as lek locations in 2020.

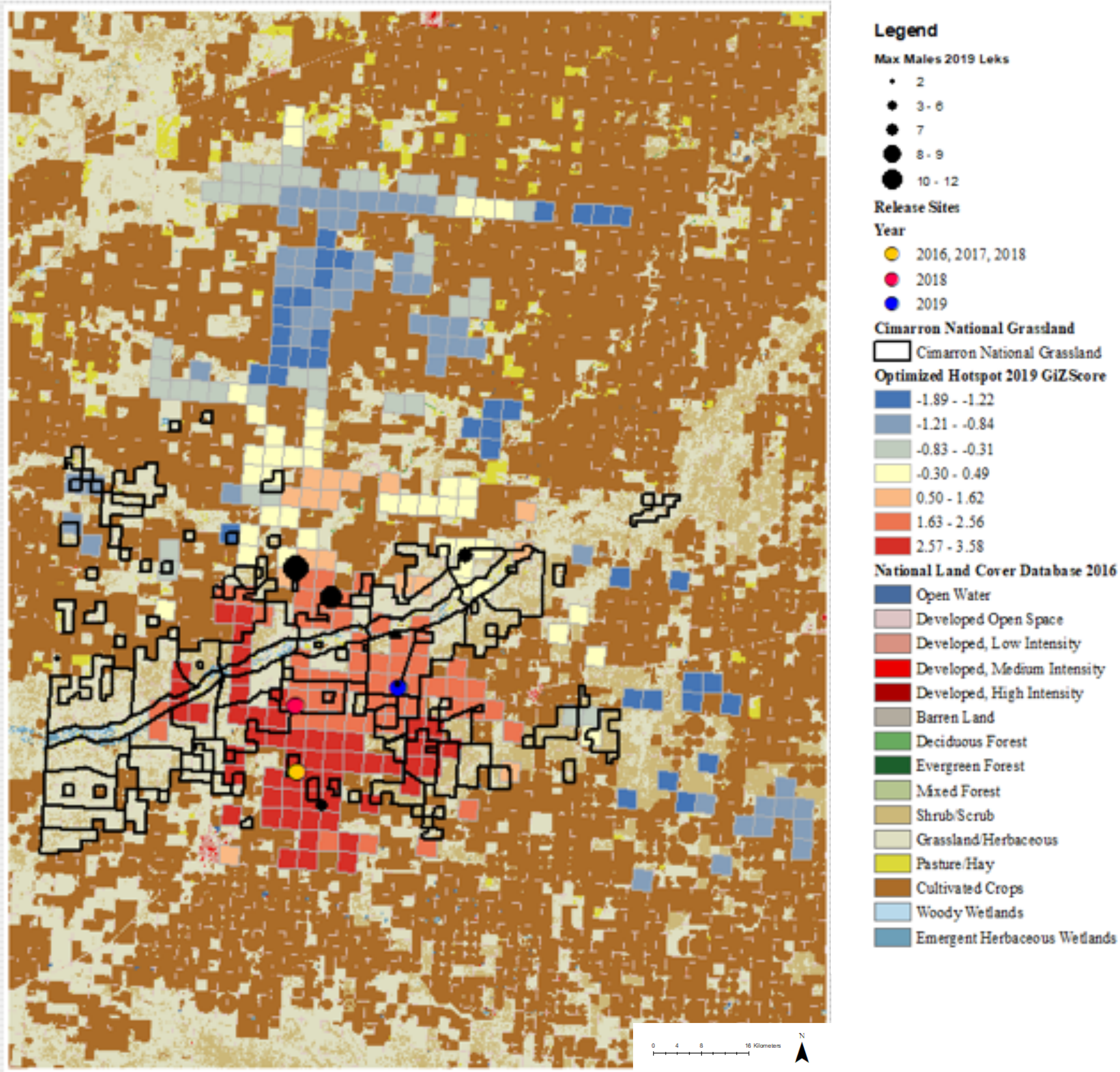

Figure 3.10 Optimized hot spot map of same year female locations and 2019 max male numbers in the Sand Sagebrush prairie of southwestern Kansas.

Fishnet polygon cell size for 2019 was 1868 m, with an optimal fixed distance of 16791.61 m, and 302 weighted polygons ($\bar{x}$ = 59.46, SD = 215.16). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. Leks that form after the translocation of birds in the 2019 breeding season are in concentrated areas of female locations, including the lek that formed nearby the primary release site of 2019.

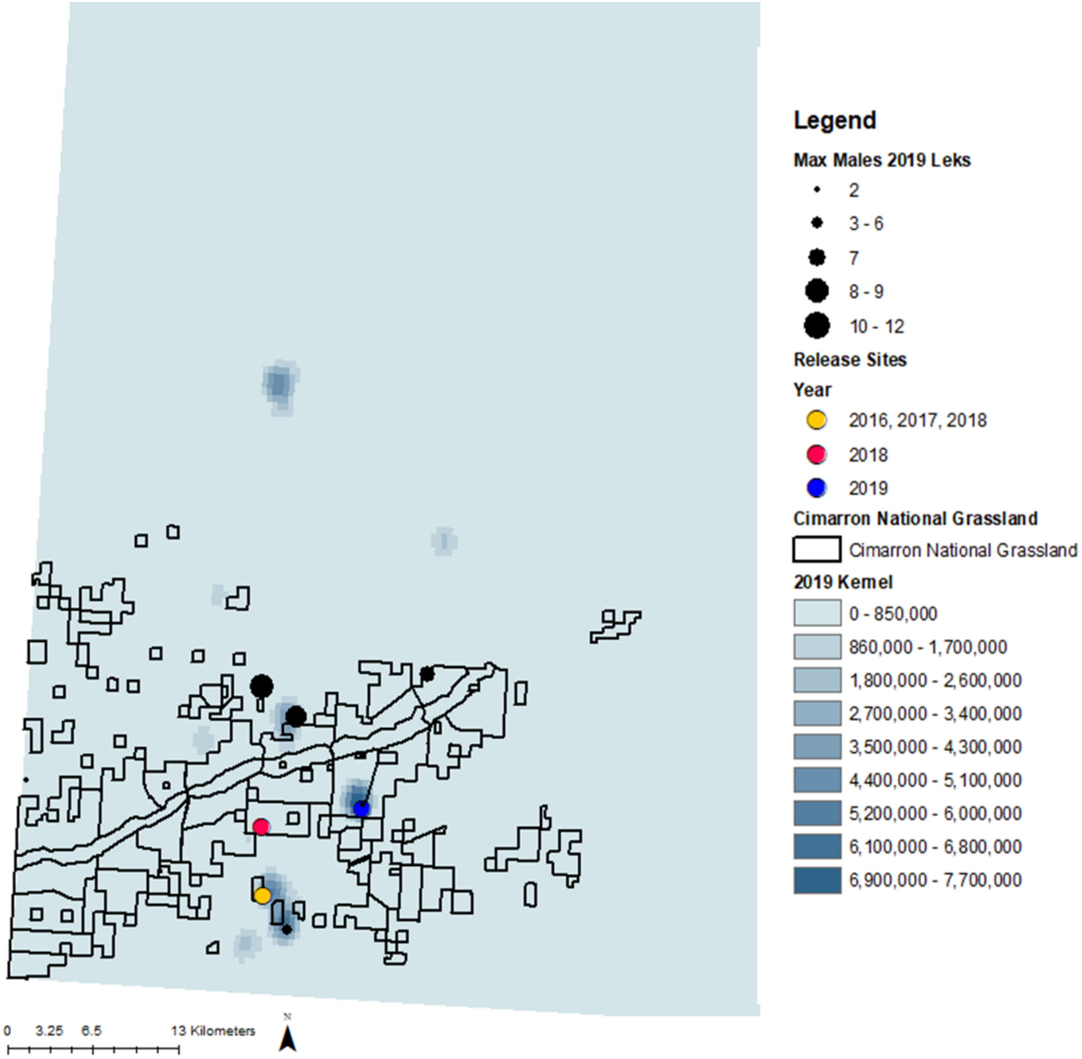

Figure 3.11 Kernel density map of same year female locations and 2019 max male numbers at translocation leks in Sand Sagebrush Prairie of southwestern Kansas.

Same year female locations match closely to where translocated males formed leks. The concentration of locations to the north suggests that leks discovered in 2020 were likely present the at least the year prior to their documentation. In conjunction with the kernel map of 2018 female locations (Figure 3.7), it is probable that there were undiscovered leks during these years.

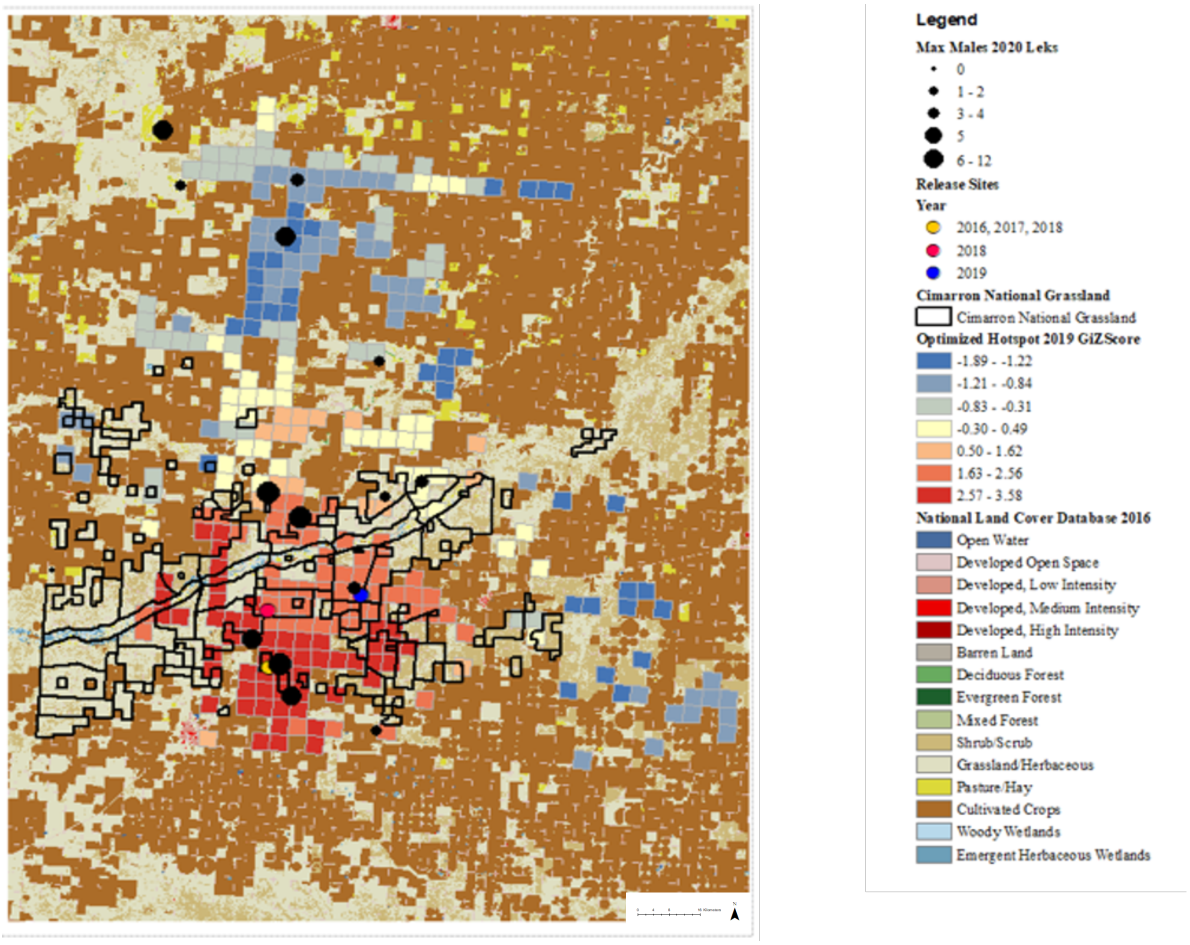

Figure 3.12 Lag female points from 2019 in Sand Sagebrush Prairie of southwestern Kansas were used to create the optimized hot spot map.

Fishnet polygon cell size for 2019 was 1868 m, with an optimal fixed distance of 16791.61 m, and 302 weighted polygons ($\bar{x}$ = 59.46, SD = 215.16). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. Clustered female locations follow closely to where large leks are located as well as leks that have persisted through multiple breeding seasons. Northern leks fall within areas of female space use, although these locations are not a significant hot spot of locations.

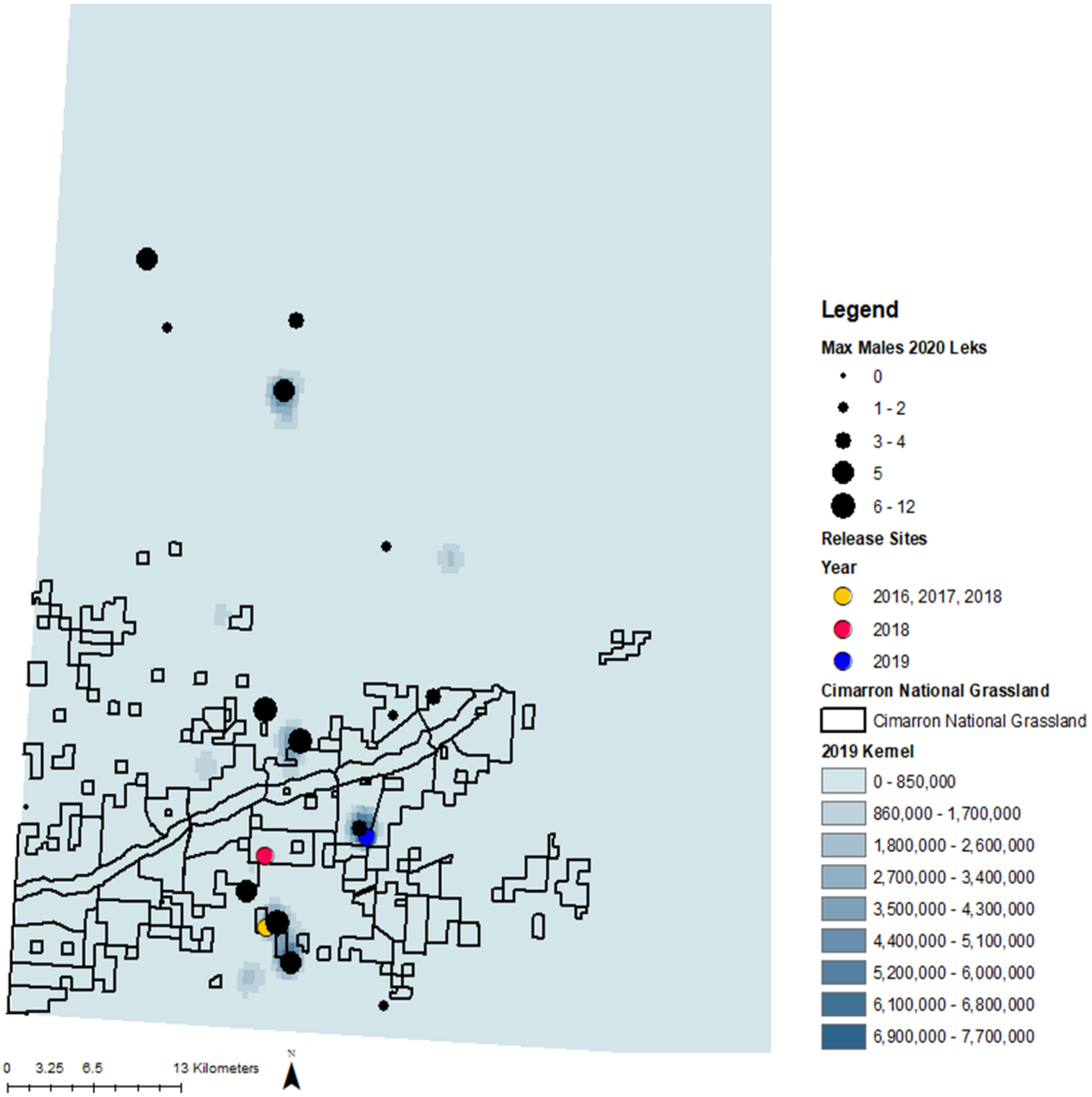

Figure 3.13 Kernel density map of lag female GPS and VHF points from 2019 within the same year of male observations at translocation leks in Sand Sagebrush Prairie in southwestern Kansas.

Concentrations of female points follow closely to the formation of leks. For those leks, especially in the northern extent of the map, female locations may have been missed by VHF monitoring.

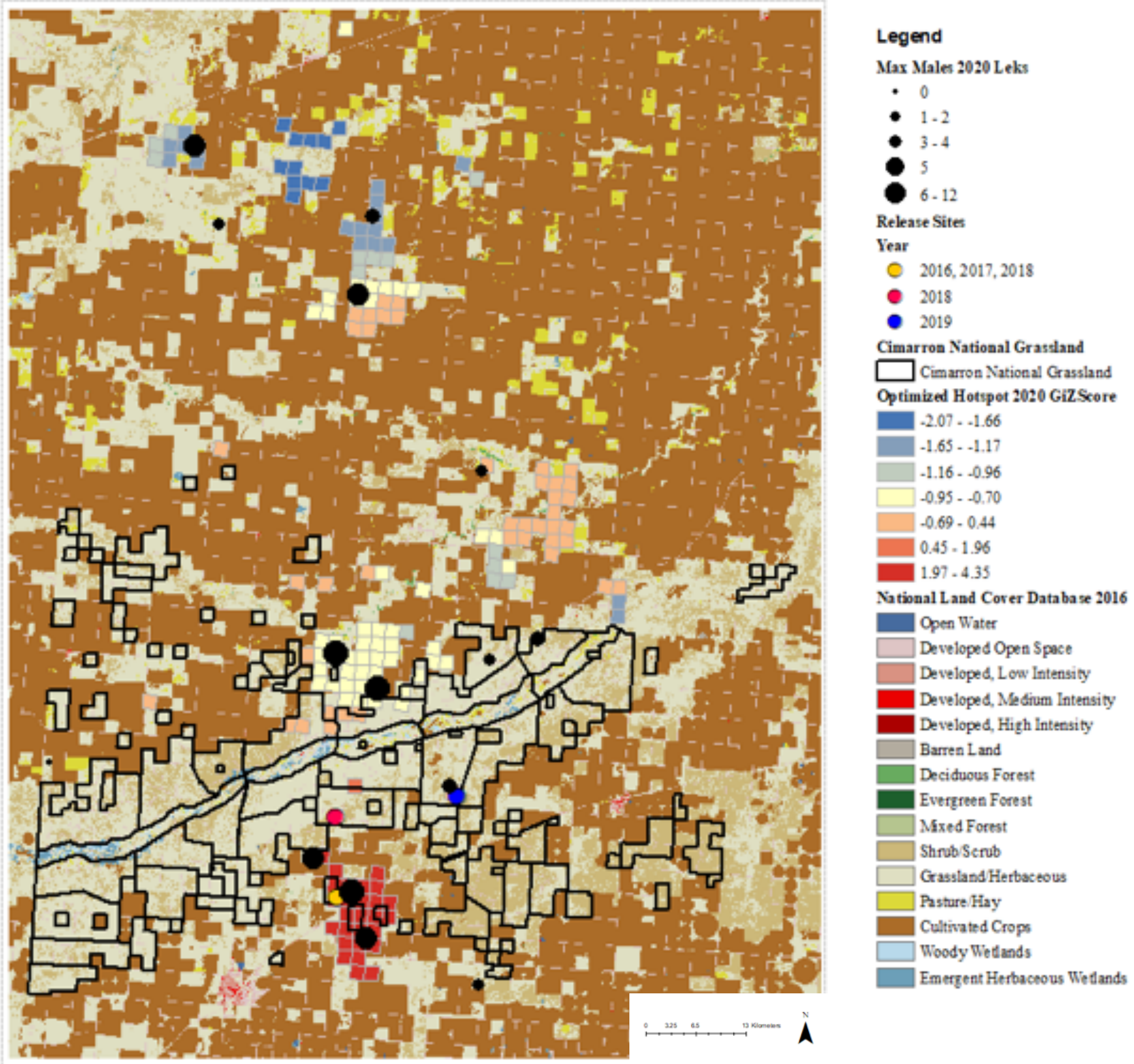

Figure 3.14 Optimized hot spot map of same year GPS and VHF female locations and male observations at translocation leks of Sand Sagebrush Prairie in southwestern Kansas in 2020.

Fishnet polygon cell size for 2020 was 1111 m, with an optimal fixed distance of 8256.68 m, and 166 weighted polygons ($\bar{x}$ = 33.97, SD = 96.19). Increased clustering of locations is depicted with warm colors and areas with decreasing point clustering in cool colors. Z-scores (± 1.96) depict statistically significant cold and hot spots at a 95% confidence interval, with larger values indicating more intensive clustering. There has been a southern and northern shift in lek formation that is reflected by female locations. While the northern extent does not have statistically significant cluster of female points, there has been clear utilization of these areas by hens since 2018.

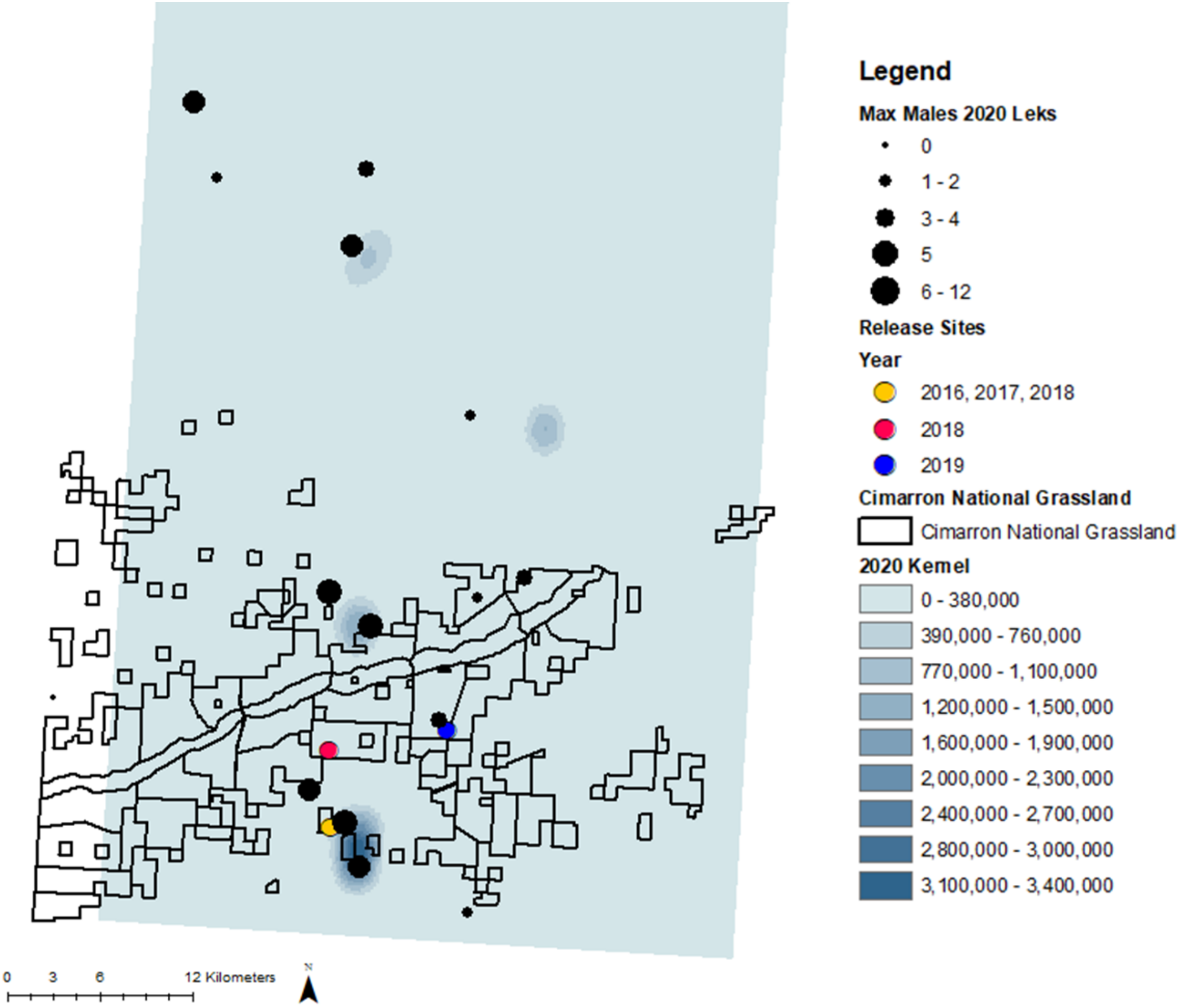

Figure 3.15 Kernel density map of same year GPS and VHF female locations and male observations at leks in 2020 in Sand Sagebrush southwestern Kansas.

Some of the northern leks are closely associated with concentrations of female points and many that are not closely associated with concentrated areas of female points appear to be small groups of males (<3). For many of the larger leks there appears to be a shift in female utilization.

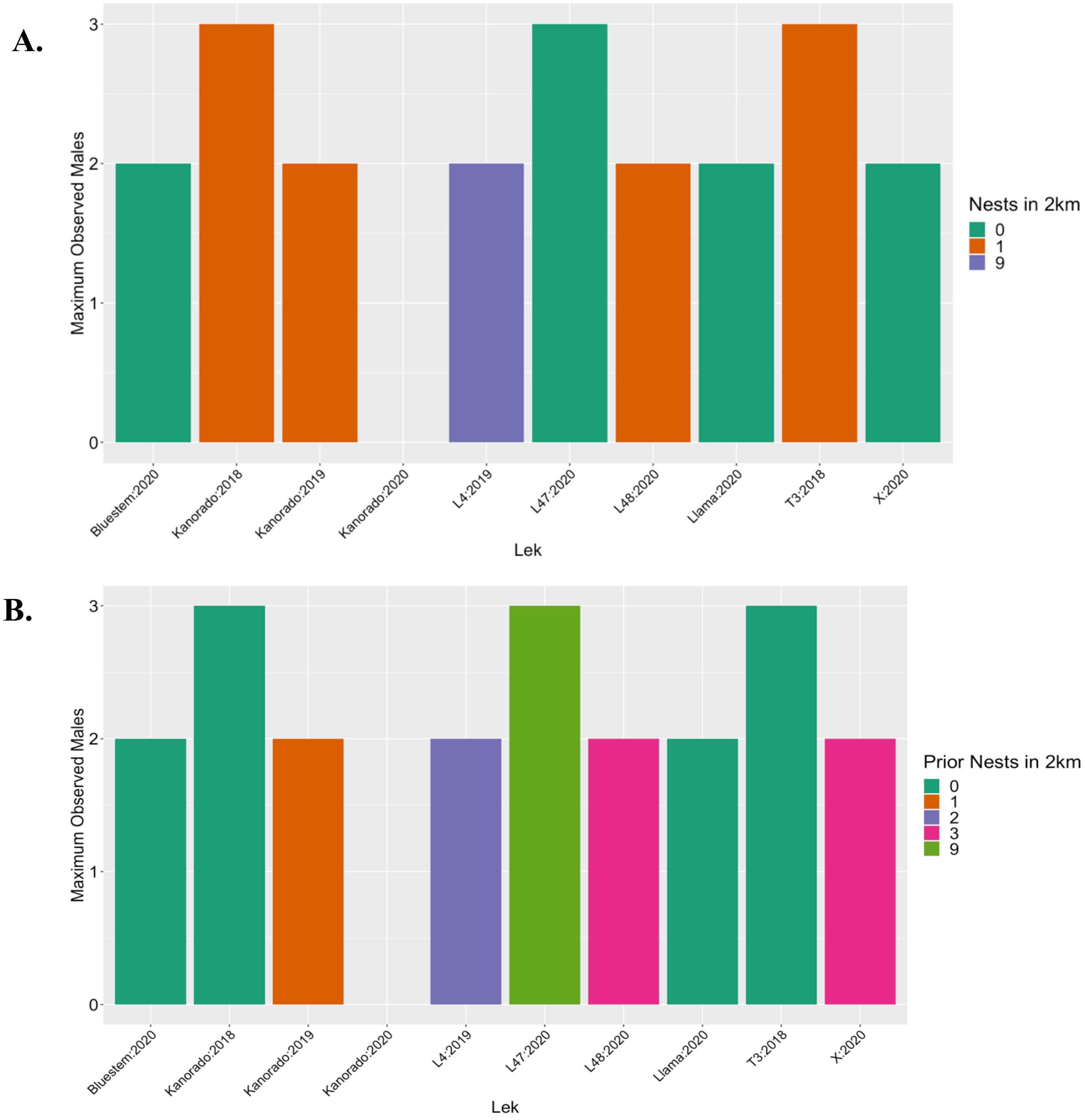

Figure 3.16 Smaller translocation leks (<4) and groupings of two males also follow female habitat constraints in Sand Sagebrush Prairie of southwestern Kansas.

Same year nesting efforts (A) are likely a determinant of whether a lek will be ephemeral or persist into subsequent breeding seasons. An example of this is the L4 grouping, where males shifted to a form L47 in nearby location, following female shifts after a change in grazing regime. (B) Prior nesting efforts were high in this area, allowing this small group to persist to become a small lek. Similarly, it can be inferred that the leks discovered in 2020 with three prior nests were likely home to at least small display groups in 2019.

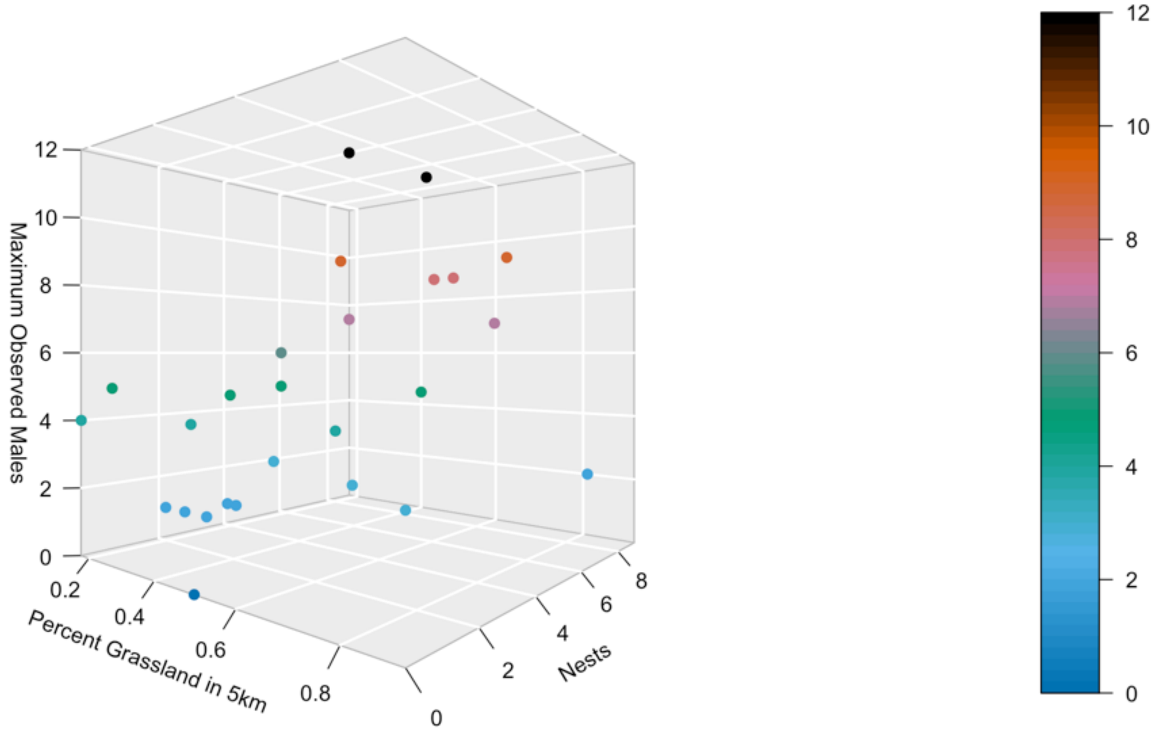

Figure 3.17 The number of observed males at leks increases with the number of active same year nests within 5 km of translocated leks in Sand Sagebrush Prairie of southwestern Kansas.

The number of nesting efforts, however, are tied to increasing percentages of grassland within the 5 km distance. This implicates that males cue to female nest site selection rather than the presence of grasslands alone.

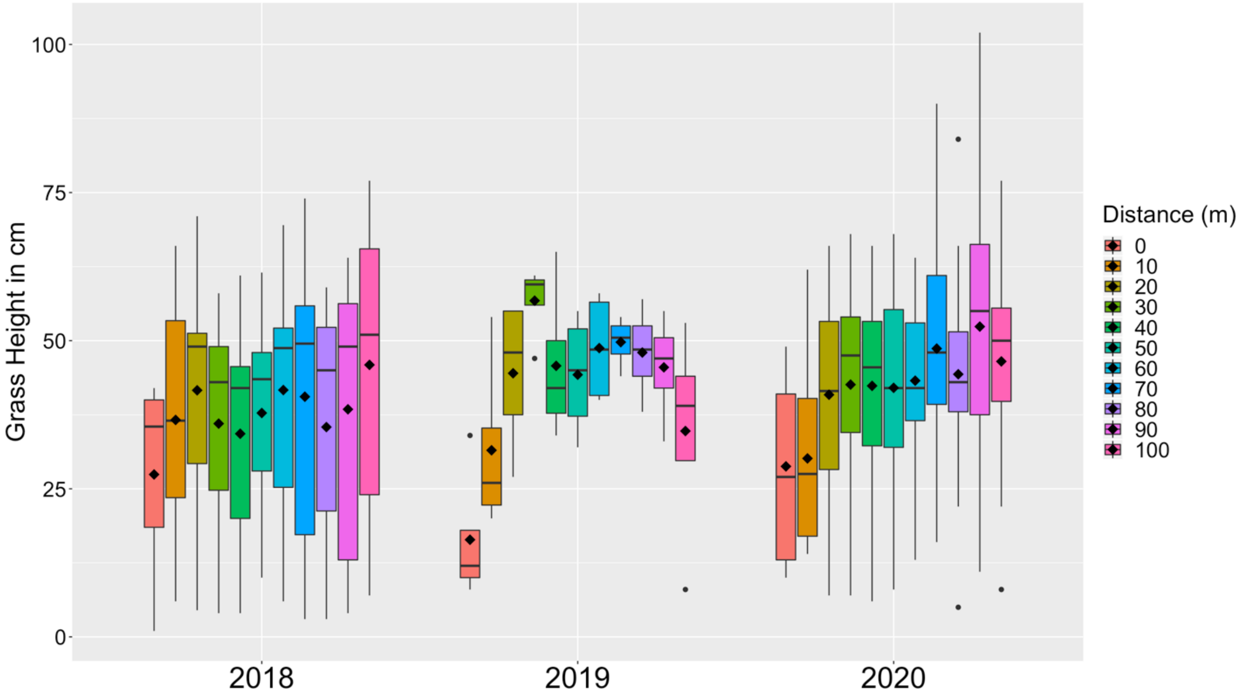

Figure 3.18 Translocation lek grass height by distance for 2018-2020 in Sand Sagebrush in southwestern Kansas.

Outer edges of grassland leks measured in 2020 are greater than that of 2018 and 2019, although other distances are comparable.

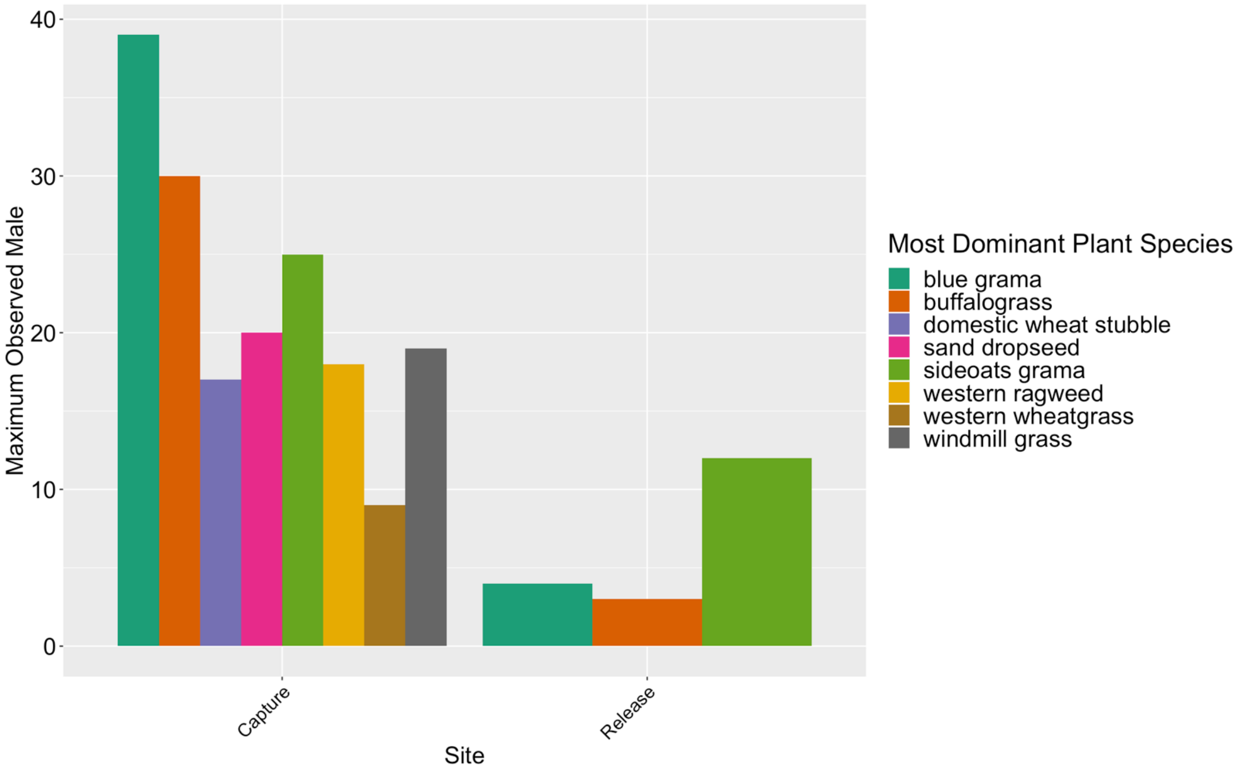

Figure 3.19 Dominant plant species within the 100 m circumference of the lek center were determined after conducting lek vegetation measurements.

Regardless of site, almost leks in Short-Grass and Sand Sagebrush prairie share grass species expected in grazed working lands. Blue grama, buffalograss, and side oats grama are all grass species associated with grazing and would offer little visual obstruction.

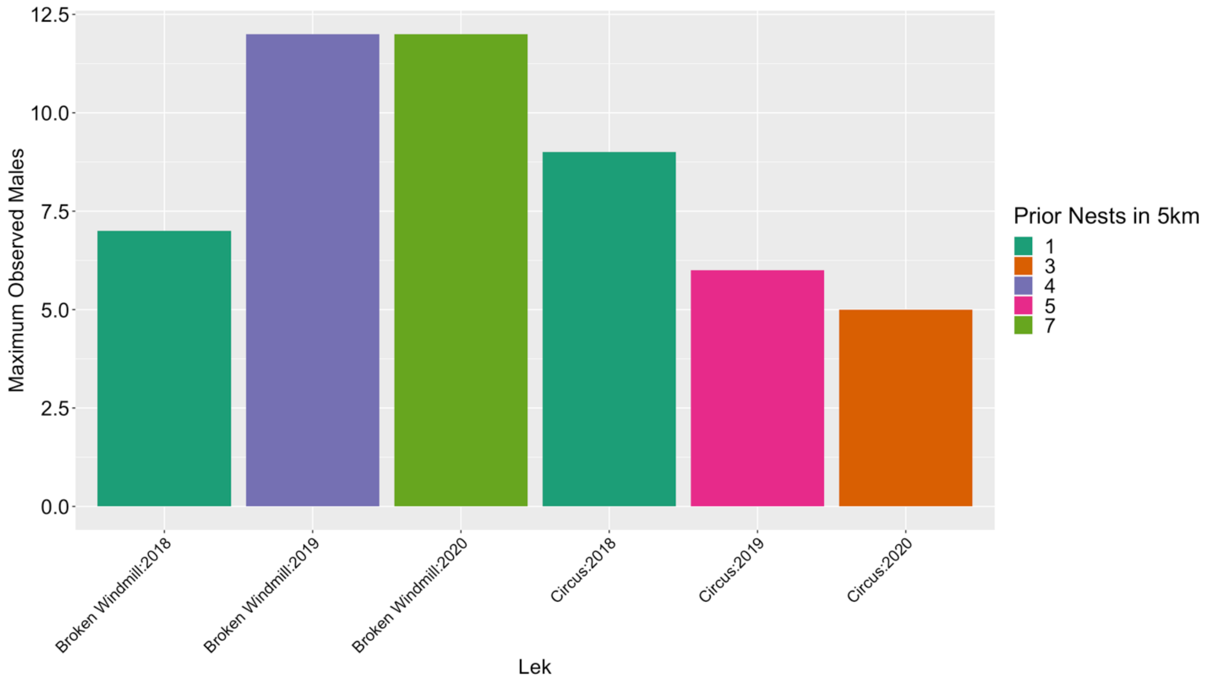

Figure 3.20 Prior nesting effort for the two leks active for the majority of the translocation effort of lesser prairie-chickens to southwestern Kansas during 2017-2020.

Broken Windmill was a grassland lek active since 2017. Circus was located in cropland, where males displayed in the stubble after harvest, and active since 2017. Together they bound the northern and southern edges of the Cimarron National Grasslands on private land. Circus' male numbers were declining as each subsequent year there was reduced nesting effort within 5 km of the lek site.

Tables

Table 3.1 Number of birds translocated to the Cimarron and Comanche National Grasslands from 2016-2019.

	Cimarron (KS)		Comanche (CO)		
	Males	Females	Males	Females	**Totals**
Fall 2016	13	0	13	1	27
Spring 2017	16	19	29	19	83
Spring 2018	32	37	39	36	144
Spring 2019	40	49	22	46	157
Totals	101	107	103	102	**411**

Table 3.2 Lek vegetation measurements for Short-Grass prairie capture site and Sand Sagebrush prairie translocation leks.

Male lesser prairie-chickens typically concentrate displays within 30 m of the lek center, where vegetation is shortest.

	Capture Leks 0-30 m (center)						Capture Leks 40-100 m				
	N	x̄	SE	Min	Max		N	x̄	SE	Min	Max
Grass Height (cm)	562	22.27	0.58	1	133	Grass Height (cm)	980	33.08	0.5	1	151
Litter Depth (cm)	562	1.24	0.04	0	13	Litter Depth (cm)	980	1.64	0.05	0	13
Robel (DM)	562	0.02	0.01	0	2	Robel (DM)	980	0.07	0.01	0	2
Percent Grass	562	68.22	1.06	3	98	Percent Grass	980	68.4	0.78	3	98
Percent Forb	562	5.7	0.36	0	63	Percent Forb	980	6.36	0.31	0	86
Percent Bare	562	14.47	0.76	0	98	Percent Bare	980	13.78	0.59	0	98
Percent Litter	562	14.49	0.58	0	86	Percent Litter	980	14.68	0.47	0	98
Percent Shrub	562	0.03	0.01	0	3	Percent Shrub	980	0.14	0.07	0	38
Translocation Leks 0-30 m (center)							Translocation Leks 40-100 m				
	N	x̄	SE	Min	Max		N	x̄	SE	Min	Max
Grass Height (cm)	160	35.63	1.34	1	71	Grass Height (cm)	280	43.66	1.05	3	102
Litter Depth (cm)	160	1.13	0.04	0	3	Litter Depth (cm)	280	1.34	0.06	0	11
Robel (DM)	160	0.09	0.02	0	1	Robel (DM)	280	0.27	0.03	0	2
Percent Grass	160	70.56	2.04	3	98	Percent Grass	280	76.68	1.41	3	98
Percent Forb	160	4.53	0.68	0	63	Percent Forb	280	5.72	0.61	0	63
Percent Bare	160	10.07	1.17	0	86	Percent Bare	280	10.5	0.88	0	86
Percent Litter	160	17.48	1.6	0	86	Percent Litter	280	10.95	0.79	0	63
Percent Shrub	160	0.49	0.34	0	38	Percent Shrub	280	0.76	0.34	0	63

Appendix C - Supplemental Tables

Table C.1 Pearson correlation results of translocation lek vegetation variables from Sand Sagebrush Prairie of southwestern Kansas.

While some characteristics are correlated, all values are below |r<0.80| and incorporated into models.

0 m

	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter
Grass Height	1	0.07	0.34	-0.01	0	-0.27	0.27
Litter Depth	0.07	1	-0.01	0.28	-0.23	-0.37	0.14
Rol DM	0.34	-0.01	1	-0.02	-0.12	-0.11	0.21
Percent Grass	-0.01	0.28	-0.02	1	-0.26	-0.72	-0.44
Percent Forb	0	-0.23	-0.12	-0.26	1	0.27	-0.39
Percent Bare	-0.27	-0.37	-0.11	-0.72	0.27	1	-0.18
Percent Litter	0.27	0.14	0.21	-0.44	-0.39	-0.18	1

10 m

	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	0.23	0.51	0.22	-0.18	-0.2	-0.05	-0.09
Litter Depth	0.23	1	0.14	0.24	-0.06	-0.38	0.1	-0.06
Robel DM	0.51	0.14	1	0.08	-0.15	-0.1	0.03	-0.04
Percent Grass	0.22	0.24	0.08	1	-0.36	-0.7	-0.53	-0.03
Percent Forb	-0.18	-0.06	-0.15	-0.36	1	0.27	-0.16	0.18
Percent Bare	-0.2	-0.38	-0.1	-0.7	0.27	1	-0.15	-0.06
Percent Litter	-0.05	0.1	0.03	-0.53	-0.16	-0.15	1	0.05
Percent Shrub	-0.09	-0.06	-0.04	-0.03	0.18	-0.06	0.05	1

Table C.1 Continued

20 m								
	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	-0.09	0.45	0.5	-0.23	-0.4	-0.31	0.12
Litter Depth	-0.09	1	0.23	-0.16	-0.21	0	0.46	0.05
Robel DM	0.45	0.23	1	0.21	-0.19	-0.25	-0.03	-0.05
Percent Grass	0.5	-0.16	0.21	1	-0.37	-0.75	-0.67	-0.2
Percent Forb	-0.23	-0.21	-0.19	-0.37	1	0.1	-0.07	-0.09
Percent Bare	-0.4	0	-0.25	-0.75	0.1	1	0.2	0.1
Percent Litter	-0.31	0.46	-0.03	-0.67	-0.07	0.2	1	0.24
Percent Shrub	0.12	0.05	-0.05	-0.2	-0.09	0.1	0.24	1

30 m								
	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	-0.29	0.43	0.21	-0.08	-0.11	-0.08	-0.27
Litter Depth	-0.29	1	-0.09	-0.33	0.04	0.29	0.11	-0.07
Robel DM	0.43	-0.09	1	0.04	0.04	-0.08	0.01	-0.09
Percent Grass	0.21	-0.33	0.04	1	-0.46	-0.56	-0.51	0.19
Percent Forb	-0.08	0.04	0.04	-0.46	1	-0.14	0.04	-0.01
Percent Bare	-0.11	0.29	-0.08	-0.56	-0.14	1	-0.16	-0.08
Percent Litter	-0.08	0.11	0.01	-0.51	0.04	-0.16	1	-0.14
Percent Shrub	-0.27	-0.07	-0.09	0.19	-0.01	-0.08	-0.14	1

Table C.1 Continued

40 m

	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	-0.08	0.36	0.16	-0.13	0.08	-0.14	-0.17
Litter Depth	-0.08	1	-0.1	-0.31	0	0.26	0.14	-0.07
Robel DM	0.36	-0.1	1	0.29	-0.08	-0.18	-0.22	-0.07
Percent Grass	0.16	-0.31	0.29	1	-0.32	-0.64	-0.48	-0.04
Percent Forb	-0.13	0	-0.08	-0.32	1	-0.15	0.03	-0.12
Percent Bare	0.08	0.26	-0.18	-0.64	-0.15	1	-0.14	-0.05
Percent Litter	-0.14	0.14	-0.22	-0.48	0.03	-0.14	1	0.03
Percent Shrub	-0.17	-0.07	-0.07	-0.04	-0.12	-0.05	0.03	1

50 m

	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	-0.1	0.4	0.26	0	-0.13	-0.19	0.01
Litter Depth	-0.1	1	-0.02	-0.24	-0.16	0.02	0.53	-0.09
Robel DM	0.4	-0.02	1	0.27	-0.14	-0.23	-0.1	-0.06
Percent Grass	0.26	-0.24	0.27	1	-0.27	-0.57	-0.58	-0.17
Percent Forb	0	-0.16	-0.14	-0.27	1	-0.12	-0.09	0.02
Percent Bare	-0.13	0.02	-0.23	-0.57	-0.12	1	-0.14	0.05
Percent Litter	-0.19	0.53	-0.1	-0.58	-0.09	-0.14	1	0.09
Percent Shrub	0.01	-0.09	-0.06	-0.17	0.02	0.05	0.09	1

Table C.1 Continued

60 m								
	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	0.17	0.55	0.19	-0.12	-0.12	-0.01	-0.14
Litter Depth	0.17	1	0.06	-0.1	0.03	-0.16	0.45	-0.14
Robel DM	0.55	0.06	1	0.22	0.09	-0.26	-0.05	0.03
Percent Grass	0.19	-0.1	0.22	1	-0.17	-0.73	-0.53	-0.19
Percent Forb	-0.12	0.03	0.09	-0.17	1	-0.05	-0.07	0.16
Percent Bare	-0.12	-0.16	-0.26	-0.73	-0.05	1	-0.1	-0.01
Percent Litter	-0.01	0.45	-0.05	-0.53	-0.07	-0.1	1	0.08
Percent Shrub	-0.14	-0.14	0.03	-0.19	0.16	-0.01	0.08	1

70 m								
	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	0.1	0.64	0.31	-0.02	-0.32	-0.05	0.03
Litter Depth	0.1	1	0.06	0	-0.15	-0.08	0.13	0.28
Robel DM	0.64	0.06	1	0.32	-0.18	-0.33	-0.02	0.08
Percent Grass	0.31	0	0.32	1	-0.31	-0.61	-0.52	-0.03
Percent Forb	-0.02	-0.15	-0.18	-0.31	1	-0.16	0.06	0.1
Percent Bare	-0.32	-0.08	-0.33	-0.61	-0.16	1	-0.18	-0.15
Percent Litter	-0.05	0.13	-0.02	-0.52	0.06	-0.18	1	0
Percent Shrub	0.03	0.28	0.08	-0.03	0.1	-0.15	0	1

Table C.1 Continued

80 m								
	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	0.45	0.56	0.07	0	-0.24	0.22	0.01
Litter Depth	0.45	1	0.23	-0.09	-0.02	-0.31	0.49	0.32
Robel DM	0.56	0.23	1	0.21	-0.01	-0.16	-0.11	0.05
Percent Grass	0.07	-0.09	0.21	1	-0.27	-0.6	-0.44	-0.06
Percent Forb	0	-0.02	-0.01	-0.27	1	-0.13	-0.18	0.21
Percent Bare	-0.24	-0.31	-0.16	-0.6	-0.13	1	-0.21	-0.17
Percent Litter	0.22	0.49	-0.11	-0.44	-0.18	-0.21	1	0.01
Percent Shrub	0.01	0.32	0.05	-0.06	0.21	-0.17	0.01	1

90 m								
	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	0.13	0.63	0.13	-0.04	-0.21	0.09	0.26
Litter Depth	0.13	1	0.15	-0.08	-0.01	-0.12	0.32	-0.06
Robel DM	0.63	0.15	1	0.01	-0.07	-0.21	0.24	0.5
Percent Grass	0.13	-0.08	0.01	1	-0.29	-0.7	-0.38	-0.28
Percent Forb	-0.04	-0.01	-0.07	-0.29	1	-0.06	-0.03	-0.08
Percent Bare	-0.21	-0.12	-0.21	-0.7	-0.06	1	-0.26	0.03
Percent Litter	0.09	0.32	0.24	-0.38	-0.03	-0.26	1	0.35
Percent Shrub	0.26	-0.06	0.5	-0.28	-0.08	0.03	0.35	1

Table C.1 Continued

100 m								
	Grass Height	Litter Depth	Robel DM	Percent Grass	Percent Forb	Percent Bare	Percent Litter	Percent Shrub
Grass Height	1	0.22	0.59	0.44	-0.23	-0.34	-0.05	0.02
Litter Depth	0.22	1	0.12	-0.17	0.04	-0.22	0.51	-0.1
Robel DM	0.59	0.12	1	0.37	-0.26	-0.28	-0.08	-0.1
Percent Grass	0.44	-0.17	0.37	1	-0.15	-0.64	-0.54	-0.01
Percent Forb	-0.23	0.04	-0.26	-0.15	1	-0.15	-0.17	0
Percent Bare	-0.34	-0.22	-0.28	-0.64	-0.15	1	-0.15	-0.04
Percent Litter	-0.05	0.51	-0.08	-0.54	-0.17	-0.15	1	0.09
Percent Shrub	0.02	-0.1	-0.1	-0.01	0	-0.04	0.09	1

Table C.2 Maximum observed male numbers and translocation grassland lek vegetation model selection by distance from lek center in Sand Sagebrush Prairie of southwestern Kansas.

0 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Grass Height + Percent Grass	0.88	0.86	56.22	4, 31	116.38	0	0.61	<0.001
Year + Grass Height + Robel + Percent Grass	0.88	0.86	45.72	5, 30	117.92	1.54	0.28	<0.001
Year + Grass Height + Robel + Percent Grass + Percent Forb	0.89	0.86	38.16	6, 29	120.12	3.74	0.09	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb	0.89	0.86	32.08	7, 28	123.21	6.83	0.02	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.89	0.86	27.17	9, 27	126.97	10.59	0	<0.001

10 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Grass Height	0.84	0.82	55.03	3, 32	124.02	0	0.64	<0.001
Year + Grass Height + Percent Forb	0.84	0.82	41.25	4, 31	125.97	1.95	0.24	<0.001
Year + Grass Height + Litter Depth + Percent Forb	0.85	0.82	33.02	5, 30	128.07	4.04	0.09	<0.001
Year + Grass Height + Litter Depth. + Robel + Percent Forb	0.85	0.82	27.39	6, 29	130.5	6.48	0.03	<0.001
Year + Grass Height. + Litter Depth + Robel + Percent Forb + Percent Litter	0.85	0.81	22.79	7, 28	133.93	9.91	0	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.85	0.81	19.24	8, 27	137.78	13.76	0	<0.001

Table C.2 Continued

20 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Grass Height + Percent Litter	0.88	0.87	58.9	4, 31	114.9	0	0.70	<0.001
Year + Grass Height + Robel + Percent Litter	0.89	0.87	46.84	5, 30	117.15	2.25	0.05	<0.001
Year + Grass Height + Robel + Percent Litter + Percent Shrub	0.89	0.86	38.22	6, 29	120.07	5.17	0.05	<0.001
Year + Grass Height+ Litter Depth + Robel + Percent Litter + Percent Shrub	0.89	0.86	32.14	7. 28	123.14	8.24	0.01	<0.001
Year + Grass Height + Litter Depth+ Robel + Percent Forb + Percent Litter + Percent Shrub	0.89	0.86	27.4	8. 27	126.7	11.80	0	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.89	0.85	23.56	9. 26	130.75	15.85	0	<0.001

30 m

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Year + Grass Height + Robel	0.92	0.91	86.92	4, 31	102.26	0	0.73	<0.001
Year + Grass Height. + Robel+ Percent Litter	0.92	0.91	68.53	5, 30	104.76	2.50	0.21	<0.001
Year + Grass Height + Robel+ Percent Litter + Percent Shrub	0.92	0.9	56.19	6, 29	107.51	5.25	0.05	<0.001
Year + Grass Height+ Litter Depth + Robel + Percent Litter + Percent Shrub	0.92	0.9	46.65	7, 28	111	8.73	0.01	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Litter + Percent Shrub	0.92	0.9	39.41	8, 27	114.83	12.57	0	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.92	0.89	33.81	9, 26	118.96	16.70	0	<0.001

Table C.2 Continued

40 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Litter + Percent Shrub	0.9	0.86	28.8	8, 27	125.09	0	0.8	<0.001
Year + Grass Height + Litter Depth+ Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.9	0.86	25.81	9, 26	127.81	2.72	0.2	<0.001

50 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Grass Height + Litter Depth + Percent Grass + Percent Litter	0.94	0.92	69.93	6, 29	100.2	0	0.81	<0.001
Year + Grass Height+ Litter Depth + Robel + Percent Grass + Percent Litter	0.94	0.92	58.19	7, 28	103.61	3.41	0.15	<0.001
Year + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter	0.94	0.92	49.17	8, 27	107.44	7.24	0.02	<0.001

Table C.2 Continued

60 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Grass Height + Robel+ Percent Litter	0.89	0.88	50.41	5, 30	114.79	0	0.71	<0.001
Year + Grass Height + Robel+ Percent Grass + Percent Litter	0.9	0.87	41.72	6, 29	117.25	2.46	0.21	<0.001
Year + Grass Height + Robel + Percent Grass + Percent Forb + Percent Litter	0.9	0.87	35.83	7, 28	119.65	4.86	0.06	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter	0.9	0.87	31.55	8, 27	112.14	7.35	0.02	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.9	0.87	27.18	9, 26	126.13	11.34	0	<0.001

70 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Grass Height	0.85	0.83	58.97	3, 32	121.97	0	0.53	<0.001
Year + Grass Height + Litter Depth	0.85	0.83	45.11	4, 31	123.24	1.27	0.28	<0.001
Year + Grass Height+ Litter Depth+ Percent Litter	0.86	0.84	36.76	5, 30	124.77	2.79	0.13	<0.001
Year + Grass Height+ Litter Depth+ Percent Litter + Percent Shrub	0.86	0.84	30.56	6, 29	127.12	5.15	0.04	<0.001
Year + Grass Height + Litter Depth. + Robel + Percent Litter + Percent Shrub	0.86	0.83	25.5	7, 28	130.45	8.48	0.01	<0.001
Year + Grass Height+ Litter Depth + Robel + Percent Grass + Percent Litter + Percent Shrub	0.86	0.82	21.54	8, 27	134.3	12.33	0	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.86	0.2	18.44	9, 26	138.5	16.53	0	<0.001

Table C.2 Continued

80 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Grass Height + Robel + Percent Grass + Percent Litter	0.87	0.85	32.88	6, 29	124.83	0	0.82	<0.001
Year + Grass Height + Robel + Percent Grass + Percent Litter + Percent Shrub	0.87	0.84	27.43	7, 28	128.18	3.35	0.15	<0.001
Year + Grass Height+ Robel+ Percent Grass+ Percent Forb + Percent Litter + Percent Shrub	0.87	0.84	23.16	8, 27	132.03	7.20	0.02	<0.001
Year + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.87	0.83	19.82	9, 26	136.23	11.40	0	<0.001

90 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Percent Grass	0.83	0.81	50.54	3, 32	126.57	0	0.56	<0.001
Year + Percent Grass + Percent Litter	0.83	0.81	38.72	4, 31	127.88	1.31	0.29	<0.001
Year + Robel + Percent Grass + Percent Litter	0.84	0.81	31.18	5, 30	129.8	3.23	0.11	<0.001
Year + Grass Height + Robel + Percent Grass + Percent Litter	0.84	0.8	25.61	6, 29	132.55	5.98	0.03	<0.001
Year + Grass Height + Robel + Percent Grass + Percent Forb + Percent Litter	0.84	0.8	21.42	7, 28	135.82	9.25	0.01	<0.001
Year + Grass Height + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.84	0.8	18.21	8, 27	139.46	12.89	0	<0.001
Year + Grass Height + Litter Depth + Robel + Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.84	0.79	15.6	9, 26	143.64	17.07	0	<0.001

Table C.2 Continued

100 m								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Year + Grass Height+ Percent Forb + Percent Litter	0.87	0.85	40.89	5, 30	121.45	0	0.72	<0.001
Year + Grass Height + Percent Grass + Percent Forb + Percent Litter	0.88	0.85	34.01	6, 29	123.77	2.33	0.23	<0.001
Year + Grass Height + Litter Depth + Percent Grass + Percent Forb + Percent Litter	0.88	0.85	28.45	7, 28	127.03	5.58	0.04	<0.001
Year + Grass Height + Litter Depth + Robel+ Percent Grass + Percent Forb + Percent Litter	0.88	0.84	24.12	8, 27	130.76	9.31	0.01	<0.001
Year + Grass Height + Litter Depth+ Robel+ Percent Grass + Percent Forb + Percent Litter + Percent Shrub	0.88	0.83	20.65	9, 26	134.94	13.50	0	<0.001

Table C.3 Model selection of anthropogenic features by buffer scale around translocation leks in Sand Sagebrush Prairie in southwestern Kansas.

Only the 10 km anthropogenic features model is significant, indicating that maximum male numbers on leks are influenced by road, electric, and rail lengths.

10 km

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Road Length + Electric Length + Rail	0.35	0.26	3.94	3, 22	134.55	0	0.83	0.02
Road Length + Electric Length + Rail + Year	0.43	0.29	3.07	5, 20	138.17	3.62	0.14	0.03
Cell + Road Length + Electric Length + Rail + Year	0.46	0.29	2.70	6, 19	141.17	6.62	0.03	0.05
Cell+ Road Length+ Electric Length+ Rail+ Year+ Oil Wells	0.47	0.26	2.24	7, 18	145.68	11.13	0	0.08

5 km

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Cell + Road Length + Oil Wells	0.24	0.14	2.35	3, 22	138.51	0	0.76	0.10
Cell + Road Length + Rail + Oil Wells	0.26	0.12	1.85	4, 21	141.32	2.81	0.19	0.16
Cell + Road Length + Electric Length + Rail + Oil Wells	0.30	0.12	1.69	5, 20	143.79	5.28	0.05	0.18
Cell + Road Length + Electric Length + Rail + Year + Oil Wells	0.32	0.05	1.20	7, 18	152.00	13.49	0	0.35

2 km

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Road Length + Oil Wells	0.25	0.18	3.53	2, 21	114.59	0	0.72	0.05
Road Length + Rail + Oil Wells	0.29	0.18	2.69	3, 20	116.62	2.03	0.26	0.07
Road Length Rail+ Year+ Oil Wells	0.34	0.16	1.85	5,18	122.48	7.88	0.01	0.15

1 km

Model	R^2	Adj R^2	F	DF	AIC_c	ΔAIC_c	w_i	P
Road Length+ Year	0.07	-0.06	0.51	3, 22	143.98			0.68

Table C.4 Model selection of prior female spatial use by buffer scale after translocation to Sand Sagebrush Prairie in southwestern Kansas.

Maximum male numbers observed at translocation leks were run the year after the female spatial locations within each scale the year prior to the observed maximum male count. Models at 5 km, 2 km, and 1 km scales are significant, with maximum male numbers driven by female space use, nest site selection, and percent grassland cover.

			10 km					
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Lag Female Points + Nest	0.19	0.10	2.07	2, 18	115.28	0	0.80	0.16
Lag Female Points + Nest + Year	0.20	0.06	1.44	3, 17	118.37	3.09	0.17	0.27
Percent Grassland + Lag Female Points + Nest + Year	0.20	0.01	1.03	4, 16	122.33	7.05	0.02	0.42
Percent Grassland + Lek + Lag Female Points + Nest + Year	0.21	-0.06	0.78	5, 15	126.90	11.62	0	0.58
Percent Grassland + Lek + Lag Female Points + Nest + Prior Nest + Year	0.21	-0.130	0.60	6, 14	132.28	17.01	0	0.72
			5 km					
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Percent Grassland+ Lek+ Lag Female Points Nest	0.56	0.45	5.04	4,16	109.10	0	0.87	0.01
Percent Grassland + Lek + Lag Female Points + Nest + Prior Nest	0.57	0.43	3.1	5,15	113.95	3.95	0.12	0.02
Percent Grassland + Lek + Lag Female Points+ Nest + Prior Nest + Year	0.57	0.39	3.11	6, 14	119.33	9.33	0.01	0.04
			2 km					
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Lag Female Points + Nest	0.69	0.64	16.33	2, 15	73.65	0	0.74	<0.001
Lag Female Points + Nest + Prior Nest	0.71	0.65	11.53	3, 14	75.98	2.33	0.23	<0.001
Lag Female Points + Nest + Prior Nest + Year	0.72	0.64	8.4	4,13	80.03	6.38	0.03	0.001
Percent Grassland + Lag Female Points + Nest + Prior Nest + Year	0.72	0.61	6.22	5, 12	85.56	11.91	0	0.01

Table C.4 Continued

1 km								
Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Percent Grassland + Lag Female Points + Nest+ Year	0.78	0.71	11.78	4, 13	82.46	0	0.92	0.00
Percent Grassland + Lag Female Points + Nest + Prior Nest + Year	0.79	0.7	9.1	5,12	87.38	4.92	0.08	0.001

Table C.5 Model selection of same female spatial use by buffer scale for translocation leks in Sand Sagebrush of southwestern Kansas.

Maximum male numbers were run with the spatial locations of females documented within each scale for the same year as the maximum male count at translocation leks. Models at 5 km, 2 km, and 1 km scales are significant, with maximum male numbers driven by female space use, nest site selection, and percent grassland cover.

10 km

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Nest	0.14	0.11	4.05	1, 24	135.77	0	0.70	0.06
Lek + Nest	0.16	0.09	2.25	2, 23	137.1	2.22	0.23	0.13
Percent Grassland + Lek + Nest	0.17	0.06	1.5	3, 22	140.9	5.13	0.05	0.24
Percent Grassland + Lek + Female Points + Nest	0.18	0.02	1.15	4, 21	144.01	8.23	0.01	0.36
Percent Grassland + Lek + Female Points + Nest + Prior Nest	0.18	-0.03	0.88	5, 20	147.8	12.03	0	0.51
Percent Grassland + Lek + Female Points + Nest + Prior Nest + Year	0.22	-0.09	0.72	7, 18	155.6	19.83	0	0.66

5 km

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Percent Grassland + Lek+ Nest + Prior Nest	0.56	0.47	6.57	4, 21	128.06	0	0.87	0.001
Percent Grassland + Lek + Female Points + Nest + Prior Nest	0.56	0.44	5	5, 20	131.86	3.80	0.13	0.004
Percent Grassland + Lek + Female Points + Nest + Prior Nest + Year	0.56	0.39	3.28	7, 18	140.63	12.56	0	0.02

Table C.5 Continued

2 km

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Female Points + Nest	0.73	0.7	27.16	2, 20	86.79	0	0.89	<0.0001
Female Points + Nest + Year	0.76	0.71	14.17	4, 18	91.28	4.49	0.9	<0.0001
Female Points + Nest + Prior Nest + Year	0.76	0.69	10.81	5, 17	95.32	8.53	0.01	<0.0001
Percent Grassland + Female Points + +Nest + Prior Nest + Year	0.76	0.67	8.48	6, 16	100.14	13.35	0	0.0003

1 km

Model	**R^2**	**Adj R^2**	**F**	**DF**	**AIC_c**	**ΔAIC_c**	**w_i**	**P**
Nest + Prior Nest	0.52	0.47	10.79	2, 20	107.1	0	0.80	<0.001
Female Points + Nest + Prior Nest	0.52	0.45	6.95	3, 19	110.2	3.10	0.17	0.002
Percent Grassland + Female Points + Nest + Prior Nest	0.53	0.42	5.03	4, 18	113.69	6.59	0.03	0.007
Percent Grassland + Female Points + Nest + Prior Nest + Year	0.56	0.4	3.44	6, 16	120.93	13.82	0	0.22