Regional variation in demography, distribution, foraging, and strategic conservation of lesser prairie-chickens in Kansas and Colorado

by

Daniel S. Sullins

B.S., Texas A&M University, 2008
M.S., Stephen F. Austin State University 2013

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

2017

Abstract

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is 1 of 3 prairie-grouse species in North America. Prairie-grouse have undergone local or widespread declines due to a loss of habitat through conversion to row crop agriculture, anthropogenic development, and alteration of ecological drivers that maintain quality grasslands. For lesser prairie-chickens, habitat loss and declines were deemed significant for listing as threatened under the Endangered Species Act in 2014. Despite a judge vacating the listing decision in 2015, the lesser prairie-chicken remains a species of concern. Conservation plans are currently being implemented and developed. To maximize the effectiveness of efforts, knowledge of the distribution of lesser prairie-chickens, regional demography, foods used during critical life-stages, and where to prioritize management is needed.

To guide future conservation efforts with empirical evidence, I captured, marked with transmitters, and monitored female lesser prairie-chickens in Kansas and Colorado during 2013–2016 ($n =307$). I used location data to predict the distribution of habitat. Encounter data from individuals were used to estimate vital rates and integrated into a matrix population model to estimate population growth rates (λ). The matrix model was then decomposed to identify life-stages that exert the greatest influence on λ and vital rate contributions to differences in λ among sites. After assessing demography, I examined the diet of adults and chicks during critical brood rearing and winter periods using a fecal DNA metabarcoding approach.

Overall, potential habitat appears to compromise ~30% of the presumed lesser prairie-chicken range in Kansas with most habitat in the Mixed-Grass Prairie Ecoregion. Within occupied sites, populations were most sensitive to factors during the first year of life (chick and juvenile survival), however, the persistence of populations through drought may rely on adult

survival. Among regional populations, breeding season, nest, and nonbreeding season survival rates contributed most to differences in λ among sites, breeding season survival contributed to differences in λ among more and less fragmented sites. During critical life-stages, diets were comprised of arthropod and plant foods. Among 80 readable fecal samples, 35% of the sequences were likely from Lepidoptera, 26% from Orthoptera, 14% from Araneae, and 13% from Hemiptera. Plant sequences from 137 fecal samples were comprised of genera similar to *Ambrosia* (27%) *Latuca* or *Taraxacum* (10%), *Medicago* (6%), and *Triticum* (5%). Among cover types, lesser prairie-chickens using native grasslands consumed a greater diversity of foods.

Last, promising conservation options include the conversion of cropland to grassland through the Conservation Reserve Program (CRP) and tree removal in mixed-grass prairie landscapes. Lesser prairie-chickens mostly used CRP during nesting and the nonbreeding season, during drier periods, and in drier portions of their distribution. Strategic CRP sign-up and tree removal could recover >60,000 ha and~100,000 ha of habitat respectively.

In summary, conservation that targets management in areas within broad scale habitat constraints predicted will be most beneficial. In areas occupied by lesser prairie-chickens, management that increases brood survival in large grasslands having optimal nesting structure will elicit the strongest influence on population growth and will likely be the most resilient to stochastic drought-related effects.

Regional variation in demography, distribution, foraging, and strategic conservation of lesser prairie-chickens in Kansas and Colorado

by

Daniel S. Sullins

B.S., Texas A&M University, 2008
M.S., Stephen F. Austin State University 2013

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

2017

Approved by:

Major Professor
David A. Haukos

Copyright

Abstract

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is 1 of 3 prairie-grouse species in North America. Prairie-grouse have undergone local or widespread declines due to a loss of habitat through conversion to row crop agriculture, anthropogenic development, and alteration of ecological drivers that maintain quality grasslands. For lesser prairie-chickens, habitat loss and declines were deemed significant for listing as threatened under the Endangered Species Act in 2014. Despite a judge vacating the listing decision in 2015, the lesser prairie-chicken remains a species of concern. Conservation plans are currently being implemented and developed. To maximize the effectiveness of efforts, knowledge of the distribution of lesser prairie-chickens, regional demography, foods used during critical life-stages, and where to prioritize management is needed.

To guide future conservation efforts with empirical evidence, I captured, marked with transmitters, and monitored female lesser prairie-chickens in Kansas and Colorado during 2013–2016 ($n = 307$). I used location data to predict the distribution of habitat. Encounter data from individuals were used to estimate vital rates and integrated into a matrix population model to estimate population growth rates (λ). The matrix model was then decomposed to identify life-stages that exert the greatest influence on λ and vital rate contributions to differences in λ among sites. After assessing demography, I examined the diet of adults and chicks during critical brood rearing and winter periods using a fecal DNA metabarcoding approach.

Overall, potential habitat appears to compromise ~30% of the presumed lesser prairie-chicken range in Kansas with most habitat in the Mixed-Grass Prairie Ecoregion. Within occupied sites, populations were most sensitive to factors during the first year of life (chick and juvenile survival), however, the persistence of populations through drought may rely on adult

survival. Among regional populations, breeding season, nest, and nonbreeding season survival rates contributed most to differences in λ among sites, breeding season survival contributed to differences in λ among more and less fragmented sites. During critical life-stages, diets were comprised of arthropod and plant foods. Among 80 readable fecal samples, 35% of the sequences were likely from Lepidoptera, 26% from Orthoptera, 14% from Araneae, and 13% from Hemiptera. Plant sequences from 137 fecal samples were comprised of genera similar to *Ambrosia* (27%) *Latuca* or *Taraxacum* (10%), *Medicago* (6%), and *Triticum* (5%). Among cover types, lesser prairie-chickens using native grasslands consumed a greater diversity of foods.

Last, promising conservation options include the conversion of cropland to grassland through the Conservation Reserve Program (CRP) and tree removal in mixed-grass prairie landscapes. Lesser prairie-chickens mostly used CRP during nesting and the nonbreeding season, during drier periods, and in drier portions of their distribution. Strategic CRP sign-up and tree removal could recover >60,000 ha and~100,000 ha of habitat respectively.

In summary, conservation that targets management in areas within broad scale habitat constraints predicted will be most beneficial. In areas occupied by lesser prairie-chickens, management that increases brood survival in large grasslands having optimal nesting structure will elicit the strongest influence on population growth and will likely be the most resilient to stochastic drought-related effects.

Table of Contents

List of Figures

List of Tables

Acknowledgments

First, thanks to Dr. David Haukos for his strong leadership, guidance, support, and patience throughout the extent of the research project. He is a champion for conservation and his selfless support for graduate students is unrivaled in academia. I also thank my committee members including Dr. Brett Sandercock, Dr. Shawn Hutchinson, and Dr. Mindy Rice for all of their wisdom, support, guidance, and for being masters of constructive criticism. Thanks to Dr. Jichul Jang for serving as outside chairperson with short notice.

To all my colleagues working on the lesser prairie-chicken project, including John Kraft, Joseph Lautenbach, Jonathan Lautenbach, Reid Plumb, Samantha Robinson, Beth Ross, and David Spencer, I have been very fortunate to work with a group as supportive, talented, and fun as you all. John Kraft was largely responsible for the resource selection function analyses in Chapter 4. Also, thanks to other fellow coop lab mates including Sara Ogden, Willow Malone, Ricky Lehrter, Thomas Becker, Brian Kearns, Ryland Taylor, and Andy Stetter. Thank you for coming over to provide field assistance when needed, for breaking up monotonous long hours in the cubicles with good conversation, for insightful chalkboard sessions, informing me of deadlines and keeping me focused, hooping it up in Wilmore, guiding hunts, near death adventures on the Kansas River, and for being superb travel partners when attending conferences.

The research presented in this dissertation would not have been possible without the asssistance of all private landowners that allowed access on their properties throughout the project. Several of these landowners were exemplary stewards of the land and I thank you all for maintaining, and allowing us to work on, some of the most beautiful tracts of native prairie in Kansas. Specifically, thank you to the Gardiner family for allowing us to conduct research on

greatly from all of your hard work. Also, thanks to Randy Rodgers for providing comments on a previous draft of Chapter 4.

Most importantly, thank you to my family for all of their support throughout the years, for believing in me, and for their patience. To my dad, Rick Sullins, for showing me how to work hard and never give up. To my mom, Debbie Sullins, for her steadfast love and wisdom, and to my sister, Lisa Sullins, for her compassion and drive to take care of others.

All of the results to follow are a product of 3 years of intense field research during which the other graduate students and I demanded a tremendous amount of time and effort from underpaid and overqualified field technicians. The quality of the research presented is largely a result of the tenacity of our dedicated field technicians. After long hours in the field and completion of assigned tasks, these individuals would always ask how else they could help, no matter how exhausted. Many thanks to William White, Liz Leipold, Jenny Proescholdt, Brittany Irle, Kellie Phillips, Greg Brinkman, Jacob Decker, Jennifer Yantacha, Blake Walter, Ian Waters, Brandon Anderson, Susan Baker, Susan Bard, Kyle Broadfoot, Riley Cooper, Jake Danner, Edward Entsminger, Robert Galvin, Neil Gilbert, Alix Godar, Geoff Gould, Harcy Bennett, Sam Hoffman, Doug Holt, Talesha Karish, Austin Klais, Hanna Kruckman, Kyle Kuechle, Sam Lane, John Letlebo, Ellie Mangelinckx, Laine McCall, Ashlee Nichter, Jordan Rabon, Tyler Reed, Ashlynn Rhodes, Aaron Steed, Amber Swicegood, Peter Waldron, Eric Wiens, Jennifer Yantachka, and Alex Zarazua.

Throughout this dissertation, you will notice that I use "I" to describe tasks completed, but use of first person does not indicate that I have performed all the tasks on my own. In contrary, all tasks completed were from a much larger collaborative research project for which I have been fortunate and honored to formulate into written form. Frankly, I dislike reading my

dissertation in this form; however, for style purposes and to relieve anyone else from a

commitment to my less than perfect writing and ideas, "I" has been used throughout.

Introduction

Grassland birds have shown greater declines in population size than any other guild of birds in North America (Herkert 1995, North American Bird Conservation Initiative 2014). Declines are largely a result of grassland habitat fragmentation and degradation (Peterjohn and Sauer 1999). Less than 0.1% of native prairie remains in areas with arable soil and favorable climate for farming (Samson and Knopf 1994). Overall, 37% of the world's grassland ecoregions are classified as "highly fragmented" (Ricketts et al. 1999). Grassland birds may be particularly sensitive to fragmentation due to the stochastic "boom or bust" population fluctuations exhibited by several species including lesser prairie-chickens (*Tympanuchus pallidicinctus*; Hagen et al. 2009, Grisham et al. 2013). In addition to fragmentation of grasslands, remaining large grassland ecosystems have been degraded through removal of natural ecological drivers including fire suppression from the landscape and shifts to more intensive grazing regimes (Askins et al. 2007). Removal and alteration of ecological drivers has allowed for the succession of grassland to shrub and woodland states in some areas, has reduced the heterogeneity of remaining grasslands, and can result in a loss of native forbs that provide food for several grassland birds (Vickery et al. 1999, Fuhlendorf et al. 2009).

In the Kansas and Colorado portions of the range of lesser prairie-chickens, grasslands have undergone varying levels of fragmentation largely based on soil type and proximity to above or belowground water for irrigation. On arable soils, the marginal potential for farming can create a mosaic of grassland, cropland, and Conservation Reserve Program fields (CRP) in some locations. In northwest Kansas and southeastern Colorado, the conversion of cropland to CRP grassland has been hypothesized to drive local increases in lesser prairie-chicken abundance (Rodgers 1999, Rodgers and Hoffman 2005). The interspersion of CRP, native grassland, and

1

cropland in this area provides evidence that there is no universally most profitable land management practice in this region. The lack of a single dominant land use may be a result of strong temporal variability of precipitation in the region (Sala et al. 1988, Opie et al. 1998). The temporal variation in precipitation is further compounded by a 40 cm gradient in average annual precipitation that spans the transition from mixed-to-shortgrass prairie (Grisham et al. 2016).

The variability of land management in the lesser prairie-chicken range contrasts with the variability of land use in the eastern portions of the current greater prairie-chicken (*Tympanuchus cupido*) range (e.g., eastern Kansas and patches in Missouri, Illinois, and Iowa). Largely driven by the greater reliability of precipitation, specific land management practices have proved most profitable in the eastern range of greater-prairie-chickens. For example, annual burning and grazing in the Flint Hills of Kansas is the most profitable option for producers operating on rocky soils with fairly reliable precipitation. In portions of Illinois, arable soils make planting corn and soybeans the most profitable option. The greater variability of landuse in western Kansas translates into larger grassland landscapes being more likely to provide high quality habitat for prairie grouse. This contrasts with the effect of greater grassland composition in the Flint Hills of Kansas, which may lead to more grassland of similar structure for greater prairie-chickens. For *Tympanuchus* species in general, population change in the Flint Hills would therefore be more a direct response of individual fitness (habitat quality, whereas in western Kansas, population change may be driven by a more complicated interaction of habitat availability and quality operating at both the individual and population level (Chalfoun et al. 2007, Pidgeon et al. 2006, Rodewald 2015, Chapter 4).

In the variable environment of the southern Great Plains where lesser prairie-chickens occur, persistence of populations is achieved through a boom-or-bust life history strategy in

which annual population growth fluctuates strongly with periods of favorable environmental conditions (Sala et al. 1988, Garton et al. 2016; Ross et al. 2016a, b). The boom or bust strategy likely evolved in a temporally unstable ecosystem that was compensated by the broad spatial availability of useable grassland (Mengel 1970, Wiens 1974). Lesser prairie-chickens and other prairie grouse species have adapted to unpredictable environments through the digestion of foods of minimal nutrient quality (Sedinger 1997), foregoing nesting during intense drought (Grisham et al. 2016), regularly renesting after nest failure (Lautenbach 2015), and by dispersing moderate distances during unfavorable periods (e.g., $\bar{x}$= 16.18 km, Earl et al. 2016). In contrast, during favorable periods, lesser prairie-chickens have a high reproductive potential that can maximize population recruitment (Hagen et al. 2009). Despite these life history traits, lesser prairie-chickens still require large areas of grassland with heterogeneous structure to avoid extinction over long periods of time (Simberloff 1994, Fuhlendorf et al. 2002, Silvy et al. 2004, Ross et al. 2016b).

Other prairie grouse (*Tympanuchus* spp.) occupying more fragmented grassland regions have comparatively lower adult survival compared to individuals that occupy more contiguous grasslands (McNew et al. 2012). Lesser prairie-chickens are known to avoid areas that are less than 64% grassland, and populations are less resilient to drought in landscapes having <90% grassland (Crawford and Bohlen 1976, Ross et al. 2016). Loss of grassland habitat for lesser prairie-chickens can also result from the presence of anthropogenic features in grasslands that would otherwise support lesser prairie-chickens (Pitman et al 2006, Hagen et al. 2011, Plumb 2015). Understanding where lesser prairie-chicken occupancy is constrained by limited grassland composition and anthropogenic features would greatly benefit conservation planning.

Within large grassland areas, the spatial heterogeneity of the grassland is of particular importance for providing life-stage specific habitat for the lesser prairie-chicken and other grassland birds (Fuhlendorf et al. 2006, Hovick et al. 2015, McNew et al. 2015, Sandercock et al. 2015). The landscape niche of lesser prairie-chickens is a product of using different vegetation types and structure for lekking (Taylor 1979), nesting (Pitman et al. 2006a), brooding (Hagen et al. 2005), and winter (Salter et al. 2005). Lesser prairie-chickens require heterogeneous grassland habitat and rangeland management must provide the appropriate composition and configuration of habitats necessary for each life stage. Therefore, effective conservation requires not only a knowledge of the needs of each of the habitats used during each life stage, but also knowledge of their availability and relative influence on population growth rates. Management can then be efficiently directed at components of habitat used during critical life stages (see sensitivity analysis in Chapter 1).

The alteration of natural ecological drivers may not only influence the heterogeneity of grasslands and their ability to provide cover for lesser prairie-chickens, but also the provision of food in the form of native forbs, which are disturbance dependent, and arthropod prey that rely on forbs. Diets during critical brooding and winter periods can influence lesser prairie-chicken populations. During the brooding period, rapidly growing lesser prairie-chicken chicks have high demands for protein and energy-rich foods and are restricted to foodstuffs within their immediate surroundings. During cold winters, meeting thermoregulatory demands on available food items of limited nutrient content may be challenging. Lesser prairie-chickens are known to have high nitrogen demands and eat both plants and arthropods (Haukos and Zaveleta 2016). Food resources available to lesser prairie-chickens are not well understood and past research has

4

struggled to link arthropod abundance and plant matter abundance to lesser prairie-chicken use or fitness (Salter et al. 2005, Haukos and Zaveleta 2016).

To best address all conservation related issues I sought to identify life stages exerting the greatest overall influence on population growth rates examine demographic variability among various landscapes (Chapter 1); estimate the distribution of lesser prairie-chickens in Kansas and Colorado based on broad-scale constraining factor (Chapter 2)s; identify the diets of lesser prairie-chickens during critical periods (Chapter 3); and examine the population response of lesser prairie-chickens to the conversion of cropland to grassland through the Conservation Reserve Program (Chapter 4). Last, I examined where regional specific conservation practices would be most likely to restore habitat for lesser prairie-chickens (Chapter2).

Literature Cited

Askins, R. A., F. Chavez-Ramirez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions: Report of the AOU committee on Conservation. Ornithological Monographs 64:1–46.

Chalfoun, A. D., and T. E. Martin. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

Crawford, J. A., and E. G. Bolen. 1976. Effects of land use on lesser prairie chickens in Texas. Journal of Wildlife Management 40:96–104.

Earl, J. E., S. D. Fuhlendorf, D. A. 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: e01441.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie Jr., 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 17:617–62

Fuhlendorf, S.D., D.M. Engle, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology 23:588–598.

Garton, E. O., C. A. Hagen, G. M. Beauprez, S. C. Kyle, J. C. Pitman, D. D. Schoeling, and W. E. Van Pelt. 2016. Population dynamics of lesser prairie-chickens. Pages 49–76 *in* D. A Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

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. PLoS One 8:e68225.

Grisham, B. A., C. P. Griffin, and A. J. Godar. 2016. Climate change. Pages 221–242 *in* D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. Journal of Wildlife Management 73:1325–1332.

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. University of California Press, Berkeley, USA.

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.

Haukos, D. A., and J. C. Zaveleta. 2016. Habitat. Pages 99-132 *in* D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Herkert, J. R. 1995. An analysis of midwestern breeding bird population trends: 1966-1993. American Midland Naturalist 134:41–50.

Hovick, T. J., R. D. Elmore, S. D. Fuhlendorf, D. M. Engle, and R. G. Hamilton. 2015. Spatial heterogeneity in grassland bird communities. Ecological Applications 25:662–672.

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

McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2012. Demography of greater prairie-chickens: regional variation in vital rates, sensitivity values, and population dynamics. Journal of Wildlife Management 76:987–1000.

McNew, L. B., V. L. Winder, J. C. Pitman, and B. K. Sandercock. 2015. Alternative rangeland management strategies and the nesting ecology of greater prairie-chickens. Rangeland Ecology and Management 68:298–304.

Mengel, R. M. 1970. The North American central plains as an isolating agent in bird speciation, pages 279-340 in Pleistocene and Recent environments of the central Great Plains Department Geological University Kansas Special Publication 3.

North American Bird Conservation Initiative, U.S. Committee, 2014. The State of the Birds 2014 Report. U.S. Department of Interior, Washington, D.C., USA.

Opie, J. 1998. Moral geography in High Plains history. American Geographical Society. Geographical Review 88:241–258.

Pidgeon, A. M., V. C. Radeloff, and N. E. Mathews. 2006. Contrasting measures of fitness to classify habitat quality for the black-throated sparrow (*Amphispiza bilineata*). Biological Conservation 132:199–210.

Pitman, J. C., C. A. Hagen, B. E. Jamison, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2006. Survival of juvenile lesser prairie-chickens in Kansas. Wildlife Society Bulletin 34:675–681.

Peterjohn, B. G., and J. R. Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey 1966-1996. Studies in Avian Biology 19:27–44.

Plumb. R. T. 2015. Lesser prairie-chicken movement, space use, survival, and response to anthropogenic structures in Kansas and Colorado. Thesis. Kansas State University, Manhattan, USA.

Ricketts,T., E. Dinerstein, D. Olson, C. Loucks, W. Eichbaum, K. Kavanagh, P. Hedao, P. Hurley, K. Carney, R. Abell, and S. Walters. 1999. A conservation assessment of the terrestrial ecoregions of North America. Island Press, Washington, D.C., USA.

Rodewald, A. D. 2015. Demographic consequences of habitat. Pages 19–33 *in* M.L. Morrison and H. A. Matthewson, editors, Wildlife habitat conservation: concepts, challenges, and solutions. John Hopkins University Press Baltimore, Maryland, USA.

Rodgers, R.D. 1999. Recent expansion of lesser prairie-chickens to the northern margin of their historic range, Pages 18–19 *in* R. Baydack, editor, Proceedings of the 23rd meeting of the Prairie Grouse Technical Council, Gimli, Manitoba, Canada.

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, 6–9 June 2004, Fort Collins, Colorado, USA. USGS Biological Resources Division, Scientific Investigation Report 2005–5145, Reston, Virginia, USA.

Ross, B. E., D. A. Haukos, C. A. Hagen, and J. C. Pitman. 2016a. The relative contribution of climate to changes in lesser prairie-chicken abundance. Ecosphere 7:e01323.

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

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Salter, G. C., R. J. Robel, and K. E. Kemp. 2005. Lesser prairie-chicken use of harvested corn fields during fall and winter in southwestern Kansas. Prairie Naturalist 37:1–9.

Samson, F. B., and F. L. Knopf. 1994. Prairie conservation in North America. Bioscience 44:418–421.

Sandercock, B. K., M. Alfaro-Barrios, A. E. Casey, T. N. Johnson, T. W. Mong, K. J. Odom, K. M. Strum, and V. L. Winder. 2015. Effects of grazing and prescribed fire on resource selection and nest survival of upland sandpipers in an experimental landscape. Landscape Ecology 30:325–337.

Sedinger, J.S. 1997. Adaptation to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314–326.

Silvy, N. J., M. J. Peterson, and R. R. Lopez. 2004. The cause of the decline of pinnated grouse: the Texas example. Wildlife Society Bulletin 32:16–21.

Simberloff, D. 1994. The ecology of extinction. Acta Paleontologica Polonica 38:159–174.

Taylor, M. A. 1979. Lesser prairie chicken use of man-made leks. The Southwestern Naturalist 24:706–707.

Vickery, P. C., and J. R. Herkert. 1999. Ecology and conservation of grassland birds of the Western Hemisphere. Studies in Avian Biology No. 19. Cooper Ornithological Society, Camarillo, California, USA.

Wiens, J. A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. 76:385–400.

Chapter 1 - Regional Variation in Lesser Prairie-Chicken Demography in Kansas and Colorado

Introduction

Loss of habitat and concurrent long- and short-term population declines led to the listing of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) as a threatened species under the 1973 Endangered Species Act in May 2014 (USFWS 2014). Despite a Federal judge vacating the listing decision in September 2015, the lesser prairie-chicken remains a species of great conservation concern (Federal Register 2016). A substantial amount of effort is currently underway to develop conservation plans and management prescriptions to recover the lesser prairie-chicken to population goals (Van Pelt et al. 2013). To maximize the effectiveness of conservation efforts, an understanding of life stages providing the greatest influence on the finite rate of population change (λ) and knowledge of demographic plasticity among the landscapes they occupy would be beneficial.

Lesser prairie-chickens are known to use different vegetation types and structure for lekking (Taylor 1979), nesting (Pitman et al. 2006a), brooding (Jamison 2000, Hagen et al. 2005), and winter (Salter et al. 2005). Because lesser prairie-chickens require a landscape-scale niche of heterogeneous habitat composition, management must provide the appropriate composition and configuration of habitats necessary for each life stage. Therefore, effective conservation will require not only a knowledge of the needs provided by each habitat used during each life stage, but also knowledge of their availability, connectivity, and relative influence on population growth rates. Management can then be efficiently directed at components of habitat used during critical life stages.

10

Past research suggests that parameters associated with nest survival and fecundity of *Tympanuchus* spp. have a strong influence on the finite rate of population change (Wisdom and Mills 1997, Hagen et al. 2009), whereby management directed toward improving reproductive success may most influence growth rates (Hagen et al. 2009). Lesser prairie-chickens have a fairly short life span with an average generation time of ~2 years (Hagen et al. 2009); the oldest documented wild bird is at least 6 years old (Lautenbach personal observation); females become sexually mature in less than a year; and populations have a variable but fairly high reproductive potential (Hagen et al. 2009). The life history traits are characteristics of a more r-selected species, for which, one would expect fecundity (nest and brood survival) to play a strong role in the finite rate of population change and may explain the short-term population dynamics of lesser prairie-chicken (Saether and Bakke 2000). The simple age structure, short generation time, and ability to reproduce in the first year of life also minimizes the bias due to transient dynamics if stable age distributions are not actually realized in matrix population modelling approaches (Koons et al. 2005). High fecundity rates may allow lesser prairie-chickens to take advantage of changes in habitat availability and quality across space and time over short generation times.

Although fecundity will influence λ in lesser prairie-chickens (Wisdom and Mills 1997, Hagen et al. 2008), adult and juvenile survival also can influence population growth rates for *Tympanachus* spp. (Hagen et al. 2009, McNew et al. 2012) and other upland gamebirds (Sandercock et al. 2008). For a boom-or-bust species such as the lesser prairie-chicken, survival becomes increasingly important during years in which conditions may not be favorable for reproduction (such as drought). A study of greater prairie-chickens (*Tympanuchus cupido*) conducted during a drought in eastern Kansas concluded that adult survival had the greatest influence on λ (McNew et al. 2012). Estimates of annual variation in lesser prairie-chicken

survival in the northern extent of the distribution include results from a 6-year study conducted in Finney County, Kansas, in which 4-month survival rates varied from 0.5 to >0.9 between adults and yearlings and among intervals including the breeding season (March – June), nonbreeding season (July – October), and winter (November – February; Hagen et al. 2009).

Some of the variation in the sensitivity of population growth rates among survival and fecundity rates may be related to variation in weather conditions among the aforementioned studies and differences in landscapes at each study site. It is unlikely that lesser prairie-chicken populations operate under a universal life history strategy with similar reproductive and survival rates throughout their range. Subsequently, range-wide management prescriptions would likely be of limited success in addressing limiting factors. Landscapes vary throughout the range of lesser prairie-chicken, spanning a sharp longitudinal ~40 cm precipitation gradient from east to west, a latitudinal 2 – 4° C change in average temperature, and with various soils distributed throughout (Soil Survey Staff 2015, PRISM 2016, Grisham et al. 2016). Categorically, the range of the lesser prairie-chicken has been divided into 4 ecoregions including the Sand Shinnery Oak Prairie, Short-Grass Prairie-CRP Mosaic, Sand Sagebrush Prairie, and Mixed-Grass Prairie ecoregions based on dominant vegetation and spatial isolation of presumed lesser prairie-chicken populations (McDonald et al. 2014).

Differences in dominant vegetation can often be a function of land use in addition to climate and soil. Spatial variation in climate, soils, and water availability all influence land use, which further complicates landscape composition and configuration. Farming typically occurs in increasingly mesic areas where soil is nutrient rich and water is supplied by precipitation or irrigation well. Cattle operations mainly occur in locations with less fertile or rocky soil and where the terrain is too rough to plow. However, land use is not always spatially predictable.

12

For example, farming often occurs in less favorable locations when supported by government

subsidies and tradition (Opie 1998, Glauber 2004). Regardless, the landscapes upon which lesser

prairie-chickens evolved have been both directly and indirectly altered (Hagen et al. 2011,

Haukos and Zavaleta 2016). Landscapes have been directly altered through the conversion of

grassland to cropland and by the presence of other manmade features (e.g., oil wells, wind

turbines, fences) and indirectly altered through the loss of key ecological drivers (e.g., fire, bison

grazing).

The historical occurrence of lesser prairie-chickens among variable grassland landscapes,

and the likelihood of their persistence among altered landscapes, may be related to the

demographic plasticity of prairie grouse. *Tympanuchus* spp. can show spatial variation in life

history strategies (Patten et al. 2005a, Hagen et al. 2009, McNew et al. 2011). Some populations

may compensate for low adult survival by having high reproductive rates, or reproductive effort,

whereas other populations may persist because of high survival when reproductive rates are

comparatively lower (Patten et al. 2005a, McNew et al. 2012). Greater prairie-chicken

populations were estimated to use alternative fecundity and survivorship dominated life history

strategies in eastern Kansas among regions exposed to differing land use and levels of grassland

fragmentation (McNew et al 2011). Lesser prairie-chickens may persist in more fragmented

grasslands associated with lower survival rates due to increases in reproductive effort (i.e., larger

clutch sizes, more attempts within good years; Patten et al. 2005a). However, lesser prairie-

chickens monitored in 2 field sites within Finney County, Kansas, did not show large differences

in overall life history strategies amid variation in λ. Both sites were in the sand sagebrush prairie

and with soils mainly in the choppy sands range site category (Hagen et al. 2009). I expect

greater variation in life history strategies among lesser prairie-chicken populations located

13

throughout the mixed-grass to short-grass prairie ecotone where a longitudinal gradient in precipitation, soils, and land use creates a contrast among grassland landscapes. Similar to differences in life history strategies of greater prairie-chickens (McNew et al. 2012), I expect lesser prairie-chicken populations in landscapes of large intact grassland to differ demographically from those in a fragmented Conservation Reserve Program (CRP)/cropland mosaic. The quality of landscapes for lesser prairie-chicken may be further influenced by woody encroachment and density of anthropogenic features (Lautenbach et al. 2017). I would expect tall vertical features, such as transmission lines and oil wells, to elicit a demographic response when not outright avoided (Plumb 2015).

My research goal was to provide knowledge of lesser prairie-chicken population dynamics that can guide conservation efforts throughout the northern extent of the range of lesser prairie-chickens across years of environmental variation between drought and above-average rainfall. I hypothesize that survival and fecundity of lesser prairie-chickens will (1) affect population growth rates, and (2) vary among study sites relative to the degree of fragmented vs. contiguous grasslands. Therefore, my objectives were to (1) identify vital rates having the greatest influence on λ and (2) compare estimates of λ and lower level vital rates among lesser prairie-chicken populations. Data collection began in spring of 2013 when lesser prairie-chickens were estimated at a contemporary population low (McDonald et al. 2014; Garton et al. 2016; Ross et al. 2016a,b). Vital rates of females were estimated among 4 study sites, 3 in Kansas and 1 in Colorado, spanning the northern half of the lesser prairie-chicken range during the 3 year period of 2013-2016.

Methods

Study Area

My study area included Kansas and Colorado portions of the lesser prairie-chicken range as identified in Hagen and Giesen (2005; Figure 1.1). Throughout the northern extent of the lesser prairie-chicken range, vegetative characteristics and land uses were largely a function of precipitation and soil type. A longitudinal gradient of average annual precipitation spans from east (69 cm) to west (37 cm) across the extent of lesser prairie-chicken range in Kansas and drives the transition from mixed-grass to short-grass prairie (PRISM 2016). Patches of farmland and sand sagebrush (*Artemisia filifolia*) prairie were interspersed throughout the transitional area. Sand sagebrush prairie occurred on sandy soils in the vicinity of current or former riparian areas and was more prevalent in the western portion of lesser prairie-chicken range. Patches of CRP grasslands and agriculture were concentrated in areas with arable soils. Overall, large remaining grasslands were restricted to areas of poor or rocky soils and areas with rough terrain. Historical ecological drivers in the study area included drought, grazing, and fire that all likely interacted to maintain the dynamic treeless expanses of mixed-grass and short-grass prairie. Drought is prevalent in the study area and major long-term droughts occur almost every 20 years, with frequent occurrence of minor droughts (Chen and Newman 1988, Grisham et al. 2016). Fire and grazing disturbance regimes have greatly been altered by confined grazing through use of fenced pastures and removal of fire from most of the study area. Pastures were large and fence densities are relatively low throughout most of the study area.

Within the study area, data were collected at 6 study sites including 2 in Colorado and 4 in Kansas (Figure 1.1). Mean and SD of vegetation height, litter depth, and percent cover varied among study sites (Table 1.1). For demographic analyses, the two study areas in northwest

Kansas (Northwest site) and study areas in Colorado (Colorado study site) were grouped to increase sample sizes for parameter estimation. Temperatures ranged from -26 to 43° C (extreme minimum and maximum temperature), with average daily minimum and maximum temperatures of 5° C and 21° C, respectively, during the period of data collection (15 March 2013 to 15 March 2016; NOAA 2016a). Drought severity varied throughout the study and was estimated using the Palmer Drought Severity Index (PDSI); an index of relative dryness derived from temperature and precipitation data. The standardized index is centered at zero and ≤ -4 indicates severe drought and anything above 0 indicates wetter than average (Palmer 1965). During the breeding seasons of 2013, 2014, and 2015, Palmer drought severity indices (PDSI) were -2.55, -0.62, and 1.36, respectively. During the nonbreeding seasons, average PDSI was -1.15, -0.27, and 1.60 in 2013, 2014, and 2015, respectively (NOAA 2016b). Overall, drought intensity decreased from March 2013 to March 2016 when the study ended.

The two study sites in Colorado were dominated by *Bouteloua curtipendula* (Michx.), *Bouteloua gracilis* (Willd. ex Kunth), *Sporobolus cryptandrus* (Torr.), *Artemisia filifolia* (Torr.), *Convolvulus arvensis* (L.), *Salsola tragus* (L.), and *Kochia scoparia* (L., Haukos et al. unpublished data). The Prowers County study site (1146 ha) was comprised of dwindling patches of grassland (mostly CRP) within a landscape mosaic of dryland and irrigated row-crop agriculture. The Prowers County site was composed of 43% cropland, 28% native working grassland, and 25% CRP (Homer et al. 2015). Prowers County was dominantly comprised of loamy soils (Soil Survey Staff 2015) and receives an average of 43 cm of precipitation annually (Grisham et al. 2016, PRISM 2016). Most CRP fields were enrolled into the program in the mid-1980s and had recently undergone mid-contract management. To meet the management requirements, typically 1/3 of the CRP fields were disked creating linear strips of disturbed and

undisturbed grass (J. Reitz, Colorado Parks and Wildlife, personal communication). The study

site in Cheyenne County (16,968 ha) was comprised of large expanses of lightly and heavily

grazed sand sagebrush prairie where 30-year precipitation averages were the lowest of all the

study sites (37 cm, Grisham et al. 2016). The Cheyenne County study site was composed of

99% native working grassland and 1% cropland both largely occurring on sandy soils (Homer et

al. 2015, Soil Survey Staff 2015).

In Kansas, the four study sites were referenced as Clark, Red Hills, Gove, and Logan.

The Clark study site, primarily located in western Clark County, was on the edge of the Mixed-

Grass Prairie and Sand Sagebrush Prairie ecoregions. The site received an average of 59 cm of

rain annually and was dominated by *Sporobolus cryptandrus, Ambrosia psilostachya* (DC.),

Bouteloua gracilis, Salsola tragus, Schizacyrim scoparium (Michx.)*, Sporobolus compositus*

(Poir.)*,* and *Artemisia filifolia* (Haukos et al. unpublished data; PRISM 2016). The Clark site

was largely comprised of two privately owned ranches; one in the Cimarron River floodplain

(32,656 ha) dominated by loamy fine sands, fine sandy loams, and fine sands with a second

ranch in the rolling hills (14,810 ha) about 20 km north on mostly silty clay, clay loam, and silt

loam (Soil Survey Staff 2015). The Clark site was 77% grassland, 14% cropland, and 5.5% CRP

(Robinson et al. *in review*). Research efforts focused on the southern portion of the study site,

which can be best described as gradients of sub-irrigated alkali flats to choppy sand sagebrush

prairie. Rotational grazing systems for both cow/calf and yearling herds were used in this area.

Stocking rates were set to take half and leave half of available forage produced each growing

season on the study ranches.

The Red Hills study site (49,111 ha) was located in the mixed-grass prairie of Comanche

and Kiowa counties and represented the eastern boundary of the lesser prairie-chicken range.

17

The Red Hills study site was not only the most eastern study site, but also received the greatest annual precipitation, on average receiving 69 cm annually (PRISM 2016). Dominant plant species included *Schizachyrim scoparium, Artemisia ludiviciana* (Nutt.)*, Bouteloua curtipendula, Ambrosia psilostachya, Sporobolus cryptandrus, Bromus tectorum* (L.), and *Bouteloua gracilis* (Haukos et al. unpublished data). The Red Hills site was comprised of large contiguous grasslands with many drainages and both cow/calf and yearling (season long) grazing systems. The Red Hills study site was 87% grassland, 8.9% cropland, and 2.2% CRP (Robinson et al. in review). Research efforts focused on a large ranch that used a patch burn grazing system wherein large pastures were divided into 3, and 1 portion was sequentially burned each year. Dominant soils included sandy loam, clay loam, and clay (Soil Survey Staff 2015).

Study sites in northwestern Kansas were located in Gove and Logan counties and together are referred to as the Northwest study site. The Logan study site (41,940 ha) was comprised of more short-grass prairie and on average received less precipitation than the Gove study site (87,822 ha) to the east as the transition between semi-arid and temperate precipitation levels divided the study area. Dominant plant species at the Gove County study site included *Bouteloua curtipendula*, *B. gracilis, Sporobolus cryptandrus, Pascapyron smithii* (Poir.)*, Schizachyrim scoparium, Gutierrezia sarothrae* (Pursh), and *Bromus tectorum* (Haukos et al. unpublished data). Both study sites were mosaics of CRP, dryland agriculture, and short-grass or mid-grass prairie. The Northwest study site was a mosaic of CRP (7.4%), cropland (36%), and native short-grass or mixed-grass prairie (54%; Robinson et al. in review). Soils at the Gove and Logan study sites were predominantly silt loams (80% and 75% of soil by area, respectively) but clay loams and fine sandy loam were also present (Soil Survey Staff 2015). All Gove County study sites were located on private land. The Logan County site included Smoky Valley

Ranch (SVR), owned and operated by The Nature Conservancy. Dominant plants in the Logan county study site included *Bouteloua gracilis, Bouteloua curtipendula, Sporobolus crypandrus, Aristida purpurea* (Nutt.)*, Schizachyrim scoparium*, and *Pascopyrum smithii* (Rydb., Haukos et al. unpublished data). Additional private lands south of SVR included in the study represented mixed-grass and short-grass prairie, CRP, and dryland row crops. A wide range of grazing practices and intensities were represented across the study region. A full season, rotational grazing operation for both cow/calf and yearling herds appeared to be the dominant system used among local ranchers (Kraft 2016). The condition of CRP tracts varied throughout the study site. A significant portion of the CRP tracts were hayed in the last several years due to drought, a few tracts were inter-seeded and disked; others were undisturbed and idle. Fire was not a commonly used management practice in the area.

The Red Hills and Clark study sites were located in the Mixed-Grass Prairie Ecoregion, whereas the Logan and Gove Study sites were located in the Short-Grass/ CRP Mosaic Ecoregion of the current range of lesser prairie-chickens (McDonald et al. 2014). The Cheyenne County and Prowers County study sites each represented isolated portions of the presumed lesser prairie-chicken range in Colorado and occurred within the Sand Sagebrush Prairie Ecoregion (Hagen and Giesen 2005, McDonald et al. 2014).

Capture and Vital Rate Data Collection

Fecundity data were collected during the 2013, 2014, and 2015 breeding seasons with concurrent annual and seasonal survival estimates. Lesser prairie-chickens were captured at all study areas between early March and mid-May lekking seasons using walk-in funnel traps and drop nets (Haukos et al. 1990, Silvy et al. 1990). Lesser prairie-chickens were sexed based on coloration, pinnae length, and tail pattern. Each individual was aged as either yearling (SY) or

19

adult (ASY) depending on the color patterns, shape, and wear of the outermost primary flight feathers (P9 and P10; Ammann 1944). All individuals that could not be aged were excluded from analyses. I measured flattened wing chord (mm), pinnae length (mm), comb height (mm), comb length (mm), tarsus length (mm), and tail length (mm) using digital calipers and a wing board. I measured body mass (g) for each lesser prairie-chicken using Pesola spring scales (1,000-g scale for adults, and 100 or 300-g for chicks and juveniles).

Captured females were uniquely banded with four plastic leg bands, and tagged with either a 15-g very-high-frequency (VHF) transmitter or 22-g global-positioning-system (GPS) satellite PTT transmitter and released at the site of capture. I obtained locations for each VHF-marked female four times a week. I recorded 8-10 GPS locations/day from each satellite-marked female, contingent on available daily solar energy. GPS locations were recorded every two hours during the day with a six-hour gap between 2300 and 0500.

During the breeding season, searches for nest locations were conducted when females localized for >3 days or appearing to be nesting based on satellite data. Females were flushed upon first discovery of a nest, with Universal Transverse Mercator system coordinates recorded and eggs counted and floated to predict hatch date (McNew et al. 2012). Nests were monitored remotely using triangulation for VHF-marked lesser prairie-chickens and by examining satellite locations. Once a female left a nest location, I visited the area to determine nest success or failure from eggshell appearance and presence/absence of predator sign. If a nest was successful, I monitored brood and chick survival with brood flush counts at lesser prairie-chicken locations within 1 hour of sunrise at weekly intervals from 14 to 60 days after hatch. I thoroughly searched the area surrounding each transmittered female to maximize chick detection. If no

20

chicks were detected, I flushed the female once more to make sure the brood was no longer present.

 Fecundity Parameters

Nest propensity (NEST) was estimated using a Horvitz – Thomson estimator that accounted for bias from nests that failed before being detected (Dinsmore et al. 2002). I estimated nesting propensity only for GPS-marked females because of the greater resolution location data (8-10 locations/day) and I was typically able to verify nest establishment within 3 days of a nest being attempted. Prior to incubation, female lesser prairie-chickens typically visited nest locations each day from 1200 – 1400 to establish a nest and lay eggs while displaying unique movement patterns relative to non-nesting females (D. Haukos, unpublished data). To account for undetected nests, I divided 1 by the 3-day nest survival rate from the top ranking nest survival model, then multiplied this number by the total number of detected nests to provide an adjusted estimate of the total number of nests (Dinsmore et al. 2002). The adjusted number of nests was divided by the total number of females that were captured presumably before losing a first nest (before 22 April) and survived long enough to attempt a nest (survived to 10 May). I estimated propensity to renest (RENEST) following a similar protocol, but estimated the proportion of females that attempted a second nest after losing their first nest. I recorded average clutch size for all first (CLUTCH1) and second (CLUTCH2) nest attempts. I estimated hatchability following Pitman et al. (2006) as the number of chicks hatched per egg laid (HATCH). I assumed that an equal ratio of males to females when estimating fecundity.

Daily nest survival rates for yearling and adults and first and second nest attempts were estimated following the nest survival procedure within Program MARK (White and Burnham 1999, Dinsmore et al. 2002). A nest attempt by age class interaction model was estimated in the

21

R package RMark (Laake 2013, R Development Core Team 2016), and was used to estimate nest

survival throughout the laying and incubation period because I was interested in differences

between age classes and nest attempts; I assessed the parsimony of incorporating age related

effects using an information criteria approach (Burnham and Anderson 2002). I extrapolated

daily survival rates across the laying and incubation period (~35 days) to estimate nest survival

for four groups: yearling first nests, renests of yearlings, first nests of adults, and renests of

adults. The delta method was used to derive standard errors for each extrapolated nest survival

rate (Powell 2007). Chick survival (CHICK) to 35-days post hatch was estimated following

Lukacs and Dreitz (2014). Juvenile survival estimates encompassing the first fall and winter of a

lesser prairie-chicken's life, August (35-days old) to March 14, were derived from Hagen et al.

(2009, Table 1.2). Fecundity was estimated for the two age classes (c) using the equation below

based on Hagen et al. (2009).

$$Fc = [(NEST \; x \; CLUTCH1 \; x \; NSURV1)$$

$$+ (1 - NSURV1) \; x \; (RENEST \; x \; CLUTCH2 \; x \; NSURV2)]$$

$$x \; (HATCH \; x \; 0.5 \; x \; CHICK)$$

Female Survival Parameters

I used Kaplan-Meier models to estimate breeding season survival for adult and yearling

lesser prairie-chickens during 2013 - 2016 (Sb; 15 March – 15 September; Pollock et al. 1989,

Plumb 2015). The same Kaplan-Meier models were used to estimate nonbreeding season (16

September – 14 March) survival (Snb) for adults and yearlings combined (Pollock et al. 1989,

Robinson 2015). I estimated nonbreeding and breeding season survival separately because of

differences in habitat use (Haukos et al. unpublished data) and mortality (Boal 2016) during

these seasons. I assessed effects of site, age, site + age, and the interaction of site and age using

a multimodel information criteria approach (Burnham and Anderson 2002). I used the output of site-specific model for estimates of both breeding and nonbreeding season survival. Annual survival was the product of survival during each 6-month season for each age class (c) as:

$$Sc = Sb \; x \; Snb$$

Matrix Population Modelling

Fecundity and survival parameters were integrated into the population matrix below (A). Wherein *Fy* represents yearling fecundity, *Fa* is adult fecundity inputs, *Sjuv* is juvenile survival, *Sy* is yearling annual survival, and *Sa* is adult annual survival.

$$A = \begin{bmatrix} Fy \; x \; Sjuv & Fa \; x \; Sjuv \\ Sy & Sa \end{bmatrix}$$

I used the R package popbio to estimate the finite rate of population change (λ), generation time in years (T), and net reproductive rate (R_0) for all birds combined and for each study area (Stubben and Milligan 2007). I estimated the mean and SD of all population matrix elements and sensitivity and elasticity values (see below) using 1,000 bootstrap iterations.

Sensitivity and Elasticity

I estimated the sensitivity of λ to changes in each matrix element (a_{ij}) and each lower-level vital rate (x_{ij}) used to estimate fecundity and annual survival of adults and yearlings. Sensitivities were estimated as the absolute change and elasticities as the proportional change of a_{ij} and x_{ij} on λ (Sensitivity; $s = \partial\lambda \, / \, \partial a_{ij}$, Elasticity; $e = \partial\ln\lambda \, / \, \partial\ln a_{ij}$). I pooled breeding season survival of adults and yearlings for lower level analyses of x_{ij}. I calculated lower level sensitivities of vital rates following Caswell (2001) and McNew et al. (2012).

$$s_x = \frac{\partial\lambda}{\partial x} = \sum_{i,j} \frac{\partial\lambda}{\partial a_{ij}} \frac{\delta a_{ij}}{\delta x} \qquad\qquad e_x = \frac{x}{\lambda} s_x$$

In addition to standard sensitivity and elasticity values, I also estimated the variance stabilized sensitivities (VSS) that minimize covariance of estimates with the variance of the vital

23

rate (Link and Doherty 2002). I calculated VSS for all binomially distributed vital rates (probabilities) using the equation

$$VSS_x = \left(\frac{\sqrt{x(1-x)}}{\lambda}\right)\frac{\partial \lambda}{\partial x}$$

I did not estimate VSS for clutch size because it was normally distributed and presents challenges for direct comparison among other vital rates. Comparisons of clutch size were limited to elasticity and sensitivity values.

Life-Stage Simulation Analysis

I followed Sandercock et al. (2008) and Wisdom et al. (2000) to create a Life-Stage simulation analysis (LSA) in which I iteratively drew vital rate estimates for the 12 parameters (Table 1.3) and estimated finite rate of population (λ) change for each set of random draws. Using 1,000 bootstrap iterations, I drew estimates for each vital rate directly from uniform distributions for clutch size and from uniform distributions of 95% confidence intervals for probability based vital rates. I used bootstrapped values to estimate fecundity and annual survival among age classes. I then performed linear regressions among the bootstrapped arrays for each parameter and respective finite rate of population change estimates. Coefficient of determination and slope estimates were acquired from each linear regression. I examined how much variation of the finite rate of population change was explained by simulated variation in each parameter using the coefficient of determination. I also assessed the strength of potential relationships among parameters and λ by assessing the slope of coefficients. I predicted that vital rates having the greatest estimated variance (as indicated by SD) would explain the greatest change in the finite rate of population growth (λ) and tested this hypothesis by regressing the SD of each estimate with the estimated coefficient of determination in the above linear regressions.

24

All regressions were performed using a least squares regression in Program R (R Core Development team 2016).

Life Table Response Experiment

I conducted a retrospective analysis to estimate vital rates that contributed (c) the most to difference in the rate of population change among female lesser prairie-chickens occupying the four study sites. I estimated contributions to the finite rate of population growth rate for each treatment using a fixed-effects life-table response experiment (Caswell 1989).

Results

I captured and marked with VHF or GPS transmitter 307 female lesser prairie-chickens during the spring lekking seasons of 2013–2016. Of the females marked with VHF of GPS transmitters 7% (21) were of unknown age, 28% (87) were adults, and 64% (199) were yearlings. Only females that could be aged as yearling (SY) or adult (ASY) were used to estimate vital rates and sample sizes used to estimate each vital rate are listed in Table 1.3. On average, 95% of female lesser prairie-chickens attempted at least one nest, laid 10.8 eggs, and nest survival rates ranged from 0.438–0.467. Of the hatched nests, ~26% of chicks survived to 35 days. Mean survival estimates for adults and yearlings ranged from 0.41–0.63 during the breeding season and was estimated at 0.73 (95% CI = 0.6490.805) with adults and yearlings pooled for the nonbreeding season (Table 1.3). Top ranking models predicting daily survival of nests included a model with year effect, the null model, and the age model (Table 1.4). However, I used the age by site interaction model because I was interested in cumulative effects among sites. For survival during the breeding and nonbreeding seasons, the model including site as a covariate was most parsimonious (Table 1.5). Survival and fecundity vital rates varied among sites (Table 1.6).

25

The time frame during which vital rates were estimated incorporated periods of variable weather, which likely resulted in variable nest propensity estimates (2013 = 89%, 2014 = 96%, 2015 = 100%) and renesting propensity estimates (2013 = 14%, 2014 = 51%, 2015 = 35%). The high-resolution location data (8–10 locations a day) from GPS transmitters likely allowed for a more accurate estimate of the propensity to nest and renest than achieved in the past using VHF marked females.

Matrix Population Model

Bootstrapped estimates of λ, the stable age distribution (w_c), reproductive values (v_c), and net reproductive rate (R_0), generation time in years (T), fecundity (F_c), and annual survival (S_c) were estimated within and across sites (Table 1.7). Among all sites, the finite rate of population change predicted that lesser prairie-chickens declined at a rate of 31% per year ($\lambda = 0.69$; 95% CI = 0.501–0.885) assuming that immigration and emigration were in equilibrium for GPS marked birds that were still monitored after making large movements, vital rates did not change for censored VHF birds that moved long distances and were no longer monitored, limited individual heterogeneity in fitness, no density dependence, and assuming vital rate estimates were not otherwise biased. The model had a relatively high damping ratio ($p = 40.22$), and the model quickly converged to the stable age distribution ($t_{20} \sim 0.819$ years). When estimated for each site, mean λ estimates ranged from 0.578 at Northwest Kansas study site to 0.826 at the Red Hills study site. Estimates of λ at the Clark, Colorado, and Red Hills study sites all overlapped 1.0 at the 95% confidence interval, suggesting that study sites other than Northwest have the potential to exhibit a stable population trajectory with number of young recruited ≥ the number of deaths. The stable age distribution achieved an asymptote near an equal proportion of both adults and yearlings among all study sites ($w_A = 0.479$, 95% CI = 0.333–0.624, $w_Y = 0.521$, 95% CI =

0.376–0.666) with a similar pattern at each study site. The estimated reproductive value (v) was near 1 for both adult and yearling female lesser prairie-chickens (Table 1.7). Female lesser prairie-chickens had a net reproductive rate (R_0) of 0.293 ± 0.150 (estimate ± SD; female chicks/female/generation) among all sites and varied from 0.191 in Northwest Kansas to 0.532 in the Red Hills. Generation times (T) were similar for lesser prairie-chickens and ranged from 3.43 to 3.86 years in the Northwest and Clark study sites, respectively.

Sensitivity and Elasticity

Sensitivity of λ to changes in the main matrix elements (a_{ij}) were evaluated based on bootstrapped ($n = 1,000$) means and SD (Table 1.7). Among the main matrix elements sensitivity and elasticities were all within 0.1 of each other, suggesting that λ is equally sensitive to both fecundity and annual survival of both age classes (Table 1.7). The same pattern was observed among sites with a relatively uniform influence of all matrix elements; however, the Northwest population may be more sensitive to the fecundity of adults while lesser prairie-chickens at all other study sites were most sensitive to the survival of adults or yearlings. Agreement between both sensitivity and elasticity support this subtle demographic variation among sites (Table 1.7).

I detected similar patterns of equal λ sensitivity to lower level survival rates with juvenile, breeding, and nonbreeding survival having near equal elasticity among all sites and breeding season survival having slightly greater VSS (Table 1.8, Figure 1.2). Although juvenile survival is technically a component of fecundity in a pre-birth pulse projection matrix, I grouped adult, yearling, and juvenile survival in table 1.8 for comparison. In contrast to the similar sensitivity of λ among survival periods, fecundity sensitivity estimates were predominantly a result of lower level sensitivity to chick survival ($s = 1.35$, $e = 0.496$, VSS = 0.848; Figure 1.2).

27

Elasticity values also indicated that λ was influenced by nest propensity and the clutch size of first nests (nestprop e = 0.438, TCL_1 = 0.438); however, elasticity estimates for these vital rates were not in agreement with absolute estimates (sensitivity) and VSS (sensitivity TCL1 = 0.028, VSS nestprop = 0.099, Table 1.8).

Life-Stage Simulation Analysis

The life-stage simulation analysis revealed patterns of both lower level vital rates (e.g., nest survival of adults) as well as cumulative effects of age-specific fecundity estimates and annual survival (Figure 1.3). The results depicted both explained variance (r^2) of the finite rate of population change (λ), within the domains of vital rate variance among all sites, as well as the relationship between vital rate and finite rate of population growth (β or slope). I expected that vital rate estimates having the greatest variance would best explain variation in λ and this pattern was apparent for the influence of juvenile survival on λ. Juvenile survival explained the greatest variance in λ and had the second greatest standard deviation estimate among all probabilities (SD = 0.089). The pattern did not hold among all variables, as there was no significant relationship between estimated SD of a vital rate and λ ($\beta = 0.653 \pm 0.856$; overlapped zero at 85% CI; Arnold 2010). Therefore, there is indication that variables have biological explanation in influencing λ outside of just variance of the estimate.

Based on the explained variance, clutch size of first nesting attempts ($r^2 = 0.405$, $\beta = 0.029 \pm 0.001$) had the greatest influence on λ followed by juvenile survival ($r^2 = 0.322$, $\beta = 0.634 \pm 0.029$). The third most influential vital rate (yearling breeding survival; $r^2 = 0.057$, $\beta = 0.381 \pm 0.045$) explained ~5 times less of the variance than juvenile survival and all the remaining variables explained 0–5% of the variation in λ (Figure 1.3). Although populations were consistently estimated to be sensitive to chick survival based on sensitivities, elasticities,

and VSS, the life-stage simulation analysis did not suggest much influence on λ based on explained variance (r^2). However, unstandardized slope estimates with chick survival affected the greatest rate of change in λ ($\beta = 1.09 \pm 0.222$), followed by juvenile survival, adult breeding survival ($\beta = 0.634 \pm 0.029$), and yearling breeding survival ($\beta = 0.381 \pm 0.045$). It should be noted that clutch size and fecundity estimates should not be compared to other vital rates using slope because of differing scale. Compared to other vital rates, chick survival exhibited a strong positive trend with λ and the slope estimate was greater than for juvenile survival (Figure 1.3).

The limited influence of nest survival among adults and yearlings on λ was surprising, given that lesser prairie-chickens have short life spans and would fall more on the r-selected side of the continuum of life history strategies. It was only when all the components contributing to fecundity were summed that the influence of reproduction on lesser prairie-chicken demography was apparent (Figure 1.3). Both the fecundity of adults and yearlings explained >9 times more of the variation in the finite rate of population change than survival of the two age classes.

Life-Table Response Experiment

I used a one-way fixed effects life-table response experiment to retrospectively assess how lower level vital rates contributed to differences in λ for each site from λ estimated among all sites. The life table response experiment estimated the contribution of vital rates (c) to differences in population growth rates (λ) estimated at each study site during the period of the study rather than projected into the future as in previous sensitivity and LSA analyses. Differences in lambda were not based on bootstrapped estimates, but using deterministic estimates from package 'popbio' in Program R, for which, the sum of all contributions should approximate the difference in λ (Stubben and Milligan 2007). The finite rate of population change (λ) differed -0.106 in Northwest, +0.135 in the Red Hills, +0.097 in Clark, and +0.083 in

29

Colorado from the mean estimate among all four sites ($\lambda = 0.683$). Lower level contribution estimates ranged from -0.055 to +0.094 (Figure 1.4). Vital rates exhibiting the greatest variation in contributions among sites included breeding survival, nest survival of adults, nonbreeding survival, and chick survival (SD of c among sites = 0.067, 0.050, 0.044, and 0.033, respectively; Figure 1.4). My findings suggest that lesser prairie-chickens exhibit the greatest demographic plasticity in breeding survival, nest survival of adults, nonbreeding survival, and chick survival among working landscapes in western Kansas and eastern Colorado.

Biotic and abiotic processes occurring on landscapes in northwest Kansas from 2013–2016 contributed to a lower demographic rate at this study site. Vital rates contributing most to the lower population growth estimate included breeding survival ($c = -0.054$) and nonbreeding survival ($c = -0.028$) of females and outweighed the positive contribution of chick survival ($c = 0.008$) at the Northwest site. The greater than average λ at the Red Hills site was largely driven by contributions of greater survival during the nonbreeding ($c = 0.067$) and breeding season ($c = 0.054$). Whereas, increases in λ at the Clark site were based on contributions from survival during the breeding season ($c = 0.094$) and chick survival ($c = 0.019$). The Colorado site was the only site to show large contributions from nest-related vital rates with adult nest survival ($c = 0.087$) and breeding survival ($c = 0.082$) contributing most to greater than average λ at this study site (Figure 1.4).

Discussion

The comprehensive demographic estimates herein are the first for lesser prairie-chickens in the Mixed-Grass Prairie and Short-Grass Prairie/CRP mosaic ecoregions of Kansas. In entirety, the Mixed-Grass Prairie and Short-Grass Prairie/CRP mosaic ecoregions may house ~80% of all extant lesser prairie-chickens (McDonald et al. 2014, 2016). Demographic estimates

for study sites in the Mixed-Grass Prairie and Short-Grass Prairie/CRP mosaic ecoregions

complements a previous demographic assessment of lesser prairie-chickens in the Sand

Sagebrush Prairie Ecoregion of Kansas (Hagen et al. 2009) and also expand knowledge of

population dynamics in the Sand Sagebrush Prairie Ecoregion by providing estimates for the

Colorado portion of this ecoregion. Among the four study sites in Kansas and Colorado, the

matrix population model projected a 31% per year decline ($\lambda = 0.693 \pm 0.098$) in lesser prairie-

chickens assuming equal immigration and emigration of GPS marked individuals in and out of

the study areas sampled, no variation in vital rates for VHF marked birds that permanently

emigrated from sites, limited individual heterogeneity, no density dependence, and vital rate

estimates were not otherwise biased. The predicted declining estimate may be depressed due to

the initiation of the study following, and during, severe drought conditions (Hoerling et al. 2014,

Su and Dickenson 2014). Although drought conditions may have limited the predictive power of

the population growth estimate, the period of study presented an opportunity to assess the

sensitivity of λ to changes in specific vital rates and assess demographic variation among

landscapes spanning a ~40 cm precipitation gradient (PRISM 2016). In summary, λ was equally

sensitive to main matrix elements (fecundity and survival, a_{ij}) and sensitivity estimates were

nearly equal among lower level survival rates for juveniles and during breeding and nonbreeding

season. Counter to survival estimates, lower level fecundity sensitivities were less uniform with

chick survival and hatchability having the greatest estimates (sensitivity, elasticity, and VSS).

Chick survival also appeared to have a strong relationship with λ in the life-stage simulation

analysis based on the slope coefficient. However, clutch size of first nests and juvenile survival

explained the greatest variance in λ. In the retrospective fixed effects life table response

experiment, breeding season survival, nest survival of nests initiated by adults, and nonbreeding

31

season survival exhibited the greatest variation in contribution to both greater than and lower than average λ among sites.

The prospective (sensitivities, elasticities, and VSS) and retrospective analyses (life-stage simulation analysis and life table response experiment) provide insight into the overall demography of lesser prairie-chicken but differ in inference provided (Caswell 200). The strength of the prospective analysis is that it shows definitively which vital rates will most impact λ and does not require rigorous estimates of the process variance of vital rates, however, prospective analyses may suggest managing for a vital rate that cannot be easily altered with management. For example, chick survival may never attain a rate of 0.95 in actual landscapes due to the inability of reducing the abundance of predators and altering all other abiotic and biotic factors to attain near perfect survival. In contrast to prospective analyses, the retrospective life stage simulation and life table response experiment contributions are based on the actual variance observed during the study. Estimates from each analysis should therefore be interpreted differently but when synthesized can provide a more holistic description of population demography among sites (Caswell 2000, McNew et al. 2012). In summary, the prospective sensitivity and elasticity values indicate breeding and nonbreeding survival, juvenile survival, chick survival, and hatchability will most influence λ in the future without considering the upper and lower boundaries of vital rates that were realized during the period of the study (Table 1.8, Caswell 2000). The life stage simulation analysis identified that λ was influenced by fecundity (incorporating juvenile survival) within the constraints of estimated vital rates among the pooled sites and years of the study (Figure 1.3). The life table response experiments provided a more spatially driven comparison among study sites and depicted variation in breeding season

32

survival, nonbreeding season survival, and nest survival of adults driving site variation in demography (Figure 1.4).

Matrix population models provide utility in estimating the cumulative effects of all vital rates on fitness while also providing a framework for decomposing the sensitivity and contribution of lower level vital rates to λ (Caswell 2001). The required estimation of overall population growth before the true importance of lower level vital rates can be deciphered provides an example of how understanding the effects at a focal level may be confounded by first having knowledge at higher levels of order (O'Neil et al. 1989, Heffernan et al. 2014). Similarly, the effects of the rate of population change on persistence of the species as a whole may not be possible without understanding factors operating at higher hierarchical levels including the episodic variation of vital rates, distribution of the species/habitat availability and connectivity throughout, carrying capacity of habitat patches, and metapopulation dynamics among habitat patches (e.g., asynchronous population growth among subpopulations; Hanski and Gyllenberg 1993). Unfortunately, some of the aforementioned higher level effects, such as the episodic variation in vital rates on overall habitat availability, likely influence population growth rate estimates using matrix modeling approaches and these effects may be readily apparent in lesser prairie-chickens (Chapter 2 & 4: Beissinger and Westphal 1998; Ross et al. 2016a,b). Therefore, the utility of my matrix population model predictions is in comparing individual level fitness among already occupied habitat, providing inference on drivers of habitat quality among differing populations, and decomposing how each vital rate influences asymptotic population growth rate estimates (Mills 2007).

Population Sensitivity

Considerable evidence suggests grouse population growth is most sensitive to chick survival and chick survival is most influenced by factors occurring within the first few weeks as a hatchling (Bergerud and Gratson 1988, Hagen et al. 2009, Lautenbach 2015). Such a strong population bottleneck during this period may result in the entire population trajectory of grouse and lesser prairie-chickens being based on events occurring in a short one or two-week period (Fields et al. 2006, Grisham 2012, Lautenbach 2015). The sensitivity and life-stage analyses provide some support for this prediction, and sensitivities suggested that chick survival may have a greater effect on λ for lesser prairie-chickens than for greater prairie-chickens (Wisdom and Mills 1997, McNew et al. 2012). Any management that increases survival of chicks would likely be of great benefit to lesser prairie-chicken populations. During this life stage, chicks require grasslands with an open understory and forbs (~20%) which provide host plants for an abundance of arthropod foods that in turn provide a protein-rich food source for growing chicks (Riley and Davis 1993, Hagen et al. 2004, Hagen et al. 2013, Lautenbach 2015). Chick survival is not spatiotemporally independent of nesting. For a chick to pass through the 7 or 14-day survival bottleneck, a nest first must be initiated and survive the laying and incubation period.

Of all the fecundity related vital rates, chick survival and hatchability (eggs hatched/ total clutch size of successful nests) exerted the greatest influence on λ based on prospective sensitivity, elasticity, and VSS estimates. In contrast, hatchability did not prove influential in the retrospective life stage simulation analysis. Suggesting that populations may be sensitive but not given the variance of hatchability estimated in my research. Hatchability includes losses due to infertility, failed development, and partial clutch loss due to predation. Although, I could not decompose hatchability among these factors, other research on lesser prairie chickens have had

similar estimates of hatchability (74%; Pitman et al. 2006), of which, 94% of eggs were fertile and most of the unhatched clutches were attributed to partial clutch size via predation by snakes (Pitman et al. 2006). Snakes and small mammals can also contribute to partial clutch losses in greater prairie-chickens (Winder et al. 2016). Knowledge of the influence of land management practices on partial clutch loss due to predation would be beneficial for lesser prairie-chicken conservation.

Although clutch size, nest propensity, and nest survival sensitivities were minimal, the cumulative effect of all metrics including chick survival to estimated fecundity explained almost all of the variance in population growth rates in the LSA. The strong explanation of λ highlights the importance of grassland structural heterogeneity for providing both nesting and brood rearing habitat in close proximity (Fuhlendorf et al. 2006, Sandercock et al. 2015, McNew et al. 2015). Further, the nest survival sensitivities may be underestimated in my analyses because nest survival was estimated separately for adults and yearlings while all survival related sensitivities were pooled among age classes. When combining nest survival sensitivity estimates for the two age classes nest survival would be of near equal importance as all of the survival sensitivity estimates (e.g. combined VSS = 0.43).

Survival (Sb, Snb, Sj) also exerted a considerable amount of influence on lesser prairie-chicken growth rates as indicated by elasticities, VSS, and the LSA. Sensitivity analyses for other prairie grouse species including sage grouse (*Centocercus urophasianus*) and greater prairie-chickens suggest that adult survival imposes the greatest influence on λ, especially in declining populations (Beissinger and Westphal 1998, McNew et al. 2012, Dahlgren et al. 2016). For sage grouse, the strong influence of adult survival is likely a result of the longer lifespan of individuals and more intermediate life history strategy on the *r*–to–*k* selected species continuum

(Dahlgren et al. 2016). For greater prairie-chickens, the strong impact of adult survival on λ could be a result of either widespread land use practices (annually burning and grazing) or a result of depressed reproductive vital rates during drought (McNew et al. 2011, 2012). My results indicated that lesser prairie-chicken population growth was of relatively equal sensitivity to both fecundity and survival at the matrix element level (*aij; FSY, FASY, SSY, SASY*). When not including absolute sensitivity, elasticity and VSS estimates among survival and most fecundity parameters were relatively similar. A previous sensitivity analysis on lesser prairie-chickens in western Kansas also indicated a relatively uniform influence of survival and fecundity related parameters on λ with elasticity values showing a strong influence of survival (Hagen et al. 2009).

I suggest that although fecundity rates may drive large increases in population growth rates as indicated in the LSA regressions surpassing λ = 1. The importance of fecundity in driving overall population growth rates corroborates the findings in Hagen et al. (2009) in which management improving nest and brood survival simultaneously had 2.5–5.3X the influence of increasing female survival. Wisdom and Mills (1997) also detected a strong correlation ($r^2 = 0.84$) of egg and brood survival parameters with λ in greater prairie-chickens when using vital rate estimates from 1978 – 1988 publications.

Although increased fecundity may drive booms in population growth as depicted in the life-stage simulation, high survival rates of individuals or extensive areas (>90% of 28km^2) of grassland are necessary for lesser prairie-chickens to persist through periods largely unfavorable for reproduction (Ross et al. 2016b). Population resilience to unfavorable periods may be particularly important in the southern Great Plains where some of the greatest variation of net primary productivity occurs (Sala et al. 1988). From a management standpoint, providing

36

optimal nesting and brood-rearing conditions for lesser prairie-chickens on a year-to-year basis within small grassland landscapes may not be achievable due to stochastic processes. For example, severe drought and above-average temperatures at the Northwest site during the 2013 breeding season resulted in a chick survival rate near zero (Lautenbach 2015). During the same year, the only successful lesser prairie-chicken nest in eastern Colorado hatched on the day of a severe hailstorm and the entire brood was lost. Extreme weather can negate successful reproduction elsewhere; for example, in west Texas only 20% of lesser prairie-chickens nested and no nests survived the worst drought in the history of the state (Grisham et al. 2014, Su and Dickinson 2014). Unfavorable weather can also influence reproduction in other sharp-tailed grouse (*Tympanuchus phasianellus*; Flanders-Wanner et al. 2006). It is imperative that enough individuals survive years of unfavorable conditions to ensure that population booms can arise during favorable years. In summary, successful management of lesser prairie-chickens should consider habitat needs both for successful reproduction and adult survival.

My prebreeding-birth pulse model incorporated juvenile survival into fecundity estimates. The strong support for the influence of juvenile survival on overall population growth as indicated in the LSA suggests that management to improve habitat quality during this life-stage would be beneficial. Unfortunately, there is a limited understanding of the needs of lesser prairie-chickens during this life-stage (Pitman et al. 2006b). I was unable to estimate juvenile survival (35 days posthatch–first March) and used an estimate from another study conducted on lesser prairie-chickens in the sand sagebrush ecoregion of Kansas (Pitman et al. 2006b, Hagen et al. 2009). The first autumn of a grouse's life is thought to function as second survival bottleneck in addition to its first two weeks of life (Hannon and Martin 2006). Management to increase food availability for juvenile lesser prairie-chickens may be beneficial as body mass has been

positively associated with juvenile survival over winter (Pitman et al. 2006b). Additionally, greater prairie-chickens and other grouse show a high propensity to disperse during this period (Bowman and Robel 1977, Hannon and Martin 2006). Therefore, increased connectivity of high quality grassland habitat may improve juvenile survival rates at a time when *Tympanuchus* spp. are highly susceptible predation (Bowman and Robel 1977).

The increased propensity for juvenile dispersal during the first fall post-hatch makes survival during this period beneficial not only to individual populations, but to a network of populations (or metapopulations). Beyond comparing demographic differences among populations, asynchronous variability in vital rates among and within populations may be the key to the persistence of lesser prairie-chicken as a species. Lesser prairie-chickens likely evolved a metapopulation structure with natural ecological drivers that maintained a spatiotemporally patchy distribution of available habitat wherein some areas may provide more reliable quality habitat. In this structure, subpopulations may go extinct but the metapopulation persists (Hanski and Gyllenberg 1993, Fuhlendorf et al. 2002, DeYoung and Williford 2016). Prior population modeling for *Tympanuchus* spp. suggests populations are reliant upon immigration from outside sources (Hagen et al. 2009, McNew et al. 2012). This includes estimates from two populations ($\lambda = 0.54$ and 0.74) using vital rates collected from 1998 – 2003 in a fragmented Sand Sagebrush Prairie landscapes in Finney County, Kansas (Hagen et al. 2009) and estimates of λ (0.53 - 0.76) for greater prairie-chickens in eastern Kansas (McNew et al. 2012). The scale at which immigration occurs is not known as there is no evidence of immigration or other movements among ecoregions (McDonald et al. 2014; D. Haukos, unpublished data), so declining estimates may be an artifact of the models themselves. I predict that some level of within ecoregion immigration and recolonization, resulting from temporal variation in vital rates, are needed to

maintain lesser prairie-chicken populations over longer periods of time. Colonization and recolonization of lesser prairie-chicken habitats may be as much of function of time as space considering that lesser prairie-chickens exhibit a boom-or-bust life history strategy (Hagen et al. 2009).

Influence of Drought

Lesser prairie-chickens have evolved a boom-or-bust life history strategy to persist in an environment that frequently experiences extreme weather conditions (Hagen et al. 2009, Grisham et al. 2013). For such a complex life history strategy projecting population growth based on the assumption that vital rates observed during the tenure of a study are maintained in the future may be ill informed (Bierzychudek 1999); particularly when vital rates are estimated over a short temporal period including a severe drought (Taylor et al. 2012). A true model exactly depicting all ecological variation for lesser prairie-chickens is probably not achievable (Levins 1966). However, I do not expect my models to be biased as a result of inadequate estimation of the stable age distribution given the simple age structure (yearling or adult) with nearly equal reproductive value (A = 1.00, Y = 0.95), the high damping ratio ($p = 40$), and quick convergence to the stable age distribution (t_{20}~0.8 years). The capability of the lesser prairie-chicken to breed within its first year of life, short life span of individuals, and limited parsimony of models examining age specific vital rates suggests that my results would not be biased by transient effects leading to an unstable age distribution (Koons et al. 2005). I also do not expect substantial immigration into the study sites. The study was initiated during the contemporary population low when quality habitat was not likely saturated and focusing my research/trapping efforts on some of the best remaining lesser prairie-chicken habitats suggests a limited potential for immigration into sites (Ross et al. 2016a).

Demographic Variability among Sites

The retrospective life table response experiment provided some indication of demographic plasticity among lesser prairie-chickens occupying the four study sites. The greatest variability among sites was in the contributions of breeding survival, nest survival of adults, nonbreeding survival, and chick survival to λ. The variation in demographic rates was similar to the variable estimates among sites for lesser prairie-chickens in Hagen et al. (2009) and greater prairie-chickens in McNew et al. (2012). Hagen et al. (2009) estimated finite rates of population change as $\lambda = 0.535$ at one study site and $\lambda = 0.739$ at the other study site, and although no life table response experiment was conducted, prospective analyses revealed differences in ranks of vital rate sensitivity among sites. For greater prairie-chickens monitored at 3 study sites spread among a gradient of habitats ranging from intensive burning and grazing cattle operations to fragmented woody encroached grasslands, vital rates differed among large contiguous grassland landscapes with more fragmented landscapes (McNew et al. 2012). In my study, differences in vital rates and population growth estimates among sites more (Northwest site) and less fragmented sites was also apparent (Red Hills and Clark; Robinson et al. in review).

The overall lower observed λ at the Northwest study site was a result of negative contributions of breeding season and nonbreeding survival and supported my prediction of lower demographic rates in regions with more fragmented grassland. In contrast, the Red Hills experienced positive contributions from adult survival vital rates. During the breeding season, lesser prairie-chicken adult survival was greater in study sites with larger contiguous grasslands compared to a study site having more fragmented grasslands (Plumb 2015). Mechanisms driving the lower adult survival rates in more fragmented landscapes remain somewhat unclear;

40

however, it appears that lesser prairie-chickens spending a greater period of time near fence lines and patch edges are at a greater risk of mortality throughout the annual cycle (Wolfe et al. 2007, Robinson et al. 2016, Robinson et al. in review). Alternatively, it could be suggested that the Red Hills study site may have herbaceous vegetation providing greater visual obstruction and concealment from predators in comparison to the Northwest study site due its more easterly location along the precipitation gradient. Contrary to this expectation, mean visual obstruction at the Red Hills site was lower than at the Northwest site and may be maintained at shorter overall heights as a result of differing grazing practices (Table 1.1, Plumb 2015).

The difference in demographic rates and vital rate contributions among regions of variable grassland fragmentation did not hold for Colorado where the Prowers County study site had the lowest grassland composition (54% grassland, CRP plus native prairie) among sites. The greater than average λ and both strong positive and negative vital rate contributions at the Colorado study site may be due to demographic stochasticity of the small population (Mills 2007). Current population estimates for lesser prairie-chickens in Colorado involved surveys of 102 historically occupied leks, of which, only 6 are currently occupied by ~27 males (Reitz 2016). Although I only monitored 10 females in Colorado throughout the study period, I effectively may have been monitoring up to 20% of the population. Therefore, the large variance of estimates may be mostly process variance depicting the true variability and instability of the population. Concerns of this population disappearing during the onset of the study in 2013 were valid; however, successful reproduction from a few individuals likely sustained the population. For example, the strong contribution of adult nest survival to λ can be attributed to one after-second-year female that successfully nested two out of the three years and reared nine and four chicks to >56 days old in 2014 and 2015, respectively. Alternatively, our clumping of the highly

41

fragmented Prowers County site and unfragmented grassland Cheyenne site to achieve a useful sample size likely confounded any potential to isolate a population effect from grassland fragmentation.

 Management Implications

A two-step approach could be used to conserve and manage for lesser prairie-chickens. First, managers should attempt to protect or restore large grassland dominated landscapes given the greater λ at the Red Hills site. In large grassland landscapes, management that promotes grassland with patches of nesting cover (20-80 cm tall grass with 4-6 cm of detached litter) adjacent to brooding habitat (20% forbs with abundant Lepidoptera larvae and Orthoptera foods) will be most beneficial. Targeting large grasslands may promote survival and successful reproduction of lesser prairie-chickens during a range of weather condition. The improved reproductive quality of habitat within the large grasslands would prime the population for rapid population growth when favorable weather conditions prevail. In small grassland landscapes, more intensive management directed at improving survival of nests, chicks, and juveniles in the first year will be necessary.

Literature Cited

Ammann, G. A. 1944. Determining the age of pinnated and sharp-tailed grouses. Journal of Wildlife Management 8:170–171.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal Wildlife Management 74:1175–1178.

Beissinger, S. R. and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821–841.

Bergerud, A. T., and M. W. Gratson. 1988. Survival and Breeding Strategies of Grouse. Pages 473–575 in A.T. Bergerud and M.W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. Volume II theory and synthesis. University of Minnesota Press, Minneapolis, USA.

Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. Ecological applications 9:1278–1287.

Boal, C. W. 2016. Predation and lesser prairie-chickens. Pages 154–159 in D. A Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Bowman, T. J., and R. J. Robel. 1977. Brood break-up and dispersal, mobility and mortality of juvenile prairie-chickens. Journal of Wildlife Management 41:27–34.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretical approach. Second edition. Springer-Verlag, New York, New York, USA.

Caswell, H. 1998. Analysis of life table response experiments I. Decomposition of effects on population growth rate. Ecological modelling 46:221–237.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619627.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Chen, P., and M. Newman. 1998. Rossby wave propagation and the rapid development of upper-level anomalous anticyclones during the 1988 US drought. Journal of Climate 11:2491–2504.

Dahlgren, D. K., M. R. Guttery, T. A. Messmer, D. Caudill, R. D. Elmore, R. Chi, and D. N. Koons. 2016. Evaluating vital rate contributions to greater sage-grouse population dynamics to inform conservation. Ecosphere 7: e01249.

43

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science
33:43–64.

Deyoung, R. W., and D. L. Williford. 2016. Genetic variation and population structure in the
prairie grouse: implications for conservation of the lesser prairie-chicken. Pages 77-99 in
D. A Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-
chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of
California Press, Berkeley, USA.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian
nest survival. Ecology 83:3476–3488.

Federal Register 2016. Federal Register. Vol. 81. No. 139: 50 CFR Part 17: Endangered and
threatened wildlife and plants; lesser prairie-chicken removed from the list of endangered
and threatened wildlife.
<http://ecos.fws.gov/ecp0/profile/speciesProfile?spcode=B0AZ#status>

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.

Flanders-Wanner, B., G. C. White, and L. L. McDaniel. 2006. Weather and prairie grouse:
dealing with effects beyond our control. Wildlife Society Bulletin 32:22–32.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie Jr., 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.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie.
2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire
and grazing. Ecological Applications 16: 1706–1716.

Garton, E. O., C. A. Hagen, G. M. Beauprez, S. C. Kyle, J. C. Pitman, D. D. Schoeling, and W.
E. Van Pelt. 2016. Population dynamics of lesser prairie-chickens. Pages 49–76 in D. A
Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens.
Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California
Press, Berkeley, USA.

Glauber, J. W. 2004. Crop insurance reconsidered. American Journal of Agricultural Economics
86:1179-1195.

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. Ph.D. dissertation, Texas Tech University, Lubbock, TX.

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

Grisham, B. A., C. P. Griffin, and A. J. Godar. 2016. Climate change. Pages 221–242 in D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA

Hagen , C. A., B. E. Jamison, K. M. Giesen, and T. Z. Riley. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. Wildlife Society Bulletin 32:69–82.

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.

Hagen, C. A., and K. M. Giesen. [online]. 2005. Lesser prairie-chicken (Tympanuchus pallidicinctus). Birds of North America 364. <http://bna.birds.cornell.edu/bna/species/364/articles/introduction> (15 May 2015).

Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. Journal of Wildlife Management 73:1325–1332.

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. University of California Press, Berkeley, USA.

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. University of California Press, Berkeley, USA.

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.

Hannon, S. J., and K. Martin. 2006. Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology 269:422–433.

Hanski, I., and M. Gyllenberg. 1993. Two general metapopulation models and the core-satellite species hypothesis. American Naturalist 142:17–41.

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

Haukos, D. A., and C. W. Boal, editors. 2016. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Heffernan, J. B., P. A. Soranno, M. J. Angilletta, L. B. Buckley, D. S. Gruner, T. H. Keitt, J. R. Kellner, J. s. Kominoski, A. V. Rocha, J. Ziao, T. K. Harms, S. J. Goring, L. E. Koenig, W. H. McDowell, H. Powell, A. D. Richardson, C. A. Stow, R. Vargas, K. C. Weathers. 2014. Macrosystem ecology: understanding ecological patterns and processes at continental scales. Frontiers in Ecology and the Environment 12:5–14.

Homer, C. G., J. A. Dewitz, L. Yang,S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Hoerling, M., J. Eischeid, A. Kumar, R. Laung, A. Mariotti, K. Mo, S. Schubert and R. Seager. 2014. Bulletin of the American Meteorolocial Society 95:269–282.

Jamison, B. E. 2000. Lesser prairie-chicken chick survival, adult survival, and habitat selection and movements of males in fragmented rangelands of southwestern Kansas. M.S. thesis, Kansas State University, Manhattan, USA.

Koons, D. N., J. B. Grand, B. Zinner, and R. F. Rockwell. 2005. Transient population dynamics: relations to life history and initial population state. Ecological Modeling 185:283–297.

Kraft, J. D. 2016. Vegetation characteristics and lesser prairie-chicken responses to land cover types and grazing management in western Kansas. Thesis. Kansas State University, Manhattan, USA.

Laake, J. L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01. Alaska Fish. Sci. Cent., NOAA, National Marine Fisheries Service, Seattle Washington. USA

Lautenbach, J. 2015. Lesser prairie-chicken reproductive success, habitat selection, and response to trees. Thesis. Kansas State University, USA. 141 pp.

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 and Management 70:78–86.

Levins, R. 1966. The strategy of model building in population biology. American Scientist 54:421–431.

Link, W. A., and P. A. Doherty. 2002. Scaling in sensitivity analysis. Ecology 83:3299–3305.

Lukacs, P. M., Dreitz, V. J., Knopf, F. L., and K. P. Burnham. 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. Condor 106: 926–931.

McDonald, L.L., G. Beauprez, G. Gardner, J. Griswold, C. Hagen, F. Hornsby, D. Klute, S. Kyle, J. Pitman, T. Rintz, D. Schoeling, and B. Van Pelt. 2014. Range-wide population size of the lesser prairie-chicken: 2012 and 2013. Wildlife Society Bulletin 38:536–546.

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, and 2016.

McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2011. Human-mediated selection on life –history traits of greater prairie-chickens. Pages 255-266 in B.K. Sandercock, K. Martin, and Gernot Segelbacher, editors. Ecology, conservation, and management of grouse. Studies in Avian Biology No. 39, Cooper Ornithological Society, University of California Press, Berkeley, USA.

McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2012. Demography of greater prairie-chickens: regional variation in vital rates, sensitivity values, and population dynamics. Journal of Wildlife Management 76:987–1000.

McNew, L. B., V. L. Winder, J. C. Pitman, and B. K. Sandercock. 2015. Alternative rangeland management strategies and the nesting ecology of greater prairie-chickens. Rangeland Ecology & Management 68:298–304.

Mills, S. L. 2007. Conservation of wildlife populations. Blackwell Publishing, Malden Massachusetts, USA.

National Oceanic and Atmospheric Administration National Climatic Data Center (NOAA). 2016a. National Environmental Satellite, Data, and Information Service. <https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp> Accessed August 11, 2016.

National Oceanic and Atmospheric Administration (NOAA). 2016b. Historical Palmer Drought Indices. National Centers for Environmental Information. < http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#>. Accessed August 11, 2016O'Neill, R. V., A. R. Johnson, and A. W. King. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology 3:193-205.

O'Neill, R. V., A. R. Johnson, and A. W. King. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology 3:193-205.

Opie, J. 1998. Moral geography in High Plains history. American Geographical Society. Geographical Review 88:241–258

Palmer, W. C. 1965. Meteorologic Drought. U.S. Weather Bureau, Research Paper No. 45, 58 pp.

Patten, M. A., D. H. Wolfe, E. Shochat, and S. K. Sherrod. 2005a. Habitat fragmentation, rapid evolution and population persistence. Evolutionary Ecology Research 7:235–249.

Patten, M. A., D. H. Wolfe, E. Shochat, and S. K. Sherrod. 2005b. Effects of microhabitat and microclimate selection on adult survivorship of the lesser prairie-chicken. Journal of Wildlife Management 69:1270–1278.

Pitman, J. C., C. A. Hagen, B. E. Jamison, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2006a. Nesting ecology of lesser prairie-chickens in sand sagebrush prairie of southwestern Kansas. Wilson Journal of Ornithology 118:23–35.

Pitman, J. C., C. A. Hagen, B. E. Jamison, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2006b. Survival of juvenile lesser prairie-chickens in Kansas. Wildlife Society Bulletin 34:675–681.

Plumb. R. T. 2015. Lesser prairie-chicken reproductive success, habitat selection, and response to trees. Thesis. Kansas State University, Manhattan, USA.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109:949–954.

PRISM Climate Group.2016. Oregon State University. <http://www.prism.oregonstate.edu/normals/> Accessed 11 January 2017.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reitz, J. 2016. Lesser prairie-chicken survey Colorado 2016. Colorado Parks and Wildlife report, Fort Collins, Colorado, USA.

Riley, T. Z., and C. A. Davis. 1993. Vegetative characteristics of lesser prairie-chicken brood foraging sites. Prairie Naturalist 25:243–238.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

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. 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. Effects of landscape characteristics on annual survival of lesser prairie-chickens *In review*

Ross, B. E., D. A. Haukos, C. A. Hagen, and J. C. Pitman. 2016a. The relative contribution of climate to changes in lesser prairie-chicken abundance. Ecosphere 7:e01323. 10.1002/ecs2.1323

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

Sæther, B. E., and Ø. Bakke. 2000. Avian life history variation in contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Sandercock, B. K., M. Alfaro-Barrios, A. E. Casey, T. N. Johnson, T. W. Mong, K. J. Odom, K. M. Strum, and V. L. Winder. 2015. Effects of grazing and prescribed fire on resource selection and nest survival of upland sandpipers in an experimental landscape. Landscape Ecology 30: 325–337.

Sandercock, B.K., W.E. Jensen, C.K. Williams, and R.D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. Journal of Wildlife Management 72:970–982.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Salter, G. C., R. J. Robel, and K. E. Kemp. 2005. Lesser prairie-chicken use of harvested corn fields during fall and winter in southwestern Kansas. Prairie Naturalist 37:1–9.

Silvy, N. J., M. E. Morrow, E. Shanley, and R. D. Slack. 1990. An improved drop net for capturing wildlife. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 44:374–378.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. 2015. Web Soil Survey. <http://websoilsurvey.nrcs.usda.gov/> Accessed 27 July 2015.

Stubben, C. J., and Milligan, B. G. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:11.

Su, H., and R. E. Dickinson. 2014. On the spatial gradient of soil moisture-precipitation feedback strength in the 2011 April drought in the Southern Great Plains. Journal of Climate 213:109–218.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

USFWS. 2014. Endangered and threatened wildlife and plants; determination of threatened status for the lesser prairie-chicken. Federal Register 79:19974–20071.

Van Pelt, W. E., S. Kyle, J. Pitman, D. Klute, G. Beauprez, D. Schoeling, A. Janus, J. Haufler, 2013. The Lesser Prairie-Chicken Range-wide Conservation Plan. Western Association of Fish and Wildlife Agencies. Cheyenne, Wyoming, pp.367

White, G. C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120–138.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chicken as an example. Journal of Wildlife Management 61:302–312.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life-stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.

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.

Table 1.1 Differences of vegetation structure among lesser prairie-chicken study sites in Kansas and Colorado, 2013–2016. Mean vegetation height was based on reading of 0% visual obstruction (Robel et al. 1970). Percent cover of grass and shrub were estimated in 60 X 60-cm Daubenmire frames (Daubenmire 1959). Litter depth (litdepth) was estimated by measuring detached litter.

Site	$\overline{X}$ vegetation height (dm)	SD vegetation height (dm)	$\overline{X}$ grass (%)	SD grass (%)	$\overline{X}$ forbs (%)	SD forbs (%)	$\overline{X}$ shrub (%)	SD shrub (%)	$\overline{X}$ litdepth (cm)	SD litdepth (cm)
Clark	6.0	3.0	45.3	24.5	15.6	15.2	2.1	7.2	1.3	1.6
Colorado	4.7	1.9	36.3	15.5	11.6	10.5	3.9	6.9	1.2	0.9
Gove	5.3	2.5	61.5	21.0	9.4	11.5	1.4	4.7	2.1	1.6
Red Hills	4.1	1.5	45.2	22.4	22.0	14.9	1.4	5.3	0.8	0.6
Logan	4.7	2.2	58.6	20.2	8.1	11.8	0.9	4.4	1.3	1.1

Table 1.2 Fecundity parameters and descriptions to estimate population growth rates for lesser prairie-chickens in Kansas and Colorado. Each was estimated for transmittered second-year (SY) and after-second-year (ASY) birds.

Parameter	Description
NEST	proportion of females that nest at least once
RENEST	proportion of females that renest after loss of first nest
CLUTCH1	clutch size for first nest
CLUTCH2	clutch size for second nest
HATCH	# of chicks hatched per egg laid for successful nests
NSURV1	probability that first nest will survive laying and incubation
NSURV2	probability that second nest will survive laying and incubation
CHICK	probability of chick survival to 56 days old

Table 1.3 Mean vital rate estimates, sample size, and standard error for all lesser prairie-chickens marked with 15-g very-high-frequency (VHF) transmitter or 22-g global-positioning-system (GPS) satellite transmitters and monitored from 2013–2016 in Kansas and Colorado. Total Clutch Laid is the clutch size for first (1) and second (2) nests. Nestsurv are nest survival estimates for adults (ASY) and yearling (SY) lesser prairie-chickens for first and renesting attempts. Hatchability is the proportion of eggs that hatch from successful nests.

Parameter	n	$\overline{X}$	SE
		All Sites	
Fecundity			
Nest Propensity[1]	118	0.951	0.044
Renest Propensity	75	0.334	0.152
Total Clutch Laid 1	185	10.8	2.17
Total Clutch Laid 2	50	8.17	2.02
Nestsurv ASY first	83	0.438	0.049
Nestsurv SY first	107	0.467	0.043
Nestsurv ASY renest	27	0.330	0.084
Nestsurv SY renest	26	0.504	0.096
Hatchability	72	0.796	0.047
Chick Survival[2]	63	0.255	0.014
Survival[3]			
Juvenile [4]	32	0.539	0.089
Nonbreeding[5]	135	0.727	0.040
ASY breeding	123	0.493	0.051
SY breeding	159	0.484	0.063

[1] SD for nest propensity, renest propensity, and clutch size. Standard error for nest and renest propensity was estimated among yearly estimates.
[2] Sample size indicates number of broods monitored
[3] Sample size indicative of bird-years, some birds survived multiple seasons
[4] Parameter estimates obtained from Hagen et al. 2009
[5] Estimate for pooled age classes from *Robinson et al. in review*

Table 1.4 Number of parameters (K), -2 log likelihood (-2 log *L*), ΔAICc (Akaike Information Criterion), and AICc weights (wi) of daily nest survival rate (S) models for lesser prairie-chickens in Kansas and Colorado during 2013-2015. Age class (age), year, nest attempt (attempt) and site were tested as covariates.

Model	K	-2 log *L*	ΔAICc[1]	w_i
S(year)	3	1461	0.00	0.37
S(.)	1	1466	0.47	0.29
S(age)	2	1465	1.63	0.16
S(attempt)	2	1466	2.24	0.12
S(attempt* age)	4	1464	4.33	0.04
S(site)	4	1465	5.85	0.02
S(Site*attempt*age)	14	1460	20.52	0.00

[1]Minimum AICc = 1467

Table 1.5 Number of parameters (K), -2 log likelihood (-2 log *L*), ΔAICc (Akaike Information Criterion), and AICc weights (*w*i) of breeding season and nonbreeding season (September 16–March 14) survival rate (S) models for lesser prairie-chickens in Kansas and Colorado during 2013-2016. Age class (age) and site were tested as covariates. Breeding season included all 4 study sites (Northwest, Red Hills, and Clark, Kansas, and Colorado); nonbreeding season included 3 Kansas study sites.

	K	-2 log *L*	ΔAICc[1]	w_i
Breeding season				
Model				
S(site)	4	1269	0.00	0.56
S(.)	1	1277	1.35	0.28
S(Site + age)	6	1269	3.41	0.10
S(age)	3	1276	4.62	0.06
S(Site*age)	12	1266	13.67	0.00
Nonbreeding season				
S(site)	3	303	0.00	0.46
S(.)	1	308	0.15	0.43
S(Site + age)	6	303	4.20	0.06
S(age)	3	308	4.22	0.06
S(Site*age)	9	301	10.84	0.00

[1] Minimum AIC$_c$ = 1276.

Table 1.6 Vital rate estimates used in the projection matrix for lesser prairie-chicken populations in Kansas and Colorado during 2013-2016. Total Clutch Laid is the clutch size for first (1) and second (2) nests. Nest Surv are nest survival estimates for adult (ASY) and yearling (SY) lesser prairie-chickens for first and renesting attempts. Hatchability is the proportion of eggs that hatch from successful nests.

Parameter		Northwest			Red Hills			Clark			Colorado	
	n	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Mean	SE
Fecundity												
Nest Propensity[1]	58	0.900	0.075	39	1.00	0.00	11	1.00	0.00	10	1.00	0.00
Renest Propensity	22	0.328	0.142	29	0.382	0.147	20	0.358	0.090	4	0.500	0.500
Total Clutch Laid 1	80	10.3	2.31	59	11.2	2.09	40	11.0	1.5	6	10.5	2.59
Total Clutch Laid 2[2]	23	7.26	2.73	19	8.42	2.12	7	8.57	2.44	1	7	N/A
Nestsurv ASY first	33	0.420	0.076	30	0.398	0.075	15	0.390	0.117	5	0.758	0.210
Nestsurv SY first	47	0.437	0.064	30	0.443	0.079	25	0.457	0.093	5	0.335	0.259
Nestsurv ASY renest	12	0.354	0.130	11	0.339	0.130	4	0.156	0.146			
Nestsurv SY renest[2]	11	0.557	0.146	9	0.538	0.167	5	0.351	0.214	1	1.00	0.000
Hatchability[3]	72	0.796	0.047	-	-	-	-	-	-	-	-	-
Chick Survival[4]	34	0.261	0.071	21	0.252	0.019	5	0.269	0.034	3	0.215	0.0413
Survival[5]				-	-	-	-	-	-	-	-	-
Juvenile Survival[6]	32	0.539	0.089	-	-	-	-	-	-	-	-	-
Breeding survival[7]	140	0.414	0.047	88	0.563	0.059	56	0.63	0.082	12	0.600	0.155
Nonbreeding Survival[8]	58	0.666	0.0066	45	0.856	0.055	32	0.677	0.0897			

[1] SD for nest propensity, renest propensity, and clutch size

[2] Only one second nesting attempt in Colorado; used the mean SE for clutch size and mean renest survival and SE estimates among all sites

[3] Averaged among all sites and repeated value for all 4 sites

[4] Sample size indicates number of broods monitored

[5] Sample size indicative of bird-years, some birds survived multiple seasons

[6] Parameter estimates obtained from Hagen et al. 2009 and repeated value for all 4 sites

[7] Breeding season survival was from March 15September15

[8] We used the average nonbreeding survival estimate for Colorado because of low sample size; Nonbreeding season survival was from September 16March 14

Table 1.7 Bootstrapped (n = 1,000) projection matrix mean and SE estimates of the finite rate in population change (λ), stable age distribution (w), reproductive value (v), net reproductive rates (Ro), generation time (T), fecundity (F), survival (S), sensitivities (sens), and elasticities (elas) for adult (ASY) and yearling (SY) female lesser prairie-chickens in Kansas and Colorado from 2013–2016. Matrix elements having the greatest sensitivity and elasticity estimates are in bold.

Parameter	All Sites mean	SD	Northwest mean	SD	Red Hills mean	SD	Clark mean	SD	Colorado mean	SD
λ	0.693	0.098	0.578	0.133	0.826	0.110	0.786	0.126	0.788	0.169
W_A	0.479	0.074	0.503	0.108	0.410	0.071	0.452	0.086	0.429	0.101
W_Y	0.521	0.074	0.497	0.108	0.590	0.071	0.548	0.086	0.571	0.101
V_A	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000
V_Y	0.971	0.108	0.981	0.128	0.964	0.122	0.945	0.165	1.366	0.428
R_0	0.293	0.150	0.191	0.177	0.532	0.307	0.467	0.334	0.551	0.534
T	3.602	0.247	3.426	0.415	3.907	0.320	3.856	0.414		
F_Y	0.657	0.141	0.566	0.217	0.672	0.162	0.721	0.174	0.402	0.296
F_A	0.596	0.133	0.540	0.214	0.606	0.147	0.628	0.190	0.835	0.318
S_Y	0.352	0.050	0.276	0.043	0.482	0.060	0.425	0.078	0.441	0.121
S_A	0.359	0.042	0.276	0.043	0.481	0.060	0.426	0.080	0.444	0.121
sens F_A	0.488	0.079	**0.509**	0.112	0.421	0.080	0.469	0.094	0.369	0.113
sens F_Y	0.471	0.077	0.496	0.112	0.401	0.070	0.437	0.092	0.480	0.145
sens S_A	**0.531**[1]	0.083	0.505	0.119	**0.605**	0.084	**0.572**	0.115	0.491	0.129
sens S_Y	0.512	0.079	0.491	0.112	0.579	0.080	0.531	0.094	**0.631**	0.113
elas F_A	0.252	0.077	**0.275**	0.114	0.189	0.070	0.238	0.093	0.112	0.101
elas F_Y	0.236	0.016	0.235	0.023	0.232	0.021	0.231	0.025	0.258	0.052
elas S_A	0.236	0.016	0.235	0.023	0.232	0.021	0.231	0.025	0.258	0.052
elas S_Y	**0.276**	0.085	0.256	0.114	**0.347**	0.093	**0.299**	0.101	**0.373**	0.144

[1]SD for nest propensity, renest propensity, and clutch size

Table 1.8 Lower level vital rate elasticities and variance stabilized sensitivities (VSS) to the finite rate of population growth (λ) estimated among all sites and separately among study sites for lesser prairie-chickens in Kansas and Colorado in 2013–2016. Lower level vital rates that ranked as the top 3 most sensitive based on either elasticity or VSS are underlined.

Parameter	All Sites			Northwest			Red Hills			Clark			Colorado		
	sens	elasticity	VSS	sens	elasticity	VSS	sens	elasticity	VSS	sens	elasticity	VSS	sens	elasticity	VSS
Fecundity															
Nest Prop	0.274	0.404	0.092	0.251	0.425	0.142	0.259	0.333	0.000	0.277	0.376	0.000	0.245	0.329	0.000
Renest Prop	0.102	0.053	0.075	0.101	0.062	0.089	0.113	0.056	0.071	0.125	0.061	0.081	0.056	0.025	0.035
Total Clutch laid 1[1]	0.024	0.404	NA	0.022	0.425	NA	0.023	0.333	NA	0.025	0.376	NA	0.023	0.329	NA
Total Clutch laid 2[1]	0.004	0.053	NA	0.005	0.062	NA	0.005	0.056	NA	0.005	0.061	NA	0.003	0.025	NA
Nestsurv ASY first	0.292	0.198	0.225	0.244	0.192	0.226	0.342	0.176	0.216	0.341	0.181	0.226	0.206	0.209	0.118
Nestsurv SY first	0.223	0.161	0.172	0.226	0.186	0.211	0.207	0.118	0.132	0.243	0.151	0.164	0.159	0.072	0.101
Nestsurv ASY renest[2]	0.048	0.025	0.035	0.041	0.032	0.038	0.066	0.034	0.042	0.065	0.035	0.043	0.013	0.014	0.008
Nestsurv SY renest	0.037	0.028	0.028	0.037	0.030	0.034	0.038	0.021	0.024	0.042	0.026	0.028	0.026	0.011	0.016
Hatchability	0.369	<u>0.457</u>	0.228	0.324	<u>0.487</u>	0.243	0.377	<u>0.389</u>	0.194	0.402	<u>0.436</u>	0.218	0.330	<u>0.354</u>	0.177
Chick Survival	<u>1.158</u>	<u>0.457</u>	<u>0.781</u>	<u>0.993</u>	<u>0.487</u>	<u>0.819</u>	<u>1.198</u>	<u>0.389</u>	<u>0.669</u>	<u>1.194</u>	<u>0.436</u>	<u>0.719</u>	<u>1.228</u>	<u>0.354</u>	<u>0.676</u>
Survival															
Juvenile Survival[3]	<u>0.548</u>	<u>0.457</u>	<u>0.422</u>	<u>0.481</u>	<u>0.487</u>	<u>0.450</u>	<u>0.560</u>	<u>0.389</u>	<u>0.359</u>	<u>0.596</u>	<u>0.436</u>	<u>0.403</u>	0.490	<u>0.354</u>	0.327
Breeding Survival	<u>0.712</u>	<u>0.543</u>	<u>0.551</u>	<u>0.660</u>	<u>0.513</u>	<u>0.611</u>	<u>0.844</u>	<u>0.611</u>	<u>0.539</u>	<u>0.659</u>	<u>0.564</u>	<u>0.432</u>	<u>0.803</u>	<u>0.646</u>	<u>0.527</u>
Nonbreeding Survival[4]	0.483	<u>0.543</u>	0.333	0.410	<u>0.513</u>	0.363	0.555	<u>0.611</u>	0.251	0.613	<u>0.564</u>	0.389	<u>0.657</u>	<u>0.646</u>	<u>0.390</u>

[1] VSS for total clutch laid not estimated because data was normally distributed

[2] Only one second nesting attempt in Colorado; used the mean SE for clutch size and mean renest survival and SE estimates among all sites

[3] Parameter estimates obtained from Hagen et al. 2009

[4] I used the average nonbreeding survival estimate among all sites for Colorado because of low sample size

Figure 1.1 Study sites where lesser prairie-chickens were captured, marked with 15-g very-high-frequency (VHF) transmitter or 22-g global-positioning-system (GPS) satellite and monitored from 2013–2016 in Kansas and Colorado. Areas in green are minimum convex polygons encompassing all locations of female birds within each site during the study.
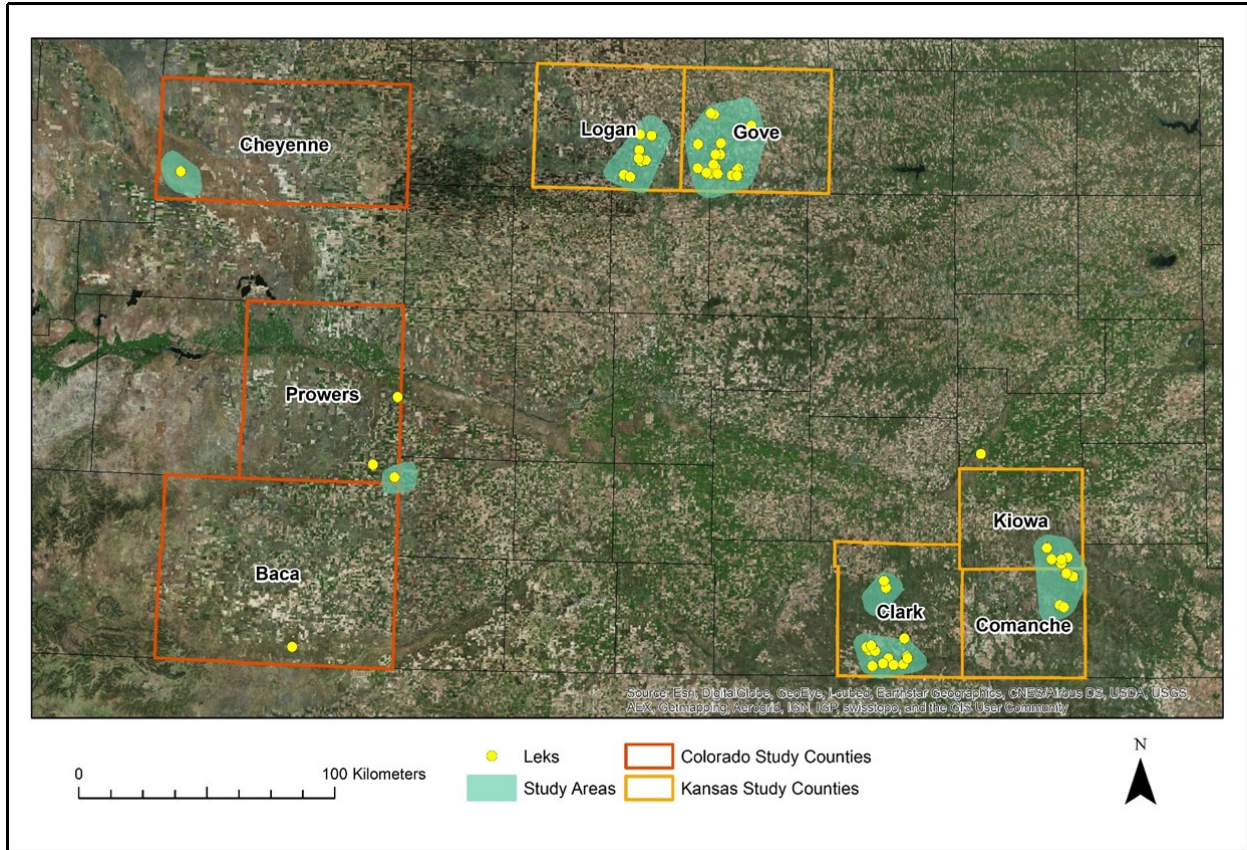
Figure 1.2 Lower level vital rate sensitivity, elasticity, and variable stabilized sensitivity(VSS) to the finite rate of population change (λ) for lesser prairie-chickens. Calculations were made among all sites in Kansas and Colorado in 2013–2016. Vital rates included clutch size of first (tcl1) and second (tcl2) nests, nest survival rates of nests initiated by adults (nestA) and yearlings (nestY), survival of renesting attempts for adults and years, hatchability (hatch), chick survival (chick), juvenile survival (Sj), nonbreeding season survival (Snb), breeding season survival (Sb), nesting propensity(nestprop), and renesting propensity(renestprop).
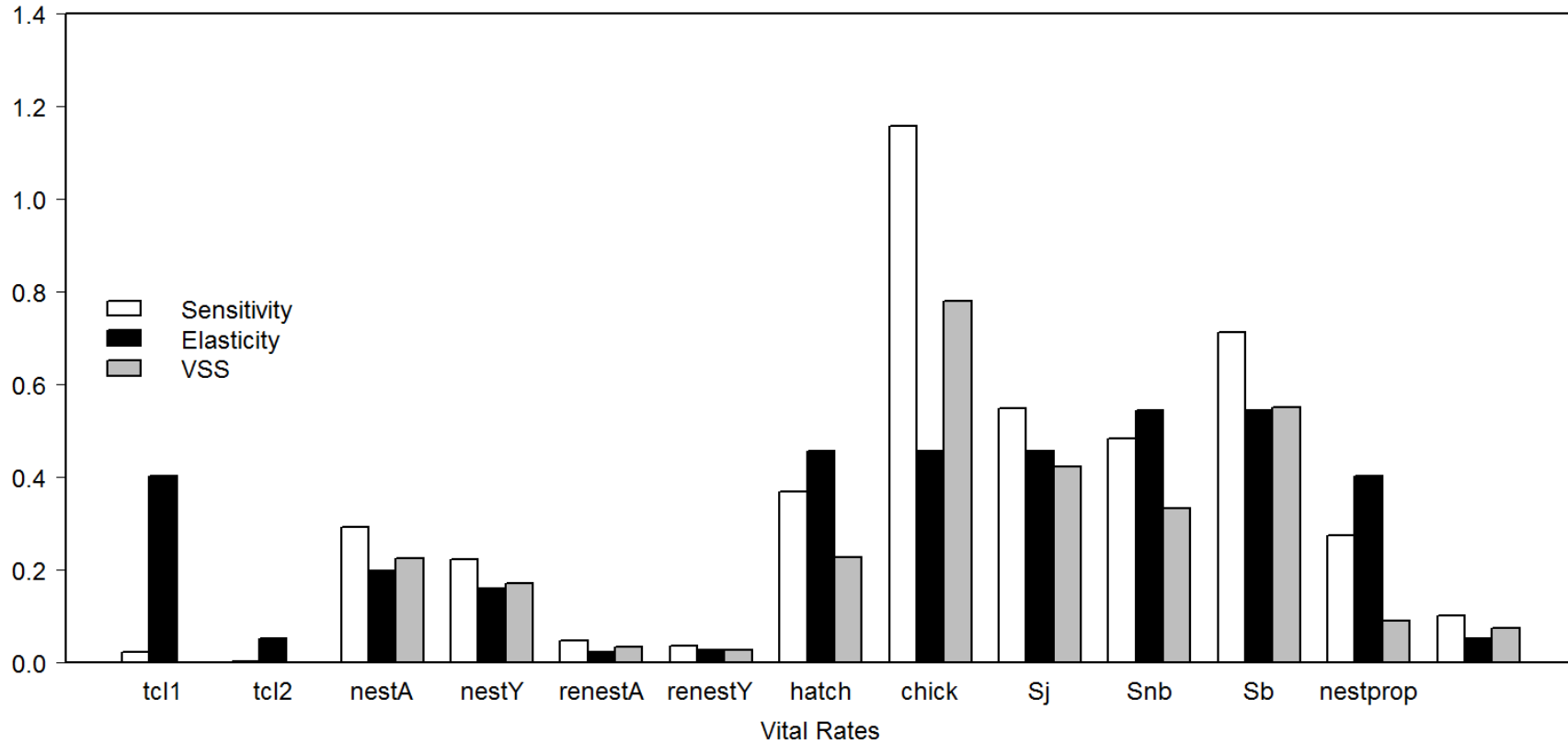
Figure 1.3 Life-stage simulation analysis results depicting linear regressions of bootstrapped (n = 1,000) parameter estimates and respective finite rate of population change for female lesser prairie-chickens among all study sites in Kansas and Colorado during 2013, 2014, and 2015. Slope estimates are from least squares regression beta coefficients. Estimates of explained variance are also provided (r^2). Excluding clutch size for second nests ($r^2=0$, $\beta = 0$) and hatchability ($r^2=0$, $\beta = -0.02$) all other lower level vital rates are displayed in panel A. Results from main matrix elements are displayed in panel B.

61
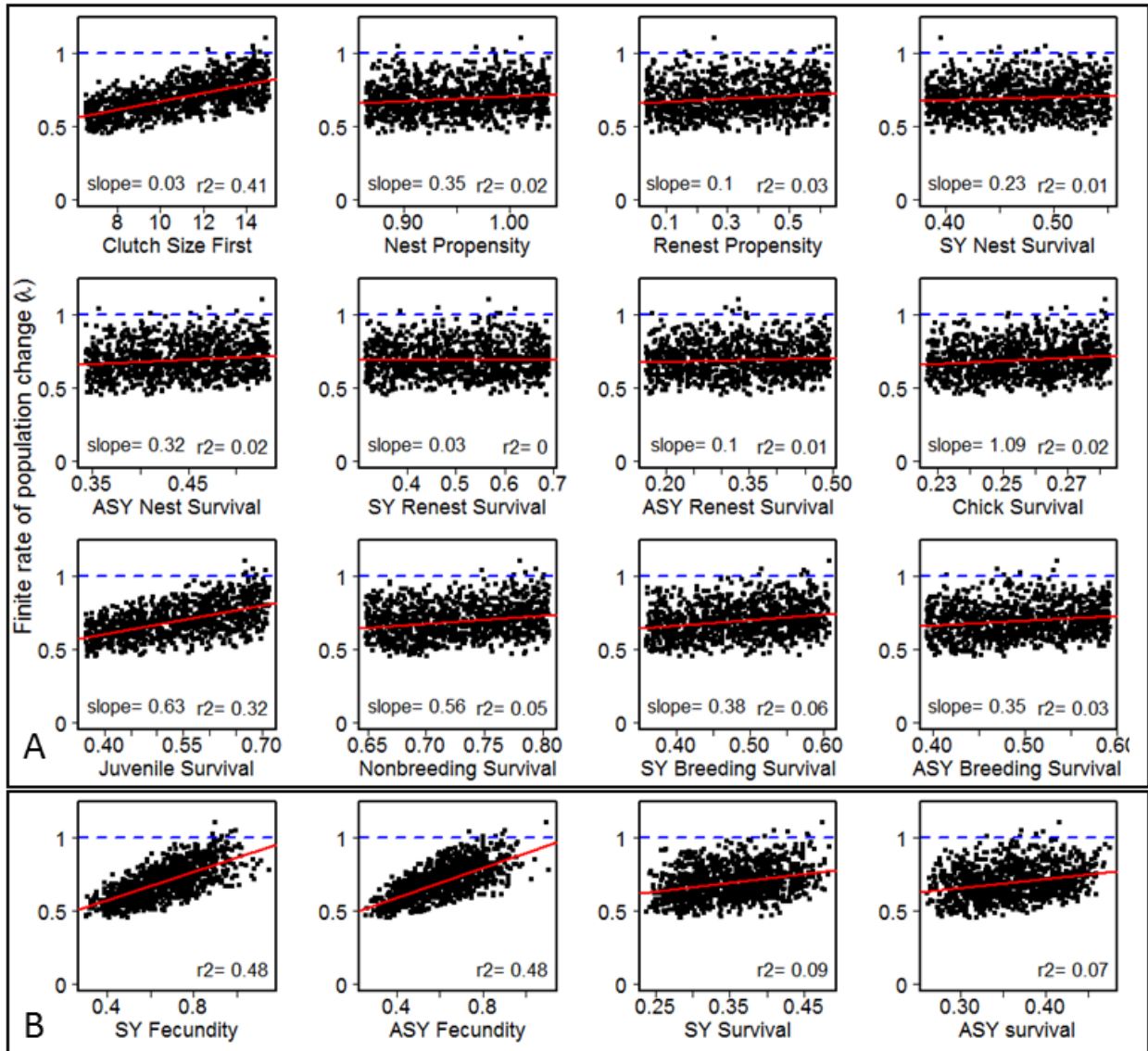
Figure 1.4 Lower level vital rate contributions to difference in the finite rate of lesser prairie-chicken population change (λ) among study sites in Kansas and Colorado in 2013–2016. Vital rates included clutch size of first (tcl1) and second (tcl2) nests, nest survival rates of nests initiated by adults (nestA) and yearlings (nestY), survival of renesting attempts for adults and yearlingss, chick survival (chick), juvenile survival (Sj), nonbreeding season survival (Snb), breeding season survival (Sb), nesting propensity(nestprop), and renesting propensity(renestprop).
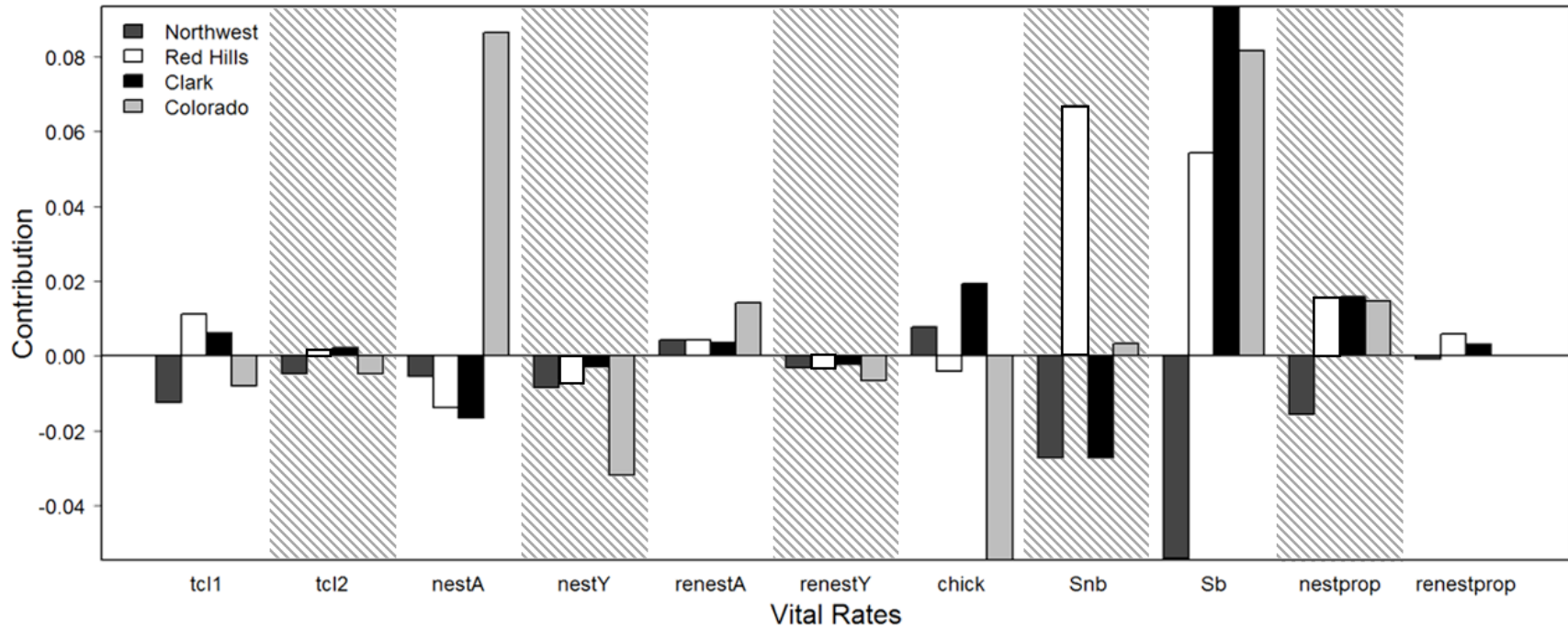
Chapter 2 - Distribution and Strategic Conservation of Lesser Prairie-Chickens in Kansas and Colorado

Introduction

The distribution of a species is a product of both unwavering broad scale (extra hierarchical) boundaries as well as of emergent processes operating at lower levels (King 1997). Extra hierarchical boundaries operate outside of the complex system and limit the distribution of a species among all possible combinations and interactions of lower level elements. In contrast, the distribution of a species can also be constrained as a result of interactions and processes occurring at finer scales (emergent processes; Bertuzzo et al. 2011). In complex non-equilibrium systems, assembling all fine-scale individual components to predict a species distribution over broad geographic extents may be futile as the hierarchical nature of the system is likely not completely decomposable (O'Neill 1989, King 1997). Distributions may be better predicted after first identifying broad scale constraints related to both emergent and extrahierarichal processes. For example, the ability of a landscape to provide resources for resident grassland birds in a non-equilibrium grassland system is not only contingent on the status quo of the landscape, and what may be measured during a short term study, but also a full spectrum of potential interacting weather and disturbance scenarios (Wiens 1974, Merchant 1982, Chapter 4). The provision of optimal habitat (food or cover) at one time may be outweighed by the lack of available habitat during other life stages or years, particularly for resident grouse species such as the lesser prairie-chicken (*Tympanuchus pallidicinctus*; Willis 1966, Wiens 1974).

In the variable environment of the southern Great Plains where lesser prairie-chickens occur, persistence of lesser prairie-chicken populations is achieved through a boom-or-bust life history strategy in which annual population growth fluctuates strongly with periods of favorable

63

environmental conditions, even in quality grassland landscapes (Sala et al. 1988, Garton et al. 2016; Ross et al. 2016a, b). The boom or bust strategy likely evolved as an adaption to temporal environmental instability buffered by the historic broad availability of useable grasslands (Mengel 1970, Wiens 1974). Lesser prairie-chickens and other prairie grouse species have adapted to unpredictable environments through the digestion of foods of minimal nutrient quality (Sedinger 1997), foregoing nesting during intense drought (Grisham et al. 2016, Sullins et al. in review), regular renesting after nest failure (Lautenbach 2015), and through dispersing moderate distances during unfavorable periods (e.g., $\bar{x}$= 16.18 km, Earl et al. 2016). In contrast, during favorable periods lesser prairie-chickens have a high reproductive potential that can maximize population recruitment (Hagen et al. 2009). Amid all the adaptations, lesser prairie-chickens require large areas of grassland with heterogeneous structure to stave off extinction over long periods of time (Simberloff 1994, Fuhlendorf et al. 2002, Silvy et al. 2004, Ross et al. 2016b).

Unfortunately, large grassland dominated landscapes available for lesser prairie-chicken populations have become increasingly rare due to conversion of grassland to cropland, establishment of anthropogenic features, and woody encroachment (Hagen et al. 2011, Plumb 2015, Rodgers 2016, Lautenbach et al. 2017, Spencer et al. 2017). However, the extent of habitat lost due to grassland conversion and the presence of anthropogenic features is not known. These factors are likely contributing to long-term declines of lesser prairie-chickens in relatively varying levels of importance across the species range (Garton et al. 2016, Ross et al. 2016a). Although in some instances, extirpation of native forb food sources from grasslands may be ameliorated by the presence of cultivated grains or alfalfa in croplands (Larsson et al. 2013), lesser prairie-chickens are a grassland obligate species that require >2,500 ha landscapes that are

64

>64% grassland and grassland loss that falls below this threshold will likely have negative consequences (Crawford and Bolen 1976, Vickery and Herkert 1999).

To estimate the effects of lost grassland habitat due to conversion to cropland and the addition of anthropogenic features on lesser prairie-chickens, knowledge as to how grassland composition and anthropogenic feature densities constrains the distribution of lesser prairie-chickens at broad scales is needed. To handle the complexity of the system and predict the distribution of wildlife in non-equilibrium systems, machine learning distribution modeling that can incorporate nonlinear relationships and interactions, appear promising and complementary to traditional approaches. Currently, the distribution of lesser prairie-chickens in the northern extent of their range (i.e., Kansas and Colorado) has been assembled largely from anecdotal evidence (Hagen and Giesen 2005). In addition to the delineation of potential lesser prairie-chicken range using anecdotal evidence, local habitat relationships have been identified at spatial scales within study areas (Pitman et al. 2005, Hagen et al. 2013, Lautenbach 2014). It remains unclear what constrains the distribution of lesser prairie-chickens outside of ~40,000 ha study site scales and how available habitat is distributed in Kansas and Colorado. To fill knowledge gaps, a machine learning Random Forest modeling approach can provide spatially explicit predictions of available habitat and the current distribution of lesser prairie-chickens (Liaw and Wiener 2002). The Random Forest algorithm may be best suited to extrapolate the potential distribution of lesser prairie-chickens outside of study areas because it has shown strong abilities to project values into new variable space which is enabled by the out of bag error estimation that can limit over prediction issues common in other classification and regression tree approaches (Hegel et al. 2010, Evans et al. 2011).

A species distribution model can be used to identify areas to target conservation and restoration. Specifically, an empirically-derived distribution could be used to spatially prioritize management practices. For lesser prairie-chicken populations, it is unlikely that a universal management practice will benefit populations similarly across the 40-cm precipitation gradient in Kansas and Colorado (PRISM 2016). For example, woody encroachment is more of a threat in mixed-grass portions of the eastern extent of the lesser prairie-chicken distribution (Bond 2008), whereas the conversion of native grasslands to cropland is a prominent threat to habitat loss in northwest Kansas and eastern Colorado (Dahlgren et al. 2016, Haukos et al. 2016). In response to regional diverse threats, management actions to remove trees and stop future encroachment are needed in the mixed-grass prairie (Lautenbach et al. 2016). In contrast, the conversion of cropland to grassland through the Conservation Reserve Program can improve habitat availability for lesser prairie-chickens in northwest Kansas (Rodgers and Hoffman 2005, Chapter 4). Both of these conservation practices can be profitable for producers in the lesser prairie-chicken range of Kansas and Colorado where >90% of the species occupied range is privately owned. However, tree removal and enrollment in CRP will only benefit lesser prairie-chickens when surrounding landscapes are capable of supporting sustainable populations, indicating a need for strategic application of these conservation practices (Plumb 2015, Winder et al. 2015, Robinson et al. in review).

Therefore, I predicted the distribution of lesser prairie-chicken habitat in Kansas and Colorado based on grassland composition and anthropogenic feature density constraints, which may be a product of lower level interactions or extra hierarchical boundaries. I used a Random Forest model that incorporated 9,985 locations from marked lesser prairie-chickens and 9,985 available locations to create spatially-explicit predicted probabilities of use through the northern

extent of the lesser prairie-chicken range. I then used the predicted distribution to identify locations at which tree removal and the enrollment of cropland into the Conservation Reserve Program (CRP) would have the greatest benefit to lesser prairie-chicken populations by increasing the grassland composition and structural heterogeneity in local landscapes (Kraft 2016, Lautenbach et al. 2017, Chapter 4).

Methods

Study Area

The study area encompassed the mixed- to short-grass portions of the lesser prairie-chicken range in Kansas and Colorado, USA (Figure 2.1). A longitudinal precipitation gradient spanned from east (~69 cm) to west (~37 cm) across the extent of Kansas into eastern Colorado with a concomitant transition from mixed- to short-grass prairie (PRISM 2016, Grisham et al. 2016). Pockets of sand sagebrush (*Artemisia filifolia*) prairie were interspersed on sandy soils, especially in the southwest portion of the study area. Mosaics of CRP and row-crop agriculture were associated in areas with arable soils. Most of the large remaining grasslands were restricted to areas of poor or rocky soils and areas with rough terrain (Spencer et al. 2017). Within the study area, data were collected at 6 study sites including 3 in Colorado and 3 in Kansas (Figure 2.1, Table 2.1). Temperatures ranged from -26 to +43° C (extreme minimum and maximum temperature), with average daily minimum and maximum temperatures of 5° C and 21° C, respectively, during the period of data collection (15 March 2013 to 15 March 2016; NOAA 2016a).

The study site in northwest Kansas was located in Gove and Logan counties. The portion of the study site occurring in Logan County (41,940 ha) was comprised of relatively more short-grass prairie and less precipitation than the Gove County (87,822 ha) portion to the east as the

transition between semi-arid and temperate precipitation levels divided the study site (Plumb 2015). The study site was a mosaic of CRP (7.4%), cropland (36%), and native short-grass or mixed-grass prairie (54%; Robinson et al. in review). Research was mostly conducted on private, working grasslands, but also included the Smoky Valley Ranch (SVR) in Logan County, owned and operated by The Nature Conservancy. Historical ecological drivers that maintained grasslands at the northwest study site included periods of drought, bison grazing, and fire. However, fire is largely absent from the current landscape and grazing by cattle is within fenced pastures. A full season, rotational grazing operation for both cow/calf and yearling herds was the dominant system used among local ranchers. A significant portion of CRP was hayed prior to and during the study due to drought conditions, a few tracts were inter-seeded and disked, and others were undisturbed and idle. Annual precipitation was 39 cm, 48 cm, and 49 cm in 2013, 2014, and 2015, respectively (NOAA 2016a).

The Red Hills/Clark study site included locations in Clark County and on the border of Comanche and Kiowa counties. Location one was in western Clark County, Kansas, on the transition between of the mixed-grass prairie and sand sagebrush prairie. The Clark site was 77% grassland, 14% cropland, and 5.5% CRP (Robinson et al. in review) and largely comprised of 2 privately owned ranches; one in the Cimarron River floodplain (32,656 ha) dominated by loamy fine sands, fine sandy loams, and fine sands with the other in rolling hills (14,810 ha) 20 km north on mostly silty clay, clay loam, and silt loam (Soil Survey Staff 2015). Rotational grazing systems for both cow/calf and yearling herds were used in this area. Stocking rates were set to utilize 50% of available forage produced each growing season on the study ranches. The Red Hills site (49,111 ha), was in the mixed-grass prairie of Comanche and Kiowa counties and represented the eastern boundary of the lesser prairie-chicken range. The Red Hills study site

was 87% grassland, 8.9% cropland, and 2.2% CRP (Robinson et al. in review). The site was comprised of large contiguous grasslands with many drainages and both cow/calf and yearling (season long) grazing systems. Research efforts focused on a large ranch that implemented a patch-burn grazing system wherein large pastures were divided into thirds or fourths and a portion was sequentially burned annually.

The Cimarron NG study site encompassed the Cimarron National Grasslands, which are managed for multiple uses by the U.S. Forest Service (USFS). Grassland was abundant within the USFS managed portion of the study site, however, the surrounding matrix for which lesser prairie-chickens can disperse encompassed a substantial amount of cropland. The Comanche NG study site depicted in Figure 2.1 was 32.3% grassland, 47.1% cropland, and 16.7% CRP grassland. The study site incorporates areas that were heavily cultivated in the early 1900s. The area was severely degraded by soil erosion during the dustbowl and many farms and ranches were abandoned. The land first became part of the Franklin Roosevelt administration's national soil conservation program and later a National Grassland in the 1960s. The area has been restored to resemble a pre-cultivation sand sagebrush grassland state; however, trees may be more abundant along riparian areas than prior to European settlement (McDonald et al. 2014, Cable 1996).

The 3 study sites in Colorado received less annual average precipitation in comparison to the sites in Kansas. The Prowers County study site (1,146 ha) was comprised of dwindling patches of grassland (largely CRP) within a landscape mosaic of dryland and irrigated row-crop agriculture. The study site was composed of 43% cropland, 28% native working grassland, and 25% CRP (Homer et al. 2015). Prowers County was dominantly comprised of loamy soils (Soil Survey Staff 2015) and received 43 cm of precipitation annually (PRISM 2016). Most CRP

69

fields were enrolled into the program in the mid-1980s. Many tracts had recently undergone

mid-contract management. To meet the management requirements, typically 1/3 of the CRP

fields were disked creating linear strips of disturbed and undisturbed grass (J. Reitz, Colorado

Parks and Wildlife, pers. comm.).

The study site in Cheyenne County (16,968 ha) was comprised of large expanses of

lightly and heavily grazed sand sagebrush prairie where 30-year precipitation averages were

lowest of all study sites (37 cm, PRISM 2016). The Cheyenne County study site was composed

of 99% native working grassland and 1% cropland both largely occurring on sandy soils (Homer

et al. 2015, Soil Survey Staff 2015). The Comanche NG landscape was 71.2% grassland, 13.2%

cropland, and 13.0% CRP and is managed for multiple uses similar to the Cimarron NG study

site but differs by having a surrounding matrix that is predominantly grassland.

Although, urban sprawl was minimal throughout the study area, anthropogenic

development was present in the form of oil wells, transmission lines, county roads, major roads

and other vertical features (e.g., cell towers, windfarms, grain elevators, etc.). The Red

Hills/Clark study site was located in the Mixed- Grass Prairie Ecoregion while the Logan and

Gove Study sites were located in the Shortgrass/CRP Mosaic Ecoregion of their current range

(McDonald et al. 2014). The Cheyenne County and Prowers County study sites each represent

isolated portions of their current range in Colorado and occurred within the Sand Sagebrush

Prairie (Hagen and Giesen 2005, McDonald et al. 2014).

Capture and Marking

I captured lesser prairie-chickens at all study areas between early March and mid-May

lekking seasons using walk-in drift fences and funnel traps and drop nets (Haukos et al. 1990,

Silvy et al. 1990). Upon capture, lesser prairie-chickens were sexed based on coloration, pinnae

length, and tail pattern. Each individual was aged as either yearling (SY) or adult (ASY) depending on the color patterns, shape, and wear of the outermost flight feathers (P9 and P10; Ammann 1944). I uniquely marked females with 4 colored leg bands and a 22-g GPS (global positioning system) satellite PTT transmitter (SAT-PTT; PTT-100, Microwave Technology, Columbia, MD, USA or North Star Science and Technology, King George, VA, USA) and released (Robinson et al. 2016). GPS transmitters generally have a spatial error of ± 5m; well within the 30m X 30 m resolution pixels used in my analyses (Davis et al. 2013). I typically downloaded 8-10 GPS locations/day from each satellite-marked female using the ARGOS system, contingent on available daily solar charge. GPS locations were recorded every 2 hours during the day with a 6-hour gap between 2300 and 0500 when birds were assumed to be roosting.

To model species distribution from 15 March 2013 – 14 March 2016 and limit any spatial or temporal autocorrelation issues, I randomly selected 2 points each week from each satellite-marked bird. Available points were randomly generated throughout each study site. Study sites were delineated by first developing minimum convex polygons (MCP) around all point locations from marked birds to provide an estimate of area available for use by lesser prairie-chickens. The area available to lesser prairie-chickens included the MCP plus areas within an effective dispersal distance of the MCP perimeter. Each MCP was buffered by the average net displacement dispersal distance (16.18 km) estimated among individuals lesser prairie-chickens (Earl et al. 2016). I randomly generated one pseudo absence record for each location used by lesser prairie-chickens throughout the study area to account for the lack of true absence data; therefore, making the interpretation of probability of use relative rather than absolute (Barbet-Massin et al. 2012).

71

Landcover Covariates

I derived landcover type classifications at a 30 m X 30 m resolution from the 2011 National Landcover database and a shapefile identifying the distribution of Conservation Reserve Program (CRP) grasslands provided under agreement with the U.S. Department of Agriculture, Farm Service Agency (Homer et al. 2015). I created smoothed continuous rasters of grassland and shrubland composition from the NLCD land cover classification using focal point statistics (moving window analysis) in ArcGIS 10.2. To create smoothed continuous rasters, I first assigned all grassland cover type (i.e. Grassland/Herbaceous, Pasture/Hay) pixels a value of 1 whereas all other pixels were given a 0 value. I then took the mean of all pixels occurring within 400 m, 800 m, 1200 m, 1600 m, 2400 m, 3200 m, 4000 m, and 5000 m radii (circular window) of each center pixel and reclassified the mean to each pixel. I examined multiple scales because of the uncertainty of scale that best predicts lesser prairie-chicken occupancy but bounded scales assessed to be ≤ 5 km based on lesser prairie-chicken demography influences at the 3km scale and the selection of nest sites within 4.8 km of lek of capture (Ross et al. 2016b, Giesen et al. 1994). In the final predictive model, I used the scale having the greatest scaled model importance in previous model runs with all scales combined.

Anthropogenic Feature Covariates

To estimate the distance to anthropogenic features, I acquired shapefile layers of oil wells, transmission lines, major roads, county roads, and cell phone towers. All shapefiles were converted to raster files with 30 m X 30 m pixels in ArcGIS 10.2 to enable the creation of continuous density of anthropogenic feature surfaces. I used the Euclidean distance tool to generate rasters depicting distance to feature and focal statistics tool (e.g., moving window analysis) to estimate summed densities of features within circular radii (0.5 km, 1 km, 2 km) of

72

each pixel. The range of radii were selected to encompass known avoidance distances published in past literature (Braun 1994, Pruett et al. 2009b, Hagen et al. 2011, Hovick et al. 2014, Plumb 2015).

I used outside sources to validate the location of anthropogenic features within the extent of study sites using basemap aerial imagery provided in ArcGIS 10.2 (product of: ESRI, i-cubed, USDA FSA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGP). Operating oil well locations since the 1930s were derived from a shapefile created by the Kansas Geological Survey that is updated weekly (http://www.kgs.ku.edu/PRS/petroDB.html). I queried and used only the wells that were producing. Oil well locations in Colorado were obtained from the Colorado Oil and Gas Conservation Commission, which updated data daily; I queried wells that had statuses of active, producing, or temporarily abandoned. Locations of active oil wells in Oklahoma were obtained from the National Energy Technology Laboratory Energy Data Exchange (https://edx.netl.doe.gov/dataset /Oklahoma-well-locations-and-operators) and the available shapefile was compiled from data compiled by the Oklahoma Corporation Commission which was updated yearly.

Road and electric transmission locations in Kansas were obtained from the Kansas Geographic Information Systems Data Access and Support Center (DASC; http://www.kansasgis.org/) as shapefiles. Locations of roads in Oklahoma and Colorado were gathered per county from the USDA geospatial data gateway (https://gdg.sc.egov.usda.gov/) and based on Topologically Integrated Geographic Encoding and Referencing (TIGER) 2010 census data. To account for potential differences in behavioral avoidance of more heavily and lighter travelled roads, I placed roads into two categories; major roads and county roads. Major roads

73

included all federal and state highways receiving heavy use and were largely paved while county roads included the smaller secondary roads, which were almost entirely gravel based.

Transmission line data in Colorado was obtained from a shapefile displaying all transmission lines in the western USA available on arcgis.com (Hanser 2011). The locations of transmission lines in Oklahoma were identified from data used in the Oklahoma lesser prairie-chicken spatial planning tool (Horton et al. 2010). Due to presumed security threats, electric distribution line data was not publicly available and was only obtained for Kansas from the Kansas Corporation Commission. Cell phone tower locations for all study areas were downloaded from arcgis.com and derived from data provided by the Federal Communications Commission (FCC). All linear feature densities were estimated by summing the number of pixels where a linear feature (e.g., road or transmission line) was present using focal statistics in ArcGIS 10.2. All vertical point features included cell towers, large buildings, wind turbines, and oil wells but did not include distribution lines.

Species Distribution Modeling and Validation

Prediction.—Lesser prairie-chicken occurrence was predicted using a Random Forest method (Brieman 2001, Cutler et al. 2007) in R (Liaw and Wiener 2002, R development core 2017). The Random Forest method was used because it has been a good predictor of plant (Evans and Cushman 2009) and animal occurrence (Baruch-Mordo et al. 2013). It is also well suited for exploring potential changes in distributions over time, likely important for a boom-and-bust species such as the lesser prairie-chicken (Hagen et al. 2009). Random Forest is a classification and regression tree method that uses bootstraps and to handle over-fitting, provides excellent predictions with the largest number of independent variables, works well with both

74

categorical and continuous covariates, and irrelevant predictors are not used to classify data (Cutler et al. 2007, Evans and Cushman 2009).

I first assessed multicollinearity of all variables at $\alpha = 0.05$ using a leave one out assessment. Explanatory variables were examined for correlation with other variables, for which, no variables were correlated and no variables were removed. The most influential scale of variables were identified using a model improvement ratio (MIR; Murphy et al. 2009). The MIR ranks variables based on permuted importance. Ranks were estimated using the mean decrease in out-of-bag (OOB) error standardized from 0 to 1. The scale (grassland composition 400–5,000 m radius circles, anthropogenic features = 500 m –2000 m radius circles) achieving the greatest MIR was used in the final model for each variable. The final model included grassland composition, county road densities, major road densities, oil well densities, transmission line densities, and densities of vertical point features other than powerlines estimated at the scale exhibiting the greatest MIR. Predictions of presence or absence were generated based on majority votes across all trees using the final model. A probability raster was then created based on the most parsimonious random forest model. An occurrence threshold was estimated following methods in Jimenez-Valverde and Lobo (2007) to identify the model output probability (0–1) where occurrence or non-occurrence were most discrete.

Validation.—Models were validated using the accuracy, misclassification rate, true positive rate, false positive rate, specificity, precision, and prevalence, which were all derived from a confusion matrix. I also estimated a Cohen's Kappa statistic derived from cross validation, and area under the ROC curve (AUC; Delong et al. 1988). I validated the model using a cross validation wherein 10% of the data points were iteratively removed and the subset model was rerun 1,000 times. The model was run on the subset and then validated against the

remaining 10% of the data. Model significance was estimated by running the Random Forest

model 1000 times with a randomization of occupancy values (Murphy et al. 2009, Evans and

Cushman 2009).

Spatial Prioritization of Tree Removal

To identify priority areas where tree removal would most likely restore lesser prairie-

chicken habitat within the mixed-grass prairie, I used the above model depicting the constrained

distribution of lesser prairie-chicken habitat based on grassland composition and avoidance of

anthropogenic features. I then derived a layer depicting tree densities from Falkowski et al.

(2017), following Lautenbach et al. (2017). Areas where predicted habitat (based on grassland

composition and anthropogenic feature density) overlapped with trees densities >2/ha were areas

most likely to be restored as habitat through tree removal. Potential habitats were high priority

areas for tree removal because they met the needs of lesser prairie-chicken populations by having

requisite grassland composition and limited anthropogenic structures; therefore, represented

areas that should be targeted for tree removal.

A percent cover of conifer and mesquite (*Prosopis* spp.) raster layer (30-m resolution)

was available through the Kansas Biological Survey (http://kars.ku.edu/). In this layer, spatial

wavelet analysis was used to identify conifer tree canopy cover and model estimates were

correlated (r = 0.98) and had a root mean square error of 4% in comparison with field measured

canopy cover (Falkowski et al. 2017). To calibrate this layer to tree density (trees/ha), I first

adjusted the scale of canopy cover estimates to match the 16-ha scale of Lautenbach et al.

(2017), wherein lesser prairie-chickens did not nest in 16-ha areas having >2 trees/ha. To adjust

the scale, I used focal point statistics (e.g., moving window analysis) to estimate average canopy

coverage at the 16-ha scale from the Falkowski et al. (2017) layer. I then used raster calculator

76

in ArcGis 10.2 to convert canopy cover to tree density using the function provided in Lautenbach et al. (2017; percent canopy coverage = 0.786 + 0.389*trees/ha). Finally, I created a binary raster that identified pixels occurring in areas having tree densities >2 trees/ha at the 16-ha scale. Lautenbach et al. (2017) identified this density as a threshold separating nesting habitat from non-habitat for lesser prairie-chickens.

Spatial Prioritization of CRP Enrollment

A similar approach for prioritizing tree removal was used to identify areas where applying CRP would most likely benefit lesser prairie chickens. I first predicted the distribution of habitat for lesser prairie-chickens based on avoidance of anthropogenic features using a Random Forest model. Previous research indicated that CRP in landscapes (4-km radius) that are >60% grassland and in areas receiving less than 55 cm of annual averaging precipitation are more likely to be used by lesser prairie-chickens compared to CRP occurring in areas with less grassland and more average annual precipitation (Kraft unpubl. data, Sullins et al. in review). I then multiplied binary layers detailing the top 33% (relative probability of use > 0.66) of areas of potential habitat from the Random Forest model (coded 1), with a layer indicating where landscapes were greater than 60% grassland (coded 1), areas receiving less than 55 cm of annual average precipitation (coded 1), and areas that are currently in cropland as indicated from NLCD 2011 (coded 1; Homer et al. 2015). The product of the combined surfaces indicated pixels where converting cropland into CRP grassland would most likely benefit lesser prairie-chickens within the Short-Grass Prairie/CRP Mosaic Ecoregion (J. Kraft unpubl. data, Sullins et al. in review). The area of CRP enrollment that would have the greatest likelihood of being used by lesser prairie-chickens was calculated using ArcGIS 10.2.

77

Definition of Potential Habitat

Using the model predictions, I defined the top 66% of probabilities as potential habitat from the Random Forest model using both grassland composition and anthropogenic features for identifying priority areas for tree removal. To identify priority areas for CRP enrollment, the top 33% of predicted values from the Random Forest model using anthropogenic features plus grassland composition >60% identified potential habitat. My definition of habitat does not account for fine scale measurements of vegetation cover and forage, but identifies broad scale constraints on the distribution of lesser prairie-chickens.

Results

I subsampled a random set of 9,895 locations from a pool of 268,820 locations collected from 170 lesser prairie-chickens marked with GPS satellite transmitters. Two locations per week were sampled from an average of 29.16 (SD = 36.35; range = 2–136) weeks for each individual. Locations only from female lesser prairie-chickens were used from the Red Hills/Clark and Northwest study sites; however, low sample sizes from study sites in Colorado and Cimarron NG required the use of both male and female individuals for analyses. A total of 9,895 available (random) points were generated within the 16.18-km buffer generated around minimum convex polygons at each study site (Figure 2.1). Grassland composition at the 5-km scale exhibited the greatest model variable importance (1.0) and was 38% more important than grassland at the 4-km scale (Figures 2.2 and 2.3). For all anthropogenic features (county roads, major roads, oil wells, transmission lines, and other vertical features) densities estimated at the 2-km scale (e.g., number of transmission lines within 2km radius) had the strongest model variable importance with a mean importance of 0.28, which was on average 150% greater than densities estimated at the 1-km scale. Model importance increased with scale (0.5 km, 1 km, 2 km) for all

anthropogenic feature densities; however, model importance for grassland composition did not follow this trend with the 1200-m scale showing the least importance.

In the final Random Forest model, grassland composition within 5 km and anthropogenic features estimated at the 2-km scale were used as variables to predict available habitat. Grassland composition exhibited the greatest model importance and was 79% greater than the next variable. Optimal relative probability of use occurred at ~77% grassland composition; similar to the 76% mean of used locations (Figure 2.4, Table 2.2). Having lower model importance than grassland composition were densities of county roads, vertical point features, transmission lines, and major roads in respective order of model importance (Figure 2.3). Overall, the relative probability of use decreased as densities of anthropogenic features increased (Figure 2.4). However, the predicted probability of use increased from 0 to 300 pixels of county roads then declined sharply as densities increased beyond 300 (Figure 2.4). I expect this to partially be a function of county roads being largely gravel surfaced and often occurred in upland areas that were more likely to be used by lesser prairie-chickens (Lautenbach 2015). When county roads densities surpass a threshold (~300 pixels/2 km^2), it likely indicated the presence of greater urban development.

In addition to the county road threshold of ~300 pixels, all other anthropogenic features display patterns of sharp decreases in relative probability of use after surpassing a critical density (Figure 2.4). The occupancy threshold for vertical point feature densities occurs at ~2 vertical features/12.6 km^{2}A similar threshold was estimated for oils wells with areas having >2 oil wells/12.6 km^2 having 8X lower relative probability of use. The threshold for major roads and transmission lines was achieved at 10 pixels/12.6 km^2, which when surpassed, relative

probability of use decreased abruptly. All estimates above were derived from partial dependency plots from the Random Forest model (Figure 2.4).

Prediction.—The predicted relative probability of use output from the Random Forest model included lesser prairie-chicken GPS locations from 2013–2016 at all study sites (Figure 2.1). The Random Forest model predicted more grassland in lesser prairie-chicken habitat in the Mixed-Grass Prairie Ecoregion than in the Short-Grass Prairie/CRP Mosaic and Sand Sagebrush Prairie Ecoregions (McDonald et al. 2014). The percentage of potential habitat (top 66% of predicted values) in each ecoregion was 39.5% (584,944/1,479,000 ha) in the Mixed-Grass Prairie, 32.0% (318,731/996,414 ha) in the Sand Sagebrush Prairie Ecoregion, and 17.3% (361,276/2,084,840 ha) in the Short-Grass Prairie/CRP Mosaic Ecoregion. In the Short-Grass Prairie/CRP Mosaic Ecoregion of northwest Kansas, optimal habitat appears constrained to patches within 12 km of the Smoky Hill River in Gove and Logan County, and in northeast Finney County and northeast Wallace County. In the Mixed-Grass Prairie of Kansas and northern Oklahoma, habitat became more uniformly distributed with large patches of optimal habitat on the edge of Clark and Meade County, throughout most of Clark County, Comanche County, and on the border of Kiowa and Barber County (Figure 2.1). Limited potential habitat for lesser prairie-chickens was predicted in the Cimarron NG study area; however, most of the actual grasslands managed by the U.S. Forest Service appear to provide optimal habitat as did the Comanche NG in Colorado. The large extent of optimal habitat predicted by models on the Comanche NG study site does not match with recent lek counts showing a dwindling population approaching local extinction (<10 males, J. Reitz, pers. comm). An occurrence threshold for the model was estimated at a model output probability of 0.62 using a sensitivity–specificity difference minimizer following Jimenez-Valverde and Lobo (2007).

Validation.— The model had an estimated accuracy of 85%, a misclassification rate of 14%, true positive rate of 90%, false positive rate of 19%, specificity of 81%, and a precision of 83%. The receiver operating curve AUC was 0.967. The Random Forest model significantly predicted better than random among 1,000 model permutations (P < 0.001). The cross-validation assessment estimated a Cohen's Kappa of 0.71 with an out of bag error of 0.144 and a model error variance of 2.22 x 10-6. The Cohen's Kappa of 0.71 falls within the 0.61–0.80 range indicative of "substantial" model prediction (Landis and Koch 1977).

Spatial Prioritization of Tree Removal

I estimate that 98,497 ha of habitat for lesser prairie-chickens could be regained by tree removal and an alteration of land management practices to prevent further woody encroachment in the mixed-grass prairie portions of the lesser prairie-chicken range in Kansas and northern Oklahoma (Figure 2.5a). The long-term removal of trees from the depicted areas could increase the amount of lesser prairie-chicken habitat (406,172 ha) in this region by 25%. Of the potential habitat, 16% is of low canopy cover (1–5%), 11% is of medium canopy cover (6–15%), and 1% is of high canopy cover (>15%). Priority areas for tree removal were largely clustered to the eastern extent of the lesser prairie-chicken range in Barber, Kiowa, and Comanche counties of Kansas.

Spatial Prioritization of CRP Enrollment

The enrollment of CRP in all croplands depicted would result in an increase of 60,923 ha of lesser prairie-chicken habitat (Figure 2.5B). An additional 51,266 ha of current CRP appears to provide habitat for lesser prairie-chickens and keeping these areas enrolled may be advantageous. Priority locations for CRP enrollment were well dispersed (uniformly distributed) west of the 55 cm annual average precipitation boundary.

Discussion

I provide the first empirically-driven species distribution estimate based on large scale grassland composition and anthropogenic feature densities. I estimated the presence of 1,264,951 (~15 of presumed lesser prairie-chicken range) ha of available habitat (>0.33 relative probability of use) for lesser prairie-chickens in Kansas and Colorado, with the potential to increase the amount of available habitat by 98,497 and 60,923 ha through the strategic removal of trees in portions of the mixed-grass prairie and enrollment of cropland into CRP grasslands in areas receiving <55 cm of mean annual precipitation. Predicted habitat was more abundant in the Mixed-Grass Prairie, followed by the Short-Grass/CRP Mosaic, and Sand Sagebrush Prairie Ecoregions, respectively. However, the model likely overestimated the amount of habitat west of the Prowers/Baca county study site for the Comanche NG and the remaining Colorado portion of the lesser prairie-chicken range because short-grass prairie is largely contributing to the grassland composition in the far western extent of the model, but should not be considered available habitat. Based on my predictions and partial dependence plots, it appears lesser prairie-chickens at current population abundance are constrained to areas having >70% grassland with minimal anthropogenic features (Figure 2.4; e.g. <10 vertical features in 12.6 km^2).

Grassland composition and anthropogenic features constrain the distribution of lesser prairie-chickens both directly based on absolute avoidance of areas among all circumstances and indirectly from the emergent properties required to sustain life in a non-equilibrium grassland system. Absolute distribution constraints that operate outside the complex system are termed extrahierarichal boundary conditions (King 1997). It has been suggested that extrahierarchical boundary conditions are largely limited to soils, geology, and temperature (largely abiotic) conditions; however, I suggest that grassland composition and anthropogenic feature densities

82

could constrain lesser prairie-chicken habitat indefinitely. For example, as an obligate grassland species lesser prairie-chickens largely cannot persist in large landscapes that are <30% grassland. Further, if lesser prairie-chickens completely avoid areas (among all life stages) at some threshold of anthropogenic feature densities, there is no interaction that would make such areas usable other than the removal of those features.

Direct effects of grassland loss and anthropogenic development can be straightforward when imposing extrahierarical boundaries, in contrast, emergent properties from finer scales also influence the way in which grassland composition at very broad scales limits occurrence as indicated by Hierarchy Theory (O'Neill 1986, King 1997). At broad spatial scales, the occurrence of lesser prairie-chickens is a product of the landscape scale provision of lekking, nesting, brooding, and nonbreeding habitats within the home-range scale of individuals to provide habitat throughout the annual cycle, and for dispersal to facilitate demographic and genetic rescue at broader scales. In addition to the spatial heterogeneity needed to satisfy all life-stage needs, the niche (e.g. 25–80 cm tall herbaceous cover) must also be realized among dry and wet years in a dynamic grassland ecosystem (Sala et al. 1988, Hagen et al. 2013). Currently, the natural boom and bust fluctuations may heighten the risk of extinction for lesser prairie-chickens in more fragmented landscapes (Ross et al. 2016b). When evaluating my estimates of how grassland composition constrains lesser prairie-chicken occurrence, I concluded that on average all needs for lesser prairie-chicken populations were most likely to be met when 78.5 km^2 landscapes were 77% grassland. My estimate of optimal grassland area is comparable to the estimated habitat requirement for long term persistence of lesser prairie-chickens. For the long-term persistence of a population of lesser prairie-chickens, the minimum amount of contiguous

habitat has been estimated at 85 km^2 and is based on the presence of 6 leks that are on average 2.6 km away from each other (Applegate and Riley 1998, Van Pelt et al. 2013).

Large intact grasslands are more likely to be more heterogeneous in structure and therefore, provide for all lesser prairie-chicken life stages among dry and wet years (Hagen et al. 2004, Fuhlendorf 2006, Kraft 2016). Although management strategies to generate grassland structural heterogeneity have been described, these practices are not widely used (Scasta et al. 2015). Therefore, any remaining heterogeneity in modern grassland systems is largely a result of accident or environmental (e.g., weather, soil) transitions rather than deliberate management. The most successful agricultural practices have long strived to reduce competition of the crop or livestock of interest with other species and maximize yields (Tilman 1999). In eastern Kansas, maximum cattle yields are largely thought to be achieved with annual spring burning and intense grazing by doubling stocking rates (Anderson et al. 1970). Whereas to the west in the mixed- and short-grass prairie, within the distribution of lesser prairie-chickens, profitable management strategies are less apparent and grazing practices range from large continuous year-round to high-intensity short-duration operations with prescribed fire almost entirely absent from the landscape.

Greater grassland structural heterogeneity could be achieved with grazing alone through two mechanisms occurring in large parcels owned by a single landowner and among smaller parcels owned by several landowners. Grassland heterogeneity can occur opportunistically in working landscapes when ranches are large and some pastures (or areas within pastures) receive greater grazing pressure due to variation in ease of access by livestock. The greater grazing inequality on larger properties would blur typical conclusions if a species was "area sensitive" or if it was more likely to find habitat on the more heterogeneous ranch that also happens to be

large (Herkert 1994). Alternatively, heterogeneity could be achieved in fragmented landscapes when parcels of property become too small to sustain profitable cattle operations. Some landowners may abandon grazing operations on the smaller grasslands while others may graze them more heavily.

Comparison to a Climatic Prediction of Distribution

The predicted distribution complements a previous model examining the role of climate on lesser prairie-chicken distribution by providing inference on where habitat availability within the extent of climate boundaries (Dunn and Milne 2014). Precipitation during the brood period can be the most important characteristic of the niche-based on model permutations; however, winter precipitation can also influence distribution (Dunn and Milne 2014). Within the domain of suitable climate predicted by Dunn and Milne (2014), limited grassland composition at the 5-km scale and anthropogenic features densities at the 2-km scale may preclude lesser prairie-chicken occupancy in optimal climatic regions. Surprisingly, a high proportion of the region predicted to have a high probability of use based on climate based predictors in the Dunn and Milne(2014) model had either limited grassland composition or had high densities of anthropogenic features based on my model. Combining results from these two models suggests that lesser prairie-chickens may be confined to climatic regions of lower habitat quality. Dunn and Milne (2014) suggested that biotic processes (e.g., grazing) may have a stronger effect on restricting the distribution further east. The role of biotic processes in restricting the eastward distribution likely emerges from a complex hierarchical system; however, similar complex emergent properties likely constrain the distribution of lesser prairie-chickens elsewhere.

Effects of Anthropogenic Feature Densities

Grasslands providing cover requirements for female lesser prairie-chickens are not always available because of constrained use to nearby leks (Giesen et al. 1994, Plumb 2015, Robinson 2015, Winder et al. 2015). In addition, the presence of tall vertical structures at high densities in a surrounding landscape can make an area that would otherwise function as habitat unavailable to lesser prairie-chickens (Hagen et al. 2011, Hovick et al. 2014). Lesser prairie-chickens have evolved mechanisms to avoid tall vertical structures likely to minimize risk of predation from perching raptors (Reinert 1984, Manzer and Hannon 2005). Tall vertical structures that are known to be avoided by prairie grouse include trees, transmission lines, oil wells, wind turbines, and cell phone towers (Pitman et al. 2005, Hagen et al. 2011, Lautenbach 2015, Plumb 2015). The avoidance of tall vertical features is not absolute and largely contingent on the density of features at a landscape scale, life-stage of individual birds, and may be reduced if access to high quality habitat outweighs the presence of vertical features (Plumb 2015, Lautenbach et al. 2017). For example, lesser prairie-chickens avoided areas having >2 trees/ha at the 16-ha scale when nesting and avoided areas having >8 trees/ha throughout remaining portions of the breeding season and nonbreeding season (Lautenbach et al. 2017). Such constitutive relationships and interactions among life stages likely drive the complex hierarchical system from which population occupancy emerges. Although there is considerable variation of the effect of anthropogenic features on lesser prairie-chickens based on life-stage and the landscapes in which they occur, I provide evidence of thresholds where anthropogenic feature densities may act as extra hierarchical constraints.

Spatial Prioritization of Tree Removal

To increase the amount of potential habitat for lesser prairie-chickens, I have identified strategic areas where tree removal would have maximum benefits (Figure 2.5). However, it is imperative that trees are not merely removed then allowed to return (estimated encroachment: 2.3% forest cover/year; Briggs et al. 2002). I suggest that on-site tree removal could follow methods outlined in Lautenbach et al. (2017) and include a prescribed fire component to be implemented following the mechanical removal of trees (Ortmann et al. 1998). Additionally, lower canopy cover areas could be prioritized first followed by medium and high percent canopy coverage areas which vary respectively in cost.

Mechanical removal of trees at low (1–5%), medium (6–15%), and a high canopy cover (>15%) are estimated to cost $158.63/ha, $400.46/ha, and $1035.72/ha respectively (Lautenbach et al. 2017, C. Hagen Lesser Prairie-Chicken Initiative, personal communication). Based on these estimates, it will cost $10.2 million to remove all identified priority areas (15,780 ha) of low percent canopy cover, $17.3 million in medium percent canopy cover areas (10,835 ha), and $5.1 million to remove areas (985 ha) having high percent canopy cover. Overall, my predictions suggest it would cost $32.6 million to overcome some of the habitat losses from removing fire as an ecological driver in the mixed-grass prairie. My predictions do not account for trees killed in the Anderson creek fire of 2016 which burned 148,771 ha in northern Oklahoma and in eastern Comanche and Barber counties of Kansas. Interestingly, the location of this fire overlaps considerably with identified priority areas for tree removal (Figure 2.6). Of the trees that were killed by the fire, a substantial number remain standing as skeletons which will likely still be avoided by lesser prairie-chickens as the skeletons will continue to provide perches for large raptors (Errington and Breckinridge 1938, Reinert 1984).

To expedite the restoration of habitat available for lesser prairie-chickens, I suggest that standing dead eastern red cedar should be removed from burned areas using either skid steer with a cutting attachment or potentially by chaining. Chaining is a mechanical tree removal method that involves dragging a anchor chain (54-mm diameter) between two crawler tractors (Stevens and Monsen 2004). Although using a skid steer with a cutting attachment may be the preferred practice for removing still living trees, chaining can be an effective method to remove juniper trees for grassland restoration especially when removing standing dead trees post fire (Miller et al. 2005, Stevens and Monsen 2004). There is conflicting evidence regarding the effects of chaining on soil erosion and compaction and decisions on which tool to be used should be made per each individual site (Stevens and Monsen 2004, Miller et al. 2005). A one direction chaining useful for removing dead standing trees can cost anywhere from $27–$112/ha and therefore is competitive with skid steer based prices detailed above (Johnson et al. 1999, Ansley et al. 2006).

Spatial Prioritization of CRP Enrollment

The targeted enrollment of cropland into CRP grasslands would allow further progression of the program to benefit wildlife species (Figure 2.5; North American Bird Conservation Initiative 2015). The utility of the program for conservation has progressed greatly from initial objectives to stabilize the food and fiber industry and prevent soil erosion (Johnson 2005, Rodgers 2016). The underlying ability of CRP to benefit both producer and grassland wildlife will likely always be the ultimate reason for its conservation success in areas >90% privately owned (Reynolds et al. 1994, Best et al. 1997, Igl and Johnson 1999, Johnson 2005, Rodgers and Hoffman 2005). To build on the underlying conservation success on working lands, current continuous CRP signup programs pay more per acre than traditional CRP signup (Stubbs 2014). These additional payments are used to encourage further management within the CRP field to

88

benefit pollinators, waterfowl, and upland game birds by requiring interseeding with native forbs and desired native grasses (North American Bird Conservation Initiative 2015). In contrast to incentives based on within CRP field management, I provide insights that could be used to incentivize locations where the surrounding landscape is favorable for lesser prairie-chickens. Both within site and spatially targeted approaches provide mechanisms to benefit wildlife populations at broad scales as there is >700,000 ha of CRP grassland within the estimated lesser prairie-chicken range (Spencer et al. 2017, Sullins et al. in review).

The areas I have depicted as priority for enrollment may vary with future enrollment and agricultural expansion. In general, more area is enrolled in CRP during years of lower grain prices and more area is converted to cropland when contract expirations are paired with above-average grain prices (Secchi et al. 2009). Based on this added complexity an adaptive management framework to CRP enrollment may be beneficial. The adaptive approach would involve reassessing the current grassland composition within 4 km of each current and prospective CRP grassland on a regular basis, followed by reprioritizing enrollment to landscapes having >60% grassland composition. I also suggest that once a >80% grassland composition within the 5 km scale is achieved that incentives for currently enrolled CRP are maintained while incentives for future enrollment are decreased because the relative probability of use did not increase once grassland composition surpassed this threshold.

Conclusion

The distribution of lesser prairie-chickens is constrained both through emergent and extrahierarchical processes related to grassland composition and anthropogenic feature densities. In general, landscapes comprised of >77% grassland at the 5-km scale having minimal anthropogenic feature densities will be more likely to support sustainable lesser prairie-chicken

populations. Within areas having optimal grassland composition and anthropogenic feature

densities tree removal and the enrollment of cropland into CRP are two options that can align

with the goals of producers and likely to benefit lesser prairie-chickens. The spatial

prioritization of both tree removal and CRP enrollment at locations depicted could restore

~150,000 ha of grassland habitat for lesser prairie-chickens.

Literature Cited

Ammann, G. A. 1944. Determining the age of pinnated and sharp-tailed grouses. Journal of Wildlife Management 8:170–171.

Anderson, K.L., E. F. Smith, and C. E. Owensby, C.E. 1970. Burning bluestem range. Journal of Range Management 23:81–92.

Ansley, R. J., H. T. Wiedemann, M. J. Castellano, and J. E. Slosser. 2006. Herbaceous restoration of juniper dominated grasslands with chaining and fire. Rangeland Ecology and Management 59:171–178.

Barbet-Massin, M. F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where, and how many? Methods in Ecology and Evolution 3:327-338.

Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J. M. Kiesecker, M. J. Falkowski, C. A. Hagen, and K. P. Reese. 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biological Conservation 167:233–241.

Cutler, D. R., T. C. Edwards, Jr., K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. Random Forests for Classification in Ecology. Ecology 88:2783–2792.

Bertuzzo, E., S. Suweis, L. Mari, A. Maritan, I. Rodriguez-Iturbe, and A. Rinaldo. 2011. Spatial effects on species persistence and implications for biodiversity. Proceedings of the National Academy of Science 108:4346–4351.

Best, L. B., H. Campa, III, K. E. Kemp, R. J. Robel, M. R. Ryan, J. A. Savidge, H. P. Weeks, Jr., and S. R. Winterstein. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. Wildlife Society Bulletin 25:864–877.

Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? Annual Review of Ecology, Evolution, and Systematics 39:641–659.

Braun, C. E., K. Martin, T. E. Remington, and J. R. Young. 1994. North American grouse: issues and strategies for the 21st century. Transactions of the North American Wildlife and Natural Resources Conference 59:428-435.

Briggs, J. M, G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystem 5:578–586

Breiman L. 2001. Random forests. Machine Learning 45:5–32.doi:10.1023/A:101093340432.

Crawford, J. A., and E. G. Bolen. 1976. Effects of land use on lesser prairie chickens in Texas. Journal of Wildlife Management 40:96–104.

Cutler D. R., T. C. Edwards Jr., K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

DeLong E. R., D. M. DeLong, and D. L. Clarke-Pearson. 1988. Comparing the area under two or more correlated receiver operating characteristics curves: a nonparametric approach. Biometrics 59:837–845.

Davis, M. J., S. Thokala, X. Xing, T. Hobbs, M. W. Miller, R. Han, S. Mishra. 2013. Testing the functionality and contact error of a GPS-based wildlife tracking network. Wildlife Society Bulletin 37:855–861.

Dunn, W. C., and B. T. Milne. 2014. Implications of climatic heterogeneity for conservation of the lesser prairie-chicken (*Tympanuchus pallidicinctus*). Ecosphere 5:1-17. 10.1890/ES13-00333.1.

Earl, J. E., S. D. Fuhlendorf, D. A. 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: e01441. 10.1002/ecs2.1441.

Errington, P. L., and W. J. Breckenridge. 1938. Food habits of *Buteo* hawks in northcentral United States. Wilson Bulletin 50:113–121.

Evans J. S, and S. A. Cushman.2009. Gradient modeling of conifer species using random forests. Landscape Ecology 24:673–683.

Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. Modeling species distribution and change using random forest. Pages 139–159 in Predictive species and habitat modeling in landscape ecology. Editors: C. A. Drew, Y. F. Wiersma, and F. Huettmann. Springer Science, Berlin, Germany.

Falkowski, M. J., J. S. Evans, D. E. Naugle, C. A. Hagen, S. A. Carleton, J. D. Maestas, A. H. Khalyani, A. J. Poznanovic, A. J. Lawrence. 2017. Mapping tree canopy cover in support of proactive prairie grouse conservation in western North America. Rangeland Ecology and Management 70:15–24.

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 Jr., 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.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16: 1706–1716.

Garton, E. O., C. A. Hagen, G. M. Beauprez, S. C. Kyle, J. C. Pitman, D. D. Schoeling, and W. E. Van Pelt. 2016. Population dynamics of lesser prairie-chickens. Pages 49–76 in D. A Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Grisham, B. A., C. P. Griffin, and A. J. Godar. 2016. Climate change. Pages 221–242 in D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Giesen, K. M. 1994. Breeding range and population status of lesser prairie-chickens in Colorado. Prairie Naturalist 26:175–182.

Hagen, C. A., B. E. Jamison, K. M. Giesen, and T. Z. Riley. 2004. Guidelines for managing Lesser Prairie-Chicken populations and their habitats. Wildlife Society Bulletin 32:69–82.

Hagen, C. A., and K. M. Giesen. [online]. 2005. Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Birds of North America 364. <http://bna.birds.cornell.edu/bna/species/364/articles/introduction> (15 May 2015).

Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. Journal of Wildlife Management 73:1325–1332.

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. University of California Press, Berkeley, USA.

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.

Hanser, S., Powerlines in the western United States. 2011. USGS-FREC, Snake River Field Station, Idaho, USA. <https://databasin.org/datasets/b386900d8bcd4287a4dad09a24ac1e6f> Accessed 24 February 2017.

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

Haukos, D. A, A. A. Flanders, C. A. Hagen, and J. C. Pitman. 2016. Lesser prairie-chickens of the sand sagebrush prairie. Pages 281299 in D.A Haukos and C.W. Boal. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, CA.

93

Hegel, T. M., S. A. Cushman, J. Evans, and F. Huettmann. 2010. Current state of the art for statistical modelling of Species Distributions. Pages 273–311 in S. A. Cushman and F. Huettmann. Spatial complexity, informatics, and wildlife conservation. Springer, New York.

Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. Ecological Applications 4:461–471.

Homer, C. G., J. A. Dewitz, L. Yang,S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Horton, R., L. Bell, C. M. O'Meilia, M. McLachlan, C. Hise, D. Wolfe, D. Elmore and J. D. Strong. 2010. A spatially-based planning tool designed to reduce negative effects of development on the lesser prairie-chicken (*Tympanuchus pallidicinctus*) in Oklahoma: a multi-entity collaboration to promote lesser prairie-chicken voluntary habitat conservation and prioritized management actions. Oklahoma Department of Wildlife Conservation. Oklahoma City, Oklahoma. 79 pp.

Hovick, T. J., R. D. Elmore, D. K. Dahlgren, S. D. Fuhlendorf, and D. M. Engle. 2014. Review: Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. Journal of Applied Ecology, 51: 1680–1689. doi: 10.1111/1365-2664.12331.

Igl, L. D., and D. H. Johnson. 1999. Le Conte's sparrows breeding in Conservation Reserve Program fields: precipitation and patterns of population change. Studies in Avian Biology 19:178–186.

Jimenez-Valverde, A., and J. M. Lobo. 2007. Threshold criteria for conversion of probability of species presence to either-or presence-absence. Acta Oecologica 31:361-369

Johnson, P., A. Gerbolini, D. Ethridge, C. Britton, and D. Ueckert. 1999. Economics of redberry juniper control in the Texas Rolling Plains. Journal of Range Management 52:569–574.

Johnson, D. H. 2005. Grassland bird use of Conservation Reserve Program fields in the Great Plains. Pages 17–32 in J. B. Haufler, editor. Fish and wildlife benefits of Farm Bill conservation programs: 2002-2005 update. The Wildlife Society Technical Review 05-02, Bethesda, Maryland, USA.

King, A. W. 1997. Hierarchy theory: a guide to system structure for wildlife biologists pages 185–212 in J. A. Bissonette, editor, Wildlife and Landscape Ecology. Springer, New York, New York, USA.

Kraft. J. D. 2016. Vegetation characteristics and lesser prairie-chicken responses to land cover types and grazing management in western Kansas. Thesis. Kansas State University, USA. 173 pp.

Landis, J. R., and G. G. Koch. 1977. The measurement of observer agreement for categorical data. Biometrics 33:159–174.

Larsson, L. C., C. L. Pruett, D. H. Wolfe, and M. A. Patten. 2013. Fine-scale selection of habitat by the lesser prairie-chicken. Southwestern naturalist 58:135–149.

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 and Management 70:78–86.

Liaw, A., and M. Wiener. 2002. Classification and Regression by randomForest. R News 2(3), 18-22.

Manzer, D. L., S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

McDonald, L., G. Beauprez, G. Gardner, J. Griswold, C. Hagen, D. Klute, S. Kyle, J. Pitman, T. Rintz, and B. Van Pelt. 2014. Range-wide population size of the lesser prairie-chicken: 2012 and 2013. Wildlife Society Bulletin 38:536–546.

Mengel, R. M. 1970. The North American central plains as an isolating agent in bird speciation, pages 279-340 in Pleistocene and Recent environments of the central Great Plains Department Geological University Kansas Special Publication 3.

Merchant, S. S. 1982. Habitat-use, reproductive success, and survival of female Lesser Prairie-Chickens in two years of contrasting weather. M.S. thesis, New Mexico State University, Las Cruces, NM.

Miller, R. F., J. D. Bates, T. J. Svejcar, B. F. Pierson, and L. E. Eddleman. 2005. Biology, ecology, and management of western juniper. Oregon State University Agricultural Experiment Station Technical, Bulletin 152.

Murphy M. A., J. S. Evans, A. S. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91:252–261.

National Oceanic and Atmospheric Administration National Climatic Data Center (NOAA). 2016a. National Environmental Satellite, Data, and Information Service. <https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp> Accessed August 11, 2016.

North American Bird Conservation Initiative, U.S. Committee. 2015. 2014 Farm bill field guide to fish and wildlife Conservation. 58 pages. <http://bringbackbobwhites.org/download/2014-farm-bill-field-guide-to-fish-and-wildlife-conservation/> Accessed 10 November 2016.

O'Neill, R. V., A. R. Johnson, and A. W. King. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology 3:193-205.

Ortmann, J., J. Stubbendieck, R. A. Masters, G. H. Pfeiffer, and T. B. Bragg, 1998. Efficacy and costs of controlling eastern red cedar. Journal of Range Management 51:158–163.

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 69:1259–1269.

Plumb. R. T. 2015. Lesser prairie-chicken movement, space use, survival, and response to anthropogenic structures in Kansas and Colorado. Thesis. Kansas State University, USA. 133 pp.

PRISM Climate Group.2016. Oregon State University. <http://www.prism.oregonstate.edu/normals/> Accessed 11 January 2017.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. Avoidance behavior by prairie grouse: implications for development of wind energy. Conservation Biology 23:1253–1259.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reinert, S. E., 1984. Use of introduced perches by raptors: experimental results and management implications. Raptor Research 18:25–29.

Reynolds, R. E., T. L. Shafper, J. R. Sauer, and B. G. Peterjohn. 1994. Conservation Reserve Program: benefit for grassland birds in the Northern Plains. Transactions of the North American Wildlife Natural Resource Conference 59:328–336.

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. Effects of landscape characteristics on annual survival of lesser prairie-chickens In review.

Rodgers. R. D. 2016. A history of lesser prairie-chickens. Pages 15–38 in D.A Haukos and C.W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

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, 6–9 June 2004, Fort Collins, Colorado, USA. USGS Biological Resources Division, Scientific Investigation Report 2005–5145, Reston, Virginia, USA.

Ross, B. E., D. A. Haukos, C. A. Hagen, and J. C. Pitman. 2016a. The relative contribution of climate to changes in lesser prairie-chicken abundance. Ecosphere 7:e01323. 10.1002/ecs2.1323

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

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Scasta, J. D., E. T. Thacker, T. J. Hovick, D. M. Engle, B. W. Allred, S. D. Fuhlendorf, and J. R. Weir. 2015. Patch-burn grazing (PBG) as a livestock management alternative for fire-prone ecosystems of North America. Renewable Agriculture and Food Systems doi:10.1017/S1742170515000411.

Secchi, S., P. W. Gassman, J. R. Williams, B. A. Babcock. Corn-based ethanol production and environmental quality: a case of Iowa and the Conservation Reserve Program. Environmental management 44:732–744.

Sedinger, J. S. 1997. Adaptation to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314–326.

Silvy, N. J., M. E. Morrow, E. Shanley, and R. D. Slack. 1990. An improved drop net for capturing wildlife. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 44:374–378.

Silvy, N. J, M. J. Peterson, and R. R. Lopez. 2004. The cause of the decline of Pinnated Grouse: the Texas example. Wildlife Society Bulletin 32:16–21.

Simberloff, D. 1994. The ecology of extinction. Acta Paleontologica Polonica 38:159–174.

Stevens, R. and S. B. Monsen. 2004. Mechanical plant control. Pages 65-87. In Restoring Western Ranges and Wildlands. S. B. Monsen, R. Stevens, and N. L. Shaw (compilers). USDA Forest Service RMS-GTR- 136 vol 1.

Stubbs, M. 2014. Conservation reserve program (CRP): Status and issues. Congressional research service 7-5700. <www.crs.gov> Accessed 14 March 2017

Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. Proceedings of the National Academy of sciences of the United States of America 96:5995–6000.

Spencer, D., D. A. Haukos, C. A. 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.

Vickery, P. C., and J. R. Herkert. 1999. Ecology and conservation of grassland birds of the Western Hemisphere. Studies in Avian Biology No. 19. Cooper Ornithological Society, Camarillo, California, USA.

Wiens, J. A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. 76:385–400.

Willis, E. 1966. Interspecific competition and the foraging behavior of Plain-brown woodcreepers. Ecology 47:667–672.

Winder V. L., K. M. Carrlson, A. J. Gregory, C. A. Hagen, D. A. Haukos, D.C. Kesler, L. C. Larsson, T. W. Matthews, L. B. McNew, M. A. Patten, J. C. Pitman, L. A. Powell, J. A. Smith, T. Thompson, D. H. Wolfe, and B. K. Sandercock. 2015. Factors affecting female space use in ten populations of prairie chickens. Ecosphere 6:1–17.

Table 2.1 Environmental conditions at 6 study sites used in the Random Forests species distribution model using location data from VHF and GPS transmittered lesser prairie-chickens monitored from 2013–2016 in Kansas and Colorado. The units for linear features (roads and transmission lines) are displayed as number of 30 m x 30 m pixels while the vertical point features (e.g., cell towers, large buildings, wind turbines, and oil wells) are represented by independent features.

	Study Area					
Site Characteristics	**Red Hills/Clark**	**Northwest**	**Prowers/Baca**	**Cheyenne**	**Comanche NG**	**Cimarron NG[4]**
N[1]	4,228	3,312	1,263	488	16	588
Annual Precipitation	63.1	51.7	43.2	380	42.2	44.3
Soils	variable, fine sand to Clay	silt loam, clay loam, fine sandy loam	loam	sand, sandy loam	sand, loamy fine sand, sandy loam	sand, loamy fine sand, sandy loam
Dominant Plants[2]	little bluestem	sideoats grama	sideoats grama	blue grama	blue grama	sand dropseed
	sand dropseed	blue grama	blue grama	sand dropseed	sand dropseed	blue grama
	Louisiana sagewort	sand dropseed	little bluestem	sand sagebrush	sand sagebrush	plains yucca
	western ragweed	western wheatgrass	Field bindweed	Russian thistle	annual buckwheat	sand sagebrush
	sideoats grama	little bluestem				
Anthropogenic features[3]						
County roads	248 ± 185	285 ± 159	399 ± 173	258 ± 235	470 ± 250	316 ± 167
Major roads	23.7 ± 50.78	18.4 ± 44.1	18.0 ± 42.0	21.4 ± 47.0	14.9 ± 38.6	24.4 ± 50.5
Oil wells	3.34 ± 4.71	3.19 ± 5.42	0.07 ± 0.46	0.23 ± 1.33	0.29 ± 1.28	7.02 ± 7.14
Transmission lines	20.2 ± 51.9	17.0 ± 46.2	0.15 ± 2.68	15.4 ± 39.8	30.6 ± 54.6	9.01 ± 32.0
Vertical point features	3.62 ± 5.03	3.41 ± 5.59	0.11 ± 0.49	0.25 ± 1.34	0.29 ± 1.28	7.16 ± 7.20
Grassland Composition[4]	0.67 ± 0.23	0.40 ± 0.21	0.47 ± 0.21	0.79 ± 0.18	0.84 ± 0.16	0.49 ± 0.20

[1] N is the number of bird locations subsampled for each site

[2] dominant plants were determined from point-step transects (see diet chapter) and from Cable et al. (1996)

[3] Anthropogneic feature densities were estimated within a 2km radius for each 30x30m pixel then averaged

[4] Grassland composition was estimated within a 5 km radius for each 30x30m pixel within each study site

[4] Soil and dominant plants for the Cimarron national grasslands were identified from Birds of Cimarron National Grassland (Cable et al. 1996).

Table 2.2 Mean and standard deviation of grassland composition (5-km scale) and anthropogenic feature densities (2-km scale) estimated at locations (n = 9,895) used by lesser prairie-chickens from 2013–2016, at random locations (n = 9,895) distributed within dispersal range of Kansas and Colorado, and throughout the entire extent analyzed for the species distribution model. The units for linear features (roads and transmission lines) are displayed as number of 30 m x 30 m pixels while the vertical features (e.g., cell towers, large buildings, wind turbines, and oil wells) are represented by actual numbers.

Variables	Used Mean	SD	Random Mean	SD	Entire Extent Mean	SD
Grassland composition	0.76	0.18	0.55	0.26	0.51	0.27
Anthropogenic features						
County roads	260	157	292	187	332	235
Major roads	6.33	26.0	20.8	46.9	22.4	48.8
Oil wells	2.42	3.89	2.95	5.04	3.49	6.67
Transmission lines	3.93	20.5	15.2	44.3	28.9	65.6
Vertical point features	2.43	3.91	3.16	5.28	3.82	7.41

Figure 2.1 Locations of the 6 study sites where lesser prairie-chickens were marked, captured, and monitored in Kansas and Colorado during 2013–2016 to estimate species distribution using a Random Forests model. Study sites were established by creating minimum convex polygons from all locations used by lesser prairie-chickens marked with VHF and GPS satellite transmitters then buffering the minimum convex polygons with the average nest displacement during dispersal (16.18 km) following Earl et al. (2016). Values range from 0 (light tan) to 1(dark blue) indicating the relative probability of use by lesser prairie chickens and predict the extent of habitat based on grassland composition within 5 km and anthropogenic feature densities within 2 km.
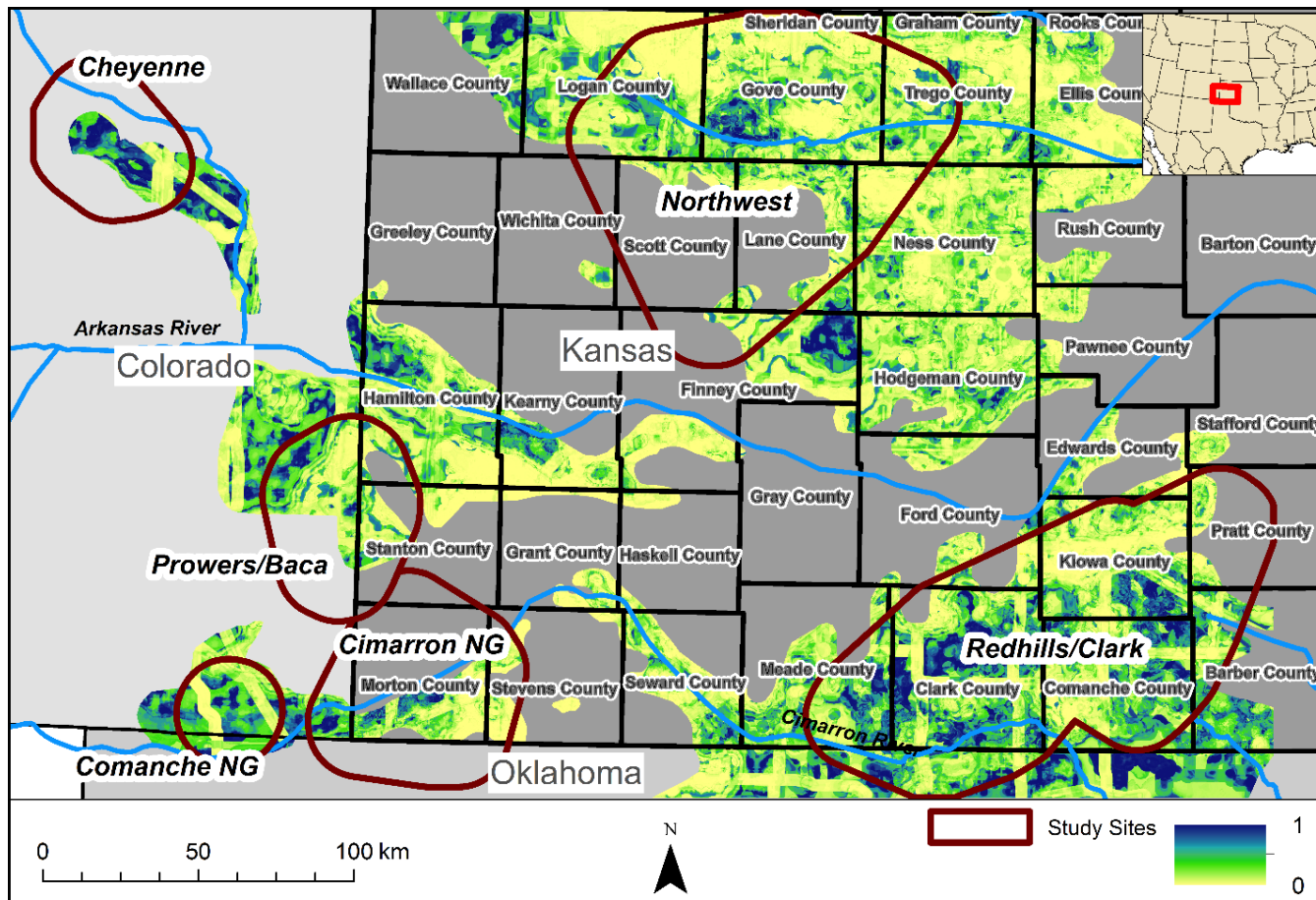
Figure 2.2 Model-scaled variable importance (Evans et al. 2011) used to identify scales for modeling grassland composition and anthropogenic features for lesser prairie-chickens in Kansas and Colorado. The scale exhibiting the greatest model variable importance for each variable (e.g., grassland composition, oil well density) was used in the final Random Forest model. All variable names describe the variable and the radius within which the variable was estimated (e.g. grassland composition within a 5km radius). Vertical point features included all tall features including cell towers, large buildings, wind turbines, and oil wells.
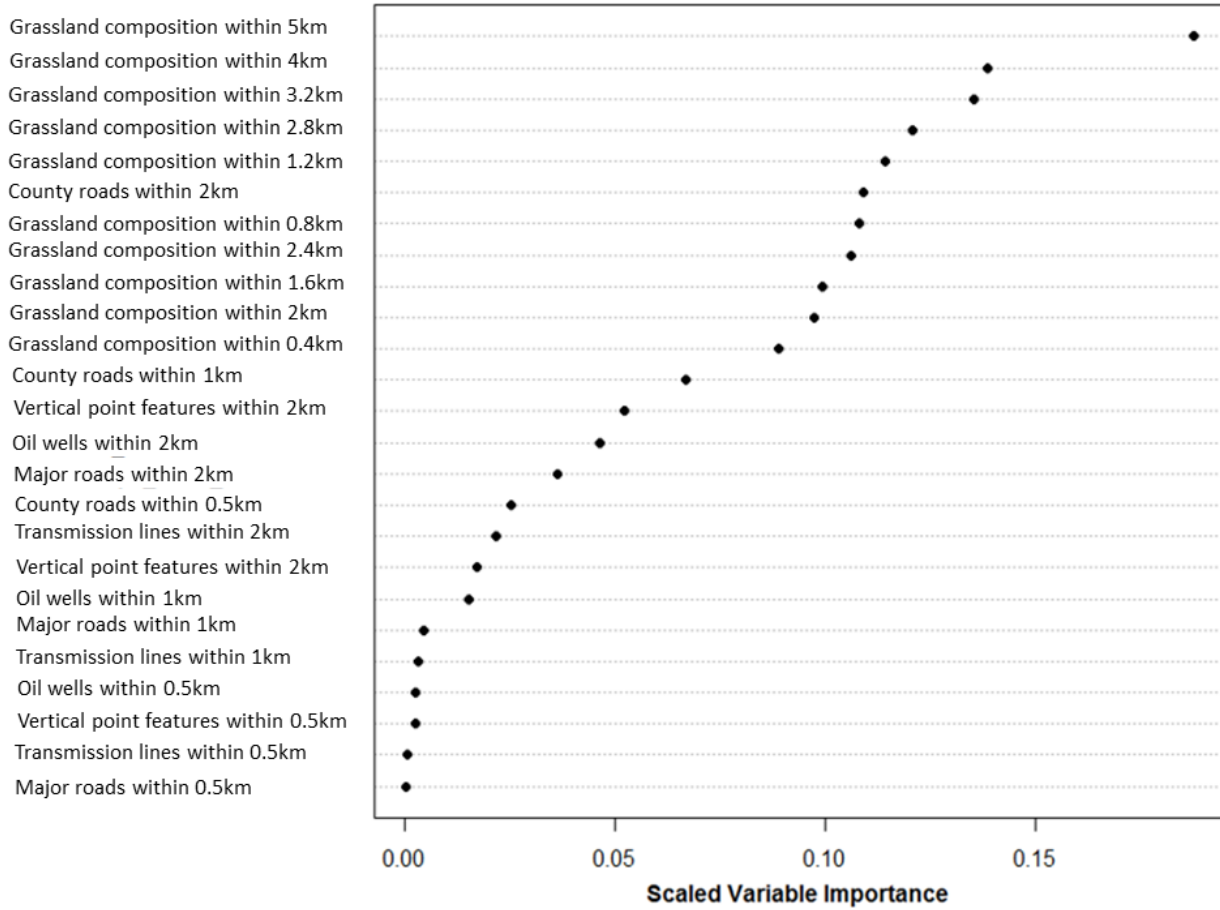
Figure 2.3 Model scaled variable importance (Evans et al. 2011) among variables used in the final species distribution model. The scale exhibiting the greatest model variable importance for each variable (e.g. grassland composition within 5 km, oil well density within 2 km) was used in the final Random Forest model based on the output in Figure 2.2. All variable names describe the variable and the radius within which the variable was estimated (e.g. grassland composition within a 5km radius). Vertical point features included all tall features including cell towers, large buildings, wind turbines, and oil wells.
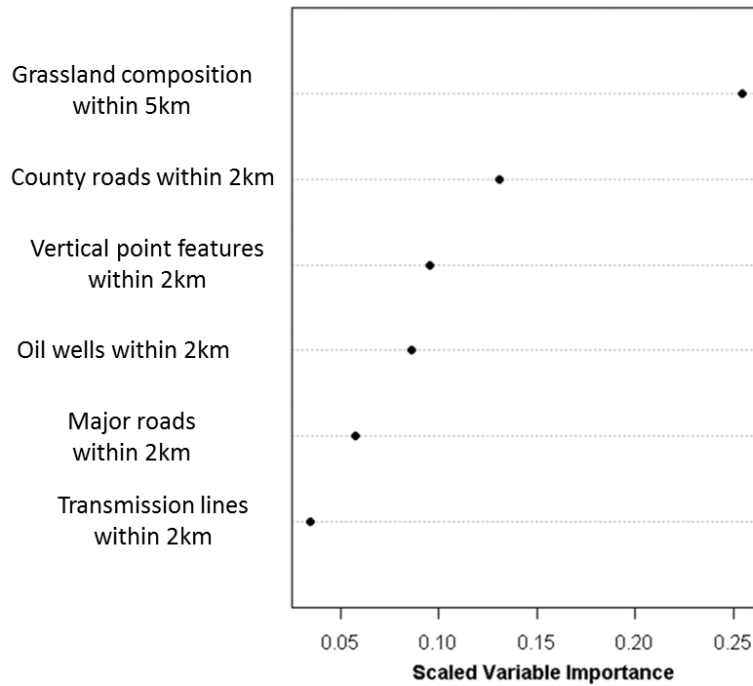
Figure 2.4 Partial dependence plots for all grassland composition and anthropogenic feature densities used to predict the distribution of lesser prairie-chickens in Kansas and Colorado as depicted in Figure 2.1. Scales having the greatest influence for each variable were identified in Figure 2.2. The raw relative probability of use distribution is plotted as grey dashes and a lowess polynomial regression is plotted in as a solid black line.
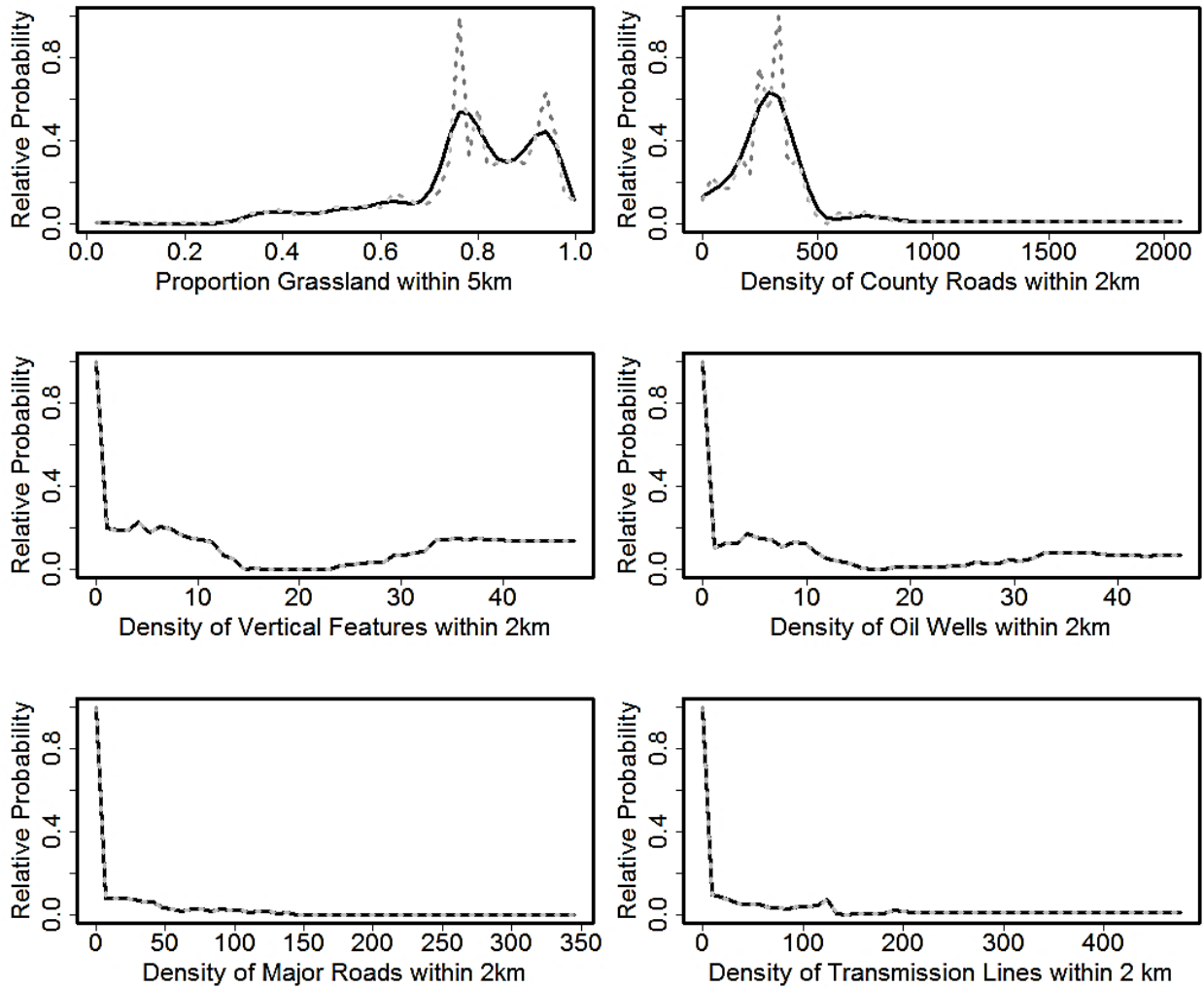
Figure 2.5 Predicted areas of low (1–5%), medium (6–15%), high (>15%) tree canopy cover where tree removal is most likely to restore lesser prairie-chicken habitat in Kansas and Colorado based on grassland composition within 5 km and anthropogenic feature densities (A). Areas having a high priority for tree removal are where the top 66% of predicted values from the Random Forests model occurred and where there was >2 trees/ha (Falkowski et al. 2017, Lautenbach et al. 2017). Predicted areas where current CRP grasslands (blue) and cropland that could be converted to CRP (red) is most likely to be used by lesser prairie-chickens following results from Chapter 4 (B). Priority areas that are currently enrolled CRP grassland and areas currently cultivated were in locations having greater than 60% grassland within 4 km and where the top 33% of values from a Random Forests model using only anthropogenic features occurred.
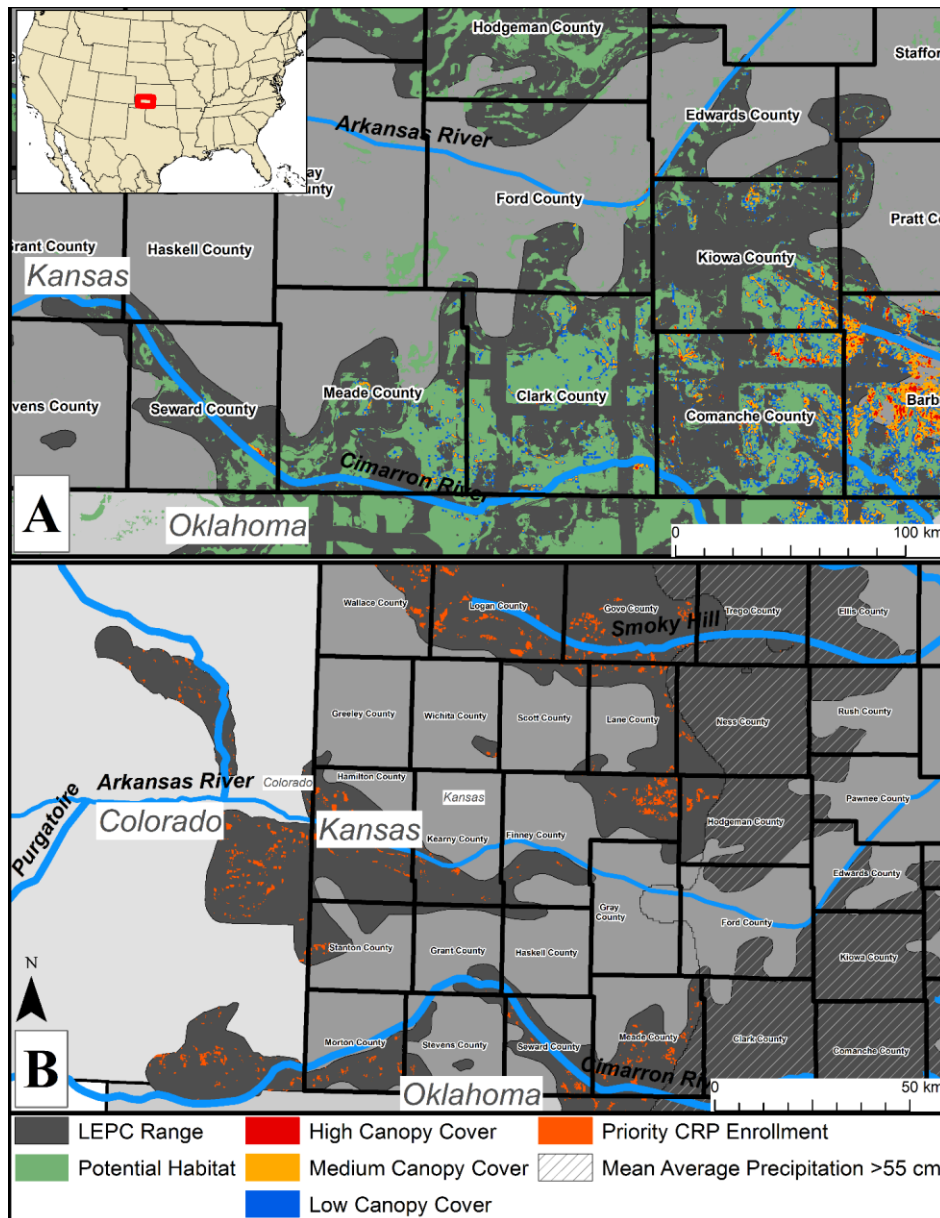
Figure 2.6 Predicted areas of low (1–5%), medium (6–15%), and high (>15%) tree canopy cover where tree removal is most likely to restore lesser prairie-chicken habitat in Kansas and perimeter of the Anderson creek fire that burned 148,771 ha in March 2016 (A). Areas having a high priority for tree removal are where the top 66% of predicted values from the Random Forests model occurred and where there was > 2 trees/ha (Falkowski et al. 2017, Lautenbach et al. 2017).
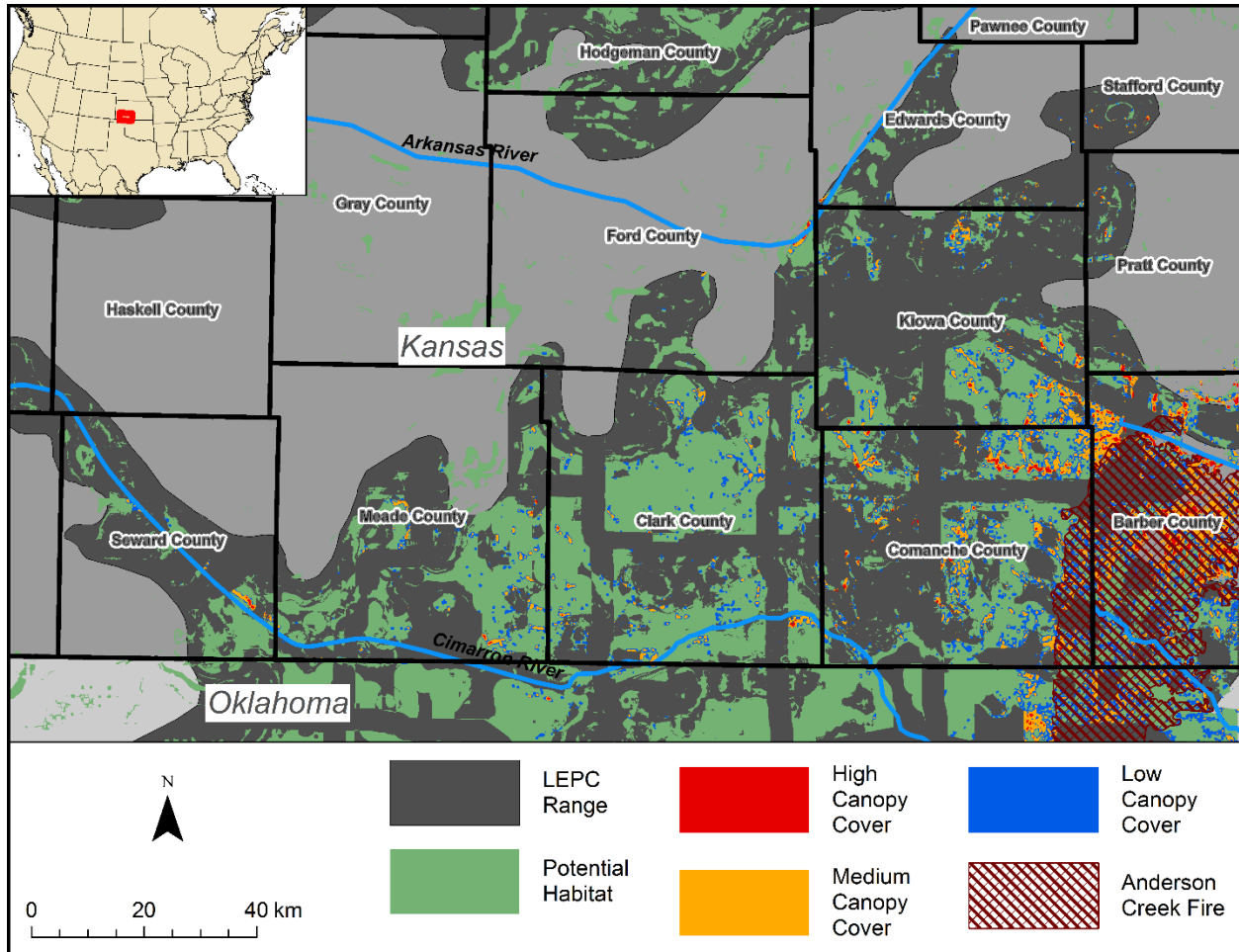
Chapter 3 - Lesser Prairie-Chicken Diets during Brooding and winter

Introduction

The first flying birds, and reptilian ancestors, evolved simplified digestive systems in which mass was lessened by the replacement of teeth with gizzards, ammonia and urea with greater processing to a dry form of uric acid, and an overall shortening of gastrointestinal tracts (Gill 2006). Flight allowed birds to move great distances over short periods of time and take advantage of seasonally abundant resources rich in nutrients (Gill 2006). Upon further evolutionary refinement, grouse developed mechanisms to make use of less digestible resources, particularly during winter, and have large ceca that may weigh more than in comparably sized waterfowl, but are thought to improve the uptake of protein from lower quality foods (Sedinger 1997). Outside of winter, prairie-chickens (*Tympanuchus* spp.) may have diverged a stronger specialization on protein-rich arthropods from other grouse species (Martin et al. 1951, Jones 1963, Haukos and Zaveleta 2016). The lesser prairie-chicken (*T. pallidicinctus*) has high protein demands and consumes both plant and invertebrate material throughout their life history (Haukos and Zavaleta 2016). Plant and arthropod taxa available to and selected by lesser prairie-chickens are not well understood and past research has struggled to link invertebrate and plant matter abundance to lesser prairie-chicken habitat use or fitness (fitness=offspring output based on survival and reproduction; Salter et al. 2005, Zaveleta 2012). Although lesser prairie-chickens have mechanisms that allow them to obtain nutrients from less than optimal foods, the nonmigratory nature of this species makes them sensitive to immediate surroundings, for which, the species is experiencing long-term population declines similar to several other migratory and nonmigratory grassland birds (NABCI 2014, Garton et al. 2016).

107

Lesser prairie-chicken diets have not been well described and are variable throughout the year (Haukos and Zaveleta 2016). Most diet information is based on information that is >30 years old from fall-collected individuals in limited areas relative to the range of the lesser prairie-chicken (Haukos and Zaveleta 2016). During the brooding period, lesser prairie-chicken adults and chicks consume an array of invertebrate taxa and are thought to specialize on grasshoppers (Orthoptera; Suminski 1977, Davis et al. 1980). There are likely some size and mobility constraints within which arthropods can be considered prey for lesser prairie-chicken chicks. For instance, a flying adult threebanded grasshopper (*Hadrotettix trifasciatus*) would be a formidable prey item for a 0–14-day-old chick to capture and consume. However, a first instar of the same species would lack an ability to fly, be much smaller and slower, and may be an optimal prey item (Pfadt 1994). In this case, the phenology of predator and prey must match. Variation in prey vulnerability and availability, even within species, must be considered to identify optimal diets of a species; a lack of accounting for this association may lead to erroneous conclusions (Sih and Christensen 2001). Specific life histories may make certain species either available as prey during the brooding period or too large or difficult for 0–14-day-old chicks to consume.

Although arthropods are important food sources during the summer and fall, during winter and spring lesser prairie-chickens typically rely upon plant matter to fulfill energetic demands (Haukos and Zaveleta 2016). Several research efforts have assessed winter diets in sand shinnery oak (*Quercus havardii*) prairie where lesser prairie-chickens readily use oak catkins and acorns when available (Jones 1964, Suminski 1977, Pettit 1986, Riley et al. 1993). Outside of periods when acorns are produced, and outside of the sand shinnery oak prairie, winter foods are less well known (Salter et al. 2005, McDonald et al. 2015). The reliance on persistent woody vegetation is known among grouse species during this time and lesser prairie-

chickens can make use of woody vegetation other than sand shinnery oak (Schmidt 1936, Schwilling 1955, Bergerud and Gratson 1988). For example, budding willows (*Salix* spp.) and cottonwoods (*Populus deltoides*) can be used during winter as can portions of sand sagebrush (*Artemisia filifolia*) and skunkbrush sumac (*Rhus aromatica*; Schwilling 1955, Jones 1963). However, the consumption of budding woody vegetation may be minimized in pinnated grouse (*Tympanuchus* spp., Schmidt 1936).

Prairie-chickens are sometimes considered to specialize on forb seeds and waste grain during winter (Schmidt 1936). Waste grain (e.g., *Sorghum* spp*., Zea* spp.) can provide an energy-rich food source for adult upland gamebirds (Evans and Dietz 1974, Bogenschuztz et al. 1995, Guthery 2000). Use of grain fields by lesser prairie-chickens has been reported during fall through early spring (Jamison et al. 2002); however, occurrence in cultivated fields by lesser prairie-chickens is not correlated with the amount of waste grain or related to increased body condition, survival, or reproductive output (Salter et al. 2005, Haukos and Zavaleta 2016). In addition to corn and sorghum, alfalfa (*Medicago* spp.) may be an important foodstuff in early spring (Jamison 2000, Larsson et al. 2013). It has been suggested that lesser prairie-chickens use alfalfa fields primarily for the moisture content of this forage and provision of moisture may make alfalfa fields more attractive than wheat (*Triticum* spp.*, Larsson et al. 2013). Alfalfa could additionally be used because of its high protein composition compared to other herbaceous foods (Mowat 1965). In portions of their range removed from cultivation, broom snakeweed (*Gutierrezia sarothrae*), annual buckwheat (*Eriogoum annum*), and Johnny-jump-up (*Viola* spp.) may be the primary winter food sources for lesser prairie-chickens (Jones 1963).

Although the general use of croplands may indicate the utility of cultivated foods, true impacts on demography and contribution of such foodstuffs in the diet will be difficult to

estimate using traditional methods based on crop contents or scat dissection. For example, analysis of crop contents usually requires the harvesting of individuals and thus preclude any estimated impact on survival. On the other hand, use of microhistological analyses of feces will underestimate easily digestible items. DNA metabarcoding of fecal samples may be the best option for linking avian diets to fitness. It has been proven as an effective way to identify prey items for a species of conservation concern when collection of individuals is not practical (Pompanon et al. 2011). It can be a particularly useful method for identifying soft-bodied arthropod prey items, which are typically unidentifiable using past methods involving examination of gut contents or histology of fecal samples (Zeale et al. 2011, Trevelline et al. 2016).

To identify prey taxa consumed, a standardized DNA region, or barcode, is identified, which varies among taxa of interest. The DNA strand is amplified using a Polymerase Chain Reaction (PCR), then amplified portions are compared to sequences from a reference database. For the DNA barcoding approach to work, sequence divergence at genetic markers must be large enough to allow for the separation of species or taxa of interest and neutral within taxa of interest. Second, reference sequences for each potential prey species must be known. Reference DNA sequences can be obtained from public libraries, such as the Barcode of Life Database (Ratnasingham and Hebert 2007) or can be acquired from samples collected on site. Dietary predictions using DNA metabarcoding may be further improved when assessing fecal samples of individuals marked with transmitters and substantial vegetation and arthropod surveys are conducted. Location data provided by transmitters combined with knowledge of potentially available plants and arthropod foods could be used to constrain DNA reads to food available based on movements of the individual and local plant and arthropod communities.

Seasonal and spatial variation in lesser prairie-chicken diets may largely follow predictions from optimal diet theory. Optimal diet theory, a version of optimal foraging theory based on prey choice, suggests that prey providing greater energy per unit handling time will be preferred, when the abundance of higher quality prey increases the lower quality prey will not be used, and predators will decide which prey items will be selected or rejected based on some threshold of abundance (Sih and Christensen 2001). Optimal diet theory describes the interaction between availability (within size and mobility constraints) and quality (nutrient content and digestibility) in determining prey consumption. At the current state of knowledge, we lack understanding of which foods are of high quality and which are available to most wildlife species throughout the annual cycle. Use of DNA metabarcoding may allow for a more efficient estimate of foods spanning the annual cycle and over larger spatial scales in the future. For now, I focused on two periods (brooding and winter) during which available forage may have the greatest influence on demography of lesser prairie-chickens and other grouse species (Wise 1982, Bergerud and Gratson 1988, Sedinger 1997, Hagen et al. 2009).

As evidence from previous sensitivity analyses, the brood-rearing period is a survival bottleneck for lesser prairie-chickens and other grouse (Hagen et al. 2009, McNew et al. 2012). Successful passage through this vulnerable period is enabled with abundant high quality forage during the summer growing season (Wise 1982, Bergerud and Gratson 1988). Food may also be particularly important during winter as evidenced by strong evolutionary processes that have shaped the digestive systems of grouse and, potentially, the divergent migratory behavior of several birds (Sedinger 1997). For these reasons, I predict that food availability may most limit lesser prairie-chicken populations during the brooding and winter periods.

To eventually estimate the effects of food availability on populations, a stronger foundational understanding of foods used during these critical periods is needed. Particularly, in the under examined northern extent of the lesser prairie-chicken range, which supports ~2/3 of the extant population (McDonald et al. 2015, Garton et al. 2016). Therefore, my primary objective was to quantify arthropod and plant taxa consumed by lesser prairie-chickens during the brooding period and winter using a DNA metabarcoding approach combined with vegetation and arthropod survey data collected among 4 study sites in Kansas and Colorado. I predicted that of available food items, a few specific plant foods will dominate diets of lesser prairie-chickens during winter and arthropods will be used based upon availability during the brooding period, but will be predominantly grasshoppers (Orthopterans). I also predicted that chicks would be restricted to smaller arthropod prey of limited mobility following optimal foraging theory (Suminski 1977, Sih and Christensen 2001). I expected to be able to identify foods consumed to the genus level using plant and arthropod sequences extracted from fecal samples through DNA metabarcoding.

Methods

Study Area

The study area encompassed the northern extent of the lesser prairie-chicken distribution in Kansas and Colorado and included 4 study areas spread among the Mixed-Grass Prairie (Red Hills, Clark), Short-Grass Prairie/CRP Mosaic (Northwest), and Sand Sagebrush Prairie (Colorado, Clark) Ecoregions (Figure 3.1, McDonald et al. 2014). However, much of the Colorado study site within the Sand Sagebrush Prairie ecoregion was predominantly comprised of Conservation Reserve Program grasslands on the border of Prowers and Baca counties. Dominant grasses, forbs, subshrubs, shrubs, mean annual precipitation, and soil texture varied

among study sites (Table 3.1). For example, subshrubs (e.g., *Gutierrezia sarothrae, G. dracunculoides*) were more abundant than forbs in Northwest Kansas and more abundant than shrubs at the Red Hills study site (Table 3.1). Forbs were predominantly *Salsola tragus* and *Kochia scoparia,* which comprised 2 of the top 3 most abundant forbs at all sites excluding the Red Hills.

 Sample Collection

I collected fecal samples from marked lesser prairie-chickens during the brooding period (May – September) and winter (November – March). Lesser prairie-chickens were captured at leks at all study sites between early March and mid-May using walk-in funnel traps and drop nets (Haukos et al. 1990, Silvy et al. 1990). Upon capture, lesser prairie-chickens were sexed based on plumage coloration, pinnae length, and tail pattern (Copelin 1963). I marked female lesser prairie-chickens with either a 15-g very-high-frequency (VHF) transmitter or 22-g global-positioning-system (GPS) satellite PTT transmitter. I obtained locations for each VHF-marked female 3–4 times a week whereas 8–10 GPS locations/day were obtained from each GPS-marked female, contingent on available daily solar energy. GPS locations were recorded every two hours during the day with a six-hour gap between 2300 and 0500. I prepared protocols and obtained collection permits to capture and handle through the Kansas State University Institutional Animal Care and Use Committee protocols #3241 and #3703, Kansas Department of Wildlife, Parks, and Tourism scientific collection permits SC-042-2013, SC-079-2014, and SC-001-2015 and the Colorado Parks and Wildlife scientific collection license numbers 13TRb2053, 14TRb2053, and 15TRb2053.

I collected fecal samples from marked hens and chicks (separate vials for each) during brood capture and during weekly flush counts occurring within an hour of sunrise (2–98 days

old). Fecal samples were classified as chick and adult samples by size differences. During

winter and early spring (December–March), I collected fecal samples (≥1 pellet) at roost sites.

Fresh fecal samples that appeared to have been dropped the previous night were placed in Fisher

20-ml vials using small plastic sampling spoons to minimize DNA contamination. Vials labeled

with the date, unique bird ID, and coordinates of the collection location were stored in a freezer

at field sites and Kansas State University before being shipped frozen overnight to the

Cooperative Institute for Research in Environmental Sciences, University of Colorado, for DNA

analyses.

 Sequencing

I extracted genomic DNA from fecal samples using the MoBio PowerSoil htp-96 well

Isolation Kit (Carlsbad, CA). For arthropods, a fragment of the Folmer region of the

Cytochrome oxidase I (COI) gene was amplified using arthropod-specific primers (Bohmann et

al. 2011, Zeale et al. 2011). To determine the contribution of plants to diets, a portion of the

chloroplast trnL intron was PCR amplified from each genomic DNA sample using the c and h

trnL primers (Taberlet et al. 2007), but modified to include appropriate barcodes and adapter

sequences for Illumina multiplexed sequencing. The barcodes used were 12-bp error-correcting

barcodes unique to each sample (Caporaso et al. 2012). Each 25-µL PCR reaction was mixed

according to the Promega PCR Master Mix specifications (Promega Corporation; Madison, WI),

with 2 µL of genomic DNA template. For trnL, the thermocycling program used an initial step

at 94° C for 1 minute, a final extension at 72° C for 2 minutes and the following steps cycled 36

times: 1 minute at 94° C, 30 seconds at 55° C, and 30 seconds at 72° C. For COI, the

thermocycling program used an initial step at 94° C for 5 minutes, a final extension at 72° C for

10 minutes and the following steps cycled 45 times: 30 seconds at 94° C, 45 seconds at 45° C,

and 45 seconds at 72° C. Amplicons from each sample were cleaned and normalized using SequalPrep Normalization Plates (Life Technologies, Carlsbad, CA) prior to being pooled together for sequencing on an Illumina MiSeq (Illumina Inc.; San Diego, CA) running the 2 x 150bp chemistry.

 Assignment of Reads to Arthropod Genera

For COI reads indicating arthropod taxa, sequences were demultiplexed using 'prep_fastq_for_uparse.py' (https://github.com/leffj/helper-code-for-uparse). Read 2s were used for downstream analysis due to higher quality scores. Sequences were filtered and Operational Taxonomic Unit (OTU) picking was performed using the UPARSE pipeline (USEARCH 7). Quality filtering included trimming sequences to the expected amplicon length (158 bp – only for 250 bp length reads), filtering by quality score (maxee value of 1.5), removing sequences below the minimum expected amplicon length (90 bp), and removing singletons. Sequences were clustered de novo at 99% similarity for OTU picking. Taxonomy assignment to genera was performed in QIIME, using the hierarchical naïve Bayesian classifer RDP, retrained with a custom reference database curated from the Bar Code of Life Database (v3). Taxonomy was assigned at 99% similarity, with a 50% confidence threshold. Sequences were then further filtered to remove non-arthropod sequences by removing sequences that were not resolved to at least the family level. All samples with <10 COI reads were excluded from analysis for arthropods in diet.

For each sample, I calculated the percentages of all sequences assigned to a given OTU for each sample. This is referred to as RRA (Relative Read Abundance; Kartzinel et al. 2015). For COI, an average of 9.67% of all sequences were matched to genera in the order Diptera, almost exclusively during summer. Due to observations of contact between fecal material and

Dipterans, I assumed that Dipteran DNA entered fecal material through secondary contact after defecation and before collection. Therefore, I excluded all Dipteran reads from analyses. I limited assignment of OTU to genera present among all study sites as estimated from arthropod sweep net survey (see details below).

Arthropod Availability

I constrained assignments to genera available for consumption in western Kansas and eastern Colorado. To sample available arthropod prey, I used sweep-net surveys at brood locations from May to August in 2013 and 2014. Sweep netting is an efficient method to sample a wide array of invertebrate species (Yi et al. 2012). At sites where fecal samples were collected and at nearby random locations, three 100-sweep surveys were conducted moving north-to-south passing along 3 parallel transects 10 m apart with the center transect passing directly through the bird location. I restricted DNA metabarcoding assignments to genera that were sampled during arthropod sweep net surveys among all sites. I did not make comparisons among biomass of arthropods in sweep nets and diets (resource selection) at the genera resolution due to potential biases among available species at the genera resolution (Spafford and Lortie 2013). However, I did make comparisons among cumulative biomass (g) of arthropod orders (broader taxonomic resolution) at study sites to help explain differences in diets among sites.

Spatial and Temporal Influence on the Consumption of Arthropods

After RRA was estimated for all arthropod (COI) reads indicative of potential foods available in the study area. I then summed arthropod genera specific RRA to estimate RRA at the order level. I assessed RRA data for multivariate normality using the Henze-Zirkler's normality test in the MVN package in the R statistical environment (Korkmaz et al. 2016, R core development team 2017). Prior to assessing normality, all RRA data were $\arcsin\sqrt{x}$ transformed

(Warton and Hui 2011). After assessing multivariate normality, I determined that no multivariate statistic approach was suitable for these data. Therefore, I identified the orders contributing the most to lesser prairie-chicken diets during the brood rearing period and winter, and then assessed these orders as single dependent variables.

To assess patterns in the orders contributing most to lesser prairie-chicken diets, I used a regression based on a parameterization of the beta distribution to examine differences among periods (brooding period and winter), age classes (chick and adult) during the brood-rearing period, and among study sites (Northwest, Red Hills, Clark, and Colorado; Ferrari and Cribari-Neto 2004). I developed boxplots to depict the median, 1st and 3rd quartiles, and maximum and minimum values of RRA for the 4 predominantly consumed orders at each site. After screening for differences among periods, site, and age classes, I used a multimodel inference approach to examine how difference in spatially and temporally related covariates influenced the composition of arthropods in the diet during the brood-rearing and winter periods separately. I examined these periods separately due to the differences in available foods based on phenology and because lesser prairie-chickens can use a greater abundance of arthropods in the brood rearing period than in the winter, regardless of the composition of arthropods consumed (Jones 1963).

Spatial covariates were based on the location of the fecal sample and included binary covariates (occurred in cover type = 1, otherwise = 0) for native grassland, Conservation Reserve Program grassland (CRP), and cropland. Also, included in the model set was landcover type as a categorical covariate with multiple levels including native grassland, CRP, and cropland as separate factors and a study site model having multiple levels (Northwest, Red Hills, Clark, and Colorado). Native grasslands referred to grasslands occurring on soil never previously tilled and

117

were typically maintained for cattle production. Temporally related covariates included Julian date, chick age in days, and age class during the brood rearing period (adult, juvenile). Julian date was set sequentially from 1, as the earliest date of bird use for a fecal sample collected, to the latest date of bird use for collected fecal samples in a period (brood rearing and winter). I conducted regression and performed multimodel inference using package 'betareg' (Zeileis 2016) and 'AICmodavg' (Mazerolle 2016) in R (R Development Core Team 2017).

After fitting beta distribution regression models, I screened for period, age, and site effects based on informative beta coefficients. Beta coefficients were considered informative if not overlapping zero at the 85% confidence interval (Arnold 2010). For multimodel inference, I ranked and selected the most parsimonious model based on AIC_c ; Akaike Information Criterion for small sample sizes, that also incorporated informative beta coefficients; Models with ΔAIC_c ≤ 2 were considered competitive (Burnham and Anderson 2002, Arnold 2010). Last, I developed boxplots to display variation in the 4 most predominantly consumed arthropod orders based on RRA.

Assignment of Reads to Plant Taxa and Functional Groups

For trnL, sequences were demulitplexed using a Python script available from: https://github.com/leffj/helper-code-for-uparse/blob/master/prep_fastq_for_uparse_paired.py. Paired end reads were then merged using fastq_merge pairs (Edgar 2010). Because merged reads often extended beyond the amplicon region of the sequencing construct, I used fastx_clipper to trim primer and adaptor regions from both ends (https://github.com/agordon/fastx_toolkit). Sequences lacking a primer region on both ends of the merged reads were discarded. Sequences were quality trimmed to have a maximum expected number of errors per read of less than 0.1 and only sequences with more than 3 identical

replicates were included in downstream analyses. BLASTN 2.2.30+ was run locally, with a representative sequence for each OTU as the query and the current NCBI nucleotide and taxonomy database as the reference. The tabular BLAST hit tables for each OTU representative were then parsed so only hits with >97% query coverage and identity were kept using the usearch7 approach (Edgar 2013, Craine et al. 2015). The National Center for Biotechnology Information (NCBI) genus names associated with each hit were used to populate the OTU taxonomy assignment lists. All samples with <50 trnL reads were excluded from analyses of trnL RRA (Kartzinel et al. 2015). I estimated OTU specific RRA and defined a representative genus for each OTU. Then I estimated genera specific RRA using the following Bayesian approach. I used the genera specific RRA when grouping RRA estimates of genera into functional groups. I assigned RRA to genera within operational taxonomic units using the equation (below).

$$RRA_{fg=i} = \left(\frac{I_{g=i}}{\sum_{\text{OTU}=i}(I_g)} \ X \ RRA_{OTU=i} \right)$$

I estimated an adjusted RRA for each functional group (RRA $_{fg=i}$) by dividing the identity value for each genus (I_g) by the sum of all identity values for all genera within each OTU. I then multiplied the quotient by the RRA estimated for each OTU (RRA$_{OTU=i}$). The adjusted RRA accounts for the probability that each read is from a particular genus among all OTUs that contained the genus. I limited plant genera within OTU to those detected during extensive vegetation surveys among sites (Table A3.1).

For trnL, an average of 4% of sequences was from *Pinus* (range = 0 – 51%). Due to the unlikelihood of *Pinus* biomass being consumed and the presence of Pinus DNAs in the blanks, the one OTU that matched with *Pinus* species were removed from the dataset. For trnL, among the top 10 OTUs, OTU 23 did not match at 97% levels for coverage and identity for any species

119

in the NCBI database. However, OTU 23 matched at 100% coverage and 95% identity with a *Chenopodium* species and was considered a species similar to *Chenopodium* for the purposes of this study.

 Functional Group Assignments

Because OTUs often encompassed multiple genera, I grouped RRA from different plant genera into functional groups including forbs, shrubs, subshrub (mostly *Gutierrezia*), legumes, grass, crop (not including alfalfa), and alfalfa. Placing genera into each functional group presented challenges because the OTUs frequently encompassed genera indicative of multiple groups (see Results). Linking plant foods consumed to specific functional groups was necessary to allow for among site comparisons and make direct connections to utility of landscapes with an agricultural component. In some instances, OTUs that included genera related to both grass and crop as well as shrub and subshrub functional groups included repeat values and therefore, added values could surpass 100%.

 Plant Availability

To minimize the overlap of certain OTUs encompassing multiple functional groups, I combined DNA metabarcoding inference with telemetry and extensive plant survey data to gain a better understanding of female lesser prairie-chicken diets in the northern extent of their range. I created home ranges encompassing the previous 48-hour period visited by each individual lesser prairie-chicken. I used minimum convex polygons for GPS-marked and buffered VHF-marked bird locations in ArcGIS 10.2 by maximum moved distance by GPS-marked birds during the 48-hour period. Home ranges were estimated separately for each GPS-marked bird and separately for VHF birds during the nonbreeding season and brooding data collection periods. For example, I created a minimum convex polygon encompassing the 48 hours prior to fecal

120

sample collection for GPS birds. Then I calculated the maximum distance moved among all GPS-marked birds during the nonbreeding and brood-rearing period. I used maximum distances to buffer sampled locations for VHF birds during each season respectively. A 48-hour home range was used because it should encompass the spatiotemporal foraging extent incorporated into the fresh fecal sample. The 48-hour home interval encompass a 9.9 hour fluid retention in rock ptarmigan (*Lagopus muta*), while providing enough locations to ensure visitation of foraging locations (Stevens and Hume 1998). I excluded dispersing birds with straight line movements >5 km from home range size estimates.

In addition to constraining potential plant foods to species available within landcover used in the previous 48 hours. I limited native plant food availability to those genera detected during point-step transects among all study sites (Table A3.1). At each study site, user-defined habitat patches were delineated and digitized in ArcGIS 10.2 using aerial imagery from the Bing aerial basemap layer (product of: ESRI, i-cubed, USDA FSA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGP). Patches were identified as areas of homogenous vegetation >2 ha in size, placed in categories (e.g., grassland, grassland. lowland, or CRP), and confirmed upon ground truthing. Within each patch, three 250-m point-step transects were conducted. Each point-step transect involved identifying the plant species for each pace (Evans and Love 1957). All delineated patches were surveyed during summer for each study site and 20% of patches using a stratified random sample approach were surveyed during the fall and winter to encompass changes in plant food availability throughout the year. In addition, I used occurrence of cultivated foods (row-crops, alfalfa) within an individual's home range to determine if a bird had access to cultivated foods. I excluded cultivated crops as potential food items if there were no croplands in the 48-hour home range. After accounting for the availability of crop and shrub

121

foods to each individual based on 48-hour home range, I adjusted RRA to reflect availability by adding functional group possibilities. I did not account for the availability of forbs and grasses because they were ubiquitous throughout all study areas and cover types.

Spatial and Temporal Influence on the Consumption of Plants

After RRA was estimated for all plant functional groups (e.g., forbs, shrub, subshrub, legume, grass, and crop), I assessed RRA data for multivariate normality using the Henze-Zirkler's normality test in the MVN package in the R statistical environment (Korkmaz et al. 2016, R core development team 2017). Prior to assessing normality, all RRA data was $\arcsin\sqrt{x}$ transformed (Warton and Hui 2011). After assessing multivariate normality, I determined that no multivariate statistic approach was suitable for these data and focused on univariate variation of specific functional groups among spatial and temporal factors.

Similar to methods above I used package 'betareg' to examine differences between periods (brooding period and winter) and among study sites (Northwest, Red Hills, Clark, and Colorado; Ferrari and Cribari-Neto 2004). Then, I used a multimodel inference approach to test how differences in spatially and temporally related covariates influenced the composition of functional groups in the diet during the brood-rearing and winter periods separately.

I used the same spatially related covariates mentioned earlier including CRP, native grassland, crop, alfalfa, and landcover type. Temporally related covariates included Julian date, and quadratic effect of Julian date. I expected that the composition of functional plant groups may change later in the brood-rearing period and plant composition of winter diets may change as only the most persistent shrub and crop-based foods may remain available during the coldest portions of winter. I conducted regressions and performed multimodel inference using package 'betareg' (Zeileis 2016) and 'AICmodavg' (Mazerolle 2016) in R (R Development

122

Core Team 2017). I followed the same multimodel inference protocol based on AIC_c and informative beta coefficients (85% confidence interval) described earlier (Burnham and Anderson 2002, Arnold 2010).

Evaluation of Sampled Taxonomic Richness

To examine if sample sizes were sufficient to detect all arthropod and plant foods used by lesser prairie-chickens at each study site, I used species accumulation curves. Species accumulation curves depicted the relationship between number of OTUs and number of fecal samples. Species accumulation curves were generated in the R package vegan with the specaccum function using the Lomolino function to describe the curves (Oksanen et al. 2015). From the function, I estimated an asymptote and the number of OTU achieving a mid-point of the asymptote. I also estimated extrapolated species richness using poolaccum within package 'vegan' following Chao (1987).

Factors Influencing Detection of DNA

Last, to improve the design of future DNA metabarcoding studies, I used a logistic regression approach to identify covariates that influenced the detection of DNA. I modeled the detection of either plant or animal, plant, and animal DNA as separate response variables in different model sets. Models tested the detection (1) or nondetection (0) of DNA to the following covariates: period (brood rearing, winter), date, exposure (number of days after use that the fecal sample was collected), maximum temperature (tmax), chick (chick or adult), daily precipitation, cumulative 2 day precipitation, cumulative 7 day precipitation, study site, nest (fecal sample collected at nest site), and cecal dropping (yes or no). I created single variable models for each covariate and assessed one model with an interaction between period and exposure based on an *a priori* prediction that DNA would degrade more quickly during the

123

summer brooding period than during winter. Models were ranked based on AIC_c then coefficients from the top-ranking models were examined for informative beta coefficients (overlapping 0 at the 85% confidence interval). Top ranking models having beta coefficients not overlapping zero were then plotted and estimates of detection probability were generated.

Results

A total of 314 fecal samples were collected from females during the brood-rearing period ($n = 211$) and winter ($n = 103$) of 2014–2015. Number of samples collected varied by site and season (Table 3.2). Among all sites and seasons, readable animal DNA was obtained from 96 of the 314 samples and readable plant DNA was sequenced in 152 of the 314 samples. A total of 334 plant and arthropod OTUs (unique DNA groupings) were identified among all fecal samples. Among the 96 samples that produced at least 10 COI sequences (Arthropod DNA), there was an average of 376 sequences per sample. Among the 152 samples that produced at least 50 trnL sequences (Plant DNA), there was an average of 4,591 sequences per sample.

Arthropods

A total of 75 arthropod OTUs were identified in diets of lesser prairie-chickens using COI analyses. Results from OTUs encompassed 5 classes including Insecta (63), Arachnida (9), Collembola (1), and Malacostraca (1). Among these 5 classes, 12 different orders and 50 families were represented. Twenty-eight of the genera were Lepidoptera, 7 Araneae, and 6 Hemiptera (Table A 3.2). On average, 35% of the RRA was from Lepidoptera, 26% from Orthoptera, 14% from Araneae, and 13% from Hemiptera (Figure 3.2).

Arthropod communities, based on sweep-net transects, varied among sites. Orthoptera had the greatest percent biomass among taxa at each site (Clark = 90.2%, Red Hills = 71.5%, Northwest = 73.1%, and Colorado = 46.5%) followed by Lepidoptera, Phasmatodea, and

Coleoptera (Figure 3.3). Lepidopterans comprised >2 times more of the arthropod community biomass in Northwest and Colorado sites in comparison to the Clark and Red Hills study site.

Spatial and temporal influence on the consumption of arthropods.— Multivariate data were not normally distributed (HZ = 6.76, $P < 0.001$). The non-normality of these data and limited sample sizes precluded my ability to test for multivariate differences among period, age, site, and landcover. Instead I focused on differences in the main prey items (Lepidoptera, Orthoptera, Araneae, and Hemiptera) using beta distribution regressions. I found no differences among Lepidoptera, Orthoptera, Hemiptera, and Araneae composition in diets during the brooding period and winter (winter $\beta = 0.054 \pm 0.303$, 0.269 ± 0.293, 0.210 ± 0.265, -0.265 ± 0.279). However, the amount of Araneae consumed decreased in the winter (winter $\beta = -0.265 \pm 0.279$).

Chick and adult diets during the brood-rearing period did not differ in consumption of Lepidoptera, Orthoptera, Araneae, and Hemiptera (chick $\beta = 0.013 \pm 0.403$, 0.205 ± 0.386, 0.122 ± 0.388, -0.199 ± 0.370). Beta regressions also suggested no differential consumption of foods by age for Lepidoptera, Orthoptera, Araneae, and Hemiptera (age of chick days $\beta = -0.004 \pm 0.00779$, 0.00732 ± 0.00788, -0.000999 ± 0.007839, -0.00218 ± 0.00700). However, there was indication of more complicated nonlinear trends in the consumption of Lepidoptera and Orthoptera with minimal use of Lepidoptera after 40 days in age and greater consumption of Orthoptera when chicks surpass 40 days in age, which warrants further investigation (Figure 3.4).

I found limited evidence of difference in the composition of arthropod foods in the diets of lesser prairie-chickens among periods and ages but this does not indicate that lesser prairie-chickens consume the same number of arthropods in the winter as in the summer. Instead, it

indicates that of the arthropods consumed by lesser prairie-chickens, composition of

Lepidoptera, Orthoptera, and Hemiptera remains similar. The lack of variation among periods

and ages is further indicated by stronger model support for landcover and site based covariates

which suggest that variation in arthropod diet consumption is more influenced by spatial

characteristics than temporal factors (Tables 3.3 and 3.4). The combined effect of spatially

related covariates in predicting the composition of each order during both brood rearing and

winter carried an average model weight of 72% (Tables 3.3 and 3.4). However, juliandate

carried 86% of the model weight for Othroptera during winter.

Spatial variation in dietary composition was indicated by RRA among sites during brood

rearing when birds from Northwest consumed 1.9 times more Lepidoptera than birds at Clark

($41.6 \pm 8\%$ vs. $21.7 \pm 10\%$, mean RRA $\pm$ SE, respectively; $\beta = 0.691 \pm 0.401$, Figure 3.5). In

contrast, birds from Northwest consumed 5.5 times less Orthoptera than Clark birds ($36.4 \pm 10\%$

vs. $6.56\% \pm 4.1\%$, respectively; $\beta = -0.782 \pm 0.390$).

During the brood-rearing period, presence of native grassland had the greatest influence

on arthropod diet composition. The contribution of Lepidoptera in diets during the brood-rearing

period decreased in native grasslands (native grassland $\beta = -0.657 \pm 0.405$, Table 3.4).

Consumption of lepidopterans was 2.12 times less in native grassland in comparison to cropland

($23.2 \pm 6.00\%$ vs. $49.2 \pm 11.8\%$, Figure 3.6). Similarly, the categorical native grassland

covariate was the best predictor of the consumption of Araneae based on AIC_c and the beta

coefficient did not overlap zero at the 85% confidence interval (native grassland $\beta = 0.559 \pm$

0.379, Table 3.4). Araneae contributed 65 times more to arthropod foods in native grasslands

than in other cover types and Araneae was rarely consumed in cropland ($26.2 \pm 7.02\%$ vs. 0.04

$\pm 0.004\%$, Figure 3.6). For Orthoptera, the model including a native grassland categorical

126

covariate was the top ranked model and the beta coefficient was informative (native grassland β = 0.585± 0.366, Table 3.4). In native grasslands, Orthoptera contributed 2.4 times as much to diet as in other cover types (21.7 ± 6.50% vs. 10.7 ± 6.71%). Hemiptera appeared to contribute more to diets of birds using CRP grasslands and native grassland than using cropland; however, the beta coefficient predicting Hemiptera consumption in grassland overlapped zero at the 85% confidence interval (Figure 3.6).

In winter, Lepidoptera, Orthoptera, and Hymenoptera contributed most to arthropod based food for lesser prairie-chickens (Figure 3.2). Of the top four orders contributing to winter diets, Orthoptera was the only order that changed (decreased) as the winter progressed from 21 November 2014 and was significant at the 85% confidence interval (Julian date β = -0.035 ± 0.0131, Table 3.4). Among sites, Clark birds had greater percentages of Orthoptera in their winter diet than all other sites and was significant at the 85% confidence interval (51.7 ± 12.6% in Clark vs. 18.3 ± 7.7% in Colorado vs. 0% in Red Hills and Northwest, Clark β = 1.86 ± 0.613).

Plants

Metabarcoding of fecal samples indicated that lesser prairie-chickens consumed foods encompassing 2 classes (Magnoliopsida and Liliopsida), 19 orders (predominantly Asterales, Poales, and Fabales), 30 families, and 90 genera. A total of 235 OTUs were found to represent at least 1% of the plant diet for a given bird at a given time. In contrast to the assignment of OTU to specific arthropod taxa, trnL OTUs were not genera specific and on average were comprised of 4.15 ± 4.79 genera and ranged from 1 to 28 potential genera that were present at all study sites combined. Of the 235 recorded OTUs, 70 represented at least 10% of the diet for at least one of the samples. The most abundant OTUs were from species in genera similar to *Ambrosia* (27%

OTU specific RRA of all reads) followed by species in genera similar to *Latuca* or *Taraxacum* (10%), *Medicago* (6%), and *Triticum* (5%).

For the brood-rearing period, the 10 most abundant OTU included species similar to *Ambrosia* (16.2%), *Latuca* (8.5%), *Triticum* (5.5%), *Chenopodium* (4.3%), *Physalis* (3.9%), *Commelina* (3.1%), *Trifolium* (1.8%), and *Elymus* (1.4%). *Ambrosia* and *Triticum* were represented by two separate OTUs as part of the top 10 most abundant summer OTU foods. During winter, the 10 most abundant OTUs consumed included species similar to *Ambrosia* (21.0%), *Latuca* (5.6%), *Medicago* (4.8%), *Triticum* (4.4%), *Bromus* (1.1%), *Oenothera* (0.9%), *Elymus* (0.7%), *Sorghum* (0.6%), and *Chenopodium* (0.6%). *Triticum* was represented by two separate OTUs as part of the top 10 most winter OTUs.

Although DNA metabarcoding provided some indication of most likely consumed plant genera when combined with vegetation surveys, the inclusion of multiple genera within OTUs precluded further analyses at the genera resolution. It should be noted that there are other genera similar to the representative genera listed above that also contributed to the percent estimates. However, based on the literature and availability at the study area, I suggest the genera listed above were the most likely consumed forage. All further analyses involved genera aggregated into functional groups.

Functional Groups.— Placing OTUs into functional groups (forb, shrub, subshrub, grass, crop, legume, and alfalfa) presented challenges because some OTUs contained genera that could be assigned to multiple groups. For example, 17/33 OTUs that identified either grass or crop foods included both crop and native grass genera (e.g., *Triticum* and *Elymus*); 2/45 OTUs of genera including shrub, subshrub, and forb species included representatives of >1 functional group (e.g., *Artemisia* and *Ambrosia*); and 1/5 OTUs for genera of legumes included both

cultivated and native species (e.g., *Medicago* and *Vicia*). To overcome functional group overlap within OTUs, I constrained use of crop and shrub foods to instances when each land cover type occurred within 48-hour home ranges. Home ranges (48-hour) averaged 45.06 ± 44.50 ha during the nonbreeding season and 11.17 ± 8.84 ha during brood rearing for GPS-marked birds. I then used the maximum size home ranges of nondispersing GPS-marked individuals during each time period to estimate home ranges for VHF-marked lesser prairie-chickens. Home ranges for VHF birds were derived from the higher resolution GPS-marked bird data because locations were obtained frequently enough to generate 48-hour home range. Max home range size during the nonbreeding and brooding period was 191.52 ha and 32.83 ha, respectively, from which, I derived 781-m and 323-m buffer distances around VHF fecal collection locations to account for all potentially used food sources.

A Henze-Zirklers multivariate normality test indicated the data were not normal ($HZ = 12$, $P < 0.001$) at the functional group specificity. I subsequently examined average contributions of individual functional groups during the brood-rearing and winter periods. Then, I assessed variation among sites and landcover types.

In both the brood-rearing and winter period, forbs were the predominant plant-based food source (winter $53.7 \pm 3.7\%$, brooding $60.67 \pm 5.5\%$; Figure 3.7). Differences in the overall use of functional groups among the winter and brood rearing periods were minimal. However, during winter, subshrub plants (e.g., *Gutierrezia* spp.) and grasses contributed 1.5 times ($43.4 \pm 3.7\%$ vs. $29.8 \pm 5.7\%$) more to lesser prairie-chicken diets than during brood rearing (winter $\beta = 0.564 \pm 0.220$, 0.287 ± 0.195). In contrast, there was no difference in the consumption of forbs, legumes, shrubs, crops between periods (brooding $\beta = 0.198 \pm 0.230$, -0180 ± 0.209, 0.222 ± 0.175, -0.265 ± 0.185 respectively).

129

I assessed differences among all sites for winter and brood rearing combined and separately for each period. When the brood rearing and winter periods were combined, the composition of forbs, grasses, and legumes in the diet did not differ among sites. All site-specific (Northwest, Red Hills, Clark, Colorado) beta coefficients predicting forbs, grass, and legume composition were uninformative. However, use of shrubs was greater at the Red Hills than at all other sites (Red Hills $\beta = 1.13 \pm 0.358$), use of crops was greater in Colorado than at other sites (Colorado $\beta = 0.4694 \pm 0.257$), and the use of subshrubs was greater in the Red Hills than at other sites (Red Hills $\beta = 0.8624 \pm 0.369$).

Within the brood rearing period alone, foods in the forb, grass, and legume functional groups did not differ among sites. Shrub and sub shrub based foods contributed more to diets during the brood rearing period in the Red Hills and Northwest Kansas compared to Clark and Colorado ($\beta = 1.82 \pm 0.782$, 0.769 ± 0.430, 1.22 ± 0.779, 0.836 ± 0.4445). Crop-based foods provided a greater contribution to brood-rearing diets in Colorado compared to other sites ($\beta = 3.67 \pm 0.509$).

During winter, grass composition varied among sites with more grasses consumed during winter at the Northwest study site compared to the Clark study site ($23.0 \pm 2.6\%$ vs. $11.0 \pm 1.7\%$; $\beta = 0.855 \pm 0.289$; Figure 3.8). Shrub foods contributed more to foods at the Red Hills study site in winter than in Clark ($\beta = 0.908 \pm 0.391$). Crop foods contributed more to diets at the Northwest site during winter than in Clark ($\beta = 0.443 \pm 0.288$). Last, subshrub foods contributed more to diets in Northwest and Red Hills study sites during winter compared to Clark ($\beta = 0.836 \pm 0.445$, 1.22 ± 0.779 respectively); interestingly, *Gutierizza* spp. were more abundant at these two sites (Figure 3.8). In summary for winter diets, forbs were predominantly

130

consumed among all sites, legumes contributed more to diets at the Clark field site; whereas, use of cultivated foods was greatest at the Northwest study site.

After screening for differences among periods and sites. I focused on winter diets using a multimodel inference approach because lesser prairie-chickens predominantly consumed plant material during this period. The functional group composition of winter plant foods was best predicted by spatially related covariates within winter. Models including spatially related covariates carried on average 99% of model weight (AIC$_c$ weight, Table 3.5). The top-ranking predictor for forb diet composition was the occurrence in alfalfa and crop fields (Table 3.5). Forbs were consumed less in winter by lesser prairie-chickens using alfalfa fields and crop fields in general (β = -1.57 ± 0.467; identical betas for alfalfa and crop). Forbs were more readily consumed in native grassland and CRP (Figure 3.9). The proportion of grass in diets was best predicted by site (Table 3.5; see differences above) with use of native grassland ranking second among models (native grassland β = 0.386 ± 0.238). For legumes, birds using alfalfa and crop fields had the greatest composition (β = 4.60 ± 0.507; identical betas for alfalfa and crop). All fecal samples collected in cropland were collected in cultivated alfalfa which confirms that birds can use alfalfa fields in the winter as a food source. Shrubs contributed more to the diets of lesser prairie-chickens using native grassland (native grassland β = 1.55 ± 0.254; Table 3.5). The relative diet composition of subshrub appears to be most strongly influenced by use of alfalfa and crop fields with consumption of subshrub lower in each (β = -1.38 ± 0.454; identical betas for alfalfa and crop).

Evaluation of Sampled Taxonomic Richness

Among all sites, the arthropod species accumulation curve achieved an estimated asymptote at 156 OTUs suggesting I did not sample all the available forage; the mid-point for

131

achieving an asymptote was estimated at 105 fecal samples (Figure 3.10). The extrapolated species richness at the OTU level based on Chao (1987) was 101. The plant species accumulation curve achieved an estimated asymptote at 282 OTUs suggesting I sampled nearly all used plant forage at the OTU level. The mid-point for achieving the asymptote was estimated at 17 fecal samples (Figure 3.10). The extrapolated species richness at the OTU level based on Chao (1987) was 262.

Factors Influencing the Detection of DNA

The most parsimonious model to explain the detection and nondetection of DNA among samples included the period by exposure interaction (Table 3.6). The interactive model suggested that detection of DNA increased in the winter months (winter $\beta = 4.89 \pm 1.12$) and decreased with longer periods of exposure (exposure $\beta = -0.070 \pm 0.078$) on trends alone. However, the interactive term was inestimable. Therefore, the top ranked model with an informative beta was based on period alone where the probability of detecting DNA in a fecal sample was greater during winter (0.981 ± 0.028) compared to during the brood-rearing period (0.403 ± 0.033) for both plant and arthropod DNA combined.

The top model for the detection of arthropod DNA included chick (adult or chick) as a categorical covariate (Table 3.6). The chick model had an AIC_c weight of 1.00; however, the beta estimate overlapped 0 at the 85% confidence interval. All the other models also failed to produce an informative beta coefficient.

I found a similar pattern for the detection of plant DNA alone in which the probability of detecting plant DNA increased during winter. However, in contrast to the detection of either plant or arthropod DNA being best explained by period, detection of plant DNA was best explained by a quadratic date model (Table 3.6). The plotted quadratic model indicated that

132

detection probability varied from nearly 1 during winter to <0.25 during the summer. This pattern may not purely be a product of detection because lesser prairie-chickens, especially chicks, are known to consume more arthropods during summer brood rearing (Jones 1963, Haukos and Zaveleta 2016). Regardless, it appears that the plant DNA is less likely to be extracted from fecal samples collected during warmer summer days, which was further indicated by the model using maximum temperature as a covariate (tmax β = -0.096 ± 0.011).

I examined DNA in 4 ceccal droppings to assess if the greater digestive potential and if the hypothesized catabolism of proteins might degrade DNA contents. The limited sample size precluded use in a logistic regression; however, I detected plant DNA in ¾ of the samples but no arthropod DNA. The three detections were collected during winter and the 1 ceccal dropping for which no readable DNA was extracted was collected during the summer.

Discussion

Using a combination of tools including DNA metabarcoding of fecal samples, telemetry data, and local plant and arthropod surveys, I identified foods consumed by lesser prairie-chickens among 4 study sites where available food items differed. The DNA metabarcoding approach was successful at identifying plant food matter to OTU containing ~4 genera on average and identified arthropod foods to genus using Bayesian classifier methods. Reliable plant DNA was obtained from ~1/2 and reliable arthropod DNA from ~1/3 of the collected fecal samples. Overall, lesser prairie-chickens in the northern portion of their range largely consumed forb species during winter and used arthropods from families Orthoptera and Lepidoptera during the brood-rearing period. Diets of chicks and adults did not differ during the brood-rearing period. However, chicks may transition from a lepidopteran dominated diet to one predominantly Orthopteran as they age to 90 days old.

In landscapes having a row-crop agriculture component, lesser prairie-chickens largely used alfalfa when available during winter and females and chicks, unexpectedly, preyed mostly on lepidopteran foods during brood rearing (likely larvae). Of the DNA reads of Lepidopteran foods, most were similar to two genera (*Euxoa* and *Dargida*) that are largely comprised of agricultural pest species (i.e., cutworms), providing evidence of a direct ecological service provided by lesser prairie-chickens in landscapes with a cropland component. The use of shrub-based foods varied among sites, but is likely not as important as in other grouse species in other regions (e.g., sand shinnery oak prairie) and may differ from historic studies due to woody encroachment.

Arthropods in Lesser Prairie-Chicken Diets

The predominant consumption of Lepidopteran food sources during both brood-rearing and winter was unexpected. The greater consumption of Lepidoptera in this study compared to past research is likely a product of both the limited detection of soft bodied prey using traditional methods and inclusion of study sites having a strong row-crop agriculture component. Lesser prairie-chickens are known to use lepidopteran larvae food sources; however, most literature suggests a minimal consumption of Lepidoptera in comparison to Orthoptera (Davis et al. 1980). The traditional use of fecal dissection may not be effective in detecting Lepidopteran larvae (e.g, caterpillars). No study using this method identified Lepidoptera as a prey item for lesser prairie-chickens (Jones 1963, Doerr and Guthery 1983). Only studies that examine crop contents have reported consumption of lepidopteran larvae (Crawford and Bolen 1976, Suminski 1977, Smith 1979, Davis et al. 1980, Riley et al. 1993). However, not all studies examining crop contents have explicitly identified Lepidoptera as a food item and foods from the order may be clumped as "other insects" (Olawsky 1987); making comparisons among other studies challenging.

Regardless, the soft bodied nature of caterpillars likely makes them easier to digest and subsequently harder to detect using traditional dissection approaches (Trevelline et al. 2016). DNA metabarcoding may be the least biased tool for comparing dietary composition among soft and hard bodied prey, however, the method is not free of error or bias.

In addition to palatability, use of Lepidopteran larvae during the brood-rearing period may be related to the ease of capture by a small, ~15-g chick. Lepidopteran larvae (caterpillars and moths) would be easy for lesser prairie-chicken chicks to obtain when occurring within reach on the ground or in shorter vegetation. Although I did not expect a greater consumption of Lepidoptera than Orthoptera by lesser prairie-chicken chicks, I predicted that chicks would be restricted to smaller arthropod prey of limited mobility following optimal diet theory (Suminski 1977, Sih and Christensen 2001). The use of lepidopteran larvae by lesser prairie-chicken chicks supports this prediction. The potential selection for caterpillars further identifies the necessity of matching life histories among predator and prey; suggesting that the life history strategies of arthropod species may largely determine their importance as a prey item.

Although Lepidoptera was used as a food source among all landcover types and sites, specific genera, within Lepidoptera, were used in agricultural landscapes. In landscapes with an agricultural component, diets of lesser prairie-chickens during the brooding period were largely supported by the genera *Euxoa* and *Dargida*. These two genera included several known agricultural pest species including army cutworms (*Euxoa auxiliaris*). Consumption of agricultural pests provides evidence of one ecological service provided by lesser prairie-chickens that may be of considerable importance to gaining conservation support in the private working landscapes throughout their range (Wenny et al. 2011). Crawford and Bolen (1976) also

135

detected the consumption of cutworms by lesser prairie-chickens during fall in fragmented sand shinnery oak prairie.

In contrast to the prevalent consumption of Lepidoptera among all study sites, the predominant use of orthopteran foods by lesser prairie-chickens is well supported by other published research (Jones 1964, Suminski 1977, Davis et al. 1980, Doerr and Guthery 1983). The difference in predominant foods (Orthoptera vs. Lepidoptera) may be a result of spatial variation among study areas in addition to potential biases in detecting soft bodied prey using traditional methods. Even within this study, I detected substantial variation in the diets of females and chicks among study sites. DNA reads from fecal samples in Clark County were predominantly assigned to Orthoptera in contrast to fecal samples from all other sites. The greater consumption of Orthopterans at the Clark study site could be driven by the limited availability of lepidopterans and a match with a concurrent increased abundance of *Melanoplus* spp. grasshoppers at the Clark site (Haukos unpublished data). The *Melanoplus* genera was the main genera of Orthopterans used as a food across all sites. At the Clark study site, *Melanoplus sanguinipes* was substantially more abundant and the roosting and morning basking of this species on bare ground may make them an easily obtainable prey item for lesser prairie-chickens (Haukos et al. unpublished data).

Unfortunately, there is no clear-cut landscape explanation as to why birds would consume more Orthoptera than Lepidoptera at the Clark site. Although the Clark site was composed of less cropland (14.2%) than the Northwest site (36%), the Red Hills site had even less cropland (8.9%) than Clark but orthoptera consumption was not greater (Robinson et al. in review). The greater consumption of Orthoptera by birds using grassland compared to cropland or CRP also does not provide any indication of difference in use of Lepidoptera vs. Orthoptera

in grasslands. Although Orthoptera composition was greatest in grasslands, the RRA of Orthoptera was nearly identical to that of Lepidoptera in native grasslands. Because RRA data are proportional among arthropod orders, an estimate close to 25% (split among 4 main foods) within one cover type would indicate that individuals using that cover type have more diverse diets. It appears that lesser prairie-chickens using native grasslands are consuming a more diverse arthropod diet, which contrasts with my hypothesis that lesser prairie-chickens would specialize on Orthopteran prey. In contrast, lesser prairie-chicken broods using native grasslands may be opportunistic predators when diets are assessed over 0-90 days in age.

It should be noted that classifying lesser prairie-chickens as opportunists or specialists is scale dependent (O'Neill 1989, Chase 2014). Lesser prairie-chickens could exhibit opportunistic foraging characteristics at broader temporal scales that emerge from specialized foraging among finer temporal intervals (King 1997). Although there is no definitive linear relationship to support this in my data, it appears that lesser prairie chickens may consume more Lepidoptera within the first three weeks of life and more Orthoptera when surpassing 60 days in age. The pattern may be nonlinear and is apparent based on locally weighted scatterplot smoothing. Interestingly, the smoothing regression produced no indication of change in diet based on Julian date alone. Based on these data, I predict that Lepidoptera are a preferred food for chicks during the first 21 days post-hatch in hopes of more rigorous examination in the future.

Understanding diets during the first 21 days of a lesser prairie-chicken's life may be crucial for understanding what drives overall population growth rates (Hagen et al. 2009, McNew et al. 2012, Lautenbach 2015). The 0–21 day-old period is a known survival bottleneck for grouse and the finite rate of population growth (λ) has been consistently shown sensitive to variation in survival during this bottleneck among prairie grouse, sage grouse, and other

137

galliformes (*Tympanuchus* spp.; Wisdom and Mills 1997, Hagen et al. 2009, McNew et al. 2012, Taylor et al. 2012, Sandercock et al. 2008). Food availability may be particularly important for survival through this life-stage as indicated by strong variation in the mass of chicks and observations of dead undepredated chicks (Lautenbach 2015). There is no documented demographic data relating foods to chick survival for prairie-grouse. Knowledge on the effects of food availability on chick survival is largely limited to inference from a closely related species (sage grouse) within the subfamily Tetraoninane. Sage grouse chick survival can increase with the availability of Lepidoptera, slender phlox (*Phlox gracilis*), and total forb cover (Gregg and Crawford 2009). The influence of food availability on chick survival may contrast with the remainder of a grouse's life when there is strong support that predation poses the greater survival risk (Bergerud and Gratson 1988). However, if food availability drives passage through the most influential life-stage and survival bottleneck, even if only lasting up to 21 days (first 7 days may be most influential, Lautenbach 2015), the influence of food availability may be paramount and materialize in population level trajectories at much broader scales. Ultimately, I expect that predation, thermoregulation, and starvation interact during this period to limit chick survival (McNamara and Houston 1987, Bergerud and Gratson 1988). Therefore, isolating a singular univariate factor is unlikely and challenging to quantify.

Comparative Nutrient Values of Lepidopterans and Orthopterans

At the nutrient level, Lepidopteran and Orthopteran foods both provide greater concentrations of protein than any plant-based foods (Lassiter and Edwards 1982, Savory 1989, Rumpold and Schluter 2013). Protein in arthropod foods is also likely more digestible than in plants (Stiven 1961, Savory 1989). On average, Orthopteran foods may provide a food source that is 61% protein and 13% fat whereas Lepidopteran are 45% protein and 27% fat (Sugimura et

138

al. 1984). However, there is variation among species and differences in digestibility of protein from chitin-rich grasshoppers and soft-bodied lepidopterans that may result in a similar assimilation of proteins from the two different foods amid differences in nutrient composition (Sugimura et al. 1984). Sugimura et al. (1984) estimated that 75% of the crude protein within soft-bodied earthworms (*Eisenia foetia*) was digestible in contrast to 61% of the protein in grasshoppers. Mineral and amino acid composition provided by the two families appear similar with a fair amount of variation among prey species (Rumpold and Schluter 2013). The strong selection of protein-rich invertebrate foods by prairie-chickens is likely driven by the need to develop pectoral muscles for flight and to help with thermoregulation. The strong selection, even among other grouse, further suggests that protein may be particularly important for lesser prairie-chickens (Savory 1989).

In addition to having high protein requirements, growing grouse may also be limited by the availability of specific amino acids. Meeting the minimum requirements for all essential amino acids, carbohydrates, fats, and minerals may be best achieved by consuming a balanced meal of various arthropods (Ramsay et al. 2003). A balanced diet was best achieved in native grasslands where lesser prairie-chickens used a diverse array of arthropod foods. Lesser prairie-chicken females and chicks not only consumed a relatively even proportion of Lepidoptera and Orthoptera in native grasslands, broods also consumed arthropods from the orders Araneae and Hemiptera on a regular basis. Overall, lesser prairie-chickens occupying native grasslands used a greater diversity of arthropod foods in comparison to birds using CRP grasslands and agricultural areas. Inclusion of Araneae in the diets of individuals using grasslands may be particularly important for fulfilling nutrient requirements. Araneae were nearly absent in fecal samples from croplands and CRP grasslands. The higher trophic level of Araneae has been

139

related to greater concentrations of otherwise limiting amino acids, especially taurine which has been associated with bile production and bone growth in young domestic chickens (Martin and Patrick 1961, Ramsay et al. 2003).

Pros and Cons of DNA Metabarcoding

The potential benefits of using DNA metabarcoding for understanding diets of wildlife species are numerous, but the current utility of the method hinges on ancillary data. I was unable to distinguish among potential plant foods that were from grass and crop functional groups using DNA metabarcoding alone. The addition of 48-hour home range data allowed for greater inference on the use of cultivated foods. Additionally, reference DNA sequences available through the NCBI provided plant sequences similar to those sequenced in fecal samples for many plant species that did not occur at any of the field sites. Without information of available food sources provided by concurrent vegetation and invertebrate surveys, predicted foods could be inaccurate.

Amplification of plant and arthropod DNA in 1/2 and 1/3 of the samples respectively may be a problem unique to lesser prairie-chickens and potentially other grouse species. For example, DNA was successfully amplified in all fecal samples from Louisiana waterthrush (*Parkesia motacilla)*, in 100% of bison (*Bison bison*) fecal samples, and 74% of fecal samples from bats (Bohman et al. 2011, Craine et al. 2015, Trevelline et al. 2016). The comparatively low percentage of reads detected in fecal samples may be a result of the well-developed digestive systems with larger cecae of lesser prairie-chickens, and other grouse, which are effective in acquiring needs from nutrient-poor foods (Moss 1983). Differences in the detection of reads was more strongly influenced by period of collection (brood rearing or winter) than study site or if the sample came from a grassland, CRP field, or agricultural area.

Plants

The predominant use of forbs as a food source during both brood-rearing and winter periods highlights the need for maintaining disturbance regimes that support healthy forb populations (Hagen et al. 2004). Among all sites, use of forbs differed from the predominant availability of grass in vegetative communities (on average 2.9 times more grass than forbs among 3 most dominant species). Forbs provided a critical habitat component for lesser prairie-chickens as food resources, even though they often comprised <10% of the available vegetation. Further, the abundance of preferred native forbs may be maintained at even lower compositions through the successful establishment of invasive forb species including *Salsola tragus* and *Kochia scoparia* at almost all sites (Beckie et al. 2012).

I detected greater RRA of forbs among brood rearing and winter, with specific forbs showing greater use during specific periods. During the brood-rearing period, forbs consumed by lesser prairie-chickens were largely from *Chenopodium-,* and *Abutilon*-like species. *Chenopodium album* (lamb's quarters) was abundant at all field sites during summer. The leaves of *C. album* are known to be palatable and high in calcium, which may be particularly important for growing lesser prairie-chicken chicks (Adedapo et al. 2011). The use of *Abutilon*-like species may be indicative of the consumption of *Callirhoe involucrate* (purple poppy mallow) or *Sphaeralcea coccinea* (scarlet globemallow) both of which were present at all sites and actively growing during the brood-rearing period (Haukos et al. unpubl. data). Leaves of *S. coccinea* are high in vitamin A, calcium, and protein and can be a preferred food of scaled quail (*Callipepla squamata*; Ault et al. 1983, Arthun et al. 1992). Although documentation of *C. involucrate* as food for grassland birds is limited, the plant is of adequate phosphorus and crude protein content to benefit white-tailed deer (*Odocoileus virginianus*; Everitt and Gonzalez 1981).

141

It also functions as a known larval host for gray hairstreak butterflies (*Strymon melinus*, butterfliesandmoths.org) and can be planted to attract butterflies (Fernandez-Canero and Gonzalez-Redondo 2010). Observations were made of several caterpillar larvae on the receptacles of *Callirhoe involucrate* flowers at the Clark study site during the brooding period (D. Sullins personal observation). In addition, *S. coccinea* is also a known larval host for several butterfly species as well (Scott 2014).

Outside of the brooding period, plant matter becomes particularly important in lesser prairie-chicken diets during winter and spring as available forage decreases, thermoregulatory needs are maximized, and stored energy becomes particularly important with the onset of lekking and nesting behavior (Haukos and Zaveleta 2016). Winter diets of grouse are often limited to only a few items that can provide sustenance and are typically high in fiber, low in nutrient content, and require longer digestive tracts to process (Moss 1983). In this study, the greater consumption of forbs compared to all other functional groups suggests a reliance on noncultivated foods in the lesser prairie-chicken range in Kansas and Colorado. Use of forbs by lesser prairie-chickens contrasts with grouse of more ancestral arctic and boreal origins that largely consume woody vegetation during winter (Schmidt 1936, Moss 1983, De Young and Wiliford 2016), but is consistent with a comparatively greater predation of "weed seeds" by pinnated grouse (*Tympanuchus* spp.; greater prairie-chickens) in comparison to sharp-tailed grouse (*T. phasianellus*; Schmidt 1936). However, forb DNA was nearly absent from fecal samples collected in croplands suggesting that current use of herbicides may reduce the availability of forbs in croplands and lesser prairie-chickens are only using cultivated plant foods in croplands.

Use of DNA metabarcoding does not indicate what portion of the plant is consumed (e.g., seeds, or leafs). In Texas, lesser prairie-chicken fecal samples can be largely composed of seeds during winter (December – February) and mostly plant foliage in spring (March – May, Doerr and Guthery 1983). Greater prairie-chickens (*T. cupido*) using agricultural and pure grassland landscapes both largely consume native plant seeds (Horak 1985). However, green leafy material can also be the predominant winter food source of lesser prairie-chickens, which may consume a greater composition of green vegetation than greater prairie-chickens (Jones 1964).

Although forbs were dominant plant foods, based on RRA, used by lesser prairie-chickens during brood rearing and winter, relative importance of crops, shrubs, legume, and subshrub plants as a food source increased from brood rearing to winter. The amount of grass consumed remained the same in contrast to Jones (1963), which documented a slight increase in grasses consumed during the winter. The increased use of shrubs and subshrubs may be related to the persistence of shrub and subshrub-based foods during the winter. Broom snakeweed was present at all study sites. This subshrub maintains green basal leaves longer into the fall and winter compared to other plants in the region thus providing a persistent source of green leafy vegetation (Ralphs and Wiedmeier 2004). Broom snakeweed is a known food for lesser prairie-chickens and has protein and nutrient content similar to green grass, but also numerous secondary metabolite compounds (Jones 1963, Davis et al. 1980, Ralphs and Wiedmeier 2004). Although subshrubs such as broom snakeweed may not be easy to digest, they may provide a food source that is persistent throughout the winter for which grouse have evolved advanced digestive systems to procure nutrients as indicated by seasonal changes in gut morphology (Olawsky 1987, Sedinger 1997, Donaldson et al. 2006).

Shrub-based foods can be important for lesser prairie-chickens (Jones 1964, Crawford and Bolen 1976, Summinski 1977, Olawsky 1987, Riley et al. 1993) and other grouse (Patterson 1952, Remington and Braun 1985). Most research that indicates shrubs are important for lesser prairie-chickens have focused on the use of sand shinnery oak where available in Texas and New Mexico (Suminski 1977, Olawsky 1987, Riley et al. 1993). Sand sagebrush, sumac species (*Rhus* spp.), willow (*Salix* spp.)*, and cottonwood (*Populus* spp.) have also provided food for lesser prairie-chickens (Schwilling 1955; Jones 1963, 1964). The increased use of shrub-based foods during the winter corresponded with the increased consumption of sand sagebrush from December to February in northwest Oklahoma (Jones 1963). However, use of sand sagebrush in winter differed from the greater consumption of fragrant sumac during the summer months at the same study site (Jones 1963).

Outside of using persistent winter foods in the form of shrubs and subshrubs, cultivated crops can be used by lesser prairie-chickens (Salter et al. 2005). Use of cultivated legumes during winter was restricted largely to the Clark field site where the OTU containing alfalfa (*Medicago* spp., 100% identity and coverage) was consumed 1.95 times more than the next leading OTU containing *Triticum* -like species. Cultivated alfalfa was available at the Clark study site and consumed by lesser prairie-chickens in distinct cropland areas. The use of alfalfa croplands at this site may explain differential within home range space use compared to the other study sites (Robinson 2015).

Conclusion

Use of DNA metabarcoding is a promising tool for understanding avian diets that minimizes bias of soft bodied prey items and in its noninvasive nature may allow for future research into the functional relationship between foods consumed and individual fitness. The

method is no silver bullet for understanding diets of lesser prairie-chickens as readable animal and plant DNA was only extracted from ⅓ and ½ of fecal samples, respectively.

From the samples producing readable DNA, I identified that Lepidoptera contributes most to the diets of brooding females and chicks compared to other arthropod orders. However, use of arthropod orders varied among study sites during the brooding period. Overall, lesser prairie-chickens using native grasslands used a greater diversity of arthropod orders (Lepidoptera, Orthoptera, Araneae, and Hemiptera).

Plant foods that contributed most to the diets of lesser prairie-chickens were of the forb functional group. Forbs should be maintained in native grasslands through a regionally specific disturbance regime (e.g., prescribed fire and grazing plans; Hagen et al. 2004). Although forbs composed the greatest proportion of winter diets during winter, the availability of persistent food sources in the form of subshrubs, shrubs, and alfalfa croplands may help sustain populations throughout winter.

Literature Cited

Adedapo, A., F. Jimoh, and A. Afolayan. 2011. Comparison of the nutritive value and biological activities of the acetone, methanol and water extracts of the leaves of Bidens pilosa and Chenopodium album. Acta Poloniae Pharmaceutica, 68:83–92.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal Wildlife Management 74:1175–1178.

Arthun, D., J. L. Holechek, J. D. Wallace, M. L. Galyean, M. Cardenas, and S. Rafique. 1992. Forb and shrub influences on steer nitrogen retention. Journal of Range Management. 45: 133–136.

Ault, S. C., and F. A. Stormer. 1983. Seasonal food selection by scaled quail in northwest Texas. Journal of Wildlife Management 47:222–228.

Beckie, H. J., R. M. Weiss, J. Y. Leeson, and O. O. Olfert. 2012. Range expansion of kochia (Kochia scoparia) in North America under a changing climate. Pages 33–46 in J. A. Ivany, and R. E., Blackshaw, eds. Climate Change and the Canadian Agricultural Environment. Topics in Canadian Weed Science Volume 8. Canadian Weed Science Society, Pinawa, Manitoba, CA.

Bergerud, A. T., and M.W. Gratson. 1988. Survival and Breeding Strategies of Grouse. Pages 473–575 in A.T. Bergerud and M.W. Gratson, eds. Adaptive Strategies and population ecology of northern grouse. Volume II theory and synthesis. University of Minnesota Press, Minneapolis, USA.

Bogenschutz, T. R., D. E., Hubbard, and A. P. Leif. 1995. Corn and sorghum as a winter food source for ring-necked pheasants. Journal of Wildlife Management 59:776–784.

Bohmann, K., A. Monadjem, C. Lehmkuhl Noer, M. Rasmussen, M. R. Zeale, E. Clare, G. Jones, E. Willerslev, and M. T. Gilbert. 2011. Molecular diet analysis of two african free-tailed bats (Molossidae) using high throughput sequencing. PLoS One 6:e21441.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretical approach. Second edition. Springer-Verlag, New York, NY, USA.

Caporaso, J. G., C. L. Lauber, W. A. Walters, D. Berg-Lyons, J. Huntley, N. Fierer, S. M. Owens, J. Betley, L. Fraser, and M. Bauer. 2012. Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. ISME journal 6:1621–1624.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics 43:783–791.

Chase, J. M. 2014. Spatial scale resolves the niche versus neutral theory debate. Journal of Vegetation Science 25:319–322.

Copelin, F. F. 1963. Lesser prairie chicken in Oklahoma. Pittman-Robertson Project Number W-62-R, Oklahoma Wildlife Conservation Department, Oklahoma City, USA.

Craine, J. M., and R. D. Jackson. 2010. Plant nitrogen and phosphorus limitation in 98 North American grassland soils. Plant and Soil 334:73–84.

Craine J. M., E. G. Towne, M. Miller, and N. Fierer. 2015. Climatic warming and the future of bison as grazers. Scientific Reports. 5:16738 doi: 10.1038/srep16738.

Crawford, J. A. and E. G. Bolen. 1976. Fall diet of the lesser prairie chickens in west Texas. Condor 78:142–144.

Davis, C. A., T. Z. Riley, R. A. Smith, and M. J. Wisdom. 1980. Spring-summer foods of Lesser Prairie Chickens in New Mexico. Pages 75–80 in P. A.Vohs and F. L. Knopf, eds, Proceedings of prairie grouse symposium, Oklahoma State University, Stillwater, OK.

DeYoung, R. W., and D. L. Williford. 2016. Genetic variation and population structure in the prairie grouse: implications for conservation of the lesser prairie-chicken. Pages 77–98 in D.A Haukos and C.W. Boal. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, CA, USA.

Doerr, T. B., and F. S. Guthery. 1983. Food selection by lesser prairie chickens in northwest Texas. Southwestern Naturalist 28:381–383.

Donaldson, J. R., M. T. Stevens, H. R. Barnhill, and R. L. Lindroth. 2006. Journal of Chemical Ecology 32:1415–1429.

Edgar, R. C. 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26:2460–2461.

Edgar, R. C. 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nat Methods 10:996–998.

Evans, R. A., and R. M. Love. 1957. The step-point method of sampling-a practical tool in range research. Journal of Range Management 10:289-297.

Evans, K. E., D. R. Dietz. 1974. Nutritional energetics of sharp-tailed grouse during winter. Journal of Wildlife Management 38:622–629.

Everitt, J. H., and C. L. Gonzalez. 1981. Seasonal nutrient content in food plants of white tailed deer on the South Texas Plains. Journal Range Management 34:506–510.

Ferrari, S. L., and F. Cribari-Neto. 2004. Beta regression modeling rates and proportions. Journal of Applied Statistics 31:799–815.

Fernandez-Canero, R. and P. Gonzalez-Redondo, 2010. Green roofs as a habitat for birds: a review. Journal Animal Veterinary Advances 9:2041–2052.

147

Garton, E. O., C. A. Hagen, G. M. Beauprez, S. C. Kyle, J. C. Pitman, D. D. Schoeling, and W. E. Van Pelt. 2016. Population dynamics of lesser prairie-chickens. Pages 49–76 in D.A Haukos and C.W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Gill, F. B. 2006. Ornithology, 3rd ed. Freeman. New York, NY, USA.

Giesen, K. M. 1994. Breeding range and population status of lesser prairie-chickens in Colorado. Prairie Naturalist 26:175–182.

Guthery, F. S. 2000. On bobwhites. Texas A&M University Press, College Station, USA.

Hagen, C. A., B. E. Jamison, K. M. Giesen, and T. Z. Riley. 2004. Guidelines for managing Lesser Prairie-Chicken populations and their habitats. Wildlife Society Bulletin 32:69–82.

Hagen, C. A., and K. M. Giesen. 2005. Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Birds of North America 364. <http://bna.birds.cornell.edu/bna/species/364/articles/introduction> Accessed 15 May 2015.

Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. Journal of Wildlife Management 73:1325–1332.

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

Haukos, D. A., and J. C. Zaveleta. 2016. Habitat. Pages 99–132 in D.A Haukos and C.W. Boal. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, CA, USA.

Horak, G. J. 1985. Kansas prairie chickens. Kansas Fish and Game Commission, Pratt, USA.

Jamison, B. E. 2000. Lesser Prairie-Chicken chick survival, adult survival, and habitat selection and movements of males in fragmented rangelands of southwestern Kansas. M.S. thesis, Kansas State University, Manhattan.

Jamison, B. E., R. J. Robel, J. S. Pontius, and R. D. Applegate. 2002. Invertebrate biomass: associations with Lesser Prairie-Chicken habitat use and sand sagebrush density in southwestern Kansas. Wildlife Society Bulletin 30:517–526.

Jones, R. E. 1963. Identification and analysis of lesser and greater prairie chicken habitat. Journal of Wildlife Management 27:757–778.

Jones, R. E. 1964. Habitat used by lesser prairie chickens for feeding related to seasonal behavior of plants in Beaver County, Oklahoma. Southwestern Naturalist 9:111–117.

148

Kartzinel, T. R., P. A. Chen, T. C. Coverdale, D. L. Erickson, W. J. Kress, M. L. Kuzmina, D. I. Rubenstein, W. Wang, and R. M. Pringle. 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proceedings of the National Academy of Sciences 112:8019–8024.

King, A. W. 1997. Hierarchy theory: a guide to system structure for wildlife biologists pages 185–212 in J. A. Bissonette, editor, Wildlife and Landscape Ecology. Springer, New York, NY, USA.

Korkmaz, S., D. Goksuluk, and G. Zarasiz. 2016. Package 'MVN', version 4.02. R Foundation for Statistical Computing, Vienna. <http://cran.r-project.org> Accessed 15 March 2016.

Larsson, L. C., C. L. Pruett, D. H. Wolfe, and M. A. Patten. 2013. Fine-scale selection of habitat by the lesser prairie-chicken. Southwestern Naturalist 58:135–149.

Lassiter, J. W., and H. M. Edwards. 1982. Animal nutrition. Reston Publishing Company, Reston, VA, USA.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1951. American wildlife and plants: a guide to wild food habits. Dover Publications, New York, NY, USA.

Martin, W. G., and H. Patrick. 1961. The effect of taurine on the Sulphate-S35 retention by chicks. Poultry Science 40: 267–268.

Mazerolle, M. J. 2016. Package 'AICcmodavg', version 2.00. R Foundation for Statistical Computing, Vienna. <http://cran.r-project.org> Accessed 15 March 2016.

McDonald, L., G. Beauprez, G. Gardner, J. Griswold, C. Hagen, D. Klute, S. Kyle, J. Pitman, T. Rintz, and B. Van Pelt. 2014. Range-wide population size of the lesser prairie-chicken: 2012 and 2013. Wildlife Society Bulletin 38:536–546.

McDonald, L. L., K. Adachi, T. Rintz, and G. Gardner. 2015. Range-wide population size of the Lesser Prairie-Chicken: 2012, 2013, 2014, and 2015. Technical report prepared for the Western Association of Fish and Wildlife Agencies. Western EcoSystems Technology, Laramie, WY, USA.

McNamara, J. M., and A. I. Houston. Starvation and predation as factors limiting population size. Ecology 68:1515–1519.

McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2012. Demography of greater prairie-chickens: regional variation in vital rates, sensitivity values, and population dynamics. Journal of Wildlife Management 76:987–1000.

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

Mowart, D. N., R. S. Fulkerson, W. E. Tossell, and J. E. Winch. 1965. The in vitro digestibility and protein content of leaf and stem portions and forages. Canadian Journal of Plant Science 45:321–331.

North American Bird Conservation Initiative, U.S. Committee. 2014. The State of the Birds 2014 Report. U.S. Department of Interior, Washington, D.C. 16 pages.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2015. vegan: Community Ecology Package. R package version 2.4-2. <http://CRAN.R-project.org/package=vegan> accessed on 9 March 2017.

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

O'Neill, R. V., A. R. Johnson, and A. W. King. 1989. A hierarchical framework for the analysis of scale. Landscape Ecology 3:193-205.

Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado, USA.

Pettit, R. D. 1986. Sand shinnery oak control and management. Management Note 8, Natural Resources Management, Texas Tech University, Lubbock, TX, USA.

Pfadt, R. E. 1994. Threebanded grasshopper (*Hadrotettix trifasciatus*). Wyoming Agricultural Experiment Station Bulletin 912.

Pompanon, F., B. E. Deagle, W. O. C. Symondson, D. S. Brown, S. N. Jarman, and P. Taberlet. 2011. Who is eating what: diet assessment using next generation sequencing. Molecular Ecology 21:1931–1950.

Ralphs, M. H., and R. D. Wiedmeier. 2004. Conditioning cattle to graze broom snakeweed (*Gutierrezia sarothrae*). Journal of Animal Science 82:3100–3106.

Ramsay, S. L., and D. C. Houston. 2003. Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. Ibis 145:227–232.

Ratnasingham S, and P. D. N. Hebert. 2007. BOLD: the barcode of life data system (http://www.barcodinglife.org). Molecular Ecology Notes 7:355–364.

Remington, T. E., and C. E. Braun. Sage grouse food selection in winter, North Park, Colorado. Journal of Wildlife Management 49:1055–1061.

Riley, T. Z., C. A. Davis, and R. A Smith. 1993. Autumn and winter foods of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) (Galliformes: tetraonidae). Great Basin Naturalist 53:186–189.

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

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. Effects of landscape characteristics on annual survival of lesser prairie-chickens In review.

Rumpold, B. A., and O. K. Schlüter. 2013. Nutritional composition and safety aspects of edible insects. Molecular Nutrition Food Research 57:802–823.

Salter, G. C., R. J. Robel, and K. E. Kemp. 2005. Lesser prairie-chicken use of harvested corn fields during fall and winter in southwestern Kansas. Prairie Naturalist 37:1–9.

Sandercock, B.K.,W.E. Jensen, C.K. Williams, and R.D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. Journal of Wildlife Management 72:970–982.

Savory, C. J. 1989. The importance of invertebrate food to chicks of gallinaceous species. Proceedings of the Nutrition Society 48:113–133.

Schmidt, F. 1936. Winter food of the sharp-tailed grouse and pinnated grouse in Wisconsin. Wilson Bulletin, 48: 186–203.

Schwilling, M. D. 1955. Study of the lesser prairie chicken in southwest Kansas. Kansas Fish and Game 10–12.

Scott, J. A. 2014. Lepidoptera of North America 13. Flower visitation by Colorado butterflies (40,615 records) with a review of the literature on pollination of Colorado plants and butterfly attraction (Lepidoptera: Hesperioidea and Papilionoidea). Contributions C.P. Gillette Museum Arthropod Diversity, Colorado State University 190 pages, Fort Collins, USA.

Sedinger, J. S. 1997. Adaptation to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99:314–326.

Sih, A., and B. Christensen. 2001. Optimal diet theory: when does it work, and when and why does it fail? Animal Behavior 61:379–390.

Silvy, N. J., M. E. Morrow, E. Shanley, and R. D. Slack. 1990. An improved drop net for capturing wildlife. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 44:374–378.

Smith, R. A. 1979. Fall and winter habitat of lesser prairie chickens in southeastern New Mexico. Thesis, New Mexico State University, Las Cruces, USA.

Spafford, R., and C. Lortie. 2013. Sweeping beauty: is grassland arthropod community composition effectively estimated by sweep netting? Ecology and Evolution 3:3347–3358.

Stevens, C. E., and I. D. Hume. 1998. Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. Physiological Reviews 78:393–427.

151

Stiven, A. E. 1961. Food energy available for and required by the blue grouse chick. 42:547–553.

Sugimura, K., E. Hori, Y. Kurihara, and S. Itoh. 1984. Nutritional value of earthworms and grasshoppers as poultry feed. Japanese Poultry Science 21:1–7.

Suminski, H. R. 1977. Habitat evaluation for Lesser Prairie Chickens in eastern Chaves, New Mexico. M.S. thesis, New Mexico State University, Las Cruces, USA.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Taberlet, P., E. Coissac, F. Pompanon, L. Gielly, C. Miquel, A. Valentini, T. Vermat, G. Corthier, C. Brochmann, and E. Willerslev. 2007. Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. Nucleic Acids Research 35:e14–e14.

Trevelline, B. K., S. C. Latta, L. C. Marshall, T. Nuttle, and B. A. Porter. 2016. Molecular analysis of nestling diet in a long-distance neotropical migrant, the Louisiana waterthrush (*Parkesia motacilla*). Auk 133:415–428.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197–215.

Zeale, M. R., R. K. Butlin, G. L. Barker, D. C. Lees, and G. Jones. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular Ecology Resources 11:236–244.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

Wenny, D. G., T. L. DeVault, M. D. Johnson, D. Kelly, C. H. Sekercioglu, D. F. Tomback, and C. J. Whelan. 2011. The need to quantify ecosystem services provided by birds. Auk 128:1–14.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chicken as an example. Journal of Wildlife Management 61:302–312.

Wise, D. R. 1982. Nutrition of wild red grouse (*Lagopus lagopus scoticus*). Ibis 119:1–9.

Yi Z., F. Jinchao, X. Dayuan, S. Weiguo, and J. C. Axmacher. 2012. A comparison of terrestrial arthropod sampling methods. Journal of Resources and Ecology 3:174–182.

Zaveleta, J. 2012. Community response to use of prescribed grazing and tebuthiuron herbicide for restoration of sand shinnery oak communities. M.S. thesis, Texas Tech University, Lubbock, USA.

Zeale, M. R. K., R. K. Butlin, G. L. A. Barker, D. C. Leess, and G. Jones. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular ecology resources 11: 236–244.

Zeileis A., F. Cribari-Neto, B. Gruen, and I. Kosmidis. 2016. Package ''betareg''. <http://cran.r-project.org/web/packages/betareg/ betareg.pdf.> Accessed 15 March 2016.

Table 3.1 Proportional abundance of the 3-top ranked abundant grass, forbs, and shrub species estimated from point-step transects by study site for the northern portion of the lesser prairie-chicken range in Kansas and Colorado during 2014-2015. Mean annual precipitation (PRISM climate group averaged from a PRISM 800-m resolution raster file) and dominant soil textures (Soil Survey Staff 2016) are also included.

	Colorado		*Kansas*					
	Prowers		**Clark**		**Northwest**		**Red Hills**	
Mean Annual Precipitation (cm)								
	43.4		58.6		49.4		69.2	
Dominant Soil Textures								
	Loam		loamy fine sands, fine sandy loams, fine sands		silt loams		sandy loam, clay loam, and clay	
Grasses								
	Bouteloua curtipendula	0.453	*Sporobolus airoides*	0.037	*Bouteloua curtipendula*	0.266	*Schizachyrim scoparium*	0.064
	Bouteloua gracilis	0.063	*Sporobolus cryptandrus*	0.037	*Bouteloua gracilis*	0.163	*Bouteloua curtipendula*	0.046
	Schizacyrim scoparium	0.057	*Bouteloua gracilis*	0.032	*Pascopyrum smithii*	0.099	*Bouteloua gracilis*	0.026
Forbs								
	Kochia scoparia	0.110	*Ambrosia psilostachya*	0.037	*Ambrosia psilostachya*	0.027	*Artemisia ludiviciana*	0.053
	Salsola tragus	0.090	*Salsola tragus*	0.033	*Salsola tragus*	0.019	*Ambrosia psilostachya*	0.037
	Convolvulus arvensis	0.028	*Kochia scoparia*	0.014	*Kochia scoparia*	0.013	*Pediomelum spp.*	0.006
Subshrubs								
	Gutierrezia sarothrae	0.005	*Guiterrizia dracunculoides*	0.002	*Gutierrezia sarothrae*	0.033	*Guiterrizia dracunculoides*	0.011
			Gutierrezia sarothrae	0.002			*Gutierrezia sarothrae*	0.003
Shrubs								
	Yucca glauca	0.011	*Artemisia filifolia*	0.011	*Artemisia filifolia*	0.013	*Artemisia filifolia*	0.004
	Artemisia filifolia	0.001	*Prunus angustifolia*	0.002	*Yucca glauca*	0.004	*Prunus angustifolia*	0.002
	Ericameria spp.	0.001	*Rhus aromatia*	0.001			*Rhus glabra*	0.001

154

Table 3.2 Number of collected fecal samples and those with readable plant and animal DNA (in parentheses) at each study site in the northern portion of lesser prairie-chicken range in Kansas and Colorado during the brooding period and winter 2014-2015.

Site	All seasons	Brood rearing	Winter
Animal DNA			
Colorado	28 (11)	6 (1)	22 (10)
Clark, KS	124 (37)	81 (25)	43(12)
Northwest, KS	117 (30)	93 (28)	24 (2)
Red Hills, KS	45 (12)	31 (6)	14 (6)
Total	314 (90)	211 (60)	103 (30)
Plant DNA			
Colorado	28 (28)	6 (6)	22 (22)
Clark, KS	124 (52)	81 (10)	43 (42)
Northwest, KS	117 (54)	93 (31)	24 (23)
Red Hills, KS	45 (18)	31 (4)	14 (14)
Total	314 (152)	211 (51)	103 (101)

155

Table 3.3 Beta regression model results for the consumption of Lepidoptera, Orthoptera, and Araneae by female lesser prairie-chickens in Kansas and Colorado during the brood-rearing period (June-September) of 2014 and winter 2014–2015.

Lepidoptera Covariate[1]	K[2]	AICc	ΔAICc	w_i
native grassland[3]	3	-43.24	0	0.37
CRP	3	-42.61	0.64	0.27
crop	3	-40.88	2.36	0.11
landcover	4	-40.87	2.37	0.11
date	3	-40.55	2.69	0.1
chick	4	-38.41	4.83	0.03
site	6	-36.77	6.47	0.01
age	3	-23.82	19.42	0
Orthoptera				
native grassland	3	-66.62	0	0.34
CRP	3	-66.07	0.55	0.26
juliandate	3	-64.63	1.99	0.13
crop	3	-64.29	2.33	0.11
landcover	4	-64.24	2.38	0.1
chick	4	-62.34	4.28	0.04
site	5	-60.75	5.88	0.02
age	3	-34.05	32.58	0
Araneae				
native grassland	3	-124.93	0	0.33
CRP	3	-124.45	0.48	0.26
date	3	-123.36	1.57	0.15
crop	3	-122.96	1.98	0.12
landcover	4	-122.55	2.38	0.1
chick	4	-120.99	3.94	0.05
site	6	-116.97	7.96	0.01
age	3	-69.6	55.34	0

[1] Covariates represent study site(site), Julian date (juliandate), adult or chick feces (chick), age in days of chick samples (age), fecal sample located in cropland (crop), Conservation Reserve Program grassland (CRP), native working grassland, or each cover type (landcover).
[2] K = no. of parameters, AIC_c =Akaike's Information Criterion adjusted for small sample sizes, ΔAIC_c = difference in AIC_c relative to smallest value, w = model weight.
[3] Models with beta coefficients not overlapping zero at the 85% confidence interval are underlined.

Table 3.4 Beta regression model results for the consumption of Lepidoptera, Orthoptera, and Hymenoptera by lesser prairie-chickens in Kansas and Colorado brood-rearing period (June-September) of 2014.

	Covariate[1]	K^2	AICc	ΔAICc	w
Lepidoptera	<u>Landcover[3]</u>	3	-30.08	0	0.30
	<u>native grassland</u>	3	-30.08	0	0.30
	CRP	3	-30.08	0	0.30
	juliandate	3	-27.66	2.42	0.09
	site	5	-24.8	5.27	0.02
Orthoptera	<u>juliandate</u>	3	-41.49	0	0.86
	<u>site</u>	5	-37.25	4.25	0.10
	landcover	3	-32.75	8.74	0.01
	native grassland	3	-32.75	8.74	0.01
	CRP	3	-32.75	8.74	0.01
Hymenoptera	juliandate	3	-62.4	0	0.24
	CRP	3	-62.4	0.01	0.24
	landcover	3	-62.4	0.01	0.24
	native grassland	3	-62.4	0.01	0.24
	site	5	-57.91	4.49	0.03

[1] Covariates represent study site (site), Julian date (juliandate), fecal sample located in in Conservation Reserve Program grassland (CRP), located in native working grassland (native grassland), or each cover type (landcover).

[2] k= no. of parameters, AICc =Akaike's Information Criterion adjusted for small sample sizes, ΔAICc = difference in AICc relative to smallest value, w = model weight.

[3]Models with beta coefficients not overlapping zero at the 85% confidence interval are underlined.

157

Table 3.5 Model AICc, number of parameters, delta AICc, and model weight of beta regression models explaining winter plant diets of lesser prairie-chickens in Kansas and Colorado 2013-2014.

	Covariate[1]	K^2	AICc	ΔAICc	*w*
Forb	alfalfa	3	-139	0	0.42
	crop	3	-139	0	0.42
	landcover	4	-137	2.1	0.15
	native grassland	3	-130	8.4	0.01
	CRP	3	-127	11.9	0
	juliandate	3	-127	11.9	0
	site	5	-126	12.3	0
	quadjuliandate	4	-125	13.2	0
Grass	site	5	-398	0	0.73
	native grassland	3	-393	4.4	0.08
	CRP	3	-393	4.5	0.08
	landcover	4	-392	6.4	0.03
	juliandate	3	-391	6.5	0.03
	alfalfa	3	-391	7	0.02
	crop	3	-391	7	0.02
	quadjuliandate	4	-390	7.8	0.01
Legume	alfalfa	3	-249	0	0.42
	crop	3	-249	0	0.42
	landcover	4	-247	2.2	0.14
	native grassland	3	-241	8	0.01
	quadjuliandate	4	-241	8.3	0.01
	CRP	3	-239	9.8	0
	juliandate	3	-239	10.2	0
	site not estimable[4]				

[1] Covariates represent study site (site), Julian date (juliandate), quadratic effect of julian date (quadjuliandate), fecal sample located in in Conservation Reserve Program grassland (CRP), located in native working grassland (native grassland), alfalfa field (alfalfa), cropland(crop) or each cover type (landcover).

[2] k= no. of parameters, AIC_c =Akaike's Information Criterion adjusted for small sample sizes, $ΔAIC_c$ = difference in AIC_c relative to smallest value, *w* = model weight.

[3] Models with beta coefficients not overlapping zero at the 85% confidence interval are underlined.

Table 3.5. Cont

	Covariate[1]	K^2	AICc	ΔAICc	*w*
Shrub	native grassland	3	-479	0	0.62
	landcover	4	-478	1.5	0.3
	site	5	-475	4.1	0.08
	quadjuliandate	4	-461	18.4	0
	juliandate	3	-445	33.7	0
	alfalfa	3	-443	36.2	0
	crop	3	-443	36.2	0
	CRP not estimable				
Crop	native grassland	3	-984	0	0.18
	alfalfa	3	-984	0.08	0.17
	crop	3	-984	0.08	0.17
	site	5	-983	0.75	0.12
	CRP	3	-983	1.04	0.11
	juliandate	3	-983	1.35	0.09
	landcover	4	-983	1.58	0.08
	quadjuliandate	4	-982	1.99	0.07
Subshrub	alfalfa	3	-249	0	0.42
	crop	3	-249	0	0.42
	landcover	4	-247	2.2	0.14
	native grassland	3	-241	8	0.01
	quadjuliandate	4	-241	8.3	0.01
	site	5	-239	9.7	0
	CRP	3	-239	9.8	0
	juliandate	3	-239	10.2	0

[1] Covariates represent study site (site), Julian date (juliandate), fecal sample located cropland (crop), in in Conservation Reserve Program grassland (CRP), located in native working grassland (native grassland), alfalfa cropland (alfalfa), or each cover type (landcover).
[2] K = no. of parameters, AICc =Akaike's Information Criterion adjusted for small sample sizes, ΔAICc = difference in AICc relative to smallest value, *w* = model weight.
[3] Models with beta coefficients not overlapping zero at the 85% confidence interval are underlined.
[4] Some models were not estimable due to having too many zeroes.

Table 3.6 Model selection for detection probability of DNA in fecal sample model results for lesser prairie-chickens in Kansas and Colorado during the brood rearing period (June – September) and winter of 2014 – 2015.

	Covariate[1]	AICc[2]	K	ΔAICc	w
Plant or Animal	period*exposure	307.68	3	0	0.51
	period[3]	308.26	2	0.58	0.38
	Quadratic date	310.87	3	3.19	0.1
	tmax	327.7	2	20.03	0
	chick	363.67	2	55.99	0
	exposure	392.51	2	84.84	0
	site	397.69	5	90.02	0
Animal DNA	chick	341.8	2	0	1
	exposure	365.5	2	23.7	0
	period*exposure	367.14	3	25.35	0
	precip	367.23	2	25.43	0
	sevenday	367.24	2	25.45	0
	twoday	367.25	2	25.45	0
	nest	367.58	2	25.78	0
Plant DNA	Quadratic date	254.89	3	0	0.64
	period	257.15	2	2.26	0.21
	period*exposure	257.84	3	2.95	0.15
	tmax	284.17	2	29.28	0
	chick	362.26	2	107.37	0
	exposure	385.5	2	130.61	0
	site	388.13	5	133.25	0

[1] K = no. of parameters, AICc =Akaike's Information Criterion adjusted for small sample sizes, ΔAICc = difference in AICc relative to smallest value, w = model weight.

[2] Covariates represent study site(site), date, time between use of location and collection of feces (exposure), fecal sample collected after hatch from nest (nest), brood rearing or winter (period), adult or chick feces (chick), daily precipitation (precip), cumulative precipitation over 7 days (sevenday), cumulative precipitation over 2 days (twoday), and maximum daily temperature (tmax).

[3] Models with beta coefficients not overlapping zero at the 85% confidence interval are underlined.

Figure 3.1 Study area extent as determined by minimum convex polygons of VHF and GPS marked lesser prairie-chickens in western Kansas and eastern Colorado. Study sites in Gove and Logan counties, Kansas, were combined for analyses and referred to as Northwest. The study site on the edge of Comanche and Kiowa counties, Kansas, is referred to as the Red Hills. The study areas are depicted in red and the estimated current distribution of lesser prairie-chickens is indicated by hatch marks (Hagen and Giesen 2005).

161
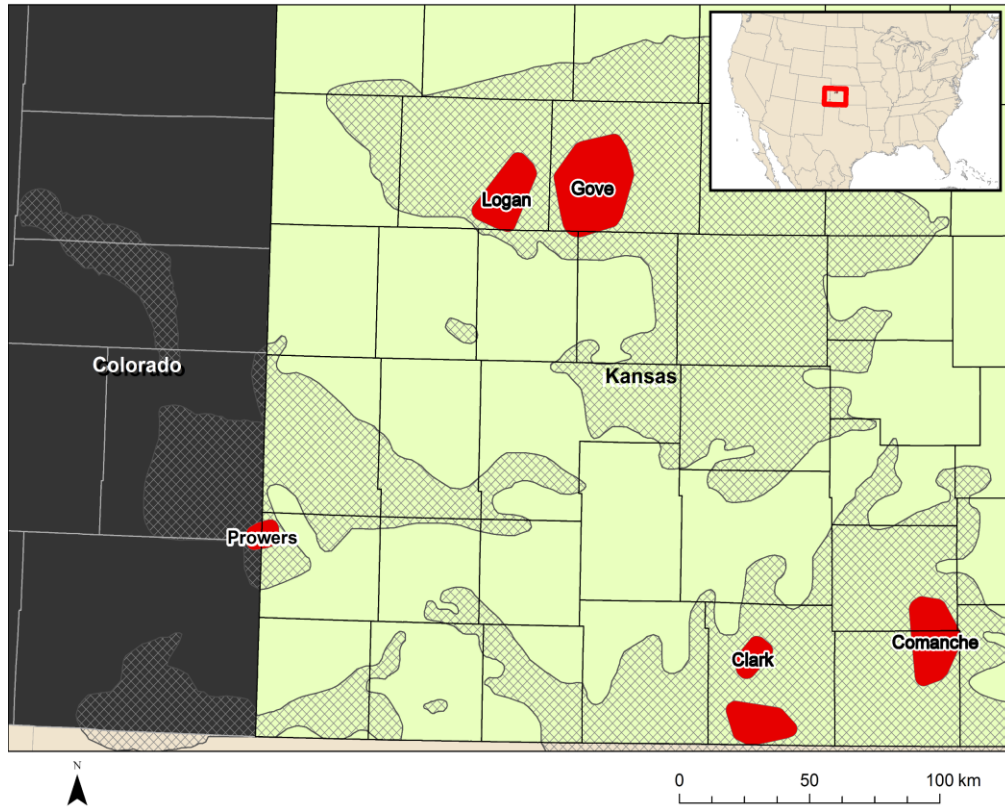
Figure 3.2 Arthropod orders detected in lesser prairie-chicken fecal samples using DNA metabarcoding collected during winter (2014–2015; top) and brood rearing (summer 2014; bottom) in Kansas and Colorado. Fecal samples were pooled among study sites in Clark County, Kansas (Clark), Gove and Logan counties, Kansas (NW), Kiowa and Comanche counties, Kansas (RH), and in Prowers and Baca counties, Colorado (CO) during summer 2014 (Panel A; hatch to 98 days old) from brooding females and chicks and from adults during the winter of 2014 –2015 (Panel B; November to March).
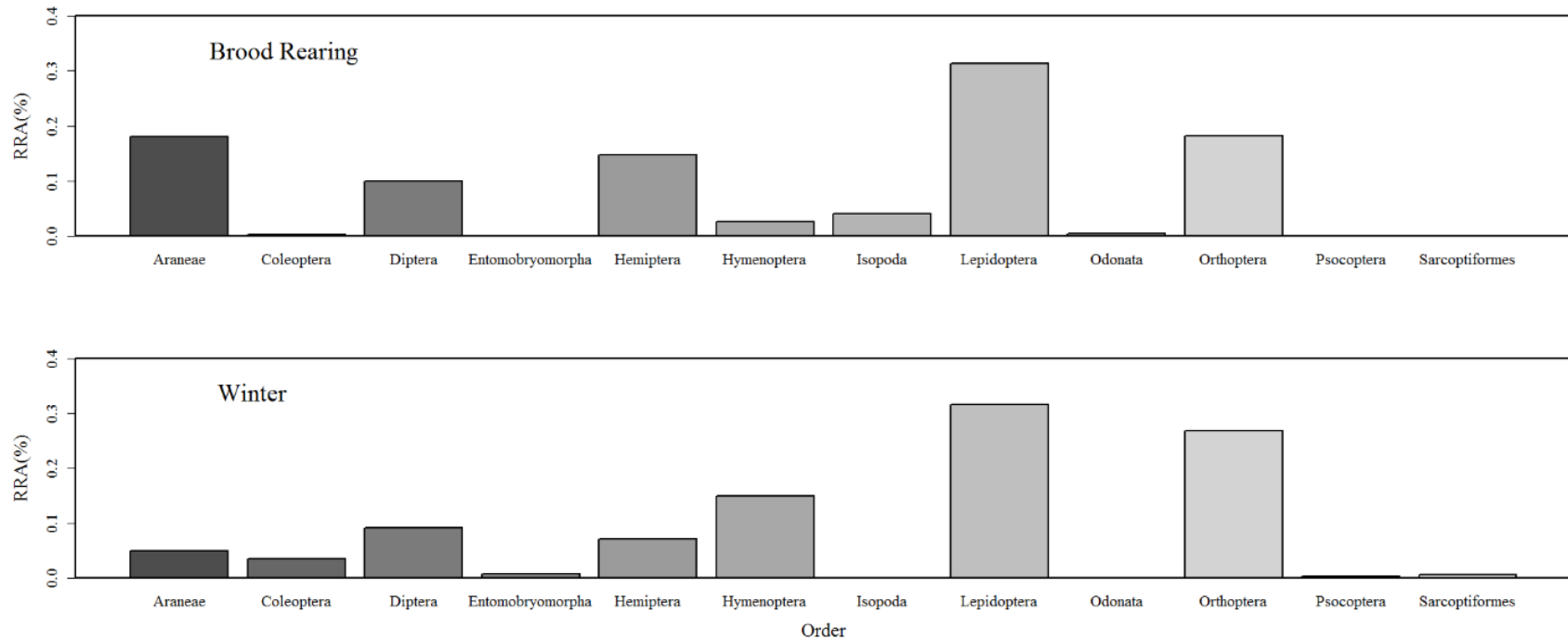
Figure 3.3 The composition of arthropod orders available to lesser prairie-chicks in Clark County, Kansas (Clark), Gove and Logan counties, Kansas (Northwest), Kiowa and Comanche counties, Kansas (Red Hills), and in Prowers and Baca counties, Colorado (Colorado) during the summers of 2013 and 2014. The composition of orders was estimated using sweep net surveys at each study site and is based on biomass of each arthropod order.
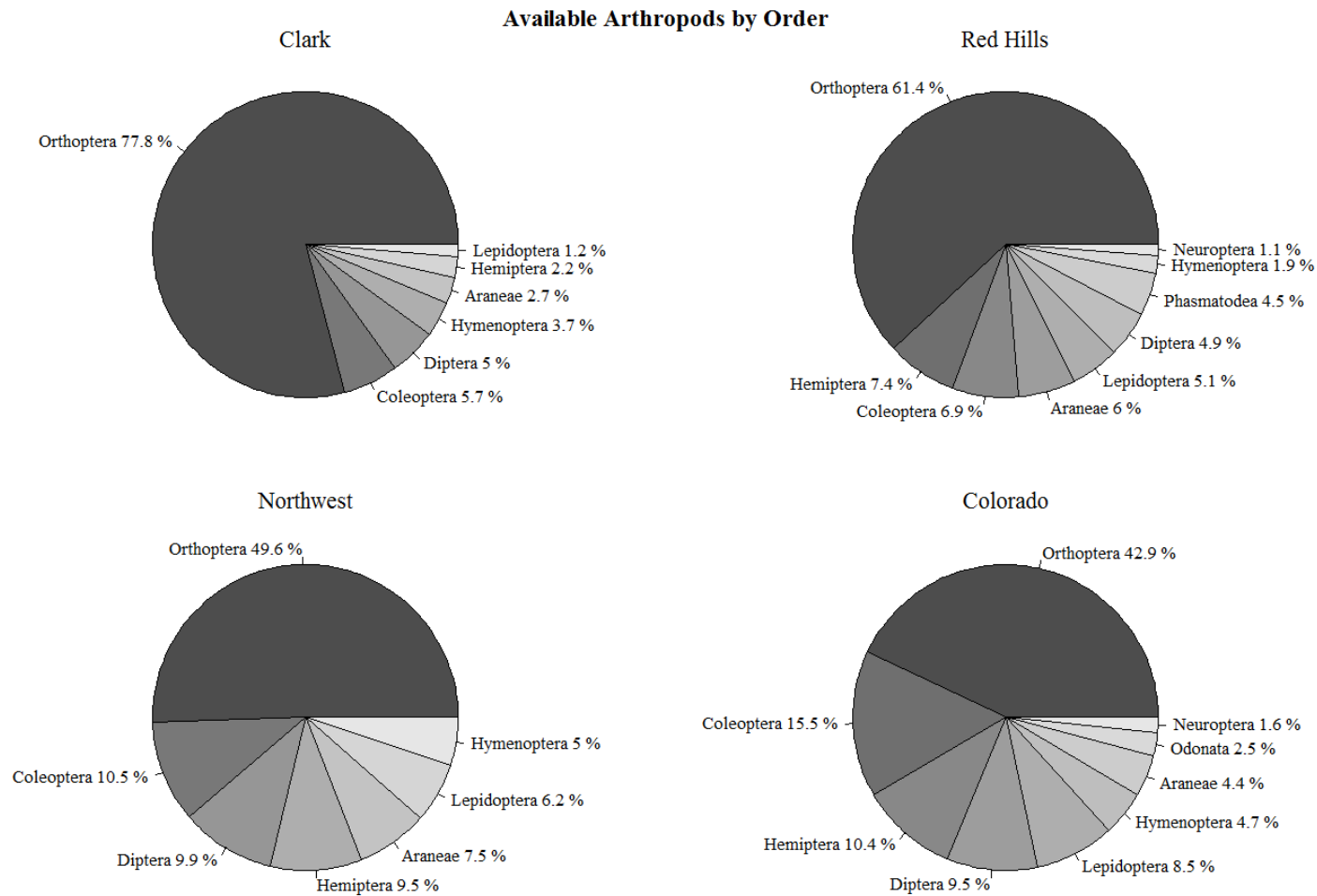
Figure 3.4 Scatter plots fitted with least squares (red) and locally weighted scatterplot smooth lines (blues) to depict patterns in the composition of Orthoptera and Lepidoptera in the diets of lesser prairie-chicken chickens during the brood rearing period of 2014 in Kansas and Colorado. Julian dates encompass 27 May 2014 (147) to 29 August 2014 (241) while age of chicks depicted range from 2 to 98 days old.
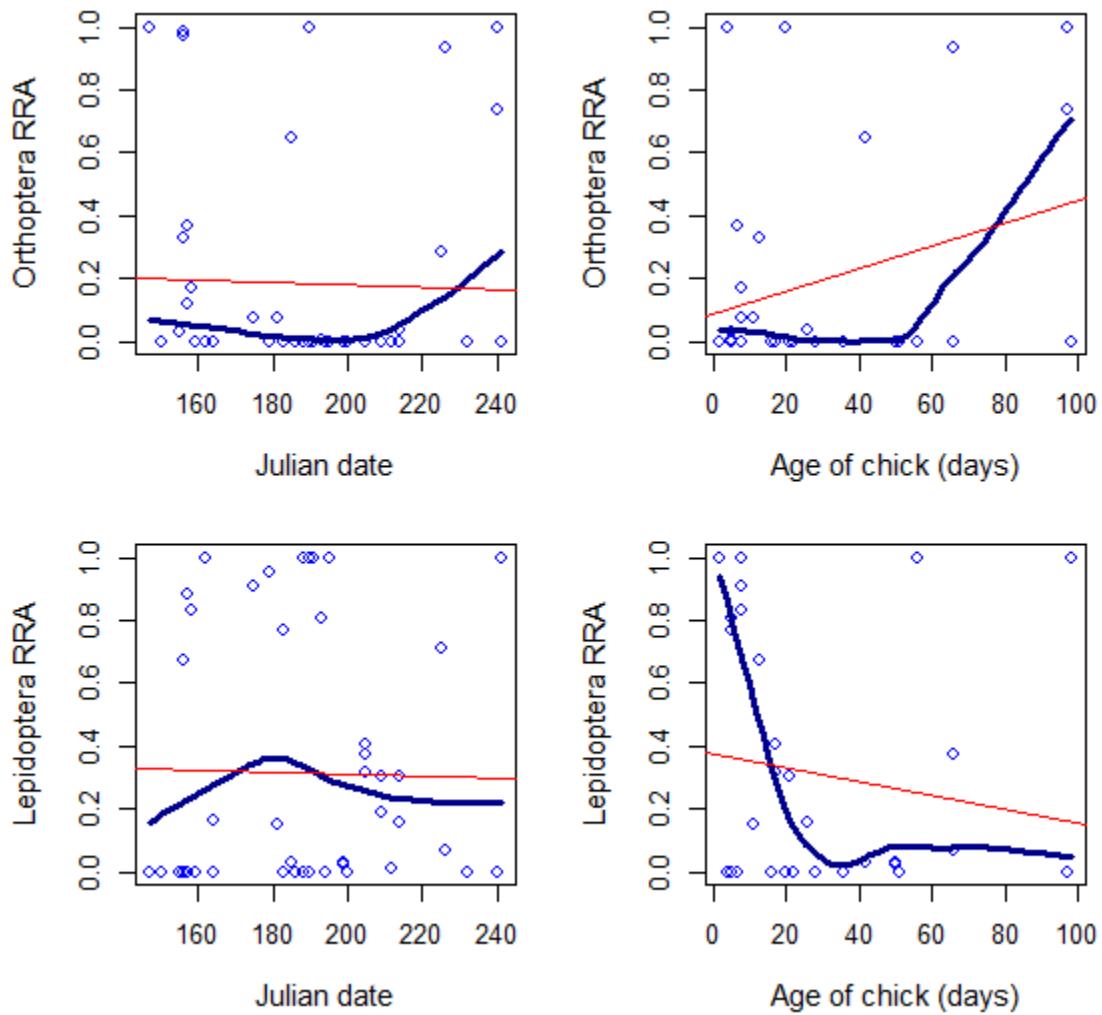
Figure 3.5 The Relative Readable Abundance (proportion) of DNA within lesser prairie-chicken fecal samples matching barcodes similar to arthropod orders of Lepidoptera, Orthoptera, Araneae, and Hemiptera grouped by site. Fecal samples were pooled among study sites in Clark County, Kansas (Clark), Gove and Logan counties, Kansas (NW), Kiowa and Comanche counties, Kansas (RH), and in Prowers and Baca counties, Colorado (CO) and were collected during summer 2014 (hatch to 98 days old) from brooding females and chicks.
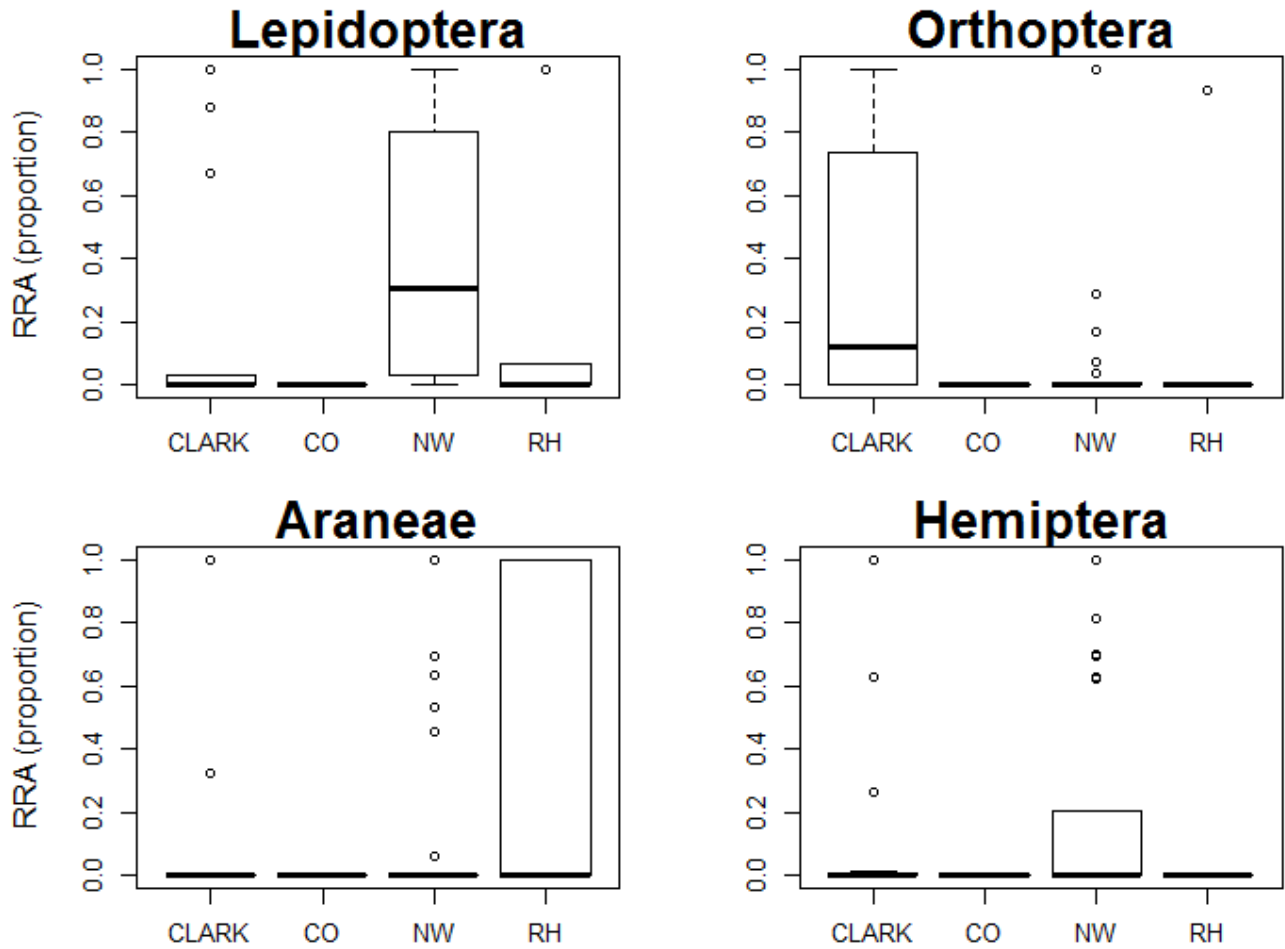
Figure 3.6 The Relative Readable Abundance (proportion) of DNA within lesser prairie-chicken fecal samples matching barcodes similar to arthropods orders of Lepidoptera, Orthoptera, Araneae, and Hemiptera grouped by landcover type where collected. Landcover types included cropland, Conservation Reserve Program grasslands (CRP), and native working grasslands (native grassland). Fecal samples were pooled among study sites in Clark County, Kansas (Clark), Gove and Logan counties, Kansas (NW), Kiowa and Comanche counties, Kansas (RH), and in Prowers and Baca counties, Colorado (CO) and were collected during summer 2014 (hatch to 98 days old) from brooding females and chicks.
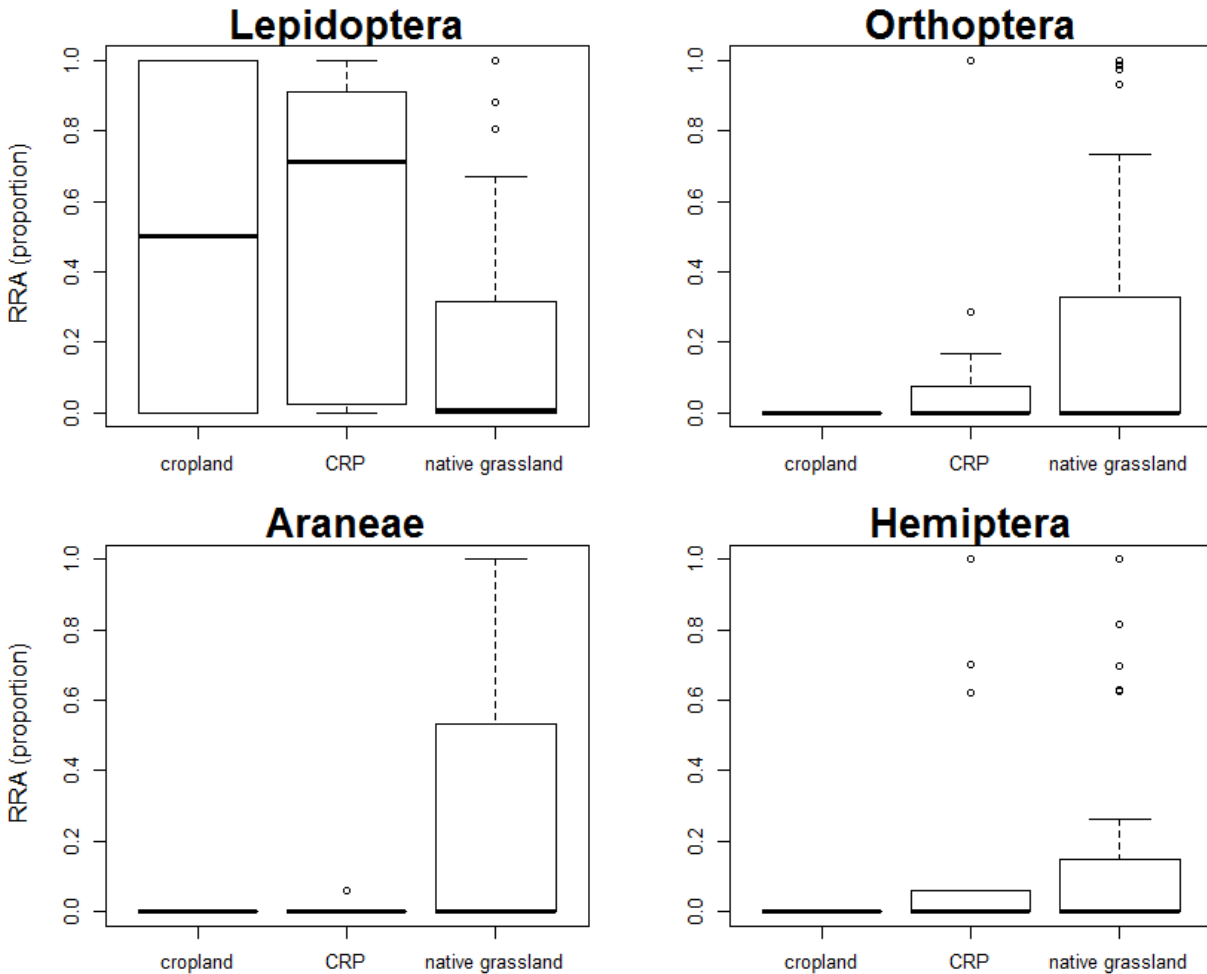
Figure 3.7 The adjusted Relative Readable Abundance (proportion) of DNA within lesser prairie-chicken fecal samples matching barcodes indicative of plant functional groups including forbs, grasses, legumes, and crops. Fecal samples were collected during summer 2014 (Panel A; hatch to 98 days old) from brooding females and chicks and from adults during winter of 2014 – 2015 (Panel B; November to March) in Kansas and Colorado.
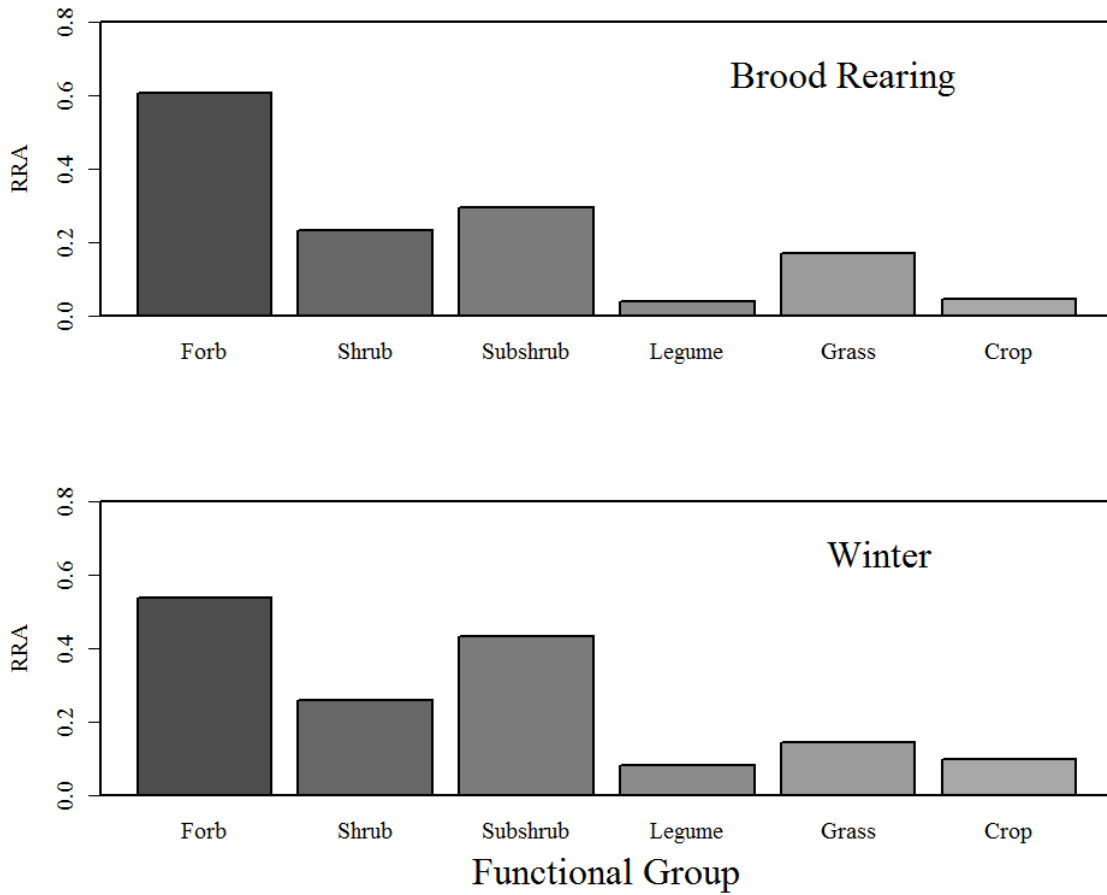
Figure 3.8 The adjusted Relative Readable Abundance (proportion) of DNA within lesser prairie-chicken fecal samples matching barcodes indicative of plant functional groups including forbs, grasses, legumes, and crops grouped by study site. Fecal samples were collected from study sites in Clark County, Kansas (Clark), Gove and Logan counties, Kansas (NW), Kiowa and Comanche counties, Kansas (RH), and in Prowers and Baca counties, Colorado (CO) during winter of 2014 – 2015 (November to March).
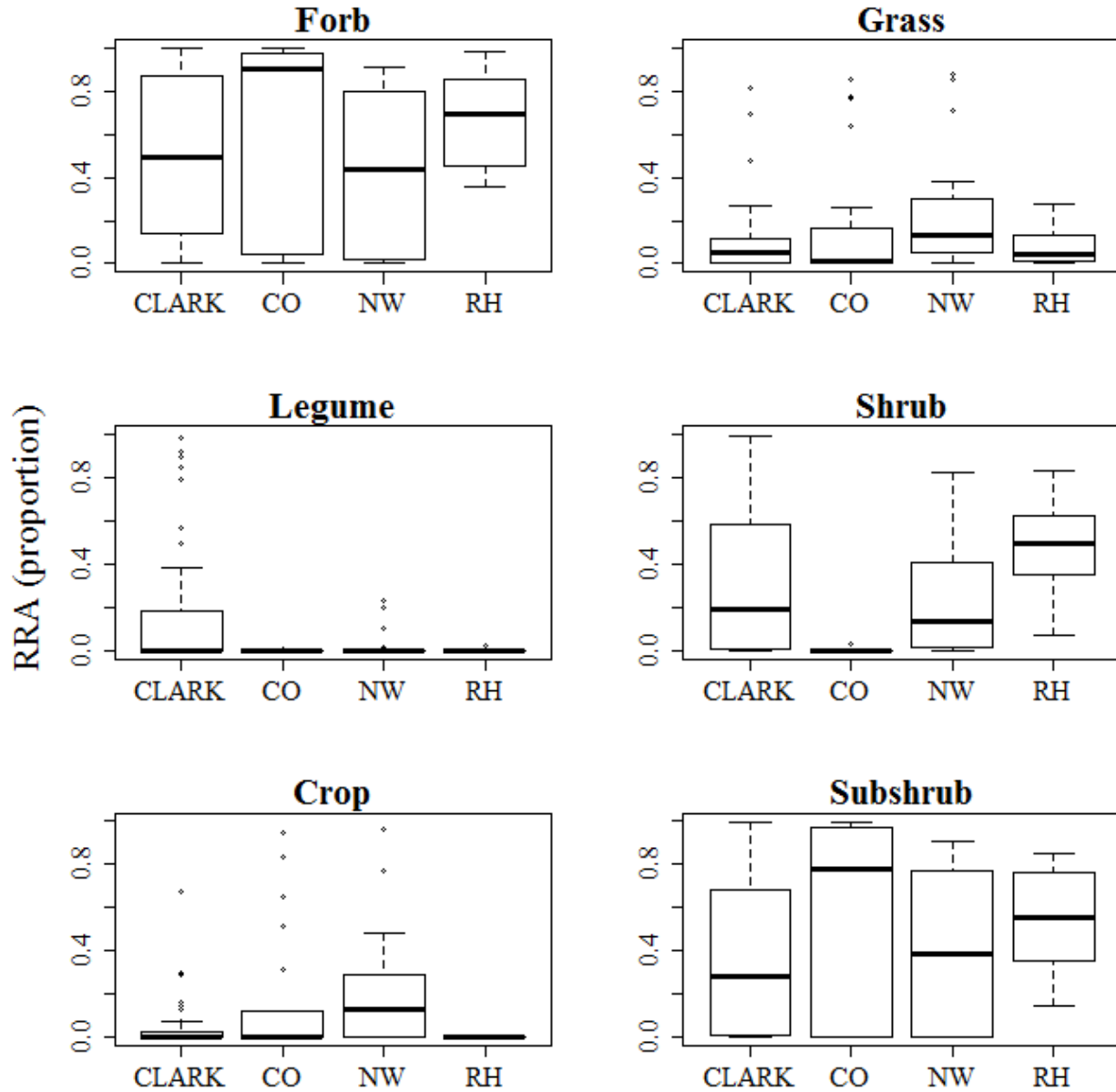
Figure 3.9 The adjusted Relative Readable Abundance (proportion) of DNA within lesser prairie-chicken fecal samples matching plant barcodes indicative of functional groups including forbs, grasses, legumes, and crops grouped by landcover type. Landcover types included cropland, Conservation Reserve Program grasslands (CRP), and native working grasslands (native grassland). Fecal samples were pooled among study sites in Clark County, Kansas (Clark), Gove and Logan counties, Kansas (NW), Kiowa and Comanche counties, Kansas (RH), and in Prowers and Baca counties, Colorado (CO) and were collected during winter of 2014 – 2015 (November to March).
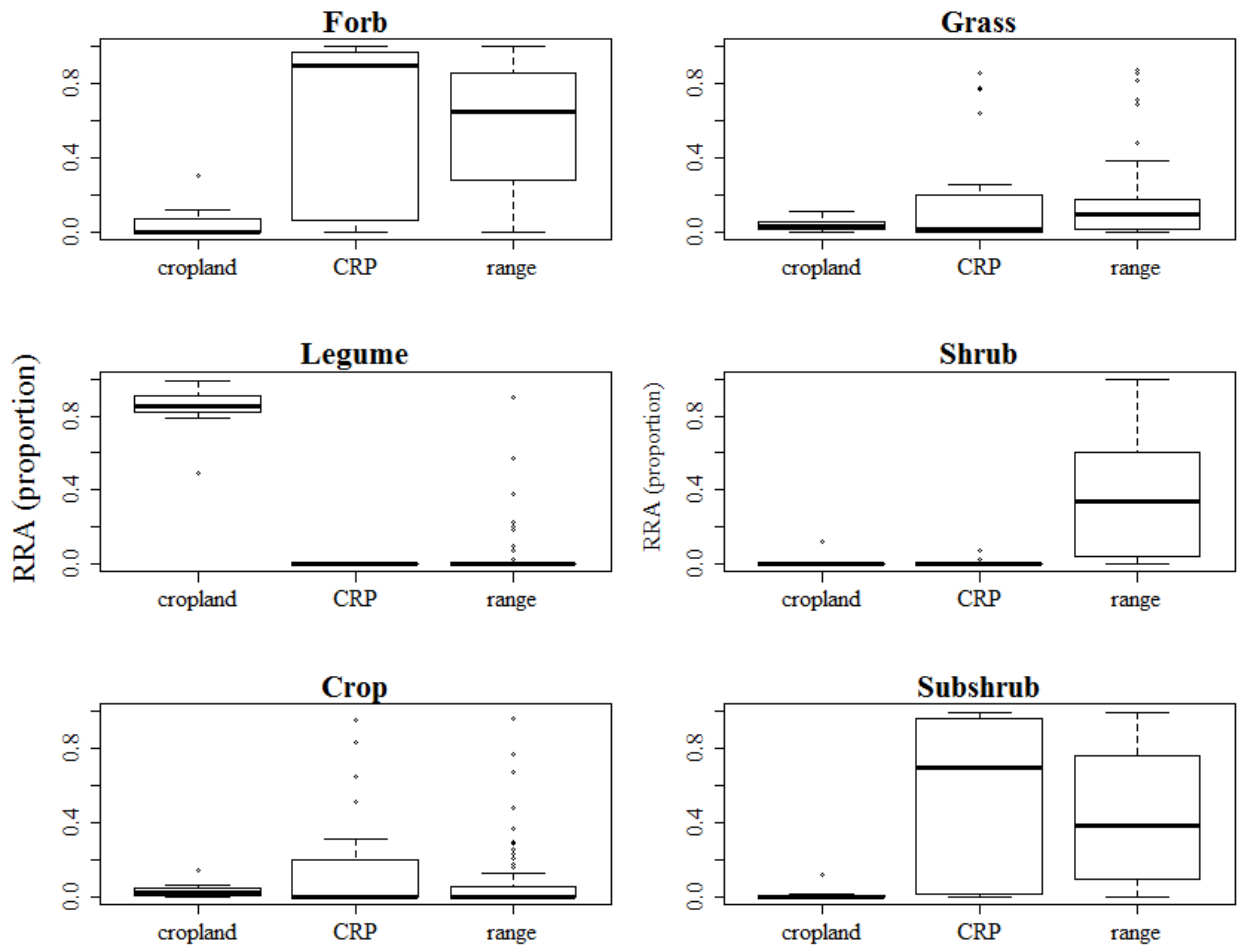
Figure 3.10 Species accumulation curves for plants and arthropods estimated using the r package 'vegan' (Oksanen et al. 2015). The curves depict the relationship between number of Operational Taxonomic Units (OTUs) detected in lesser prairie-chicken fecal samples collected during brood rearing and winter of 2014–2015 in Kansas and Colorado. Lomolino curves: Plants 282.7/(1+17.1^log(2.3/x)) Arthropods: 156.0/(1+105.3^log (2.25/x)).
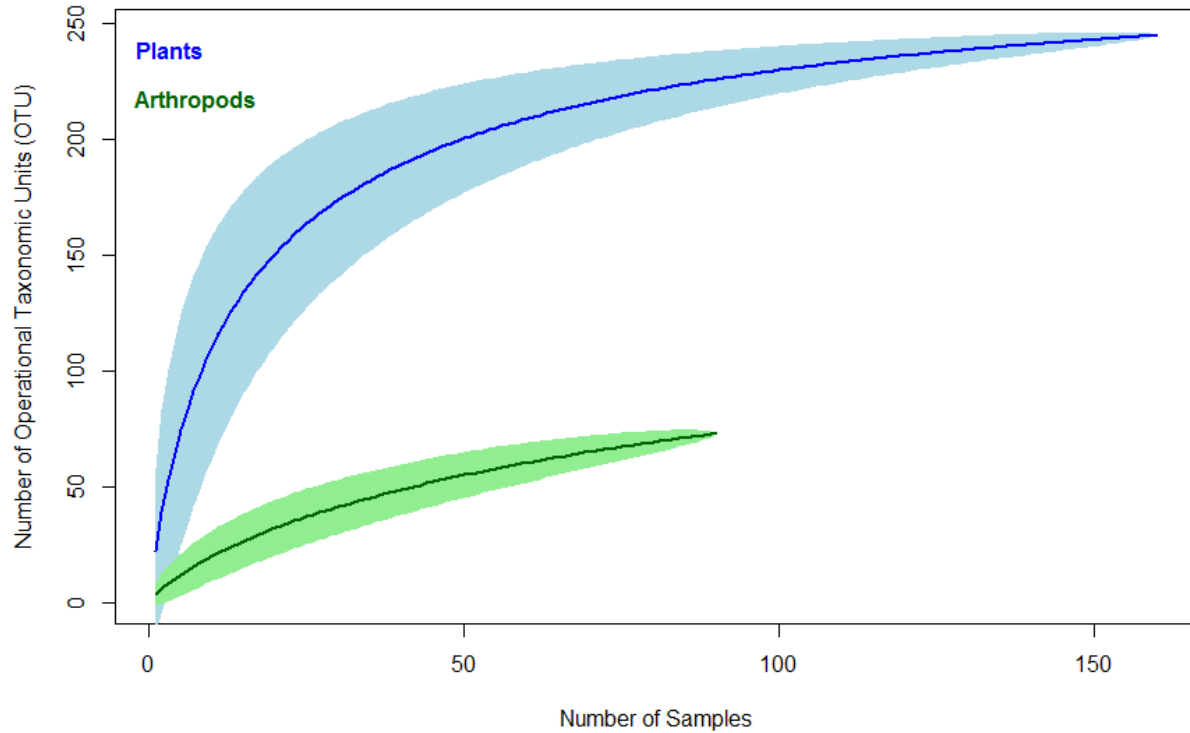
Appendix

Table Error! No text of specified style in document.**.1 Part I of II genera sampled (n = 257) during vegetation surveys in western Kansas and eastern Colorado study sites 2013–2016.**

Available Plant Genera Part I				
Acer	Bouteloua	Cornus	Eriogonum	Indigofera
Achillea	Brickellia	Corydalis	Erioneuron	Ipomoea
Achnatherum	Bromus	Croptilon	Escobaria	Ipomopsis
Aegilops	Buchloe	Croton	Eupatorium	Iva
Agrostis	Calamovilfa	Cryptantha	Euphorbia	Juglans
Allium	Callirhoe	Cucurbita	Euphorbiaceae	Juncus
Amaranthus	Calylophus	Cuscuta	Evolvulus	Juniperus
Ambrosia	Cannabis	Cynodon	Fabaceae	Krameria
Amorpha	Carduus	Cyperaceae	Ferocactus	Lactuca
Andropogon	Carex	Cyperus	Froelichia	Lepidium
Androsace	Castilleja	Dalea	Gaillardia	Lespedeza
Anemone	Catalpa	Delphinium	Galium	Liatris
Antennaria	Celtis	Descurainia	Geum	Linum
Aphanostephus	Cenchrus	Desmanthus	Glandularia	Lithospermum
Apocynum	Cephalanthus	Dianthus	Gleditisia	Lotus
Argemone	Ceris	Dichanthelium	Glycyrrhiza	Lygodesmia
Aristida	Chaeropyllum	Digitaria	Gomphrena	Machaeranthera
Artemisia	Chaetopappa	Distichlis	Grindelia	Maclura
Aruncus	Chamaecrista	Draba	Gutierrezia	Marsilea
Asclepia	Chamaesaracha	Echinacea	Haplopappus	Medicago
Asclepias	Chamaesyce	Echinochloa	Helianthus	Melampodium
Aster	Chenopodium	Elaeagnus	Hesperostipa	Melilotus
Asteraceae	Chloris	Eleocharis	Heterotheca	Menispermum
Astragalus	Cirsium	Elymus	Hibiscus	Mentzelia
Atriplex	Cleome	Engelmannia	Hoffmannseggia	Microseris
Baccharis	Comandra	Equisetum	Hordeum	Mimosa
Baptisia	Commelina	Eragrostis	Hybanthus	Minuartia
Bassia	Convulvulus	Ericameria	Hydrocotyle	Mirabilis
Boltonia	Conyza	Erigeron	Hymenopappus	Monarda
Bothriochloa	Coreopsis	Eriochloa	Hypericum	Muhlenbergia

Table A.1. Cont

Available Plant Genera (Part II)

Nama	Populus	Senecio	Tribulus
Nothoscordum	Portulaca	Setaria	Tridens
Nuttallanthus	Proboscidea	Silphium	Trifolium
Oenother	Prunus	Sisymbrium	Triodanis
Oenothera	Psilostrophe	Sisyrinchium	Tripsacum
Opuntia	Psoralidium	Smilax	Triticum
Oxalis	Pyrrhopappus	Solanum	Typha
Oxytropis	Pyrus	Solidago	Ulmus
Packera	Quincula	Sophora	Urtica
Panicum	Ranunculs	Sorghastrum	Verbascum
Paronychia	Ranunculus	Sorghum	Verbena
Parthenocissus	Ratibida	Spartina	Vernonia
Pascopyron	Rayjacksonia	Sphaeralcea	Vicia
Paspalum	Rhus	Sporobolus	Viola
Pediomelum	Ribes	Stellaria	Vitus
Penstemon	Robinia	Stenaria	Vulpia
Phemeranthus	Rudbeckia	Stenosiphon	Yucca
Phyla	Rumex	Stillingia	Zea
Physalis	Salix	Streptanthus	
Physaria	Salsola	Symphyotrichum	
Phytolacca	Salvia	Tamarix	
Plantago	Sambucus	Taraxacum	
Poa	Sanguisorba	Tephrosia	
Poaceae	Sapindus	Tetraneuris	
Polanisia	Schedonnardus	Thelesperma	
Polygala	Schedonorus	Townsendia	
Polygonaceae	Schizachyrium	Toxicodendron	
Polygonum	Schoenoplectus	Tradescantia	
Polytaenia	Scirpus	Tragia	
Pomaria	Securigera	Tragopogon	

Table Error! No text of specified style in document.**.2 Family and genera of arthropods consumed by lesser prairie-chickens during brood rearing and winter identified with DNA barcoding in Kansas and Colorado 2014-2015.**

Northwest		Clark		Red Hills		Colorado	
Family	*Genus*	*Family*	*Genus*	*Family*	*Genus*	*Family*	*Genus*
Acrididae	Melanoplus	Acrididae	Melanoplus	Acrididae	Melanoplus	Acrididae	Melanoplus
Noctuidae	Dargida	Noctuidae	Dargida	Noctuidae	Dargida	Noctuidae	Dargida
Pentatomidae	Thyanta	Pentatomidae	Thyanta	Pentatomidae	Thyanta	Pentatomid.	Thyanta
Pieridae	Pieris	Pieridae	Pieris	Pieridae	Pieris	Pieridae	Pieris
Araneidae	Argiope	Acrididae	Arphia	Agaonidae	Valisia	Braconidae	Cotesia
Braconidae	Cotesia	Aphididae	Aphis	Araneidae	Argiope	Crambidae	Loxostege
Braconidae	Microplitis	Caeciliusidae	Valenzuela	Cynipidae	Andricus	Cynipidae	Andricus
Caeciliusidae	Valenzuela	Cicadidae	Tibicen	Erebidae	Halysidota	Dermestidae	Anthrenus
Carabidae	Cyclotrachel.	Coreidae	Leptogloss.	Noctuidae	Ponometia	Erebidae	Halysidota
Chrysomelid.	Leptinotarsa	Cynipidae	Andricus	Philodromid.	Philodrom.	Erebidae	Spilosoma
Coccinellidae	Harmonia	Delphacidae	Muirodelphax			Gryllidae	Allonemob.
Crambidae	Loxostege	Diplopoda	Brachyiulus			Gryllidae	Gryllus
Culicidae	Psorophora	Entomobryid.	Entomobrya			Miridae	Lygus
Dermestidae	Anthrenus	Gryllidae	Allonemobius			Noctuidae	Agrotis
Erebidae	Caenurgina	Gryllidae	Gryllus			Noctuidae	Athetis
Erebidae	Pyrrharctia	Muscidae	Musca			Noctuidae	Dargida
Geometridae	Narraga	Noctuidae	Athetis			Noctuidae	Spodoptera
Gryllidae	Gryllus	Noctuidae	Euxoa			Proctophyll.	Monojoube.
Libellulidae	Sympetrum	Noctuidae	Noctua			Salticidae	Phidippus
Miridae	Lygus	Noctuidae	Sunira			Sphingidae	Hyles
Noctuidae	Chrysodeixis	Notodontidae	Dunama			Tineidae	Tinea
Noctuidae	Helicoverpa	Philosciidae	Burmoniscus				
Noctuidae	Leucania	Ptinidae	Stegobium				
Noctuidae	Ponometia	Salticidae	Phidippus				
Noctuidae	Psectrotarsia	Tenthredinidae	Dolerus				
Noctuidae	Spodoptera	Tetragnathidae	Leucauge				
Notodontidae	Dunama	Theridiidae	Latrodectus				
Nymphalidae	Chlosyne	Theridiidae	Parasteatoda				
Proctophyll.	Monojouber.	Thomisidae	Xysticus				
Pterophoridae	Emmelina	Tineidae	Tinea				
Ptinidae	Stegobium						
Pyralidae	Phycitodes						
Salticidae	Phidippus						
Sphingidae	Hyles						
Sphingidae	Manduca						
Theridiidae	Latrodectus						
Tineidae	Tinea						

[*]All fly related taxa (Diptera) were removed as after defecation contamination. Taxa underlined are those common among all study sites.

Table Error! No text of specified style in document.**.3 Sample size, mean, and standard deviations of relative read abundance of arthropod orders in the diets of chicks and adults during the brooding period and adults during winter in Kansas and Colorado 2014–2015. Only one sample had readable DNA from CO; SD = NA.**

		NW			RH			Clark			CO	
Order	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Brood rearing												
Araneae	25	0.135	0.283	5	0.400	0.548	17	0.196	0.392	1	0.000	NA
Coleoptera	25	0.007	0.017	5	0.000	0.000	17	0.000	0.000	1	0.000	NA
Diptera	25	0.151	0.327	5	0.200	0.447	17	0.002	0.007	1	0.000	NA
Entomobryomorpha	25	0.000	0.000	5	0.000	0.000	17	0.000	0.000	1	0.000	NA
Hemiptera	25	0.207	0.320	5	0.000	0.000	17	0.113	0.280	1	0.000	NA
Hymenoptera	25	0.010	0.037	5	0.000	0.000	17	0.000	0.000	1	1.000	NA
Isopoda	25	0.000	0.000	5	0.000	0.000	17	0.116	0.326	1	0.000	NA
Lepidoptera	25	0.416	0.385	5	0.214	0.441	17	0.217	0.393	1	0.000	NA
Odonata	25	0.008	0.038	5	0.000	0.000	17	0.000	0.000	1	0.000	NA
Orthoptera	25	0.066	0.205	5	0.187	0.417	17	0.364	0.425	1	0.000	NA
Psocoptera	25	0.000	0.001	5	0.000	0.000	17	0.000	0.000	1	0.000	NA
Sarcoptiformes	25	0.001	0.003	5	0.000	0.000	17	0.000	0.000	1	0.000	NA
Winter												
Araneae	2	0.000	0.000	6	0.167	0.408	12	0.025	0.069	10	0.020	0.054
Coleoptera	2	0.375	0.530	6	0.000	0.000	12	0.023	0.057	10	0.002	0.007
Diptera	2	0.500	0.707	6	0.000	0.000	12	0.046	0.113	10	0.120	0.313
Entomobryomorpha	2	0.000	0.000	6	0.000	0.000	12	0.021	0.073	10	0.000	0.000
Hemiptera	2	0.000	0.000	6	0.167	0.408	12	0.046	0.105	10	0.058	0.183
Hymenoptera	2	0.000	0.000	6	0.333	0.516	12	0.112	0.287	10	0.114	0.314
Isopoda	2	0.000	0.000	6	0.000	0.000	12	0.000	0.000	10	0.000	0.000
Lepidoptera	2	0.125	0.177	6	0.333	0.516	12	0.188	0.305	10	0.495	0.383
Odonata	2	0.000	0.000	6	0.000	0.000	12	0.000	0.000	10	0.000	0.000
Orthoptera	2	0.000	0.000	6	0.000	0.000	12	0.518	0.438	10	0.184	0.244
Psocoptera	2	0.000	0.000	6	0.000	0.000	12	0.010	0.035	10	0.000	0.000
Sarcoptiformes	2	0.000	0.000	6	0.000	0.000	12	0.011	0.026	10	0.007	0.022

Chapter 4 - Selection and Demographic Consequences of Conservation Reserve Program Grasslands for Lesser Prairie-Chickens

Introduction

Populations of lesser prairie-chickens (*Tympanuchus pallidicinctus*) have decreased in occupied range and density since the 1980s, leading to a temporary listing as threatened under the Endangered Species Act of 1973, as amended, from May 2014 – July 2016 (Taylor and Guthery 1980, Giesen 1994, Jensen et al. 2000, Haukos and Boal 2016, Garton et al. 2016, Van Pelt 2016, Ross et al. 2016a). Removal of the lesser prairie-chicken from the list of threatened species was in response to a judicial decision in September 2015 to vacate the final listing rule on procedural grounds (Federal Register 2016). However, environmental conditions considered to contribute to population declines, such as grassland conversion to other uses or cover types and periodic drought continue to affect the lesser prairie-chicken across its range (Fuhlendorf et al. 2002, Silvy et al. 2004, Wolfe et al. 2007, Askins et al. 2007, Lautenbach et al. 2017, Robinson et al. 2016, Haukos and Boal 2016). Although it is recognized that lesser prairie-chicken populations require large areas of grasslands with adequate vegetative cover to persist, episodic periods of drought and above-average precipitation are thought to drive a boom-or-bust life history strategy that results in considerable inter-annual variation in abundance (Grisham et al. 2013, Haukos and Zavaleta 2016, Ross et al. 2016a).

In contrast to the range-wide declining population trajectory and broad-scale habitat loss throughout much of their occupied range, lesser prairie-chickens have expanded their range and significantly increased in abundance in the Short-Grass Prairie/CRP Mosaic Ecoregion of

175

northwest Kansas, USA (north of the Arkansas River; Figure 4.1) since the mid-1990s (Rodgers 1999, Jensen et al. 2000, McDonald et al. 2014, Dahlgren et al. 2016, Garton et al. 2016, Rodgers 2016). There is limited indication of lesser prairie-chicken occurrence in this ecoregion prior to the late 1990s and a possible factor contributing to population expansion in the Short-Grass Prairie/CRP Mosaic Ecoregion is a response to the maturation of U.S. Department of Agriculture Conservation Reserve Program (CRP) grasslands (Rodgers 1999, Hagen 2003, Dahlgren et al. 2016, Rodgers 2016, Spencer et al. 2017). Alternatively, there was limited survey effort for lesser prairie-chickens in areas north of the Arkansas river prior to becoming a candidate for the Endangered Species Act in 1998 (Hagen 2003, Rodgers 2016). Hagen (2003) summarized reports of lesser prairie-chickens throughout Kansas and noted records of a harvested lesser prairie-chicken in Logan County in 1921, the occurrence of 2 small populations further south near the SW border of Lane County and near the NE corner of Finney County in 1955, and records of unknown prairie-chicken species further east in Ellis and Rush counties from 1962–1976 (Baker 1953, Schwilling 1955, Waddell 1977). The limited records suggest lesser prairie-chickens were sparsely distributed in northwest Kansas following European settlement but prior to the maturation of CRP grasslands in the region. In contrast, Short-Grass Prairie/CRP Mosaic Ecoregion may currently support ~55% of the estimated lesser prairie-chicken range-wide population (McDonald et al. 2014;2016).

Throughout the northern distribution of the lesser prairie-chicken's range, a precipitation gradient results in a distinct east-to-west transition from mixed-grass to short-grass prairie (Grisham et al. 2016). The short-grass prairie becomes increasingly predominant in the western portions of the distribution and rarely provides vegetation tall enough for use by lesser prairie-chickens without an associated shrub component (Giesen 1994). Frequent drought and lack of

176

adequate vegetation structure may have limited lesser prairie-chicken occupancy and abundance to low, apparently undetectable levels prior to the advent of CRP (Rodgers and Hoffman 2005, Dahlgren et al. 2016, Rodgers 2016). Some experts suggest that lesser prairie-chickens were formerly confined to relatively small patches of mixed-grass, sand sagebrush (*Artemsia filifolia*), and sand shinnery oak (Quercus havardii) prairie throughout much of their estimated range west of the 100th Meridian in the High Plains (Haukos and Zaveleta 2016, Rodgers 2016). The addition of CRP grasslands to landscapes of short-grass prairie in northwest Kansas, may mimic these natural patches of taller vegetation which typically occur on sandy soils, in somewhat moister microclimates, on north facing slopes, or in drainages.

Adding taller vegetation with dense litter in the form of CRP grasslands to a short-grass prairie landscape would not only increase the amount of cover, it would also increase landscape heterogeneity. Spatial heterogeneity can be particularly important for generating stability and maintaining habitat for multiple species within the grassland bird community (Knopf 1996, Hovick et al. 2015), and multiple life stages of prairie-chickens and other ground-nesting birds (Knopf 1996, Fuhlendorf et al. 2006, McNew et al. 2015, Sandercock et al. 2015). Heterogeneity established by the taller vegetation and thick litter layer of CRP in a matrix of short-grass prairie with more open canopy may create a landscape capable of supporting both nesting and brood rearing life-stages for lesser prairie-chickens (Hagen et al. 2013). Additionally, a lack of grazing and the native tallgrass species composition of CRP may ensure the presence of habitat during drought, when short-grass prairie growth is limited and contributes little to available lesser prairie-chicken habitat. Spatial heterogeneity is important in ensuring available habitat in the Southern Great Plains, which exhibit strong temporal and spatial variation in net primary productivity (Sala et al. 1998, Grisham et al. 2016).

Managing for heterogeneity at a landscape scale in grasslands will improve the odds of providing some quality habitat for all life stages in a stochastic ecosystem. However, at the patch scale, there are some predictable characteristics of CRP in comparison to native working grasslands such as the provision of residual cover suitable for nesting. Further, CRP could provide habitat that is otherwise limited during unfavorable environmental periods. Amid the variability of grasslands in the Southern Great Plains, the presence or absence of a limiting factor at one critical point in time may determine long term population dynamics (Edwards and Fowle 1955). Understanding predictable aspects will be key to achieving the optimal composition and configuration of CRP in a landscape design for lesser prairie-chickens. I would expect relatively undisturbed CRP grasslands dense in thatch and taller vegetative cover to meet the needs of nesting lesser prairie-chickens and potentially for adult birds seeking concealment from predators (Rodgers and Hoffman 2005, Fields et al. 2006). A previous study in the Short-Grass Prairie/CRP Mosaic Ecoregion found 70% (41/59) of detected lesser prairie-chicken nests in CRP; however, only 37% (10/27) of broods spent the majority of time in CRP compared to other cover types (Fields et al. 2006). Nesting cover may be readily available throughout native working grassland during wet years; however, during drought years, patches of shrubs and CRP grasslands may provide the only available nesting habitat (Grisham et al. 2013, Haukos and Zaveleta 2016). In short-grass dominated landscapes, the added refugia and stability of CRP grasslands would likely increase the resistance and resiliency of populations to intensive drought. In contrast, the more limited habitat may increase risk of predation if predators conduct area concentrated searches in quality habitat (Ringelman 2014).

Alternatively, the ecological response of lesser prairie-chickens to CRP grasslands in the short-grass prairie may have nothing to do with the structure of the grasslands. Grasslands in

northwest Kansas are comparatively more fragmented than other areas of the state occupied by lesser prairie-chickens (Spencer et al. 2017). In landscapes that consist of <60% grassland, general availability of grasslands may be most limiting for lesser prairie-chickens (Crawford and Bolen 1976). Conversion of marginal croplands back into grasslands through the CRP could allow landscapes to surpass a critical threshold. Further, the increased grassland composition provides an additional mechanism to stabilize populations. Ross et al. (2016b) linked the amount of available grassland within a 3-km landscape surrounding leks to the resilience of lesser prairie-chicken populations to drought.

Beyond increasing available habitat, CRP could provide greater quality habitat than available on the landscape for lesser prairie-chickens. During a 2-year study, Fields et al. (2006) determined that lesser prairie-chickens use CRP in the Short-Grass Prairie/CRP Mosaic Ecoregion as reproductive habitat, but individuals accrued no added fitness benefits compared to those nesting in other cover types. Although CRP may not improve reproductive fitness at the individual level, population level mechanisms by which CRP grasslands influence lesser prairie-chickens are unknown. Specifically, it remains unclear if CRP grasslands provide high quality habitat for lesser prairie-chickens, merely increase the amount of available habitat above an extinction threshold, or provide for a limiting life-stage specific habitat at a landscape scale. . Through some combination of these three mechanisms, addition of CRP to northwest Kansas landscapes was likely a culminating beneficial influence in an area of appropriate climate, landscape composition, and landscape configuration (Rodgers and Hoffman 2005, Dahlgren et al. 2016, Rodgers 2016).

I did not expect typical CRP grasslands to meet the needs of all stages of the lesser prairie-chicken life cycle because it may produce cover that is too thick or coarse for use by

chicks and provide limited food due to lack of forbs; therefore, utility of CRP is likely influenced by the surrounding matrix at a landscape scale (Fields et al. 2006). Additionally, I did not expect CRP grasslands to influence populations throughout the distribution of lesser prairie-chickens in the same manner because of differing vegetative structures realized based on annual average precipitation. Last, in landscapes where CRP is used by lesser prairie-chickens, we need knowledge of how CRP influences vital rates at both individual and population levels. It remains uncertain if lesser prairie-chickens maximize fitness when selecting CRP, as depicted in an ideal free distribution (Fretwell and Lucas 1970), or if CRP grasslands may be functioning as ecological traps (Gates and Gysel 1978). In sum, this information can be used to target conservation efforts and develop management strategies. To fill knowledge gaps, I first identified landscape and regional climatic constraints in which CRP becomes usable by lesser prairie-chickens. I then assessed the fitness of individuals using CRP and other grassland cover types based on their finite rate of population growth (λ) and vital rates (e.g., nest, chick, and adult survival). Overall, I describe the circumstances in which CRP provides habitat for lesser prairie-chickens and demographic performance of birds using CRP.

Methods

Study Area

The study area encompassed the mixed- to short-grass portions of the lesser prairie-chicken range in Kansas and Colorado, USA (Figure 4.1). A longitudinal precipitation gradient spanned from east (~69 cm) to west (~37 cm) across the extent of Kansas into eastern Colorado with a concomitant transition from mixed- to short-grass prairie (PRISM 2016, Grisham et al. 2016). Pockets of sand sagebrush prairie were interspersed on sandy soils, especially in the southwest portion of the study area. Mosaics of CRP and row-crop agriculture were associated

in areas with arable soils. Most of the large grasslands that still remain were restricted to areas of, sandy/rocky soils or areas with rough terrain (Spencer et al. 2017). Within the study area, habitat selection and vital rate data were collected at 5 study sites including 2 in Colorado and 3 in Kansas (Figure 4.1). Temperatures ranged from -26 to +43° C (extreme minimum and maximum temperature), with average daily minimum and maximum temperatures of 5° C and 21° C, respectively, during the period of data collection (15 March 2013 to 15 March 2016; NOAA 2016a).

Both the Red Hills and Clark study sites were located in the Mixed- Grass Prairie Ecoregion while the Logan and Gove Study sites were located in the Shortgrass/CRP Mosaic Ecoregion of their current range (McDonald et al. 2014). The Cheyenne County and Prowers County study sites each represent isolated portions of their current range in Colorado and occurred within the Sand Sagebrush Prairie (Hagen and Giesen 2005, McDonald et al. 2014). All study sites were used to assess the influence of average annual precipitation on use of CRP by lesser prairie-chickens: however, demographic modeling and landscape scale resource selection results in this study focused on northwest Kansas study sites in Gove and Logan Counties (Figure 4.1).

The northwest Kansas study site was located in Gove and Logan counties. Annual average long-term (30 year) precipitation varies between 47 and 52 cm in Gove and Logan counties respectively (PRISM 2016). The portion of the study site occurring in Logan County (41,940 ha) was comprised of relatively more short-grass prairie and less precipitation than the Gove County (87,822 ha) portion to the east as the transition between semi-arid and temperate precipitation levels divided the study site (Plumb 2015, Robinson 2015). Dominant plant species on the northwest Kansas study site included sideoats grama (*Bouteloua curtipendula*), blue

grama (*Bouteloua gracilis*), sand dropseed, western wheatgrass (*Pascapyron smithii*), little bluestem (*Schizachyrim scoparium*), broomed snakeweed (*Gutierrezia sarothrae*), purple threeawn (*Aristida purpurea*), and annual bromes (*Bromus tectorum*; D.A. Haukos, unpublished data). The study site was a mosaic of CRP (7.4%), cropland (36%), and native short-grass or mixed-grass prairie (54%; Robinson et al. in review). Soils were predominantly silt loams (80% and 75% of soil type by site, respectively), but clay loams and fine sandy loams were also present (Soil Survey Staff 2015). Research was mostly conducted on private, working grasslands, but also included the Smoky Valley Ranch (SVR; 6,600 ha) in Logan County, owned and operated by The Nature Conservancy. Historical ecological drivers that maintained grasslands at the northwest study site included periods of drought, bison grazing, and fire. However, fire is largely absent from the current landscape and grazing by cattle is standardized within fenced pastures. A full season, rotational grazing operation for both cow/calf and yearling herds was the dominant system used among local ranchers. A significant portion of CRP was hayed prior to and during the study due to drought conditions, a few tracts were inter-seeded and disked, and others were undisturbed and idle. Precipitation varied and Palmer Drought Severity Indices (PDSI; smaller number = more severe drought) were -3.4, -0.67, and 0.39 during the breeding season (March – August) and -1.85, -0.16, and 0.38 during the nonbreeding season (September – February) of 2013, 2014, and 2015, respectively (Augustine 2010, NOAA 2016b). During the nesting period (April to July), PDSI were estimated at -3.44, -1.58, and 0.57 in 2013, 2014, and 2015, respectively (NOAA 2016b). Annual precipitation was 39 cm, 48 cm, and 49 cm in 2013, 2014, and 2015 respectively (NOAA 2016a).

The Clark study site was primarily located in western Clark County, Kansas, on the transition between of the mixed-grass prairie and sand sagebrush prairie. On average, the site

received 59 cm of rain annually and was dominated by sand dropseed (*Sporobolus cryptandrus*), western ragweed (*Ambrosia psilostachya*), blue grama, Russian thistle (*Salsola tragus*), little bluestem, alkali sacaton (*Sporobolus airoides*), and sand sagebrush (D.A. Haukos, unpublished data; PRISM 2016). The Clark site was 77% grassland, 14% cropland, and 5.5% CRP (Robinson et al. in review) and was largely comprised of 2 privately owned ranches; one in the Cimarron River floodplain (32,656 ha) dominated by loamy fine sands, fine sandy loams, and fine sands with the other in rolling hills (14,810 ha) 20 km north on mostly silty clay, clay loam, and silt loam (Soil Survey Staff 2015). Rotational grazing systems for both cow/calf and yearling herds were used in this area. Stocking rates were set to achieve 50% utilization rates for forage produced each growing season on the study ranches.

The Red Hills study site (49,111 ha) was located in the mixed-grass prairie of Comanche and Kiowa counties and represented the eastern boundary of the current lesser prairie-chicken range. The Red Hills study site was not only the most eastern study area, but also received the greatest annual precipitation, where average annual precipitation is 69 cm (PRISM 2016). Dominant plant species included little bluestem, Louisiana sagewort (*Artemisia ludiviciana*), sideoats grama, western ragweed, sand dropseed, annual bromes, and blue grama (D.A. Haukos, unpubl. data). The Red Hills study site was 87% grassland, 8.9% cropland, and 2.2% CRP (Robinson et al. in review). The site was comprised of large contiguous grasslands with many drainages and both cow/calf and yearling (season long) grazing systems. Research efforts focused on a large ranch that implemented a patch-burn grazing system wherein large pastures were divided into thirds or fourths and a portion was sequentially burned annually. Dominant soils include sandy loam, clay loam, and clay (Soil Survey Staff 2015).

183

Two study sites in Colorado were dominated by sideoats grama, blue grama, sand dropseed, sand sagebrush, field bindweed (*Convolvulus arvensis*), Russian thistle, and kochia (*Kochia scoparia*; J. Reitz, unpubl. data). The Prowers County study site (1,146 ha) was comprised of relict patches of grassland (largely CRP) within a landscape mosaic of dryland and irrigated row-crop agriculture. The study site was composed of 43% cropland, 28% native working grassland, and 25% CRP (Homer et al. 2015). Prowers County was dominantly comprised of loamy soils (Soil Survey Staff 2015) and received 43 cm of precipitation annually (PRISM 2016). Most CRP fields were enrolled into the program in the mid-1980s. Many tracts had recently undergone mid-contract management to increase forb abundance and diversity. To meet the management requirements, typically 1/3 of the CRP fields were disked creating linear strips of disturbed and undisturbed grass (J. Reitz, Colorado Parks and Wildlife, pers. comm.). The study site in Cheyenne County (16,968 ha) was comprised of large expanses of lightly and heavily grazed sand sagebrush prairie where 30-year precipitation averages were lowest of all study sites (37 cm, PRISM 2016). The Cheyenne County study site was composed of 99% native working grassland and 1% cropland both largely occurring on sandy soils (Homer et al. 2015, Soil Survey Staff 2015).

Capture and Marking

Lesser prairie-chickens were captured on leks at all study sites between early March and mid-May using walk-in funnel traps and drop nets (Haukos et al. 1990, Silvy et al. 1990). Upon capture, lesser prairie-chickens were sexed based on plumage coloration, pinnae length, and tail pattern (Copelin 1963). Each individual was aged as either yearling (SY) or adult (ASY) depending on the color patterns, shape, and wear of the outermost flight feathers (P9 and P10; Ammann 1944). I prepared protocols and obtained collection permits to capture and handle

184

through the Kansas State University Institutional Animal Care and Use Committee protocols #3241 and #3703, Kansas Department of Wildlife, Parks, and Tourism scientific collection permits SC-042-2013, SC-079-2014, and SC-001-2015 and the Colorado Parks and Wildlife scientific collection license numbers 13TRb2053, 14TRb2053, and 15TRb2053.

Captured females were fitted with 4 plastic leg bands corresponding to region, year, and lek to identify and resight individuals in the field. They were tagged with either a 15-g very-high-frequency (VHF; A3960, Advanced Telemetry System, Isanti, MN, USA) transmitter or 22-g GPS (global positioning system) satellite PTT transmitter (SAT-PTT; PTT-100, Microwave Technology, Columbia, MD, USA and North Star Science and Technology, King George, VA, USA) and released (Robinson et al. 2016). I obtained locations for each VHF-marked female 4 times per week using triangulation and Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary). I typically downloaded 8-10 GPS locations/day from each satellite-marked female using the ARGOS system, contingent on available daily solar charge. GPS locations were recorded every 2 hours during the day with a 6-hour gap between 2300 and 0500 when birds were assumed to be roosting.

 Vegetation Characteristics of CRP and Native Working Grasslands

Measurements of grassland variables were collected at random point locations distributed among CRP and native working grasslands available to lesser prairie-chickens within the northwest Kansas study site. Available points were randomly generated throughout the study sites at a rate of 1 per 4 ha with a maximum of 10 points per patch. User-defined habitat patches were delineated and digitized in ArcGIS 10.2 using aerial imagery available in the basemap layer (product of: ESRI, i-cubed, USDA FSA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGP). Patches were identified as areas of homogenous vegetation >2 ha in size and placed in categories

(e.g., grassland, grassland lowland, and CRP) and confirmed upon ground truthing. Vegetation was measured at points within all delineated patches during summer and within a stratified random sample of 20% of patches during fall and winter.

At all random locations, a point-center measurement of percent canopy cover of forbs, bare ground, grass, shrub, and annual bromes were estimated within a 60 x 60-cm modified Daubenmire frame (Daubenmire 1959). Four additional estimates of canopy cover were estimated 4 m from point center at all cardinal directions (5 estimates/point). Visual obstruction readings were taken 4 m from point center at all cardinal directions and I recorded height in dm at which 100%, 75%, 50%, 25%, and 0% cover were estimated (4 estimates/point; Robel et al. 1970). Litter depth (cm) was measured at 0.5-m increments stretching 4 m north, east, south, and west of point center (32 estimates/point; Davis et al. 1979). The 3 most abundant species within a 4-m radius of each point was estimated ocularly.

From the top 3 most abundant plant species data, I estimated the frequency of tall grass species occurrence at locations with CRP and native working grasslands. Dominant Tallgrass species included little bluestem, big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*). The occurrence of these tall-grass species is suggested to be an indicator of quality nesting cover for lesser prairie-chickens (Hagen et al. 2013). I also directly estimated the proportion of random points that met characteristics of available nesting habitat following Lautenbach (2015). Available nesting locations had a 75% VOR in the range of 1.5–3.5 dm and bare ground cover estimates <20% when averaged among measurements taken at each random point (e.g., 4-m radius microhabitat; Lautenbach 2015). I used a Hotelling T2 test to examine a multivariate difference among vegetation measured in CRP and native working grasslands (Johnson and Wichern 1988). Once a significant variation was

identified in multivariate space ($p < 0.05$), I then used an unequal variances Welch two sample t-test to examine differences in all vegetative measurements among CRP and native working grasslands.

Use of CRP

To describe frequency and timing of lesser prairie-chicken use of CRP grasslands in northwest Kansas, I estimated the proportion of locations from GPS marked individuals that occurred in cropland, native working grassland, and CRP grassland during the breeding (15 March–15 September) and nonbreeding seasons (16 September–14 March) from 2013–2016. I used GIS layers from the National Landcover Database (NLCD) 2011 and a CRP layer provided under agreement by the U.S. Department of Agriculture Farm Services Agency to delineate cropland, native working grassland, and CRP grassland land cover types (Homer et al. 2015). I then overlaid all locations from GPS marked individuals and estimated the proportion of locations occurring in each cover type during each season and all seasons combined.

Selection of CRP

All the resource selection methods below were conceived and conducted by John Kraft. I synthesized the results with all demographic, use, and vegetation data to develop this chapter. I used "we" below to describe tasks largely conducted by John Kraft with minor support from myself.

Influence of temporal and spatial variability of precipitation on selection. —We investigated selection of CRP grasslands from 2 perspectives. First, we evaluated the influence of longitude and average annual precipitation on the use of CRP lands across lesser prairie-chicken populations in Kansas and Colorado (all study sites). Second, we investigated the influence of PDSI (Palmer Drought Severity Index) on selection of land cover types within the

northwest Kansas site (Gove and Logan counties). We used PDSI to estimate drought severity to make results comparable to other lesser prairie-chicken research and because of the utility of PDSI in large areas of uniform topography (Hayes 1998, Ross et al. 2016a,b).

To examine how the east-to-west spatial variability of 30-year average annual precipitation influenced selection of cover type by lesser prairie-chickens in Kansas and Colorado from April 2013-March 2016, we compared locations for lesser prairie-chickens that occurred in CRP (coded 1) to bird locations occurring in non-CRP cover types (coded 0) using logistic regression. We used longitude and average annual precipitation as covariates. Average annual precipitation was assigned to each bird location using the 30-year normal precipitation values calculated and made available by the PRISM Climate Group (PRISM 2016). We investigated both longitude and average annual precipitation as single variable models alongside a null model and used a model ranking protocol outlined below to identify the most parsimonious model.

After we tested how the long-term spatial variability of precipitation influences the use of CRP among individual lesser prairie-chickens throughout the study area, we also investigated how selection of CRP grasslands varied temporally with change in precipitation at the northwest Kansas site. Further analysis employed a used vs. available resource selection framework at the population scale. Used locations from marked birds were assigned a value of 1 as the response variable. We sub-sampled the pool of bird locations using the sample() command in Program R to one location per bird per day to limit potential temporal and spatial autocorrelation associated with SAT-PTT locations. To define resources available to the population, we distributed one random location for each bird location. Random/paired locations were constrained within the northwest study site boundary (Figure 4.1) and assigned the same date as the corresponding used

location. All random/paired locations were assigned a response variable of 0. For all locations (used and random/paired), we identified a cover type category following Spencer et al. (2017). Three different PDSI values were assigned to each location as well. Lag PDSI described the average PDSI value calculated during the previous 12-month period from April-March. Thus, a location recorded during July of 2014 would be assigned the mean PDSI value calculated from April 2013-March 2014. Monthly PDSI described the PDSI value associated with the same month during which the location was recorded. Average Growing Season PDSI was the mean value of PDSI calculated during the growing season (April-September) of the current year. For example, the PDSI value associated with a location recorded in October 2014 was the mean PDSI calculated during April-September 2014. From these covariates (landcover type, Lag PDSI, Monthly PDSI, and Average Growing Season PDSI), we developed a priori models and ranked them post model fitting using the model ranking protocol described below.

Influence of the surrounding matrix.—Efforts to assess the influence of the surrounding matrix on lesser prairie-chicken selection of CRP grasslands were focused on the northwest Kansas study site. We compared landscapes associated with CRP tracts used by lesser prairie-chickens to random landscapes that also had a CRP component.

Similar to selection analyses described previously, we employed logistic regression in the form of a resource selection function to investigate the influence of the matrix surrounding CRP grasslands on selection (Manly et al. 1992, Boyce et al. 2002). With the used vs. available framework, we identified bird locations from April 2013-March 2016 that were located in CRP lands and distributed the same number random or available locations in CRP lands located throughout the Short-Grass Prairie/CRP Mosaic Ecoregion encompassing the northwest Kansas study site (McDonald et al. 2014). Landscapes were delineated by buffering each location by 4

km using the Buffer Tool in ArcGIS using landcover maps created through concurrent research (Spencer et al. 2017). In northwest Kansas, the surrounding matrix for CRP grasslands was largely restricted to either cropland or working native grassland cover types. Thus, what was not working native grassland was typically cropland. We evaluated the influence of total area of grassland on lesser prairie-chicken use of CRP grasslands. In doing so, we also provide inference on the potential effect of total area of cropland on the response variable. Total area (TA) of working native grassland in the 4-km radius landscapes was estimated using FRAGSTATS (McGarigal et al. 2012). The 4-km radius scale outcompeted other models incorporating landscapes within a 2-km radius based on AICc (J. Kraft, unpubl. data). We only evaluated total area grassland to provide a relationship that would be implemented by wildlife managers, and because the patterns of habitat fragmentation are rarely as influential as total habitat loss (Andren 1994).

Model selection and evaluation. —We employed resource selection functions to evaluate the temporal and spatial influence of precipitation and influence of surrounding matrix on selection of CRP grasslands by lesser prairie-chickens (Manly et al. 2002, Boyce et al. 2002). Correlations between pairs of covariates were examined, and correlated variables ($r > 0.70$) were not allowed within the same model. After model fitting, we ranked and selected the most parsimonious model based AICc and informative beta coefficients (Burnham and Anderson 2002). Models with ΔAICc ≤ 2 were considered competitive. Untransformed beta estimates from the top ranking model were informative when coefficients differed from zero at the 95% confidence interval. To visualize predicted probability of use curves for top models in each model set, we used the following logistic function where x1 and x2 are two explanatory factors:

$$F(x) = [\exp(\beta 0 + \beta 1(x1) + \beta 2(x2))] / [\ 1 + \exp(\beta 0 + \beta 1(x1) + \beta 2(x2))]$$

190

We conducted all resource selection functions in Program R (R Development Core Team 2016) using the glm package for generalized linear models.

Demographic Rates

Vital Rate Data Collection.— Vital rates and population growth were estimated only for lesser prairie-chickens at the northwest Kansas study site to assess to population level influence of CRP in the region. Fecundity and survival data were collected during the breeding seasons (15 March – 15 September) and nonbreeding seasons (16 March –14 September) of 2013–2016 (Table 4.1). During the breeding season, searches for nest locations occurred when females localized for >3 days or appeared to be nesting based on satellite data. Upon discovery of the nest, with nest location recorded in GPS and eggs were counted and floated to predict hatch date. Nests were monitored remotely by telemetry for VHF transmittered lesser prairie-chickens and by examining satellite locations for GPS transmittered birds. Once a female left a nest location, I visited the area to identify nest success or failure based on eggshell appearance and presence/absence of predator sign at the nest site. If a nest was successful, I monitored brood and chick survival by conducting brood flush counts at lesser prairie-chicken female locations within 1 hr of sunrise at weekly intervals from 14 to 60 days after hatch. I thoroughly searched the area surrounding each transmittered female to maximize chick detection. If no chicks were detected, I flushed the female once more to make sure the brood was no longer present. Between flushes, I located VHF marked brooding females, and chicks when possible, daily until chicks were 14 days old then 4 times a week after reaching the 14-day old mark.

Fecundity Parameters.—Nesting propensity (NEST) was estimated using a Horvitz – Thomson estimator that accounted for bias from nests that failed before being detected (Dinsmore et al. 2002). I estimated nesting propensity only for GPS-marked females because of

the greater resolution location data (8-10 locations/day) and typically verified nest establishment within 3 days of a nest being attempted. Prior to incubation, female lesser prairie-chickens typically visited nests locations each day from 1200 – 1400 to establish a nest and lay eggs while displaying unique movement patterns relative to non-nesting females (D. Haukos, unpublished data). To account for undetected nests, I used the inverse of the 3-day nest survival rate estimated from the DSR, then multiplied this number by the total number of detected nests to provide an adjusted estimate of the total number of nests (Dinsmore et al. 2002). The adjusted number of nests was divided by the total number of females that were captured presumably before losing a first nest (before 22 April) and survived long enough to attempt a nest (survived to 10 May). I estimated propensity to renest (RENEST) following a similar protocol, but estimated the proportion of females that attempted to renest after losing their first nest but not dying during the nest predation events.

I counted clutch size for all first (CLUTCH1) and known second (CLUTCH2) nest attempts, and tested for differences in average clutch size between birds that nested in CRP and native working grasslands (i.e., grazed) using a 2-sample t-test assuming equal variance. I estimated hatchability following Hagen et al. (2009) as the proportion of chicks hatched per egg laid (HATCH). I estimated daily nest survival rates for yearling and adults, and separately for first (NSURV1) and second nest attempts (NSURV2) with the nest survival procedure within Program MARK (White and Burnham 1999, Dinsmore et al. 2002). Models were ranked based on Akaike's Information Criterion corrected for small sample sizes (AICc) and evaluated based on model weight (Burnham and Anderson 2002). Ultimately, the single covariate CRP model as estimated in the R package RMark interface was used to estimate nest survival throughout the laying and incubation period, because I were interested in differences between birds nesting in

and out of CRP (Laake 2013, R Development Core Team 2016). I calculated nest survival rates

from daily survival rates for a 35-day exposure period with a 10 day laying period and a 25-day

incubation period to estimate nest survival for yearling first nests and renests of yearlings and

first nests and renests of adults. I used the delta method to calculate standard errors for each nest

survival rate (Powell 2007). Chick survival (CHICK) to 35-days post hatch using models of

Lukacs et al. (2004). I did not estimate chick survival separately for CRP and native working

grasslands because only one brood that survived >7 days used CRP. The 35-day survival was

estimated as the product of weekly survival rates over 5 week-long intervals and the standard

error was estimated for chick survival using the delta method assuming independence of input

values. Fecundity rates were estimated for the 2 nesting attempts (a) using the equation below

based on Hagen et al. (2009).

$$Fa = [(NEST \; x \; CLUTCH1 \; x \; NSURV1) + (1 - NSURV1)x \; (RENEST \; x \; CLUTCH2 \; x \; NSURV2)]$$
$$x \; (HATCH \; x \; 0.5 \; x \; CHICK)$$

Nest Densities.—Even if nest survival was not higher in CRP grasslands compared to

native working grasslands, the addition of CRP grasslands could benefit lesser prairie-chickens

by increasing the landscape-scale carrying capacity for lesser prairie-chickens nests (Pidgeon et

al. 2006, Chalfoun and Martin 2007). I estimated cover type specific nest densities to compare

the nesting capacity between CRP and native working grasslands in northwest Kansas. Nest

densities of transmittered lesser prairie-chickens were estimated within a 5-km radius of each lek

trapped during spring 2013-2016. The 5-km radius buffer around leks represented an estimate of

the perceptual range of habitat selection for female lesser prairie-chickens. Greater than 85% of

females established nests within this distance from lek of capture (J.M. Lautenbach and D.

Sullins, unpublished data).

Landscape Scale Reproduction.—I estimated the proportions of female lesser prairie-chickens with 7 day old broods using CRP, native working grassland, or croplands that also nested in CRP. I used the nest location (e.g., CRP or native working grassland) and location occurring closest to the 7-day mark, which encompassed the critical brood survival period; lesser prairie-chicken broods are often lost in the first week of life (Lautenbach 2015). The percentage of females using CRP to nest and native working grasslands for broods will provide inference on how lesser prairie-chickens use the CRP/native working grassland mosaic for reproduction.

Female Survival Parameters.—I used Kaplan–Meier models to estimate breeding season survival for adult and yearling lesser prairie-chickens during 2013–2016 breeding season (Sb;15 March – 15 September) in Program MARK. The same Kaplan–Meier models were used to estimate nonbreeding season (16 September – 14 March) survival (Snb) for adults and yearlings combined (White and Burnham 1999). Juvenile survival (35 days posthatch to first breeding season; Sjuv) was derived from a previous study on lesser prairie-chickens in western Kansas, and set at 0.539 ± 0.089 (Hagen et al. 2009) because I did not obtain a sufficient sample size to estimate this demographic parameter for my study population in northwest Kansas. I estimated nonbreeding and breeding season survival separately because of differences in habitat use during these 6- month seasons (Haukos and Zaveleta 2016). Annual survival was then estimated for each age class (c) and season (breeding=b, nonbreeding=nb) as:

$$Sc \ = \ Sb \text{ x } Snb$$

Matrix Population Model.—Fecundity and survival parameters for female lesser prairie-chickens using CRP and native working grasslands were integrated into a matrix population model (A). If sample sizes were too small (n < 20) to estimate a parameter, the vital rate was obtained from previous research conducted in western Kansas between 1998 and 2003

194

(Hagen et al. 2009). Wherein Fy represented yearling fecundity, Fa was adult fecundity, Sjuv was juvenile survival, Sy was yearling annual survival, and Sa was adult annual survival.

$$A = \begin{bmatrix} Fy \ x \ Sjuv & Fa \ x \ Sjuv \\ Sy & Sa \end{bmatrix}$$

I used 1,000 bootstrap iterations of the R package popbio (Stubben and Milligan 2007) to generate estimates and standard deviations of the finite rate of population change (λ), generation time in years (T), and net reproductive rate (R0) for birdsgrouped as using CRP and not using CRP. I also conducted a retrospective analysis to estimate vital rates that contributed the most to difference in population growth rates among female lesser prairie-chickens that used native working grassland and CRP grasslands. I estimated contributions to the finite rate of population growth rate for each treatment using a fixed-effects life-table response experiment and used 1,000 bootstrap iterations to estimate standard deviations for the contribution values (Caswell 1989).

Results

I captured, marked, and monitored 280 female lesser prairie-chickens from 2013–2016 among all sites. Overall, 156 individuals were marked with GPS transmitters and 124 individuals were marked with VHF transmitters. At the northwest Kansas site, a total of 146 female lesser prairie-chickens were marked with GPS or VHF transmitters and used to estimate the demographic response to CRP. Of the females monitored in northwest Kansas 10% were of unknown age, 63% were SY, and 28% were ASY.

Vegetation Differences between CRP and Native Working Grasslands

Overall, CRP grasslands supported taller vegetation with a greater litter depth, a smaller shrub composition, less bare ground, more tallgrass species, and provided a greater number of suitable nesting microhabitats (Hotelling's $T^2 = 69.73$, P < 0.0001, Table 4.2).

195

Use of CRP

Although nest densities were greater in CRP grasslands compared to native working grasslands, lesser prairie-chickens ($n = 79$) used native working grasslands more frequently than CRP in northwest Kansas during both the breeding and nonbreeding seasons of 2013–2016 (Table 4.3). Of the locations from GPS marked birds, 70% of locations were in native working grasslands with 20% in CRP grasslands (Table 4.3).

Selection of CRP

Influence of Temporal and Spatial Variability of Precipitation on Selection.—At a regional scale, CRP grasslands were 7 times more likely to be used by lesser prairie-chickens in regions receiving 55 cm compared to 70 cm of average annual precipitation ($\beta = -0.0152 \pm 0.002$, $P < 0.05$, Figure 4.2A). Within the northwest Kansas study site, probability of use of CRP increased with increased drought severity as indicated by the lag PDSI value. The predicted probability of using CRP was 1.89 times greater when the lag PDSI value equaled -4 (more severe drought) compared to a value of 4 (less severe drought; $\delta 1 = -0.1963 \pm 0.0322$, marginal effect of PDSI lag on predicted probability of using CRP, Figure 4.2B). In contrast, the predicted probability of using native working grassland was 1.18 times less when the lag PDSI value was   -4 compared to +4 and overlapped zero at the 95% confidence interval ($\delta 1 = -0.0278 \pm 0.0272$, marginal effect of PDSI lag on predicted probability of using native working grassland, Figure 4.2B).

Influence of the Surrounding Matrix.—I sampled an array of landscapes with variation in the amount of grassland in the surrounding matrix. In northwest Kansas, CRP grasslands were 5.13 times more likely to be used by lesser prairie-chickens when local landscapes (~5,027 ha)

196

were comprised of ~70% (~3,500 ha) native grassland compared to ~20% (1,000 ha) native grassland (β= 0.00125 ± 0.0000541, P < 0.001; Figure 4.3).

Demographic Rates

Nests.—I monitored 102 lesser prairie-chicken nests during 2013, 2014, and 2015 in northwest Kansas. Total clutch size did not vary among females that nested in CRP (9.70 ±3.17) and native working grassland (9.61 ± 2.56; t_{99} = 0.13, P = 0.90; Table 4.4). Females on average laid 10.33 (SE = 0.25) eggs for their first nest and 7.23 (SE = 0.58) eggs for their second clutch (t_{99} = 5.35, P = <0.001). Renesting attempts in CRP and native working grasslands were limited and too few to provide estimates of renesting survival (n = 4 & 15 respectively; Table 4.4).

Nesting propensity varied among years and was estimated at 82.0%, 88.0%, and 100% in 2013, 2014, and 2015, respectively. Low nesting propensity corresponded with index of drought severity (PDSI) during the nesting season. The probability of a marked female renesting following the loss of a first nest was estimated at 15.3%, 53.7%, and 35.7% in 2013, 2014, and 2015, respectively. To explore parameter space, I used uniform distributions encompassing the range of nesting propensity and renesting propensity for matrix model calculations.

The highest ranked nest survival model based on AICc was the null model (w_i = 0.25), followed by a year (w_i = 0.21), CRP (w_i = 0.17), age class model (w_i = 0.11), and nesting attempt model (w_i = 0.09), all of which had a ΔAICc < 2. Support for the null model suggested that daily survival rates of lesser prairie-chicken nests was similar among land cover types, years of the study, age classes, and nesting attempts. Lesser prairie-chickens that nested in CRP had an estimated nest survival rate of 0.505 (SE = 0.079) while those that used native working grasslands had an estimated nest survival of 0.405 (SE = 0.053; Table 4.4). The top ranking model with a covariate included year and nest survival was estimated at 0.365 (SE = 0.068),

197

0.422 (SE = 0.066), and 0.604 (SE = 0.101) in 2013, 2014, and 2015, respectively. However, the effect size between these two estimates was not measurably different from zero. Because my goal was to evaluate any potential cumulative effects of CRP on lesser prairie-chicken population demography, I used estimates from the CRP model to estimate nest survival.

Of the nests monitored in northwest Kansas, 34% produced young. Of the nests that failed, 78% were depredated and 18% abandoned (Table 4.5). Only 4% of nests were trampled by cattle; all occurred within native working grassland pastures. The proportion of eggs that successfully hatched within a successful nest (hatchability) was estimated as 0.75 (SE = 0.048) from 35 successful nests in northwest Kansas. Among nests, hatchability varied from 0.1 to 1.0 of eggs successfully hatching. Hatchability included losses to predation, egg viability, and infertility. Unfortunately, we were unable to distinguish among factors reducing hatchability rates.

Nest Densities. — Approximately 40% of nests occurred in CRP grassland in 2013 and 2014 whereas only 10% of nests were in CRP in 2015. Across the 5-km lek buffers, CRP made up 17.3% of the available grassland. Overall, nest density of marked lesser prairie-chickens was ~2 times greater in CRP grasslands than in native working grassland (CRP = $3.63/10 \text{ km}^2$, native working grassland = $1.78/10 \text{ km}^2$).

Landscape Scale Reproduction. — In northwest Kansas, 14.3% (1/7) of female lesser prairie-chickens successfully used CRP as both nesting and brooding habitat to successfully rear chicks to 7 days. The remaining females (85%) that used CRP grasslands as nesting substrate moved broods to other cover types within the first 7 days of life. Of these females half moved their broods to native working grasslands and the other half were moved to cropland.

Chick Survival. — The strong selection of non-CRP cover types for brood rearing did not allow for the estimation of chick survival in both CRP and non-CRP cover types. Pooling across strata, I estimated an overall 35-day individual chick survival from 34 broods for northwest Kansas at 0.261 ± 0.071 (estimate $\pm$ SE).

Survival. —I estimated survival for 128 adult females during the breeding season and 53 during the nonbreeding season in 2013, 2014, and 2015 combined. For birds that did not use CRP grasslands during the breeding season survival was estimated as 0.440 ± 0.077 and 0.565 ± 0.097 for non-breeding season. For female lesser prairie-chickens that used CRP, survival was 0.421 ± 0.067 and 0.711 ± 0.100 for breeding and non-breeding season, respectively. Although not statistically different, survival rates suggest that CRP is providing habitat at a level of quality at least comparable to that of used native working grasslands

Population Matrix.—Population growth rate point estimates for birds that used CRP (λ $=0.601$, SD $= 0.135$) compared to those that only used native working grasslands ($\lambda= 0.491$, SD $= 0.114$) overlapped at 95% confidence intervals (95% CI; CRP $= 0.336$–0.8656, NonCRP $= 0.268$–0.714). Female lesser prairie-chickens had a net reproductive rate of R0$=0.094 \pm 0.0695$ (estimate $\pm$ SD; female chicks/female/generation) when using CRP at a landscape scale and a net reproductive rate of R0$=0.0547 \pm 0.0396$ when not using CRP suggesting that breeding females are not replacing themselves. However, generation times were similar for lesser prairie-chickens using CRP (3.340 ± 0.303 years) and those that never used CRP (3.183 ± 0.254 years). The larger point estimate for generation time for lesser prairie-chickens using CRP likely resulted from the greater adult survival rates (slightly longer lifespans) and did not indicate lesser prairie-chickens using CRP had lower fecundity. The fixed effects life table response experiment decomposed the difference in λ (difference $= +0.110$ for CRP) among birds using CRP and

199

native prairie. The life table response experiment revealed that nonbreeding survival contributed (contribution [c] = 0.0592 ± 0.0600, 53.0% of difference, Figure 4.4) most to the difference in population growth rates between lesser prairie-chickens using CRP at a landscape scale and those not using CRP (Figure 4.4). Contributions from nest survival for second-year (c = 0.0240 ± 0.0284, 21.8% of difference) and after-second-year (c = 0.0224 ± 0.0224, 20.4% of difference) contributed the second and third most to the difference in population growth rates between female lesser prairie-chickens using and not using CRP.

Discussion

I provide evidence of landscape scale mechanisms that may have allowed lesser prairie-chickens to expand their range and increase regionally in abundance during the past 3 decades in northwest Kansas despite ongoing population declines elsewhere throughout much of its 5-state range (Van Pelt et al. 2013). Understanding mechanisms that have allowed lesser prairie-chickens to expand in the northern edge of the range may be key to the foreseeable persistence of this species on privately owned working lands, especially in light of current climate change predictions (Rodgers and Hoffman 2005, Cook et al. 2015, Haukos and Zaveleta 2016, Rodgers 2016, Grisham et al. 2016). My combined resource selection and demographic results provide a holistic estimation of individual and population level effects of CRP on lesser prairie-chickens based on long-term evolved behavioral cues (selection) and realized fitness over the 3-year window of data collection. Data collection encompassed the entire life cycle of lesser prairie-chickens as well as severe drought and wet years. The results herein should be interpreted, in context of the current population status (Garshelis 2000), at a landscape spatial scale and within the temporal scale of the study to understand true population response. In summary, CRP

grasslands provide habitat during the nesting and nonbreeding period and are of particular importance during drought years in northwest Kansas, and in drier portions of the lesser prairie-chickens range (e.g., Colorado). Lesser prairie-chickens appear to follow aspects of the ideal free distribution model in northwest Kansas wherein individuals perceive and select habitat that maximize fitness as opposed to selecting areas that may function as ecological traps (Fretwell and Lucas 1970, Gates and Gysel 1978). Last, under the current regulatory guidelines and successional state, CRP benefits lesser prairie-chickens where lands occur in areas of appropriate climate and where the surrounding matrix of the fields are predominantly grassland. Therefore, strategic conservation efforts that spatially prioritize CRP to areas within grassland dominated landscapes of favorable regional climate in which CRP grasslands achieve optimal structure for use by lesser prairie-chickens and increase spatial heterogeneity would, currently, be most beneficial. However, use of grazing, burning, and disking also appear promising to extend the utility of CRP grasslands for lesser prairie-chickens outside of the nesting and nonbreeding periods (J. Reitz, Colorado Parks and Wildlife, pers. com.) as well as in the eastern extent of the species range where average annual precipitation is >65 cm and supports mixed grass prairie (Hagen et al. 2004).

Selection of High Quality Habitat

Following the ideal free distribution model and the effects of natural selection, I would expect that species select habitats that maximize their demographic potential and will be most likely to do so at low population densities (Fretwell and Lucas 1970, Whitman 1980). Lesser prairie-chickens were at a contemporary population low at the onset of this research (Ross et al. 2016b), and distributed among cover types of similar demographic consequence supporting an ideal free distribution. If exhibiting an ideal free distribution, lesser prairie-chickens would be

201

able to discern habitat quality and their distribution would provide a reasonable long-term estimate of habitat quality when habitat is not saturated and recent changes to the environment are minimal (Rodewald 2015). During the spring of 2013, estimates of the lesser prairie-chicken population size in Kansas were lower than any estimate since large-scale monitoring began in 1978 (Ross et al. 2016b). Therefore, any locations still occupied by lesser prairie-chickens likely represented a core area of optimal habitat quality (Guthery et al. 2005) or, alternatively, a location that provided refugia during drought events. In either case, demographic assessments during a population low will likely not encompass the full spectrum of habitat quality. Assessing the full spectrum of habitat quality, if achievable, may require a significantly longer study for a boom or bust species such as the lesser prairie-chicken. Regardless, understanding habitat quality at a population low is essential to understanding how populations resist extinction (Simberloff 1994).

To evaluate the quality of a cover type as habitat, vital rates of individuals must be estimated. Similar to Fields et al. (2006), nest survival was not different between CRP and native working grasslands; however, nest densities were greater in CRP grasslands. Whether nesting in CRP or native working grasslands, lesser prairie-chickens appear to select microhabitats resulting in similar fitness. Nesting microhabitats appear to be more readily available in CRP grasslands in this region as indicated by the greater nesting densities (2X) and vegetation data. By incorporating nesting densities, estimated from marked individuals, I have provided evidence of population-level demographic effects on reproduction that would benefit lesser prairie-chickens occurring in landscapes with CRP (Van Horne 1983, Rodewald 2015). Higher densities likely translated into increased lesser prairie-chicken reproductive output in landscapes with more CRP in northwest Kansas. Such increased reproductive output may offset

higher mortality for lesser prairie-chickens in northwest Kansas where adult survival estimates are lowest among populations in Kansas (Plumb 2015, Robinson 2015).

Regional and Life-Stage Variation in Benefits of CRP

Conservation Reserve Program grasslands in northwest Kansas benefit lesser prairie-chickens by increasing adult survival and reproductive output. The contribution of nonbreeding season survival to changes in population growth has not been previously documented. However, nonbreeding survival of adults ranked first and second in importance based on elasticity values for a population of lesser prairie-chickens inhabiting sand sagebrush prairie (Hagen et al. 2009). The positive influence of CRP during this period may be related to the provision of denser cover that is more likely to remain following winter snow storms or may be related to the close proximity of CRP to waste grain in adjacent crop fields. A nearly 3-fold increase in use of croplands during the nonbreeding season may indicate the use of these locations when foods become limited outside of the growing season. I provide some evidence that birds using CRP may have greater survival during the nonbreeding season, but benefits of CRP in this region were largely realized during the nesting period.

The documented utility of CRP as nest habitat and the regional population increase following the addition of CRP suggests that nest habitat may have been previously limiting in northwest Kansas. In northwest Kansas, juxtaposition of patches of native mixed-grass prairie plant species (CRP grasslands), which are not grazed, throughout short-grass prairie has increased the amount of grassland cover and heterogeneity of grasslands in the region. The same effects may not be realized further to the east where nesting habitat may not be as limiting and CRP may become too dense and tall even for use as nesting habitat (>30 – 50 cm tall; Rodgers and Hoffman 2005). In addition to being too tall or thick, CRP in the eastern portion of the

LEPC range is more likely to be adjacent to woodlands, both conditions are an underlying result of increased average annual precipitation (Bond 2008, Grisham et al. 2016). Therefore, the universal application of one management practice for a species requiring heterogeneous grasslands and that occupies a strong precipitation gradient, such as the lesser prairie-chicken, would not be advisable.

Making CRP useable by lesser prairie-chickens outside of broad-scale climatic and fine-scale life-stage constraints will rely on the proper application of disturbance. The lack of disturbance (e.g., grazing and burning) outside of mid-contract management (Negus et al. 2010) for CRP grasslands in areas receiving greater than 65 cm of precipitation may make them unavailable for nesting lesser prairie-chickens. Alternatively, the lack of disturbance throughout the northern distribution of lesser prairie-chickens may make CRP unavailable as brood-rearing habitat. In northwest Kansas, CRP grasslands were not used by lesser prairie-chicken broods likely because the ground layer was too dense and thick for a small chick (<15 g) to move around and limited accessibility to food resources due to a lack of forbs (Hagen et al. 2013). The CRP grasslands in northwest Kansas provided nesting habitat adjacent to more disturbed native working grassland (~20% forb cover, Lautenbach 2015) and cropland used by broods in the first 7 days of life. In contrast, adding ungrazed CRP to landscapes in the mixed-grass eastern extent of the lesser prairie-chicken range would be less likely to achieve this pairing of nest and brood habitat. Further, the addition of CRP is less likely to address a limiting factor in the eastern extent of the lesser prairie-chicken range where mean annual net primary productivity is ~200 g/m^2 greater than at my western most study site (Sala et al. 1988). Conservation Reserve Program grassland establishment may increase habitat quality in landscapes for lesser prairie-

chickens only when increasing the spatial heterogeneity of those landscapes or by increasing the amount of grassland in landscapes past an extinction threshold.

Role of CRP in Surpassing Habitat-based Thresholds

Lesser prairie-chickens were most likely to use CRP grasslands when local landscapes (~50 km^2) were >70% (~35 km^2) native working grasslands. My estimates of habitat selection document the influence of factors at scales larger than the typical home range of lesser and greater prairie-chickens (*Tympanuchus cupido*) and are comparable to previous research that estimated support for stable populations when >25 km^2 areas were comprised of greater than 63% native prairie (Crawford and Bolen 1976, Plumb 2015, Robinson 2015, Winder et al. 2015). To maintain a genetically healthy lesser prairie-chicken population, the minimum amount of contiguous habitat has been estimated at 85 km^2 (32 mile^2) and is based on the presence of 6 leks that are on average 1.6 km away from each other (Westemeier et al. 1998, Applegate and Riley 1998, Van Pelt et al. 2013, DeYoung and Williford 2016). However, estimates have ranged from 49 km^2 to ~20 km^2 of contiguous native prairie based on providing habitat for a single lek or at the population level (Haukos and Zaveleta 2016). Ultimately, the conservation of lesser prairie-chickens will require the maintenance of a geographic range large enough and of sufficient quality to rebound from detrimental stochastic processes (demographic and genetic rescue) and unpredictable environmental conditions prevalent within the extant distribution of lesser prairie-chickens (Sala et al. 1988, Simberloff 1994, Grisham et al. 2016, Ross et al. 2016a).

The loss of grassland through conversion to cropland in the early 1900s in the Short-Grass Prairie/CRP Mosaic Ecoregion may have reduced the amount of available grassland cover and structure below a threshold to overcome stochastically driven extinction by lesser prairie-chickens (Simberloff 1994, Spencer et al. 2017). Larger areas of intact grasslands are more

likely to provide heterogeneity sourced refugia during drought and generate population momentum to resist negative stochastic events (Simberloff 1994, Ross et al. 2016b). It is much less likely for a small patch of grassland to predictably provide microhabitats capable of supporting nesting, brooding, and winter habitat in comparison to larger grasslands. Additionally, a greater grassland component would also result in greater reproductive output during periods of favorable weather (Garton et al. 2016, Ross et al. 2016a). Maximizing reproductive output during periodic favorable periods may be particularly important population strategy in the semi-arid portion of the southwestern Great Plains, where precipitation-driven net primary productivity varies greatly on an annual basis (Sala et al. 1988). Amid such climatic and photosynthetic variability, population resilience of lesser prairie-chickens to drought periods has been empirically related to greater grassland composition within 4 km of leks with an optimum value of 90% grassland (Ross et al. 2016b).

The population resilience to drought may stem from the decision to nest or forego nesting during a particular season. My results and past reports from a study in west Texas have documented the decreased propensity to nest during intensive drought (Grisham et al. 2014). In west Texas, only 20% of marked female lesser prairie-chickens nested during a record extreme drought (Grisham et al. 2014, Su and Dickinson 2014). In my study, nesting propensity was lowest in 2013 (82%) and greatest in 2015 (100%), which were the years of the most and least severe Palmer Drought Severity Index, respectively (NOAA 2016b). Further, I documented that female lesser prairie-chickens were more likely to select CRP grasslands as drought severity increased. Given my observations, it is plausible that lesser prairie-chickens reduce nesting effort when environmental conditions are not favorable for nest survival. This behavior may differentiate lesser prairie-chickens from greater prairie-chickens, which appear to exhibit high

206

nest propensity even during drought and result from the occurrence of greater prairie-chickens in more mesic environments (McNew et al. 2012).The decision to nest or not could be controlled by the availability of nesting habitat that should increase with CRP on the landscape in northwest Kansas, or, alternatively, by water availability (Robinson et al. 2016), both of which are likely main factors in the boom-bust population fluctuation

Influence of Climate Change on Lesser Prairie-Chicken Distribution

In addition to the integration and management of CRP fields for lesser prairie-chickens into landscapes in the northwestern extent of their range (Rodgers 1999), there is also the possibility that climate change has played a role in the putative northward expansion of lesser prairie-chickens. Higher temperatures and drier conditions with increased frequency of drought are expected in the southwestern Great Plains due to climate change (Karl et al. 2009, Grisham et al. 2016).

Climate-related constraints on the distribution and niche of lesser prairie-chicken are possible and could be imposed on multiple life-stages. To date, inference of relationships among climate and demographics of lesser prairie-chicken populations are limited to the influence of temperature on nest survival, brood survival, and lek abundance, for which, temperature is negatively related to both life stages and drier previous summers (lower PDSI) can lead to lower male abundance on leks (Fields et al. 2006, Grisham et al. 2013, Lautenbach 2015, Ross et al. 2016a). The future projections for climates to be warmer and drought more severe does not bode well for lesser prairie-chickens (Grisham et al. 2013). Further, climate models suggest a shift from favorable nesting conditions needed for viable populations in the southern extent of the lesser prairie-chicken range by 2050 (Grisham et al. 2013). Although estimates of a narrowing southern breeding distribution are available, we lack knowledge of how the distribution may

207

expand northward with climate change. The minimum temperature threshold for the lesser

prairie-chicken reproductive niche has not been documented; however, I expect that climate

change would allow for a northern shift of this abiotic constraint. I predict a northward

progression of this reproductive niche constraint matched with an increased provision of nesting

habitat with the addition of CRP may be key to the future persistence of lesser prairie-chicken.

Falling below a threshold of ~60% grasslands through the removal of CRP grasslands in

northwest Kansas may result in localized extinction. The loss of this population could be

detrimental for lesser prairie-chickens overall, as it appears to be the only population showing

positive growth over the last decade and it currently supports an estimated ~55% of the entire

population (Garton et al. 2016).

Overall Influence of CRP on Grassland Birds

Following periods of agricultural intensification in the 1960s and 1970s, the CRP was

initially implemented in 1986 to reduce topsoil erosion and stabilize the food and fiber industry

by taking marginal cropland out of production and establishing perennial grasslands (Rodgers

2016). Most CRP grasslands in northwest Kansas were planted with native species from 1986-

1989, and much of this was interseeded with legumes in the late-1990s (Fields et al. 2006,

Rodgers 2016). In 2014, >700,000 ha (1.7 million acres) of CRP grasslands occurred within the

lesser prairie-chicken range, with 270,000 ha in the Short-Grass Prairie/CRP Mosaic Ecoregion

(McDonald et al. 2014, Spencer et al. 2017). Although not an initial objective, CRP also benefits

nesting grassland birds (Reynolds et al. 1994, Best et al. 1997, Igl and Johnson 1999, Johnson

2005, Rodgers and Hoffman 2005). In North Dakota, USA, population trends reversed from

declining to increasing for 4 of 9 grassland bird species following the establishment of CRP

(Reynolds et al. 1994). Currently, providing and enhancing wildlife habitat is considered a

primary objective of CRP (North American Bird Conservation Initiative 2015). Recognizing the unique ability of this program to benefit ecosystems and producers over large spatial scales has made it a rare conservation success (>7 million ha in Great Plains; Johnson 2005). One of which includes the expanded range of lesser prairie-chickens (Rodgers et al. 1999).

Management Implications

Managers interested in maximizing ecological benefits of CRP to lesser prairie-chicken populations could concentrate CRP incentives in areas receiving <55 cm of average annual precipitation and in ~50 km^2 landscapes that would surpass a 65% grassland threshold with the addition of CRP grasslands. Within these landscapes, a management strategy for CRP signup could include further incentives for areas adjacent to large tracts of remnant prairie. Continued planting of native mixed- and tall-grass species when seeding CRP grassland in Kansas and Colorado would provide maximum benefits for lesser prairie-chickens. A potential approach to improving attractiveness of CRP in the eastern portion of the lesser prairie-chicken range would be to increase disturbance either by way of grazing, burning, haying, and/or disking, which could be examined in an adaptive management framework.

Literature Cited

Ammann, G. A. 1944. Determining the age of pinnated and sharp-tailed grouses. Journal of Wildlife Management 8:170–171.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat: a review. Oikos 71:355–366.

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

Askins, R.A., F. Chavez-Ramirez, B.C. Dale, C.A. Haas, J.R. Herkert, F.L. Knopf, and P.D. Vickery. 2007. Conservation of grassland birds in North America: Understanding Ecological processes in different regions: Report of the AOU committee on Conservation. Ornithological Monographs 64:1–46.

Augustine, D. J. 2010. Spatial versus temporal variation in precipitation in a semiarid ecosystem. Landscape Ecology 25:913–925.

Baker, M. F. 1953. Prairie chickens of Kansas. State biological survey, University of Kansas, Lawrence, Kansas, USA.

Best, L. B., H. Campa, III, K. E. Kemp, R. J. Robel, M. R. Ryan, J. A. Savidge, H. P. Weeks, Jr., and S. R. Winterstein. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. Wildlife Society Bulletin 25:864–877.

Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? Annual Review of Ecology, Evolution, and Systematics 39:641–659.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretical approach. Second edition. Springer-Verlag, New York, New York, USA.

Caswell, H. 1989. The analysis of life table response experiments I. Decomposition of effects on population growth rate. Ecological Modelling 46:221–237.

Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:1–7.

Copelin, F. F. 1963. Lesser prairie chicken in Oklahoma. Pittman-Robertson Project Number W-62-R, Oklahoma Wildlife Conservation Department, Oklahoma City, USA.

Chalfoun, A. D., and T. E. Martin. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

Crawford, J. A., and E. G. Bolen. 1976. Effects of land use on lesser prairie chickens in Texas. Journal of Wildlife Management 40:96–104.

Dahlgren, D. K., R. D. Rodgers, R. D. Elmore, and M. R. Bain. 2016. Grasslands of western Kansas, north of the Arkansas River. Pages 259–281 in D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

Davis, C. A., T. Z. Riley, H. R. Suminski, and M. J. Wisdom. 1979. Habitat evaluation of lesser prairie chickens in eastern Chaves County, New Mexico. Final Report to Bureau of Land Management, Roswell, Contract YA-512-CT6-61. Department of Fishery and Wildlife Sciences, New Mexico State University, Las Cruces.

DeYoung, R. W., and D. L. Williford. 2016. Genetic variation and population structure in the prairie grouse: implications for conservation of the lesser prairie-chicken. Pages 77–98 in D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Edwards, R. Y., and C. D. Fowle. 1955. The concept of carrying capacity. Transactions North American Wildlife Conference 20:589–602.

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.

Federal Register 2016. Federal Register. Vol. 81. No. 139: 50 CFR Part 17: Endangered and threatened wildlife and plants; lesser prairie-chicken removed from the list of endangered and threatened wildlife.
<http://ecos.fws.gov/ecp0/profile/speciesProfile?spcode=B0AZ#status>

Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds I. Theoretical development. Acta Biotheoretica 19:16–36.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie Jr., 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

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16: 1706-1716.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 in L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University Press, New York, New York, USA.

Garton, E. O., C. A. Hagen, G. M. Beauprez, S. C. Kyle, J. C. Pitman, D. D. Schoeling, and W. E. Van Pelt. 2016. Population dynamics of lesser prairie-chickens. Pages 49–76 in D. A Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field–forest ecotones. Ecology 95:871–883.

Giesen, K. M. 1994. Breeding range and population status of lesser prairie-chickens in Colorado. Prairie Naturalist 26:175–182.

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. PLoS One 8: e68225. doi: 10.1371/journal.pone.0068225.

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., C.P. Griffin, and A.J. Godar. 2016. Climate change. Pages 221–242 in D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Guthery, F. S., A. R. Rybak, W. R. Walsh, S. D., Fuhlendorf, and T. L. Hiller. 2005. Quantifying usable space for wildlife with use–availability data. Journal of Wildlife Management 69:655–663.

Hagen, C. A. 2003. A demographic analysis of Lesser Prairie-Chicken populations in southwestern Kansas: survival, population viability, and habitat use. Ph.D. dissertation, Kansas State University, Manhattan, KS.

Hagen, C. A., B.E. Jamison, K. M. Giesen, and T. Z. Riley. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. Wildlife Society Bulletin 32:69–82.

Hagen, C. A., and K. M. Giesen. [online]. 2005. Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Birds of North America 364. <http://bna.birds.cornell.edu/bna/species/364/articles/introduction> Accessed 10 November 2016.

Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. Journal of Wildlife Management 73:1325–1332.

212

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.

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

Haukos, D. A., and C. W. Boal. 2016. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Haukos, D. A., and J. C. Zaveleta. 2016. Habitat. Pages 99-132 in D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Hayes, M. 1998. Drought Indices. National Drought Mitigation Center, Lincoln, Nebraska.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Hovick, T. J., R. D. Elmore, S. D. Fuhlendorf, D. M. Engle, and R. G. Hamilton. 2015. Spatial heterogeneity in grassland bird communities. Ecological Applications 25:662–672.

Igl, L. D., and D. H. Johnson. 1999. Le Conte's sparrows breeding in Conservation Reserve Program fields: precipitation and patterns of population change. Studies in Avian Biology 19:178–186.

Jensen, W. E., D. A. Robinson, and R. D. Applegate. 2000. Distribution and population trend of lesser prairie-chicken in Kansas. Prairie Naturalist 32:169–176.

Johnson, D. H. 2005. Grassland bird use of Conservation Reserve Program fields in the Great Plains. Pages 17–32 in J. B. Haufler, editor. Fish and wildlife benefits of Farm Bill conservation programs: 2002-2005 update. The Wildlife Society Technical Review 05-02, Bethesda, Maryland, USA.

Johnson, R. A., and D. W. Wichern. 1988. Applied multivariate statistical analysis. Second Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.

Karl, T. R., J. M. Melillo, and T. C. Peterson. 2009. Global climate change impacts in the United States. Cambridge University Press, New York, New York, USA.

Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, WA, USA. <www.afsc.noaa.gov/Publications/ProcRpt/PR2013-01.pdf.> Accessed 10 November 2016.

213

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

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 and Management 70:78–86.

Lukacs, P. M., Dreitz, V. J., Knopf, F. L., & Burnham, K. P. 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. Condor 106: 926–931.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second Edition. Kluwer Academic Publishers, Dordrecht, Netherlands.

McDonald, L., G. Beauprez, G. Gardner, J. Griswold, C. Hagen, D. Klute, S. Kyle, J. Pitman, T. Rintz, and B. Van Pelt. 2014. Range-wide population size of the lesser prairie-chicken: 2012 and 2013. Wildlife Society Bulletin 38:536–546.

McDonald, L., K. Nasman, T. Rintz, F. Hornsby, and B. Van Pelt. 2016. Range-wide population size of the lesser prairie-chicken: 2012, 2013, 2014, 2015, and 2016. Wildlife Society Bulletin 38:536–546.

McGarigal, K., S.A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html> accessed 10 November 2016.

McNew, L.B., A.J. Gregory, S.M. Wisely, and B. K. Sandercock. 2012. Demography of greater prairie-chickens: regional variation in vital rates, sensitivity values, and population dynamics. Journal of Wildlife Management 76:987–1000.

McNew, L. B., V. L. Winder, J. C. Pitman, and B. K. Sandercock. 2015. Alternative rangeland management strategies and the nesting ecology of Greater Prairie-Chickens. Rangeland Ecology and Management 68: 298-304.

National Oceanic and Atmospheric Administration National Climatic Data Center (NOAA). 2016a. National Environmental Satellite, Data, and Information Service. <https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp> Accessed August 11, 2016.

National Oceanic and Atmospheric Administration (NOAA). 2016b. Historical Palmer Drought Indices. National Centers for Environmental Information. < http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#>. Accessed August 11, 2016.

North American Bird Conservation Initiative, U.S. Committee. 2015. 2014 Farm bill field guide to fish and wildlife Conservation. 58 pages. <http://bringbackbobwhites.org/download/2014-farm-bill-field-guide-to-fish-and-wildlife-conservation/> Accessed 10 November 2016.

Negus, L. P., C. A. Davis, and S. E. Wessel. 2010. Avian response to mid-contract management of Conservation Reserve Program fields. American Midland Naturalist 164:296–310.

Pidgeon, A. M., V. C. Radeloff, and N. E. Mathews. 2006. Contrasting measures of fitness to classify habitat quality for the black-throated sparrow (*Amphispiza bilineata*). Biological Conservation 132: 199–210.

Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. Condor 109:949–954.

Plumb. R. T. 2015. Lesser prairie-chicken movement, space use, survival, and response to anthropogenic structures in Kansas and Colorado. Thesis. Kansas State University, Manhattan, USA.

PRISM Climate Group.2016. Oregon State University. <http://www.prism.oregonstate.edu/normals/> Accessed 11 January 2017.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org> Accessed 10 November 2016.

Reynolds, R. E., T. L. Shafper, J. R. Sauer, and B. G. Peterjohn. 1994. Conservation Reserve Program: benefit for grassland birds in the Northern Plains. Transactions of the North American Wildlife Natural Resource Conference 59:328–336.

Ringelman, K. M. 2014. Predator foraging behavior and patterns of avian nest success: what can we learn from agent-based model? Ecological Modelling 272:141–149.

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

Robinson, S. G., D. A. Haukos, D. S. Sullins, R. T. Plumb. 2016. Use of free water by nesting lesser prairie-chickens. Southwestern Naturalist 61:187–193.

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. Effects of landscape characteristics on annual survival of lesser prairie-chickens In review.

Rodewald, A. D. 2015. Demographic consequences of habitat. Pages 19–33 in M.L. Morrison and H. A. Matthewson, editors, Wildlife habitat conservation: concepts, challenges, and solutions. John Hopkins University Press Baltimore, Maryland, USA.

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, 6–9 June 2004, Fort Collins, Colorado, USA. USGS Biological Resources Division, Scientific Investigation Report 2005–5145, Reston, Virginia, USA.

Rodgers, R.D. 1999. Recent expansion of lesser prairie-chickens to the northern margin of their historic range, Pages 18–19 in R. Baydack, editor, Proceedings of the 23rd meeting of the Prairie Grouse Technical Council, Gimli, Manitoba, Canada.

Rodgers. R.D. 2016. A history of lesser prairie-chickens. Pages 15–38 in D.A Haukos and C.W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Ross, B. E., D. A. Haukos, C. A. Hagen, and J. C. Pitman. 2016a. The relative contribution of climate to changes in lesser prairie-chicken abundance. Ecosphere 7:e01323. 10.1002/ecs2.1323

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

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Sandercock, B. K., M. Alfaro-Barrios, A. E. Casey, T. N. Johnson, T. W. Mong, K. J. Odom, K. M. Strum, and V. L. Winder. 2015. Effects of grazing and prescribed fire on resource selection and nest survival of upland sandpipers in an experimental landscape. Landscape Ecology 30: 325-337.

Schwilling, M. D. 1955. A study of the lesser prairie-chicken in Kansas. Kansas Forestry, Fish and Game Commission, Pratt, Kansas, USA.

Silvy, N. J., M. E. Morrow, E. Shanley, and R. D. Slack. 1990. An improved drop net for capturing wildlife. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 44:374–378.

Silvy, N. J., M. J. Peterson, and R. R. Lopez. 2004. The cause of the decline of pinnated grouse: the Texas example. Wildlife Society Bulletin 32:16–21.

Simberloff, D. 1994. The ecology of extinction. Acta Paleontologica Polonica 38:159–174.

Spencer, D., D. A. 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.

Stubben, C. J., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software 22:1–22.

Su, H., and R. E. Dickinson. 2014. On the spatial gradient of soil moisture-precipitation feedback strength in the 2011 April drought in the Southern Great Plains. Journal of Climate 213:109–218.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. 2015. Web Soil Survey. <http://websoilsurvey.nrcs.usda.gov/> Accessed 27 July 2015.

Taylor, M. A., and F. S. Guthery. 1980. Status, ecology, and management of the Lesser Prairie Chicken. U. S. Department of Agriculture, Forest Service General Technical Report RM-77. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Van Horne, G. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Van Pelt, W. E., S. Kyle, J. Pitman, D. Klute, G. Beauprez, D. Schoeling, A. Janus, and J. Haufler, 2013. The lesser prairie-chicken range-wide conservation plan. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Van Pelt, W. E. 2016. Legal status of the lesser prairie-chicken. Pages 39–46 in D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48, Cooper Ornithological Society, University of California Press, Berkeley, USA.

Waddell, B. H. 1977. Lesser prairie-chicken investigations – current status evaluation. Kansas Forestry, Fish and Game Commission, Pratt, Kansas, USA.

Westemeier, R. L., J. D. Brawn, S. A. Simpson, T. L. Esker, R. W. Jansen, J. W. Walk, E. L. Kershner, J. L. Bouzat, and K. N. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. Science 282:1695–1698.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement, 120–138.

Whitman, T. G. 1980. The theory of habitat selection: examined and extended using pemphigus aphids. American Naturalist 115:449–466.

Winder V. L., K. M. Carrlson, A. J. Gregory, C. A. Hagen, D. A. Haukos, D.C. Kesler, L. C. Larsson, T. W. Matthews, L. B. McNew, M. A. Patten, J. C. Pitman, L. A. Powell, J. A. Smith, T. Thompson, D. H. Wolfe, and B. K. Sandercock. 2015. Factors affecting female space use in ten populations of prairie chickens. Ecosphere 6:1–17.

Wolfe, D. H., M. A. Patten, E. Schocat, 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.

Table 4.1 Fecundity parameters and descriptions to estimate population growth rates for lesser prairie-chickens among 6 study sites in Kansas and Colorado, during 2013-2016. Each parameter was estimated for transmittered second-year (SY) and after-second- year (ASY) birds.

PARAMETER	DESCRIPTION
NEST	proportion of females that attempt at least 1 nest
RENEST	given failed first nest, proportion of females that renest
CLUTCH1	clutch size for first nest
CLUTCH2	clutch size for second nest
HATCH	# of chicks hatched per egg laid in a successful nest
NSURV1	probability that first nest will survive laying and incubation
NSURV2	probability that second nest will survive laying and incubation
CHICK	probability of chick survival to 35 days old

Table 4.2 Sample sizes, means, and standard deviation of vegetation measurements collected at random locations distributed within the northwest Kansas study site in 2013 – 2016.

Vegetation Measurements	Native Working Grasslands			CRP Grasslands			t	DF	P≤
	Mean	SD	*n*	Mean	SD	*n*	*t*	DF	*P*≤
Visual Obstruction Readings									
25% VOR (dm)	1.95	1.64	6,918	3.34	2.04	3,372	-33.7	5,475	0.001
75% VOR (dm)	0.98	1.29	6,918	2.06	1.64	3,372	-34.4	5,550	0.001
Horizontal Cover Estimates									
Litter (%)	19.37	18.07	8,674	23.14	20.05	4,229	-10.3	7,387	0.001
Grass (%)	59.17	26.77	8,674	64.54	26.63	4,229	-11.1	8,289	0.001
Shrub (%)	1.83	8.95	8,674	0.01	0.31	4,228	18.2	8,707	0.001
Bare (%)	15.35	20.23	8,674	7.98	14.79	4,229	22.7	11,367	0.001
Forb (%)	8.11	13.05	8,674	7.02	18.11	4,230	0.83	5,727	0.41
Litter Depth (cm)	1.2	1.57	55,520	2.72	3.26	27,072	-72.7	33,345	0.001
Grass Height (cm)	17.07	15.75	1,720	32.34	19.81	841	-19.5	1,375	0.001
Frequency of Tallgrass Occurrence	0.13	0.33	1,735	0.63	0.48	846			
Proportion Suitable Nesting Locations	0.2		1,713	0.46		834			

[1] Vegetation measurements include visual obstruction readings collected using a 2-m tall Robel pole marked at alternating decimeters, Horizontal cover estimates were collected using a 60-cm^2 Daubenmire frame, litter depth and grass height were measured using a ruler, the frequency of tall-grass occurrence is an estimate of the number or locations having a tall-grass species as one of the 3 most abundant plants, proportion suitable nesting locations is the proportion of location having suitable nesting habitat as described in Lautenbach (2015; 75%VOR:1.5–3.5, Bare (%): 0–20).

[2]Tallgrass species included: little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*)

Table 4.3. Locations used by, and available to, lesser prairie-chickens in Northwest Kansas. Proportion of locations (n = 89,297) of lesser prairie-chickens (n= 148) marked with GPS transmitters occurring in cropland, CRP grasslands, and native working grasslands during the breeding (15 march –14 September), nonbreeding (16 September–14 March), and all seasons combined in northwest Kansas during 2013–2016. Proportional availability of cover types is based on minimum convex polygons drawn around all point at the northwest Kansas study sites (Plumb 2015, Robinson 2015).

Used

Season	Cropland	CRP	Native working grassland
Breeding	0.07	0.20	0.73
Nonbreeding	0.20	0.19	0.61
All seasons	0.10	0.20	0.70

Available

	Cropland	CRP	Native working grassland
All seasons[1]	0.07	0.36	0.54

[1]Availability of landcover types remained the same among seasons.

Table 4.4 Fecundity and survival variables estimated for female lesser prairie-chickens that used Conservation Reserve Program (CRP) grasslands at some point in their life cycle and those that never used CRP (NonCRP) cover types in northwest Kansas, during the breeding season (BS; 15 March – 15 September) and nonbreeding season (NBS; 15 September – 15 March) during 2013-2016. Chick survival and hatchability were estimated among all cover types and estimates are provided in the text.

Variable	CRP			NonCRP		
	Estimate	*SE*	*n*	*Estimate*	*SE*	*n*
Nest Survival	0.505	0.079	34	0.405	0.053	75
CLUTCH1	10.52	0.45	30	10.25	0.3	56
CLUTCH2	4.5	1.04	4	7.83	0.6	19
Nest Density	3.63/1000ha		31	1.78/1000ha		73
Percentage of broods*	14.29		1	86.00		6
BS Survival	0.421	0.064	65	0.440	0.066	63
NBS Survival	0.711	0.100	22	0.565	0.097	31

**Estimate of the percentage of 7-day-old broods occurring in CRP or NonCRP grasslands from nests that hatched in CRP.

Table 4.5 Fate of 102 lesser prairie-chicken nests occurring in Conservation Reserve Program (CRP) grasslands and native working grasslands in northwest Kansas, during 2013, 2014, and 2015.

Cover Type	*n*	Proportion			
		Successful	Depredated	Abandoned	Trampled
non-CRP	69	0.30	0.55	0.12	0.04
CRP	33	0.44	0.47	0.09	0.00
Total	102	0.34	0.52	0.11	0.03

223

Figure 4.1 Locations of the 5 study sites where lesser prairie-chickens were marked, captured, and monitored in 2013–2016 to estimate regional use of Conservation Reserve Program grasslands in Kansas and Colorado, USA. Study sites are highlighted with a blue box to identify the spatial extent of landscape scale resource selection function and demographic estimates herein. The estimated contemporary lesser prairie-chicken range is identified by black crosshatches.
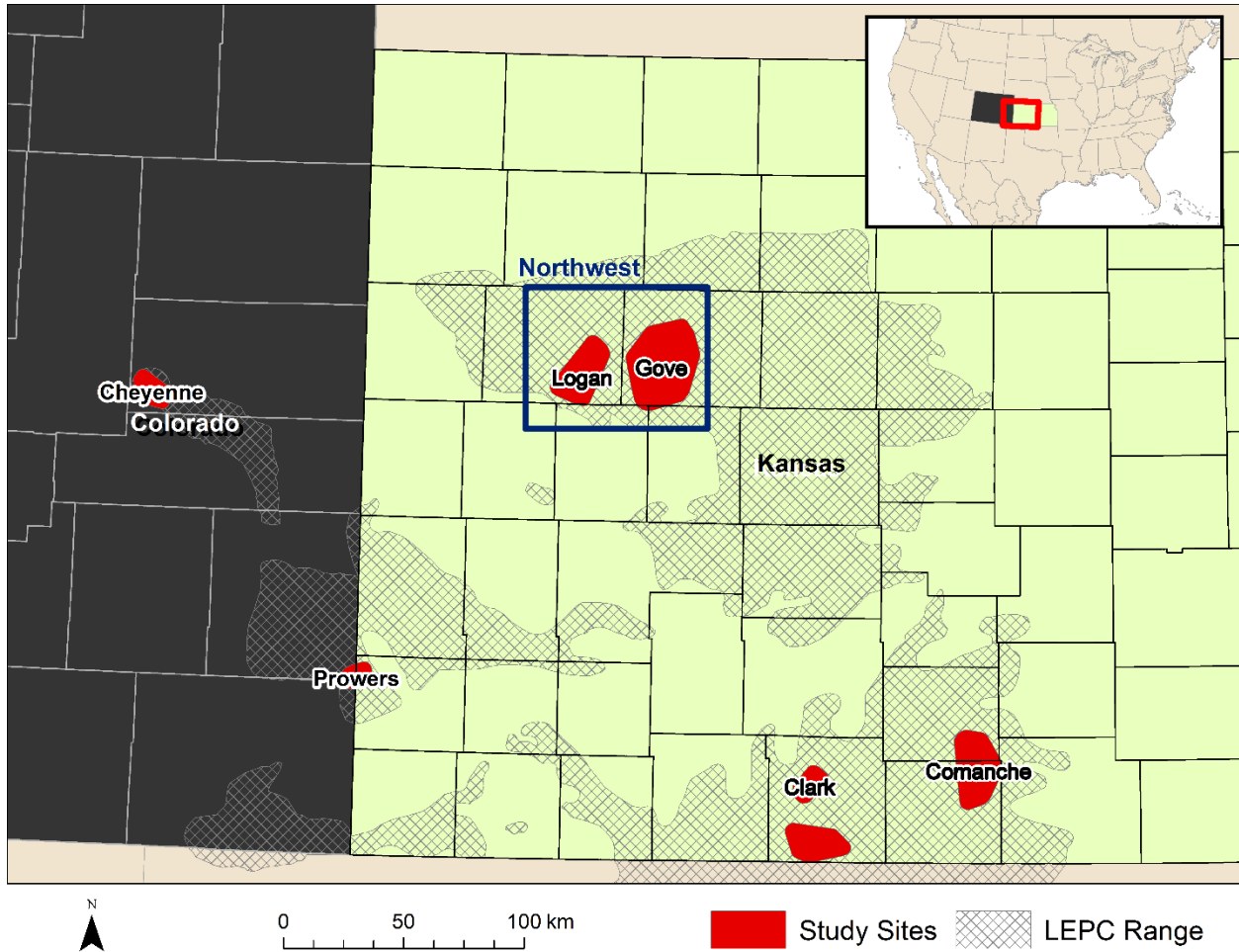
Figure 4.2 Predicted probability of use of Conservation Reserve Program grasslands by lesser prairie-chickens in northwest Kansas in 2013, 2014, and 2015 as a function of average annual precipitation estimated in 800 m x 800 m pixels (A; PRISM2016) and as a function of the drought severity (B; PDSI; Palmer Drought Severity Index) during the previous year (low numbers = greater drought severity).
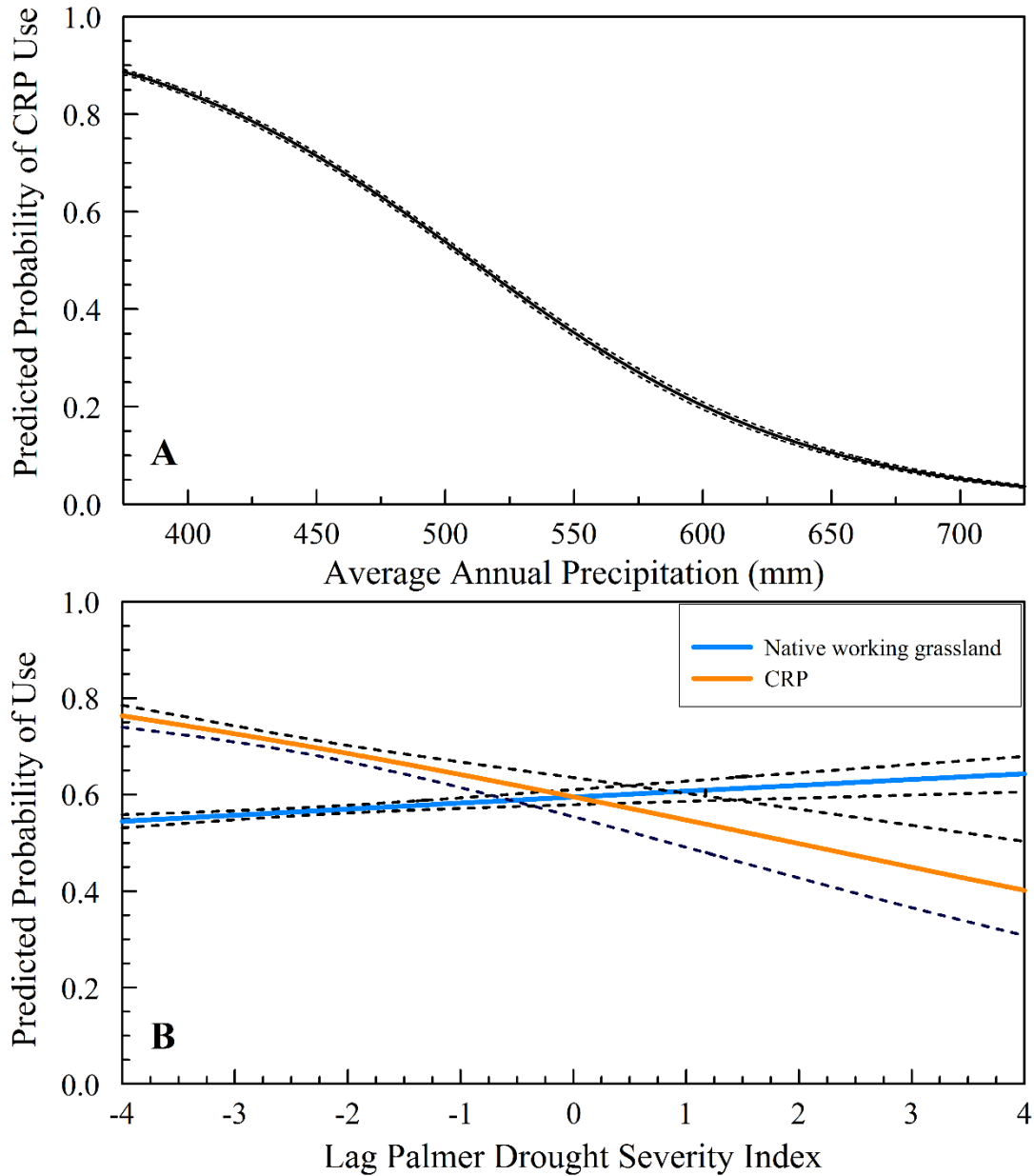
Figure 4.3 Predicted probability of use of Conservation Reserve Program grasslands by lesser prairie-chickens in northwest Kansas in 2013, 2014, and 2015 as a function of the amount of native grassland in a ~3,000-ha landscape.
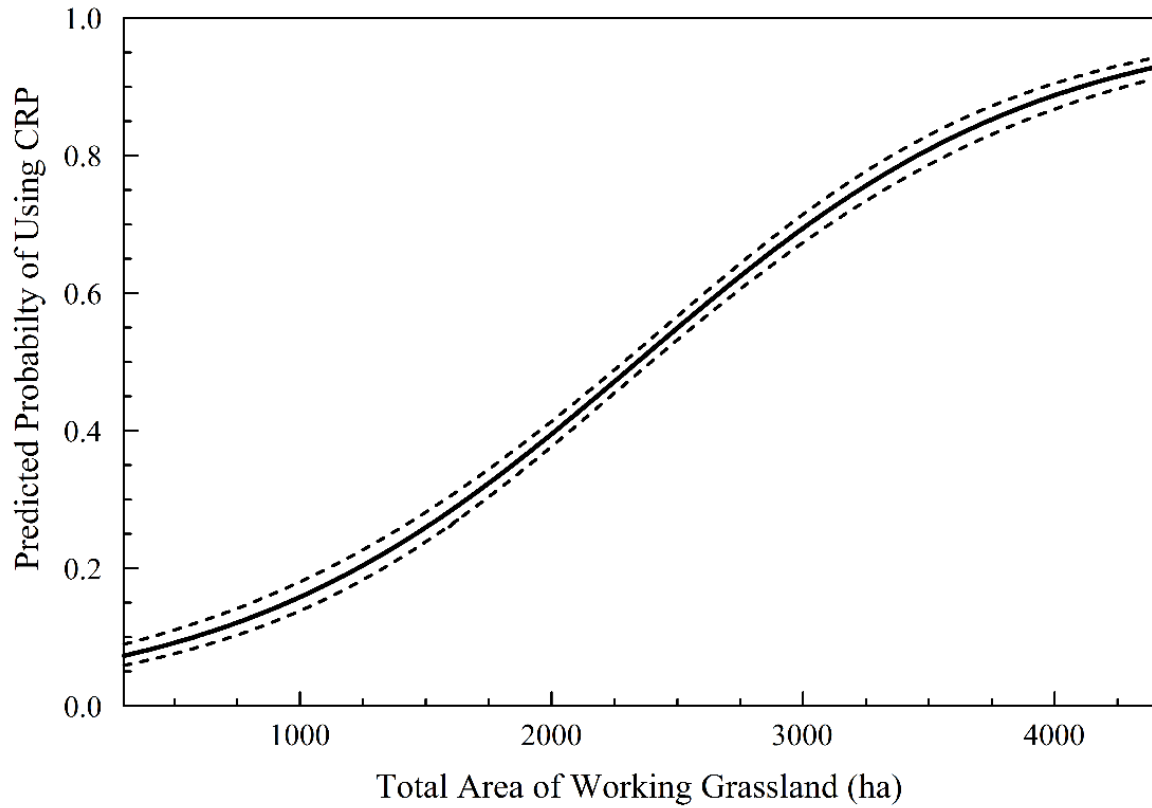
Figure 4.4