Final Report
USDA Natural Resources Conservation Service LPCI and CEAP

Great Plains CESU 68-7482-16-538

Grazing Management and Prescribed Fire for Conservation of Lesser Prairie-Chickens

Dan Sullins, John Kraft, Jonathan Lautenbach, Chris Gulick, Bram Verheijen, and David Haukos
Kansas Cooperative Fish and Wildlife Research Unit
Kansas State University
Manhattan, Kansas 66506
dhaukos@ksu.edu
(785) 532-5761
(806) 939-9404

December 2021

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is endemic to the High Plains of the western Great Plains of Kansas, Oklahoma, Colorado, Texas, and New Mexico. Despite the judicial decision to vacate the listing rule in September 2015 for the recent listing of the lesser prairie-chicken as threatened under the Endangered Species Act in May 2014, threats and stressors continue to prioritize the species for conservation actions. In 2021, the U.S. Fish and Wildlife Service proposed listing the lesser prairie-chicken as threatened in its northern range and endangered in its southern range, highlighting the continued concern for the species.

Core habitat for the species is associated with a variety of vegetation types and hetergeneity necessary to complete their life cycle. Quality habitat for lekking, nesting, brood rearing, and nonbreeding periods differ in vegetation associations and structure, indicating a need for a heterogeneous landscape to support populations of lesser prairie-chickens. Historical ecological drivers creating landscape heterogeneity of lesser prairie-chicken habitat include drought, grazing, and fire. However, natural grazing and fire patterns have been altered during the past 150 years and current application (or lack of application) of these drivers contribute little to development of habitat for lesser prairie-chickens.

Although the amount of habitat necessary for the persistence of lesser prairie-chickens is frequently debated, it is readily acknowledged that areas exceeding 10,000 – 20,000 ha may be the minimum space requirement for population persistence as long as the habitat components are present. If necessary components of habitat are not present, then lesser prairie-chickens must have sufficient connections among available quality habitat locations across landscapes to access necessary vegetation structure and composition to maximize survival and recruitment. Therefore, for habitat management to be effective, it must be implemented at large spatial scales. Unfortunately, there has not been any assessment or evaluation of the potential response of lesser prairie-chickens to large-scale management efforts. In addition, strategic application of large-scale management for lesser prairie-chicken populations would greatly enhance conservation efforts.

One potential large-scale conservation strategy would be determining the use of U.S. Department of Agriculture Conservation Reserve Program (CRP) land. The CRP allows landowners to convert cropland with highly erodible soils to permanent perennial cover (usually grass) for 10-15 year contracts in exchange for annual rental payments. Tracts of CRP contribute to the total amount of grassland on the landscape where the threshold for supporting lesser prairie-chicken >60%. In addition, most CRP tracts in lesser prairie-chicken range of Kansas and Colorado are planted to mid- and tall grasses, providing vegetation structure not found in the predominant short-grass prairie of much of the lesser prairie-chicken range. However, the importance of CRP to the persistence of lesser prairie-chickens is unknown.

Because livestock grazing, tree removal, fire, and application of CRP are the primary management options available for large-scale conservation actions, information to guide planning and implementation of these management actions is needed. Recent research has found that lesser prairie-chickens maximize use in relatively large pastures (>500 ha) under moderately intense grazing pressure, with hypothesized relationships among grazing intensity, annual biomass production, and visual obstruction that influence use, survival, and recruitment. However, these relationships need additional clarification prior to incorporation in management plans. Preliminary investigations into the use of fire indicates that a patch-burn approach provides landscape heterogeneity needed for lesser prairie-chickens as areas >2 years since burn provide nesting habitat and areas 1-2 years since burn are good brood-rearing habitat. However, additional information on use and vital rates in burned ys unburned areas is needed to fully understand the potential role of fire in population ecology of lesser prairie-chickens. In addition, information on livestock response to use of fire in lesser prairie-chicken habitat is needed to assist landowners and producers in decisions regarding the use of fire.

Funding under this agreement allowed for the expansion of on-going lesser prairie-chicken investigations into aspects of grazing, fire, and CRP as management tools in Kansas and Colorado. Our study objectives were to (1) evaluate lesser prairie-chicken and livestock response to large-scale patch-burn prescribed fire in the Red Hills, (2) quantify relationships of vegetation response (composition and structure) to prescribed fire and grazing management strategies in the Red Hills of Kansas, (3) compare lesser prairie-chicken population response among different grazing systems and intensities as well as burned versus unburned landscapes, (4) in-depth analysis of >400,000 lesser prairie-chicken locations and movements to quantify use of CRP during the entire year - with comparisons among ecoregions, (5) probabilistic evaluation of relative movements and locations by lesser prairie-chickens and cattle between patch-burn and rotational grazing systems including the influence of vegetation composition and structure, and (6) measure lesser prairie-chicken response to removal of eastern red cedar from the landscape.

Because these objective spanned multiple investigations across numerous study sites and research efforts and results are found in multiple theses, dissertations, and published journal articles, our intent is provide the abstracts of each with links to theses and dissertation and copies of published journal articles rather than an extensive, repetitive, stand-alone document. This will allow readers access to the primary literature of interest. All of the objectives were addressed during the work. Only objective (6) remains to be completed as the onset of the pandemic delayed completing this objective. However, we plan on continuing this work. With one exception, resource selection results, all other objectives were completed. The resource selection analyses are complete and the manuscript is being prepared. Additional work is on-going building these initial results.

Products

Post-Doctoral Research Associates

Beth Ross (2013-2016) – Ecological and landscape influences of CRP on lesser prairie-chicken populations in Kansas and Colorado.
Dan Sullins (2017-2019) – Lesser prairie-chicken population response to landscape management strategies.
Bram Verheijen (2017-2021) –Movements and resource selection by lesser prairie-chickens.

Theses and Dissertations

Gulick, C. (2019) Spatial ecology and resource selection by female lesser prairie-chickens within their home ranges and during dispersal. Thesis, Kansas State University, Manhattan. (https://krex.k-state.edu/dspace/handle/2097/40072)
Sullins, D. (2017) - Regional variation in demography, distribution, foraging, and strategic conservation of lesser prairie-chickens in Kansas and Colorado. Dissertation, Kansas State University, Manhattan. (https://krex.k-state.edu/dspace/handle/2097/35604)

Lautenbach, J. (2017). The role of fire, microclimate, and vegetation in lesser prairie-chicken habitat selection. Thesis, Kansas State University, Manhattan. (https://krex.k-state.edu/dspace/handle/2097/35395)

Kraft, J. (2016). Vegetation characteristics and lesser prairie-chicken responses to land cover types and grazing management in western Kansas. Thesis, Kansas State University, Manhattan. (https://krex.k-state.edu/dspace/handle/2097/34550)

Professional Presentations (56)

Gulick, C., and D. Haukos. 2018. Spatial patterns of lesser prairie-chickens in response to different disturbance regimes. International Grouse Symposium, Logan, Utah.

Gulick, C., and D.A. Haukos. 2018. Factors affecting habitat availability for lesser prairie-chickens across different land management regimes. Kansas Natural Resources Conference, Manhattan, Kansas.

Gulick, C., and D.A. Haukos. 2019. Influence of grassland management systems on fine-scale distribution of lesser prairie-chickens and their habitat. Annual Meeting of the Society for Range Management, Minneapolis, Minnesota.

Gulick, C., and D.A. Haukos. 2019. Influence of landscape features on female lesser prairie-chicken dispersal routes. Kansas Natural Resource Conference, Manhattan, Kansas.

Gulick, C., D. Haukos, and J. Lautenbach. 2018. Effect of grazing management systems on space use by cattle and lesser prairie-chickens. Annual Meeting of The Wildlife Society, Cleveland, Ohio.

Gulick, C., J. Lautenbach, and D.A. Haukos. 2017. Space use by cattle, and its cascading effects on lesser prairie-chicken habitat selection. Annual conference of The Wildlife Society, Albuquerque, NM.

Kraft, J.D. 2015. Third-order selection of a prairie specialist lesser prairie-chicken habitat selection in varying landscapes. Division of Biology, Graduate Student Forum.

Kraft, J.D., and D.A. Haukos. 2015. Landscape level habitat selection of female lesser prairie-chickens in western Kansas and eastern Colorado. International Grouse Symposium, Reykjavík, Iceland.

Kraft, J.D., D. Haukos, and C. Hagen. 2016. Implications of pasture area, grazing strategy, and region on lesser prairie-chicken habitat selection and vegetation. Annual Meeting of the Society of Range Management, Corpus Christi, TX

Kraft, J.D., D. Haukos, C. Hagen, and J. Pitman. 2016. Are larger pastures and sparser herds the way to manage grassland birds? A case-study of the lesser prairie-chicken. Annual Meeting of The Wildlife Society, Raleigh, NC. (Invited)

Kraft, J.D., D. Haukos, J. Pitman, and C. Hagen. 2015. Identifying drivers of lesser prairie-chicken habitat selection within western Kansas grazed lands. Annual Meeting of the Kansas Ornithological Society, Emporia, KS

Kraft, J.D., D. Sullins, and D.A. Haukos. 2016. Dynamic interactions of Conservation Reserve Program, native grasslands, and lesser prairie-chicken habitat selection. Kansas Natural Resource Conference, Wichita, KS.

Kraft, J.D., D. Sullins, and D.A. Haukos. 2016. Evaluation of lesser prairie-chicken brood habitat selection across categorical habitats. Kansas Natural Resource Conference, Wichita, KS.

Kraft, J.D., D.A. Haukos, M.R. Bain, M. Rice, S. Robinson, D.S. Sullins, C.A. Hagen, J. Pitman, J. Lautenbach, R. Plumb, and J. Lautenbach. 2017. Sparser herds, larger pastures, and imperiled birds: heterogeneity-based grazing management is essential for a heterogeneity-dependent grassland. Prairie Grouse Technical Council, Dickinson, ND.

Kraft, J.D., J. Lautenbach, D. Haukos, J. Pitman, and C. Hagen. 2015. Female lesser prairie-chicken response to grazing in western Kansas grasslands. Biennial meeting of the Prairie Grouse Technical Council, Nevada, Missouri.

Kraft, J.D., J. Lautenbach, D. Haukos, J. Pitman, and C. Hagen. 2015. Female lesser prairie-chicken response to grazing in western Kansas grasslands. Annual meeting of the Central Mountains and Plains Section of The Wildlife Society, Manhattan, Kansas.

Kraft, J.D., J. Lautenbach, D.A. Haukos, and J.C. Pitman. 2015. Seasonal habitat selection by female lesser prairie-chickens in varying landscapes. Kansas Natural Resource Conference, Wichita.

Kraft, J.D., J. Lautenbach, D.A. Haukos, J.C. Pitman, and C.A. Hagen. 2015. Female lesser prairie-chicken response to grazing practices in western Kansas grasslands. Annual Meeting of the Society of Range Management, Sacramento, CA.

Kraft, J.D., S.G. Robinson, R.T. Plumb, and D.A. Haukos. 2015. Landscape characteristics of home ranges of lesser prairie-chickens. Joint meeting of American Ornithologists' Union and Cooper Ornithological Society, Norman, OK.

Lautenbach, J. D. Haukos, J. Lautenbach, J. Kraft, and D. Sullins. 2016. Satisfying the quilt work of habitat needs of the lesser prairie-chicken: the role of patch-burn grazing. Annual Meeting of The Wildlife Society, Raleigh, NC. (Invited)

Lautenbach, J., and D. Haukos. 2017. Quantifying landscape and vegetation characteristics of lesser prairie-chicken habitat during extreme temperature events. Annual meeting of the Society of Range Management, St. George, UT.

Lautenbach, J., D. Haukos, and B.A. Grisham. 2017. Fried Chicken: Identifying areas of thermal refugia for lesser prairie-chickens in a changing climate. Annual meeting of the Midwest Fish and Wildlife Agencies, Lincoln, NE.

Lautenbach, J., D. Haukos, and B.A. Grisham. 2017. Quantifying landscape and vegetative characteristics of lesser prairie-chicken habitat during extreme temperature events. Annual meeting of The Wildlife Society, Albuquerque, NM.

Lautenbach, J., D. Haukos, and C. Hagen. 2016. Satisfying the quilt work of habitat needs of the lesser prairie-chicken: the role of patch-burn grazing. Annual meeting of The Wildlife Society, Raleigh, NC.

Lautenbach, J., D. Haukos, and C. Hagen. 2017. Influence of patch-burn grazing on lesser prairie-chicken habitat selection in Kansas. Prairie Grouse Technical Council, Dickinson, ND.

Lautenbach, J., J. Lautenbach, and D. Haukos. 2016. Response of lesser prairie-chicken habitat and habitat use to patch-burn grazing. Annual Meeting of the Midwest Fish and Wildlife Conference, Grand Rapids, MI.

Lautenbach, J., J. Lautenbach, and D. Haukos. 2016. Using patch-burn grazing to maintain prairie for lesser prairie-chickens. Kansas Natural Resource Conference, Wichita, KS.

Sullins, D. S., B. E., Ross, and D. A. Haukos. 2018. Potential bias of lesser prairie-chicken population estimates when not accounting for individual heterogeneity. Kansas Natural Resources Conference, Manhattan, Kansas.

Sullins, D., D. Haukos, and C. Hagen. 2019. Hierarchical ecological benefits of the Conservation Reserve Program in the Southern Great Plains. Annual Meeting of The Wildlife Society, Reno, Nevada. (Invited)

Sullins, D., W. Conway, C. Comer, K. Hobson, and I. Wassenaar. 2013. American woodcock connectivity as indicated by hydrogen isotope. Annual Meeting of The Texas Chapter of The Wildlife Society, Houston, Texas

Sullins, D.A., W. Conway, and D. Haukos. 2012. American woodcock (Scolopax minor) habitat suitability and occupancy in eastern Texas. 48th Annual Meeting, Texas Chapter of The Wildlife Society, Fort Worth, Texas.

Sullins, D.S., and D.A. Haukos. 2015. Lesser prairie-chicken diets during brooding and winter. Annual Meeting of the Kansas Ornithological Society, Emporia, KS

Sullins, D.S., and D.A. Haukos. 2015. Optimal nesting substrate drives lesser prairie-chicken habitat use in Kansas and Colorado. Kansas Natural Resource Conference, Wichita.

Sullins, D.S., and D.A. Haukos. 2016. Available foods and diets of lesser prairie-chickens in native and CRP grasslands of Kansas and Colorado. Kansas Natural Resource Conference, Wichita, KS.

Sullins, D.S., and D.A. Haukos. 2016. Lesser prairie-chicken foraging in native and CRP grasslands of Kansas and Colorado. Annual Meeting of The Wildlife Society, Raleigh, NC.

Sullins, D.S., and D.A. Haukos. 2016. Lesser prairie-chicken foraging in native and CRP grasslands of Kansas and Colorado. Annual Meeting of the Society of Range Management, Corpus Christi, TX

Sullins, D.S., B.E. Ross, and D.A. Haukos. 2018. Influence of individual heterogeneity on lesser prairie-chicken population persistence. Annual Meeting of The Wildlife Society, Cleveland, Ohio.

Sullins, D.S., D.A. Haukos, and B.K. Sandercock. 2015. Population demographic sensitivity for the threatened lesser prairie-chicken. Joint meeting of American Ornithologists' Union and Cooper Ornithological Society, Norman, OK.

Sullins, D.S., D.A. Haukos, and B.K. Sandercock. 2015. Regional demographic variability for lesser prairie-chickens in Kansas and Colorado. Biennial meeting of the Prairie Grouse Technical Council, Nevada, Missouri.

Sullins, D.S., D.A. Haukos, and B.K. Sandercock. 2015. Regional demographic variability for lesser prairie-chickens in Kansas and Colorado. Annual meeting of the Central Mountains and Plains Section of The Wildlife Society, Manhattan, Kansas.

Sullins, D.S., D.A. Haukos, and B.K. Sandercock. 2016. Impacts of Conservation Reserve Program grasslands on lesser prairie-chicken populations in the northern extent of their range. Kansas Natural Resource Conference, Wichita, KS.

Sullins, D.S., D.A. Haukos, J. Kraft, J. Lautenbach, J. Lautenbach, R. Plumb, S. Robinson, B. Ross, and B.K. Sandercock. 2017. Strategic regional conservation for lesser prairie-chickens among landscapes adjacent to western Kansas rivers. Kansas Natural Resource Conference, Wichita, KS.

Sullins, D.S., D.A. Haukos, J. Kraft, J. Lautenbach, J. Lautenbach, R. Plumb, S. Robinson, and B. Ross. 2016. Conservation planning for lesser prairie-chickens among reproductive and survivorship landscapes of varying anthropogenic influence. North American Congress for Conservation Biology, Madison, WI. (Invited)

Sullins, D.S., D.A. Haukos, J.M. Lautenbach, and J.D. Kraft. 2018. Tradeoffs of nest and brood habitat availability for lesser prairie-chickens. International Grouse Symposium, Logan, Utah.

Sullins, D.S., J. Kraft, D.A. Haukos, and B.K. Sandercock, 2017. Selection and demographic consequences of Conservation Reserve Program grasslands for lesser prairie-chickens. Annual meeting of the Midwest Fish and Wildlife Agencies, Lincoln, NE.

Sullins, D.S., J.M. Lautenbach, and D.A. Haukos. 2017. Tradeoffs of nest and brood habitat availability for lesser prairie-chickens. Annual conference of The Wildlife Society, Albuquerque, NM.

Sullins, D.S., M.S. Sirch, J. Kraft, and David A. Haukos. 2019. Lesser prairie-chicken response to herbaceous vegetation change following intensive wildfire. Kansas Natural Resource Conference, Manhattan, Kansas.

Sullins, D.S., W.C. Conway, D.A. Haukos, and C.E. Comer. 2017. Using pointing dogs and hierarchical models to estimate American woodcock winter habitat availability. 11th Woodcock Symposium, Roscommon, MI.

Sullins, D.S., W.C. Conway, D.A. Haukos, K.A. Hobson, L.I. Wassenaar, and C.E. Comer. 2015. American woodcock migratory connectivity as indicated by hydrogen isotopes. Joint meeting of American Ornithologists' Union and Cooper Ornithological Society, Norman, OK.

Sullins, D.S., D.A. Haukos, C.A. Hagen, and K.C. Olson. 2021. Targeted tree removal to benefit prairie grouse and cattle operations. Annual Conference of The Wildlife Society (invited, virtual).

Verheijen, B.H.F, C.K.J. Gulick, J.D. Kraft, J.D. Lautenbach, J.M. Lautenbach, R.T. Plumb, S.G. Robinson, D.S. Sullins, and D.A. Haukos. 2019. How can breeding stage-specific estimates of movements and space use of female lesser prairie-chickens (Tympanuchus pallidicinctus) aid conservation efforts? Annual Meeting of The Wildlife Society, Reno, Nevada.

Verheijen, B.H.F., and D.A. Haukos. 2019. How can breeding stage-specific estimates of movements and space use of female lesser prairie-chickens aid conservation efforts? 33rd Biennial Meeting of the Prairie Grouse Technical Council, Bartlesville, Oklahoma.

Verheijen, B.H.F., C.K.J. Gulick, C.A. Hagen, J.D. Kraft, J.D. Lautenbach, J.M. Lautenbach, R.T. Plumb, S.G. Robinson, D.S. Sullins, and D.A. Haukos. 2020. Extrinsic and intrinsic drivers of resource selection by female lesser prairie-chickens. Annual Meeting of The Wildlife Society, Louisville, Kentucky.

Verheijen, B.H.F., C.K.J. Gulick, J.D. Kraft, J.D. Lautenbach, J.M. Lautenbach, R.T. Plumb, S.G. Robinson, D.S. Sullins, and D.A. Haukos. 2021. Is grassland always grassland? Spatiotemporal variation in grassland patch selection by lesser prairie-chickens. Midwest Fish and Wildlife Conference, virtual.

Verheijen, B.H.F., C.K.J. Gulick, J.D. Kraft, J.D. Lautenbach, J.M. Lautenbach, R.T. Plumb, S.G. Robinson, D.S. Sullins, and D.A. Haukos. 2020. Is grassland always grassland? Spatiotemporal variation in grassland patch selection by lesser prairie-chickens. Annual meeting of the Kansas Ornithological Society, virtual.

Verheijen, B.H.F., D.A. Haukos, and D.S. Sullins. 2021. Spatiotemporal variation and individual heterogeneity in resource selection by lesser prairie-chickens. Annual Conference of The Wildlife Society (virtual).

Primary Journal Articles

Kraft, J. D., D. A. Haukos, M. R. Bain, M. B. Rice, S. G Robinson, D. S. Sullins, C. A. Hagen, J. Pitman, J. Lautenbach, R. Plumb, and J. Lautenbach. 2021. Using grazing to manage herbaceous structure for a heterogeneity-dependent bird. Journal of Wildlife Management 85:354–368. DOI: 10.1002/jwmg.21984

Lautenbach, J.D., D.A. Haukos, J.M. Lautenbach, and C.A. Hagen. 2021. Ecological disturbance through patch-burn grazing drives lesser prairie-chicken space use. Journal of Wildlife Management 85:1699-1710.

Sullins, D.S., D. A. Haukos, J. Craine, J. M. Lautenbach, S. G. Robinson, J. D. Lautenbach, J. D. Kraft, R. T. Plumb, B. K. Sandercock, and N. Fierer. 2018. Identifying diet of a declining prairie grouse using DNA metabarcoding. Auk 135:583–608.

Sullins, D.S., J.D. Kraft, D.A. Haukos, S.G. Robinson, J. Reitz, R.T. Plumb, J.M. Lautenbach, J.D. Lautenbach, B.K. Sandercock, and C.A. Hagen. 2018. Selection and demographic consequences of Conservation Reserve Program grasslands for lesser prairie-chickens. Journal of Wildlife Management 82:1617-1632.

Sullins, D.S., D.A. Haukos, J.M. Lautenbach, J.D. Lautenbach, S.G. Robinson, M.B. Rice, B.K. Sandercock, J.D. Kraft, R.T. Plumb, J.H. Reitz, J.M.S. Hutchinson, and C.A. Hagen. 2019. Strategic regional conservation for lesser prairie-chickens among landscapes of varying anthropogenic influence. Biological Conservation 238 (2019) 108213.

Sullins, D.S., M. Bogaerts, B.H.F. Verheijen, D.E. Naugle, T. Griffiths, and C.A. Hagen. 2021. Increasing durability of voluntary conservation through strategic implementation of the Conservation Reserve Program. Biological Conservation 259:109177.

Verheigen, B.H.F., R.T. Plumb, C.K.J. Gulick, C.A. Hagen, S.G. Robinson, D.S. Sullins, and D.A. Haukos. 2021. Breeding season space use by lesser prairie-chickens (Tympanuchus pallidicinctus) varies among ecoregions and breeding stages. American Midland Naturalist 185:149-174.

Secondary Journal Articles (used data generated by this funding)

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

Lautenbach, J.M., D.A. Haukos, D.S. Sullins, C.A. Hagen, J.D. Lautenbach, J.C. Pitman, R.T. Plumb, S,G. Robinson, and J.D. Kraft. 2019. Factors influencing nesting ecology of lesser prairie-chickens. Journal of Wildlife Management 83:205-215.

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

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

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

Robinson, S.G., D.A. Haukos, R.T. Plumb, J.M. Lautenbach, D.S. Sullins, J.D. Kraft, J.D. Lautenbach. C.A. Hagen, and J.C. Pitman. 2018. Nonbreeding home range size and survival of lesser prairie-chickens. Journal of Wildlife Management 82:374–382.

Ross, B.E., D.A. Haukos, C. Hagen, and J. Pitman. 2018. Combining multiple sources of data to inform conservation of Lesser Prairie-Chicken populations. Auk 135:228-239.

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

Ross, B.E., D.S. Sullins, and D.A. Haukos. 2019. Using an individual-based model to assess common biases in lek-based count data to estimate population trajectories of lesser prairie-chickens. PLoS ONE 14(5): e0217172.

Schindler, A.R., D.A. Haukos, C.A. Hagen, and B.E. Ross. 2020. A decision-support tool to prioritize candidate landscapes for lesser prairie-chicken conservation. Landscape Ecology 35:1417-1434.

Schindler, A.R., D.A. Haukos, C.A. Hagen, and B.E. Ross. 2020. A multi-species approach to manage effects land cover and weather on upland game birds. Ecology and Evolution 10:14330–14345.

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

Effects of working grassland management on lesser prairie-chicken resource selection within home ranges and during dispersal events

Gulick, Christopher Kevin

The lesser prairie-chicken (Tympanuchus pallidicinctus) is a grassland obligate whose decline has been associated with anthropogenic fragmentation and land use change. Historical habitat drivers (i.e., natural fires and free roaming grazers) created vegetation heterogeneity across the species' range, providing resources for each of their life stages. Currently, most of the lesser prairie-chicken's eastern range consists of rangelands managed with confined continuous livestock grazing without fire as a disturbance. Lesser prairie-chicken habitat is also fragmented at larger scales, limiting dispersals and threatening genetic connectivity. A need exists to determine optimum landscape management that provides seasonal habitat at small scales, and allows for dispersal and metapopulation connectivity at large scales. My first objective was to determine the relationship between cattle distributions and lesser prairie-chicken habitat among patch-burn and rotationally grazed rangelands. My second objective was to determine differences in seasonal selection by female lesser prairie-chickens, relative to fine-scale cattle distributions on these two rangelands. My final objective was to determine movement patterns and resource selection of lesser prairie-chickens during dispersal. I tracked cattle (Bos taurus) and lesser prairie-chickens via satellite telemetry in patch-burn and rotationally grazed pastures to model their space use at fine scales. I estimated vegetation change along the resulting gradient of cattle distributions. I determined seasonal selection of lesser prairie-chickens relative to cattle distributions within each management treatment. I tracked GPS-tagged lesser prairie-chickens in the Mixed-Grass Prairie and Short-Grass Prairie/CRP Mosaic ecoregions and delineated dispersals. I used step selection analysis to determine differences in resource selection along each dispersal route. Year-of-fire patches drove cattle site-selection on patch-burn grazed rangelands, which created greater vegetation heterogeneity within pastures. Lesser prairie-chickens selected for different cattle densities during different life stages. On rotationally grazed pastures, lesser prairie-chickens selected for moderate cattle densities during breeding, moderate-to-high densities during post-breeding, and selected for the greatest fine-scale cattle densities during nonbreeding. Within the patch-burn grazed treatment, females avoided moderate cattle densities during breeding and post-breeding, and selected for the lowest cattle densities during nonbreeding. Patch-burn grazed pastures were more heterogeneous and contained greater forb abundance in areas with low cattle densities, which could create better brooding and post-breeding habitat near nesting habitat. In the Mixed-Grass Prairie Ecoregion, lesser prairie-chickens selected for lower tree densities and increased grassland cover at the landscape scale during dispersal. On the Short-Grass Prairie Ecoregion, lesser prairie-chickens avoided areas containing electrical transmission lines. During dispersal, young females traveled further and took longer movement steps. Successful dispersals were also shorter distances than failed dispersals. Drivers of dispersal may be innate and could occur regardless of annual variation in local habitat; however, there is likely a fitness cost associated with increased dispersal length. Land-use alterations influenced habitat within home ranges and affected population

connectivity by altering dispersals. Managers can benefit lesser prairie-chickens by altering grazing management to mimic historical drivers of habitat. Population connectivity could be increased by limiting electrical transmission line establishment along corridors in the Short-Grass Prairie Ecoregion and by removing trees and increasing grassland within the Mixed Grass-Prairie Ecoregion.

The role of fire, microclimate, and vegetation in lesser prairie-chicken habitat selection

Lautenbach, Jonathan David

The lesser prairie-chicken is a prairie grouse native to the southwestern Great Plains that has experienced significant population and habitat declines since European settlement. Ongoing declines prompted the U.S. Fish and Wildlife Service to list lesser prairie-chickens as threatened under the Endangered Species Act in spring of 2014. In fall of 2015, the listing was vacated on procedural grounds and the lesser prairie-chicken was removed from listing in summer 2016. Despite the legislative change, considerable conservation efforts emerged with the initial listing and have continued following the removal of the species from the threatened and endangered species list. Understanding how lesser prairie-chickens use landscapes and how management actions can influence their space use is important for long-term strategies to meet conservation goals. I modeled lesser prairie-chicken habitat selection relative to landscape mosaics of vegetation patches generated through patch-burn grazing, microclimate, and vegetation characteristics across their range. I captured, attached GPS satellite or VHF radio transmitters to, tracked, and measured vegetation characteristics used by and available to female lesser prairie-chickens across the northern portion of their range in Kansas and Colorado. Female lesser prairie-chickens use all patch types created in a patch-burn grazing mosaic, with female selecting greater time-since-fire patches (>2-years post-fire) for nesting, 2-year post-fire patches during the spring lekking season, 1- and 2-year post-fire patches during the summer brooding period, and 1-year post-fire units during the nonbreeding season. Available vegetation structure and composition in selected patches during each life-cycle stage was similar to the needs of female lesser prairie-chickens during that life-cycle stage. To assess their selected microclimate conditions, I deployed Maxim Integrated Semiconductor data loggers (iButtons) at female flush locations and across a landscape inhabited by lesser prairie-chickens. Females selected locations that minimized thermal stress at microsite, patch, and landscape scales during peak midday temperatures during summer. Females selected midday locations based on vegetation characteristics; where selected sites had >60% forb cover and <25% grass cover, or >75% grass cover and <10% forb cover. In addition, females selected sites with greater visual obstruction. I measured vegetation composition and structure at use and available sites at four study areas located along the precipitation gradient characterizing the full extent of the lesser prairie-chicken range. Vegetation structure use by females varied in relation to long-term precipitation patterns. Females used sites with lower visual obstruction than available during the fall and spring. However, they used vegetation composition that was similar to available within each study area. Overall, my findings indicate that lesser prairie-chickens require structural and compositional heterogeneity to support a suite of habitat needs throughout the year. Therefore, management should focus on providing structural and compositional heterogeneity across landscapes. Greater heterogeneity in vegetation conditions can be achieved through management practices that allow domestic grazers to select grazing locations, such as patch-burn grazing or increased pasture area.

Vegetation characteristics and lesser prairie chicken responses to land cover types and grazing management in western Kansas

Kraft, John Daniel

In the southern Great Plains, the lesser prairie-chicken (Tympanuchus pallidicinctus; hereafter LEPC), an obligate grassland species, has experienced significant population declines and range contractions with subsequent conservation concern. Management actions often use land cover types to make inference about habitat quality. Relatively little information is available related to grazed rangelands to guide conservation. The influences of land cover types and livestock grazing on LEPC habitat selection have not been researched extensively in western Kansas. I evaluated the influence of land cover types and grazing management on vegetation characteristics, habitat selection, and nest/adult survival of LEPC in western Kansas. Females were captured and radio-marked to monitor habitat use, nest success, and adult survival. Grazing and vegetation data were collected via producer correspondence and vegetation surveys, respectively. Vegetation composition and structure differed across land cover types, which can be used to make inferences about LEPC habitat quality. Habitat selection analyses corroborated the importance of breeding habitat in close proximity to leks (<3 km) and identified land cover types selected for nesting (Conservation Reserve Program, Limy Upland, Saline Subirrigated) and brooding (Conservation Reserve Program, Red Clay Prairie, Sands, Sandy Lowland). Conservation Reserve Program patches positioned near rangelands contributed to LEPC reproductive success in northwest Kansas. In grazed lands, LEPC selected habitat close to leks (<3 km) and large pastures (>400 ha), exhibiting low-moderate stocking densities (<0.4 AU/ha), and low-moderate levels of deferment during the grazing season (60-100 days). Nest site selection was negatively influenced by increasing distance from a lek and grazing pressure. Daily nest survival rates were negatively influenced by increasing grazing pressure and high levels of stocking density. Annual adult female survival was negatively influenced as forage utilization (% forage removed) increased. Heterogeneity (coefficient of variation and standard deviation) of visual obstruction was decreased at stocking densities > 0.26 AU/ha. Future conservation actions should consider the potential of land cover types to create adequate vegetation structure, and manage rangelands with low-moderate stocking densities and deferment and greater pasture areas. The relationship between habitat selection and proximity of lek sites (< 5 km) should be used to identify quality LEPC habitat.

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

Sullins, Daniel S.

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.

Increasing durability of voluntary conservation through strategic implementation of the Conservation Reserve Program

Working lands are an attractive solution for conservation in the conterminous United States where 76% of area is privately owned. Conservation of private lands often relies on participation in temporary incentive-based programs. As incentives expire landowners make decisions that determine whether environmental benefits continue. In the U.S., the Conservation Reserve Program (CRP) contracts for 10–15 years to replant ~90–140.5 thousand km2 of cropland back to grassland. Temporary set-aside programs, such as CRP, are implemented with minimal planning to retain durable investments after payments end. We used known fate models and remotely-sensed cropland layers to estimate durability of CRP after contract expiration and to identify areas of greater predicted durability. The durability of conservation through CRP is the probability of continued provision of grass cover after incentive-based payments have ended. We expected durability would vary among landscapes and regions. Overall, 58% (SE = 0.40) of expired fields remained in grassland. However, durability ranged widely (36–76%) across six U.S. states for 13,231 contracts that expired in 2007. Reversion to cropland increased for CRP grasslands with an inherently high tillage risk, in more northerly regions, and for larger fields including those surrounded by cropland. Temporally, conversion was prevalent within five years of contract expiration, during years with higher corn prices, and in wetter years. Findings provide guidance for allocating CRP contracts in areas where grassland conservation benefits may be maximized and where transition from set-aside programs to working grasslands may promote durability.

Breeding season space use by lesser prairie-chickens (Tympanuchus pallidicinctus) varies among ecoregions and breeding stages

Large-scale declines of grassland ecosystems in the conterminous United States since European settlement have led to substantial loss and fragmentation of lesser prairie-chicken (Tympanuchus pallidicinctus) habitat and decreased their occupied range and population numbers by ~85%. Breeding season space use is an important component of lesser prairie-chicken conservation, because it could affect both local carrying capacity and population dynamics. Previous estimates of breeding season space use are largely limited to one of the four currently occupied ecoregions, but potential extrinsic drivers of breeding space use, such as landscape fragmentation, vegetation structure and composition, and density of anthropogenic structures, can show large spatial variation. Moreover, habitat needs vary greatly among the lekking/prelaying, nesting, brood-rearing, and post-breeding stages of the breeding season, but space use by female lesser prairie-chickens during these stages remain relatively unclear. We tested whether home range area and daily displacement (the net distance between the first and last location of each day) of female lesser prairie-chickens varied among ecoregions and breeding stages at four study sites in Kansas and Colorado, U.S.A., representing three of the four currently occupied ecoregions. We equipped females with very-high-frequency (VHF) or Global Positioning System (GPS) transmitters, and estimated home range area with kernel density estimators or biased random bridge models, respectively. Across all ecoregions, breeding season home range area averaged 190.4 ha (619.1 ha SE) for birds with VHF and 283.6 ha (623.1 ha) for birds with GPS transmitters, whereas daily displacement averaged 374.8 m (614.3 m). Average home range area and daily displacement of bird with GPS transmitters were greater in the Short-Grass Prairie/Conservation Reserve Program Mosaic and Sand Sagebrush Prairie Ecoregions compared to sites in the Mixed-Grass Prairie Ecoregion. Home range area and daily displacement were greatest during lekking/prelaying and smallest during the brood-rearing stage, when female movements were restricted by mobility of chicks. Ecoregion- and breeding stage-specific estimates of space use by lesser prairie-chickens will help managers determine the spatial configuration of breeding stage-specific habitat on the landscape. Furthermore, ecoregion and breeding stage-specific estimates are crucial when estimating the amount of breeding habitat needed for lesser prairie-chicken populations to persist.

Ecological disturbance through patch-burn grazing influences lesser prairie-chicken space use

Across portions of the western Great Plains in North America, natural fire has been removed from grassland ecosystems, decreasing vegetation heterogeneity and allowing woody encroachment. The loss of fire has implications for grassland species requiring diverse vegetation patches and structure or patches that have limited occurrence in the absence of fire. The lesser prairie-chicken (Tympanuchus pallidicinctus) is a declining species of prairie-grouse that requires heterogeneous grasslands throughout its life history and fire has been removed from much of its occupied range. Patch-burn grazing is a management strategy that re-establishes the fire-grazing interaction to a grassland system, increasing heterogeneity in vegetation structure and composition. We evaluated the effects of patch-burn grazing on lesser prairie-chicken space use, habitat features, and vegetation selection during a 4-year field study from 2014–2017. Female lesser prairie-chickens selected 1- and 2-year post-fire patches during the lekking season, ≥4-year post-fire patches during the nesting season, and year-of-fire and 1-year post-fire patches during post-nesting and nonbreeding seasons. Vegetation selection during the lekking season was not similar to available vegetation in selected patches, suggesting that lesser prairie-chickens cue in on other factors during the lekking season. During the nesting season, females selected nest sites with greater visual obstruction, which was available in ≥4-year post-fire patches; during the post-nesting season, females selected sites with 15–25% bare ground, which was available in the year-of-fire, 1-year post-fire, and 2-year post-fire patches; and during the nonbreeding season they selected sites with lower visual obstruction, available in the year-of-fire and 1-year post-fire patches. Because lesser prairie-chickens selected all available time-since-fire patches during their life history, patch-burn grazing may be a viable management tool to restore and maintain lesser prairie-chicken habitat on the landscape.

Using grazing to manage herbaceous structure for a heterogeneity-dependent bird

Grazing management recommendations often sacrifice the intrinsic heterogeneity of grasslands by prescribing uniform grazing distributions through smaller pastures, increased stocking densities, and reduced grazing periods. The lack of patch-burn grazing in semi-arid landscapes of the western Great Plains in North America requires alternative grazing management strategies to create and maintain heterogeneity of habitat structure (e.g., animal unit distribution, pasture configuration), but knowledge of their effects on grassland fauna is limited. The lesser prairie-chicken (Tympanuchus pallidicinctus), an imperiled, grassland-obligate, native to the southern Great Plains, is an excellent candidate for investigating effects of heterogeneity-based grazing management strategies because it requires diverse microhabitats among life-history stages in a semi-arid landscape. We evaluated influences of heterogeneity-based grazing management strategies on vegetation structure, habitat selection, and nest and adult survival of lesser prairie-chickens in western Kansas, USA. We captured and monitored 116 female lesser prairie-chickens marked with very high frequency (VHF) or global positioning system (GPS) transmitters and collected landscape-scale vegetation and grazing data during 2013‑2015. Vegetation structure heterogeneity increased at stocking densities ≤0.26 animal units/ha, where use by nonbreeding female lesser prairie-chickens also increased. Probability of use for nonbreeding lesser prairie-chickens peaked at values of cattle forage use values near 37% and steadily decreased with use ≥40%. Probability of use was positively affected by increasing pasture area. A quadratic relationship existed between growing season deferment and probability of use. We found that 70% of nests were located in grazing units in which grazing pressure was <0.8 animal unit months/ha. Daily nest survival was negatively correlated with grazing pressure. We found no relationship between adult survival and grazing management strategies. Conservation in grasslands expressing flora community composition appropriate for lesser prairie-chickens can maintain appropriate habitat structure heterogeneity through the use of low to moderate stocking densities (<0.26 animal units/ha), greater pasture areas, and site-appropriate deferment periods. Alternative grazing management strategies (e.g., rest-rotation, season-long rest) may be appropriate in grasslands requiring greater heterogeneity or during intensive drought. Grazing management favoring habitat heterogeneity instead of uniform grazing distributions will likely be more conducive for preserving lesser prairie-chicken populations and grassland biodiversity.

Demographic consequences of Conservation Reserve Program grasslands for lesser prairie-chickens

Knowledge of landscape and regional circumstances where conservation programs are successful on working lands in agricultural production are needed. Converting marginal croplands to grasslands using conservation programs such as the United States Department of Agriculture Conservation Reserve Program (CRP) should be beneficial for many grassland obligate wildlife species; however, addition of CRP grasslands may result indifferent population effects based on regional climate, characteristics of the surrounding landscape, or species planted or established. Within landscapes occupied by lesser prairie-chickens (*Tympanuchuspallidicinctus*), CRP may provide habitat only for specific life stages and habitat selection for CRP may vary between wet and dry years. Among all study sites, we captured and fitted 280 female lesser prairie-chickens with very high frequency (VHF) and global positioning system (GPS) transmitters during the spring lekking seasons of 2013–2015 to monitor habitat selection for CRP in regions of varying climate. We also estimated vital rates and habitat selection for 148 individuals, using sites in northwest Kansas, USA. The greatest ecological services of CRP became apparent when examining habitat selection and densities. Nest densities were approximately 3 times greater in CRP grasslands than native working grasslands (i.e., grazed), demonstrating a population-level benefit (CRP = 6.0 nests/10 km^2 ±1.29 [SE], native working grassland = 1.7 nests/10 km^2 ± 0.62). However, CRP supporting high nest density did not provide brood habitat; 85% of females with broods surviving to 7 days moved their young to other cover types. Regression analyses indicated lesser prairie-chickens were approximately 8 times more likely to use CRP when 5,000-ha landscapes were 70% rather than 20% grassland, indicating variation in the level of ecological services provided by CRP was dependent upon composition of the larger landscape. Further, CRP grasslands were 1.7timesmore likely to be used by lesser prairie-chickens in regions receiving 40 cm compared to 70 cm of average annual precipitation and during years of greater drought intensity. Demographic and resource selection analyses revealed that establishing CRP grasslands in northwest Kansas can increase the amount nesting habitat in a region where it may have previously been limited, thereby providing refugia to sustain populations through periods of extreme drought. Nest survival, adult survival during breeding, and nonbreeding season survival did not vary between lesser prairie-chickens that used and did not use CRP grasslands. The finite rate of population growth was also similar for birds using CRP and using only native working grasslands, suggesting that CRP provides habitat similar to that of native working grassland in this region. Overall, lesser prairie-chickens may thrive in landscapes that are a mosaic of native working grassland, CRP grassland, with a minimal amount of cropland, particularly when nesting and brood habitat are in close proximity.

Identifying the diet of a declining prairie grouse using DNA metabarcoding

Diets during critical brooding and winter periods likely influence the growth of Lesser Prairie-Chicken (Tympanuchus pallidicinctus) populations. During the brooding period, rapidly growing Lesser Prairie-Chicken chicks have high calorie demands and are restricted to foods within immediate surroundings. For adults and juveniles during cold winters, meeting thermoregulatory demands with available food items of limited nutrient content may be challenging. Our objective was to determine the primary animal and plant components of Lesser Prairie-Chicken diets among native prairie, cropland, and Conservation Reserve Program (CRP) fields in Kansas and Colorado, USA, during brooding and winter using a DNA metabarcoding approach. Lesser Prairie-Chicken fecal samples (n = 314) were collected during summer 2014 and winter 2014–2015, DNA was extracted, amplified, and sequenced. A region of the cytochrome oxidase I (COI) gene was sequenced to determine the arthropod component of the diet, and a portion of the trnL intron region was used to determine the plant component. Relying on fecal DNA to quantify dietary composition, as opposed to traditional visual identification of gut contents, revealed a greater proportion of soft-bodied arthropods than previously recorded. Among 80 fecal samples for which threshold arthropod DNA reads were obtained, 35% of the sequences were most likely from Lepidoptera, 26% from Orthoptera, 14% from Araneae, 13% from Hemiptera, and 12% from other orders. Plant sequences from 137 fecal samples were composed of species similar to Ambrosia (27%), followed by species similar to Lactuca or Taraxacum (10%), Medicago (6%), and Triticum (5%). Forbs were the predominant (.50% of reads) plant food consumed during both brood rearing and winter. The importance both of native forbs and of a broad array of arthropods that rely on forbs suggests that disturbance regimes that promote forbs may be crucial in providing food for Lesser Prairie-Chickens in the northern portion of their distribution.

Strategic conservation for lesser prairie-chickens among landscapes of varying anthropogenic influence

For millennia grasslands have provided a myriad of ecosystem services and have been coupled with human resource use. The loss of 46% of grasslands worldwide necessitates the need for conservation that is spatially, temporally, and socioeconomically strategic. In the Southern Great Plains of the United States, conversion of native grasslands to cropland, woody encroachment, and establishment of vertical anthropogenic features have made large intact grasslands rare for lesser prairie-chickens (Tympanuchus pallidicinctus). However, it remains unclear how the spatial distribution of grasslands and anthropogenic features constrain populations and influence conservation. We estimated the distribution of lesser prairie-chickens using data from individuals marked with GPS transmitters in Kansas and Colorado, USA, and empirically derived relationships with anthropogenic structure densities and grassland composition. Our model suggested decreased probability of use in 2-km radius (12.6 km^2) landscapes that had greater than two vertical features, two oil wells, 8 km of county roads, and 0.15 km of major roads or transmission lines. Predicted probability of use was greatest in 5-km radius landscapes that were 77% grassland. Based on our model predictions, ~10% of the current expected lesser prairie-chicken distribution was available as habitat. We used our estimated species distribution to provide spatially explicit prescriptions for CRP enrollment and tree removal in locations most likely to benefit lesser prairie-chickens. Spatially incentivized CRP sign up has the potential to provide 4189 km2 of additional habitat and strategic application of tree removal has the potential to restore 1154 km^2. Tree removal and CRP enrollment are conservation tools that can align with landowner goals and are much more likely to be effective on privately owned working lands.

Biological Conservation 259 (2021) 109177

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Policy analysis

Increasing durability of voluntary conservation through strategic implementation of the Conservation Reserve Program

Daniel S. Sullins [a,*], Meghan Bogaerts [b], Bram H.F. Verheijen [c], David E. Naugle [d], Tim Griffiths [e], Christian A. Hagen [f]

[a] Department of Horticulture and Natural Resources, Kansas State University, 1712 Claflin Rd., Manhattan, KS 66506, USA
[b] Playa Lakes Joint Venture, 2675 Northpark Drive, Suite 208, Lafayette, CO 80026, USA
[c] Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, 205 Leasure Hall, 1128 N. 17th Street, Manhattan, KS 66506, USA
[d] W.A. Franke College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA
[e] United States Department of Agriculture, Natural Resources Conservation Service, 10 East Babcock Street, Bozeman, MT 59718, USA
[f] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

ARTICLE INFO

Keywords:
Cultivation
CRP
Durability
Farm Bill
Grassland
Great Plains
Land use
Set-aside program

ABSTRACT

Working lands are an attractive solution for conservation in the conterminous United States where 76% of area is privately owned. Conservation of private lands often relies on participation in temporary incentive-based programs. As incentives expire landowners make decisions that determine whether environmental benefits continue. In the U.S., the Conservation Reserve Program (CRP) contracts for 10–15 years to replant ~90–140.5 thousand km^2 of cropland back to grassland. Temporary set-aside programs, such as CRP, are implemented with minimal planning to retain durable investments after payments end. We used known fate models and remotely-sensed cropland layers to estimate durability of CRP after contract expiration and to identify areas of greater predicted durability. The durability of conservation through CRP is the probability of continued provision of grass cover after incentive-based payments have ended. We expected durability would vary among landscapes and regions. Overall, 58% (SE = 0.40) of expired fields remained in grassland. However, durability ranged widely (36–76%) across six U.S. states for 13,231 contracts that expired in 2007. Reversion to cropland increased for CRP grasslands with an inherently high tillage risk, in more northerly regions, and for larger fields including those surrounded by cropland. Temporally, conversion was prevalent within five years of contract expiration, during years with higher corn prices, and in wetter years. Findings provide guidance for allocating CRP contracts in areas where grassland conservation benefits may be maximized and where transition from set-aside programs to working grasslands may promote durability.

1. Introduction

The extent of contemporary human land modification is substantial (Theobald et al., 2020), which when coupled with global climatic shifts, portends unprecedented conservation challenges in the Anthropocene (Steffen et al., 2011). Setting aside preserves or refugia alone may provide too small of an ecological footprint within ecosystems, and even biomes, where vast areas of working lands sustain people (Kremen and Merenlender, 2018). Biome-scale conservation needed to stem declines in biodiversity and ecosystem services (Allred et al., 2015; Ripple et al., 2017), begs inclusion of privately stewarded working grasslands, forests, and shrublands worldwide and may necessitate voluntary incentive-based temporary set-aside programs for widespread implementation (Naugle et al., 2019; Augustine et al., 2019). Use of temporary set-aside programs to achieve lasting conservation in working landscapes will require strategic implementation based on knowledge of the persistence, or durability, of conservation investments and the biophysical factors that influence durability over space and time.

Temperate grasslands are often maintained as working lands and are among the most altered systems globally (Hoekstra et al., 2005). Grassland conversion to cropland, energy infrastructure, and housing sustain humans but pose challenges to conservation. In North America, grassland losses have reaccelerated in the 2000s (Lark, 2020) following widespread cultivation dating back to the Dust Bowl (Samson et al.,

---

* Corresponding author at: Department of Horticulture and Natural Resources, 1602 Throckmorton Hall, Manhattan, KS 66506, USA.
E-mail address: sullins@ksu.edu (D.S. Sullins).

https://doi.org/10.1016/j.biocon.2021.109177
Received 15 October 2020; Received in revised form 6 May 2021; Accepted 8 May 2021

2004; Augustine et al., 2019). Cultivation has focused in areas with nutrient rich soil and available water from precipitation, river, or groundwater sources (Ashworth, 2007; Cotterman et al., 2018). In the U. S., 85% of remaining grasslands are privately-owned (NABCI, 2013), making the U.S. Department of Agriculture's voluntary and incentive-based programs all more relevant (Kamal et al., 2015). The Conservation Reserve Program (CRP) is the largest of these programs in the country, covering 22.3 million acres (90,000 km^2; USDA, 2019).

Since 1985, CRP annually enrolls landowners in 10- to 15-year contracts for establishing grasses or other perennial cover on environmentally sensitive agricultural lands in exchange for annual rental payments. The associated economic infusions of $2 billion into rural communities from CRP payments is considerable (FSA, 2016), with concomitant benefits to wildlife (e.g., Reynolds et al., 2006), water quality (Johnson et al., 2016) and soil productivity (De et al., 2020). An estimated 700 million birds have been lost from North America's grassland biome since 1970 (Rosenberg et al., 2019); yet in 2016, CRP in the southern Great Plains conserved 4.5 million grassland songbirds, and met or exceeded population recovery goals for eight imperiled species (Pavlacky et al., 2020). Restoring grasslands also represents the largest natural opportunity in the agricultural sector to address climate change (Fargione et al., 2018).

Despite the substantial benefits of the program, CRP is currently administered as a temporary set-aside program with less spatial planning to retain initial investments after payments end. Prioritization for long-term post contract expiration benefits are incorporated based on landowner interest in high-investment conservation practices (e.g. planting of trees and establishing pollinator or rare and declining habitat), however, efforts to incorporate spatial factors are limited (Ribaudo et al., 2001; FSA, 2021). As CRP contracts expire, producers face a decision: reenroll, revert to cropland, or maintain grass cover without reenrolling (Barnes et al., 2020). Conservationists have long-assumed satisfied landowners progress from enrollment to reenrollment to persistence (Dayer et al., 2018), but recent insights indicate a portion of CRP re-enrollment decisions may be predetermined with landowners having no intention of leaving the most productive fields in grass after contract expiration (Barnes et al., 2020). The opposite is likely for CRP fields with lower cropland potential; landowners are likely to keep these fields in grass long-term. With fluctuating federally set acreage caps, competition to stay in the program can be intense. In recent sign-ups, half (55%) of willing participants surveyed were unable to re-enroll expiring CRP fields (Barnes et al., 2020). This outlook is concerning because acreage exiting CRP comprises the largest source of grassland conversion nationally (Hendricks and Er, 2018; Lark et al., 2015).

In the Great Plains, decisions to retain a CRP grassland in grass cover after contract expiration is likely influenced by regional, landscape, drought, and socioeconomic factors (Secchi and Babcock, 2007; Jack et al., 2008; Philip et al., 2016). Most of the factors are intertwined with the overall arability of the grassland (Skaggs et al., 1994; Roberts and Lubowski, 2007). Other landscape factors might include the accessibility of tilling the former CRP grassland and may interact with spatially driven socioeconomic factors (Wang et al., 2017). Last, temporal variation in weather that would be favorable for planting crops and maximizing profit during years of high crop prices might influence the decision to convert former CRP grassland to cropland (Heimlich and Kula, 1990; Wang et al., 2017; Hendricks and Er, 2018).

Patterns and drivers of decisions to maintain fields in grassland are poorly understood but can move millions of hectares of land in and out of crop production with lasting impacts. Legacy effects of coupled human and natural systems are known to influence landcover change (Waylen et al., 2015). Legacies detrimental to grassland conservation in the Great Plains are widely known (e.g., 1862 Homestead Act; Opie, 1998) but enduring effects of beneficial actions are largely unexplored. Legacy effects of CRP that benefit grassland conservation will be inherently related to widespread durability of the program (Bottema and Bush, 2012). Hereafter we define ‘durability’ as the probability of CRP to persist in grassland cover a decade or more after voluntary and incentive-based payments have ended. We use ‘legacy grasslands’ to describe durable CRP investments that have persisted in a grassland state over the 10 year study period.

With a better understanding of CRP durability and the factors that influence durability, natural resource managers and policymakers could effectively target future conservation with long-lasting benefits. To date, no long-term approach exists to account for iterations of contract enrollment, expiration, and land status after set-aside payments end. There is also a need for spatially-explicit science to implement strategic targeting of future CRP in the most durable landscapes. Our study begins to fill this spatial knowledge gap by examining biophysical drivers of grassland durability after CRP. We selected for study the southern Great Plains, a region of the U.S. with a high acreage of CRP enrollment, and a substantial number of expired acres. Specifically, we 1) estimated durability of CRP grasslands 10 years post-contract, and 2) quantified geographic variability in CRP durability throughout the southern Great Plains.

2. Methods

2.1. Study area

The Southern Great Plains is a hotspot of CRP enrollment, ranching, and agricultural production, as well as home to several declining grassland birds including the iconic lesser prairie-chicken (Herkert, 2009; Hagen et al., 2016). The region contains over 50,000 playa lakes, which provide critical habitat for millions of birds migrating through the Central Flyway and associated economic benefits from wildlife tourism and hunting (Verheijen et al., 2018). The study area included counties within the Great Plains states of Colorado, Kansas, New Mexico, Oklahoma, Nebraska and Texas (Fig. 1). We studied the cohort of CRP fields that expired in 2007 allowing for 10 years of post-expiration observation. The United States Department of Agriculture, Farm Service Agency maintains spatial CRP data that are not publicly available to maintain privacy for participants. We obtained CRP data under an agreement with the Farm Service Agency.

2.2. CRP dataset and analysis overview

We estimated durability based on the persistence of grass cover in 13,231 CRP grasslands that expired in 2007 in the southern Great Plains. Only former CRP fields that were not reenrolled in the program were used in analyses. Monitoring former fields for 10 years avoided known lag effects of reversion up to seven years post-contract (Barnes et al., 2020).

Using a novel application of known fate modeling (Therneau, 2018) typically applied to radio-marked animal populations, we identified whether a field ‘survived’ as a grassland or reverted to cropland, based on imagery from the National Agricultural Statistic Service's (NASS) Cropland Data Layer (Supporting information). We first converted CRP field polygon shapefiles to 30-m raster files and then used NASS to estimate percent cropland for each field. We defined as cropland former CRP fields with >20% of their area in cropland for two consecutive years, and the rest we recorded as persistent grasslands. This resulted in a survival record for each CRP field for the years 2008–2018. We used survival analyses to evaluate the influence of covariates on durability of CRP.

2.3. Covariates

Known fate models incorporated covariates affecting the durability of expired CRP fields in four categories: regional, landscape, economic, and drought-related predictors. Our explanatory variables were a mixture of stationary and time-varying covariates over the 10-year

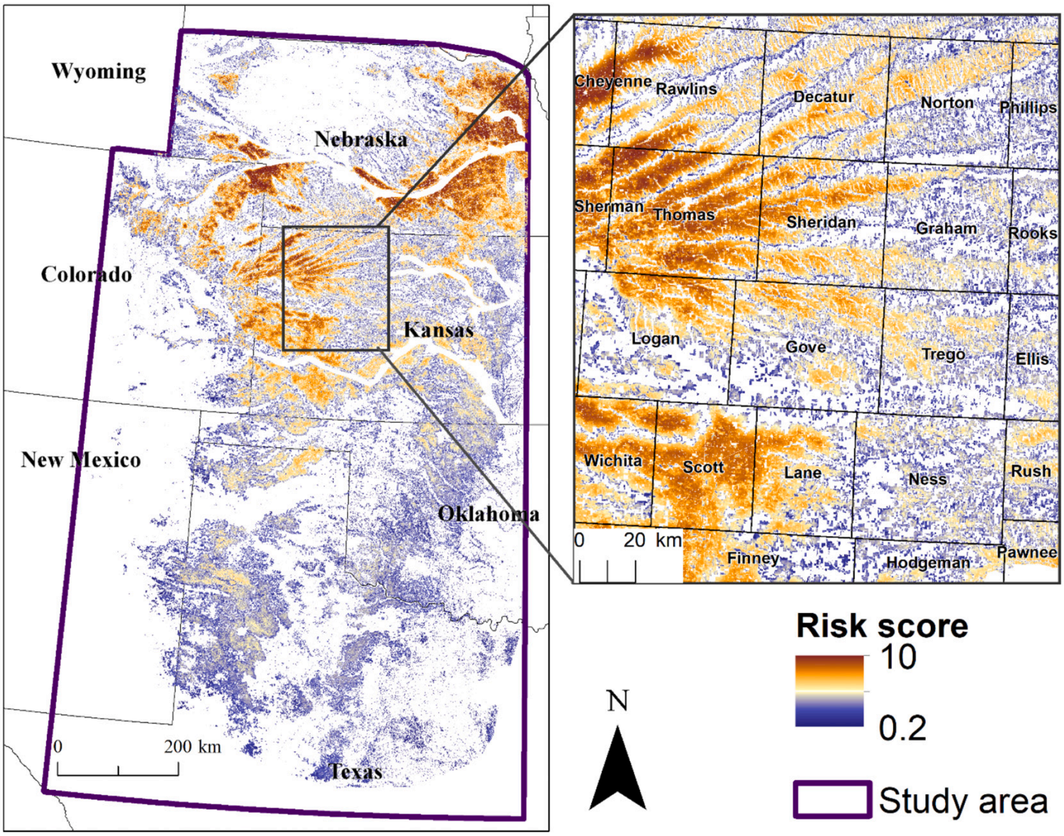


Fig. 1. Study area and predicted risk of conversion from a grassland to a cropland state. Risk is depicted using spatially-explicit attributes from our best supported cox proportional hazards model (Supporting information). Spatial attributes include proportion grassland within a 4-km radius, tillage index developed following Smith et al. (2016), and mean annual average temperature (PRISM, 2016). Risk scores are only displayed for cropland areas identified using Augustine et al. (2019) and outside of urban areas from the 2010 U.S. census. An inset of Northwest Kansas is displayed to highlight utility at finer scales.

timeframe (Supporting information).

2.4. Regional

At a regional scale, we included time-constant variables of tillage risk, 30-year average estimates of annual precipitation and temperature, and a fixed effect of the state in which the field was located. To quantify the inherent risk from tillage to grassland durability, we spatially extended to the southern Great Plains a remotely-sensed ‘cultivation risk layer’ that was originally used to target conservation easements in the northern Great Plains (Smith et al., 2016; https://rangelands.app; Supporting information). This spatial layer predicts the probability of tillage using soils, climate, topography, and other inputs, within the non-parametric weak learner model, Random Forests (Cutler et al., 2007). Our estimates of precipitation and temperature represented variation in east-to-west and north-to-south gradients in regional climate, and were obtained from Prism (2016) at 4-km (precipitation) and 800-m (temperature) spatial resolutions. We included each U.S. state to incorporate potential spatial and sociopolitical influences.

2.5. Field and landscape

We included four time-constant variables related to the field itself, or to the landscape immediately surrounding it: field area (ha), CRP practice, and proportions of grassland and CRP within 4 km of each field. We restricted CRP practice to include introduced grasses (CP1), native grasses (CP2), and already established grasses (CP10). We excluded other practices because they were rare (<230 fields) throughout the study area. We included landscape composition within a 4-km radius, which is known to influence habitat use of CRP fields by an imperiled prairie-grouse (Sullins et al., 2018).

2.6. Economics

We initially examined the correlation of crop prices among years for corn, cotton, wheat, sorghum, and soybeans, and then selected the uncorrelated types broadly planted throughout the study area (Leff et al., 2004). We used time-dependent pricing to evaluate financial market influences. We acquired state-specific data on annual crop prices and total acreage planted for all five crop types from NASS (USDA, 2019; https://quickstats.nass.usda.gov). We also included crop prices from the previous year to assess influence of the prior year's market on grassland reversion to cropping. We obtained data in $USD per pound for cotton and per bushel for corn, soybeans and wheat, and in $USD per hundredweight (45.4 kg) for sorghum.

2.7. Drought

We used as model covariates the Palmer Drought Severity Index (PDSI; lower numbers equate to higher severity) from both the current and previous year to account for possible lag effects. We obtained PDSI values within U.S. climatological divisions that divide each state into 5–10 regions of similar climate (Guttman and Quayle, 1996).

2.8. Estimating grassland durability

We fit Kaplan-Meier models to estimate survival for all CRP fields combined, and separately for each of the six U.S. states in the southern Great Plains (Survival package in Program R; Therneau, 2018, R Core Team, 2019). Kaplan-Meier models fit survival curves over time by generating estimates within categorical variables. We expected tillage risk to be a strong predictor of durability and sought to validate its potential predictive power. To examine the effect of tillage risk as a categorical variable, we grouped this continuous estimate of risk into three equal categories (low 0–0.32, medium 0.33–0.65 and high 0.66–1.00).

2.9. *Relationships with covariates*

We used an Andersen-Gill framework of time-dependent Cox proportional hazards to assess risk of a former CRP grassland reverting to cropland. We fit models and assessed model assumptions with the Survival package in R (Therneau, 2018; R Core Team, 2019). We generated means and standard deviations for covariates during the year of reversion or within a randomly selected year for persistent grassland fields. We standardized covariates before fitting models and performed a log transformation of area of CRP fields to approximate a normal distribution.

For model selection, we hierarchically fit models within the four categories of covariates (i.e., regional, landscape, economics, drought), and then formulated composite models by combining covariates from top ranking models within each category (see Supporting information).

Candidate composite models included all combinations of covariates used in top ranking models from the initial regional, landscape, economic, and drought-related model groups. We ranked candidate models using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson, 2002). All candidate models with a $\Delta\text{AICc} \leq 2$ were considered equally parsimonious. We deemed uninformative any top ranked models with coefficients overlapping zero at 95% confidence intervals, and we instead selected the next parsimonious model with informative covariates. For our final model, we evaluated goodness of fit using a measure of concordance for which values >0.5 indicate predictive power greater than by chance alone (Therneau, 2018).

2.10. *Spatial prediction of durability*

We predicted the durability of grasslands using spatial covariates that were identified as important to durability in the best-supported composite model. We depicted risk spatially as maps to help practitioners make decisions on placement of new CRP contracts. We predicted risk scores using the predict.coxph tool in package survival in Program R (Therneau, 2018). We created the predictive surface using the raster package in R (Hijmans et al., 2020). Masked from spatial predictions are urban areas with >2500 people (U.S. Census Bureau, 2012), and lands already in cropland (from Augustine et al., 2019).

3. Results

3.1. *Estimates of grassland durability*

Durability of former CRP grasslands 10 years after set-aside payments ended was an estimated 0.580 (SE = 0.004) in the southern Great Plains (Fig. 2). Temporally, durability was 0.630 (SE = 0.004) by 2012, suggesting that conversion was most prevalent within five years of contract expiration. Spatially, conversion rate increased for grasslands with an inherently high tillage risk (Figs. 1, 2, 3). Grassland durability was three times greater in landscapes classified as low versus high risk as categorized by the remotely-derived tillage risk layer (low [0.870, SE = 0.005], medium [0.626, SE = 0.007], high [0.268, SE = 0.006]). Durability also varied widely between states (77–37%), and was highest in Oklahoma (0.765; SE = 0.009) and lowest in Colorado (0.366; SE = 0.017). Intermediate in state-level durability were New Mexico (0.626; SE = 0.026), Texas (0.613; SE = 0.008), Kansas (0.564; SE = 0.007), and Nebraska (0.404; SE = 0.012; Fig. 2).

3.2. *Covariates associated with durability*

Our hierarchical model selection process revealed that model parsimony increased when main effects from best supported regional, landscape, economic and drought models were combined ($w = 1.0$, Table 1, Supporting information). Top model components were tillage risk (standardized β ± SE; 0.75 ± 0.02), temperature (0.36 ± 0.02), grassland abundance at a 4-km scale (0.35 ± 0.02), log of field area (0.19 ± 0.01), corn prices (0.56 ± 0.08) and drought (PDSI; 0.15 ± 0.02). Tillage risk exhibited the greatest magnitude of effect on durability (Fig. 3) with grassland cover maintained most often in landscapes less conducive to cropping. Grassland dominated landscapes in areas with warmer climates also were less likely to be converted (Table 2; Fig. 3). In contrast, rate of reversion increased for CRP fields that were larger in area and for those with less grassland in the surrounding landscape (4-km scale; Fig. 3). Durability was inversely related to corn prices (Fig. 3), especially in 2011 and 2012 when corn prices throughout the study area topped $6USD (Supporting information). Fields were more likely to revert to cropland in wetter years (higher PDSI values) than in randomly selected years for CRP fields that remained in grass (Table 2).

Concordance of the best supported model was 0.773 (SE = 0.003) indicating relatively good model fit (Therneau, 2018). Schoenfield residuals initially suggested that coefficients for grassland cover, log area, and PDSI coefficients had violated the proportionality assumption (cox.zph(); Therneau, 2018). Further graphical inspection of residuals from >10,000 fields indicated no substantial trends of beta coefficients over

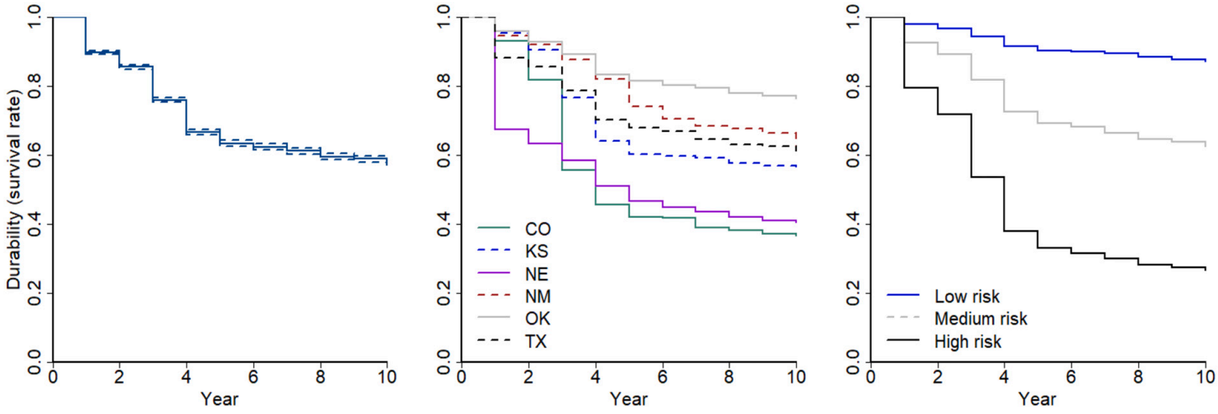


Fig. 2. Plot of Kaplan-Meier durability curves for all expired CRP fields combined (left), individual states (middle) and within tillage risk categories (right). Combined model includes 95% confidence intervals (CIs) as dashed lines. The CIs were omitted for clarity from other plots. Tillage risk corresponds to low (0–0.32), medium (0.33–0.65), and high (0.66–1.00) values derived from methods described in Smith et al. (2016). Years correspond to 2008 to 2018 (year 0 = 2008).

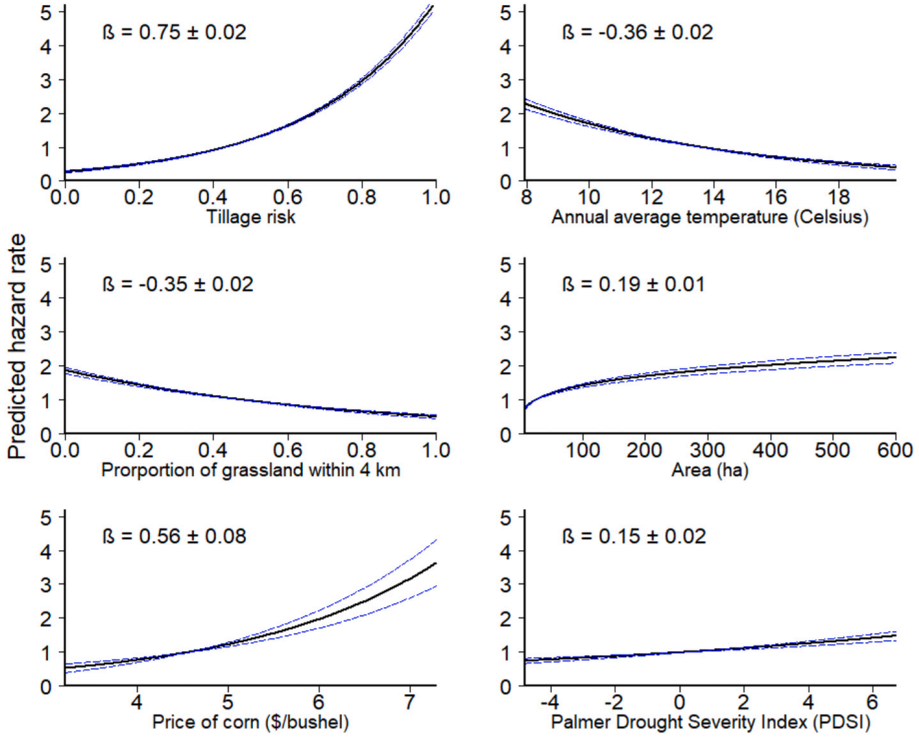


Fig. 3. Estimated relationship of grassland composition within 4 km, area of CRP field, tillage risk, annual average temperature, price of corn, PDSI, and predicted hazard rate of CRP conversion to cropland (2008–2018). Black lines indicate predictions fitted by Andersen-Gill modeling framework. Blue dashed lines are upper and lower 95% confidence intervals. Within each plot the standardized beta coefficient from the final model is displayed as untransformed β ± SE. Beta coefficients are on a standardized scale (x variables all converted to z-scores) to facilitate direct comparison; plotted lines are displayed in observed units. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Overall model selection included top ranked variables from landscape, regional, economic, and drought model groups (see Tables S2–5). Landscape covariates included grassland within 4 km of each CRP field (Grass) and area of the CRP field (area). Regional models included tillage risk and temperature. Economic and drought variables included corn prices (Corn) and Palmer drought severity index (PDSI) respectively. Model selection was based on the number of parameters (K), Deviance, AIC$_c$ and ΔAIC$_c$ values, and Akaike weights (w_i).

Model structure	K	Deviance	AIC$_c$	ΔAIC$_c$	w_i
Grass + area + tillage risk + temperature + corn + PDSI	7	97,652.54	97,664.54	0.00	1.000
Grass + area + tillage risk + temperature + corn	6	97,699.66	97,709.66	45.12	0.000
Grass + area + tillage risk + temperature + PDSI	6	97,702.16	97,712.15	47.61	0.000
Grass + area + tillage risk + temperature	5	97,782.14	97,790.13	125.59	0.000
Tillage risk + temperature + corn + PDSI	5	98,178.12	98,186.12	521.57	0.000
Tillage risk + temperature + corn	4	98,212.70	98,218.69	554.15	0.000
Tillage risk + temperature + PDSI	4	98,230.64	98,236.63	572.09	0.000
Tillage risk + temperature	3	98,285.86	98,289.86	625.32	0.000
Grass + area + corn + PDSI	5	101,047.98	101,055.98	3391.44	0.000
Grass + area + PDSI	4	101,165.66	101,171.66	3507.12	0.000
Grass + area + Corn	4	101,606.06	101,612.06	3947.52	0.000
Grass + area	3	101,679.60	101,683.60	4019.06	0.000
PDSI	2	102,602.14	102,604.15	4939.60	0.000
Corn + PDSI	3	102,601.16	102,605.15	4940.61	0.000
Constant	1	102,758.16	102,758.15	5093.61	0.000
Corn	2	102,757.32	102,759.32	5094.77	0.000

Table 2
Means and standard deviations of CRP field characteristics distributed throughout the study site in 2008–2018. Comparisons for time dependent variables (economic and drought) were facilitated by comparing the variable at the year of conversion for fields converted to croplands (N = 5559) to values from a randomly selected year for CRP fields that remained in grassland (N = 7672).

Covariates	Durable grasslands		Reverted to crops		t	$P\leq$
	Mean	SD	Mean	SD		
Regional						
Tillage index	0.38	0.24	0.67	0.22	71.34	0.001
Precipitation (mm)	603.06	122.74	561.06	128.20	18.94	0.001
Temperature (C)	13.75	2.41	12.69	2.53	24.15	0.001
Field and landscape						
Area (ha)	32.31	31.74	46.94	44.73	20.88	0.001
Proportion grassland	0.49	0.27	0.38	0.22	25.24	0.001
Proportion CRP	0.04	0.05	0.05	0.06	7.40	0.001
Economics						
Corn price	4.56	1.15	5.01	1.10	474.97	0.001
Wheat price	5.65	1.33	6.20	1.13	528.02	0.001
Sorghum price	7.37	2.12	8.13	2.21	403.71	0.001
Drought						
PDSI	0.11	2.49	1.08	2.34	24.11	0.001

time. Incorporating time interaction terms with these covariates did not improve model parsimony.

3.3. Spatial prediction of durability

Tillage risk, grassland abundance (4-km scale) and annual temperature (Table 2) were the three spatial covariates from the best-supported model (Supporting information) and were used to predict durability (Fig. 1). Tillage risk was highest in more northerly and eastern regions of the central Great Plains (Fig. 1). The positive influence of grassland abundance on durability (Fig. 3) was apparent in the clustering of grassland strongholds throughout the region (Fig. 1). Higher annual average temperatures along south and east gradients was positively associated with increased durability of grasslands (Fig. 3).

4. Discussion

4.1. Enduring benefits of CRP

A durability rate of 58% a decade after CRP payments ended indicated that more than half of all grassland CRP fields remain in grass cover a decade after contract expiration. Our reported durability rate is the most concrete evidence to date that legacy effects are substantive for this voluntary and incentive-based Farm Bill program. Others surveying landowner intent report comparable (55–66%; Barnes et al., 2020) or lower (15–52%; Caldas et al., 2016, Roberts and Lubowski, 2007, Atkinson et al., 2011) rates, but ours is first to employ time-stamped spatial imagery to assign known fates to former CRP fields including persistence or year of subsequent cultivation (2008–2018). This continuing legacy of CRP (2609 km^2; ~1000 mi^2) equates to an area equivalent to Rhode Island in a biome plagued by cultivation (Hoekstra et al., 2005). With more than 90,000 km^2 currently enrolled, our findings add to the growing body of evidence that CRP provides a scale of ecosystem services that rivals in acreage other post-1920 conservation efforts.

Our durability estimates indicate that legacy effects of CRP are not keeping pace with continued cropland expansion across the U.S. (>4040 km^2 annually, and 7122 km^2 from 2008 to 2016 in our 6-state region; Lark et al., 2020). The disparate range of durability (36–76%) across U.S. states is indicative of a reversion to cropland in more productive landscapes where farming communities are predominant (Fig. 1). Such economic decisions likely operate at landscape and regional scales as evidenced by our climate, soils and topographic relationships that favor grain production over grassland retention. Governed by broad-scale biophysical traits, our findings reinforce that durability at local scales is ultimately constrained by crop prices (Philip et al., 2016). Known fate models also highlighted landscape effects documented in previous research with larger and more isolated CRP grasslands more likely to revert to cropland (Skaggs et al., 1994). Such landscape effects are likely influenced by more than just cropland profitability and suggests greater durability in working grassland dominated landscapes where grazing is socially supported and the equipment and infrastructure are present (Dayer et al., 2018).

4.2. Factors influencing durability

Grassland durability was spatially dependent upon the arability of fields selected for CRP enrollment. Legacy grasslands (CRP fields that remained in a grassland state) were more likely to persist in landscapes that were too rocky, dry, or erodible, or that lacked groundwater resources for farming; effects captured within our index of tillage risk (Figs. 1 & 3; Supporting information). Quantifying grassland durability that was three times greater in low- versus high-risk landscapes provided a robust test of the tillage risk layer using data not used to create it. Spatially, our insights into tillage risk were strengthened by controlling for landscape, drought and crop prices which are known to influence durability (Jack et al., 2008; Philip et al., 2016).

Water and soil covariates used to fit the tillage risk index (Smith et al., 2016) seemed adept at predicting the effects of groundwater availability on grassland durability. Although precipitation is more reliable for growing crops farther east, tillage risk was higher in the drier western extents of Kansas, Oklahoma, and Texas (Fig. 1). Water resources from the Ogallala Aquifer and from rivers which drain the Rocky Mountains (e.g., Arkansas and Platte Rivers) increase water availability in drier climates farther west which likely influenced the steep drop in durability in Colorado in 2010 (Ashworth, 2007). In the future, groundwater availability for irrigation may decrease as water in the aquifer becomes more depleted. Predictions suggest that irrigated corn and wheat acreage will decrease by 50–60% by the year 2100 (Cotterman et al., 2018). When subsurface water availability wanes, formerly irrigated acres could revert to dryland farming or grassland. Temperature will be a contributing factor, as modeled here, but durability of grasslands in northern latitudes will hinge on whether changing climatic conditions are conducive to growing corn (USDA, 2019).

4.3. Corn prices and ethanol policy

Grain markets remain uncertain even though conditions fueling the most recent bout of cropland expansion (2007–2012)—high corn prices, buildout of the biofuels industry, and reductions in CRP availability—have subsided (Lark et al., 2020). Recent estimates from this period attribute 13% of the reduction in CRP acreage to ethanol production (Chen and Khanna, 2018). From 2008 to 2012, an additional 18% of corn harvest was used to produce ethanol with a corresponding 75% increase in price per bushel (Wright et al., 2017). Such a connection to CRP conversion may explain the immediate decrease in the durability of Nebraska CRP grasslands where corn production is most predominant among our study states (Lark et al., 2015). Past experience shows that price spikes can be exacerbated by drought and subsidies made available to ethanol and biofuel industries (Hoerling et al., 2014; Wright and Wimberly, 2013; Wright et al., 2017). Although currently unlikely, stabilization of grain markets would likely enhance grassland durability and resulting ecosystem services (Jack et al., 2008). Paradoxically, the ethanol and biofuel industries are largely subsidized through the same Farm Bill that administers the CRP. Conversion from grass to grain production could therefore be driven less by the free market and more by a shift from one government program to another (Jack et al., 2008). Moreover, Congress's recent limitations on CRP rental rates will likely reduce sign-ups on productive soils, and instead push enrollment to more marginal lands.

4.4. Functionality of legacy grasslands

Our models do not account for changes in grassland structure if set-aside CRP acres are later used to expand grazing operations. We expect that most legacy grasslands will be functionally similar to grazed pastures (Sala and Paruelo, 1997) as 77% of enrollees surveyed by Heimlich and Kula (1990) would graze, hay, or seed CRP fields if granted the opportunity. Ecosystem services might change because CRP is typically not grazed while under contract (Hellerstein, 2017). For soil and water quality related ecosystem services, a change from an ungrazed CRP to grazed pastureland is superior to cropland (Fuhlendorf et al., 2002; Hubbard et al., 2004). Soil retention and carbon sequestration would continue under moderate grazing prescriptions (Schuman et al., 2002; Fuhlendorf et al., 2002). Changes in vegetation structure from grazing will increase habitat quality for some species and decrease it for others. In the eastern Great Plains, grazing could improve herbaceous structure for a variety of imperiled grassland songbirds and upland nesting shorebirds (Klute and Robel, 1997; Rahmig et al., 2009). Moderate grazing pressure could also be beneficial for prairie grouse (Kraft et al., 2021). However, habitat quality will be lessened for prairie grouse when grazing reduces their requisite dense nesting cover, particularly in western regions (Sullins et al., 2018; Kraft et al., 2021).

5. Conclusions

Long-term strategies are necessary to maintain the efficacy of CRP because congressional enrollment caps have decreased ~50,000 km^2 since 2007 (Hellerstein, 2017). We hope depicting durability spatially (Fig. 1) is a catalyst for more strategic planning for CRP enrollment. For example, extrapolating the average rate of durability to a national scale (0.58) suggests that enrolling 98,000 km^2 into CRP annually could net 155,000 km^2 of legacy grasslands in the year 2030 assuming no re-enrollment. However, durability varies spatially (36–76%; Fig. 1), so the long-term outlook for grasslands conservation will in part depend on whether CRP administrators enroll heavily in tillage-prone landscapes, or instead steer investments to less productive areas.

The next logical step to help Farm Bill administrators extend the benefits of initial investments is to incorporate durability into simulations depicting future placement and loss of CRP over time and space. After evaluating simulations, administrators could incorporate expected durability into the Environmental Benefits Index currently used to prioritize CRP placement (Ribaudo et al., 2001). Initial placement of CRP can influence ecosystem services provided (Adkins et al., 2020) and will influence durability of ecosystem services, which are manifested through landowner decisions. Competition is intense to stay in CRP as evidenced by 55% of willing participants unable to re-enroll expiring fields (Barnes et al., 2020). Landowner surveys corroborate the importance of accounting for durability as 28% of former CRP enrollees converted CRP to cropland and at least one survey respondent had no intention of leaving the most productive fields in grass (Barnes et al., 2020). The opposite is likely true for CRP fields with lower cropland potential that landowners said they should not have cultivated (Barnes et al., 2020). Rapid decay in durability five years post-contract (0.63 [SE = 0.004]) suggests there is some urgency in helping landowners find innovative ways to keep fields in grassland.

A vision is emerging for transitioning CRP grasslands into working lands that are intrinsically valued components of grazing operations. This innovation is complimentary to CRP rather than a replacement. Piecing back together lower-productivity landscapes that are better suited for grazing than farming has the potential to restore grasslands at unprecedented scales. Pilot projects show promise such as an initiative in the Nebraska Panhandle that helped producers voluntarily transition 83 km^2 of expiring CRP into working lands by providing grazing infrastructure and technical assistance (Augustine et al., 2019). Mechanisms are evolving for willing landowners to move between Farm Bill programs (Barnes et al., 2020), and an understanding of producer needs to make the transition (e.g., water for cattle; Barnes et al. 2019). Despite landowner interest in the southern Great Plains, only 5% of fields coming out of CRP are typically enrolled in another conservation program 1–7 years after expiration (Barnes et al., 2020). Early adopters of this approach may view it as compatible with landowners' motivations in low tillage risk landscapes where grazing is socially supported (Dayer et al., 2018).

CRediT authorship contribution statement

Daniel S. Sullins: Methodology, Formal analysis, Writing, Editing, Visualization. **Meghan Bogaerts**: Methodology, Formal analysis, Writing, Editing. **Bram H. F. Verheijen**: Methodology, Formal analysis, Writing, Editing, Visualization. **Christian A. Hagen**: Conceptualization, Writing, Editing, Project administration. **David E. Naugle**: Writing, Editing, Supervision. **Tim Griffiths**: Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank D. Haukos for research and financial support. Funding for the project was provided by United States Department of Agriculture (USDA) Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62), Conservation Effects Assessment Project which is part of the Natural Resources Conservation Service, and USDA-led Lesser Prairie-Chicken Initiative. We also thank the Associate Editor and anonymous reviewers for providing helpful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109177.

References

Adkins, K., Roy, C.L., Wright, R.G., Andersen, D.E., 2020. Simulating strategic implementation of the CRP to increase greater prairie-chicken abundance. J. Wildl. Manag. https://doi.org/10.1002/jwmg.21960.

Allred, B.B.W., Smith, W.K., Twidwell, D., Haggerty, J.H., Running, S.W., Naugle, D.E., Fuhlendorf, S.D., 2015. Ecosystem services lost to oil and gas in North America. Science 348, 401–402.

Ashworth, W., 2007. Ogallala Blue: Water and Life on the Plains. W. W. Norton and Company, New York, NY.

Atkinson, L.M., Romsdahl, R.J., Hill, M.J., 2011. Future participation in the conservation reserve program in North Dakota. Great Plains Res. 21, 203–214.

Augustine, D., Davidson, A., Dickinson, K., Van Pelt, B., 2019. Thinking like a grassland: challenges and opportunities for biodiversity conservation in the Great Plains of North America. Rangel. Ecol. Manag. https://doi.org/10.1016/j.rama.2019.09.001.

Barnes, J.C., Sketch, M., Gramza, A.R., Sorice, M.G., Iovanna, R., Dayer, A.A., 2020. Land use decisions after the Conservation Reserve Program: re-enrollment, reversion, and persistence in the southern Great Plains. Conserv. Sci. Pract. 2, e254. https://doi.org/10.1111/csp2.254.

Bottema, M.J.M., Bush, S.R., 2012. The durability of private sector-led marine conservation: a case study of two entrepreneurial marine protected areas in Indonesia. Ocean Coast. Manag. 61, 38–48.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA.

Caldas, M.M., Bergtold, J.S., Peterson, J.M., Earnhart, D.H., 2016. Land-use choices: the case of conservation reserve program (CRP) re-enrollment in Kansas, USA. J. Land Use Sci. 11, 579–594.

Chen, X., Khanna, M., 2018. Effect of corn ethanol production on Conservation Reserve Program acres in the US. Appl. Energy 225, 124–134.

Cotterman, K.A., Kendall, A.D., Basso, B., Hyndman, D.W., 2018. Groundwater depletion and climate change: future prospects of crop production in the Central High Plains Aquifer. Clim. Chang. 146, 187–200.

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

Dayer, A.A., Lutter, S.H., Sesser, K.A., Hickey, C.M., Gardali, T., 2018. Private landowner conservation behavior following participation in voluntary incentive programs: recommendations to facilitate behavioral persistence. Conserv. Lett. 11, 1–11.

De, M., Riopel, J.A., Cihacek, L.J., Lawrinenko, M., Baldwin-Kordick, R., Hall, S.J., McDaniel, M.D., 2020. Soil health recovery after grassland reestablishment on cropland: the effects of time and topographic position. Soil Sci. Soc. Am. J. 84, 568–586.

Fargione, J.E., et al., 2018. Natural climate solutions for the United States. Sci. Adv. 4, 1–15.

Farm Service Agency, 2016. The Conservation Reserve Program: 49th Signup Results. USDA, Washington, DC. Accessed 11 January 2019.

Farm Service Agency, 2021. Conservation Reserve Program: 56th General Enrollment Period Environmental Benefits Index Fact Sheet January 2021. USDA, Washington, DC. Accessed 26 March 2021.

Fuhlendorf, S.D., Zhang, H., Tunnell, T.R., Engle, D.M., Cross, A.F., 2002. Effects of grazing on restoration of southern mixed prairie soils, 10, 401–407.

Guttman, N.B., Quayle, R.G., 1996. A historical perspective of U.S. climate divisions. Bull. Am. Meteorol. Soc. 77, 293–303.

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

Heimlich, R.E., Kula, O.E., 1990. Grasslands: the future of CRP land after contracts expire. J. Prod. Agric. 3, 7–12.

Hellerstein DM. 2017. The US Conservation Reserve Program: the evolution of an enrollment mechanism. Land Use Policy 63:601–610. Available from doi:https://doi.org/10.1016/j.landusepol.2015.07.017 (Elsevier Ltd).

Hendricks, N.P., Er, E., 2018. Changes in cropland area in the United States and the role of CRP. Food Policy 75, 15–23.

Herkert, J.R., 2009. Response of bird populations to farmland set-aside programs. Conserv. Biol. 23, 1036–1040.

Hijmans, R.J., et al., 2020. Package "raster". Available from. https://cran.r-project.org/web/packages/raster/raster.pdf.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29.

Hoerling, M., Eischeid, J., Kumar, A., Leung, R., Mariotti, A., Mo, K., Schubert, S., Seager, R., 2014. Causes and predictability of the 2012 Great Plains drought. Bull. Am. Meteorol. Soc. 95, 269–282.

Hubbard, R.K., Newton, G.L., Hill, G.M., 2004. Water quality and the grazing animal. J. Anim. Sci. 82, 255–263.

Jack, B.K., Kousky, C., Sims, K.R.E., 2008. Designing payments for ecosystem services: lessons from previous experience with incentive-based mechanisms. PNAS 105, 9465–9470.

Johnson, K.A., Dalzell, B.J., Donahue, M., Gourevitch, J., Johnson, D.L., Karlovits, G.S., Keeler, B., Smith, J.T., 2016. Conservation Reserve Program (CRP) lands provide ecosystem service benefits that exceed land rental payment costs. Ecosyst. Serv. 18, 175–185.

Kamal, S., Grodzińska-Jurczak, M., Brown, G., 2015. Conservation on private land: a review of global strategies with a proposed classification system. J. Environ. Plan. Manag. 58, 576–597.

Klute, D.S., Robel, R.J., 1997. Will conversion of conservation reserve program lands to pasture be detrimental for grassland birds in Kansas? Am. Midl. Nat. 137, 206–212.

Kraft, J.D., Haukos, D.A., Bain, M.R., Rice, M.B., Robinson, S., Sullins, D.S., Hagen, C.A., Pitman, J., Lautenbach, J.M., Plumb, R., Lautenbach, J.D., 2021. Using grazing to manage herbaceous structure for a heterogeneity-dependent bird. J. Wildl. Manag. 85, 354–368.

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science 362, 1–9.

Lark, T.J., 2020. Protecting our prairies: research and policy actions for conserving America's grasslands. Land Use Policy 97. https://doi.org/10.1016/j.landusepol.2020.104727.

Lark, T.J., Meghan Salmon, J., Gibbs, H.K., 2015. Cropland expansion outpaces agricultural and biofuel policies in the United States. Environ. Res. Lett. 10 https://doi.org/10.1088/1748-9326/10/4/044003.

Lark, T.J., Spawn, S.A., Bougie, M., Gibbs, H.K., 2020. Cropland expansion in the United States produces marginal yields at high costs to wildlife. Nat. Commun. 11, 4295. https://doi.org/10.1038/s41467-020-18045-z.

Leff, B., Ramankutty, N., Foley, J.A., 2004. Geographic distribution of major crops across the world. Glob. Biogeochem. Cycles 18. https://doi.org/10.1029/2003GB002108.

Naugle, B.D.E., Maestas, J.D., Allred, B.W., Hagen, C.A., Jones, M.O., Falkowski, M.J., Randall, B., Rewa, C.A., 2019. CEAP quantifies conservation outcomes for wildlife and people on western grazing lands. Rangelands 41, 211–217.

North American Bird Conservation Initiative. 2013. The State of the Birds 2013: Report on Private Lands. Washington, DC: U.S. Department of Interior 48 pp.

Opie, J., 1998. Moral geography in High Plains history. Geogr. Rev. 88, 241–258 (American Geographical Society).

Pavlacky Jr., D.C., Hagen, C.A., Bartuszevige, A.M., Iovanna, R., George, T.L., Naugle, D. E., 2020. Scaling up private land conservation to meet recovery goals for grassland birds. Conserv. Biol. https://doi-org.er.lib.k-state.edu/10.1111/cobi.13731 (accepted).

Philip, E.M., Stephen, D.L., Christopher, M.C., Richard, I., 2016. Grasslands, wetlands, and agriculture: the fate of land expiring from the Conservation Reserve Program in the Midwestern United States. Environ. Res. Lett. 11, 94005.

PRISM Climate Group, 2016. Oregon State University. http://www.prism.oregonstate.edu/normals/ accessed January 11, 2019.

R Development Core Team, 2019. 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.

Rahmig, C.J., Jensen, W.E., With, K.A., 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. Conserv. Biol. 23, 420–432.

Reynolds, R.E., Shaffer, T.L., Loesch, C.R., Cox, R.R., 2006. The Farm Bill and duck production in the Prairie Pothole Region: increasing the benefits. Wildl. Soc. Bull. 34, 963–974.

Ribaudo, M.O., Hoag, D.L., Smith, M.E., Heimlich, R., 2001. Environmental indices and the politics of the Conservation Reserve Program. Ecol. Indic. 1, 11–20.

Ripple, W.J., Wolf, C., Newsome, T.M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M. I., Laurance, W.F., 2017. World scientists' warning to humanity: a second notice. BioScience 67, 1026–1028.

Roberts, M.J., Lubowski, R.N., 2007. Enduring impacts of land retirement policies: evidence from the conservation reserve program. Land Econ. 83, 516–538.

Rosenberg, K.V., et al., 2019. Decline of the North American avifauna. Science 366, 120–124.

Sala, O.E., Paruelo, J.M., 1997. Ecosystem services in grasslands. In: Daily, G.C. (Ed.), Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, D.C., USA, pp. 237–252.

Samson, F.B., Knopf, F.L., Ostlie, W.R., 2004. Great Plains ecosystems: past, present, and future. Wildl. Soc. Bull. 32, 6–15.

Schuman, G.E., Janzen, H.H., Herrick, J.E., 2002. Soil carbon dynamics and potential carbon sequestration by rangelands. Environ. Pollut. 116, 391–396.

Secchi, S., Babcock, B.A., 2007. Impact of high corn prices on conservation reserve program acreage. Iowa Ag Rev. 13, 4–7.

Skaggs, A.R.K., Kirksey, R.E., Harper, W.M., Skaggs, R.K., Kirksey, R.E., Harper, W.M., 1994. Determinants and implications of post-CRP land use decisions. J. Agric. Resour. Econ. 19, 299–312.

Smith, J.T., Evans, J.S., Martin, B.H., Baruch-Mordo, S., Kiesecker, J.M., Naugle, D.E., 2016. Reducing cultivation risk for at-risk species: predicting outcomes of conservation easements for sage-grouse. Biol. Conserv. 201, 10–19.

Steffen, W., Grinevald, J., Crutzen, P., Mcneill, J., 2011. The anthropocene: conceptual and historical perspectives. Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 369, 842–867.

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

Theobald, D.M., Kennedy, C., Chen, B., Oakleaf, J., Baruch-mordo, S., Kiesecker, J., 2020. Earth transformed: detailed mapping of global human modification from 1990 to 2017. Earth Syst. Sci. Data 12, 1953–1972.

Therneau, T.M., 2018. Package "survival". https://cran.r-project.org/package=survival.

U.S. Census Bureau, 2012. 2010 tiger/line shapefiles. Available at. https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html. (Accessed 11 January 2019).

USDA National Agricultural Statistics Service Cropland Data Layer. 2019. Published Crop-specific Data Layer. Available at https://nassgeodata.gmu.edu/CropScape. USDA-NASS, Washington, DC. accessed January 11, 2019 (Online).

Verheijen BHF, Varner DM, Haukos DA. 2018. Effects of large-scale wetland loss on network connectivity of the Rainwater Basin, Nebraska. Landsc. Ecol. 33: 1939–1951. Springer Netherlands.

Wang, T., Luri, M., Janssen, L., Hennessy, D.A., Feng, H., Wimberly, M.C., Arora, G., 2017. Determinants of motives for land use decisions at the margins of the Corn Belt. Ecol. Econ. 134, 227–237.

Waylen, K.A., Blackstock, K.L., Holstead, K.L., 2015. How does legacy create sticking points for environmental management? Insights from challenges to implementation of the ecosystem approach. Ecol. Soc. 20 https://doi.org/10.5751/ES-07594-200221.

Wright, C.K., Wimberly, M.C., 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proc. Natl. Acad. Sci. 110, 4134–4139.

Wright, C.K., Larson, B., Lark, T.J., Gibbs, H.K., 2017. Recent grassland losses are concentrated around U.S. ethanol refineries. Environ. Res. Lett. 12 https://doi.org/10.1088/1748-9326/aa6446.

Breeding Season Space Use by Lesser Prairie-Chickens (Tympanuchus Pallidicinctus) Varies Among Ecoregions and Breeding Stages

Authors: Verheijen, Bram H.F., Plumb, Reid T., Gulick, Chris K.J., Hagen, Christian A., Robinson, Samantha G., et al.

Source: The American Midland Naturalist, 185(2) : 149-174

Published By: University of Notre Dame

URL: https://doi.org/10.1674/0003-0031-185.2.149

Am. Midl. Nat. (2021) 185:149–174

Breeding Season Space Use by Lesser Prairie-Chickens (Tympanuchus Pallidicinctus) Varies Among Ecoregions and Breeding Stages

BRAM H.F. VERHEIJEN[1], REID T. PLUMB AND CHRIS K.J. GULICK
Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan 66506

CHRISTIAN A. HAGEN
Department of Fisheries and Wildlife, Oregon State University, Corvallis 97331

SAMANTHA G. ROBINSON AND DANIEL S. SULLINS
Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan 66506

AND

DAVID A. HAUKOS
U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan 66506

ABSTRACT.—Large-scale declines of grassland ecosystems in the conterminous United States since European settlement have led to substantial loss and fragmentation of lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat and decreased their occupied range and population numbers by ~85%. Breeding season space use is an important component of lesser prairie-chicken conservation, because it could affect both local carrying capacity and population dynamics. Previous estimates of breeding season space use are largely limited to one of the four currently occupied ecoregions, but potential extrinsic drivers of breeding space use, such as landscape fragmentation, vegetation structure and composition, and density of anthropogenic structures, can show large spatial variation. Moreover, habitat needs vary greatly among the lekking/prelaying, nesting, brood-rearing, and postbreeding stages of the breeding season, but space use by female lesser prairie-chickens during these stages remain relatively unclear. We tested whether home range area and daily displacement (the net distance between the first and last location of each day) of female lesser prairie-chickens varied among ecoregions and breeding stages at four study sites in Kansas and Colorado, U.S.A., representing three of the four currently occupied ecoregions. We equipped females with very-high-frequency (VHF) or Global Positioning System (GPS) transmitters, and estimated home range area with kernel density estimators or biased random bridge models, respectively. Across all ecoregions, breeding season home range area averaged 190.4 ha (±19.1 ha SE) for birds with VHF and 283.6 ha (±23.1 ha) for birds with GPS transmitters, whereas daily displacement averaged 374.8 m (±14.3 m). Average home range area and daily displacement of bird with GPS transmitters were greater in the Short-Grass Prairie/Conservation Reserve Program Mosaic and Sand Sagebrush Prairie Ecoregions compared to sites in the Mixed-Grass Prairie Ecoregion. Home range area and daily displacement were greatest during lekking/prelaying and smallest during the brood-rearing stage, when female movements were restricted by mobility of chicks. Ecoregion- and breeding stage-specific estimates of space use by lesser prairie-chickens will help managers determine the spatial configuration of breeding stage-specific habitat on the landscape. Furthermore, ecoregion- and breeding stage-specific estimates are crucial when estimating the amount of breeding habitat needed for lesser prairie-chicken populations to persist.

---

[1] Corresponding author: E-mail: bramverheijen@gmail.com

INTRODUCTION

Since European settlement, grassland ecosystems in the conterminous United States have seen large-scale declines in their extent and quality (Samson and Knopf, 1994; Hoekstra *et al.*, 2005; Augustine *et al.*, 2019). Widespread conversion of grassland to row-crop agriculture and other intensive land uses have created a fragmented landscape (Fuhlendorf *et al.*, 2006). Furthermore, many remaining grasslands are now heavily grazed by cattle (*Bos taurus*), thereby decreasing spatial heterogeneity in the composition and structure of vegetation reducing overall quality of extant grasslands (Knapp *et al.*, 1999; Fuhlendorf *et al.*, 2006). As a result, grassland birds have shown some of the greatest population declines among bird communities in North America (Sauer and Link, 2011; North American Bird Conservation Initiative, 2016; Rosenberg *et al.*, 2019).

The lesser prairie-chicken (*Tympanuchus pallidicinctus*), a grassland-obligate species of grouse, has been especially affected by habitat loss, reduced quality of remaining habitat patches, and increased abundance of anthropogenic structures (*e.g.*, roads, oil wells, powerlines; Hagen *et al.*, 2011; Haukos and Zavaleta, 2016; Plumb *et al.*, 2019; Sullins *et al.*, 2019). Once widely distributed across the southwestern Great Plains of Texas, New Mexico, Oklahoma, Kansas, and Colorado, U.S.A., the estimated occupied range and population abundance of lesser prairie-chickens have been reduced by 85% compared to assumed historical conditions (Boal and Haukos, 2016). However, despite ongoing conservation and management strategies, population numbers of lesser prairie-chickens remain at a contemporary low (Ross *et al.*, 2016; Hagen *et al.*, 2017).

Lesser prairie-chickens are short-lived (~18 mo) and population growth rates are sensitive to breeding season survival and reproductive success (Hagen *et al.*, 2009; Sullins, 2017; Ross *et al.*, 2018). Demographic rates of lesser prairie-chickens have been linked to landscape configuration and individual space use (Robinson *et al.*, 2018a). Therefore, a clear understanding of what drives space use and movements by lesser prairie-chickens during the breeding season could provide useful insights in the population dynamics of the species.

During the breeding season, lesser prairie-chickens can show large variation in home range area (236–850 ha) and average daily displacements (net distance between the first and last location of each day; 220–390 m/d; Winder *et al.*, 2015, *see* review by Haukos and Zavaleta, 2016), and this variation has been linked to heterogeneity in vegetation structure and composition, landscape fragmentation, and anthropogenic influences (Southwood, 1977; Robinson *et al.*, 2018a; Sullins *et al.*, 2019). Because all these factors vary considerably throughout the currently occupied range (Fuhlendorf, 2002; Haukos and Zavaleta, 2016; Spencer *et al.*, 2017; Robinson *et al.*, 2018a), large spatial variation in space use and movements by lesser prairie-chickens is likely.

Variation in resource needs of individuals throughout the breeding season could also drive temporal variation in breeding season space use. Although most breeding-season activities of female lesser prairie-chickens take place near active leks (Hagen and Giesen, 2005; Boal *et al.*, 2014; Grisham *et al.*, 2014; Winder *et al.*, 2015; Gehrt *et al.*, 2020), resource needs and space use of females depend on whether they are in the lekking/prelaying, nesting, brood-rearing, or postbreeding stage of their reproductive attempts (Lautenbach, 2015; Boal and Haukos, 2016; Lautenbach *et al.*, 2019; Plumb *et al.*, 2019). Female lesser prairie-chickens tend to move relatively long distances during the lekking/prelaying stage while visiting leks and searching for nest sites, shorter distances while attending eggs or chicks, and longer distances again after completing successful or failed breeding attempts (Merchant, 1982; Riley *et al.*, 1994). However, relative availability of breeding stage-specific habitat varies throughout the lesser prairie chicken range, potentially resulting in spatial variation in breeding-stage specific space use (Gehrt *et al.*, 2020).

Whereas previous studies have identified several drivers of the space use and movements by lesser prairie-chickens, they have focused primarily on only one of four currently occupied ecoregions, representing only ∼10–15% of the total remaining birds (Sand Shinnery Oak Prairie Ecoregion; Merchant, 1982; Riley *et.al.,* 1994; Leonard, 2008; Borsdorf, 2013; McDonald *et al.*, 2014; Boggie *et al.,* 2017; but *see* Toole, 2005; Winder *et al.*, 2015). Most previous studies also described space use over the entire breeding season, with few providing breeding stage-specific estimates (Merchant, 1982; Riley *et al.*, 1994). Spatial variation in local and regional environmental variables may prohibit the extrapolation of current estimates to other ecoregions, and patterns in breeding stage-specific resource selection and resulting space use could vary among ecoregions as a result. Inference from previous studies is further complicated by low sample sizes of radio-marked individuals and low temporal resolution of bird locations (very-high-frequency [VHF] telemetry; Haukos and Zavaleta, 2016), which in combination with large individual variation in space use and movements has led to considerable uncertainty around published estimates. Unbiased ecoregion- and breeding stage-specific estimates of space use and movements by lesser prairie-chickens are necessary to strategically inform management, especially in the three northernmost ecoregions for which estimates are lacking.

Our goal was to assess breeding-season space use and movements by female lesser prairie-chickens in the northern portion of the species' range. Our first objective was to estimate home range area and daily displacement for the three northernmost occupied ecoregions to improve our general understanding of breeding season space use. As a second objective, we compared home range areas, mean daily displacements, and variation in daily displacements among study sites and breeding stages to test their relative effects on breeding season space use. Our estimates of home range area and daily displacement by female lesser prairie-chickens can inform existing and future management plans and conservation strategies for a large portion of their range, as well as help managers determine the spatial distribution and relative size of breeding stage-specific habitat patches necessary for current populations to persist.

STUDY AREA

We estimated home range area and daily displacement during the breeding season at four study sites within three of the four currently occupied ecoregions, which together support >85% of the extant lesser prairie-chickens (Van Pelt *et al.*, 2013; McDonald *et al.*, 2014; Boal and Haukos, 2016; Hagen *et al.*, 2017; Fig. 1). The Northwest site was dominated by native short- and mixed-grass prairie, grassland enrolled in the U.S. Department of Agriculture Conservation Reserve Program (CRP), and row-crop agriculture on silt-loam soils. In the Short-Grass Prairie/CRP Mosaic Ecoregion in northwestern Kansas, we collected data from 2013–2015 on the Smoky Valley Ranch—owned and managed by The Nature Conservancy—and surrounding private lands in Gove and Logan counties (collectively termed Northwest; Fig. 1). Within the Mixed-Grass Prairie Ecoregion of south-central Kansas, Oklahoma, and the Texas panhandle, we collected data at two separate study sites in Kansas: Clark and Red Hills. In 2014 and 2015, we collected data in Clark County in south-central Kansas located in the transition between the Mixed-Grass Prairie and Sand Sagebrush Ecoregions. Clark was dominated by native mixed-grass prairie, interspersed with sand sagebrush (*Artemisia filifolia*), limited amounts of CRP-grasslands and row-crop agriculture, and large alkali flats along drainages. We collected data in the Red Hills of south-central Kansas from 2013–2018

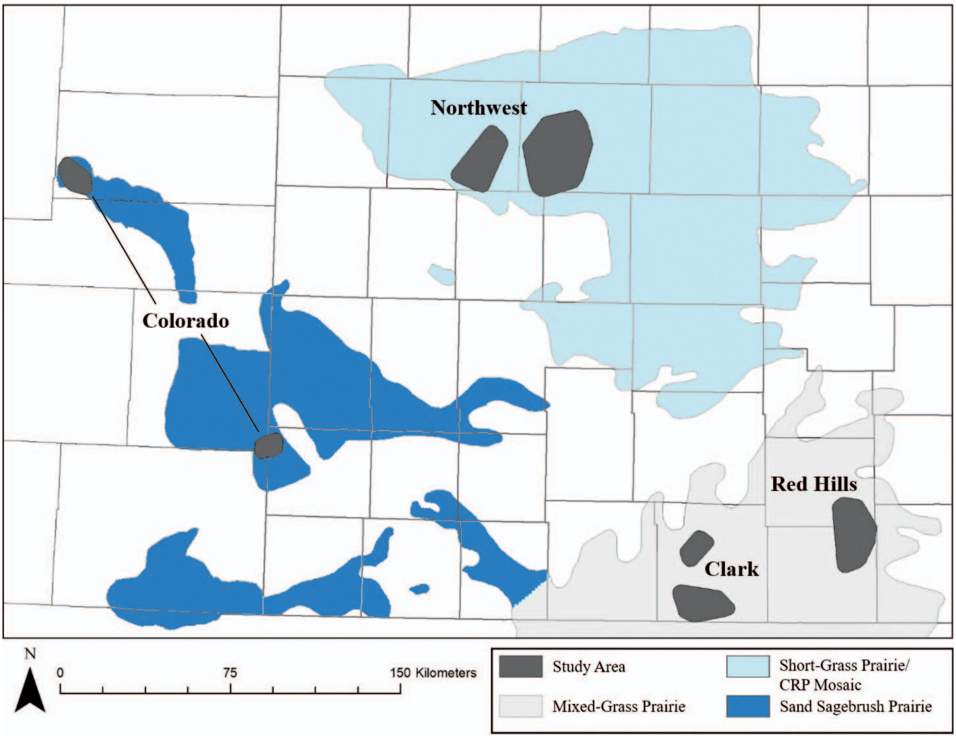


FIG. 1.—Locations of four study sites in Kansas and Colorado, U.S.A., where we captured female lesser prairie-chickens to monitor breeding season space use and movements during 2013–2018. Study sites are shown in dark grey; The Clark (Clark County) and Red Hills sites (Comanche and Kiowa counties) are both located in the Mixed-Grass Prairie Ecoregion (shown in light grey), the Colorado site (Baca, Cheyenne, and Prowers counties) is located in the Sand Sagebrush Prairie Ecoregion (blue), and the Northwest site (Gove and Logan counties) is located in the Short-Grass Prairie/CRP Mosaic ecoregion (light blue). Data from the Baca/Prowers and Cheyenne study sites were pooled to form one Colorado site to increase sample sizes for parameter estimation for the Sand Sagebrush Ecoregion

on private lands in Comanche and Kiowa counties. The Red Hills consisted of mixed-grass prairie rangelands on loamy soils, with only some row-crop agriculture and CRP-grasslands present on the landscape. Last, our study site in the Sand Sagebrush Prairie Ecoregion was in Baca, Cheyenne, and Prowers counties, Colorado, where we collected data from 2013–2015. The landscape in Baca and Prowers counties consisted of native rangeland and CRP-grasslands within a landscape mosaic of row-crop agriculture, whereas Cheyenne County was dominated by grazed sand sagebrush prairie. Although distinct in geographical location and to a certain extent in landscape composition, we pooled data from our Baca/Prowers and Cheyenne sub-sites to form one Colorado site to increase sample sizes for parameter estimation for the Sand Sagebrush Prairie Ecoregion. More detailed descriptions of all four study sites are available online as Supplemental Information (Table Appendix 1).

TABLE 1.—Sample sizes of female lesser prairie-chickens captured in Kansas and Colorado, U.S.A, during 2013–2018 shown separately by study sites, years, and whether females were equipped with a very-high-frequency (VHF) or GPS transmitter. Sample sizes include only females for which there were at least 30 (VHF) or 100 (GPS) unique locations during the entire breeding season (15 March–15 September) after excluding locations that were part of long-distance (>5 km) movements

Study Site	Transmitter	2013	2014	2015	2016	2017	2018	Total
Clark	VHF	.	3	5	.	.	.	8
	GPS	.	16	9	.	.	.	25
Colorado	VHF	.	.	.	.	.	.	.
	GPS	5	1	3	.	.	.	9
Northwest	VHF	3	10	5	.	.	.	18
	GPS	29	20	11	.	.	.	60
Red Hills	VHF	6	7	.	.	.	.	13
	GPS	12	13	11	14	8	5	63
Total	VHF	9	20	10	.	.	.	39
	GPS	46	50	34	14	8	5	157

METHODS

CAPTURE

During the lekking period (March–May) of each year, we captured lesser prairie-chickens with walk-in traps and drop nets (Haukos *et al.*, 1990; Silvy *et al.*, 1990). We sexed and aged lesser prairie-chickens based on plumage and marked individuals with a unique combination of plastic color bands and a numbered aluminum leg band (Copelin, 1963; Sullins *et al.*, 2018). Captured females received either a 12 or 15 g bib style very-high-frequency (VHF) transmitter (A3960, Advanced Telemetry System, Isanti, MN, U.S.A.) or a rump-mounted 22 g, solar-powered, Global Positioning System (GPS) transmitter (Solar Argos/GPS PTT 100 by Microwave Telemetry Inc., Columbia, MD, U.S.A., or 22 GPS PTT by NorthStar Science and Technology LLC, King George, VA, U.S.A.). We attached satellite transmitters using leg harnesses made of Teflon ribbon with elastic at the front of the harness to accommodate the bird's movement or changes in body condition (Bedrosian and Craighead, 2007; Dzialak *et al.*, 2011). Transmitters did not exceed 3% of body mass of captured individuals. We released individuals within 30 min after capture. Capture and handling methods do not decrease survival probabilities of individuals (Grisham *et al.*, 2015) or affect movements as average daily movements of recently captured birds were similar to those of birds captured >2 wk earlier (B.H.F. Verheijen, unpubl. data). All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee under protocols #3241 and #3703; Kansas Department of Wildlife, Parks and Tourism scientific collection permits SC-042-2013 SC-079-2014, SC-001-2015), SC-014-2016, SC-018-2017, and SC-024-2018; and Colorado Parks and Wildlife scientific collection permits 13TRb2053, 14TRb20153, and 15TRb2053.

TRACKING

Throughout the breeding season, we located females with VHF transmitters 3–4 times per wk using triangulation from 3–5 observer locations using three-piece handheld Yagi antennas and an Advanced Telemetry Systems receiver (R4000, R4500; Isanti, MN, U.S.A.)

or a Communications Specialists receiver (R1000; Orange, CA, U.S.A.). We determined the Universal Transverse Mercator (UTM) position of the observer's location with a handheld GPS receiver (average accuracy: ±5 m; Garmin 64; Olathe, KS, U.S.A.) and recorded the compass bearing from each observer location to the bird's estimated location. Bearings of observer locations were on average 15 degrees apart and taken within 20 min to minimize error from bird movements. We estimated the UTM location and associated error of each bird with the Location of a Signal program (LOAS; Ecological Software Solutions, Hegymagas, Hungary). We generally used bird locations with error polygons $<$ 0.1 ha, but we did use some locations with error polygons between 0.1–1 ha when the number of locations for an individual were limited ($<$20% of all locations). Throughout the field season, we varied our survey routes through the study area such that individuals were located at different times of day across surveys. If individuals left the immediate study area, we would attempt to relocate individuals with a fixed-wing Cessna plane twice a year during May and July at each site. GPS transmitters recorded female locations every 2 h between 4:00 and 22:00 local time for a total of ~10 locations per day. GPS transmitter locations were recorded with ±18 m accuracy (which approximates an error polygon of ~0.1 ha), uploaded to an Argos satellite, and downloaded every 3–4 d using the Argos System.

ASSIGNING BIRD LOCATIONS TO BREEDING STAGES

We monitored lesser prairie-chicken nests and broods to assign individual bird locations to specific breeding stages and estimate breeding stage-specific home range area and daily displacement. Overall, we followed monitoring protocols as described in Lautenbach (2015) and Lautenbach *et al.*, (2019), but will briefly describe our methodology here. First, we located nests of females with VHF transmitters by homing once a female was recorded in the same location for three consecutive locations (Pitman *et al.*, 2005). We located nests of females with GPS transmitters as the GPS location that females consistently visited or at which they were stationary (7–10 locations/d) over a three-d period. When located, we briefly ($<$5 min) visited each nest once to count the number of eggs and estimate nest initiation date, start of incubation, and predicted hatch date (Coats, 1955; Pitman *et al.*, 2006; McNew *et al.*, 2009; Grisham *et al.*, 2013). Most hens were flushed once during the initial nest check, but overall abandonment rates were low (6.9%; Lautenbach *et al.*, 2019). If telemetry or GPS locations showed females off the nest for $>$1 d, we approached the nest to determine its fate (Pitman *et al.*, 2005). If a nest was successful, we continued monitoring broods with weekly brood-flushes and counted the number of fledglings until no fledglings or fecal pellets were encountered during three subsequent visits, female movements increased beyond the limited mobility of young fledglings (*e.g.*, $>$1.5 km in 1–2 d), or active broods reached independence and disbanded (~15 September; Pitman *et al.*, 2006; Boal and Haukos, 2016).

Based on our nest and brood monitoring data, we then assigned individual bird locations to one of four breeding stages: lekking/prelaying, nesting, brood-rearing, and postbreeding. We considered a bird to be in a lekking/prelaying stage from date of capture or start of the breeding season (15 March; Boal and Haukos, 2016) to initiation of its first nest, as well as during the period between a failed nesting attempt and initiation of a renesting attempt (Plumb *et al.*, 2019). Nest propensity of lesser prairie-chickens is generally high (95%; Ross *et al.*, 2019) and only two females seemingly did not initiate any nests. We assigned bird locations collected between the initiation of any nest until nest fate was determined to the nesting stage. Females with successful nests entered the brood-rearing stage until brood failure was determined by brood flushes or when broods disbanded (September 15; Boal and

Haukos, 2016). Last, we assigned bird locations to the postbreeding stage after females had failed their last reproductive attempt during the current breeding season until the end of the breeding season (September 15; Boal and Haukos, 2016). Because of our conservative decision to consider a brood to have failed the day after the brood was last known to be alive, some bird locations might have been assigned to the postbreeding stage while broods were still alive. However, the misclassification of several days will likely lead to only a small underestimation of home range area during the postbreeding stage, which generally encompassed >4 wk for females with failed broods.

ESTIMATING HOME RANGE AREA

We estimated home range area of female lesser prairie-chickens with either kernel density estimators (VHF birds) or biased random bridge movement models (GPS birds) with the *adehabitatHR* package in Program R (Worton, 1989; Seaman and Powell, 1996; Calenge, 2006; Benhamou and Cornelis, 2010; Benhamou, 2011; R Core Team, 2020). We first excluded any locations that were part of movements >5 km away from the center of the home range, which we considered dispersal events or other exploratory movements and are not part of the daily movements that generally take place inside a home range (Earl *et al.*, 2016; Robinson *et al.*, 2018a). For each female with a VHF transmitter for which we obtained at least 30 unique locations over the entire breeding season or during specific breeding stages, we estimated the home range area as the 95% isopleth of the utilization distribution calculated with a kernel density estimator. Previous studies have shown that 30 unique locations can provide an unbiased estimate of home range area (Worton, 1989; Seaman *et al.*, 1999; Leonard *et al.*, 2008; Patten *et al.*, 2011). When using kernel density estimation, selection of an appropriate smoothing parameter can have a strong effect on the area of estimated home ranges, as it constrains the area over which individual locations are affecting the utilization distribution (Silverman, 1986; Hemson *et al.*, 2005; Fieberg, 2007; Leonard *et al.*, 2008). We estimated the smoothing parameter with least-squares cross-validation (LSCV) techniques, which is often recommended when studying animal space use (Seaman *et al.*, 1999; Horne and Garton, 2006). However, LSCV-techniques may fail to converge when datasets contain many identical points or points that are very close together, as could be the case with incubating lesser prairie-chickens (Silverman, 1986; Hemson *et al.*, 2005). For VHF birds in which LSCV techniques failed to converge ($n = 21$ of 39), we used the average smoothing parameter of the remaining birds, similar to Robinson *et al.* (2018a).

For each female equipped with a GPS transmitter for which we obtained at least 100 unique locations over the entire breeding season or during specific breeding stages, we estimated the home range area as the 95% isopleth of the utilization distribution calculated with biased random bridge movement models available in the *adehabitatHR* package in R. Although dependent on the frequency of data collection, a minimum of 100 unique locations is likely necessary to obtain an unbiased estimate of home range area based on biased random bridge and related movement models (Girard *et al.*, 2002; Robinson *et al.*, 2018a; Plumb *et al.*, 2019). Biased random bridge models account for the time lag between successive locations, path between two successive locations, transmitter error, and temporal autocorrelation, and are therefore more appropriate than fixed kernel density estimators when handling spatially autocorrelated data (Benhamou and Cornelis, 2010; Benhamou, 2011). Furthermore, biased random bridge models do not assume a purely diffusive movement, unlike the commonly used Brownian bridge movement models. Instead, they assume a certain amount of directional drift between successive relocations and are assumed to more realistically model animal movements compared to Brownian bridge movement models (Benhamou, 2011). Because we did not collect locations during a six-hr period overnight, we considered all locations collected on different days to belong to unique activity segments. We set the minimum smoothing parameter to 6 m – the standard deviation of the accuracy of our GPS transmitters and determined the diffusion coefficient (D) with the maximum likelihood approach.

ESTIMATING DAILY DISPLACEMENT

We estimated daily displacement by each female as the absolute distance between the first and last location of each day using base functions in R (R Core Team, 2020). We only estimated daily displacement for females with GPS transmitters, because we did not record multiple locations per day for females with VHF transmitters. Last, we estimated mean daily displacement and its standard deviation for each female for the whole breeding season as well as for each individual breeding stage.

STATISTICAL ANALYSES

We used linear regressions to assess a potential relationship between home range area and the number of unique locations of birds with VHF (30) or GPS (100) transmitters ($\alpha = 0.05$). We then used a one-way analysis of variance (ANOVA; $\alpha = 0.05$) to test whether breeding season home range areas and daily displacements by female lesser prairie-chickens varied among study sites. We analyzed females equipped with VHF or GPS transmitters separately and pooled our data across years because of low samples sizes during some site-year combinations (Table 1). To test whether home range areas or daily displacements by female lesser prairie-chickens varied among breeding stages, we limited our dataset to females with GPS transmitters only, because no females with VHF transmitters had a sufficient number of unique locations (>30) during any breeding stage. We then used two-way ANOVAs ($\alpha = \leftarrow 0.05$) to test effects of study site, breeding stage, and their interaction on home range areas or daily displacements. For both analyses, we log-transformed home range areas and daily displacements so that residuals would be normally distributed. If we found significant effects in our ANOVAs, we used Tukey HSD tests ($\alpha = 0.05$) with Bonferroni corrections to determine statistical differences among sites or breeding stages. We conducted all our analyses using the base functions in R (R Core Team, 2020).

RESULTS

Our final dataset included a total of 196 female lesser prairie-chickens that met our analysis criteria (VHF: 30 locations, $n = 39$; GPS: 100 locations, $n = 157$; Table 1). The number of locations was not correlated with the resulting home range area for females equipped with VHF ($r = 0.07$, $P = 0.70$) or GPS transmitters ($r = \leftarrow 0.06$, $P = 0.48$), indicating that 30 (VHF) or 100 (GPS) locations per female were sufficient to estimate home range area (Fig. 2).

HOME RANGE AREA

Over the entire breeding season, home range area for females equipped with VHF transmitters averaged 190.4 ha (SE = 19.1, range = 50.3–566.3) and did not vary among sites ($F_{2,36} = \leftarrow 2.02$, $P = \leftarrow 0.15$; Table 2). Home range area for females equipped with GPS transmitters averaged 283.6 ha (SE = 23.1, range = 17.7–2448.1) for the whole breeding season and did vary among sites ($F_{3,153} = 17.72$, $P < 0.001$), with home range areas being

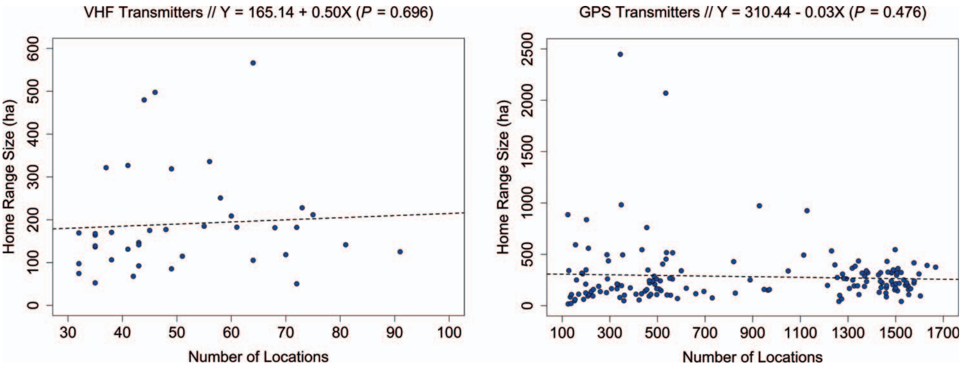


FIG. 2.—Linear relationships between the number of locations of each female and resulting home range area estimated with kernel density estimators for birds equipped with very-high-frequency (VHF) transmitters ($r = 0.065$, $n = 39$, left panel) or with biased random bridge models for birds equipped with GPS transmitters ($r =$-~~0~~.057, $n = 157$, right panel) of females captured at four sites in Kansas and Colorado, U.S.A., during the breeding seasons of 2013–2018. Home range areas represent the 95% isopleth, were measured in hectares, and represent the entire breeding season (15 March–15 September). Linear relationships and P-values are listed above each panel

∼2.3 times larger at the Northwest site and ∼1.9 times larger in Colorado compared to Clark and the Red Hills (NW vs. CL and NW vs. RH: $P < 0.001$, CO vs. CL: $P = 0.02$, CO vs. RH: P =← 0.004, CO vs. NW: $P = 0.99$; Table 2).

Home range area of female lesser prairie-chickens varied among breeding stages ($F_{3,324}$ =← 18.91, $P < 0.001$) and were ∼1.5–1.8 times larger during the lekking/prelaying stage compared to the nesting ($P < 0.001$) and postbreeding stages ($P < 0.001$), whereas home ranges were ∼1.8–2.1 times smaller during the brood-rearing stage compared to the nesting ($P < 0.001$) and postbreeding stages ($P = 0.003$; Table 2). Relative differences between specific breeding stages did not vary among sites ($F_{8,324} = 0.98$, $P = 0.45$). Breeding stage-specific home ranges were consistently greater at the Colorado and Northwest sites compared to the Clark and Red Hills sites ($P < 0.001$ for all listed combinations; Table 2).

MEAN DAILY DISPLACEMENT

During the breeding season, mean daily displacement of females averaged 374.8 m (SE =← 14.3) and was highly variable among females ranging from 115.6 to 1171.4 m (Table 3). Mean daily displacement varied across study sites ($F_{3,153} = 12.32$, $P < 0.001$) and was ∼1.7 times greater for females at the Northwest site compared to the Clark site ($P < 0.001$) and ∼1.5 times greater compared to the Red Hills site ($P < 0.001$; Table 3). In Colorado, mean daily displacement was intermediate but not different from any other site (vs. Clark: $P = 0.09$, vs. Northwest: $P = 0.88$, vs. Red Hills: $P = 0.29$; Table 3).

Mean daily displacement varied greatly across breeding stages ($F_{3,323} = 100.27$, $P < 0.001$). Females moved similar distances during nesting and brood-rearing stages ($P = 0.91$), but moved ∼1.3 times farther during the postbreeding stage compared to the nesting stage ($P < 0.001$) and tended to move farther than during the brood-rearing stage ($P = 0.07$; Table 3). During the lekking/prelaying stage, mean daily displacement was ∼2.3 times greater than the nesting stage ($P < 0.001$), ∼2.4 times greater than during the brood-rearing stage ($P < 0.001$), and ∼1.8 times greater than during the postbreeding stage ($P < 0.001$; Table 3).

TABLE 2.—Average breeding season home range areas of female lesser prairie-chickens captured in Kansas and Colorado, U.S.A, during 2013–2018. Shown are sample sizes (*n*), and means, standard deviations, standard errors, and observed range in hectares. Estimates are separated by transmitter type (VHF vs. GPS), breeding stage, and study sites, but were pooled across years

Transmitter	Breeding stage	Study site	n	Mean	SD	SE	Range
GPS	Lekking/Prelaying	Clark	21	177.5	131.0	28.6	53.9–521.8
		Colorado	6	285.7	151.4	61.8	109.5–523.1
		Northwest	50	396.7	356.7	50.4	50.1–1978.0
		Red Hills	54	145.2	101.9	13.9	17.7–523.6
		All Sites	131	252.8	263.5	23.0	17.7–1978.0
GPS	Nesting	Clark	19	92.0	50.9	11.7	31.7–177.4
		Colorado	8	210.9	164.8	58.3	76.6–594.5
		Northwest	33	309.6	300.9	52.4	49.5–1444.2
		Red Hills	48	99.6	62.8	9.1	19.4–344.7
		All Sites	108	170.7	201.2	19.4	19.4–1444.2
GPS	Brood-rearing	Clark	5	65.8	53.0	23.7	4.6–125.4
		Colorado	0	.	.	.	.
		Northwest	9	106.1	55.9	18.6	47.7–213.6
		Red Hills	7	60.7	39.1	14.8	9.1–123.9
		All Sites	21	81.4	52.5	11.5	4.6–213.6
GPS	Postbreeding	Clark	12	118.9	97.6	28.2	19.4–343.7
		Colorado	6	217.9	79.8	32.6	125.7–291.5
		Northwest	25	172.0	144.1	28.8	30.8–798.6
		Red Hills	28	114.9	72.6	13.7	10.9–280.0
		All Sites	71	144.4	110.9	13.2	10.9–798.6
GPS	Whole Breeding Season	Clark	25	183.9	106.2	21.2	41.7–496.3
		Colorado	9	347.7	99.5	33.2	156.9–533.9
		Northwest	60	420.8	408.8	52.8	94.2–2448.1
		Red Hills	63	183.3	110.2	13.9	17.7–545.9
		All Sites	157	283.6	288.8	23.1	17.7–2448.1
VHF	Whole Breeding Season	Clark	8	146.4	46.4	16.4	92.2–227.9
		Colorado	0	.	.	.	.
		Northwest	18	233.0	147.0	34.7	52.5–566.3
		Red Hills	13	158.6	91.0	25.2	50.3–335.9
		All Sites	39	190.4	119.6	19.1	50.3–566.3

Relative differences in mean daily displacement among breeding stages did not vary across sites ($F_{8,323} = \leftarrow 0.90$, P $= \leftarrow 0.52$). For all breeding stages, mean daily displacement was consistently greater at the Colorado and Northwest sites compared to the Clark and Red Hills sites (Clark vs. Colorado: P $= 0.003$, Clark vs. Northwest: P < 0.001, Red Hills vs. Colorado: P $= 0.04$, Red Hills vs. Northwest: P < 0.001; Table 2).

STANDARD DEVIATION OF DAILY DISPLACEMENT

Over the entire breeding season, the standard deviation of daily displacements of individual female lesser prairie-chickens averaged 445.7 m (SE $= \leftarrow 16.6$ m) and varied significantly among field sites ($F_{3,153} = 5.79$, P < 0.001). Daily displacements of individual females were ~1.4 times more variable at the Northwest site than Clark (P $= 0.008$) and ~1.3

TABLE 3.—Average breeding season daily displacements (absolute distance between first and last location of each day) of female lesser prairie-chickens captured in Kansas and Colorado, U.S.A. and equipped with GPS transmitters during 2013–2018. Shown are sample sizes (*n*), and means, standard deviations, standard errors, and observed range in meters. Estimates are separated by breeding stage, and study sites, but were pooled across years

Breeding stage	Study site	n	Mean	SD	SE	Range
Lekking/Prelaying	Clark	21	451.1	187.5	40.9	249.3–952.4
	Colorado	6	595.4	162.3	66.2	370.1–789.5
	Northwest	50	620.7	216.3	30.6	231.2–1192.7
	Red Hills	54	492.8	225.9	30.7	208.9–1414.7
	All Sites	131	539.7	223.0	19.5	208.9–1414.7
Nesting	Clark	19	173.9	93.7	21.5	67.2–410.3
	Colorado	8	258.5	152.7	54.0	94.8–571.3
	Northwest	33	300.5	212.3	37.0	70.8–1046.4
	Red Hills	48	204.0	91.5	13.2	71.0–443.4
	All Sites	108	232.2	150.4	14.5	67.2–1046.4
Brood-rearing	Clark	5	200.7	67.9	30.4	99.4–265.9
	Colorado	0	.	.	.	.
	Northwest	9	256.5	69.4	23.1	187.7–372.0
	Red Hills	7	190.8	27.5	10.4	160.6–231.4
	All Sites	21	221.3	63.7	13.9	99.4–372.0
Postbreeding	Clark	12	246.4	96.2	27.8	132.3–485.9
	Colorado	6	404.5	83.4	34.0	309.5–526.3
	Northwest	24	294.4	85.2	17.4	49.5–427.1
	Red Hills	28	294.6	102.2	19.3	123.2–525.4
	All Sites	70	295.7	99.7	11.9	49.5–526.3
Whole Breeding Season	Clark	25	281.0	80.2	16.0	141.7–442.2
	Colorado	9	397.1	100.1	33.4	195.1–521.3
	Northwest	60	468.5	228.0	29.4	139.7–1171.4
	Red Hills	63	319.5	109.9	13.8	115.6–740.5
	All Sites	157	374.8	178.9	14.3	115.6–1171.4

times more variable than Red Hills sites ($P = 0.002$), but similar to Colorado ($P = 0.74$; Table 4).

Variability in daily displacement within female lesser prairie-chickens also differed among breeding stages ($F_{3,315} = 44.87$, $P < 0.001$). Daily displacements were least variable for females during the brood-rearing stage and ~1.6 times more variable during the nesting stage ($P < 0.001$), ~1.8 times more variable during the postbreeding stage ($P < 0.001$), and ~2.8 times more variable during the lekking/prelaying stage ($P < 0.001$; Table 4). Daily displacement was ~1.7 times more variable during the lekking/prelaying stage compared to the nesting stage ($P < 0.001$) and ~1.6 times more variable than during the postbreeding stage ($P < 0.001$; Table 4). Relative differences in the variability of daily displacement within female prairie-chickens among breeding stages did not vary among sites ($F_{8,315} = 1.29$, P =← 0.25) and were consistently most variable at the Northwest site and least variable at the Clark and Red Hills sites (except during the postbreeding stage; Table 4).

Table 4.—Standard deviations of breeding season daily displacements (absolute distance between first and last location of each day) of female lesser prairie-chickens captured in Kansas and Colorado, U.S.A. and equipped with GPS transmitters during 2013–2018. Shown are sample sizes (*n*), and means, standard deviations, standard errors, and observed range in meters. Estimates are separated by breeding stage, and study sites, but were pooled across years

Stage	Site	n	Mean	SD	SE	Range
Lekking/Prelaying	Clark	21	461.0	183.3	40.0	180.1–855.1
	Colorado	6	460.3	171.4	70.0	240.2–690.8
	Northwest	50	586.1	251.6	35.6	251.5–1136.3
	Red Hills	54	499.3	301.9	41.1	145.8–1534.5
	All Sites	131	524.5	264.3	23.1	145.8–1534.5
Nesting	Clark	19	222.7	88.6	20.3	97.3–513.1
	Colorado	8	420.9	184.1	65.1	209.0–714.9
	Northwest	33	402.6	233.3	40.6	127.5–872.3
	Red Hills	48	252.8	81.8	11.8	103.9–511.1
	All Sites	108	305.7	170.7	16.4	97.3–872.3
Brood-rearing	Clark	5	158.9	70.4	31.5	66.3–257.0
	Colorado	0	.	.	.	.
	Northwest	8	227.4	56.8	18.9	132.2–326.3
	Red Hills	7	157.6	35.0	13.2	116.6–203.8
	All Sites	20	187.8	62.3	13.6	66.3–326.3
Postbreeding	Clark	12	309.3	274.0	79.1	99.0–1128.4
	Colorado	6	390.3	108.9	44.5	298.7–565.7
	Northwest	24	320.8	148.0	30.2	110.5–689.9
	Red Hills	28	341.5	201.1	38.0	91.7–903.4
	All Sites	70	333.1	190.9	22.8	91.7–1128.4
Whole Breeding Season	Clark	25	374.1	142.6	28.5	161.0–661.0
	Colorado	9	440.6	129.1	43.0	261.3–644.4
	Northwest	60	524.5	240.7	31.1	211.1–1198.9
	Red Hills	63	399.9	183.9	23.2	145.8–1102.1
	All Sites	157	445.7	208.3	16.6	145.8–1198.9

Discussion

We present the first estimates of breeding season space use by female lesser prairie-chickens for the Short-Grass Prairie/CRP Mosaic Ecoregion and the first estimates based on GPS transmitters for the three northernmost occupied ecoregions. Both breeding season home range areas and daily displacements by lesser prairie-chickens showed large variation among ecoregions and breeding stages. Home range areas and daily displacements were consistently greater in the Sand Sagebrush Prairie and Short-Grass Prairie/CRP Mosaic Ecoregions compared to the Mixed-Grass Prairie Ecoregion, greatest during the lekking/prelaying stage, and smallest during the brood-rearing stage of the breeding season.

DRIVERS OF BREEDING SEASON SPACE USE

Observed spatial variation in breeding season space use by female lesser prairie-chickens could be caused by several key differences among ecoregions. Although lesser prairie-chickens seem to select for a certain degree of landscape heterogeneity (Robinson *et al.*, 2018b; Sullins *et al.*, 2019), they generally select areas with large amounts of grassland (>70%), while avoiding anthropogenic structures, such as powerlines, roads, or oil wells (Winder *et al.*, 2015; Plumb *et al.*, 2019; Sullins *et al.*, 2019). Both cropland and anthropogenic structures are more abundant in the Sand Sagebrush Prairie and Short-Grass Prairie/CRP Mosaic Ecoregions compared to the Mixed-Grass Prairie Ecoregion (Haukos and Zavaleta, 2016; Spencer *et al.*, 2017; Robinson *et al.*, 2018a; Plumb *et al.*, 2019). Croplands fragment the prairie landscape, increasing the spatial distribution of important breeding resources. Avoidance of powerlines, roads, and oil wells may also increase female space use as well. As a result, landscape features, such as croplands and anthropogenic structures, could explain some of the variation in space use that we observed among ecoregions.

As expected, female space use was most limited during the brood-rearing stage when movements were largely restricted by the low mobility of recently hatched chicks. Brood-rearing home ranges were only 28.7% of the home range area of the entire breeding season and daily displacements were up to 2.4 times smaller than during any other breeding stage. More interestingly, we found large site differences in space use by brood-rearing females, with home range areas ~1.6–1.7 times and daily displacements ~1.3 times larger in the Short-Grass Prairie/CRP Mosaic Ecoregion than the Mixed-Grass Prairie Ecoregion. Only relatively small parts of our study areas meet habitat requirements for nesting (1.1–30.5%) or brood-rearing (6.9–35.7%) lesser prairie-chickens, but brood-rearing habitats are especially limited in the Short-Grass Prairie/CRP Mosaic Ecoregion (6.9–11.6%; Gerht *et al.*, 2020). Moreover, nesting and brood-rearing habitats differ in vegetation structure and composition and rarely overlap on the landscape (Lautenbach, 2015; Lautenbach *et al.*, 2019; Gehrt *et al.*, 2020). Low availability of brood-rearing habitat in the Short-Grass Prairie/CRP Mosaic Ecoregion could force brood-rearing females to move larger distances from nest sites to brood-rearing habitat and among brood-rearing habitat patches compared to other ecoregions. The short daily movements of brood-rearing females at all study sites (range: 99.4–372.0 m/d), even where brood-rearing habitat was scarce, suggest that females with newly hatched chicks may not have the option of traveling large distances to find brood-rearing habitat. The amount of available brood-rearing habitat on the landscape could be even more limited than previous estimates based on habitat requirements alone (Gehrt *et al.*, 2020).

Female lesser prairie-chickens used almost as much space during the lekking/prelaying stage (89.1%) as during the entire breeding season and show daily displacements that are ~1.8–2.4 times larger than during other breeding stages. Female lesser prairie-chickens seem to visit a variety of habitat patches before and between nesting attempts, potentially scouting parts of the landscape they will use during nesting and brood-rearing. However, 10.9% of space used during the entire breeding season remains unvisited in the lekking/prelaying stage. Whereas habitat use during the lekking/prelaying stage could provide a useful means of identifying key breeding habitats for conservation, it could also exclude certain areas crucial for nesting and brood-rearing female lesser prairie-chickens.

COMPARISON TO PREVIOUS ESTIMATES

Previous estimates of breeding season home range area have been based on relatively small samples of females equipped with VHF radio-transmitters and may only be comparable to our VHF estimates (Merchant, 1982; Toole, 2005; Leonard, 2008; Borsdorf, 2013; Winder *et al.*, 2015). In contrast to GPS transmitters, locations collected with VHF transmitters are subject to coarser temporal resolution (VHF: 3–7 locations/wk; GPS: ~70 locations/wk), more frequent missing observations, and different analytical tools (VHF: minimum convex polygons or kernel density estimators, GPS: biased random bridge or similar models). Estimates from the two transmitter types are, therefore, not directly comparable and are often larger when using GPS transmitters (this study, Robinson *et al.*, 2018a). Previous studies based on VHF transmitters might therefore have systematically underestimated lesser prairie-chicken space use.

When focusing solely on birds with VHF transmitters, our overall estimates of breeding season home range area (190.4 ha, site means: 146.4–233.0 ha) were on the low end of the range of previous estimates (236–671.4 ha; Merchant, 1982; Toole, 2005; Leonard, 2008; Borsdorf, 2013; Winder *et al.*, 2015). Two key differences between our work and previous studies could help explain those differences. First, with the exception of Toole (2005) and Winder *et al.* (2015), all previous estimates are from the Sand Shinnery Oak Prairie Ecoregion in New Mexico and Texas (Merchant, 1982; Riley *et al.*, 1994; Leonard, 2008; Borsdorf, 2013), whereas our study spanned the other three ecoregions. Large-scale habitat loss, reduced quality of remaining habitat patches, and an overall drier and hotter climate than in other ecoregions (Peterson and Boyd, 1998; Wester, 2007; Haukos, 2011; Grisham *et al.*, 2016) could have affected the distribution and availability of resources in the Sand Shinnery Oak Prairie Ecoregion, forcing female lesser prairie-chickens to travel larger distances. Moreover, overall breeding season home ranges in our study were only slightly larger than during any single breeding stage, but were close to the sum of all four stages in the Sand Shinnery Oak Prairie Ecoregion (lekking/prelaying: 32.4%, nesting: 11.7%, brood-rearing: 26.2%, postbreeding: 26.2% of total breeding season; Merchant, 1982; Riley *et al.*, 1994; Leonard, 2008; Borsdorf, 2013). Breeding stage-specific habitats therefore seem less interspersed and more spatially separated in the Sand Shinnery Oak Prairie Ecoregion than in the northern three ecoregions, potentially increasing female space use over the breeding season.

Second, we excluded locations that were part of dispersal movements before calculating breeding season home range areas, a step not mentioned in previous studies (Merchant, 1982; Toole, 2005; Leonard, 2008; Borsdorf, 2013; Winder *et al.*, 2015). This methodological difference could also help explain why our estimates from the Sand Sagebrush Prairie and Mixed-Grass Prairie Ecoregions were 3.8–4.5 (VHF) or 2.5–3.0 times (GPS) smaller than previously published estimates from the same ecoregions (Winder *et al.*, 2015). Although long-distance movements (*e.g.*, foray loops, dispersal, and round-trip movements) are an integral part of the ecology of the lesser prairie-chicken, they do not reflect day-to-day space use and are only shown by ∼28% of females (Earl *et al.*, 2016). Therefore, breeding season space use may be better represented when long-distance movements are excluded. As a result, lesser prairie-chickens in the Sand Sagebrush Prairie and Mixed-Grass Prairie Ecoregions could have smaller home ranges during the breeding season than previously reported.

COMPARISON TO OTHER SPECIES OF PRAIRIE GROUSE

Previous studies have also estimated breeding season space use of females in two other closely related species of prairie grouse: greater prairie-chicken (*Tympanuchus cupido*) and sharp-tailed grouse (*Tympanuchus phasianellus*). Compared to lesser prairie-chickens, overall breeding season home range areas based on VHF transmitters are much larger for the larger-bodied greater prairie-chicken (Colorado: 213–624 ha, Kansas: 1060–2460 ha, Missouri: 800 ha, Nebraska: 360 ha, and Oklahoma: 3670 ha; Schroeder, 1991; Winder *et al.*, 2015, 2017), whereas estimates for sharp-tailed grouse are relatively comparable but equally variable (Colorado: 87 ha, Idaho: 187 ha, Montana and North Dakota: 361–838 ha, Washington: 1066 ha; Saab and Marks ,1992; Boisvert *et al.*, 2005; Stonehouse *et al.*, 2015;

Milligan *et al.*, 2020). Female greater prairie-chickens that move larger distances and maintain larger home ranges may have reduced annual survival and reproductive success (Burger, 1988), which suggests that if a similar link exists in lesser prairie-chickens, greater space use in some ecoregions could have consequences for local population dynamics. Moreover, although absolute breeding season space use varies among species, similarities in response to spatial patterns in extrinsic factors, such as landscape fragmentation and densities of anthropogenic structures (Patten *et al.*, 2011) or rangeland management practices (Milligan *et al.*, 2020), could mean that all three species of prairie grouse may be similarly affected by common challenges in their conservation.

Previous studies on greater prairie-chickens and sharp-tailed grouse have been unable to estimate home range areas for specific breeding stages likely due to low sample sizes and limitations from the use of VHF transmitters, but home ranges of female greater prairie-chickens were smaller during early spring (213 ha) versus late spring (624 ha; Schroeder, 1991). Similar to lesser prairie-chickens, daily movements of greater prairie-chickens are generally smaller during the breeding season than the nonbreeding season (Hamerstrom and Hamerstrom, 1949; Burger *et al.,* 1991; Johnson *et al.,* 2020), but estimates for minimum daily movements within stages of the breeding season are sparse and inconsistent (nesting: 469–521 m/d, postnesting: 294–471 m/d, Burger *et al.*, 1991; spring: 461 m/d, summer: 272 m/d, Patten *et al.*, 2011). Although breeding stage-specific movements may be similar among these closely related species, ecological and geographical differences among species could affect breeding stage-specific patterns in home ranges areas and daily movements, thereby providing an opportunity for future research.

COMPARISON TO THE NONBREEDING SEASON

Factors restricting space use and movements by lesser prairie-chickens and the spatial scale at which these factors operate likely differ between the breeding and nonbreeding season. Breeding season home ranges were 1.4 2.5 (VHF) and ∼3.5 times (GPS) smaller and daily displacements were ∼1.2 1.8 times shorter than existing estimates from the nonbreeding season (Candelaria, 1979; Toole, 2005; Pirius *et al.*, 2013; Robinson *et al.*, 2018a). Moreover, differences found among ecoregions were opposite from the only study on nonbreeding season space use in the northern three ecoregions (Robinson *et al.*, 2018a), in which home ranges were smallest in the Short-Grass Prairie/CRP Mosaic Ecoregion. During the nonbreeding season, space use by female lesser prairie-chickens may be driven by factors, such as availability of food and cover for thermal regulation (Riley *et al.*, 1994; Hagen and Giesen, 2005; Grisham *et al.*, 2014; Boal and Haukos, 2016), rather than by the availability of breeding resources around leks. Although breeding resources, such as nesting and brood-rearing habitat, are less abundant in the Short-Grass Prairie/CRP Mosaic Ecoregion (Gehrt *et al.*, 2020), food availability during the nonbreeding season could be greater in this ecoregion compared to the Mixed-Grass Prairie Ecoregion, which is reflected by a ∼20g greater body mass of females at capture (C. Aulicky, unpublish. data). Lesser prairie-chickens are known to forage on waste grains during the nonbreeding season, especially during drought conditions when other food sources are less abundant (Copelin, 1963; Boal and Haukos, 2016). The greater proportion of croplands and potentially increased availability of waste grains in the Short-Grass Prairie/CRP Mosaic Ecoregion could allow lesser prairie-chickens to move shorter distances during the nonbreeding season compared to other ecoregions (Spencer *et al.*, 2017). Given the apparent variation in lesser prairie-chicken space use and its drivers across the year, a full life-cycle approach would be necessary for appropriate management recommendations.

CONCLUSIONS

Observed variation in breeding season space use among ecoregions could have potential consequences for the population dynamics of lesser prairie-chickens. Spatial patterns in home range areas and daily displacements coincided with spatial variation in several demographic parameters. Estimates of brood and adult survival during the breeding season are (or tend to be) lower in the Short-Grass Prairie/CRP Mosaic Ecoregion compared to the Mixed-Grass Prairie Ecoregion (Lautenbach, 2015; S. Robinson, unpubl. data), suggesting that increased space use could be associated with demographic costs. However, a direct link between breeding-season space use and demographic rates of lesser prairie-chickens is currently missing. Simultaneously assessing space use and demographic rates at the individual level could help managers understand how space use and its drivers affect population dynamics of the species. Regardless of demographic consequences, our results emphasize the heterogeneity in lesser prairie-chicken space use and habitat needs across ecoregions and breeding stages. Ecoregion- and breeding stage-specific estimates of space use in combination with breeding stage-specific resource selection could therefore prove important for land managers for determining the amount and juxtaposition of breeding habitat that is needed for populations to persist.

Acknowledgments.—We like to thank J. Kraft, J. D. Lautenbach, J. M. Lautenbach, and the many technicians who helped to collect our field data, and all private landowners that allowed us access to their land. We thank J. Gehrt, J. Lamb, B. Ross, and E. Weiser for providing helpful comments on earlier drafts of this manuscript. We greatly appreciate the logistical and technical support provided by J. Pitman, J. Kramer, D. Dahlgren, J. Prendergast, K. Fricke, C. Berens, G. Kramos, A. Flanders, J. Reitz, M. Bain, and the Smoky Valley Ranch of The Nature Conservancy. We thank K. Schultz and A. Chappell for providing GPS data from lesser prairie-chickens captured on the Cimarron National Grasslands. Funding for the project was provided by Kansas Department of Wildlife, Parks and Tourism (Federal Assistance Grant KS W-73-R-3); United States Department of Agriculture (USDA) Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62); and USDA Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

AUGUSTINE, D., A. DAVIDSON, K. DICKINSON, AND B. VAN PELT. 2019. Thinking like a Grassland: Challenges and Opportunities for Biodiversity Conservation in the Great Plains of North America. *Range. Ecol. Manag.*, https://doi.org/10.1016/j.rama. 2019.09.001.

BEDROSIAN, B. AND D. CRAIGHEAD. 2007. Evaluation of techniques for attaching transmitters to common raven nestlings. *Northwestern Nat.*, **88**:1–6.

BENHAMOU, S. AND D. CORNELIS. 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. *J. Wildl. Manag.*, **74**:1353–1360.

———. 2011. Dynamic approach to space and habitat use based on biased random bridges. *PLoS ONE* **6**:e14592.

BOAL, C. W. AND D. A. HAUKOS. 2016. The lesser prairie-chicken: a brief introduction to the grouse of the southern Great Plains. p. 1–11. *In*: D. A. Haukos and C. W. Boal (eds.). Ecology and conservation of lesser prairie–chickens. CRC Press, Boca Raton, Florida, U.S.A.

BOISVERT, J. H., R. W. HOFFMAN, AND K. P. REESE. 2005. Home range and seasonal movements of Columbian sharp-tailed grouse associated with Conservation Reserve Program and mine reclamation. *West. N. Am. Nat.*, **65**:36–44.

BORSDORF, P. K. 2013. Lesser prairie-chicken habitat selection across varying land use practices in eastern New Mexico and west Texas. Thesis, Texas Tech University, Lubbock, U.S.A. 95 p.

BURGER, L. W. 1988. Survival, movements, and home range of female greater prairie-chickens in relation to prairie distribution in southwest Missouri. Thesis, University of Missouri, Columbia, U.S.A. 107 p.

———, M. R. RYAN, D. P. JONES, AND A. P. WYWIALOWSKI. 1991. Radio transmitters bias estimation of movements and survival. *J. Wildl. Manag.*, **55**:693–697.

CANDELARIA, M. A. 1979. Movements and habitat-use by lesser prairie chickens in eastern New Mexico. Thesis, New Mexico State University, Las Cruces, U.S.A. 45 p.

CALENGE, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.*, **197**:516–519.

COATS, J. 1955. Raising lesser prairie chickens in captivity. Kansas Fish and Game **13**:16–20.

COPELIN, F. F. 1963. The lesser prairie chicken in Oklahoma. Technical Bulletin No. 6, Oklahoma Department of Wildlife Conservation, Oklahoma City, U.S.A.

CRAWFORD, J. A. AND E. G. BOLEN. 1976. Effects of land use on Lesser Prairie Chickens in Texas. *J. Wildl. Manag.*, **40**:96–104.

DAHLGREN, D. K., R. D. ROGERS, R. D. ELMORE, AND M. R. BAIN. 2016. Grasslands of western Kansas, north of the Arkansas River. p. 259–280. *In:* D. A. Haukos and C. W. Boal (eds.). Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, U.S.A.

DZIALAK, M. R., C. V. OLSON, S. M. HARJU, S. L. WEBB, J. P. MUDD, J. B. WINSTEAD, AND L. D. HAYDEN-WING. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. *PLoS One,* **6**:1–19

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.

FIEBERG J. 2007. Kernel density estimators of home range: Smoothing and the autocorrelation red herring. *Ecology*, **88**:1059–1066.

FUHLENDORF, S. D., AND D. M. ENGLE. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience, **51**:625–632.

———, A. J. W. WOODWARD, D. M. LESLIE JR., AND J. S. SHACKFORD. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landsc. Ecol.*, **17**:617–628.

———, W. C. HARRELL, D. M. ENGLE, R. G. HAMILTON, C. A. DAVIS, AND D. M. LESLIE JR. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol. Appl.*, **16**:1706–1716.

GARTON, E. O., C. A. HAGEN, G. M. BEAUPREZ, S. C. KYLE, J. C. PITMAN, D. S. SCHOELING, AND W. E. VAN PELT. 2016. Population dynamics of the lesser prairie-chicken. p. 49–76. *In*: D. A. Haukos and C. W. Boal (eds.). Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, U.S.A.

GEHRT, J. M., D. S. SULLINS, AND, D. A. HAUKOS. 2020. Looking at the bigger picture: how abundance of nesting and brooding habitat influences lek-site selection by lesser prairie-chickens. *Am. Midl. Nat.*, **183**:52–77.

GIRARD, I., J. OUELLET, R. COURTOIS, C. DUSSAULT, AND L. BRETON. 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. *J. Wildl. Manag.*, **66**:1290–1300.

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.

———, 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. *J. Wildl. Manag.*, **78**:857–866.

———, C. W. BOAL, N. R. MITCHELL, T. S. GICKLHORN, P. K. BORSDORF, D. A. HAUKOS, AND C. E. DIXON. 2015. Evaluation of capture techniques on lesser prairie-chicken trap injury and survival. *J. Fish Wildl. Manag.*, **6**:318–326.

———, J. C. ZAVALETA, A. C. BEHNEY, P. K. BORSDORF, D. R. LUCIA, C. W. BOAL, AND D. A. HAUKOS. 2016. Ecology and conservation of lesser prairie-chickens in sand shinnery oak prairie. p. 315–344. *In*:

D. A. Haukos and C. W. Boal (eds.). Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, U.S.A.

HAGEN, C. A., AND K. M. GIESEN. 2005. Lesser prairie-chicken. Account 364. *In*: A. Poole (ed.). The birds of North America. Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A. <https://birdsna.org/Species-Account/bna/species/lepchi>. Accessed 5 June 2020.

———, 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. *J. Wildl. Manag.*, **73**:1325–1332.

———, 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. p. 63–75. *In*: B. K. Sandercock, K. Martin, and G. Segelbacher (eds). Ecology, conservation, and management of grouse. Studies in Avian Biology 39, University of California Press, Berkeley, California, U.S.A.

———, D. C. PAVLACKY, K. ADACHI, F. E. HORNSBY, T. J. RINTZ, AND L. L. MCDONALD. 2016. Multiscale occupancy modeling provides insights into range-wide conservation needs of lesser prairie-chicken (*Tympanuchus pallidicinctus*). *Condor*, **118**:597–612.

———, E. O. GARTON, G. BEAUPREZ, B. S. COOPER, K. A. FRICKE, AND B. SIMPSON. 2017. Lesser prairie-chicken population forecasts and extinction risks: an evaluation 5 years post–catastrophic drought. *Wildl. Soc. Bull.*, **41**:624–638.

HAMERSTROM, JR. F. N. AND F. HAMERSTROM. 1949. Daily and seasonal movements of Wisconsin prairie chickens. *Auk*, **66**:313–337.

HAUKOS, D. A., L. M. SMITH, AND G. S. BRODA. 1990. Spring trapping of lesser prairie-chickens (captura durante la primavera de individuos de *Tympanuchus pallidicinctus*). *J. Field Ornithol.*, **61**:20–25.

———. 2011. Use of tebuthiuron to restore sand shinnery oak grasslands of the Southern High Plains. p. 103–124. *In*: M. Naguib and A. E. Hasaneen (eds.). Herbicide: mechanisms and mode of action. Intech, Rijeka, Croatia.

——— AND J. C. ZAVALETA. 2016. Habitat. p. 99–132. *In*: D. A. Haukos and C. W. Boal (eds). Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, U.S.A.

HEMSON, G., P. JOHNSON, A. SOUTH, R. KENWARD, R. RIPLEY, AND D. MACDONALD. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel homerange analyses with least-squares cross-validation. *J. Anim. Ecol.*, **74**:455–463.

HOEKSTRA, J. M., T. M. BOUCHER, T. H. RICKETTS, AND C. ROBERTS. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.*, **8**:23–29.

HORNE, J. S., AND E. O. GARTON. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *J. Wildl. Manag.*, **70**:641–648.

JOHNSON, J. A., M. A. SCHROEDER, AND L. A. ROBB. 2020. Greater prairie-chicken (*Tympanuchus cupido*), version 1.0. *In*: A. Poole (ed.). Birds of the World. Cornell Lab of Ornithology, Ithaca, New York, U.S.A. <https://doi-org.er.lib.k-state.edu/10.2173/bow.grpchi.01>. Accessed 26 July 2020.

KNAPP, A. K., J. M. BLAIR, J. M. BRIGGS, S. L. COLLINS, D. C. HARTNETT, L. C. JOHNSON, AND E. G. TOWNE. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience*, **49**:39–50.

LAUTENBACH, J. M. 2015. Lesser prairie-chicken reproductive success, habitat selection, and response to trees. Thesis, Kansas State University, Manhattan, U.S.A. 159 p.

———, D. A. HAUKOS, D. S. SULLINS, C. A. HAGEN, J. D. LAUTENBACH, J. C. PITMAN, R. T. PLUMB, S. G. ROBINSON, AND J. D. KRAFT. 2019. Factors influencing nesting ecology of lesser prairie-chickens. *J. Wildl. Manag.*, **83**:205–215.

LEONARD, J. P. 2008. The effects of shinnery oak removal on lesser prairie chicken survival, movement, and reproduction. Thesis, Texas A&M University, College Station, U.S.A. 50 p.

LEONARD, T. D., P. D. TAYLOR, AND I. G. WARKENTIN. 2008. Landscape structure and spatial scale affect space use by songbirds in naturally patchy and harvested boreal forests. *Condor*, **110**:467–481.

MCDONALD, 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. *Wildl. Soc. Bull.*, **38**:536–546.

MCNEW, L. B., A. J. GREGORY, S. M. WISELY, AND B. K. SANDERCOCK. 2009. Estimating the stage of incubation for nests of greater prairie-chickens using egg flotation: a float curve for grousers. *Grouse News*, **38**:12–14.

MERCHANT, S. S. 1982. Habitat-use, reproductive success, and survival of female lesser prairie-chickens in two years of contrasting weather. Thesis, New Mexico State University, Las Cruces, U.S.A. 72 p.

MILLIGAN, M. C., L. I. BERKELEY, AND L. B. MCNEW. 2020. Habitat selection of female sharp-tailed grouse in grasslands managed for livestock production. *PLoS ONE*, **15**:e0233756.

NORTH AMERICAN BIRD CONSERVATION INITIATIVE. 2016. The State of the Birds 2016 Report. U.S. Department of Interior, Washington, D.C., U.S.A.

PATTEN, M. A., C. L. PRUETT, AND D. H. WOLFE. 2011. Home range size and movements of Greater Prairie-Chickens. *Studies Avian Biol.*, **39**:51–62.

PETERSON, R. S., AND C. S. BOYD. 1998. Ecology and management of sand shinnery communities: a literature review. General Technical Report RMRS-GTR-16. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, U.S.A.

PIRIUS, N. E., C. W. BOAL, D. A. HAUKOS, AND M. C. WALLACE. 2013. Winter habitat use and survival of lesser prairie-chickens in west Texas. *Wildl. Soc. Bull.*, **37**:759–765.

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. *J. Wildl. Manag.*, **69**:1259–1269.

———, C. A. HAGEN, B. E. JAMISON, R. J. ROBEL, T. M. LOUGHIN, AND R. D. APPLEGATE. 2006. Nesting ecology of lesser prairie-chickens in sand sagebrush prairie of southwestern Kansas. *Wilson J. Ornithol.*, **118**:23–35.

———, B. E. JAMISON, C. A. HAGEN, R. J. ROBEL, AND R. D. APPLEGATE. 2006. Brood break-up and juvenile dispersal of lesser prairie-chicken in Kansas. *Prairie Nat.*, **38**:85–99.

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, U.S.A. 150 p.

———, J. M. LAUTENBACH, S. G. ROBINSON, D. A. HAUKOS, V. L. WINDER, C. A. HAGEN, D. S. SULLINS, J. C. PITMAN, AND D. K. DAHLGREN. 2019. Lesser prairie-chicken space use in relation to anthropogenic structures. *J. Wildl. Manag.*, **83**:216–230.

R CORE TEAM. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

RILEY, T. Z., C. A. DAVIS, M. A. CANDELARIA, AND H. R. SUMINSKI. 1994. Lesser prairie-chicken movements and home ranges in New Mexico. *Prairie Nat.*, **26**:183–186.

ROBINSON, S. G., D. A. HAUKOS, R. T. PLUMB, J. M. LAUTENBACH, D. S. SULLINS, J. D. KRAFT, J. D. LAUTENBACH, C. A. HAGEN, AND J. C. PITMAN. 2018a. Nonbreeding home-range size and survival of lesser prairie-chickens. *J. Wildl. Manag.*, **82**:413–423.

———, ———, ———, J. D. KRAFT, D. S. SULLINS, J. M. LAUTENBACH, J. D. LAUTENBACH, B. K. SANDERCOCK, C. A. HAGEN, A. BARTUSZEVIGE, AND M. A. RICE. 2018b. Effects of landscape characteristics on annual survival of lesser prairie-chickens. *Am. Midl. Nat.*, **180**:66–86.

ROSENBERG, K. V., A. M. DOKTER, P. J. BLANCHER, J. R. SAUER, A. C. SMITH, P. A. SMITH, J. C. STANTON, A. PANJABI, L. HELFT, M. PARR, AND P. P. MARRA. 2019. Decline of the North American avifauna. *Science*, **366**:120–124.

ROSS, B. E., D. A. HAUKOS, C. A. HAGEN, AND J. C. PITMAN. 2016. Landscape composition creates a threshold influencing lesser prairie-chicken population resilience to extreme drought. *Global Ecol. Conserv.*, **6**:179–188.

———, ———, ———, and ———. 2018. Combining multiple sources of data to inform conservation of lesser prairie-chicken populations. *Auk*, **135**:228–239.

———, D. S. SULLINS, AND D. A. HAUKOS. 2019. Using an individual-based model to assess common biases in lek-based count data to estimate population trajectories of lesser prairie-chickens. *PLoS ONE* **14**:e0217172.

SAAB, V. A. AND J. S. MARKS. 1992. Summer habitat use by Columbian sharp-tailed grouse in western Idaho. *Great Basin Nat.*, **52**:166–173.

SAMSON, F., AND F. KNOPF. 1994. Prairie conservation in North America. *BioScience*, **44**:418–421.

SAUER, J. R., AND W. A. LINK. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. *Auk*, **128**:87–98.

SCHROEDER, M. A. 1991. Movement and lek visitation by female greater prairie-chickens in relation to predictions of Bradbury's female preference hypothesis of lek evolution. *Auk*, **108**:896–903.

SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**:2075–2085.

———, J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *J. Wildl. Manag.*, **63**:739–747.

SILVERMAN, B. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, U.K.

SILVY, N. J., M. E. MORROW, E. J. SHANLEY, AND R. D. SLACK. 1990. An improved drop net for capturing wildlife. *Proc. Southeastern Assoc. Fish Wildl. Agencies*, **44**:374–378.

SOUTHWOOD, T. R. E. 1977. Habitat, the templet for ecological strategies? *J. Anim. Ecol.*, **46**:336–365.

SPENCER, D., D. HAUKOS, C. HAGEN, M. DANIELS, AND D. GOODIN. 2017. Conservation Reserve Program mitigates grassland loss in the lesser prairie-chicken range of Kansas. *Global Ecol. Conserv.*, **9**:21–38.

STONEHOUSE, K. F., L. A. SHIPLEY, J. LOWE, M. T. ATAMIAN, M. E. SWANSON, AND M. A. SCHROEDER. 2015. Habitat selection and use by sympatric, translocated greater sage-grouse and Columbian sharp-tailed grouse. *J. Wildl. Manag.*, **79**:1308–1326.

SULLINS, D. D. 2017. Regional variation in demography, distribution, foraging, and strategic conservation of lesser prairie-chickens in Kansas and Colorado. Dissertation, Kansas State University, Manhattan, U.S.A. 256 p.

———, J. D. KRAFT, D. A. HAUKOS, S. G. ROBINSON, J. H. REITZ, R. T. PLUMB, J. M. LAUTENBACH, J. D. LAUTENBACH, B. K. SANDERCOCK, AND C. A. HAGEN. 2018. Demographic Consequences of Conservation Reserve Program Grasslands for Lesser Prairie-Chickens. *J. Wildl. Manag.*, **82**:1617–1632.

———, D. A. HAUKOS, J. M. LAUTENBACH, J. D. LAUTENBACH, S. G. ROBINSON, M. B. RICE, B. K. SANDERCOCK, J. D. KRAFT, R. T. PLUMB, J. H. REITZE, J. M. S. HUTCHINSON, AND C. A. HAGEN. 2019. Strategic conservation for lesser prairie-chickens among landscapes of varying anthropogenic influence. *Biol. Conserv.*, **238**:108213.

TAYLOR, M. A., AND F. S. GUTHERY. 1980. Status, ecology, and management of lesser prairie chicken. USDA Forest Service General Technical Report RM-77. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, U.S.A.

TOOLE, B. E. 2005. Survival, seasonal movements, and cover use by lesser prairie chickens in the Texas panhandle. Thesis, Texas A&M University, College Station, U.S.A. 48 p.

VAN PELT, W. E., S. KYLE, J. C. 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, U.S.A.

WINDER, V. L., K. M. CARRLSON, A. J. GREGORY, C. A. HAGEN, D. A. HAUKOS, 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**:166.

———, L. B. MCNEW, J. C. PITMAN, AND B. K. SANDERCOCK. 2017. Space use of female greater prairie-chickens in response to fire and grazing interactions. *Rang. Ecol. Manag.*, **70**:165–174.

WOODWARD, A. J. W., S. D. FUHLENDORF, D. M. LESLIE, JR., AND J. SHACKFORD. 2001. Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. *Am. Midl. Nat.*, **145**:261–274.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**:164–168.

SUBMITTED 30 JULY 2020 ACCEPTED 8 JANUARY 2021

Appendix Table 1.—Description of study sites including years of data collection, Lesser Prairie-chicken Ecoregion[1], counties, latitude, longitude, total area (km^2)[2], landcover composition (% native grassland, % CRP grassland, % cropland, and % other categories [forest, urban, water])[2,3], contagion values (smaller value = less aggregated landscape)[2], mean patch size (ha)[2], annual precipitation in study counties (mm)[4], range of average daily temperatures in study counties (C)[4], and dominant land uses, flora, and fauna[3]. We used the following data sources: [1] Boal and Haukos, 2016, [2] Robinson *et al.*, 2018, [3] Sullins *et al.*, 2018, [4] Kansas State University 2020, [5] Colorado Climate Center 2020

Study site	Clark	Colorado	Northwest	Red Hills
Years of Data Collection	2014–2015	2013–2015	2013–2015	2013–2018
Ecoregion	Mixed-Grass Prairie	Sand Sagebrush Prairie	Short-Grass Prairie/CRP Mosaic	Mixed-Grass Prairie
Counties	Clark	Baca/Prowers, Cheyenne	Gove, Logan	Comanche/Kiowa
Lat	37.0733	37.6629, 38.6989	38.8539, 38.8183	37.3548
Long	99.8693	102.038, 103.001	100.621, 101.007	99.1204
Total Area (km^2)	712.1	181.1	1,714.4	491.1
% Native Grassland	77.0	28.0, 99.0	54.0, 56.0	87.0
% CRP Grassland	5.5	25.0, 0	8.0, 8.0	2.2
% Cropland	14.0	43.0, 1.0	34.0, 32.0	8.9
% Other	3.5	5.0, 0	3.0, 3.0	1.9
Contagion	60.25	64.09	59.67	66.28
Mean Patch Size (ha) ± SD	34.9 ± 231.7	29.4 ± 231.7	39.5 ± 288.42	32.05 ± 387.3
Precipitation (mm)				
Long-term Average	586.7	402.8, 407.7	523.2, 485.1	646.4
2013	569.0	338.3, 304.0	477.5, 431.8	675.6
2014	579.1	419.6, 400.3	556.3, 553.7	642.6
2015	815.3	610.9, 471.2	538.5, 551.2	776.0
2016	-	-	-	640.1
2017	-	-	-	589.3
2018	-	-	-	809.0
Range of Long-term Monthly Average Temperatures (C)	0.8–27.0	1.2–25.4, 2.4–24.0	1.0–25.7, 1.1–25.4	0.4–26.8
Dominant Land Uses	livestock grazing with, extraction of fossil fuels, row-crop agriculture	Livestock grazing, CRP-grasslands, row-crop agriculture	livestock grazing, energy extraction, row-crop agriculture	livestock grazing with, extraction of fossil fuels, row-crop agriculture

APPENDIX TABLE 1.—Continued

Study site	Clark	Colorado	Northwest	Red Hills
Dominant Flora	sand dropseed (*Sporobolus cryptandrus*), western ragweed (*Ambrosia psilostachya*), blue grama (*Bouteloua gracilis*), Russian thistle (*Salsola tragus*), little bluestem (*Schizacyrim scoparium*), alkalai sacaton (*Sporobolus airoides*), sand sagebrush (*Artemisia filifolia*)	blue grama, hairy grama (*Bouteloua hirsuta*), sideoats grama (*Bouteloua. curtipendula*), little bluestem, sand sagebrush, kochia (*Bassia scoparia*), Russian thistle	blue grama, sideoats grama, sand dropseed, little bluestem, broom snakeweed (*Gutierrezia sarothrae*), and purple three-awn (*Aristida purpurea*)	little bluestem, Louisiana sagewort (*Artemisia ludoviciana*), sideoats grama, western ragweed, sand dropseed, cheatgrass (*Bromus tectorum*), and blue grama
Dominant Fauna	coyote (*Canis latrans*), American badger (*Taxidea taxus*), red-tailed hawk (*Buteo jamaicensis*), northern harrier (*Circus cyaneus*)	coyote, swift fox (*Vulpes velox*), striped skunk (*Mephitis mephitis*), American badger, northern harrier, red-tailed hawk	Coyote, swift fox, northern harrier, Swainson's hawk (*Buteo swainsoni*)	coyote, red-tailed hawk, northern harrier

SUPPLEMENTAL LITERATURE CITED

BOAL, C. W. AND D. A. HAUKOS. 2016. The lesser prairie-chicken: a brief introduction to the grouse of the southern Great Plains. p.1–14. *In:* D. A. Haukos and C. W. Boal (eds.). Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, U.S.A.

Colorado Climate Center. 2020. <https://climate.colostate.edu/>. Accessed 2 June 2020.

Kansas State University. 2020. Monthly Precipitation Maps. <http://climate.k-state.edu/precip/county/>. Accessed 2 June 2020.

ROBINSON, S. G., D. A. HAUKOS, R. T. PLUMB, J. M. LAUTENBACH, D. S. SULLINS, J. D. KRAFT, J. D. LAUTENBACH, C. A. HAGEN, AND J. C. PITMAN. 2018. Nonbreeding home-range size and survival of lesser prairie-chickens. J. Wildl. Manage. **82**:413–423.

SULLINS, D. S., J. D. KRAFT, D. A. HAUKOS, S. G. ROBINSON, J. H. REITZ, R. T. PLUMB, J. M. LAUTENBACH, J. D. LAUTENBACH, B. K. SANDERCOCK, AND C. A. HAGEN. 2018. Demographic Consequences of Conservation Reserve Program Grasslands for Lesser Prairie-Chickens. J. Wildl. Manage., **82**:1617–1632.

Appendix Table 2.—Annual variation in home range areas of female lesser prairie-chickens (*Tympanuchus pallidicinctus*) captured in Kansas and Colorado, U.S.A., and equipped with GPS or very-high-frequency (VHF) transmitters during 2013–2018. Shown are means (ha) and standard errors split by breeding stage and for the entire breeding season. Sample sizes are displayed within brackets

Site	2013	2014	2015	2016	2017	2018	All Years
GPS – Lekking/Prelaying							
Clark	.	209.5 ± 42.3 (13)	125.5 ± 22.5 (8)	.	.	.	177.5 ± 28.5 (21)
Colorado	270.4 ± 95.1 (4)	.	316.0 ± 40.6 (2)	.	.	.	285.6 ± 61.8 (6)
Northwest	346.8 ± 48.1 (26)	272.2 ± 45.1 (13)	661.6 ± 175.1 (11)	.	.	.	396.7 ± 50.4 (50)
Red Hills	128.5 ± 17.4 (12)	231.8 ± 38.9 (12)	158.8 ± 25.9 (6)	83.5 ± 12.9 (13)	181.3 ± 50.7 (6)	78.1 ± 23.8 (5)	145.2 ± 13.8 (54)
All Sites	**277.2 ± 34.4 (42)**	**238.0 ± 24.2 (38)**	**365.4 ± 85.3 (27)**	**83.5 ± 12.9 (13)**	**181.3 ± 50.7 (6)**	**78.1 ± 23.8 (5)**	**252.8 ± 23.0 (131)**
GPS – Nesting							
Clark	.	102.6 ± 16.1 (11)	77.5 ± 16.5 (8)	.	.	.	92.0 ± 11.7 (19)
Colorado	123.4 ± 25.4 (4)	153.6 (1)	346.7 ± 124.6 (3)	.	.	.	210.9 ± 58.3 (8)
Northwest	198.6 ± 28.8 (13	347.6 ± 110.8 (12)	433.1 ± 123.2 (8)	.	.	.	309.6 ± 52.4 (33)
Red Hills	88.5 ± 13.3 (10)	135.4 ± 24.3 (13)	98.1 ± 15.4 (7)	63.8 ± 9.8 (8)	111.0 ± 30.0 (6)	68.6 ± 12.6 (4)	99.6 ± 9.1 (48)
All Sites	**146.7 ± 17.9 (27)**	**194.9 ± 40.3 (37)**	**223.5 ± 50.3 (26)**	**63.8 ± 9.8 (8)**	**111.0 ± 30.0 (6)**	**68.6 ± 12.6 (4)**	**170.7 ± 19.4 (108)**
GPS – Brooding							
Clark	.	50.9 ± 23.8 (4)	125.4 (1)	.	.	.	65.8 ± 23.7 (5)
Colorado	.	.	.	.	.	.	.
Northwest	64.9 (1)	98.2 ± 25.0 (6)	150.4 ± 10.8 (2)	.	.	.	106.1 ± 18.6 (9)
Red Hills	96.0 ± 27.9 (2)	38.7 (1)	48.0 ± 25.9 (3)	50.1 (1)	.	.	60.7 ± 14.8 (7)
All Sites	**85.6 ± 19.2 (3)**	**75.6 ± 17.2 (11)**	**95.0 ± 24.5 (6)**	**50.1 (1)**	**.**	**.**	**81.4 ± 11.5 (21)**
GPS – Postbreeding							
Clark	.	138.6 ± 34.6 (9)	59.6 ± 26.8 (3)	.	.	.	118.9 ± 28.2 (12)
Colorado	259.4 ± 30.3 (4)	.	134.9 ± 9.3 (2)	.	.	.	217.9 ± 32.6 (6)
Northwest	168.7 ± 16.4 (12)	109.2 ± 8.0 (7)	251.8 ± 114.7 (6)	.	.	.	172.0 ± 28.8 (25)
Red Hills	99.0 ± 46.5 (5)	95.5 ± 20.0 (5)	101.9 ± 29.0 (6)	145.1 ± 25.0 (6)	135.9 ± 36.9 (4)	109.0 ± 98.1 (2)	114.9 ± 13.7 (28)
All Sites	**169.4 ± 18.7 (21)**	**118.6 ± 15.7 (21)**	**151.2 ± 43.9 (17)**	**145.1 ± 25.0 (6)**	**135.9 ± 36.9 (4)**	**109.0 ± 98.1 (2)**	**144.4 ± 13.2 (71)**
GPS – Whole Breeding Season							
Clark	.	205.2 ± 27.5 (16)	145.9 ± 30.8 (9)	.	.	.	183.9 ± 21.2 (25)
Colorado	342.3 ± 14.0 (5)	156.9 (1)	420.1 ± 61.9 (3)	.	.	.	347.6 ± 33.1 (9)
Northwest	363.9 ± 40.9 (29)	364.1 ± 112.5 (20)	673.7 ± 160.2 (11)	.	.	.	420.8 ± 52.7 (60)
Red Hills	180.7 ± 20.0 (12)	227.5 ± 34.7 (13)	181.9 ± 28.2 (11)	132.2 ± 24.4 (14)	227.6 ± 61.3 (8)	148.8 ± 32.1 (5)	183.2 ± 13.8 (63)
All Sites	**313.8 ± 28.7 (46)**	**273.6 ± 47.2 (50)**	**352.5 ± 65.8 (34)**	**132.2 ± 24.4 (14)**	**227.6 ± 61.3 (8)**	**148.8 ± 32.1 (5)**	**283.5 ± 23.0 (157)**

APPENDIX TABLE 2.—Continued

Site	2013	2014	2015	2016	2017	2018	All Years
VHF – Whole Breeding Season							
Clark	.	132.9 ± 26.0 (3)	154.4 ± 22.5 (5)	.	.	.	146.3 ± 16.4 (8)
Colorado	.	.	.	.	.	.	.
Northwest	384.2 ± 104.7 (3)	170.0 ± 27.7 (10)	268.1 ± 76.7 (5)	.	.	.	232.9 ± 34.6 (18)
Red Hills	158.8 ± 39.8 (6)	158.5 ± 35.0 (7)	.	.	.	.	158.6 ± 25.2 (13)
All Sites	**233.9 ± 54.6 (9)**	**160.4 ± 18.3 (20)**	**211.3 ± 42.2 (10)**	**.**		**.**	**190.4 ± 19.1 (39)**

APPENDIX TABLE 3.—Annual variation in daily displacements of female lesser prairie-chickens (*Tympanuchus pallidicinctus*) captured in Kansas and Colorado, USA, and equipped with GPS transmitters during 2013–2018. Shown are means (m) and standard errors split by breeding stage and for the entire breeding season. Sample sizes are displayed within brackets

Site	2013	2014	2015	2016	2017	2018	All Years
GPS – Lekking/Prelaying							
Clark	.	464.5 ± 62.2 (13)	429.3 ± 40.6 (8)	.	.	.	451.1 ± 40.9 (21)
Colorado	529.5 ± 77.4 (4)	.	727.1 ± 62.4 (2)	.	.	.	595.4 ± 66.2 (6)
Northwest	596.7 ± 37.6 (26)	615.5 ± 77.4 (13)	683.6 ± 58.8 (11)	.	.	.	620.7 ± 30.6 (50)
Red Hills	452.3 ± 46.8 (12)	626.2 ± 84.3 (12)	531.1 ± 92.0 (6)	422.0 ± 51.6 (13)	588.0 ± 84.8 (6)	294.7 ± 41.7 (5)	492.8 ± 30.7 (54)
All Sites	**549.1 ± 29.0 (42)**	**567.2 ± 43.7 (38)**	**577.6 ± 39.4 (27)**	**422.0 ± 51.6 (13)**	**588.0 ± 84.8 (6)**	**294.7 ± 41.7 (5)**	**539.7 ± 19.5 (131)**
GPS – Nesting							
Clark	.	188.5 ± 30.0 (11)	153.8 ± 30.8 (8)	.	.	.	173.9 ± 21.5 (19)
Colorado	195.6 ± 45.1 (4)	118.3 (1)	389.2 ± 93.0 (3)	.	.	.	258.5 ± 54.0 (8)
Northwest	302.2 ± 72.9 (13)	306.6 ± 62.5 (12)	288.6 ± 41.5 (8)	.	.	.	300.5 ± 37.0 (33)
Red Hills	196.0 ± 24.5 (10)	249.2 ± 28.7 (13)	207.8 ± 47.1 (7)	176.9 ± 29.9 (8)	189.5 ± 19.3 (6)	146.0 ± 27.2 (4)	204.0 ± 13.2 (48)
All Sites	**247.1 ± 37.4 (27)**	**246.2 ± 25.1 (37)**	**237.0 ± 26.2 (26)**	**176.9 ± 29.9 (8)**	**189.5 ± 19.3 (6)**	**146.0 ± 27.2 (4)**	**232.2 ± 14.5 (108)**
GPS – Brooding							
Clark	.	184.4 ± 33.1 (4)	265.9 (1)	.	.	.	200.7 ± 30.4 (5)
Colorado	.	.	.	.	.	.	.
Northwest	195.6 (1)	244.8 ± 26.1 (6)	321.8 ± 50.2 (2)	.	.	.	256.5 ± 23.1 (9)
Red Hills	223.3 ± 8.0 (2)	160.6 (1)	176.0 ± 10.3 (3)	200.6 (1)	.	.	190.8 ± 10.4 (7)
All Sites	**214.1 ± 10.4 (3)**	**215.2 ± 20.4 (11)**	**239.6 ± 32.7 (6)**	**200.6 (1)**	**.**	**.**	**221.3 ± 13.9 (21)**
GPS – Postbreeding							
Clark	.	263.4 ± 34.5 (9)	195.7 ± 30.4 (3)	.	.	.	246.4 ± 27.8 (12)
Colorado	449.7 ± 29.3 (4)	.	314.3 ± 4.8 (2)	.	.	.	404.5 ± 34.0 (6)
Northwest	325.5 ± 20.1 (12)	231.3 ± 33.6 (7)	308.1 ± 35.9 (5)	.	.	.	294.4 ± 17.4 (24)
Red Hills	245.6 ± 28.8 (5)	293.0 ± 43.8 (5)	256.3 ± 34.2 (6)	369.4 ± 36.6 (6)	347.7 ± 68.9 (4)	205.8 ± 82.6 (2)	294.6 ± 19.3 (28)
All Sites	**330.1 ± 20.3 (21)**	**259.7 ± 20.9 (21)**	**268.4 ± 19.9 (16)**	**369.4 ± 36.6 (6)**	**347.7 ± 68.9 (4)**	**205.8 ± 82.6 (2)**	**295.7 ± 11.9 (70)**
GPS – Whole Breeding Season							
Clark	.	284.3 ± 18.4 (16)	275.2 ± 31.7 (9)	.	.	.	281.0 ± 16.0 (25)
Colorado	425.8 ± 33.8 (5)	195.1 (1)	416.5 ± 43.4 (3)	.	.	.	397.1 ± 33.4 (9)
Northwest	500.6 ± 42.1 (29)	422.0 ± 58.5 (20)	468.4 ± 48.1 (11)	.	.	.	468.5 ± 29.4 (60)
Red Hills	312.1 ± 32.9 (12)	360.1 ± 39.7 (13)	311.1 ± 34.5 (11)	318.2 ± 21.8 (14)	331.0 ± 31.0 (8)	235.2 ± 38.5 (5)	319.5 ± 13.8 (63)
All Sites	**443.3 ± 30.3 (46)**	**357.3 ± 27.3 (50)**	**361.8 ± 24.9 (34)**	**318.2 ± 21.8 (14)**	**331.0 ± 31.0 (8)**	**235.2 ± 38.5 (5)**	**374.8 ± 14.3 (157)**

APPENDIX TABLE 4.—Annual variation in the standard deviation of daily displacements of female lesser prairie-chickens (*Tympanuchus pallidicinctus*) captured in Kansas and Colorado, U.S.A., and equipped with GPS transmitters during 2013–2018. Shown are mean standard deviations (m) and standard errors split by breeding stage and for the entire breeding season. Sample sizes are displayed within brackets

Site	2013	2014	2015	2016	2017	2018	All Years
GPS – Lekking/Prelaying							
Clark	.	478.5 ± 56.4 (13)	432.4 ± 54.2 (8)	.	.	.	461.0 ± 40.0 (21)
Colorado	429.6 ± 80.8 (4)	.	521.7 ± 169.0 (2)	.	.	.	460.3 ± 70.0 (6)
Northwest	562.9 ± 49.9 (26)	586.6 ± 70.7 (13)	640.5 ± 77.1 (11)	.	.	.	586.1 ± 35.6 (50)
Red Hills	397.8 ± 76.4 (12)	610.5 ± 102.9 (12)	543.4 ± 113.5 (6)	473.0 ± 70.8 (13)	615.2 ± 172.9 (6)	352.7 ± 75.6 (5)	499.3 ± 41.1 (54)
All Sites	**503.1 ± 39.7 (42)**	**557.2 ± 44.6 (38)**	**548.5 ± 45.7 (27)**	**473.0 ± 70.8 (13)**	**615.2 ± 172.9 (6)**	**352.7 ± 75.6 (5)**	**524.5 ± 23.1 (131)**
GPS – Nesting							
Clark	.	211.7 ± 17.6 (11)	237.8 ± 43.2 (8)	.	.	.	222.7 ± 20.3 (19)
Colorado	319.0 ± 39.2 (4)	220.4 (1)	623.6 ± 48.0 (3)	.	.	.	420.9 ± 65.1 (8)
Northwest	361.3 ± 62.0 (13)	436.3 ± 71.9 (12)	419.2 ± 86.8 (8)	.	.	.	402.6 ± 40.6 (33)
Red Hills	241.0 ± 21.6 (10)	282.0 ± 26.1 (13)	266.1 ± 35.7 (7)	219.2 ± 28.0 (8)	263.8 ± 9.9 (6)	214.9 ± 55.4 (4)	252.8 ± 11.8 (48)
All Sites	**310.5 ± 32.5 (27)**	**309.5 ± 29.2 (37)**	**345.8 ± 39.3 (26)**	**219.2 ± 28.0 (8)**	**263.8 ± 9.9 (6)**	**214.9 ± 55.4 (4)**	**305.7 ± 16.4 (108)**
GPS – Brooding							
Clark	.	134.4 ± 25.5 (4)	257.0 (1)	.	.	.	158.9 ± 31.5 (5)
Colorado	.	.	.	.	.	.	.
Northwest	228.1 (1)	216.7 ± 27.7 (6)	259.3 ± 3.3 (2)	.	.	.	227.4 ± 18.9 (9)
Red Hills	185.0 ± 9.8 (2)	137.9 (1)	130.5 ± 12.4 (3)	203.8 (1)	.	.	157.6 ± 13.2 (7)
All Sites	**199.4 ± 15.4 (3)**	**179.6 ± 21.1 (11)**	**194.5 ± 29.2 (6)**	**203.8 (1)**	**.**	**.**	**187.8 ± 13.6 (21)**
GPS – Postbreeding							
Clark	.	359.5 ± 100.7 (9)	158.6 ± 29.1 (3)	.	.	.	309.3 ± 79.1 (12)
Colorado	420.1 ± 63.4 (4)	.	330.9 ± 15.9 (2)	.	.	.	390.3 ± 44.5 (6)
Northwest	367.7 ± 37.4 (12)	216.2 ± 29.0 (7)	354.8 ± 93.5 (5)	.	.	.	320.8 ± 30.2 (24)
Red Hills	207.5 ± 20.0 (5)	391.1 ± 143.1 (5)	299.5 ± 73.0 (6)	430.2 ± 77.5 (6)	412.3 ± 95.8 (4)	270.8 ± 131.6 (2)	341.5 ± 38.0 (28)
All Sites	**339.5 ± 29.4 (21)**	**319.2 ± 55.4 (21)**	**294.3 ± 41.7 (16)**	**430.2 ± 77.5 (6)**	**412.3 ± 95.8 (4)**	**270.8 ± 131.6 (2)**	**333.1 ± 22.8 (70)**
GPS – Whole Breeding Season							
Clark	.	386.2 ± 35.2 (16)	352.4 ± 50.7 (9)	.	.	.	374.1 ± 28.5 (25)
Colorado	415.3 ± 43.8 (5)	261.3 (1)	542.5 ± 69.0 (3)	.	.	.	440.6 ± 43.0 (9)
Northwest	536.2 ± 43.2 (29)	475.1 ± 57.1 (20)	583.7 ± 71.9 (11)	.	.	.	524.5 ± 31.1 (60)
Red Hills	348.9 ± 52.7 (12)	482.3 ± 68.8 (13)	361.0 ± 49.1 (11)	415.7 ± 46.7 (14)	405.6 ± 48.0 (8)	339.8 ± 46.6 (5)	399.9 ± 23.2 (63)
All Sites	**474.2 ± 32.9 (46)**	**444.3 ± 31.3 (50)**	**446.8 ± 35.9 (34)**	**415.7 ± 46.7 (14)**	**405.6 ± 48.0 (8)**	**339.8 ± 46.6 (5)**	**445.7 ± 16.6 (157)**

The Journal of Wildlife Management 85(2):354–368; 2021; DOI: 10.1002/jwmg.21984

Research Article

Using Grazing to Manage Herbaceous Structure for a Heterogeneity-Dependent Bird

JOHN D. KRAFT, *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
DAVID A. HAUKOS,[1] *U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan, KS 66506, USA*
MATTHEW R. BAIN, *Kansas Chapter of The Nature Conservancy, Smoky Valley Ranch, Oakley, KS 67748, USA*
MINDY B. RICE, *U.S. Fish and Wildlife Service, National Wildlife Refuge System, Fort Collins, CO 80525, USA*
SAMANTHA ROBINSON,[2] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
DAN S. SULLINS,[3] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
CHRISTIAN A. HAGEN, *Department of Fisheries and Wildlife, Oregon State University, Bend, OR 97702, USA*
JAMES PITMAN,[4] *Conservation Delivery Director, Western Association of Fish and Wildlife Agencies, Emporia, KS 66801, USA*
JOSEPH LAUTENBACH,[5] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
REID PLUMB,[6] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
JONATHAN LAUTENBACH,[7] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

ABSTRACT Grazing management recommendations often sacrifice the intrinsic heterogeneity of grasslands by prescribing uniform grazing distributions through smaller pastures, increased stocking densities, and reduced grazing periods. The lack of patch-burn grazing in semi-arid landscapes of the western Great Plains in North America requires alternative grazing management strategies to create and maintain heterogeneity of habitat structure (e.g., animal unit distribution, pasture configuration), but knowledge of their effects on grassland fauna is limited. The lesser prairie-chicken (*Tympanuchus pallidicinctus*), an imperiled, grassland-obligate, native to the southern Great Plains, is an excellent candidate for investigating effects of heterogeneity-based grazing management strategies because it requires diverse microhabitats among life-history stages in a semi-arid landscape. We evaluated influences of heterogeneity-based grazing management strategies on vegetation structure, habitat selection, and nest and adult survival of lesser prairie-chickens in western Kansas, USA. We captured and monitored 116 female lesser prairie-chickens marked with very high frequency (VHF) or global positioning system (GPS) transmitters and collected landscape-scale vegetation and grazing data during 2013–2015. Vegetation structure heterogeneity increased at stocking densities $\leq$0.26 animal units/ha, where use by nonbreeding female lesser prairie-chickens also increased. Probability of use for nonbreeding lesser prairie-chickens peaked at values of cattle forage use values near 37% and steadily decreased with use $\geq$40%. Probability of use was positively affected by increasing pasture area. A quadratic relationship existed between growing season deferment and probability of use. We found that 70% of nests were located in grazing units in which grazing pressure was <0.8 animal unit months/ha. Daily nest survival was negatively correlated with grazing pressure. We found no relationship between adult survival and grazing management strategies. Conservation in grasslands expressing flora community composition appropriate for lesser prairie-chickens can maintain appropriate habitat structure heterogeneity through the use of low to moderate stocking densities (<0.26 animal units/ha), greater pasture areas, and site-appropriate deferment periods. Alternative grazing management

Received: 21 April 2020; Accepted: 2 October 2020

---

[1] *E-mail: dhaukos@ksu.edu*
[2] *Current affiliation: Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*
[3] *Current affiliation: Department of Horticulture and Natural Resources, Kansas State University, KS 66506, USA*
[4] *Current affiliation: National Wild Turkey Federation, Emporia, KS 66801, USA*
[5] *Current affiliation: Ohio Department of Natural Resources, 2045 Morse Road, Columbus, OH 43229, USA*
[6] *Current affiliation: Voyageurs National Park, 360 MN-11, International Falls, MN 56649, USA*
[7] *Current affiliation: Department of Ecosystem Science and Management, University of Wyoming, 1000 E. University Avenue, Laramie, WY 82071, USA*

strategies (e.g., rest-rotation, season-long rest) may be appropriate in grasslands requiring greater heterogeneity or during intensive drought. Grazing management favoring habitat heterogeneity instead of uniform grazing distributions will likely be more conducive for preserving lesser prairie-chicken populations and grassland biodiversity. © 2021 The Wildlife Society.

KEY WORDS Andersen-Gill, deferment, forage use, grassland heterogeneity, lesser prairie-chicken, pasture area, resource selection function, stocking density, *Tympanuchus pallidicinctus*.

Grasslands are among the most imperiled ecosystems across the globe (Samson et al. 2004, Hoekstra et al. 2005), and extant grasslands are highly susceptible to anthropogenic disturbance with >3.5 million ha managed as pastureland for grazing (Goldewijk 2001). Grazing and periodic fire are the principal keystone drivers in maintenance and enhancement of grassland biodiversity in the Great Plains in North America. Mistargeted grazing practices, however, can negatively affect grassland species diversity, composition, function, and structure (Milchunas et al. 1988, Fleischner 1994, Knapp et al. 1999, Samson et al. 2004). Grazing intensity (i.e., forage use, grazing pressure, stocking rate), classification of grazers (i.e., sex, age, species), and spatiotemporal patterns of grazing are the primary determinants of grazing-associated effects (Fuhlendorf and Engle 2001). Grazing management designed to maximize annual livestock performance (e.g., management for vegetation homogeneity) is potentially harmful to grassland ecosystem function (Fleischner 1994; Hovick et al. 2014, 2015). Although a few wildlife species may benefit from habitat created by homogenous grazing disturbance, it is detrimental to most species, such as grassland birds, reliant on variable vegetation structure at a landscape scale (Knopf 1994). A shift in management strategy towards creating and maintaining landscape heterogeneity (i.e., variation in plant composition and structure) has been proposed to remedy these effects (Fuhlendorf et al. 2006).

The recoupling of fire and grazing (i.e., pyric herbivory) is commonly suggested and implemented as a means of creating landscape heterogeneity (Fuhlendorf et al. 2009), but a cultural pattern of fire suppression has limited the implementation of pyric-herbivory as a management tool in certain geographies (Taylor 2005). Moreover, in semi-arid systems such as the short-grass steppe of northeastern Colorado, USA, patch-burn grazing strategies alone fail to produce adequate nesting habitat for grassland bird species requiring relatively robust herbaceous microhabitat (Augustine and Derner 2015). In the absence of pyric-herbivory, alternative methods for creating structural heterogeneity across spatiotemporal scales, particularly in semi-arid landscapes, may be valuable. Traditional grazing systems tend to create uniform grazing disturbances by increasing stocking density (i.e., number of animal units per unit area), reducing pasture area, and increasing deferment during the growing season (i.e., proportion of growing season [Apr to 1 Oct] in which livestock were absent from a pasture). Thus, reversing these management actions should promote variation in spatiotemporal grazing disturbance and, subsequently, a heterogeneity-based vegetation response to grazing (Fuhlendorf and Engle 2001). A growing body of evidence describes how domestic grazers perceive, interact with, and affect their environment on the Great Plains (Launchbach and Howery 2005, Derner et al. 2009, Allred et al. 2011). Additional insights from experimental design focused on the effects of grazing disturbances on vegetation structure metrics empirically related to a wildlife species resource selection and fitness would also be valuable (Fritts et al. 2018; Smith et al. 2018; Milligan et al. 2020*a*, *b*).

In the Great Plains, prairie grouse are grassland-obligate species that require vegetation heterogeneity across broad landscapes to complete their life cycle (Haukos and Zavaleta 2016, Milligan et al. 2020*a*). Livestock grazing on extant grasslands has the potential to affect habitat quality for prairie grouse through changes in vegetation composition and structure. Previous investigations have assessed prairie grouse response to grazing strategies intended to promote landscape heterogeneity (e.g., patch-burn grazing, rest-rotation grazing) in vegetation relative to traditional grazing strategies (e.g., continuous grazing, annual burning and high intensity grazing) that create vegetation homogeneity across pastures. Milligan et al. (2020*a*, *b*, *c*) reported that rest-rotational grazing did not influence nest success or female survival of sharp-tailed grouse (*Tympanuchus phasianellus*) but found a weak positive relationship with placement of home range during the breeding season. Female greater prairie-chickens (*T. cupido*) monitored on lands managed with patch-burn grazing had annual survival estimates 35% greater than those managed with annual burning and intensive early cattle stocking (Winder et al. 2018). Female greater prairie-chickens monitored at properties managed with patch-burn grazing selected areas with low stocking rates and high fire frequencies but avoided recently burned areas (Winder et al. 2016). Smith et al. (2018) reported equivocal effects of livestock presence and indices of local livestock use on nest-site selection and survival of greater sage-grouse (*Centrocercus urophasianus*). No published studies relate space use, resource selection, and demographics of prairie grouse populations to specific grazing metrics such as intensity, deferment, forage use, and pasture size.

The lesser prairie-chicken (*T. pallidicinctus*) occupies semi-arid grasslands and shrublands of the southwestern Great Plains and requires heterogeneous environments to fulfill all life-stage needs (Fig. 1; Haukos and Zavaleta 2016). In particular, as primary factors influencing population demography, female lesser prairie-chickens transition among

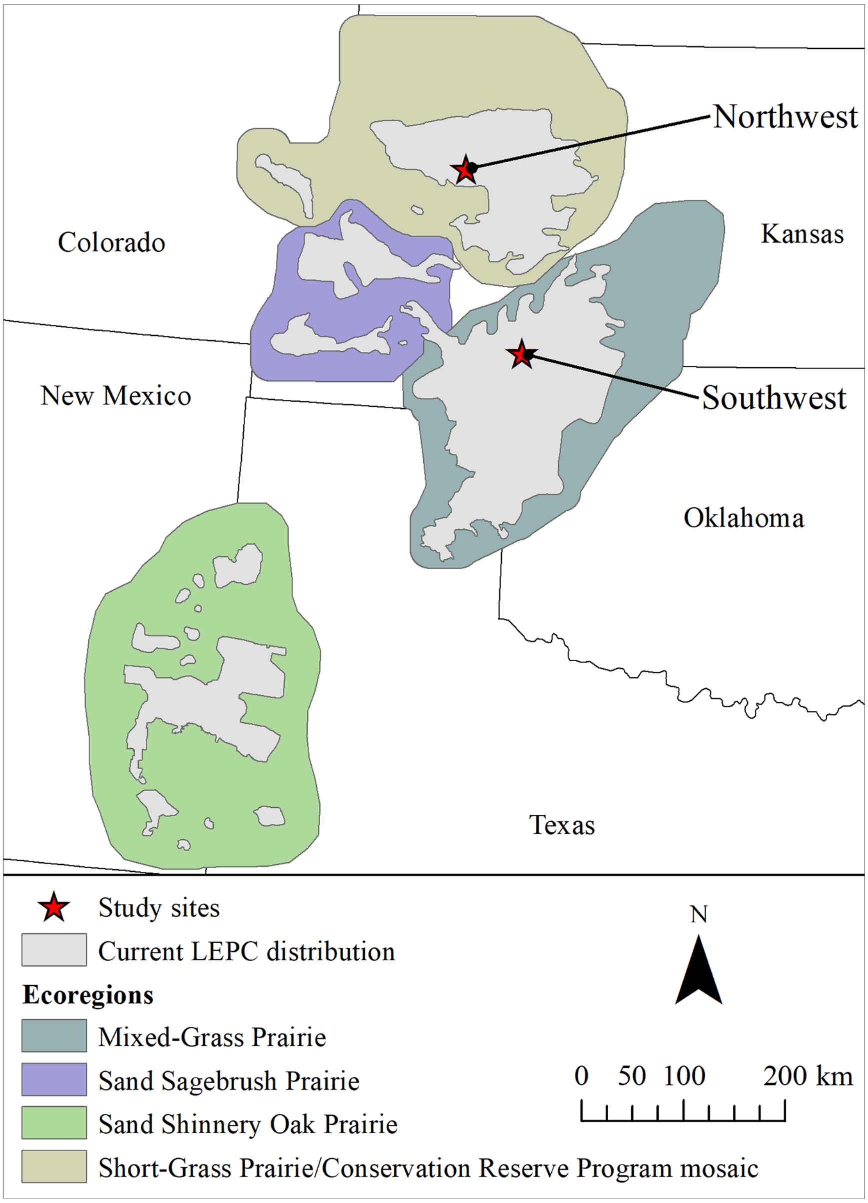


Figure 1. Study area locations where we assessed lesser prairie-chicken (LEPC) population response to livestock grazing from 2013–2015 in relation to lesser prairie-chicken distribution and ecoregions in the Southern Great Plains, USA (McDonald et al. 2014). The Northwest study area was located within Logan and Gove counties, Kansas, USA, and the Southwest study area was located within Clark County, Kansas.

a wide range of vegetation composition and structure types across all reproductive states (Hagen et al. 2009, 2013; Lautenbach 2015; Haukos and Zavaleta 2016; Lautenbach et al. 2019). When grazing management objectives are conceptualized with a goal of creating lesser prairie-chicken microhabitat, recommendations often include creation of habitat heterogeneity to accommodate nesting and brooding habitat needs by referencing a range of structural vegetation metrics (e.g., visual obstruction, height, and canopy cover; Fritts et al. 2016, Haukos and Zavaleta 2016, Lautenbach et al. 2019). Typically, a negative relationship between lesser prairie-chicken habitat quality and grazing disturbance is assumed, with recommendations generally including a light to moderate stocking rate or forage use (e.g., 33–50%; Hagen et al. 2004, Kansas Natural Resources Conservation Service 2014). Short-duration grazing at moderate grazing intensity (~50% forage use) was benign or beneficial to lesser prairie-chicken nesting ecology and adult survival, respectively, in sand shinnery oak (*Quercus havardii*) ecosystems of southeastern New Mexico, USA (Fritts et al. 2016, 2018). The effectiveness of managed grazing to create landscape heterogeneity, conditional on regional variation in precipitation, soils, and vegetation productivity, for conservation of lesser prairie-chickens on private lands is poorly understood (Giesen 1994, Hagen and Elmore 2016, Hagen et al. 2017).

Grazing management prescriptions developed to enhance lesser prairie-chicken habitat may influence management of livestock operations. Landowner incentive programs such as the Lesser Prairie-Chicken Initiative through the United States Department of Agriculture Natural Resources

Conservation Service and Western Association of Fish and Wildlife Agencies Range-wide Conservation Plan targeted potential monetary gaps between livestock production and grazing management to improve lesser prairie-chicken habitat (Van Pelt et al. 2013). Assessing the ability for heterogeneity-based grazing management to balance lesser prairie-chicken habitat and livestock production goals would be useful to optimize cost-effectiveness of future conservation efforts on private working lands.

Our objectives were to evaluate how heterogeneity-based grazing influenced vegetation structure in semi-arid environments, and could be used to manage habitat for female lesser prairie-chickens. We predicted that larger pastures, exhibiting reduced stocking densities and deferment periods, would contain the greatest habitat heterogeneity at the pasture scale. We hypothesized that lesser prairie-chickens would respond differentially to variation in grazing disturbance. We predicted a nonlinear relationship between probability of use and increasing grazing pressure. We predicted a positive relationship between female lesser prairie-chicken resource use (nonbreeding space use and nest-site selection) and larger pastures, decreased stocking density, and shorter deferment period. Third, we predicted that nest survival and adult female survival would mirror relationships between habitat use and grazing management.

STUDY AREA

Our research was concentrated on portions of 3 large ranches located in 2 distinct areas of the Short-Grass Prairie/Conservation Reserve Program (CRP) Mosaic Ecoregion (i.e., Northwest) and confluence of the Sand Sagebrush Prairie and Mid-Grass Prairie (i.e., Southwest) ecoregions where densities of lesser prairie-chickens were relatively high in western Kansas, USA, during 2013–2015 (Fig. 1; McDonald et al. 2014). The Northwest study area was focused on 2 study sites dominated by private land within Logan and Gove counties in northwest Kansas (~785 m elevation). Topography included numerous draws, ravines, and wooded riparian areas intersecting a relatively level landscape. The Southwest study area was located on private lands south of Ashland, Kansas, within Clark County (~615 m elevation). Topography was primarily flat with little change in elevation, and included the Cimarron river on the southern edge of the study area. The ranches comprised 25,259 ha, of which we included 13,398 ha in 33 pastures in this study. Primary land uses for both study areas were livestock grazing, energy exploration and extraction, and both dryland and irrigated row-crop agriculture. Conservation Reserve Program grasslands and row-crop agriculture were more abundant in Northwest than Southwest (Robinson et al. 2018). In the Northwest study area, mean annual precipitation was 48.7 cm with an overall average annual temperature of 11.1°C. Average annual maximum temperature was 20.0°C and average annual minimum temperature was 2.1°C (United States Climate Data, http://usclimatedata.com, accessed 15 Jan 2018). Annual precipitation during the 2013–2015 study period was similar to the long-term average: 45.0, 55.1, and 49.4 cm, respectively. The Southwest study area had a mean annual precipitation of 61.8 cm with an overall average annual temperature of 13.3°C. Average annual maximum temperature was 21.3°C and average annual minimum temperature was 5.2°C (United States Climate Data, http://usclimatedata.com, accessed 15 Jan 2018). Annual precipitation during the 2013–2015 study period was slightly less than the long-term average in 2013 (41.0 cm), similar to the long-term average in 2014 (59.7 cm), and slightly greater than the long-term average in 2015 (78.7 cm). Primary occurrence of precipitation was from April to August as thunderstorms, with occasional precipitation as frontal events during fall (Sep–Dec). Winter was usually dry and windy with occasional snow events.

Predominant soil and community types (ecological sites) in the Northwest study area included limy upland, loamy upland, chalk flats, and loamy lowland. The Southwest study area was dominated by saline subirrigated, subirrigated, sandy, and sands sites. Dominant grasses in the Northwest study area included blue grama (*Bouteloua gracilis*), buffalograss (*B. dactyloides*), and western wheatgrass (*Pascopyrum smithii*). In addition to blue grama, dominant grasses in the Southwest study area were alkali sacaton (*Sporobolous airoides*) and sand dropseed (*S. cryptandrus*). Dominant fauna in the Northwest study site consisted of coyote (*Canis latrans*), swift fox (*Vulpes velox*), striped skunk (*Mephitis mephitis*), northern harrier (*Circus cyaneus*), Swainson's hawk (*Buteo swainsoni*), red-tailed hawk (*Buteo jamaicensis*), ring-necked pheasant (*Phasianus colchicus*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Dominant fauna in the Southwest study site consisted of coyote, striped skunk, American badger (*Taxidea taxus*), northern harrier, red-tailed hawk, ring-necked pheasant, and white-tailed deer.

METHODS

Capture and Bird Locations

We used walk-in funnel traps and drop nets to capture female lesser prairie-chickens on leks during spring (mid-Mar through mid-May) of 2013–2015 (Haukos et al. 1990, Silvy et al. 1990). We fitted captured females with either a very high frequency (VHF) radio-transmitter or global positioning system (GPS) satellite-transmitter (platform transmitting terminals [PTT]). We attached VHF transmitters (12 g or 15 g) with an estimated battery life of 790 days using a bib-style harness to individuals >500 g (Advanced Telemetry Systems, Isanti, MN, USA). We fitted solar-powered GPS-PTT (22 g, PTT-100, Microwave Telemetry, Columbia, MD, USA) transmitters to females weighing >700 g using a rump-style harness method (Dzialak et al. 2011). We released marked lesser prairie-chickens at the lek of capture. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocol 3241) and Kansas Department of Wildlife, Parks and

Tourism scientific wildlife permits (SC-042-2013, SC-079-2014, SC-001-2015).

We monitored radio-tagged birds from March 2013 through February 2016. We located VHF-fitted females using fixed-location triangulation 3–4 times/week throughout the lifespan of the bird or transmitter (Cochran and Lord 1963). We used handheld receivers and 3-element Yagi antennae to collect ≥3 bearings/location. We entered telemetry bearings into Location of a Signal software (Ecological Software Solutions, Hegymagas, Hungary) to obtain Universal Transverse Mercator coordinates of the estimated location. We generally limited error polygons of each estimated bird location to 0.1 ha. We monitored status of each VHF-tagged female via an 8-hour mortality switch installed in the transmitter. We obtained fixes of GPS-PTT locations every 2 hours during 0600–2400 (depending on sunlight and battery charge). Recorded GPS fixes uploaded to ARGOS satellites every 3 days. Potential error of these points was <18 m. If we obtained a mortality signal, we used either homing (VHF) or previous GPS locations to locate the transmitter and identify cause-specific mortality or another reason for transmitter loss.

Grazing Management Information

Fifty-five pastures across the 3 ranches represented a gradient of grazing intensities and management strategies available to relatively high densities of lesser prairie-chickens. For functionality and efficiency, ranch managers within our study sites generally rotated cattle through pastures while keeping animal units (i.e., herd size) and forage consumption goals constant (e.g., 50% forage use for all pastures). Producers provided grazing management records of animal class (e.g., female and calf, male) herd size, average mass, and grazing duration in each pasture. We delineated pasture boundaries and calculated area (ha) for each pasture using the calculate geometry tool in ArcGIS 10.2 (Esri, Redlands, CA, USA).

We categorized 3 metrics in grazing management as indicators of potential increased within-pasture microhabitat heterogeneity: increased pasture size, decreased stocking density, and shorter period of livestock deferment during the growing season. Collectively, we defined implementation of these patterns as heterogeneity-based grazing management. We used recorded grazing data and pasture area calculations to determine grazing pressure (animal unit months/ha [AUM/ha]), stocking density (animal unit/ha [AU/ha]), and deferment (proportion of growing season in which cattle were absent [Apr–Sep]). We calculated grazing pressure at weekly intervals during each grazing period for each year.

In conjunction with pasture boundaries, we created ecological site maps using ArcGIS 10.2 (U.S. Department of Agriculture [USDA] 2013). We estimated the area (ha) within each pasture occupied by unique ecological sites (USDA 2013). We obtained expected average annual forage production estimates from state and transition models unique to each defined ecological site (USDA 2013). We estimated the expected forage available in each pasture by multiplying the area (ha) of each unique ecological site by the average predicted annual forage production (kg/ha). We summed each unique ecological site present within a given pasture to obtain an estimate for available forage expected during average precipitation conditions. This would be the likely approach to estimate available forage by producers with large ranches and multiple grazing units. Using grazing pressure calculations, we determined forage consumption estimates for each pasture based on an expected forage efficiency of 50% and a consumption rate of 363 kg/month/1.0 AU (454-kg female; Holechek et al. 1989). To estimate forage use for each pasture, we multiplied the forage consumption estimate by 2 (to account for the destruction of forage via trampling, urinating, and defecating) and divided by the expected available forage. We estimated forage use values at weekly intervals during grazing periods to provide a cumulative measure of disturbance as grazing events progressed. Summary of the spatial and temporal scale for grazing variables are available online in Supporting Information (Table S1).

Vegetation Heterogeneity

To determine effects of vegetation heterogeneity on selection by lesser prairie-chickens, we conducted standardized vegetation surveys at each ranching operation using 33 existing pastures as experimental units with an average area of 406 ha (Table S2, available online in Supporting Information). We completed surveys during October to March 2014–2015. We either randomly generated vegetation survey points within monitored pasture units (i.e., available) using the create random points tool in ArcGIS 10.2 or randomly selected points from a pool of locations obtained from marked female lesser prairie-chickens. All survey points were limited to grassland pastures in which we collected grazing management data.

At each survey point, we recorded a 100% visual obstruction reading (VOR; the maximum height in cm completely visually obscured by vegetation) in each cardinal direction using a Robel pole at plot center from a distance of 4 m and height of 1 m (Robel et al. 1970). We recorded the tallest vegetation present within a 60 × 60-cm quadrat located at plot center, and 4 m out from plot center in each cardinal direction (Daubenmire 1959).

We then binned averaged readings for each survey point with others of identical sampling period and pasture. Secondarily, we calculated the mean, coefficient of variation, and standard deviation of 100% VOR (cm) and vegetation height (cm) across each bin of survey points (binned by pasture). We also calculated grazing management components (grazing pressure, forage use, stocking density, pasture area, deferment) for each pasture and paired components with the appropriate vegetation calculations. We did not perform vegetation surveys in a given pasture until grazing was completed for the year. For each grazing management component, we divided survey points into 2 groups: above the median and below the median. We used 2-sample *t*-tests to compare vegetation values above and below the median for each grazing management component. We set $\alpha = 0.05$.

Nonbreeding Habitat and Nest-Site Selection

We evaluated habitat selection during 2013–2016 using mixed-effect resource selection functions (RSF; Boyce et al. 2002, Manly et al. 2002, Gillies et al. 2006). We employed RSFs to evaluate nonbreeding habitat (Oct–Mar) and nest-site selection by female lesser prairie-chickens. Each RSF incorporated a used versus available study design limited to contiguous portions of each ranch with available grazing data (Boyce et al. 2002, Manly et al. 2002).

For each nonbreeding RSF, we distributed 1 random location for each time- and date-stamped lesser prairie-chicken location using the create random points tool in ArcGIS 10.2. We constrained random locations to pastures within each study site to facilitate comparison among used and available pastures. Within study sites, pastures were well within the average dispersal distance of lesser prairie-chickens (~16 km) and therefore available (Earl et al. 2016). The development of RSF model sets was a 2-fold process. First, we developed a nonbreeding RSF model set to establish baseline habitat selection response of nonbreeding females to the intensity of grazing observed within our study sites. Second, we evaluated effects of heterogeneity-based grazing management strategies in the context of increasing grazing intensity. The grazing intensity model set included linear and nonlinear (quadratic) predictors of grazing pressure (AUM/ha) and forage use (%). We included the grazing intensity variable found to be the most influential in nonbreeding habitat selection in all secondary model sets as important context to interpreting the multifaceted response of female lesser prairie-chickens to grazing. Additionally, we suspected the inclusion of an objective grazing intensity metric in secondary model sets would be essential for applicable interpretation of results. We developed 3 secondary model sets (1 for each heterogeneity-based management strategy) to investigate our questions and hypotheses regarding linear and nonlinear predictors of deferment, stocking density, and pasture area. These will be referred to individually as the deferment, stocking density, and pasture area models.

Our nest dataset for testing included nest locations from successful (≥1 egg hatched/nest) and unsuccessful (failed nest or no recorded nest attempt) breeders. Because of our limited sample of nests due to the lag effect of grazing factors affecting nest-site selection (e.g., 2015 nest-site selection in response to grazing practices in 2014), we developed 1 set of models to evaluate nest-site selection. Nests require residual vegetation cover and at the time of nest-site selection, current year grazing disturbance generally has little influence on available nest sites (Hagen et al. 2004). Thus, we assigned grazing management components from the previous year to used and available nest sites. For example, a covariate associated with a nest in May of 2015 describes grazing during the 2014 grazing year (Apr 2014–Mar 2015). The nest-site RSF model set included 17 *a priori* models that evaluated our predictions for grazing disturbance and heterogeneity-based grazing management strategies.

In nonbreeding and nest-site-selection RSFs, we did not include explanatory variables exhibiting a correlation of $|r| > 0.7$ in the same model. We included bird and nest identification as a random effect (random intercept) in nonbreeding RSFs and nest-site selection models, respectively (Gillies et al. 2006). Additionally, we included a random intercept of ranch in all RSF model sets. We z-transformed all continuous variables to address scaling issues among predictors and back-transformed variables for plotting response curves. We included a null (constant) model in each model set. We excluded year and site variables from our model set because the range of grazing intensities represented would have been reduced. We conducted all RSF analyses in Program R (version 3.0.1, R Foundation for Statistical Computing, Vienna, Austria) using the glmer() function within the lme4 package (Bates et al. 2015).

Nest Location and Survival

We identified nest locations by homing in on VHF-marked females after females were in the same relative location for 3 consecutive days (Pitman et al. 2005, Lautenbach et al. 2019). We monitored females marked with GPS-PTTs remotely until GPS locations indicated nest initiation or early incubation. We approached nests wearing rubber boots and latex gloves to reduce possible scent trails. At first nest visit, we flushed the female and floated her eggs to estimate date of incubation (McNew et al. 2009). We monitored each nesting female daily during 2013–2015 until locations indicated that the female had left the nest. We considered nests successful if we found ≥1 egg exhibiting pipping, intact egg membranes, or chicks with females following hatching; otherwise, we classified the nest as unsuccessful.

We used the nest survival model in Program MARK to determine if grazing disturbance influenced nest survival of lesser prairie-chickens (White and Burnham 1999). We tested linear effects of grazing pressure, forage use, stocking intensity, deferment, pasture area, and date of the nesting season on nest survival. We examined correlations of covariates and did not include correlated ($|r| > 0.7$) covariates in the same model. We developed 24 models in an *a priori* model set that tested hypotheses related to grazing management components and daily survival rate, and estimated overall nest survival for an average exposure period of 38 days (Lautenbach et al. 2019).

Adult Survival

We used an Anderson-Gill model to evaluate how continuous, encounter-specific grazing management covariates affect hazard rates for female lesser prairie-chickens throughout the study period (Dinkins et al. 2014). We used Cox proportional hazard models to evaluate the influence of our grazing management strategies (Andersen and Gill 1982). We used all available locations for encounters of VHF-marked lesser prairie-chickens. We randomly selected PTT-marked bird locations at the rate of 1 point per bird per day from 8–10 points available per day. The frequency of locations allowed for modeling of daily survival using a daily encounter history. We randomly selected available locations for each day using the r.sample command in Geospatial Modeling Environment

(Beyer 2012). We used only points and mortalities located within monitored cattle operations. We created an *a priori* model set using predictors of grazing intensity and heterogeneity-based grazing management tools. We limited models to single variables because we recorded few mortalities. We tested model diagnostics with the cox.zph function to determine if these data met assumptions for proportional hazard functions (Fox and Weisberg 2011). Additionally, we used Kaplan-Meier methodology to estimate annual survival (Kaplan and Meier 1958).

For all analyses, we used an information-theoretic approach, Akaike's Information Criterion adjusted for small sample sizes (AIC_c), to rank and select individual models for inference within each model suite (Anderson and Burnham 2002). We considered models with $\Delta AIC_c \leq 2$ to be equally parsimonious. If beta estimates from top models differed from zero (i.e., 95% CIs did not overlap zero), then we determined the variable to be influential and plotted the relative probability of use curve (effects package; Ihaka and Gentleman 1996).

RESULTS

We captured 116 female lesser prairie-chickens during spring 2013–2015. Our pooled nonbreeding VHF and GPS-PTT location dataset included 7,018 nonbreeding lesser prairie-chicken locations and an equal number of random points. Grazing pressure ranged from 0–2.31 AUM/ha ($\bar{x} = 0.47 \pm 0.37$ [SD] AUM/ha). Estimated forage use values ranged from 0–77% ($\bar{x} = 15.0 \pm 12.2\%$). Stocking density ranged from 0–0.96 AU/ha ($\bar{x} = 0.31 \pm 0.25$ AU/ha). Pasture area ranged from 33–736 ha ($\bar{x} = 464.29 \pm 166.69$ ha). Growing season deferment across all locations ranged from 0–100% of the growing season ($\bar{x} = 73.32 \pm 18.41\%$). Density distributions varied between used and available locations for forage use, pasture area, deferment, and stocking density (Fig. 2).

Vegetation Heterogeneity

We sampled 914 random points in 33 pastures ($\bar{x} =$ 27.7 points/pasture) to assess effect of grazing management on vegetation heterogeneity. We calculated means, coefficients of variation, and corresponding standard deviations of visual obstruction (100% cm) and vegetation height (cm) for 2 grazing intensity predictors (grazing pressure and forage use) and 3 heterogeneity-based grazing management tools (stocking density, pasture area, deferment) across 33 pastures; we used 26 pastures for stocking density models during 2 sampling years (Table S2, available online in Supporting Information). As stocking density decreased, vegetation density was more variable (i.e., heterogeneous). Pastures subjected to relatively lower values of stocking density (<0.26 AU/ha) had more heterogeneous vegetation density, exhibiting roughly 40% greater values of standard deviation ($t_{21.067} = 2.79$, $P = 0.01$) and coefficient of variation ($t_{18.89} = 3.17$, $P = 0.005$) for 100% VOR than pastures subjected to relatively greater values of stocking density (>0.26 AU/ha; Fig. 3; Table S3, available online in Supporting Information). We did not detect any other significant relationships during vegetation response analyses.

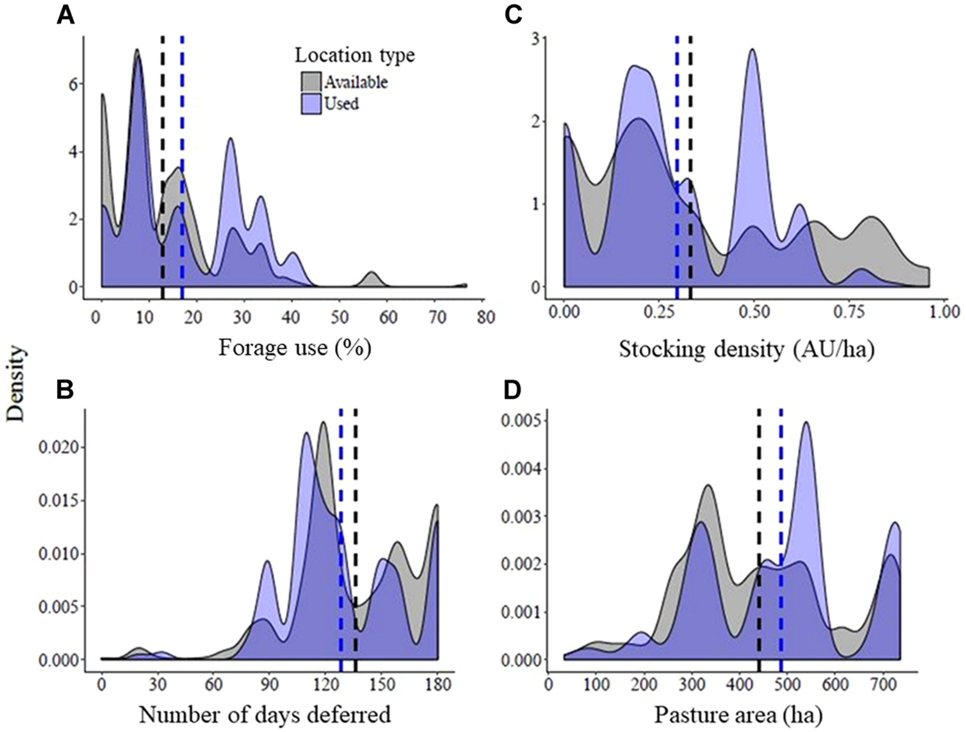


Figure 2. Density distributions of available and used locations obtained for resource selection functions evaluating the influence of grazing management components A) forage use, B) number of growing season days deferred, C) stocking density (animal units [AU]/ha), and D) pasture area on nonbreeding habitat selection by female lesser prairie-chickens in monitored grasslands, western Kansas, USA, 2013–2016. Vertical dashed lines represent the means associated with each set of available (black) and used (blue) locations.

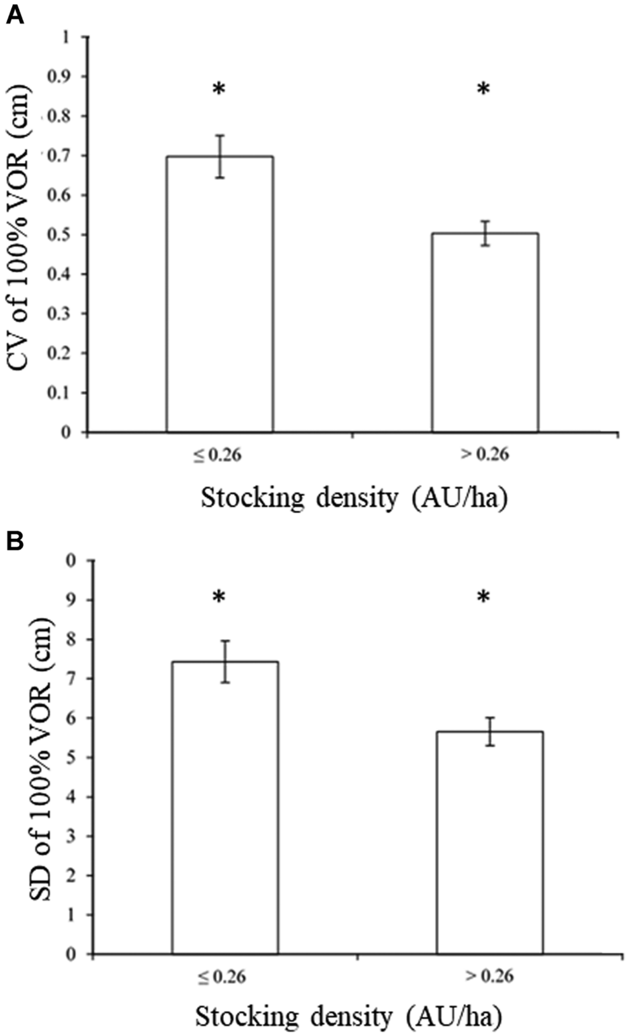


Figure 3. Mean estimates and standard errors of A) coefficient of variation (CV) of 100% visual obstruction (VOR; cm) and B) standard deviation (SD) of 100% VOR (cm) associated with 2 categories of stocking density (≤0.26 and >0.26 animal units/ha [AU/ha]) applied to pastures in western Kansas, USA, 2013–2015. An asterisk (*) denotes that means differed as determined by a 2-sample *t*-test ($P < 0.05$).

Nonbreeding Habitat and Nest-Site Selection

For nonbreeding habitat selection, the results of the grazing intensity model set identified a quadratic relationship with forage use with 100% of model weight (Table 1). The variance associated with the random effects of bird and ranch were 0.025 (SD = 0.159) and 0.088 (SD = 0.029), respectively. Relative probability of use exhibited a quadratic relationship with forage use and lesser prairie-chicken habitat selection, with selection being the greatest close to 40% (Fig. 4). The quadratic effect of forage use was included in all secondary nonbreeding RSF model sets because it was the best predictor of the baseline response of lesser prairie-chickens to increasing grazing disturbance.

The top-ranked RSF model in the pasture area model set included additive influences of forage use, forage use^2, and pasture area (Table 1). The variance associated with the random effects of bird and ranch were 0.026 (SD = 0.160) and 0.059 (SD = 0.243), respectively. The positive beta associated with pasture area and our model output indicated a positive linear relationship between pasture size and habitat selection by female lesser prairie-chickens (Table 2; Fig. 4).

The top-ranked model in our deferment model set was an interaction between forage use^2 and deferment^2 (Table 1). The variance associated with the random effects of bird and ranch were 0.048 (SD = 0.229) and 0.139 (SD = 0.374), respectively. Probability of use was lowest when pastures were deferred for approximately 40% of the growing season (Fig. 4). The second-ranked model of the additive version forage use^2 and deferment^2 was equally parsimonious ($\Delta AIC_c = 0.92$; Table 1).

The top-ranked model in the stocking density model set included additive effects of forage use, forage use^2, and stocking density and an interaction between stocking density and forage use^2 (Table 1). The variance associated with the random effects of bird and ranch were 0.052 (SD = 0.229) and 0.444 (SD = 0.666), respectively. Beta estimates indicated a negative relationship between stocking density and probability of lesser prairie-chicken use (Table 2). At mean values of forage use, the stocking density response curve indicated a 75% drop in relative probability of use when stocking densities were near zero AU/ha and a relative probability of use of approximately 15% as stocking density approached 1.0 AU/ha. The relationship between stocking density and forage use yields an increase in probability of use as stocking density decreases at forage use values from 0–80% (Fig. 4).

Five models of nest-site selection were equally parsimonious with values ≤2 ΔAIC_c, all of which included the quadrat relationship of grazing pressure (Table 3). The top model reported variances of 0.000 (SD = 0.000) and 1.703 (SD = 1.305) for unique nest and ranch, respectively. Our results indicated that only the quadratic relationship of grazing pressure was an influential predictor of nest-site placement being a variable in 7 of the 8 top-ranked models (Tables 2, 3). The quadratic relationship of grazing pressure illustrated that the relative probability of nest-site placement was maximized near 1.2 AUM/ha (Fig. 5).

Nest-Site Location and Survival

We located and monitored 37 nests within grazed pastures in our study sites. All nests were located in pastures exhibiting forage use values below 40%. Twenty-six of 37 (70%) nests were located where grazing pressure was <0.8 AUM/ha.

We modeled daily nest survival for 34 nests; we censored 3 nests because they failed before we located them. Of the 34 nests, 28 were first attempts and 6 were renests. Drawing inference from our constant model, the daily survival rate of monitored nests was 0.983 (95% CI = 0.972–0.989). Nest success for the 38-day exposure incubation period was 50.1%. Seven of our 24 *a priori* nest survival models had a $\Delta AIC_c \leq 2$, but all of these models included a quadratic trend of day over the nesting season (date + date^2; Table 4). The top-ranked model excluded all grazing metrics but supported a quadratic trend of day over the nesting season (date + date^2), indicating that all other variables in the

Table 1. Model ranking for resource selection functions, based on Akaike's Information Criterion corrected for small sample size (AIC$_c$), evaluating habitat selection by female lesser prairie-chickens within monitored working grasslands in Kansas, USA, 2013–2015. We developed model sets to investigate grazing intensity (1), and heterogeneity-based grazing management (2, 3, 4) influences on nonbreeding habitat selection. Model sets include the following variables: forage use (% of forage consumed or destroyed), grazing pressure (index of grazing units per area over time; animal unit month [AUM]/ha), pasture area (size of pasture unit; ha), deferment (number of days during the grazing season [Apr–Sep] a pasture unit is void of cattle), and stocking density (number of grazing units per unit area; animal unit [AU]/ha). We include number of parameters (*K*), deviance (Dev), and Akaike weight (w_i) for each model.

Model set	Model structure	*K*	Dev	ΔAIC$_c$	w_i
1) Grazing intensity	Forage use	4	18,756.86	0.00	1.00
	Forage use	3	18,894.92	136.06	<0.001
	Grazing pressure^2	4	19,289.18	532.31	<0.001
	Grazing pressure	3	19,295.28	536.41	<0.001
	Null	2	19,459.42	698.55	<0.001
2) Pasture area	Forage use^2 + pasture area	5	18,692.18	0.00	0.54
	Forage use^2 × pasture area	6	18,690.50	0.32	0.46
	Forage use^2	4	18,756.86	62.68	<0.001
	Pasture area	3	19,200.62	504.45	<0.001
	Null	2	19,459.42	761.23	<0.001
3) Deferment	Forage use^2 × deferment^2	7	17,648.46	0.00	0.44
	Forage use^2 + deferment^2	6	17,647.38	0.92	0.28
	Forage use^2 + deferment	5	17,650.52	2.06	0.16
	Forage use^2 × deferment	6	17,652.88	2.42	0.13
	Deferment^2	4	18,061.26	408.79	<0.001
	Deferment	3	18,143.36	488.88	<0.001
	Forage use^2	4	18,756.86	1,104.39	<0.001
	Null	2	19,459.42	1,802.94	<0.001
4) Stocking density	Forage use^2 × stocking density	6	18,183.54	0.00	0.81
	Forage use^2 + stocking density	5	18,188.46	2.92	0.19
	Forage use^2	4	18,756.86	569.32	<0.001
	Stocking density	3	19,271.14	1,081.61	<0.001
	Null	2	19,459.42	1,267.88	<0.001

potentially competitive models were spurious. Grazing pressure occurred in the second- and third-best supported models (Table 4). Stocking density also occurred in the second-ranked model but was an uninformative parameter. Daily nest survival estimates were lowest (0.968–0.970) between days 25 and 32 of the exposure period for each nest. The top-ranked model with grazing effects predicted a negative relationship between grazing pressure and daily survival, but it was not measurably different from zero ($\beta_{\text{grazing pressure}} = -1.53$, 95% CI = −3.36–0.29; Fig. 6). Although a positive relationship was indicated by the stocking density beta estimate ($\beta_{\text{stocking density}} = 2.49$, 95% CI = −1.06–6.04), it was not measurably different from zero.

Adult Survival

We used 14 mortality events and 39 bird years to model the effect of grazing management components on hazard rates. Our model selection indicated the null model was the best predictor of survival within our model set, but there was considerable model uncertainty ($\Delta AIC_c \leq 2$; Table 5). The overall annual survival rate of female lesser prairie-chickens across all study sites was 0.317 (SE = 0.107, 95% CI = 0.16–0.62).

DISCUSSION

Overall, our results suggest that lesser prairie-chickens respond positively to light to moderate grazing disturbances (e.g., forage use <50% and stocking densities <0.26 AU/ha) in semi-arid environments based on expected production for the ecological sites defined by soil types and precipitation. Heterogeneity-based grazing strategies also promoted habitat quality for an increased number of grassland species compared to grazing strategies prioritizing standardized, uniform grazing distributions (Pavlacky et al. 2019). Our research concentrated on ranching operations that had a relatively long history of implementing light to moderate grazing intensities that supported high densities of lesser prairie-chickens. Ranches within our study areas that implemented heavy grazing (>60% forage use) intensities did not support lesser prairie-chickens in sufficient numbers to be included in the study, but each of our study ranches contained pastures that sustained heavy grazing intensities and emulated what was occurring on adjacent properties but at larger scales. Our results support the conclusion of Fritts et al. (2016) that increasing levels of grazing disturbance, past critical thresholds (i.e., 40% forage use, grazing pressure >1.2 AUM/ha), negatively affected female habitat selection and potentially nest success. We concur with Milligan et al. (2020*a*) that a wider range of forage use rates may have revealed stronger effects on selection and possibly demographic rates, but our findings were consistent with the conclusion that greater than moderate grazing intensity negatively influence use by lesser prairie-chickens.

In continuous grazing systems, the creation of heterogeneity is contingent on the awareness of forage quality, subsequent competition among grazers for quality forage, and realized distribution of grazing pressure across a pasture (Hart et al. 1988, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). The forage quality-grazing

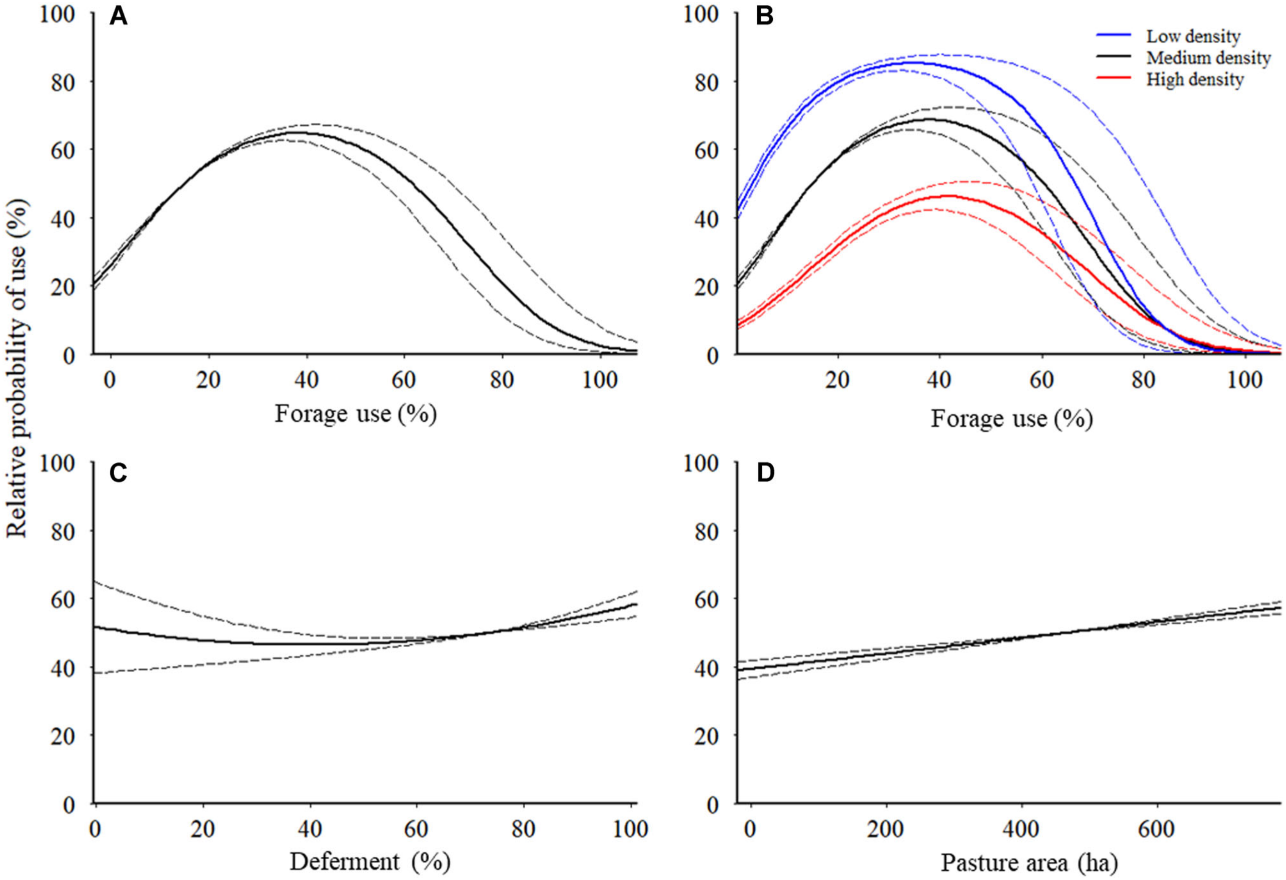


Figure 4. Relative probability of use response curves illustrating nonbreeding habitat selection by female lesser prairie-chickens in relation to A) forage use (%), B) forage use at 3 levels of stocking density ($\bar{x} \pm 1$ SD; animal units/ha [AU/ha]; low [0.06 AU/ha], medium [0.13 AU/ha], and high [0.56 AU/ha]), C) deferment (proportion of growing season), and D) pasture area (ha) within monitored grasslands grazed by cattle in western Kansas, USA, 2013–2015. We developed response curves using output from resource selection functions. We calculated forage use assuming a 50% grazing efficiency (proportion of the allocated forage consumed by livestock). The prediction curves are bounded by 95% confidence intervals (dashed lines).

distribution process is primarily influenced by stocking density. Cattle perceive variation in forage quality across a pasture and selectively graze accordingly. At high levels of stocking density, competition for high quality forage increases and cattle are forced to graze in lower quality areas (Barnes et al. 2008). Increased competition for high quality forage associated with high stocking densities leads to greater uniformity of grazing pressure (use of the entire gradient of forage quality), resulting in uniformity in microhabitat structure across a pasture (Fuhlendorf et al. 2006). When

Table 2. Summary of beta coefficients (β) and 95% upper (UCI) and lower (LCI) confidence intervals from top-ranked resource selection functions identified using Akaike's Information Criterion for nonbreeding habitat selection (2013–2016) and nest-site selection (2013–2015) by female lesser prairie-chickens within monitored working grasslands in western Kansas, USA, 2013–2016.

Model set	Variables	β	95% LCI	95% UCI
1) Grazing intensity	Forage use	0.6397	0.5908	0.6885
	Forage use^2	−0.1681	−0.1959	−0.1404
2) Pasture area	Forage use	0.5739	0.5226	0.6252
	Forage use^2	−0.1504	−0.1790	−0.1218
	Pasture area	0.1546	0.1169	0.1923
3) Deferment	Forage use	0.7825	0.7049	0.8600
	Forage use^2	−0.1878	−0.2215	−0.1542
	Deferment^2	0.0442	0.0055	0.0830
	Deferment	0.1594	0.1002	0.2186
	Forage use^2: deferment^2	−0.0301	−0.0650	0.0048
4) Stocking density	Forage use	0.8440	0.7909	0.8971
	Forage use^2	−0.2274	−0.2719	−0.1828
	Stocking density	−1.0697	−1.1698	−0.9696
	Forage use^2: stocking density	0.0331	0.0049	0.0612
5) Nest-site selection	Grazing pressure	1.0067	0.2557	1.7577
	Grazing pressure^2	−0.3285	−0.6787	0.0216
	Pasture area	0.3154	−0.0701	0.7009

Table 3. Model ranking of resource selection functions, based on Akaike's Information Criterion corrected for small sample size (AIC_c), evaluating nest-site selection by lesser prairie-chickens within monitored working grasslands in western Kansas, USA, 2014–2015. We developed model sets to investigate influences of grazing intensity and heterogeneity-based grazing management. Variables in models sets include forage utilization (% of forage consumed or destroyed), grazing pressure (index of grazing units per area over time; animal unit month [AUM]/ha), pasture area (size of pasture unit; ha), deferment (number of days during the grazing season [Apr–Sep] a pasture unit is void of cattle), and stocking density (number of grazing units per unit area; AU/ha). We include number of parameters (K), deviance (Dev), and Akaike weight (w_i) for each model.

Model structure	K	Dev	ΔAIC_c	w_i
Grazing pressure^2 + pasture area	5	181.28	0.00	0.18
Grazing pressure^2	4	183.86	0.45	0.14
Grazing pressure^2 × stocking density	6	179.64	0.48	0.14
Grazing pressure^2 + deferment	5	182.06	0.77	0.12
Grazing pressure^2 × pasture area	6	180.88	1.72	0.08
Forage use^2 + pasture area	5	183.50	2.21	0.06
Grazing pressure^2 × deferment	6	181.54	2.39	0.05
Grazing pressure^2 + stocking density	5	183.84	2.56	0.05
Forage use^2	4	185.96	2.56	0.05
Pasture area	3	189.58	4.08	0.02
Forage use^2 × pasture area	6	183.50	4.35	0.02
Forage use^2 + stocking density	5	185.78	4.49	0.02
Forage use^2 + deferment	5	185.84	4.55	0.02
Forage use^2 × deferment	6	185.36	6.21	0.01
Deferment	3	191.78	6.28	0.01
Null	2	193.88	6.33	0.01
Forage use^2 × stocking density	6	185.76	6.61	0.01
Stocking density	3	193.72	8.23	0.00

stocking densities are held at low to moderate values, the pattern of grazing disturbance across a pasture mimics the pattern of forage quality (Chapman et al. 2007). Subsequently, a gradient of light to heavy grazing disturbance develops as pasture size increases. The gradient in grazing disturbance creates a corresponding gradient of vegetation structure and thus microhabitat heterogeneity. As predicted, results indicated that female lesser prairie-chickens select habitat based on the microhabitat heterogeneity created at lower values of stocking density.

Table 4. Model ranking based on Akaike's Information Criterion corrected for small sample size (AIC_c) of lesser prairie-chicken nest survival estimation for nests in working grasslands monitored in western Kansas, USA, during 2015. *A priori* models included variable combinations of date during the nesting season (date), a quadratic function of date (date^2), grazing pressure (animal unit month [AUM]/ha), stocking density (animal unit [AU]/ha), pasture area (ha), forage use (proportion of forage consumed or destroyed), deferment (number of days deferred during the grazing season), and a constant model. We include number of parameters (K), deviance (Dev), and Akaike weight (w_i) for each model.

Model structure	K	Dev	ΔAIC_c	w_i
Date + date^2	3	164.62	0.00	0.16
Date + date^2 + grazing pressure + stocking density	5	161.38	0.79	0.11
Date + date^2 + grazing pressure	4	163.62	1.02	0.10
Date + date^2 + pasture area	4	163.83	1.22	0.09
Date + date^2 + stocking density	4	164.14	1.54	0.07
Date + date^2 + forage use	4	164.52	1.92	0.06
Date + date^2 + deferment	4	164.55	1.94	0.06
Date + date^2 + grazing pressure + pasture area	5	162.66	2.08	0.06
Date + date^2 + grazing pressure + deferment	5	163.30	2.72	0.04
Null	1	171.76	3.12	0.03
Date + date^2 + forage use + pasture area	5	163.77	3.19	0.03
Date + date^2 + forage use + stocking density	5	163.90	3.31	0.03
Date + date^2 + forage use + deferment	5	164.34	3.75	0.02
Grazing pressure	2	170.74	4.11	0.02
Grazing pressure + stocking density	3	168.84	4.22	0.02
Pasture area	2	171.00	4.37	0.02
Stocking density	2	171.43	4.80	0.01
Forage use	2	171.61	4.98	0.01
Deferment	2	171.70	5.06	0.01
Grazing pressure + pasture area	3	169.78	5.16	0.01
Grazing pressure + deferment	3	170.43	5.81	0.01
Forage use + pasture area	3	170.88	6.26	0.01
Forage use + stocking density	3	171.13	6.51	0.01
Forage use + deferment	3	171.42	6.80	0.01

Previous researchers have assumed that increases in grazing disturbance (i.e., forage use, grazing pressure) result in negative effects on microhabitat quality for lesser prairie-chickens (Hagen et al. 2004, Dahlgren et al. 2016,

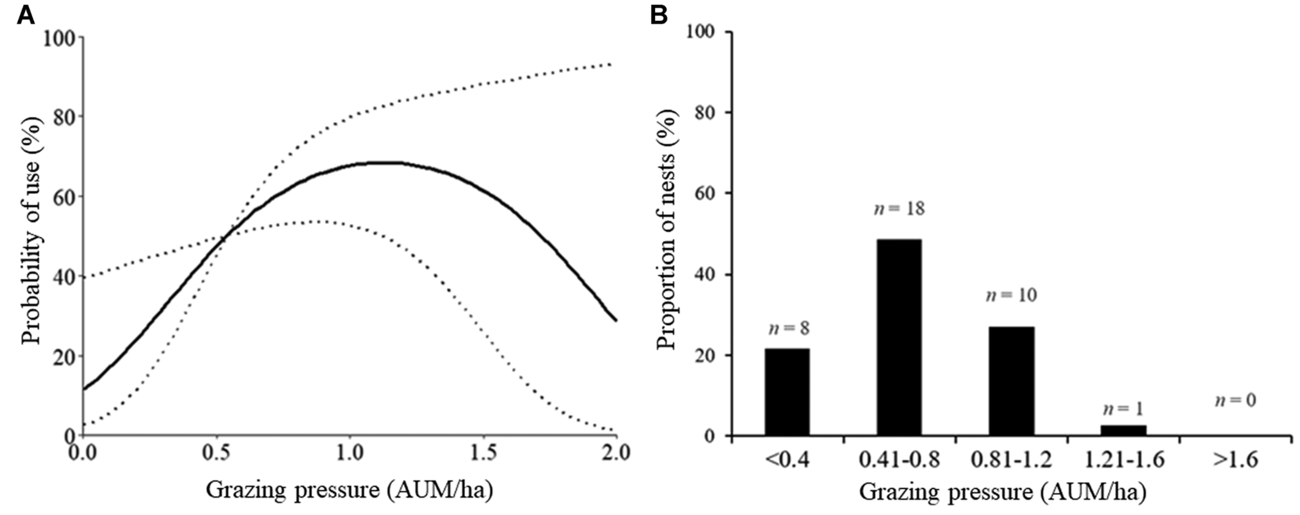


Figure 5. A) Relative probability of use curve (bounded by 95% CIs) describing nest-site selection by female lesser prairie-chickens in relation to grazing pressure (animal units/ha [AU/ha]) during the 2015 nesting season in monitored grasslands in western Kansas, USA. B) Proportions of nest-site locations used to estimate nest-site selection observed within 0.4 animal unit months (AUM)/ha interval bins of grazing pressure estimates.

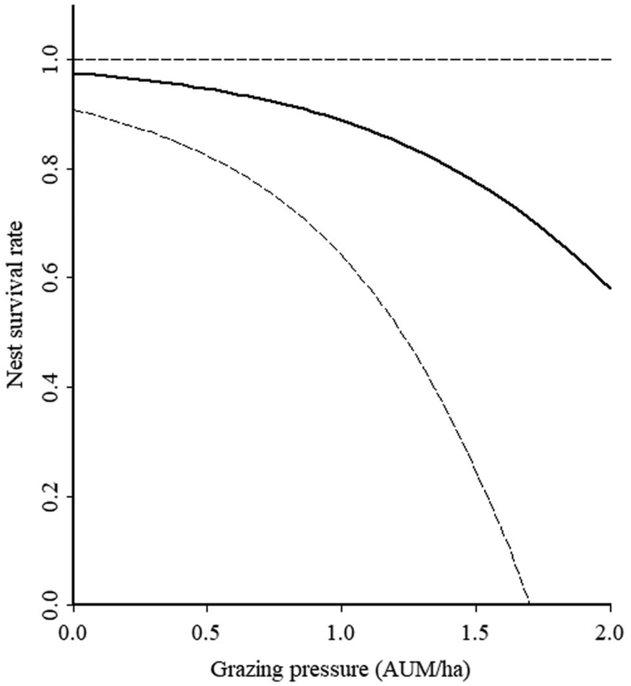


Figure 6. Daily nest survival response curve (bounded by 95% CIs) of lesser prairie-chickens in relation to grazing pressure (animal unit months [AUM]/ha]) in monitored grasslands of western Kansas, USA, 2014–2015. We held stocking density and date^2 at their mean during modeling. Response curves are enveloped within 95% confidence intervals (dashed lines).

Hagen and Elmore 2016). We observed a threshold effect on lesser prairie-chicken habitat use in the northern portion of the species' distribution where relative probability of use was maximized near 40% forage use and steadily decreased at forage use beyond this threshold. These values corroborate prescriptions of forage use values between 30–50% recommended by Western Association of Fish and Wildlife Agencies in the Lesser Prairie-Chicken Range-Wide Conservation Plan and Natural Resources Conservation Service Lesser Prairie-Chicken Initiative (Van Pelt et al. 2013, Kansas Natural Resources Conservation Service 2014). Effects of forage use likely fluctuate as plant community composition, precipitation, and forage production vary. Thus, average expected forage production within monitored grasslands in our study was 2,639 kg/ha. Consideration for site-specific conditions (i.e., precipitation, plant community composition, forage production potential, historical management) will be essential for prescribing forage use values to achieve desired vegetation structural goals.

Table 5. Model ranking for Anderson-Gill models, based on Akaike's Information Criterion corrected for small sample size (AIC$_c$), for 5 models identifying the effects of grazing strategies on annual survival of female lesser prairie-chickens within working grasslands monitored in western Kansas, USA, during 2013–2016. *A priori* models included single-variable models of forage use (proportion of forage consumed or destroyed), grazing pressure (animal unit month [AUM]/ha), stocking density (animal unit [AU]/ha), and pasture area (ha). We include number of parameters (K), deviance (Dev), and Akaike weight (w_i) for each model.

Model structure	K	Dev	ΔAIC$_c$	w_i
Null	1	73.37	0.00	0.36
Stocking density	2	74.77	1.40	0.18
Grazing pressure	2	74.79	1.42	0.15
Forage use	2	75.18	1.81	0.15
Pasture area	2	75.37	2.00	0.13

Previous research indicates that lesser prairie-chicken nest-site placement is characterized by the tendency of females to place nests in areas of greater grass cover, litter cover, and visual obstruction with relatively lower area of bare ground (Davis 2009, Hagen et al. 2013, Grisham et al. 2014, Haukos and Zavaleta 2016, Lautenbach et al. 2019). Nest-site selection had the greatest relative probability of occurrence at forage use values of 15–20% and declined rapidly as forage use increased past 20%. This result concurred with previously established patterns of nest-site selection by lesser prairie-chickens and importance of lightly disturbed habitat (Fritts et al. 2016, Haukos and Zavaleta 2016).

Baseline responses of habitat selection by lesser prairie-chickens to grazing disturbance provided insights into effects of heterogeneity-based grazing management. Variation of environmental characteristics such as soils, plant communities, and microhabitat structure is positively correlated with spatial scale (Wiens 1989, 2000). Thus, there is likely an inherent positive relationship between habitat heterogeneity and increasing pasture size within our study sites. Intuitively, an increase in pasture size also increased the probability of a required lesser prairie-chicken female resource (i.e., leks, nest habitat, brood habitat, winter cover) being present. Despite the increased probability of lesser prairie-chicken microhabitat presence at larger scales, it is unlikely that the relationship between pasture area and presence of quality habitat is independently creating the increased probability of use by female lesser prairie-chickens as pasture area increases. Our results combined with established concepts of grazing ecology indicate that grazing management strategies associated with larger pasture areas, such as stocking density, may be a more significant influence on microhabitat heterogeneity and lesser prairie-chicken occurrence than pasture size alone.

There was a threshold effect of deferment where probability of use increased at low and high values of deferment. We hypothesize that site-specific variation is influencing this pattern. For example, long periods of rest or deferment are likely beneficial for grasslands that exhibit relatively low potential for the production of nesting habitat. Alternatively, in grasslands exhibiting high potential for biomass production, longer grazing periods may be required to achieve desired habitat outcomes. Additional investigations focusing on the influence of deferment with consideration for regional variation is required to understand this pattern.

We did not observe a definitive pattern of lesser prairie-chicken adult survival and nest success in response to heterogeneity-based grazing strategies as we did with patterns of habitat selection. Our data suggested, however, that increasing grazing disturbance during the year previous to nest initiation may have negative influence on lesser prairie-chicken nest success. This pattern was contrary to grazing studies on other prairie grouse that reported equivocal effects

(Fritts et al. 2016, Smith et al. 2018, Milligan et al. 2020*a*). Although in some cases, grazing indirectly affected nesting success by providing (or removing) adequate vegetation visual obstruction. Increasing female survival during the breeding season, combined with improving recruitment is often a priority for lesser prairie-chicken population management (Hagen et al. 2009, 2013). Development of ranch-scale heterogeneity (among pastures) may mitigate effects of grazing disturbance by providing pastures with quality nesting or brood-rearing microhabitat (Fritts et al. 2018). For example, a manager could prioritize nest success within certain pastures by applying specific grazing prescriptions. In our study systems, models suggest pastures with an annual grazing pressure of 0.5 AUM/ha would result in nest success of approximately 61% based on expected available forage. Nest success at this level would be above average and representative of a stable or growing population (Hagen et al. 2013). Additionally, areas managed for greater nest success may also provide habitat that favors adult female survival during the breeding season because significant portions of adult female mortality occurs during nesting and survival is positively correlated with greater values of overhead cover (Hagen et al. 2007). Other pastures could then be grazed at levels convenient for livestock production or brood habitat. Adaptive grazing may promote heterogeneity among pastures following a deferred-rotation grazing strategy (Merrill 1954) and ensure the presence of quality habitat as weather and climate amplify the negative effects of forage use on vegetation structure (Ross et al. 2016*a, b*; Fritts et al. 2018). At finer scales (i.e., within pasture), success of heterogeneity-based grazing prescriptions may hinge on the development of interspersion of nesting, brooding, and nonbreeding habitats (Hagen et al. 2009, Gehrt et al. 2020).

Applying site-specific grazing prescription may also be beneficial for overall participation in lesser prairie-chicken conservation strategies by private landowners. If recommendations for grazing management inhibit profitability, they will not be relevant in providing certainty for this imperiled species. Long-term grazing extension research in the region of our study suggests that moderate stocking rates (i.e., 45–50% forage use) optimize forage production and livestock gains (Launchbaugh 1957). Recent market data applied to the same long-term research suggest that moderate stocking rates also maximize profitability (K. R. Harmoney, Kansas State University, personal communication).

Although effective grazing prescriptions are site-specific, our results indicate that some grazing is beneficial for lesser prairie-chickens, whereas intensive grazing can be harmful or cause avoidance of potential habitat. Our results offer an alternative for creating heterogeneous habitat for female lesser prairie-chickens through grazing management when prescribed fire may not be feasible. Heterogeneity-based grazing management strategies may not be optimum for some working grasslands where plant community composition and relatively low precipitation may not promote lesser prairie-chicken nest microhabitat under the influence of even light grazing disturbances. The prevalence of short-grass prairie dominated by buffalo grass and blue grama in the Short-Grass Prairie/CRP Mosaic Ecoregion may require a rest-rotation grazing management scheme including season-long rest of pastures to create beneficial microhabitat for nesting (e.g., 100% visual obstruction >20 cm; Lautenbach et al. 2019). Only with the addition of mid- and tall grasses through the CRP were populations of lesser prairie-chickens sustainable in this ecoregion (Sullins et al. 2018). Therefore, a moderate grazing disturbance at the landscape scale is likely within the range of forage use goals adequate for maintaining lesser prairie-chicken habitat throughout much of the species' range.

MANAGEMENT IMPLICATIONS

Some of the largest contemporary recorded lesser prairie-chicken population densities were recorded within our study sites on landscapes characterized by long-term grazing management. Therefore, our findings are primarily in the context of maintaining and improving existing occupied habitat. Although other factors (e.g., energy development, habitat fragmentation) may be involved, lesser prairie-chickens were not present in detectable densities on neighboring sites that used more intensive grazing strategies. In regions with similar plant species composition and environmental characteristics to our study sites, heterogeneity-based grazing management may benefit lesser prairie-chickens by establishing strategies that include large pastures, low stock densities, and relatively long grazing periods. Grazing disturbance would best be targeted at 10–25% forage use in areas capable of producing nesting structure, but we encourage variation in forage use (15–50%) to meet heterogeneity needs among pastures. If the potential for nesting vegetation structure is limited or inconsistent because of the plant community or precipitation, maintenance of available nesting habitat may be possible through targeted deferment or forage use <15%. Management considerations to increase quality of lesser prairie-chicken habitat might not be as applicable to sites exhibiting less-favorable conditions resulting from the deleterious effects of long-term, heavy, continuous grazing or recent intensive drought events. More likely, our findings are better suited to sites exhibiting site potential and soil qualities conducive for supporting quality lesser prairie-chicken habitat.

ACKNOWLEDGMENTS

The contents and opinions herein do not necessarily reflect the views or policies of the United States Fish and Wildlife Service or the Kansas Department of Wildlife, Parks and Tourism. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank K. E. Sexson, J. L. Kramer, M. W. Mitchener, D. K. Dahlgren, J. A. Prendergast, K. A. Fricke, D. J. Kraft, R. W. Tacha, P. G. Kramos, A. A. Flanders, and B. S. T. Hyberg for their assistance with the project. We thank 2 anonymous reviewers for reviewing earlier versions of this manuscript. Research was funded by the USDA, Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative;

Kansas Department of Wildlife, Parks, and Tourism (Federal Assistance Grant KS W-73-R-3); The Kingsbury Family Foundation; and USDA Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA7, KSCFWRU RWO 62).

LITERATURE CITED

Allred, B. W., S. D. Fuhlendorf, and R. G. Hamilton. 2011. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. Ecosphere 2:26.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66:912–918.

Andersen, P. K., and R. D. Gill. 1982. Cox's regression model for counting processes: a large sample study. Annals of Statistics 10:1100–1120.

Augustine, D. J., and J. D. Derner. 2015. Patch-burn grazing management, vegetation heterogeneity, and avian responses in a semi-arid grassland. Journal of Wildlife Management 79:927–936.

Barnes, M. K., B. E. Norton, M. Maeno, and J. C. Malechek. 2008. Paddock size and stocking density affect spatial heterogeneity of grazing. Rangeland Ecology & Management 61:380–388.

Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beyer, H. L. 2012. Geospatial Modelling Environment (version 0.7.3.0). <http://www.spatialecology.com/gme>. Accessed 10 Mar 2020.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Chapman, D. F., A. J. Parsons, G. P. Cosgrove, D. J. Barker, D. M. Marotti, K. J. Venning, S. M. Rutter, J. Hill, and A. N. Thompson. 2007. Impacts of spatial patterns in pasture on animal grazing behavior, intake, and performance. Crop Science 47:399–415.

Cochran, W. W., and R. D. Lord, Jr. 1963. A radio-tracking system for wild animals. Journal of Wildlife Management 27:9–24.

Dahlgren, D., R. Rodgers, R. Elmore, and M. Bain. 2016. Grasslands of western Kansas north of the Arkansas River. Pages 259–280 *in* D. Haukos and C. Boal, editors. Ecology and management of lesser prairie-chickens. CRC Press, Boca Raton, Florida, USA.

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

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

Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the western Great Plains of North America. Rangeland Ecology & Management 62:111–118.

Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2014. Greater sage-grouse (*Centrocercus urophasianus*) female survival: effects of raptors, anthropogenic and landscape features, and female survival. Canadian Journal of Zoology 92:319–330.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. Hayden–Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood rearing habitat for conservation in human–modified landscapes. PLoS ONE 6:e26273.

Earl, J. E., S. D. Fuhlendorf, D. Haukos, A. M. Tanner, D. Elmore, and S. A. Carleton. 2016. Characteristics of lesser prairie-chicken (*Tympanuchus pallidicinctus*) long-distance movements across their distribution. Ecosphere 7:e01441.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

Fox, J., and S. Weisberg. 2011. Cox proportional–hazards regression for survival data in R. Pages 1–20 *in* J. Fox and S. Weisberg, editors. An appendix to an R companion to applied regression. Second edition. SAGE Publications, Washington, D.C., USA.

Fritts, S. F., B. A. Grisham, D. A. Haukos, C. W. Boal, M. A. Patten, D. H. Wolfe, C. E. Dixon, R. D. Cox, and W. R. Heck. 2016. Long-term evaluation of lesser prairie-chicken nest ecology in response to grassland restoration at two spatial scales. Journal of Wildlife Management 80:527–539.

Fritts, S. R., B. A. Grisham, R. D. Cox, C. W. Boal, D. A. Haukos, P. McDaniel, C. A. Hagen, and D. U. Greene. 2018. Interactive effects of severe drought and grazing on the life history cycle of a bioindicator species. Ecology and Evolution 8:9550–9562.

Fuhlendorf, S., and D. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625–632.

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

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

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

Giesen, K. M. 1994. Movements and nesting habitat of lesser prairie-chicken hens in Colorado. Southwestern Naturalist 39:96–98.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Goldewijk, K. K. 2001. Estimating global land use change over the past 300 years: the HYDE database. Global Biogeochemical Cycles 15:417–433.

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.

Hagen, C. A., and R. D. Elmore. 2016. Synthesis, conclusions, and a path forward. Pages 345–352 *in* D. Haukos and C. Boal, editors. Ecology and management of lesser prairie-chickens. CRC Press, Boca Raton, Florida, USA.

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

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

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

Hagen, C. A., 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.

Hart, R. H., M. J. Samuel, P. S. Test, and M. A. Smith. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. Journal of Range Management 41:282–286.

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. Zavaleta. 2016. Habitat. Pages 99–132 *in* D. Haukos and C. Boal, editors. Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, USA.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Holechek, J. L., R. D. Pieper, and C. H. Herbel. 1989. Range management: principles and practices. Prentice–Hall, Englewood Cliffs, New Jersey, USA.

Hovick, T. J., R. D. Elmore, and S. D. Fuhlendorf. 2014. Structural heterogeneity increases diversity of non-breeding grassland birds. Ecosphere 5:62.

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

Ihaka, R., and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299–314.

Kansas Natural Resources Conservation Service. 2014. Identifying and creating lesser and greater prairie-chicken habitat. Kansas Range

Technical Note, KS-9, Natural Resources Conservation Service, Saline, Kansas, USA. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/ks/people/employees/?cid=nrcs142p2_033405. Accessed 27 Sep 2016.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, and D. C. Hartnett. 1999. The keystone role of bison in North American tallgrass prairie—bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. Bioscience 49:39–50.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. Studies in Avian Biology 15:247–257.

Launchbaugh, J. L. 1957. The effect of stocking rate on cattle gains and on native shortgrass vegetation in west central Kansas. Bulletin 394, Kansas Agricultural Experiment Station, Hays, USA.

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

Lautenbach, J. M., D. A. Haukos, D. S. Sullins, C. A. Hagen, J. D. Lautenbach, J. C. Pitman, R. T. Plumb, S. G. Robinson, and J. D. Kraft. 2019. Northern exposure: factors influencing nesting ecology of lesser prairie-chickens in Kansas and Colorado. Journal of Wildlife Management 83:205–215.

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, F. Hornsby, D. Klute, S. Kyle, J. Pitman, and T. Rintz. 2014. Range-wide population size of the lesser prairie-chicken: 2012 and 2013. Wildlife Society Bulletin 38:536–546.

McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2009. Estimating the stage of incubation for nests of greater prairie-chickens using egg flotation: a float curve for grousers. Newsletter of the Grouse Group, Grouse News 38:12–14.

Merrill, L. B. 1954. A variation of deferred rotation grazing for use under southwest range conditions. Journal of Range Management 7:152–154.

Milchunas, D. G., O. E. Sala, and W. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132:87–106.

Milligan, M. C., L. I. Berkeley, and L. B. McNew. 2020*a*. Effects of rangeland management on the nesting ecology of sharp-tailed grouse. Rangeland Ecology & Management 73:128–137.

Milligan, M. C., L. I. Berkeley, and L. B. McNew. 2020*b*. Habitat selection of female sharp-tailed grouse in grasslands managed for livestock production. PLoS ONE 15:e0233756.

Milligan, M. C., L. I. Berkeley, and L. B. McNew. 2020*c*. Survival of sharp-tailed grouse under variable livestock grazing management. Journal of Wildlife Management 84:1296–1305.

Pavlacky, D. C., B. B. Woiderski, R. A. Sparks, A. Van Boer, and A. W. Green. 2019. Effectiveness monitoring of the lesser prairie-chicken initiative and conservation reserve program for managing the biodiversity and population size of grassland birds. Technical Report # LPCI-16-02, Bird Conservancy of the Rockies, Fort Collins, Colorado, USA.

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.

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, J. D. Kraft, D. S. Sullins, J. M. Lautenbach, J. D. Lautenbach, B. K. Sandercock, C. A. Hagen, A. Bartuszevige, et al. 2018. Effects of landscape characteristics on annual survival of lesser prairie-chickens. American Midland Naturalist 180:66–86.

Ross, B. E., D. Haukos, C. Hagen, and J. Pitman. 2016*a*. The relative contribution of climate to changes in lesser prairie-chicken abundance. Ecosphere 7(6):e01323.

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

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6–15.

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, J. T., J. D. Tack, L. I. Berkeley, M. Szczypinski, and D. E. Naugle. 2018. Effects of livestock grazing on nesting sage-grouse in central Montana. Journal of Wildlife Management 82:1503–1515.

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

Taylor, C. A., Jr. 2005. Prescribed burning cooperatives: empowering and equipping ranchers to manage rangelands. Rangelands 27:18–23.

United States Department of Agriculture [USDA]. 2013. Interagency ecological site handbook for rangelands. USDA, Washington, D.C., USA.

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.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–97.

Wiens, J. A. 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. Pages 9–31 *in* M. J. Hutchings, E. A. John, and A. J. A. Stewart, editors. Ecological consequences of environmental heterogeneity. Blackwell Science, Oxford, England, United Kingdom.

Winder, V. L., L. B. McNew, J. C. Pitman, and B. K. Sandercock. 2016. Space use of female greater prairie-chickens in response to fire and grazing interactions. Rangeland Ecology & Management 70:165–174.

Winder, V. L., L. B. McNew, J. C. Pitman, and B. K. Sandercock. 2018. Effects of rangeland management on survival of female greater prairie-chickens. Journal of Wildlife Management 82:113–122.

Associate Editor: Anthony Roberts.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

The Journal of Wildlife Management 85(8):1699–1710; 2021; DOI: 10.1002/jwmg.22118

Research Article

Ecological Disturbance Through Patch-Burn Grazing Influences Lesser Prairie-Chicken Space Use

JONATHAN D. LAUTENBACH,[1,2] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

DAVID A. HAUKOS, *U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University, Manhattan, KS 66506, USA*

JOSEPH M. LAUTENBACH,[3] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

CHRISTIAN A. HAGEN, *Oregon State University, Bend, OR 97702, USA*

ABSTRACT Across portions of the western Great Plains in North America, natural fire has been removed from grassland ecosystems, decreasing vegetation heterogeneity and allowing woody encroachment. The loss of fire has implications for grassland species requiring diverse vegetation patches and structure or patches that have limited occurrence in the absence of fire. The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a declining species of prairie-grouse that requires heterogeneous grasslands throughout its life history and fire has been removed from much of its occupied range. Patch-burn grazing is a management strategy that re-establishes the fire-grazing interaction to a grassland system, increasing heterogeneity in vegetation structure and composition. We evaluated the effects of patch-burn grazing on lesser prairie-chicken space use, habitat features, and vegetation selection during a 4-year field study from 2014–2017. Female lesser prairie-chickens selected 1- and 2-year post-fire patches during the lekking season, ≥4-year post-fire patches during the nesting season, and year-of-fire and 1-year post-fire patches during post-nesting and nonbreeding seasons. Vegetation selection during the lekking season was not similar to available vegetation in selected patches, suggesting that lesser prairie-chickens cue in on other factors during the lekking season. During the nesting season, females selected nest sites with greater visual obstruction, which was available in ≥4-year post-fire patches; during the post-nesting season, females selected sites with 15–25% bare ground, which was available in the year-of-fire, 1-year post-fire, and 2-year post-fire patches; and during the nonbreeding season they selected sites with lower visual obstruction, available in the year-of-fire and 1-year post-fire patches. Because lesser prairie-chickens selected all available time-since-fire patches during their life history, patch-burn grazing may be a viable management tool to restore and maintain lesser prairie-chicken habitat on the landscape. © 2021 The Wildlife Society.

KEY WORDS disturbance, habitat selection, Kansas, lesser prairie-chicken, prescribed fire, pyric herbivory, *Tympanuchus pallidicinctus*.

Disturbances are ecological processes defined as a shift from normal ecosystem function but necessary to maintain spatial and temporal heterogeneity and biodiversity (White 1979, Rykiel 1985, Pickett et al. 1989, Fuhlendorf et al. 2009). As with other ecological processes, disturbances occur at multiple spatial and temporal scales and are system dependent. Alterations to historical disturbance regimes (either spatial, temporal, or both) results in a transformed contemporary disturbance regime. For example, frequent fire in sagebrush (*Artemisia* spp.) steppe might be considered an altered, contemporary disturbance transforming vegetation communities (Whisenant 1990, Bradley et al. 2018); whereas, in tall grass prairie, frequent fire is a historical disturbance required to maintain community composition and structure (Turner et al. 2003, Fuhlendorf et al. 2009).

There are 3 main factors influencing vegetation conditions in grasslands: fire, grazing, and climate (Fuhlendorf and Engle 2001, Askins et al. 2007, McGranahan et al. 2012, Hovick et al. 2014*a*). These factors are dynamic and interact to create vegetation conditions that are spatially and temporally heterogeneous (Fuhlendorf and Smeins 1999, McGranahan et al. 2012). For example, grazing pressure is strongly influenced by the presence of fire, with large grazers

Received: 5 March 2020; Accepted: 23 July 2021

---

[1] *E-mail: jlauten1@uwyo.edu*

[2] *Present address: Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY, 82071, USA*

[3] *Present address: Ohio Department of Natural Resources, Columbus, OH 43229, USA*

(e.g., cattle, bison [*Bison bison*]) selecting recently burned areas (i.e., the fire-grazing interaction; Fuhlendorf et al. 2009, Allred et al. 2011). If long-term shifts in the frequency of these factors occur, there is the potential that altered, contemporary disturbance regimes will occur, causing an ecological state change, such as tree encroachment, reduced vegetation diversity, and lower species abundances (Fuhlendorf and Smeins 1999; Ratajczak et al. 2011, 2012; Scholtz et al. 2017).

In the southern mixed-grass prairies of North America's Great Plains, fire has been suppressed for >100 years throughout much of the region, allowing trees and shrubs to encroach into grasslands (e.g., eastern redcedar [*Juniperus virginiana*]; Engle et al. 2008). This expansion of trees has converted significant areas of prairie into redcedar savannas or forests (Briggs et al. 2002) and decoupled fire-grazing interactions (Fuhlendorf et al. 1996, 2009; Allred et al. 2014). Decoupling fire-grazing interactions can lead to structural homogeneity across grasslands and reduce available habitat for grassland fauna including birds (Coppedge et al. 2001, Chapman et al. 2004, Samson et al. 2004, Engle et al. 2008).

Across their range, lesser prairie-chickens (*Tympanuchus pallidicinctus*) have experienced a >90% decline in abundance and perceived occupied range during the past century and, as a result, is a species of conservation concern (Taylor and Guthery 1980, McDonald et al. 2014, Hagen and Giesen 2020). Lesser prairie-chickens are grassland obligates that require a diversity of vegetation structure and composition to complete their life history (Fuhlendorf and Engle 2001, Haukos and Zavaleta 2016). The primary cause of population declines for the species is habitat loss resulting from large-scale conversions of prairie to cropland, energy development, and tree encroachment (Woodward et al. 2001, Fuhlendorf et al. 2002, Pitman et al. 2005, Rogers 2016, Falkowski et al. 2017). Further, grassland mismanagement, such as unmanaged grazing, compounded with extended severe drought has the potential to stress current populations (Grisham et al. 2013, Ross et al. 2016, Fritts et al. 2018). Because lesser prairie-chickens have diverse vegetation requirements across life-history stages, they are considered an umbrella species for grassland species (Pruett et al. 2009). Thus, managing grasslands for lesser prairie-chickens should result in tangential benefits for multiple avian species within the grassland community (Pavlacky et al. 2019). Therefore, it is imperative to identify management systems that promote the retention of grasslands for lesser prairie-chickens and reduce the probability of ecological state changes for multiple species (Samson and Knopf 1994, With et al. 2008, Rosenberg et al. 2019).

Tree encroachment into the southern mixed-grass prairie reduces habitat availability for lesser prairie-chickens because females do not place nests in areas with >2 trees/ha (Lautenbach et al. 2017). One effective conservation action to remedy this increasing threat is to reintroduce fire at a historical fire return interval (e.g., 4–10 yr for the southern mixed grass prairie; Wright and Bailey 1982, Bragg 1995, Bragg and Steuter 1996, Frost 1998) into the system (Ortmann et al. 1998, Thacker and Twidwell 2014, Lautenbach et al. 2017). The ecological response (e.g., space use, demography) of lesser prairie-chickens to historical or prescribed fire is unknown but assumed to be beneficial (Thacker and Twidwell 2014, Hagen and Elmore 2016) and should be examined to enable the strategic implementation of conservation practices for lesser prairie-chickens (Thacker and Twidwell 2014).

Our primary goal was to measure the influence of prescribed fire on lesser prairie-chicken habitat selection and use. We were specifically interested in exploring lesser prairie-chicken response to patch-burn grazing where land managers annually burn a portion of each pasture and allow livestock to select a grazing patch within the pasture, with grazers typically concentrating their activities in burned areas (Fuhlendorf and Engle 2001, Vermeire et al. 2004, Allred et al. 2011). Rotation of burned patches among years generates multi-scale vegetation heterogeneity based on time since fire, increasing variation in vegetation structure within a pasture. In addition, patch-burn grazing offers the opportunity to investigate the response by lesser prairie-chickens to availability of multiple time-since-fire patches (i.e., patches). Specifically, our objectives were to quantify effects of patch-burn grazing on vegetation composition and structure in different patches generated through patch-burn grazing, evaluate lesser prairie-chicken time-since-fire patch selection during different life stages, and evaluate lesser prairie-chicken selection of vegetation structure and composition responding to patch-burn grazing management regime.

STUDY AREA

We conducted our research on 14,000 ha of private lands in Kiowa and Comanche counties, Kansas, USA, during 2014–2017 (Fig. 1). We collected data during 4 biological seasons, lekking (15 Mar–nest incubation start), nesting (incubation start–nest completion), post-nesting (nest completion–15 Sep; brooding and nonbrooding females), and nonbreeding (15 Sep–14 Mar) seasons. Our study area was located within the Red Hills region of south-central Kansas and characterized by mixed-grass prairie on loamy soils. Topography at the site was rolling hills with an average elevation of 560 m above sea level. The dominant land use was cattle production and grassland (87%) with some row-crop agriculture (8.9%), and United States Department of Agriculture Conservation Reserve Program grasslands (2.2%; Robinson et al. 2018*a*). Native vegetation in the study area included little bluestem (*Schizachyrium scoparium*), hairy grama (*Bouteloua hirsuta*), blue grama (*B. gracilis*), sideoats grama (*B. curtipendula*), buffalograss (*B. dactyloides*), big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), sand dropseed (*Sporobolus cryptandrus*), western ragweed (*Ambrosia psilostachya*), Louisiana sagewort (*Artemisia ludoviciana*), sand sagebrush (*Artemisia filifolia*), Chickasaw plum (*Prunus angustifolia*), and eastern redcedar. Common mammalian and avian species included coyote (*Canis latrans*), thirteen-lined ground-squirrel

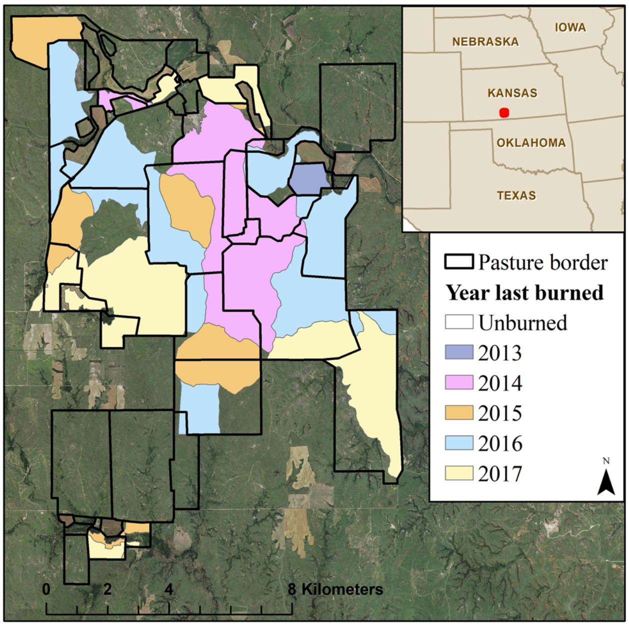


Figure 1. Location of the study area investigating the influence of prescribed fire on lesser prairie-chickens in Kiowa and Comanche counties, Kansas, USA, 2014–2017. Different colors represent year last burned. Black lines represent the property where patch-burn grazing is used as a management strategy and pasture borders within the property. Inset map shows the location of the study area.

(*Ictidomys tridecemlineatus*), white-tailed deer (*Odocoileus virginianus*), red-tailed hawk (*Buteo jamaicensis*), eastern meadowlark (*Sturnella magna*), western meadowlark (*S. neglecta*), grasshopper sparrow (*Ammodramus savannarum*), and dickcissel (*Spiza americana*).

Climate was characterized by warm summers and mild winters. During our study, the mean daily January minimum temperature was −5.9°C (range = −7 to −5.1; 30-yr average = −7.4°C) and average daily maximum in July was 33.6°C (range = 32.4–34.3; 30-yr average = 33.2°C). The average annual precipitation during our study was 62.2 cm (range = 53.5–69.6; 30-yr average = 63.9 cm) with an average of 73% occurring during the growing season (range = 62.9–88.3; http://mesonet.k-state.edu/weather/historical/#!, accessed 28 Sep 2018; http://www.usclimatedata.com, accessed 28 Sep 2018).

The study site contained 18 pastures with an average size of 550 ha (range = 123–1,346 ha). Management varied among pastures; 12 pastures were managed using patch-burn grazing and 6 pastures were grazed with either no prescribed fire or the entire pasture was subjected to prescribed fire, both lacking within-pasture heterogeneity. Within patch-burn grazing pastures, approximately 20–33% of each pasture was burned on a rotational basis during spring, with the entirety of each pasture burned every 3–6 years depending on weather and time considerations, which generally falls within the expected mean fire return interval for our study area (Wright and Bailey 1982, Bragg 1995, Bragg and Steuter 1996, Frost 1998, LANDFIRE 2014). Prescribed fires occurred between 1 March and 30 April. Average burn patch size was 485.4 ha (range = 95.7–1,172.5 ha) with generally ≥80% of the burn patch burned; fires were cooler spring burns (mean temperature at fire line was 213.5°C, range = 79.9–551°C) with some hotter fires in areas with greater fuel (D. A. Haukos, U.S. Geological Survey, unpublished data). Pastures were stocked with yearling or adult female-calf pair domestic cattle at moderate stocking rates (0.80–1.0 ha/animal unit month). Pastures stocked with female-calf pairs were grazed year-round and yearling-stocked pastures were grazed from approximately 15 April through 15 October. Because this property was managed for livestock production, grazing duration of yearlings varied from approximately 60 days to 180 days depending on the cattle market. Pastures containing female-calf pairs and yearlings were rotated every 3–4 years. The amount of land burned each year depended on weather conditions and amount of time that conditions were suitable for burning; therefore, total area burned varied among years. There were no prescribed fires conducted at the study site during 2011 and 2012, and 1 100-ha (~1% of study area) fire in 2013 because of extensive drought in the region during 2011–2013. In 2014, 1,780 ha (13% of study area) were burned in 6 pastures; in 2015, 1,120 ha (8% of study area) were burned in 7 pastures; in 2016, 2,600 ha (19% of study area) were burned in 13 pastures; and in 2017, 2,251 ha (16.5% of study area) were burned in 6 pastures (Fig. 1).

METHODS

Lesser Prairie-Chicken Use of Burned Patches

To assess female lesser prairie-chicken response to the availability of burned patches, we captured lesser prairie-chickens at lek sites using walk-in traps (Haukos et al. 1990, Schroeder and Braun 1991) and drop nets (Silvy et al. 1990). We trapped leks continuously throughout the lekking season (~15 Mar–1 May). Upon capture, we sexed birds using tail coloration, pinnae length, and presence of an eye comb (Copelin 1963). We fitted females with either a 22-g global positioning system (GPS) satellite transmitter (platform transmitting terminal [PTT]; Microwave Telemetry, Columbia, MD, USA) or a 15-g very-high-frequency (VHF) radio transmitter (Advanced Telemetry Systems, Isanti, MN, USA). Transmitters were <3.5% of body mass. In 2014 and 2015, we assigned GPS and VHF transmitters to every other bird. During 2016 and 2017, we deployed only GPS transmitters. The GPS transmitters were rump-mounted using a Teflon® ribbon harness around the legs (Dzialak et al. 2011). All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocols 3241 and 3703), and Kansas Department of Wildlife, Parks and Tourism scientific collection permits (SC-042-2013, SC-079-2014. SC-001-2015, SC-014-2016, and SC-018-2017).

We located female lesser prairie-chickens fitted with VHF radio transmitters 3–4 times per week throughout the year. We triangulated individuals from 3 to 5 locations using a 3-element hand-held Yagi antenna and either an Advanced Telemetry Systems receiver (R4000, R4500) or a Communications Specialists receiver (R1000, Communications Specialists, Orange, CA, USA; Cochran and Lord 1963) from 50–100 m to minimize observer influence on the bird's location. We determined approximate locations and error polygons associated with the triangulations using Location of a Signal (Ecological Software Solutions, Hegymagas, Hungary). To maintain consistent accuracy between transmitter types, we used only locations with <1,000-m^2 error polygons, similar to GPS transmitter error of 1,018 m^2, to estimate location of VHF-tagged birds. We tracked lesser prairie-chickens marked with satellite transmitters using the GPS-Argos system. The system recorded daily GPS locations approximately every 2 hours between 0600 and 2400, resulting in 10 locations per day; we downloaded locations weekly. Potential location error associated with the use of these transmitters was <18 m. When a female appeared to be sitting on a nest (≥2 days of the same location), we walked to her location and flushed her from her nest to note its precise location.

Used and Available Vegetation Structure and Composition

We divided the study area into patches stratified by time since fire and pasture to quantify available vegetation structure and composition (Fig. 1). Within each patch, we randomly generated 20–50 vegetation surveys points using ArcMap 10.2 (Esri, 2013, Redlands, CA, USA). We measured vegetation in each patch 3 times a year (spring [Apr–May], summer [Jun–Aug], and winter [Nov–Feb]) for the duration of the study (e.g., patches burned in 2014 were surveyed in 2014–2017, with 2014 data categorized as a year-of-fire patch, 2015 as a 1-year post-fire patch, 2016 as a 2-year post-fire patch, and 2017 as a 3-year post-fire patch).

Random vegetation surveys followed the protocol adopted by the United States Department of Agriculture Natural Resources Conservation Service Lesser Prairie-Chicken Initiative and Lesser Prairie-Chicken Interstate Working Group as sampling strategies for standardization among field sites (Pitman et al. 2005, Grisham 2012). At each random point, we centered 2 perpendicular 8-m transects in a north-south and east-west orientation. At point center and 4 m to the north, south, east, and west, we estimated the percent cover of grasses, forbs, shrubs, litter, and bare ground using a 60-cm × 60-cm quadrat (vegetation composition; Daubenmire 1959). At point center, we also estimated height of visual obstruction at 100%, 75%, 50%, 25%, and 0% obstruction classes to the nearest decimeter from a distance of 4 m and a height of 1 m using a Robel pole (vegetation structure; Robel et al. 1970), where we measured 100% obstruction as the highest decimeter that we were not able to see; 75%, 50%, and 25% obstruction as the highest decimeter for the respective percent of obstruction; and 0% obstruction as the lowest decimeter where no vegetation obstructed the pole.

We conducted vegetation surveys at used locations during each biological season to determine patch types and vegetation characteristics used by lesser prairie-chickens. During lekking, post-nesting, and nonbreeding seasons, we randomly selected 2 telemetry location points per bird per week to conduct vegetation surveys for non-nesting birds. During the nesting season, we conducted vegetation surveys only at nesting sites. We followed the same vegetation sampling protocol at these locations as specified above for available locations. We collected a different number of used and available samples during each season because of differences in the number of birds and observer effort.

Data Analysis

Available vegetation.—To assess if patch-burn grazing generated heterogeneous vegetation patches, we used a multivariate analysis of variance (MANOVA) to test compositional (% cover) and structural characteristics (visual obstruction readings) among seasons and patch types (time-since-fire patches). When a significant interaction between these variables (patch and season; Wilks' lambda $P < 0.05$) was present, we proceeded with separate analyses by season. Following a significant MANOVA (Wilks' lambda $P < 0.05$), we used an analysis of variance (ANOVA) with a Tukey *post hoc* analysis to identify univariate differences among patch types ($P < 0.05$) separately for each dependent variable.

Habitat selection relative to time since fire.—To assess lesser prairie-chicken nest-site selection in relation to time-since-fire patches, we used the Neu et al. (1974) method with the recommended Bailey (1980) confidence intervals (Cherry 1996, Aldredge and Griswold 2006). We used this method to assess nest-site selection because of limited sample sizes in some of the time-since-fire patches. This method requires that expected and used proportions are calculated and confidence intervals are developed around the used proportions (Neu et al. 1974). We derived the expected number of nests in each patch for each year independently because the number of nests and availability in each patch category changed annually based on burning patterns that year. To identify selection or avoidance by lesser prairie-chickens of certain patch types for nest placement, we calculated and compared the Bailey (1980) confidence intervals of the used proportions of that patch type to the available proportion of that patch type. If the confidence intervals around use overlapped the proportion available, no selection occurred. If the confidence intervals did not overlap available, then lesser prairie-chickens were selecting (use > available) or avoiding (use < available) nesting within that patch.

We used a use versus available study design within a resource selection framework to estimate habitat (i.e., patch) selection by female lesser prairie-chickens outside the nesting season (Boyce et al. 2002, Manly et al. 2002). We evaluated differential patch use throughout the year using seasonal periods (lekking, post-nesting, and nonbreeding). We censored locations for 4 days after capture because movements may not be normal during this period as the bird adjusts to the transmitter. To define availability, we buffered each of 7 lek locations within our study area by 3.2 km, the average distance that typical movement occurs and the area surrounding leks that conservation actions are targeted around active leks (Hagen et al. 2004, Hagen and Giesen 2020); once each lek was buffered, we merged all buffered leks to create an availability polygon that we used for each bird. To assess availability, we used the spsample function from package sp (version 1.4-2; Pebesma and Bivand 2005) in Program R (version 4.0.2; R Core Team 2020) to generate an equal number of random points as used points throughout the available area. We then extracted time-since-fire patch for each random and used location. We used a binomial generalized linear mixed-effects regression model with a logit link in a logistic framework to evaluate patch selection by season (Manly et al. 2002). In this model, we used number of years post fire as a fixed effect and bird identification as a random effect of the intercept. Using this model, we compared the different time-since-fire patches to areas that had not been burned in ≥4 years (unburned). We fit these models for each season using the glmer() function in the lme4 package (version 1.1-23; Bates et al. 2015) in Program R.

Vegetation selection.—We assessed vegetation characteristics selected by female lesser prairie-chickens using a use versus available study design within a resource selection function framework (Boyce et al. 2002, Manly et al. 2002). We modeled selection during each season for both vegetation composition and structure. For each season, we fit sub-models for composition and structure variable and then combined these in a final stage (Bromaghin et al. 2013, Morin et al. 2020). We compared linear and quadratic models of each vegetation variable (% cover of bare ground, forbs, grass, litter, shrubs, and visual obstruction) to identify the most likely relationship (linear or quadratic) for each variable. Once we identified the relationship of each variable, we generated models based on ecological possibility (Tables S1–S4, available in Supporting Information). These models included a model for each composition variable, herbaceous vegetation (grass + forbs), herbaceous + litter, herbaceous + bare, each composition model previously mentioned + visual obstruction, visual obstruction, and a null model. During some seasons, grass cover and litter were correlated ($|r^2| > 0.6$), so we did not include these variables in the same model during that season; in these cases, the herbaceous + litter model only included forbs + litter. We ranked candidate models using Akaike's Information Criterion adjusted for small sample size (AIC_c); we considered models with $\Delta\text{AIC}_c \le 2$ equally parsimonious and averaged all models with $\Delta\text{AIC}_c \le 2$ to obtain model coefficients (Burnham and Anderson 2002).

RESULTS

Available Vegetation

We sampled vegetation at 3,274 available vegetation plots across all seasons; 1,186 during the lekking season, 1,559 during the post nesting season, and 529 during the nonbreeding season. Available vegetation differed among patches for both visual obstruction (Wilks lambda = 0.71, $P < 0.001$) and composition (Wilks lambda = 0.91, $P < 0.001$). As time since fire increased, visual obstruction increased by an average of 4.78 times in each visual obstruction class during the lekking and nesting season, 2.23 times during the post-nesting season, and 1.93 times during the nonbreeding season, with >2-year post-fire patches having the greatest vertical structure (Table 1). For composition, grass increased (1.66 times during lekking and nesting, 0.85 times during post-nesting, and 0.82 times during the nonbreeding season) and bare ground decreased (3.28 times during lekking and nesting, 2.60 times during post-nesting, and 2.45 times during the nonbreeding season) as time since fire increased. There were no clear trends in relation to time since fire for litter, forb, and shrub cover (Table 2).

Time-Since-Fire Patch Selection

Nesting season.—We captured 66 female lesser prairie-chickens; 39 and 27 were fitted with satellite and VHF transmitters, respectively. Ten of these birds left the study area ($n = 4$) or died ($n = 6$) before nesting. We located 52 nests and 4 renest attempts from these

Table 1. Mean (±95% CI) visual obstruction (VOR; dm) based on time-since-fire patches available to female lesser prairie-chickens during each season, south-central Kansas, USA, 2014–2017. We measured visual obstruction using a Robel pole and estimated it at 100%, 75%, 50%, 25%, and 0% obstruction classes. Means followed by the same superscript do not differ ($P > 0.05$) among time-since-fire patch types within each VOR class by season.

Season	100% VOR	75% VOR	50% VOR	25% VOR	0% VOR
Lekking and nesting					
Year of fire	0.07 ± 0.03^{A}	0.22 ± 0.05^{A}	0.39 ± 0.07^{A}	0.81 ± 0.10^{A}	2.67 ± 0.14^{A}
1 year post fire	0.40 ± 0.08^{B}	0.86 ± 0.12^{B}	1.27 ± 0.14^{B}	1.85 ± 0.17^{B}	4.80 ± 0.29^{B}
2 years post fire	$0.53 \pm 0.13^{B,C}$	$1.04 \pm 0.17^{B,C}$	$1.42 \pm 0.21^{B,C}$	1.95 ± 0.26^{B}	4.33 ± 0.36^{B}
>2 years post fire	0.65 ± 0.06^{C}	1.21 ± 0.08^{C}	1.69 ± 0.10^{C}	2.42 ± 0.12^{C}	5.55 ± 0.19^{C}
Post-nesting					
Year of fire	0.33 ± 0.09^{A}	0.92 ± 0.14^{A}	1.35 ± 0.15^{A}	1.99 ± 0.16^{A}	4.07 ± 0.18^{A}
1 year post fire	0.90 ± 0.12^{B}	1.65 ± 0.14^{B}	2.21 ± 0.17^{B}	2.95 ± 0.19^{B}	5.34 ± 0.21^{B}
2 years post fire	0.87 ± 0.16^{B}	1.67 ± 0.20^{B}	$2.31 \pm 0.25^{B,C}$	$3.13 \pm 0.29^{B,C}$	5.10 ± 0.34^{B}
>2 years post fire	1.28 ± 0.08^{C}	2.03 ± 0.09^{C}	2.58 ± 0.10^{C}	3.38 ± 0.11^{C}	6.00 ± 0.13^{C}
Nonbreeding					
Year of fire	0.42 ± 0.10^{A}	0.89 ± 0.12^{A}	1.20 ± 0.14^{A}	2.00 ± 0.19^{A}	6.31 ± 0.55^{A}
1 year post fire	0.60 ± 0.17^{A}	1.13 ± 0.28^{A}	1.40 ± 0.31^{A}	2.12 ± 0.36^{A}	$6.78 \pm 0.68^{A,B}$
>2 years post fire	1.00 ± 0.10^{B}	1.82 ± 0.14^{B}	2.53 ± 0.18^{B}	3.71 ± 0.22^{B}	7.66 ± 0.32^{B}

Table 2. Mean (±95% CI) available percent cover of litter, grass, forbs, bare ground, and shrubs, as measured with a 60-cm × 60-cm Daubenmire frame, within time-since-fire patches available to female lesser prairie-chickens within lekking and nesting, post-nesting, and nonbreeding seasons, south-central Kansas, USA, 2014–2017. Means followed by the same superscript do not differ ($P > 0.05$) among time-since-fire patch types within each vegetation composition variable by season.

Season	Litter	Grass	Forbs	Bare ground	Shrubs
Lekking and nesting					
Year of fire	16.57 ± 1.48^{C}	39.39 ± 2.05^{A}	8.81 ± 0.81^{A}	35.31 ± 2.46^{C}	0.70 ± 0.31^{A}
1 year post fire	6.38 ± 0.71^{A}	59.95 ± 2.39^{B}	17.70 ± 1.29^{B}	17.25 ± 2.33^{B}	0.38 ± 0.22^{A}
2 years post fire	$4.47 \pm 0.66^{A,B}$	$66.29 \pm 4.29^{B,C}$	15.57 ± 1.98^{B}	$13.22 \pm 4.23^{B,C}$	0.70 ± 0.60^{A}
≥3 years post fire	8.22 ± 0.60^{B}	65.29 ± 1.56^{C}	16.25 ± 0.81^{B}	10.75 ± 1.37^{A}	1.06 ± 0.38^{A}
Post-nesting					
Year of fire	6.13 ± 0.56^{A}	54.82 ± 1.94^{A}	16.59 ± 1.10^{A}	22.02 ± 1.90^{C}	$0.69 \pm 0.24^{B,C}$
1 year post fire	6.66 ± 0.84^{A}	60.70 ± 2.35^{B}	20.17 ± 1.36^{B}	13.38 ± 2.51^{B}	$0.43 \pm 0.23^{A,B}$
2 years post fire	6.01 ± 0.82^{A}	$62.47 \pm 3.96^{B,C}$	$17.59 \pm 1.82^{A,B}$	15.08 ± 4.65^{B}	$0.69 \pm 0.44^{B,C}$
≥3 years post fire	8.01 ± 0.47^{B}	64.46 ± 1.19^{C}	18.46 ± 0.74^{B}	8.48 ± 0.87^{A}	1.33 ± 0.32^{C}
Nonbreeding					
Year of fire	6.74 ± 0.98^{A}	56.70 ± 2.90^{A}	$15.02 \pm 1.75^{B,C}$	22.11 ± 2.73^{B}	0.77 ± 0.39^{A}
1 year post fire	6.96 ± 1.18^{A}	61.61 ± 3.80^{A}	16.89 ± 2.30^{C}	15.59 ± 3.40^{C}	0.69 ± 0.80^{A}
≥2 years post fire	7.99 ± 0.65^{A}	69.80 ± 1.69^{B}	13.79 ± 0.97^{A}	9.01 ± 1.27^{A}	0.51 ± 0.23^{A}

transmitter-equipped birds within the study area: 29, 17, 6, and 4 nests in 2014–2017, respectively. The number of nests in 2016 and 2017 was lower because fewer individuals were captured within the study area. There was a difference between the number of expected and observed nests in time-since-fire patches ($\chi^2_3 = 12.2$, $P = 0.007$; Table 3). Females avoided nesting in year-of-fire patches and selected locations to nest in ≥4-year post-fire patches (Table 3). The observed number of nests in 1- and 2-year post-fire patches did not differ from expected based on availability (Table 3).

Non-nesting seasons.— We recorded 13,774 locations from 38 satellite and 12 VHF females during the lekking season; 15,081 locations from 22 satellite and 11 VHF females during the post-nesting season; and 13,685 locations from 18 satellite and 8 VHF females in the nonbreeding season. Female lesser prairie-chickens had different responses to time-since-fire patches relative to unburned areas throughout their life cycle. During the lekking season, females avoided year-of-fire (odds ratio = 0.470, 95% CI = 0.431, 0.512) and 3-year post-fire patches (odds ratio = 0.600, 95% CI = 0.488, 0.738) and selected 1- (odds ratio = 1.646, 95% CI = 1.501, 1.806) and 2-year post-fire (odds ratio = 4.094, 95% CI = 3.611, 4.641) patches relative to unburned areas within the study site (Table 4). Post-nesting, females selected year-of-fire (odds ratio = 1.978, 95% CI = 1.840, 2.127), 1- (odds ratio = 3.624, 95% CI = 3.339, 3.933), and 2-year post-fire patches (odds ratio = 2.143, 95% CI = 1.901, 2.416) and avoided 3-year post-fire patches (odds ratio = 0.004, 95% CI = 0.001, 0.029) relative to unburned patches (Table 4). In the nonbreeding season, females selected year-of-fire (odds ratio = 1.093, 95% CI = 1.018, 1.174) and 1-year post-fire (odds ratio = 1.590, 95% CI = 1.473, 1.715) patches and used 2-year post-fire (odds ratio = 0, 95% CI = 0, ∞) patches equal to their availability relative to unburned areas (Table 4).

Vegetation Selection

We sampled vegetation at 551 used locations and 1,186 random locations during the lekking season, 582 used locations and 1,559 random locations during the post-nesting season, and 722 used locations and 529 random locations during the nonbreeding season. During the lekking season, our top model predicting lesser prairie-chicken habitat selection was the grass ($\beta = -0.003$; 95% CI = −0.027, 0.021) + grass^2 ($\beta = -0.00009$; 95% CI = −0.0003, 0.0001) + forbs ($\beta = -0.005$; 95% CI = −0.031, 0.02) + forbs^2 ($\beta = 0.0003$; 95% CI = −0.0002, 0.0007) + bare ground ($\beta = -0.007$; 95% CI = −0.026, 0.013) + bare ground^2 ($\beta = -0.0003$; 95% CI = −0.0006, −0.00003) + visual obstruction ($\beta = 0.781$; 95% CI = −0.535, 1.04) + visual obstruction^2 ($\beta = -0.122$, 95% CI = −0.168, −0.079) model (Table S1). This model indicates that lesser prairie-chickens select sites with 25% visual obstruction of 2–4 dm, sites with less bare ground, more forb cover, and less grass cover (Fig. 2).

Table 3. The cumulative proportion of available time-since-fire patch type to nesting lesser prairie-chickens compared to the proportion of nests in each time-since-fire patch type in south-central Kansas, USA, 2014–2017. The presented 95% confidence interval is for proportion used; if this range does not overlap the proportion available, then there is selection or avoidance for the specific patch type.

			95% CI		
Patch type	Proportion available (expected number of nests)	Proportion used (observed number of nests)	Lower	Upper	Selection or avoidance[a]
Year of fire	0.18 (10)	0.00 (0)	0.00	0.09	–
1 year post fire	0.09 (5)	0.07 (4)	0.01	0.20	.
2 years post fire	0.04 (2)	0.05 (3)	0.00	0.18	.
3 years post fire	0.01 (1)	0.00 (0)	0.00	0.08	.
≥4 years post fire	0.69 (38)	0.88 (49)	0.71	0.96	+

[a] (–) represents avoidance, (.) represents proportional use, and (+) represents selection.

Table 4. Beta estimates (β), standard error (SE), test statistic (*P* value), and 95% confidence intervals (CI) for the probability of use from a linear mixed effects logistic regression model for different time-since-fire patches when compared to patches ≥4 years post fire (unburned) during the lekking, post-nesting, and non-breeding seasons for lesser prairie-chickens in south-central Kansas, USA, 2014–2017. During the nonbreeding season, 3-year post-fire patches were not on the landscape.

Season	Predictors	β	SE	*P*	95% CI
Lekking	Year of fire	−0.755	0.044	<0.001	(−0.843, −0.669)
	1 year post fire	0.499	0.047	<0.001	(0.406, 0.591)
	2 years post fire	1.409	0.064	<0.001	(1.284, 1.535)
	3 years post fire	−0.510	0.105	<0.001	(−0.716, −0.303)
Post-nesting	Year of fire	0.682	0.037	<0.001	(0.610, 0.755)
	1 year post fire	1.288	0.042	<0.001	(1.206, 1.369)
	2 years post fire	0.762	0.061	<0.001	(0.642, 0.882)
	3 years post fire	−5.500	1.004	<0.001	(−7.467, −3.532)
Non-breeding	Year of fire	0.089	0.020	0.014	(0.018, 0.160)
	1 year post fire	0.463	0.039	<0.001	(0.388, 0.539)
	2 years post fire	−25.840	20,770	0.999	(−40,739, 40,687)

The top-ranked models during the nesting season were the litter + visual obstruction model (Akaike weight [w_i] = 0.51) and litter + herbaceous (forbs) + visual obstruction model ($\Delta\text{AIC}_c = 1.22$, $w_i = 0.28$; Table S2). We averaged these models, with results indicating that the probability of nest-site selection increased with increased litter availability (β = 0.093; 95% CI = 0.029, 0.157), showed no relationship with forbs (β = −0.035; 95% CI = −0.106, 0.036), and increased as 50% visual obstruction increased (β = 3.366; 95% CI = 2.033, 4.698; Fig. 3).

The top-ranked models during the post-nesting season were the forbs^2 + bare ground^2 + visual obstruction^2 ($w_i = 0.59$) and herbaceous (grass^2 + forbs^2) + bare ground^2 + visual obstruction^2 ($\Delta\text{AIC}_c = 0.70$, $w_i = 0.41$; Table S3) models. We averaged these models and lesser prairie-chickens selected 0–30% bare ground (bare ground β = 0.058; 95% CI = 0.036, 0.080, bare ground^2 β = −0.001; 95% CI = −0.002, −0.0009), 30–50% forb cover (forb β = 0.03; 95% CI = 0.005, 0.055, forb^2 β = −0.0004; 95% CI = −0.0008, 0.0001), showed no selection for grass cover (grass β = −0.006; 95% CI = −0.042, 0.012, grass^2 β = 0.00003; 95% CI = −0.0002, 0.0003), and selected 50% visual obstruction between 3–5 dm (visual obstruction β = 0.472; 95% CI = 0.025, 0.696, visual obstruction^2 β = −0.061; 95% CI = −0.098, −0.024; Fig. 4).

During the nonbreeding season, the top-ranked model was the grass (β = −0.024; 95% CI = −0.052, −0.005) grass^2 (β = 0.0004; 95% CI = 0.0001, 0.0006) + forbs (β = 0.103; 95% CI = 0.072, 0.136) + forbs^2 (β = −0.001; 95% CI = −0.002, −0.0007) + litter (β = 0.079; 95% CI = 0.044, 0.115) + litter^2 (β = −0.002; 95% CI = −0.003, −0.0004) + visual obstruction (β = −0.739; 95% CI = −1.023, −0.44) + visual obstruction^2 (β = −0.061; 95% CI = −0.098, −0.024; Table S4) model. This model indicated that lesser prairie-chickens selected 20–40% litter, 30–50% forb cover, avoided areas of intermediate grass cover, and selected sites with <1 dm of 100% visual obstruction during the nonbreeding season (Fig. 5).

DISCUSSION

Information on the influence of prescribed fire and patch-burn grazing on grassland vegetation and lesser prairie-chicken habitat selection provides information for future habitat management. Our study demonstrates that grasslands modified with prescribed fire through patch-burn grazing provide a structurally heterogeneous landscape and lesser prairie-chickens select different time-since-fire patches during different stages of their life history. Female lesser prairie-chickens selected 1- and 2-year post-fire patches during the lekking season, ≥4-year post-fire patches during the nesting season, year-of-fire and 1- and 2-year post-fire patches during the post-nesting season, and year-of-fire and 1-year post-fire patches during the nonbreeding season. Specifically, our work documented that patch-burn grazing generated a diverse array of vegetation conditions across the landscape and lesser prairie-chickens selected patches with different times since fire depending on their vegetation resource needs during each life-history stage.

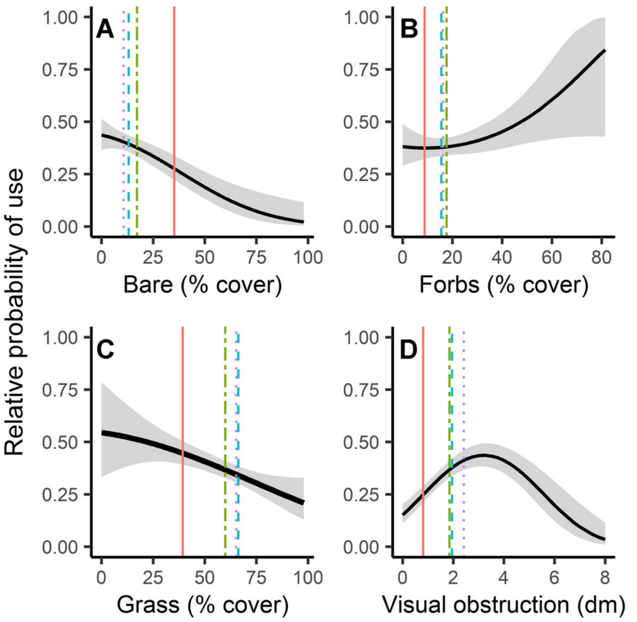


Figure 2. Relative probability of use by lesser prairie-chickens generated from the top logistic regression model during the lekking season for 4 vegetation variables: A) bare ground (% cover), B) forbs (% cover), C) grass (% cover), and D) 25% visual obstruction (dm), south-central Kansas, USA, 2014–2017. Vertical lines represent mean percent cover available in each time-since-fire patch: year of fire (solid red), 1 year post fire (double dashed green), 2 years post fire (dashed blue), and >2 years post fire (dotted purple).

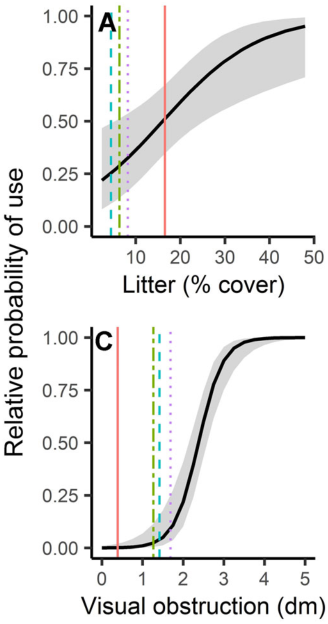


Figure 3. Relative probability of use by lesser prairie-chickens generated from the top logistic regression model during the nesting season for 3 vegetation variables: A) litter (% cover), B) forbs (% cover), and C) 50% visual obstruction (dm), south-central Kansas, USA, 2014–2017. Vertical lines represent mean percent cover available in each time-since-fire patch: year of fire (solid red), 1 year post fire (double dashed green), 2 years post fire (dashed blue), and >2 years post fire (dotted purple).

Time-since-fire patch selection by lesser prairie-chickens was influenced by their selection for visual obstruction. Across all seasons, visual obstruction varied with time-since-fire patches, and generally increased as time since fire increased. Within the nesting and nonbreeding seasons, females selected time-since-fire patches where available vegetation structure was similar to vegetation conditions that females selected for. Lesser prairie-chickens select nest sites with greater visual obstruction than available to conceal their nests (Pitman et al. 2005, Hagen et al. 2013, Grisham et al. 2014, Lautenbach et al. 2019). Nest success increases with increased visual obstruction (Lautenbach et al. 2019), which we observed in the ≥4-year post-fire patches. Similarly, prescribed fire in a sand-shinnery oak (*Quercus harvardii*) community resulted in similar prediction, with the reduction in nesting habitat for lesser prairie-chickens in year-of-fire and 1-year post-fire and potential nesting habitat being found in ≥2-year post-fire patches (Boyd and Bidwell 2001). During the nonbreeding season, lesser prairie-chickens selected sites with lower visual obstruction that was prevalent in year-of-fire and 1-year post-fire patches, which may provide greater forage quality and potentially aid their ability to detect predators (Lautenbach 2017).

Selected time-since-fire patch and available vegetation composition within that patch rarely matched selection for vegetation composition features. This pattern may have resulted from lesser prairie-chicken females cuing in on vegetation structure over composition (Hagen et al. 2013). Selection for visual obstruction may have diluted any effects related to changes in composition as it pertained to time since fire. During the post-nesting season, females selected patches <2 years post fire that generally maintained a proportion of bare ground similar to what they select (10–30% bare ground). Females likely select these areas because they facilitate movement for predator avoidance, while still providing forb cover that provides increased food abundance (Hagen et al. 2005, Fields et al. 2006, Hannon and Martin 2006, Lautenbach 2015). The overall mismatch between composition selection and patch selection indicates that females were rarely cuing in on vegetation composition differences among time-since-fire patches and suggests patch selection was primarily influenced by differences in vegetation structure relative to time since fire. Our observed patch selection supported predictions that lesser prairie-chickens would nest in ≥4-year post-fire patches and lead broods (i.e., post-nesting) to 2- and 3-year post-fire patches (Boyd and Bidwell 2001, Thacker and Twidwell 2014).

Because patch selection varied among seasons, it is important to maintain availability of a suite of time-since-fire patches on the landscape for lesser prairie-chickens. It is also important that these patches are proximate to each other to facilitate bird movement, minimizing distance moved and associated potential hazards such as predation (Robinson et al. 2018*b*). Proximity of recently burned patches may be important after a successful nest, when a female must relocate her brood to an available patch with sufficient food and cover resources (Fuhlendorf and Engle 2001, Hagen et al. 2005, Bell et al. 2010, Lautenbach 2015).

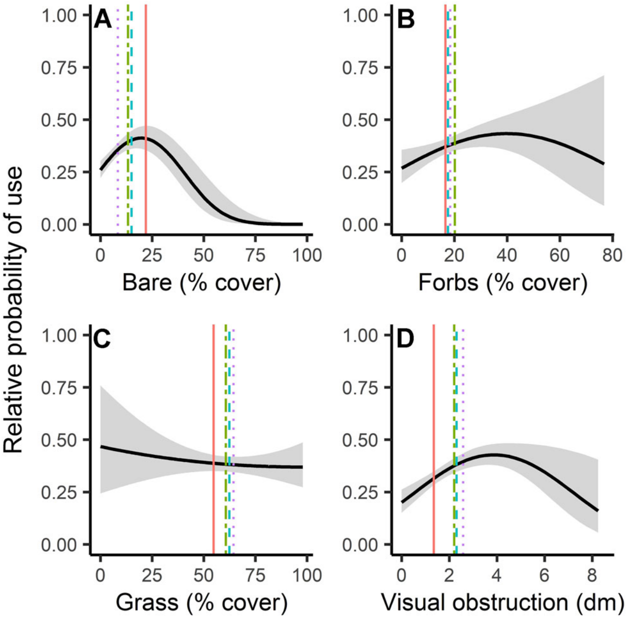


Figure 4. Relative probability of use by lesser prairie-chickens generated from the top logistic regression model during the post-nesting season for 4 vegetation variables: A) bare ground (% cover), B) forbs (% cover), C) grass (% cover), and D) 50% visual obstruction (dm), south-central Kansas, USA, 2014–2017. Vertical lines represent mean percent cover available in each time-since-fire patch: year of fire (solid red), 1 year post fire (double dashed green), 2 years post fire (dashed blue), and >2 years post fire (dotted purple).

With a patch-burn grazing management system, consistent use of fire across the landscape helps maintain lesser prairie-chicken habitat by providing heterogenous vegetation patches on the landscape required throughout their life cycle (Hagen et al. 2013, Haukos and Zaveleta 2016). Furthermore, because prescribed fire helps reduce tree cover in grasslands (Buehring et al. 1971, Owensby et al. 1973, Twidwell et al. 2013, Smit et al. 2016) and patch-burn grazing reduces woody encroachment (Capozzelli et al. 2020), prescribed fire has the potential to control woody encroachment and protect lesser prairie-chicken habitat from potential tree invasion. Maintaining landscapes free of trees is an important conservation action because lesser prairie-chickens avoid trees (Lautenbach et al. 2017).

Previous research on lesser prairie-chicken response to fire is limited to Cannon and Knopf (1979) showing that lesser prairie-chickens move leks to recently burned areas in a previously unburned landscape. Studies on greater prairie-chickens (*Tympanuchus cupido*) indicate that patch-burn grazing improves landscape conditions compared to traditional management practices (McNew et al. 2015, Winder et al. 2017). Female greater prairie-chickens select >1-year post-fire patches during the breeding season and <1-year post-fire patches during the nonbreeding season (Winder et al. 2017). These findings are similar to ours, in that female lesser prairie-chickens selected areas with intermediate time since fire during the post-nesting season and females selected patches with less time since fire during the nonbreeding season. In greater prairie-chicken studies, traditional management practices predominately include annual burning followed by short duration high-intensity stocking, a practice that is not implemented within the lesser prairie-chicken range. Future work on patch-burn grazing should examine fitness consequences of lesser prairie-chickens at the site level between patch-burn grazing systems and traditional management practices (whole pasture grazing with no prescribed fire).

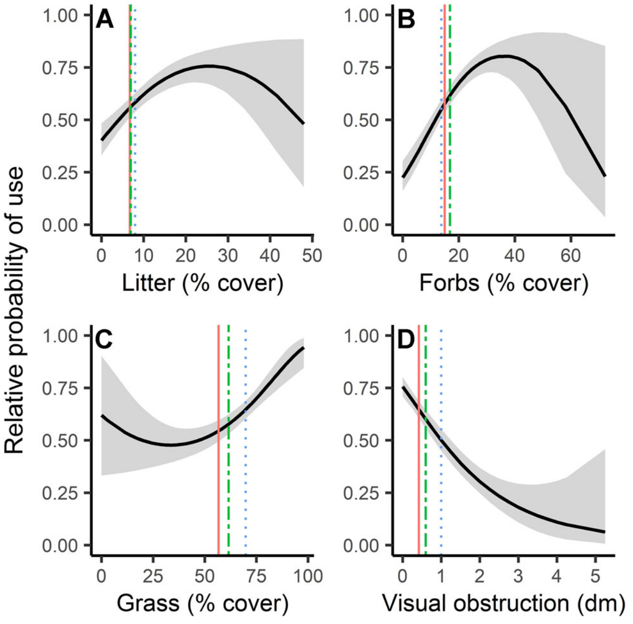


Figure 5. Relative probability of use by lesser prairie-chickens generated from the top logistic regression model during the nonbreeding season for 4 vegetation variables: A) litter (% cover), B) forbs (% cover), C) grass (% cover), and D) 100% visual obstruction (dm), south-central Kansas, USA, 2014–2017. Vertical lines represent mean percent cover available in each time-since-fire patch: year of fire (solid red), 1 year post fire (double dashed green), and >2 years post fire (dotted purple).

Our results demonstrate that female lesser prairie-chickens respond to heterogeneity generated through patch-burn grazing by selecting patches with vegetation characteristics matching their resource needs. Our data further demonstrate that patch-burn grazing can provide the necessary vegetation heterogeneity required throughout different stages of the lesser prairie-chicken annual cycle and has the potential to help maintain quality habitat by controlling tree encroachment (Hagen et al. 2013, Haukos and Zaveleta 2016, Lautenbach et al. 2017, Capozzelli et al. 2020). Our results also emphasize that lesser prairie-chickens readily use a heterogeneous landscape generated through patch-burn grazing, selecting patches that should maintain or potentially enhance survival and recruitment similar to greater prairie-chickens (Hovick et al. 2014*b*; McNew et al. 2012, 2015; Winder et al. 2017).

MANAGEMENT IMPLICATIONS

Maintaining structural heterogeneity on the landscape ensures that there is adequate habitat for lesser prairie-chickens throughout the year. Implementing patch-burn-grazing with a 3–5-year rotation, similar to historical fire return intervals in this area, will help maintain vegetation structural heterogeneity on the landscape required by lesser prairie-chickens. Perhaps most importantly, prescribed fire is one of the most effective tools in controlling the spread of eastern redcedar. Prescribed fire during our study was applied during years of average to above average precipitation in the eastern portion of the lesser prairie-chickens range, with prudent management necessary during drought conditions to avoid reducing habitat. Maintenance of large landscapes and increasing usable space is paramount for the species' occurrence and success in the southern Great Plains. Further, using lesser prairie-chickens as an umbrella species for managing grasslands will aid in the conservation of multiple taxa of grassland-obligate small mammals, birds, reptiles, amphibians, and insects.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank K. E. Sexson, J. L. Kramer, M. W. Mitchener, D. K. Dahlgren, J. A. Prendergast, K. A. Fricke, D. J. Kraft, P. G. Kramos, A. A. Flanders, and our many field assistants who helped collected the data for their assistance with the project. We thank C. Williams, B. E. Ross, and 3 anonymous reviewers for providing feedback on earlier versions of this manuscript. Research was funded by the United States Department of Agriculture (USDA), Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative; Kansas Department of Wildlife, Parks, and Tourism (Federal

Assistance Grant KS W-73-R-3); and USDA Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62).

LITERATURE CITED

Aldredge, J. R., and J. Griswold. 2006. Design and analysis of resource selection studies for categorical resource variables. Journal of Wildlife Management 70:337–346.

Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. Ecology and Evolution 1:132–144.

Allred, B. W., J. D. Scasta, T. J. Hovick, S. D. Fuhlendorf, and R. G. Hamilton. 2014. Spatial heterogeneity stabilizes livestock productivity in a challenging climate. Agriculture, Ecosystems, and Environment 193:37–41.

Askins, R. A., F. Chávez-Ramírez, 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. Ornithological Monographs 64:1–46.

Bailey, B. J. R. 1980. Large sample simultaneous confidence intervals for the multinomial probabilities based on transformations of the cell frequencies. Technometrics 22:583–589.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed effects models using lme4. Journal of Statistical Software 67:1–48.

Bell, L. A., S. D. Fuhlendorf, M. A. Patten, D. H. Wolfe, and S. K. Sherrod. 2010. Lesser prairie-chicken hen and brood habitat use on sand shinnery oak. Rangeland Ecology & Management 63:478–486.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Boyd, C. S., and T. G. Bidwell. 2001. Influence of prescribed fire on lesser prairie-chicken habitat in shinnery oak communities in western Oklahoma. Wildlife Society Bulletin 29:938–947.

Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M. N. Tuanmu. 2018. Cheatgrass *(Bromus tectorum)* distribution in the intermountain western United States and its relationship to fire frequency, seasonality, and ignitions. Biological Invasions 20:1493–1506.

Bragg, T. B. 1995. The physical environment of Great Plains grasslands. Pages 49–81 *in* A. Joern and K. H. Keeler, editors. The changing prairie: North American grasslands. Oxford University Press, New York, New York, USA.

Bragg, T. B., and A. A. Steuter. 1996. Prairie ecology—the mixed prairie. Pages 53–65 *in* F. B. Samson and F. L. Knopf, editors. Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington, D.C., USA.

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. Ecosystems 5:578–586.

Bromaghin, J. F., R. L. McDonald, and S. C. Amstrup. 2013. Plausible combinations: an improved method to evaluate the covariate structure of Cormack-Jolly-Seber mark-recapture models. Open Journal of Ecology 3:11–22.

Buehring, N., P. W. Santelmann, and H. M. Elwell. 1971. Responses of eastern red cedar to control procedures. Journal of Range Management 24:378–382.

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

Cannon, R. W., and F. L. Knopf. 1979. Lesser prairie-chicken response to range fires at the booming ground. Wildlife Society Bulletin 7:44–46.

Capozzelli, J. F., J. R. Miller, D. M. Debinski, and W. H. Schacht. 2020. Restoring the fire–grazing interaction promotes tree–grass coexistence by controlling woody encroachment. Ecosphere 11:e02993.

Chapman, R. N., D. M. Engle, R. E. Masters, and D. M. Leslie, Jr. 2004. Tree invasion constrains the influence of herbaceous structure in grassland bird habitats. EcoScience 11:56–63.

Cherry, S. 1996. A comparison of confidence interval methods for habitat use-availability studies. Journal of Wildlife Management 60: 653–658.

Cochran, W. W., and R. D. Lord. 1963. A radio-tracking system for wild animals. Journal of Wildlife Management 27:9–24.

Copelin, F. F. 1963. The lesser prairie-chicken in Oklahoma. Technical Bulletin No. 6, Oklahoma Department of Wildlife Conservation, Oklahoma City, USA.

Coppedge, B. R., D. M. Engle, S. D. Fuhlendorf, R. E. Masters, and M. S. Gregory. 2001. Urban sprawl and juniper encroachment effects on abundance of wintering passerines in Oklahoma. Pages 225–242 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Springer, New York, New York, USA.

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

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PLoS ONE 6:e26273.

Engle, D. M, B. R. Coppedge, and S. D. Fuhlendorf. 2008. From the dust bowl to the green glacier: human activity and environmental change in Great Plains grasslands. Pages 253–271 *in* O. W. Van Auken, editor. Western North American Juniperus communities: a dynamic vegetation type. Springer, New York, New York, USA.

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

Fields, T. L., G. C. White, W. G. 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.

Fritts, S. R., B. A. Grisham, R. D. Cox, C. W. Boal, D. A. Haukos, P. McDaniel, C. A. Hagen, and D. U. Greene. 2018. Interactive effects of severe drought and grazing on the life history cycle of a bioindicator species. Ecology and Evolution 8:9550–9562.

Frost, C. C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. Tall Timbers Fire Ecology Conference Proceedings 1:76–95.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51:625–632.

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.

Fuhlendorf, S. D., and F. E. Smeins. 1999. Scaling effects of grazing in a semi-arid grassland. Journal of Vegetation Science 10:731–738.

Fuhlendorf, S. D., F. E. Smeins, and W. E. Grant. 1996. Simulation of a fire-sensitive threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecological Modeling 90:245–255.

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

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

Hagen, C. A., and R. D. Elmore. 2016. Synthesis, conclusions, and a path forward. Pages 345–351 *in* D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, USA.

Hagen, C. A., and K. M. Giesen. 2020. Lesser prairie-chicken (*Tympanuchus pallidicinctus*), version 1.0. Account *in* A. Poole, editor. The birds of the world. The Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/364, accessed 19 Jul 2021.

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

Hagen, C. A., D. E. Jamison, K. M. Giesen, and T. Z. Riley. 2004. Guidelines for managing lesser prairie-chicken population 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 habitat in sand sagebrush: invertebrate biomass and vegetation. Wildlife Society Bulletin 33:1080–1091.

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

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. Zavaleta. 2016. Habitat. Pages 99–132 *in* D. A. Haukos and C. W. Boal, editors. Ecology and conservation of lesser prairie-chickens. CRC Press, Boca Raton, Florida, USA.

Hovick, T. J., R. D. Elmore, and S. D. Fuhlendorf. 2014*a*. Structural heterogeneity increases diversity of non-breeding grassland birds. Ecosphere 5:62.

Hovick, T. J., R. D. Elmore, S. D. Fuhlendorf, and D. K. Dahlgren. 2014*b*. Weather constrains the influence of fire and grazing on nesting greater prairie-chickens. Rangeland Ecology & Management 68:186–193.

LANDFIRE. 2014. LANDFIRE mean fire return interval. Wildland Fire Science, Earth Resources Observation and Science Center, U.S. Geological Survey. https://landfire.gov/fri.php. Accessed 28 Oct 2020.

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

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

Lautenbach, J. M., D. A. Haukos, D. S. Sullins, C. A. Hagen, J. D. Lautenbach, J. C. Pitman, R. T. Plumb, S. G. Robinson, and J. D. Kraft. 2019. Factors influencing nesting ecology of lesser prairie-chickens. Journal of Wildlife Management 83:205–215.

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

Manly, B. F., 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. Springer, New York, New York, USA.

McDonald, L., G. Beauprez, G. Gardner, J. Griswold, C. Hagen, F. Harnsby, 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.

McGranahan, D. A., D. M. Engle, S. D. Fuhlendorf, S. J. Winter, J. R. Miller, and D. M. Debinski. 2012. Spatial heterogeneity across five rangelands managed with pyric-herbivory. Journal of Applied Ecology 49:903–910.

McNew, L. B., T. J. Prebyl, and B. K. Sandercock. 2012. Effects of rangeland management on the site occupancy dynamics of prairie-chickens in a protected prairie preserve. Journal of Wildlife Management 76:38–47.

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

Morin, D. J., C. B. Yackulic, J. E. Diffendorfer, D. B. Lesmeister, C. K. Nielsen, J. Reid, and E. M. Schauber. 2020. Is your ad hoc model selection strategy affecting your multimodel inference? Ecosphere 11:e02997.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541–545.

Ortmann, J., J. Stubbendieck, R. A. Masters, G. H. Pfeiffer, and T. B. Bragg. 1998. Efficacy and costs of controlling eastern redcedar. Journal of Range Management 58:158–163.

Owensby, C. E., K. R. Blan, B. J. Eaton, and O. G. Russ. 1973. Evaluation of eastern redcedar infestations in the northern Kansas Flint Hills. Journal of Range Management 26:256–260.

Pavlacky, D. C., B. B. Woiderski, R. A. Sparks, A. Van Boer, and A. W. Green. 2019. Effectiveness monitoring of the lesser prairie-chicken initiative and conservation reserve program for managing the biodiversity and population size of grassland birds. Technical Report # LPCI-16-02, Bird Conservancy of the Rockies, Fort Collins, Colorado, USA.

Pebesma, E. J., and R. S. Bivand. 2005. Classes and methods for spatial data in R. R News 5(2):9–113.

Pickett, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129–136.

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.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. It's not easy being green: wind energy and a declining grassland bird. BioScience 59:257–262.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93:697–703.

Ratajczak, Z., J. B. Nippert, J. C. Hartman, and T. W. Ocheltree. 2011. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. Ecosphere 2:121.

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

Robinson, S. G., D. A. Haukos, R. T. Plumb, J. M. Lautenbach, D. S. Sullins, J. D. Kraft, J. D. Lautenbach, C. A. Hagen, and J. C. Pitman. 2018*b*. Nonbreeding home-range size and survival of lesser prairie-chickens. Journal of Wildlife Management 82:413–423.

Rogers, 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. CRC Press, Boca Raton, Florida, USA.

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

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

Rykiel, E. J., Jr. 1985. Towards a definition of ecological disturbance. Australian Journal of Ecology 10:361–365.

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

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6–15.

Scholtz, R., J. A. Polo, S. D. Fuhlendorf, and G. D. Duckworth. 2017. Land cover dynamics influence distribution of breeding birds in the Great Plains, USA. Biological Conservation 209:323–331.

Schroeder, M. A., and C. E. Braun. 1991. Walk-in traps for capturing greater prairie-chickens on leks. Journal of Field Ornithology 62:378–385.

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

Smit, I. P. J., G. P. Asner, N. Govender, N. R. Vaughn, and B. W. van Wilgen. 2016. An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas. Journal of Applied Ecology 53:1623–1633.

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.

Thacker, E., and D. Twidwell. 2014. Synthesis of the effects of fire on lesser prairie-chickens. Great Plains Fire Science Exchange GPE publication 2014–6, Lincoln, Nebraska, USA.

Turner, M. G., S. L. Collins, A. L. Lugo, J. J. Magnuson, T. S. Rupp, and F. J. Swanson. 2003. Disturbance dynamics and ecological response: the contribution of long-term ecological research. BioScience 53:46–56.

Twidwell, D. W., W. E. Rogers, S. D. Fuhlendorf, C. L. Wonkka, D. M. Engle, J. R. Weir, U. P. Kreuter, and C. A. Taylor. 2013. The rising Great Plains fire campaign: citizens' response to woody plant encroachment. Frontiers in Ecology and the Environment 11: e64–e71.

Vermeire, L. T., R. B. Mitchell, S. D. Fuhlendorf, and R. L. Gillen. 2004. Patch burning effect on grazing distribution. Rangeland Ecology & Management 57:248–252.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's River Plains: ecological and management implications. Pages 4–10 *in* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller, editors. Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. USDA Forest Service Intermountain Research Station General Technical Report INT-276, Ogden, Utah, USA.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229–299.

Winder, V. L., L. B. McNew, J. C. Pitman, and B. K. Sandercock. 2017. Space use of female greater prairie-chickens in response to fire and grazing interactions. Rangeland Ecology & Management 70:164–174.

With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152–3167.

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

Wright, H. A., and A. W. Bailey. 1982. Fire ecology: United States and southern Canada. John Wiley and Sons, New York, New York, USA.

Associate Editor: Christopher Williams.

SUPPORTING INFORMATION

Additional supporting information may be found in the-online version of this article at the publisher's website.

The Journal of Wildlife Management; DOI: 10.1002/jwmg.21553

Research Article

Demographic Consequences of Conservation Reserve Program Grasslands for Lesser Prairie-Chickens

DANIEL S. SULLINS,[1] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
JOHN D. KRAFT, *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
DAVID A. HAUKOS, *U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
SAMANTHA G. ROBINSON,[2] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
JONATHAN H. REITZ, *Colorado Parks and Wildlife Department, Lamar, CO 81052, USA*
REID T. PLUMB,[3] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
JOSEPH M. LAUTENBACH,[4] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
JONATHAN D. LAUTENBACH,[5] *Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
BRETT K. SANDERCOCK,[6] *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
CHRISTIAN A. HAGEN, *Department of Fisheries and Wildlife, Oregon State University, Bend, OR 97702, USA*

ABSTRACT Knowledge of landscape and regional circumstances where conservation programs are successful on working lands in agricultural production are needed. Converting marginal croplands to grasslands using conservation programs such as the United States Department of Agriculture Conservation Reserve Program (CRP) should be beneficial for many grassland-obligate wildlife species; however, addition of CRP grasslands may result in different population effects based on regional climate, characteristics of the surrounding landscape, or species planted or established. Within landscapes occupied by lesser prairie-chickens (*Tympanuchus pallidicinctus*), CRP may provide habitat only for specific life stages and habitat selection for CRP may vary between wet and dry years. Among all study sites, we captured and fitted 280 female lesser prairie-chickens with very high frequency (VHF)- and global positioning system (GPS) transmitters during the spring lekking seasons of 2013–2015 to monitor habitat selection for CRP in regions of varying climate. We also estimated vital rates and habitat selection for 148 individuals, using sites in northwest Kansas, USA. The greatest ecological services of CRP became apparent when examining habitat selection and densities. Nest densities were approximately 3 times greater in CRP grasslands than native working grasslands (i.e., grazed), demonstrating a population-level benefit (CRP = 6.0 nests/10 km^2 1.29 [SE], native working grassland = 1.7 nests/10 km^2 0.62). However, CRP supporting high nest density did not provide brood habitat; 85% of females with broods surviving to 7 days moved their young to other cover types. Regression analyses indicated lesser prairie-chickens were approximately 8 times more likely to use CRP when 5,000-ha landscapes were 70% rather than 20% grassland, indicating variation in the level of ecological services provided by CRP was dependent upon composition of the larger landscape. Further, CRP grasslands were 1.7 times more likely to be used by lesser prairie-chickens in regions receiving 40 cm compared to 70 cm of average annual precipitation and during years of greater drought intensity. Demographic and resource selection analyses revealed that establishing CRP grasslands in northwest Kansas can increase the amount nesting habitat in a region where it may have previously been limited, thereby providing refugia to sustain populations through periods of extreme drought. Nest survival, adult survival during breeding, and nonbreeding season survival did not vary between lesser prairie-chickens that used and did not use CRP grasslands. The finite rate of population growth was also similar for birds using CRP and using only native working grasslands, suggesting that CRP provides habitat similar to that of native working grassland in this region. Overall, lesser prairie-chickens may thrive in landscapes that are a mosaic of native working grassland, CRP grassland, with a minimal amount of cropland, particularly when nesting and brood habitat are in close proximity. © 2018 The Wildlife Society

KEY WORDS Conservation Reserve Program, demography, landscape effects, lesser prairie-chicken, nest density, population, resource selection, strategic conservation, survival.

Received: 28 June 2017; Accepted: 28 June 2018

---

[1] *E-mail: sullins@ksu.edu*
[2] *Present Address: Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA.*
[3] *Present Address: California Department of Fish and Wildlife, 1724 Ball Mountain Rd., Montague, CA 96067, USA.*
[4] *Present Address: Ohio Department of Natural Resources, Delaware, OH 43015, USA.*
[5] *Present Address: Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA.*
[6] *Present Address: Department of Terrestrial Ecology, Norwegian Institute for Nature Research, Trondheim, Norway.*

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 to July 2016 (Taylor and Guthery 1980, Haukos and Boal 2016, Ross et al. 2016*a*). The lesser prairie-chicken was removed from the list of threatened species in response to a judicial decision in September 2015 (U.S. Fish and Wildlife Service 2016). However, environmental conditions 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, Haukos and Boal 2016, Robinson et al. 2016*a*). Lesser prairie-chickens require large areas of grassland with specific vegetation structure (Haukos and Zaveleta 2016). Large grasslands may allow lesser prairie-chickens to persist among episodic periods of drought and above-average precipitation that influence population fluctuations (Grisham et al. 2013, Haukos and Zavaleta 2016, Ross et al. 2016*a*).

In contrast to the range-wide declining population trajectory and broad-scale habitat loss throughout much of their distribution, the lesser prairie-chicken has expanded its range and significantly increased in abundance in the Shortgrass/CRP Mosaic Ecoregion of northwest Kansas, USA (SGPR; north of the Arkansas River; Fig. 1) since the mid-1990s (Rodgers 1999, Jensen et al. 2000, Dahlgren et al. 2016). Although survey efforts were minimal prior to becoming a candidate for the Endangered Species Act in 1998, there is limited indication of lesser prairie-chicken occurrence in this ecoregion prior to the late 1990s (Hagen 2003, Rodgers 2016). A possible factor contributing to population expansion in the SGPR Ecoregion is a response to the maturation of United States Department of Agriculture Conservation Reserve Program (CRP) grasslands (Rodgers 1999, 2016; Dahlgren et al. 2016; Spencer et al. 2017). 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 farther south near the southwest border of Lane County and near the northeast corner of Finney County in 1955, and records of unknown prairie-chicken species farther east in Ellis and Rush counties from 1962 to 1976 (Baker 1953, Schwilling 1955, Waddell 1977). In contrast to the isolated historical sightings, the SGPR Ecoregion may currently support approximately 55% of the estimated lesser prairie-chicken range-wide population (McDonald et al. 2014, 2016).

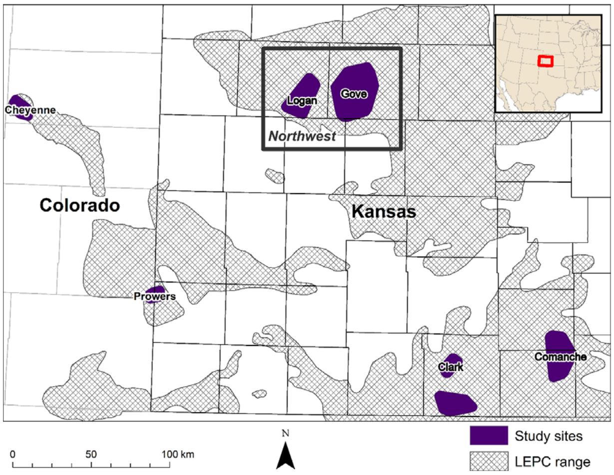


Figure 1. Locations of the 5 study sites where we marked, captured, and monitored lesser prairie-chickens (LEPC) in 2013–2016 to estimate regional use of Conservation Reserve Program grasslands in Kansas and Colorado, USA. The northwest Kansas study sites are highlighted with a black box to identify the spatial extent of landscape-scale resource selection functions and demographic estimates herein. The estimated contemporary lesser prairie-chicken range is identified by black crosshatches.

Throughout the northern distribution of the lesser prairie-chicken's range that encompasses the SGPR Ecoregion, a precipitation gradient results in a distinct east-to-west transition from mixed-grass to short-grass prairie (McDonald et al. 2014, Grisham et al. 2016). In the short-grass prairie, frequent drought and lack of 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). Experts suggest that lesser prairie-chickens in the short-grass prairie, and other areas west of the 100th meridian, were formerly confined to relatively small patches of mixed-grass, sand sagebrush (*Artemisia filifolia*), and sand shinnery oak (*Quercus havardii*; Giesen 1994, Haukos and Zaveleta 2016, Rodgers 2016). The addition of CRP grasslands to landscapes of short-grass prairie in northwest Kansas may mimic natural patches of taller vegetation, which formerly occurred only on sandy soils, in somewhat moister microclimates, on north facing slopes, or in drainages.

Adding taller vegetation in the form of CRP grasslands to a short-grass prairie landscape would increase the amount of cover and increase heterogeneity at the landscape scale. Spatial heterogeneity can be particularly important for generating habitat stability and maintaining habitat for multiple life stages of grassland 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 nesting and brood-rearing life stages for lesser prairie-chickens (Hagen et al. 2013). For example, a previous study in the SGPR Ecoregion detected 70% (41/59) of lesser prairie-chicken nests in CRP; however, only 37% (10/27) of broods spent most of their time in CRP (Fields et al. 2006).

Additionally, a lack of grazing and the native tall-grass 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. 1988, Grisham et al. 2016). Nesting cover may be readily available throughout native working grasslands (i.e., grazed) during wet years and nearly absent during drought (Grisham et al. 2013, Haukos and Zaveleta 2016). During drought 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.

Last, the ecological response of lesser prairie-chickens to CRP grasslands is likely influenced by a general increase in grassland abundance at the landscape scale. Grasslands in northwest Kansas are comparatively more fragmented than the occupied mixed grass prairie portions of the state (Spencer et al. 2017). In landscapes that consist of <60% grassland, general availability of grasslands may be the most limiting for lesser prairie-chickens (Crawford and Bolen 1976, Ross et al. 2016*b*). Conversion of marginal croplands back into grasslands through CRP could allow landscapes to surpass a critical threshold. Further, the increased grassland abundance provides an additional mechanism to stabilize populations. For example, the amount of available grassland within a 3-km landscape surrounding leks can influence the resilience of lesser prairie-chicken populations to drought (Ross et al. 2016*b*).

Although increased grassland abundance at the landscape scale can be beneficial, not all grasslands provide habitat equal in quality (Hagen et al. 2009, Lautenbach 2015, Robinson 2015). Conservation Reserve Program grasslands are often smaller in size than native working grasslands (grazed grasslands) and occur in landscapes where grassland has been fragmented through conversion to row crop agriculture (Dahlgren et al. 2016, Rodgers 2016). The potential for more concentrated small patches of habitat in CRP may increase risk of predation and create ecological traps, particularly if predators conduct area-concentrated searches (Gates and Gysel 1978, Ringelman 2014). Based on results from a previous 2-year study in the SGPR Ecoregion, it appears that CRP grasslands do not function as ecological traps for lesser prairie-chickens; demographic performance was similar in CRP grasslands compared to other cover types (Fields et al 2006). Alternatively, the use of CRP grasslands by lesser prairie-chickens may follow an ideal free distribution model if individuals select habitat that maximize individual fitness (Fretwell and Lukas 1970, Whitman 1980). In an ideal free distribution, when densities within a patch increase, the fitness of individuals within the patch decrease. Individuals move into marginal habitats only after a density is surpassed in more optimal habitat (Fretwell and Lucas 1970). In such a distribution, estimates of individual demographic performance would only be beneficial when linked with inference from resource selection, densities, and carrying capacity, which are needed to discern habitat quality at the population level (Van Horne 1983, Rodewald 2015).

Overall, it remains unclear if CRP grasslands merely increase the amount of available habitat above an extinction threshold, increase the spatial heterogeneity of certain grassland landscapes, provide high-quality habitat for lesser prairie-chickens by increasing the fitness of individuals, or provide for a limiting life-stage-specific habitat at a landscape scale. In sum, this information can be used to target conservation efforts and develop management strategies. To fill knowledge gaps, our objectives included identifying landscape and regional climatic constraints in which CRP becomes usable by lesser prairie-chickens. We then assessed the individual-level habitat quality of CRP and other grassland cover types based on the finite rate of population growth (λ) and vital rates among individuals using CRP and native working grasslands (Rodewald 2015). Last, we estimated nesting densities to provide inference of population-level habitat quality. Overall, this study describes the circumstances in which CRP provides habitat for lesser prairie-chickens and demographic performance of birds using CRP.

STUDY AREA

The study area encompassed the mixed- to short-grass portions of the lesser prairie-chicken range in Kansas and Colorado, USA (Fig. 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 (Grisham et al. 2016, PRISM 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 remain were restricted to areas of sandy or rocky soils or areas with rough terrain (Spencer et al. 2017). Within the study area, we collected resource selection and vital rate data at 5 study sites including 2 in Colorado and 3 in Kansas (Fig. 1). Temperatures ranged from 26°C to 43°C (extreme min. and max. temp), with average daily minimum and maximum temperatures of 5°C and 21°C, respectively, during the period of data collection (15 Mar 2013 to 15 Mar 2016; National Oceanic and Atmospheric Administration [NOAA] 2016*a*).

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

At the northwest Kansas study site, annual average long-term (30-year) precipitation varied between 47 cm 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. The transition between semi-arid and temperate precipitation levels divided the counties (Plumb 2015, Robinson 2015). Dominant plant species on the northwest Kansas study site included sideoats grama (*Bouteloua curtipendula*), blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), western wheatgrass (*Pascapyron smithii*), little bluestem (*Schizachyrim scoparium*), broomed snakeweed (*Gutierrezia sarothrae*), purple threeawn (*Aristida purpurea*), and annual bromes (*Bromus* spp.; Lauver et al. 1999). The northwest study site was a mosaic of CRP (7.4%), cropland (36%), and native short-grass or mixed-grass prairie (54%; Robinson 2015). The Gove County portion was composed of 8.0% CRP, 34% cropland, and 54% native working grassland and the Logan County portion was composed of 8.0% CRP, 32% cropland, and 56% native working grassland. 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 (6,600 ha) in Logan County, owned and operated by The Nature Conservancy. Historical ecological factors that maintained grasslands at the northwest study site included periods of drought, bison (*Bison bison*) grazing, and fire. However, fire is largely absent from the current landscape and grazing by cattle is controlled within fenced pastures. Full season or rotational grazing operations for cow-calf and yearling herds were the dominant system used among local ranchers. A significant portion of CRP was hayed prior to and during the study because of drought conditions, a few tracts were inter-seeded and disked, and others were undisturbed and idle. Mammalian and avian fauna at the site included coyote (*Canis latrans*), swift fox (*Vulpes velox*), black-tailed prairie-dog (*Cynomys ludovicianus*), thirteen-lined ground-squirrel (*Ictidomys tridecemlineatus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), western meadowlark (*Sturnella neglecta*), grasshopper sparrow (*Ammodramus savannarum*), and horned lark (*Eremophila alpestris*).

Precipitation varied during the study. Data collection began during an exceptional drought in the spring and summer of 2013 with a shift to more normal conditions in 2014 and 2015 (NOAA 2016*a*, *b*). Palmer Drought Severity Indices (PDSI; smaller number = more severe drought) were 3.4, 0.67, and 0.39 during the breeding season (Mar–Aug) and 1.85, 0.16, and 0.38 during the nonbreeding season (Sep–Feb) of 2013, 2014, and 2015, respectively (Augustine 2010, NOAA 2016*b*). During the nesting period (Apr–Jul), PDSI were estimated at 3.44, 1.58, and 0.57 in 2013, 2014, and 2015, respectively (NOAA 2016*b*). Annual precipitation was 39 cm, 48 cm, and 49 cm in 2013, 2014, and 2015, respectively (NOAA 2016*a*). These data indicated the occurrence of a drought during the first spring and summer of the study.

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, western ragweed (*Ambrosia psilostachya*), blue grama, Russian thistle (*Salsola tragus*), little bluestem (*Schizacyrim scoparium*), alkali sacaton (*Sporobolus airoides*), and sand sagebrush (PRISM 2016). The Clark site was 77% grassland, 14% cropland, and 5.5% CRP (Robinson 2015) and was was largely comprised of 2 privately owned ranches: 1 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 cow-calf and yearling herds were used in this area.

The Red Hills study site (49,111 ha) was 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 received the greatest annual precipitation, where average annual precipitation was 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. The Red Hills study site was 87% grassland, 8.9% cropland, and 2.2% CRP (Robinson 2015). The site was comprised of large contiguous grasslands with many drainages and 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 included sandy loam, clay loam, and clay (Soil Survey Staff 2015).

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, Colorado Parks and Wildlife, unpublished 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 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 of the grassland tract. To meet the management requirements, typically a third of the CRP fields were disked, creating linear strips of disturbed and undisturbed grass (J. Reitz, 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 lowest of all study sites (37 cm; PRISM 2016). The Cheyenne County study site was composed of 99% native working grassland, 1% cropland, and no CRP grassland; the site largely occurred on sandy soils (Homer et al. 2015, Soil Survey Staff 2015). Although there was no CRP within the minimum convex polygon used to delineate the Cheyenne County study site, CRP grasslands were present <4 km to the north and south of the study site, within the mean dispersal distance of lesser prairie-chickens (16.18 km; Earl et al. 2016).

METHODS

We captured lesser prairie-chickens at leks between early March and mid-May using walk-in funnel traps and drop nets (Haukos et al. 1990, Silvy et al. 1990). Upon capture, we sexed lesser prairie-chickens based on plumage coloration, pinnae length, and tail pattern (Copelin 1963). We aged each individual as yearling (second-year; SY) or adult (after-second-year; ASY) depending on the color patterns, shape, and wear of the outermost flight feathers (P9 and P10), which are retained from juvenal plumage in SY birds (Ammann 1944). We prepared protocols and obtained collection permits to capture and handle birds 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, SC-001-2015); and the Colorado Parks and Wildlife scientific collection license numbers 13TRb2053, 14TRb2053, and 15TRb2053.

We captured females and marked them with 4 plastic leg bands corresponding to region, year, and lek to identify and resight individuals in the field. We tagged birds with a 15-g very-high-frequency transmitter (VHF; A3960, Advanced Telemetry System, Isanti, MN, USA), or 22-g global positioning system (GPS) satellite Platform Transmitter Terminal (SAT-PTT) transmitter (PTT-100, Microwave Technology, Columbia, MD, USA and North Star Science and Technology, King George, VA, USA). We attached VHF transmitters as a necklace with whip antennae down the middle of the back and GPS transmitters were rump mounted using straps that were fastened around each thigh. We released all birds immediately at the site of capture. We obtained diurnal locations for each VHF-marked female 4 times/week using triangulation and Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary). We typically downloaded 8–10 GPS locations/day from each satellite-marked female using the ARGOS system, contingent on available daily solar charge. We recorded GPS locations every 2 hours during the day with a 6-hour gap between 2300 and 0500 when birds were assumed to be roosting.

Selection of CRP

We investigated lesser prairie-chicken use of CRP grasslands from 3 perspectives: the influence of spatial variability of precipitation, the influence of temporal variability of precipitation, and the influence of the surrounding matrix. We evaluated the influence of average annual precipitation on the use of CRP grasslands among lesser prairie-chicken populations in Kansas and Colorado (all study sites; Fig. 1). We investigated the influence of PDSI on selection of land cover types within the northwest Kansas site (Gove and Logan counties). Last, we assessed the influence of the surrounding matrix on use of CRP fields within the SGPR Ecoregion, which encompassed the northwest Kansas site (McDonald et al. 2014).

Influence of spatial variability of precipitation on use.—Use of CRP grasslands by lesser prairie-chickens may vary regionally because of changes in average annual precipitation, which is a primary factor influencing cover and food production. To examine the relationship of average annual precipitation on use of CRP by lesser prairie-chickens in Kansas and Colorado, we first subsampled 2 locations per bird per week from all sites. We then generated 5 random locations within a 4-km radius of each subsampled location used by a marked lesser prairie-chickens. The 4-km-radius scale outcompeted other models incorporating landscapes within a 2-km radius based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) and was also used to assess landscapes surrounding CRP described below (J. D. Kraft, Kansas State University, unpublished data). We assigned a value of 1 to all locations used by lesser prairie-chickens and a 0 to all random locations. We used a logistic regression to describe the combined influence of CRP and precipitation on point use among lesser prairie-chickens among all study sites. Random locations and associated designation as CRP or non-CRP controlled for variation in CRP availability among sites. We assigned average annual precipitation to each location using the 30-year normal precipitation values made available by the PRISM Climate Group (PRISM 2016). Candidate models included single-variable models of CRP presence (0 or 1), annual average precipitation, and additive and interactive models including effects of CRP and average annual precipitation on the probability of use of a location.

Influence of temporal variability of precipitation on selection.—After we examined how the long-term spatial variability of precipitation influenced the use of CRP among individual lesser prairie-chickens throughout the study area, we investigated how selection of CRP grasslands varied temporally with short-term changes in precipitation (drought severity) at the northwest Kansas site. We assigned used locations from marked birds a value of 1 for the response variable. We sub-sampled our pool of bird locations using the sample() command in Program R to 1 location per bird per day to limit potential temporal and spatial autocorrelation associated with SAT-PTT locations. We generated 1 random location for each bird location to define resources available to the population. We constrained random paired locations within the northwest study site boundary (Fig. 1) and assigned the same date to the random location as the corresponding used location. We assigned all random locations a response variable value of 0. For all locations (used and random), we identified a cover type category following Spencer et al. (2017). We assigned 3 different PDSI values to each location. Lag PDSI described the average PDSI value calculated during the previous 12-month period from April to March. Thus, a location recorded during July of 2014 would be assigned the mean PDSI value calculated from April 2013 to March 2014. Monthly PDSI described the PDSI value associated with the same month during which a location was recorded. Average growing season PDSI was the mean value of PDSI calculated during the growing season (Apr–Sep) 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. We developed single-variable models for each covariate (landcover type, lag PDSI, monthly PDSI, and average growing season PDSI) and ranked them 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 all landscapes associated with CRP tracts used by lesser prairie-chickens to random landscapes that also had a CRP component. Similar to habitat use 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 (Boyce et al. 2002, Manly et al. 2002). With the used versus available framework, we identified CRP fields used by lesser prairie-chickens based on the presence of bird locations from April 2013 to March 2016. We then distributed the same number of random locations in CRP lands located throughout the SGPR Ecoregion encompassing the northwest Kansas study site (McDonald et al. 2014). We delineated landscapes by buffering each location by 4 km using the buffer tool in ArcGIS (Environmental Systems Research Institute [ESRI], Redlands, CA, USA) and using landcover maps created through concurrent research (Spencer et al. 2017). In northwest Kansas, the surrounding matrix for CRP grasslands was largely restricted to 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 selection of CRP grasslands. We measured total area of working native grassland in the 4-km-radius landscapes using FRAGSTATS (McGarigal et al. 2012). We limited landscape metrics to total area grassland for the main text of the manuscript in hopes to provide a simple relationship that would be implemented by wildlife managers, and because the patterns of habitat fragmentation are rarely as influential as total habitat loss, particularly for focal species that are sensitive to habitat loss (Andren 1994, Villard and Metzger 2014). However, fragmentation can exert broader scale influence among metapopulations and results from a more detailed landscape analysis are included in Supporting Information (Hanski 2015).

Model selection and evaluation.—We examined correlations between pairs of covariates and did not allow correlated variables ($r > 0.70$) within the same model. After model fitting, we ranked and selected the most parsimonious model based AIC_c and informative beta coefficients (Burnham and Anderson 2002). We considered models with $\Delta\mathrm{AIC}_c$ 2 to be equal to the top-ranked model. Untransformed beta estimates from the top-ranking model were informative when coefficients did not overlap zero at the 95% confidence interval. We plotted predicted probability of use curves for top models in each model set. We conducted all resource selection functions in Program R (R Development Core Team 2016) using the glm package for generalized linear models.

Use of CRP in Northwest Kansas

We measured the proportion of locations from GPS-marked individuals that occurred in cropland, native working grassland, and CRP grassland during the breeding (15 Mar–15 Sep) and nonbreeding seasons (16 Sep–14 Mar) from 2013 to 2016. Such an approach can complement inference from resource selection functions that are imperfect because of constitutive relationships with the resource composition of study areas evaluated (Garshelis 2000). We used GIS layers from the National Landcover Database (NLCD) 2011 and a CRP layer provided under agreement by the United States Department of Agriculture Farm Services Agency to delineate cropland, native working grassland, and CRP grassland land cover types (Homer et al. 2015). We 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. The GPS transmitters generally have a spatial error of 5 m; well within the 30-m 30-m resolution pixels used in our analyses (Davis et al. 2013).

Vegetation Characteristics of CRP and Native Working Grasslands

We assessed the fine-scale vegetative characteristics of CRP and native working grasslands to provide inference on the potential for each cover type to provide quality microhabitat for lesser prairie-chickens. We collected measurements of grassland variables at random point locations distributed among CRP and native working grasslands available to lesser prairie-chickens within the northwest Kansas study site. We randomly generated available points throughout the study sites at a rate of 1 per 4 ha with a maximum of 10 points per patch. We delineated user-defined habitat patches and digitized them in ArcGIS 10.2 using aerial imagery available in the basemap layer (product of ESRI, i-cubed, U.S. Department of Agriculture Farm Service Agency, U.S. Geological Survey, Automating Equipment Information Exchange, GeoEye, Getmapping, Aerogrid, Instituto Geografico Português). We identified patches as areas of homogenous vegetation >2 ha and placed them in categories (i.e., native working grassland and CRP) and confirmed categories using ground truthing. We refer to grasslands that were typically managed for cattle production, privately owned, and composed of native grass species as native working grassland throughout the text. We measured vegetation at points within all delineated patches during summer and within a stratified random sample of 20% of patches during fall and winter. We captured vegetation data at more points during the spring breeding season to provide a robust estimate of available reproductive habitat.

At all random locations, we estimated a point-center measurement of percent canopy cover of forbs, bare ground, grass, shrub, and annual bromes within a 60 60-cm modified Daubenmire frame (Daubenmire 1959). We estimated 4 additional estimates of canopy cover 4 m from point center at all cardinal directions (5 estimates/point). We obtained visual obstruction readings 4 m from point center at all cardinal directions and we recorded height in dm at which we estimated 100%, 75%, 50%, 25%, and 0% visual obstruction (4 estimates/point; Robel et al. 1970). We measured litter depth (cm) at 0.5-m increments stretching 4 m north, east, south, and west of point center (32 estimates/

point; Davis et al. 1979). We visually estimated the 3 most abundant species within a 4-m radius of each point.

From the top 3 most abundant plant species, we estimated the frequency of tall-grass species occurrence at locations within CRP and native working grasslands. Dominant tall-grass 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 a reasonable indicator of quality nesting cover for lesser prairie-chickens (Hagen et al. 2013). We also directly estimated the proportion of random points that met characteristics of available nesting habitat following Lautenbach (2015). Available nesting locations had a 75% visual obstruction 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). We used a Hotelling T^2 test to examine a multivariate difference among vegetation measured in CRP and native working grasslands (Johnson and Wichern 1988). Once we identified a significant variation in multivariate space ($P < 0.05$), we then used an unequal variances Welch 2-sample *t*-test to examine differences in all vegetative measurements among CRP and native working grasslands.

Demographic Rates

Vital rate data collection.—We estimated vital rates and population growth for lesser prairie-chickens that used and did not use CRP grasslands at the northwest Kansas study site to assess the demographic influence of CRP in the region. We classified a lesser prairie-chicken as using CRP if it had 1 location in CRP during a season. We collected fecundity and survival data during the breeding seasons (15 Mar–15 Sep) and nonbreeding seasons (16 Mar–14 Sep) of 2013–2016. 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 a nest, we recorded the location of the nest and counted and floated eggs to predict hatch date. We monitored nests 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, we visited the area to identify nest success or failure based on eggshell appearance and presence or absence of predator sign at the nest site. If a nest was successful, we monitored brood and chick survival by conducting brood flush counts at lesser prairie-chicken female locations within 1 hour of sunrise at weekly intervals from 14 to 60 days after hatch. We thoroughly searched the area surrounding each transmittered female to maximize chick detection. If we did not detect chicks, we flushed the female once more to make sure the brood was no longer present. Between flushes, we 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.—We estimated nesting propensity (NEST; probability a female decides to nest) using a Horvitz–Thomson estimator that accounted for bias from nests that failed before being detected (Dinsmore et al. 2002). We 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 each day from 1200 to 1400 to establish a nest and lay eggs while displaying unique movement patterns relative to non-nesting females (Sullins 2017). To account for undetected nests, we divided 1 by the 3-day nest survival rate estimated from the daily survival rate, 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). We divided the adjusted number of nests by the number of females that were captured presumably before losing a first nest (before 22 Apr) and survived long enough to attempt a nest (survived to 10 May). We estimated propensity to re-nest (RENEST) following a similar protocol but estimated the proportion of females that attempted to re-nest after losing their first nest but not dying during the nest predation events.

We 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. We estimated hatchability following Hagen et al. (2009) as the proportion of chicks hatched per egg laid (HATCH). We estimated daily nest survival rates over a 35-day exposure period with a 10-day laying period and a 25-day incubation period for yearlings and adults. Small sample sizes precluded our ability to estimate nest survival separately for first and re-nest attempts in CRP and native working grassland. We estimated nest survival among attempts for CRP and native working grassland (NSURV) with the nest survival procedure within Program MARK (White and Burnham 1999, Dinsmore et al. 2002). We ranked models based on AIC_c and evaluated models based on model weight (w_i; Burnham and Anderson 2002). Ultimately, we used the model including CRP as a covariate estimated in the R package RMark interface to estimate nest survival throughout the laying and incubation period because we were interested in differences between birds nesting in and out of CRP (Laake 2013, R Development Core Team 2016). We used the delta method to calculate standard errors for each nest survival rate (Powell 2007). We estimated chick survival (CHICK) to 35 days post hatch using models of Lukacs et al. (2004). We did not estimate chick survival separately for CRP and native working grasslands because only 1 brood that survived >7 days used CRP. However, we did estimate the proportion of broods that had 1 chick survive to >7 days post-hatch from nests that were in CRP versus native working grasslands. We estimated 35-day survival as the product of weekly survival rates over 5 week-long intervals and estimated the standard error for chick survival using the delta method assuming independence. We estimated fecundity (*F*) for the 2 nesting attempts (*a*) using the equation below based on Hagen et al. (2009).

$$\begin{aligned} Fa = [(NEST \quad CLUTCH1 \quad NSURV) + (1 \quad NSURV) \\ (RENEST \quad CLUTCH2 \quad NSURV) \\ (HATCH \quad 0.5 \quad CHICK) \end{aligned}$$

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). We estimated cover type-specific nest densities within 5-km-radius landscapes surrounding each lek to compare the nesting capacity between CRP and native working grasslands in northwest Kansas. We estimated nest densities of transmittered lesser prairie-chickens within a 5-km radius of each lek trapped during spring 2013–2016. We then averaged nest densities in CRP and native working grassland among all leks and estimated the standard deviation of nest densities among landscapes associated with leks. 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 in our study, which is comparable to the typical use of nesting habitat within 3 km of leks (Hagen and Giesen 2005, Sullins 2017).

Landscape-scale reproduction.—We 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. We 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. Most lesser prairie-chicken broods die in the first week of life (Lautenbach 2015). The percentage of females using CRP to nest and native working grasslands to brood will identify how lesser prairie-chickens use the CRP or native working grassland mosaic for reproduction.

Female survival parameters.—We used Kaplan–Meier models to estimate breeding season survival for adult and yearling lesser prairie-chickens during 2013–2016 breeding seasons (*Sb*; 15 Mar–15 Sep) in Program MARK. We used the same Kaplan–Meier models to estimate nonbreeding season (16 Sep–14 Mar) survival (*Snb*) for adults and yearlings combined (White and Burnham 1999). We used a juvenile survival (35 days post-hatch to first breeding season; *Sjuv*) estimate from a previous study on lesser prairie-chickens in western Kansas: 0.539   0.089 (SE; Hagen et al. 2009). We did not obtain a sufficient sample size to estimate this demographic parameter for our study population in northwest Kansas. We estimated nonbreeding and breeding season survival separately because of differences in habitat use during these 6-month seasons (Haukos and Zaveleta 2016). We then estimated annual survival (*S*) for each age class (*c*) as:

$$Sc = Sb \quad Snb$$

Population matrix.—We integrated fecundity and survival parameters for female lesser prairie-chickens using CRP and native working grasslands into a matrix population model (**A**) wherein *Fy* represented yearling fecundity, *Fa* was adult fecundity, *Sjuv* was juvenile survival, *Sy* was yearling annual survival, and *Sa* was adult annual survival.

$$\mathrm{A} = \begin{bmatrix} Fy \quad Sjuv & Fa \quad Sjuv \\ Sy & Sa \end{bmatrix}$$

We 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 (R_0) for birds using CRP and not using CRP. To explore parameter space, we used uniform distributions encompassing the range of nesting propensity and renesting propensity for matrix model calculations. We 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. Vital rates estimated separately among CRP and native working grasslands included nest survival, clutch size, breeding season survival, and nonbreeding season survival. We grouped individuals as CRP or native working grassland based on the location of the nest for nest survival and clutch size and based on the use or complete avoidance of CRP for adult survival estimates. We estimated contributions to λ 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

We captured, marked, and monitored 280 female lesser prairie-chickens from 2013 to 2016 among all sites. Overall, we marked 156 individuals with GPS-transmitters and 124 individuals with VHF-transmitters. At the northwest Kansas site, we marked 146 female lesser prairie-chickens with GPS- or VHF-transmitters and used these birds to estimate the demographic response to CRP. Of the females monitored in northwest Kansas, 10% were of unknown age, 28% were ASY, and 63% were SY.

Selection of CRP

Influence of spatial variability of precipitation on selection.—Using 7,462 locations from 96 female lesser prairie-chickens marked with GPS-transmitters and 37,310 random locations, we examined the influence of average annual precipitation and CRP on the probability of use by lesser prairie-chickens among all study sites. At a regional scale, CRP grasslands were 1.7 times more likely to be used by lesser prairie-chickens in regions receiving 40 cm compared to 70 cm of average annual precipitation ($\delta 1 = -0.0314 \quad 0.0048$, marginal effect of annual average precipitation on predicted probability of using CRP; Fig. 2). The model including the interactive effect of CRP presence

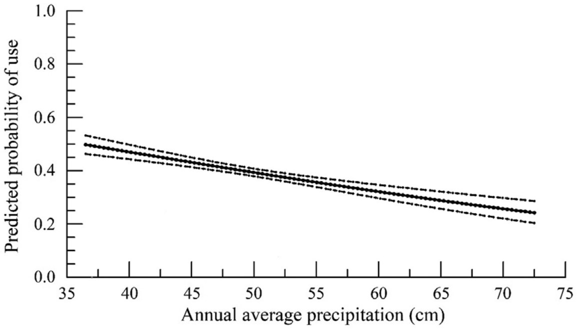


Figure 2. Predicted probability of use of Conservation Reserve Program (CRP) grasslands by lesser prairie-chickens in Kansas and Colorado, USA, 2013–2016 as a function of average annual precipitation estimated in 800-m 800-m pixels (PRISM 2016). The displayed relationship of annual average precipitation and probability of use is only for CRP grasslands based on the interaction model that included presence of CRP and average annual precipitation. Dashed lines indicate 95% confidence intervals.

and annual average precipitation outcompeted all other candidate models and had an AIC_c model weight of 1.0.

Influence of temporal variability of precipitation on selection.—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 positively related to PDSI and was 1.89 times greater when the lag PDSI value equaled 4 (more severe drought) compared to a value of 4 (less severe drought; δ_1 =- 0.1963 0.0322, marginal effect of PDSI lag on predicted probability of using CRP; Fig. 3). In contrast, the predicted probability of using native working grassland was negatively related to PDSI and was 1.18 times less when the lag PDSI value was 4 compared to 4 and overlapped zero at the 95% confidence interval (δ_1 =- 0.0278 0.0272, mar-ginal effect of PDSI lag on predicted probability of using native working grassland; Fig. 3).

Influence of the surrounding matrix.—We sampled 62 used and 62 random CRP fields and their surrounding 4-km landscapes in the SGPR Ecoregion within the estimated distribution of lesser prairie-chickens. The matrix surrounding each CRP field varied in the amount (716–4,209 ha) and percent of grassland (14–84%) and clumpiness of grasslands (0.7230.961; see Fig. A1, available online in Supporting Information). In northwest Kansas, CRP grasslands were 8.6 times more likely to be used by lesser prairie-chickens when local landscapes (5,027 ha) were comprised of approximately 70% (3,500 ha) native grassland compared to approximately 20% (1,000 ha) native grassland (β_{area} = 0.00155 0.000331, $P < 0.001$; Fig. 4).

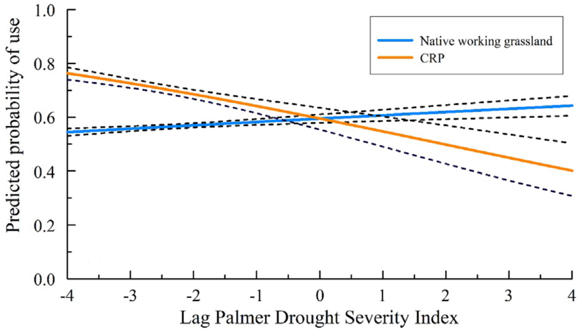


Figure 3. Predicted probability of lesser prairie-chickens in Kansas and Colorado, USA, 2013–2016 using Conservation Reserve Program (CRP) or native working grassland as a function of drought severity (Palmer Drought Severity Index) during the previous year (low numbers = greater drought severity). Dashed lines indicate 95% confidence intervals.

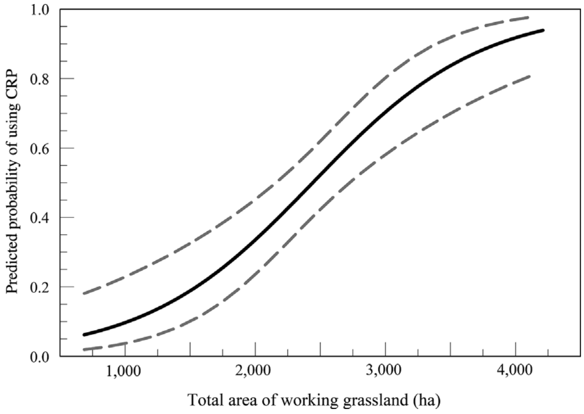


Figure 4. Predicted probability of use of Conservation Reserve Program (CRP) grasslands by lesser prairie-chickens in northwest Kansas, USA, 2013–2016 as a function of the amount of native working grassland in a 5,026-ha (4-km radius) landscape. Dashed lines indicate 95% confidence intervals.

Use of CRP

Lesser prairie-chickens ($n = 79$) used native working grasslands more frequently than CRP in northwest Kansas during the breeding and nonbreeding seasons of 2013–2016 (Table 1). Of the locations from GPS-marked birds, 70% of locations were in native working grasslands with 20% in CRP grasslands (Table 1).

Vegetation Differences Between CRP and Native Working Grasslands

Overall, CRP grasslands supported taller vegetation with a greater litter depth, had less shrub cover, less bare ground,

Table 1. Locations used by, and available to, lesser prairie-chickens in northwest Kansas, USA. We present proportion of locations ($n = 89{,}297$) of lesser prairie-chickens ($n = 148$) marked with GPS-transmitters occurring in cropland, Conservation Reserve Program (CRP) grasslands, and native working grasslands during the breeding (15 Mar–14 Sep), nonbreeding (16 Sep–14 Mar), and all seasons combined in northwest Kansas during 2013–2016. Proportional availability of cover types is based on minimum convex polygons drawn around all points at the northwest Kansas study sites (Plumb 2015, Robinson 2015).

Season	Cropland	CRP	Native working grassland
Used			
Breeding	0.07	0.20	0.73
Nonbreeding	0.20	0.19	0.61
All seasons	0.10	0.20	0.70
Available			
All seasons[a]	0.35	0.08	0.57

[a] Availability of landcover types remained the same among seasons.

Table 2. Sample sizes, means, and standard deviation of microsite (4-m radius) vegetation measurements collected at random locations distributed within the northwest Kansas, USA study site in 2013–2016.

	Native working grasslands			CRP grasslands					
Vegetation measurements[a]	*x*	**SD**	*n*	*x*	**SD**	*n*	*t*	**Df**	*P*
Visual obstruction readings (VOR)									
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	0.8	5,727	0.410
Litter depth (cm)	1.20	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 tall-grass occurrence[b]	0.13	0.33	1,735	0.63	0.48	846			
Proportion suitable nesting locations	0.20		1,713	0.46		834			

[a] Vegetation measurements include visual obstruction readings collected using a 2-m-tall Robel pole marked at alternating decimeters. We measured horizontal cover estimates using a 60-cm^2 Daubenmire frame, and litter depth and grass height using a ruler. The frequency of tall-grass occurrence is an estimate of the number or locations having a tall-grass species as 1 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 dm, bare [%]: 0–20).

[b] Tall-grass species included little bluestem, big bluestem, switchgrass, and indiangrass.

more tall-grass species, and provided a greater number of suitable nesting microhabitats (Hotelling's $T^2 = 69.73$, $P < 0.001$; Table 2).

Demographic Rates

Nests.—We monitored 109 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 [SE]) and native working grassland (9.61 2.56; $t_{99} = 0.13$, $P = 0.90$; Table 3). Females on average laid 10.33 0.25 eggs for their first nest and 7.23 0.58 eggs for their second clutch ($t_{99} = 5.35$, P 0.001). Re-nesting attempts in CRP and native working grasslands were limited and too few to provide estimates of re-nesting survival ($n = 4$ and 15 respectively; Table 3).

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 re-nesting following the loss of a first nest was estimated at 15.3%, 53.7%, and 35.7% in 2013, 2014, and 2015, respectively.

The highest-ranked nest survival model based on AIC_c was the null model ($w_i = 0.25$), followed by a year ($w_i = 0.21$), CRP ($w_i = 0.17$), age class ($w_i = 0.11$), and nesting attempt model ($w_i = 0.09$), all of which had a $\Delta\text{AIC}_c < 2$. 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 0.079, whereas those that used native working grasslands had an estimated nest survival of 0.405 0.053 (Table 3). The top-ranking model with a covariate included year and nest survival was estimated at 0.365 0.068, 0.422 0.066, and 0.604 0.101 in 2013, 2014, and 2015, respectively. Because our goal was to determine cumulative effects of CRP on lesser prairie-chicken population demography, we used the CRP model to estimate nest survival.

Of the nests monitored in northwest Kansas, 34% produced young, 52% were depredated, and 11% abandoned. Only 3% of nests were trampled by cattle, all within native working grassland pastures. The proportion of eggs that successfully

Table 3. 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 (Non-CRP) cover types in northwest Kansas, USA, during the breeding season (15 Mar–15 Sep) and nonbreeding season (15 Sep–15 Mar) during 2013–2016. We estimated chick survival and hatchability among all cover types.

	CRP				Non-CRP			
Variable	**Estimate**	**SE**	**95% CI**	*n*	**Estimate**	**SE**	**95% CI**	*n*
Nest survival	0.51	0.079	0.35–0.66	34	0.41	0.05	0.30–0.51	75
Clutch size of first nest	10.5	0.45	9.6–11.4	30	10.3	0.31	9.7–10.8	56
Clutch size of second nest	4.5	1.04	2.5–6.5	4	7.8	0.62	6.7–9.0	19
Nest density (nests/10 km^2)[a]	6.0	1.29	3.5–8.6	20	1.7	0.62	0.41–3.03	18
Percentage of broods[b]	14.3			1	86.0			6
Breeding season survival	0.42	0.064	0.30–0.55	65	0.44	0.07	0.31–0.57	63
Nonbreeding season survival	0.71	0.100	0.52–0.91	22	0.57	0.1	0.35–0.76	31

[a] We estimated nest density within the 5-km-radius area surrounding each lek and sample sizes reflect the number of leks.

[b] Estimate of the percentage of 7-day-old broods occurring in CRP or Non-CRP grasslands from nests that hatched in CRP.

hatched within a successful nest (hatchability) was estimated as 75% 0.048 from 35 successful nests in northwest Kansas. Among nests, hatchability varied from 10% to 100% of eggs successfully hatching.

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 point estimates of marked lesser prairie-chickens were 3 times greater in CRP grasslands than in native working grassland (CRP = 6.0/10 km^2 1.29, native working grassland = 1.7/10 km^2 0.62). Nest densities were greater in CRP grasslands compared to native working grassland in 85% (17/20) of 5-km-radius landscapes surrounding each lek.

Landscape-scale reproduction.—In northwest Kansas, 1 out of 7 female lesser prairie-chickens successfully used CRP as nesting and brooding habitat to rear chicks to 7 days. The remaining females (85%) used CRP grasslands as nesting substrate, and successfully raised chicks to 7 days old, 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. All successful broods that hatched in native working grassland nests, excluding 1 brood that used CRP for a half day, remained in native working grassland for the first 7 days of life.

Chick survival.—The strong selection of non-CRP cover types for brood rearing did not allow for the estimation of chick survival in CRP and non-CRP cover types. Pooling across strata, we estimated an overall 35-day chick survival from 34 broods for northwest Kansas at 0.261 0.071. Although our sample sizes precluded estimating chick survival for individuals using CRP and native working grassland as brooding habitat, we estimated the proportion of broods that successfully survived >7 days post-hatch from nests in CRP and native working grasslands. Of broods from successful nests in CRP, 7 of 11 survived and 9 of 20 broods from nests in native working grassland survived to >7 days post-hatch.

Survival.—We 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 (95% CI = 0.289–0.591) and 0.565 (95% CI = 0.371–0.755) for nonbreeding season. For female lesser prairie-chickens that used CRP, survival was 0.421 (95% CI = 0.290–0.552) for the breeding season and 0.711 (95% CI = 0.515–0.907) for the nonbreeding season.

Population matrix.—Population growth rate point estimates for birds that used CRP ($\lambda = 0.601$, 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 = 0.336–0.866, Non-CRP = 0.268–0.714). Female lesser prairie-chickens had a net reproductive rate of R0 = 0.094 0.0695 (estimate SD; female chicks/female/generation) when using CRP at a landscape scale and a net reproductive rate of R0 = 0.0547 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, SD = 0.303 years) and those that never used CRP (3.183 SD = 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.

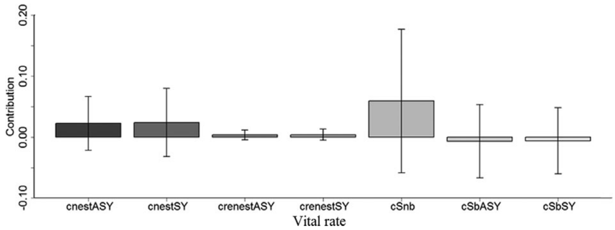


Figure 5. Life-stage contributions for after-second-year (ASY) and second-year (SY) female lesser prairie-chickens to greater population growth rate estimates of birds using Conservation Reserve Program grasslands compared to birds using only native working grasslands (reference) in northwest Kansas, USA, 2013, 2014, and 2015. Life-stage contributions included nest survival (cnestASY, cnestSY), survival of subsequent nesting attempts (crenestASY, cnestSY), nonbreeding adult survival (cSnb), and breeding season survival of adults (cSbASY) and yearlings (cSbSY). We calculated contributions following Caswell (1989) and errors bars represent 95% confidence intervals.

The fixed-effects life-table response experiment decomposed the difference in λ (difference = +0.110 for CRP) among birds using CRP and native prairie. The life-table response experiment revealed that nonbreeding survival contributed most to the difference in population growth rates between lesser prairie-chickens using CRP at a landscape scale and those not using CRP (contribution [c] = 0.0592, SD = 0.0600, 53.0% of difference; Fig. 5). Contributions from nest survival for SY (c = 0.0240, SD = 0.0284, 21.8% of difference) and ASY (c = 0.0224, SD = 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

We 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 this region may be key to the foreseeable persistence of this species on privately owned working lands, especially considering current climate change predictions (Rodgers and Hoffman 2005, Cook et al. 2015, Grisham et al. 2016, Haukos and Zaveleta 2016, Rodgers 2016). Our combined habitat use 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 (resource selection) and realized fitness over the 3-year window of data collection. 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 importance during drought years in northwest Kansas, and in drier portions of the lesser prairie-chicken's range (e.g., Colorado). 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 is predominantly grassland. Therefore, the most beneficial strategic conservation efforts would be those 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. In Kansas, this is already being partially implemented through the establishment of conservation priority areas (Rodgers 2016). Other research and management experiments in this system suggest that the 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, personal communication) and 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

Lesser prairie-chickens were distributed among cover types of similar demographic consequence, supporting an ideal free distribution and providing no evidence of one cover type functioning as higher quality habitat among all life stages and when not accounting for densities (Van Horne 1983). Although it could be suggested that CRP fields function as ecological traps, for which avian species are attracted to suitable cover in small grassland patches, our results indicated that lesser prairie-chickens had similar fitness in CRP and native working grasslands (Gates and Gyel 1978). If exhibiting an ideal free distribution, lesser prairie-chickens would be 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 (Fretwell and Lucas 1970, Whitman 1980, Rodewald 2015).

During spring 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. 2016*b*). Therefore, any locations still occupied by lesser prairie-chickens may represent a core area of optimal habitat quality (Guthery et al. 2005) or, alternatively, a location that provided refugia during drought events as reported in our study. 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 may require a significantly longer study for a boom or bust species such as the lesser prairie-chicken, or an analytical framework linking changes in densities with individual fitness.

The ideal free distribution model provides insight into how densities can be related to the fitness of individuals using certain habitats (habitat quality; Fretwell and Lucas 1970). In an ideal free distribution when densities within a patch increase, fitness of individuals within the patch decrease. Individuals move into marginal habitats only after a density is surpassed in more optimal habitat (Fretwell and Lucas 1970). Therefore, in circumstances where the ideal free distribution exists, individuals should have similar fitness among differing habitat patches and densities must be considered when evaluating habitat quality (Fretwell and Lucas 1970, Van Horne 1983). The similar nest survival estimates for lesser prairie-chickens using CRP and native working grasslands in comparison to contrasting nest densities among cover types supports patterns predicted in the ideal free distribution. Congruent with our results, Fields et al. (2006) estimated that nest survival was not different between CRP and native working grasslands of northwest Kansas. Although we provided densities of marked lesser prairie-chickens only during the nesting period, estimates indicated greater nest densities (3) in CRP compared to native working grassland and agreed with vegetation data that indicated CRP provided over twice the number of suitable nesting locations.

Nesting microhabitats appear to be more readily available in CRP grasslands in this region as indicated primarily by the greater nesting densities by marked female lesser prairie-chickens and secondarily by the greater proportion of suitable nesting locations based on vegetative characteristics (Table 2). By incorporating nesting densities (estimated from marked individuals), we 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 may translate 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 benefited lesser prairie-chickens by increasing habitat equal in quality to native working grasslands for adults and by increasing 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 at 2 study sites 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, albeit the estimated λ was still <1, 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 proximity of CRP to waste grain in adjacent crop fields. Some experts suggest that prairie-chicken populations achieve peak abundance in landscapes having 10–15% of the area in grain production and lesser prairie-chickens may have boomed in the presence of small-scale farming in the early 1900s (Baker 1953, Jackson and DeArment 1963, Rodgers 2016). A nearly 3-fold increase in use of croplands during the nonbreeding season may indicate the use of grain fields when foods become limited outside of the growing season. Although confidence intervals overlapped, we 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 purported 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 structural heterogeneity of grasslands in the region (Table 2). The same effects may not be realized farther to the east where nesting habitat is likely not 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 lesser prairie-chicken range is more likely to be adjacent to woodlands; these conditions are an underlying result of increased average annual precipitation (Bond 2008, Grisham et al. 2016). Although we were not able to control for availability of CRP grasslands among all our sites, our results indicated a greater use of CRP among all life stages in areas of lower annual average precipitation (Fig. 2).

Making CRP useable for 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 >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 because a lack of forbs limited accessibility to food resources (Bergerud and Gratson 1988, 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 approximately 200 g/m^2 greater than at our western most study site (Sala et al. 1988). Conservation Reserve Program grassland establishment may improve habitat quality in landscapes for lesser prairie-chickens only when increasing the spatial heterogeneity of those landscapes or the amount of grassland 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 ha) were >70% (35 km^2) native working grasslands, and when CRP fields were established in areas where patches of native grasslands were clumped together or contiguous (Figs. A1 and A2, available online in Supporting Information). Our 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 and is based on the presence of 6 leks that are on average 1.6 km away from each other (Applegate and Riley 1998, Westemeier et al. 1998, Van Pelt et al. 2013, DeYoung and Williford 2016). However, estimates have ranged from 49 km^2 to approximately 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 (Sala et al. 1988, Simberloff 1994, Grisham et al. 2016, Ross et al. 2016*a*).

The loss of grassland through conversion to cropland in the early 1900s in the SGPR Ecoregion may have reduced the amount of available grassland cover 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. 2016*b*). 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, landscapes having a greater grassland abundance would also result in greater reproductive output during periods of favorable weather (Garton et al. 2016, Ross et al. 2016*a*). Maximizing reproductive output during periodic favorable periods may be a 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 area within 3 km of leks with an optimum value of 90% grassland (Ross et al. 2016*b*).

The population resilience to drought may stem from the decision to nest or forego nesting during a season. Our 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 our study, nesting propensity was lowest in 2013 (82%) and greatest in 2015 (100%), which were the years of the most and least severe PDSI, respectively (NOAA 2016*b*). Further, we documented that female lesser prairie-chickens were more likely to select CRP grasslands as drought severity increased. Given our 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 nest propensity even during drought (McNew et al. 2012). Alternatively, drought may not restrict the availability of nesting habitat, and therefore the propensity to nest, in wetter portions of the greater prairie-chicken distribution. 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*b*), both of which are likely main factors in the boom-bust population fluctuation.

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. Management practices (e.g., grazing, burning, haying, or disking) to achieve the optimal structure for nesting and increase the amount of brood habitat within CRP grasslands in the eastern portion of the lesser prairie-chicken range could be examined in an adaptive management framework.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank R. D. Rodgers for providing comments and edits on a previous draft of the manuscript. B. Anderson, S. Baker, S. Bard, G. Brinkman, K. Broadfoot, R. Cooper, J. Danner, J. Decker, E. D. Entsminger, R. M. Galvin, N. Gilbert, A. Godar, G. Gould, B. Hardy, S.P. Hoffman, D. Holt, B. M. Irle, T. Karish, A. Klais, H. Kruckman, K. Kuechle, S. J. Lane, E. A. Leipold, J. Letlebo, E. Mangelinckx, L. McCall, A. Nichter, K. Phillips, J. K. Proescholdt, J. Rabon, T. Reed, A. Rhodes, B. E. Ross, D. Spencer, A. M. Steed, A. E. Swicegood, P. Waldron, B. A. Walter, I. Waters, W. J. White, E. Wiens, J. B. Yantachka, and A. Zarazua, provided much needed assistance with data collection. We greatly appreciate the logistic and technical support provided by J. C. Pitman, J. Kramer, M. Mitchener, D. K. Dahlgren, J. A. Prendergast, C. Berens, G. Kramos, A. A. Flanders, and S. Hyberg. Funding for the project was provided by Kansas Wildlife, Parks, and Tourism (Federal Assistance Grant KS W-73-R-3); United States Department of Agriculture (USDA) Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62); and USDA Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative.

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.

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, USA.

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.

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. 2007. 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, USA.

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

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.

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.

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.

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., 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.

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.

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(7):e68225.

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

Grisham, B. A., 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. Dissertation, Kansas State University, Manhattan, USA.

Hagen, C. A., and K. M. Giesen. 2005. Lesser prairie-chicken (T*ympanuchus pallidic* in ctus). Account 364 *in* A. F. Poole, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/364/articles/introduction. Accessed 10 Nov 2016.

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

Hagen, C. A., 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., 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.

Hanski, I. 2015. Habitat fragmentation and species richness. Journal of Biogeography 42:989–993.

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., 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, editors. Ecology and conservation of lesser prairie-chickens. Studies in Avian Biology No. 48. Cooper Ornithological Society, University of California Press, Berkeley, USA.

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.

Jackson, A. S., and R. DeArment. 1963. The lesser prairie chicken in the Texas panhandle. Journal of Wildlife Management 27:733–737.

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, R. A., and D. W. Wichern. 1988. Applied multivariate statistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Knopf, F. L. 1996. Prairie legacies—birds. Pages 135–148 *in* F. B. Samson and F. L. Knopf, editors. Preserving North America's most endangered ecosystem. Island Press, Covello, California and Washington, D.C., USA.

Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, Washington, USA. www.afsc.noaa.gov/Publications/ProcRpt/P R2013-01.pdf. Accessed 10 Nov 2016.

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

Lauver, C. L., K. Kindscher, F. L. Don, and R. Schneider. 1999. A classification of the natural vegetation of Kansas. Southwestern Naturalist 44:421–443.

Lukacs, P. M., V. J. Dreitz, F. L. Knopf, and K. P. Burnham. 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, The 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. University of Massachusetts, Amherst, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 10 Nov 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 & Management 68:298–304.

National Oceanic and Atmospheric Administration National Climatic Data Center [NOAA]. 2016*a*. National Environmental Satellite, Data, and Information Service. https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp. Accessed 11 Aug 2016.

National Oceanic andAtmospheric Administration [NOAA]. 2016*b*. Historical Palmer Drought Indices. National Centers for Environmental Information. http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#. Accessed 11 Aug 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.

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.

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 Jan 2017.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed 10 Nov 2016.

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.

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

Robinson, S. G., D. A. Haukos, D. S. Sullins, and R. T. Plumb. 2016*b*. Use of free water by nesting lesser prairie-chickens. Southwestern Naturalist 61:187–193.

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. 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. 2016*a*. 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. 2016*b*. 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, 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.

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

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.

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

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.

U.S. Fish and Wildlife Service. 2016. Endangered and threatened wildlife and plants; lesser prairie-chicken removed from the list of endangered and threatened wildlife. Federal Register 81(139):47047–47048.

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.

Villard, M. A., and J. P. Metzger. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51:309–318.

Waddell, B. H. 1977. Lesser prairie-chicken investigations—current status evaluation. Kansas Forestry, Fish and Game Commission, Pratt, 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.

Associate Editor: Adam Janke.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

The Auk
Ornithological Advances

AmericanOrnithology.org

Volume 135, 2018, pp. 583–608
DOI: 10.1642/AUK-17-199.1

RESEARCH ARTICLE

Identifying the diet of a declining prairie grouse using DNA metabarcoding

Daniel S. Sullins,[1]* David A. Haukos,[2] Joseph M. Craine,[3] Joseph M. Lautenbach,[1a] Samantha G. Robinson,[1b] Jonathan D. Lautenbach,[1] John D. Kraft,[1] Reid T. Plumb,[1c] Jonathan H. Reitz,[4] Brett K. Sandercock,[5d] and Noah Fierer[6]

[1] Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, Kansas, USA
[2] U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, Kansas, USA
[3] Jonah Ventures, LLC, Manhattan, Kansas, USA
[4] Colorado Parks and Wildlife Department, Lamar, Colorado, USA
[5] Division of Biology, Kansas State University, Manhattan, Kansas, USA
[6] Cooperative Institute for Research in Environmental Science, University of Colorado, Boulder, Colorado, USA
[a] Current address: Sault Ste. Marie Tribe of Chippewa Indians, Sault Ste. Marie, Michigan, USA
[b] Current address: Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia, USA
[c] Current address: California Department of Fish and Wildlife, Montague, California, USA
[d] Current address: Department of Terrestrial Ecology, Norwegian Institute for Nature Research, Trondheim, Norway
* Corresponding author: sullins@ksu.edu

Submitted October 10, 2017; Accepted February 24, 2018; Published May 16, 2018

ABSTRACT

Diets during critical brooding and winter periods likely influence the growth of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) populations. During the brooding period, rapidly growing Lesser Prairie-Chicken chicks have high calorie demands and are restricted to foods within immediate surroundings. For adults and juveniles during cold winters, meeting thermoregulatory demands with available food items of limited nutrient content may be challenging. Our objective was to determine the primary animal and plant components of Lesser Prairie-Chicken diets among native prairie, cropland, and Conservation Reserve Program (CRP) fields in Kansas and Colorado, USA, during brooding and winter using a DNA metabarcoding approach. Lesser Prairie-Chicken fecal samples ($n = 314$) were collected during summer 2014 and winter 2014–2015, DNA was extracted, amplified, and sequenced. A region of the cytochrome oxidase I (COI) gene was sequenced to determine the arthropod component of the diet, and a portion of the *trn*L intron region was used to determine the plant component. Relying on fecal DNA to quantify dietary composition, as opposed to traditional visual identification of gut contents, revealed a greater proportion of soft-bodied arthropods than previously recorded. Among 80 fecal samples for which threshold arthropod DNA reads were obtained, 35% of the sequences were most likely from Lepidoptera, 26% from Orthoptera, 14% from Araneae, 13% from Hemiptera, and 12% from other orders. Plant sequences from 137 fecal samples were composed of species similar to *Ambrosia* (27%), followed by species similar to *Lactuca* or *Taraxacum* (10%), *Medicago* (6%), and *Triticum* (5%). Forbs were the predominant (>50% of reads) plant food consumed during both brood rearing and winter. The importance both of native forbs and of a broad array of arthropods that rely on forbs suggests that disturbance regimes that promote forbs may be crucial in providing food for Lesser Prairie-Chickens in the northern portion of their distribution.

Keywords: arthropods, diet, DNA metabarcoding, foraging, forbs, grasslands, grouse, invertebrates, Lesser Prairie-Chicken, *Tympanuchus pallidicinctus*

Identificación de la dieta de un urogallo de la pradera en disminución usando meta-códigos de barra de ADN

RESUMEN

La dieta durante los períodos críticos de incubación y de invierno probablemente influencian el crecimiento de las poblaciones de *Tympanuchus pallidicinctus*. Durante el período de incubación, los polluelos en rápido crecimiento de *T. pallidicinctus* tienen altas demandas de calorías y están restringidos a alimentos dentro del entorno inmediato. Para los adultos y los juveniles durante los inviernos fríos, alcanzar las demandas de termorregulación a partir de los ítems alimenticios con contenido limitado de nutrientes puede ser un desafío. Nuestro objetivo fue determinar los componentes principales de animales y plantas de la dieta de *T. pallidicinctus* en praderas nativas, cultivos y campos del Programa de Reservas de Conservación (PRC) en Kansas y Colorado, EEUU, durante la incubación y el invierno, usando un enfoque de meta-códigos de barra de ADN. Las muestras de heces de *T. pallidicinctus* ($n = 314$) fueron colectadas durante el verano de 2014 y el invierno de 2014–2015 y el ADN fue extraído, amplificado y secuenciado. Una región del gen de citocromo oxidasa I (COI) fue secuenciada para determinar el contenido de artrópodos de la dieta y una porción de la región del intrón trnL fue usada para el componente de las plantas. El uso de AND de heces para cuantificar la composición de la dieta en contraposición con la identificación visual tradicional del contenido intestinal reveló una mayor proporción de artrópodos de cuerpo blando que lo registrado previamente. Entre 80 muestras de heces de las cuales se obtuvieron umbrales de lectura del ADN de artrópodos, 35% de las secuencias fueron probablemente de Lepidoptera, 26% de Orthoptera, 14% de Araneae y 13% de Hemiptera y 12% fueron de otros órdenes. Las secuencias de plantas a partir de 137 muestras de heces estuvieron comprendidas por especies similares a *Ambrosia* (27%) seguidas de especies similares a *Lactuca* o *Taraxacum* (10%), *Medicago* (6%) y *Triticum* (5%). Los forbes fueron la planta principal (>50% de las lecturas) consumida durante la crianza de la nidada y en el invierno. La importancia de los forbes nativos y de una amplia gama de artrópodos que dependen de los forbes sugieren que los regímenes de disturbio que promueven a los forbes pueden ser críticos para brindarle alimentos a *T. pallidicinctus* en la porción norte de su distribución.

Palabras clave: ADN, artrópodos, dieta, forbes, forrajeo, invertebrados, meta-códigos de barra, pastizales, *Tympanuchus pallidicinctus*, urogallo

INTRODUCTION

Knowledge of how starvation, predation, and thermoregulation interact to regulate Lesser Prairie-Chicken populations (*Tympanuchus pallidicinctus*) is limited, in part, by a lack of knowledge of diets during critical ecological periods (McNamara and Houston 1987, Newton 1998, Patten et al. 2005, Haukos and Zavaleta 2016). Lesser Prairie-Chicken populations have experienced long-term declines and continue to decline in areas that appear to provide good-quality habitat at broad scales (Garton et al. 2016, Rodgers 2016, Spencer et al. 2017). Minimizing the degradation of remaining available habitat will require a comprehensive understanding of Lesser Prairie-Chicken biology, including dietary needs. Lesser Prairie-Chicken diets have not been well described but appear to be variable throughout the year (Olawsky 1987, Haukos and Zavaleta 2016). Most diet information is based on information from individuals collected in autumn over a small part of the species' range (Crawford and Bolen 1976, Smith 1979, Riley et al. 1993, Haukos and Zavaleta 2016). However, availability of food resources during brood rearing and winter may be most limiting for galliforms (Sedinger 1997, Sandercock et al. 2008, Hagen et al. 2009). Rapidly growing Lesser Prairie-Chicken, and other grouse (Phasianidae), chicks have high calorie demands and are restricted to foods within their immediate surroundings (Bergerud and Gratson 1988, Lautenbach 2015). For adults and juveniles, meeting thermoregulatory demands with available food items of limited nutrient content may be challenging during cold winters (Moss 1983, Olawsky 1987, Sedinger 1997).

During the brooding period, adult Lesser Prairie-Chickens and chicks consume an array of invertebrate taxa and are thought to specialize on grasshoppers (Orthoptera; Jones 1964, Suminski 1977, Davis et al. 1980). Yet this conclusion is based on only a few studies that assessed diets from crop and fecal contents and from sampling available invertebrates at locations visited by Lesser Prairie-Chickens (Haukos and Zavaleta 2016). Sampled plant and arthropod abundance may not always be a good estimator of food availability, and diets cannot always be assumed on the basis of association (Jones 1964, Davis et al. 1980, Litvaitis 2000). At feeding sites, the size, mobility, and phenology of invertebrates should constrain which arthropods are considered available prey for Lesser Prairie-Chicken chicks. Variation in arthropod prey vulnerability and availability at feeding sites, even within species, must be considered to identify optimal diets; a lack of accounting for this association may lead to erroneous conclusions (Sih and Christensen 2001).

Although arthropods are important food sources for Lesser Prairie-Chickens during summer and fall, Lesser Prairie-Chickens typically rely on plant matter to fulfill energetic demands during winter and spring (Haukos and Zavaleta 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 known (Salter et al. 2005, McDonald et al. 2014). The reliance on persistent woody vegetation during the winter months is well documented for grouse species, 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, consumption of budding woody vegetation may be minimal in prairie-chickens in comparison to other grouse (Schmidt 1936).

Compared to other grouse, prairie-chickens may 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, Bogenschutz 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 of Lesser Prairie-Chickens in cultivated fields has not been 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 food resource 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, and provision of moisture may make alfalfa fields more attractive than wheat (*Triticum* spp.; Larsson et al. 2013). Additionally, alfalfa may be used by prairie-chickens because it is richer in protein than other herbaceous foods (Mowat et al. 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 primary winter food sources for Lesser Prairie-Chickens (Jones 1963).

True impacts on demography and contributions of food sources in the diet are 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 precludes any estimated impact on survival. Such post mortem analyses are not practical for species of concern. Microhistological analyses of feces are another option that can provide inference, and are noninvasive, but may underestimate easily digestible items (Bartolome et al. 1995, Litvaitis 2000). Additionally, not all contents in the crop are ultimately digested. Some of the material stored in the crop can be regurgitated (Jordan 2005). Therefore, DNA metabarcoding of fecal samples might be the best option for linking avian diets to fitness because it can identify prey items for species of conservation concern when collection of individuals is not practical (Pompanon et al. 2012). Instead of collecting individual crop samples, a standardized DNA region, or barcode, is identified that varies among, but is neutral within, taxa of interest. The DNA barcode region is amplified from fecal samples and compared to sequences from a reference database; then the relative contribution of food items can be estimated, based on the frequency of sequences (Ratnasingham and Hebert 2007, Zeale et al. 2011, Craine et al. 2015). DNA metabarcoding can be a particularly useful method for identifying soft-bodied arthropod prey items, which can be detected only by expert examination of gut contents or by histology of fecal samples (Burger et al. 1999, Zeale et al. 2011, Trevelline et al. 2016).

To estimate the effects of food availability on Lesser Prairie-Chicken populations, a stronger foundational understanding of diets used during critical life stages is needed, particularly in the northern extent of the species' range, which supports approximately two-thirds of the extant population (Garton et al. 2016, McDonald et al. 2016). Therefore, we used DNA metabarcoding of Lesser Prairie-Chicken fecal samples to quantify arthropod and plant taxa consumed by Lesser Prairie-Chickens during the brooding period and winter. We further used vegetation and arthropod survey data collected among 4 study sites in Kansas and Colorado, USA, to verify results.

METHODS

Study Area

The study area encompassed the northern extent of the Lesser Prairie-Chicken's distribution in Kansas and Colorado and included 4 study sites spread among the Mixed-Grass Prairie (Red Hills, Clark), Short-Grass Prairie/CRP Mosaic (Northwest), and Sand Sagebrush Prairie (Colorado, Clark) ecoregions (McDonald et al. 2014; Figure 1). Although the Colorado study site occurred within the Sand Sagebrush Prairie ecoregion, this site was predominantly composed of Conservation Reserve Program grassland (CRP) and cropland on the border of Prowers and Baca counties. Dominant grasses, forbs, subshrubs, shrubs, mean annual precipitation, and soil texture varied among study sites (Appendix Table 5). For example, subshrubs (e.g., *Gutierrezia sarothrae* and *Amphiachyris dracunculoides*) were more abundant than forbs in northwest Kansas and more abundant than shrubs at the Red Hills study site (Appendix Table 5). Forbs were predominantly *Salsola tragus* and *Kochia scoparia*, which were 2 of the top 3 most abundant forbs at all sites, excluding the Red Hills.

Sample Collection

We collected fecal samples during the brooding period (May–September) and winter (November–March) from Lesser Prairie-Chickens captured at leks between early March and mid-May using walk-in funnel traps and drop nets (Haukos et al. 1990, Silvy et al. 1990). We sexed the birds on the basis of plumage coloration, length of pinnae, and tail pattern (Copelin 1963). We marked female Lesser Prairie-Chickens with either a 15 g VHF transmitter or a 22 g GPS satellite PTT transmitter. We obtained locations for each VHF-marked female 3–4 times wk ^{1}, whereas females marked with GPS PTT transmitters accrued 8–10 locations day ^{1}, contingent on available daily solar energy. GPS locations were recorded every 2 hr during the day, with a 6 hr gap between 2300 and 0500 hours.

During the brooding season, we collected fecal samples from marked hens and chicks (separate vials for each)

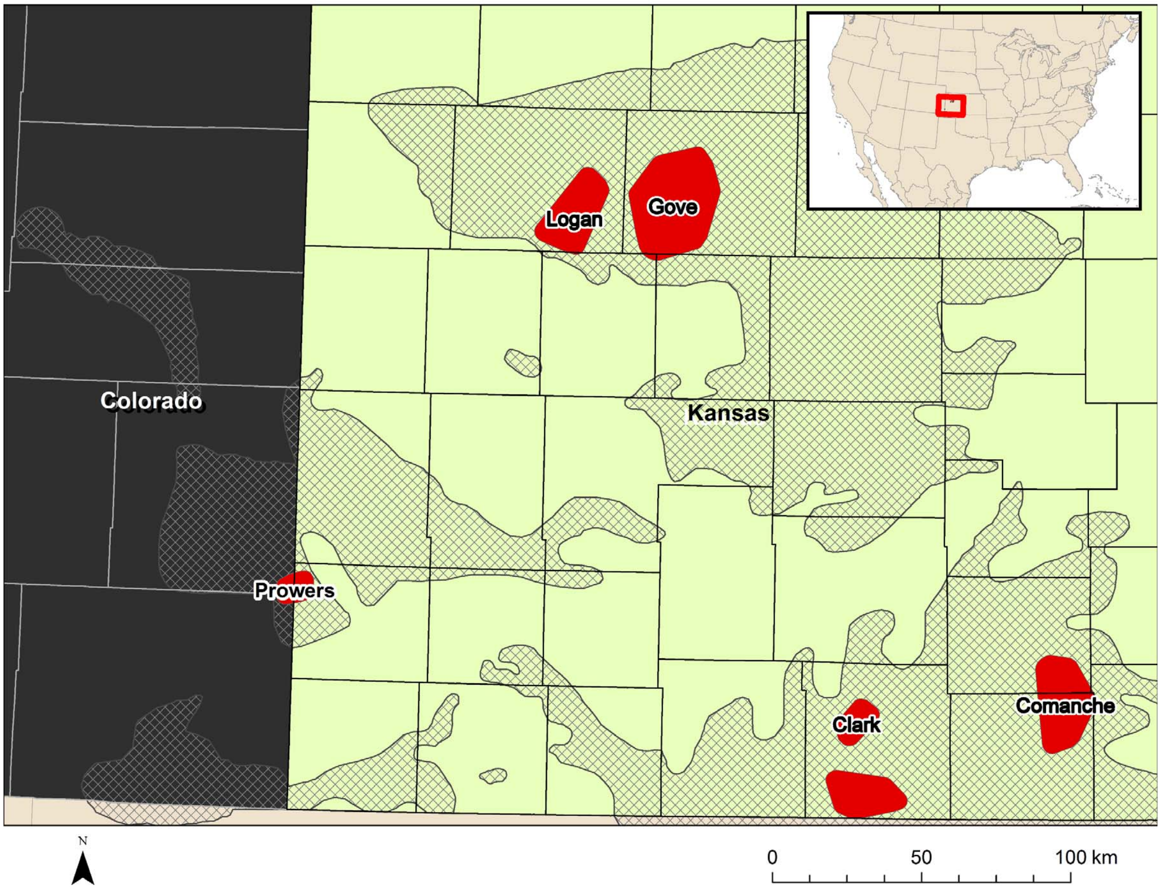


FIGURE 1. Extent of study area as determined by minimum convex polygons (shown in red) of VHF- and GPS-marked Lesser Prairie-Chickens in western Kansas and eastern Colorado, USA, 2014–2015. Study sites in Gove and Logan counties, Kansas, were combined for analyses and are referred to as "Northwest." The study site on the edge of Comanche and Kiowa counties, Kansas, is referred to as "Red Hills." The estimated current distribution of Lesser Prairie-Chickens is indicated by hatch marks (Hagen and Giesen 2005).

during brood capture and weekly flush counts occurring within 1 hr of sunrise (2–98 days old). We classified fecal samples as either chick or adult samples on the basis of their relative size differences. During winter and early spring (December–March), we collected fecal samples (1 pellet) at roost sites. Fresh fecal samples that were still moist and appeared to have been dropped the previous night were placed in 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 at Kansas State University before being shipped frozen overnight for laboratory analyses.

Sequencing

We extracted Genomic DNA from fecal samples using the PowerSoil-htp 96-well Soil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, California, USA). For arthropods, we amplified a fragment of the Folmer region of the cytochrome oxidase I (COI) gene 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 *trn*L intron was PCR-amplified from each genomic DNA sample using the c and h *trn*L primers (Taberlet et al. 2007), but modified to include appropriate barcodes and adapter sequences for Illumina multiplexed sequencing. The barcodes used were 12 base pair (bp) error-correcting barcodes unique to each sample (Caporaso et al. 2012). Each 25 μL PCR reaction was mixed according to PCR Master Mix specifications (Promega, Madison, Wisconsin, USA), with 2 μL of genomic DNA template. For *trn*L, the thermocycling program used an initial step at 94°C for 1 min, a final extension at 72°C for 2 min, and the following steps cycled 36 times: 1 min at 94°C, 30 s at 55°C, and 30 s at 72°C. For COI, the thermocycling program used an initial step at 94°C for 5 min, a final extension at 72°C for 10 min, and the following steps cycled 45 times: 30 s at 94°C, 45 s at 45°C, and 45 s at 72°C. We cleaned amplicons from each sample and normalized them using SequalPrep Normalization Plates

(Life Technologies, Carlsbad, California) before pooling them for sequencing on a MiSeq (Illumina, San Diego, California) running the 2 × 150 bp chemistry.

Assignment of Reads to Arthropod Genera

For COI reads indicating arthropod taxa, we demultiplexed sequences using "prep_fastq_for_uparse.py" (Leff 2018). 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 reads), filtering by quality score (maxee value of 1.5), removing sequences below the minimum expected amplicon length (90 bp), and removing singletons. We clustered sequences de novo at 99% similarity for OTU picking. We performed taxonomy assignment in QIIME, using the hierarchical naive Bayesian classifer RDP, retrained with a custom reference database curated from the Barcode of Life Database (version 3). Taxonomy was assigned at 99% similarity, with a 50% confidence threshold. We further filtered sequences 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.

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

Arthropod availability. We constrained assignments to taxa available for consumption in western Kansas and eastern Colorado. We used sweep-net surveys at brood locations from May to August in 2013 and 2014 to sample available arthropod prey. Sweep netting is an efficient method for sampling a wide array of invertebrate species (Yi et al. 2012). However, sweep netting can be biased toward capture of Araneae, Orthoptera, Lepidoptera, and Thysanoptera (Doxon et al. 2011, Spafford and Lortie 2013). Therefore, we didn't compare biomass estimates from sweep-net surveys directly to items detected in diet using a resource-selection type analysis. Instead, we restricted DNA metabarcoding assignments to taxa detected among all sites including genera within Orthoptera, families within Hemiptera, families detected within Coleoptera, families within Araneae, and all other taxa to the order resolution.

To perform sweep-net surveys, three 100-sweep surveys were conducted at sites where fecal samples were collected and at nearby paired random locations. Survey sweeps moved north to south, passing along 3 parallel transects 10 m apart, with the center transect passing directly through the bird location (Hagen et al. 2005). We compared cumulative biomass (g) of arthropod orders (broader taxonomic resolution) at study sites to help explain relative 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, we summed genus-specific RRA to estimate RRA at the order level. Using RRA, we documented the relative contribution of all orders to Lesser Prairie-Chicken diets during the brood-rearing period and winter, and then assessed orders as dependent variables in separate beta regression model sets.

We used a regression based on a parameterization of the beta distribution to examine differences in RRA for orders that were predominant in fecal samples. We evaluated the relationships of RRA values among independent variables including period (brooding period and winter), chick (yes or no) during the brood-rearing period, and study sites (Northwest, Red Hills, Clark, and Colorado; Ferrari and Cribari-Neto 2004). We developed box plots to depict the median, first, and third quartiles, and maximum and minimum values of RRA for the 4 predominantly consumed orders at each site. After screening for differences among period, site, and age class, we used a multimodel inference approach to examine how spatially and temporally related covariates influenced the composition of arthropods in the diet during the brood-rearing and winter periods, separately. We examined periods separately because of the differences in available foods based on phenology and because Lesser Prairie-Chickens use a greater abundance of arthropods in the brood-rearing period than in 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, CRP, and cropland. Also included in the model set was land cover type as a categorical covariate with multiple levels, including native grassland, CRP, and cropland as separate factors and a study-site model with multiple levels (Northwest, Red Hills, Clark, and Colorado). "Native grassland" refers to grasslands occurring on soil never previously tilled and that were typically maintained for cattle production (but note that all CRP grasslands assessed were planted with native grasses and forbs). Temporally related covariates included day since start of period, chick age in days, and age class during the brood-rearing period (adult, juvenile). Day since start of period 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). We conducted regression and performed multi-model inference using the packages "betareg" (Zeileis et al. 2016) and "AICmodavg" (Mazerolle 2016) in R (R Development Core Team 2016).

After fitting beta distribution regression models, we screened for period, age, and site effects based on informative beta coefficients. Beta coefficients were considered informative, or statistically meaningful, if not overlapping zero at the 85% confidence interval (CI; Arnold 2010). For multimodel inference, we ranked and selected the most parsimonious model based on Akaike's Information Criterion corrected for small sample sizes (AIC_c), for the 3 most abundant orders based on RRA. Models with $\Delta\mathrm{AIC}_c$ 2 were considered equal in parsimony (Burnham and Anderson 2002, Arnold 2010).

Assignment of Reads to Plant Taxa and Functional Groups

Sequences were demultiplexed for *trn*L 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). We used "fastx_clipper" to trim primer and adaptor regions from both ends (https://github.com/agordon/fastx_toolkit) because merged reads often extended beyond the amplicon region of the sequencing construct. 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 <0.1, and only sequences with >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 National Center for Biotechnology Information (NCBI) nucleotide and taxonomy database as the reference. The tabular BLAST hit tables for each OTU representative were then parsed so that only hits with >97% query coverage and identity were kept, using the "usearch7" approach (Edgar 2013, Craine et al. 2015). The NCBI genus names associated with each hit were used to populate the OTU taxonomy assignment lists. All samples with <50 *trn*L reads were excluded from analyses of *trn*L RRA (Kartzinel et al. 2015). We estimated OTU-specific RRA and defined a representative genus for each OTU to describe composition in diet. We used the representative genera when summarizing OTU composition in diets. For example, OTUs were from species in genera similar to *Ambrosia*. We limited plant genera within OTU to those detected during extensive vegetation surveys among sites (Appendix A).

For *trn*L, an average of 4% of sequences was from *Pinus* (range: 0–51%). Because of the unlikelihood of *Pinus* biomass being consumed and the presence of *Pinus* DNA in the blanks, the one OTU that matched with *Pinus* species was removed from the dataset. For *trn*L, among the top 10 OTUs, OTU 23 did not match at 97% levels for coverage and identity for any species in the NCBI database. However, OTU 23 matched at 100% coverage and 95% identity with a *Chenopodium* species in the NCBI database and was considered a species similar to *Chenopodium* for the purposes of this study.

Functional group assignments. Because OTUs often encompassed multiple genera, we grouped RRA from different plant genera into functional groups including forbs, shrubs, subshrubs (mostly *Gutierrezia*), legumes, grasses, crops (not including alfalfa), and alfalfa. Placing genera into each functional group presented challenges because the OTUs frequently encompassed genera indicative of multiple groups (see below). However, linking plant foods consumed to specific functional groups was necessary to allow for comparisons among sites and to make direct connections to the 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%. For example, 17 of 33 OTUs that identified either grass or crop foods included both crop and native grass genera (e.g., *Triticum* and *Elymus*); 2 of 45 OTUs of genera including shrub, subshrub, and forb species included representatives of >1 functional group (e.g., *Artemisia* and *Ambrosia*); and 1 of 5 OTUs for genera of legumes included both cultivated and native species (e.g., *Medicago* and *Vicia*). To overcome functional-group overlap within OTUs, we constrained the use of crop and shrub foods to instances when each land cover type occurred within 48 hr home ranges; and we used the Bayesian approach, similar to regional assignments in Royle and Rubenstein (2004), to estimate RRA for each functional groups using identity values as a prior probability:

$$\mathrm{RRA}_{fg=k} = \leftarrow \left(\frac{I_{g=i}}{\sum_{\mathrm{OTU}=j} (I_g) \leftarrow} \times \mathrm{RRA}_{\mathrm{OTU}=j} \right)$$

We estimated an adjusted RRA for each functional group ($\mathrm{RRA}_{fg=k}$) by estimating the average identity value (I_g) among genera within an OTU and then dividing I_g by the sum of identity values for functional groups within each OTU. We then multiplied the quotient by the RRA estimated for each OTU ($\mathrm{RRA}_{\mathrm{OTU}\,=\,j}$). The adjusted RRA accounts for the probability that each read is from a particular functional group based on the identity value. The identity value is a measure of the match between the OTU detected in the fecal sample and genus-specific reference sequence.

Plant availability. To limit plant forage possibilities to those available, and to minimize the overlap of certain OTUs encompassing multiple functional groups, we combined DNA metabarcoding inference with telemetry and extensive plant survey data. We limited native plant food availability to those genera detected during point-step transects among all study sites (Appendix A). At each study site, 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) or the National Agriculture Imagery Program (NAIP) 2012 satellite imagery. Patches were identified as areas of homogeneous vegetation >2 ha in size, placed in categories (e.g., 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 fall and winter.

To minimize overlap of certain OTUs that included multiple functional groups, we created home ranges encompassing the previous 48 hr period visited by each individual and identified the presence–absence of crop or shrub functional groups. We 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 hr period. We used maximum distances to buffer sampled locations for VHF birds during each season. We excluded dispersing birds with straight-line movements >5 km from analyses. A 48 hr home range was used because it should encompass the spatiotemporal foraging extent incorporated into the fresh fecal sample. The 48 hr home interval encompassed a 9.9 hr fluid retention in Rock Ptarmigan (*Lagopus muta*), while providing enough locations to include foraging locations (Stevens and Hume 1998). We used occurrence of cultivated foods (row crops, alfalfa) and shrubs within an individual's home range to determine whether a bird had access to cultivated foods. We excluded cultivated crops as potential food items if there was no cropland in the 48 hr home range. After accounting for the availability of crop and shrub foods to each individual, we adjusted RRA to reflect availability by adding, or removing, functional-group possibilities. All home ranges included CRP or native grassland; therefore, forbs and grasses were included as possibilities for all individuals.

Spatial and temporal influence on the consumption of plants. After RRA was estimated for all plant functional groups (e.g., forbs, shrubs, subshrubs, legumes, grasses, and crops), we focused on univariate variation of specific functional groups among spatial and temporal independent covariates. Similar to methods described above, we used the package "betareg" in R 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 we used a multi-model 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.

We used the same spatially related covariates as we did for arthropods, including CRP, native grassland, crop, alfalfa, and land cover type. Temporally related covariates included day since start of period and the quadratic effect of day since start of period. We expected that the composition of functional plant groups may change later in the brood-rearing period and that plant composition of winter diets may change because only the most persistent shrub- and crop-based foods remain available during the coldest portions of winter. We followed the same multi-model inference protocol based on AIC_c and informative coefficients of beta regression models (85% CI) described above for arthropods (Burnham and Anderson 2002, Arnold 2010, Mazerolle 2016, Zeileis et al. 2016).

Evaluation of Sampled Taxonomic Richness

To examine whether sample sizes were sufficient to detect all arthropod and plant foods used by Lesser Prairie-Chickens at each study site, we used species accumulation curves depicting 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, and the "Lomolino" function was used to describe the curves (Oksanen et al. 2015). From the function, we estimated an asymptote and the number of OTUs achieving a midpoint of the asymptote. We also estimated extrapolated species richness using the function "poolaccum" within package "vegan" following Chao (1987).

RESULTS

We collected a total of 314 fecal samples from Lesser Prairie-Chickens during the brood-rearing period ($n =$← 211) and winter ($n = 103$) of 2014–2015. The number of samples collected varied by site and season (Table 1). Among all sites and seasons, arthropod DNA were 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)

TABLE 1. Number of collected fecal samples and those with readable plant or animal DNA (in parentheses) at each study site in the northern portion of the Lesser Prairie-Chicken range in Kansas (KS) and Colorado, USA, during the brooding period and winter 2014–2015.

	Site	All seasons	Brood rearing	Winter
Animal DNA	Colorado	28 (13)	6 (3)	22 (10)
	Clark, KS	124 (29)	81 (17)	43(12)
	Northwest, KS	117 (27)	93 (25)	24 (2)
	Red Hills, KS	45 (11)	31 (5)	14 (6)
	Total	314 (80)	211 (50)	103 (30)
Plant DNA	Colorado	28 (28)	6 (6)	22 (22)
	Clark, KS	124 (51)	81 (9)	43 (42)
	Northwest, KS	117 (53)	93 (30)	24 (23)
	Red Hills, KS	45 (18)	31 (4)	14 (14)
	Total	314 (150)	211 (49)	103 (101)

were identified among all fecal samples. Among the 80 samples that produced 10 COI sequences, there was an average of 376 sequences per sample. An average of 4,591 sequences per sample were present among the 150 samples that produced 50 *trn*L sequences (plant DNA). During the brood-rearing period, 6% (4) of the 48 hr home ranges included CRP, 22% (15) included cropland, and 72% (48) included native grassland. Of the winter 48 hr home ranges, 15% (21) included CRP, 27% (38) included cropland, and 57% (79) included native grassland.

Arthropods

A total of 75 arthropod OTUs were identified in diets of Lesser Prairie-Chickens using COI analyses. Results from OTUs encompassed 4 classes: Insecta (63), Arachnida (9), Collembola (1), and Malacostraca (1). Among these 4 classes, 12 orders and 50 families were represented. Twenty-eight of the genera were Lepidoptera, 7 Araneae, and 6 Hemiptera (Appendix Table 6). On average, 35% of the RRA was from Lepidoptera, 26% from Orthoptera, 14% from Araneae, and 13% from Hemiptera (Appendix Figure 8 and Appendix Table 7).

Sweep-net transects indicated that arthropod communities varied among study 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 (Appendix Figure 9). Lepidopterans comprised >4 times more of the arthropod community biomass in Northwest and Colorado sites than in the Red Hills site and 1.6 times more than in the Clark study site.

Beta regressions suggested no differences among Lepidoptera, Orthoptera, Hemiptera, and Araneae composition in diets between the brooding period and winter (winter $\beta = 0.054 \pm 0.303$, 0.269 ± 0.293, 0.210 ± 0.265, 0.265 ± 0.279, respectively; brooding period as reference intercept). However, average reads per sample were fewer in the winter than in the brooding period for all sites except Colorado (Appendix Table 7). Given our sample size, the power of detecting a difference at an 85% CI was 0.24, 0.43, 0.47, and 0.56, respectively. 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, respectively). Beta regressions also indicated 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, respectively). There was an indication of more complicated nonlinear trends in the consumption of Lepidoptera and Orthoptera with minimal use of Lepidoptera after 40 days of age and greater consumption of Orthoptera when chicks surpassed 40 days of age (Figure 2).

The lack of variation among periods and ages is further indicated by stronger model support for land cover (Native Prairie, CRP, cropland) and site-based covariates for Lepidoptera and Araneae, which suggest that variation in arthropod diet consumption is more influenced by landscape characteristics than by temporal factors (Table 2). For Orthoptera during brood rearing, the model including date as a covariate was ranked highest but was equally parsimonious ($\Delta \text{AIC}_c < 2$) with the native grassland, crop, and CRP models, and its beta coefficient overlapped zero at the 85% CI (Table 2). 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 2 and 3).

Spatial variation in dietary composition was indicated by RRA among sites (Figure 3). During the brood-rearing period, presence of native grassland had the greatest influence on arthropod diet composition among Lepidoptera, Orthoptera, and Araneae but carried, on average, 30% of model weight (Table 2), which suggests that several variables were likely influential. The contribution of Lepidoptera in diets during the brood-rearing period decreased in native grassland (native grassland $\beta =\leftarrow 0.657 \pm 0.405$; Table 2). Consumption of lepidopterans was 2.12× less in native grassland in comparison to cropland (23.2 ± 6.00% vs. 49.2 ± 11.8%; Figure 4). 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% CI (native grassland $\beta = 0.559 \pm 0.379$). Araneae contributed 65× more to diets in native grassland than in other cover types and was rarely consumed in cropland (26.2 ± 7.02% vs. 0.04 ± 0.004%; Figure 4). For Orthoptera, the model including native grassland as a covariate was not informative (native grassland $\beta = 0.154 \pm 0.361$). Despite not providing a statistically meaningful

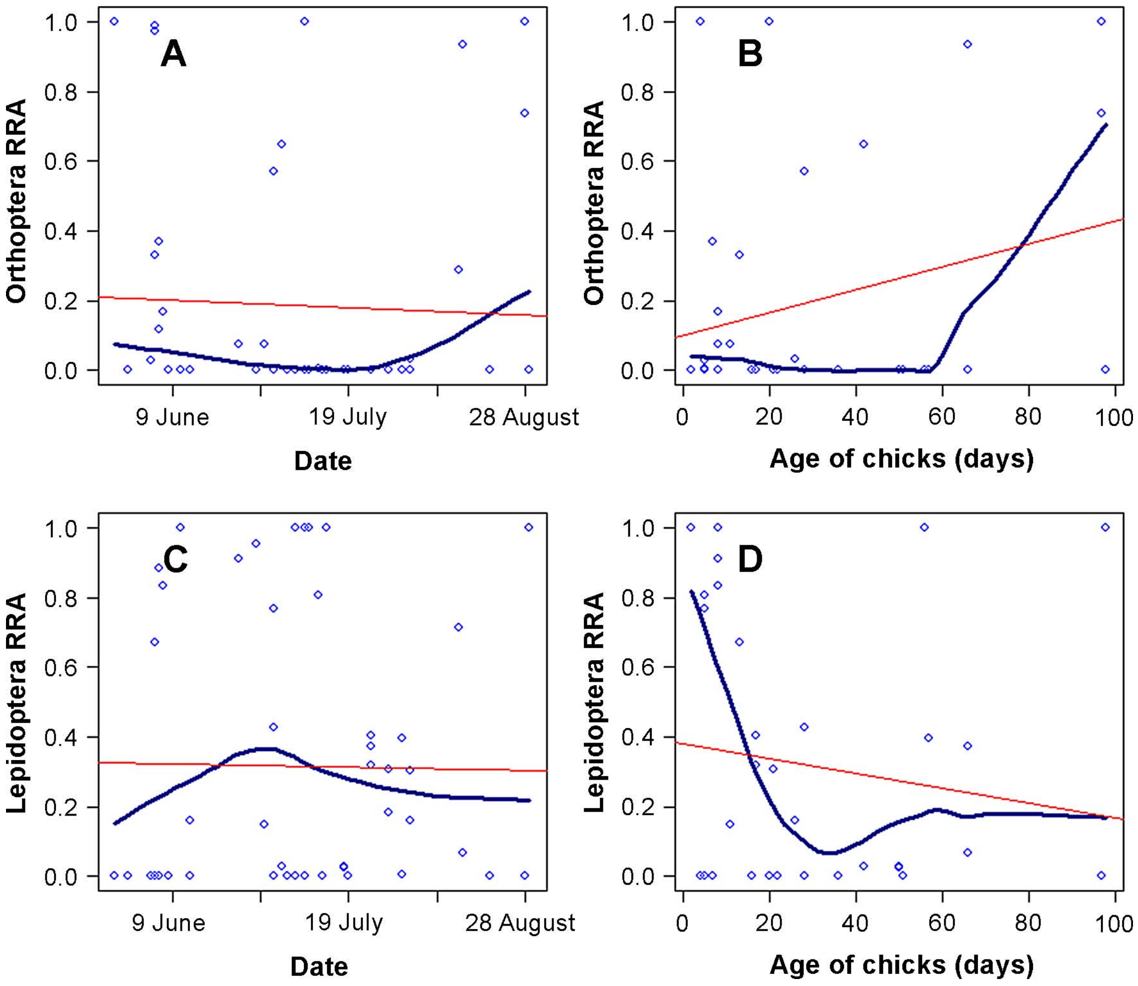


FIGURE 2. Scatter plots fitted with least squares (red) and locally weighted scatterplot smooth lines (blue) to depict patterns in the composition of Orthoptera (**A**, **B**) and Lepidoptera (**C**, **D**) in the diets of Lesser Prairie-Chicken chickens during the brood-rearing period of 2014 in Kansas and Colorado, USA. Days encompass May 27, 2014, to August 29, 2014; ages of chicks depicted range from 2 to 98 days.

difference, point estimates for Orthoptera RRA was 21.7 ± 6.50% in native grassland vs. 12.7 ± 6.71% in other cover types. Hemiptera contributed relatively equally to diets among Lesser Prairie-Chickens using CRP grassland, native grassland, and cropland (Figure 4).

In winter, Lepidoptera, Orthoptera, and Hymenoptera (most likely galls) contributed most to arthropod-based food for Lesser Prairie-Chickens (Appendix Figure 8 and Appendix Table 7). Of the top 4 orders contributing to winter diets, Orthoptera was the only order that changed (decreased) as the winter progressed, which was significant at the 85% CI (day since start of period β =-0.035 ± 0.0131). Among sites, Clark birds had the greatest percentages of Orthoptera in their winter diet when compared to all other sites, and this was significant at the 85% CI (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 1% of the plant diet for a given bird at a given time. In contrast to the assignment of OTU to specific arthropod taxa, *trn*L OTUs were not genus specific and, on average, comprised 4.15 ± 4.79 genera, ranging from 1 to 28 potential genera that were present at all study sites combined. Of the 235 recorded OTUs, 70 represented 10% of the diet for 1 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 *Lactuca* or *Taraxacum* (10%), *Medicago* (6%), and *Triticum* (5%).

For the brood-rearing period, the 10 most abundant OTUs included species similar to *Ambrosia* (16.2%),

TABLE 2. Results of beta regression model for the consumption of Lepidoptera, Orthoptera, and Araneae by Lesser Prairie-Chickens in Kansas and Colorado, USA, during the brood-rearing period (June–September) of 2014. *K* is the number of parameters, AIC_c is Akaike's Information Criterion adjusted for small sample size, ΔAIC_c is the difference in AIC_c compared to the smallest value, and w_i is model weight. Models with beta coefficients not overlapping zero at the 85% confidence interval are in bold.

	Covariate [a]	K	AIC_c	ΔAIC_c	w_i
Lepidoptera	**Native grassland**	3	66.03	0	0.38
	CRP	3	64.98	1.05	0.22
	Crop	3	63.68	2.35	0.12
	Land cover	4	63.67	2.36	0.12
	Date	3	63.21	2.82	0.09
	Site	5	61.59	4.44	0.04
	Chick	3	61.02	5.00	0.03
	Age	3	37.34	28.68	0
Orthoptera	Date	3	109.7	0.00	0.2
	Native grassland	3	109.59	0.11	0.19
	Crop	3	109.49	0.21	0.18
	CRP	3	109.48	0.22	0.18
	Site	5	108.62	1.08	0.12
	Chick	3	107.42	2.28	0.06
	Land cover	4	107.24	2.46	0.06
	Age	3	65.88	43.82	0
Araneae	**Native grassland**	3	133.12	0	0.34
	CRP	3	132.42	0.7	0.24
	Date	3	131.3	1.82	0.14
	Crop	3	131.1	2.03	0.12
	Land cover	4	130.76	2.36	0.1
	Chick	3	129.09	4.03	0.04
	Site	5	127.48	5.65	0.02
	Age	3	76.71	56.41	0

[a] Covariates represent study site (site), day since start of period (date), adult or chick feces (chick), age in days of chick samples (age), and fecal sample located in cropland (crop), Conservation Reserve Program grassland (CRP), native working grassland, or each cover type (land cover).

TABLE 3. Beta regression model results for the consumption of Lepidoptera, Orthoptera, and Hymenoptera by Lesser Prairie-Chickens in Kansas and Colorado, USA, during winter 2014–2015. *K* is the number of parameters, AIC_c is Akaike's Information Criterion adjusted for small sample size, ΔAIC_c is the difference in AIC_c compared to the smallest value, and w_i is model weight. Models with beta coefficients not overlapping zero at the 85% confidence interval are in bold.

	Covariate [a]	K	AIC_c	ΔAIC_c	w_i
Lepidoptera	**Land cover**	3	30.08	0	0.30
	Native grassland	3	30.08	0	0.30
	CRP	3	30.08	0	0.30
	Date	3	27.66	2.42	0.09
	Site	5	24.8	5.27	0.02
Orthoptera	**Date**	3	41.49	0	0.86
	Site	5	37.25	4.25	0.10
	Land cover	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	Date	3	62.4	0	0.24
	CRP	3	62.4	0.01	0.24
	Land cover	3	62.4	0.01	0.24
	Native grassland	3	62.4	0.01	0.24
	Site	5	57.91	4.49	0.03

[a] Covariates represent study site (site), day since start of period (date), and fecal sample located in Conservation Reserve Program grassland (CRP), native working grassland (native grassland), or each cover type (land cover).

Lactuca (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 2 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%), *Lactuca* (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 2 separate OTUs as part of the top 10 most abundant winter OTUs.

Functional groups. Home ranges (48 hr) averaged 45.06 ± 44.50 ha during the nonbreeding season and 11.17 ± 8.84 ha during brood rearing for GPS-marked birds. We 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 GPS locations were obtained frequently enough to generate 48 hr home ranges. Maximum home range sizes during the nonbreeding and brooding periods were 191.52 ha and 32.83 ha, respectively, from which we derived 781 m and 323 m buffer distances around VHF fecal collection locations to account for all potentially used food sources.

In both the brood-rearing and winter periods, forbs were the predominant plant-based food source (winter 53.7 ± 3.7%, brooding 60.67 ± 5.5%; Appendix Figure 10). Differences in the overall use of functional groups among the winter and brood-rearing periods were minimal. However, subshrubs (e.g., *Gutierrezia* spp.) and grasses contributed 1.5 times (43.4 ± 3.7% vs. 29.8 ± 5.7%) more to Lesser Prairie-Chicken diets during winter than during brood rearing (winter $\beta = 0.564 \pm 0.220$, 0.287 ± 0.195). By contrast, there was no difference in the consumption of forbs, legumes, shrubs, and crops between periods (brooding $\beta = 0.198 \pm 0.230$, 0180 ± 0.209, 0.222 ± 0.175, 0.265 ± 0.185, respectively).

We assessed differences among all sites separately for each period. Within the brood-rearing period alone, foods in the forb, grass, and legume functional groups did not differ among sites. Shrub- and subshrub-based foods contributed more to diets during the brood-rearing period in the Red Hills and northwest Kansas compared to Clark

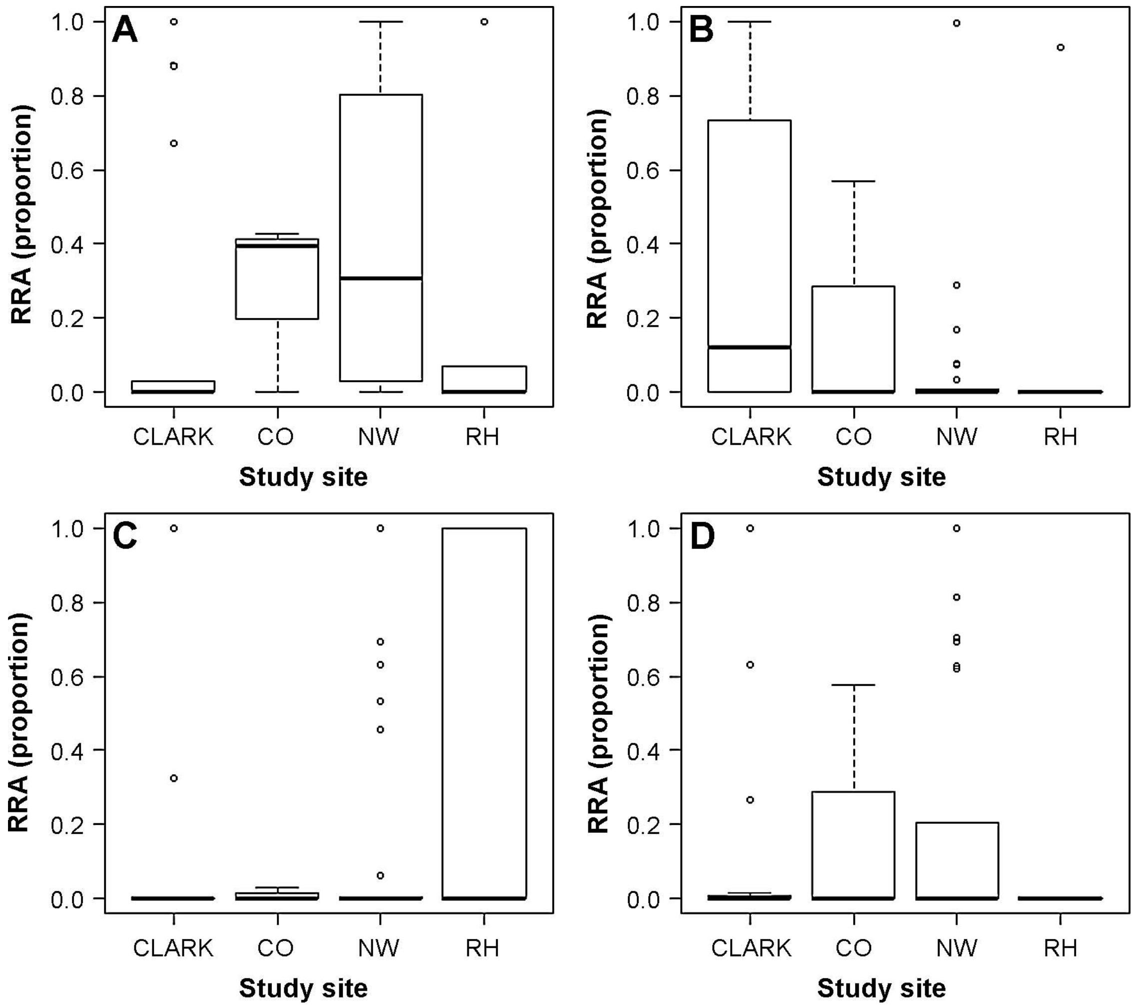


FIGURE 3. Relative readable abundance (RRA; proportion) of DNA within Lesser Prairie-Chicken fecal samples matching barcodes similar to arthropod orders (**A**) Lepidoptera, (**B**) Orthoptera, (**C**) Araneae, and (**D**) Hemiptera, grouped by study site. Fecal samples were pooled among study sites in Clark County, Kansas (Clark); Gove and Logan counties, Kansas (NW); Kiowa and Comanche counties, Kansas (RH); and Prowers and Baca counties, Colorado (CO), USA, and were collected during summer 2014 (hatch to 98 days old) from brooding females and chicks.

and Colorado (Red Hills β = 1.82 ± 0.782, Northwest β =← 0.769 ± 0.430, Clark β = 1.22 ± 0.779, Colorado β = 0.836 ± 0.444). Crop-based foods provided a greater contribution to brood-rearing diets in Colorado compared to other sites (β = 3.67 ± 0.509).

During winter, grass composition in diets varied among sites. More grasses were consumed during winter at the Northwest study than at the Clark study site (23.0 ± 2.6% vs. 11.0 ± 1.7%; β = 0.855 ± 0.289; Figure 5). Shrub foods contributed more in winter at the Red Hills study site than at Clark (β = 0.908 ± 0.391). Crop foods contributed more in winter to diets at the Northwest site than at Clark (β =← 0.443 ± 0.288). Last, subshrub foods contributed more in winter to diets at the Northwest and Red Hills study sites than at Clark (β =←0.836 ± 0.445, 1.22 ± 0.779, respectively; Figure 5).

After screening for differences among periods and sites, we focused on winter diets, using a multimodel inference approach, because Lesser Prairie-Chickens predominantly consume plant material during winter (Jones 1963). Models including spatially related covariates carried, on average, 99% of model weight (AIC$_c$ weight; Table 4). The top-ranking predictor for forb diet composition was occurrence in alfalfa and crop fields (Table 4). Forbs were consumed less in winter by Lesser Prairie-Chickens using alfalfa fields and crop fields in general (β =←1.57 ± 0.467; identical beta values for alfalfa and crop). Forbs were more readily consumed in native grassland and CRP (Figure 6). The proportion of grass in diets was best predicted by site (Table 4; see differences above), with use of native grassland ranking second among models (native grassland β = 0.386 ± 0.238). Birds using alfalfa and crop fields had

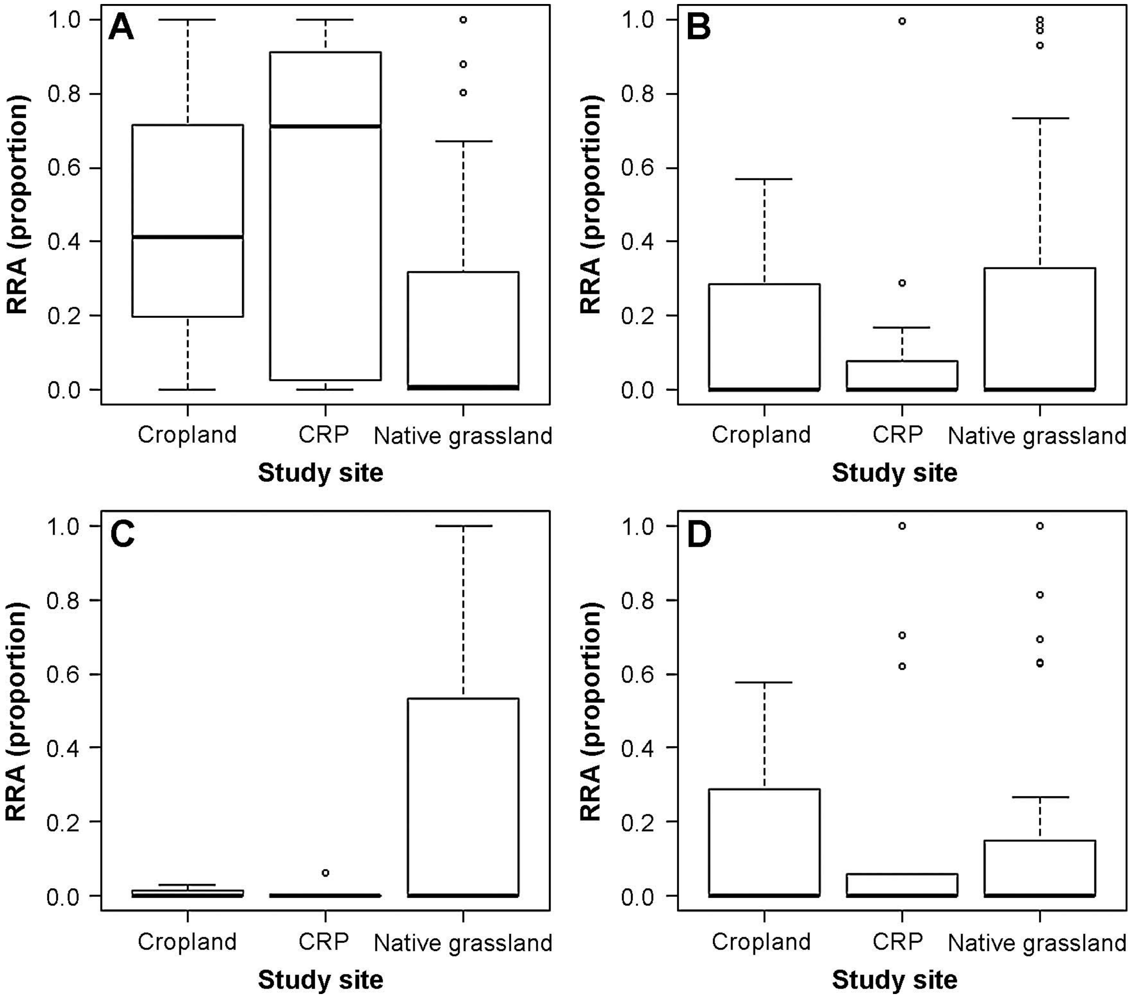


FIGURE 4. Relative readable abundance (RRA; proportion) of DNA within Lesser Prairie-Chicken fecal samples matching barcodes similar to arthropod orders (**A**) Lepidoptera, (**B**) Orthoptera, (**C**) Araneae, and (**D**) Hemiptera, grouped by land cover type where collected. Land cover types included cropland, Conservation Reserve Program grassland (CRP), and native working grassland (native grassland). Fecal samples were pooled among study sites in Clark County, Kansas; Gove and Logan counties, Kansas; Kiowa and Comanche counties, Kansas; and Prowers and Baca counties, Colorado, USA, and were collected during summer 2014 (hatch to 98 days old) from brooding females and chicks.

the greatest relative proportion of legumes in their diet ($\beta = 4.60 \pm 0.507$ for both alfalfa and crop). All fecal samples collected in cropland were collected in cultivated alfalfa, which confirms that birds can use alfalfa fields in winter as a food source. Shrubs contributed more to the diets of Lesser Prairie-Chickens using native grassland than to those in other cover types (native grassland $\beta = 1.55 \pm 0.254$; Table 4). The relative diet composition of subshrub appears to be most strongly influenced by use of crop fields, with consumption of subshrub lower in cropland ($\beta = \leftarrow 1.38 \pm 0.454$).

Evaluation of Sampled Taxonomic Richness

Among all sites, the arthropod species accumulation curve achieved an estimated asymptote at 156 OTUs, which suggests that we didn't sample all available forage; the midpoint for achieving an asymptote was estimated at 105 fecal samples (Figure 7). 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, which suggests that we sampled nearly all used plant forage at the OTU level. The midpoint for achieving the asymptote was estimated at 17 fecal samples (Figure 7). The extrapolated species richness at the OTU level (based on Chao 1987) was 262.

DISCUSSION

Using a combination of tools including DNA metabarcoding of fecal samples, telemetry data, and local plant and

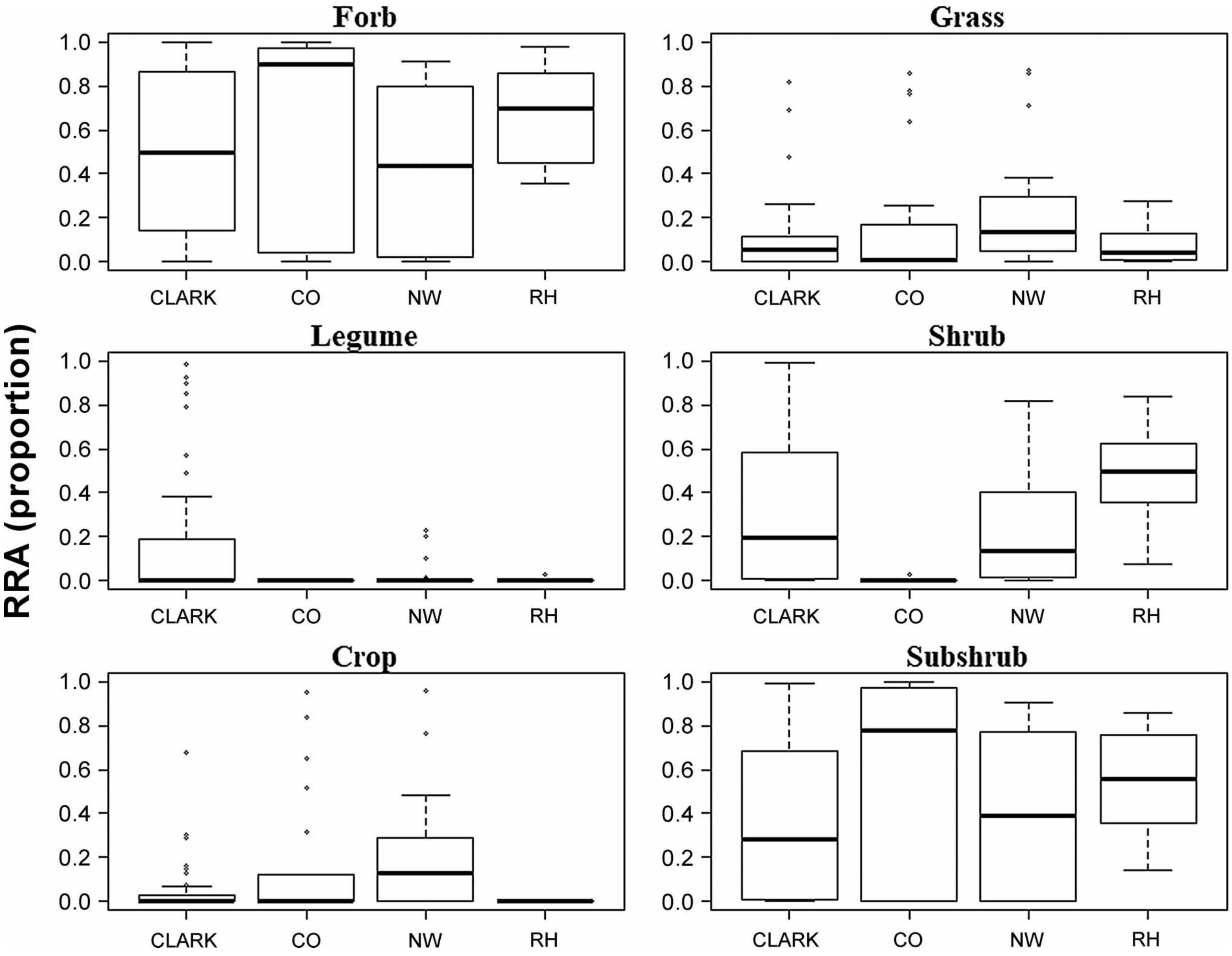


FIGURE 5. Adjusted relative readable abundance (RRA; proportion) of DNA within Lesser Prairie-Chicken fecal samples matching barcodes indicative of plant functional groups, including forbs, grasses, legumes, shrubs, crops, and subshrubs, grouped by study site. Fecal samples were collected from study sites in Clark County, Kansas (Clark); Gove and Logan counties, Kansas (NW); Kiowa and Comanche counties, Kansas (RH); and Prowers and Baca counties, Colorado (CO), USA, during winter 2014–2015 (November–March).

arthropod surveys, we identified foods consumed by Lesser Prairie-Chickens among 4 study sites. Lesser Prairie-Chickens that used native grassland maintained for cattle production consumed a greater diversity of arthropods and plant functional groups. In 48 hr home ranges that had a row-crop agriculture component, Lesser Prairie-Chickens largely used alfalfa when it was available during winter. Females and chicks, unexpectedly, preyed mostly on lepidopteran foods (likely larvae) during brood rearing. The use of shrub-based foods varied among sites but is likely not as important as in other regions (e.g., sand shinnery oak prairie) or in other grouse species (Schmidt 1936, Moss 1983, Olawsky 1987).

Arthropods in Lesser Prairie-Chicken Diets

The greater consumption of Lepidoptera in this study than was found in past research is likely a product of both the limited detection of soft-bodied prey using traditional methods and inclusion of study sites that have a strong row-crop agriculture component. Lesser Prairie-Chickens are known to consume lepidopteran larvae, yet the results of previous research suggest 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., butterfly and moth caterpillars). No study using fecal dissection identified Lepidoptera as a prey item for Lesser Prairie-Chickens (Jones 1963, Doerr and Guthery 1983). Only studies that examined 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 this order may be clumped as "other

TABLE 4. Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c compared to the smallest value (ΔAIC_c), and model weight (w_i) for beta regression models explaining winter plant diets of Lesser Prairie-Chickens in Kansas and Colorado, USA, 2013–2014. K is the number of parameters. Models with beta coefficients not overlapping zero at the 85% confidence interval are in bold.

	Covariate [a]	K	AIC_c	ΔAIC_c	w_i
Forb	**Alfalfa**	3	139	0	0.42
	Crop	3	139	0	0.42
	Land cover	4	137	2.1	0.15
	Native grassland	3	130	8.4	0.01
	CRP	3	127	11.9	0
	Julian date	3	127	11.9	0
	Site	5	126	12.3	0
	Quad date	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
	Land cover	4	392	6.4	0.03
	Julian date	3	391	6.5	0.03
	Alfalfa	3	391	7	0.02
	Crop	3	391	7	0.02
	Quad date	4	390	7.8	0.01
Legume	**Alfalfa**	3	249	0	0.42
	Crop	3	249	0	0.42
	Land cover	4	247	2.2	0.14
	Native grassland	3	241	8	0.01
	Quad date	4	241	8.3	0.01
	CRP	3	239	9.8	0
	Julian date	3	239	10.2	0
	Site not estimable [b]				
Shrub	**Native grassland**	3	479	0	0.62
	Land cover	4	478	1.5	0.3
	Site	5	475	4.1	0.08
	Quad date	4	461	18.4	0
	Date	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
	Date	3	983	1.35	0.09
	Land cover	4	983	1.58	0.08
	Quad date	4	982	1.99	0.07
Subshrub	**Alfalfa**	3	249	0	0.42
	Crop	3	249	0	0.42
	Land cover	4	247	2.2	0.14
	Native grassland	3	241	8	0.01
	Quad date	4	241	8.3	0.01
	Site	5	239	9.7	0
	CRP	3	239	9.8	0
	Date	3	239	10.2	0

[a] Covariates represent study site (site), day since start of period (date), and fecal sample located in cropland (crop), Conservation Reserve Program grassland (CRP), native working grassland (native grassland), alfalfa cropland (alfalfa), or each cover type (land cover).

[b] Some models were not estimable because they had too many zeros.

insects" (Olawsky 1987), making comparisons among other studies challenging. Overall, 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.

In addition to palatability, use of lepidopteran larvae during the brood-rearing period may be related to the ease of capture by a small, 13–35 g chick. Lepidopteran larvae would be easy for Lesser Prairie-Chicken chicks to obtain when occurring within reach on the ground or in shorter vegetation. It is possible that soft-bodied larvae from other orders (e.g., Coleoptera) could also be consumed when available. Although we didn't expect a greater consumption of Lepidoptera than of Orthoptera by Lesser Prairie-Chicken chicks, we 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 dietary selection of lepidopterans further identifies the necessity of matching life histories among predator and prey. The life-history strategies of arthropod species may largely determine their importance as a prey item.

Although Lepidoptera were used as a food source among all land cover types and sites, specific lepidopteran genera were used in agricultural landscapes. Diets of Lesser Prairie-Chickens during the brooding period were largely supported by the genera *Euxoa* and *Dargida*. These 2 genera comprise several known agricultural pest species, including army cutworms (*Euxoa auxiliaris*). Dietary use of cutworms by Lesser Prairie-Chickens was also detected in fall by Crawford and Bolen (1976) in fragmented sand shinnery oak prairie. Consumption of agricultural pests provides evidence of one ecological service provided by Lesser Prairie-Chickens that could be used to gain conservation support in private working landscapes throughout their distribution (Wenny et al. 2011).

In contrast to the prevalent consumption of Lepidoptera in their northern range, 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 the present study, we detected substantial variation in diets among study sites. The greater consumption of orthopterans at the Clark study site could be driven by the limited availability of lepidopterans and an increased abundance of grasshoppers in the genus *Melanoplus* at the Clark site (Appendix Figure

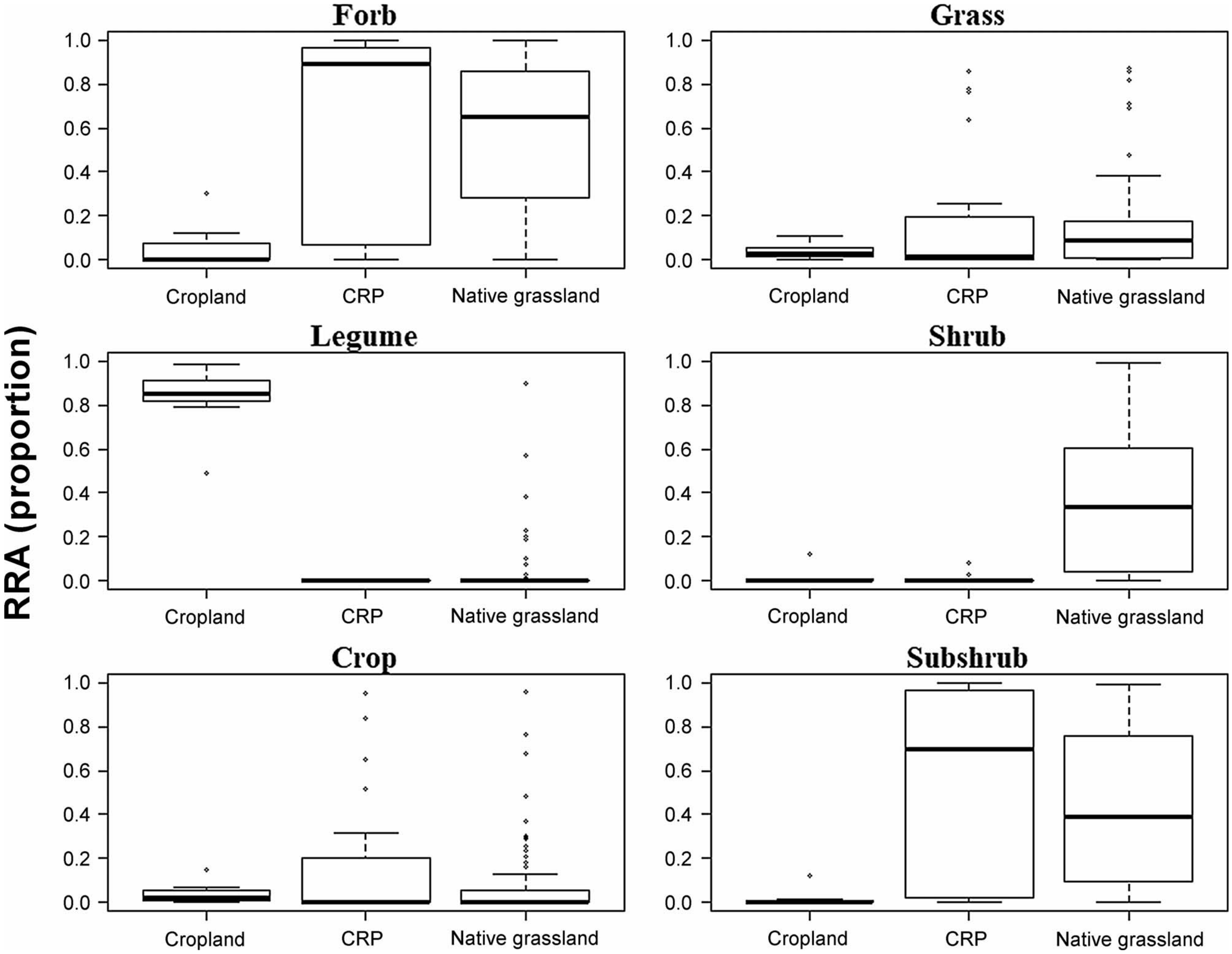


FIGURE 6. Adjusted relative readable abundance (RRA; proportion) of DNA within Lesser Prairie-Chicken fecal samples matching barcodes indicative of plant functional groups, including forbs, grasses, legumes, shrubs, crops, and subshrubs, grouped by land cover type. Land cover types included cropland, Conservation Reserve Program grassland (CRP), and native working grassland (native grassland). Fecal samples were pooled among study sites in Clark County, Kansas; Gove and Logan counties, Kansas; Kiowa and Comanche counties, Kansas; and Prowers and Baca counties, Colorado, USA, and were collected during winter 2014–2015 (November–March).

9; D. A. Haukos et al. personal observation). *Melanoplus* was the main genus 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 it an easily obtainable prey item for Lesser Prairie-Chickens (Pfadt 1994, D. A. Haukos et al. personal observation).

The similar consumption of Orthoptera by Lesser Prairie-Chickens using grassland compared to cropland or CRP also doesn't provide any indication of difference in use of Lepidoptera vs. Orthoptera in grassland. Although Orthoptera composition was greatest in grassland, the RRA of Orthoptera was nearly identical to that of Lepidoptera in native grassland. Because RRA data are proportional among arthropod orders, an estimate close to 25% (split among 4 main foods) within one cover type would suggest that individuals using that cover type have more diverse diets. Although the split among the 4 orders was not perfectly uniform, Lesser Prairie-Chickens that used native grassland consumed a more diverse arthropod diet, which contrasts with our hypothesis that Lesser Prairie-Chickens would specialize on Orthopteran prey. Lesser Prairie-Chicken broods using native grassland may be opportunistic predators when diets are assessed during 0–90 days of age (Davis et al. 1980).

Despite the fact that brood diets appeared to be opportunistic when examining the brooding period as a whole, there was some indication of a nonlinear transition from Lepidoptera- to Orthoptera-dominated diets as

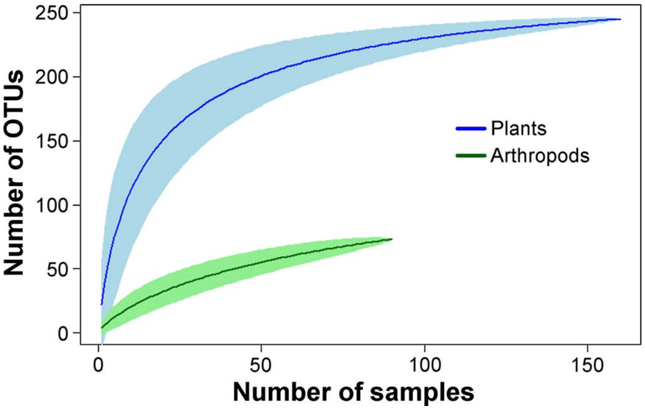


FIGURE 7. Species accumulation curves for plants and arthropods estimated using the R package "vegan" (Oksanen et al. 2015), depicting the relationship to number of operational taxonomic units (OTUs) detected in Lesser Prairie-Chicken fecal samples collected during brood rearing and winter, 2014–2015, in Kansas and Colorado, USA. Lomolino curves: plants $282.7/[1+17.1\^\log(2.3/x)]$; arthropods: $156.0/[1+105.3\^\log(2.25/x)]$.

chicks surpassed ~40 days of age. We were particularly interested in diet during the first few weeks of a Lesser Prairie-Chicken's life. Knowledge of factors influencing survival during the first 21 days can be crucial for understanding what drives overall population growth rates (Hagen et al. 2009, McNew et al. 2012, Lautenbach 2015). The finite rate of population growth (λ) among prairie grouse and other galliformes has consistently been shown to be sensitive to variation in the 0- to 21-day-old survival bottleneck (*Tympanuchus* spp.; Wisdom and Mills 1997, Sandercock et al. 2008, Hagen et al. 2009, McNew et al. 2012, Taylor et al. 2012). Food availability may be particularly important for survival through this life stage, as indicated by strong variation in the mass of chicks and by observations of dead, undepredated chicks that may have died from starvation or thermal stress (Lautenbach 2015). Knowledge of the effects of food availability on chick survival is largely limited to inference from a closely related species within the subfamily Tetraoninane, the Greater Sage-Grouse (*Centrocercus urophasianus*). 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 (the 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.

Comparative Nutrient Values of Lepidopterans and Orthopterans

Lepidopteran and orthopteran foods both provide greater concentrations of protein than any plant-based foods at the nutrient level (Lassiter and Edwards 1982, Savory 1989, Rumpold and Schlüter 2013). Protein in arthropod foods are also likely more digestible than that in plants (Stiven 1961, Savory 1989). On average, orthopterans can provide a food source that is 61% protein and 13% fat, whereas lepidopterans are 45% protein and 27% fat (Sugimura et al. 1984). Among protein estimates, there is interspecific variation and differences in digestibility. Furthermore, assimilation of protein from chitin-rich orthopterans and soft-bodied lepidopterans may be similar amid differences in nutrient composition (Sugimura et al. 1984). Mineral and amino acid composition provided by the 2 families appears to be similar, with variation among prey species (Rumpold and Schlütter 2013).

The Need for Ancillary Data

The potential benefits of using DNA metabarcoding to understand diets of wildlife species are numerous, but the current utility of the method hinges on ancillary data that can be used to constrain and evaluate the completeness of reference databases. We were unable to distinguish among certain plant foods that were from grass and crop functional groups using the primers we selected. The addition of 48 hr home range data allowed for greater inference on the use of cultivated foods. Additionally, reference DNA sequences for species that did not occur at any of the field sites sometimes matched sequences in fecal samples. To avoid inaccurate predictions, we constrained possible food sources to those detected during vegetation and arthropod surveys. The amplification of plant and arthropod DNA in only a proportion of the samples 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 in 74% of fecal samples from bats (Bohmann et al. 2011, Craine et al. 2015, Trevelline et al. 2016).

Plants

The predominant use of forbs as a food source during both brood-rearing and winter periods highlights the need to maintain disturbance regimes that support healthy forb populations (Hagen et al. 2004). Forbs provided a critical habitat component for Lesser Prairie-Chickens as food resources, even though they often comprised <10% of the available vegetation.

We detected greater RRA of forbs during 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 present 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 indicate consumption of *Callirhoe involucrata* (purple poppy mallow) or *Sphaeralcea coccinea* (scarlet globemallow), both of which were present at all sites and actively growing during the brood-rearing period (D. A. Haukos et al. personal observation). Leaves of *S. coccinea* are high in vitamin A, calcium, and protein and can be selected as food by scaled quail (*Callipepla squamata*; Ault et al. 1983, Arthun et al. 1992). Although documentation of *C. involucrata* as food for grassland birds is limited, the plant has adequate phosphorus and crude protein content (*Odocoileus virginianus*; Everitt and Gonzalez 1981). It also functions as a known larval host and food source for several butterflies (Fernandez-Canero and Gonzalez-Redondo 2010, Scott 2014). Observations were made of several caterpillar larvae on the receptacles of *C. involucrate* flowers at the Clark study site during the brooding period (D. Sullins personal observation). The presence of *Abutilon*-like plants in Lesser Prairie-Chicken diets could be from either direct or indirect consumption mediated through lepidopteran herbivory. The presence of arthropod foods can be attained only by first providing necessary host plants.

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 approaching lekking and nesting seasons (Haukos and Zavaleta 2016). Winter diets of grouse are often limited to only a few items that can provide sustenance—typically high in fiber, low in nutrient content, and requiring longer digestive tracts to process (Moss 1983). In the present study, the greater consumption of forbs compared to all other functional groups suggests a reliance on noncultivated foods in the northern portion of the Lesser Prairie-Chicken range. 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, DeYoung and Williford 2016) but is consistent with comparatively greater predation of "weed seeds" by pinnated grouse (e.g., Greater Prairie-Chickens [*Tympanuchus cupido*]) in comparison to Sharp-tailed Grouse (*T. phasianellus*; Schmidt 1936). Forb DNA was nearly absent from fecal samples collected in cropland, which suggests that current use of herbicides may reduce the availability of forbs in cropland.

Although forbs were dominant plant foods used by Lesser Prairie-Chickens during brood rearing and in winter, the relative importance of crops, shrubs, legumes, and subshrubs as food sources increased from brood rearing to winter. The amount of grass consumed remained the same, in contrast to the results of Jones (1963), who documented a slight increase in grasses consumed during winter. The increased use of shrubs and subshrubs may be related to the persistence of shrub- and subshrub-based foods during 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 leafy green 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 numerous secondary metabolite compounds make broom snakeweed challenging to digest (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, 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, Suminski 1977, Olawsky 1987, Riley et al. 1993) and other grouse (Patterson 1952, Remington and Braun 1985). Most research indicating that shrubs are important for Lesser Prairie-Chickens has focused on the use of sand shinnery oak where available in Texas and New Mexico, USA (Suminski 1977, Olawsky 1987, Riley et al. 1993). Sand sagebrush, sumac (*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 winter corresponded with the increased consumption of sand sagebrush from December to February in northwest Oklahoma, USA (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 largely restricted to the Clark study site, where the OTU containing alfalfa (*Medicago* spp., 100% identity and coverage) was consumed 1.95× more than the next leading OTU containing *Triticum*-like species. Cultivated alfalfa was available at the Clark study site and was consumed by Lesser Prairie-Chickens in distinct cropland areas. The use of alfalfa cropland at this site may explain differences in space use among regions (Robinson 2015).

Diversity and Food Stability

The greater diversity of forage in native working grassland may be key to food and nutrient stability in Lesser Prairie-Chickens. Lesser Prairie-Chickens occur in a region with the greatest variability of net primary productivity in the Great Plains (Sala et al 1998, Grisham et al. 2016). In such a variable environment, population viability may be more influenced by a stable presence of foods from year to year than by an abundance at any one time. Various arthropod and plant taxa can boom or bust in response to years of above-average precipitation or drought, and therefore food stability may be linked to a diversity of forage (Haglund 1980, Tilman and Downing 1994, Gutbrodt et al. 2011, Craine et al. 2013). Our results indicated that native working grassland provided forage for Lesser Prairie-Chickens, in addition to providing cover for reproduction and adult survival (Hagen et al. 2013). However, in some landscapes it is possible that the presence of small-scale row-crop agriculture adjacent to grassland could diversify food options (Rodgers 2016).

ACKNOWLEDGMENTS

We thank all the landowners who allowed access during the research project and all our technicians, including B. Anderson, S. Baker, S. Bard, G. Brinkman, K. Broadfoot, R. Cooper, J. Danner, J. Decker, E. Entsminger, R. Galvin, N. Gilbert, A. Godar, G. Gould, B. Hardy, S. Hoffman, D. Holt, B. Irle, T. Karish, A. Klais, H. Kruckman, K. Kuechle, S. Lane, E. Leipold, J. Letlebo, E. Mangelinckx, L. McCall, A. Nichter, K. Phillips, J. Proescholdt, J. Rabon, T. Reed, A. Rhodes, B. Ross, D. Spencer, A. Steed, A. Swicegood, P. Waldron, B. Walter, I. Waters, W. White, E. Wiens, J. Yantachka, and A. Zarazua for assisting with data collection. We greatly appreciate the logistic and technical support provided by J. Pitman, C. Hagen, J. Prendergast, K. Fricke, D. Tacha, D. Kraft, J. Ungerer, D. Krehbiel, A. Elliott, D. Dahlgren, G. Kramos, and A. Flanders. Thanks to J. Zavaleta for thought-provoking conversations related to Lesser Prairie-Chicken diets. We thank C. Conway for reviewing an earlier version of this publication.

Funding statement: Funding for the project was provided by Kansas Wildlife, Parks, and Tourism (Federal Assistance Grant KS W-73-R-3); USDA Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62); and USDA Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative.

Ethics statement: We complied with the *Guidelines to the Use of Wild Birds in Research* for all components of this research. We prepared protocols and obtained collection permits to capture and handle through the Kansas State University Institutional Animal Care and Use Committee protocol nos. 3241 and 3703; Kansas Department of Wildlife, Parks, and Tourism scientific collection permits SC-042-2013, SC-079-2014, and SC-001-2015; and Colorado Parks and Wildlife scientific collection license numbers 13TRb2053, 14TRb2053, and 15TRb2053.

Author contributions: D.S.S. and D.A.H. conceived the idea, design, and experiment. J.M.C., N.F., D.S.S., J.M.L., S.G.R., J.D.L., J.D.K., R.T.P., and J.H.R. performed the experiments (collected data and conducted the research). D.S.S., J.M.C., and N.F. developed or designed the methods. D.S.S. and J.M.C. analyzed the data. D.S.S., D.A.H., J.M.C., and B.K.S. wrote the paper.

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.

Bartolome, J., J. Franch, M. Gutman, and N. G. Seligman (1995). Technical note: Physical factors that influence fecal analysis estimates of herbivore diets. Journal of Range Management 48:267–270.

Bergerud, A. T., and M. W. Gratson (1988). Survival and breeding strategies of grouse. In Adaptive Strategies and Population Ecology of Northern Grouse, vol. 2: Theory and Synthesis (A. T. Bergerud and M. W. Gratson, Editors). University of Minnesota Press, Minneapolis, MN, USA. pp. 473–575.

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. K. Zeale, E. Clare, G. Jones, E. Willerslev, and M. T. P. Gilbert (2011). Molecular diet analysis of two African Free-tailed Bats (Molossidae) using high throughput sequencing. PLOS One 6: e21441.

Burger, J. C., M. A. Patten, J. T. Rotenberry, R. A. Redak (1999). Foraging ecology of the California Gnatcatcher deduced from fecal samples. Oecologia 120:304–310.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, second edition. Springer, 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, M. Bauer, N. Gromley, et al. (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.

Copelin, F. F. (1963). Lesser Prairie Chicken in Oklahoma. Pittman-Robertson Project W-62-R. Oklahoma Wildlife Conservation Department, Oklahoma City, OK, USA.

Craine, J. M., T. W. Ocheltree, J. B. Nippert, E. G. Towne, A. M. Skibbe, S. W. Kembel, and J. E. Fargione (2013). Global diversity of drought tolerance and grassland climate-change resilience. Nature Climate Change 3:63–67.

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.

Crawford, J. A., and E. G. Bolen (1976). Fall diet of Lesser Prairie Chickens in west Texas. The 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. In Proceedings of Prairie Grouse Symposium (P. A. Vohs, Jr., and F. L. Knopf, Editors). Oklahoma State University Press, Stillwater, OK, USA. pp. 75–80.

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. Studies in Avian Biology 48:77–98.

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). Age-related shifts in leaf chemistry of clonal aspen (*Populus tremuloides*). Journal of Chemical Ecology 32:1415–1429.

Doxon, E. D., C. A. Davis, and S. D. Fuhlendorf (2011). Comparison of two methods for sampling invertebrates: Vacuum and sweep-net sampling. Journal of Field Ornithology 82:60–67.

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. Nature Methods 10:996–998.

Evans, K. E., and D. R. Dietz (1974). Nutritional energetics of Sharp-tailed Grouse during winter. Journal of Wildlife Management 38:622–629.

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.

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.

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

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

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. Studies in Avian Biology 48:49–76.

Gregg, M. A., and J. A. Crawford (2009). Survival of Greater Sage-Grouse chicks and broods in the northern Great Basin. Journal of Wildlife Management 73:904–913.

Grisham, B. A., C. P. Griffin, and A. J. Godar (2016). Climate change. Studies in Avian Biology 48:221–242.

Gutbrodt, B., K. Mody, and S. Dorn (2011). Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. Oikos 120:1732–1740.

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

Hagen, C. A., and K. M. Giesen (2005). Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*), version 2.0. In Birds of North Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/364/articles/introduction

Hagen, C. A., B. A. Grisham, C. W. Boal, and D. A. Haukos (2013). A meta-analysis of Lesser Prairie-Chicken nesting and brood-rearing habitats: Implications for habitat management. Wildlife Society Bulletin 37:750–758.

Hagen, C. A., 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., 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.

Haglund, B. M. (1980). Proline and valine—cues which stimulate grasshopper herbivory during drought stress? Nature 288: 697–698.

Haukos, D. A., and J. C. Zavaleta (2016). Habitat. Studies in Avian Biology 48:99–132.

Haukos, D. A., L. M. Smith, and G. S. Broda (1990). Spring trapping of Lesser Prairie-Chickens. Journal of Field Ornithology 61:20–25.

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, KS, USA.

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.

Jordan, M. J. R. (2005). Dietary analysis for mammals and birds: A review of field techniques and animal-management applications. International Zoo Yearbook 39:108–116.

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 USA 112:8019–8024.

Larsson, L. C., C. L. Pruett, D. H. Wolfe, and M. A. Patten (2013). Fine-scale selection of habitat by the Lesser Prairie-Chicken. The Southwestern Naturalist 58:135–149.

Lassiter, J. W., and H. M. Edwards, Jr. (1982). Animal Nutrition. Reston Publishing, Reston, VA, USA.

Lautenbach, J. (2015). Lesser Prairie-Chicken reproductive success, habitat selection, and response to trees. M.S. thesis, Kansas State University, Manhattan, KS, USA.

Leff, J. W. (2018). Helper-code-for-uparse. https://github.com/leffj/helper-code-for-uparse

Litvaitis, J. A. (2000). Investigating food habits of terrestrial vertebrates. In Research Techniques in Animal Ecology: Controversies and Consequences (L. Boitani and T. K. Fuller, Editors). Columbia University Press, New York, NY, USA. pp. 165–190.

Mazerolle, M. J. (2016). Package 'AICcmodavg', version 2.00. R Foundation for Statistical Computing, Vienna. http://cran.r-project.org

McDonald, 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. 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 (1987). 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. The Condor 85:185–193.

Mowat, 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 of forages. Canadian Journal of Plant Science 45: 321–331.

Newton, I. (1998). Population Limitation in Birds. Academic Press, San Diego, CA, USA.

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

Olawsky, C. D. (1987). Effects of shinnery oak control with tebuthiuron on Lesser Prairie-Chicken populations. M.S. thesis, Texas Tech University, Lubbock, USA.

Patten, M. A., D. H. Wolfe, E. Shochat, and S. K. Sherrod (2005). Effects of microhabitat and microclimate selection on adult survivorship of the Lesser Prairie-Chicken. Journal of Wildlife Management 69:1270–1278.

Patterson, R. L. (1952). The Sage Grouse in Wyoming. Sage Books, Denver, CO, 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). Migratory Grasshopper: *Melanoplus sanguinipes* (Fabricius). Species Fact Sheet. Wyoming Agricultural Experiment Station Technical Bulletin 912.

Pompanon, F., B. E. Deagle, W. O. C. Symondson, D. S. Brown, S. N. Jarman, and P. Taberlet (2012). 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.

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.

R Development Core Team (2016). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Remington, T. E., and C. E. Braun (1985). 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. M.S. thesis, Kansas State University, Manhattan, KS, USA.

Rodgers, R. D. (2016). A history of Lesser Prairie-Chickens. Studies in Avian Biology 48:15–38.

Royle, J. A., and D. R. Rubenstein (2004). The role of species abundance in determining breeding origins of migratory birds with stable isotopes. Ecological Applications 14:1780–1788.

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

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.

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. The Wilson Bulletin 48:186–203.

Schwilling, M. D. (1955). A study of the Lesser Prairie-Chicken in Kansas. Kansas Forestry, Fish and Game Commission, Pratt, KS, USA.

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 of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, CO, USA.

Sedinger, J. S. (1997). Adaptation to and consequences of an herbivorous diet in grouse and waterfowl. The 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 Behaviour 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 Annual Conference 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. M.S. thesis, New Mexico State University, Las Cruces, NM, USA.

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

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.

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.

Stiven, A. E. (1961). Food energy available for and required by the Blue Grouse chick. Ecology 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, NM, USA.

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 *trn*L (UAA) intron for plant DNA barcoding. Nucleic Acids Research 35:e14.

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.

Tilman, D., and J. A. Downing (1994). Biodiversity and stability in grasslands. Nature 367:363–365.

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*). The Auk: Ornithological Advances 133: 415–428.

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. The Auk 128:1–14.

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

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.

Zeale, M. R. K., R. K. Butlin, G. L. A. 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.

Zeileis, A., F. Cribari-Neto, B. Gruen, and I. Kosmidis (2016). Package "betareg". https://cran.r-project.org/web/packages/betareg/betareg.pdf

APPENDIX A

Plant Genera Detected ($n = 257$) during Vegetation Surveys at Study Sites in Western Kansas and Eastern Colorado, USA, 2013–2016

Acer
Achillea
Achnatherum
Aegilops
Agrostis
Allium
Amaranthus
Ambrosia
Amorpha
Amphiachyris
Andropogon
Androsace
Anemone
Antennaria
Aphanostephus
Apocynum
Argemone
Aristida
Artemisia
Aruncus
Asclepia
Asclepias
Aster
Asteraceae
Astragalus
Atriplex
Baccharis
Baptisia
Bassia
Boltonia
Bothriochloa
Bouteloua
Brickellia
Bromus
Buchloe
Calamovilfa
Callirhoe
Calylophus
Cannabis
Carduus
Carex
Castilleja
Catalpa
Celtis
Cenchrus
Cephalanthus
Ceris
Chaeropyllum
Chaetopappa
Chamaecrista
Chamaesaracha
Chamaesyce
Chenopodium
Chloris
Cirsium
Cleome
Comandra
Commelina
Convulvulus
Conyza
Coreopsis
Cornus
Corydalis
Croptilon
Croton
Cryptantha
Cucurbita
Cuscuta
Cynodon
Cyperaceae
Cyperus
Dalea
Delphinium
Descurainia
Desmanthus
Dianthus
Dichanthelium
Digitaria
Distichlis
Draba
Echinacea
Echinochloa
Elaeagnus
Eleocharis

Elymus
Engelmannia
Equisetum
Eragrostis
Ericameria
Erigeron
Eriochloa
Eriogonum
Erioneuron
Escobaria
Eupatorium
Euphorbia
Euphorbiaceae
Evolvulus
Fabaceae
Ferocactus
Froelichia
Gaillardia
Galium
Geum
Glandularia
Gleditisia
Glycyrrhiza
Gomphrena
Grindelia
Gutierrezia
Haplopappus
Helianthus
Hesperostipa
Heterotheca
Hibiscus
Hoffmannseggia
Hordeum
Hybanthus
Hydrocotyle
Hymenopappus
Hypericum
Indigofera
Ipomoea
Ipomopsis
Iva
Juglans
Juncus
Juniperus
Krameria
Lactuca
Lepidium
Lespedeza
Liatris
Linum
Lithospermum
Lotus
Lygodesmia
Machaeranthera
Maclura
Marsilea
Medicago
Melampodium
Melilotus
Menispermum
Mentzelia
Microseris
Mimosa
Minuartia
Mirabilis
Monarda
Muhlenbergia
Nama
Nothoscordum
Nuttallanthus
Oenother
Oenothera
Opuntia
Oxalis
Oxytropis
Packera
Panicum
Paronychia
Parthenocissus
Pascopyron
Paspalum
Pediomelum
Penstemon
Phemeranthus
Phyla
Physalis
Physaria
Phytolacca
Plantago
Poa
Poaceae
Polanisia
Polygala
Polygonaceae
Polygonum
Polytaenia
Pomaria
Populus
Portulaca
Proboscidea
Prunus
Psilostrophe
Psoralidium
Pyrrhopappus
Pyrus
Quincula
Ranunculs
Ranunculus
Ratibida
Rayjacksonia
Rhus
Ribes
Robinia
Rudbeckia
Rumex
Salix
Salsola
Salvia
Sambucus
Sanguisorba
Sapindus
Schedonnardus
Schedonorus
Schizachyrium
Schoenoplectus
Scirpus
Securigera
Senecio
Setaria
Silphium
Sisymbrium
Sisyrinchium
Smilax
Solanum
Solidago
Sophora
Sorghastrum
Sorghum
Spartina
Sphaeralcea
Sporobolus
Stellaria
Stenaria
Stenosiphon
Stillingia
Streptanthus
Symphyotrichum
Tamarix
Taraxacum
Tephrosia
Tetraneuris
Thelesperma
Townsendia
Toxicodendron
Tradescantia
Tragia
Tragopogon
Tribulus
Tridens
Trifolium
Triodanis
Tripsacum
Triticum
Typha
Ulmus
Urtica
Verbascum
Verbena
Vernonia
Vicia
Viola
Vitus
Vulpia
Yucca
Zea

APPENDIX TABLE 5. Proportional abundance of the most common grass, forb, subshrub, 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, USA, 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	*Amphiachyris dracunculoides*	0.002	*Gutierrezia sarothrae*	0.033	*Amphiachyris 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

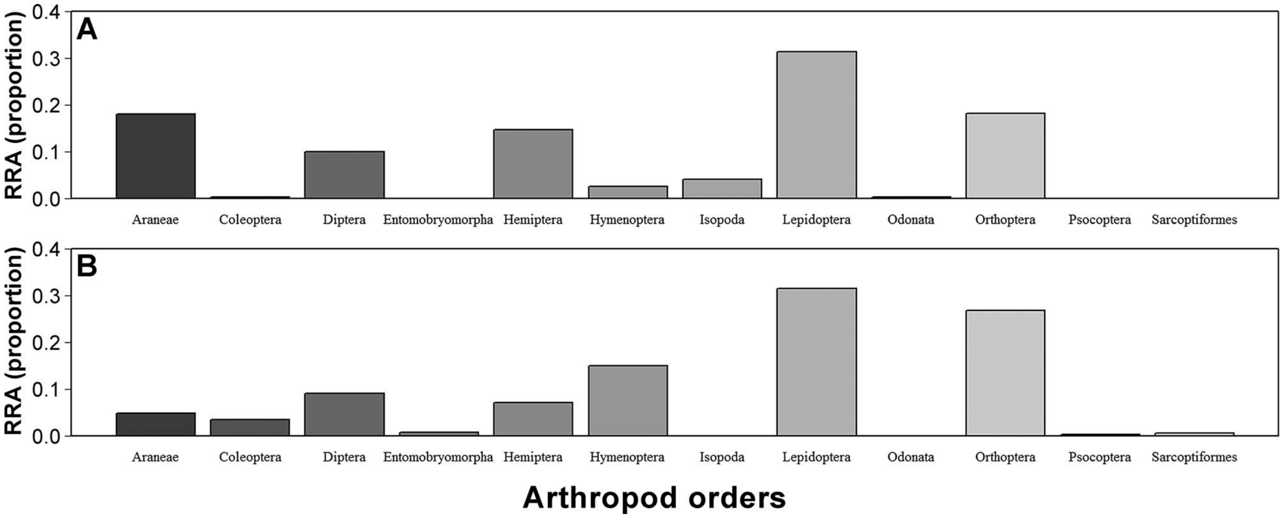
APPENDIX TABLE 6. Families and genera of arthropods detected using DNA barcoding in fecal samples of Lesser Prairie-Chickens during brood rearing and winter at 4 study sites in Kansas and Colorado, USA, 2014–2015.

Northwest		Clark		Red Hills		Colorado	
($n = 27$ fecals, 29,073 reads)		($n = 29$ fecals, 8,064 reads)		($n = 14$ fecals, 5,810 reads)		($n = 13$ fecals, 833 reads)	
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*	Noctuidae	*Halysidota*	Dermestidae	*Anthrenus*
Carabidae	*Cyclotrachel*	Coreidae	*Leptogloss*	Philodromid	*Ponometia*	Erebidae	*Halysidota*
Chrysomelid	*Leptinotarsa*	Cynipidae	*Andricus*		*Philodrom*	Erebidae	*Spilosoma*
Coccinellidae	*Harmonia*	Delphacidae	*Muirodelpha*			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*						

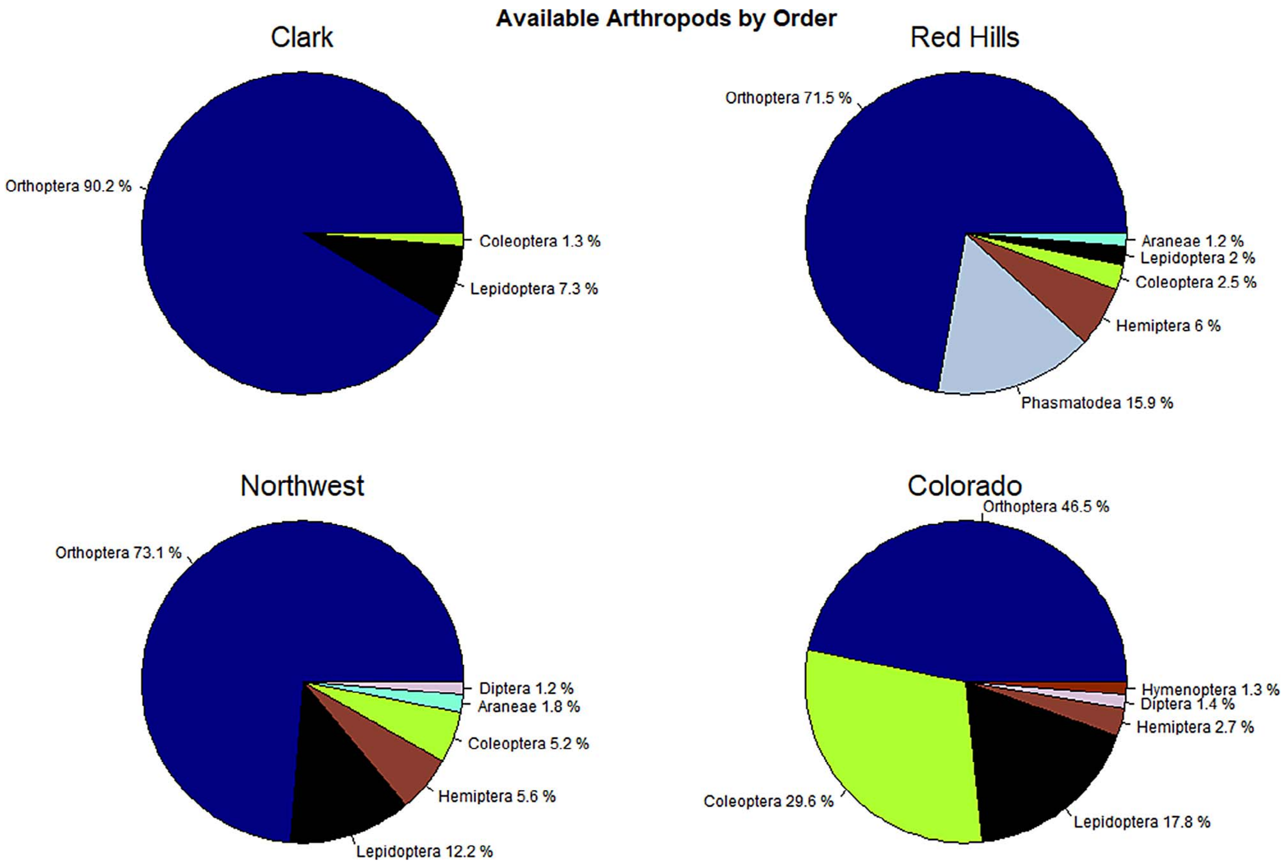
Notes: All fly-related taxa (Diptera) were removed because they likely reflect post-defecation contamination. Taxa in bold are those common among all study sites.

APPENDIX TABLE 7. Relative read abundance (sample size, mean, and SD) of arthropod orders in the diets of Lesser Prairie-Chicken chicks and adults during the brooding period, and of adults during winter, from 4 study sites in Kansas and Colorado, USA, 2014–2015. Only one brood sample had readable DNA from Colorado.

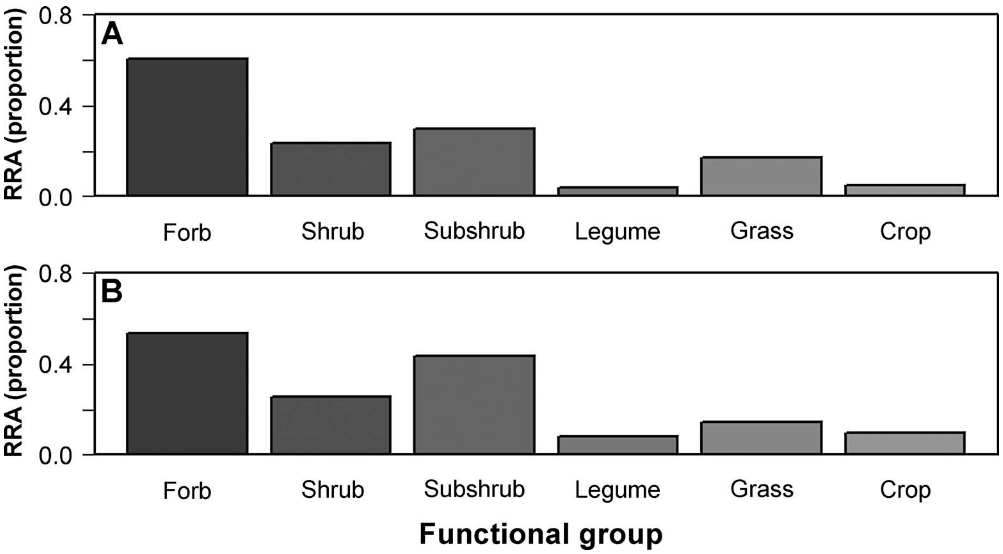
	Northwest			Red Hills			Clark			Colorado		
Order	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
Brood rearing		28,879 reads			1,722 reads			4,283 reads			178 reads	
Araneae	25	0.135	0.283	5	0.400	0.548	17	0.196	0.392	3	0.009	0.003
Coleoptera	25	0.007	0.017	5	0.000	0.000	17	0.000	0.000	3	0.000	0.000
Diptera	25	0.151	0.327	5	0.200	0.447	17	0.002	0.007	3	0.000	0.000
Entomobryomorpha	25	0.000	0.000	5	0.000	0.000	17	0.000	0.000	3	0.000	0.000
Hemiptera	25	0.207	0.320	5	0.000	0.000	17	0.113	0.280	3	0.193	0.070
Hymenoptera	25	0.010	0.037	5	0.000	0.000	17	0.000	0.000	3	0.333	0.149
Isopoda	25	0.000	0.000	5	0.000	0.000	17	0.116	0.326	3	0.000	0.000
Lepidoptera	25	0.416	0.385	5	0.214	0.441	17	0.217	0.393	3	0.274	0.035
Odonata	25	0.008	0.038	5	0.000	0.000	17	0.000	0.000	3	0.000	0.000
Orthoptera	25	0.066	0.205	5	0.187	0.417	17	0.364	0.425	3	0.190	0.085
Psocoptera	25	0.000	0.001	5	0.000	0.000	17	0.000	0.000	3	0.000	0.000
Sarcoptiformes	25	0.001	0.003	5	0.000	0.000	17	0.000	0.000	3	0.000	0.000
Winter		194 reads			410 reads			1,527 reads			655 reads	
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



APPENDIX FIGURE 8. Arthropod orders detected, using DNA metabarcoding, in Lesser Prairie-Chicken fecal samples collected (**A**) from brooding females and chicks during summer 2014 (hatch to 98 days old; $n = 50$ samples; $n = 35{,}062$ sequences) and (**B**) from adults during winter 2014–2015 (November–March; $n = 30$ samples; $n = 2{,}786$ sequences) in Kansas and Colorado, USA. Fecal samples were pooled among study sites in Clark County, Kansas; Gove and Logan counties, Kansas; Kiowa and Comanche counties, Kansas; and Prowers and Baca counties, Colorado.



APPENDIX FIGURE 9. Composition of arthropod orders available to Lesser Prairie-Chicken chicks in Clark County, Kansas (Clark); Gove and Logan counties, Kansas (Northwest); Kiowa and Comanche counties, Kansas (Red Hills); and Prowers and Baca counties, Colorado (Colorado), USA, 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 the biomass of each arthropod order.



APPENDIX FIGURE 10. Adjusted relative readable abundance (RRA; 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 (**A**) from brooding females and chicks during summer 2014 (hatch to 98 days old; $n = 49$ samples; $n = 223{,}660$ sequences) and (**B**) from adults during winter 2014–2015 (November–March; $n = 101$ samples; $n = 516{,}960$ sequences) in Kansas and Colorado, USA.

Biological Conservation 238 (2019) 108213

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Strategic conservation for lesser prairie-chickens among landscapes of varying anthropogenic influence

Daniel S. Sullins[a,*,1], David A. Haukos[b], Joseph M. Lautenbach[a,2], Jonathan D. Lautenbach[a,3], Samantha G. Robinson[a,4], Mindy B. Rice[c], Brett K. Sandercock[d], John D. Kraft[a], Reid T. Plumb[a,6], Jonathan H. Reitz[e], J.M. Shawn Hutchinson[f], Christian A. Hagen[g]

[a] Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS 66506, USA
[b] U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, 66506 Manhattan, KS, USA
[c] U.S. Fish and Wildlife Service, National Wildlife Refuge System, 1201 Oakridge Drive, Suite 320, Fort Collins, CO 80525, USA
[d] Department of Terrestrial Ecology, Norwegian Institute for Nature Research, Trondheim, Norway
[e] Colorado Parks and Wildlife Department, Lamar, CO 81052, USA
[f] Department of Geography, Kansas State University, Manhattan, KS 66506, USA
[g] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

ARTICLE INFO

Keywords:
Conservation reserve program
Grassland
Prairie grouse
Random Forest
Species distribution
Working lands

ABSTRACT

For millennia grasslands have provided a myriad of ecosystem services and have been coupled with human resource use. The loss of 46% of grasslands worldwide necessitates the need for conservation that is spatially, temporally, and socioeconomically strategic. In the Southern Great Plains of the United States, conversion of native grasslands to cropland, woody encroachment, and establishment of vertical anthropogenic features have made large intact grasslands rare for lesser prairie-chickens (*Tympanuchus pallidicinctus*). However, it remains unclear how the spatial distribution of grasslands and anthropogenic features constrain populations and influence conservation. We estimated the distribution of lesser prairie-chickens using data from individuals marked with GPS transmitters in Kansas and Colorado, USA, and empirically derived relationships with anthropogenic structure densities and grassland composition. Our model suggested decreased probability of use in 2-km radius ($12.6\,km^2$) landscapes that had greater than two vertical features, two oil wells, 8 km of county roads, and 0.15 km of major roads or transmission lines. Predicted probability of use was greatest in 5-km radius landscapes that were 77% grassland. Based on our model predictions, ~10% of the current expected lesser prairie-chicken distribution was available as habitat. We used our estimated species distribution to provide spatially explicit prescriptions for CRP enrollment and tree removal in locations most likely to benefit lesser prairie-chickens. Spatially incentivized CRP sign up has the potential to provide $4189\,km^2$ of additional habitat and strategic application of tree removal has the potential to restore $1154\,km^2$. Tree removal and CRP enrollment are conservation tools that can align with landowner goals and are much more likely to be effective on privately owned working lands.

1. Introduction

Conservation on working lands may require not only efforts to protect remaining tracts of high biodiversity but efforts to strategically apply management practices that simultaneously consider human well-being and wildlife (Samson et al., 2004; Kareiva and Marvier, 2012). Since the start of the Progressive Era > 100 years ago, those that have strived to protect wildlife and wild areas have disagreed on whether to preserve by protecting and leaving areas alone, or by conserving wildlife friendly habitat through human imposed management (Fox,

---

* Corresponding author.
E-mail address: sullins@ksu.edu (D.S. Sullins).

[1] Present Address: Department of Horticulture and Natural Resources, Kansas State University, KS 66506, USA.
[2] Ohio Department of Natural Resources, Delaware, OH, 43015, USA.
[3] Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY, 82071, USA.
[4] Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA, 24061, USA.
[6] California Department of Fish and Wildlife, 1724 Ball Mountain Rd., Montague, CA, 96067, USA.

https://doi.org/10.1016/j.biocon.2019.108213
Received 14 February 2019; Received in revised form 7 August 2019; Accepted 11 August 2019

1981; Miller et al., 2011). More recently, this discussion has evolved to include ideas on land sparing verse land sharing and a "new conservation" that demonstrates human benefit to gain conservation success through public approval (Miller et al., 2011; Kareiva and Marvier, 2012; Kremen, 2015). Such considerations are relevant for prairie-grouse (*Tympanuchus* and *Centrocercus* spp.) management that occurs in areas that are either privately owned or leased for agricultural production (Ciuzio et al., 2013). To improve landowner participation, slogans such as "what's good for the bird, is good for the herd" have been developed to disseminate wildlife-friendly land management practices to more widespread audiences (Wiklund, 2015). Outside of efforts to preserve large remaining tracts of grassland, the "new conservation" approach may be the best, and only, foreseeable option in the Great Plains of Kansas and Colorado, USA, where historical ecological drivers that once maintained habitat for numerous grassland dependent species have been greatly altered (Askins et al., 2007). Management that closely mimics site-specific historical ecological drivers is likely the best option to manage for biodiversity in grasslands; however, due to the extent of alterations and global change, more novel approaches to provide grassland on working lands may be beneficial. For example, free-ranging bison (*Bison bison*) have been replaced by cattle in fenced pastures, fire has largely been removed from the landscape, woody species are encroaching, the climate is changing, and increased food, fiber, and energy needs for growing human populations have greatly changed the Great Plains since pre-European settlement (Samson et al., 2004; Haukos and Boal, 2016).

It is estimated that grasslands have decreased 46% worldwide and only 4.5% of grasslands are protected (Hoekstra et al., 2005). In the Great Plains of North America, grasslands have decreased by an estimated 70% (Samson et al., 2004). This is especially problematic for grassland-dependent wildlife that need broad grassland availability to cope with weather driven variation in habitat availability (Wiens, 1974, Sala et al., 1998, Winter et al., 2005). Large grassland-dominated landscapes available for lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations and other grassland birds have become rare due to conversion of native grasslands to cropland, establishment of anthropogenic features, and woody encroachment due to grassland management practices (Hagen et al., 2011; Rodgers, 2016; Lautenbach et al., 2017; Plumb et al., 2019).

Knowledge of how grassland composition (i.e., proportion of grassland in a landscape) and anthropogenic feature densities constrain the distribution of lesser prairie-chickens at multiple scales and among years of variable climate are needed. It remains unclear what constrains the distribution of lesser prairie-chickens and how available habitat is distributed in Kansas and Colorado, which together support > 80% of extant lesser prairie-chickens (McDonald et al., 2014). To fill knowledge gaps, a machine-learning approach can provide spatially explicit predictions of potential habitat of lesser prairie-chickens (Cutler et al., 2007). Once an empirically derived species distribution is estimated, the predicted distribution can be used to identify grassland strongholds to be protected and areas within those strongholds that can be spatially prioritized for conservation on working lands.

Two conservation actions that could increase habitat include tree removal in south-central Kansas and conversion of cropland to perennial grassland through the USDA Conservation Reserve Program (CRP) in northwest Kansas and eastern Colorado (Lautenbach et al., 2017; Sullins et al., 2018). For *Tympanuchus* spp., it is unlikely that a universal management practice will benefit populations similarly across their range, with a 40-cm annual precipitation gradient in our study area from Kansas to Colorado (McNew et al., 2013; PRISM, 2016). Therefore, we propose two distinct conservation practices that are spatially dependent, but potentially capable of large-scale application on working lands. Both conservation practices can be profitable for producers in the lesser prairie-chicken range of Kansas and Colorado where > 95% of the species-occupied range is privately owned (Becerra et al., 2016). However, tree removal and enrollment in CRP will only benefit lesser prairie-chickens when surrounding landscapes can support sustainable populations. Conservation practices should be strategically applied where they are most likely to reap benefits within large grassland areas having limited anthropogenic structures (Winder et al., 2015; Sullins et al., 2018; Plumb et al., 2019).

Merely protecting a grassland as a wildlife-friendly grassland is not possible due to the dependence of the grassland itself, and its quality for wildlife, on ecological drivers that have been greatly altered (Askins et al., 2007). Alterations to ecological drivers (processes) that once maintained quality grasslands in this area have led to declines and distribution shifts in several grassland bird species (Peterjohn and Sauer, 1999). For example, there is evidence that prairie-grouse (*Tympanuchus* spp.), grasshopper sparrows (*Ammodramus savannarum*), and Henslow's sparrows (*A. henslowii*) exhibit declining trends in traditional portions of their range but have increased in areas where cropland has been converted to ungrazed grassland through the Conservation Reserve Program (CRP; Herkert, 1998, Johnsgard, 2001, Rodgers and Hoffman, 2005). The benefit of CRP for these species is a clear example, albeit by accident, of "new conservation" because the program incentivizes landowners to take land out of agricultural production. The financial benefit of CRP makes this a favorable tool for wildlife conservation.

Tree removal is another management practice that can benefit both cattle producer and prairie grouse by expanding grasslands that provide cover for prairie grouse and forage for cattle (Lautenbach et al., 2017; Severson et al., 2017). Deploying such management practices have promise of being well received and implemented by producers; however, because of various environmental and abiotic constraints, and our inability to preserve a pre-European settlement state at an appropriate scale, most conservation benefits are site dependent and therefore, must be spatially targeted (Samson et al., 2004; Ciuzio et al., 2013).

We provide an example of strategic conservation to target management practices on privately owned land that may benefit both producer and lesser prairie-chickens alike. Our first objective was to predict the distribution of lesser prairie-chicken habitat in Kansas and Colorado based on grassland composition, tree occurrence, and anthropogenic feature density constraints. We used a Random Forest model that incorporated locations from marked lesser prairie-chickens and available locations to create spatially-explicit predictions of use through the northern extent of the lesser prairie-chicken range. Our second objective was to use the predicted distribution to identify locations at which tree removal and enrollment of cropland into the CRP would have the greatest benefit to lesser prairie-chicken populations (Lautenbach et al., 2017; Sullins et al., 2018).

2. Study area

Our study area encompassed the northern portion of the extant lesser prairie-chicken distribution including portions of the Short-Grass Prairie/CRP mosaic (SGP), Mixed-Grass Prairie (MGP), and Sand Sagebrush Prairie Ecoregions (SSP; Fig. 1, McDonald et al., 2014). A longitudinal annual 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). 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 that were unsuitable for cultivation (Spencer et al., 2017). 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.). Within the study area, data were collected at 6 study sites that varied in anthropogenic feature densities including 3 in Colorado (Prowers/Baca, Cheyenne, Comanche National Grasslands[NG]) and 3 in Kansas (Red Hills/Clark, Northwest,

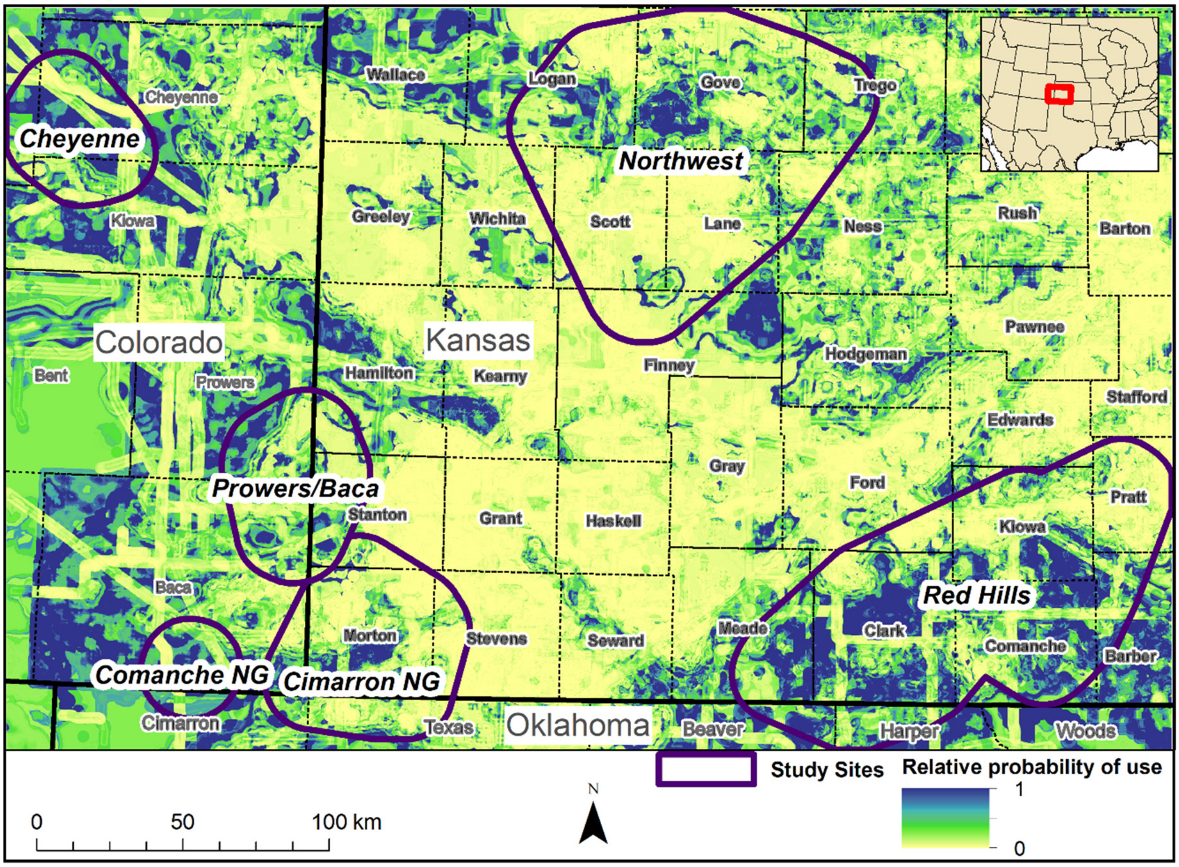


Fig. 1. Locations of the 6 study sites where lesser prairie-chickens were marked, captured, and monitored in Kansas and Colorado, USA, during 2013–2016 to estimate species distribution using a Random Forests model relative to presumed occupied range of lesser prairie-chickens. Study sites were established by creating minimum convex polygons from the subset of locations used by lesser prairie-chickens marked with GPS satellite transmitters then buffering the minimum convex polygons with the average net displacement during dispersal (16.18 km) following Earl et al. (2016; A). Values range from 0 (yellow) 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 (B). The species distribution model encompasses 3 of 4 ecoregions used by the lesser prairie-chicken including the Short Grass Prairie/CRP mosaic (Northwest study site), Mixed Grass Prairie (Red Hills study site), and Sand Sagebrush Prairie Ecoregions (Cimarron NG, Comanche NG, Prowers/Baca, and Cheyenne study sites) as defined in McDonald et al. (2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Cimarron NG; Fig. 1, Table S1, see supplemental material for further description of each study site). 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 data collection (15 March 2013 to 15 March 2016; NOAA, 2016).

3. Methods

3.1. Capture and marking

We captured lesser prairie-chickens at all study sites on leks during spring (March to mid-May) and uniquely marked individuals with rump-mounted 22-g GPS (global positioning system) satellite PTT transmitters (SAT-PTT; PTT-100, Microwave Technology, Columbia, MD, USA, or North Star Science and Technology, King George, VA, USA; Robinson et al., 2018) or a 15-g very-high-frequency transmitter attached as a necklace with whip antennae down the middle of the back (VHF; A3960, Advanced Telemetry System, Isanti, MN, USA). We alternated attachment of GPS and VHF transmitters on every other bird captured. The GPS transmitters had a spatial error of ± 18 m, which was less than the 30-m × 30-m (900 m^2) resolution pixels used in our analyses. We limited VHF location data to those with error polygons < 1000 m^2 (Robinson et al., 2018). Locations were recorded every 2 h during the day for GPS transmitters, with a 6-hour and 8-hour nocturnal gap during summer and winter, respectively. We attached VHF transmitters as a necklace with whip antennae down the middle of the back and estimated diurnal locations four times per week using triangulation and using Location of a Signal software to estimate error polygons (Ecological Software Solutions LLC, Hegymagas, Hungary).

3.2. Landcover covariates

We obtained landcover type classifications at a 30-m × 30-m resolution from the 2011 National Landcover database (NLCD) and a shapefile identifying the distribution of Conservation Reserve Program (CRP) grasslands in 2014 provided under agreement with the U.S. Department of Agriculture, Farm Service Agency (Homer et al., 2015). We created continuous rasters of grassland and shrubland composition from the NLCD land cover classification using focal-point statistics in ArcGIS 10.2. We created surfaces using multiple windows that estimated grassland composition within 0.4 km–5 km to represent potential scales of selection for lesser prairie-chickens. Throughout, we refer to the scale used as the length of the radius (e.g., 5-km scale). We examined multiple scales because of the uncertainty of the scale at which emergent and extrahierarchical properties of the landscape would best predict lesser prairie-chicken occupancy (King, 1997). We bounded scales assessed to be ≤5 km based on past lesser prairie-chicken literature, which included demographic influences at the 3-km scale and selection of nest sites within 4.8 km of capture lek (Giesen, 1994, Ross et al., 2016a). We used the 0.4-km radius as a minimum scale because it is less than estimates for habitat requirements in Haukos and Zaveleta (2016).

3.3. Anthropogenic feature covariates

To estimate the distance to, and densities of, anthropogenic features, we acquired shapefile layers of oil wells, transmission lines, major roads, county roads, and cell phone towers (see Supplemental Materials for sources of anthropogenic feature data). In ArcGIS 10.2, we used the Euclidean distance tool to generate rasters depicting distance to feature and focal statistics tool to estimate summed densities of features within circular radii (0.5 km, 1 km, 2 km) of each pixel. The range of radii was selected to encompass known avoidance distances (~0.5–2 km) published in past literature (Pruett et al., 2009; Hagen et al., 2011; Plumb et al., 2019).

3.4. Species distribution modeling and validation

Predicted species distribution.— To model species distribution and potentially limit autocorrelation issues, we randomly selected two used locations weekly from each marked bird (Segurado et al., 2006). We then separated location data from GPS- and VHF-marked individuals to create a model training and independent validation data samples, respectively. Study sites were delineated using minimum convex polygons (MCP) around all marked bird locations. We then buffered the MCP by the average net displacement distance (16.18 km) to estimate the area available to all marked lesser prairie-chickens (Earl et al., 2016). Average net displacement distance provides an estimate of dispersal distance that is not based on circular movement but linear distance away from initial capture location, which we used to infer areas available to the lesser prairie-chickens at the population level (Earl et al., 2016). We randomly generated one pseudo absence location for each location used by lesser prairie-chickens throughout the estimated available area and to account for the lack of true absence data; the response variable was relative probability of use (Barbet-Massin et al., 2012).

Lesser prairie-chicken occurrence was predicted using a Random Forest method (package ‘randomForest’; Liaw and Wiener, 2002, R Development Core, 2017). Random Forest is a classification and regression tree method that uses bootstraps to handle over-fitting (Cutler et al., 2007). We first assessed multicollinearity of all variables at $\alpha = 0.05$ using a leave one out assessment. Then, the most influential scales of variables were identified using a model improvement ratio (MIR) based on predictions from a global model of all variables at all scales that also included distance to anthropogenic feature (Evans et al., 2011). Ranks were estimated using the mean decrease in out-of-bag error standardized from 0 to 1. The scale (grassland composition = 0.4–5-km radius circles, anthropogenic features = 0.5–2-km radius circles) achieving the greatest MIR was used in the final model for each variable. Predictions of presence or absence were generated based on majority votes across all trees using the final model. An occurrence threshold was estimated following Jimenez-Valverde and Lobo (2007) to identify the model output probability (0–1) where occurrence or non-occurrence were most discrete and to identify potential habitat.

Validation.— We validated the model using VHF location data that were not used to train the predictive model and collected concurrently with GPS locations. Models were validated based on accuracy, specificity, and sensitivity of the model in predicting presence or pseudoabsence of locations from the independent validation set. We also estimated an area under the receiver operating characteristic curve to evaluate the predictive power of the model (AUC; DeLong et al., 1988).

3.5. Spatial prioritization of tree removal

To identify priority areas where tree removal would most likely restore lesser prairie-chicken habitat within the MGP, we defined potential habitat from the Random Forest model using both grassland composition and anthropogenic features. We used the threshold that included the top 95% predicted values (values > 0.33) from VHF locations in the validation to incorporate a greater area for potential conservation than obtained following Jimenez-Valverde and Lobo (2007). We then derived a layer depicting tree densities from Falkowski et al. (2017), following methods of Lautenbach et al. (2017; see Supplemental Materials for tree canopy cover). Areas where predicted habitat overlapped with tree densities > 2 per ha were most likely to be restored as habitat through tree removal based on a habitat relationship in Lautenbach et al. (2017). Last, we identified predicted habitat areas affected by low (1–5%), medium (6–15%), and high (> 15%) canopy coverage identified in Falkowski et al. (2017).

3.6. Spatial prioritization of CRP enrollment

To identify areas where applying CRP would most likely benefit lesser prairie-chickens, we first predicted the distribution of habitat using the occurrence threshold estimated from the Random Forest model, based on avoidance of anthropogenic features (Jimenez-Valverde and Lobo, 2007). Previous research indicated that CRP in landscapes (4-km radius) with < 56 cm of annual average precipitation and > 30% grassland were most likely to be used by lesser prairie-chickens (Sullins et al., 2018). We multiplied binary layers detailing areas of predicted habitat, a layer indicating where landscapes were > 30% grassland, areas receiving < 56 cm of annual average precipitation, and areas that were currently in CRP to indicate priority areas for conservation as well as cropland as indicated from NLCD 2011 to indicate priority areas for enrollment (Homer et al., 2015). Priority areas for conservation included CRP grasslands that provided habitat for lesser prairie-chickens based on our model. Priority areas for enrollment were areas that were cropland but if enrolled as CRP would likely provide habitat.

We then estimated the composition of priority enrollment and conservation of CRP by tillage risk. To identify tillage risk, we used a layer developed by Smith et al. (2016) that predicts areas of high and low tillage risk based on soil, climate, and topography related variables. We identified areas of low (0.00–0.32), medium (0.33–0.66), and high (0.67–1.00) tillage risk for descriptive purposes.

4. Results

We randomly selected a subset of 9895 locations from 170 lesser prairie-chickens marked with GPS satellite transmitters monitored from 2013 to 2016 to build our species distribution model. We sampled two locations a week from an average of 29.16 (SD = 36.35; range = 2–136) weeks for each individual. The model included only locations from female lesser prairie-chickens from the Red Hills/Clark and Northwest study sites; however, small sample sizes from study sites in Colorado and Cimarron NG required the use of both male and female individuals for analyses.

Grassland composition at the 5-km scale had the greatest model variable importance (1.0) and was 38% more important than at the 4-km scale (Figs. S1 and S2). For all anthropogenic features (county roads, major roads, oil wells, transmission lines, and other vertical features) densities estimated at the 2-km scale had the greatest model variable importance with a mean importance of 0.28, which was 150% greater than densities estimated at the 1-km scale. We used grassland composition within 5 km and anthropogenic features within 2 km as covariates in the final model to predict available habitat.

Grassland composition was 79% greater in model importance compared to the next predictor in the final model. Peak relative

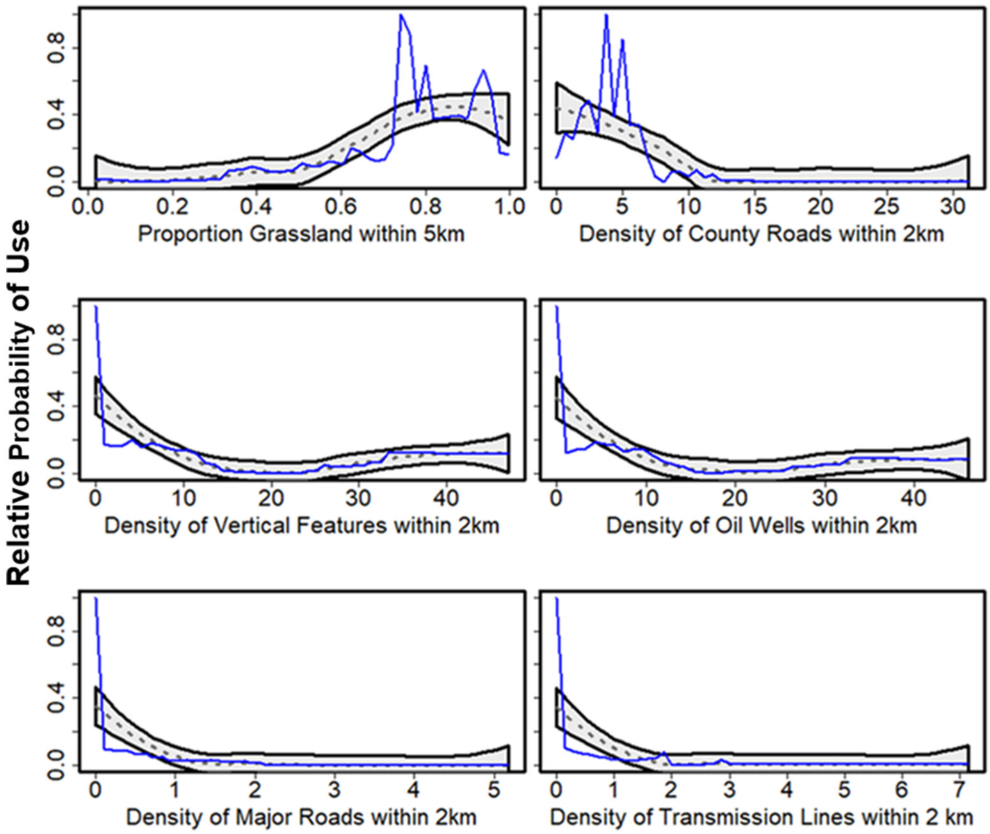


Fig. 2. Partial dependence plots for all grassland composition and anthropogenic feature densities used to predict the distribution of lesser prairie-chickens in Kansas and Colorado, USA, as depicted in Fig. 1 based on data from 2013 to 2016. A loess polynomial regression is plotted in as a dashed grey line with 95% prediction intervals highlighted in grey and the raw relative probability of use distribution is plotted as a blue line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Mean and standard deviation of grassland composition as a proportion of a 5-km radius scale and anthropogenic feature densities (2-km radius scale) estimated at lesser prairie-chicken locations (n = 9895) from 2013 to 2016, and random locations (n = 9895) distributed within dispersal range of Kansas and Colorado, USA, and throughout the entire extent analyzed for the species distribution model. The units for linear features (roads and transmission lines) are displayed as linear km densities within the 2 km (12.6 km^2) of each location while the vertical features (e.g., cell towers, large buildings, wind turbines, and oil wells) are represented by the densities of individual features. Estimates for the entire extent are based on the mean and variance of all pixel values estimated using a moving window analysis within the study area.

Variables	Used		Random		Entire extent	
	Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*
Grassland composition	0.76	0.18	0.55	0.26	0.51	0.27
Anthropogenic features						
County roads (km/12.6 km^2)	3.90	2.36	4.38	2.81	4.98	3.53
Major roads (km/12.6 km^2)	0.09	0.39	0.31	0.70	0.34	0.73
Oil wells/12.6 km^2	2.42	3.89	2.95	5.04	3.49	6.67
Transmission lines (km/12.6 km^2)	0.06	0.31	0.23	0.66	0.43	0.98
Vertical point features/12.6 km^2	2.43	3.91	3.16	5.28	3.82	7.41

probability of use occurred at ~77% grassland composition; similar to the 76% mean of used locations (Fig. 2, Table 1). Having lower model importance than grassland composition were densities of county roads, vertical point features, transmission lines, and major roads in decreasing order of model importance (Fig. S2). Overall, the relative probability of use decreased as cumulative densities of anthropogenic features increased (Fig. 2). However, the raw predicted probability of use increased from 0 to 5 km per 12.6 km^2 of county roads then declined sharply as densities increased beyond 5 km per 12.6 km^2 and was close to zero at densities > 10 km per 12.6 km^2 (Fig. 2). When county road densities surpassed a threshold of 8–10 km per 12.6 km^2 area, it indicated an urban environment based on visual observations.

In addition to the county road threshold of ~8 km/12.6 km^2, all other anthropogenic features displayed patterns of sharp decreases in relative probability of use after surpassing a feature-specific density (Fig. 2). Based on the raw probability distribution, the occupancy threshold for vertical point feature densities occurred at ~2 vertical features per 12.6 km^2 (Fig. 2). A similar threshold was estimated for oil wells with areas having > 2 oil wells per 12.6 km^2 having 8 times lower relative probability of use. The threshold for major roads and transmission lines was achieved at 0.15 km per 12.6 km^2; relative probability of use decreased abruptly when surpassed.

Predicted species distribution.— The predicted relative probability of use output from the Random Forest model predicted a greater area of lesser prairie-chicken habitat in the MGP than in the SGP or SSP Ecoregions (Fig. 1; McDonald et al., 2014). An occurrence threshold for the model was estimated at a model output probability of 0.60 for the model incorporating both grassland composition and anthropogenic structures and 0.70 for the model including only anthropogenic structure densities based on maximizing the sum of model sensitivity and specificity (Jimenez-Valverde and Lobo, 2007).

The percentage of potential habitat (> 0.6 predicted occurrence threshold) within the northern extent of presumed range of the lesser prairie-chicken in Kansas and Colorado as delineated in McDonald et al. (2014) was 16% (3099/14,790 km^2) in the MGP Ecoregion, 9% (2613/27,899 km^2) in the SSP Ecoregion, and 8% (3671/43,641 km^2) in the SGP Ecoregion. In the SGP Ecoregion of northwest Kansas, optimal habitat appears constrained to patches within 12 km of the Smoky Hill River in Gove and Logan counties; northeast Finney County; and northeast Wallace County. The model also predicted a substantial amount of habitat in the western most extent of the SGP in Kiowa and Cheyenne Counties of Colorado where a large expanse of undeveloped sand sagebrush prairie occurs within what is technically delineated as the SGP Ecoregion. Within the delineated SSP Ecoregion, predicted habitat is largely clumped in the western extent as well. In the MGP of

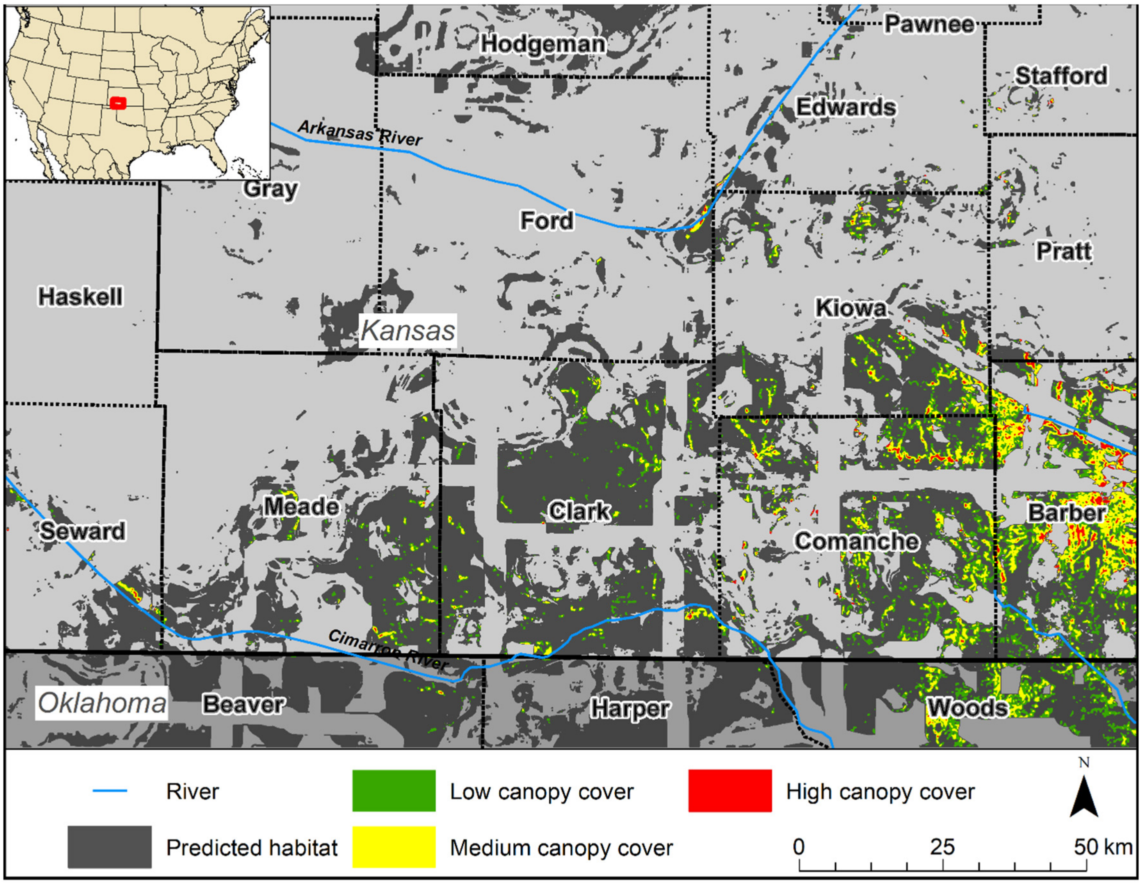


Fig. 3. Predicted areas of low (1–5%), medium (6–15%), high (> 15%) tree canopy cover where tree removal is most likely to restore lesser prairie-chicken habitat in Kansas and Colorado, USA, based on grassland composition within 5 km and anthropogenic feature densities (A). Areas having a high priority for tree removal were the top 66% of predicted values from the Random Forests model and where tree densities were > 2 trees/ha (Falkowski et al., 2017, Lautenbach et al., 2017, B).

Kansas and northern Oklahoma, habitat was more uniformly distributed (Fig. 1).

Validation.— We used subsampled VHF locations (2 locations per week from 113 individuals) to validate our predictions ($n = 4043$). Model performance was good with an estimated accuracy of 84%. The model correctly predicted 83% of VHF locations as habitat (sensitivity) and 83% of pseudoabsences as nonhabitat (specificity). The area under the receiver operating characteristics was 0.91 suggesting a fairly strong dichotomy between predicted habitat and nonhabitat (DeLong et al., 1988).

4.1. Spatial prioritization of tree removal

Based on our identification of areas with limited anthropogenic influence and adequate grassland availability, we estimated that 1154 km^2 of habitat for lesser prairie-chickens could be gained by tree removal and an alteration of land management practices to prevent further woody encroachment in the MGP of Kansas and northern Oklahoma (Fig. 3). Of the potential habitat, 12% is affected by low canopy cover (1–5%), 8% by medium canopy cover (6–15%), and 1% by high canopy cover (> 15%). Priority areas for tree removal were largely clustered to the eastern extent of the lesser prairie-chicken range.

4.2. Spatial prioritization of CRP enrollment

Our model suggests that 1570 km^2 of current CRP provides habitat for lesser prairie-chickens and should remain CRP if lesser prairie-chickens are a priority (Fig. 4). There were 4189 km^2 of cropland that reside in areas where enrollment would benefit lesser prairie-chickens. However, based on our results, enrolling cropland into CRP would be most beneficial when increasing grassland composition within 5-km to approximately 80% in areas receiving < 56 cm of precipitation. Predicted effects of anthropogenic features resulted in a 7211 km^2 decrease in priority cropland for enrollment and 4312 km^2 decrease in priority areas to conserve CRP and highlights the importance of considering anthropogenic feature densities. Our model highlighted areas on the Lane, Ness, and Finney county lines in addition to areas near our study sites.

The proportion of area that was predicted as high, medium, and low risk for tillage varied among priority areas for enrollment and conservation. Priority areas for enrollment were 7%, 32%, and 61% of low, medium, and high risk to tillage respectively. Priority areas to conserve CRP were comprised of 25%, 48%, and 28% of low, medium, and high risk respectively.

5. Discussion

We provide empirical evidence that can be used to preserve remaining grassland strongholds of low anthropogenic feature densities as well as spatially target management practices that are likely to acquire voluntary participation on working lands. Our model indicates how the broad-scale availability of large grasslands unencumbered by anthropogenic features is limited within the study area and likely imposes strong constraints on the distribution of grassland-obligate wildlife; especially those requiring large spatial extents for populations to persist (e.g., lesser prairie-chicken). We estimated the presence of 9383 km^2 of available habitat (> 0.60 relative probability of use) for

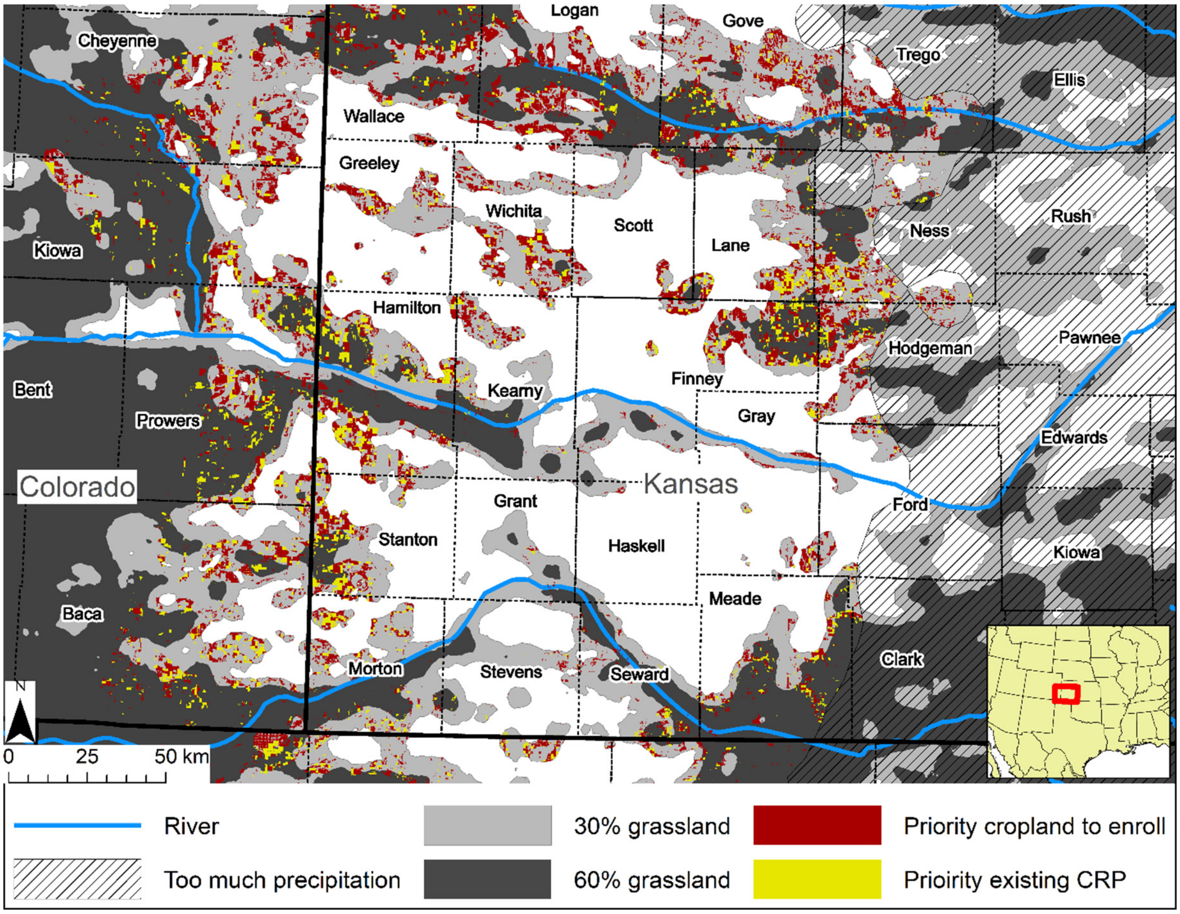


Fig. 4. Predicted priority areas where current CRP grasslands (yellow) and cropland that could be enrolled in CRP (red) were most likely to be used by lesser prairie-chickens in Kansas and Colorado, USA (A). Priority areas occur in locations having > 30% native working grassland (light grey) within 4 km and where the top 30% of values from a Random Forests model using only anthropogenic features occurred. Also, shown are areas that had > 60% native working grassland (dark grey) within 4 km (B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lesser prairie-chickens in the study area. There is potential to increase available habitat by 1154 and 4189 km^2 (57%) through strategic removal of trees and conversion of cropland to CRP grasslands. Area of predicted habitat was greatest in the SGP ecoregion, followed by the MGP and SSP ecoregions. However, the model likely overestimated the amount of available habitat in the far western extent of the distribution where short-grass prairie is largely contributing to the grassland composition of the model and may not provide habitat due to insufficient vegetation structure (Giesen, 1994). In contrast, the area in the far northwestern extent of the lesser prairie-chicken range is predominantly sand sagebrush prairie that is free of anthropogenic features and may become more important for lesser prairie-chickens given climate change projections (Grisham et al., 2016). Based on our predictions, it appears lesser prairie-chickens at current population abundance are constrained to areas having > 70% grassland within a 5-km radius (78.5 km^2) and with minimal anthropogenic features (e.g., < 10 vertical features in 12.6 km^2).

In the working landscapes of the Southern Great Plains, the need for strategic conservation is critical (Samson et al., 2004). Future expected increases in global food and energy needs may take a further toll on biodiversity in this region. There has been much discussion on whether approaches that would "spare" land parcels and allow for intensification of production elsewhere or whether landscapes should be "shared" to provide large areas that are marginal for both agriculture and biodiversity (Kremen, 2015). We did not explicitly test these ideas but the optimization of lesser prairie-chicken habitat at 77% grassland, the purported population increase following low intensity agriculture at the turn of the century, and the underlying spatial variability in farming suitability suggest that a combination of "sparing" and "sharing" strategies may be best (Kremen, 2015; Rodgers, 2016). Diet analyses have also demonstrated the use of some crops and crop pests as foods (Sullins et al., 2018). Our results and past literature highlight the utility of large grassland areas adjacent to low intensity row crop agriculture for lesser prairie-chickens. Our model does not account for the influence of dispersal on population persistence. Successful conservation will likely need to consider how the cropland matrix, adjacent to, and within grassland dominated landscapes facilitates successful dispersal. Having a matrix that facilitates movement by grassland dependent wildlife from one optimal habitat patch to another is likely important (Simberloff, 1994; Kremen and Merenlender, 2018).

Grassland abundance in a landscape likely influences the occurrence of lesser prairie-chickens both directly, as extrahierarchical boundaries, and indirectly through emergent properties operating at finer scales (King, 1997). Occurrence of lesser prairie-chickens is a product of the finer scale availability of lekking, nesting, brooding, and nonbreeding habitats that are properly abundant and configured to allow the establishment of home ranges and populations at subsequently broader scales (Hagen et al., 2013; Winder et al., 2015; Robinson et al., 2018). In addition to the spatial heterogeneity needed to satisfy all life-stage needs, the vegetation structure requirement (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; Ross et al., 2016a; Ross et al., 2016b). Habitat must also be abundant enough, and properly configured when fragmented, for dispersal to facilitate demographic and genetic rescue at even broader scales (Simberloff, 1994; Ross et al., 2016a). Our estimate of optimal grassland area (77% of 78.5 km^2 landscape) lies between the 49 km^2 and 202 km^2 estimates of habitat to support a single lek and overall population respectively (Haukos and Zaveleta, 2016). The estimate also falls within a range of scales at which established CRP grasslands and prescribed grazing influence lesser prairie-chicken occupancy (Hagen et al., 2016). Our predictions are based on the landscape rather than a single contiguous patch of grassland and suggest that landscapes that have limited vertical structures (e.g., oil wells, trees) and ≥ 60.5 km^2 of grassland within a 78.5 km^2 area would be optimal – assuming the grasslands are managed properly.

5.1. *Effects of anthropogenic feature densities*

The presence of vertical structures at high densities can make a landscape that would otherwise function as habitat unavailable to lesser prairie-chickens (Hagen et al., 2011; Plumb et al., 2019). Lesser prairie-chickens have evolved mechanisms to avoid vertical structures likely to minimize risk of predation from perching raptors (Reinert, 1984; Manzer and Hannon, 2005). Vertical structures avoided by lesser prairie-chickens include trees, transmission lines, oil wells, wind turbines, and cell phone towers (Pitman et al., 2005; Hagen et al., 2011; Lautenbach et al., 2017; Plumb et al., 2019). The avoidance of tall vertical features is not absolute and is 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 (Lautenbach et al., 2017, Plumb et al., 2019). For example, lesser prairie-chickens avoid areas having > 2 trees/ha at the 16-ha scale when nesting and areas having > 8 trees/ha otherwise (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 landscapes in which they occur, we provide evidence of thresholds where anthropogenic feature densities may act as overall constraints.

The lack of avoidance of county roads suggests that they do not affect lesser prairie-chicken occurrence at low densities (< 15 km per 12.6 km^2). Locations of roads in upland areas may additionally be a result of overlapping desirable conditions for road placement and lesser prairie-chicken habitat. We expect this to partially be a function of county roads being largely gravel surfaced and often occurred in upland areas of relatively higher elevation that are more likely used by lesser prairie-chickens (Lautenbach, 2015). Additionally, traffic volume on certain roads may dictate avoidance more than presence of the road itself (Blickley et al., 2012).

Although our reported avoidance density thresholds are specific for lesser prairie-chickens, there are other grassland birds that avoid anthropogenic structures and exhibit area sensitivity (Ribic et al., 2009; Ludlow et al., 2015; Londe et al., 2019). The area sensitivity of several grassland songbirds likely make them more susceptible to the fragmentation effects of anthropogenic structures and infrastructure (Ribic et al., 2009). Some grassland birds may not be negatively affected by anthropogenic structures and more species-level information is needed (Ludlow et al., 2015). However, our model predictions identify areas where anthropogenic feature densities are minimal and due to the lesser prairie-chicken's strong sensitivity to anthropogenic features may provide an estimate based on a worst case scenario for many grassland birds.

5.2. *Spatial prioritization of tree removal*

To increase the amount of potential habitat for lesser prairie-chickens, we identified strategic areas where tree removal, primarily eastern red cedar (*Juniperus virginiana*), would have maximum benefits. 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). We suggest that on-site tree removal follow Lautenbach et al. (2017) and implementation of a prescribed fire component 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 to be cost effective. Based on cost estimates in Lautenbach et al. (2017), it would cost US$32.6 million to remove trees in priority areas in Kansas and Colorado (more details in supplemental material). Tree removal in predicted priority areas would likely benefit cattle producers by increasing available forage and therefore may be more likely to be implemented (Ciuzio et al., 2013; Severson et al., 2017).

5.3. *Spatial prioritization of CRP enrollment*

The underlying ability of CRP to benefit both producer and grassland dependent wildlife is likely the reason for its conservation importance in areas > 95% privately owned (Johnson, 2005; Sullins et al., 2018). To build on the underlying conservation importance of CRP on working lands, current continuous CRP signup programs were developed that pay more per acre than traditional CRP signup (Stubbs, 2014). Increased payments are used to encourage further management within CRP tracts to benefit pollinators, waterfowl, and upland game birds by requiring interseeding with native forbs and desired native grasses (North American Bird Conservation Initiative, 2015).

Although CRP can benefit wildlife, the future of CRP remains uncertain and its ability to provide habitat for lesser prairie-chickens is contingent on renewal of the program with each new Farm Bill and the enrollment and reenrollment of CRP grasslands in contracts that typically span 10–15 years (Stubbs, 2014). Based on our model estimates of 1570 km^2 of current CRP providing habitat for lesser prairie-chickens, US$11.7 million annually in rental rates will conserve these areas for lesser prairie-chickens in addition to providing several other ecological services (Johnson, 2005; more details in supplemental material). Financial support may be necessary to maintain conservation gains achieved through CRP, as voluntary participation can decline when financial incentives are removed (Mascia and Mills, 2018). Efforts to connect CRP, or other forms of grassland restoration, with existing community actions and social movements may be other options for increasing participation on private lands (Kremen and Merenlender, 2018).

6. Conclusion

For grassland birds in the Great Plains, conservation on working lands is the only feasible option to provide habitat at a relevantly broad scale. Implementation of conservation practices that simultaneously create wildlife habitat and improve human well-being will be the most likely to positively affect wildlife populations (Samson et al., 2004; Kareiva and Marvier, 2012). Broad scale (78.5 km^2) grassland composition and anthropogenic feature densities appear to exert constraints on the distribution of lesser prairie-chickens and likely other grassland-obligate wildlife in our study area. The study area was > 95% privately owned and using tree removal and CRP at landscape scales may be the best management options to improve habitat availability for lesser prairie-chickens due to their likelihood of achieving voluntary participation (Lautenbach et al., 2017; Sullins et al., 2018). Comparing costs of tree removal to CRP enrollment suggest that CRP enrollment may be more cost efficient. However, lesser prairie-chickens use of habitat at a landscape scale make tree removal and CRP enrollment not directly comparable. Efforts to preserve remaining habitat matched with strategic management efforts that take into account human well-being have the greatest potential to conserve lesser prairie-chickens and other grassland-dependent wildlife on working lands.

Acknowledgement

We thank Kent Fricke, three anonymous reviewers, and the associate editor for providing reviews that improved the quality of the manuscript. We thank K. Schultz and A. Chappell for capturing and providing GPS data from lesser prairie-chickens captured on the Cimarron National Grasslands. B. Anderson, S. Baker, S. Bard, G. Brinkman, K. Broadfoot, R. Cooper, J. Danner, J. Decker, E. D. Entsminger, R. M. Galvin, N. Gilbert, A. Godar, G. Gould, B. Hardy, S.P. Hoffman, D. Holt, B. M. Irle, T. Karish, A. Klais, H. Kruckman, K. Kuechle, S. J. Lane, E. A. Leipold, J. Letlebo, E. Mangelinckx, L. McCall, A. Nichter, K. Phillips, J. K. Proescholdt, J. Rabon, T. Reed, A. Rhodes, B. E. Ross, D. Spencer, A. M. Steed, A. E. Swicegood, P. Waldron, B. A. Walter, I. Waters, W. J. White, E. Wiens, J. B. Yantachka, and A. Zarazua, provided much needed assistance with data collection. We greatly appreciate the logistic and technical support provided by J. C. Pitman, J. Kramer, M. Mitchener, D. K. Dahlgren, J. A. Prendergast, C. Berens, G. Kramos, and A. A. Flanders. Funding for the project was provided by Kansas Wildlife, Parks, and Tourism (Federal Assistance Grant KS W-73-R-3); United States Department of Agriculture (USDA) Farm Services CRP Monitoring, Assessment, and Evaluation (12-IA-MRE CRP TA#7, KSCFWRU RWO 62); and USDA Natural Resources Conservation Service, Lesser Prairie-Chicken Initiative. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108213.

References

Askins, R.A., Chavez-Ramirez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L., Vickery, P.D., 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Ornithol. Monogr. 64, 1–6.

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

Becerra, T.A., Engel, D.M., Fuhlendorf, S.D., Elmore, R.D., 2016. Preference for grassland heterogeneity: implications for biodiversity in the Great Plains. Soc. Nat. Resour. https://doi.org/10.1080/08941920.2016.1239293.

Blickley, J.L., Blackwood, D., Patricelli, G.L., 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage grouse at leks. Conserv. Biol. 26, 461–471.

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

Ciuzio, E., Hohman, W.L., Martin, B., Smith, M.D., Stephens, S., Strong, A.M., VerCauteren, T., 2013. Opportunities and challenges to implementing bird conservation on private lands. Wildl. Soc. Bull. 37, 267–277.

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

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

Earl, J.E., Fuhlendorf, S.D., Haukos, D.A., Tanner, A.M., Elmore, D., Carleton, S.A., 2016. Characteristics of lesser prairie-chicken (*Tympanuchus pallidicinctus*) long-distance movements across their distribution. Ecosphere 7, e01441.

Evans, J.S., Murphy, M.A., Holden, Z.A., Cushman, S.A., 2011. Modeling species distribution and change using random forest. In: Drew, C.A., Wiersma, Y.F., Huettmann, F. (Eds.), Predictive Species and Habitat Modeling in Landscape Ecology. Springer Science, Berlin, Germany, pp. 139–159.

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

Fox, S., 1981. John Muir and his Legacy: The American Conservation Movement. Little Brown, Boston, Massachusetts, USA.

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

Grisham, B.A., Griffin, C.P., Godar, A.J., 2016. Climate change. In: Haukos, D.A., Boal, C.W. (Eds.), Ecology and Conservation of Lesser Prairie-Chickens. Studies in Avian Biology No. 48 Cooper Ornithological Society, University of California Press, Berkeley, USA, pp. 221–242.

Hagen, C.A., Pitman, J.C., Loughin, T.M., Sandercock, B.K., Robel, R.J., Applegate, R.D., 2011. Impacts of anthropogenic features on habitat use by lesser prairie-chickens. In: Sandercock, B.K., Martin, K., Segelbacher, G. (Eds.), Ecology, Conservation, and Management of Grouse. University of California Press, Berkeley, USA, pp. 63–75.

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

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

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

Haukos, D.A., Zaveleta, J.C., 2016. Habitat. In: Haukos, D.A., Boal, C.W. (Eds.), Ecology and Conservation of Lesser Prairie-Chickens. Studies in Avian Biology No. 48 Cooper Ornithological Society, University of California Press, Berkeley, USA, pp. 99–132.

Herkert, J.R., 1998. The influence of the CRP on grasshopper sparrow population trends in the mid-continental United States. Wildl. Soc. Bull. 26, 227–231.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29.

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

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

Johnsgard, P.A., 2001. Prairie Birds: Fragile Splendor in the Great Plains. University Press of Kansas, Lawrence, Kansas, USA.

Johnson, D.H., 2005. Grassland bird use of conservation reserve program fields in the Great Plains. In: Haufler, J.B. (Ed.), Fish and Wildlife Benefits of Farm Bill Conservation Programs: 2002–2005 Update. The Wildlife Society Technical Review 05-02pp. 17–32 (Bethesda, Maryland, USA).

Kareiva, P., Marvier, M., 2012. What is conservation science? BioScience 62, 962–969.

King, A.W., 1997. Hierarchy theory: A guide to system structure for wildlife biologists. In: Bissonette, J.A. (Ed.), Wildlife and Landscape Ecology. Springer, New York, New York, USA, pp. 185–212.

Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. Ann. N. Y. Acad. Sci. 1335, 52–76.

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science 362.

Lautenbach, J., 2015. Lesser Prairie-Chicken Reproductive Success, Habitat Selection, and Response to Trees. Thesis. Kansas State University, Manhattan, USA.

Lautenbach, J.M., Plumb, R.T., Robinson, S.G., Hagen, C.A., Haukos, D.A., Pitman, J.C., 2017. Lesser prairie-chicken avoidance of trees in a grassland landscape. Rangel. Ecol. Manag. 70, 78–86.

Liaw, A., Wiener, M., 2002. Classification and regression by random. Forest. R News 2, 18–22.

Londe, D.W., Fuhlendorf, S.D., Elmore, R.D., Davis, C.A., 2019. Landscape heterogeneity influences the response of grassland birds to energy development. Wildl. Biol. https://doi.org/10.2981/wlb.00523.

Ludlow, S.M., Brigham, R.M., Davis, S.K., 2015. Oil and natural gas development has mixed effects on the density and reproductive success of grassland songbirds. Condor 117, 64–75.

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

Mascia, M.B., Mills, M., 2018. When conservation goes viral: the diffusion of innovative biodiversity conservation policies and practices. Conserv. Lett. 11, 1–9.

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

McNew, L.B., Gregory, A.J., Sandercock, B.K., 2013. Spatial heterogeneity in habitat selection: nest site selection by greater prairie-chickens. J. Wildl. Manag. 77, 791–801.

Miller, T.R., Minteer, B.A., Malan, L., 2011. The new conservation debate: the view from practical ethics. Biol. Conserv. 144, 948–957.

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

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

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

Peterjohn, B.G., Sauer, J.R., 1999. Population status of North American grassland birds from the North American breeding bird survey, 1966–1996. Stud. Avian Biol. 19, 27–44.

Pitman, J.C., Hagen, C.A., Robel, R.J., Loughin, T.M., Applegate, R.D., 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. J. Wildl. Manag. 69, 1259–1269.

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

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

Pruett, C.L., Patten, M.A., Wolfe, D.H., 2009. Avoidance behavior by prairie grouse:

implications for development of wind energy. Conserv. Biol. 23, 1253–1259.

R Development Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria 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.

Ribic, C.A., Koford, R.R., Herkert, J.R., Johnson, D.H., Niemuth, N.D., Naugle, D.E., Bakker, K.K., Sample, D.W., Renfrew, R.B., 2009. Area sensitivity in North American grassland birds: patterns and processes. Auk 126, 233–244.

Robinson, S.G., Plumb, R.T., Kraft, J.D., Sullins, D.S., Lautenbach, J.M., Lautenbach, J.D., Hagen, C.A., Rice, M.A., 2018. Effects of landscape characteristics on annual survival of lesser prairie-chickens. Am. Midl. Nat. 180, 62–82.

Rodgers, R.D., 2016. A history of lesser prairie-chickens. In: Haukos, D.A., Boal, C.W. (Eds.), Ecology and Conservation of Lesser Prairie-Chickens. Studies in Avian Biology No. 48. Cooper Ornithological Society, University of California Press, Berkeley, USA, pp. 15–38.

Rodgers, R.D., Hoffman, R.W., 2005. Prairie grouse population response to conservation reserve program grasslands: An overview. In: Allen, A.W., Vandever, M.W. (Eds.), 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, pp. 120–128.

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

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

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

Samson, F.B., Knopf, F.L., Ostlie, W.R., 2004. Great Plains ecosystems: past, present, and future. Wildl. Soc. Bull. 32, 6–15.

Segurado, P., Araújo, M.B., Kunin, W.E., 2006. Consequences of spatial autocorrelation for niche-based models. J. Appl. Ecol. 43, 433–444.

Severson, J.P., Hagen, C.A., Maestas, J.D., Naugle, D.E., Forbes, J.T., Reese, K.P., 2017. Restoring sage-grouse nesting habitat through removal of early successional conifer. Restor. Ecol. 25, 1026–1034.

Simberloff, D., 1994. The ecology of extinction. Acta Palaeontol. Pol. 38, 159–174.

Smith, J.T., Evans, J.S., Martin, B.H., Baruch-Mordo, S., Kiesecker, J.M., Naugle, D.E., 2016. Reducing cultivation risk for at-risk species: predicting outcomes of conservation easements for sage-grouse. Biol. Conserv. 201, 10–19.

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

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

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

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

Wiklund, J., 2015. Lesser Prairie-Chickens, Unite! Cowboys and Indians. (30 June 2015).

Winder, V.L., Carrlson, K.M., Gregory, A.J., Hagen, C.A., Haukos, D.A., Kesler, D.C., Larsson, L.C., Matthews, T.W., McNew, L.B., Patten, M.A., Pitman, J.C., Powell, L.A., Smith, J.A., Thompson, T., Wolfe, D.H., Sandercock, B.K., 2015. Factors affecting female space use in ten populations of prairie chickens. Ecosphere 6, ES14–00536.1.

Winter, M., Johnson, D.H., Shaffer, J.A., 2005. Variability in vegetation effects on density and nesting success of grassland birds. J. Wildl. Manag. 69, 185–197.