

Effectiveness Monitoring of the Conservation Reserve Program and Lesser Prairie-Chicken Initiative for Managing the Biodiversity of Grassland Birds in the Southern Great Plains



June 2018

David C. Pavlacky Jr. and Adam W. Green



Connecting People, Birds and Land

Bird Conservancy of the Rockies

14500 Lark Bunting Lane

Brighton, CO 80603

303-659-4348

www.birdconservancy.org

Tech. Report # AG-3151-P-15-0039

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3. Contribute to bird population viability and help sustain working lands by partnering with landowners and managers to enhance wildlife habitat.
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Suggested Citation:

Pavlacky, D. C., Jr., and A. W. Green. 2018. Effectiveness monitoring of the Conservation Reserve Program and Lesser Prairie-Chicken Initiative for managing the biodiversity of grassland birds in the Southern Great Plains. Technical Report AG-3151-P-15-0039. Bird Conservancy of the Rockies, Brighton, Colorado, USA.

Cover Photos: J. Forbes; T. Benson; B. Trentler; A. Schmierers;
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Contact Information:

David Pavlacky
david.pavlacky@birdconservancy.org
Bird Conservancy
14500 Lark Bunting Lane
Brighton, CO 80603
303-659-4348

Executive Summary

The long-term population declines of grassland birds have elevated the recovery of the grassland avifauna to among the highest conservation priorities in North America. The lesser prairie-chicken (LEPC, *Tympanuchus pallidicinctus*) is the species of greatest conservation concern, yet several other grassland bird species show long-term population declines in the Great Plains. Because a large percentage of the southern Great Plains are privately owned, the recovery of the LEPC and other grassland bird species depends on conservation initiatives with strong partnerships between private landowners and resource professionals. The Conservation Reserve Program (CRP) and Natural Resource Conservation Service, Lesser Prairie Chicken Initiative (LPCI) are two programs used to manage the abundance and distribution of the LEPC and its habitat while promoting the overall health and long-term sustainability of farming and ranching operations. The overall conservation goal of this project is to integrate the conservation needs of the LEPC with those of other grassland bird species of conservation concern by evaluating practices that minimize the loss, fragmentation and degradation of grasslands, promote the overall health of grazing and restored lands, and improve the long-term sustainability of farming and ranching operations. The objectives are to 1) evaluate the effectiveness of LEPC conservation practices for increasing the site occupancy and biodiversity of grassland birds, and 2) to understand the mechanisms involving relationships with landscape and local vegetation structure for increasing the site occupancy and biodiversity of grassland birds.

We found native and introduced CRP plantings to restore agricultural lands are important conservation practices for increasing the biodiversity of grassland birds in the southern Great Plains. We found both native and introduced CRP plantings increased the species richness of grassland obligates relative to agricultural lands, whereas introduced CRP plantings increased the species richness of grassland generalists. Similar to findings of other studies, we were unable to confirm the hypothesis for greater species richness in native CRP plantings relative to introduced CRP plantings, but a shift in species composition indicated grassland obligates showed larger positive responses to native CRP relative to introduced CRP than generalist species. Overall, the treatment effect for planting agricultural land into introduced CRP was more important for the species composition of grassland obligates and declining species than native CRP plantings

Our findings indicated LPCI prescribed grazing to improve rangeland condition is an important practice for the biodiversity of grassland obligates and species currently experiencing population declines. Lands enrolled in LPCI prescribed grazing showed greater species richness of grassland obligates than grassland generalists, and the species richness of grassland generalists was lower on LPCI rangelands than reference grasslands. However, we were unable to confirm the hypothesis for greater species richness of grassland obligates on LPCI rangelands relative to reference grasslands. Nevertheless, LPCI prescribed grazing appeared to shift species composition toward a community of grassland obligates and species that are currently declining.

The study of landscape relationships suggested declining species and grassland obligates were more sensitive to the loss of grassland than the fragmentation of native vegetation, but more grassland obligates also favored landscapes with large patch sizes of native vegetation. We were unable to confirm hypotheses for variation in species richness along gradients of landscape composition or configuration. We observed greater variation in species composition along the gradient of landscape composition than the gradient of landscape configuration, suggesting the grassland bird community may be responding to the

loss rather than the fragmentation of native vegetation. This result suggested implementing CRP in a way that maximizes the percentage of suitable habitat in any spatial configuration may be a more effective conservation strategy than managing the patch configuration of native vegetation.

The study of local vegetation structure suggested CRP and LPCI prescribed grazing practices that increase the ground cover of herbaceous vegetation play an important role in increasing the biodiversity of grassland birds. The species richness of grassland obligates and generalists increased with increasing herbaceous ground cover, but the species richness of obligates and generalists did not vary with grass height. Our results suggested land enrolled in CRP and LPCI prescribed grazing practices at the low-end of shrub cover and height provided important habitat for obligate grassland species of conservation concern, and LPCI rangelands with a substantial shrub component promoted the species richness of grassland generalists. The species richness of grassland generalists increased with shrub canopy cover and height, but we were unable to confirm hypotheses for declining species richness of grassland obligates with increasing gradients of shrub cover and height.

We investigated habitat relationships for tree canopy cover and height to predict the responses of grassland bird species to LEPC management actions for the encroachment of woodland vegetation. We were unable to confirm hypotheses for variation in species richness along gradients of tree canopy cover and height. Nevertheless, we observed a shift in species composition with a greater number of declining species and grassland obligates occurring at low levels of tree canopy cover and tree height, and a greater number of declining generalists at high levels of tree canopy cover and tree height. Our results suggest tree removal may benefit several grassland obligates currently experiencing population declines, but may be detrimental to several declining grassland generalists.

Acknowledgements

We are grateful to Eric Banks, Andy Burr, Casey Cardinal, Russell Castro, Christopher Hamilton, Sheldon Hightower, Dan Meyerhoff, Chanda Pettie, Michael Sams and Jon Ungerer from the Natural Resources Conservation Service (NRCS) for coordinating private landowner participation. Thank you to Christian Hagen and Sandra Murphy from the Lesser Prairie-Chicken Initiative (LPCI), Skip Hyberg and Rich Iovanna from the Farm Service Agency (FSA), Anne Bartuszevige and Alex Daniels from the Playa Lakes Joint Venture (PLJV), Cal Baca and Grant Beauprez from the New Mexico Game and Fish, and Barth Crouch from the Kansas Grazing Lands Coalition for providing insight and direction for the project. We are grateful to Bill Van Pelt from the Western Association of Fish and Wildlife Agencies (WAFWA), Ron Leathers and Sara Marquart from Pheasants Forever, Beth Bardwell from Audubon New Mexico and Teal Edelen, Alyssa Hildt, Michael Laguna, Seth Gallagher and Michaela Gold from the National Fish and Wildlife Foundation (NFWF) for project support. A large measure of project success belongs to Gillian Bee, Jenny Berven, Adam Beh, William Bevil, Angela Dwyer, T. Luke George, Michael Getzy, David Hanni, Valerie Marshal, Peggy Marston, Matthew McLaren, Duane Pool, Laura Quattrini, Rob Sparks, Jen Timmer, Alex Van Boer, Nick Van Lanen, Tammy VerCauteren, Mindi Walker, Chris White and Kristen Winter from the Bird Conservancy of the Rockies. Thank you to crew leader Jason Beason, Brittany Woiderski and Jeff Birek and many field technicians for their bird identification skills. We thank NFWF (grant # 39676), NRCS-LPCI and Pheasants Forever (grant # 68-3A75-14-120) and FSA (grant # AG-3151P-15-0039) for funding this project, with thanks to the Dorothy Marcille Wood Foundation, United States Forest Service, Gates Family Foundation, PLJV, Colorado Parks and Wildlife, and WAFWA Grassland Initiative for in-kind financial assistance. Last but not least, we thank the 17 livestock producers and many landowners for allowing access to their properties. Ultimately, we have landowners to thank for successful wildlife conservation outcomes in the southern Great Plains.

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Introduction

The long-term population declines of grassland birds has elevated the recovery of the grassland avifauna to among the highest conservation priorities in North America (Vickery and Herkert 2001, Brennan and Kuvlesky 2005). Of greatest conservation concern, the lesser prairie-chicken (LEPC, *Tympanuchus pallidicinctus*) has experienced a 90% reduction in population size since European settlement, and was recently delisted as a “threatened” species under the Endangered Species Act (USFWS 2016). According to the Breeding Bird Survey, several grassland obligate bird species show long-term population declines in the Great Plains (Sauer et al. 2017), including the eastern meadowlark (*Sturnella magna*), grasshopper sparrow (*Ammodramus savannarum*), horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), mountain plover (*Charadrius montanus*), northern harrier (*Circus cyaneus*) and western meadowlark (*S. neglecta*). In addition, several grassland generalists are also declining in the Great Plains (Sauer et al. 2017), including the American kestrel (*Falco sparverius*), Brewer’s blackbird (*Euphagus cyanocephalus*), canyon towhee (*Melospiza fusca*), common nighthawk (*Chordeiles minor*), common yellowthroat (*Geothlypis trichas*), eastern kingbird (*Tyrannus tyrannus*), field sparrow (*Spizella pusilla*), killdeer (*C. vociferous*), lark sparrow (*Chondestes grammacus*), loggerhead shrike (*Lanius ludovicianus*), mourning dove (*Zenaida macroura*), northern bobwhite (*Colinus virginianus*), rufous-crowned sparrow (*Aimophila ruficeps*), red-winged blackbird (*Agelaius phoeniceus*) and scissor-tailed flycatcher (*T. forficatus*). Habitat loss, fragmentation and degradation are widely considered to be the primary threats to the population viability of the LEPC (Van Pelt et al. 2013, Haukos and Zavaletta 2016), and other grassland bird species (Ribic et al. 2009).

Because a large percentage of the southern Great Plains are privately owned, the recovery of the LEPC and other grassland bird species depends on conservation initiatives with strong partnerships between private landowners and resource professionals (Van Pelt et al. 2013). The Natural Resource Conservation Service (NRCS), Lesser Prairie Chicken Initiative (LPCI) was established in 2008 to increase the abundance and distribution of the LEPC and its habitat while promoting the overall health of grazing lands and the long-term sustainability of ranching operations (USFWS 2011, Van Pelt et al. 2013). The core LPCI conservation practices include Upland Wildlife Management and Prescribed Grazing is a secondary core practice when livestock are present (USFWS 2011). The Conservation Reserve Program (CRP) is a voluntary program for agricultural producers administered by Farm Service Agency, addressing a threat to the LEPC from agricultural conversion by providing incentives to landowners to take cropland out of production and plant it back into grassland (Van Pelt et al. 2013). The U. S. Fish and Wildlife Service recently ruled the implementation of CRP is consistent with the long-term recovery goals of the LEPC (USFWS 2014a). The implementation of the Prescribed Grazing or CRP practices requires the development of grazing management or conservation plans, and the NRCS provides technical and financial assistance to private landowners through the Farm Bill (USFWS 2011, Van Pelt et al. 2013).

Habitat management for the LPCH will likely improve vegetation conditions for other grassland bird species of conservation concern (USFWS 2011, Haukos and Boal 2016), yet monitoring data are often necessary to establish the effectiveness of umbrella species conservation for increasing biodiversity (Favreau et al. 2006, Seddon and Leech 2008). Umbrella species are those requiring large areas of habitat, and the umbrella species concept assumes protection of the species’ habitat simultaneously protects other, less spatially demanding species (Favreau et al. 2006). The evaluation of species responses to available

conservation measures used to manage habitat for umbrella species provides a direct evaluation of the umbrella species concept (Roberge and Angelstam 2004). Because patterns of species co-occurrence vary across different spatial scales (Favreau et al. 2006), the umbrella species hypothesis may be best addressed using a hierarchical theory for community ecology (Whittaker et al. 2001). Applying a hierarchical model of community ecology to land management activities provides a framework for linking umbrella species conservation to biodiversity at multiple scales (Bestelmeyer et al. 2003). Effectiveness monitoring (Lyons et al. 2008) to determine the ability of LEPC conservation practices for increasing the biodiversity of grassland birds may ultimately be useful for evaluating the success of Farm Bill rangeland practices toward a program of evidence-based conservation (Briske et al. 2017). The treatment effects for the effectiveness of conservation practices can be applied to decision making (Sauer et al. 2013) and adaptive management (Williams 2011) of the grassland bird community in the southern Great Plains.

The long-term conservation goal of this project is to integrate the conservation needs of the LEPC with those of other grassland bird species of conservation concern by evaluating practices that minimize the loss, fragmentation and degradation of grasslands, promote the overall health of grazing and restored lands, and improve the long-term sustainability of farming and ranching operations. The objectives are to determine 1) the effectiveness of LEPC conservation practices for increasing the site occupancy and biodiversity of grassland birds, and 2) the influence of landscape and local vegetation relationships on the site occupancy and biodiversity of grassland birds.

Methods

Study Area

The study took place within the occupied range of the LEPC plus a 16 km buffer (SGP CHAT 2011) in Colorado, Kansas, Oklahoma, New Mexico and Texas, 2015 - 2017 (Fig. 1). We subdivided the occupied range by four ecoregions from the LEPC range-wide conservation plan (Van Pelt et al. 2013). The occupied range of the LEPC occurred within portions of the Shortgrass Prairie, Central Mixed-Grass Prairie and Chihuahuan Desert BCRs (US NABCI Committee 2000a;b).

The Sand Sagebrush Prairie (SSPR) ecoregion (Fig. 1) is characterized by a sparse to moderately dense woody layer dominated by sand sagebrush (*Artemisia filifolia*) interspersed within a sparse to moderately dense ground cover of tall, mid-, or short grasses (USFWS 2014b). Common grass species include sand bluestem (*Andropogon hallii*), sand dropseed (*Sporobolus cryptandrus*), prairie sandreed (*Calamovilfa longifolia*), giant sandreed (*C. gigantea*), needle and thread (*Hesperostipa comata*), and grammas (*Bouteloua* spp.). Other shrub species include soapweed yucca (*Yucca glauca*), honey mesquite (*Prosopis glandulosa*), and skunkbush sumac (*Rhus trilobata*).

The Shortgrass/CRP Mosaic Prairie (SGPR) ecoregion (Fig. 1) is a mixture of native shortgrass prairie and CRP grasslands planted with a mix of native warm season grasses (USFWS 2014b). Blue grama (*B. gracilis*) and buffalograss (*B. dactyloides*) are the dominant species, and sideoats grama (*B. curtipendula*), hairy grama (*B. hirsuta*), little bluestem (*Schizachyrium scoparium*), and western wheatgrass (*Pascopyrum smithii*) are also present.

The Mixed Grass Prairie (MGPR) ecoregion (Fig. 1) is primarily comprised of blue grama and buffalograss, with blue grama as the dominant species (USFWS 2014b). Other common plant species include sideoats grama, threeawns (*Aristida* spp.), sand dropseed, vine mesquite (*P. obtusum*), little bluestem, sand bluestem, Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), Canada wildrye (*Elymus canadensis*), and western wheatgrass. Shrubs such as sand sagebrush, shinnery oak (*Quercus havardii*), soapweed yucca, pricklypear (*Opuntia* spp.), winterfat (*Krascheninnikovia lanata*), and skunkbush sumac are also common.

The Sand Shinnery Oak Prairie (SOPR) ecoregion (Fig. 1) is comprised of shinnery oak and sand sagebrush, with little bluestem, sand bluestem, soapweed yucca, purple threeawn (*A. purpurea*), hairy grama, black grama (*B. eriopoda*), fall witchgrass (*Digitaria cognata*), New Mexico needlegrass (*Stipa neomexicana*), and dropseeds (*Sporobolus* spp.) (USFWS 2014b). Grasslands are common throughout this ecoregion in flat and rolling plains interspersed within shinnery oak-dominated areas. Soapweed yucca is the dominant shrub species in the grasslands. Other common grassland species include sand bluestem, giant dropseed (*S. giganteus*), broom snakeweed (*Gutierrezia sarothrae*), honey mesquite, tobosa (*Hilaria mutica*), little bluestem, sand sagebrush, catclaw mimosa (*Mimosa aculeaticarpa*), shinnery oak, and collegeflower (*Hymenopappus flavescens*).

Study Species

We detected 45 bird species during the course of study (Table A1) and classified the species as obligate (16) or facultative (29) grassland species according to Vickery and Herkert (1999), and Johnsgard (2009). Facultative species are those not entirely dependent on grasslands but use grasslands as a substantial part of their habitat requirements (Vickery and Herkert 1999). Because facultative species use a variety of vegetation types in addition to grasslands, we defined facultative species as grassland generalists in the current study. We queried species

detections from the IMBCR database and defined the species pool as 74 grassland species, including 24 obligates and 50 generalists (Vickery and Herkert 1999, Johnsgard 2009), known to breed in the Shortgrass Prairie, Central Mixed-Grass Prairie and Chihuahuan Desert BCRs (US NABCI Committee 2000a;b).

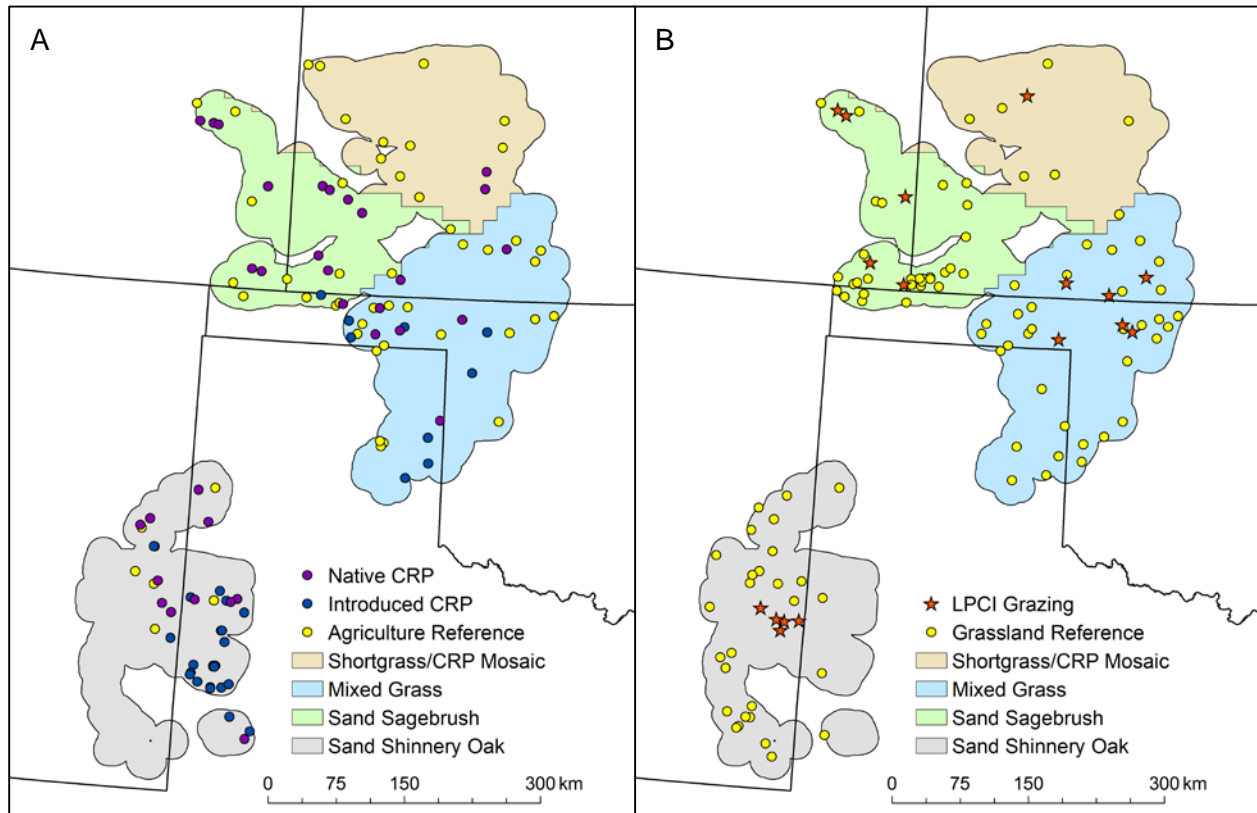


Figure 1. The location of (A) sampling grids for native Conservation Reserve Program (CRP) plantings (CP2), introduced CRP plantings (CP1) and reference agricultural lands, and (B) the general location of Lesser Prairie-Chicken Initiative (LPCI) prescribed grazing properties and sampling grids for reference grasslands within the occupied range of the lesser prairie-chicken (LEPC) plus a 16 km buffer, Colorado, Kansas, New Mexico, Oklahoma, and Texas, 2015 - 2017. Ecoregions from the LEPC Range-wide Conservation Plan are shown by the color-coded regions.

Sampling Design

We developed an impact-reference design (Morrison et al. 2008) within the Integrated Monitoring in Bird Conservation Regions (IMBCR, Box 1, White et al. 2013, Pavlacky et al. 2017) program for Playa Lakes Joint Venture (PLJV, Brennan and Kuvlesky 2005) to monitor avian community responses to treatments relative to reference lands within the occupied range of the LEPC (Fig. 1). The treatment strata included lands enrolled in native CRP plantings (CP2), introduced CRP plantings (CP2) and LPCI prescribed grazing, and the reference strata included random samples of grassland and agricultural lands from the IMBCR for PLJV program.

Box 1. Integrated Monitoring in Bird Conservation Regions

The Integrated Monitoring in Bird Conservation Regions (IMBCR) is a collaborative partnership between policy-makers, land managers, conservationists and scientists to leverage a common data platform over large spatial scales, promoting the efficient use of monitoring resources (Pavlacky et al. 2017). The Program was designed meet the North American Bird Conservation Initiative (NABCI) goals for improving avian monitoring and is well suited for addressing multiple management and conservation objectives (US NABCI Monitoring Subcommittee 2007). The IMBCR program uses modern sampling and analysis to provide reliable knowledge about bird populations (Pollock et al. 2002, Nichols et al. 2009). The design involves spatially balanced sampling (Stevens and Olsen 2004) to ensure representative geographic variation and data collection protocols to estimate population size and site occupancy while accounting for incomplete detection (Pavlacky et al. 2017). The spatially balanced properties of the design are maintained when sampling units are inaccessible and when sampling intensity varies between years. Accordingly, the spatially balanced design is well suited for regions with large amounts private land, when permission to access selected sampling units is denied, and is able to accommodate fluctuations in sampling intensity over time. The common data platform provides an economy of scale that allows pooling detection data across the monitoring region, allowing robust estimates of distribution and abundance in management units that have insufficient sample sizes on their own. The design of the IMBCR program provides an ecologically realistic framework for understanding hierarchical habitat use at local and landscape scales (Pavlacky et al. 2017), and the avian population metrics in local management units can be aggregated-up at multiple scales relevant to conservation and management objectives (Conroy et al. 2012).

We developed the sampling frames for reference lands in 2016 and 2017 by superimposing the 1 km × 1 km U. S. National Grid (USNG, FGDC 2001) over the LEPC occupied range plus 16 km buffer (SGP CHAT 2011) within a Geographic Information System (GIS; ArcGIS Version 10.1, Environmental Systems Research Institute, Redlands, CA). In 2015, the sampling frame for reference grasslands comprised all grid cells within the LEPC occupied range containing ≥40% grassland or shrub-land vegetation as mapped by the PLJV (2009) and Southwest Region Gap (Prior-Magee et al. 2007) spatial databases. We stratified the sampling frames for the reference lands by the SSPR, SGPR, MGPR and SOPR ecoregions (Fig. 1) from the LEPC Range-Wide Conservation Plan (Van Pelt et al. 2013).

The sampling units for the IMBCR for PLJV design are defined by 1 km² grid cells, each containing 16 point count stations located 250 m apart and ≥125 m from the grid cell boundaries. The IMBCR for PLJV program uses Generalized Random Tessellation Stratification (GRTS, Stevens and Olsen 2004) to select a spatially balanced sample. We post-stratified the point count plots by reference agriculture lands or reference grasslands using primary vegetation types collected at the point count locations. The reference agriculture lands comprised the agricultural and rural primary vegetation type, and the reference grasslands comprised the grassland, shrub-land, and emergent wetland primary vegetation types (Fig. 1, Table 1). The plant species composition of the reference grasslands varied by ecoregion and is described above in the Study Area section.

Table 1. The sample sizes of 1 km² grid cells and 5 ha point count plots for the impact-reference design within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas, 2015 - 2017.

Impact-reference level	Grid cells			Point count plots		
	2015	2016	2017	2015	2016	2017
LPCI grazing lands	31	30	30	368	333	373
Reference grasslands	38	51	50	356	392	439
Native CRP plantings		33			293	
Introduced CRP plantings		33			322	
Reference agriculture lands	7	30	29	19	177	153

Conservation Reserve Program

The CRP program administered by the FSA plays a role in addressing habitat loss and fragmentation of the LEPC, and involves planting rangeland and critical areas in regions converted cropland to indirectly promote landscape connectivity (USFWS 2011, Van Pelt et al. 2013). We evaluated two CRP practices within the occupied range of the LEPC, including permanent introduced grasses and legumes (CP1) and permanent native grasses (CP2). From an extensive survey of CRP species composition in the LEPC range (Ripper et al. 2008), introduced CRP plantings (CP1) were dominated by two exotic warm-season grasses, weeping lovegrass (*Eragrostis curvula*) and old-world bluestem (*Bothriochloa ischaemum*), but also included native warm-season grasses such as big bluestem (*A. gerardii*), red three-awn (*A. purpurea*), sideoats grama, switchgrass and silver bluestem (*B. saccharoides*). Native CRP plantings (CP2) were dominated by native warm-season grasses such as sideoats grama, blue grama, switchgrass, sand dropseed, silver bluestem, big bluestem, little bluestem, tall dropseed (*S. compositus*), red three-awn, and the cool-season western wheatgrass, but also included exotic warm-season grasses such as cheatgrass (*Bromus* spp.), foxtail bristlegrass, weeping lovegrass and old-world bluestem (Ripper et al. 2008).

We used an auxiliary stratification scheme for the IMBCR for PLJV program to develop the sampling frames for native CRP (CP2) and introduced CRP (CP1) plantings. We intersected the 1 km² USNG (FGDC 2001) and the 2015 U. S. Department of Agriculture Common Land Unit geospatial data (USDA 2014) within a GIS environment. Within the LEPC occupied range, the sampling frame for native CRP plantings (CP2) comprised all grid cells containing ≥40% land cover of native CRP and the sampling frame for introduced CRP plantings (CP1) comprised all grid cells containing ≥40% land cover of introduced CRP. We stratified the sampling frames by the Shortgrass Prairie and Central Mixed Grass Prairie Bird Conservation Regions (BCR, US NABCI 2000a;b), and post-stratified the sampling frame by the SSPR, SGPR, MGPR and SOPR ecoregions (Fig 1.) from the LEPC Range-Wide Conservation Plan (Van Pelt et al. 2013). We selected a spatially balanced sample of 1,200 grid cells from the native CRP (CP2) and introduced CRP (CP1) sampling frames using GRTS (Stevens and Olsen 2004) sample selection. In partnership with the Farm Service Agency (FSA), we mailed 1,430 Landowner Information Return Cards to the producers to ask permission to access the CRP lands. Of the 1,430 Return Cards, 105 producers granted permission to access the CRP lands. In 2016, we selected a spatially balanced sample of 33 introduced and 33 native granted grid cells in proportion to the areas of Shortgrass Prairie (BCR 18) and Central Mixed Grass Prairie (BCR 19) in the LEPC occupied range (Fig. 1, Table 1).

Prescribed Grazing

The LPCI prescribed grazing practice plays a role in addressing habitat degradation of the LEPC and is defined as managing the harvest of vegetation with grazing and/or browsing animals (USFWS 2011). The practice involves the management of stocking rates, rotation patterns, grazing intensity and duration, and includes an objective to meet nesting and brood rearing habitat requirements of the LEPC (Van Pelt et al. 2013). Recommendations for grazing management of LEPC nesting and brooding habitat include maintaining suitable vegetation structure for mean plant height (55 cm), bare ground (23%), plant foliar cover (78%), desirable LEPC plant cover (36.5%), and desirable LEPC shrub cover (11%) (Hagen et al. 2004).

We developed the sampling frame for LPCI prescribed grazing using an auxiliary stratification scheme for the IMBCR for PLJV program. We recruited landowners participating the LPCI prescribed grazing program within a partnership between the National Fish and Wildlife Foundation, and the NRCS state offices of Colorado, Kansas, Oklahoma and New Mexico. We intersected the 1 km² USNG (FGDC 2001) and project boundaries for 17 ranches enrolled in the LPCI prescribed grazing practice within a GIS environment (Fig. 1). The sampling frame for LPCI rangelands included all grid cells completely contained within the project boundaries of the 17 LPCI ranches. We stratified the sampling frame by the SSPR, SGPR, MGPR and SOPR ecoregions (Fig. 1) from the LEPC Range-Wide Conservation Plan (Van Pelt et al. 2013).

In 2015, we selected a spatially balanced sample of 31 grid cells within the occupied range of the LEPC using GRTS (Stevens and Olsen 2004), and ensured ≥ 1 grid cell was selected in each of the 17 ranches (Fig.1, Table 1). In 2016 and 2017, we selected 30 grid cells from 16 ranches enrolled in LPCI prescribed grazing because one of the ranches unsubscribed from the program.

Data Collection

We sampled avian occurrence using 6 min point counts (Buckland 2006) between one-half hour before sunrise and 1100 h at each accessible point count location, and measured the distance to each bird detection using a laser rangefinder (White et al. 2013, Pavlacky et al. 2017). We binned the 6 min point count duration into three, two min time occasions in order to maintain a constant detection rate in each interval and ensure a monotonic decline in the detection frequency histogram through time (Pavlacky et al. 2012). Before beginning each 6 min point count, surveyors recorded vegetation data within a 50 m radius of the point rapid using ocular estimation. The vegetation data included primary vegetation type, and percent cover and mean height of trees and shrubs; as well as ground cover and grass height.

We measured 2 continuous covariates at the level of 1 km² grid cells using remotely sensed data to represent landscape configuration and composition. We quantified the mean patch size of native vegetation and land cover of shrub-land (Table 1) within a GIS environment using the LANDFIRE spatial data (USGS 2014). We measured 6 continuous covariates at the level of point count plots using data collected in the IMBCR for PLJV monitoring program to represent local vegetation structure. We quantified the canopy cover and height of ground, shrub and tree vegetation with 50 m radius of the point count location (Table 1). We measured a covariate representing the start time of each point count survey using data recorded in the IMBCR for PLJV program (Table 1). In addition to the continuous covariates, we considered a treatment factor effect with levels for native CRP (CP2), introduced CRP (CP1), LPCI prescribed grazing, agriculture reference and grassland reference, and an ecoregion factor covariate with

Effectiveness monitoring of the Conservation Reserve Program and Lesser Prairie-Chicken Initiative levels for the SSPR, SGPR, MGPR and SOPR ecoregions. We standardized the continuous covariates using the z-transformation (Sokal and Rohlf 1981, Schielzeth 2010).

Table 2. The name, description, and mean and range of covariates for grid cells and point count plots within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas, 2015 - 2017.

Covariate	Description	Mean (range)
Patch size	Mean patch size of native vegetation (km ²) within 1 km ² grid cells, including grassland and shrub-land.	0.42 km ² (0.00 km ² - 1.00 km ²)
Shrub-land	Proportion (<i>P</i>) of shrub-land cover within 1 km ² grid cells.	0.25 <i>P</i> (0.00 <i>P</i> - 1.00 <i>P</i>)
Herb cover	Percentage (%) of herbaceous live grass and forb ground cover within a 50 m radius of the point count locations.	18.6 % (0.0 % - 90.0 %)
Grass height	Mean height (cm) of live or residual grass cover within a 50 m radius of the point count locations.	36.8 cm (0.0 cm - 142.0 cm)
Shrub cover	Percentage (%) of shrub canopy cover within a 50 m radius of the point count locations.	6.8 % (0.0 % - 60.0 %)
Shrub height	Mean height (m) of shrubs within a 50 m radius of the point count locations.	0.46 m (0.00 m - 2.75 m)
Tree cover	Percentage (%) of tree canopy cover within a 50 m radius of the point count locations.	0.2 % (0.0 % - 40.0 %)
Tree height	Mean height (m) of trees within a 50 m radius of the point count locations.	0.45 m (0.00 m - 25.00 m)
Time	Start time (h) of the point count survey measured as fractional time.	6.98 h (4.73 h - 10.80 h)

Hypotheses and Model Justification

We used predictive models and the method of multiple working hypotheses (Chamberlin 1965) to evaluate *a priori* hypotheses for the effects of CRP plantings, LPCI prescribed grazing and vegetation structure on avian community structure at multiple scales. We defined the spatial scales using the grain and extent of ecological processes (Turner et al. 2001) operating in the southern Great Plains. The landscape scale corresponded to a grain of 1 km² grid cells, the local scale corresponded to a grain of 5 ha point count plots and the extent for both scales corresponded to the occupied range of the LEPC. We estimated the site occupancy of all grassland bird species in the community at landscape and local scales (Pavlacky et al. 2012), and estimated gamma species richness at the landscape scale and alpha species richness at the local scale (Whittaker et al. 2001, Bestelmeyer et al. 2003).

At the landscape scale, we used patterns of vegetation composition to evaluate hypotheses for the effects of native vegetation loss, and patterns of patch configuration to evaluate hypotheses about the effects of native vegetation fragmentation on the biodiversity of grassland birds (Fischer and Lindenmayer 2007). The landscape covariate for the proportion of shrub-land vegetation quantified the relative composition of shrub-land or grassland vegetation, and this covariate predicted biodiversity responses to the loss of shrub-land or grassland

vegetation (Table 2). We hypothesized gamma species richness of grassland obligates would decline with increasing proportion of shrub-land vegetation in landscapes with low land cover of grassland vegetation. In contrast, we hypothesized species richness of grassland generalists would increase with increasing proportion of shrub-land vegetation in landscapes with high land cover of shrub-land vegetation. In general, we hypothesized community composition of grassland obligates would show negative occupancy responses, and grassland generalists would show positive occupancy responses to the proportion of shrub-land vegetation. The landscape covariate for the mean patch size of native vegetation quantified the extent of patch discontinuity, and this covariate predicted biodiversity responses to the fragmentation of native vegetation (Table 2). We hypothesized gamma species richness of grassland obligates would decline with increasing fragmentation of native vegetation, and hypothesized that species richness of generalists would be insensitive or increase with the fragmentation of native vegetation. In general, we hypothesized the community composition of grassland obligates would show negative occupancy responses to the fragmentation of native vegetation, and grassland generalists would show positive or stable occupancy responses to the fragmentation of native vegetation. In addition, we evaluated an ecoregion factor covariate with levels for the SSPR, SGPR, MGPR and SOPR regions (Fig. 1) from the LEPC Range-Wide Conservation Plan (Van Pelt et al. 2013). We hypothesized species richness of grassland obligates would be greatest in the SGPR ecoregion, which is most important to LEPC occupancy, followed by the MGPR, SOPN and SSPR ecoregions (Hagen et al. 2016).

At the local scale, we used the LEPC core conservation practices and patterns of vegetation structure to evaluate hypotheses for the effects of vegetation degradation and condition on the biodiversity of grassland birds (Fischer and Lindenmayer 2007). The comparison of CRP plantings and agricultural reference lands represent treatment effects for enrollment of cropland into the CRP program within the occupied range of the LEPC. We hypothesized the alpha species richness of grassland obligates would be greater on native than introduced CRP plantings (Bakker and Higgins 2009), and greater on native CRP plantings than agricultural reference lands. In contrast, we predicted the species richness of grassland generalists would be lower on native than introduced CRP plantings, and greater on introduced CRP plantings than agricultural reference lands. In general, we hypothesized community composition of grassland obligates would show positive occupancy responses to native CRP plantings, and grassland generalists would show positive occupancy responses to introduced CRP plantings. In addition, we predicted species richness and composition of native CRP plantings would be more similar to reference grasslands than species richness and composition of introduced CRP plantings because the dominant plants found in native CRP plantings were similar to those in the reference grasslands (Bakker and Higgins 2009).

The comparison of LPCI prescribed grazing lands to reference grasslands represent the departure of LPCI grazing lands from average grassland conditions in the occupied range of the LEPC. Because the LPCI prescribed grazing practice employed a rotational grazing system, we hypothesized grassland obligates would show greater alpha species richness on lands enrolled in prescribed grazing than reference grasslands (Derner et al. 2009). In contrast, we hypothesized the species richness of grassland generalists would be lower on lands enrolled in prescribed grazing than reference grasslands. In general, we hypothesized the community composition of grassland obligates would show positive occupancy responses, and grassland generalists would show negative occupancy responses to LPCI prescribed grazing.

We used local scale covariates for the canopy cover and height of herbaceous, shrub and tree vegetation to represent hypotheses for heterogeneity in grassland condition (Derner et al. 2009). We hypothesized that alpha species richness of obligates and generalists would increase with increasing cover and height of herbaceous ground cover. In general, we

hypothesized the community composition of grassland species would vary according to the known habitat associations of the species (Knopf 1996). We hypothesized alpha species richness of grassland obligates would decline, and generalist grassland species would increase with increasing cover and height of shrubs and trees (Coppedge et al. 2001). Overall, we hypothesized the community composition of grassland obligates would show negative occupancy responses, and grassland generalists would show positive occupancy responses to the cover and height of trees and shrubs.

We accounted for the incomplete observation of avian species using covariates to explain temporal and spatial variation in the detection probabilities of species (Table 1). We hypothesized the year factor would explain differences in detection due to annual turn-over in the field crew and variable bird abundance in different years. We hypothesized the ecoregion factor covariate would explain spatial differences in detection due to variation in the geographic ranges and abundances of the species. The shrub cover and height covariates represented hypotheses that increasing shrub cover and height may interfere with the ability of the observers to detect the bird species. In addition, we hypothesized that increasing grass at the point count plot would inhibit the ability of the observers to detect birds. The time of day covariate represented the hypothesis that the singing frequency of bird species would decline later in the morning.

Statistical Analysis

We extended the hierarchical Bayes multi-scale occupancy model of Mordecai et al. (2011) to accommodate multiple species (Dorazio and Royle 2005, Royle and Dorazio 2008) and two spatial scales (Pavlacky et al. 2012). For each species, we estimated the probability of large-scale occupancy (ψ) for grid cells, probability of small-scale occupancy (θ) for point count plots given presence at the grid cells, and probability of detection (p) in min intervals given presence at point count plots (Pavlacky et al. 2012). The multi-scale model provides an ecologically realistic framework for understanding hierarchical habitat use of species (Pavlacky et al. 2012). The theory of hierarchical habitat selection suggests species first select habitat at the landscape scale based on the composition or configuration suitable vegetation types, and then within suitable landscapes, species select territories based on suitable vegetation structure at the local scale (Hutto 1985). Multi-scale habitat relationships have an advantage over single-scale relationships because they tease apart species absence from suitable habitat at local scales when imbedded in unsuitable landscapes, and also species absence from unsuitable habitat at local scales when imbedded in otherwise suitable landscapes (Pavlacky et al. 2012). In addition, because the 16 point count plots within the randomly located grid cells are not independent, the multi-scale model allows habitat relationships at the point-scale while accounting for variation between grid cells (Pavlacky et al. 2012). Finally, estimating detection probabilities was important for reliable estimates of site occupancy (MacKenzie 2005). Count data from bird surveys often suffer from false absences because few, if any species are so conspicuous that they are detected with certainty when present during a survey (Nichols et al. 2009). We used detection probabilities related to the conspicuousness of bird species to adjust the occupancy estimates upward, and this corrected false absences and ensured the occupancy estimates reflect accurate prevalence of the species rather than artifacts of incomplete detection (MacKenzie 2005).

We used a series of logistic regression equations to model the effects of treatment, vegetation structure, ecoregion and year on large-scale (ψ) and small-scale (θ) occupancy, and the effects vegetation structure, ecoregion and year on the probability of detecting the species (p):

$$\begin{aligned}\text{logit}(\psi_{itk}) &= d_{0i} + d_{1i}x_{1k} + \dots + d_{hi}x_{hk}, \\ \text{logit}(\theta_{itkj}) &= b_{0i} + b_{1i}x_{1kj} + \dots + b_{hi}x_{hkj}, \\ \text{logit}(p_{itkj}) &= a_{0i} + a_{1i}x_{1kj} + \dots + a_{hi}x_{hkj},\end{aligned}$$

where d_{0i} is the random intercept, d_{li} is the beta regression coefficient of covariate x_l ($l = 1, \dots, h$) for the large-scale occupancy of species i , year t and grid cell k . The parameters b_{0i} and a_{0i} are the random intercepts, b_{li} and a_{li} are the beta regression coefficients of covariate x_l ($l = 1, \dots, h$) for the small-scale occupancy and detection, respectively of species i , year t , grid cell k and point j . The random intercepts were drawn from a multivariate distribution and each of the beta coefficients were drawn from a random effect accounting for variation among species (Appendix A). The beta parameters represented effect sizes for introduced and native CRP relative to agricultural lands (Fig. 1A, Table 1), LPCI grazing relative to reference grasslands (Fig. 1B, Table 1), as well as ecoregion, year and the covariates listed in Table 2.

We used data augmentation to estimate the number of unobserved species in the community (Dorazio et al. 2006, Iknayan et al. 2014). The observed data comprised encounter histories for 45 species and we augmented the observed data with “all zero” encounter histories for 29 unobserved species known to breed in the BCRs, resulting in a species pool of 74 grassland species. Data augmentation provides occupancy estimates for all 74 species in the species pool, including unobserved species, in a way that accounts for correlations between detection and occupancy of the species. This approach is particularly useful for understanding how the entire community of species responds to management actions and environmental covariates (Zipkin et al. 2010, Sauer et al. 2013). This approach has advantages over alternate approaches that only incorporate species with sufficient data because patterns for a subset of abundant species may not correspond to patterns for the entire community, including rare and undetected species (Kéry and Royle 2009, Iknayan et al. 2014).

We estimated model parameters using Markov Chain Monte Carlo (MCMC) simulation implemented in program JAGS (Plummer 2003, JAGS Version 4.3.0, www.sourceforge.net, accessed 5 April 2018) using package jagsUI in the R statistical computing environment (R Version 3.4.3, www.r-project.org, accessed 5 April 2018). We used vague and weakly informative prior distributions for all estimated parameters (Appendix A). We generated 10,000 MCMC samples, specified a burn-in period of 5,000 iterations, and used $\hat{R} < 1.1$ as an indication of model convergence (Gelman and Rubin 1992). We estimated the beta parameters using the mean and standard deviation of the MCMC samples of the posterior distributions, calculated 95% Credible Intervals (CI) using the quantiles of the posterior distributions, and calculated Bayesian P -values to determine the probability the beta parameter was greater than ($P > 0$) or less than ($P < 0$) zero using posterior predictive distributions (Hobbs and Hooten 2015). A 95% CI excluding zero indicated the probability of observing a beta parameter equaling zero was less than 95%, whereas the P -value indicated the probability the beta parameter was less than or greater than zero. We considered beta regression coefficients with P -values > 0.9 as strong support for the associated hypotheses.

We estimated gamma and alpha species richness for the 24 grassland obligates and 50 grassland generalists in the avian community. We derived estimates of species richness from the posterior MCMC samples (Hobbs and Hooten 2015) by summing the species occupancy estimates for each treatment and ecoregion, and along gradients of the continuous covariates (Appendix A). We defined gamma species richness at the landscape scale (Whittaker et al. 2001) as the mean number of species among 1 km² grid cells for each guild (Box 2). Alternatively, we defined alpha species richness at the local scale (Whittaker et al. 2001) as the mean number of species among 5 ha point count plots for each guild (Box 2).

Bird Conservancy of the Rockies

Conserving birds and their habitats

Box 2. Species richness and composition at multiple-scales

Species richness is defined as the number of species in the community. And while species richness is an important aspect of biodiversity, the usefulness of species richness to conservation is limited by lack of attention to geographic scale and species composition (Whittaker et al. 2001). Alpha species richness represents the number of species at local scales, gamma richness corresponds to the number of species at landscape scales and epsilon richness represents the total number of species at regional scales. Beta species richness represents the turnover among species between the sampling locations at local or landscape scales (Whittaker et al. 2001). We did not report measures of epsilon and beta richness in the present study, but the approach easily accommodates these additional measures (Dorazio et al. 2011). Adopting a hierarchical framework for species richness allows the study of biodiversity along environmental gradients at multiple scales that are relevant to land management and species conservation (Bestelmeyer et al. 2003). Because bird species composition may shift in response management with no apparent changes in species richness, we developed a multi-species approach that estimates both species richness and composition from the bottom-up responses of individual species (Iknayan et al. 2014). In the present study, alpha species richness at the local scale corresponds to the average number of species among 5 ha point count plots. At the landscape scale, gamma richness represents the average number of species among 1 km² grid cells. This approach allowed us to simultaneously investigate biodiversity responses of the grassland bird community to environmental gradients operating at two spatial scales. In the present study, we investigated gamma richness along gradients of grassland loss and fragmentation at the landscape scale, and alpha richness in response to conservation practices and vegetation condition at the local scale.

Results

The alpha species richness of obligates on reference grasslands was greater in the Sand Sagebrush Prairie than in the Sand Shinnery Oak Prairie ($\beta = 0.96$, $SD = 0.24$, $CI = [0.52, 1.50]$, $P = 1.00$) and Mixed Grass Prairie ($\beta = 0.62$, $SD = 0.35$, $CI = [-0.17, 1.31]$, $P = 0.95$, Fig. 2A). The alpha species richness of generalists on reference grasslands was greater in the Mixed Grass Prairie than the Sand Shinnery Oak Prairie ($\beta = 1.40$, $SD = 0.54$, $CI = [0.49, 2.55]$, $P = 1.00$) and Sand Sagebrush Prairie ($\beta = 1.40$, $SD = 0.64$, $CI = [0.19, 2.72]$, $P = 0.99$, Fig. 2B). In addition, the alpha species richness of obligates was greater than generalists on reference grasslands in the Sand Sagebrush Prairie ($\beta = 1.01$, $SD = 0.70$, $CI = [-0.47, 2.27]$, $P = 0.92$, Fig. 2).

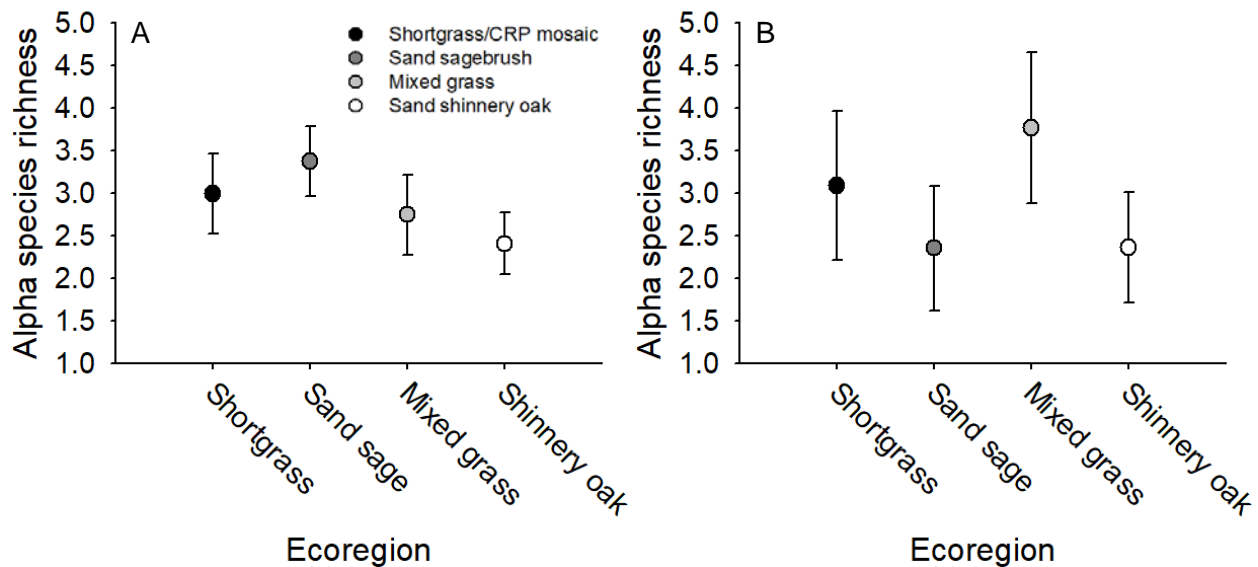


Figure 2. The alpha species richness of 5 ha point count plots for reference grasslands by ecoregion for grassland (A) obligates and (B) generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas, 2016. The round symbols represents the mean number of species among point count plots and the error bars are 1 standard deviation.

Species composition varied by ecoregion in the occupied range of the LEPC (Fig. 3, available in Supporting Information). Several obligates showed high small-scale occupancy on reference grasslands in the Sand Sagebrush Prairie relative to the other ecoregions, including the Cassin's sparrow (*Peucaea cassinii*, $P \leq 1.00$), horned lark ($P \leq 1.00$), lark bunting ($P \leq 1.00$) and western meadowlark ($P \leq 1.00$, Fig. 3). Generalists showing low small-scale occupancy on reference grasslands in the Sand Sagebrush Prairie relative to the other ecoregions included the common nighthawk ($P \leq 0.98$), eastern kingbird ($P \leq 0.93$), killdeer ($P \leq 1.00$), lark sparrow ($P \leq 1.00$), red-winged blackbird ($P \leq 0.92$), scissor-tailed flycatcher ($P \leq 0.97$) and western kingbird (*T. verticalis*, $P \leq 0.98$, Fig. 3). Generalists with greater small-scale occupancy on reference grasslands in the Mixed Grass Prairie relative to the Sand Sagebrush Prairie included the eastern kingbird ($P = 0.92$), killdeer ($P = 1.00$), lark sparrow ($P = 1.00$), red-winged blackbird ($P = 0.92$) and scissor-tailed flycatcher ($P = 0.97$, Fig. 3C)

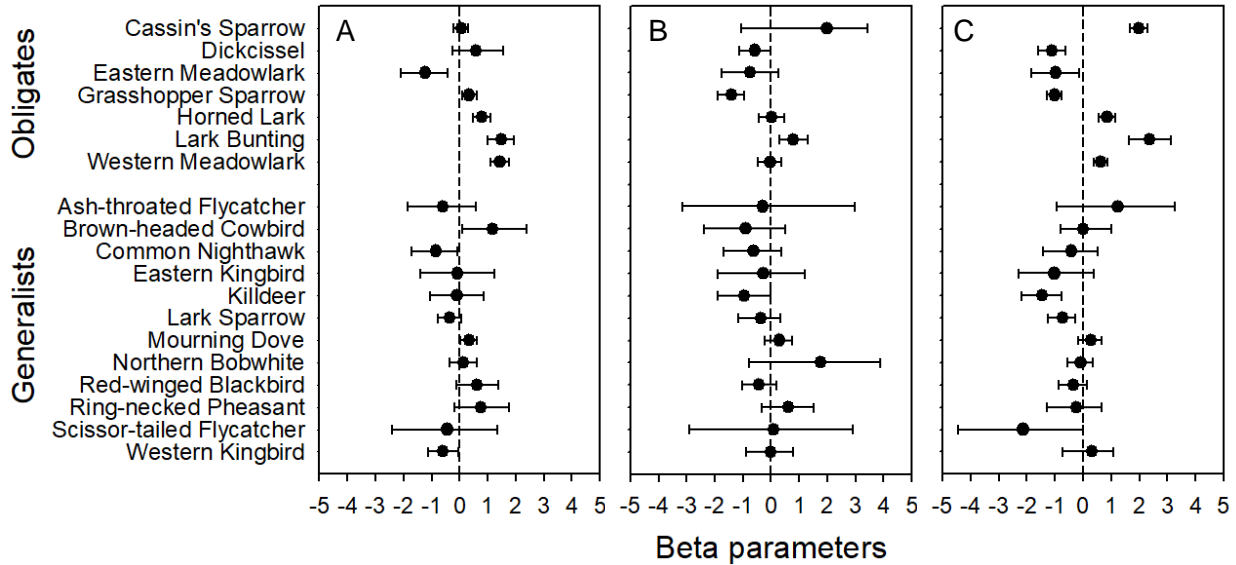


Figure 3. The beta coefficients for the small-scale occupancy of 5 ha point count plots for reference grasslands within the Sand Sagebrush Prairie relative to (A) Shinnery Oak Prairie ecoregion, (B) Shortgrass/CRP Mosaic and (C) Mixed Grass Prairie ecoregions for grassland obligates and generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas. The round symbols represent beta coefficients graphed relative to zero and the error bars are 95% credible intervals.

Conservation Reserve Program

We confirmed the hypothesis that alpha species richness of grassland obligates was greater on native CRP plantings ($\beta = 0.65$, $SD = 0.17$, $CI = [0.28, 1.00]$, $P = 1.00$) and introduced CRP plantings ($\beta = 0.59$, $SD = 0.16$, $CI = [0.28, 0.93]$, $P = 1.00$) than agricultural reference lands (Fig. 4A). In contrast, there was little support for the hypothesis that alpha species richness of obligates was greater on native CRP than on introduced CRP ($P = 0.73$, Fig. 4A), or the hypothesis that the alpha species richness of generalists was lower on native CRP than on introduced CRP ($P = 0.84$, Fig. 4A). We found evidence for greater alpha species richness of generalists in introduced CRP plantings relative to agricultural reference lands ($\beta = 0.35$, $SD = 0.26$, $CI = [-0.14, 0.93]$, $P = 0.92$), but little evidence for a difference between native CRP plantings and agricultural lands ($P = 0.56$, Fig. 4A).

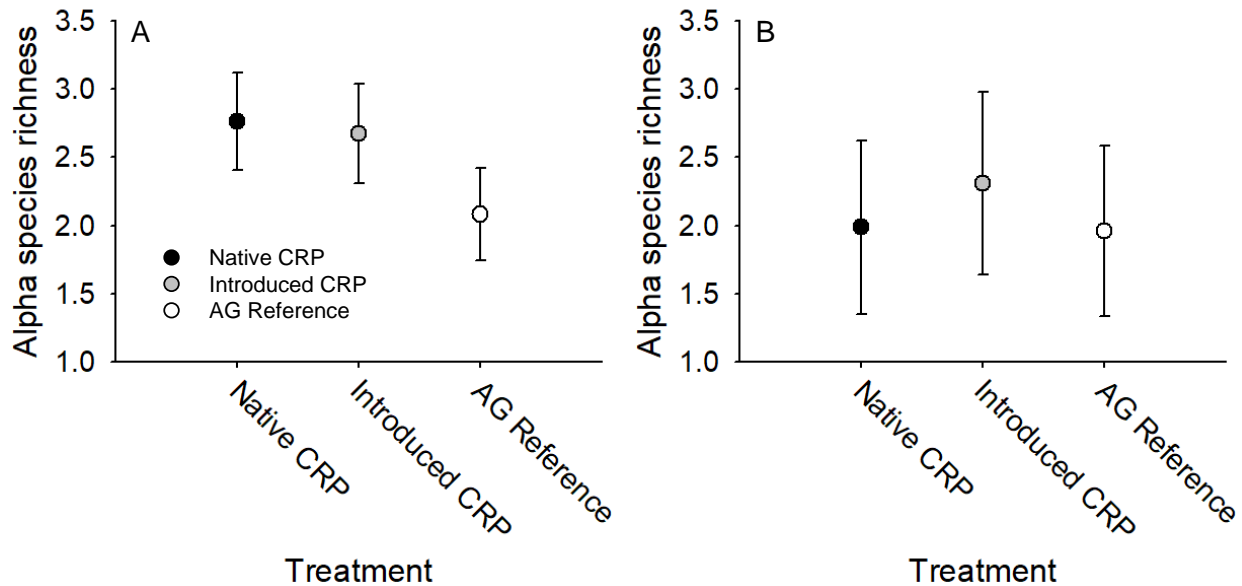


Figure 4. The alpha species richness of 5 ha point count plots for native Conservation Reserve Program (CRP) plantings, introduced CRP plantings and agricultural reference lands for grassland (A) obligates and (B) generalists within the Sand Shinnery Oak Prairie ecoregion, occupied range of the lesser prairie-chicken, New Mexico and Texas, 2016. The round symbols represents the mean number of species among point count plots and the error bars are 1 standard deviation.

We found large shifts in species composition in the CRP treatments relative to agricultural lands (Fig. 5, available in Supporting Information). The dickcissel (*Spiza americana*, $P = 1.00$), eastern meadowlark ($P = 1.00$), grasshopper sparrow ($P = 1.00$), brown-headed cowbird (*Molothrus ater*, $P = 0.98$) and mourning dove ($P = 1.00$) showed greater small-scale occupancy on native CRP plantings than agricultural lands (Fig. 5A). The small-scale occupancy of the Cassin's sparrow ($P = 1.00$), eastern meadowlark ($P = 1.00$), grasshopper sparrow ($P = 1.00$), lark bunting ($P = 1.00$), mourning dove ($P = 1.00$) and northern bobwhite ($P = 1.00$) was greater on introduced CRP plantings than agricultural lands (Fig. 5A). In contrast, the common nighthawk ($P \leq 0.92$), eastern kingbird ($P \leq 0.91$), killdeer ($P = 1.00$), western kingbird ($P \leq 0.99$), horned lark ($P = 1.00$) and red-winged blackbird ($P = 1.00$) showed greater small-scale occupancy on agricultural lands than the CRP plantings (Fig. 5A, Fig. 5B).

Although there was little evidence for differences in alpha species richness of obligates and generalists between the native and CRP plantings, there was strong evidence of shifts in species composition (Fig. 5C, available in Supporting Information). The small-scale occupancy of the dickcissel ($P = 0.97$), grasshopper sparrow ($P = 1.00$), western meadowlark ($P = 0.96$) and brown-headed cowbird ($P = 0.96$) was greater on native CRP plantings than introduced CRP plantings (Fig. 5C). The Cassin's sparrow ($P = 1.00$), lark bunting ($P = 0.98$), killdeer ($P = 0.91$), mourning dove ($P = 0.98$), northern bobwhite ($P = 0.99$) and western kingbird ($P = 0.94$) showed greater small-scale occupancy on introduced CRP plantings than native CRP plantings (Fig. 5C).

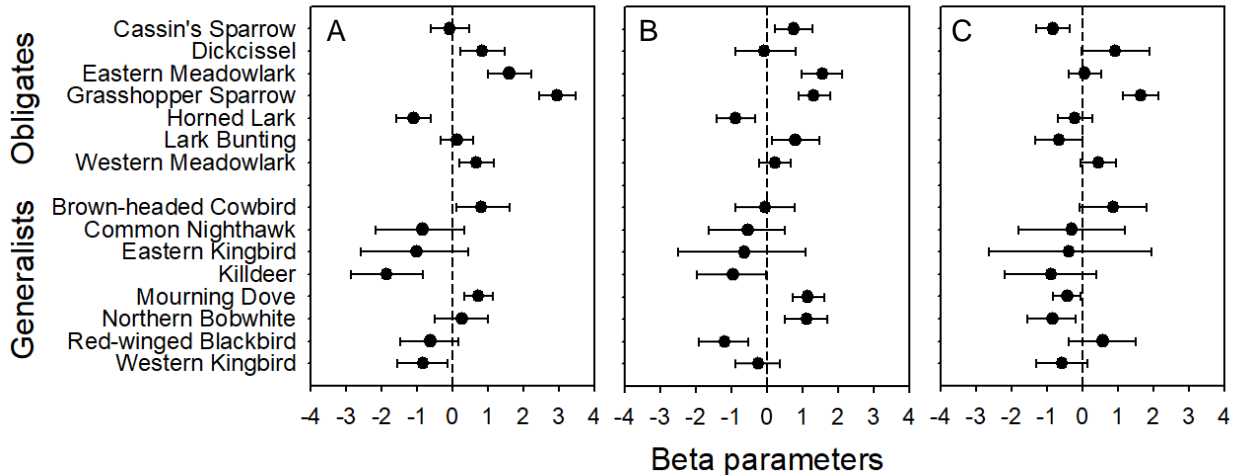


Figure 5. The beta coefficients for the small-scale occupancy of 5 ha point count plots for (A) native Conservation Reserve Program (CRP) plantings relative to agricultural lands, (B) introduced CRP plantings relative to agricultural lands, and (C) native CRP plantings relative to introduced CRP plantings for grassland obligates and generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas. The round symbols represent beta coefficients graphed relative to zero and the error bars are 95% credible intervals.

Prescribed Grazing

There was little support for the hypothesis that alpha species richness of grassland obligates was greater on LPCI prescribed grazing lands than on reference grasslands ($P = 0.86$, Fig. 6A, available in Supporting Information). However, we confirmed the hypothesis for lower alpha species richness of generalists in LPCI prescribed grazing lands relative to reference grasslands ($\beta = 0.55$, $SD = 0.34$, $CI = [-0.06, 1.28]$, $P = 0.96$, Fig. 6B). We confirmed the hypothesis for greater alpha species richness of obligates than generalists in LPCI grazing lands ($\beta = 0.82$, $SD = 0.63$, $CI = [-0.65, 1.90]$, $P = 0.90$, Fig. 6).

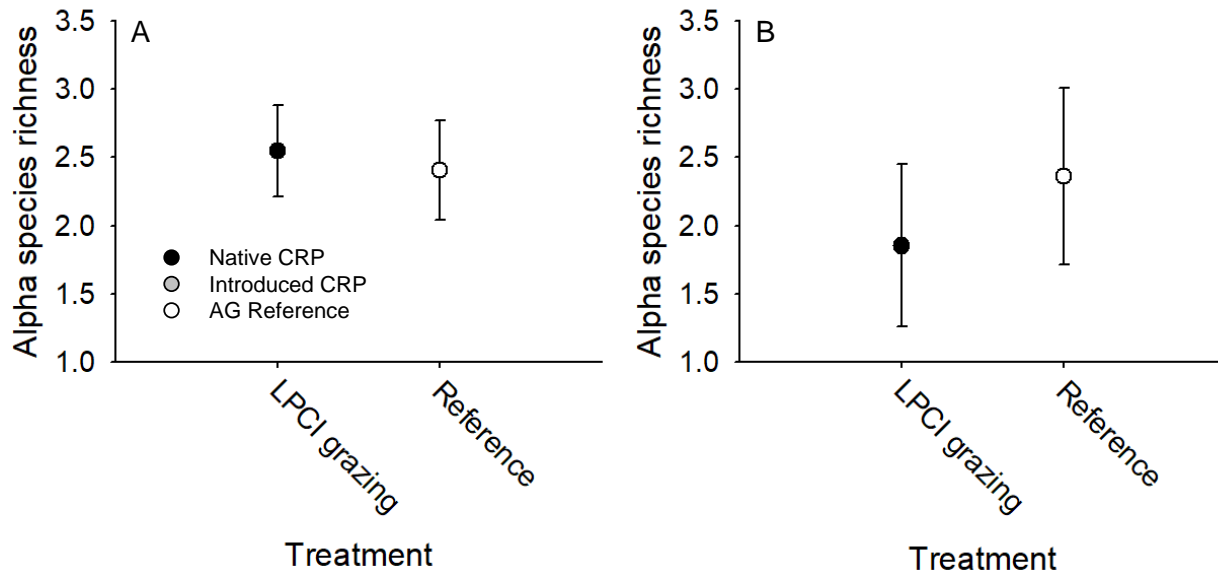


Figure 6. The alpha species richness of 5 ha point count plots for Lesser Prairie-Chicken Initiative prescribed grazing and reference grasslands for grassland (A) obligates and (B) generalists within the Sand Shinnery Oak Prairie ecoregion, occupied range of the lesser prairie-chicken, New Mexico and Texas, 2016. The round symbols represents the mean number of species among point count plots and the error bars are 1 standard deviation.

We found strong evidence for shifts in species composition between LPCI prescribed grazing lands and reference grasslands (Fig. 7, available in Supporting Information). The small-scale occupancy of the Cassin's sparrow ($P = 1.00$), common nighthawk ($P = 0.99$), dickcissel ($P = 0.91$), eastern meadowlark ($P = 0.99$), killdeer ($P = 0.94$), lark bunting ($P = 1.00$), lesser prairie-chicken ($P = 0.99$) and eastern kingbird ($P = 0.98$) was greater on LPCI prescribed grazing lands than reference grasslands (Fig. 7). In contrast, the ash-throated flycatcher (*Myiarchus cinerascens*, $P = 1.00$), canyon towhee ($P = 0.98$), field sparrow ($P = 1.00$), grasshopper sparrow ($P = 0.98$), lark sparrow ($P = 0.98$), loggerhead shrike ($P = 0.99$), mallard (*Anas platyrhynchos*, $P = 0.92$), northern bobwhite ($P = 0.93$), red-winged blackbird ($P = 0.99$), ring-necked pheasant (*Phasianus colchicus*, $P = 0.94$), scaled quail (*Callipepla squamata*, $P = 1.00$), scissor-tailed flycatcher ($P = 1.00$), vesper sparrow ($P = 0.90$) and western kingbird ($P = 1.00$) showed lower small-scale occupancy in LPCI prescribed grazing lands than reference grasslands (Fig. 7).

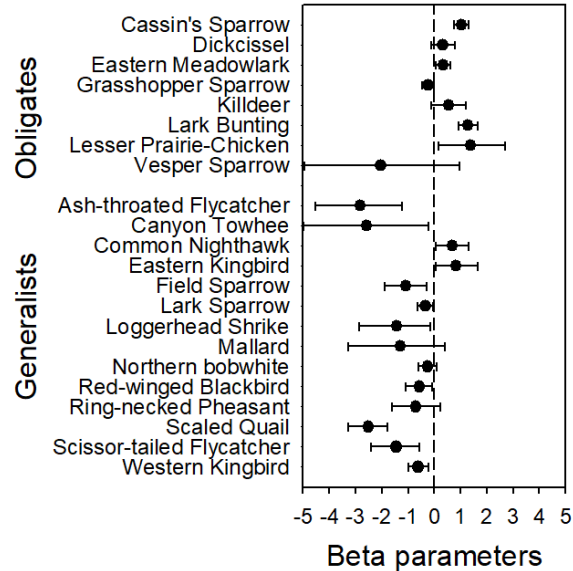


Figure 7. The beta coefficients for the small-scale occupancy of 5 ha point count plots for Lesser Prairie-Chicken Initiative prescribed grazing relative to reference grasslands for grassland obligates and generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas. The round symbols represent beta coefficients graphed relative to zero and the error bars are 95% credible intervals.

Landscape and Local Vegetation Structure

At the landscape scale, we found little evidence for the hypothesis that gamma species richness of grassland obligates declined with increasing fragmentation of native vegetation ($P = 0.51$), or the hypothesis that gamma species richness of grassland generalists increased with increasing fragmentation of native vegetation ($P = 0.29$). Likewise, we found little evidence for the hypothesis that gamma species richness of grassland obligates declined with increasing land-cover of shrub-land vegetation ($P = 0.72$), or the hypothesis that gamma species richness of grassland generalists increased with increasing land-cover of shrub-land vegetation ($P = 0.28$).

Nevertheless, species composition varied by the fragmentation of native vegetation (Fig. 8A, available in Supporting Information) and the relative land-cover of shrub-land vegetation (Fig. 8B). The large-scale occupancy of the Cassin's sparrow ($P = 0.98$), eastern meadowlark ($P = 0.90$), canyon towhee ($P = 0.92$), Chihuahuan raven (*Corvus cryptoleucus*, $P = 0.92$), field sparrow ($P = 0.93$) and lark sparrow ($P = 0.96$) increased with increasing mean patch size of native vegetation (Fig. 8A). In contrast, the dickcissel ($P = 0.93$), killdeer ($P = 0.94$), northern bobwhite ($P = 0.99$), red-winged blackbird ($P = 1.00$) and ring-necked pheasant ($P = 0.97$) showed declining large-scale occupancy with increasing mean patch size of native vegetation (Fig. 8A). Along the shrub-land land-cover gradient, the large-scale occupancy of the burrowing owl (*Athene cunicularia*, $P = 0.97$), vesper sparrow (*Poocetes gramineus*, $P = 0.90$), ash-throated flycatcher ($P = 0.99$), field sparrow ($P = 0.91$), scaled quail ($P = 1.00$), scissor-tailed flycatcher ($P = 1.00$) and western kingbird ($P = 0.97$) increased with increasing land-cover of shrub-land vegetation (Fig. 8B). In contrast, the dickcissel ($P = 1.00$), grasshopper sparrow ($P = 1.00$), horned lark ($P = 1.00$), long-billed curlew (*Numenius americanus*, $P = 0.94$), western meadowlark ($P = 1.00$), killdeer ($P = 1.00$), lark sparrow ($P = 0.95$), red-winged blackbird ($P = 0.93$) and ring-necked pheasant ($P = 1.00$) showed declining large-scale occupancy with increasing land-cover of shrub-land vegetation (Fig. 8B).

Bird Conservancy of the Rockies

Conserving birds and their habitats

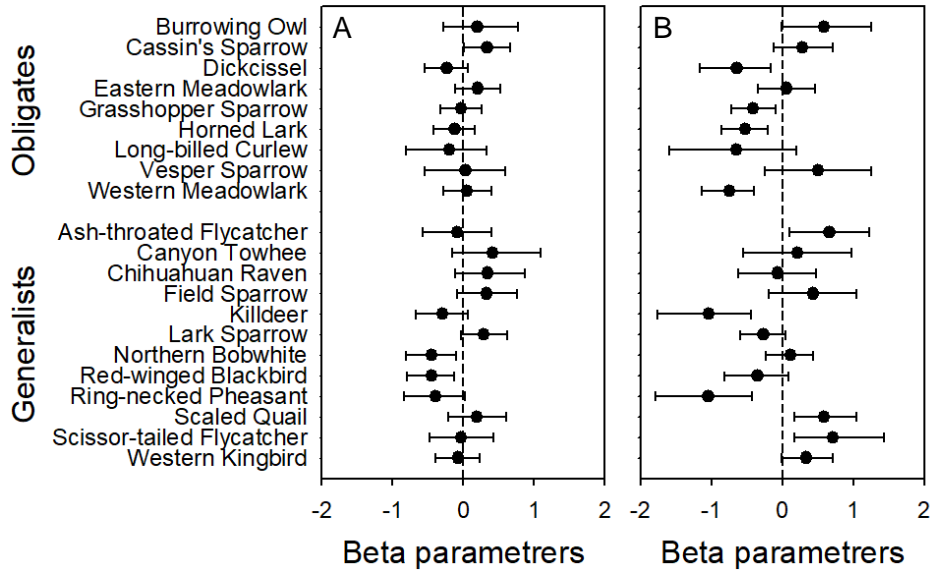


Figure 8. The beta coefficients for the large-scale occupancy of 1 km² grid cells for the (A) mean patch size of native vegetation and (B) relative land-cover of shrub-land vegetation for grassland obligates and generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas. The round symbols represent beta coefficients graphed relative to zero and the error bars are 95% credible intervals.

At the local scale, we confirmed the hypothesis that the alpha species richness of grassland obligates ($\beta = 0.10$, $SD = 0.04$, $CI = [0.02, 0.19]$, $P = 0.99$) and generalists ($\beta = 0.08$, $SD = 0.04$, $CI = [0.00, 0.17]$, $P = 0.98$) increased with increasing ground cover of herbaceous vegetation (Fig. 9). In contrast, there was little evidence that the alpha species richness of grassland obligates ($P = 0.56$) and generalists ($P = 0.73$) increased with increasing grass height.

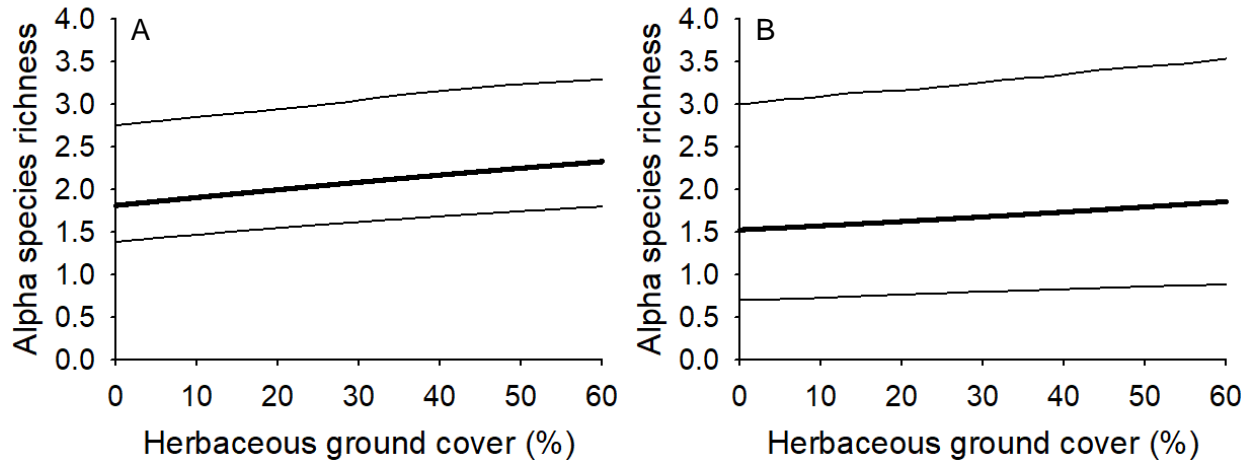


Figure 9. The alpha species richness of 5 ha point count plots by herbaceous ground cover for grassland (A) obligates and (B) generalists in reference grasslands within the Sand Shinnery Oak Prairie ecoregion, occupied range of the lesser prairie-chicken, New Mexico and Texas, 2016. The bold trend line represents the mean number of species among point count plots and the bounding lines are 95% credible intervals.

We found evidence for shifts in species composition according variation in herbaceous ground cover (Fig. 10A, available in Supporting Information) and grass height (Fig. 10B, available in Supporting Information). The small-scale occupancy of the Cassin's sparrow ($P = 1.00$), grasshopper sparrow ($P = 0.98$), horned lark ($P = 0.99$), western meadowlark ($P = 1.00$), brown-headed cowbird ($P = 0.97$), northern bobwhite ($P = 1.00$), red-winged blackbird ($P = 0.97$) and scaled quail ($P = 0.91$) increased with increasing herbaceous ground cover (Fig. 10A). In terms of grass height, the dickcissel ($P = 1.00$), lark bunting ($P = 0.97$), mallard ($P = 0.93$), mourning dove ($P = 1.00$), red-winged blackbird ($P = 1.00$) and ring-necked pheasant ($P = 0.98$) showed increasing small-scale occupancy with increasing grass height, whereas horned lark ($P = 0.96$) and western meadowlark ($P = 0.96$) occupancy declined with increasing grass height (Fig. 10B).

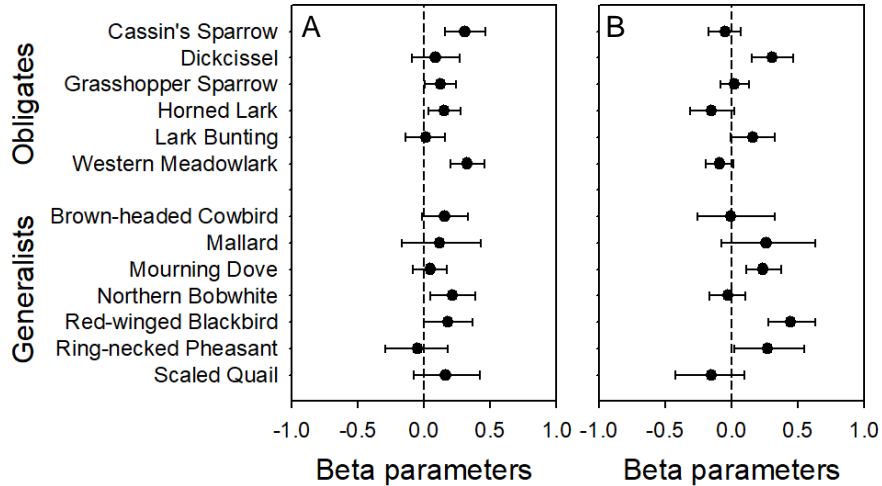


Figure 10. The beta coefficients for the small-scale occupancy of 5 ha point count plots for (A) herbaceous ground cover and (B) mean grass height for grassland obligates and generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas. The round symbols represent beta coefficients graphed relative to zero and the error bars are 95% credible intervals.

With respect to the shrub component, we found little support for declining alpha species richness of grassland obligates with increasing shrub canopy cover ($P = 0.42$) and shrub height ($P = 0.19$). In contrast, we confirmed the hypothesis for increasing species richness of generalists with increasing shrub cover ($\beta = 0.09$, $SD = 0.06$, $CI = [-0.03, 0.20]$, $P = 0.93$, Fig. 11A) and shrub height ($\beta = 0.15$, $SD = 0.06$, $CI = [0.03, 0.27]$, $P = 0.99$, Fig. 11B).

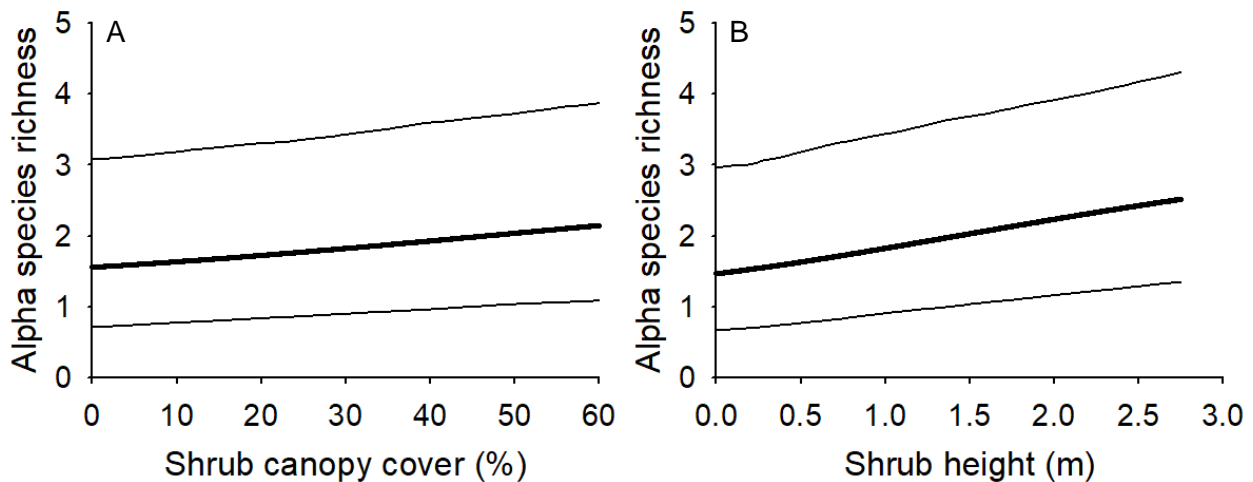


Figure 11. The alpha species richness of 5 ha point count plots for grassland generalists by shrub canopy cover in reference grasslands within the Sand Shinnery Oak Prairie ecoregion, occupied range of the lesser prairie-chicken, New Mexico and Texas, 2016. The bold trend line represents the mean number of species among point count plots and the bounding lines are 95% credible intervals.

We found strong evidence for shifts in species composition along gradients of shrub cover (Fig. 12A, available in Supporting Information) and shrub height (Fig. 12B, available in Supporting Information). The Cassin's sparrow ($P = 1.00$), lesser prairie-chicken ($P = 0.97$), field sparrow ($P = 1.00$), mourning dove ($P = 0.99$), northern bobwhite ($P = 1.00$), scaled quail ($P = 1.00$), scissor-tailed flycatcher ($P = 0.99$) and western kingbird ($P = 0.90$) showed increasing small-scale occupancy with increasing shrub cover, whereas grasshopper sparrow ($P = 1.00$), lark bunting ($P = 0.99$) and western meadowlark ($P = 0.98$) occupancy declined with increasing shrub cover (Fig. 12A). Along the gradient of shrub height, the small-scale occupancy of the Cassin's sparrow ($P = 1.00$), eastern meadowlark ($P = 0.99$), vesper sparrow ($P = 0.90$), American kestrel ($P = 1.00$), ash-throated flycatcher ($P = 0.99$), canyon towhee ($P = 0.91$), eastern kingbird ($P = 0.99$), field sparrow ($P = 0.97$), lark sparrow ($P = 1.00$), loggerhead shrike ($P = 0.96$), mourning dove ($P = 0.99$), northern bobwhite ($P = 1.00$), Say's phoebe (*Sayornis saya*, $P = 0.92$), scaled quail ($P = 1.00$) and western kingbird ($P = 1.00$) increased with increasing shrub height (Fig. 12B). In contrast, the grasshopper sparrow ($P = 1.00$), horned lark ($P = 1.00$), western meadowlark ($P = 0.98$) and red-winged blackbird ($P = 0.99$) showed declining small-scale occupancy with increasing shrub height (Fig. 12B).

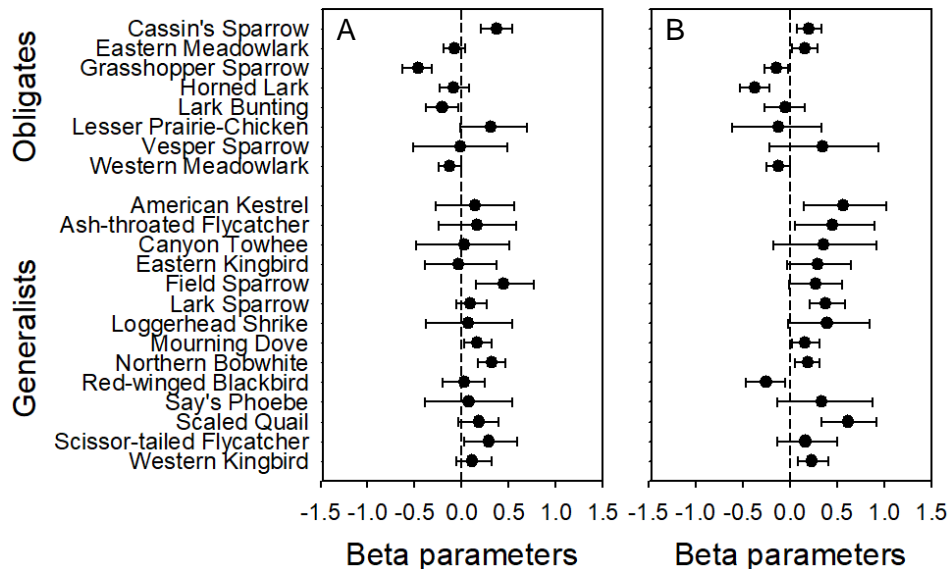


Figure 12. The beta coefficients for the small-scale occupancy of 5 ha point count plots for (A) shrub canopy cover and (B) mean shrub height for grassland obligates and generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas. The round symbols represent beta coefficients graphed relative to zero and the error bars are 95% credible intervals.

With respect to the tree component, we found little support for declining alpha species richness of grassland obligates with increasing tree canopy cover ($P = 0.85$) and tree height ($P = 0.82$). In a similar fashion, there was little support for increasing alpha species richness of grassland generalists with increasing tree canopy cover ($P = 0.33$) and tree height ($P = 0.86$).

We observed evidence for shifts in species composition along the gradients of tree canopy cover (Fig. 13A, available in Supporting Information) and tree height (Fig. 13B, available in Supporting Information). Along the tree canopy cover gradient, the small-scale occupancy of the grasshopper sparrow ($P = 0.96$), horned lark ($P = 0.93$) and western meadowlark ($P = 0.92$)

declined, whereas the occupancy of the northern bobwhite ($P = 0.98$) increased with increasing tree canopy cover (Fig. 13A). Along the gradient of tree height, the Cassin's sparrow ($P = 1.00$), grasshopper sparrow ($P = 1.00$), horned lark ($P = 1.00$), lark bunting ($P = 0.99$), western meadowlark ($P = 1.00$) and killdeer ($P = 0.97$) showed declining small-scale occupancy with increasing tree height, whereas American kestrel ($P = 0.91$), ash-throated flycatcher ($P = 0.98$), eastern kingbird ($P = 1.00$), lark sparrow ($P = 1.00$), loggerhead shrike ($P = 0.90$), mourning dove ($P = 1.00$), red-winged blackbird ($P = 0.97$) and rufous-crowned sparrow ($P = 0.92$) occupancy increased with increasing tree height (Fig. 13B).

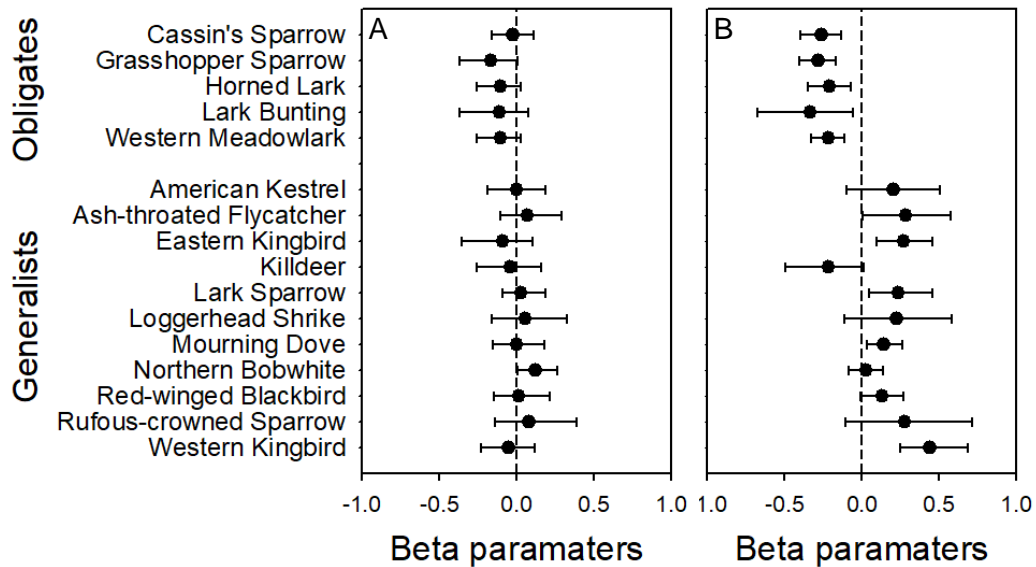


Figure 13. The beta coefficients for the small-scale occupancy of 5 ha point count plots for (A) tree canopy cover and (B) mean tree height for grassland obligates and generalists within the occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas. The round symbols represent beta coefficients graphed relative to zero and the error bars are 95% credible intervals.

Discussion

We developed a hierarchical framework for evaluating the responses of avian biodiversity (Whittaker et al. 2001, Bestelmeyer et al. 2003) to Farm Bill conservation practices (Briske et al. 2017) aimed at the recovery of the LEPC (USFWS 2011, Van Pelt et al. 2013). We investigated avian species richness at two spatial scales. At the landscape scale, gamma richness represented the average number of species among 1 km² grid cells. At the local scale, alpha richness corresponded to the average number of species among 5 ha point count plots. This approach allowed us to simultaneously investigate biodiversity responses of the grassland bird community to environmental gradients operating at two spatial scales. We investigated gamma richness along gradients of grassland loss and fragmentation at the landscape scale, and the responses of alpha richness to conservation practices and vegetation structure at the local scale. We used min intervals of point count surveys to estimate the detection probabilities of the species, which allowed us to estimate site occupancy while accounting for false absences. We used the patterns of landscape composition and configuration to make inference about land use associated with the loss and fragmentation of native vegetation (Fischer and Lindenmayer 2007), and the landscape relationships allowed us to control for large-scale processes while evaluating treatment effects at the local scale. The evaluation of treatments effects at the local scale is relevant to vegetation responses to conservation practices and this allowed us to study avian responses to heterogeneity in vegetation structure (Derner et al. 2009). We accounted for differences in species richness and composition between ecoregions, and this allowed the estimation of treatment effects while controlling for variation in the geographic ranges of the species. Finally, the multi-species occupancy model (Iknayan et al. 2014) provided a framework for estimating species richness and composition for all 74 grassland species in the community, including unobserved species.

Conservation Reserve Program

Our results indicated native and introduced CRP plantings to restore agricultural lands are important conservation practices for increasing the biodiversity of grassland bird in the southern Great Plains. Land enrolled in the CRP program is an important conservation practice for increasing the large-scale occupancy of the LEPC in the SGPR and MGPR ecoregions (Carlisle et al. 2018). We found both native and introduced CRP plantings increased the alpha species richness of grassland obligates relative to agricultural lands. In contrast to the findings of Bakker and Higgins (2009), introduced CRP plantings increased the species richness of grassland generalists, whereas species richness of generalists was similar in native CRP and agricultural lands. Similar to the findings of Thompson et al. (2009), we were unable to confirm the hypothesis for greater species richness in native CRP plantings relative to introduced CRP plantings, but a shift in species composition indicated grassland obligates showed larger positive responses to native CRP plantings relative to introduced CRP plantings than generalist species. Of the 4 species favoring native over introduced CRP plantings, 75% are obligates and 50% are declining. Of the 6 species favoring introduced over native CRP plantings, 60% are obligates and 50% are declining. Overall, the treatment effect for taking cropland out of production and planting introduced CRP was more important than native CRP plantings for the species composition of grassland obligates and declining species. Of the 5 species favoring native CRP over agricultural reference lands, 60% are obligates and 60% are declining. Of the 6 species favoring introduced CRP over agricultural reference lands, 67% are obligates and 83% are declining.

Prescribed Grazing

Our findings indicated LPCI prescribed grazing to improve rangeland condition is an important practice for increasing the biodiversity of grassland obligates and declining species. Although overgrazing is one of the largest threats to LEPC nesting habitat (Hagen et al. 2004), conservative grazing practices are known to be compatible with LEPC nesting habitat and nest survival (Fritts et al. 2016). The rest-rotation grazing systems employed by the LPCI prescribed grazing practice were expected to produce heterogeneity in grassland structure and increase the biodiversity of grassland birds (Derner et al. 2009). Lands enrolled in LPCI prescribed grazing showed greater species richness of grassland obligates relative to grassland generalists. The species richness of grassland generalists was lower on LPCI rangelands than reference grasslands. However, we were unable to confirm the hypothesis for greater alpha species of grassland obligates on LPCI rangelands relative to reference grasslands. Nevertheless, LPCI prescribed grazing appeared to shift species composition toward a community of grassland obligates and species that are currently declining. Of the 9 species favoring LPCI rangelands over reference grasslands, 67% are obligates and 78% are declining. In contrast, of the 9 species favoring reference grasslands over LPCI rangelands, 11% are obligates and 44% are declining.

Landscape and Local Vegetation Structure

We investigated landscape relationships to better understand biodiversity responses to the loss and fragmentation of native vegetation in the occupied range of the LEPC. Our results suggested declining grassland obligates were more sensitive to the loss of grassland land-cover than the fragmentation of native vegetation, but more grassland obligates favored landscapes with large patches of native vegetation. The mean patch size of native grassland and land-cover of shrub-land are important drivers of the large-scale occupancy distribution of the LEPC (Carlisle et al. 2018). However, we were unable to confirm hypotheses for changes in gamma species richness of obligates or generalists along gradients of mean patch size of native vegetation or land-cover of shrub-land vegetation. Nevertheless, we observed greater variation in species composition along the gradient of landscape composition than the gradient of landscape configuration, suggesting that the grassland bird community may be responding to the loss rather than the fragmentation of native vegetation (Fahrig 2003). Future research to investigate the interaction between landscape composition and configuration may reveal additional insight to the fragmentation of grassland and shrub-land vegetation. The relative importance of habitat loss and fragmentation to biodiversity has important conservation implications (Fischer and Lindenmayer 2007). For example, when habitat loss is more important than habitat fragmentation, implementing CRP in a way that maximizes the percentage of suitable habitat in any configuration may be a more effective conservation strategy than managing the patch configuration of native vegetation. Of the 6 species favoring large patches of native vegetation, 33% are obligates and 50% are declining. Of the 5 species favoring small patches of native vegetation, 20% are obligates and 60% are declining. In terms of landscape composition, of the 9 species favoring grassland land-cover, 63% are obligates and 75% are declining. Of the 8 species favoring shrub-land land-cover, 25% are obligates and 25% are declining.

We investigated local vegetation relationships to better understand the mechanisms for biodiversity responses to the LEPC conservation practices. Herbaceous ground cover and grass height, as well as shrub cover and height, have important implications for LEPC nesting habitat and nest survival (Hagen et al. 2004). In addition, variation in species responses to

heterogeneity in vegetation structure is expected to result in high species richness at larger spatial scales (Derner et al. 2009, Hovick et al. 2015). Our results suggested CRP and LPCI prescribed grazing practices that increase the ground cover of herbaceous vegetation play an important role in increasing the biodiversity of grassland birds. The alpha species richness of grassland obligates and generalists increased with increasing herbaceous ground cover, but the species richness of obligates and generalists did not vary with grass height. Of the 8 species favoring high herbaceous ground cover, 50% are obligates and 63% are declining. None of the grassland species increased with declining herbaceous ground cover. Of the 6 species favoring tall grass height, 33% are obligates and 50% are declining. Of the 2 species favoring short grass height, both are obligates and both are declining.

In terms of the shrub component, the alpha species richness of grassland generalists increased with shrub cover and height, but we were unable to confirm hypotheses for declining species richness of grassland obligates with increasing shrub cover and height. However, the majority of species responding negatively to shrub cover and height were grassland obligates currently experiencing population declines. Our results suggested land enrolled in CRP and LPCI prescribed grazing practices at the low-end of shrub cover and height provide important habitat for obligate grassland species of conservation concern, and LPCI rangelands with a substantial shrub component promote the species richness of grassland generalists. Of the 8 species favoring high shrub canopy cover, 25% are obligates and 63% are declining. Of the 3 species favoring low shrub cover, all 3 are obligates and all 3 are declining. In terms of shrub height, of the 15 species favoring tall shrub height, 20% are obligates and 60% are declining. Of the 4 species favoring low shrub height, 75% are obligates and 75% are declining.

We investigated habitat relationships for tree canopy cover and height to predict the responses of grassland bird species to LEPC management actions for the encroachment of woodland vegetation. The large-scale occupancy distribution of the LEPC is negatively influenced by woodland cover (Carlisle et al. 2018), and tree removal may facilitate grassland habitat restoration and range expansion of the LEPC (Lautenbach et al. 2017). We were unable to confirm hypotheses for declining species richness of grassland obligates or increasing species richness of generalists along gradients of tree canopy cover and height. The range of covariate values for tree canopy cover and height (Table 2) may not have contained enough information to evaluate hypotheses for variation in species richness along gradients of woody vegetation. Nevertheless, similar to the findings of Coppedge et al. (2001), we observed a shift in species composition with a greater number of declining grassland obligates occurring at low levels of tree canopy cover and tree height, and a greater number of declining generalists at high levels of tree canopy cover and tree height. Our results suggest tree removal may benefit several grassland obligates currently experiencing population declines, but may be detrimental to several declining species of grassland generalists. Of the 3 species favoring low tree canopy cover, all three are obligates and all three are declining. Only one species, the declining generalist, northern bobwhite increased with increasing tree canopy cover. In terms of tree height, of the 6 species declining with tree height, 83% are obligates and 83% are declining. Of the 8 species increasing with tree height, none are obligates and 88% are declining.

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Appendix A

Details of the Statistical Analysis

We extended the hierarchical Bayes multi-scale occupancy model of Mordecai et al. (2011) to accommodate multiple species (Dorazio and Royle 2005, Royle and Dorazio 2008) and two spatial scales (Pavlacky et al. 2012). For each species, we estimated the probability of large-scale occupancy (ψ) for grid cells, probability of small-scale occupancy (θ) for point count plots given presence at the grid cells, and probability of detection (p) in min intervals given presence at point count plots (Pavlacky et al. 2012). We used a state-space formulation (Royle and Dorazio 2008) composed of two sub-models for partially observed processes of large-scale and small-scale occupancy and an observation model for repeated detections (Mordecai et al. 2011). The latent state z_{itk} is the estimated presence ($z = 1$) or absence ($z = 0$) of species i , year t and grid cell k , and the latent state u_{itkj} is the estimated presence ($u = 1$) or absence ($u = 0$) of species i , year t , grid cell k and point j . The observations y_{itkj} are the frequency of detections for species i , year t , grid cell k and point j using a removal design for 3, 2-minute time occasions (Pavlacky et al. 2012, MacKenzie et al. 2018). The state process model is comprised of two equations, one for the occupancy state of grid cells $z_{itk}|w_i \sim \text{Bernoulli}(\psi_{itk}w_i)$, where the latent variable w_i is explained below, and the other for the occupancy state of point count plots conditional on the occupancy of grid cells $u_{itkj}|z_{itk} \sim \text{Bernoulli}(\theta_{itk}z_{itk})$. The observation model for the frequency of detections $y_{itkj}|u_{itkj} \sim \text{Binomial}(p_{itkj}u_{itkj}, J_{itkj})$ is conditional on the occupancy state of point count plots, where J_{itkj} is the time occasion in which species i was first detected for year t , grid cell k and point j using a removal design (Pavlacky et al. 2012, MacKenzie et al. 2018). When a species was not detected, or when a species was detected on the last time occasion, $J = 3$.

We used a series of logistic regression equations to model the effects of treatment, vegetation structure, ecoregion and year on large-scale (ψ) and small-scale (θ) occupancy, and the effects vegetation structure, ecoregion and year on the probability of detecting the species (p):

$$\begin{aligned}\text{logit}(\psi_{itk}) &= d_{0i} + d_{1i}x_{1k} + \dots + d_{hi}x_{hk}, \\ \text{logit}(\theta_{itkj}) &= b_{0i} + b_{1i}x_{1kj} + \dots + b_{hi}x_{hkj}, \\ \text{logit}(p_{itkj}) &= a_{0i} + a_{1i}x_{1kj} + \dots + a_{hi}x_{hkj},\end{aligned}$$

where d_{0i} is the random intercept, d_{li} is the beta coefficient of covariate x_l ($l = 1, \dots, h$) for the large-scale occupancy of species i , year t and grid cell k . The parameters b_{0i} and a_{0i} are the random intercepts, b_{li} and a_{li} are the beta coefficients of covariate x_l ($l = 1, \dots, h$) for the small-scale occupancy and detection, respectively of species i , year t , grid cell k and point j .

We used data augmentation to estimate the number of unobserved species in the community (Dorazio et al. 2006, Iknayan et al. 2014). The observed data comprised encounter histories for 45 species and we augmented the observed data with “all zero” encounter histories for 29 unobserved species known to breed in the region, resulting in a species pool of 74 grassland species. The latent state w_i is the estimated presence ($w = 1$) or absence ($w = 0$) of species i in the community of species. The state process for the membership of unobserved species in the community is $w_i \sim \text{Bernoulli}(\Omega_g)$, where Ω_g is the probability a species in the augmented data set is a member of the community of species that are present and vulnerable to

detection (Dorazio et al. 2011) for guild g . We estimated the membership of species in the avian community by sharing information and accounting for correlation between the large-scale occupancy, small-scale occupancy and detection of the species (Dorazio et al. 2006, Iknayan et al. 2014).

We used the multivariate normal distribution to specify the variation and correlation of occupancy and detection probabilities among bird species (Dorazio et al. 2011),

$$\begin{bmatrix} a_{0i} \\ b_{0i} \\ d_{0i} \end{bmatrix} \sim \text{Normal} \left(\begin{bmatrix} \alpha_0 \\ \beta_0 \\ \delta_0 \end{bmatrix}, \begin{bmatrix} \sigma_{a_0}^2 & \rho_{ab}\sigma_{a_0}\sigma_{b_0} & 0 \\ \rho_{ab}\sigma_{a_0}\sigma_{b_0} & \sigma_{b_0}^2 & \rho_{bd}\sigma_{b_0}\sigma_{d_0} \\ 0 & \rho_{bd}\sigma_{b_0}\sigma_{d_0} & \sigma_{d_0}^2 \end{bmatrix} \right),$$

where α_0 is mean detection, β_0 is mean small-scale occupancy, and δ_0 is mean large-scale occupancy among the i species. The parameters $\sigma_{a_0}^2$, $\sigma_{b_0}^2$ and $\sigma_{d_0}^2$ represent the variance of detection, small-scale occupancy and large-scale occupancy, respectively among the i species. The parameter ρ_{ab} estimates the correlation between detection and small-scale occupancy, and the ρ_{bd} estimates the correlation between small-scale occupancy and large-scale occupancy. The parameters a_{0i} , b_{0i} , d_{0i} represent the random intercepts for detection, small-scale occupancy and large-scale occupancy, respectively for species i .

In addition, we assumed the species-level beta coefficients were drawn from normal distributions for the 74 species in the community (Dorazio et al. 2006, Royle and Dorazio 2008). We defined the community-level random effects according to:

$$d_{iI} \sim \text{Normal}(\mu_{d_I}, \sigma_{d_I}^2)$$

$$b_{iI} \sim \text{Normal}(\mu_{b_I}, \sigma_{b_I}^2),$$

and

$$a_{iI} \sim \text{Normal}(\mu_{a_I}, \sigma_{a_I}^2),$$

where μ is the mean and σ^2 is the variance for the I beta coefficients of large-scale occupancy (d), small-scale occupancy (b) and detection (a) for species i .

We estimated model parameters using Markov Chain Monte Carlo (MCMC) simulation implemented in program JAGS (Plummer 2003, JAGS Version 4.3.0, www.sourceforge.net, accessed 5 April 2018) using package jagsUI in the R statistical computing environment (R Version 3.4.3, www.r-project.org, accessed 5 April 2018). We used vague and weakly informative prior distributions for all estimated parameters (Dorazio et al. 2011):

$$\Omega_g \sim \text{Uniform}(0,1),$$

$$\rho_{ab}, \rho_{bd} \sim \text{Uniform}(-1,1),$$

$$\alpha_0, \beta_0, \delta_0, \mu_{a_I}, \mu_{b_I}, \mu_{d_I} \sim t(\sigma, \nu),$$

and

$$\sigma_{a_0}, \sigma_{b_0}, \sigma_{d_0}, \sigma_{a_I}, \sigma_{b_I}, \sigma_{d_I} \sim \text{half-Cauchy}(\alpha),$$

where the scale parameter $\sigma = 1.566$ and degrees of freedom $\nu = 7.763$ for the t-distribution. The scale parameter α for the half-Cauchy distribution has the probability density function $f(\alpha) = 2/[\pi(1+\alpha^2)]$, and we used the Student t-distribution prior approximation to the half-Cauchy distribution with mean $\mu = 0$, degrees of freedom = 1 and non-centrality parameter $\Delta = 1$

(Dorazio et al. 2011). We generated 10,000 MCMC samples, specified a burn-in period of 5,000 iterations, and used $\hat{R} < 1.1$ as an indication of model convergence (Gelman and Rubin 1992). We estimated the parameters using the mean and standard deviation of the MCMC samples of the posterior distributions, calculated 95% credible intervals using the quantiles of the posterior distributions, and calculated Bayesian P -values for parameter estimates $P > 0$ or $P < 0$ using posterior predictive distributions (Hobbs and Hooten 2015).

We estimated gamma and alpha species richness for the 24 grassland obligates and 50 grassland generalists in the avian community. We derived estimates of species richness from the posterior MCMC samples (Hobbs and Hooten 2015) by summing the species occupancy estimates for each treatment and ecoregion, and along gradients of the continuous covariates while holding the other effects in the model constant at mean covariate values. We estimated gamma species richness at the landscape scale (Whittaker et al. 2001) by $R = \sum_{m=1}^M \hat{\Psi}_m$, where M is the number of m species in each guild and $\hat{\Psi}$ is the estimate of large-scale occupancy for each species (Zipkin et al. 2009, MacKenzie et al. 2018), and this corresponds to the mean number of species among 1 km² grid cells. We estimated alpha species richness at the local scale (Whittaker et al. 2001) by $R = \sum_{m=1}^M \hat{\Psi}_m \hat{\theta}_m$, where M is the number of m species in each guild, $\hat{\Psi}$ is the estimate of large-scale occupancy and $\hat{\theta}$ is the estimate of small-scale occupancy for each species, and this corresponds to the mean number of species among 5 ha point count plots.

Appendix B

Table B1. The common name, scientific name, guild (Vickery and Herkert 1999, Johnsgard 2009) and declining trends in the Great Plains from the Breeding Bird Survey (Sauer et al. 2017) for the 45 grassland bird species observed in the study, occupied range of the lesser prairie-chicken, Colorado, Kansas, New Mexico, Oklahoma, and Texas, 2015 - 2017.

Common name	Scientific name	Guild	Trend
Burrowing Owl	<i>Athene cunicularia</i>	Obligate	No
Cassin's Sparrow	<i>Peucaea cassinii</i>	Obligate	No
Dickcissel	<i>Spiza americana</i>	Obligate	No
Eastern Meadowlark	<i>Sturnella magna</i>	Obligate	Yes
Ferruginous Hawk	<i>Buteo regalis</i>	Obligate	No
Grasshopper Sparrow	<i>Ammodramus savannarum</i>	Obligate	Yes
Horned Lark	<i>Eremophila alpestris</i>	Obligate	Yes
Lark Bunting	<i>Calamospiza melanocorys</i>	Obligate	Yes
Lesser Prairie-Chicken	<i>Tympanuchus pallidicinctus</i>	Obligate	-
Long-billed Curlew	<i>Numenius americanus</i>	Obligate	No
Mountain Plover	<i>Charadrius montanus</i>	Obligate	Yes
Northern Harrier	<i>Circus cyaneus</i>	Obligate	Yes
Short-eared Owl	<i>Asio flammeus</i>	Obligate	No
Swainson's Hawk	<i>Buteo swainsoni</i>	Obligate	No
Vesper Sparrow	<i>Pooecetes gramineus</i>	Obligate	No
Western Meadowlark	<i>Sturnella neglecta</i>	Obligate	Yes
American Kestrel	<i>Falco sparverius</i>	Facultative	Yes
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	Facultative	No
Blue-winged Teal	<i>Anas discors</i>	Facultative	No
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	Facultative	Yes
Brown-headed Cowbird	<i>Molothrus ater</i>	Facultative	No
Canyon Towhee	<i>Melospiza fusca</i>	Facultative	Yes
Cassin's Kingbird	<i>Tyrannus vociferans</i>	Facultative	No
Cattle Egret	<i>Bubulcus ibis</i>	Facultative	No
Chihuahuan Raven	<i>Corvus cryptoleucus</i>	Facultative	No
Common Nighthawk	<i>Chordeiles minor</i>	Facultative	Yes
Common Yellowthroat	<i>Geothlypis trichas</i>	Facultative	Yes
Eastern Bluebird	<i>Sialia sialis</i>	Facultative	No
Eastern Kingbird	<i>Tyrannus tyrannus</i>	Facultative	Yes
Field Sparrow	<i>Spizella pusilla</i>	Facultative	Yes
Killdeer	<i>Charadrius vociferus</i>	Facultative	Yes
Lark Sparrow	<i>Chondestes grammacus</i>	Facultative	Yes
Loggerhead Shrike	<i>Lanius ludovicianus</i>	Facultative	Yes
Mallard	<i>Anas platyrhynchos</i>	Facultative	No
Mourning Dove	<i>Zenaidura macroura</i>	Facultative	Yes
Northern Bobwhite	<i>Colinus virginianus</i>	Facultative	Yes
Northern Shoveler	<i>Anas clypeata</i>	Facultative	No
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Facultative	Yes
Ring-necked Pheasant	<i>Phasianus colchicus</i>	Facultative	No
Rufous-crowned Sparrow	<i>Aimophila ruficeps</i>	Facultative	Yes
Say's Phoebe	<i>Sayornis saya</i>	Facultative	No

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Common name	Scientific name	Guild	Trend
Scaled Quail	<i>Callipepla squamata</i>	Facultative	No
Scissor-tailed Flycatcher	<i>Tyrannus forficatus</i>	Facultative	Yes
Turkey Vulture	<i>Cathartes aura</i>	Facultative	No