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Research Article

Landscape-Scale Greater Prairie-Chicken–Habitat Relations and the Conservation Reserve Program

KALYSTA ADKINS,[1,2] *Minnesota Cooperative Fish and Wildlife Research Unit, University of Minnesota, 1980 Folwell Avenue, 200 Hodson Hall, St. Paul, MN 55108, USA*

CHARLOTTE L. ROY, *Minnesota Department of Natural Resources, 1201 E Highway 2, Grand Rapids, MN 55744, USA*

DAVID E. ANDERSEN, *U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit, 1980 Folwell Avenue, 200 Hodson Hall, St. Paul, MN 55108, USA*

ROBERT G. WRIGHT, *Minnesota Information Technology Services at Department of Natural Resources, 5463-C W Broadway, Forest Lake, MN 55025, USA*

ABSTRACT Both the abundance of greater prairie-chickens (*Tympanuchus cupido pinnatus*) and the area of grassland enrolled in the Conservation Reserve Program (CRP) in northwestern Minnesota, USA, have recently declined. Although wildlife conservation is a stated objective of the CRP, the impact of the CRP on greater prairie-chicken populations has not been quantified. To address that information need, we evaluated the association between greater-prairie chicken lek density (leks/km^2), the number of males at leks (males/lek), and CRP enrollments in the context of landscape structure and composition in northwestern Minnesota. Using data from standardized prairie-chicken surveys and land cover in 17 41-km^2 survey blocks during 2004–2016, we used a mixed-effect model and a layered approach in an information-theoretic framework at multiple spatial scales to identify covariates related to prairie-chicken abundance. At the landscape scale, lek density was best explained by the amount of CRP grassland and wetland, grassland and wetland with long-term conservation goals (state, federal, and The Nature Conservancy owned); other wetlands managed with variable or no continuity in conservation goals; the contiguity of grasslands; and the number of patches of grasslands and wetlands in each survey block each year. Increasing the amount of CRP grassland in 41-km^2 survey blocks by 1 km^2 (2.4%) resulted in a corresponding increase of 6% in lek density. At the lek scale, the number of males per lek was best explained by the amount of CRP grassland and other grassland, CRP wetland and other wetland, forests, developed areas, shrubland, and the contiguity of CRP grassland. Increasing the amount of CRP grassland in the 2-km breeding-cycle habitat radius around a lek by 25% (3 km^2) corresponded to a 5% increase in males per lek. Our results suggest that both increasing the quantity of grassland CRP and wetland CRP enrollments and aggregating CRP grassland enrollments may increase greater prairie-chicken abundance.

KEY WORDS Conservation Reserve Program, grassland, greater prairie-chicken, landscape, Minnesota, *Tympanuchus cupido pinnatus*.

Over much of their distribution, greater prairie-chicken (*Tympanuchus cupido pinnatus*) abundance has declined since the early twentieth century, resulting in heightened conservation concern and focused management efforts to increase and re-establish sustainable populations. Declines of greater prairie-chicken abundance are strongly associated with decreases in the extent of the tallgrass prairie ecosystem, which once spanned over 380,000 km^2 in the midwestern United States (Noss et al. 1995, Steiner and Collins 1996, Ryan 2000). The conversion of the tallgrass prairie plant community to row-crop agriculture production or pasture and invasion of exotic grasses led to alteration and loss of 83–99% of its area throughout the Midwest (Noss et al. 1995, Herkert et al. 1996, Steiner and Collins 1996, Ryan 2000, Burger et al. 2006). For example, in Minnesota, USA, the tallgrass prairie ecosystem once covered approximately a third of the state but now <2% of that area remains as tallgrass prairie (Minnesota Prairie Plan Working Group 2011) and >90% of the loss of tallgrass prairie resulted from conversion to row-crop agriculture. Other grassland cover types are also declining across many agricultural landscapes; in Minnesota agricultural grasslands such as hay, pasture, and small grain crops were lost at a rate of 6%/year from 1987–1997 (Giudice and Haroldson 2007). Although

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[1]*E-mail: kadkins24@gmail.com*
[2]*Current affiliation: Oregon Department of Fish and Wildlife, 3701 13th Street, The Dalles, OR 97058, USA*

extensive row-crop agriculture is typically negatively associated with greater prairie-chicken abundance, a small amount of agriculture amid extensive grasslands seems to benefit greater prairie-chicken populations by providing food and cover (Partch 1973, Svedarsky et al. 2000).

Greater prairie-chicken conservation in Minnesota and elsewhere has focused on maintaining and re-establishing grassland cover types within expansive landscapes. Greater prairie-chickens use grasslands during all portions of their life history for nesting, brood rearing, roosting, concealment from predators, mating rituals, and foraging (Kobriger 1965, Merrill et al. 1999, Niemuth 2000). Prairie grouse (greater prairie-chickens, lesser prairie-chickens [*T. pallidicinctus*], and sharp-tailed grouse [*T. phasianellus*]) are generally resident, area-sensitive, and philopatric to their natal areas. For example, greater prairie-chickens use a 2-km radius surrounding leks (Merrill et al. 1999, Niemuth 2011) throughout their breeding cycle. Therefore, landscape characteristics such as amount, types, and configuration of land cover are expected to have an effect on the presence, abundance, and persistence of greater prairie-chickens at various spatial scales (Merrill et al. 1999; Niemuth 2000, 2003; Larson and Bailey 2007; Hovick et al. 2015).

In the face of loss, fragmentation, and isolation of tallgrass prairie and other grassland cover types, federal and state agricultural policy and programs have the potential to influence greater prairie-chicken abundance and distribution. Specifically, the Conservation Reserve Program (CRP) can influence the amount of grassland in an agriculture-dominated landscape. The CRP is the largest federal private land retirement program in the United States (Stubbs 2014). Established in 1985, the CRP is authorized to remove land from crop production with the objectives to reduce soil erosion, improve water quality, and restore and protect wildlife habitats by providing financial incentives to reseed agricultural land to sod-forming or ecologically native vegetation for 10–15 years. A variety of programs within the CRP focus on different types of wildlife habitat restoration including field buffers, bottomland hardwood forest, pollinator habitat, restoring farmed wetlands, and riparian cover (Riley 2004), some of which can increase the amount of tallgrass prairie and other grassland cover types in agricultural landscapes.

The protection and restoration of wildlife habitat is a stated objective of the CRP, but the relationship between grassland CRP enrollments, landscape composition, and greater prairie-chicken populations at multiple spatial scales is not well understood. In northwestern Minnesota, greater prairie-chickens use CRP for nesting habitat (Toepfer 1988, Svedarsky et al. 2000) and large amounts of CRP grassland have been associated with the presence of greater prairie-chicken leks (Merrill et al. 1999). Multiple studies (Niemuth 2000, 2003; Larson and Bailey 2007; Hovick et al. 2015) have linked greater prairie-chicken presence, abundance, and persistence with the amount, types, and configuration of land cover, but none have explicitly addressed greater prairie-chicken abundance relationships with CRP.

Area enrolled in the CRP has declined nationwide since its peak enrollment of approximately 149,000 km^2 in 2007 (Stubbs 2014). This decrease is scheduled to continue because the 2014 Farm Bill decreased the enrollment cap from approximately 130,000 km^2 to <100,000 km^2 by 2018 (Stubbs 2014). In greater prairie-chicken range in Minnesota, area enrolled in the CRP (all conservation practice codes) declined 16–52% across 17 established greater prairie-chicken survey blocks from 2004 to 2014 and greater prairie-chicken populations declined over this period (Roy 2016), indicating a correlation warranting further investigation. Stronger inferences about the relationship between the CRP and greater prairie-chickens can be obtained by examining spatially explicit patterns that are replicated temporally with a large sample.

Our objective was to quantify the relationship between greater prairie-chicken populations, CRP enrollments, and the resulting landscape structure in northwestern Minnesota at multiple spatial scales. Specifically, we investigated the relationship between population metrics (i.e., leks/km^2 and males/lek) of greater prairie-chickens and landscape metrics (i.e., composition, contiguity, and fragmentation) at the landscape and lek scales. Based on previous studies documenting greater prairie-chicken use of areas with CRP grassland, we expected that greater prairie-chicken abundance would be associated with the extent and distribution of CRP enrollments that result in grassland cover types in the agricultural landscape in northwestern Minnesota.

STUDY AREA

Our study area included portions of an 8-county region in northwestern Minnesota approximately 24,000 km^2 in size. The region was part of the bed of glacial Lake Agassiz, making it relatively flat with elevation ranging from approximately 100 m to 300 m. During the study period (2004–2016), this region was dominated by various agricultural croplands (>60% of total area; U.S. Department of Agriculture [USDA]-National Agricultural Statistics Service [NASS] 2016) where soybeans, corn, and wheat comprised >50% of the total area. The rest of the landscape consisted of low amounts of developed areas (~5%), forested areas (<10%), and shrubland (<5%). Herbaceous cover (i.e., herbaceous wetlands, pasturelands, grasslands) was approximately 15% of the total area (USDA-NASS 2016). Fragmented prairie grasslands and wetlands that exist within the region are dominated by grass and sedge species such as big bluestem (*Andropogon gerardii*), side oats grama (*Bouteloua curtipendula*), and fox sedge (*Carex vulpinoidea*) with a mix of broad-leaf forbs and low shrub species. Greater prairie-chickens use these grasslands throughout their annual life cycles including lekking through early spring (late Mar–Apr) and nesting and brood rearing through late spring and summer (May–Aug). Fauna within the area include various grassland birds such as dicksissel (*Spiza americana*), eastern meadowlark (*Sturnella magna*), grasshopper sparrow (*Ammodramus savannarum*), and red-tailed hawk (*Buteo jamaicensis*), and common mammals include coyote (*Canis latrans*), red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), and raccoon (*Procyon lotor*). The climate is continental, with seasonality including cold winters with average low temperatures below −12° C and warm summers with average high temperatures above 27° C. Within this region, greater prairie-chickens have been surveyed annually using standardized protocols in 17 41-km^2 survey blocks since 2004 (Fig. 1; Roy 2016). This survey provided an opportunity to assess greater prairie-chicken–habitat relations at a landscape scale because survey blocks were non-randomly selected to represent different grassland land ownerships that vary in management approaches across the greater prairie-chicken range in Minnesota (J. H. Giudice, Minnesota Department of Natural Resources, unpublished report). Open cover types in 2 of the 17 blocks were comprised of a majority of state and federally managed lands, in 5 blocks open cover types were mostly under CRP enrollment in 1997, and in 10 blocks open cover types were a combination of CRP and holdings owned and managed by the Minnesota Department of Natural Resources (MNDNR), the U.S. Fish and Wildlife Service (USFWS), and The Nature Conservancy (TNC).

METHODS

Annual surveys of greater prairie-chickens were collected through a program coordinated by MNDNR and adhered to MNDNR animal welfare standards in place at the time surveys were conducted. Surveys were executed in collaboration with the Minnesota Prairie Chicken Society (MPCS), TNC, USFWS, and other volunteers. Data from the greater prairie-chicken spring survey consisted of count and location information for leks from 2004–2016 within the 17 41-km^2 survey blocks. The survey protocol consisted of surveyors being assigned 4 Public Land Survey sections within a survey block and attempting to observe mating display behavior on multiple visits to these sections. Surveyors observed mating display behavior with the use of binoculars and counted the number of males (displaying) and females (not displaying when most other birds displayed) at each visit to each lek. Surveyors recorded sex as unknown if they flushed prairie-chickens to obtain a count because of viewing obstructions (Roy 2016). Location data were available for 58–114 leks/year within these survey blocks, typically recorded to the level of quarter-section or global positioning system (GPS) coordinates. From these survey

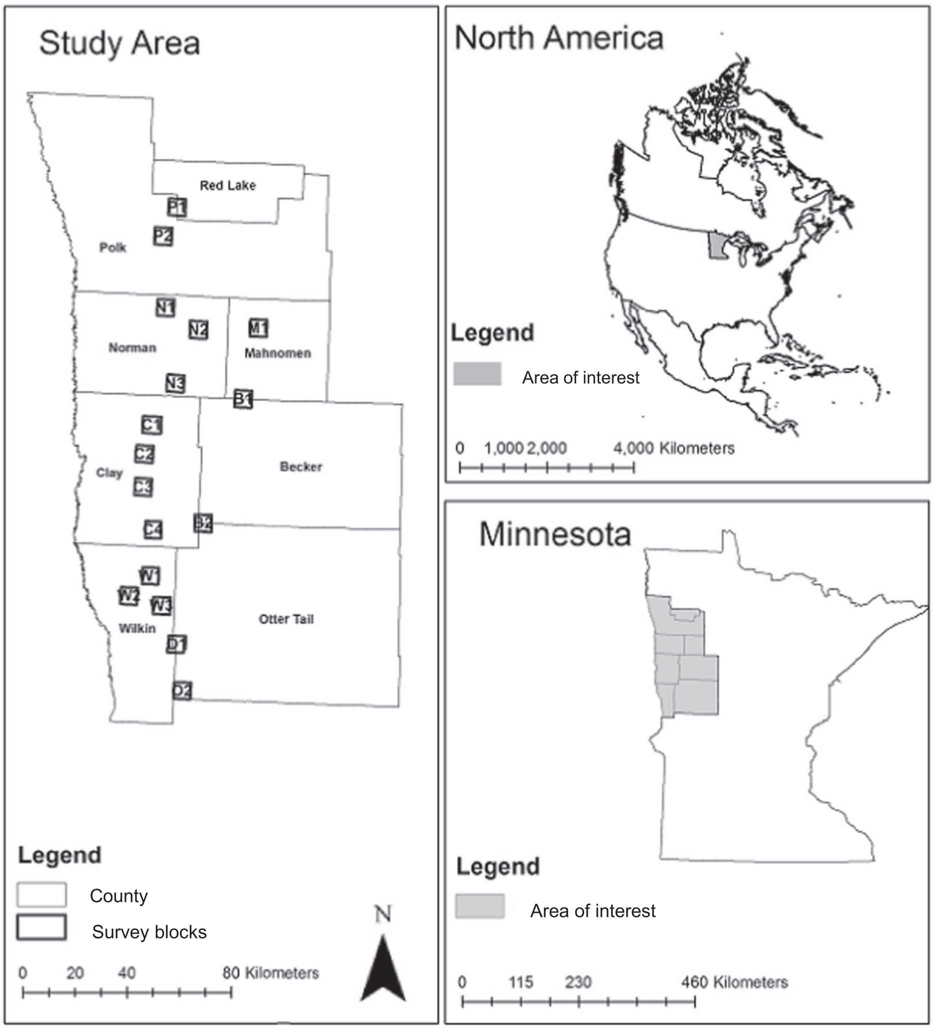

Figure 1. Location of the 17 greater prairie-chicken survey blocks (black labeled squares, 41 km^2) in northwestern Minnesota, USA, surveyed during 2004–2016. Survey blocks are labeled with the first letter of the respective county (gray border) and corresponding number (from north to south).

data, we derived data for analysis at survey-block and lek scales. The survey-block scale refers to the entirety of the 41-km^2 blocks; the lek scale considers a fixed buffer of 2 km around each recorded lek location to encompass the breeding-cycle habitat radius of greater prairie-chickens (Merrill et al. 1999, Hovick et al. 2015).

We created shapefiles of lek locations by importing GPS coordinates of lek locations and Public Land Survey coordinates collected by survey volunteers into a geographic information system (ArcGIS; Esri, Redlands, California, USA). If lek locations were only recorded to the accuracy of the section, we examined notes included with lek observations and surrounding lek locations in the current, previous, and later years to more precisely estimate lek locations. If we could not estimate a lek location from the survey data or if the survey data indicated the lek was at the center of the section, we placed the lek location in the center of the section (4% of recorded leks). In addition, to reduce error due to drift of lek locations between years, we created a 250-m buffer around lek locations (Hovick et al. 2015). If a lek location with high fidelity was not recorded in a particular year, we examined the distance to the nearest lek the following year. If the 250-m buffers of the 2 leks overlapped, we combined lek locations based on the assumption that the same group of birds used both leks between years.

We then derived population metrics at survey-block and lek scales. For these metrics, we considered a lek to be >1 displaying male at the survey location for ≥1 of the years surveyed (Schroeder and Braun 1993, Merrill et al. 1999). At the lek scale we considered the number of males/lek as the dependent variable. At the survey-block scale we used the number of leks/km^2 in each of the 17 survey blocks as the dependent variable. The metrics of males/lek and leks/km^2 have been used previously as indices of greater prairie-chicken population size and habitat quality (Hamerstrom and Hamerstrom 1973, Niemuth 2011).

Land-Cover Data

We obtained shapefiles of CRP enrollments and corresponding conservation practice codes within survey blocks from the Farm Service Agency for 1997, 2006–2011, and 2013–2016. Shapefiles had data missing from 2004, 2005, and 2012 and for some locations in 2 counties (Polk and Otter Tail counties). We reconstructed missing enrollment shapefiles for those years in ArcGIS by examining enrollment expiration dates provided in the available shapefiles and aerial photography. We also analyzed enrollment inconsistencies (e.g., different expiration dates recorded or a break in the enrollment data but consistent aerial photography coverage) in years with provided shapefiles and reconstructed these inconsistences, as necessary. After reconstruction, we analyzed approximately 1,100 CRP enrollments totaling approximately 15,000 ha from 2004–2016. During June–August 2016, we visited and verified mapped areas of CRP enrollment reconstruction within survey blocks to ensure that land-cover data were correct. Because the shapefiles obtained from the Farm Service Agency included all CRP practice codes within survey blocks, we distinguished the CRP practice codes that provide grassland cover types used by greater prairie-chickens (Table S1, available online in Supporting Information) using classification categories of Nielson et al. (2008) and Drum et al. (2015).

Because CRP grassland is not the only land-cover type that provides suitable greater prairie-chicken breeding-season habitat in northwestern Minnesota, we also identified and quantified non-CRP grassland cover within the study area during 2004–2016. To delineate other cover types, we examined infrared imagery, light detection and ranging (LiDAR) data layers, the Minnesota Land Cover Classification (MLCC) and Impervious Surface Area by Landsat and LiDAR (2013 update), the NASS Cropscape Cropland Data Layer (CDL) and National Land Cover Database (NLCD) land cover in ArcGIS, and histories of state-, federal-, and TNC-managed areas within the study area. The MLCC layer is a raster-based land-cover data set for the state of Minnesota with 15-m accuracy (University of Minnesota 2013). The CDL land-cover data layer is a raster-based, georeferenced, crop-specific land-cover data layer with 30-m accuracy. The source of the CDL non-agricultural land-cover classes relies on the most recently released NLCD for that year (i.e., 2001, 2006, or 2011; USDA-NASS 2016).

To determine the best land-cover classification to use for each year of our study period, we compared the accuracy of each land-cover data layer at classifying known areas of grassland (e.g., grassland CRP enrollments or state-, federal-, and TNC-managed areas) by placing 200 random points within known areas of grassland and extracting the land-cover value at those points. We reclassified the land-cover data layers in each of the 17 survey blocks for each of the 13 years of our study period into 7 vegetation classes with 30-m accuracy (Table S1, available online in Supporting Information). We also classified grassland and wetland cover types into 3 more-specific management categories: CRP; permanently conservation-focused (state-, federal-, and TNC-managed areas); and other open cover types (i.e., grassland and wetland that did not fall into the other 2 categories).

We divided grassland and wetland cover types into more-specific management categories for analysis based on the management goals published for each category. Although the protection and restoration of wildlife habitat is a stated objective of the CRP and state-, federal-, and TNC-managed areas (Minnesota Prairie Plan Working Group 2011, MNDNR 2016, USDA 2017), CRP grasslands and open cover types managed specifically for wildlife are subject to different management regimes. For example, landowners enrolled in the CRP are only required to conduct management actions (e.g., disk, spray, burn, interseed) to increase plant community species and structural diversity once throughout the duration of a 10- or 15-year enrollment (USDA 2017), whereas managers of state, federal, and TNC areas have the goal to introduce disturbance as part of their management at least every 4 years (Minnesota Prairie Plan Working Group 2011). Conversely, upon examination of aerial photography, grassland areas on the landscape that did not fall into the 2 previously identified management categories included mostly agricultural grasslands such as pasture and hayfields. Although pasture and hayfields serve as a source of grassland or wetland on the landscape, they are managed for agricultural purposes. In addition to using these management categories for analysis, we also considered all grassland and wetland types on the landscape pooled into a single category.

We verified our reclassification of CRP, permanently conservation-focused grassland and wetland, and other known natural cover types (i.e., forest, shrubland, and open water) by visiting 500 random points in the 17 survey blocks during June–August 2016. We placed 200 points randomly, stratified by CRP practice code (e.g., CP 1, Establishment of Permanent Introduced Grasses and Legumes) and then placed the remaining 300 points by including ≥50 random points in each cover type placed within a 50-m buffer of a road in ArcGIS (Nelson 2010, Nelson and Andersen 2013). We then located and identified the cover type at each random point ≤50 m perpendicular distance from the road with the aid of a laser rangefinder (Nelson 2010, Nelson and Andersen 2013). Based on these points, we calculated overall accuracy, user's accuracy, and producer's accuracy of our cover-type classification. Overall accuracy represents percentage of correctly classified points from all random points surveyed. User's accuracy assesses the commission error, or the probability of classifying a point in a category when it does not belong in that land-cover category. Producer's accuracy assesses the omission error or the probability of excluding a point from the classification to which it belongs. We did not evaluate classification accuracy for remaining cover classes (i.e., cropland, developed and barren land) because these land-cover types did not occur within the reclassification of CRP and permanently conservation-focused areas, except that we confirmed the rare food plots in permanently conservation-focused areas by communicating with the managers of these properties. We calculated the accuracy of our reclassification of CRP and other cover types within permanently conservation-focused areas by using error matrices and the Kappa statistic (Congalton and Green 1999). Because the 2016 CDL layer was released in January 2017 and we collected ground-truth data during June–August 2016, we used ground-truth data collected from a map created with the 2015 CDL layer.

Following cover-type reclassification, we used the spatial pattern analysis program FRAGSTATS (McGarigal et al. 2012) to calculate landscape metrics potentially related to abundance indices of greater prairie-chickens at both the survey-block and lek scales. Based on habitat–greater prairie-chicken relations from previous studies (Merrill et al. 1999, Niemuth 2000) and published information concerning greater prairie-chicken ecology (Stempel and Rodgers 1961, Niemuth 2011), we considered composition, contiguity, and fragmentation metrics (Table 1) of each land-cover class for each survey block or lek buffer.

Composition metrics included the area (ha) of each land-cover type in each survey block and the percent landscape of each land-cover type in each lek buffer (Table 1) derived using FRAGSTATS (McGarigal et al. 2012). We also considered logarithmic and quadratic transformations of the area of grassland to allow for a non-linear response of greater prairie-chicken population indices to amount of grassland at the survey-block or lek scale (Larson and Bailey 2007, Niemuth 2011). We calculated the ratio of cropland to grassland at both scales to allow for a relationship where greater prairie-chickens may tolerate and benefit from some amount of conversion to cropland (similar to providing food plots), but then decline when the abundance of cropland far exceeds that of grassland (Stempel and Rodgers 1961).

We measured contiguity with the contiguity index, which represents the size and connectivity of patches of a given land-cover type on a scale of 0 to 1. Large, contiguous patches result in contiguity index values closer to 1. We used the area-weighted mean of these patches of the same land-cover type at each scale to calculate the contiguity index for each land-cover type (McGarigal et al. 2012). We only considered the contiguity of land-cover types that were positively associated with greater prairie-chicken abundance indices (i.e., wetland and grassland cover types, based on assessment of models only including composition covariates).

We measured fragmentation using number of patches, which sums the number of patches of a given land-cover type at the survey-block or lek scale. An increased number of patches represents an increase of fragmentation of a given land-cover type. We only considered the effect of fragmentation on land-cover types that were positively associated with greater prairie-chicken abundance indices (i.e., wetland and grassland-cover types, based on assessment of models only including composition covariates).

Data Analysis

We assessed models relating greater prairie-chicken population metrics (i.e., leks/km^2 and males/lek) to landscape metrics using a layered approach in an information-theoretic framework (Burnham and Anderson 2002) based on Akaike's Information Criterion (AIC; Akaike 1973). Using package lme4 (Bates et al. 2015) in software package R (R Core Team 2013), we created multiple *a priori* models of greater prairie-chicken metrics for each of 3 levels (composition, contiguity, and fragmentation; Table 1) and scale (survey-block and lek). We included covariates in models based on findings of previous studies and knowledge of greater prairie-chicken ecology. We evaluated the same set of mixed-effect models for the survey-block and lek scales but used leks/km^2 as the response variable for the survey-block scale and the log transformation of males/lek as the response variables at the lek scale. We derived values of composition, contiguity, and fragmentation covariates for each year during 2004–2016 and considered these to be fixed (Table 1). We considered each survey block (or lek, depending on analysis) and year as random effects in models because these are not the effects of primary interest and to account for repeated measurements of the same survey blocks and leks.

We first evaluated models with covariates related to cover-type composition and identified the best-supported model (lowest AIC value) of greater prairie-chicken population metrics. We then used this model as the base model to assess covariates related to cover-type contiguity to again identify the best-supported model of greater prairie-chicken

Table 1. Land-cover covariates at each level (composition, contiguity, fragmentation) of model development of greater prairie-chicken (GRPC) abundance (leks/km^2 and males/lek) in northwestern Minnesota, USA, during 2004–2016, their hypothesized relationship with GRPC population indices, and literature basis for the prediction.

Land cover categories	Hypothesized relationship to GRPC density	Literature basis
Composition: area within each survey block or percent area within the lek buffer		
Grassland Conservation Reserve Program (CRP)	+	Merrill et al. (1999), Niemuth (2003)
Conservation-focused (i.e., state, federal, The Nature Conservancy [TNC]) grassland	+	Niemuth (2000, 2003), Hovick et al. (2015)
Other grassland (e.g., hay and pasture)	−	Niemuth (2003)
Wetland CRP	+	Merrill et al. (1999)
Conservation-focused (i.e., state, federal, TNC) wetland	+	Niemuth (2000, 2003)
Other wetland (e.g., wet areas in pasture or hay fields)	+	Niemuth (2000, 2003)
Forest	−	Merrill et al. (1999), Niemuth (2000), Hovick et al. (2015)
Developed	−	Merrill et al. (1999), Larson and Bailey (2007), Hovick et al. (2015)
Shrubland	+	Niemuth (2000)
Cropland	−	Niemuth (2000)
Open water	−	Non-habitat
All types of grassland	+	Niemuth (2000, 2003, 2011), Larson and Bailey (2007), Hovick et al. (2015)
All types of wetland	+	Niemuth (2000, 2003)
Ratio of area of cropland to area of all types of grassland within each survey block or lek buffer	quadratic	Stempel and Rodgers (1961)
Contiguity: contiguity index within each survey block or lek buffer		
All types of grassland	+	Niemuth (2011)
All types of wetland	+	Niemuth (2011)
Grassland CRP	+	Niemuth (2011)
Wetland CRP	+	Niemuth (2011)
Conservation-focused (i.e., state, federal, TNC) grassland	+	Niemuth (2011)
Conservation-focused (i.e., state, federal, TNC) wetland	+	Niemuth (2011)
Other grassland (i.e., not CRP or state, federal TNC managed grassland)	−	Niemuth (2011)
Other wetland (i.e., not CRP or state, federal TNC managed wetland)	+	Niemuth (2011)
Fragmentation: number of patches within each survey block or lek buffer		
All types of grassland	+	Niemuth (2003)
All types of wetland	+	Niemuth (2003)
Grassland CRP	+	Niemuth (2003)
Wetland CRP	+	Niemuth (2003)

population metrics that included both composition and contiguity. We repeated this process using the best-supported model that considered composition and contiguity covariates as the base model to evaluate fragmentation covariates, in a layered process similar to that used by Amundson and Arnold (2010) and Daly et al. (2015). We considered composition, contiguity, and fragmentation metrics in that order based on published information regarding greater prairie-chicken ecology and results of previous studies of greater prairie-chicken–habitat relations (Table 1). At each step in our model-selection process, we evaluated support for covariates in competing models ($\Delta AIC \leq 2$) based on peak frequency by summing the Akaike weights for each model in which that covariate occurred (Symonds and Moussalli 2010) in addition to evaluating the direction and magnitude of parameter estimates; however, in all cases we proceeded to the next step using only the best-supported model. We used *k*-fold cross validation ($k = 5$, iterations = 100) and the normalized root-mean-square error (NRMSE) of the best-supported models at the survey-block and lek scales to assess model accuracy (Refaeilzadeh et al. 2009). The NRMSE is a measure of the difference between the predicted and observed values after *k*-fold cross validation. The *a priori* suite of models included 1 base model (random effects only), 11 composition models, 7 contiguity models, and 4 fragmentation models (Table 1). Finally, we evaluated the predicted relationships from our best-supported models of lek density and leks/km^2 and increasing amounts of CRP on the landscape using bootstrapping ($n = 10,000$ iterations), holding covariates other than CRP at their average values, to illustrate the potential influence of adding CRP grassland to northwestern Minnesota landscapes.

RESULTS

At the survey-block scale, lek density ranged from 0.02 leks/km^2 to 0.32 leks/km^2. At 311 leks, the number of males per lek ranged from 2 to 67. We classified land cover at 481 of 500 points (19 points were unusable because they were not within a 50-m buffer of a road after creation of a new land-cover map for 2016 after release of the 2016 CDL layer in Jan 2017). Overall accuracy of known grassland cover types in 2016 was 74% (Kappa-statistic = 0.64; Table S2, available online in Supporting Information). The user's accuracy of classification of the 5 land-cover types we assessed ranged from 50% (shrubland) to 84% (grassland). The producer's accuracy of classification of these 5 land-cover types ranged from 47% (forest) to 87% (wetland and open water).

Survey-Block-Scale Model

The best-supported composition model of leks/km^2 ($n = 17$ blocks surveyed each year from 2004 through 2016) at the survey-block scale included area of CRP grassland, permanently conservation-focused grasslands, CRP wetland, permanently conservation-focused wetlands, and other wetlands (Table 2). Although there were competing models ($\Delta AIC \leq 2$) at each step in our model-selection process, competing models did not suggest substantively different relationships than indicated in the best-supported models. Covariates in competing models that were excluded in the best-supported model at each level included the area of other grassland at the composition level and the contiguity of all wetlands at the contiguity level (Table 2). Two models at the contiguity level had a lower AIC than the best-supported (base) model from the composition level (Table 2); the best-supported model included grassland contiguity. Two models at the fragmentation level had a lower AIC than the best-supported model from the contiguity level (Table 2); the best-supported model included the number of grassland patches and the number of wetland patches.

All covariates included in the best-supported model had a positive association with the number of leks/km^2 except the area of other wetlands and number of grassland patches (Table 3). Based on k-fold validation, this best-supported model had an average NRMSE of 13.15% (SD = 0.27%) and predicted lek density had a strong, positive relationship with the amount of CRP grassland (Fig. 2A).

Lek-Scale Model

At the lek scale (log[males/lek]; $n = 311$ leks that were tallied 1–13 times), the best-supported model among those considered with only composition covariates included the percent area of CRP grassland, permanently

Table 2. Number of parameters (K), difference from Akaike's Information Criterion of the best-supported model (ΔAIC), model weight (w), and deviance (d) for models of greater prairie-chicken lek density at the survey-block scale (leks/km^2) in northwestern Minnesota, USA, during 2004–2016. We then used the top-ranked composition model as the base model to assess covariates related to cover-type contiguity. We repeated this process using the best-supported model that considered composition and contiguity covariates as the base model to evaluate fragmentation covariates. The column ΔAIC compares models at each level of model development, whereas ΔAIC^i compares models to the best-supported model of the previous level; negative values indicate a decrease in AIC. All models included random effects of survey block and year.

Model[a]	K	ΔAIC	ΔAIC^i	w	d
Composition					
CRP grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland	9	0.00		0.4	−798.7
CRP grassland + other grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland +	10	0.38		0.39	−800.3
CRP grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland + forest + developed + shrub	12	2.35		0.14	−802.3
Cropland + developed land + forest + open water + shrub + grassland + wetland	11	22.24		0.00	−780.4
Wetland + grassland	6	23.17		0.00	−769.5
Grassland	5	23.56		0.00	−767.1
CRP grassland + conservation-focused grassland + other grassland	7	25.44		0.00	−769.2
Logarithmic transformation of grassland	5	27.52		0.00	−763.9
Quadratic transformation of grassland	8	27.64		0.00	−769.0
Wetland	5	33.79		0.00	−756.9
Ratio of cropland to grassland	5	37.13		0.00	−753.5
Only random effects	4	36.76		0.00	−751.9
Composition and Contiguity					
Comp[b] + all grassland contiguity	10	0.00	−2.54	0.47	−803.2
Comp + all grassland contiguity + all wetland contiguity	11	1.04	−1.50	0.28	−804.2
Comp + CRP grassland contiguity	10	2.92	0.38	0.11	−800.6
Comp + CRP wetland contiguity	10	3.98	1.44	0.06	−799.2
Comp + CRP grassland contiguity + CRP wetland contiguity	11	4.58	2.05	0.05	−800.6
Comp + other grassland contiguity + conservation-focused grassland contiguity + CRP grassland contiguity	12	5.20	2.66	0.03	−802.0
Comp + other grassland contiguity + conservation-focused grassland contiguity + CRP grassland contiguity + other wetland contiguity + conservation-focused wetland contiguity + CRP wetland contiguity	15	8.81	6.28	0.01	−804.4
Composition, Contiguity, and Fragmentation					
Contig[c] + number of all wetlands + number of all grasslands	12	0.00	−2.66	0.56	−809.9
Contig + number of all grasslands	11	1.16	−1.50	0.31	−806.7
Contig + number of CRP grasslands	11	3.66	1.00	0.09	−804.2
Contig + number of CRP grasslands + number of CRP wetlands	12	5.24	2.58	0.04	−804.6

[a] CRP = Conservation Reserve Program, conservation-focused = land managed by state or federal agencies or The Nature Conservancy, other = not CRP and not conservation-focused.

[b] Comp = covariates in the top-ranked composition model (CRP grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland).

[c] Contig = covariates in the top-ranked contiguity model (CRP grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland + contiguity of all grassland).

Table 3. Parameter estimates for best-supported models of greater prairie-chicken abundance in northwestern Minnesota, USA, 2004–2016, at each scale of analysis and each layer of model building with their associated standard errors, and *P*-value of the test of whether 95% confidence intervals around those estimates include zero.

Model level	Parameter	Estimate of coefficient	SE	*P*
Survey block composition				
	Area Conservation Reserve Program (CRP) grassland	5.50E-05	1.28E-05	≤0.001
	Area conservation-focused grassland	7.54E-05	1.92E-05	≤0.001
	Area CRP wetland	9.87E-05	2.27E-05	≤0.001
	Area conservation-focused wetland	5.23E-05	1.94E-05	0.013
	Area other wetland	−4.25E-05	1.53E-05	0.006
Survey block contiguity				
	Area CRP grassland	4.67E-05	1.33E-05	≤0.001
	Area conservation-focused grassland	7.00E-05	1.86E-05	≤0.001
	Area CRP wetland	1.18E-04	2.39E-05	≤0.001
	Area conservation-focused wetland	5.75E-05	1.88E-05	0.005
	Area other wetland	−2.87E-05	1.61E-05	0.077
	Contiguity of all grassland	1.16E-02	1.16E-02	0.040
Survey block fragmentation				
	Area CRP grassland	4.95E-05	1.33E-05	≤0.001
	Area conservation-focused grassland	6.24E-05	1.91E-05	0.002
	Area CRP wetland	1.41E-04	2.49E-05	≤0.001
	Area conservation-focused wetland	7.57E-05	2.03E-05	≤0.001
	Area other wetland	−1.66E-05	1.67E-05	0.322
	Contiguity of all grassland	6.44E-03	5.90E-03	0.276
	Number of all wetlands	4.18E-05	2.38E-05	0.081
	Number of all grasslands	−9.42E-05	3.69E-05	0.012
Lek composition				
	Percent CRP grassland	2.22E-02	1.32E-02	0.092
	Percent conservation-focused grassland	3.66E-02	1.32E-02	0.006
	Percent CRP wetland	1.89E-02	1.06E-02	0.074
	Percent conservation-focused wetland	3.99E-03	1.37E-02	0.771
	Percent other wetland	−1.19E-02	1.22E-02	0.331
	Percent forest	−1.79E-02	1.40E-02	0.204
	Percent developed area	−3.46E-02	1.46E-02	0.018
	Percent shrub	7.21E-03	1.20E-02	0.547
Lek contiguity				
	Percent CRP grassland	1.16E-02	1.40E-02	0.405
	Percent conservation-focused grassland	3.21E-02	1.34E-02	0.017
	Percent CRP wetland	2.13E-02	1.06E-02	0.044
	Percent conservation-focused wetland	9.05E-03	1.39E-02	0.515
	Percent other wetland	−5.66E-03	1.25E-02	0.651
	Percent forest	−1.94E-02	1.40E-02	0.167
	Percent developed area	−3.25E-02	1.46E-02	0.026
	Percent shrub	4.36E-03	1.20E-02	0.716
	Contiguity CRP grassland	3.14E-02	1.37E-02	0.022

conservation-focused grasslands, CRP wetland, permanently conservation-focused wetlands, other wetlands, forest, developed land, and shrubland (Table 4). Covariates in competing models that were excluded in the best-supported model at each level included the contiguity of other grasslands, permanently conservation-focused grasslands, and CRP wetlands at the contiguity level, and the number of grassland, wetland, and CRP wetland patches at the fragmentation level (Table 4). Three models at the contiguity level had a lower AIC than the best-supported model from the composition level (Table 4). The best-supported model at the contiguity level included the contiguity of CRP grassland. No models at the fragmentation level had a lower AIC value than the best-supported model from the contiguity level (Table 4).

All covariates included in the best-supported model had a positive association with the number of males/lek except the percent of other wetlands, the percent of forest, and the percent of developed area (Table 3). This model had an average NRMSE of 17.38% (SD = 0.11%) and the predicted number of males/lek had a small, positive relationship with the amount of CRP grassland (Fig. 2B), although there was considerable uncertainty associated with the predicted number of males/lek.

DISCUSSION

The CRP and other land-conservation programs that commonly occur within an agriculture-dominated landscape have the potential to influence greater prairie-chicken abundance by influencing the amount and configuration of grassland (Merrill et al. 1999, Niemuth 2003). Our models indicated that higher lek density and a higher number of males per lek were related to the amount and configuration of CRP enrollments in the agricultural landscape of northwestern Minnesota. At the landscape scale, increasing the amount of CRP grassland in 41-km^2 survey blocks by 1 km^2 (2.4%) resulted in a corresponding increase of 6% in lek density (Fig. 2A). At the individual lek scale, increasing the amount of CRP grassland in the 2-km breeding-cycle habitat radius around a lek by 25% (3 km^2) corresponded to

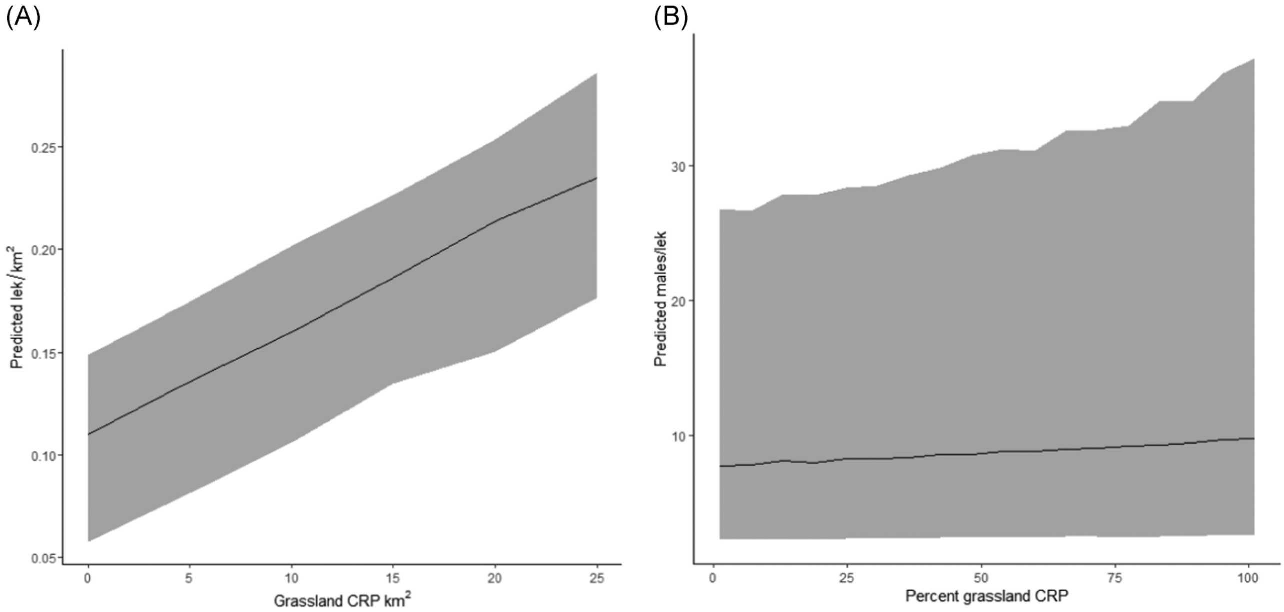

Figure 2. Predicted relationships between Conservation Reserve Program (CRP) grassland and greater prairie-chicken abundance in northwestern Minnesota, USA, 2004–2016, based on the best-supported models at the survey block and lek scales. All other covariates were held at their average values. Shaded error bands (95% CIs) are derived from bootstrapping (number of simulations = 10,000).

a 5% increase in males per lek (Fig. 2B). Therefore, increasing the quantity of grassland, specifically aggregating CRP grassland enrollments in areas of known lek locations, may increase greater prairie-chicken abundance, at least in landscapes comparable to those we assessed in northwestern Minnesota. Additionally, our results suggest that CRP grassland and wetland play an important role in contributing to contiguity and reducing fragmentation of grassland and wetland cover types at a larger landscape scale.

Survey-Block-Scale Model

At the survey-block scale, greater prairie-chicken lek density was related to the composition, contiguity, and fragmentation of land-cover types, particularly the amount and distribution of grassland and wetland cover types. The importance of the amount of grassland cover for predicting lek density is consistent with the majority of existing literature (Niemuth 2000, 2003, 2011; Larson and Bailey 2007; Hovick et al. 2015); the amount of grassland cover is typically thought of as the resource limiting greater prairie-chicken abundance. Although not generally thought of as high-quality habitat for greater prairie-chickens, our findings and several other studies (Niemuth 2000, 2003) indicate that the amount of wetland cover, specifically CRP wetland, may also be an important component of prairie-chicken habitat, at least in the landscapes of northwestern Minnesota we studied.

At the composition level, the amount of grassland and wetland cover types in different management categories (i.e., CRP, conservation-focused, and other) were important predictors of greater prairie-chicken lek density, likely because these different management categories varied in their continuity of management through the study period. For example, based on information published in management guidelines, after state-, federal-, and TNC-managed areas are established, management goals are consistently focused on wildlife habitat in perpetuity (Minnesota Prairie Plan Working Group 2011, MNDNR 2016). In contrast, although CRP grassland and wetland areas may be established and undergo mid-enrollment management with the goal of meeting wildlife habitat objectives, they can then be converted to cropland when enrollments expire after 10–15 years (USDA 2017); therefore, CRP lands are more temporary feature on the landscape than areas managed with a permanent conservation focus. Furthermore, other grasslands and wetlands (i.e., pastures and hayfields) are not necessarily managed with wildlife conservation as a priority. Because we did not measure vegetation in each of the 3 management categories (i.e., CRP, conservation-focused, and other), we are limited to assuming that management and the resulting vegetation followed published guidelines or common practices (Minnesota Prairie Plan Working Group 2011, MNDNR 2016, USDA 2017).

The relationships between the area in these management categories and greater prairie-chicken lek density were all positive with the exception of other wetlands (Table 3). We did not expect the amount of other wetland to have a negative relationship with lek density because we presumed that all the grassland and wetland management categories provided suitable herbaceous cover for greater prairie-chickens. However, based on examination of aerial photography, the other wetland type was comprised primarily of wet areas within pastures and hayfields. The type and timing of agricultural practices in pastures and hayfields may have an adverse effect on greater prairie-chicken lek density (Niemuth 2003, USDA 2008), and these areas are not generally managed with providing wildlife habitat as a

Table 4. Number of parameters (*K*), difference from Akaike's Information Criterion of the best-supported model (ΔAIC), model weights (*w*), deviance (*d*), and model comparisons for composition, contiguity, and fragmentation model levels of the number of greater prairie-chickens at leks in northwestern Minnesota, USA, 2004–2016. The column ΔAIC compares models at each level of model development, whereas ΔAIC[i] compares models to the best-supported model of the previous level; negative values indicate a decrease in AIC.

Model[a]	*K*	ΔAIC	ΔAIC[i]	*w*	*d*
Composition					
CRP grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland + forest + developed + shrub	12	0.00		0.43	230.7
CRP grassland + conservation-focused grassland + CRP wetland + other wetland + conservation-focused wetland	9	1.59		0.19	238.2
CRP grassland + other grassland + conservation-focused grassland + CRP wetland + other wetland + conservation-focused wetland	10	3.11		0.09	237.8
Logarithmic transformation of grassland	5	3.69		0.07	248.3
CRP grassland + conservation-focused grassland + other grassland	7	3.83		0.06	244.5
Cropland + developed land + forest + open water + shrub + grassland + wetland	11	4.30		0.05	237.0
Quadratic transformation of grassland	8	4.65		0.04	243.3
Grassland	5	5.21		0.03	249.9
Wetland + grassland	6	6.21		0.02	248.9
Only random effects	4	8.48		0.01	255.1
Wetland	5	10.14		0.00	254.8
Ratio of cropland to grassland	5	10.48		0.00	255.1
Composition and Contiguity					
Comp[b] + CRP grassland contiguity	13	0.00	−3.36	0.47	225.3
Comp + other grassland contiguity + conservation-focused grassland contiguity + CRP grassland contiguity	15	0.41	−2.95	0.28	221.7
Comp + CRP grassland contiguity + CRP wetland contiguity	14	1.96	−1.40	0.11	225.3
Comp + all grassland contiguity	13	5.02	1.66	0.06	230.3
Comp + CRP wetland contiguity	13	5.35	1.99	0.05	230.6
Comp + all grassland contiguity + all wetland contiguity	14	6.01	2.64	0.03	229.3
Comp + other wetland contiguity + conservation-focused wetland contiguity + CRP wetland contiguity	15	9.31	5.94	0.01	230.6
Composition, Contiguity, and Fragmentation					
Contig[c] + number of CRP grasslands	14	0.00	1.80	0.36	225.1
Contig + number of all grasslands	14	0.16	1.97	0.31	225.3
Contig + number of CRP grasslands + number of CRP wetlands	15	1.70	3.51	0.15	224.8
Contig + number of all grasslands + number of all wetlands	15	1.72	3.52	0.15	224.8

[a] CRP = Conservation Reserve Program, conservation-focused = land managed by state or federal agencies or The Nature Conservancy, other = not CRP and not conservation-focused.
[b] Comp = covariates in the top-ranked composition model (CRP grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland + forest + developed + shrub).
[c] Contig = covariates in the top-ranked contiguity model (CRP grassland + conservation-focused grassland + CRP wetland + conservation-focused wetland + other wetland + forest + developed + shrub + CRP grassland contiguity).

consideration. Although greater prairie-chickens are grassland-obligate birds, these herbaceous cover types may not meet the habitat needs of greater prairie-chickens and may serve as sink habitat on the landscape (Niemuth 2003). For example, herbaceous cover in agricultural fields may be subjected to intensive grazing or removed by haying multiple times throughout the year, whereas CRP enrollments and properties managed with a long-term conservation focus have restrictions preventing the removal of cover during the nesting period (USDA 2008).

Contiguity and fragmentation of suitable herbaceous cover types (i.e., grasslands and wetlands) were related to prairie-chicken lek density, but the continuity of management goals of grasslands and wetlands was not as important as for composition. Greater prairie-chickens are thought to be area-sensitive in that they require large patches of habitat (Niemuth 2003, 2011), and federal properties tended to be larger than other land ownerships within specific survey blocks. However, the relationship of area of other wetland to lek density was negative, and the relationship of lek density to fragmentation or number of patches of wetland was positive. Multiple explanations may exist for these relationships. First, more xeric areas within herbaceous wetlands may act as a supplementary source of suitable cover for roosting, whereas grasslands are acting as the primary source during other parts of the life cycle (Svedarsky 1979). Second, considerable ambiguity exists in distinguishing between grasslands and wetlands via remote sensing; 85% of the 47 misclassified wetland points in our study were grassland and 77% of the 20 misclassified grassland points were wetland (Table S2, available online in Supporting Information). The error caused by misclassification may exaggerate the extent of wetland fragmentation by creating a patchier herbaceous-land-cover matrix than what was present on the landscape. Because of this tendency to confound wetlands and grasslands in our cover-type classification, the apparent positive relationship between lek density and fragmentation may be spurious. Finally, these observed relationships may also be due to the type or size of wetland cover. Different types of wetlands (e.g., seasonally flooded wetland, wet meadows, marshes, swamps, bogs) have different vegetation characteristics, amounts of water throughout the year, and in turn, differing contiguity. Additionally, these characteristics also make some wetlands more suitable for greater prairie-chickens than others. Small wetlands with shallow water may be classified as less contiguous than large open-water wetlands but are likely more suitable for greater prairie-chickens.

Lek-Scale Model

At the lek scale, males/lek was related to composition and contiguity but not fragmentation of grassland and wetland cover types surrounding leks. The amount of habitat (i.e., grassland and wetland cover types) is also associated with lek-scale abundance of greater prairie-chickens (Niemuth 2000, 2003, 2011; Larson and Bailey 2007; Hovick et al. 2015).

The relationships between grassland and wetland area in our lek-scale model were the same as at the survey-block scale; at both scales, different management goals of grassland and wetland cover are related to the abundance of greater prairie-chickens. At the survey-block and lek scales, greater amounts of grassland and wetland CRP and areas managed with a long-term conservation focus were positively related to abundance of greater prairie-chickens. This result is similar to the conclusions of Merrill et al. (1999) that leks were in areas with more CRP than randomly selected non-lek locations. Additionally, at the survey-block and lek scales, categories of grassland not managed for conservation goals were not important predictors of lek abundance and non-CRP grassland was not positively related to abundance of greater prairie-chickens. Our findings regarding the relationship between males/lek and forest, developed areas, and shrublands are consistent with other studies (Table 1) and what are thought to be key ecological needs of greater prairie-chickens.

Although not included as a covariate in the best-supported model of the number of males at leks, the relationship between the contiguity of all grasslands and males/lek was positive ($\beta = 1.99\text{E-}02$, SE = 1.13E-03, $P = 0.591$), which is consistent with the well-accepted idea that greater prairie-chickens are area sensitive, or that they require large aggregations of appropriate cover types that together provide habitat (Niemuth 2003, 2011). However, the relationship between the contiguity of CRP wetland and the number of males at leks was negative in our assessment ($\beta = -2.57\text{E-}03$, SE = 3.43E-03, $P = 0.454$), with higher numbers of males associated with less-connected CRP wetland surrounding leks. This negative relationship is likely because herbaceous wetlands serve as supplementary and not primary habitat for greater prairie-chickens, and they occur as smaller, less-connected patches within the herbaceous land-cover matrix of northwestern Minnesota. The best-supported model of males/lek included only the contiguity of CRP grassland, indicating that aggregating CRP grassland enrollments in areas of known lek locations may increase greater prairie-chicken abundance. This finding highlights the importance of protecting existing and establishing new contiguous CRP grassland enrollments in areas immediately surrounding known lek locations to maintain or increase the number of males/lek.

MANAGEMENT IMPLICATIONS

Our research provides new insight into the importance of management goals with specific wildlife objectives at the survey-block and lek scales for greater prairie-chickens. Management efforts that focus on enrolling contiguous grassland CRP enrollments at the lek scale around known lek locations are likely to increase greater prairie-chicken lek density and the number of males at leks. Also at the lek scale, management efforts that protect the areas surrounding known lek locations from encroachment of forested and developed areas are likely to increase or maintain the number of males at individual leks. Additionally, because models of lek density and the number of males at leks had a relatively low NRMSE, they would be suitable for predicting the effects of potential land-cover changes to greater prairie-chicken populations within our study area and perhaps in comparable landscapes, which may be a useful tool to help inform management decisions.

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SUPPORTING INFORMATION

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