WILDLIFE SURVEY REPORT

Prairie grouse occurrence models for South Dakota

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Prairie grouse occurrence models for South Dakota

ABSTRACT

Loss and fragmentation of required grassland habitat has reduced the distribution and abundance of prairie grouse throughout their range. The primary cause of this decline in the Great Plains is conversion of grassland to other uses, mostly cropland. Spatial models are a useful tool for understanding the spatially-explicit habitat relationships that influence species occurrence or abundance. We developed statewide spatially-explicit habitat-based breeding season occurrence models for sharp-tailed grouse, greater prairie-chickens, and for prairie grouse in general. We determined presence or absence of prairie grouse leks on 421, 1.6 by 1.6 km survey units from 2014–2016. We found 43 sharp-tailed grouse leks, 23 greater prairie chicken leks, and 4 mixed leks. Habitat variables based primarily on National Land Cover Database (NLCD) and from manually digitized land covers were used as covariates to develop occurrence models. Because our presence/absence data were drawn from random samples, we used logistic regression to model the conditional probability of occurrence. Percent grass was a positive predictor for all 3 models. Percent of landscape in woody and developed areas were strong negative predictors for occurrence of prairie-chickens. Percent of landscape in developed was also a negative predictor for sharp-tailed grouse. We found some evidence of increased occurrence in less fragmented landscapes for both species. The models based on digitized habitat variables had better performance than NLCD-based models. Predictive occurrence GIS layers have been developed for sharp-tailed grouse, greater prairie-chicken, and prairie grouse, which should serve as a tool to prioritize conservation efforts.

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INTRODUCTION

Loss and fragmentation of required grassland habitat has reduced the distribution and abundance of prairie grouse throughout their range. Specifically, the greater prairie-chicken (*Tympanuchus cupido*, hereafter prairie-chicken) was once found in portions of 17 U.S. states and 4 Canadian provinces, but now only occurs in 11 states (Ross et al. 2006). Sharp-tailed grouse (*T. phasianellus*) were originally found in 21 states and 8 provinces, but have been extirpated from 8 states and some existing populations are isolated (Connelly et al. 1998).

In South Dakota, prairie-chickens historically occurred in far eastern and southeastern portions of the state where tallgrass prairies once dominated the landscape. However, their range exploded north and west well into Canada as settlers converted some grassland to cropland in the late 1800s (Johnsgard and Wood 1968). Prairie-chickens were thought to benefit from winter food provided by crops which allowed them to expand their range (reviewed in Flake et al. 2010). As more grassland was converted to cropland and cattle grazing reduced grass height, their range in South Dakota quickly constricted to their current stronghold in central portions of the state. The prairie-chicken range is thought to be limited by winter food and grass height to the west and climate to the north. Sharp-tailed grouse were common throughout most of South Dakota prior to European settlement. They are now most common in central and western South Dakota where large blocks of contiguous grasslands remain (reviewed in Flake et al. 2010).

Grassland habitat loss remains a concern for prairie grouse populations in South Dakota. During the 15-year period of 1982–1997, 736,528 ha of grassland were converted to cropland in the state (U.S. GAO 2007). A more recent study found 744,622 ha of grassland were lost, primarily to conversion to cropland, from 2006–2012 (Reitsma et al. 2014). Wright and Wimberly (2013) estimated 182,109 ha of grassland were converted to corn or soybeans between 2006 and 2011. Grassland to cropland conversion continues at a rate of approximately 20,000 ha per year (Stubbs 2007) and the rate of conversion appears to be accelerating (Rashford et al. 2011). Using these statistics, it is reasonable to estimate that since the early 1980s SD has lost an estimated 1.82 million ha of grassland to cropland conversion. Much of the recent conversions are occurring within the Missouri Coteau (Stubbs 2007, Stephens et al. 2008) which also represents the eastern fringe of the prairie grouse range in SD. This region contains vast grasslands that are vulnerable to future conversion (Stephens et al. 2008, Rashford et al. 2011).

Landscape level habitat loss is particularly concerning for prairie grouse because they require large blocks of habitat to persist (Ammann 1957, Niemuth 2000, Woodward et al. 2001). Lek persistence, density and reproductive success are all correlated with the amount of suitable habitat (Ryan et al. 1998, Merrill et al. 1999, Fuhlendorf et al. 2002, Niemuth 2005, Aldridge et al. 2008, Gregory et al. 2011). Because prairie grouse occurrence and demographic performance are sensitive to landscape conditions, an opportunity exists to utilize spatial modeling as a means of predicting habitat conditions across broad areas. Spatially explicit models specify relationships between landscape characteristics and species in a way that is useful in conservation applications. This concept has most notably been applied to waterfowl management where landscape models are used in part to prioritize habitat conservation (Abraham et al. 2007), but more recent modeling efforts have been developed for several grassland birds (Niemuth et al. 2017). A landscape approach has been suggested for prairie grouse conservation (Vodehnal and Haufler 2007), but fine scale habitat models/maps are lacking across much of their range including South Dakota.

Leks are a focal point for prairie grouse ecology and management (Hamerstrom and Hamerstrom 1973, Giesen and Connelly 1993), and have been used to develop spatial models (Merrill et al. 1999, Niemuth 2000, Hanowski et al. 2000, Gregory et al. 2011). Models have generally been based on a census of leks in a region (Niemuth 2000), or a list of known lek sites from opportunistic surveys (Merrill et al. 1999, Hanowski et al. 2000, Gregory et al. 2011). Results are generally useful for ranking habitat quality across the landscape, but not for estimating probability of use (Keating and Cherry 2004). Because nonrandom sampling designs have varying and often unknown levels of contaminated controls, results are often difficult to compare and interpret among studies. This issue is obvious when results of models with different sampling designs are displayed in maps. Although habitat value may be ranked in a useful manner for each study area, the results are not directly comparable and are unlikely to edge match.

The use of readily available data is convenient, but there are advantages to collecting data specifically for spatial modeling. Most notably, conditional probability of use can be estimated when presence/absence data are collected from random samples (Keating and Cherry 2004). Further, random sampling designs can be developed to avoid geographic bias, and to assure samples are collected across a gradient of important land cover variables. Opportunistic data could be biased if lek searches only occur from roads, or if searches are skewed toward high quality habitat areas or a limited portion of the occupied range. Random sampling designs also require a defined sampling unit which is useful for estimating density in addition to occurrence.

Our objective was to design and implement a practical data collection framework to develop a spatial-explicit habitat-based breeding season occurrence model for prairie grouse in South Dakota. Our approach involved collecting spatially-balanced random samples which were stratified across a wide range of grassland availability.

STUDY AREA

Our 163,061 km^2 study area encompassed the state of South Dakota, excluding the White River Badlands and Black Hills (Foothills, Plateau, and Core Highlands) ecoregions (Bryce et al. 1996) and portions of extreme southeastern South Dakota (Figure 1). Sharp-tailed grouse are known to occur in portions of the Black Hills, particularly where open grasslands exist (Flake et al. 2010). However, our objective was to evaluate the coarse habitat needs of prairie grouse in the open grassland/cropland dominated landscapes of the rest of the state. The White River Badlands is a unique ecoregion dominated by mud buttes with limited vegetation cover. Sharp-tailed grouse do occur in the White River Badlands, but much of the area lacks enough grassland cover for them to persist. Prairie grouse are rare in southeastern South Dakota where much of the landscape has been converted to cropland.

East of the Missouri River nearly all of the study area is characterized as Glaciated Plains (Bryce et al. 1996). Where native vegetation still exists, the tall grass prairies of the eastern fringe of the state transition to mixed grass prairie as you move west into central portions of the state (Johnson and Larson 1999). The Great Plains west of the Missouri River is a mix of short and mixed grass prairie. Much of the native grassland vegetation in the study area has been converted to cropland. In 2016, the state harvested 2.3 million ha of corn, 2.1 million ha of soybean, 0.92 million ha of wheat, and 0.49 million ha acres of other crops (NASS 2017). An additional 1.25 million ha of hay was harvested (NASS 2017). Another 0.39 million ha of farmland was enrolled in the Conservation Reserve Program (CRP) (USDA 2016).

Temperature and precipitation patterns exhibit substantial spatial and temporal variation. Temperatures are highest in July and coldest in January. Precipitation is highest in May–July and lowest during November–February. Except for the Black Hills, western South Dakota receives less precipitation than the eastern part of the state. Annual snowfall is higher and the average temperature is lower in northern South Dakota when compared to the southern part of the state.

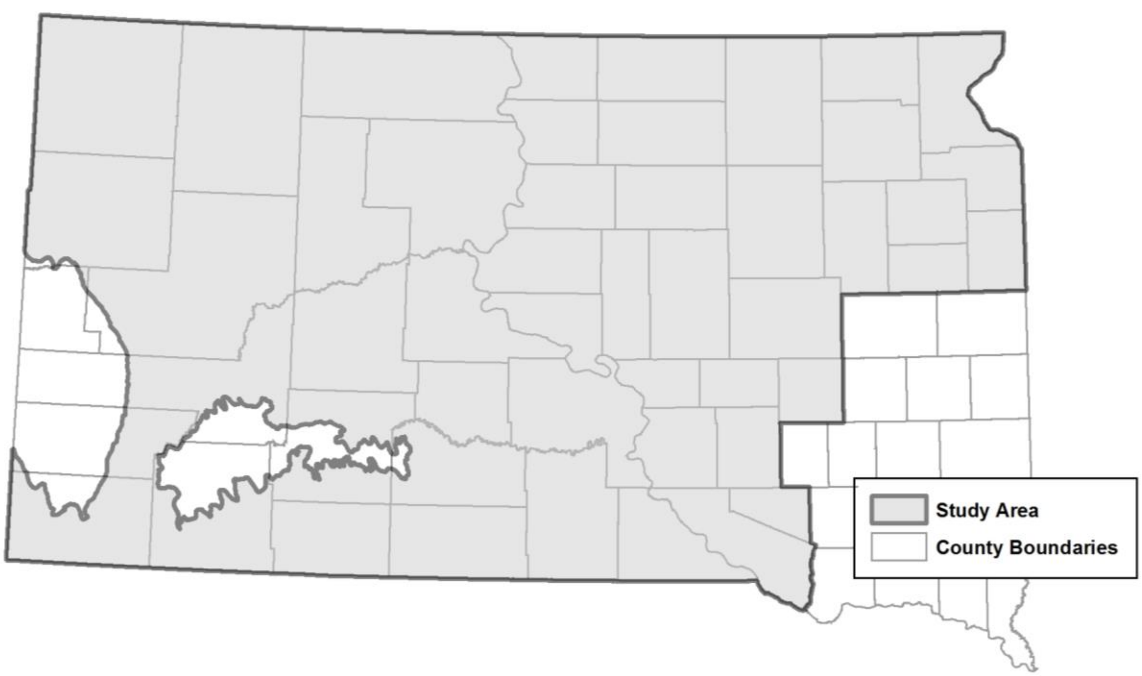

Figure 1. South Dakota study area where we studied occurrence of prairie grouse leks during spring, 2014–2016.

METHODS

Sampling Framework

We developed a sampling framework similar to methodology in the recently developed national sampling framework for secretive marsh birds (Johnson et al. 2009). This approach has been recommended for prairie grouse because samples are spatially balanced and collected across a gradient of predictive variables thought to influence occurrence Niemuth (2011). Our sampling unit was 1.6 by 1.6 km square and centered on a Public Land Survey System (PLSS) section. Prairie grouse occurrence has been linked to grassland availability at approximately the 1.6 km scale (Merrill et al. 1999, Niemuth 2000, Niemuth 2003), so we stratified our samples within a wide range of this habitat variable. Probabilistic sampling was used to stratify survey effort by grassland strata with a disproportionate amount of samples within landscapes of intermediate grassland availability.

Specifically, we divided the study area into 7 approximately equal-sized survey regions which consisted of grouped counties. All PLSS sections were categorized by grassland strata by first combining the grassland/herbaceous and pasture/hay classes of National Land Cover Database 2011 (NLCD, Homer et al. 2015) geographic information system (GIS) layer into a single class. All other classes were ignored in this process. The focal statistics tool (ArcGIS) was used to convert the new grassland cover class layer into a spatially-explicit layer based on percent of landscape in a 1.6 km radius circular moving window. The zonal statistics (ArcGIS) tool was used to append the average cell value of the spatially-explicit grass layer to each overlapping PLSS section. Within each survey region, 175 sample sections were randomly selected within the high (>80%), medium (20-80%), and low (<20%) grassland strata category

(Figure 2). Sample allocation was 10%, 80%, and 10% for the high, medium, and low grassland categories respectively.

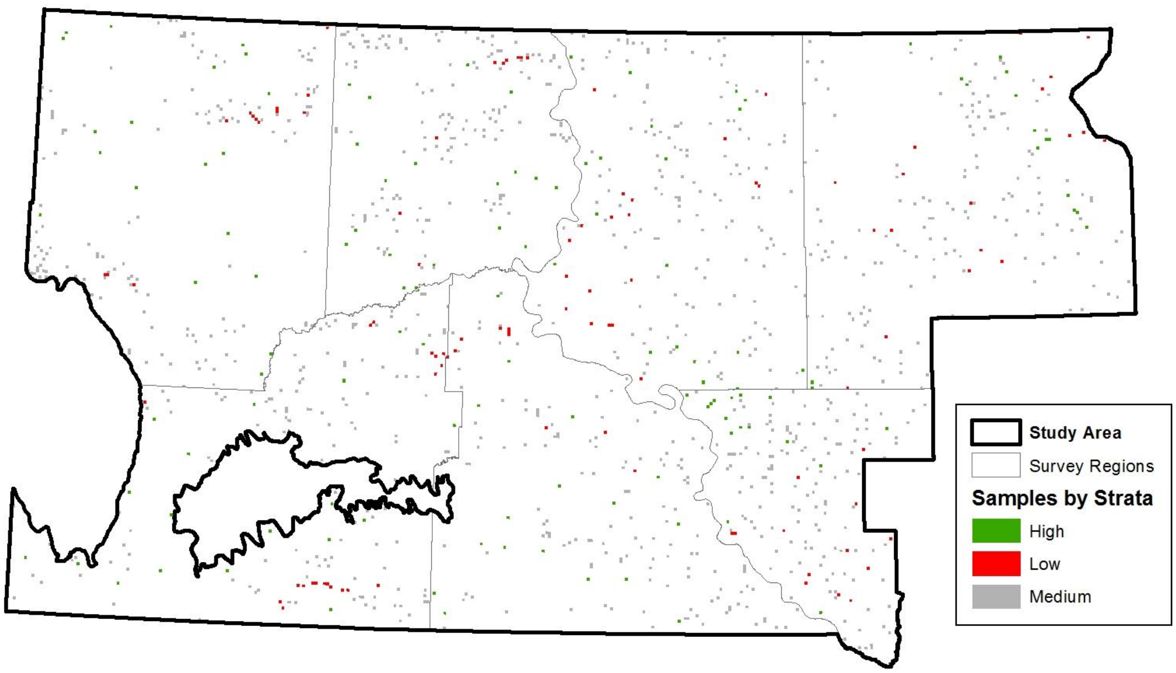

Figure 2. Pre-determined sample units for studying prairie grouse occurrence in South Dakota 2014-2016. Each sample unit was 1.6 by 1.6 km and centered on a public land survey section. Samples were first stratified by region (175 per region), then by grassland strata within region. Sampling units were randomly selected within high (>80%), medium (20-80%), and low (<20%) grassland strata. Sample allocation was 10%, 80%, and 10% for the high, medium, and low grassland categories respectively.

Lek searches

We determined the presence or absence of sharp-tailed grouse or greater prairie-chicken leks and male lek attendance within each sampling unit. Each sampling unit was intensively searched for leks by looking and listening for lek activity from outside of a vehicle. Observers were required to look and listen for activity within 400 m of all areas within the sampling unit. If a road completely surrounded a section, the observer could look and listen for lek activity from stopping points on the road. However, they were still required to navigate to the center of the section to look and listen for lekking activity to meet the 400 m requirement. This usually required acquiring permission to access private property by foot. At least 2 searches were conducted between 30 minutes prior to sunrise until 2 hours after sunrise from 15 March–15 May, but at least one search and lek count occurred during 1 April–30 April. Searches were conducted during mostly clear skies and winds <19 km/hr. Detected leks were marked with a Global Positioning System (GPS), and all males counted and identified to species. Evening searches were permitted, but only supplemental to morning searches (i.e., at least 2 morning searches required). If a lek was detected during the first visit and a valid count was completed, the sample was considered completed and a revisit was not required.

Habitat variables

The NLCD 2011 layer was used for most habitat variables (Homer et al. 2015; Table 1). However, we also included alfalfa from the 2011 CDL (NASS CDL 2011) and the 2016 CRP layer as provided directly from the Farm Service Agency. The standard deviation of the National Elevation Dataset (NED, USGS 2005) was included as an indication of landscape ruggedness. Universal Transverse Mercator (UTM) coordinates were also used as relative northing and easting variables. All variables were assessed in a circular moving windows analysis with a radius of 0.4, 0.8, 1.2, 1.6, 2.4, and 3.2 km. The resulting variables were reported as % of landscape except for the NED layer which was the standard deviation of cells within the moving window and grass cover type which was a count of the unique herbaceous cover classes present within the moving window.

Because of known inaccuracies with NLCD 2011 (Wickham et al. 2010), we created our own land use layer for comparison. All land use within a 1.6 km buffer of the sampling unit was verified in the field to identify any recent major land use changes such as grassland conversion to cropland. Maps were provided to observers for each sampling unit with the most recently available Cropland Data Layer (CDL) and the most recent National Agricultural Imagery Program (NAIP) imagery. Observers compared the maps to the actual land use types at and surrounding the sampling unit and made note of any field-level deviations.

In ArcGIS 10.3 (ESRI, Redlands, CA), we used the NAIP and CDL layers as a guide to heads-up digitize land use layers for sampling units. We classified the landscape into 5 categories; grassland, tree, developed, water, and cropland with a 0.1 ha minimum mapping unit. Developed areas included road and rail rights-of-way, farmsteads, buildings, towns, and trees directly surrounding building sites. Right-of-way included hard surface and gravel roads, but not unimproved grass trails. The grassland land use category included grass, hay, and alfalfa. We processed this GIS layer with a similar moving window analysis as the NLCD layer.

Table 1. Habitat variables used to evaluate prairie grouse lek occurrence in South Dakota, 2014–2016.

Variable Name	Variable Type	Description (NLCD[a] 2011 unless otherwise noted)
Alfalfa	% of landscape	Alfalfa (from 2011 CDL[b])
All Water	% of landscape	Open water + emergent wetland + woody wetland
Barren	% of landscape	Barren land
Crop	% of landscape	Cultivated crops
CRP	% of landscape	Conservation Reserve Program (CRP; from FSA[c] - 2016)
Developed	% of landscape	Developed (open space + low, medium, and high intensity)
Emergent wetland	% of landscape	Emergent herbaceous wetland
Forest	% of landscape	Forest (deciduous + evergreen + mixed)
Forest/shrub	% of landscape	Forest (deciduous + evergreen + mixed)+ shrub/scrub
Forest/woody wetland	% of landscape	Forest (deciduous + evergreen + mixed) + woody wetland
Grass cover type	Count of unique types	Range 0–4; based on alfalfa, CRP, grass/herbaceous, and pasture/hay
Grass	% of landscape	Grassland/herbaceous + pasture/hay
Grass patches	Count	Count of grass patches
Herbaceous	% of landscape	grassland/herbaceous
LSI	Shape index	FRAGSTATS[d] Landscape Shape Index metric
LSI (grass)	Shape index	FRAGSTATS Landscape Shape Index metric for grass variable
Open water	% of landscape	Open water
Pasture/hay	% of landscape	Pasture/hay
Ruggedness index	Ruggedness index	Sd[e] of National Elevation Dataset + 1[f]
Shrub	% of landscape	Shrub/scrub
UTM[g] latitude	Relative northing	UTM zone 14 latitude
UTM longitude	Relative easting	UTM zone 14 longitude
Woody	% of landscape	Forest (deciduous + evergreen + mixed) + woody wetland + shrub/scrub
Woody wetland	% of landscape	Woody wetland

[a]National Land Cover Database 2011 (Homer et al. 2015)
[b]Cropland Data Layer (NASS CDL 2011)
[c]Farm Service Agency
[d]McGarigal et al. 2012
[e]Standard deviation
[f]USGS 2005
[g]Universal Transverse Mercator

Statistical Analyses and Model Development

Because our presence/absence data were drawn from random samples, we used logistic regression to model the conditional probability of occurrence of a prairie grouse lek (Keating and Cherry 2004). Our approach assumes perfect detection of leks for the results to be interpreted as conditional probability of occurrence. Since we required ≥ 2 on the ground lek searches during favorable conditions, we believe our practical data collection approach yields results approximately equal to probability of occurrence. We developed models for the occurrence of sharp-tailed grouse, greater prairie-chickens and for the presence of any prairie grouse lek.

Although we reported summary statistics for a full suite of habitat variables, we opted to limit our model development to a manageable level of biologically relevant variables. We did not have specific information to determine differential preference/avoidance of the individual components of the grass, woody, and developed variables, so we opted to use the aggregated variables. Additionally, inaccuracies are common with NLCD so we opted to use aggregated habitat class variables (Wickham et al. 2010). We only considered one fragmentation variable, LSI (grass), because LSI and LSI (grass) were highly correlated. We also considered ruggedness index and UTM northing and easting as potential variables.

We first developed simple models with the grass, woody and developed variables at the 1.2, 1.6, 2.4, and 3.2 km scales to assess model fit at various scales. Summary analysis showed observed differences in means between lek sites and unoccupied section centers for these 3 variables for sharp-tailed grouse, prairie-chicken and with the data combined. We did not consider scales ≤ 1.2 km because we measured our habitat variables from the section center and thus wanted predictor variables to be at least inclusive of our sample unit. We ranked our identical models of different scales by Akaike's Information Criterion corrected for small sample size (AICc), and then selected the most supported scale.

The 1.2 km scale was most supported, so we developed a suite of candidate models for our 3 species groups at this scale. The grass variable was included in all models because of its obvious importance to most aspects of prairie grouse ecology. We built models with all combinations of grass, woody, developed and ruggedness index. From this set of candidate models, we selected models within 2 AICc units of the top model, and then added relevant combinations of UTM latitude and longitude and LSI (grass). We included LSI (grass) as an additive effect, but also considered an interaction effect with grass. We considered the linear and quadratic forms of UTM latitude and longitude for greater prairie-chickens and for the all prairie grouse models.

We hypothesized that the ruggedness index may be important because more rugged areas may have more diverse plant assemblages and potentially shrubby draws, both of which could be beneficial to prairie grouse, especially sharp-tailed grouse. However, we thought there could be a threshold to the potential benefit. We compared support for the linear and pseudo threshold ($\log_e x + 1$) form of the variable via a single variable model and there was overwhelming support for the pseudo threshold form (Franklin et al. 2000). Thus we only included the pseudo threshold form of the ruggedness index.

We inspected our final model set for models that differed from the top ranked model by one variable and were within 2 AICc of the top model. Those models with uninformative variables were not considered competitive (Burnham and Anderson 2002). We selected the top ranked model as most parsimonious when no other models with informative variables were within 2 AICc units. If model selection uncertainty occurred, we full model averaged the competitive models within 2 AICc units of the top model (Lukacs et al. 2009). We evaluated predictive strength of models by calculating the area under the curve (AUC) of receiver operating characteristics (ROC); values between 0.7 and 0.8 were considered acceptable and values higher than 0.8 were considered excellent (Hosmer and Lemeshow 2000). All analyses and plots were conducted in Program R (R Core Team 2017) using packages MuMIn (Barton 2017), ROCR (Sing et al. 2015), and ggplot2 (Wickham 2009).

RESULTS

Lek searches

A total of 421 sections were sampled throughout our study area (Figure 3). We completed 34, 349, and 38 samples in the high, medium, and low grassland strata, respectively. At least one grouse lek was located on 64 sections with a total of 70 leks found. We found 43 sharp-tailed grouse leks, 23 greater-prairie chicken leks, and 4 mixed leks.

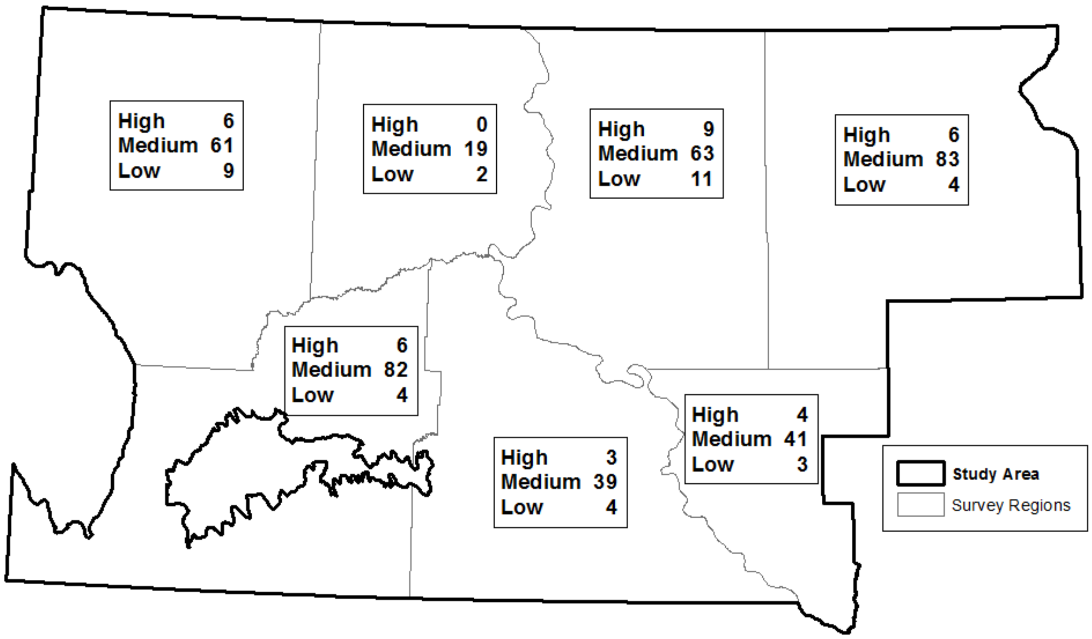

Figure 3. Distribution of 421 sample units searched for prairie grouse leks by grassland strata and region in South Dakota 2014–2016. Grassland strata were categorized as high (>80%), medium (20–80%), and low (<20%).

Lek Site Habitat Characteristics

Lek sites for both species were generally associated with higher amounts of grasslands and lower amounts of woody and developed habitats than unoccupied sites (Figures 4, 5, and 6; Appendices 1, 2 and 3). Grassland and cropland variables were negatively correlated so lek sites also had less cropland than unoccupied sites. The differences in grassland between lek and unoccupied sites were less apparent for greater prairie-chickens, but this could have been because many samples were located outside their known occupied range. Lek sites had higher ruggedness index values than unoccupied sites, but the difference was more apparent for sharp-tailed grouse than greater prairie-chickens. The aggregation variables, LSI and LSI (grass), had lower values for leks sites vs. unoccupied sites which suggest preference for more intact grassland landscapes. Similarly, unoccupied sites had more grass patches than lek sites. Full results for all variables at all scales for each species are available in Appendices 1, 2 and 3.

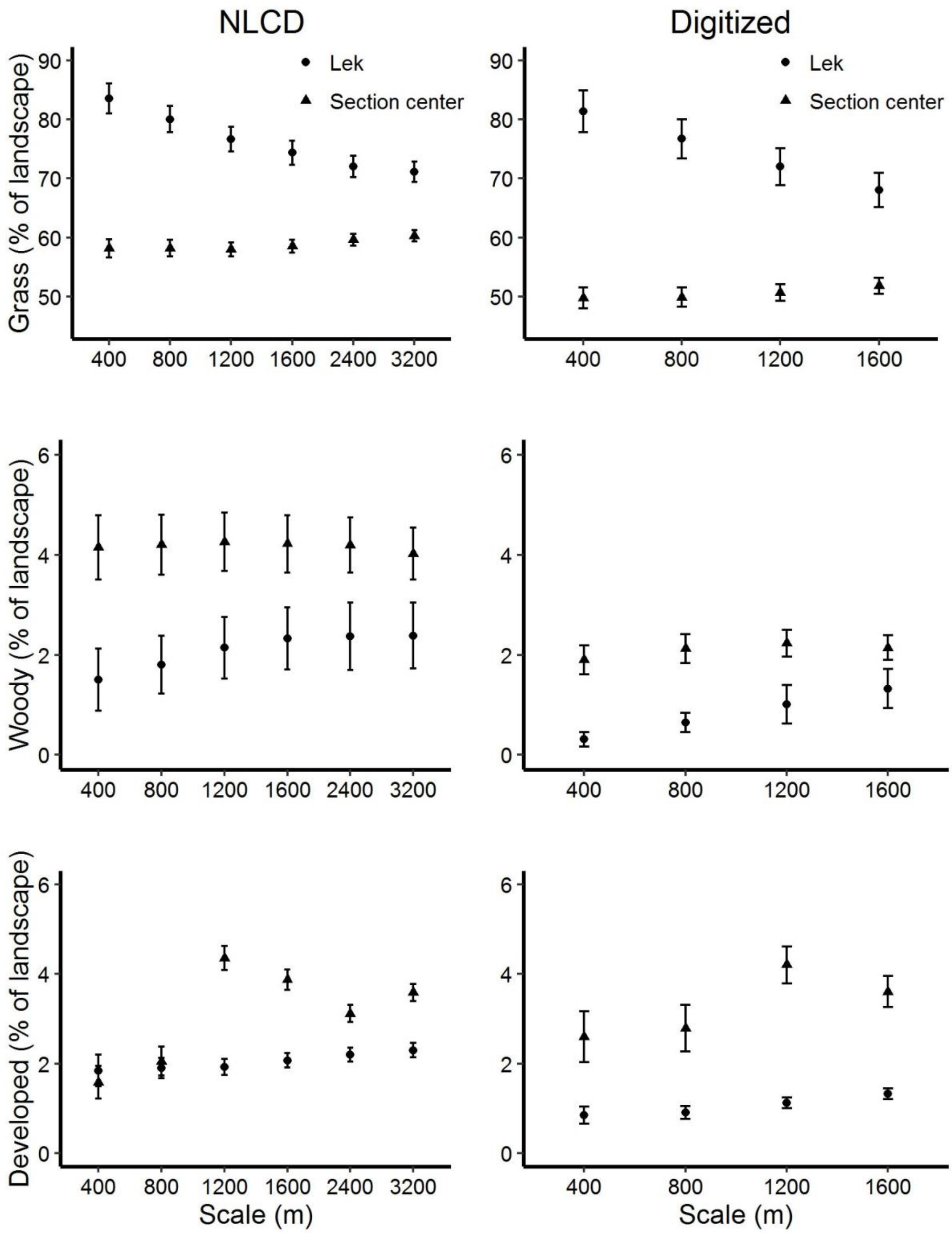

Figure 4. Comparison of selected habitat variables between prairie grouse leks (n = 70) and unoccupied section centers (n = 357) in South Dakota, 2014–2016. Habitat variables were derived from either National Land Cover Dataset 2011 (NLCD, Homer et al. 2015) or from manually digitized landscapes. Error bars indicate standard errors.

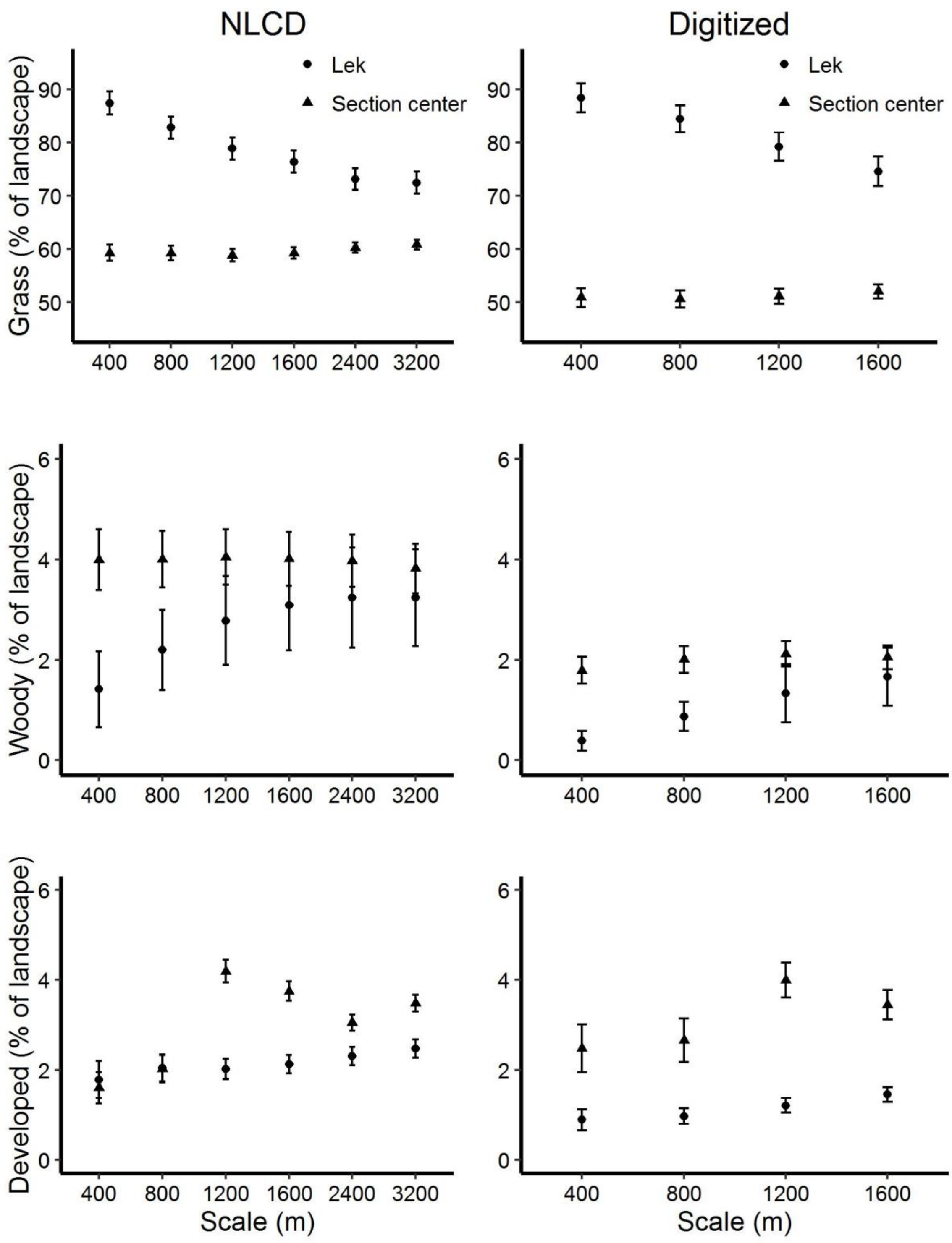

Figure 5. Comparison of selected habitat variables between sharp-tailed grouse leks (n = 47) and unoccupied section centers (n = 377) in South Dakota, 2014–2016. Habitat variables were derived from either National Land Cover Dataset 2011 (NLCD, Homer et al. 2015) or from manually digitized landscapes. Error bars indicate standard errors.

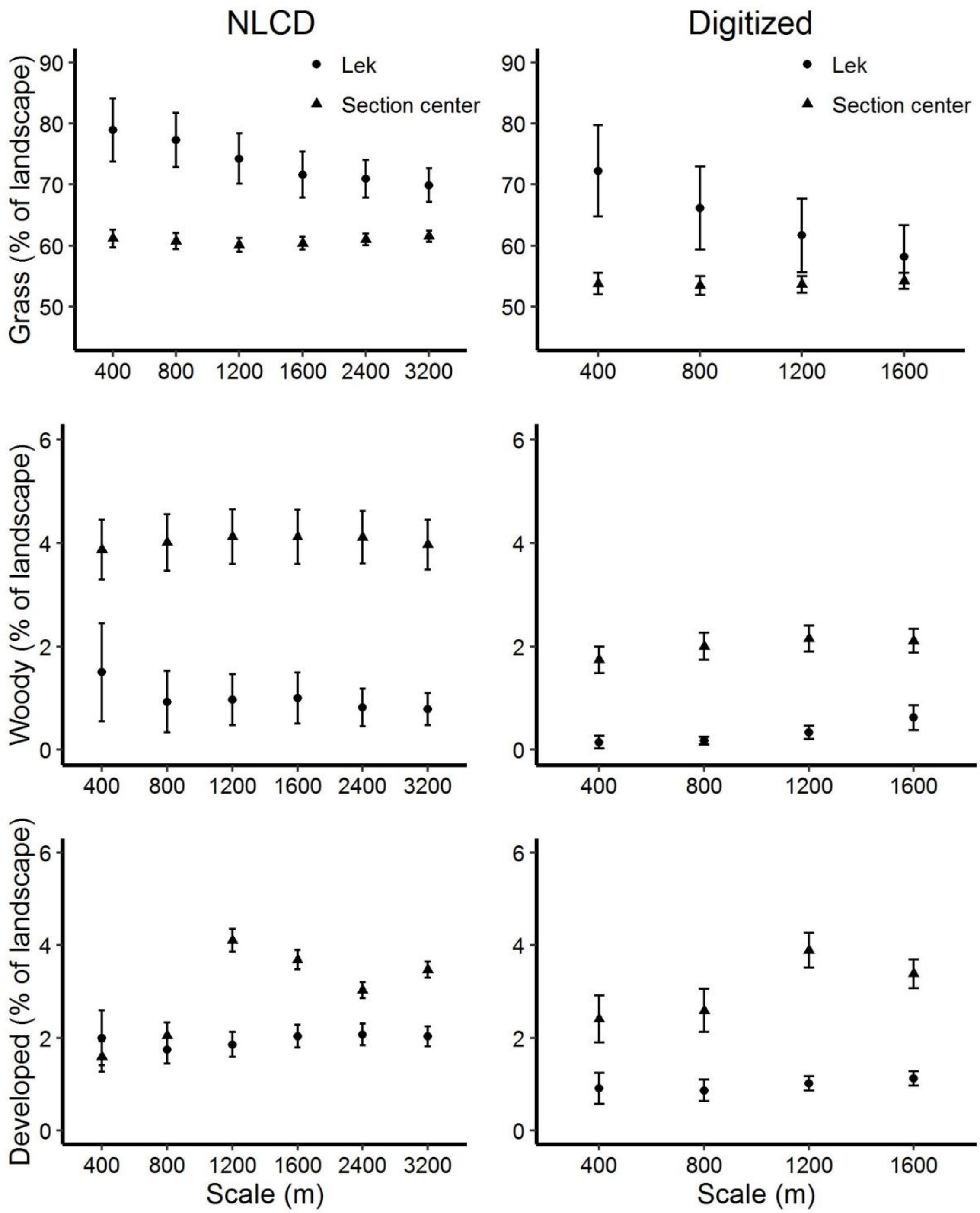

Figure 6. Comparison of selected habitat variables between greater prairie-chicken leks (n = 27) and unoccupied section centers (n = 397) in South Dakota, 2014–2016. Habitat variables were derived from either National Land Cover Dataset 2011 (NLCD, Homer et al. 2015) or from manually digitized landscapes. Error bars indicate standard errors.

Habitat Models

All Prairie Grouse – NLCD-based

There were 6 models within 2 AICc of the top ranked model (Table 2). The sixth ranked model only differed from the top ranked model by one uninformative variable, so we model averaged the top 5 models. The final model included grass and ruggedness index as positive predictors, developed and woody as negative predictors and the quadratic form of UTM longitude (Table 3; Figures 7 and 8). The LSI (grass) variable had a very small coefficient and was not considered a very important variable. The apex of the quadratic response to the UTM longitude variable was 392571, or an area with a relative easting value similar to the town of Pierre. The model had an AUC of 0.76. The model map can be viewed in Appendix 4.

Table 2. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by prairie grouse leks to unoccupied samples in South Dakota, 2014–2016. Only models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented. We also provide number of parameters (K) and model weights (ωi).

Model[a] (1.2 km scale)[b]	**AIC_c**	**ΔAICc**	**K**	**ωi**
Grass + woody + developed + $\log_e$ ruggedness index	319.9	0.00	4	0.19
Grass + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	319.9	0.01	5	0.19
Grass + woody + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	320.6	0.73	6	0.13
Grass + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2	321.5	1.67	6	0.08
Grass + developed + $\log_e$ ruggedness index	321.8	1.97	3	0.07
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass)	321.8	1.98	5	0.07
Grass + developed + $\log_e$ ruggedness index + LSI (grass)	321.9	2.04	4	0.07
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2	322.7	2.79	7	0.05
Grass + $\log_e$ ruggedness index	323.2	3.33	2	0.04
Grass*LSI (grass) + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	323.6	3.73	7	0.03
Grass*LSI (grass) + woody + developed + $\log_e$ ruggedness index	323.8	3.98	6	0.03

[a] Variables for % of landscape include grass = National Land Cover Database 2011 (NLCD; Homer et al. 2015) classes 71 and 81 combined, developed = NLCD classes 21–24 combined, woody = NLCD classes 41–43, 52, and 90 combined. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. Relative northing and easting were included as Universal Transverse Mercator (UTM) latitude and UTM longitude coordinates for UTM Zone 14 North. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

[b] Measured as a circle from the sample unit center.

Table 3. Variables, beta (β) estimates, and standard errors (SE) from model average results comparing sample units (1.6 by 1.6 km) occupied by prairie grouse leks to unoccupied samples in South Dakota, 2014–2016. Model average estimates were generated only from models within 2 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model which had informative variables.

Variable[a]	β Estimate	SE
Intercept	-5.62	1.52
Grass	0.03	0.01
Woody	-0.02	0.02
Developed	-0.16	0.09
$\log_e$ ruggedness index	0.66	0.29
UTM longitude	6.63E-06	6.77E-06
UTM longitude^2	-8.44E-12	8.67E-12
LSI (grass)	-0.01	0.05

[a] Variables for % of landscape include grass = National Land Cover Database 2011 (NLCD; Homer et al. 2015) classes 71 and 81 combined, developed = NLCD classes 21–24 combined, woody = NLCD classes 41–43, 52, and 90 combined. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. Relative northing and easting were included as Universal Transverse Mercator (UTM) latitude and UTM longitude coordinates for UTM Zone 14 North. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

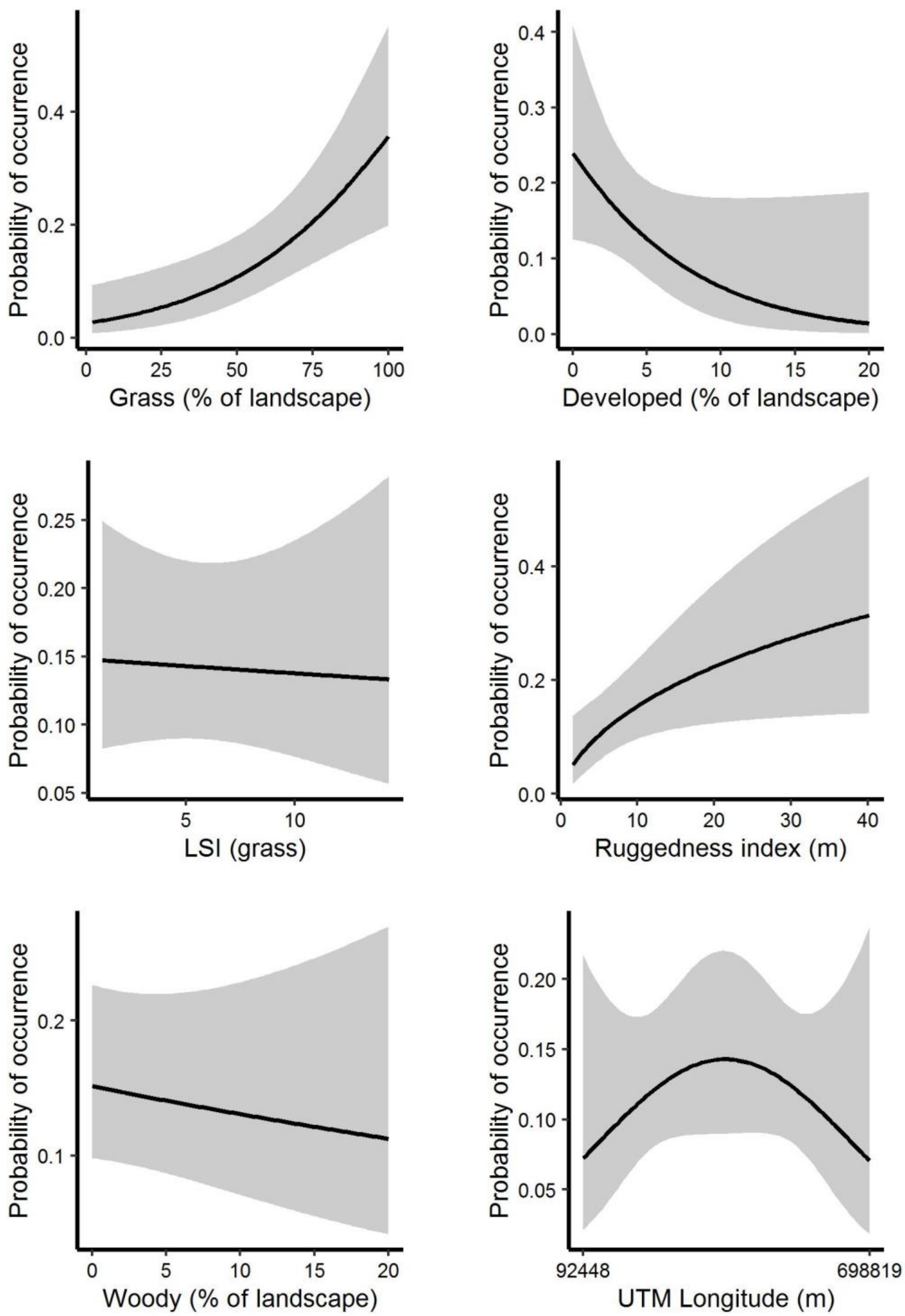

Figure 7. Probability of occurrence of prairie grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Each variable was plotted within the range of its observed values while all other variables were held at their observed mean. Shaded areas represent 95% confidence intervals. The ruggedness index was natural log transformed and UTM longitude was quadratic transformed (Franklin et al. 2000).

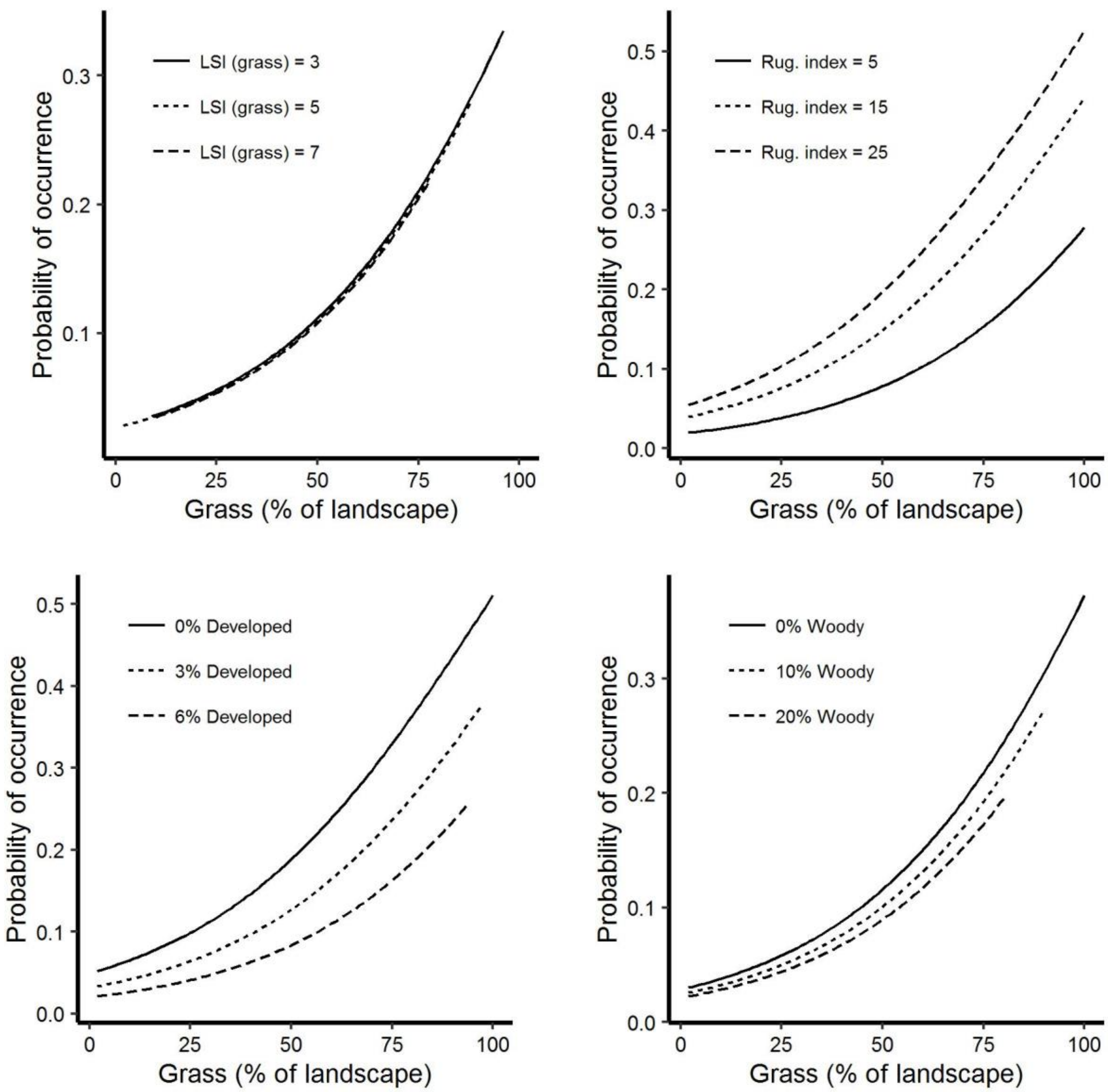

Figure 8. Probability of occurrence of prairie grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Specifically, the probability of occurrence was modeled as a function of % of landscape in grass at three common levels of woody (% of landscape), developed (% of landscape), LSI (grass) and ruggedness index. Variables not plotted were held at their observed mean.

Sharp-tailed grouse – NCLD-based

There were 2 models within 2 AICc of the top ranked model (Table 4). The second ranked model only differed from the top ranked model by one uninformative variable, so we selected the top ranked model as the most parsimonious. The selected model included grass and ruggedness index as positive predictors (Table 5; Figures 9 and 10). The model had an AUC of 0.78. The model map can be viewed in Appendix 5.

Table 4. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by sharp-tailed grouse leks to unoccupied samples in South Dakota, 2014–2016. Only models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented. We also provide number of parameters (K) and model weights (ωi).

Model[a] (1.2 km scale)[b]	**AIC_c**	**ΔAICc**	**K**	**ωi**
grass + $\log_e$ ruggedness index	250.7	0.00	2	0.34
grass + developed + $\log_e$ ruggedness index	251.6	0.89	3	0.22
grass + $\log_e$ ruggedness index + LSI (grass)	252.7	2.01	3	0.13
grass + woody + developed + $\log_e$ ruggedness index	253.4	2.67	4	0.09
grass + developed + $\log_e$ ruggedness index + LSI (grass)	253.6	2.92	4	0.08

[a] Variables for % of landscape include grass = National Land Cover Database 2011 (NLCD; Homer et al. 2015) classes 71 and 81 combined, developed = NLCD classes 21–24 combined, woody = NLCD classes 41–43, 52, and 90 combined. Ruggedness index is the standard deviation of National Elevation Dataset + 1 (USGS 2005). The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

[b] Measured as a circle from the sample unit center

Table 5. Variables, beta (β) estimates, and standard errors (SE) from the top model comparing sample units (1.6 by 1.6 km) occupied by sharp-tailed grouse leks to unoccupied samples in South Dakota, 2014–2016.

Variable[a]	**β Estimate**	**SE**
Intercept	-7.32	1.00
Grass	0.05	0.01
$\log_e$ ruggedness index	0.78	0.28

[a] Grass =% of landscape of National Land Cover Database 2011 (NLCD; Homer et al. 2015) classes 71 and 81 combined. Ruggedness index is the standard deviation of National Elevation Dataset + 1 (USGS 2005). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

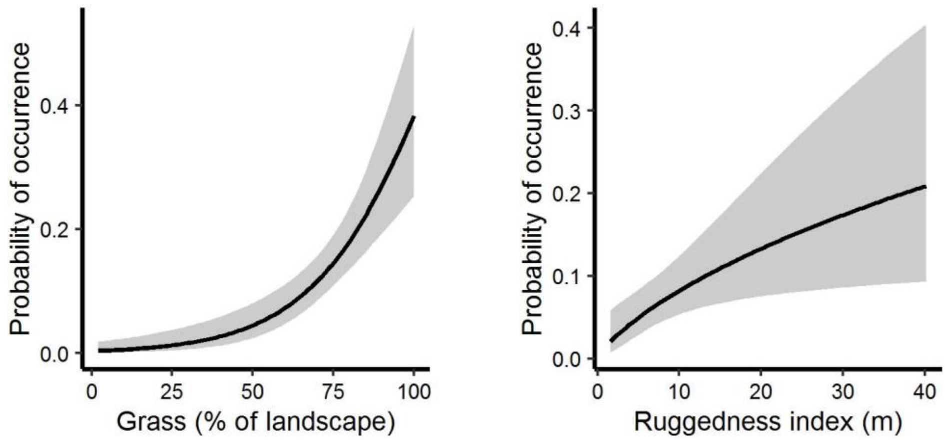

Figure 9. Probability of occurrence of sharp-tailed grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Each variable was plotted within the range of its observed values while the other variable was held at its mean. Shaded areas represent 95% confidence intervals. The ruggedness index was natural log transformed (Franklin et al. 2000).

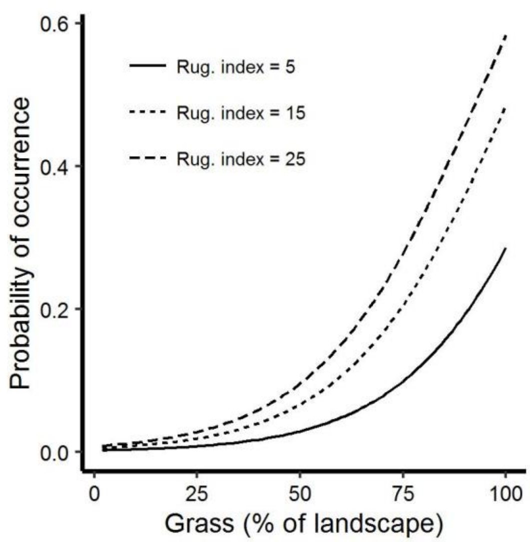

Figure 10. Probability of occurrence of sharp-tailed grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Specifically, the probability of occurrence was modeled as a function of % of landscape in grass at three common levels of the ruggedness index (standard deviation of National Elevation Dataset + 1; USGS 2005).

Greater Prairie-chicken – NLCD-based

There were 3 models within 2 AICc of the top ranked model (Table 6). The second ranked model contained the same variables as the top model, except LSI (grass) variable was entered as an interaction term with the grass variable. The third ranked model only differed from the top ranked model by one uninformative variable. We selected the top model as the most parsimonious. The model included grass as a positive predictor; developed, woody, and LSI (grass) as negative predictors; and the quadratic form of UTM latitude and UTM longitude (Table 7; Figures 11 and 12). The apex of the quadratic responses to the UTM longitude and UTM latitude variables was 392571 and 4859498 or a point approximately 60 km south of Pierre. The model had an AUC of 0.93. The model map can be viewed in Appendix 6.

Table 6. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by greater prairie-chicken leks to unoccupied samples in South Dakota, 2014–2016. Only models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented. We also provide number of parameters (K) and model weights (ωi).

Model[a] (1.2 km scale)[b]	**AIC_c**	**ΔAICc**	**K**	**ωi**
Grass + woody + developed + LSI (grass) + UTM latitude + UTM latitude^2 + UTM longitude + UTM longitude^2	136.2	0	8	0.46
Grass*LSI (grass) + woody + developed + UTM latitude + UTM latitude^2 + UTM longitude + UTM longitude^2	137.6	1.33	9	0.24
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass) + UTM latitude + UTM latitude^2 + UTM longitude + UTM longitude^2	137.9	1.73	9	0.19
Grass*LSI (grass) + woody + developed + $\log_e$ ruggedness index + UTM latitude + UTM latitude^2 + UTM longitude + UTM longitude^2	139.2	2.94	10	0.11

[a] Variables for % of landscape include grass = National Land Cover Database 2011 (NLCD; Homer et al. 2015) classes 71 and 81 combined, developed = NLCD classes 21–24 combined, Woody = NLCD classes 41–43, 52, and 90 combined. Ruggedness index is the standard deviation of National Elevation Dataset + 1 (USGS 2005). The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

[b]Measured as a circle from the sample unit center

Table 7. Variables, beta (β) estimates, and standard errors (SE) from the top model comparing sample units (1.6 by 1.6 km) occupied by greater prairie-chicken leks to unoccupied samples in South Dakota, 2014–2016.

Variable[a]	β Estimate	SE
Intercept	-4.68E+03	2.37E+03
Grass	0.02	0.02
Woody	-0.08	0.08
Developed	-0.38	0.18
LSI (grass)	-0.05	0.21
UTM latitude	1.92E-03	9.71E-04
UTM latitude^2	-1.97E-10	9.94E-11
UTM longitude	9.41E-05	2.74E-05
UTM longitude^2	-1.19E-10	3.47E-11

[a] Variables for % of landscape include grass = National Land Cover Database 2011 (NLCD; Homer et al. 2015) classes 71 and 81 combined, developed = NLCD classes 21–24 combined, woody = NLCD classes 41–43, 52, and 90 combined. Relative northing and easting were included as Universal Transverse Mercator (UTM) latitude and UTM longitude coordinates for UTM Zone 14 North. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

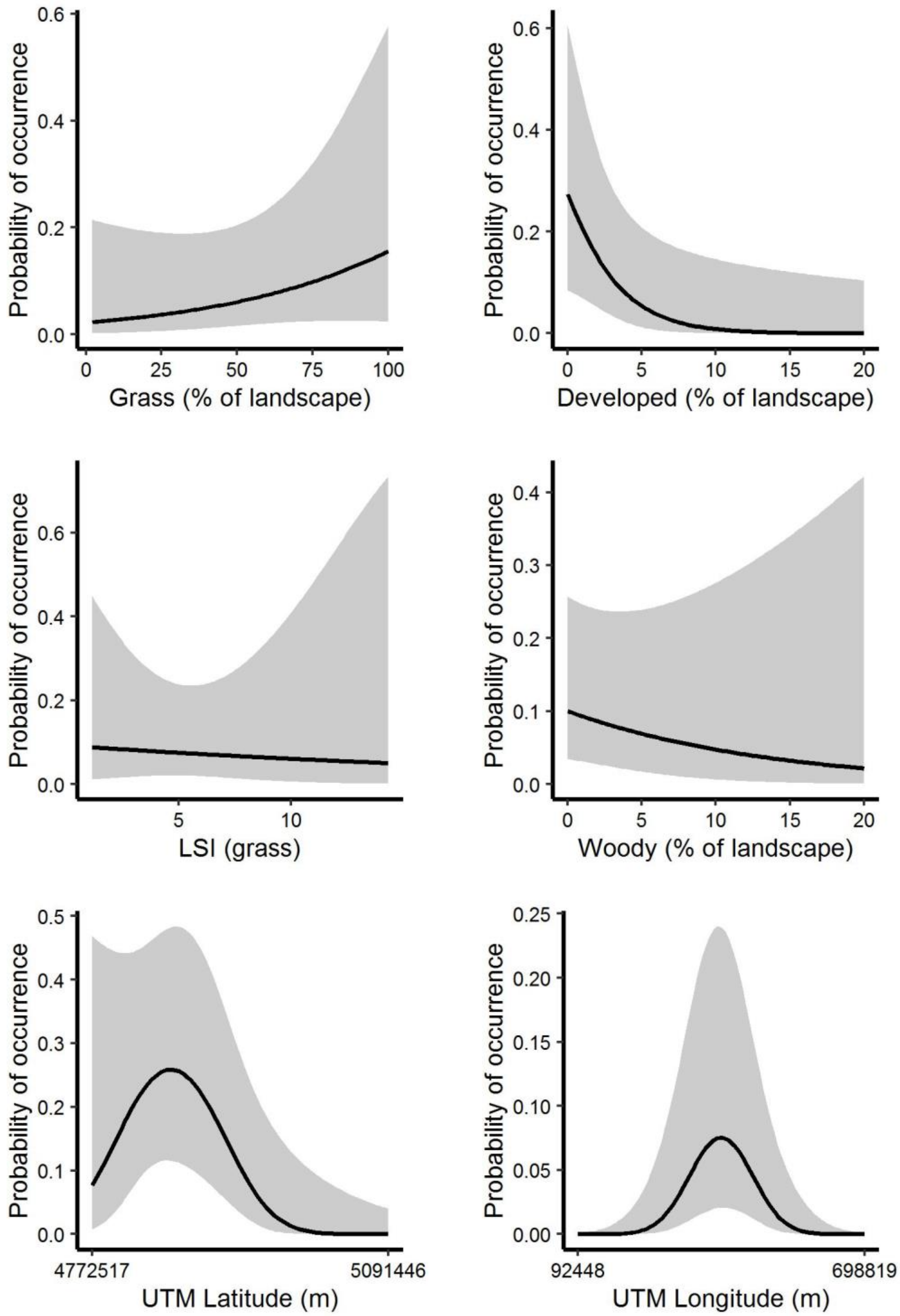

Figure 11. Probability of occurrence of greater prairie-chicken leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Each variable was plotted within the range of its observed values while all other variables were held at their observed mean. Shaded areas represent 95% confidence intervals.

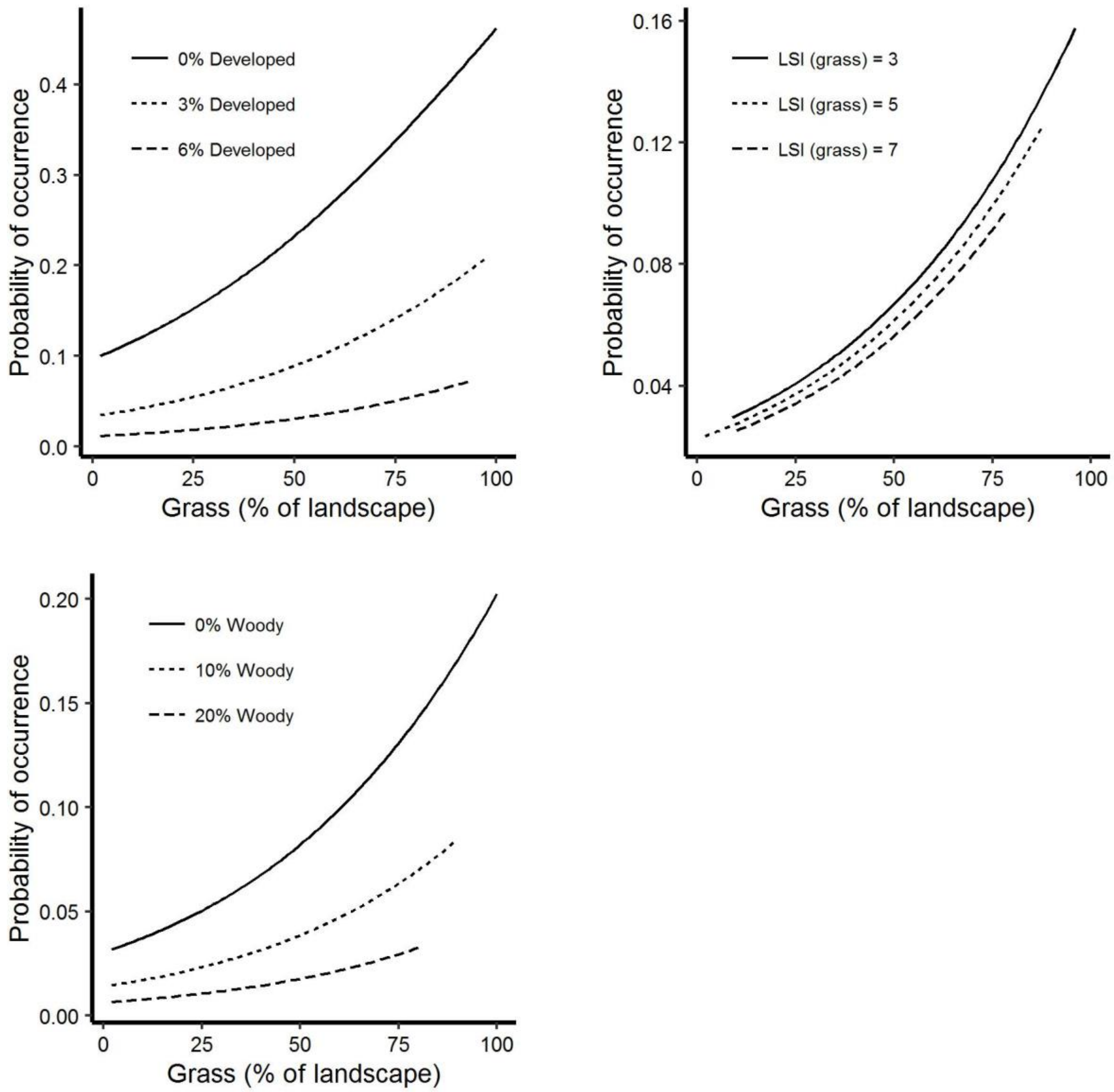

Figure 12. Probability of occurrence of greater prairie-chicken leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Specifically, the probability of occurrence was modeled as a function of % of landscape in grass at three common levels of developed (% of landscape), woody (% of landscape), and LSI (grass). Variables not plotted were held at their observed mean.

All Prairie Grouse – Digitized Landscape-based

There were 3 models within 2 AICc of the top ranked model (Table 8). The second ranked model contained the same variables as the top model, except LSI (grass) variable was entered as an interaction term with the grass variable. The third ranked model only differed from the top ranked model by one uninformative variable. We selected the top model as the most parsimonious. The model included grass and ruggedness index as positive predictors; developed and LSI (grass) as negative predictors; and the quadratic form of UTM longitude (Table 9; Figures 13 and 14). The apex of the quadratic response to the UTM longitude variable was 435445, or an area with a relative easting value similar to 37 km east of Pierre. The model had an AUC of 0.80.

Table 8. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by prairie grouse leks to unoccupied samples in South Dakota, 2014–2016. Only models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented. We also provide number of parameters (K) and model weights (ωi). Land use variables were manually digitized from aerial imagery interpretation.

Model[a] (1.2 km scale)[b]	**AIC_c**	**ΔAICc**	**K**	**ωi**
Grass + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2	303.6	0	6	0.35
Grass*LSI (grass) + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	304.8	1.23	7	0.19
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2	305.6	1.99	7	0.13
Grass + developed + LSI (grass) + UTM longitude + UTM longitude^2	306.3	2.69	5	0.09
Grass*LSI (grass) + woody + developed + UTM longitude + UTM longitude^2	306.7	3.14	8	0.07
Grass*LSI (grass) + developed + UTM longitude + UTM longitude^2	307.1	3.58	6	0.06

[a] Variables for % of landscape include grass = upland herbaceous vegetation such as grass and hayland including alfalfa, developed = road and railroad right-of-ways, towns, and farmsteads, woody = trees and shrubs. Trees directly adjacent to farmsteads were classified as developed. Only roads with impermeable surfaces such as gravel, concrete, or asphalt were classified as developed. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. Relative easting was included as Universal Transverse Mercator (UTM) longitude coordinates for UTM Zone 14 North. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

[b] Measured as a circle from the sample unit center.

Table 9. Variables, beta (β) estimates, and standard errors (SE) from the top model comparing sample units (1.6 by 1.6 km) occupied by prairie grouse leks to unoccupied samples in South Dakota, 2014–2016. Land use variables were manually digitized from aerial imagery interpretation.

Variable[a]	**β Estimate**	**SE**
Intercept	-4.66	1.44
Grass	0.02	0.01
Developed	-0.25	0.12
$\log_e$ ruggedness index	0.64	0.30
LSI (grass)	-0.55	0.18
UTM longitude	1.49E-05	5.35E-06
UTM longitude^2	-1.71E-11	7.10E-12

[a] Variables for % of landscape include grass = upland herbaceous vegetation such as grass and hayland including alfalfa, developed = road and railroad right-of-ways, towns, and farmsteads, woody = trees and shrubs. Trees directly adjacent to farmsteads were classified as developed. Only roads with impermeable surfaces such as gravel, concrete, or asphalt were classified as developed. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. Relative easting was included as Universal Transverse Mercator (UTM) longitude coordinates for UTM Zone 14 North. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

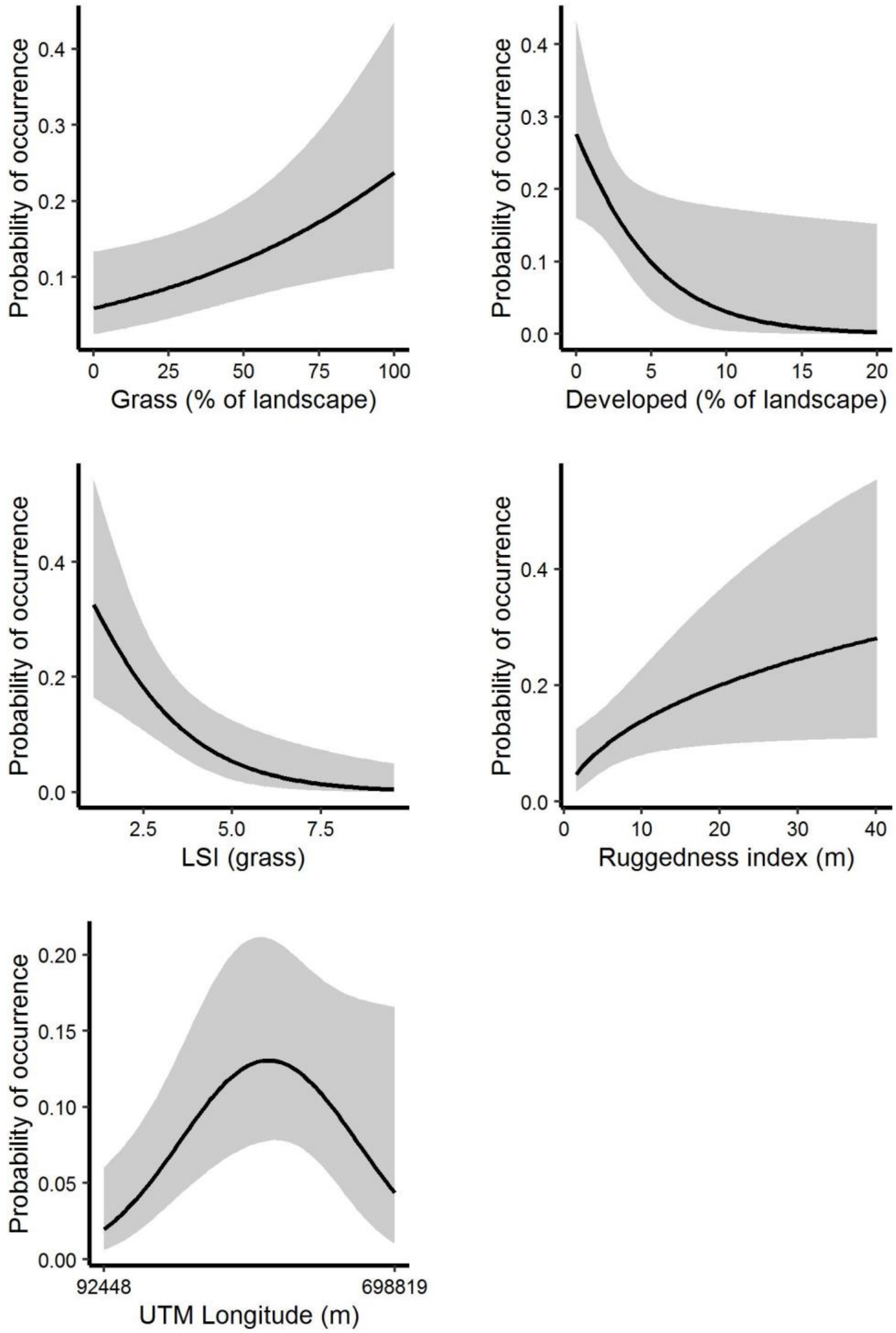

Figure 13. Probability of occurrence of prairie grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Each variable was plotted within the range of its observed values while all other variables were held at their observed mean. Shaded areas represent 95% confidence intervals. The ruggedness index was natural log transformed and UTM longitude was quadratic transformed (Franklin et al. 2000). Land use variables were manually digitized from aerial imagery interpretation.

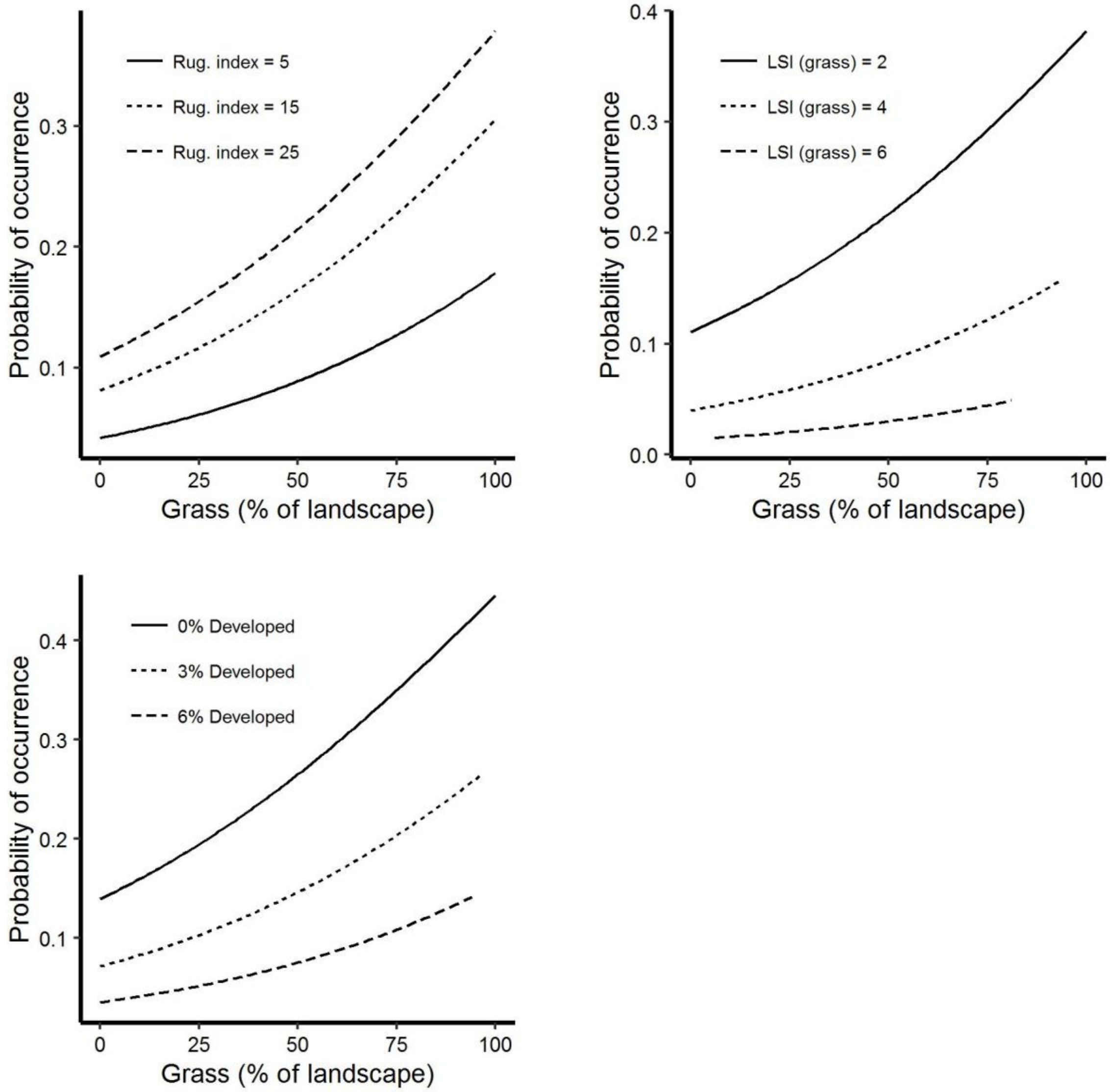

Figure 14. Probability of occurrence of prairie grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Specifically, the probability of occurrence was modeled as a function of % of landscape in grass at three common levels of ruggedness index, LSI (grass) and developed (% of landscape). Variables not plotted were held at their observed mean. Land use variables were manually digitized from aerial imagery interpretation.

Sharp-tailed Grouse – Digitized Landscape-based

There were 5 models within 2 AICc of the top ranked model (Table 10). The third and fourth ranked models were similar to the top two models except LSI (grass) was included as an interaction with the grass variable. We model averaged the 3 models which did not include the LSI (grass) variable as an interaction. The final model included grass and ruggedness index as positive predictors and developed and LSI (grass) as negative predictors (Table 11; Figures 15 and 16). The model had an AUC of 0.80.

Table 10. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by sharp-tailed grouse leks to unoccupied samples in South Dakota, 2014–2016. Only models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented. We also provide number of parameters (K) and model weights (ωi). Land use variables were manually digitized from aerial imagery interpretation.

Model[a] (1.2 km scale)[b]	**AIC_c**	**ΔAICc**	**K**	**ωi**
Grass + developed + $\log_e$ ruggedness index + LSI (grass)	250.0	0.00	4	0.23
Grass + developed + LSI (grass)	250.4	0.40	3	0.19
Grass*LSI (grass) + developed + $\log_e$ ruggedness index	250.9	0.95	5	0.14
Grass*LSI (grass)+ developed	251.0	1.01	4	0.14
Grass + developed	251.5	1.51	2	0.11
Grass + developed + $\log_e$ ruggedness index	252.3	2.35	3	0.07
Grass + woody + developed	253.5	3.51	3	0.04
Grass + woody + developed + $\log_e$ ruggedness index	253.8	3.86	4	0.03

[a] Variables for % of landscape include grass = upland herbaceous vegetation such as grass and hayland including alfalfa, developed = road and railroad right-of-ways, towns, and farmsteads, woody = trees and shrubs. Trees directly adjacent to farmsteads were classified as developed. Only roads with impermeable surfaces such as gravel, concrete, or asphalt were classified as developed. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

[b] Measured as a circle from the sample unit center.

Table 11. Variables, beta (β) estimates, and standard errors (SE) from model average results comparing sample units (1.6 by 1.6 km) occupied by sharp-tailed grouse leks to unoccupied samples in South Dakota, 2014–2016. Land use variables were manually digitized from aerial imagery interpretation.

Variable [a]	**β Estimate**	**SE**
Intercept	-3.14	1.05
Grass	0.03	0.01
Developed	-0.16	0.13
$\log_e$ ruggedness index	0.22	0.33
LSI (grass)	-0.29	0.24

[a] Variables for % of landscape include grass = upland herbaceous vegetation such as grass and hayland including alfalfa and developed = road and railroad right-of-ways, towns, and farmsteads. Only roads with impermeable surfaces such as gravel, concrete, or asphalt were classified as developed. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

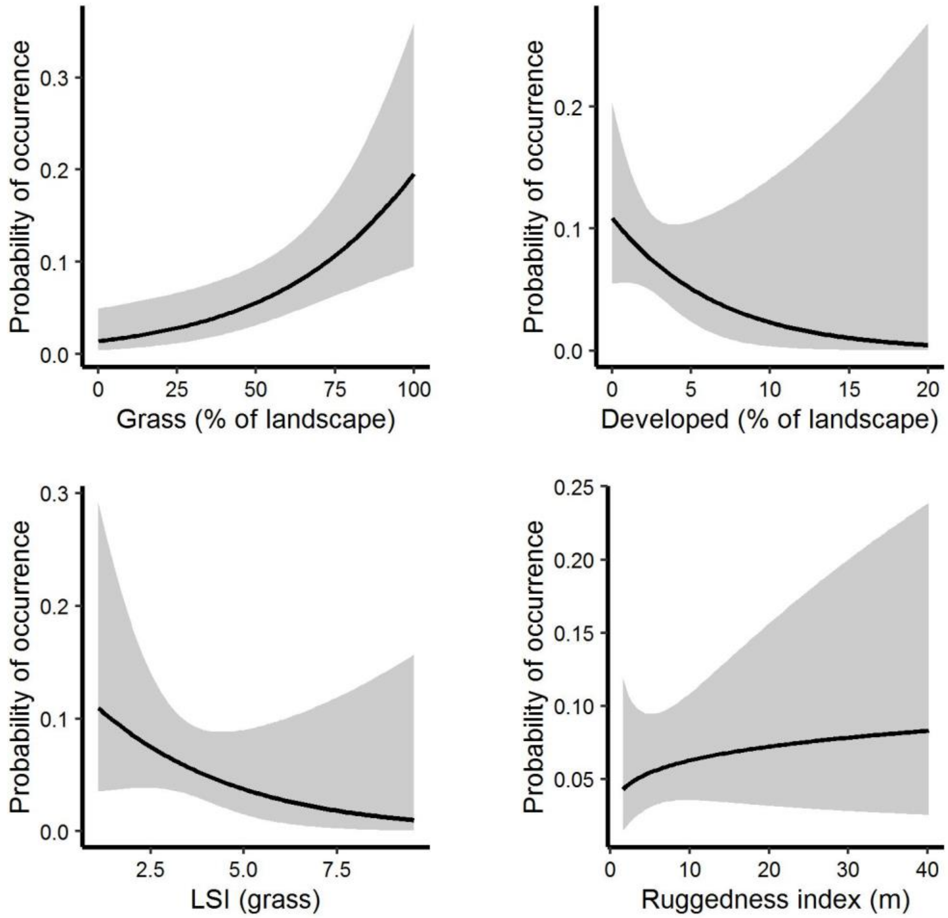

Figure 15. Probability of occurrence of sharp-tailed grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Each variable was plotted within the range of its observed values while all other variables were held at their observed mean. Shaded areas represent 95% confidence intervals. The ruggedness index was natural log transformed (Franklin et al. 2000). Land use variables were manually digitized from aerial imagery interpretation.

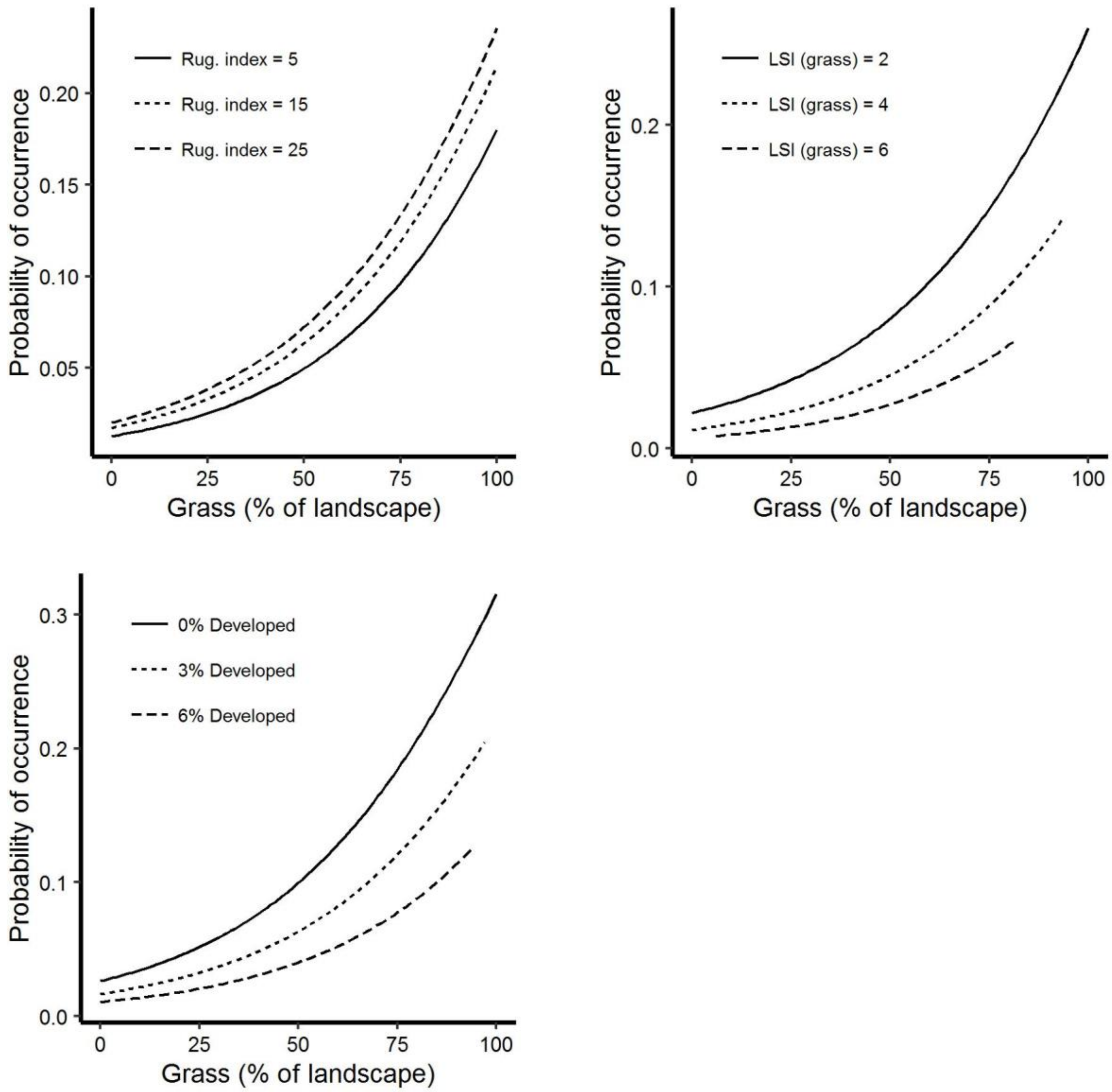

Figure 16. Probability of occurrence of sharp-tailed grouse leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Specifically, the probability of occurrence was modeled as a function of % of landscape in grass at three common levels of ruggedness index, LSI (grass) and developed (% of landscape). Variables not plotted were held at their observed mean. Land use variables were manually digitized from aerial imagery interpretation.

Greater prairie-chicken – Digitized Landscape-based

There were 3 models within 2 AICc of the top ranked model (Table 12). The third ranked model only differed from the top ranked model by one uninformative variable, so we model averaged the top two models. The final model included grass as a positive predictor; developed, woody, and LSI (grass) as negative predictors; and the quadratic form of UTM latitude and UTM longitude (Table 13; Figures 17 and 18). The apex of the quadratic responses to the UTM longitude and UTM latitude variables was 398695 and 4862719 or a point approximately 50 km south of Pierre. The model had an AUC of 0.95.

Table 12. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by greater prairie-chicken leks to unoccupied samples in South Dakota, 2014–2016. Only models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented. We also provide number of parameters (K) and model weights (ωi). Land use variables were manually digitized from aerial imagery interpretation.

Model[a] (1.2 km scale)[b]	**AIC_c**	**ΔAICc**	**K**	**ωi**
Grass + developed + woody + LSI (grass) + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	121.2	0	8	0.33
Grass + developed + woody + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	121.6	0.39	7	0.27
Grass + developed + woody + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	123.0	1.77	9	0.14
Grass*LSI (grass) + developed + woody + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	123.2	2.06	9	0.12
Grass + developed + woody + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	123.6	2.39	8	0.10
Grass*LSI (grass) + developed + woody + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	125.0	3.81	10	0.05

[a] Variables for % of landscape include grass = upland herbaceous vegetation such as grass and hayland including alfalfa, developed = road and railroad right-of-ways, towns, and farmsteads, woody = trees and shrubs. Trees directly adjacent to farmsteads were classified as developed. Only roads with impermeable surfaces such as gravel, concrete, or asphalt were classified as developed. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. Relative northing and easting were included as Universal Transverse Mercator (UTM) longitude and latitude coordinates for UTM Zone 14 North. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

[b] Measured as a circle from the sample unit center.

Table 13. Variables, beta (β) estimates, and standard errors (SE) from model average results comparing sample units (1.6 by 1.6 km) occupied by greater prairie-chicken leks to unoccupied samples in South Dakota, 2014–2016. Land use variables were manually digitized from aerial imagery interpretation.

Variable[a]	β Estimate	SE
Intercept	-7610.00	3088.00
All grass	0.01	0.01
Developed	-0.73	0.27
Woody	-0.23	0.17
LSI (grass)	-0.35	0.45
UTM longitude	8.94E-05	2.72E-05
UTM longitude^2	-1.12E-10	3.44E-11
UTM latitude	3.12E-03	1.27E-03
UTM latitude^2	-3.21E-10	1.30E-10

[a] Variables for % of landscape include grass = upland herbaceous vegetation such as grass and hayland including alfalfa, developed = road and railroad right-of-ways, towns, and farmsteads, woody = trees and shrubs. Trees directly adjacent to farmsteads were classified as developed. Only roads with impermeable surfaces such as gravel, concrete, or asphalt were classified as developed. Ruggedness index is the standard deviation of National Elevation Dataset (USGS 2005) + 1. Relative northing and easting were included as Universal Transverse Mercator (UTM) longitude and latitude coordinates for UTM Zone 14 North. The LSI (grass) variable is the FRAGSTATS Landscape Shape Index class metric for grass (McGarigal et al. 2012). Variables may include non-linear forms such as quadratic and natural log transformation (Franklin et al. 2000).

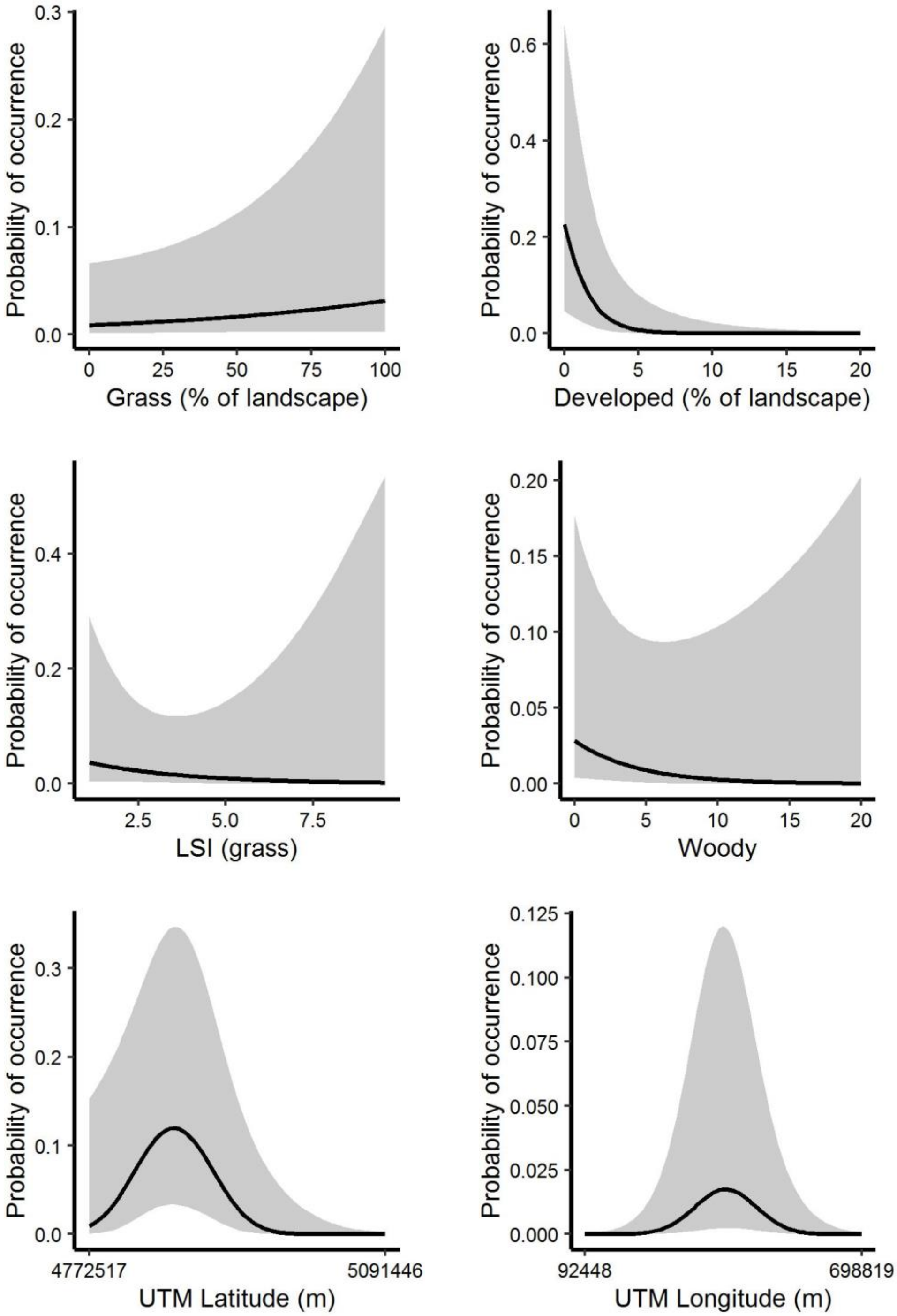

Figure 17. Probability of occurrence of greater prairie-chicken leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Each variable was plotted within the range of its observed values while all other variables were held at their observed mean. Shaded areas represent 95% confidence intervals. The ruggedness index was natural log transformed and the UTM longitude and latitude variables were quadratic transformed (Franklin et al. 2000). Land use variables were manually digitized from aerial imagery interpretation.

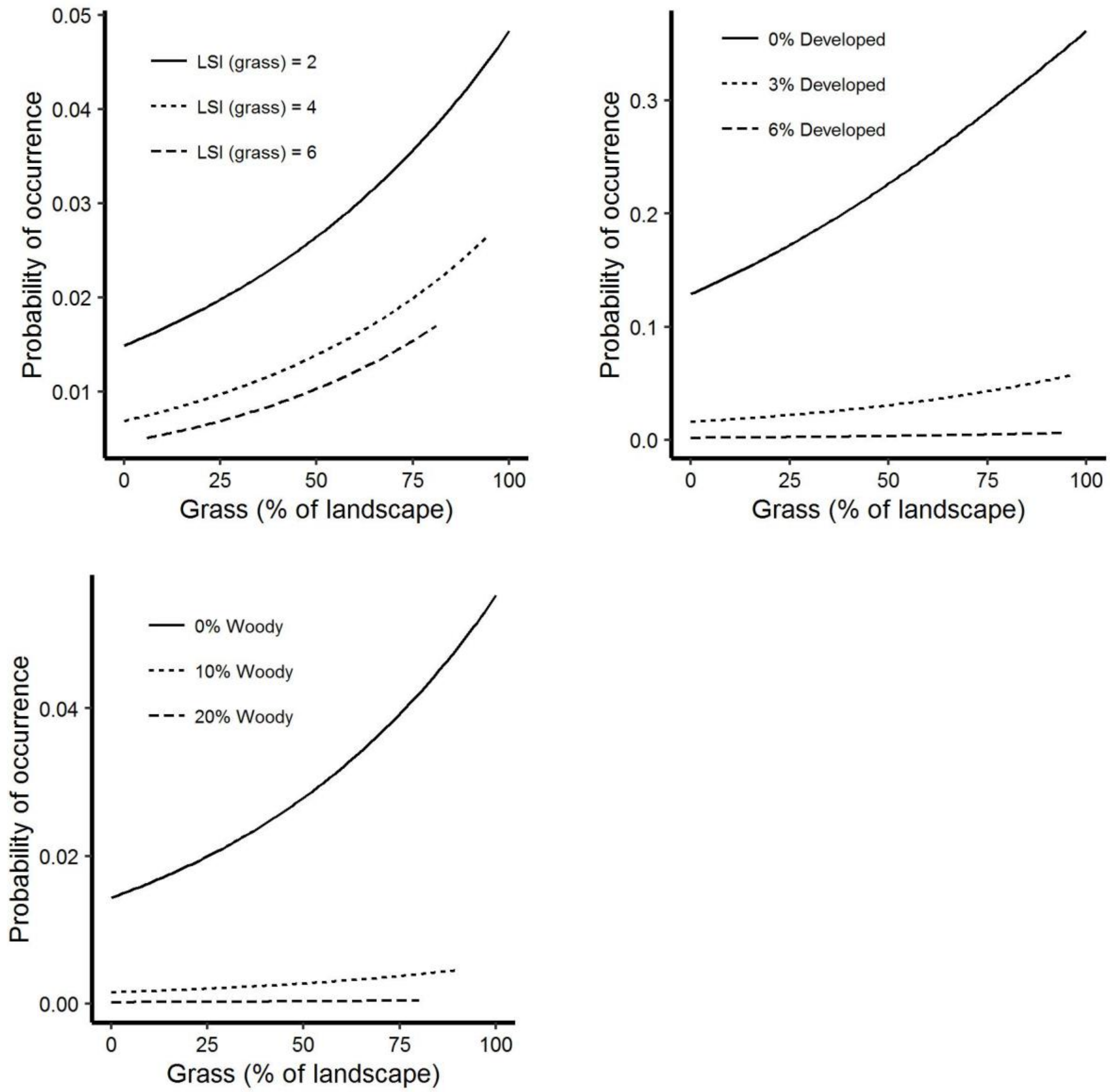

Figure 18. Probability of occurrence of greater prairie-chicken leks within 1.6 by 1.6 km sampling units as a function of habitat variables within a 1.2 km radius circle from the sample center in South Dakota, 2014–2016. Specifically, the probability of occurrence was modeled as a function of % of landscape in grass at three common levels of LSI (grass), developed (% of landscape), and woody (% of landscape). Variables not plotted were held at their observed mean. Land use variables were manually digitized from aerial imagery interpretation.

Comparison of NLCD-based models versus digitized landscape models

Models based on the digitized land use variables consistently outperformed models base on NLCD land use variables, although the difference was less apparent for sharp-tailed grouse (Table 14, 15, and 16). Differences in classification were also observed between our digitized land use layer and the NLCD layer (Table 17). The top ranked prairie grouse model based on the digitized variables was 16.30 AICc units higher than the top ranked NLCD-based model. Final models from both data sets contained the variables grass, developed, ruggedness index, LSI (grass) and UTM longitude, but woody was also included in the NLCD-based model. The AUC for the final NLCD-based model was 0.76 while the digitized-based model was slightly higher at 0.80.

For sharp-tailed grouse, the final NLCD-based model contained the variables grass and ruggedness index while the digitized-based model contained the same variables with the addition of developed and LSI (grass). The digitized-based models generally ranked higher when compared by AICc, but the difference was not large. The NLCD-based model had an AUC of 0.78 while the digitized-based model was 0.80.

The final models for prairie-chickens contained the same variables of grass, woody, developed, LSI (grass), UTM longitude, and UTM latitude. However, the top ranked digitized-based model was 15.03 AICc units better than the top ranked NLCD model. All models based on digitized variables ranked higher than NLCD models. The effect sizes for woody and developed were substantially larger for the digitized based models than the NLCD-based models. The NLCD-based model had an AUC of 0.93 while the digitized-based model was 0.95.

Table 14. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by prairie grouse leks to unoccupied samples in South Dakota, 2014–2016. Models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented for analyses based both on NLCD variables and digitized variables. We also provide number of parameters (K) and model weights (ωi). Bolded models were developed from digitized landscape variables.

Model (1.2 km scale)	AICc	ΔAICc	K	ωi
Grass + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2	303.6	0.00	6	0.39
Grass*LSI (grass) + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	304.8	1.23	7	0.21
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2	305.6	1.99	7	0.15
Grass + developed + LSI (grass) + UTM longitude + UTM longitude^2	306.3	2.69	5	0.10
Grass*LSI (grass) + woody + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	306.7	3.14	8	0.08
Grass*LSI (grass) + developed + UTM longitude + UTM longitude^2	307.1	3.58	6	0.07
Grass + woody + developed + $\log_e$ ruggedness index	319.9	16.30	4	0.00
Grass + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	319.9	16.31	5	0.00
Grass + woody + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	320.6	17.03	6	0.00
Grass + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	321.5	17.97	6	0.00
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass)	321.8	18.28	5	0.00
Grass + developed + $\log_e$ ruggedness index + LSI (grass)	321.9	18.34	4	0.00
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2	322.7	19.09	7	0.00
Grass + $\log_e$ ruggedness index	323.2	19.63	2	0.00
Grass*LSI (grass) + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2	323.6	20.04	7	0.00
Grass*LSI (grass) + woody + developed + $\log_e$ ruggedness index	323.8	20.28	6	0.00

Table 15. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by sharp-tailed grouse leks to unoccupied samples in South Dakota, 2014–2016. Models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented for analyses based both on NLCD variables and digitized variables. We also provide number of parameters (K) and model weights (ωi). Bolded models were developed from digitized landscape variables.

Model (1.2 km scale)	**AICc**	**ΔAICc**	**K**	**ωi**
Grass + developed + $\log_e$ ruggedness index + LSI (grass)	250.0	0.00	4	0.17
Grass + developed + LSI (grass)	250.4	0.40	3	0.14
Grass + $\log_e$ ruggedness index	250.7	0.71	2	0.12
Grass*LSI (grass) + developed + $\log_e$ ruggedness index	250.9	0.95	5	0.11
Grass*LSI (grass) + developed	251.0	1.01	4	0.10
Grass + developed	251.5	1.51	2	0.08
Grass + developed + $\log_e$ ruggedness index	251.6	1.59	3	0.08
Grass + developed + $\log_e$ ruggedness index	252.3	2.35	3	0.05
Grass + $\log_e$ ruggedness index + LSI (grass)	252.7	2.72	3	0.04
Grass + woody + developed + $\log_e$ ruggedness index	253.4	3.38	4	0.03
Grass + developed + woody	253.5	3.51	3	0.03
Grass + developed + $\log_e$ ruggedness index + LSI (grass)	253.6	3.63	4	0.03
Grass + woody + developed + $\log_e$ ruggedness index	253.8	3.86	4	0.03

Table 16. Logistic regression model selection results comparing sample units (1.6 by 1.6 km) occupied by greater prairie-chicken leks to unoccupied samples in South Dakota, 2014–2016. Models within 4 AICc (Akaike's Information Criterion corrected for small sample size) units of the best model are presented for analyses based both on NLCD variables and digitized variables. We also provide number of parameters (K) and model weights (ωi). Bolded models were developed from digitized landscape variables.

Model (1.2 km scale)	**AICc**	**ΔAICc**	**K**	**ωi**
Grass + developed + woody + LSI (grass) + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	121.2	0.00	8	0.33
Grass + developed + woody + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	121.6	0.39	7	0.27
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	123.0	1.77	9	0.14
Grass*LSI (grass) + developed + woody + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	123.2	2.06	9	0.12
Grass + woody + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	123.6	2.39	8	0.10
Grass*LSI (grass) + woody + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	125.0	3.81	10	0.05
Grass + woody + developed + LSI (grass) + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	136.2	15.03	8	0.00
Grass*LSI (grass) + woody + developed + UTM longitude+ UTM longitude + UTM latitude + UTM latitude^2	137.6	16.36	9	0.00
Grass + woody + developed + $\log_e$ ruggedness index + LSI (grass) + UTM longitude + UTM longitude^2 + UTM latitude + UMT latitude^2	137.9	16.76	9	0.00
Grass*LSI (grass) + woody + developed + $\log_e$ ruggedness index + UTM longitude + UTM longitude^2 + UTM latitude + UTM latitude^2	139.2	17.97	10	0.00

Table 17. Comparative classification of landcover between digitized landscape and NLCD in South Dakota, 2014–2016.

Digitized Classification	NLCD Classification	%
Grass	Grass	81
	Developed	2
	Crop	9
	Tree	4
Tree	Grass	39
	Developed	3
	Crop	11
	Tree	33
Developed	Grass	38
	Developed	45
	Crop	13
	Tree	2
Crop	Grass	33
	Developed	2
	Crop	63
	Tree	1

DISCUSSION

The strong association between prairie grouse occurrence and landscape level grassland availability was once again demonstrated in this study and is consistent with past research (Merrill et al. 1999, Hanowski et al. 2000, Niemuth 2000, Niemuth and Boyce 2004, Gregory et al. 2011, Hamilton and Manzer 2011). Prairie grouse rely on grasslands for most life cycle needs and the biological traits that make them sensitive to landscape grassland conditions have been thoroughly established (reviewed in Niemuth 2011). Our analysis also revealed important non-grassland variables which influence occurrence. Because we manually digitized our sample sites, we were able to scrutinize our NLCD-based models and identify potential shortcomings in statewide occurrence maps.

For sharp-tailed grouse, the model based on the digitized variables had a higher AUC value (0.80 vs. 0.78) and lower AICc value (250.0 vs. 250.7) compared to the best NLCD-based model. For greater prairie-chicken, the model based on the digitized variables had a higher AUC value (0.95 vs. 0.93) and lower AICc value (121.2 vs. 136.2) compared to the best NLCD-based model. The prairie grouse model followed a similar pattern with better performance for the digitized-based models.

Both sharp-tailed grouse models included grass and ruggedness index, but the digitized-based model also included the variables developed and LSI (grass). Both greater prairie-chicken models included the same variables. The influence was stronger for developed, woody, and LSI (grass) for the digitized-based model. Our model comparison suggests potentially important influences of developed and LSI (grass) were not detected with the NLCD-based habitat variables for sharp-tailed grouse. The affect size for some variables was also substantially different between the greater prairie-chicken models.

The ruggedness index could have been a positive predictor of sharp-tailed grouse occurrence for several reasons. Shrubby draws, a habitat type commonly used by sharp-tailed grouse (Sisson 1976, Flake et al. 2010), could be associated with areas with higher ruggedness index values. High ruggedness index areas could have less tillage history (i.e. current grassland more likely to be native) and be less fragmented than flatter areas. Finally, the ruggedness could create more microhabitat diversity which could have positive influences on sharp-tailed grouse ecology (Sisson 1976). Sharp-tailed grouse are more known to use shrubby draws than greater prairie-chickens which may explain why the ruggedness index did not occur in the greater prairie-chicken model (Flake et al. 2010).

Interestingly, ruggedness index was only marginally important in the digitized-based sharp-tailed grouse model. The LSI (grass) variable indicated higher occurrence in landscapes with more intact grasslands for both species. Fragmentation has been associated with lower reproductive success in greater prairie-chickens (Ryan et al. 1998) and in many other upland nesting birds (Stephens et al. 2003). The NLCD layer is a coarse representation of the landscape with many misclassified cells. Although a relatively low number of misclassified cells may not have a large influence on % of landscape variables, misclassified cells do contribute substantially to fragmentation calculations (e.g. one misclassified 30m cell is equal to 120 meters of false edge). This may explain why LSI (grass) was not an important variable in our NLCD-based models but was in our digitized-based models.

There was less than a 50% concordance rate for the developed variable between NLCD and our digitized layer. The coarse resolution of NLCD may have poorly classified developed areas. Additionally, we were easily able to digitize farmsteads and rural residences as developed while tree canopy cover and intermixed herbaceous vegetation may have resulted in these areas being classified as grass or trees by NLCD. We also observed unimproved roads (i.e. not gravel or paved) being classified as developed by NLCD. We consider our digitized layer as a more accurate representation of the landscape. For a landscape with 75% grass, the probability of sharp-tailed grouse occurrence was approximately double for landscapes with 0% developed versus 6% developed and for landscapes with LSI (grass) of 2 versus 6. The affect size was even larger for greater prairie-chickens.

In North Dakota, sharp-tailed grouse exhibited higher nest survival in a landscape fragmented by oil and gas development, presumably because fewer mesopredators were present (Burr et al. 2017). However, Runia and Solem (2015) found lower prairie grouse nest survival in proximity to developed areas such as roads and building sites. Prairie-chickens avoided power lines in Oklahoma (Pruett et al. 2009) and greater-prairie chicken leks had higher abandonment rates near wind energy developments in Kansas (Winder et al. 2015).

Although woody was only a negative predictor for the greater prairie-chicken and prairie grouse model, our lek-based habitat analysis showed higher % of landscape in woody habitat at all spatial scales for both species. Trees can provide perch sites for raptors which could be important as raptors can be a major source of adult mortality (Burger 1988). Trees are negatively associated with a suite of area sensitive grassland birds (Greer et al. 2016, Niemuth et al. 2017).

MANAGEMENT IMPLICATIONS

Spatially-explicit habitat-based models provide a means of rapidly assessing landscape suitability so targeted conservation can occur. Landscapes with high probability of prairie grouse occurrence would be appropriate areas to maintain or protect from development/habitat conversion. High value landscapes would also be key areas to implement beneficial local-scale management actions such as grazing regimes expected to alter vegetation composition and structure beneficial for prairie grouse. Habitat models provide a useful way to assess less suitable landscapes so management actions with the greatest return on investment can be implemented. For example, increasing landscape level grassland availability from 0 to 50% is expected to have minimal influence on probability of occurrence of sharp-tailed grouse, but increasing from 75 to 100% increases probability of occurrence from 15 to 38%. Relatedly, managers should be aware that presence of developed areas reduces the prairie grouse habitat benefit that can be achieved by increasing grassland availability alone. Similarly, the presence of trees vastly reduces the benefit of increasing grassland availability for greater prairie-chickens. In other words, some landscapes will require reduction in trees or developed areas before the benefit from increasing grass is substantial. Fortunately, spatial models can be used to project the response from management actions so return on investment from various scenarios can be compared.

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APPENDICES

Appendix 1. Mean and standard error (SE) for habitat variables surrounding section centers occupied or unoccupied by a prairie grouse lek in South Dakota, 2014–2016. See table 1 and methods section for variable definitions. Note, only areas ≤ 1,600 m from section centers were manually digitized by photointerpretation.

	NLCD habitat layers				Digitized habitat layers			
Variable	**Occupied (n = 64)**		**Unoccupied (n = 357)**		**Occupied**		**Unoccupied**	
400 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	0.95	0.43	2.09	0.36				
All water	1.38	0.38	5.25	0.60				
Barren	0.02	0.02	0.07	0.05				
Crop	16.97	3.11	31.77	1.64	24.47	4.43	43.01	1.87
CRP	1.78	0.94	3.02	0.55				
Developed	0.61	0.20	1.58	0.37	0.20	0.09	2.60	0.57
Emergent wetland	0.27	0.10	1.31	0.21				
Forest	0.70	0.35	0.94	0.23				
Forest/shrub	1.66	0.67	3.16	0.59				
Forest/woody wetland	1.33	0.50	1.92	0.33				
Grass	79.39	3.16	58.17	1.57	73.88	4.40	49.76	1.79
Grass cover type	1.69	0.10	1.74	0.05				
Grass patches	2.64	0.49	3.83	0.23				
Grassland/herbaceous	63.05	4.02	39.29	1.79				
Open water	0.47	0.17	2.94	0.48				
Pasture/hay	13.64	3.48	13.79	1.28				
Ruggedness index	5.73	0.55	3.79	0.18	5.73	0.55	3.79	0.18
Shrub	0.95	0.58	2.23	0.49				
Woody	2.28	0.76	4.14	0.64	0.95	0.47	1.90	0.28
Woody wetland	0.63	0.33	0.98	0.25				

800 m Scale	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Alfalfa	1.48	0.48	2.17	0.32				
All water	2.42	0.68	5.07	0.47				
Barren	0.05	0.03	0.08	0.06				
Crop	16.38	2.70	31.28	1.47	24.49	3.96	42.65	1.67
CRP	1.80	0.78	2.70	0.43				
Developed	0.91	0.14	2.06	0.32	0.44	0.08	2.79	0.52
Emergent wetland	0.36	0.15	1.20	0.15				
Forest	0.64	0.30	0.95	0.22				
Forest/shrub	1.73	0.65	3.24	0.56				
Forest/woody wetland	1.34	0.57	1.90	0.30				
Grass	78.53	2.70	58.20	1.39	72.96	3.86	49.85	1.62
Grass cover type	2.13	0.12	2.30	0.05				
Grass patches	7.48	1.29	12.15	0.67				
Grassland/herbaceous	61.31	3.71	39.48	1.63				
Open water	1.28	0.39	2.89	0.37				
Pasture/hay	13.84	3.30	13.81	1.19				
Ruggedness index	7.96	0.69	5.94	0.27	7.96	0.69	5.94	0.27
Shrub	1.06	0.55	2.27	0.47				
Woody	2.44	0.80	4.20	0.60	1.20	0.54	2.13	0.29
Woody wetland	0.70	0.46	0.96	0.20				

1200 m Scale	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Alfalfa	1.56	0.37	2.02	0.24				
All Water	2.75	0.64	4.90	0.42				
Barren	0.06	0.03	0.08	0.06				
Crop	18.08	2.25	29.27	1.24	26.83	3.38	40.41	1.43
CRP	1.69	0.50	2.55	0.29				
Developed	2.61	0.21	4.35	0.26	1.67	0.15	4.21	0.41
Emergent wetland	0.59	0.17	1.05	0.12				
Forest	0.86	0.34	0.97	0.21				

Forest/shrub	1.91	0.64	3.37	0.56				
Forest/woody wetland	1.50	0.51	1.86	0.28				
Grass	74.50	2.21	57.94	1.17	68.89	3.28	50.64	1.42
Grass cover type	2.53	0.13	2.81	0.05				
Grass patches	18.13	2.39	26.13	1.24	3.59	0.35	5.40	0.19
Grassland/herbaceous	58.83	3.27	39.67	1.50				
LSI	4.14	0.20	4.97	0.08				
LSI (grass)	4.20	0.25	5.33	0.11	2.44	0.12	3.40	0.07
Open Water	1.45	0.44	2.92	0.34				
Pasture/hay	12.39	2.83	13.60	1.09				
Ruggedness index	9.75	0.78	7.42	0.32	9.75	0.78	7.42	0.32
Shrub	1.03	0.52	2.36	0.47				
Woody	2.55	0.74	4.26	0.58	1.49	0.50	2.23	0.27
Woody wetland	0.64	0.33	0.89	0.17				
1,600 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.56	0.32	2.02	0.21				
All water	3.16	0.70	4.91	0.40				
Barren	0.06	0.04	0.08	0.06				
Crop	19.44	2.19	29.20	1.15	28.78	3.18	39.96	1.36
CRP	1.69	0.45	2.50	0.25				
Developed	2.44	0.19	3.87	0.23	1.62	0.16	3.61	0.35
Emergent wetland	0.64	0.21	1.01	0.11				
Forest	0.89	0.40	0.94	0.20				
Forest/shrub	1.92	0.66	3.37	0.55				
Forest/woody wetland	1.55	0.53	1.80	0.26				
Grass	72.89	2.10	58.48	1.10	66.49	3.05	51.80	1.35
Grass cover type	2.66	0.13	2.97	0.04				
Grass patches	30.39	3.61	42.18	1.96	4.39	0.44	6.80	0.26
Grassland/herbaceous	57.45	3.16	40.29	1.46				
LSI	5.11	0.25	6.02	0.10				

LSI (grass)	5.32	0.31	6.53	0.14	2.99	0.16	3.98	0.08
Open Water	1.78	0.54	2.95	0.33				
Pasture/hay	12.03	2.74	13.66	1.06				
Ruggedness index	11.41	0.88	8.75	0.36	11.41	0.88	8.75	0.36
Shrub	1.02	0.51	2.42	0.47				
Woody	2.58	0.74	4.22	0.57	1.67	0.52	2.14	0.25
Woody wetland	0.66	0.30	0.85	0.16				
2,400 m Scale	**Mean**	**SE**	**Mean**	**SE**				
Alfalfa	1.67	0.28	1.88	0.17				
All Water	3.63	0.81	4.94	0.37				
Barren	0.14	0.10	0.08	0.05				
Crop	21.14	2.07	28.79	1.05				
CRP	1.56	0.32	2.37	0.21				
Developed	2.14	0.15	3.13	0.19				
Emergent wetland	0.70	0.22	0.94	0.09				
Forest	0.94	0.50	0.92	0.18				
Forest/shrub	1.84	0.67	3.36	0.53				
Forest/woody wetland	1.69	0.67	1.75	0.23				
Grass	70.88	1.96	59.58	1.00				
Grass cover type	3.03	0.12	3.21	0.04				
Grass Patches	68.45	7.09	88.23	4.02				
Grassland/herbaceous	55.97	3.00	41.27	1.42				
LSI	7.01	0.32	8.13	0.15				
LSI (grass)	7.45	0.42	8.95	0.20				
Open Water	2.09	0.64	3.06	0.33				
Pasture/hay	11.64	2.58	14.03	1.05				
Ruggedness index	14.49	1.13	11.02	0.42				
Shrub	0.91	0.43	2.41	0.45				
Woody	2.59	0.79	4.19	0.55				
Woody wetland	0.75	0.38	0.83	0.13				

3,200 m Scale	Mean	SE	Mean	SE
Alfalfa	1.67	0.24	1.76	0.15
All water	3.84	0.80	5.01	0.36
Barren	0.19	0.15	0.08	0.06
Crop	21.16	1.87	27.65	0.97
CRP	1.66	0.30	2.26	0.18
Developed	2.48	0.17	3.59	0.19
Emergent wetland	0.88	0.26	0.99	0.08
Forest	0.95	0.53	0.93	0.17
Forest/shrub	1.83	0.67	3.29	0.51
Forest/woody wetland	1.66	0.64	1.66	0.21
Grass	70.30	1.77	60.30	0.94
Grass cover type	3.30	0.11	3.45	0.04
Grass Patches	124.95	11.78	152.94	6.67
Grassland/herbaceous	55.39	2.86	42.14	1.40
LSI	9.16	0.39	10.54	0.19
LSI (grass)	9.74	0.49	11.51	0.25
Open water	2.19	0.68	3.22	0.33
Pasture/hay	11.55	2.47	14.10	1.05
Ruggedness index	16.98	1.27	13.17	0.50
Shrub	0.83	0.42	2.33	0.43
Woody	2.53	0.75	4.03	0.52
Woody wetland	0.70	0.29	0.74	0.11

Appendix 2. Mean and standard error (SE) for habitat variables surrounding section centers occupied or unoccupied by a sharp-tailed grouse lek in South Dakota, 2014–2016. See table 1 and methods section for variable definitions. Note, only areas ≤ 1,600 m from section centers were manually digitized by photointerpretation.

	NLCD habitat layers				Digitized habitat layers			
Variable	**Occupied (n = 46)**		**Unoccupied (n = 375)**		**Occupied**		**Unoccupied**	
400 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.33	0.59	1.99	0.34				
All water	1.11	0.42	5.09	0.58				
Barren	0.02	0.02	0.06	0.05				
Crop	11.98	2.89	31.67	1.60	16.99	4.19	43.09	1.84
CRP	2.24	1.29	2.90	0.53				
Developed	0.74	0.26	1.52	0.35	0.28	0.13	2.47	0.54
Emergent wetland	0.28	0.13	1.26	0.20				
Forest	0.98	0.48	0.89	0.22				
Forest/shrub	2.30	0.92	3.01	0.56				
Forest/woody wetland	1.59	0.66	1.86	0.32				
Grass	83.87	3.13	58.63	1.54	81.71	4.18	49.95	1.77
Grass cover type	1.78	0.12	1.73	0.04				
Grass patches	2.78	0.61	3.75	0.22				
Grassland/herbaceous	69.15	4.27	39.68	1.75				
Open water	0.22	0.10	2.86	0.46				
Pasture/hay	11.22	3.57	14.08	1.28				
Ruggedness index	6.25	0.74	3.81	0.17	6.25	0.74	3.81	0.17
Shrub	1.33	0.80	2.12	0.47				
woody	2.91	1.02	3.97	0.61	0.96	0.59	1.85	0.27
Woody wetland	0.61	0.41	0.97	0.24				
800 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.89	0.64	2.08	0.30				

All water	2.65	0.91	4.91	0.45				
Barren	0.07	0.04	0.08	0.06				
Crop	11.22	2.21	31.20	1.44	16.38	3.48	42.78	1.65
CRP	2.20	1.04	2.61	0.41				
Developed	0.89	0.17	2.01	0.31	0.53	0.11	2.66	0.50
Emergent wetland	0.41	0.20	1.15	0.14				
Forest	0.87	0.41	0.91	0.21				
Forest/shrub	2.39	0.88	3.09	0.53				
Forest/woody wetland	1.70	0.77	1.83	0.28				
Grass	82.85	2.48	58.64	1.36	80.74	3.43	50.00	1.60
Grass cover type	2.26	0.13	2.27	0.05				
Grass patches	7.91	1.67	11.87	0.65				
Grassland/herbaceous	67.11	3.81	39.82	1.60				
Open water	1.30	0.50	2.81	0.36				
Pasture/hay	11.52	3.23	14.09	1.20				
Ruggedness index	8.77	0.89	5.94	0.26	8.77	0.89	5.94	0.26
Shrub	1.48	0.76	2.17	0.45				
Woody	3.22	1.08	4.02	0.57	1.42	0.73	2.05	0.28
Woody wetland	0.83	0.63	0.93	0.19				
1,200 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.74	0.48	1.98	0.23				
All water	3.33	0.86	4.73	0.40				
Baren	0.09	0.04	0.08	0.06				
Crop	13.57	1.89	29.29	1.20	18.88	2.89	40.73	1.42
CRP	1.76	0.64	2.50	0.28				
Developed	2.54	0.25	4.28	0.25	1.74	0.19	4.08	0.39
Emergent wetland	0.78	0.23	1.01	0.11				
Forest	1.15	0.47	0.93	0.20				
Forest/shrub	2.61	0.87	3.21	0.53				
Forest/woody wetland	1.87	0.70	1.79	0.26				

Grass	77.87	2.07	58.32	1.15	76.15	2.86	50.63	1.40
Grass cover type	2.65	0.13	2.78	0.05				
Grass patches	19.13	3.08	25.62	1.20	3.41	0.38	5.34	0.19
Grassland/herbaceous	63.74	3.33	39.99	1.47				
LSI	4.21	0.25	4.93	0.08				
LSI (grass)	4.19	0.29	5.27	0.11	2.45	0.14	3.35	0.07
Open water	1.76	0.60	2.81	0.33				
Pasture/hay	10.52	2.78	13.77	1.09				
Ruggedness index	10.63	1.02	7.43	0.31	10.63	1.02	7.43	0.31
Shrub	1.43	0.72	2.25	0.45				
Woody	3.33	1.00	4.08	0.56	1.82	0.67	2.16	0.26
Woody wetland	0.72	0.44	0.87	0.16				
1,600 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.65	0.42	1.99	0.20				
All water	3.91	0.94	4.73	0.38				
Barren	0.09	0.05	0.08	0.06				
Crop	15.28	2.01	29.24	1.13	21.25	2.92	40.35	1.34
CRP	1.78	0.59	2.45	0.24				
Developed	2.37	0.22	3.81	0.22	1.68	0.20	3.51	0.33
Emergent wetland	0.83	0.28	0.97	0.10				
Forest	1.20	0.54	0.90	0.19				
Forest/shrub	2.63	0.90	3.21	0.52				
Forest/woody wetland	2.00	0.72	1.73	0.25				
Grass	75.65	2.08	58.83	1.07	73.14	2.86	51.69	1.32
Grass cover type	2.78	0.13	2.94	0.05				
Grass patches	32.39	4.67	41.37	1.89	4.35	0.54	6.69	0.25
Grassland/herbaceous	61.48	3.33	40.62	1.43				
LSI	5.25	0.32	5.96	0.10				
LSI (grass)	5.37	0.37	6.47	0.13	3.05	0.20	3.93	0.08
Open water	2.22	0.74	2.84	0.32				

Pasture/hay	10.52	2.80	13.77	1.06				
Ruggedness index	12.40	1.16	8.75	0.34	12.40	1.16	8.75	0.34
Shrub	1.41	0.70	2.30	0.44				
woody	3.43	1.00	4.04	0.55	2.03	0.71	2.07	0.23
Woody wetland	0.80	0.40	0.83	0.15				
2,400 m Scale	**Mean**	**SE**	**Mean**	**SE**				
Alfalfa	1.85	0.36	1.85	0.17				
All water	4.63	1.10	4.75	0.36				
Barren	0.20	0.14	0.08	0.05				
Crop	17.17	2.12	28.91	1.02				
CRP	1.48	0.41	2.34	0.20				
Developed	2.11	0.19	3.08	0.19				
Emergent wetland	0.93	0.30	0.90	0.08				
Forest	1.28	0.69	0.88	0.17				
Forest/shrub	2.54	0.91	3.20	0.50				
Forest/woody wetland	2.26	0.91	1.68	0.22				
Grass	73.02	2.14	59.86	0.97				
Grass cover type	3.17	0.13	3.18	0.04				
Grass patches	71.26	8.88	86.93	3.87				
Grassland/herbaceous	59.11	3.28	41.59	1.39				
LSI	7.17	0.40	8.06	0.14				
LSI (grass)	7.48	0.48	8.88	0.19				
Open water	2.70	0.87	2.94	0.31				
Pasture/hay	10.63	2.73	14.04	1.04				
Ruggedness index	15.68	1.49	11.04	0.41				
Shrub	1.26	0.59	2.29	0.43				
Woody	3.52	1.07	4.00	0.53				
Woody wetland	0.98	0.52	0.80	0.13				
3,200 m Scale	**Mean**	**SE**	**Mean**	**SE**				
Alfalfa	1.89	0.30	1.73	0.14				

All water	4.87	1.07	4.82	0.35
Barren	0.26	0.20	0.08	0.05
Crop	17.57	2.03	27.78	0.93
CRP	1.63	0.35	2.23	0.17
Developed	2.50	0.22	3.53	0.18
Emergent wetland	1.15	0.35	0.95	0.08
Forest	1.30	0.73	0.89	0.16
Forest/shrub	2.52	0.91	3.13	0.48
Forest/woody wetland	2.20	0.88	1.60	0.20
Grass	72.04	2.05	60.56	0.91
Grass cover type	3.39	0.13	3.43	0.04
Grass patches	132.11	15.10	150.72	6.42
Grassland/herbaceous	57.83	3.18	42.47	1.36
LSI	9.46	0.49	10.43	0.18
LSI (grass)	9.93	0.60	11.40	0.24
Open water	2.76	0.94	3.10	0.32
Pasture/hay	10.72	2.64	14.07	1.03
Ruggedness index	18.31	1.69	13.19	0.48
Shrub	1.15	0.57	2.22	0.41
Woody	3.41	1.02	3.85	0.50
Woody wetland	0.89	0.40	0.71	0.11

Appendix 3. Mean and standard error (SE) for habitat variables surrounding section centers occupied or unoccupied by a greater prairie-chicken lek in South Dakota, 2014–2016. See table 1 and methods section for variable definitions. Note, only areas ≤ 1,600 m from section centers were manually digitized by photointerpretation.

Variable	Occupied (n = 26)		Unoccupied (n = 395)		Occupied		Unoccupied	
400 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	0.50	0.46	2.01	0.33				
All water	1.62	0.56	4.86	0.55				
Barren	0.00	0.00	0.06	0.05				
Crop	21.50	5.79	30.05	1.54	37.43	8.13	40.42	1.79
CRP	0.42	0.42	2.99	0.52				
Developed	0.38	0.27	1.50	0.33	0.16	0.16	2.37	0.51
Emergent wetland	0.19	0.12	1.21	0.19				
Forest	0.73	0.69	0.91	0.21				
Forest/shrub	0.73	0.69	3.07	0.54				
Forest/woody wetland	1.19	0.77	1.87	0.31				
Grass	75.77	5.65	60.45	1.50	61.34	8.06	52.90	1.74
Grass cover type	1.54	0.16	1.75	0.04				
Grass patches	1.92	0.55	3.76	0.22				
Grassland/herbaceous	55.12	6.83	42.10	1.74				
Open water	0.92	0.39	2.68	0.44				
Pasture/hay	19.73	6.42	13.38	1.21				
Ruggedness index	5.43	0.81	3.99	0.18	5.43	0.81	3.99	0.18
Shrub	0.00	0.00	2.17	0.46				
Woody	1.19	0.77	4.03	0.59	0.66	0.54	1.83	0.27
Woody wetland	0.46	0.39	0.96	0.23				
800 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.19	0.90	2.12	0.29				
All water	1.46	0.53	4.88	0.44				

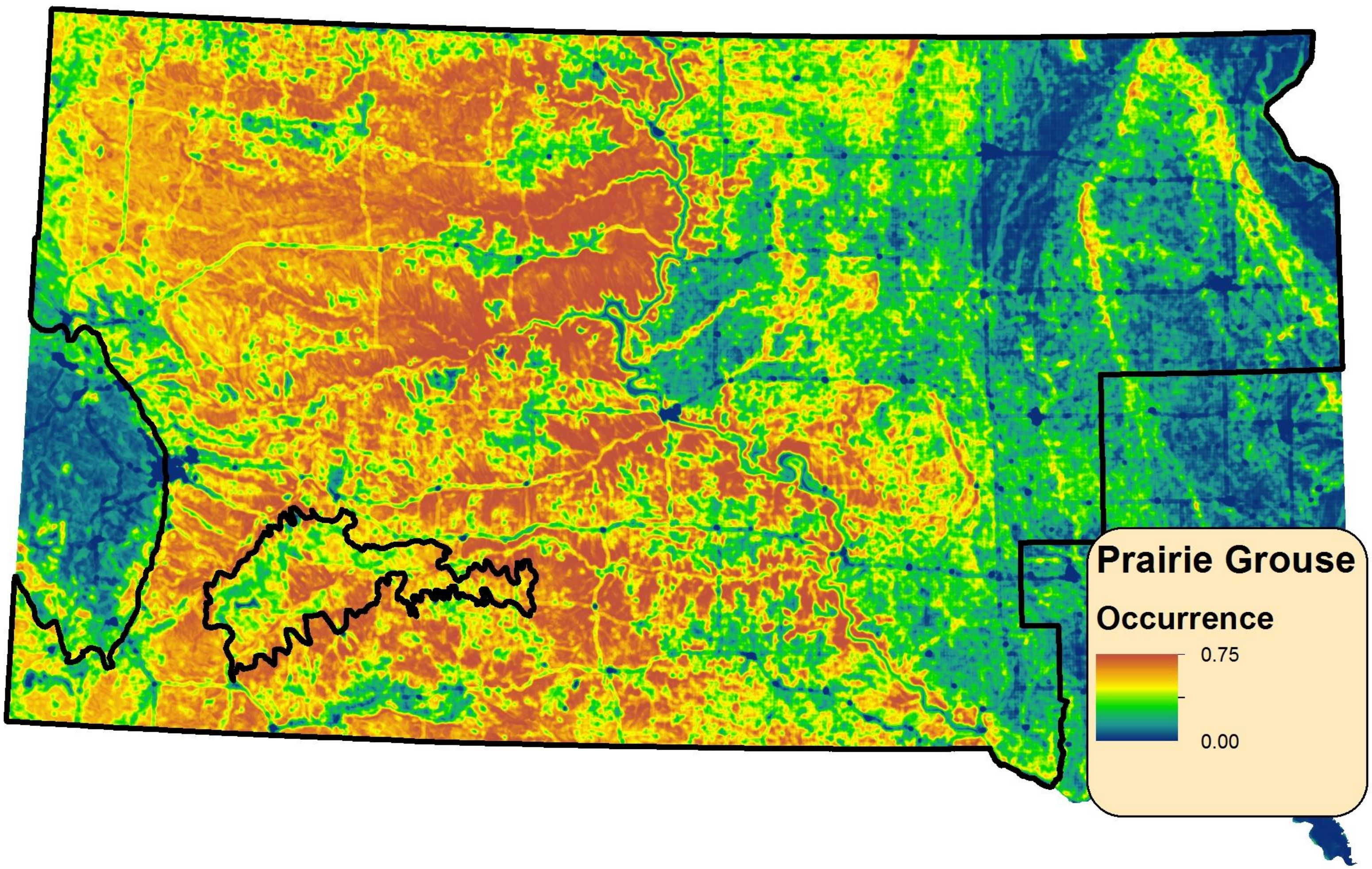
Barren	0.00	0.00	0.08	0.06				
Crop	22.27	5.31	29.46	1.38	36.13	7.28	40.14	1.61
CRP	0.69	0.55	2.68	0.40				
Developed	0.81	0.22	1.96	0.29	0.27	0.09	2.57	0.47
Emergent wetland	0.15	0.11	1.13	0.14				
Forest	0.50	0.46	0.93	0.20				
Forest/shrub	0.54	0.46	3.18	0.51				
Forest/woody wetland	0.81	0.52	1.89	0.28				
Grass	74.77	5.13	60.40	1.33	62.50	7.17	52.76	1.58
Grass cover type	1.81	0.19	2.30	0.05				
Grass patches	5.27	1.24	11.85	0.64				
Grassland/herbaceous	54.50	6.66	42.03	1.58				
Open water	0.92	0.41	2.76	0.34				
Pasture/hay	18.42	6.27	13.51	1.13				
Ruggedness index	7.39	0.97	6.17	0.26	7.39	0.97	6.17	0.26
Shrub	0.00	0.00	2.23	0.43				
Woody	0.85	0.53	4.13	0.55	0.49	0.34	2.08	0.27
Woody wetland	0.31	0.23	0.96	0.20				
1,200 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.50	0.61	1.98	0.22				
All water	1.42	0.42	4.78	0.39				
Barren	0.04	0.04	0.08	0.06				
Crop	23.38	4.37	27.85	1.16	37.74	6.21	38.38	1.37
CRP	1.27	0.56	2.50	0.27				
Developed	2.50	0.33	4.19	0.24	1.41	0.19	3.98	0.38
Emergent wetland	0.15	0.07	1.04	0.11				
Forest	0.50	0.39	0.98	0.20				
Forest/shrub	0.58	0.40	3.32	0.51				
Forest/woody wetland	0.92	0.45	1.86	0.26				
Grass	71.85	4.23	59.70	1.12	59.77	6.12	53.00	1.37

Grass cover type	2.23	0.23	2.80	0.05				
Grass patches	13.46	2.60	25.67	1.17	3.58	0.59	5.23	0.18
Grassland/herbaceous	53.50	5.98	41.87	1.44				
LSI	3.75	0.27	4.92	0.08				
LSI (grass)	3.87	0.38	5.24	0.11	2.25	0.17	3.32	0.07
Open water	0.81	0.34	2.82	0.32				
Pasture/hay	15.65	5.41	13.27	1.03				
Ruggedness index	9.25	1.09	7.68	0.31	9.25	1.09	7.68	0.31
Shrub	0.12	0.12	2.30	0.43				
Woody	1.00	0.48	4.19	0.54	0.57	0.29	2.22	0.25
Woody wetland	0.42	0.22	0.88	0.16				
1,600 m Scale	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Alfalfa	1.42	0.42	1.98	0.20				
All water	1.77	0.67	4.83	0.38				
Barren	0.00	0.00	0.09	0.05				
Crop	23.96	4.08	27.96	1.08	38.47	5.61	38.25	1.30
CRP	1.38	0.55	2.45	0.23				
Developed	2.42	0.29	3.73	0.21	1.37	0.18	3.43	0.31
Emergent wetland	0.15	0.07	1.00	0.10				
Forest	0.38	0.31	0.97	0.19				
Forest/shrub	0.58	0.36	3.32	0.50				
Forest/woody wetland	0.73	0.37	1.83	0.25				
Grass	71.15	3.92	59.98	1.04	58.62	5.42	53.73	1.29
Grass cover type	2.46	0.24	2.96	0.04				
Grass patches	21.35	3.88	41.64	1.84	4.08	0.57	6.58	0.25
Grassland/herbaceous	53.46	5.69	42.20	1.40				
LSI	4.48	0.32	5.98	0.10				
LSI (grass)	4.71	0.45	6.45	0.13	2.68	0.19	3.90	0.08
Open water	1.19	0.66	2.88	0.31				
Pasture/hay	14.81	5.14	13.32	1.00				

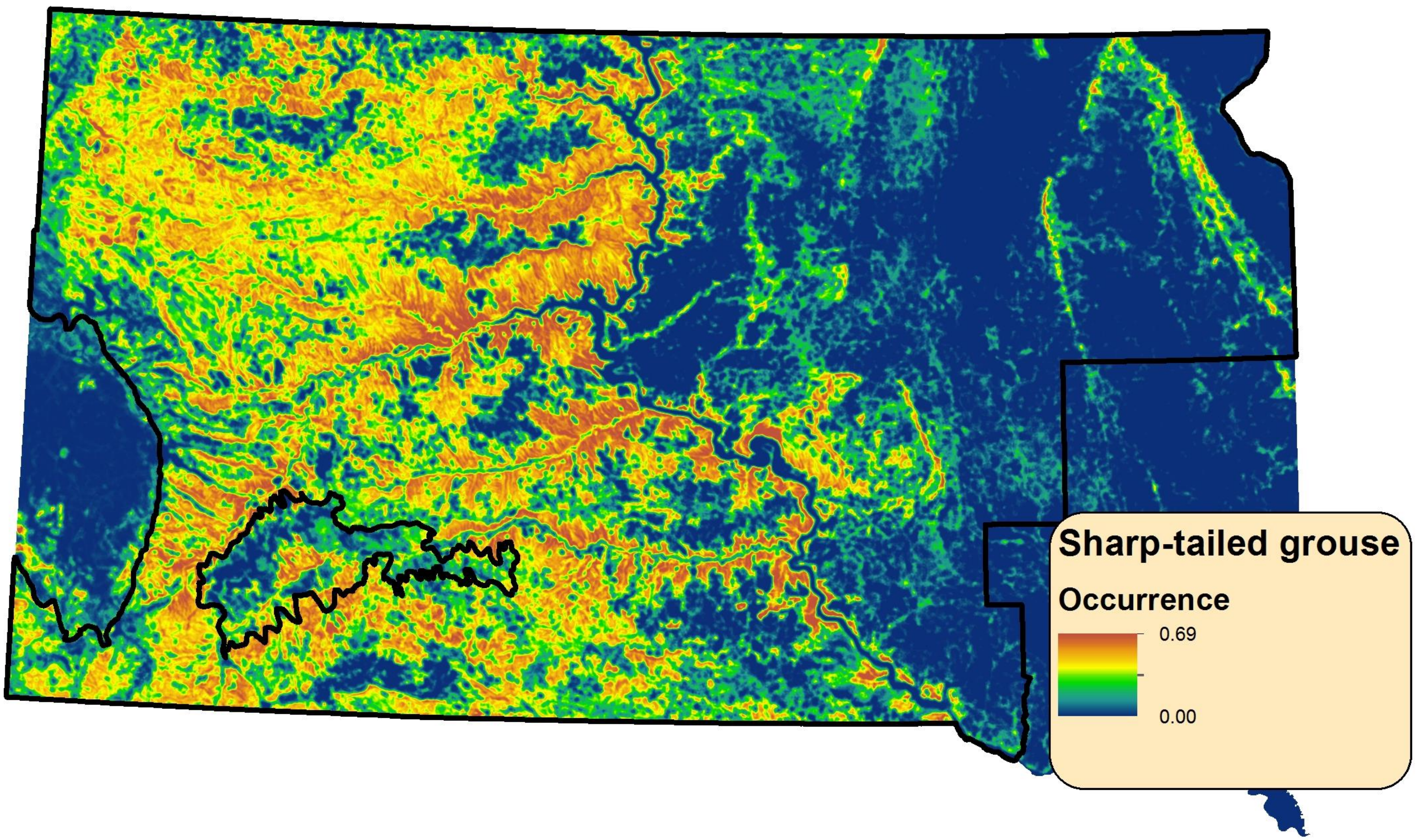
Ruggedness index	10.95	1.23	9.03	0.35	10.95	1.23	9.03	0.35
Shrub	0.15	0.15	2.34	0.43				
Woody	0.92	0.45	4.17	0.53	0.74	0.25	2.16	0.24
Woody wetland	0.35	0.19	0.86	0.15				
2,400 m Scale	**Mean**	**SE**	**Mean**	**SE**				
Alfalfa	1.23	0.32	1.89	0.16				
All water	2.31	1.17	4.90	0.35				
Barren	0.00	0.00	0.10	0.05				
Crop	25.27	3.53	27.78	0.99				
CRP	1.69	0.50	2.28	0.19				
Developed	2.04	0.23	3.04	0.18				
Emergent wetland	0.08	0.08	0.96	0.09				
Forest	0.27	0.23	0.97	0.18				
Forest/shrub	0.42	0.27	3.31	0.49				
Forest/woody wetland	0.58	0.27	1.82	0.23				
Grass	70.04	3.37	60.72	0.95				
Grass patches	51.35	8.67	87.45	3.75				
Grassland cover type	2.81	0.23	3.21	0.04				
Grassland/herbaceous	53.19	5.23	42.87	1.35				
LSI	6.14	0.43	8.08	0.14				
LSI (grass)	6.64	0.65	8.86	0.19				
Open water	1.77	1.18	2.99	0.30				
Pasture/hay	13.69	4.72	13.67	0.99				
Ruggedness index	14.02	1.52	11.39	0.42				
Shrub	0.15	0.15	2.31	0.41				
woody	0.73	0.34	4.16	0.51				
Woody wetland	0.31	0.15	0.85	0.13				
3,200 m Scale	**Mean**	**SE**	**Mean**	**SE**				
Alfalfa	1.04	0.27	1.79	0.14				
All water	2.65	1.39	4.97	0.34				

Barren	0.00	0.00	0.10	0.06
Crop	24.81	3.01	26.78	0.91
CRP	1.54	0.47	2.21	0.16
Developed	2.27	0.23	3.50	0.17
Emergent wetland	0.15	0.07	1.02	0.08
Forest	0.27	0.23	0.97	0.17
Forest/shrub	0.38	0.25	3.24	0.47
Forest/woody wetland	0.62	0.26	1.73	0.21
Grass	69.73	2.88	61.30	0.89
Grass cover type	3.08	0.19	3.45	0.04
Grass patches	92.42	12.52	152.39	6.24
Grassland/herbaceous	53.81	4.91	43.52	1.33
LSI	7.90	0.48	10.49	0.18
LSI (grass)	8.48	0.69	11.42	0.23
Open water	2.12	1.40	3.13	0.31
Pasture/hay	13.15	4.46	13.74	0.99
Ruggedness index	16.42	1.59	13.57	0.49
Shrub	0.08	0.08	2.23	0.40
Woody	0.73	0.31	4.00	0.49
Woody wetland	0.35	0.15	0.76	0.11

Appendix 4. Occurrence model for prairie grouse in South Dakota.



Appendix 5. Occurrence model for sharp-tailed grouse in South Dakota.



Appendix 6. Occurrence model for greater prairie-chicken in South Dakota.