

## CHAPTER TWO

# Hierarchical Modeling of Lek Habitats of Greater Prairie-Chickens

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*Abstract.* Greater Prairie-Chickens (*Tympanuchus cupido*) are a lek-mating prairie grouse of the central Great Plains. Males gather each spring at communal display grounds or leks to compete for mating opportunities with females, and lek sites are essential for the reproductive biology of prairie-chickens. We obtained geographic coordinates for 166 active leks located in eastern Kansas. Using GIS analysis, we developed a spatially explicit model to identify landcover and geomorphological variables associated with lek locations. We used a hierarchical approach to model selection to identify the best predictor variables at three spatial scales (0 m, 200 m, and 5 km), and then combined factors from the best models into a global multi-scale model. We found that a synthetic variable, weighted elevation or the point elevation standardized by the elevation of the surrounding landscape, best explained lek occurrence at a lek point scale of 0 m. At broader spatial scales of 200 m and 5 km, avoidance of agricultural, urban, and

forest habitats, avoidance of high densities of roads, and a preference for grassland cover were the best predictors of lek site locations. Next, we created an entropy model based on factors from our minimum Bayesian Information Criterion global model to create an index of suitable lek habitat across the Flint Hills, Smoky Hills, and Osage Plains ecoregions of eastern Kansas. The entropy model showed that >85% of lek sites were in habitat strata that comprised <20% of the regional landscape, suggesting that prairie-chickens may be utilizing areas that are of marginal quality. Our research results have important implications for conservation because Kansas prairies are the core of extant distribution of Greater Prairie-Chickens and include the largest remaining intact grasslands in the United States.

*Key Words:* entropy modeling, landscape ecology, lek habitat, niche modeling, tallgrass prairie, *Tympanuchus cupido*.

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Conversion of native grasslands to agriculture has caused dramatic declines in prairie habitats since European settlement, and tallgrass prairie is one of the most highly endangered ecosystems in North America, with <5% of the original area remaining (Samson and Knopf 1994). Eastern Kansas includes >90% of the tallgrass prairie ecosystem left in North America, and the Smoky Hills, Flint Hills, and Osage Plains ecoregions have been recognized as ecologically important because they are core areas for grassland birds, an avian community of conservation concern (Fitzgerald et al. 2000, Pashley et al. 2000, Brennan and Kuvlevsky 2005). Unfortunately, long-term changes in land use and rangeland management practices may be negatively impacting the regional population viability of grassland birds in Kansas (Powell 2006, With et al. 2008, Rahmig et al. 2009).

Greater Prairie-Chickens (*Tympanuchus cupido*, hereafter "prairie-chickens") are a prairie grouse that are native to the grasslands of North America (Schroeder and Robb 1993). Prairie-chickens have been extirpated from much of their historical range, and historic losses were likely due to anthropogenic conversion of grasslands to row crop agriculture. The core of the remaining range of the species is in eastern Kansas and adjacent states, and populations in Kansas have been declining for over 30 years (Svedarsky et al. 2000, Rodgers 2008). The underlying causes for ongoing population declines are poorly understood but may be related to changes in land use practices or predator communities. Regardless of the cause, ongoing population declines are a serious conservation concern. Kansas is the core of the remaining range, and translocations of birds from source populations in Kansas have been used to bolster population numbers and increase genetic diversity within relict populations of prairie-chickens in Illinois and Missouri (Bouzat et al. 1998, B. E. Jamison, pers. comm.). A better understanding of the distribution and habitat requirements of prairie-chickens will aid conservation for this species and the associated community of grassland birds.

Wildlife habitat use is hierarchical, and animals make decisions about which areas to use at multiple spatial scales (Johnson 1980). At broad scales of ~10 km, prairie-chickens may avoid unsuitable habitats within their large home ranges (Hamerstrom and Hamerstrom 1960, Prose 1985).

At finer scales of ~1 km, prairie-chickens may use different vegetative cover types for different purposes such as nesting, feeding, and roosting (Svedarsky 1988, McCarthy et al. 1994, Ryan et al. 1998). When engaged in these activities, prairie-chickens may select patches to reduce predation risk, to optimize their thermal environment, or to forage on important food plants (Buhnerkempe et al. 1984, Ryan et al. 1998). Heterogeneity among patches within landcover types provides different resources, and consequently some patches may be more desirable than others. At each spatial scale, prairie-chickens must make decisions about where to allocate time and energy, and habitat preferences at broader scales likely impact the choices available at finer spatial scales.

We evaluated the suitability of the Flint Hills, Smoky Hills, and Osage Plains ecoregions of Kansas based on multiscale geospatial modeling of lek site locations for Greater Prairie-Chickens. Leks or booming grounds are communal display sites where male prairie-chickens congregate to display and mate with females. Male prairie-chickens show high site fidelity to leks from one breeding season to the next, and lek locations can be relatively stable over time (Robel 1970, Nooker and Sandercock 2008). Most mating is thought to occur at lek sites, and consequently suitable lekking sites are a necessary component of prairie-chicken habitat (Hamerstorm and Hamerstrom 1960, Schroeder and Robb 1993). Female prairie-chickens usually nest in the vicinity of leks ( $\leq$  km; Hamerstrom 1939, Schroeder 1991), and lek site location ought to serve as a proxy for the occurrence of suitable nesting habitat at a landscape scale. Indeed, one proposed mechanism for lek evolution (the hot spot hypothesis) hypothesizes that leks evolved as males settled and clustered on pathways used preferentially by females to travel between needed resources (Beehler and Foster 1988, Schroeder and White 1993).

The primary goal of our landscape model was to identify suitable versus unsuitable habitat based on the location attributes of lek sites. We used a hierarchical modeling approach with three spatial scales of 0 m, 200 m, and 5 km, based on the movements and space use of prairie-chickens in Kansas (Robel et al. 1970). When modeling habitat suitability, even the most refined spatial scales are a coarse-grained approach to conservation, because we must assume that microhabitat features within identified habitat patches have

the potential to be improved with management practices. Prairie-chickens could be considered an umbrella species for grassland communities because the species requires large tracts of grasslands (Svedarsky 1988, Poiani et al. 2001). Our main goal was to identify areas in need of conservation or enhancement for prairie-chickens, but our modeling approach and research results also have conservation implications for other sensitive species of grassland birds (Herkert 1994, Brennan and Kuvlesky 2005).

## METHODS

To create an index of suitable prairie-chicken habitat for our study region, we performed a geospatial analysis of 166 lek locations distributed across the Flint Hills, Smoky Hills, and Osage Plains ecoregions of Kansas (Fig. 2.1; Griffith et al. 2008). Geographical coordinates of leks were collected as part of a 3-year population study of prairie-chickens in eastern Kansas (2006–2008; L. B. McNew et al., this volume, chapter 15) and from lek surveys conducted by the Kansas Department of Wildlife and Parks (KDWP, 2005–2007). KDWP survey routes were originally established in the late 1950s at a sampling density of 1 route

surveying 57.8 km<sup>2</sup> per county, but sampling efforts are being continually expanded. KDWP survey routes were not established in targeted areas with known prairie-chicken populations, but rather were selected based on the presence of large tracts of grassland habitat and relatively good access via county roads. For the purposes of KDWP surveys, leks were defined as  $\geq 3$  males displaying in an area, and were located by listening for prairie-chicken booming at 1-mile intervals along the survey routes and by performing flush counts on located leks (R. D. Rodgers, pers. comm.). Our intensive population study was primarily conducted in Cloud, Geary, and Elk counties. For the intensive surveys, leks were also defined as  $\geq 3$  males displaying in an area and were located via listening along all county roads within the identified counties. We also sought landowner permission to survey large road-free tracts of land either on foot or with all-terrain vehicles.

We used Arc Info 9.2 (Environmental Systems Research Institute, Redlands, CA) for all geospatial analysis and data extraction. We acquired all data sets from the Kansas Geospatial Community Commons ([www.kansasgis.org](http://www.kansasgis.org)). For land cover analyses, we used the 30-m resolution, 2005 land cover map of the State of Kansas (Kansas Applied

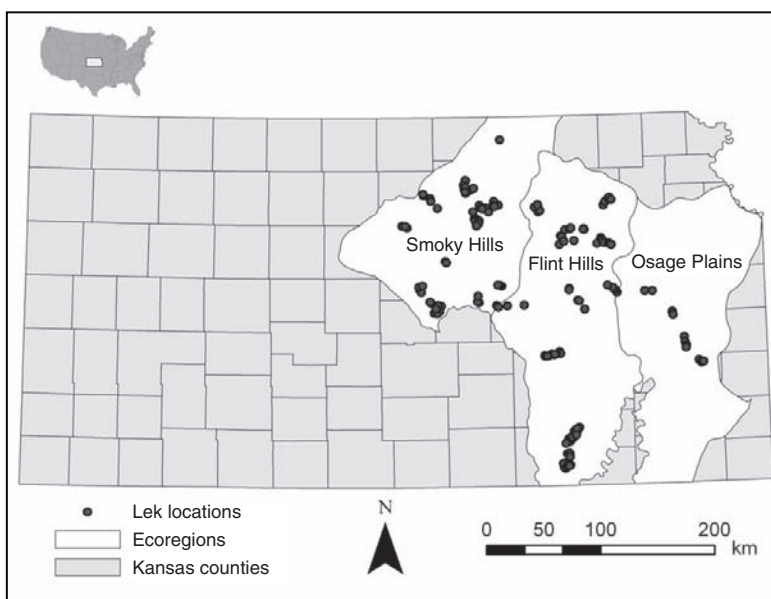


Figure 2.1. Study area and lek sites of Greater Prairie-Chickens in eastern Kansas, 2005–2008. Ecoregions represent areas of similar ecosystems and geomorphological characteristics. Black dots are locations of leks used for model development and validation. Inset map indicates the location of Kansas within the United States.

Remote Sensing Program 2005; Whistler et al. 2006), which we reclassified to an Anderson Level I classification scheme, depicting five biologically relevant landcover classes: grassland, row crop agriculture, urban, forested, and water (Anderson et al. 1971). Grasslands included all CRP (Conservation Reserve Program) lands, or grazed and ungrazed pastures of native prairie. Row crop agriculture included croplands plus all tillable acres. Urban areas were defined as all cities, towns, roads, and human dwellings. Forested lands included gallery forests and riparian corridors, whereas water included rivers, streams, stock ponds, and reservoirs. For geomorphological analyses, we used the 30-m resolution 1999 National Elevation Dataset (U.S. Geological Survey, EROS Data Center). We also included a 1991 Riparian Inventory data set for the state of Kansas (U.S. Department of Agriculture, Natural Resources Conservation Service) and a roadway data set that combined the 2006 Kansas State and Non-State Road System data sets (Kansas Department of Transportation, Bureau of Transportation Planning). Each land cover data set was aggregated to 100-m grain size prior to landscape analysis.

To assess differences in landscape and habitat features of lek sites versus potentially available landscape features and habitats, 132 random points were generated within the same spatial extent as lek locations using Arc Info 9.2 and were later used in logistic regression model fitting. Prior to model fitting procedures, we randomly selected 34 of 166 (20%) lek locations and an additional 34 randomly generated locations and withheld them from model development to be used for model validation.

To evaluate characteristics of the area surrounding lek sites at a landscape spatial scale, we buffered each lek site with a 5-km neighborhood radius which evaluated landscape patterns at large spatial scale. Females typically choose nesting sites within 2 km of lek locations (Hamerstrom 1939, Schroeder 1991), and the average home range size of a prairie-chicken in Kansas is 500 ha (Robel 1970). Thus a 5-km buffer was selected to encompass possible nesting habitats around lek sites. For the intermediate spatial scale, we analyzed lek habitat characteristics within overlapping neighborhoods of 200 m radii, a distance that would likely characterize the habitat used for lekking itself. Analysis at these two spatial scales tested whether characteristics

of the landscape surrounding lek sites influenced the presence or absence of leks. We used neighborhood statistics to calculate the percent area for each of the six landcover types and Fragstats 3.3 to calculate the total core area of grassland patches using the eight neighbor patch rule and 100 m edge depth (McGarigal and Marks 1995). Within neighborhoods, we calculated the density of all roads (km per km<sup>2</sup>) as an index of disturbance, and the density of 10-m elevational contour lines as an index of habitat complexity or topographic relief.

At the finest spatial scale at 0 m or the point of the lek, we measured attributes of the geographic center of the lek. We recorded four variables: distance to riparian areas, distance to urban areas, distance to roads, and weighted elevation. Weighted elevation was a synthetic variable that compared the absolute elevation of the lek site relative to the surrounding landscape, calculated as the elevation of the lek location divided by the average elevation of all grid centroid points within 1 km of the location. Use of weighted elevations standardized the topographic positions of leks within our study region to values ranging from 0.7 to 2.0. All measured variables were extracted from landscape data for both known lek sites and an equal number of random points.

Prior to model construction, all variables were standardized by z-transformations to normal distributions with a mean of zero and a standard deviation of 1, so that  $\beta$  coefficients from the resulting models were in the same units and would be directly comparable. We employed a hierarchical approach to model selection. Factors from each spatial scale were first entered into separate logistic regression models, and then significant factors were combined into a global model that pooled important variables across multiple scales. Our hierarchical model selection process consisted of Bayesian model selection at each of three spatial scales, followed by a second round of model selection for models with factors at multiple spatial scales (Schwarz 1978, Hosmer et al. 1997). Hierarchical procedures were used to avoid spatial autocorrelation between data sets. Spatial autocorrelation between scales can occur because scales are nested within each other hierarchically. Hierarchical procedures adjust for spatial autocorrelation by allowing models to be developed for each scale independently and then concatenated across scales. During the concatenation

process, if variables are correlated across scales they are unlikely to be included because of the penalty associated with adding extra parameters. Bayesian model selection (BIC) procedures were used for model selection (Anderson et al. 2000, Johnson and Omland 2004), because these statistics tend to be more conservative and less likely to over-fit data than Akaike's Information Criterion (Burnham and Anderson 2004). A conservative approach to model selection was desirable to compensate for highly spatially correlated data sets. Principal components analysis or factor analysis could have been used to address this issue, but we did not use multivariate techniques because we were primarily interested in the effects of our original landscape variables. Use of the untransformed landscape data was important because we wanted to apply model predictions directly to spatially explicit ecological niche modeling. Improved GIS analysis techniques allow many landscape metrics to be calculated, but our goal was to ensure that only biologically relevant and statistically meaningful metrics were included in our analysis (McGarigal and Marks 1995).

Landscape variables from the minimum BIC multiscale model were used as data inputs for ecological niche modeling using program MaxEnt. Program MaxEnt uses entropy theory to model landscape suitability based only on presence data and to integrate analyses across spatial scales (Phillips et al. 2004); it has several advantages compared to other software for ecological niche modeling, including program GARP (Phillips et al. 2006, Austin 2007). However, program MaxEnt and other niche modeling software packages tend to overestimate landscape suitability when many environmental variables are used, but a conservative model selection procedure based on BIC should have ameliorated this possibility (Phillips et al. 2006). Ecological niche modeling yielded a preliminary index of suitable prairie-chicken lek habitat across the Flint Hills, eastern Smoky Hills, and Osage Plains regions of Kansas. We validated our model by using a random 20% subset of our lek points that were withheld from model development, and assessed the proportion of leks that mapped onto each of the suitability categories of our index. We also compared the suitability of the landscape as predicted from our hierarchical model to the suitability of the landscape as predicted by models based on each of the single spatial scales.

## RESULTS

### Environmental Covariates

At each spatial scale, our analysis indicated different features of the landscape were influencing lek presence. At the broadest scale, which described the area adjacent to leks in a 5-km neighborhood, five of six competing models each received some support ( $w_i > 0.11$ ; Table 2.1). In general, the broad-scale models indicated that lek occurrence was negatively associated with percent forest area, road density, and urban area within the region, but was weakly and positively associated with percent grassland cover and the total core grassland area in a 5-km neighborhood. All possible candidate models for these variables were considered. Using a logistic model describing relative probability of lek occurrence conditional on habitat variables, the minimum BIC model included three variables: percent urban cover, road density, and percent forest cover:  $\text{leks} = 1.08 - 5.92 \times \text{percent urban area} - 1.39 \times \text{road density} - 0.76 \times \text{percent forest}$ .

At the lek habitat scale of a 200-m neighborhood, the global model included percent land coverage for forest, agriculture, urban, grassland, crop, and an estimate of topographic relief based on density of contour lines. All possible candidate models for the variables included in the global model were evaluated. Our selection procedure indicated that a single candidate model received 99% of the model support (Table 2.1), which indicated that lek habitat at a neighborhood of 200 m was most strongly influenced by a negative association with cover of row crop agriculture:  $\text{leks} = 0.01 - 0.46 \times \text{percent agriculture}$ .

At a lek point scale of 0 m, the global model included four variables: distance to roads, urban areas, forest, and weighted elevation. Of all possible candidate models for these four variables, two models received similar levels of support ( $w_i > 0.45$ ; Table 2.1). The minimum BIC model, which received 49% of the model support, modeled lek sites as a function of both the weighted elevation and the distance from urban centers:  $\text{leks} = 0.003 + 1.34 \times \text{weighted elevation} + 0.36 \times \text{distance to urban areas}$ . A second model, which received 46% of the model support, modeled lek site location as a function of weighted elevation.

To understand the importance of different spatial scales in habitat selection, we reran the model selection procedure combining different scales.



TABLE 2.1  
*Bayesian model selection to identify landscape attributes associated with lek sites of Greater Prairie-Chickens  
 in eastern Kansas, 2005–2008.*

Model	K	-2 ln (K)	BIC	ΔBIC	$w_i$	Hosmer-Lemeshow	
						C	P
Habitat Models 5 km							
%Urban, % Frst, Rd. Den	4	286.9	309.3	0.0	0.33	0.80	0.03
%Grass, %Urban, %Frst	4	287.7	310.0	0.7	0.24	0.78	0.07
%Frst, Rd. Den	3	293.8	310.6	1.3	0.18	0.79	0.04
%Urban, %Frst, Rd. Den, ALGP	5	283.1	310.9	1.6	0.14	0.80	0.04
%Grass, %Urban, %Frst, Rd. Den	5	283.5	311.4	2.1	0.12	0.80	0.04
C-Den, %Ag, %CRP, &Grass, %Urban, %H <sub>2</sub> O, %Frst, Rd. Den, ALGP	10	270.5	326.2	16.9	<0.01	0.82	0.86
Habitat Models 200 m							
%Ag	2	227.3	271.9	0.0	0.99	0.66	0.01
C-Den, %Ag, %CRP, %Grass, %Urban, %H <sub>2</sub> O	8	353.0	364.1	92.0	0.01	0.86	0.02
%Frst							
Points Models 0 m							
D-Urb, Wt-Elev	3	281.3	298.1	0.0	0.49	0.82	0.01
Wt-Elev	2	287.0	298.1	0.1	0.46	0.82	0.01
Multi-Scale Model							
%Grass 5 km, %Urban 5 km, Wt-Elev	4	230.2	262.7	0.0	0.42	0.85	0.05
%Urban 5 km, %Frst 5 km, Rd. Den 5 km, Wt-Elev	5	259.3	263.2	0.6	0.32	0.88	0.06
%Urban 5 km, %Frst 5 km, Rd. Den 5 km, ALGP, Wt-Elev	6	259.2	263.6	0.9	0.26	0.88	0.09
%Grass 5 km, %Urban 5 km, %Frst 5 km, Rd. Den 5 km, D-Urb, ALGP, Wt-Elev	8	223.4	273.6	10.9	<0.01	0.89	0.30

NOTE: Variables are defined as follows: ALGP = area in m<sup>2</sup> of the largest contiguous grassland patch in the 5-km neighborhood, C-Den = contour line density, D-RIP = distance to riparian area, D-URB = distance to urban town or city, D-Road = distance to nearest road, %Ag = % of the neighborhood in row crop agriculture, %CRP = % of the neighborhood Conservation Reserve Program, %Frst = % of the neighborhood in forest, %Grass = % of the neighborhood in grassland, %H<sub>2</sub>O = % of the neighborhood in water, %Urban = % of the neighborhood in urban cover, Rd.Den = road density in km per km<sup>2</sup> of the neighborhood, and Wt-Elev = weighted elevation. Column heading labels are as follows: K = number of parameters, -2Ln(K) = maximum likelihood estimate from logistic model, BIC is the Schultz Criterion, and Hosmer-Lemeshow statistics are a goodness-of-fit test for the logistic model.

From the first set of analyses at different spatial scales (0 m, 200 m, and 5 km), we identified a set of eight landscape attributes from the subset of models that had high BIC weights and were equally parsimonious ( $\Delta BIC \leq 2$ ). The global model combining factors from multiple spatial scales included eight factors: percent grassland,

urban or forest at 5 km, road density at 5 km, total core grassland area at 5 km, percent agriculture at 200 m, distance to urban areas, and weighted elevation. We included all possible combinations of variables in the candidate models in the selection procedure, and three of these models received strong model support ( $w_i > 0.25$ ; Table 2.1). The



minimum BIC model, which received 42% of the total model support, indicated strong avoidance of urban areas and preference for relatively high sites with grassland cover:  $\text{leks} = 1.02 - 6.62 \times \text{percent urban area at 5 km} + 1.21 \times \text{weighted elevation} + 0.43 \times \text{percent grassland at 5 km}$ . Other parsimonious models had similar coefficients for these three factors, but also included weak effects for avoidance of areas with high road density or forests and a preference for lek sites close to large grassland patches.

### Niche Modeling

We used the minimum BIC multiscale model and program MaxEnt to create an index of suitable lek habitat for the three ecoregions in our study area (Fig. 2.2). Our niche model predicted that highly suitable habitat for leks was found at or near the highest point on the surrounding landscape. The average weighted elevation was  $1.07 \pm 0.07$  SE, and highly suitable areas were comprised of 90% grassland and 8% agriculture, with <2% of the landscape surrounding leks being forest, water, or urban habitats. Moderately suitable areas were similar to highly suitable areas in having an average weighted elevation of  $1.02 \pm 0.07$  SE, but had less grassland (77%) and more agriculture

(20%) than highly suitable areas; other habitats accounted for ~3% of the landscape. In contrast, low suitability areas were usually distributed in low-lying areas of the landscape and had an average weighted elevation of  $0.87 \pm 0.22$  SE. Low-elevation habitats in our study area frequently included gallery forests, river beds and flood plains, row crop agricultural areas, and urbanized developments. Overall, low-suitability areas were comprised of 51% grassland, 33% agriculture, 9% forests, 4% urban, and 3% water.

Overall, our model predicted that lek sites would occur at or near the highest point on the landscape away from forests, large bodies of water, or urban centers, in areas comprised primarily of grassland with slight to moderate amounts of row crop agriculture. We created similar indices of lek habitat suitability for the minimum BIC models at each single spatial scale and compared the area of suitable habitat predicted by these indices to the area predicted by the multiscale grand model. Predictions from models based on a spatial scale of 0 m and 5 km were most similar to the predictions of the multiscale model (Fig. 2.3), presumably because environmental covariates at these spatial scales had the strongest effects on lek occurrence, as measured by the slope coefficients for z-transformed landscape covariates.

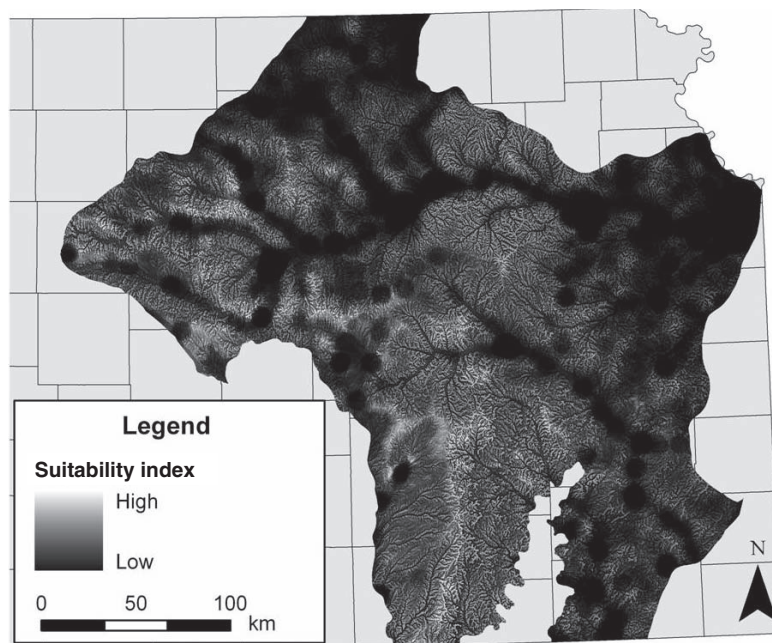


Figure 2.2. Map of habitat suitability based on maximum entropy modeling of lek sites of Greater Prairie-Chickens in eastern Kansas, 2005–2008.

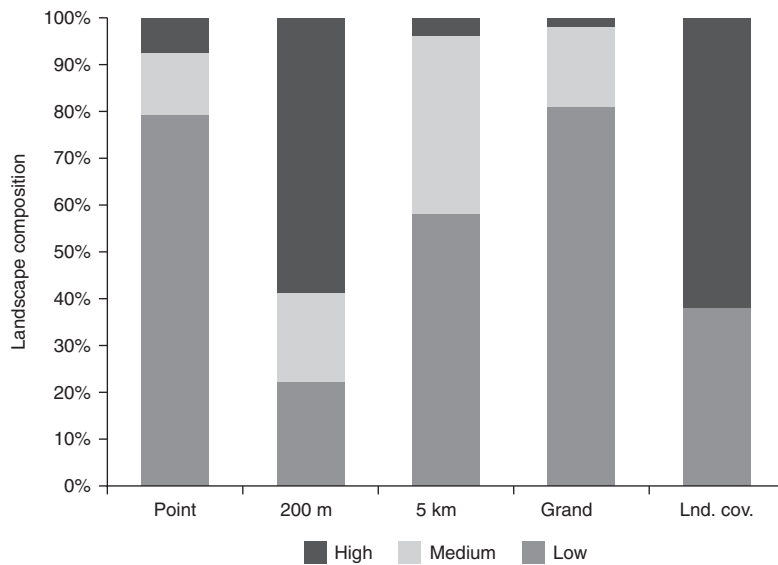


Figure 2.3. Comparisons of habitat suitability of our study area as predicted by models for three spatial scales (0 m, 200 m, and 5 km), a multi-scale model (Grand), and a model based solely on land cover (Lnd. cov.).

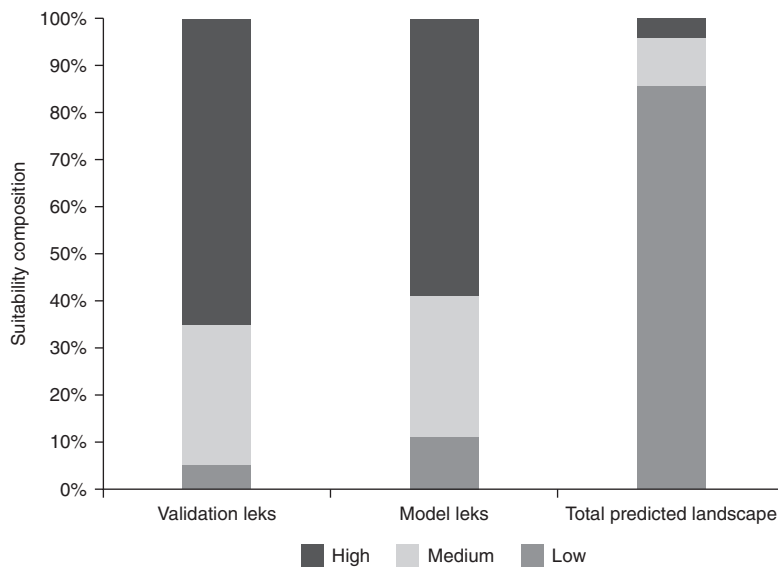


Figure 2.4. Comparisons of habitat suitability among a random set of leks used for model validation ( $n = 34$ ), lek locations used for model development ( $n = 132$ ), and the entire study area (Landscape).

During validation procedures, the final multi-scale model was able to distinguish between randomly selected lek sites and randomly plotted points ( $t = -3.9$ ,  $df = 35$ ,  $P \leq 0.001$ ). Moreover, 88.2% of the randomly selected validation leks ( $n = 34$ ) were correctly classified into suitable habitat. We next plotted geographic coordinates

of random leks onto the multiscale lek habitat suitability index to determine what proportion of these leks occurred in each of the three suitability categories, and compared the proportions to the frequency of occurrence of each habitat type in the landscape as a whole (Fig. 2.4). The top three models gave similar predictions, and in all cases



the leks had substantially higher levels of suitability than the entire landscape. A total of 85–90% of the lek sites occurred in habitat areas of moderate to high suitability, yet only 5–20% of the total landscape included habitats that met these criteria for Greater Prairie-Chickens (Fig. 2.4).

## DISCUSSION

Our hierarchical approach to ecological niche modeling showed that >85% of lek sites of Greater Prairie-Chickens were in habitat strata that comprised <20% of the regional landscape in eastern Kansas. Our results are somewhat discouraging because Kansas prairies are considered to be the last remaining strongholds for conservation of grassland birds in the U.S. (Fitzgerald et al. 2000, Pashley et al. 2000). We expected that the environmental correlates of lek site selection might vary across the geographic distribution of prairie-chickens if differences in the degree of habitat fragmentation affected lek placement. An estimated 36–45% of the landscape of our Kansas study area is comprised of intact grasslands (Applegate et al. 2003, A. J. Gregory and D. G. Goodin, unpubl. data). Previous analyses of lek habitat suitability have been conducted in more fragmented landscapes in Minnesota and Wisconsin, where grasslands are part of a patchy mosaic in a matrix of forest, wetlands, and row crop agriculture (Merrill et al. 1999, Niemuth 2003).

Despite potential differences in landscape configuration, our major findings were consistent with previous analyses of lek site selection for prairie-chickens. Grassland cover at 5 km was a relevant factor in our multiscale model for Kansas, which is consistent with previous studies that have identified cover or size of grassland patches as important factors in determining the presence of prairie-chicken leks elsewhere in their range (Hamerstrom et al. 1957, Kirsch 1974, Merrill et al. 1999, Niemuth 2003). Although grassland cover was relevant in Kansas, we found that relative elevation at the lek location, a lack of agriculture within 200 m, and a lack of urban areas, forest, and roads within 5 km were better predictors of lek presence. Grassland cover alone has previously been found to be a poor predictor of lek location in fragmented landscapes, and avoidance of areas with residential development and forest cover appears to be a general finding for lek site selection by prairie-chickens

(Merrill et al. 1999, Niemuth 2003). In the prairie-dominated landscapes of eastern Kansas, the amount of grassland available may be of less concern for prairie-chicken habitat conservation than the degree of fragmentation and configuration of remaining grassland habitats.

Our multiscale approach to modeling prairie-chicken habitat had two advantages over single-scale niche modeling approaches. First, by using data at different spatial scales and in a combined model, we obtained different suitability estimates of the landscape for the study species. Second, animal habitat use is predicted to be a hierarchical set of decisions (Johnson 1980), and our modeling indicated that different habitat attributes were preferred at different spatial scales. Our point model indicated that prairie-chicken lek sites were located at the highest portion of the surrounding landscape and distant from urban areas. Thus, prairie-chickens may choose display grounds with high visibility, good auditory projection, or areas free from ambient noise (Hamerstrom and Hamerstrom 1960, Aspbury and Gibson 2004, Slabbekoorn and Ripmeester 2008). This combination of features may assist females in locating lek sites or males in detecting and avoiding approaching predators. At the spatial scales of 200 m and 5 km, we observed lek sites being placed in areas that avoided urban areas, row crop agriculture, and roads, indicating avoidance of anthropogenic disturbance at spatial scales relevant to grassland conservation (Schroeder and Robb 1993).

Our model offers insights into the current suitability of the Kansas tallgrass prairies for prairie-chickens. Eastern Kansas represents >90% of the remaining tallgrass prairie in the U.S. (Samson and Knopf 1994). However, >80% of this area was predicted by our model to be of relatively low suitability (Figs. 2.2 and 2.3). Moreover, ~15–20% of the active lek sites in our analysis were in areas of low suitability, which may indicate use of marginal habitats. Prairie-chickens show high site fidelity to lek sites, but landscapes and habitat suitability can change rapidly. Site fidelity may result in a lag period between the time of landscape degradation and habitat abandonment or local extirpation. Thus, males may continue to display at lek sites that are effectively demographic sinks before the population is eventually extirpated (Schroeder and Robb 1993, Nooker and Sandercock 2008). Consequently, lek count surveys that are routinely used for population

monitoring of prairie-chickens may be slow to reveal the impacts of environmental change. Our lek habitat suitability index does not account for the effects of land management on the demographic performance of prairie-chickens attending leks in marginal habitats, and caution should be used when interpreting our map. However, if the habitat requirements for lek and nest sites are closely associated, then our model suggests that much of the landscape in eastern Kansas is unsuitable for prairie-chickens, and habitat may be a limiting factor contributing to ongoing population declines (Rodgers 2008).

Spatial models for prairie-chickens in eastern Kansas, Minnesota, and Wisconsin (Merrill et al. 1999, Niemuth 2003, this study) have shown that lek sites are usually associated with grassland cover and negatively associated with anthropogenic disturbance and forest habitats. One goal for conservation of prairie-chickens should be to preserve large remaining tracts of natural grasslands with little development. A second goal should be to expand connectivity among unfragmented grassland habitats by removal of hedgerows and encroaching woody plants, and by enrollment of agriculture fields into the Conservation Reserve Program. The microhabitats required by prairie-chickens were not identified by our landscape approach, but the suitable habitats identified by our model could represent sites where improved land management would be beneficial. Rangeland management in eastern Kansas frequently includes use of early season burning to enhance forage quality for cattle production (With et al. 2008, Rahmig et al. 2009). Spring burning removes the vegetation that provides nesting cover for female prairie-chickens during the breeding season (L. B. McNew et al., this volume, chapter 15). Changes in land management from annual spring burns to a patch-burn rotational system could benefit Greater Prairie-Chickens and associated species of grassland birds by providing additional cover for ground-nesting species in a more heterogeneous landscape.

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#### LITERATURE CITED

- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- Anderson, J. R., E. E. Hardy, J. T. Roach, and R. E. Witmier. 1971. A land use and land cover classification system for use with remote sensor data. U.S. Geological Survey Professional Paper 964.
- Applegate, R. D., B. E. Flock, and E. J. Finck. 2003. Changes in land use in eastern Kansas, 1984–2000. *Transactions of the Kansas Academy of Science* 106:192–197.
- Aspbury, A. S., and R. M. Gibson. 2004. Long-range visibility of Greater Sage-Grouse leks: a GIS-based analysis. *Animal Behavior* 67:1127–1132.
- Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modeling* 200:1–19.
- Beehler, B. M., and M. S. Foster. 1988. Hotshots, hotspots, and female preferences in the organization of lek mating systems. *American Naturalist* 131:203–219.
- Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. L. Westemeier, J. D. Brawn, and K. N. Paige. 1998. Genetic evaluation of a demographic bottleneck in the Greater Prairie-Chicken. *Conservation Biology* 12:836–843.
- Brennan, L. A., and W. P. Kuvlesky. 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69:1–13.
- Buhnerkempe, J. E., W. R. Edwards, D. R. Vance, and R. L. Westemeier. 1984. Effects of residual vegetation on prairie-chicken nest placement and success. *Wildlife Society Bulletin* 12:382–386.
- Burnham, K. P., and D. R. Anderson. 2004. Understanding AIC and BIC model selection. *Sociological Methods and Research* 33:261–304.
- Fitzgerald, J., B. Busby, M. Howery, R. Klatske, D. Reinking, and D. Pashley. 2000. Partners in

- Flight Bird Conservation Plan for the Osage Plains (Physiogeographic Area 33), Version 1.0. American Bird Conservancy, The Plains, VA.
- Griffith, G. E., J. M. Omernik, and M. McGinley. 2008. Ecoregions of Kansas and Nebraska (EPA). In C. J. Cleveland (editor), *Encyclopedia of earth*. Environmental Information Coalition, National Council for Science and the Environment, Washington, DC.
- Hamerstrom, F. N. 1939. A study of Wisconsin prairie-chicken and Sharp-tailed Grouse in Wisconsin. *Wilson Bulletin* 51:105–120.
- Hamerstrom, F. N., O. E. Matson, and F. Hamerstrom. 1957. A guide to prairie-chicken management. Wisconsin Department of Natural Resources Technical Bulletin 15. Wisconsin Conservation Department, Game Management Division, Madison, WI.
- Hamerstrom, F. N., Jr., and F. Hamerstrom. 1960. Comparability of some social displays of grouse. *Transactions of the International Ornithological Congress* 12:274–293.
- Herkert, J. R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecological Applications* 4:461–471.
- Hosmer, D. W., T. Hosmer, S. Le Cessie, and S. Lemeshow. 1997. A comparison of goodness-of-fit tests for the logistic regression model. *Statistics in Medicine* 16:965–980.
- Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 6:65–71.
- Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101–108.
- Kirsch, L. M. 1974. Habitat considerations for prairie-chickens. *Wildlife Society Bulletin* 2:123–129.
- McCarthy, C., T. Pella, G. Link, and M. A. Rumble. 1994. Greater Prairie-Chicken nesting habitat, Sheyenne National Grassland, North Dakota. *Proceedings of the North Dakota Academy of Science* 48:13–18.
- McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
- Merrill, M. D., K. A. Chapman, K. A. Poiani, and B. Winter. 1999. Land-use patterns surrounding Greater Prairie-Chicken leks in northwestern Minnesota. *Journal of Wildlife Management* 63:189–198.
- Niemuth, N. D. 2003. Identifying landscapes for Greater Prairie-Chicken translocation using habitat models and GIS: a case study. *Wildlife Society Bulletin* 31:145–155.
- Nooker, J. K., and B. K. Sandercock. 2008. Correlates and consequences of male mating success in lek-mating Greater Prairie-Chickens (*Tympanuchus cupido*). *Behavioral Ecology and Sociobiology* 62:1377–1388.
- Pashley, D. N., C. J. Beardmore, J. A. Fitzgerald, R. P. Ford, W. C. Hunter, M. S. Morrison, and K. V. Rosenberg. 2000. Partners in flight: conservation of the landbirds of the United States. American Bird Conservancy, The Plains, VA.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling* 190:231–259.
- Phillips, S. J., M. Dudik, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Pp. 83 in *Proceedings of the Twenty-first International Conference on Machine Learning*. Association for Computing Machinery, Banff, AB, Canada.
- Poiani, K. A., M. D. Merrill, and K. A. Chapman. 2001. Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. *Conservation Biology* 2:513–522.
- Powell, A. F. L. A. 2006. Effects of prescribed burning and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. *Auk* 123:183–197.
- Prose, B. L. 1985. Habitat suitability index models: Greater Prairie-Chicken (multiple levels of resolution). U.S. Fish and Wildlife Service, Biological Report 82:(10.102).
- Rahmig, C. J., W. E. Jensen, and K. A. With. 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. *Conservation Biology* 23:420–432.
- Robel, R. J. 1970. Possible role of behavior in regulating Greater Prairie-Chicken populations. *Journal of Wildlife Management* 34:306–312.
- Robel, R. J., J. N. Briggs, J. J. Cebula, N. J. Silvy, C. E. Viers, and P. G. Watt. 1970. Greater Prairie-Chicken ranges, movements, and habitat usage in Kansas. *Journal of Wildlife Management* 34:286–306.
- Rodgers, R. D. 2008. Prairie-chicken lek survey—2008. Performance report statewide wildlife research and surveys, May 2008. Kansas Department of Wildlife and Parks, Pratt, KS.
- Ryan, M. R., L. W. Burger, and D. P. Jones. 1998. Breeding ecology of Greater Prairie-Chickens (*Tympanuchus cupido*) in relation to prairie landscape configuration. *American Midland Naturalist* 140:111–121.

- Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44:418–421.
- Schroeder, M. A. 1991. Movement and lek visitation by female Greater Prairie-Chickens in relation to predictions of Bradbury's female preference hypothesis of lek evolution. *Auk* 108:896–903.
- Schroeder, M. A., and L. A. Robb. 1993. Greater Prairie-Chicken (*Tympanuchus cupido*). *Birds of North America* No. 36.
- Schroeder, M. A., and G. C. White. 1993. Dispersion of Greater Prairie-Chicken nests in relation to lek location: evaluation of the hot-spot hypothesis of lek evolution. *Behavioral Ecology* 4:266–270.
- Schwarz, G. 1978. Estimating the dimension of a model. *Annals of Statistics* 6:461–464.
- Slabbekoorn, H., and E. A. P. Ripmeester. 2008. Birdsong and anthropogenic noise: Implications and applications for conservation. *Molecular Ecology* 17:72–83.
- Svedarsky, W. D. 1988. Reproductive ecology of female Greater Prairie-Chickens in Minnesota. Pp. 193–239 in A. T. Bergerud and M. W. Gratson (editors), *Adaptive strategies and population ecology of northern grouse*. University of Minnesota Press, Minneapolis, MN.
- Svedarsky, W. D., R. L. Westemeier, R. J. Robel, S. Gough, and J. E. Toepfer. 2000. Status and management of the Greater Prairie-Chicken *Tympanuchus cupido pinnatus* in North America. *Wildlife Biology* 6:277–284.
- Whistler, J. L., B. N. Mosiman, D.L. Peterson, and J. Campbell. 2006. The Kansas satellite image database 2004–2005. *Landsat Thematic Map Imagery Final Report*, No. 127.
- With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 141:3152–3167.