

LANDSCAPE GENETICS AND BEHAVIORAL ECOLOGY OF GREATER PRAIRIE-  
CHICKENS (*TYMPANUCHUS CUPIDO*)

by

ANDREW J. GREGORY

B.S., Winona State University, 2003  
M.S., Central Michigan University, 2006

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology  
College of Arts and Sciences

KANSAS STATE UNIVERSITY  
Manhattan, Kansas

2011

## Abstract

Anthropogenic activities and climate change have dramatically altered landscapes worldwide. The ability of species to cope and adapt to ongoing changes is likely a function of their behavior, movements, and sensitivity to fragmentation. Greater Prairie-Chickens (GPC) are a lek mating grouse native to the Great Plains Landscape Conservation Cooperative (GPLCC), for which inbreeding depression and anthropogenic avoidance are a concern. The goals of my dissertation were to: 1) identify genetic correlates of male performance which may influence population viability under current land use practices, 2) identify GPC habitat characteristics and delineate areas of critical GPC habitat necessary for GPC conservation, and 3) identify the relative importance of distance and habitat quality for maintaining genetic connectivity among spatially structured populations. First, I found male reproductive success and survival to be positively associated with genetic diversity. Using multistate modeling in Program Mark, male survival across the observed range of variation in number of alleles (15-22) increased more than fourfold from 0.17 to 0.77. Second, I found 35-40% of Kansas, and 1.5 % (11,000 Km<sup>2</sup>) of the GPLCC, were considered high-quality lek habitats. Top performing logistic models predicting lek presence ( $w_i=0.95$ ) included strong effects of grassland cover and avoidance of anthropogenic disturbance. When this model was applied to putative future landscapes based on climate change and current land use trends over a 70-year period, I found a 27-40% reduction in habitat area and a 137 Km southeast shift in habitat distribution. Under equilibrium conditions we expect isolation by distance (IBD) to explain the distribution of genetic diversity. However, if the landscape restricts dispersal, then we might observe isolation by resistance (IBR). I used model selection procedures to choose among competing IBR or IBD models to explain the distribution of genetic diversity among GPC populations across Kansas and the GPLCC. IBD was never supported ( $R^2<0.02$ ,  $P>0.09$ ). The best models for Kansas ( $R^2=0.69$ ,  $P<0.02$ ) and for the GPLCC ( $R^2=0.46$ ,  $P<0.02$ ) indicated that human-mediated landscape changes have influenced landscape permeability for dispersal. The integration of behavioral, landscape, and genetic data provided new insights on prairie-chicken ecology, and is a powerful approach for developing conservation strategies for sensitive species.

LANDSCAPE GENETICS AND BEHAVIORAL ECOLOGY OF GREATER PRAIRIE-  
CHICKENS (*TYMPANUCHUS CUPIDO*)

by

ANDREW J. GREGORY

B.S., Winona State University, 2003  
M.S., Central Michigan University, 2006

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology  
College of Arts and Sciences

KANSAS STATE UNIVERSITY  
Manhattan, Kansas

2011

Approved by:

Co-Major Professor  
Dr. Samantha M. Wisely

Approved by:

Co-Major Professor  
Dr. Brett K. Sandercock

# **Copyright**

ANDREW J. GREGORY

2011

## Abstract

Anthropogenic activities and climate change have dramatically altered landscapes worldwide. The ability of species to cope and adapt to ongoing changes is likely a function of their behavior, movements, and sensitivity to fragmentation. Greater Prairie-Chickens (GPC) are a lek mating grouse native to the Great Plains Landscape Conservation Cooperative (GPLCC), for which inbreeding depression and anthropogenic avoidance are a concern. The goals of my dissertation were to: 1) identify genetic correlates of male performance which may influence population viability under current land use practices, 2) identify GPC habitat characteristics and delineate areas of critical GPC habitat necessary for GPC conservation, and 3) identify the relative importance of distance and habitat quality for maintaining genetic connectivity among spatially structured populations. First, I found male reproductive success and survival to be positively associated with genetic diversity. Using multistate modeling in Program Mark, male survival across the observed range of variation in number of alleles (15-22) increased more than fourfold from 0.17 to 0.77. Second, I found 35-40% of Kansas, and 1.5 % (11,000 Km<sup>2</sup>) of the GPLCC, were considered high-quality lek habitats. Top performing logistic models predicting lek presence ( $w_i = 0.95$ ) included strong effects of grassland cover and avoidance of anthropogenic disturbance. When this model was applied to putative future landscapes based on climate change and current land use trends over a 70-year period, I found a 27-40% reduction in habitat area and a 137 Km southeast shift in habitat distribution. Under equilibrium conditions we expect isolation by distance (IBD) to explain the distribution of genetic diversity. However, if the landscape restricts dispersal, then we might observe isolation by resistance (IBR). I used model selection procedures to choose among competing IBR or IBD models to explain the distribution of genetic diversity among GPC populations across Kansas and the GPLCC. IBD was never supported ( $R^2 < 0.02$ ,  $P > 0.09$ ). The best models for Kansas ( $R^2 = 0.69$ ,  $P < 0.02$ ) and for the GPLCC ( $R^2 = 0.46$ ,  $P < 0.02$ ) indicated that human-mediated landscape changes have influenced landscape permeability for dispersal. The integration of behavioral, landscape, and genetic data provided new insights on prairie-chicken ecology, and is a powerful approach for developing conservation strategies for sensitive species.

# Table of Contents

List of Figures .....	x
List of Tables .....	xiii
Acknowledgements.....	xv
Dedication .....	xvii
Chapter 1 - INTRODUCTION .....	1
Literature Cited .....	5
Chapter 2 - GENETIC DIVERSITY DRIVES SURVIVORSHIP AND MATING	
PREFERENCE IN A LEK-MATING GROUSE .....	7
Abstract .....	7
Introduction.....	7
Methods .....	10
Field Methods .....	10
Behavioral observations .....	11
Genetic Methods .....	11
Statistical analyses .....	12
Results.....	14
Trapping and Sampling Results .....	14
Relationship between Allelic Richness and Behavior Display Rates .....	15
Number of Alleles, Mating Status and Survival .....	15
Discussion.....	16
Acknowledgements.....	19
Literature Cited .....	20
Chapter 3 - HIERARCHICAL MODELING OF LEK HABITATS OF GREATER PRAIRIE- CHICKENS .....	31
Abstract.....	31
Introduction.....	31
Methods .....	33
Results.....	37

Environmental Covariates.....	37
Niche Modeling .....	38
Discussion.....	40
Acknowledgements.....	42
Literature Cited.....	42
<b>Chapter 4 - OPTIMIZING LANDSCAPE RESISTANCE SURFACES TO UNDERSTAND     GENE FLOW: A CASE STUDY USING GREATER PRAIRIE-CHICKENS .....</b>	<b>53</b>
Abstract.....	53
Introduction.....	53
Methods .....	56
General Approach and Sampling .....	57
Influence of the Number of Land Cover Classes on IBR .....	58
Simulation Analysis .....	60
Optimization of the Number of Land Cover Resistance Classes.....	60
Resistance Surface Parameterization .....	62
Greater Prairie-Chicken Case Study .....	62
Results.....	64
Genetic Analysis .....	64
Influence of the Number of Land Cover Classes on IBR .....	65
Optimization of Land Cover Resistance Classes .....	65
Resistance Surface Parameterization .....	65
Greater Prairie-Chicken Case Study .....	65
Discussion.....	66
Acknowledgements.....	70
Literature Cited.....	70
<b>Chapter 5 - MODELING HABITAT SUITABILITY CHANGE FOR A GRASSLAND BIRD     AS A FUNCTION OF CHANGING LAND USE AND GLOBAL CLIMATE CHANGE     ACROSS THE U.S. GREAT PLAINS.....</b>	<b>88</b>
Abstract.....	88
Introduction.....	89
Critical Reproductive Habitat Distribution.....	90

Critical Dispersal Habitat Distribution .....	91
Critical Future Habitat Distribution .....	92
Methods .....	92
Environmental Data .....	93
Critical Breeding and Nesting Habitat Distribution.....	94
Climate Model Development .....	95
Ecological Niche Model Validation.....	96
Critical Dispersal Habitat.....	96
Critical Future Habitat Distribution .....	98
Results.....	100
Critical Breeding and Nesting Habitat Distribution.....	100
Variance in Habitat Estimates and Model Validation.....	102
Critical Dispersal Habitat Distribution .....	102
Critical Future Habitat Distribution .....	103
Discussion.....	103
Literature Cited.....	108
Chapter 6 - Conclusion .....	132
Literature Cited.....	134
APPENDIX A - FIELD NOTES: OFF-LEK SOLICITATION AND MULTIPLE ON LEK COPULATIONS AMONG GREATER PRAIRIE-CHICKENS ( <i>TYMPANUCHUS</i> <i>CUPIDO</i> ) IN KANSAS.....	135
Description.....	135
Off-Lek Solicitation of Females by Males .....	135
Multiple on Lek Copulations .....	136
Literature Cited.....	137
Appendix B - MANUSCRIPTS AND DATA SETS.....	138
Chapter II .....	138
GENETIC DIVERSITY DRIVES SURVIVORSHIP AND MATING PREFERENCE IN A LEK-MATING GROUSE .....	138
Chapter III.....	139



A multi-scale hierarchical modeling approach to mapping lek habitats of Greater Prairie-chickens in EASTERN Kansas .....	139
Chapter IV .....	141
Optimizing Landscape Resistance Surfaces to Increase Inferences about Gene Flow: A Case Study for a Grassland Obligate Species, the Greater Prairie-Chicken ( <i>Tympanuchus cupido pinnatus</i> ).....	141
Chapter V .....	142
Modeling habitat suitability change for a grassland specialist as a function of increasing human land use and global climate change across the U.S. Great Plains .....	142

## List of Figures

Figure 2.1. Effect of Individual Allelic Richness on Male Reproductive Status. A) Effect of Individual Allelic Richness on Male Reproductive Status. Primary males are males receiving the most copulations on each lek, each year, Secondary males are all males, not the primary male, who received some copulations on a lek each year, and Unmated males are those males never observed to copulate on a lek. Individual allelic richness values for each male reproductive class are presented with global standard errors. B) Frequency histogram of the number of males with each level of observed allelic richness by reproductive category. .... 29

Figure 2.2. Effect of genetic diversity (no. of alleles) on A) the probability of being a primary male and B) annual survival of male Greater Prairie-Chickens ( $n = 89$ ) in northeast Kansas from 2003-2006. Parameter estimates for (B) were taken from the minimum  $AIC_C$  model  $S(\text{all})$ ,  $\psi(\text{con})$ ,  $p(\text{fixed}=1)$ . Dashed lines indicate 95% CI, and are linear on the logit scale but nonlinear after back-transformation. .... 30

Figure 3.1. Study area and lek sites of Greater Prairie-Chickens in eastern Kansas, 2005-2008. Eco-regions 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. .... 49

Figure 3.2. Map of habitat suitability based on maximum entropy modeling of lek sites of Greater Prairie-Chickens in eastern Kansas, 2005-2008. .... 50

Figure 3.3. 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.). .... 51

Figure 3.4. 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). .... 52

Figure 4.1. Central prairie study region. .... 83

Figure 4.2. Example of random landscape map with  $K = 2-5$  land cover elements. .... 84

Figure 4.3. Figures 4A and 4B represent the Resistance and calculated r-square values as a function of the number of land cover elements included in the land cover resistance data set for simulated landscape and genetics data sets. The y-axis for figure 4A are r-square values x 10,000. Error bars in Figures 4A and 4B represents the range of observed values from each of our 30 randomly generated landscapes and simulated genetics data. Figure 4C represents the resulting calculated r-square values using our actual genetics data and actual landscape data using  $K = 1 - 20$  land cover classes. Figure 4D represents the resistance values calculated using Program CircuitScape for landscapes including 1 – 20 distinct landscape resistance classes. .... 85

Figure 4.4. Procedural diagram of how land cover resistance classes were merged for  $AIC_C$  model selection analysis. .... 86

Figure 4.5. Resistance map generated from the  $K = 5$  second best performing  $AIC_C$  resistance model used for Least Cost Path Analysis. The least cost path determined from the path analysis is also shown with a 3 km buffer highlighting high priority areas for on-the-ground management to enhance regional prairie-chicken genetic connectivity. .... 87

Figure 5.1. Great Plains Landscape Conservation Cooperative study area ..... 123

Figure 5.2. Predicted habitat probability of detecting prairie-chicken habitat from ecological niche modeling of lek locations map depicts the likelihood of finding suitable habitat conditions for Greater Prairie-Chicken breeding habitat at a given area. The map ranges < 0.001% (red) – 98.4% (green) likelihood. .... 124

Figure 5.3. Predicted critical connectivity habitat based on isolation by resistance model. Areas in dark green are considered high priority areas for conservation to maintain genetic connectivity and areas of lighter green indicate areas of lesser priority. Black stars represent areas where genetic data were collected. .... 125

Figure 5.4. Predicted probability of detecting prairie-chicken habitat based on ecological niche modeling excluding climate data. The probability of encountering suitable Greater Prairie-Chicken breeding habitat across the landscape ranges from 0.2% - 94.4%..... 126

Figure 5.5. Predicted probability of detecting prairie-chicken habitat based on ecological niche modeling using landscape and climatic data. The probability of encountering suitable Greater Prairie-Chicken breeding habitat across the landscape ranges from 1.0% - 98.5%. .... 127

Figure 5.6 Variance in the probability of finding prairie-chicken habitat across the GPLCC region. Red outlined area is the Sand Hills region of Nebraska, where most of our omission errors occurred. .... 128

Figure 5.7. Critical breeding and dispersal habitat regions based on combining ecological niche model output with results from the isolation by resistance model..... 129

Figure 5.8. Predicted future distribution of Greater Prairie-Chicken breeding habitat across the GPLCC. Probability of finding lek habitat across the region ranges from <0.001% – 94.6%. .... 130

Figure 5.9. Predicted change in distribution map from 2010 ecological niche model compared to the predictions of the putative future habitat areas. Areas in yellow and green are contemporary high probability of occurrence habitats, whereas the subsets of areas in green are the predicted future distribution of high probability of occurrence habitats. Also depicted is the calculated shift in the center of distribution of high probability of occurrence habitats from the contemporary center (triangle) to the future center (circle)..... 131

## List of Tables

Table 2.1. Eleven polymorphic microsatellites successfully amplified from 235 adult Greater Prairie-Chickens from 2003-2007 near Manhattan, KS.....	24
Table 2.2. Summary of the descriptive genetic data from nine polymorphic microsatellites successfully .....	25
Table 2.3. Summary of male behavioral observations recorded during 10 minute focal bouts of male Greater .....	26
Table 2.4. Multistate encounter histories for male Greater Prairie-Chickens ( $n = 89$ ) in northeast Kansas from 2003-2006. Males were recorded as breeders if a successful copulation was observed (Y), or as non-breeders if they never mated (N).....	27
Table 2.5. Model selection results for multistate models testing the effects of breeding status (state) and number of alleles (all) on the survival ( $S$ ) and transitional probability of becoming a breeder ( $\psi$ ) in male Greater Prairie-Chickens ( $n = 89$ ) in northeast Kansas from 2003-2006. ....	28
Table 3.1. Bayesian Model Selection to Identify Landscape Attributes Associated with Lek Sites of Greater Prairie-Chickens in Eastern Kansas, 2005-2008 .....	47
Table 4.1. Eleven polymorphic microsatellites successfully amplified from adult Greater Prairie-Chickens ( $n = 1,038$ ) captured at leks across Kansas and southeastern Nebraska, 2006-2008. ....	77
Table 4.2. Parameterization of the resistance values for IBR estimates. Model performance is ranked by correlation coefficients.....	78
Table 4.3. Assessment of population genetic diversity within each sub-population of prairie-chickens sampled for these analyses.....	79
Table 4.4. Pairwise analysis of genetic differentiation ( $F_{ST}$ Nei's $D$ , km), physical distance, landscape resistance, least cost distance from the most parsimonious IBR Circuit model. .	80
Table 4.5. Results of model selection procedures used to determine the number of biologically relevant habitat classes to use in IBR modeling. ....	82

Table 5.1. Cooperating organizations and number of tissue samples provided for the analysis of critical and dispersal habitat within the Great Plains Landscape Conservation Cooperative. All samples were collected in 2009-2010. ....	115
Table 5.2. Landscape and climate variables collected at each spatial scale of the hierarchical analysis approach. ....	116
Table 5.3. Description of and model parameters for the hierarchical model selection procedure. ....	118
Table 5.4. Descriptive statistics for the six microsatellite markers used for genetic analysis of Greater Prairie-Chickens (n = 235) in the Great Plains LCC. ....	119
Table 5.5. Population genetic characteristics of each population focus used in isolation by resistance analysis. ....	120
Table 5.6. Population pairwise genetic and resistance variables for Greater Prairie-Chickens sampled across the GPLCC in 2010. ....	121
Table 5.7. Model description and parameter values for the models used in the isolation by resistance analysis for 5 Greater Prairie-Chicken populations in the GPLCC. ....	122

## **Acknowledgements**

This work is the result of the collaborative and cooperative efforts of many individuals. First, I'd like to thank my adviser Dr. Samantha Wisely for her encouragement, advice, and guidance for the past five years I've spent at K-State. I also thank my co-adviser Dr. Brett Sandercock for all the time and guidance he has provided. Next, I'd like to thank the members of my research committee Dr. Doug Goodin and Dr. Kimberly With for their time and contributions to this work. Funding and equipment for this research were provided by consortium of wind energy companies and conservation organizations including: The Nature Conservancy, Kansas Department of Wildlife and Parks, U.S. Fish and Wildlife Service, Cooperative Fish and Wildlife Research Unit at Kansas State University, National Fish and Wildlife Foundation, National Renewable Energies Laboratory, National Wind Coordinating Collaborative, Horizon Wind Energy, BP Alternative Energy, PPL Energy, FPL Energy, and Competitive Power Ventures (technical monitor for this consortium was Karin Sinclair of the National Renewable Energies Lab). I'd also like to thank Kansas State University and the Division of Biology for their support of this research. In addition to the funding sources already listed I was also supported through the National Science Foundation in the form of 1-year GK-12 fellowship, a U.S. Fish and Wildlife Services Landscape Conservation Cooperative grant, and from the J.E. Weaver Competitive Grants Initiative of The Nature Conservancy.

To accomplish this work required the coordination and organization of an immense field effort, to collect prairie-chicken genetic samples, movement data, and habitat data across the entire expanse of the Kansas Flint Hills. This effort would not have been successful without the hard work, talent, and dedication of my good friend and collaborator Dr. Lance McNew – Thank You! Thanks also to my friend and lab technician Thomas Prebyl for all of his hard work and time helping me collect genetics data from prairie-chicken blood samples collected in the field each spring – good luck in grad school at UGA Tom. I also thank Paige Berry and Cody Simmons my current lab technicians for all their hard work and for putting up with me these last few months as I prepared this dissertation. The following field technicians should also be credited for all their hard work in the field: Samantha Caldwell, William White, Emilie Berry, Lyla Hunt, Tara Whitty, Derek Broman, Jim Birmingham, Casey Cardinal, Kasey Clark, Tracey

Cikanek, Logan Gill, Jenny Hancock, Victoria Hunter, Francesca Jarvis, Helen Kurkjian, Nate Libel, Deb Martel, Don Moffett, Keith Rutz, Cynthia Soria, Jason Swenson, Ryan Voetsch, Brad Wessel, Patricia Yeager, Amy Zavala, and Josh Nakash. I also thank Hannah Leventhal for her office managerial and editorial expertise.

Special thanks go to all the organizations, landowners and ranch managers that allowed access to their properties to conduct field work; including Konza Prairie Biological Station (owned by The Nature Conservancy and managed by the Division of Biology at Kansas State University), Rannells Flint Hills Prairie Preserve managed by Clenton Owensby in the Department of Agronomy at Kansas State University, private lands owned or managed by Ken Brabb, Robert Foote, James Hess, Bob and Margaret Massey, Eddie Snyder, Kent Radcliffe, Scott Tracy, Brad Jackson, Mead Ferguson, Martin Peck, Troy Phillips, Jack Bannon, Norris Cooper, Grant Poole, Rod Moyer, David Burdette, Dick Weaver, James Walker, Richard Sulanka, Adam Hupach, Raymond Kindel, Gerald and John Braun, Lyle Perry, Virgil Vesterburg, and many other landowners who allowed access to their properties. Special thanks also to Steve Richards the land-lord of our northern field research unit field housing for all his help gaining access to properties and for the ‘beer-pong’ table the 2008 field crew used so fervently.

The work presented here is the result of the synergistic efforts of the Conservation Genetics and Molecular Ecology Lab and the Avian Ecology Lab. This work represents the results of that synergy and I am very proud to have been part of this group. During my tenure working in these labs I have had the privilege of working with some truly excellent people, most notably my advisers Drs. Wisely and Sandercock. I’d also like to acknowledge some of my fellow graduate students for their contributions in helping me develop some of the ideas presented in this dissertation: Dr. Lance McNew, Dr. Heather Barton, Dr. Jackie Augustine, Dr. Page Klug, Dr. Juan Campos, Rachel Pigg, Gina Barton, Amy Erickson, Robert Kaler, and Theresa Schneider.

Finally, I wish to thank my parents for always allowing me to indulge my curiosities as a child. I also thank my previous mentors Dr. Brad Swanson, Dr. Robin Richardson, and in particular Dr. Mark Lung for their early guidance and direction in my scientific career. Lastly, I thank my wife Sarah, who remarkably stuck with me throughout this entire process, and who even more remarkably still seems to want to hang around for the next chapter.



## **Dedication**

This dissertation is dedicated to three persons or groups. First, I dedicate this dissertation to all those who made the work so ‘interesting’ - you know who you are. Second, I also dedicate this dissertation to Mr. Ripple, my seventh grade biology teacher, who is the first person to plant the notion of pursuing a career in science in my head. In essence, for better or worse this is really all his fault. Last, I dedicate this work to all my mentors past, present, and future for taking a chance on me and sharing their time, talent, and passion for both science, but also more importantly for life with me –Thank You!

## Chapter 1 - INTRODUCTION

The Greater Prairie-Chicken (*Tympanuchus cupido*; hereafter prairie-chicken) is an upland game-bird native to the Central Plains of the United States. Prairie-chickens have a lek mating system, where males gather annually at display arenas, called booming grounds, and perform a series of vocal and behavioral displays to attract mates. On each booming ground, males hold and defend discrete territories and show high philopatry to their territory and their lek both within and between breeding seasons, yet these territories provide no known resources (Schroeder and Robb 1993). Female prairie-chickens visit leks only for the purpose of choosing a mate, as male prairie-chickens provide no parental care. Typically there is high skew in male reproductive success as females tend to repeatedly choose the same subset of males (Nooker and Sandercock 2008). Finally, while the mechanism driving the evolution of this type of mating system is somewhat of a mystery, one current hypothesis is that leks are located at the intersection of necessary resources needed by females to successfully nest and fledge young, as once a female has mated she will typically nest within 1-3 Km of the lek site (*Gregory et al. unpublished data*).

The current distribution of the species has declined significantly over the past 200 years since European settlement of the plains, putatively as a result of anthropogenic-induced changes to the landscape in the form of conversion of grasslands for row crop agriculture, increased grazing and ranching, and increased urban development and exurban sprawl (Knapp et al. 1998, Svedarsky et al. 2000). Currently, prairie-chicken distribution is limited to only about 20% of its historical range and population estimates place prairie-chicken populations at 30% of their historical maximum (Schroeder and Robb 1993, Johnsgard 2002). The central Flint Hills eco-region of Kansas represents the largest relatively intact tallgrass prairies left in the U.S. today (Knapp et al. 1998) and is the core of the current prairie-chicken distribution (Svedarsky et al. 2000). Despite the general characterization of the Flint Hills as being relatively pristine prairie habitat, they have arguably been impacted by human land use. Prairie-chicken lek count data, which are frequently used as an indices of population status for grouse (Walsh 2004), have indicated that the Flint Hills prairie-chicken population has declined by approximately 30% over the last 30 years (Rogers 2008). However, while the Flint Hills, populations have been in decline, lek count data

from the adjacent Smoky Hills eco-region of Kansas suggests that over the last 25 years prairie-chicken populations in that region have remained stable, and over the last decade have shown an approximate 7% population increase (Rogers 2008). While the demographic mechanism for the Flint Hills population decline is poorly understood, it has been hypothesized that intensive rangeland management has functionally reduced the quality of habitat within the Flint Hills, and negatively impacted nesting and breeding success to a greater extent than the Smoky Hills (McNew 2010).

Declining populations are of great concern for prairie-chickens as they are one of the few species for which we have well-documented evidence for inbreeding depression (Bouzat et al. 1998). Declining populations lead to reduced population size and a smaller effective population size, which in turn can lead to the rapid loss of genetic diversity (Nunney 1995). Reduced genetic diversity leads to inbreeding depression if reduced genetic diversity is directly or indirectly linked to reduced demographic performance. In addition to declining populations, habitat fragmentation may also restrict gene flow among populations and likewise lead to increased population isolation which further exasperates the loss of genetic diversity within the population via the process of random genetic drift (Frankham et al. 2002). However, characteristics of the mating system can off-set the loss of allelic diversity if some mechanism exists such that more genetically diverse individuals produce a greater proportion of the offspring than do more homozygous individuals (Nunney 1993). Consequently, when dealing with conservation of a species with a propensity for inbreeding such as prairie-chickens (Westemeir et al. 1998; but see Johnson et al. 2003), understanding the species mating system and its genetic consequences to the population is a key consideration for effective management of the species (Hedrick et al. 1996, Gregory et al. in review).

In addition to the mating system, the ability of prairie-chickens to use habitat and disperse across the fragmented landscapes will also be important considerations for effective management. Given that the Flint Hills populations are declining, their persistence may be dependent upon immigration by individuals from the adjacent Smoky Hills eco-region where declines have not been observed. The degree to which the landscape promotes or inhibits dispersal will then be critically important for effective management and understanding of the population dynamics of this species (Hanski and Gaggiotti 2004). Moreover, identifying critical portions of the landscape that act as corridors to movement and allow for genetic connectivity

among populations is of tantamount conservation importance (McRae et al. 2008), as panmictic populations will have a functionally larger effective population size and will therefore lose alleles to random genetic drift more slowly than isolated populations (Hartl and Clark 2007).

The goals of my dissertation were to address the complex interactions that mating system, distribution of suitable habitat and landscape permeability to dispersal have on prairie-chicken conservation, and evolution. In Chapter 2, using data collected on 235 prairie-chickens sampled at five leks located ten miles southeast of Manhattan, Kansas from 2003-2006, I explore the role of individual genetic diversity in mate choice and survival. Prairie-chickens have a classic lek mating system where males congregate annually on display arenas to compete for females, which is characterized by high skew in male reproductive success (Nooker and Sandercock 2008). Thus, the potential exists for the mating system to reduce the effective population size of local populations via the repeated selection by females of the same sub-set of available males. To investigate the role of male genetic diversity on female mate choice, we combine observational data on reproductive behavior with molecular genetics to examine the effects of genetic diversity on male mating success. I also model the influence of individual male genetic diversity on male survival and the likelihood of males to transition from non-breeders to breeders over subsequent breeding seasons.

In Chapter 3, I use no genetic data, rather I use geospatial analysis and lek location data from 166 lek coordinates provided by Kansas Department of Wildlife and Parks lek survey routes conducted each year some of which date back to 1960 in an ecological niche modeling framework to evaluate landscape suitability for chicken lek habitat across three eco-regions of Kansas. Recognizing that animals make decisions about home ranges and space use in a hierarchical fashion (Johnson 1980), I measure attributes associated with lek occurrence or pseudo-absence at multiple spatial scales, create independent models predicting lek presence for each scale, and then pool variables of top performing models at each single scale into a multi-scale model predicting breeding habitat distribution across KS. I also argue that at a landscape scale, breeding habitat distribution can be used as a surrogate for nesting habitat (Schroeder 1991).

Nesting and breeding habitat are not the only habitat requirements for successful prairie-chicken conservation (Schroeder and Robb 1993). Long-term conservation will require the delineation and preservation of dispersal habitat between demes (Westemeier et al. 1998). Under

equilibrium conditions, the prediction would be that gene flow between populations is a function of the Euclidean distance between population pairs (isolation by distance; IBD; Slatkin 1993). However, most natural landscapes are not at equilibrium, as the various land cover types pose different levels of resistance to movement to species trying to disperse across them (isolation by resistance; IBR; McRae 2006). In Chapter 4, I use data on 1,038 chickens, sampled at 84 leks in Nebraska and Kansas collected from 2006-2009 to compare models of IBD to models of IBR. However, one of the chief limitations of using resistance-based path metrics such as least cost path modeling or circuit analysis is how to parameterize a resistance surface from available GIS data in a biologically meaningful way (Beier et al. 2009). To solve this problem, I used information theoretic approach to model selection and to identify the number of land cover habitat resistance classes to include in the analysis, and then used the population genetics data to elucidate the functional resistance of all included habitat classes in a causal modeling framework (Cushman et al. 2006). I also tested the necessity of using this approach using simulated data.

Last, in Chapter 5 I expand the landscape analysis in Chapter 4 to a larger ecosystem, that of the Great Plains Conservation Cooperative (GPLCC) region. This data set consists of samples from 235 individual chickens extracted from feathers collected by state agency personnel at 98 leks across the GPLCC in 2010. The GPLCC is one of 22 US Fish and Wildlife Service strategic habitat conservation regions used as organizational units for species conservation and management in light of the threats of climate change. I expand our analyses to include climate change scenarios by applying an eco-forecasting model based on current rates of grassland conversion, human population change, and predicted global climate change over a 70-year time period. By comparing the current habitat distribution with that of the putative future habitat distribution, I investigated how human land use and climate change might affect the distribution of GPC critical breeding and dispersal habitats across the GPLCC region. In summation, the analyses of the four chapters of this dissertation are directly testing hypotheses related to how anthropogenic alterations to the landscape might impact the long-term viability and evolutionary potential of prairie-chickens based on attributes of the prairie-chicken mating system, habitat requirements, and dispersal abilities. Such data will be invaluable to managers and conservationists as they strive to implement effect management scenarios for this species; moreover, the analytical approaches I have developed and describe here, should be amenable for use with many other species or landscapes of conservation concern.

## Literature Cited

- Beier, P., D.R. Majka, and W.D. Spencer. 2009. Forks in the road: choices in procedures for designing wildland linkages. *Conservation Biology* 22:836-851.
- Bouzat, J.L., H.A. Lewin, K.N. Paige. 1998. Genetic evaluation of a demographic bottleneck in the greater prairie-chicken. *Conservation Biology* 12:836-843.
- Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128:231-240.
- Frankham, R., J.D. Ballou, and D.A. Briscoe. 2002. *Introduction to conservation genetics*. Cambridge University Press, New York, NY. USA.
- Gregory, A.J. R.S.A. Kaler, T.J. Prebyl, B.K. Sandercock, and S.M. Wisely. In review. Kin avoidance and multiple paternity in a recently translocated island population of rock ptarmigan. *Conservation Genetics*.
- Hanski, I., and O.E. Gaggiotti. 2004. *Ecology, genetics, and the evolution of metapopulations*. Elsevier Academic Press, Burlington, MA, USA.
- Hartl, D.L., and A.G. Clark. 2007. *Principles of population genetics*. Sinauer Associates Inc. Sunderland, MA, USA.
- Hedrick, P.W., R.C. Lacey, F.W. Allendorf, and M.E. Soule. 1996. Directions in conservation biology: a response to Caughley. *Conservation Biology* 10:1312-1320.
- Johnsgard, P.A. 2002. *Grassland grouse and their conservation*. Smithsonian Institute. Washington D.C., USA.
- Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 6:65-71.
- Johnson, J.A., J.E. Toepfer, and P.O. Dunn. 2003. Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology* 12:3335-3347.
- Knapp, A.K., J.M. Briggs, D.C. Hartnett, and S.L. Collins. 1998. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, NY, USA.
- McNew, L.B. 2010. *An analysis of Greater Prairie-chicken demography in Kansas: The effect*

- of human land use on the population ecology of an obligate grassland species.  
Manhattan, KS: Kansas State University; 2010. 149p.
- McRae, B.H. 2006. Isolation by resistance. *Evolution* 60:1551-1561.
- McRae, B.H., B.G. Dickson, T.H. Keitt, and V.B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712-2724.
- 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.
- Nunney, L. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* 8:234-239.
- Nunney, L. 1995. Measuring the ratio of effective population size to adult numbers using genetic and ecological data. *Evolution* 49:389-392.
- Rogers, R. 2008. Prairie-chicken lek surveys—2008. Performance Report Statewide Wildlife Research Surveys. Kansas Department of Wildlife and Parks, Pratt, KS, USA.
- 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.

## **Chapter 2 - GENETIC DIVERSITY DRIVES SURVIVORSHIP AND MATING PREFERENCE IN A LEK-MATING GROUSE**

### **Abstract**

Sexual selection, particularly mate choice, places profound selective pressure on all individuals in populations with skewed reproductive success. Previous studies of Greater Prairie-Chickens (*Tympanuchus cupido*) have revealed that female mate choice is related to male behavioral display characteristics. Males obtaining copulations displayed more frequently and acted more aggressively toward other males. Combining observational data on aggressive behavior, display rate, and copulations received by males at five lek sites over four years with molecular genetics data from 11 microsatellites, we tested the influence of individual male genetic diversity on mating success and survival. We found evidence for heterosis; males with greater individual allelic richness displayed more frequently and acted more aggressively when females were not present on the lek. When females were present, we found no behavioral differences between males with different levels of diversity. Using Analysis of Variance with orthogonal contrasts, on the individual allelic richness of males in three categories of male reproductive success, males receiving the most copulations on a lek in a year, males receiving some copulations but not the most on a lek each year, and unsuccessful males, we found that genetically diverse males received more copulations than did less diverse males. Finally, using a multistate mark recapture model, we found both annual survival and probability of transitioning from a non-breeder to a breeder over successive years to be positively correlated with genetic diversity. These are some of the best data that we have for a direct link between genetic diversity, survivorship, and mate success in wild populations.

### **Introduction**

The drivers of sexual selection have been studied by evolutionary and behavioral biologists since Darwin observed that one sex has the power to modify the other sex (Alcock 2001). When beneficial traits such as attractiveness, longevity, or disease resistance are associated with heterosis, the costs associated with low individual heterozygosity and the



benefits of high heterozygosity may promote the evolution of sexual selection based on individual genetic diversity. Selection for heterosis differs from traditional directional sexual selection in which genetically heritable traits are passed down to offspring (Jennions and Petrie 2000). Although genetic diversity is not a heritable trait, if females routinely choose males with high individual genetic diversity, then their offspring will, on average, have high individual genetic diversity and derive the benefits of heterosis. Thus, traits associated with heterosis may cue females to the overall diversity of the male's genetic makeup (Mays and Hill 2004).

Heterosis in natural populations is a well-studied phenomenon. For example, male red deer (*Cervus elaphus*) with high genetic diversity tended to have large body mass which was correlated with larger harems and higher fitness than males with lower diversity (Coulson et al. 1998). Female mice (*Mus musculus*) were more likely to mate with males of either greater genetic diversity or those individuals less genetically similar to themselves (Roberts and Gosling 2003). Phenotypic traits such as growth rate, oxygen consumption, and survival have been correlated with increased heterozygosity in rainbow trout (*Oncorhynchus mykiss*; Thelen and Allendorf 2001). Female lesser kestrels (*Falco naumanni*) with greater heterozygosity laid larger clutches and had higher hatching success than less genetically diverse individuals (Ortego et al. 2007). Additionally, male Collared Flycatchers (*Ficedula albicollis*) with higher genetic diversity had greater longevity than less diverse individuals (Merilä et al. 2003). Conversely, low genetic diversity has been correlated with inbreeding depression (reduced egg viability and smaller clutch sizes) in both Greater Prairie-Chickens (*Tympanuchus cupido*) and Gunnison Sage-Grouse (*Centrocercus minimus*; Westemeier et al. 1998, Stiver et al. 2008). Finally, in Collared Flycatchers, inbreeding depression has been associated with reduced hatch rates, lower chick skeletal mass, and lower post fledgling juvenile survival (Loeske et al. 2002).

Social mating system can impact the role of heterosis in mate choice. In socially monogamous mating systems, female choice of males is constrained by settlement and mate choice by other females, thus highly heterozygous males may not be available (Alcock 2001). A classic lek mating system differs from social monogamy because female mate choice is unconstrained by choices of other females, and consequently females can each choose the same subset of the highest quality males (Höglund and Alatalo 1995). Therefore, male reproductive success is driven by male/male competition and female mate choice, both of which in turn could be influenced by genetic diversity of the male. If genetically diverse males have an advantage in

male to male competition (heterosis), then more diverse males may have higher reproductive success in current breeding attempts (Darwin 1876, Crow 1970, Wright 1977). If greater genetic diversity affords males greater innate disease resistance or a longer life expectancy, then males may gain a reproductive advantage by having more future breeding opportunities. In addition, if mating with a more genetically diverse male reduces the risk of unmasking lethal recessive traits in offspring (Hedrick 1994), then females that choose more diverse males would have greater reproductive success, and evolution should favor a mechanism for female choosiness. Ironically, while lekking may enable multiple females to choose the same high quality male and increase or maintain genetic diversity in their offspring, skew in mating success can negatively impact the genetic diversity of the population by reducing effective population size, which can increase inbreeding and the risk of inbreeding depression (Nunney 1995).

Here, we test the role that male genetic diversity plays on male reproductive success and longevity in Greater Prairie-Chickens. Greater Prairie-Chickens are a compelling model for testing the role of male genetic diversity on mating success and longevity for several reasons. First, prairie-chickens have a lek mating system and female mate choice ought to be unconstrained; indeed previous behavioral studies indicate that as few as 20% of the males on a lek site obtain > 80% of the copulations, thus making males available for multiple mating opportunities (Nooker and Sandercock 2008). Second, because most copulations take place at the lek, accurate estimates of male mating success can be made via observation of the lek. Third, male Greater Prairie-Chickens show high site fidelity with regards to their lek site territories between years (Schroeder and Robb 1993, Nooker and Sandercock 2008), so annual survival can be estimated directly by male return rates to lek sites. Last, Greater Prairie-Chickens exhibit pronounced inbreeding depression (Westemeier et al. 1998), so there are known costs associated with low genetic diversity.

Assuming that genetic diversity is an important characteristic of Greater Prairie-Chicken reproductive ecology and lekking behavior, we tested three predictions on the role of male genetic diversity on male prairie-chicken reproductive success. First, if genetically diverse males display hybrid vigor, then we should observe a greater rate, duration, or intensity of display on lek sites by males with higher levels of genetic diversity. Nooker and Sandercock (2008) noted that successful males tended to avoid mate attraction displays when females were not present and that in general more aggressive males tended to be more successful. Presumably, a greater rate,

duration, or intensity of aggressive behaviors being observed when females are not present on the leks may be indicative of over dominance, if more diverse males are able to establish their superiority over less genetically diverse males and behaviorally exclude them from mate consideration when females are present. Second, if females have evolved a mechanism for selecting more genetically diverse males, then males with greater genetic diversity should have more mating opportunities or have a greater probability of transitioning from a non-breeder to a breeder. Third, if more genetically diverse males can garner more resources and resist diseases better, then heterosis should also confer greater survival to males with greater genetic diversity than on those with lower genetic diversity.

## **Methods**

### ***Field Methods***

The research performed in the present study complied with the current laws of the countries in which they were performed and were conducted under the following research permits: Scientific, Education or Exhibition Wildlife Permit, Kansas Department of Wildlife and Parks (SC-118-2003, SC-068-2004, SC-078-2005, SC-072-2006), and all field protocols were approved by the Kansas State University Institutional Animal Care and Use Committee (Protocols 2079, 2351).

Greater Prairie-Chickens were observed on lek sites between mid-March and mid-May in a 4-year study, 2003-2006. All leks were located on cattle-grazed pastures in Riley and Geary Counties in northeast Kansas, USA (39° 05'N, 96° 34'W). Three leks were observed in 2003, and we expanded our sampling effort to four leks in 2004-2005 and five leks in 2006.

Prior to behavioral observations, birds were trapped at lek sites using walk-in funnel traps (Hamerstrom and Hamerstrom 1973, Toepfer et al. 1987), and were given a unique combination of colored leg bands and tail markings to aid in individual identification. Morphometric measurements of mass, tail length, pinnae length and tarsus length were measured for each bird. Approximately 40  $\mu$ L of blood was collected in 1 mL of Queen's lysis buffer (Seutin et al. 1991) and stored at -20°C until DNA could be extracted.

### ***Behavioral observations***

Every other morning on average, observers in blinds located 6-m from the lek recorded the identity of males and females visiting lek sites. Successful copulations were recorded by behavioral cues. Following successful copulations, females vigorously shook their wings and body feathers, preened their vent and departed the lek shortly after the copulation (Schroeder and Robb 1993). During continuous 10-min focal observations of particular males, we tallied the number of fights and boom vocalizations observed. Number of booms observed for each bird was then converted into a frequency rate of number of booms per minute observed. To control for possible effects of observer bias, observers were rotated among leks daily.

### ***Genetic Methods***

DNA was extracted from blood using Qiaquick DNeasy tissue extraction kits (Qiagen Inc.; Valencia, CA). Amplification via PCR took place on an Eppendorf epgradient thermocycler (Brinkman Inc. Westbury, NY), in standard 20  $\mu$ L PCR cocktails containing: 30 ng of template DNA, 2.5  $\mu$ M MgCl<sub>2</sub>, 0.2  $\mu$ M dNTP's, 0.12  $\mu$ g/ $\mu$ l BSA, 0.8 M betaine, 0.5  $\mu$ M of each forward and reverse primer, 0.2  $\mu$ M of M-13 universal primers (Schuelke 2000) labeled with a fluorescent dye (Hex or FAM; Operon Biotechnologies, Huntsville, AL) attached to the 5' end, and 0.5 units of Go Taq Flexi Taq polymerase (Promega, Madison, WI). Samples were amplified at 11 polymorphic microsatellite markers originally developed for use in other species of grouse, but which had previously been successfully used in Greater Prairie-Chickens (Table 2.1). Fragment analysis was conducted using an ABI 3730, and alleles were scored using GeneMarker 1.6 software (Applied Biosystems; Foster City, CA). Of 164 individual males, DNA amplified at 11 loci in this analysis, we re-ran 607 samples which included all homozygotes, and a random 15% of the heterozygotes to determine whether the error was observer-based or biochemically based.

Population-wide measures of allelic diversity as well as tests for Hardy-Weinberg Equilibrium (HWE) and genetic disequilibrium were carried out in Program GenePop 3.1 (Raymond and Rousset 1995). Estimates of genetic diversity can be calculated as allelic richness (AR, total number of different alleles per individual), heterozygosity (ratio of microsatellite loci found to be heterozygous out of the total number of microsatellite loci per individual), or  $d^2$  (sum of the squared differences between the lengths in repeat units of microsatellite alleles divided by

the number of loci; Höglund et al 2002). We quantified AR, heterozygosity and  $d^2$  for all individuals and ran all analyses using all three estimators of genetic diversity. All trends and significance levels were similar regardless of the method used to quantify genetic diversity. Here we chose to report the trends with respect to AR only, because the values are normally distributed, not bounded between 0-1, and are easily interpreted as individual genetic diversity. AR for individuals was calculated as the total number of different alleles summed across all loci used and was calculated using Microsoft Excel (Microsoft Corporation; Redmond, WA). Estimates of probability of identity and probability of identity between sibs were calculated using Program GenAlEx 6 (Peakal and Smouse 2006). Estimates of effective population size ( $N_e$ ) were calculated following Waples (1989) method for estimating  $N_e$  over short time periods as implemented in Program Neestimator (Peel et al. 2004). We tested for departures from Hardy-Weinberg Equilibrium (HWE) using program GenAlEx 6, all loci were in HWE, and no pairwise linkage disequilibrium was detected after Bonferroni corrections ( $\alpha = 0.002$ ,  $P > 0.7$  to  $P > 0.02$ ; Table 2.1).

### ***Statistical analyses***

Statistical analyses were conducted in JMP IN (Ver. 4.0.4, SAS Institute, 2001) or SAS 9.1 (SAS Institute 2003), except where otherwise noted. Sample sizes varied among analyses because it was not possible to measure every attribute for all males. Descriptive statistics are presented as mean  $\pm$  1 SD unless otherwise indicated.

In 2006, 15 male greater prairie-chickens were implanted subcutaneously with 30 mg of testosterone propionate to examine the role of testosterone on male lekking display behavior and reproductive success. Testosterone implanted birds did show moderate increases in testosterone levels over reference samples taken prior to testosterone implantation. However, testosterone levels in implanted birds were not significantly greater than the natural variation in testosterone levels found in the population and testosterone implantation did not alter display behaviors beyond the natural variation in display rate (Augustine et al. *in press*). Moreover, of the 15 males which were implanted with testosterone, only two successfully mated after being implanted, and both of those were also successful in prior years. Thus we retained all implanted males in our analysis.

With the exception of one lek where two males had equal mating success,  $\geq 60\%$  of the observed copulations were obtained by a single male. We collectively refer to this subset of males as primary males. A second subset of males (3-5 males per lek) received the remaining 40% of the copulations observed on each lek; we refer to this subset of males on each lek as secondary males. The majority of the males on each lek were not observed to receive any copulations and are referred to as unmated males. Once a male was found to be successful, they were removed from the cohort of unsuccessful males, even if in previous years they were unsuccessful, likewise once a male was classified as a primary male, they were censored from the cohort of secondary or unmated males. This was done to avoid resampling the same individual in multiple categories and also pseudoreplication because each individual was included in the analysis one time, despite being present in the population over multiple breeding seasons. We compared the individual allelic richness among males in all three groups using ANOVA with orthogonal contrasts in SAS 9.2. We also conducted a binomial logistic regression regressing observed individual allelic richness of primary males vs. unmated males, to determine the extent to which individual allelic richness is responsible for conferring reproductive success on male Greater Prairie-Chickens.

To test for the influence of individual male genetic diversity on booming frequency and the number of fights engaged in by male prairie-chickens, both when females were and were not present on lek sites, individuals were grouped into three classes. Class 1 (the medium class) contained all males with individual allelic richness values within  $\pm 1$  standard deviation (SD) of the population mean individual allelic richness. Class 2 (the high allelic richness class) contained all males with individual allelic richness values  $>1$  SD of the mean individual allelic richness, and Class 3 (the low allelic richness class) contained all males with individual allelic richness  $<1$  SD of the mean individual allelic richness. We compared the rate of booming and the number of fights engaged in by males in all three classes when females were and were not present on the leks using ANOVA. We also compared rates of booming and the number of fights engaged in by males in just the upper and lower tails of the distribution (Class 2 and Class 3 males) both when females were and were not present on the leks using a two sample t-tests.

To investigate covariates of survivorship, encounter histories for male prairie-chickens were coded with multistate information where birds were coded as receiving copulations during behavioral observations (*Y*), non-breeders that never mated (*N*), or not captured or re-sighted (*O*).

Males were genotyped at 11 microsatellite loci and number of alleles was included as an individual covariate. We estimated state-specific estimates of apparent survival ( $S$ ), the transitional probability of changing breeding states ( $\psi$ ), and encounter rates ( $p$ ) with multistate models in Program Mark (Ver. 5.1, White and Burnham 1999). In this study, estimates of apparent survival from live encounter data ( $\phi = SF$ ) approach true survival ( $S$ ) because site fidelity of male Greater Prairie-Chickens to lek territories is strong ( $F \approx 1$ , Nooker 2007, Nooker and Sandercock 2008).

Annual survival ( $S$ ) and the transitional probability of changing states ( $\psi$ ) were modeled as a function of breeding success (state) and genotype (all = number of alleles) in both factorial ( $\times$ ) and main effects models (+). We did not model time-dependence because our study was only four years in duration. Inspection of the encounter histories showed that no males were missed in an intervening year and we fixed encounter rates ( $p$ ) to one. Thus, our global model was:  $S(\text{state} \times \text{all})$ ,  $\psi(\text{state} \times \text{all})$ ,  $p(\text{fixed to } 1)$ . Goodness of fit tests were not available for models with individual covariates. We tested goodness-of-fit of the multistate model alone to the encounter histories with the median c-hat procedure in Program Mark. A single model received most of the support in our set of candidate models and we took parameter estimates from the minimum  $AIC_C$  model and did not use model-averaging.

## Results

### *Trapping and Sampling Results*

Over four years and 420 mornings of observations, 164 males were observed at five lek sites of Greater Prairie-Chickens (17 lek-years). On average,  $2.0 \pm 2.7$  females visited a lek each morning (range 0-18,  $n = 420$  mornings). Lek size varied (5-14 territorial males per lek), but male attendance was consistently high during the 7-week observation period with  $90.6 \pm 14.2\%$  of all territorial males attending per day ( $n = 420$  mornings). On average,  $87.3 \pm 9.0\%$  of males were banded on each lek (17 lek-years). Greater Prairie-Chickens at our study area exhibited a high degree of genetic diversity and low population structure with a relatively large effective population size over a small geographic extent (Table 2.2). Effective population size ( $N_e$ ) for the study population was 118.5 (95% CI: 64.2 - 286.1). Analysis of population genetic structure

using Structure 2.2 indicated greatest support ( $\text{Ln}(P) = -5,532.2$ ) for a single population with genetic admixture and correlated gene frequencies. Thus, we concluded that the leks themselves were not genetically isolated from each other and functioned as if they were one panmictic population ( $n = 235$  prairie-chickens; 164 males, 71 females).

### ***Relationship between Allelic Richness and Behavior Display Rates***

Analysis of Variance across all three genetic diversity groups did not indicate any significant trend with regards to genetic diversity and display rate when females were present (Booms:  $F_{df=2,86} = 0.30$ ,  $P = 0.741$ , Fights:  $F_{df=2,86} = 1.33$ ,  $P = 0.271$ ), nor when they were not present (Booms:  $F_{df=2,86} = 2.20$ ,  $P = 0.117$ , Fights:  $F_{df=2,86} = 3.29$ ,  $P = 0.05$ ). However, the observed trend in display rate was such that it suggested there might be a relationship between genetic diversity class and behavioral display rate, but Class 1 males had a large range in both display rate and number of fights (Table 2.3). Therefore, we analyzed the tails of the distribution looking only at Class 2 and Class 3 males using two sample-t-tests.

When female prairie-chickens were present at the lek, all males in Class 2 and Class 3 significantly increased their display rate and aggressive behavior (Booms  $\pm$  SE with females =  $4.69 \pm 0.0$ , Booms  $\pm$  SE without females present =  $1.59 \pm 0.01$ ,  $t = 16.4$ ,  $df = 132$ ,  $P < 0.001$ , and Fights  $\pm$  SE with females present =  $5.5 \pm 0.08$ , Fights  $\pm$  SE without females =  $3.68 \pm 0.02$ ,  $t = 2.5$ ,  $df = 97$ ,  $P = 0.02$ ). When females were present at leks, we detected no significant differences between the frequency of booming or the number of fights engaged in by either more (Class 2) or less (Class 3) genetically diverse males (Booms,  $t = 0.72$ ,  $df = 17$ ,  $P = 0.48$ , Fights,  $t = 0.22$ ,  $df = 40$ ,  $P = 0.83$ ). However, when females were not present, Class 2 males with greater individual allelic richness engaged in more fights and had a significantly higher rate of booming than Class 3 males with lower individual allelic richness (Booms,  $t = 2.25$ ,  $df = 29$ ,  $P = 0.03$ ; Fights,  $t = 2.9$ ,  $df = 21$ ,  $P = 0.01$ ; Table 2.3).

### ***Number of Alleles, Mating Status and Survival***

Analysis of variance indicated a significant difference in individual male allelic richness based on the breeding class of the male ( $F_{df=7,3} = 53.2$ ,  $P < 0.001$ ). Primary males had significantly greater individual allelic richness than did other male breeding classes (Fig. 2.1A).



However, it is also interesting to note that while the average allelic richness of secondary males did not differ significantly from unsuccessful males, secondary males had a bimodal distribution with regards to their observed individual allelic richness (Fig. 2.1B). Binary logistic regression indicated a significant positive relationship between individual allelic richness and the probability of being the most successful male on the lek as compared to being an unsuccessful male on the lek ( $P = 0.018$ ; Fig. 2.2A).

Of the 164 male Greater Prairie-Chickens captured, we were able to gain a comprehensive observational data set on 89 males during this 4-year study: 50 males were observed in only one year, 18 were observed in two out of four years, 18 were observed in three years, and three males were observed in all four years. The average number of alleles per male was  $18.5 \pm 1.4$  *SD* (range = 15-22; Table 2.4).

Results from the median  $\hat{c}$  procedure indicated that the multistate model was a good fit to the encounter histories without the individual covariates ( $\hat{c} < 1$ ). We set the variance inflation factor ( $\hat{c}$ ) to one and used  $AIC_C$  for model selection. The minimum  $AIC_C$  model showed that annual survival was affected by number of alleles, and the probability of changing status was constant (Table 2.5): model S(all),  $\psi(\text{con})$ ,  $p(\text{fixed}=1)$ . The next best models included an effect of state on survival, and the remaining models received little support ( $w_i < 0.1$ , Table 2.5).

Parameter estimates from the minimum  $AIC_C$  model indicated that number of alleles had a strong positive effect on annual survival with a slope coefficient of  $\beta = 0.55 \pm 0.21SE$  (95%CI = 0.13-0.96). The annual survival rate was  $0.453 \pm 0.048$  for males with an average number of alleles. Across the observed range of variation in number of alleles (15-22), survival increased more than fourfold from 0.17 to 0.77, indicating that more genetically diverse males have higher rates of survival and thus more reproductive attempts (Figure 2.2B). Males that failed to receive copulations had a lower probability of becoming breeders in a future year ( $\psi(NY) = 0.315 \pm 0.063SE$ ) than breeders had of remaining breeders ( $\psi(YY) = 0.685 \pm 0.063SE$ ).

## Discussion

Our study demonstrates a link among individual male genetic diversity, reproductive success and annual survival. Based on our ordered PLR analysis, we showed that males with

greater genetic diversity are more likely to receive the greatest number of copulations on a lek site. Mechanistically, a link between male genetic diversity and reproductive success could be accomplished in several ways. Nooker and Sandercock (2008) demonstrated that Greater Prairie-Chicken female mate choice was determined primarily by behavioral characteristics of males rather than by male territorial or morphometric attributes. Our analysis furthers their findings and suggests that genetic diversity may drive variation in behavioral characteristics. In our initial analysis we detected only a marginally significant increase in the frequency of fighting among males when females were not present. However, we did observe a trend such that males with high genetic diversity displayed more and fought more, than males with intermediate genetic diversity who also displayed and fought more than males with low genetic diversity. When we excluded Class 1 males from the analysis we found a clear trend such that males with greater genetic diversity had a higher rate of booming and greater number of fights on lek sites when females were not present. An increase in display and fighting ability could be indicative of heterosis (Crnokrak and Barrett 2002), such that more diverse individuals were able to allocate greater resources to establishing dominance on the lek, even when females were not present. Our findings are bolstered by the observations that genetically diverse males were more likely to live longer than less diverse males.

In addition, our regression analysis suggests a positive relationship between genetic diversity and the probability of male prairie-chickens being the most successful male on a lek site. For this analysis we excluded all males that had intermediate success on the lek. This group of males was excluded because of they had a bimodal distribution in the frequency plot of male individual allelic richness. This group likely consists of a mixture of individuals which that will remain secondary males and males which may go on to become primary males. Given the proclivity of lek-mating grouse species, including Greater Prairie-Chickens, to carry high genetic loads resulting in inbreeding depression (Bouzat et al. 1998, Westemeier et al. 1998, Johnson and Dunn 2006, Stiver et al. 2008), it is unsurprising that males with greater genetic diversity had higher reproductive success. For a species with a high genetic load and a breeding system that may enhance the expression of deleterious alleles, selection for highly heterozygous breeders may be one way to decrease the chance of succumbing to the genetic load. Selective pressure for maximally diverse males likely maximizes the overall genomic diversity of offspring and minimizes the expression of deleterious alleles in a female's offspring.

High skew in male reproductive success is common across many different lekking species, and begs the question why do unsuccessful males participate in lekking activities (Höglund and Alatalo 1995)? Within our study population we observed no statistical difference with regards to the observed individual allelic richness of unmated males and secondary males. Thus, even the most genetically depauperate male in the population has the potential to receive some reproductive success if he participates in lekking activities. Moreover, the relatively high success of genetically depauperate males argues that the behavioral cues used by females to choose the most genetically diverse males (Nooker and Sandercock 2008) are imperfect and thus it is still beneficial for males with low genetic diversity to participate in lekking activities because the fitness pay-off, if successful, is large relative to the costs.

We found a connection between individual genetic diversity and survival for Greater Prairie-Chickens. To date little work has been done to link genetic diversity to survival, but previous work conducted by Merilä et al. (2003) determined that male Collared Flycatchers with higher genetic variability ( $d^2$ ) lived longer and had higher lifetime reproductive success. There was no such correlation among female flycatchers, suggesting that sexual selection on genetic diversity may be acting more strongly on males. Functionally, increased survival could also increase the lifetime fitness of more genetically diverse male prairie-chickens, because more genetically diverse males not only tend to be more likely to be the most successful male on a lek in a given year, but also live longer. Consequently, genetically diverse males have more opportunities to become the dominant male on a lek and realize the high mating success of being the dominant male on the lek. As of yet, we do not understand the influence of genetic diversity on the lifetime fitness of female Greater Prairie-Chickens.

If conservation programs are to be effective, conservation biologists must understand the natural processes which maintain genetic diversity. From a fitness standpoint, mates are chosen to maximize individual fitness; however, the cumulative effects of individual mate choices can and do scale up to have population-level consequences (Nowak et al. 2010). Within our study, female mate choice for genetically diverse males may in part be responsible for the relatively high heterozygosity and low observed variance in heterozygosity within our population ( $H_O \pm SE = 0.72 \pm 0.03$ ). Selection for, and heritability of, allelic diversity differs from heritability in the classic sense defined as the proportion of total phenotypic variation due to additive genetic variation (Frankham et al. 2002). However, under neutral theory (Kimura 1983), selection by

females of males with maximal genetic diversity is likely to maintain higher levels of genetic diversity in the population longer than would random mating (Nunney 1995). From an individual standpoint, the genetic composition of males and females involved in mating will interact to determine offspring genetic diversity (Jennions and Petrie 2000). However, if selection by females for maximally diverse males increases the likelihood that at least some of her offspring will also have high genetic diversity, then we have an individual-based mechanism for mate choice with population conservation-level consequences.

In our study, selection for genetically diverse individuals appears to be asymmetric in that males with higher genetic diversity had greater mating success and higher survival than did their less genetically diverse counterparts. Therefore, genetic diversity appears to be under sexual selection in this species. On our study site, most females that visited leks were bred, suggesting that variation in genetic diversity does not play a similar role in mating success for females. Although this trend has not been documented for any other lekking species, the observation of increased male reproductive success and survival with increased individual genetic diversity in both the Passeriformes and now Galliformes may indicate a broad evolutionary trend within the Aves.

### **Acknowledgements**

We thank the following organizations and people for allowing access to their prairie-chicken leks: Konza Prairie Biological Station, a property of The Nature Conservancy managed by the Division of Biology at Kansas State University; Rannells Flint Hills Prairie Preserve managed by Dr. Clenton Owensby in the Department of Agronomy at Kansas State University; and private lands owned by Grant Poole and James Hess. Tom VanSlyke and Kenny Berg provided logistical support. We thank Tracey Adamson, Jeremy Baumgardt, Amanda Behnke, Jarrod Bowers, Tara Conkling, Seth Cutright, DeVaughn Fraser, Chris Frey, Kyle Gerstner, Chod Hedinger, 'Hoogy' Hoogheem, Nichole Lambrecht, and Kara Oberle for field assistance and Thomas Prebyl for lab assistance. Funding for field work included: a NSF Kansas EPSCOR Grant, a research grant from the American Ornithologists' Union, an NSF Doctoral Dissertation Improvement Grant to J.K. Nooker (DEB-0608477), and the National Fish and Wildlife Foundation. Partial funding for the genetic analysis was provided by the National Wind

Coordinating Collaborative and Kansas Department of Wildlife and Parks. J.K. Augustine (nee Nooker) was supported by the Konza Prairie NSF Long-Term Ecological Research Grant (DEB-0218210) and by the Division of Biology at Kansas State University. This research was conducted under the following research permits: Scientific, Education or Exhibition Wildlife Permit, Kansas Department of Wildlife and Parks (SC-118-2003, SC-068-2004, SC-078-2005, SC-072-2006), and KSU Institutional Animal Care and Use Committee (Protocols 2079, 2351).

### **Literature Cited**

- Alcock, J. 2001. *Animal Behavior: an evolutionary approach*, Seventh Edition. Sinauer Associates Inc., Sunderland, Massachusetts, 532 pages.
- Augustine, J.K., J.J. Millspaugh, and B.K. Sandercock. In press. Testosterone: a proximate factor mediating mating success in male Greater Prairie-Chickens. *Studies in Avian Biology*.
- Bouzat, J.L., H.A. Lewin, K.N. Paige. 1998. Genetic evaluation of a demographic bottleneck in the Greater Prairie-Chicken. *Conserv Biol* 12:836-843.
- Cheng, H.H., I. Levin, R.L. Vallejo, H. Khatib, J.B. Dodgson, L.B. Crittenden, and J. Hillel. 1995. Development of a genetic map of the chicken with markers of high utility. *Poultry Science*: 74: 1855-1874.
- Coulson, T.N., J.M. Pemberton, S.D. Albon, M. Beaumont, T.C. Marshall, J. Slate, F.E. Guinness, and T.H. Clutton-Brock. 1998. Microsatellites reveal heterosis in red deer. *Proceedings of the Royal Society of London B*, 265, 489-495.
- Crnokrak, P., and S.C. H. Barrett. 2002. Purging the genetic load: a review of the experimental evidence. *Evolution* 56:2347-2358.
- Crow, J.F. 1970. Genetic loads and the cost of natural selection. Pp. 128-177 in K. I. Kojima, ed. *Mathematical topics in population genetics*. Springer Inc., Berlin, Germany.
- Darwin, C. 1876. *The effects of cross and self-fertilization in the vegetable kingdom*. John Murray, London, UK.
- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. *Introduction to conservation genetics*. Cambridge University Press, New York, NY. USA.

- Hamerstrom, F. N., and F. Hamerstrom. 1973. The prairie-chicken in Wisconsin. Wisconsin Dept of Natural Resources. Technical Bulletin No. 64. Madison, WI, USA.
- Hedrick, P.W. 1994. Purging inbreeding depression and the probability of extinction: full-sib mating. *Heredity* 73:363-372.
- Höglund, J., and R. V. Alatalo. 1995. *Leks*. Princeton University Press. Princeton, NJ, USA.
- Höglund, J., S.B. Piertney, R.V. Alatalo, J. Lindell, A. Lunberg, and P. T. Rintamaki. 2002. Inbreeding depression and male fitness in black grouse. *Proceedings of the Royal Society of London B*, 269, 711-715.
- Jennions, M.D., and M. Petrie. 2000. Why do females mate multiply: a review of the genetic benefits. *Biological Review* 75:21-64.
- Johnson, J.A., J.E. Toepfer, and P.O. Dunn. 2003. Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology* 12:3335-3347.
- Johnson, J.A. and P.O. Dunn. 2006. Low genetic variation in the Heath Hen prior to extinction and implications for the conservation of prairie chicken populations. *Conservation Genetics* 7:37-48.
- Johnstone, R.A. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biological Reviews of the Royal Society of London B* 265, 1651-1657.
- Kimura, M. 1983. *The neutral theory of molecular evolution*. Cambridge University Press, Cambridge, UK.
- Leberon, J.D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Loeske, E.B.K., B.C. Sheldon, and J. Merilä. 2002. Severe inbreeding depression in collared flycatchers (*Ficedula albicollis*). *Proceedings of the Royal Society of London B*, 269, 1581–1589.
- Mays, M.L., and G.E. Hill. 2004. Choosing mates: good genes versus genes that are a good fit. *Trends Ecology and Evolution* 19:554-559.
- Merilä, J., B.C. Sheldon, and S.C. Griffith. 2003. Heterotic effects on fitness in a wild bird population. *Ann Zool Fennici* 40:269-280.

- Nooker, J.K. 2007. Factors affecting the demography of a lek-mating bird: the greater prairie-chicken. Ph.D. Dissertation, Kansas State University, Manhattan, KS, USA.
- 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.
- Nowak, M.A., C.E. Tarnita, and E.O. Wilson. 2010. The evolution of eusociality. Nature 466:1057-1062.
- Nunney, L. 1995. Measuring the ratio of effective population size to adult numbers using genetic and ecological data. Evolution 49:389-392.
- Ortego, J., J.M. Aparicio, G.C. Calabuig, and P.J. Cordero. 2007. Increase in heterozygosity in a growing population of lesser kestrels. Biology Letters 3: 585-588.
- Peakal, R., R. Smouse. 2006. Genalex 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288-295.
- Peel, D., J.R. Ovenden, and S.L. Peel. 2004. NeEstimator: Software for estimating effective population size, Version 1.3. Queensland Government, Department of Primary Industries and Fisheries.
- Piertney, S.B., and J.F. Dallas. 1997. Isolation and characterization of hypervariable microsatellites in the red grouse (*Lagopus lagopus scoticus*). Molecular Ecology 6:93-95.
- Piertney, S.B., and J. Höglund. 2001. Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). Molecular Ecology Notes 1:303-304.
- Queller, D.C., and K.F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution 43:258-288.
- Raymond, M., and F. Rousset. 1995. GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.
- Roberts, S.C., and L.M. Gosling. 2003. Genetic similarity and quality interact in mate choice decisions by female mice. Nature Genetics 35: 103-106.
- Schroeder, M.A., and L.A. Robb. 1993. Greater prairie-chicken (*Tympanuchus cupido*). In: Poole A, Stettenheim P, Gill F (eds) The birds of North America. No. 36. The American Ornithologists' Union and the Academy of Natural Sciences of Philadelphia.
- Schuelke, M. 2000. An economic method for the fluorescent labeling of PCR fragments. Nature Biotechnology 18:2:233-234.

- Seutin, G., B.N. White, and P.T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analysis. *Canadian Journal of Science* 69:82-90.
- Stiver, J.R., A.D. Apa, T.E. Remington, and R.M. Gibson. 2008. Polygyny and female breeding failure reduce effective population size in the lekking Gunnison sage-grouse. *Biological Conservation* 141:472-481.
- Taylor, S.E., S.J. Oyler-McCance, and T.W. Quinn. 2003. Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). *Molecular Ecology Notes* 3:262-264.
- Thelen, G.C., and F.W. Allendorf. 2001. Heterozygosity-fitness correlations in rainbow trout: effects of allozyme loci of associative overdominance? *Evolution* 55:1180-1187.
- Thuman, K.A., and S.C. Griffith. 2005. Genetic similarity and the nonrandom distribution of paternity in a genetically highly polyandrous shorebird. *Animal Behavior* 69:765-770.
- Toepfer, J.E., J.A. Newell, and J. Monarch. 1987. A method for trapping prairie grouse hens on display grounds. Contribution No. 2144, Montana Agricultural Experimental Station, MT, USA.
- Waples, R. 1989. A generalized approach for estimating effective population size from temporal change in allele frequencies. *Genetics* 121: 379-391.
- Westemeier, R., J. Braun, S. Simpson, T. Esker, R. Jansen, J. Walk, E. Kershner, J. Bouzat, and K. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282:1695-1698.
- Wright, S. 1977. *Evolution and the genetics of populations. Vol.3. Experimental results and evolutionary deductions.* University of Chicago Press, Chicago, IL, USA.
- White, G.C., and K.P. Burnham. 1999. Survival estimation from populations of marked animals. *Bird Study* 46:5120-5139.
- White, G.C., K.P. Burnham, and D R. Anderson. 2001. Advanced features of program MARK. Pages 368-377 in R. Field, R.J. Warren, H. Okarma, and P.R. Sievert, ed *Wildlife, land, and people: priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress.* The Wildlife Society, Bethesda, MD, USA.



**Table 2.1.** Eleven polymorphic microsatellites successfully amplified from 235 adult Greater Prairie-Chickens from 2003-2007 near Manhattan, KS.

Marker	NA	AR	H <sub>o</sub>	H <sub>E</sub>	HWE	Genetic Disequilibrium	Source of marker <sup>a</sup>
ADL-146	7	5	0.51	0.66	0.510	0.510 – 0.433	1
ADL-230	9	4	0.49	0.69	0.932	0.036 – 0.517	1
BG-12	8	3	0.42	0.41	0.080	0.009 – 0.433	2
BG-16	12	5	0.57	0.73	0.673	0.015 – 0.272	2
BG-18	23	17	0.92	0.93	0.789	0.006 – 0.903	2
LLSD-4	11	9	0.87	0.91	0.049	0.051 – 0.201	3
LLSD4	29	19	0.81	0.89	0.123	0.040 – 0.767	3
LLSD-7	33	25	0.74	0.81	0.104	0.006 – 0.757	3
LLST-1	8	5	0.68	0.69	0.229	0.041 – 0.527	3
SGCA-6	12	7	0.79	0.87	0.061	0.023 – 0.767	4
SGCA-9	26	18	0.89	0.91	0.834	0.012 – 0.188	4
<b>Pooled</b>	<b>16.18±5.9</b>	<b>11.03±5.7</b>	<b>0.70±0.2</b>	<b>0.79±0.2</b>			

Abbreviations are as follows: Marker = marker name; NA = number of alleles observed in our sample; AR = allelic richness (number of alleles after correction for sample size); H<sub>o</sub> = observed heterozygosity; H<sub>E</sub> = expected heterozygosity; HWE/Genetic Disequilibrium = P values for Hardy-Weinberg equilibrium and linkage tests. <sup>a</sup>After Bonferroni correction for multiple comparisons  $\alpha = 0.005$ . The given P-values represent the range of observed P-values for each pairwise comparison between loci. <sup>b</sup> 1: Domestic chicken (*Gallus gallus*), Cheng et al. 1995; 2: black grouse (*Tetrao tetrix*), Piertney and Hoglund 2001; 3: red grouse (*Lagopus lagopus scoticus*), Piertney and Dallas 1997; 4: greater sage grouse (*Centrocercus urophasianus*), Taylor et al. 2003.

Table 2.2. Summary of the descriptive genetic data from nine polymorphic microsatellites successfully amplified from 164 male Greater Prairie-Chickens between 2003-2006 near Manhattan, in northeast Kansas.

<b>Lek</b>	<b>N<sup>(males)</sup></b>	<b>NA</b>	<b>AR</b>	<b>H<sub>O</sub></b>	<b>H<sub>E</sub></b>	<b>F<sub>ST</sub></b>
Hess Ranch	14	7.9±0.3	5.9±0.03	0.73±0.03	0.78±0.02	0.041±0.001
Konza North	27	10.3±0.5	6.7±0.4	0.75±0.02	0.79±0.03	0.027±0.002
Konza Main	61	10.0±0.4	6.6±0.4	0.76±0.03	0.80±0.01	0.031±0.003
Rannells Ranch	37	12.0±0.7	7.2±0.7	0.78±0.02	0.80±0.01	0.032±0.03
Poole Ranch	25	9.3±0.3	7.2±0.4	0.77±0.02	0.80±0.04	0.024±0.00
<b>Pooled</b>	164	13.8±2.3	7.3±0.4	0.72±0.03	0.77±0.03	0.03±0.001

Abbreviations are as follows: N<sup>(males)</sup> = number of males, NA = average number of alleles observed across all loci within a lek;

AR = allelic richness for each lek; H<sub>O</sub> and H<sub>E</sub> = observed and expected heterozygosities within each lek.

F<sub>ST</sub> value presented for each lek is the mean pairwise lek F<sub>ST</sub> value for each lek to the other four. The

F<sub>ST</sub> presented for the whole population Pooled is the average of all inter-lek F<sub>ST</sub> values

within the population.

Table 2.3. Summary of male behavioral observations recorded during 10 minute focal bouts of male Greater Prairie-Chicken behavior on lek sites both when females were and when females were not present on the lek.

Male Status	Boom Frequency $\pm$ SE	Number of Fights $\pm$ SE
High $H_O$ with females (N = 13)	4.99 $\pm$ 0.13	4.85 $\pm$ 0.19
Low $H_O$ with females (N = 10)	5.16 $\pm$ 0.18	4.61 $\pm$ 0.17
$\pm 1SD H_O$ with females (N = 59)	4.89 $\pm$ 1.46	5.93 $\pm$ 8.36
High $H_O$ without females (N = 13)	1.56 $\pm$ 0.04	3.81 $\pm$ 0.07
Low $H_O$ without females (N = 10)	1.08 $\pm$ 0.03	2.42 $\pm$ 0.11
$\pm 1SD H_O$ without females (N = 59)	1.39 $\pm$ 0.86	3.26 $\pm$ 1.71

Males have been divided into two categories; those having an observed heterozygosity  $>$  1 SD of the population mean observed heterozygosity (High  $H_O$ ) and those with observed heterozygosity  $<$  1 SD of the population mean heterozygosity (Low  $H_O$ ).

Table 2.4. Multistate encounter histories for male Greater Prairie-Chickens ( $n = 89$ ) in northeast Kansas from 2003-2006. Males were recorded as breeders if a successful copulation was observed (Y), or as non-breeders if they never mated (N).

State 03,04,05,06	Number of alleles							
	15	16	17	18	19	20	21	22
YYYY							1	
YYNN						1		
YY00				2				
YNY0			1					
Y000			1	2	1			
NYN0					1			
NY00			2		1		1	
NNYY						1		
NNNN				1				
NNN0			2		2			1
NN00				1	1			
N000				4	2	2		
OYYYY					1	1		
OYN0				1				
OY00				2				
ONYN						1		
ONYO					2			
ONNY				1	1			
ONNN					1			
ONN0				1	1			
ON00	1	1	2	5	3	2		
O0YY				1				
O0Y0			2					
O0NN						1	2	
O0N0		1	1	3	3	2		
O00Y		1		1		1		
O00N		1	3	2	4		1	1
Total	1	4	14	26	24	13	5	2

Table 2.5. Model selection results for multistate models testing the effects of breeding status (state) and number of alleles (all) on the survival ( $S$ ) and transitional probability of becoming a breeder ( $\psi$ ) in male Greater Prairie-Chickens ( $n = 89$ ) in northeast Kansas from 2003-2006.

Model structure		Model parameters			
$S$	$\psi$	$K$	Dev	$\Delta AIC_c$	$w_i$
all	con	3	219.0	0.0	0.505
state+all	con	4	219.0	2.2	0.172
state*all	con	5	217.7	3.1	0.108
con	con	6	216.6	4.2	0.061
state*all	state	2	226.3	5.2	0.034

Model parameters include number of parameters ( $K$ ), deviance (Dev), difference in  $AIC_C$  value (minimum  $AIC_{Cmodel} = 225.2$ ), and the Akaike weights ( $w_i$ ). Probability of encounter ( $p$ ) and the variance inflation factor ( $\hat{c}$ ) were set to 1.

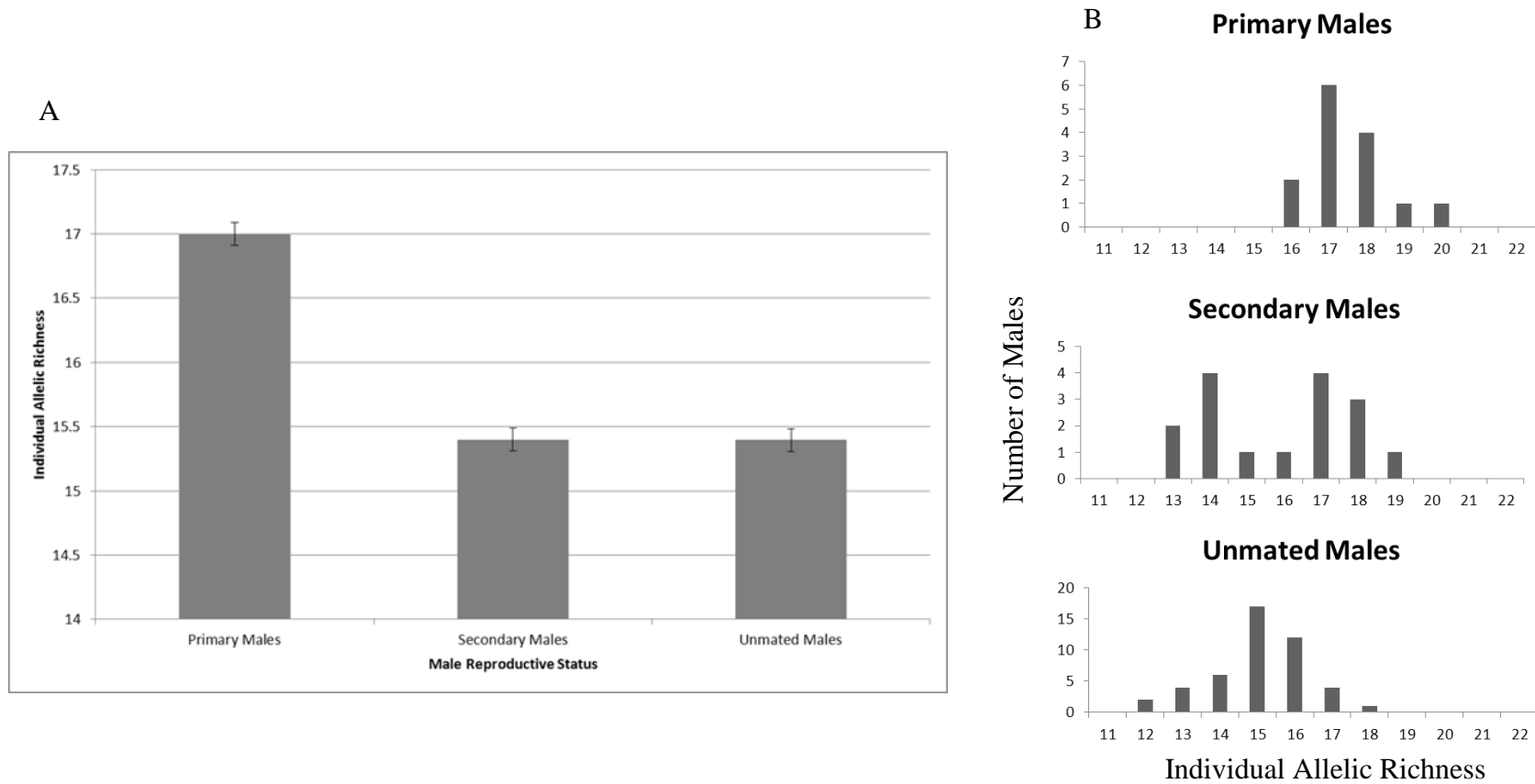


Figure 2.1. Effect of Individual Allelic Richness on Male Reproductive Status. A) Effect of Individual Allelic Richness on Male Reproductive Status. Primary males are males receiving the most copulations on each lek, each year, Secondary males are all males, not the primary male, who received some copulations on a lek each year, and Unmated males are those males never observed to copulate on a lek. Individual allelic richness values for each male reproductive class are presented with global standard errors. B) Frequency histogram of the number of males with each level of observed allelic richness by reproductive category.

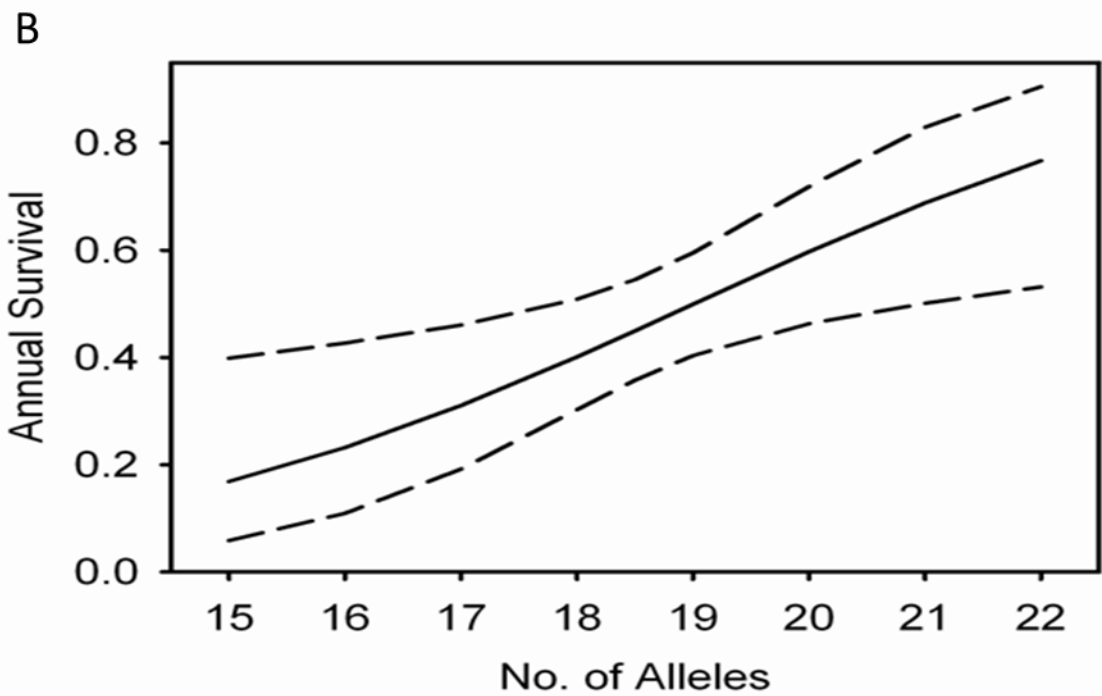
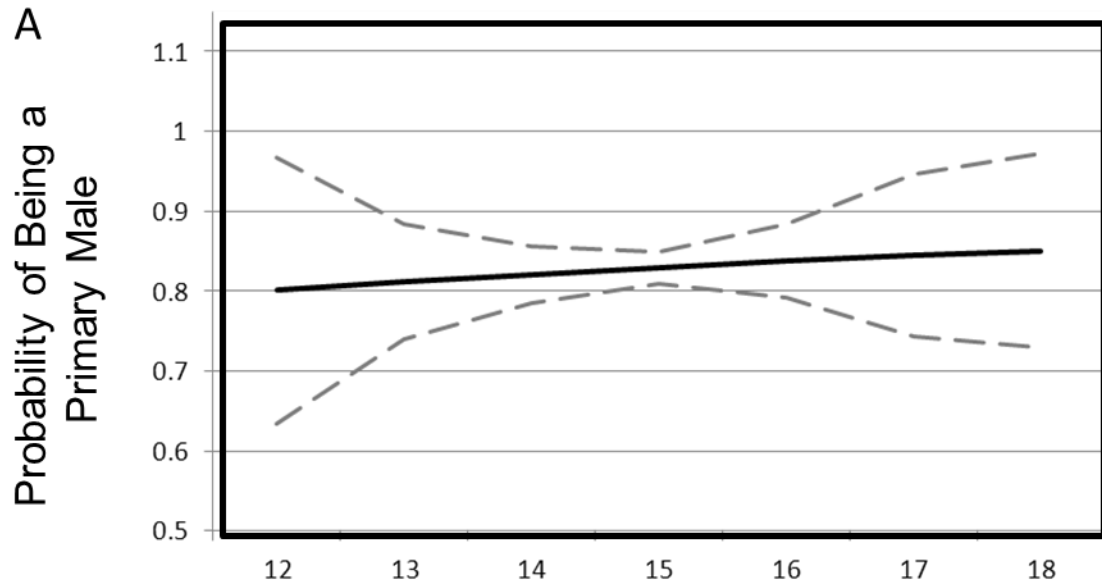


Figure 2.2. Effect of genetic diversity (no. of alleles) on A) the probability of being a primary male and B) annual survival of male Greater Prairie-Chickens ( $n = 89$ ) in northeast Kansas from 2003-2006. Parameter estimates for (B) were taken from the minimum  $AIC_C$  model  $S(\text{all})$ ,  $\psi(\text{con})$ ,  $p(\text{fixed}=1)$ . Dashed lines indicate 95% CI, and are linear on the logit scale but nonlinear after back-transformation.

# **Chapter 3 - HIERARCHICAL MODELING OF LEK HABITATS OF GREATER PRAIRIE-CHICKENS**

## **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 land cover 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, forest habitats and 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 eco-regions of eastern Kansas. The entropy model showed that >85% of lek sites were in habitat strata that comprised <20% of the regional landscape, and suggested 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.

## **Introduction**

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 eco-regions 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 historic 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 land cover 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 eco-regions of Kansas based on multi-scale 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 ( $\leq 2$  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 et al. 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 which were 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 eco-regions of Kansas (Figure 3.1, 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., *unpubl. ms*), 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 >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, personal communication). Our intensive population study was primarily conducted in Cloud, Geary, and Elk counties. For the intensive surveys, leks were also defined as >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. (Figure 3.1).

We used Arc Info 9.2 (Environmental Systems Research Institute, Redlands, CA) for all geospatial analysis and data extraction. We acquired all datasets 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 Remote Sensing Program 2005; Whistler et al. 2006) that we reclassified using Anderson Level I classification rules, depicting five biologically relevant land cover classes: grassland, row crop agriculture, urban, forested, and water (Anderson et al. 1971). Grasslands included all CRP (conservation reserve program) lands, or grazed and un-grazed 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 meter resolution 1999 National Elevation Dataset (U.S. Geological Survey, EROS Data Center). We also included a 1991 Riparian Inventory dataset for the state of Kansas (U.S. Department of Agriculture, Natural Resources Conservation Service) and roadway dataset that combined the 2006 Kansas State and Non-State Road System datasets (Kansas Department of

Transportation: Bureau of Transportation Planning). Each land cover data set was aggregated to 100 meter 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 land cover 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 which compared the absolute elevation of the lek site relative to the surrounding landscape, and was 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 one, so that  $\beta$ -coefficients from the resulting models were in the same units and would be directly comparable. We recognize there are inherent difficulties in z-transformations of categorical data, however the number of categories used was large and approximates a normal distribution; moreover models were run with both transformed and untransformed variables and the net effect of this transformation did not qualitatively alter model results or performance. 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 each data set. 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 multi-scale 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 integrate analyses across spatial scales (Phillips et al. 2004), and 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 3.1). 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:  $\text{leks} = 1.08 - 5.92 \times \text{percent urban area} - 1.39 \times \text{road density} + 0.76 \times \text{percent forest}$ . (Table 3.1)

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 3.1), 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 3.1). 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. 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 ( $\Delta\text{BIC} \leq 2$ ). The global model combined 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 3.1). 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 multi-scale model and Program MaxEnt to create an index of suitable lek habitat for the three eco-regions in our study area (Figure 3.2). 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 multi-scale grand model. Predictions from models based on a spatial scale of 0 m and 5 km were most similar to the predictions of the multi-scale model (Figure 3.3), presumably because environmental covariates at those spatial scales had the strongest effects on lek occurrence, as measured by the slope coefficients for z-transformed landscape covariates. (Figure 3.2, Figure 3.3)

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 multi-scale 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 (Figure 3.4). 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 (Figure 3.4).

## 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. ms*). 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 multi-scale 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 multi-scale 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 (Figures 3.2 and 3.3). 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., *unpubl. ms*). 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.

### **Acknowledgements**

The authors thank R. Rogers and J. Pitman of the Kansas Department of Wildlife and Parks for providing lek survey data for prairie-chickens in eastern Kansas. We also thank T. Cikanek, V. Hunter, K. Rutz, and W. White, who helped to locate and monitor lek sites in our study region. The Conservation Genetics and Molecular Ecology Lab at Kansas State University provided access to SAS statistical software and a dedicated GIS work station for analysis of spatial data. Financial support was provided by the Division of Biology at Kansas State University, and by wind industry partners, state and federal agencies and conservation groups under the National Wind Coordinating Collaborative.

### **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 Service Professional Paper 964.
- Applegate, R.D., B.E. Flock, and E.J. Fink. 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.
- 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. Kulesky. 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, USA.
- Griffith, G.E., J.M. Omernik, M. McGinley. 2008. Eco-regions 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, USA.
- 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, USA.

- 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. LeCessie, 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, USA.
- 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. Breadmore, J.A. Fitzgerald, R.P. Ford, W.C. Hunter, M.S. Morrison, and K.V. Rosenberg. 2000. Partners in flight: Conservation of the land birds of the United States. American Bird Conservancy, The Planes, VA, USA.

- 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.
- Phillips, S.J., R.P. Anderson, and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling* 190:231-259.
- 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. 2008. Prairie-chicken lek survey – 2008. Performance report statewide wildlife research and surveys, May 2008. Kansas Department of Wildlife and Parks, Pratt, KS, USA.
- Ryan, M.R., L.W. Buger, 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*). The birds of North America, Issue No. 36.
- Schwarz, G. 1978. Estimating the dimension of a model. *Annals of Statistics* 6:461-464.
- Slabbekoon, 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. Pages 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, USA.
- 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.

1 Table 3.1. Bayesian Model Selection to Identify Landscape Attributes Associated with Lek Sites of Greater Prairie-Chickens in  
 2 Eastern Kansas, 2005-2008

Model	K	-2 Log(L)	BIC	$\Delta$ BIC	$w_i$	Hosmer Lemeshow	
						C	P $\leq$
<i>Habitat Models 5 Km</i>							
%Urban, %Frst, Rd.Den	4	286.9	309.3	0	0.33	0.80	0.03
%Grass, %Urban, %Frst	4	287.7	310.0	0.68	0.24	0.78	0.07
%Frst, Rd.Den	3	293.8	310.6	1.26	0.18	0.79	0.04
%Urban, %Frst, Rd.Den, ALGP	5	283.1	310.9	1.64	0.14	0.80	0.04
%Grass, %Urban, %Frst, Rd.Den	5	283.5	311.4	2.07	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	16.93	< 0.01	0.82	0.86
<i>Habitat Models 200 m</i>							
%Ag	2	227.3	271.9	0	0.99	0.66	0.01
C-Den, %Ag, %CRP, %Grass, %Urban, %H <sub>2</sub> O, %Frst	8	353.0	364.1	92.19	0.01	0.86	0.02
<i>Point Models 0 m</i>							
D-Urb, Wt-Elev	3	281.3	298.1	0	0.49	0.82	0.01
Wt-Elev	2	287.0	298.1	0.09	0.46	0.82	0.01



*Multi-Scale Model*

%Grass 5 km, %Urban 5 km, Wt-Elev	4	230.2	262.7	0	0.42	0.85	0.05
%Urban 5 km, %Frst 5 km, Rd.Den 5 km, Wt.Elev	5	259.3	263.2	0.56	0.32	0.88	0.06
%Urban 5 km, %Frst 5 km, Rd.Den 5 km, ALGP, Wt-Elev	6	259.2	263.6	0.93	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	10.88	< 0.01	0.89	0.30

---

3  
4 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 =  
5 contour line density, D-RIP = distance to riparian area, D-URB = distance to urban town or city, D-Road = distance to nearest road,  
6 %Ag = % of the neighborhood in row crop agriculture, %CRP = % of the neighborhood Conservation Reserve Program, %Frst = % of  
7 the neighborhood in forest, %Grass = % of the neighborhood in grassland, %H2O = % of the neighborhood in water, %Urban = % of  
8 the neighborhood in urban cover, Rd.Den = road density in km per Km<sup>2</sup> of the neighborhood, and Wt-Elev = weighted elevation.  
9 Column heading labels are as follows: K = number of parameters, -2Ln(K) = maximum likelihood estimate from logistic model, BIC  
10 is the Schultz Criterion, and Hosmer-Lemeshow are goodness-of-fit test statistics for the logistic model.

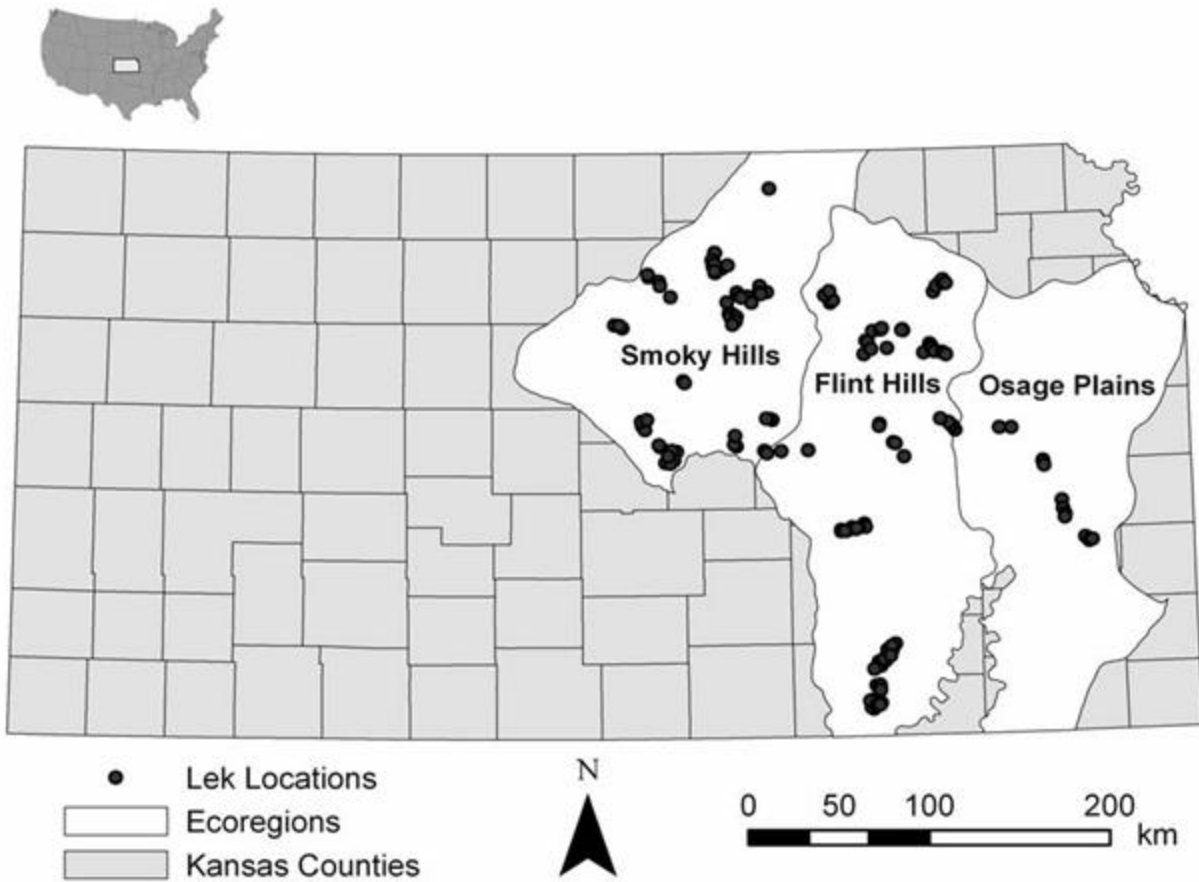


Figure 3.1. Study area and lek sites of Greater Prairie-Chickens in eastern Kansas, 2005-2008. Eco-regions represent areas of similar ecosystems and geomorphological characteristics. Black dots are locations of leks used for model development and validation. Inset map indicates the location of Kansas within the United States.

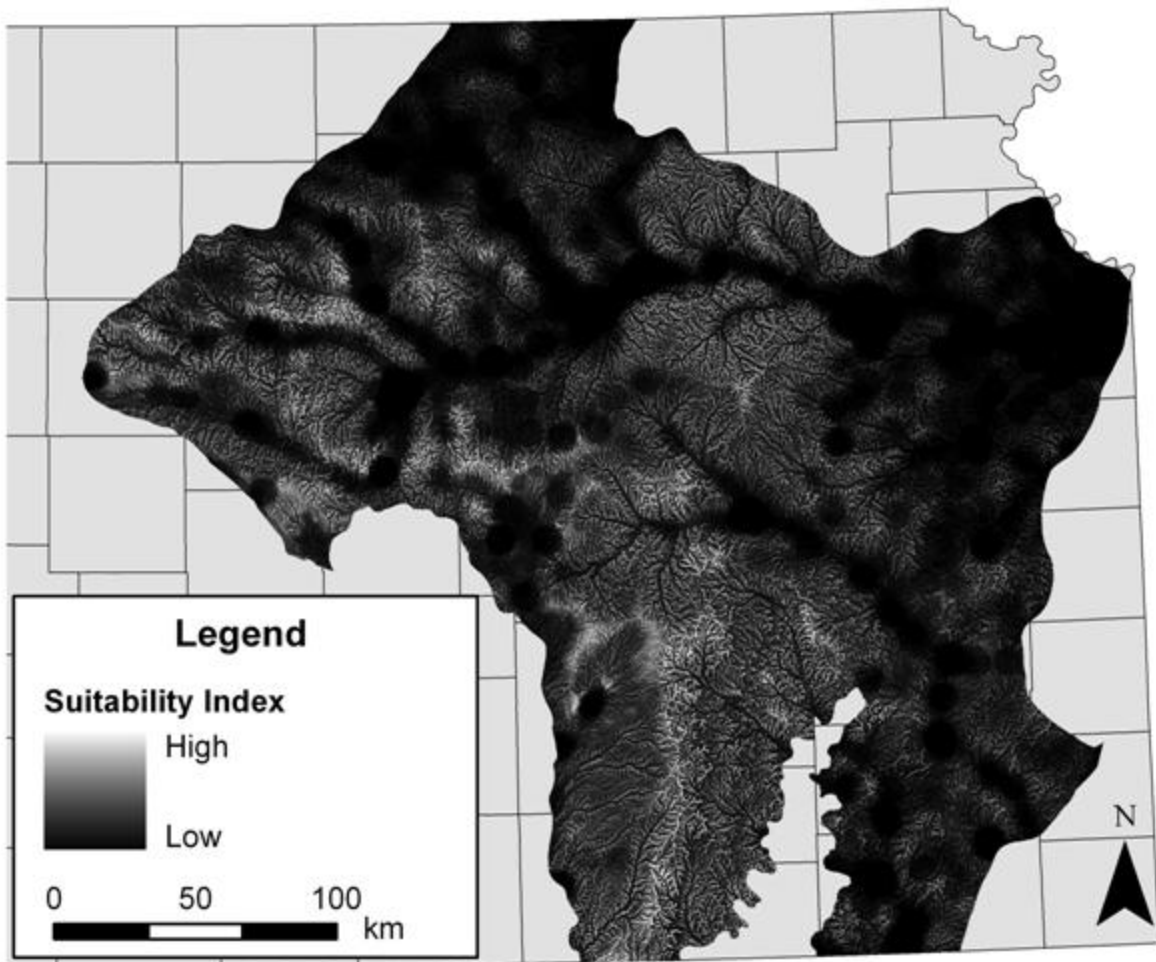


Figure 3.2. Map of habitat suitability based on maximum entropy modeling of lek sites of Greater Prairie-Chickens in eastern Kansas, 2005-2008.

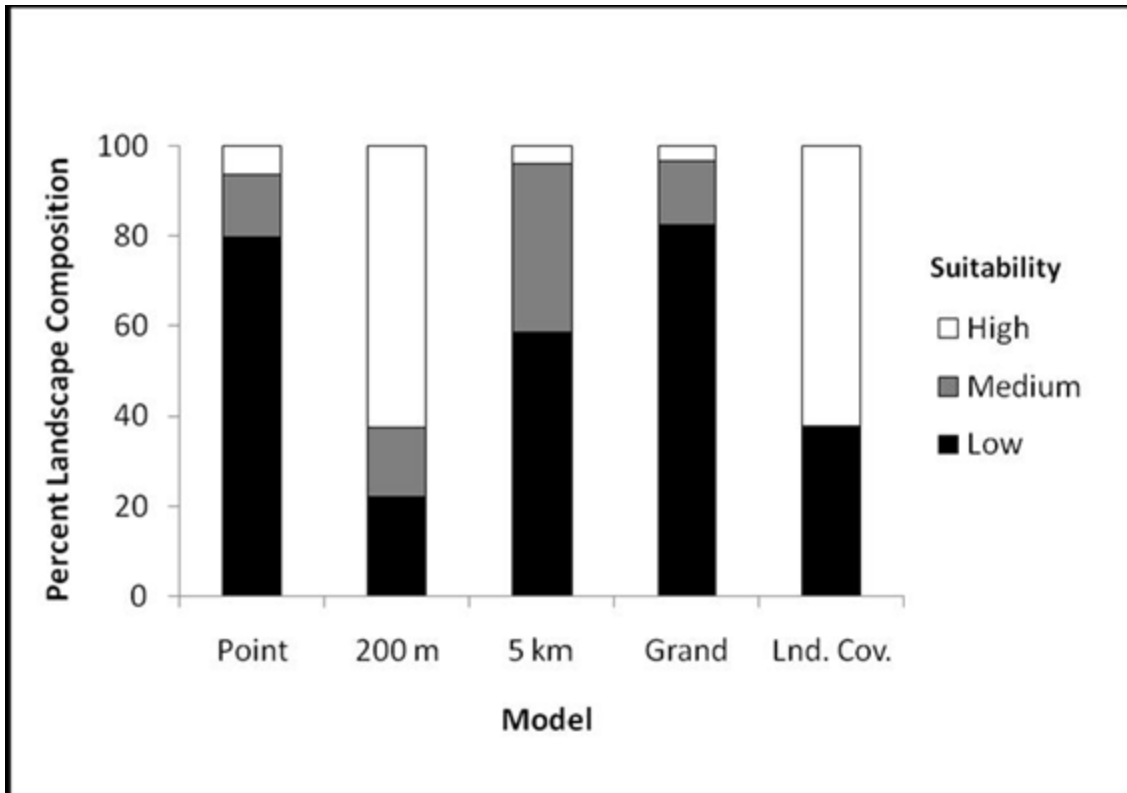


Figure 3.3. Comparisons of habitat suitability of our study area as predicted by models for three spatial scales (0 m, 200 m, and 5 km), a multi-scale model (Grand), and a model based solely on land cover (Lnd. Cov.).

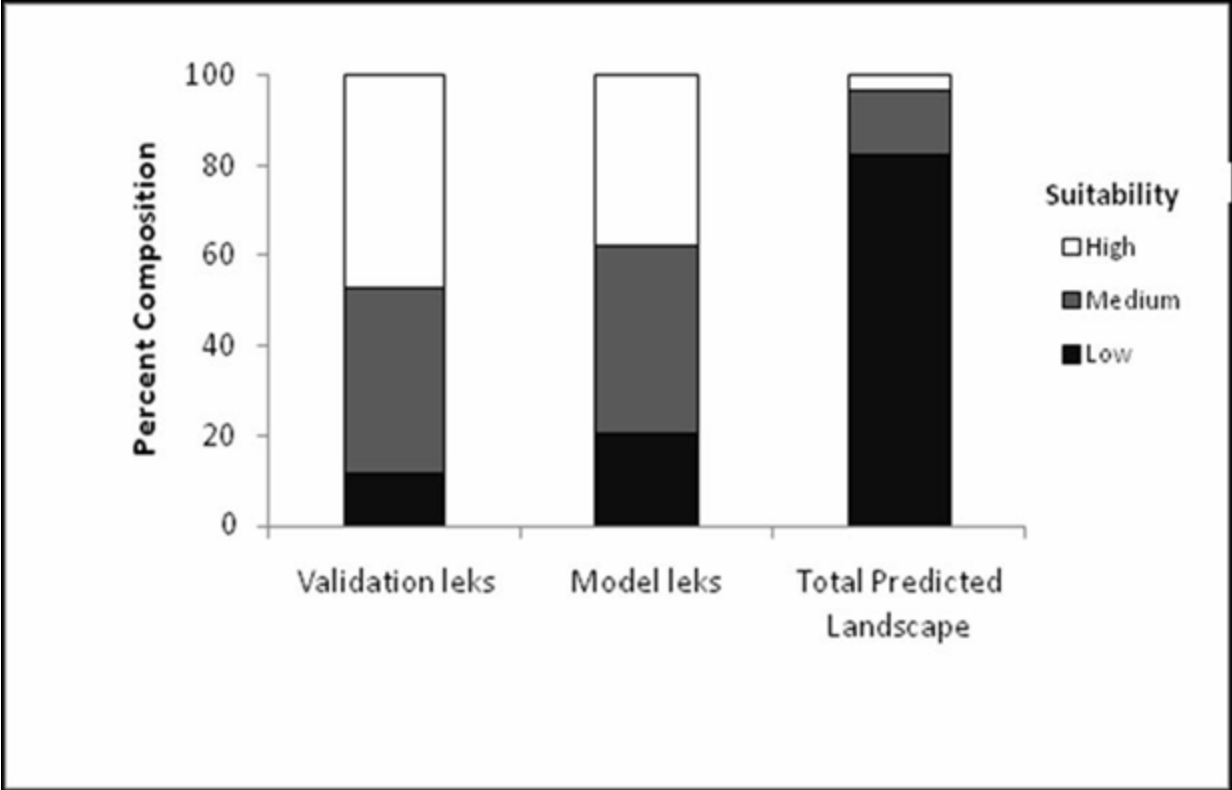


Figure 3.4. Comparisons of habitat suitability among a random set of leks used for model validation (N = 34), lek locations used for model development (N = 132), and the entire study area (Landscape).

# **Chapter 4 - OPTIMIZING LANDSCAPE RESISTANCE SURFACES TO UNDERSTAND GENE FLOW: A CASE STUDY USING GREATER PRAIRIE-CHICKENS**

## **Abstract**

Measurements of genetic differentiation among populations or individuals at spatially discrete locations are often used as surrogate measures of functional connectivity of spatially structured landscapes. Under equilibrium conditions of genetic drift and migration, isolation by distance (IBD) is expected to explain the distribution of genetic diversity. However, most landscapes are not homogenous but are composed of a patchy mosaic of different land cover types that are differentially permeable to dispersal movements. The methods used to parameterize a permeability cost surface are a critical component determining isolation by resistance (IBR) model performance, yet most IBR models neither optimize habitat permeability values, nor test the sensitivity of IBR models to changes in permeability values. Here, we present an information theoretic approach to model selection for optimizing the resistance surface for a sensitive species of grassland bird, the Greater Prairie-Chicken. We assessed sensitivity of model output to the number of land cover resistance classes included in the land cover data set, and compared our optimized cost surface to a reference cost surface optimized using expert opinion. Our top performing IBR model from our model selection procedure included two land cover classes (grassland and all other classes), three fewer than our literature model optimized resistance surfaces, and had 20% greater concordance with the population genetics data. We utilized results of our top performing IBR model to highlight areas of conservation need for Greater Prairie-Chickens across our study region. The methodologies outlined in this paper illustrate a general approach for researchers interested in quantifying the connectivity of natural landscapes.

## **Introduction**

Landscape ecology has led to a paradigm shift away from assumptions of spatial homogeneity to an understanding of the patchy structure of natural landscapes and introduction

of statistical tools necessary to assess the influence of landscape heterogeneity on ecological processes (Weins 1989, 2001). Similarly, the emerging field of landscape genetics has led to a paradigm shift in population genetics, allowing researchers to explicitly incorporate spatial and temporal heterogeneity when assessing the distribution of genetic variation within and among populations in space and time (Manel et al. 2003, Sacks et al. 2004, Knowles 2009). Human activities over the past 200 years have caused unprecedented changes to landscape cover and configuration, and habitat fragmentation and disturbance are ubiquitous. Landscape genetics, estimates how landscape structure influences gene flow and the geographic distribution of genetic diversity, and may offer unique insights into how wildlife will respond to novel environments (Manel et al. 2003, Storfer et al. 2007).

For many species, habitat alteration has been shown to inhibit dispersal (deMaynadier and Hunter 2000), decrease survival (Carr and Fahrig 2001), reduce genetic diversity (Frankham et al. 2002), and increase extinction risk (Allendorf and Luikart 2007). Historically, ecologists interested in assessing the putative impacts of landscape change to wildlife have relied on direct observation of animals marked with unique tags or radio transmitters to estimate movement rates among subpopulations. Landscape genetic techniques provide useful alternatives to more costly and less efficient methods of animal tracking because genetic methods are able to detect low but biologically meaningful rates of dispersal and can differentiate between those movements which produce population level consequences and those movements which fail to produce offspring (Edwards 1993, Lowe and Allendorf 2010). In particular, measurement of gene flow between sub-populations is an index of dispersal, which is in part regulated by the permeability of landscape matrix to the dispersing organism (Wright 1943, Slatkin 1993). Therefore, landscape genetics can be used to estimate effective dispersal and immigration among spatially structured sub-populations (Schwartz et al. 2002), providing essential information for conservation biologists and wildlife managers.

One attractive feature of landscape genetics is an ability to evaluate the responses of species to landscape management scenarios in a robust, hypothesis-driven framework. Several studies have applied causal modeling techniques to implicitly test multiple hypotheses of how landscape elements (including matrix composition) may interact to impact gene flow and landscape connectivity (Jørgensen et al. 2005, Cushman et al. 2006). Past workers have evaluated model support by ranking competing models by Mantel correlation coefficients or  $r$ -

square values. Correlation coefficient values are considered an indication of biological significance (Quinn and Keough 2002), but are sensitive to the number of parameters included in the model and care must be taken to avoid the inclusion of extraneous variables (Akaike 1981, Lebreton et al. 1992, Burnham and Anderson 1998). Model selection procedures based on Akaike's Information Criterion aim to strike a balance between the number of parameters estimated, and the precision of the parameter estimates (Akaike 1981). For example, AIC model selection procedures have been used in a regression framework to test landscape characteristics as explanatory variables of observed differences in pairwise  $F_{ST}$  values among populations of black-tailed prairie dogs (*Cynomys ludovicianus*, Roach et al. 2001, Antolin et al. 2006). Similarly, Epps et al. (2007) used least cost path analysis and Mantel tests to test alternative models for patterns of gene flow in bighorn sheep (*Ovis canadensis*). However, both sets of models have advanced our understanding of animal movements but do not account for alternate movement paths or the potential influence that matrix configuration might have on gene flow (McRae et al. 2008).

Isolation by resistance models (IBR) based on circuit theory were explicitly designed to correct for limitations of previous models (McRae 2006). By utilizing a user-defined cost surface, investigators can test the influence of habitat composition and configuration on gene flow among populations in a single resistance metric (McRae 2006, McRae et al. 2008). Since initial release of the software (McRae 2006), applications of Program CircuitScape to model IBR for field data from natural populations has become widespread (Storfer et al. 2007, McRae and Beier 2007, Barton et al. 2010, DeBarba et al. 2010). A critical element determining the performance of permeability models is how the landscape data are parameterized to a cost surface (McRae et al. 2008, Beier et al. 2008). Under ideal circumstances, cost surface values are parameterized from field data on habitat use and movements (McRae and Beier 2007). In practice, availability of comprehensive data sets on movements are limited, and cost values must be assigned by biological inference or based on expert opinion (Beier et al. 2008).

Understanding the natural history of a sensitive species is limited compared to resolution of most land cover data sets, which can include > 30 land cover classes. Reconciling the resolution of what we know about a species versus what we know about its environment can influence the outcome of the model. Thus, it would be beneficial to develop specific guidelines, or robust algorithms for parameterization of cost surfaces for use in IBR analyzes. Currently, no rigorous



quantitative methods are available for deciding how many land cover classes should be included in landscape analyses nor to estimate the relative permeability of each habitat.

Here we seek to address current knowledge gaps by providing a robust, hypothesis-driven methodology for determining the appropriate number of land cover classes to include in IBD analyzes. We also develop recommendations for inclusion of genetic data to parameterize the number and value of land cover resistance classes. Our goals are three-fold. First, we test the hypothesis that the number of land cover classes included in isolation by resistance models impacts model results and suggest a methodology to control for such impacts. Second, we propose a method to parameterize land cover data into resistance classes in situations where little is known about the habitat use or movement patterns of the study species, but for which genetic data are available. Last, we describe a case study based on our new approach with field data collected on Greater Prairie-Chickens (*Tympanuchus cupido*) in Kansas and Nebraska; a system for which a great deal is known about their habitat use and distribution. For the third aspect of this research it was important to use a species whose natural history was well understood, so that resistance values for different types of land cover were based on known habitat preferences, and movement data could be compared with model predictions. If both approaches give similar results, then this will lend credence to the validity of our approach.

## Methods

Here, we describe our general approach and the sampling scheme used to obtain our genetics data; the methods used to test the impact of the number of land cover classes included the resistance surface on IBR models, and then apply the results of this assessment to Greater Prairie-Chickens in Kansas. For purposes of consistency, we have adopted the following labeling scheme for subsequent discussion about the parameterization of IBR cost surfaces. When we refer to a *land cover class* we are referring to the habitat classifications given to different land cover elements included in the land cover data. When referring to a *land cover resistance class*, we mean a resistance value assigned by the researcher to a particular *land cover class*. The resistance surface then is the land cover data set once all *land cover classes* have been parameterized to *land cover resistance classes*. Pairwise resistance value is a cumulative resistance value calculated using the *land cover resistance class* values occurring between any

two populations distributed across the resistance surface. A landscape resistance value is the average of all pairwise resistance values distributed across the resistance surface.

### ***General Approach and Sampling***

To measure isolation by resistance we used Program CircuitScape (McRae 2006). Program CircuitScape uses electrical circuit theory to model the connectedness of two nodes (populations) on a network (resistance surface). One aspect of this modeling approach is that nodes connected by broad swaths of habitat or by habitat with lower land cover resistance values will yield lower pairwise resistance values than nodes connected by narrow swaths of habitat or by habitats with higher land cover resistance values. Therefore, land cover composition, patch shape, and matrix configuration were considered when estimating pairwise resistance (McRae 2006). The resulting matrix of pairwise resistance values was then correlated with the matrix of pairwise genetic distance values from the genetic analyses using Mantel tests (Mantel 1967).

Prairie-chickens are a good candidate species for an integrated model of landscape genetics and ecology because they are grassland obligates with a well-defined mating system and known habitat requirements (Schroeder and Robb 1993, Nooker and Sandercock 2008, Gregory et al. *Chapter 3*). Prairie-chickens require large tracts of relatively intact grasslands to fledge young (Robel et al. 1970) and they may avoid anthropogenic disturbances (Pitman et al. 2005). Moreover, male philopatry to lek locations makes them vulnerable to land cover change, and a lek mating system typified by high skew in male mating success and female nesting success can lead to rapid reductions in effective population size (Nooker and Sandercock 2008).

Prairie-chickens were captured at lek sites during the spring breeding season from 2006-2009 using walk-in funnel traps (Hamerstrom and Hamerstrom 1973, Toepfer et al. 1987). Field methods were approved by Kansas State University's Institutional Animal Care and Use Committee (Protocol Nos. 2474 and 2781). Multiple leks were surveyed at each of six distinct locations across our study area which encompassed a 98,400 km<sup>2</sup> area of the eastern Smoky Hills and Flint Hills of Kansas as well as southeastern Nebraska (Figure 4.1). At capture, each bird was given a unique combination of colored leg bands and a 40 µL blood sample was collected via toenail clipping and stored in 1,000 µL of either Queen's lysis buffer (Seutin et al. 1991) or Longmire's Solution (Longmire et al. 1997) until DNA extraction could be carried out.

DNA was extracted using commercially available Qiagen DNEasy tissue extraction kits (Qiagen Inc. Valencia, CA, USA). All samples were genotyped at 11 microsatellite loci developed for other gallinaceous birds but previously used in prairie-chicken research. Amplification of microsatellite markers via Polymerase Chain Reaction (PCR; Table 4.1) was conducted in an Eppendorf eppgradient thermocycler (Brinkman Inc. Westbury, NY, USA) in 10  $\mu$ L PCR cocktails containing 30 ng of template DNA, 2.5  $\mu$ M MgCl<sub>2</sub>, 0.2  $\mu$ M dNTP's, 0.12  $\mu$ g/ $\mu$ L BSA, 0.8 M betaine, 10  $\mu$ M of each forward and reverse primer, 0.2  $\mu$ M of M-13 universal primers (Schuelke 2000) labeled with a fluorescent dye attached to the 5' end, and 0.05 units of Taq polymerase (Go Taq Flexi, Promega, Madison, WI, USA). Fragment analysis was conducted using an ABI 3730 automated sequencer, and alleles were scored using GeneMarker 1.6 software (Applied Biosystems; Foster City, CA). We re-analyzed all homozygotes and 10% of all heterozygotes to determine rates of genotypic error and allelic dropout.

We tested for deviations from Hardy-Weinberg and linkage equilibrium and also to calculate population pairwise  $F_{ST}$ , observed and expected heterozygosity, within population  $F_{IS}$ , and allelic richness using GenePop 4.0.10 (Roussette 2008). Estimates of effective population size ( $N_e$ ) were calculated using the linkage disequilibrium method as implemented in Program LDNE (Waples 2007). We used GenAlEx ver. 6.3 (Peakall and Smouse 2006) to calculate pairwise genetic and geographic distances between sub-populations. Mantel tests of isolation by distance and isolation by resistance based on Euclidean distance or pairwise resistance verses pairwise genetic distance values ( $D$ ) and pairwise  $F_{ST}$  were implemented in SPAGeDi (Hardy and Vekemans 2002). To test for population structure, we used Program Structure 2.2 (Pritchard et al. 2000), testing for  $K = 1-6$  populations, for 100,000 iterations with a 50,000 iteration burn in period. Program Geneland (Guillot et al. 2008) was used to test if the number of distinct sub-populations identified ( $K = 6$ ) were in part structured by their geographic distribution on the landscape using the same number of iterations and burn in period as was used for Program Structure.

### ***Influence of the Number of Land Cover Classes on IBR***

Addition of land cover resistance classes to a resistance surface increases the patchiness because it affects the distance among nodes and the size of land cover resistance classes among two nodes. Thus, the pairwise resistance value for a given pair of nodes will be a function of the

number of land cover classes included in a model (McGarigal and Marks 1995, McRae and Beier 2007). Moreover, r-square values from a Mantel test for IBR may also increase as a function of the number of included land cover resistance classes (Lebreton et al. 1992, Burnham and Anderson 1998). The net effect is that results from IBR models may be sensitive to the number of land cover classes included in the model.

Our study site included portions of eastern Kansas and southeastern Nebraska (Figure 4.1). Land cover data for Kansas were summarized from the 2005 Kansas Gap Land cover database, UTM zone 14, NAD 27. The database depicts 43 land cover classes for the state of Kansas generated by the Gap Analysis Project to meet the requirements of the National Gap Analysis Program for the United States Geological Survey. The database was generated using a two-stage hybrid classification system of multi-temporal Landsat Thematic Mapper 5 imagery at 30 m resolution (Whistler et al. 2006). The database is maintained by the Kansas Applied Remote Sensing (KARS) Program, housed at the University of Kansas in Lawrence, KS, USA.

Land cover data for Nebraska were summarized from the 2005 Nebraska Land Use Map UTM zone 14, NAD 27. The Nebraska Land Use Map depicts 41 land cover land use classes for the state of Nebraska, generated by Center for Advanced Land Management Information Technologies, housed in the School of Natural Resources at the University of Nebraska-Lincoln. The database was created to provide comprehensive land cover and land use data for the state of Nebraska suitable for use in the National Gap Analysis Program. The database was generated using a three-stage hybrid classification system of multi-temporal Landsat Thematic Mapper 5 imagery at 30 m resolution (Dappen et al. 2007). All land cover data were retilled to 500 meter pixels for IBR analysis with Program CircuitScape.

To test the influence that the number of land cover resistance classes (hereafter referred to as  $K$ ) has on the calculated pairwise resistance value, we parameterized the original Kansas and Nebraska land cover data sets to include  $K = 1-20$  different land cover resistance classes and assigned resistance values to those classes based on expert opinion and merged classes following the guidelines of Anderson et al. (1971). We used multiple Mantel tests to produce the r-square value for correlations of genetic matrices and resistance matrices for landscapes with  $K=1-20$  habitat types. We tested for a significant correlation between average pairwise resistances and the IBR  $r^2$  value with the number of land cover resistance classes ( $K$ ) included in the resistance surface using Spearman's rank correlation ( $r_s$ ) as implemented in Program R.

### *Simulation Analysis*

Next, we tested the effects of the number of included land cover resistance classes on IBR with simulated landscapes and simulated genetic data ( $F_{ST}$  values). We created 30 simulated landscapes with 500 m pixels in a variety of spatial configurations and extents (e.g. simulated landscape Figure 4.2). We then created six putative populations and randomly assigned pairwise  $F_{ST}$  values ranging from 0-1 among population pairs. For each simulated landscape, we used the same genetic distance matrix, but randomly placed each population on each of the 30 different landscapes. Each of the 30 different landscapes were parameterized to have between two and five different land cover resistance classes. Separate Mantel tests were used to analyze the same matrix of pairwise genetic distance values with each different matrix of pairwise resistance values derived from the  $K = 2-5$  parameterizations of each simulated landscape. Spearman's rank correlation was used to test for a significant linear trend between the number of land cover resistance classes ( $K$ ) and the resulting average landscape resistance value and the resultant IBR r-square value for these simulated landscapes.

### *Optimization of the Number of Land Cover Resistance Classes*

The observed trend of increasing  $r^2$  and pairwise resistance values as a function of increasing  $K$  suggested that an information theoretic approach to model selection would aid in identifying the appropriate number of land cover resistance classes to include in IBR model selection (Leberton et al. 1992). While the method described here can be applied to any system or species for any number of  $K$  land cover classes, the procedure here is described as it pertains to our prairie-chicken study systems in eastern Kansas and Nebraska.

The inflection point in the plot of  $r^2$  versus  $K$  suggests an upper asymptote of about five land cover resistance classes to be considered in our model selection procedure (Figure 4.3). Therefore, to determine the appropriate number of land cover classes to be included in isolation by resistance models, we started with five land cover classes. Previous analyses suggest that the absolute value of the resistance classes is less important in determining model performance than is the differences among values (McRae et al. 2006, Jaquiere et al. 2011). Thus, the initial land cover parameterization was such that grassland land cover was assigned a resistance value of 100, row crop agriculture was assigned a resistance value of 200, forests were assigned a resistance value of 300, water was assigned a resistance of 400, and human developed land

classes were assigned a resistance value of 500. These ordinal values were chosen based on a relatively naïve estimate of how we thought prairie-chickens might respond to these different land cover classes in their environment based on Schroeder and Robb (1993). We then re-parameterized the resistance surface by merging the two least prevalent land cover resistance classes (human impacted land cover and water) into a single category with a resistance = 400 and all other resistance categories as previously specified. This process was repeated iteratively until we had a resistance surface with  $K = 2$  land cover resistance classes (Figure 4.4).

We then ran CircuitScape and calculated all relevant test statistics on all parameterizations of the resistance surface. Next we used the matrix of population pairwise resistance values as the predictor matrix and the genetic distance values matrix as a response matrix in Mantel tests for IBR. We then used the residual sum squares estimate from the Mantel test of IBR to calculate the maximum likelihood estimate following equations provided in Burnham and Anderson (1998) such that:

$$\text{LN}(\mathcal{L}(\hat{\theta})) = \frac{1}{2} n \log(\hat{\sigma}^2)$$

where  $\log(\mathcal{L}(\hat{\theta}))$  is the log likelihood of the model given the data,  $n$  is the sample size, and  $\hat{\sigma}^2$  is the maximum likelihood estimator calculated as the residual sum of squares /  $n$  (Burnham and Anderson 1998). Using the log likelihood value, we then estimated a second order AIC statistic adjusted for small sample size bias as:

$$\text{AIC}_c = -2 \log(\mathcal{L}(\hat{\theta})) + 2K \left( \frac{n}{n - K - 1} \right)$$

where  $K$  = the number of landscape elements included in the land cover resistance data set and  $n$  = the number of population pairs for which we were estimating pairwise resistance (Burnham and Anderson 1998). Using this adjusted  $\text{AIC}_c$  value we carried out traditional model selection procedures. Parsimonious models were identified as any model with a  $\Delta\text{AIC}_c \leq 6$ . The most parsimonious model was chosen as the minimum  $\text{AIC}_c$  model with the greatest Akaike weight ( $w_i$ , Burnham and Anderson 1998). Model selection procedures allowed us to identify the model which determined how many landscape resistance classes were biologically relevant for our study system.

### ***Resistance Surface Parameterization***

Once we had determined the number of land cover resistance classes to include in our resistance surface, we needed to determine biologically relevant resistance values for each land cover class. Estimates of genetic differentiation among populations such as Nei's modified genetic distance or  $F_{ST}$  contain key information about functional connectivity of populations on the landscape (Scribner and Chesser 2001). Estimates of genetic differentiation among populations are due, in part, to gene flow as a function of dispersal among adjoining or isolated populations in a patchy environment (Hanski and Gaggiotti 2004, Storfer et al. 2007). Thus, genetics data can be used to gain insights about the functional resistance to movement of the intervening matrix to dispersal between populations (Slatkin 1993). For a set number of land cover classes in the resistance surface, we iteratively adjusted the resistance values for each land cover class to determine the magnitude of difference or degree of contrast among resistance values that would yield the greatest concordance with our genetic data. Model fit was assessed by the largest possible  $r^2$  value from our Mantel tests (Cushman et al. 2006).

### ***Greater Prairie-Chicken Case Study***

For our case study with Greater Prairie-Chickens, we compared two sets of IBR models to each other and to IBD. For the first set of IBR models we applied the above methods as described by iteratively adjusting the assigned land cover resistance values of models identified by  $AIC_C$  model selection as top performing models to obtain the greatest concordance between our resistance surface and the genetics data. We refer to models parameterized in this way collectively as  $AIC_C$  models, and denote a specific  $AIC_C$  model by its  $K$  value. We also parameterized two resistance surfaces based on the suggested approach of (McRae and Beier 2007) using biological inference and data on prairie-chicken habitat use and distribution, respectively. We then compared model performance of these two parameterizations with that of our  $AIC_C$  models to evaluate the efficacy of our model selection and optimization to the genetics data approaches.

Using habitat use and movement data collected for Greater Prairie-Chickens, we developed two possible habitat resistance surfaces for prairie-chickens inhabiting our study region. The '*literature model*' was an IBR model derived using known habitat preferences for prairie-chickens taken from the literature (Robel et al. 1970, Schroder and Robb 1993). The

'*niche model*' was an IBR model based on a recent ecological niche modeling study conducted on our study system, which determined overall landscape suitability for prairie-chickens based on active lek site distribution across >80% of our study area (Gregory et al. *Chapter 3*). For consistency with AIC<sub>C</sub> models each of these resistance surfaces included five land cover resistance classes (Table 4.2). We parameterized the literature model using data on habitat characteristics taken from the literature; assigning grassland habitat the lowest land cover resistance value of 100. Recent data suggests that prairie-chickens may avoid anthropogenic structures (Pitman et al. 2005), so human-developed land cover was assigned a land cover resistance value of 1,000. Common cultivated plants in our study area were wheat, milo, and corn, which are all non-native grass species. We have observed prairie-chickens nesting in wheat fields thus, we felt agricultural fields likely represented fairly low resistance to movement and so we assigned a land cover resistance value of 200 to them. Prairie-chickens meet their water requirements from native grasses and water; wetland areas are typically avoided by prairie-chickens (Schroeder and Rob 1993). However, nests have been observed in close proximity to cattle stock-ponds on our field sites, so the water habitat class was assigned a land cover resistance value of 400. Last, prairie-chickens have been observed to make seasonal use of forested areas during severe winter weather (*pers. Obs.*), so forest land cover was given a land cover resistance value of 500 (Table 4.3).

For the niche model, we utilized the predicted distribution of highly suitable prairie-chicken lek habitat delineated across our study site using an ecological niche model developed by Gregory et al. (*Chapter 3*). The ecological niche model predicted that ~90% of highly suitable prairie-chicken lek habitat was grassland, so we assigned grassland land cover types a resistance value of 100. The model also predicted < 0.001% of highly suitable lek habitat to be human developed land cover, so this land cover class was assigned a resistance value of 1,000. Forests and water made up ~2% and 0.3% of the land cover in highly suitable areas and so were assigned resistance values of 500 and 800 respectively. Last, row crop agriculture comprised approximately 8% of highly suitable lek habitat, so we assigned row crop agriculture a resistance value of 400 (Table 4.2). After parameterizing the land cover data for the niche model we also parameterized the data for a 'reverse' model. The reverse model is simply a landscape parameterization that has resistance values assigned opposite of expectation for the species, i.e. opposite of the literature model. Thus, in our reverse model for prairie-chickens, we predicted



grassland to have the highest resistance to movement and urban areas to have the lowest resistance to movement (Table 4.4). The reverse model served for validation of our method, i.e. we sought to confirm that a model which idealized a poor representation of reality actually did perform substantially worse than models that were purportedly a good representation of reality. Last, to demonstrate the utility of this approach for conservation work, we used the habitat resistance surface from our top performing AIC<sub>C</sub> IBR model as a cost surface in least cost path analysis in Arc Info 9.3.

## Results

### *Genetic Analysis*

In the four year period from 2006 – 2009, we collected genetic samples from 1,038 adult Greater Prairie-Chickens from 84 leks sampled at six discrete populations spread across the Flint Hills and Smoky Hills of Kansas ( $N = 921$ ) and southeastern Nebraska ( $N = 117$ ; Figure 4.1). We found no significant deviations from Hardy-Weinberg Equilibrium or linkage disequilibrium among our loci, and our observed rate of allelic dropout was  $<1.0\%$  (Table 4.1). The sample was male biased (70%), but this is likely due to the lek-based sampling method and not representative of a true sex bias in these wild populations. Population-wide estimates of genetic diversity indicated a moderately high level of genetic diversity ( $H_E = 0.76$ ,  $H_O = 0.70$ , and  $AR = 13$ ). There was some indication of population structure among the six sample sites (average pairwise  $F_{ST} = 0.024 \pm 0.015$ , average pairwise genetic distance  $D = 0.04 - 0.26$ , and average within sub-population  $F_{IS} = 0.08 - 0.22$ ; Table 4.3; Table 4.4). We estimated  $N_e$  to be 230 – 820 (Table 4.3). Using our six sampling sites as putative populations, analysis of population genetic structure from Program Structure indicated greatest support for five of our *a priori* identified populations to be distinct genetic populations ( $LN(P) = -40,322 \pm 1,246$ ). Spatially explicit estimates of population structure using Program Geneland found greatest support for each of our six *a priori* sampling areas to be six distinct populations or demes ( $LN(P) = -37,211$ ). Thus each sampling unit was determined to be a distinct sub population of prairie-chickens. Isolation by distance among the six sub-populations was not observed ( $r^2 = 0.32$ ,  $P = 0.14$ ).

### ***Influence of the Number of Land Cover Classes on IBR***

As we increased the number of land cover resistance classes included in the resistance surface, we also observed a significant increase in the landscape resistance value calculated using CircuitScape ( $r_s = 0.95$ ,  $P < 0.01$ ), as well as a correlated increase in the  $r^2$  value from the IBR analysis ( $r_s = 0.93$ ,  $P < 0.01$ ; Figure 4.3). A similar trend was observed with our simulated landscapes, as 27/30 (90%) also showed increasing IBR  $r^2$  and landscape resistance values across the range of  $K$  tested (IBR  $r^2$   $r_s = 0.29$ ,  $P = 0.07$ ; IBR landscape resistance  $r_s = 0.43$ ,  $P = 0.01$ ). However, the magnitude of the effect in the simulated model was small compared to our prairie-chicken model (Figure 4.3). Half ( $n=15$ ) of the simulated data models yielded significant correlations of genetic and resistance distances, which met the expectation of a randomly generated dataset (Binomial Test,  $P = 0.50$ ).

### ***Optimization of Land Cover Resistance Classes***

Model selection procedures to determine the number of relevant land cover classes in IBR analysis indicated two potentially suitable models ( $AIC_C < 6.0$ ; Table 4.5). The first model received 82% of the model weight and indicated that prairie-chickens likely recognize two distinct land cover classes: grasslands and all other land cover classes. The second potentially suitable model, which received approximately 18% of the  $AIC_C$  weight, indicated that there were five land cover classes to which prairie-chickens likely respond (Table 4.5). No other models received strong  $AIC_C$  model support.

### ***Resistance Surface Parameterization***

We optimized the resistance surface to maximize IBR r-square for our top two performing  $AIC_C$  models. The second best performing model, which predicts population isolation to be the function of five distinct land cover resistance classes, was able to explain ~10% more of the variation in genetic diversity than the non-optimized model (Table 4.2).

### ***Greater Prairie-Chicken Case Study***

We created two resistance surfaces based on published values for habitat preferences and distributions of lek sites. The niche model based on lek sites performed much better, and in fact performed almost as well as the two  $AIC_C$  models did (Table 4.2). The reverse model, as expected, performed poorly, but was only a moderately worse model at predicting gene flow on

this landscape than was IBD (Table 4.2). Using the  $K=5$  AIC<sub>C</sub> model as a resistance surface for prairie-chickens across our study area, we conducted a least cost path distance analysis (Figure 4.5). Our least cost path distance analysis indicated that the functional distance, as a result of landscape permeability and matrix configuration between subpopulations, was 3-72% greater than linear distance, indicating strong effects of landscape quality on population genetic connectivity (Table 4.4).

## Discussion

The spatial distribution of gene flow among and within populations is a key component of successful species management (Scribner and Chesser 2001). Because of the dynamic nature of many contemporary landscapes, isolation by distance is rarely observed and isolation by resistance models have been increasingly utilized (Spear et al. 2010). In the context of landscape genetic studies, the optimization of the resistance surface parameterization is of critical importance to the performance of IBR, but the most common approach to assigning resistance values remains the use of values derived from literature review of species habitat needs or expert opinion (Murray et al. 2009). This approach will be appealing for researchers who have a great deal of experience working with their study system or when working with species that have been well studied and have well documented habitat requirements. However, our data suggest that expert opinion or literature models may not be the most viable option as our literature model explained 28-38% less of the variance in genetic diversity than either the niche or AIC<sub>C</sub> models did. Our work provides a clearly defined set of criteria for optimization of landscape resistance surface for use with genetics data.

A first consideration is how many land cover classes to include in a resistance surface. This value is not a trivial concern as some have suggested (Cushman et al. 2006), as our data indicated that approximately 20% more variance in the genetics data was explained across the range of  $K = 2 - 20$  land cover resistance values included in the resistance surface. However, our sensitivity analysis found little support for models including more than two land cover resistance classes, and the plot of r-square values as a function of the number of land cover resistance classes also suggests an asymptotic relationship between r-square and  $K$ . Plotting the response of IBR models to the number of land cover resistance classes can be a powerful tool in helping researchers determine how many land cover resistance classes to retain in their land cover data.

For our data set on prairie-chickens, no more than five land cover resistance classes would need to be retained in the optimized resistance surface.

Using the asymptotic relationship will provide some guidance to the parameterization of a land cover resistance surface. However, across the range of included land cover resistance classes, past workers have often assumed a simple linear accumulation of effects with regards to each included land cover resistance class (Coulon et al. 2004). A linear relationship is likely not accurate, as different land cover classes can interact synergistically in resistance values (Blakenhol 2009), and critical habitat thresholds can exist (With and Crist 1995). For example, data from studies with Greater Prairie-Chickens suggest that optimum landscapes contain primarily grass with up to 15-20% row crop agriculture (Svedarsky et al. 2000). We advocate use of a statistical model optimization procedure using  $AIC_C$  model selection to investigate how many of these land cover classes are functionally important. Our analysis suggested that only two land cover resistance classes were functionally important in explaining the distribution of prairie-chicken genetic diversity across Kansas and Nebraska. However, our approach also found some support for a resistance surface parameterization containing five land cover resistance classes, with little or no support for models with three or four land cover resistance classes. While we recognize that the use of  $AIC_C$  may not be sufficient or scientifically justifiable in all cases (Spear et al. 2010), for many systems it will offer a good starting point and will provide researchers with both biologically and statistically justifiable reasons for their use of a particular resistance surface parameterization.

The above procedures provide a rigorous and methodologically driven work plan to determine the most biologically relevant number of land cover resistance classes to include in a resistance surface. However, the assigned resistance values to the retained land cover resistance classes will still profoundly impact the overall IBR model performance. Ultimately, there are still three procedures that can be used to parameterize resistance surfaces. First, expert opinion can be solicited and used to parameterize the resistance surface. However, models parameterized in this manner have previously been shown to be rather unreliable (Murray et al. 2009). Additionally, a thorough literature review can be undertaken to investigate how the species uses habitat, and that information can be used to guide researchers in land cover parameterization. Within our modeling exercise however, the literature model performed relatively poorly compared to other models based on its ability to predict the distribution of genetic diversity

among populations. Second, genetic data provide information about the functional connectivity of the different demes and can be used, as we did with our  $AIC_C$  models, to reach an optimal resistance configuration. This method is time intensive and provided only moderately better congruence to the genetics data than did our niche model parameterization. Thus, if no movement or habitat data are available this is likely the best option for researchers using circuit based IBR analyses. The third option, using extensive habitat use or movement data to parameterize the resistance surface (McRae and Beier 2007, Beier et al. 2008) is likely an acceptable parameterization method once the correct number of land cover resistance classes to be included in the resistance surface have been determined.

One tool that is missing from these analyses, which would greatly increase the efficiency of IBR modeling with circuit theory, is if the software allowed for the simultaneous calculation of pairwise resistance values, Mantel Tests, and maximum likelihood estimates. For our analyses, data from each of these processes had to be transferred from one analytical software package to another and distinct analyses had to be conducted. The ability to run such analyses in a single analytical application would greatly increase end user confidence in such analyses. Furthermore, the nature of this analysis argues that a Bayesian approach may be better suited analytical approach than is maximum likelihood. However to our knowledge, at this time no Bayesian analytical methods exist. Such an approach would also allow us to test for true model independence. For example, the literature model and the niche model both include the same five land cover elements, and only differ in the relative resistances assigned to each of the included land cover elements. A Bayesian approach would allow us to test the degree to which the differing parameterizations actually justify our treating those models as independent.

When we applied these methodologies to study the spatial ecology of prairie-chickens, we found a strong influence of landscape conformation on the distribution of prairie-chicken population genetic structure. Specifically, our estimates of genetic diversity suggest that Greater Prairie-Chickens across Kansas and Nebraska maintain relatively high levels of genetic diversity, which is expected of a species with a large population being sampled near the core of the extant distribution (Hartl and Clark 2007). A lack of isolation by distance and significant genetic structure among populations suggests that contemporary land use may be limiting Greater Prairie-Chicken dispersal across this landscape. Moreover, when we applied a least cost path analysis to one of our top performing  $AIC_C$  resistance surfaces, we observed a substantial

increase in the effective distance between populations. The effect of reduced landscape permeability to dispersal will result in reduced genetical connectivity of the disparate demes distributed across this landscape (Slatkin 1993).

Previous studies conducted on prairie-chicken populations in Wisconsin have also reported strong genetic isolation effects among prairie-chicken populations due to landscape composition (Johnson et al. 2004). A recent population bottleneck among the Wisconsin populations, as a result of isolation, has also likely lead to decreased  $N_e$  within sub-populations and increased structure among sub-populations in a relatively short time period (Bellinger et al. 2003). Genetic structure and reductions in  $N_e$  are a concern for conservation because relict populations of prairie-chickens in Illinois have shown evidence of inbreeding depression (Bouzat et al. 1998). Effective management must include management to maintain or increase the genetic connectivity of disparate prairie-chicken populations on the landscape.

When paired with our least cost path analysis, our analysis delineating the perceived permeability of the various land cover classes on the landscape to prairie-chickens ought to prove useful then in delineating areas of conservation priority. Our top-performing  $AIC_C$  model indicated that only two land cover resistance classes were recognized by prairie-chickens. The second best  $AIC_C$  model indicated that five land cover resistance classes were recognized by prairie-chickens. In both models grassland habitat was observed to have the lowest resistance value. One noteworthy finding is that IBR models predict row crop agriculture to be between four- and ten-fold less permeable to movement than native grasslands. One of the dominant land use changes across the central plains is the conversion of grasslands to row crop agriculture (Halmans 1985). Thus increased protection of native grasslands is a key consideration for long-term management of this species. In addition, Conservation Reserve Program (CRP) which is a government program that pays farmers to remove land from row crop agricultural production and replant it with native grassland seeds in order to enhance wildlife habitat, may also provide beneficial grassland restoration in areas where limited native grassland still exists.

A second possible management or conservation action suggested by our top-performing models would be to conduct intensive and targeted tree removal throughout the landscape. The second predominant loss of grassland habitat throughout much of our study region is woody encroachment as a result of overgrazing and fire suppression (Sankey and Germino 2008, Stam et al. 2008). Within the five-variable model, trees are twice as resistant to gene flow as is row

crop agriculture, and eight times as resistant to gene flow, as is grassland land cover types. Thus targeted chemical or mechanical removal of trees and shrubs along the identified least cost path would likewise serve to increase both local habitat suitability as well as increase the amount of critical dispersal habitat between demes on the landscape. Collectively these two actions would be beneficial to prairie-chicken conservation and management in both the short- and long-term and may also prove beneficial to numerous other grassland species of conservation concern.

### **Acknowledgements**

Funding for this research was provided by The National Wind Coordinating Collaborative, Kansas Department of Wildlife and Parks, the National Fish and Wildlife Foundation, and The Nature Conservancy. Additional partial funding for this project was provided by the J.E. Weaver Competitive Grants Initiative of The Nature Conservancy. We thank Dr. Larkin Powell of the University of Nebraska – Lincoln, and B. Jamieson and the Missouri Department of Conservation for providing us with prairie-chicken genetic samples from Nebraska and Salina, Kansas respectively. We also thank C. Cardinal, T. Cikanek, L. Hunt, V. Hunter, K. Rutz, W. White and A. Zavala along with numerous other field technicians, and T. Prebyl and P. Berry who were our lab technicians. Support for A. Gregory, L. McNew, B. Sandercock, and S. Wisely was provided by the Division of Biology at Kansas State University.

### **Literature Cited**

- Akaike, H. 1981. Likelihood of a model and information criteria. *Journal of Econometrics* 16:3-14.
- Allendorf, F.W., and G. Luikart. 2007. *Conserving global biodiversity conservation and the genetics of populations*. Blackwell Publishing, Oxford, UK.
- 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 Service Professional Paper 964.
- Antolin, M.F., L.T. Savage, and R.J. Eisen. 2006. Landscape features influence genetic

- structure of black-tailed prairie dogs (*Cynomys ludovicianus*). *Landscape Ecology* 21:867-875.
- Barton, H.D., A.J. Gregory, R. Davis, C.A. Hanlon, and S.M. Wisely. 2010. Contrasting landscape epidemiology of two sympatric rabies virus strains. *Molecular Ecology* 19:2725-2738.
- Beier, P., D.R. Majka, and W.D. Spencer. 2008. Forks in the road: choices in procedures for designing wild land linkages. *Conservation Biology* 22:836-851.
- Bellinger, R.M., J.A. Johnson, J. Toepfer, and P.O. Dunn. 2003. Loss of genetic variation in Greater Prairie-Chickens following a population bottleneck in Wisconsin, USA. *Conservation Biology* 17:717-724.
- 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.
- Burnham, K.P., and D.R. Anderson. 1998. *Model selection and inference a practical information-theoretic approach*. Springer-Verlag Inc, New York, NY, USA.
- Carr, L.W., and L. Fahrig. 2001. Effect of traffic on two amphibian species of different vagility. *Conservation Biology* 15:1071-1078.
- Clark, R.W., W.S. Brown, R. Stechert, and K.R. Zamudio. 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. *Conservation Biology* Published online, February 2010, DOI: 10.1111/j.1523-1739.2009.01439.x
- Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128:231-240.
- Dappen, P., J. Merchant, I. Ratcliffe, and C. Robbins. 2007. *Delineation of 2005 land use patterns for the state of Nebraska Department of Natural Resources, Final Report*.
- DeBarba, M., L.P. Waits, E.O. Garton, E. Rand, A. Mustoni, and C. Groffs. 2010. The power of genetic monitoring for studying demography, ecology, and genetics of a reintroduced brown bear population. *Molecular Ecology* 19:3938-3951.
- deMaynadier, P.G., and M.L. Hunter Jr. 2000. Road effects on amphibian movements in forested landscapes. *Natural Areas Journal* 20:56-65.



- Edwards, S.V. 1993. Long-distance gene flow in a cooperative breeder detected in genealogies of mitochondrial DNA sequences. *Proceedings of the Royal Society of London B* 252:177-185.
- Epps, C.W., J.D. Wehausen, V.C. Bleich, S.G. Torres, and J.S. Brashers. 2007. Optimizing dispersal corridor models using landscape genetics. *Journal of Applied Ecology* 44:714-724.
- Frankham, R., J.D. Ballou, and D.A. Briscoe. 2002. *Introduction to conservation genetics*. Cambridge University Press, New York, NY. USA.
- Funk, W.C., M.S. Bouin, P.S. Corn, B.A. Maxell, D.S. Pilliod, S. Amish. 2005. Population genetics of Columbia spotted frogs (*Rana luteiventris*) is strongly influenced by the landscape. *Molecular Ecology* 14: 483-496.
- Gregory, A.J., L.B. McNew, T.J. Prebyl, S.M. Wisely, and B.K. Sandercock. *Chapter 3. A multi-scale hierarchical modeling approach to mapping Greater Prairie-Chicken (*Tympanuchus cupido*) lekking habitat across central Kansas*. *Studies in Avian Biology*.
- Guillot, G., F. Santos, and A. Estoup. 2008. Analyzing georeferenced population genetics data with Geneland: a new algorithm to deal with null alleles and a friendly geographical user interface. *Bioinformatics* 0:1-2.
- Halmans, J.A. 1985. Whoa to sod busting. *Rangelands* 7:27.
- Hamerstrom, F.N. 1939. A study of Wisconsin prairie-chicken and Sharp-tailed Grouse in Wisconsin. *Wilson Bulletin* 51:105-120.
- Hamerstrom, F.N, and F. Hamerstrom. 1973. *The prairie chicken in Wisconsin*. Wisconsin Dept. of Natural Resources. Technical Bulletin No. 64. Madison, WI.
- Hanski, I., and O.E. Gaggiotti. 2004. *Ecology, genetics, and evolution of metapopulations*. Elsevier Academic Press, Burlington, MA, USA.
- Hardy, O.J., and X. Vekemans. 2002. SPAGEDi: a versatile computer program to analyze spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* 2:618-620.
- Hartl, D.L., and A.G. Clark. 2007. *Principles of population genetics*. Sinauer Associates Inc. Sunderland, MA, USA.

- Jaquiere, J., T. Brouquet, A.H. Hirzel, J. Yearsley, and N. Perrin. 2011. Inferring landscape effects on dispersal from genetic distances: how far can we go? *Molecular Ecology* 20:692-705.
- Johnson, J.A., R.M. Bellinger, J.E. Toepfer, and P.O. Dunn. 2004. Temporal change in allele frequencies and low effective population size in Greater Prairie-Chickens. *Molecular Ecology* 13:2617-2630.
- Johnson, J.A., and P.O. Dunn. 2006. Low genetic variation in the Heath Hen prior to extinction and implications for the conservation of prairie-chicken populations. *Conservation Genetics* 7:37-48.
- Jørgensen, H.B.H., M.M. Hansesn, D. Bekkevold, D.E. Ruzzante, and V. Loeschecke. 2005. Marine landscapes and population genetic structure of herring (*Clupea harengus*) in the Baltic Sea. *Molecular Ecology* 14:3219-3234.
- Knowles, L.L. 2009. Statistical phylogeography. *Annual Review of Ecology, Evolution, and Systematics* 40: 593-612.
- Lebreton, J.-D., K.P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Longmire, J.L., M. Maltbie, and R.J. Baker. 1997. Use of lysis buffer in DNA isolation and its implications for museum collections. *Occasional Papers, Museum of Texas Tech University* 163:1-5.
- Lowe, W.H., and F.W. Allendorf. 2010. What can genetics tell us about population connectivity? *Molecular Ecology* 19:3038-3051.
- Manel, S., M.K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. *TRENDS in Ecology and Evolution* 18:189-197.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209-220.
- 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.
- McRae, B.H. 2006. Isolation by resistance. *Evolution* 60:1551-1561.

- McRae, B.H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. *PNAS* 104:19885-19890.
- McRae, B.H., B.G. Dickson, T.H. Keitt, and V.B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712-2724.
- Murray, J.V., A.W. Godizen, R.A. O'Leary, C.A. McAlpine, H.P. Possingham, and S.L. Choy. 2009. How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. *Journal of Applied Ecology* 46:842-851.
- 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.
- Peakall, R., and P.E. Smouse. 2006. GENEALEX 6 Genetic analysis in Excel: population genetic software for teaching and research. *Molecular Ecology Notes* 6:288-295.
- Pease, K.M., A.H. Freedman, J.P. Pollinger, J.E. McCormack, W. Buermann, J. Rodzen, J. Banks, E. Meredith, V.C. Bleich, R.J. Schaefer, K. Jones, and R.K. Wayne. 2009. Landscape genetics of California mule deer (*Odocoileus hemionus*): the roles of ecological and historical factors in generating differentiation. *Molecular Ecology* 18:1848-1862.
- Pitman, J.C., C.A. Hagen, R.J. Robel, T.M. Loughlin, and R.D. Applegate. 2005. Location and success of Lesser Prairie-Chicken nests in relation to vegetation and human disturbance. *Journal of Wildlife Management* 69:257-262.
- Pritchard, J.K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945-959.
- Quinn, G.P., and M.J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, New York, NY, USA.
- Roach, J.L., P. Stapp, B. Van Horne, and M.F. Antolin. 2001. Genetic structure of a metapopulation of black-tailed prairie dogs. *Journal of Mammalogy* 82:946-959.
- 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.

- Rousset, F., 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources* 8: 103-106.
- Sacks, B.N., S.K. Brown, and H.B. Ernest. 2004. Population structure of California coyotes corresponds to habitat-specific breaks and illuminates species history. *Molecular Ecology* 13: 1265-1275.
- Sankey, T. and M. J. Germino. 2008. Assessment of juniper encroachment with the use of satellite imagery and geospatial data. *Rangeland Ecology and Management* 61:412-419.
- Schwartz, M.K., L.S. Mills, K. McKelvey, L.S. Ruggiero, and F.W. Allendorf. 2002. DNA reveals high dispersal synchronizing the population dynamics of lynx. *Nature* 41:520-522.
- Schuelke, M. 2000. An economic method for the fluorescent labeling of PCR fragments. *Nature Biotechnology* 18:2:233-234.
- Schroeder, M.A., and L.A. Robb. 1993. Greater Prairie-Chicken (*Tympanuchus cupido*). *The birds of North America*, Issue 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.
- Scribner, K.T., and R.K. Chesser. 2001. Group-structured models in analyses of the population and behavioral ecology of poikilothermic vertebrates. *Journal of Heredity* 98:201-210.
- Seutin, G., B. N. White, and P. T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analysis. *Canadian Journal of Science* 69:82-90.
- Slatkin, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* 47:264-279.
- Spear, S.F., N. Balkenhol, M.J. Fortin, B.S. McRae, and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology* 19:3576-3591.
- Stam, B. R., J. C. Malechek, D. L. Bartos, J. E. Bowns, and E. B. Godfrey. 2008. Effect of conifer encroachment into aspen stands on understory biomass. *Rangeland Ecology and Management* 61:93-97.

- Storfer, A., M.A. Murphy, J.S. Evans, C.S. Goldberg, S. Robinson, S.F. Spear, R. Dezzani, E. Delmelle, L. Vierling, and L.P. Waits. 2007. Putting the 'landscape' in landscape genetics. *Heredity* 98:128-142.
- 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.
- Toepfer, J.E., J.A. Newell, and J. Monarch. 1987. A method for trapping prairie grouse hens on display grounds. Contribution No. 2144, Montana Agricultural Experimental Station.
- Vernesi, C., M.W. Bruford, G. Bertorelle, E. Pecchioli, A. Rizzoli, and H.C. Hauffe. 2008. Where's the conservation in conservation genetics? *Conservation Biology* 22:802-804.
- Waples, R.S. 2007. LDNE: a program for estimating effective population size from data on linkage disequilibrium. *Molecular Ecology Notes* 7:167-184.
- Weins, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Weins, J.A. 2001. The landscape context of dispersal. Pages 96-109 in J. Clobert, E. Danchin, A.A. Dhondt, and J.D. Nichols, eds. *Dispersal*. Oxford University Press, Oxford, UK.
- Westemeier, R., J. Braun, S. Simpson, T. Esker, R. Jansen, J. Walk, E. Kershner, J. Bouzat, and K. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282:1695-1698.
- 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.
- Williams, B.L., J.D. Brawn, and K.N. Paige. 2003. Landscape scale genetic effects of habitat fragmentation on a high gene flow species: *Speyeria idalia* (*Nymphalidae*). *Molecular Ecology* 12:11-20.
- Wong, M. 2003. High spatial homogeneity in a sex-biased mating system: the breeding structure of Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) in Kansas, Missouri, and Oklahoma. Master's Thesis, Kansas State University, Manhattan, KS.
- Wright, S. 1943. Isolation by distance. *Genetics* 28:139-156.

Table 4.1. Eleven polymorphic microsatellites successfully amplified from adult Greater Prairie-Chickens (n =1,038) captured at leks across Kansas and southeastern Nebraska, 2006-2008.

Marker	NA	AR	$H_O$	$H_E$	HWE	Genetic Disequilibrium <sup>a</sup>	Source of marker <sup>b</sup>
ADL-146	7	5	0.57	0.74	0.051	0.041 – 0.433	1
ADL-230	9	4	0.56	0.73	0.932	0.036 – 0.517	1
BG-12	8	3	0.41	0.45	0.800	0.009 – 0.433	2
BG-16	12	5	0.55	0.72	0.673	0.015 – 0.272	2
BG-18	23	17	0.92	0.93	0.789	0.006 – 0.903	2
LLSD-3	11	9	0.92	0.94	0.049	0.051 – 0.201	3
LLSD-4	29	19	0.89	0.94	0.123	0.040 – 0.767	3
LLSD-7	33	25	0.74	0.80	0.104	0.006 – 0.757	3
LLST-1	8	5	0.73	0.76	0.229	0.041 – 0.527	3
SGCA-6	12	7	0.85	0.94	0.061	0.023 – 0.767	4
SGCA-9	26	18	0.93	0.84	0.834	0.012 – 0.188	4
<b>Pooled ± SD</b>	<b>16.2 ± 9.6</b>	<b>10.6 ± 7.6</b>	<b>0.73 ± 0.2</b>	<b>0.80 ± 0.1</b>			

Abbreviations are as follows: Marker = marker name; NA = number of alleles observed in our sample; AR = allelic richness (number of alleles after correction for sample size);  $H_O$  = observed heterozygosity;  $H_E$  = expected heterozygosity; HWE and Genetic Disequilibrium =  $P$  values for Hardy-Weinberg equilibrium and linkage tests. <sup>a</sup>After Bonferroni correction for multiple comparisons  $\alpha = 0.005$ . The given  $P$ -values represent the range of observed  $P$ -values for each pairwise comparison between loci. <sup>b</sup>1: Domestic Chicken (*Gallus gallus*), Cheng et al. 1995; 2: Black Grouse (*Tetrao tetrix*), Piertney and Hoglund 2001; 3: Red Grouse (*Lagopus lagopus scoticus*), Piertney and Dallas 1997; 4: Greater Sage-Grouse (*Centrocercus urophasianus*), Taylor et al. 2003.

Table 4.2. Parameterization of the resistance values for IBR estimates. Model performance is ranked by correlation coefficients.

Model	(K)	GR	Ag	TR	H <sub>2</sub> O	HU	$r^2$	P-value	$\Delta AIC_c$	$\Delta AIC_c$ weight
<i>Naïve model estimates</i>										
Niche Model	5	100	400	500	800	1,000	0.61	0.05	-	-
Literature Model	5	100	200	500	400	1,000	0.41	0.04	-	-
IBD	1	-	-	-	-	-	0.32	0.14	*43.04	*<0.001
Reverse Model	5	1,000	800	200	300	100	0.28	0.48	-	-
<i>Refined model estimates based on AIC<sub>c</sub> analysis of the number of land cover elements to include</i>										
2 land cover										
resistance class										
model	2	100	1,000	1,000	1,000	1,000	0.69	0.01	* 0.00	*0.82
5 land cover										
resistance class										
model	5	100	400	800	600	1,000	0.79	0.05	*3.01	*0.18

Land cover classes coded in the model elements category are as follows: GR = grassland, Ag = row crop agriculture, TR = forested, H<sub>2</sub>O = water, HU = human structure (town, road, farm, etc). \* Values were taken from the AIC<sub>C</sub> analysis in Table 4.5, and do not necessarily reflect model performance with the assigned resistance values.

Table 4.3. Assessment of population genetic diversity within each sub-population of prairie-chickens sampled for these analyses.

Population	UTM (North, East)	$N$	$H_O$	$H_E$	$AR$	$F_{IS}$	$N_e \pm SD$
Nebraska	4475027, 728675	117	0.68	0.76	12	0.22	304.6 $\pm$ 103
Saline County	4287767, 597390	130	0.70	0.77	14	0.18	819.9 $\pm$ 295
Fort Riley	4345008, 685580	49	0.73	0.77	11	0.09	66.1 $\pm$ 13.1
Cloud County	4363026, 624085	299	0.72	0.79	15	0.17	282.2 $\pm$ 33.3
Riley County	4328420, 711738	265	0.71	0.79	15	0.18	335.8 $\pm$ 40.4
Elk County	4140109, 715017	178	0.69	0.75	14	0.16	229.9 $\pm$ 33.6
<b>Pooled</b>		<b>1,038</b>	<b>0.70</b>	<b>0.76</b>	<b>13</b>	<b>0.11</b>	<b>957.8 <math>\pm</math> 126.9</b>



Table 4.4. Pairwise analysis of genetic differentiation ( $F_{ST}$  Nei's D, km), physical distance, landscape resistance, least cost distance from the most parsimonious IBR Circuit model.

Sub-population Pair	Euclidean Distance (KM)	Circuit Resistance	Least Cost Dist.	$F_{ST}$	Nei's D
Nebraska - Ft. Riley	178.4	770	219.24	0.025	0.168
Nebraska - Saline County	220.1	866	173.26	0.016	0.116
Nebraska - Riley County	215.3	843	166.44	0.013	0.094
Nebraska - Cloud County	141.0	967	171.01	0.009	0.070
Nebraska - Elk County	377.9	961	588.10	0.024	0.163
Ft. Riley - Saline County	87.1	239	165.31	0.016	0.112
Ft. Riley – Riley County	46.3	421	47.47	0.015	0.109
Ft. Riley – Cloud County	82.0	466	128.32	0.015	0.105
Ft. Riley – Elk County	206.4	355	421.66	0.026	0.167

Saline County – Riley County	86.3	261	216.04	0.007	0.049
Saline County – Cloud County	65.1	466	113.22	0.005	0.038
Saline County – Elk County	187.1	288	645.80	0.010	0.067
Riley County – Cloud County	127.9	534	138.17	0.005	0.041
Riley County – Elk County	191.4	390	375.80	0.013	0.078
Cloud County – Elk County	242.5	588	510.69	0.012	0.081

---

Euclidean Distance is the shortest straight line distance between sub-population centers. Values for Circuit resistance are the pairwise resistance values from the top performing AIC<sub>C</sub> IBR model. LCP distance values are the pairwise Least Cost Path calculations calculated in Arc GIS 9.3, using the top performing AIC<sub>C</sub> resistance model as the cost surface.

Table 4.5. Results of model selection procedures used to determine the number of biologically relevant habitat classes to use in IBR modeling.

<u>Number of Land cover elements (K) included</u>	$r^2$	<i>P</i> -value	-Ln(K)	$\Delta AIC_C$	AIC weight
K = 2	0.41	0.04	-11,220	0.00	0.82
K = 5	0.58	0.01	-11,748	3.01	0.18
K = 1	0.26	0.51	-16,309	9.17	$\leq 0.001$
K = 3	0.47	0.03	-26,309	10.7	$\leq 0.001$
K = 4	0.55	0.09	-36,057	40.0	$\leq 0.001$
IBD (K = 1)	0.32	0.14	-18,962	9.56	$\leq 0.001$

---

Resistance values of 100 – 500 were assigned to the land cover elements included in each model in the same order that they are listed in the ‘Land cover elements included’ column above. Isolation by distance was included for comparison.

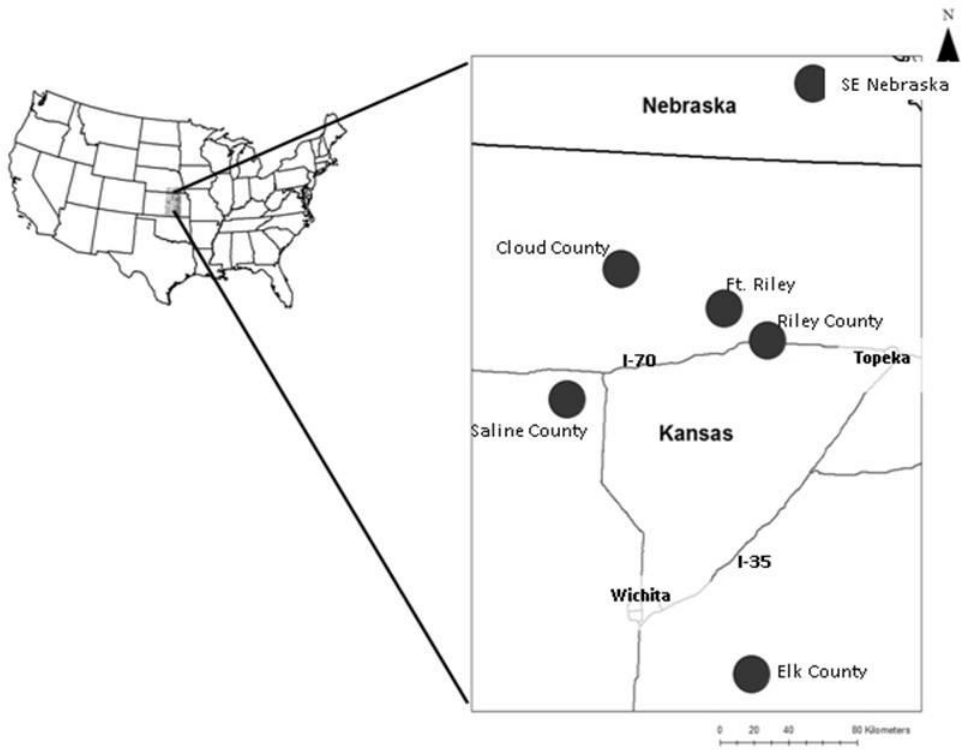


Figure 4.1. Central prairie study region.

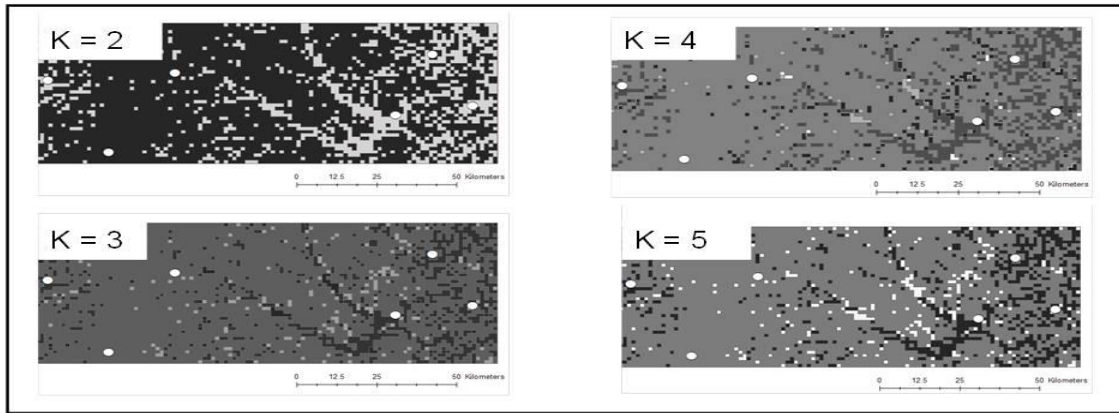


Figure 4.2. Example of random landscape map with  $K = 2-5$  land cover elements.

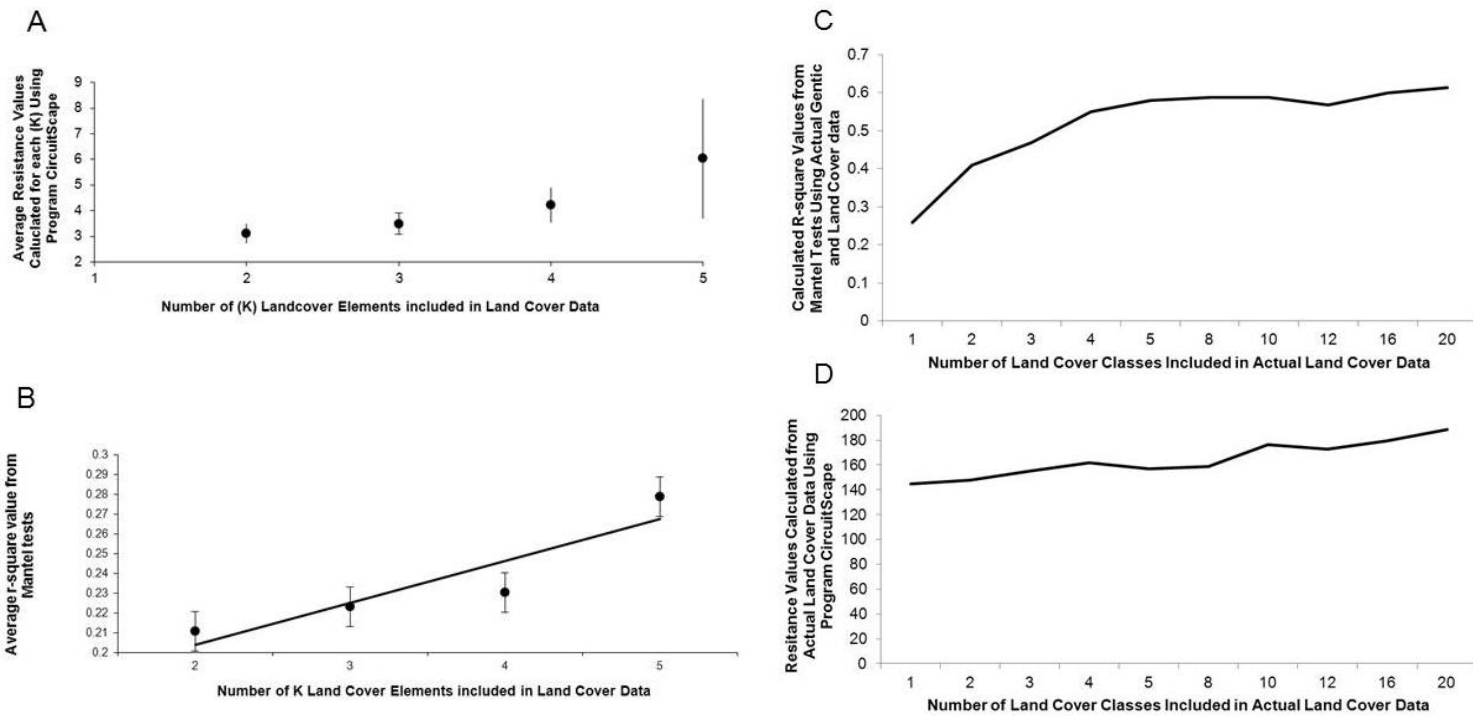


Figure 4.3. Figures 4A and 4B represent the Resistance and calculated r-square values as a function of the number of land cover elements included in the land cover resistance data set for simulated landscape and genetics data sets. The y-axis for figure 4A are r-square values x 10,000. Error bars in Figures 4A and 4B represents the range of observed values from each of our 30 randomly generated landscapes and simulated genetics data. Figure 4C represents the resulting calculated r-square values using our actual genetics data and actual landscape data using  $K = 1 - 20$  land cover classes. Figure 4D represents the resistance values calculated using Program CircuitScape for landscapes including 1 – 20 distinct landscape resistance classes.

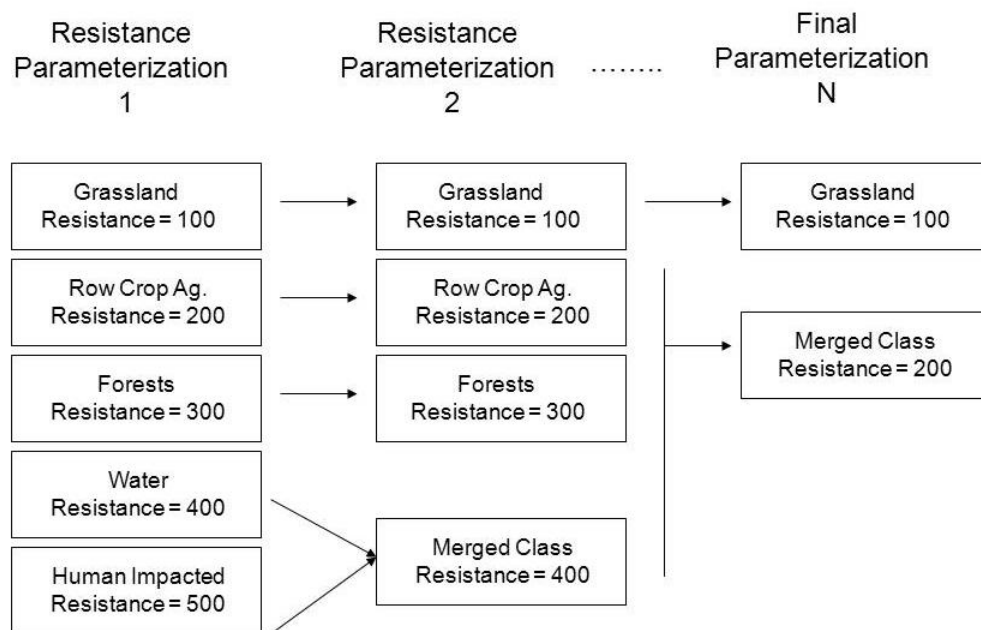


Figure 4.4. Procedural diagram of how land cover resistance classes were merged for  $AIC_C$  model selection analysis.

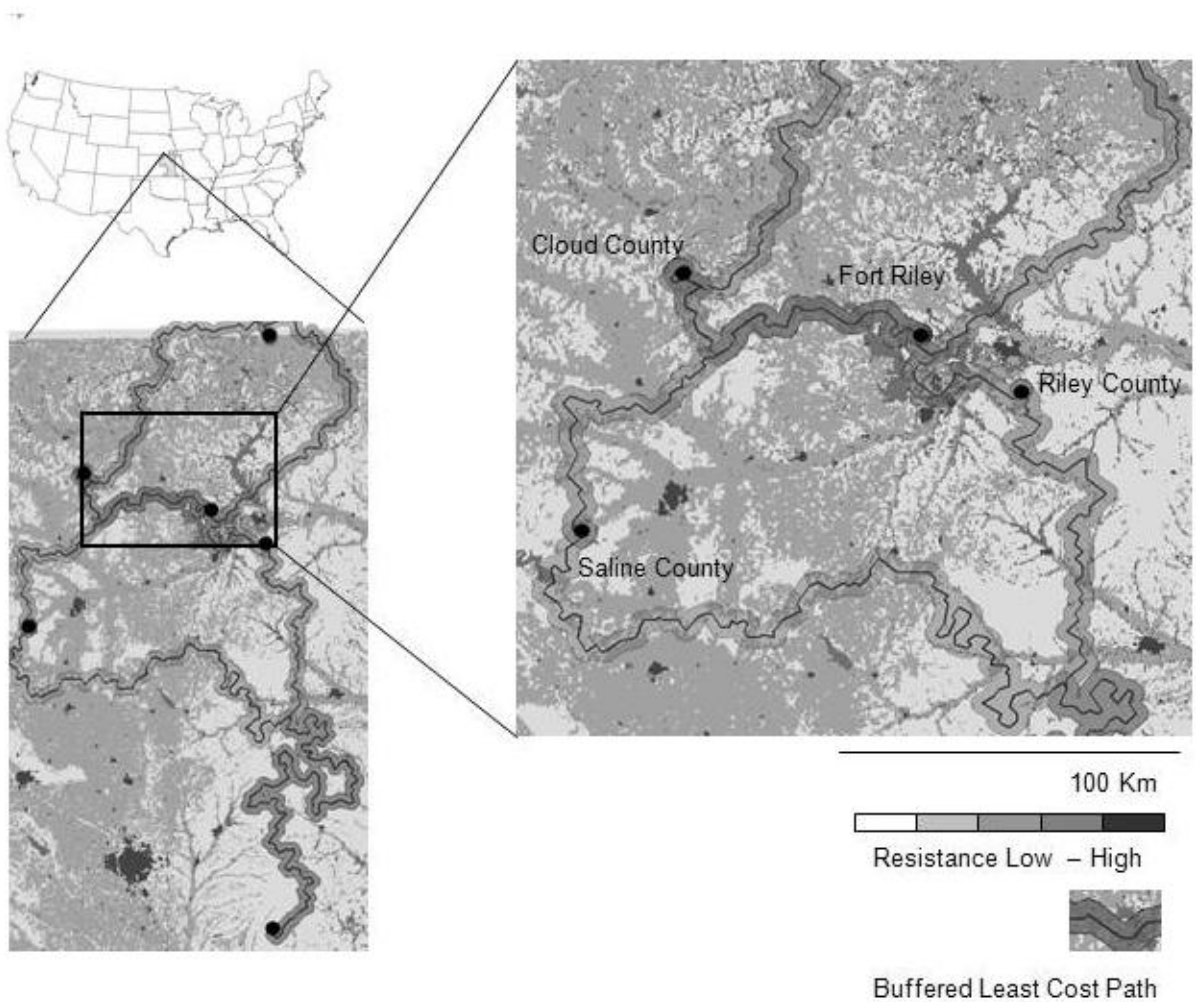


Figure 4.5. Resistance map generated from the  $K = 5$  second best performing  $AIC_C$  resistance model used for Least Cost Path Analysis. The least cost path determined from the path analysis is also shown with a 3 km buffer highlighting high priority areas for on-the-ground management to enhance regional prairie-chicken genetic connectivity.



# **Chapter 5 - MODELING HABITAT SUITABILITY CHANGE FOR A GRASSLAND BIRD AS A FUNCTION OF CHANGING LAND USE AND GLOBAL CLIMATE CHANGE ACROSS THE U.S. GREAT PLAINS**

## **Abstract**

Worldwide, the extent and integrity of grassland systems are declining due to anthropogenic pressures and climate change. Landscape Conservation Cooperatives are US Fish and Wildlife service partnerships between landscape managers and research scientists to obtain scientific knowledge about global climate change and other stressors for land managers. The Great Plains Landscape Conservation Cooperative (GPLCC) encompasses portions of eight states: South Dakota, Nebraska, Kansas, Oklahoma, Texas, New Mexico, Colorado, and Wyoming. Greater Prairie-Chickens (prairie-chickens; *Tympanuchus cupido*) are a grassland lek-breeding grouse native to the GPLCC. Prairie-chickens are a charismatic species of conservation concern due to their economic value, status as a grassland specialist, and large home range requirements. Using lek location data provided by GPLCC state agencies and publicly available land cover data, we modeled lek habitat suitability across the GPLCC using a hierarchical Bayesian model selection procedure and Program MaxEnt. We then used eco-forecasting models predicting GPLCC land cover changes over 70-years and re-ran our analyses on putative future landscapes. We found a 4% reduction in landscape quality, a 27-40% reduction in areas suitable for prairie-chickens lek habitat, and a reduction in the number of suitable lek habitat patches from 200 to 120. We also detected 137 Km southeastern shift of the center of prairie-chickens habitat distribution. Such findings are concerning to land managers because prairie-chickens are considered an umbrella species. Conservation of blocks of grassland habitat for prairie-chickens enables conservation for numerous other grassland species.

## Introduction

Ongoing environmental degradation around the world diminishes intact landscapes and fragments remaining habitats, which compounds threats to survival and persistence of native species, particularly those species which evolved in expansive contiguous habitats (Young and Clarke 2000, Collinge 2009). Consequently, as species are increasingly confined to networks of small, semi-isolated habitat patches, reliable predictions of metapopulation persistence in fragmented landscapes has become a top priority in conservation biology (Wahlberg et al. 1996, Hanski and Gaggiotti 2004). Global climate change exacerbates the threat of environmental degradation by accelerating habitat loss. Currently, climate change has been attributed to the recent rise in species extinction and this extinction inertia is predicted to continue to cause species losses well into the future (McLaughlin et al. 2002, Thomas et al. 2004, Schwartz et al. 2006). Thus, the challenges posed to conservation and management by the combined threats of habitat loss, fragmentation, and climate change are immense and synergistic (Weins et al. 2009).

In response to global conservation threats, the U.S. Fish and Wildlife Service has developed strategic habitat conservation program which sets biological goals for priority species, habitats, and landscapes, and establishes a network of Landscape Conservation Cooperatives to meet the needs of priority species, habitats, and ecosystems (Salazar 2009). Some of the most threatened ecosystems world-wide are grassland and prairie ecosystems (Samson and Knopf 1994). Since European settlement of the Americas, grassland birds have suffered greater losses in terms of habitat, numbers, and species diversity than any other bird group (Sauer et al. 2004). In the Great Plains, persistent or increasing pressures of agriculture, livestock production, natural resource extraction, and climate change will cause losses to biodiversity without proactive conservation and management plans. The Great Plains Landscape Conservation Cooperative (GPLCC; Region 7; 657,000 km<sup>2</sup>; centered at 37.543°N, -101.11°W) encompasses portions of eight states including: South Dakota, Nebraska, Kansas, Oklahoma, Texas, New Mexico, Colorado, and Wyoming (Figure 5.1). Within the region, six habitat types have been identified as conservation priorities: 1) short grass and mixed grass prairies, 2) playa wetlands, 3) riparian streams, 4) prairie rivers, 5) cross timbers savannahs forest, and 6) shrub land/sand dune systems. Within, each system a list of key indicator species of conservation concern have been developed to help guide research and management actions.

Within grassland communities of the GPLCC, the Greater Prairie-Chicken (*Tympanuchus cupido*) serves as an umbrella species for many members of the grassland bird community (Poiani et al. 2001). Greater Prairie-Chickens are a species of economic and social importance across much of their current range, yet across the core of their distribution population size has declined over the past 30 years (Schroeder and Robb 1993, Rodgers 2008). The reason for the decline of this and other grassland bird species is multifaceted, but ultimately is a result of habitat loss and changes in the remaining habitat quality due to rangeland management practices (Ryan et al. 1998). For Greater Prairie-Chickens, several proximate factors have contributed to declines in population size and range contraction. First, prairie-chickens are a grassland specialist which avoids anthropogenic structures (Pitman et al. 2005, Gregory et al. *Chapter 3*). Second, prairie-chickens have large space requirements and need large tracts of grassland to breed and fledge young, and are known to occupy large overlapping home ranges of up to 500 hectares each (Robel 1970, Schroeder and Robb 1993, Poiani et al. 2001). Last, Greater Prairie-Chickens are prone to inbreeding depression as a result of small population size and population isolation (Westemeier et al. 1998). Thus, both habitat quality and the matrix connecting populations across the landscape are important considerations for managers charged with conserving this and other sensitive grassland species of concern.

The key objective of this research was to delineate both critical breeding and nesting habitat, as well as areas necessary to maintain genetic connectivity among prairie-chicken populations (critical dispersal habitat) across the GPLCC. We then explored how climate change and continued anthropogenic land use will impact the distribution of these two necessary habitat types across the GPLCC through time, and thus affect the ability of the landscape to sustain viable prairie-chicken populations in perpetuity. To meet our objectives we address the following three hypotheses: regarding critical habitats needed for reproduction, dispersal, and future distributions.

### ***Critical Reproductive Habitat Distribution***

Sites used by males for lek arenas are likely indicative of the presence of nesting habitat at a landscape scale (Schroeder 1991), and nesting success has been correlated with the presence of large blocks of grassland habitat (Schroeder and Robb 1993, Robel et al. 1970, McNew et al. unpubl. data). Movement data collected from Lesser Prairie-Chickens (*T. pallidicinctus*) suggests

strong avoidance of anthropogenic disturbances when selecting nesting habitat (Pitman et al. 2005). Therefore, we predict that the distribution of high quality breeding and nesting habitat across the GPLCC would likely track the distribution of large tracts of relatively contiguous grasslands away from urban centers and major highways. For many species of grouse, the range of temperatures between the maximum and the minimum observed yearly temperature has been shown to be an important environmental characteristic of grouse habitat (Renqiang et al. 2010). Field data for prairie-chickens in Kansas suggests that nest success may be lower in wet years (Gregory and McNew, unpubl. data). Consequently we also predicted that in addition to the presence of large tracts of grassland, the distribution of critical habitat would also be influenced by both temperature and precipitation.

### ***Critical Dispersal Habitat Distribution***

The long term persistence of a species on a landscape is not simply a function of the presence of critical nesting and breeding habitat, but is also due to metapopulation dynamics of dispersal and genetic exchange among populations (Hanski and Gaggiotti 2004). We also sought to quantify the connectivity of the landscape and delineate areas of high quality dispersal habitat. The degree of genetic similarity among populations is indicative of the functional connectivity of those two populations and the permeability of landscape features among those populations, which can be measured using population genetic analysis (Lowe and Allendorf 2010). Under equilibrium conditions, the amount of genetic exchange and dispersal among populations is likely a function of the Euclidean distance between pairs of populations (Slatkin 1993). However, equilibrium conditions are not likely to apply to habitat specialists because the distribution of suitable and unsuitable habitat in the intervening matrix likely influences dispersal ability above and beyond geographic distance (Slatkin 1993, McRae 2006). Connectivity is of even greater concern when dispersal distances are long and gene flow between populations requires multiple generations to occur, requiring the matrix to actually contain suitable nesting and breeding habitat between the focal populations being assessed (Beier et al. 2009). Therefore, we predict that the genetical connectivity between populations across the GPLCC will not be a function of the Euclidean distance (isolation by distance; IBD), but could be related to the habitat quality of the matrix among populations (isolation by resistance; IBR).

### ***Critical Future Habitat Distribution***

Anthropogenic changes to landscapes are further exacerbated by the ongoing threats of global climate change which may shift or eliminate critical habitat. Over short evolutionary time periods, species requirements (often referred to as the niche) tend to be relatively stable (Soberón 2007). Thus, prairie-chicken habitat requirements are likely to remain unchanged despite the impacts of ongoing ecological changes on dynamic landscapes. Over time, the dynamic aspects of climate and human land use change are likely to change the distribution of critical prairie-chicken nesting and breeding habitat. By applying our niche model of current critical habitat requirements to putative future landscape, we ought to be able to identify areas on the landscape important for current and future prairie-chicken conservation. Our approach will be highly useful to conservationists seeking to plan and implement long-term conservation and management strategies as it will allow them to plan for putative changes in habitat suitability as a function of continued human land use and potential climate change, thereby ensuring that the appropriate areas have been conserved.

### **Methods**

Geographic coordinates of leks of Greater Prairie-Chickens located during annual monitoring surveys were compiled from multiple cooperating federal and state agencies across the GPLCC (Table 5.1). Location data from Colorado, Nebraska, and South Dakota were combined with location data from eastern Kansas (Gregory et al. *Chapter 3*) to create the lek location data set used for these analyses. This gave us a database of 110 known lek locations.

Land cover data were obtained from the 2001 National Land Cover Database (NLCD; Homer et al. 2007) and clipped to the geographic extent of the GPLCC. We chose this scale because the GPLCC has already been identified as a targeted management unit by the U.S. Fish and Wildlife Service, and thus, our analyses were conducted at a meaningful and relevant scale for conservation. The NLCD data set was comprised of 65 mapping zones based on LandSat Thematic Mapper and LandSat Enhanced Thematic Mapper images (Howard and Lagrasse 2004). Land cover data were collected at a 30 m resolution and were classified using multi-temporal classification scheme. A 30 m resolution has previously been deemed suitable for landscape and regional level analysis of landscape patterns (Homer et al. 2007). We used an

Anderson Level 1 habitat classification scheme to reduce the number of land cover classes from 43 to five (Anderson 1971).

### *Environmental Data*

For predictions of critical habitat, we collected a suite of environmental data at three scales. The first scale is the ‘point scale’ which refers to attributes collected at the lek location itself. The next two scales are the ‘500 m neighborhood’ and the ‘5 Km neighborhood’ scales, which refer to attributes collected in buffered regions around the lek location of the specified neighborhood size, 500 m or 5 Km respectively (Table 5.2). All point variables were developed from existing GIS data sets using Arc Info 10. To identify distance to nearest riparian area, we extracted riparian areas and riparian habitat types from the GAP Land Cover data as a distinct data layer and then calculated the distance from each lek to the nearest riparian area using Arc Info 10. We used the ESRI U.S. cities and U.S. highways data set and Arc Info 10 to estimate distance to the nearest road and city. Elevation data were obtained from the USGS national elevation model OCG Map seamless server at 30 meter resolution. Elevation data sets were mosaicked together using Arc Info 10 (Environmental Systems Research Inc., Redlands, California, USA) and edited to the extent of the GPLCC region. We used the elevation data set to calculate lek site elevation and weighted elevation. Weighted elevation is a synthetic variable derived by taking the elevation at a specific point and dividing by the average elevation of the surrounding landscape out to a specified distance buffer (in this case 1 km; Gregory et al. *Chapter 3*).

Using the land cover data and the Patch Grid application of Patch Analyst tools, we used grassland connectedness as an index of grassland contagion for 30 m pixels with 5,000 m neighborhood roving windows. The 5 km focal area to measure grassland connectedness was deemed suitable for this system based on the biology and natural history of this species. For example, prairie-chickens in Kansas living on the relatively intact grasslands of the Flint Hills have been shown to occupy overlapping 500 ha home ranges (Robel et al. 1970); a 25 km<sup>2</sup> roving window would calculate the degree of grassland connectedness in an area large enough to encompass home ranges of multiple prairie-chickens. The roving window would also calculate the degree of grassland continuity across a region large enough to form groups of leks, an essential component of prairie-chicken breeding ecology (Schroeder and Robb 1993).

County level population data for all counties in the GPLCC region Seven area were obtained from the U.S. Census Bureau for census years 2000 & 2010. Population density data were then developed by dividing the county population data from the census bureau by the area of each county. For 500 meter and 5 km neighborhood models, each lek location was buffered to the specified neighborhood and the buffers were then used to clip the land cover data using Arc info 10. The percent composition of each buffer was then calculated for each lek site (Table 5.2).

### ***Critical Breeding and Nesting Habitat Distribution***

To predict lek habitat occurrence across the GPLCC, we first identified the most predictive environmental characteristics of locations where prairie-chickens were present and absent using logistic regression, and then we extended the predictive modeling across the extent of the GPLCC using ecological niche modeling (Phillips et al. 2004). We followed the recommendations of Keating and Cherry (2004) for estimating pseudo absence data. Point location and regional attribute data were extracted for each lek location and also for a series of randomly generated absence points following the methods of Gregory et al. (*Chapter 3*). Prior to analysis with logistic regression and model selection procedures, all environmental variables were *z*-transformed (mean = 0, SD = 1) to allow for direct comparisons of model slope coefficients (McGarigal et al. 2001). We recognize there are inherent difficulties with *z*-transformations of categorical data, however the number of categories used was large and approximates a normal distribution; moreover models were run with both transformed and untransformed variables and the net effect of this transformation did not qualitatively alter model result, performance, or ranking. All input data sets were resampled at a 100 m resolution and geo-referenced to the NLCD land cover data set using majority resampling in Arc Info 10. A 100 m resolution should be acceptable for use with Greater Prairie-Chickens based on characteristics of their home range (Robel et al. 1970, Gregory et al. *Chapter 3*).

We employed a hierarchical approach to logistic model selection to identify environmental variables with high predictive power (Gregory et al. *in press*). Environmental variables were organized by the spatial scale at which they were estimated and entered into separate logistic regression models (Table 2); significant factors were combined into a global model that pooled important variables across multiple scales (Schwarz 1978, Hosmer et al.

1997). Thus, we had a hierarchical procedure for model selection, which was used to avoid spatial autocorrelation among environmental variables. Model selection was conducted with Bayesian procedures based on the Schultz Criterion (BIC; Anderson et al. 2000, Johnson and Omland 2004) because Bayesian statistics tend to be more conservative and less likely to over-fit data than Aikake's Information Criterion (AIC; Burnham and Anderson 2004, Guthry et al. 2005). A conservative approach to model selection was desirable to compensate for highly spatially correlated data sets.

All variables included in the minimum BIC multi-scale model were used as data inputs for ecological niche modeling using Program MaxEnt. Program MaxEnt uses entropy theory to create an index of landscape suitability across a predefined region based on the environmental variables associated with occurrence data (Phillips et al. 2004).

### ***Climate Model Development***

Climate data for the year 2000 were obtained from the WorldClim climate model at 1 km resolution for each lek location, and edited to the extent of the GPLCC (Hijmans et al. 2005). The resolution of 1 km was more coarse than the 100 m resolution previously used with habitat models for prairie-chickens (Gregory et al. *Chapter 3*), but was necessary given the resolution of the climate data (Fisher 1997) and the inherent uncertainty present in current eco-forecasting and climatic modeling applications (Hulme 2010). We used three climate variables: maximum annual temperature, minimum annual temperature, and average annual precipitation based on the ten year averages recorded in the WorldClim data set. We used these three variables to characterize climate because they have been previously shown to be important for Galiformes, and because more complex climate interaction variables are often highly correlated with these metrics of local climate conditions (Wang et al. 2002, Renqiang et al. 2010). Using the same subset of random point locations, we used logistic models to predict lek occurrence from climatic data. We used BIC model selection to select the best climate model and then entered the parameters of this model into a new round of regression and model selection for multi-scale models. Variables included in the best performing model were then included as additional covariates along with the variables from the best performing multi-scale combined model in ecological niche modeling using MaxEnt. Thus, we created an additional critical habitat model which included effects of climate variables.



### ***Ecological Niche Model Validation***

To validate our final niche model we used Program MaxEnt to create 1,000 replicates of regional niche model, withholding a randomly drawn 10% subset of the lek locations from each model replicate. For each replicate niche model we recorded at which probability of habitat occurrence each withheld lek was located. We also recorded the variance in the estimated habitat suitability for all areas of the GPLCC. In this way we were able to both validate the model performance using a standardized cross validation technique as well as quantify the spatial uncertainty of our niche model in a spatially explicit manner.

### ***Critical Dispersal Habitat***

We compared multiple models of landscape permeability among populations with measures of gene flow among populations, to model how intervening habitat drives connectivity among populations and to determine which habitat features are important to connectivity. In order to collect population genetic data for analyses of gene flow, federal and state agency personnel across the GPLCC collected feathers shed by prairie-chickens at known lek locations (Table 5.1). DNA was extracted from feathers using Qiagen DNA tissue extraction kits or DNA extraction kits in conjunction with Qiagen QiaShredder kits following manufacturer protocols (Qiagen Inc; Valencia, CA). Samples were amplified at six polymorphic microsatellite loci originally developed for use in other species of grouse, but which had previously been shown to be polymorphic in Greater Prairie-Chickens in Kansas. Amplification of DNA via polymerase chain reaction (PCR) took place on an Eppendorf epgradient thermocycler (Brinkman Inc. Westbury, NY) following published cycling protocols optimized for each primer. For PCR amplification we used a 14  $\mu$ L cocktail containing: 30 ng of template DNA, 2.5  $\mu$ MMgCl, 0.25  $\mu$ MdNTP's, 0.1  $\mu$ g/ $\mu$ l BSA, 0.8 M betaine, 0.5  $\mu$ M of each forward and reverse primer, 0.2  $\mu$ M of M-13 universal primers (Schuelke 2000) labeled with a fluorescent dye (Operon Biotechnologies, Huntsville, AL) attached to the 5' end, and 0.25 units of Go Taq FlexiTaq polymerase (Promega, Madison, WI). Fragment analyses were conducted using an ABI 3730 Automated Sequencer, and alleles were scored using GeneMarker 1.6 software (Applied Biosystems; Foster City, CA).

Prior to analysis, molecular genotypes for all samples collected at a common lek site were compared to each other to ensure that each sample was from a unique individual, and all duplicate samples were removed. We used GenePop 4.0.10 to test for deviations from Hardy-Weinberg, and linkage equilibrium (Roussette 2008). GenAlEx ver. 6.3 (Peakall and Smouse 2006) was used to calculate estimates of genetic diversity within population foci and for calculations of pairwise genetic distance and  $F_{ST}$  values between population foci. Estimates of effective population size ( $N_e$ ) were calculated using the linkage disequilibrium method as implemented in Program LDNE (Waples 2007).

For analysis of connectivity throughout the GPLCC, we clustered lek location data into six population foci using Ripley's K clustering algorithm and the mean center tools in Arc Info 10 to identify the maximum distance at which lek locations were significantly clustered across the GPLCC, and then identify the centroid of each cluster.

To assess the influence of landscape on the distribution of genetic diversity among our population foci, six landscape connectivity models based on geographic distance and/or land cover were created in Arc Info 10. The first *IBD Model* included only geographic distance and tested the hypothesis of isolation by distance. The other four models are all based on pairwise isolation by resistance. Isolation by resistance (IBR) uses a path resistance metric to model the functional distance among populations. This functional distance is based on putative resistances to movement of the various land cover classes in the land cover data set. Two of the additional IBR models were identified by Gregory et al. (*Gregory et al. Chapter 4*) as being top performing multi-scale models at smaller spatial scales within Kansas. These models tested hypotheses about the proportion of grassland versus other habitat types needed to maintain population connectivity. We refer to these two models as *High Low Habitat Resistance* and the *Five Habitat Resistance* models respectively. The *High Low Habitat Resistance Model* predicts grassland land cover to be of low resistance to movement and all other land cover classes to be of equally high resistance to dispersal conversely the *Five Habitat Resistance Model* predicts grassland to pose low resistance to dispersal, row crop agriculture to pose moderate resistance to dispersal, and water, forest, and urban land cover classes to pose a high resistance to dispersal. The last three models were derived from the regional scale critical habitat models developed as part of this research and tested hypotheses about the role of habitat fragmentation and habitat quality. The *Contagion Model* was a landscape fragmentation model which predicted areas of

high regional (within 25 km<sup>2</sup> roving window analyses) grassland continuity to be of low resistance to gene flow and areas with high fragmentation to be of high resistance to gene flow; we refer to this model as the *Contagion Model*. The second of the three newly developed *a priori* resistance models is based on the critical habitat model derived for the GPLCC region, where highly suitable areas are given a low resistance value and low suitability areas were given high resistance values; we refer to this model as the *Habitat Suitability Model*. The third and final model was a combination of the Contagion Model and the Habitat Suitability Model, where the original LCC *Habitat Suitability Model* resistance values were modified so that in areas where contagion was high resistance was lowered (Table 5.7).

We tested pairwise resistance values generated from each putative landscape resistance model against pairwise estimates of Nei's modified genetic distance using Mantel tests as implemented in SPAGeDi (Hardy and Vekemans 2002). We then used an information theoretic approach to model selection to choose the best model. Model selection can be challenging when comparing models that differ by a single parameter (Guthery et al. 2005), so we followed the recommendation of Arnold (2010) and used confidence intervals for slope coefficients of environmental parameters to discard uninformative models from our candidate set before applying model selection procedures. Last, using our best fit model, we mapped the least resistant areas to gene flow among population foci to delineate critical dispersal habitat using program CircuitScape (McRae 2006). We overlaid the critical breeding and nesting habitat map with the critical dispersal habitat map to generate a combined map showing the distribution of habitat areas necessary for the long-term conservation of Greater Prairie-Chickens across the GPLCC ecoregion.

### ***Critical Future Habitat Distribution***

For projected climate data for the 70-year time interval from 2010 – 2080, we used the WorldClim climate predictions model based on the Canadian Center for Climate Modeling Analysis (CCCMA) emission scenario at 1km resolution (Flato and Boer 2001), clipped to the extent of the GPLCC region seven area; all other data sets were also resampled and scaled up to 1 Km resolution for these analyses using Arc Info 10.

Future human population density estimates were derived by taking the county-specific trend for population change from 2000-2010 across all counties of the GPLCC region and

extrapolating linear population growth, to the year 2080. An exception was made for counties where populations were shown to decline. In these cases we modeled population declines to a maximum of 75% of their 2010 population and then set densities as a constant for a minimum estimate of future population density (Ahlburg and Vaupel 1990).

To project future landscapes, we used a Markov-Cellular Automaton Model (M-CA) as described in Li and Reynolds (1994) to alter contemporary land cover data in a manner consistent with current trends of landscape change. The M-CA we implemented in Program Dinamica used a simple transition matrix of the probability of habitat types transitioning within each time step based on the contemporary rates of land cover land use changes across the Great Plains (Soares-Filho et al. 2006). There are currently three main threats to grasslands across the GPLCC: 1) sod-busting or the conversion of native grasslands to tillable farmland (Mitchell 2000), 2) woody encroachment by native or exotic shrubs onto grassland systems as a result of altered grazing patterns or fire suppression (Briggs et al. 2005), and 3) urban sprawl and development into previously intact grasslands (Hilty et al. 2004). Collectively, this set of threats accounted for an approximately 3% decline in grasslands area per year throughout the Great Plains from 1982-1992 (Maczko et al. 2004). Thus, our transition matrix was set to be a vector indicating a 3% chance of any grassland pixel with a shared boundary to urban, agricultural, or forested pixels transitioning to one of those land cover types with each time step of the model. Other land cover types were considered static; so once a pixel transitioned away from grassland there was a zero probability of transitioning back. We ran the model for 70 time steps/years. Rates of loss over the given period are likely conservative, but could still amount to approximately 90% loss of habitat when extrapolated over the 70 years for which we have climate data. A 90% reduction in grasslands is not likely realistic, as approximately 30-40% of our current rangelands has protected status as either Bureau of Rangeland Management Lands, National Park Lands, or are enrolled in Conservation Reserve Programs (Mitchell 2000). In addition, given the current recognition by resource managers for the need for proactive protection and conservation of grassland habitats (Briggs et al. 2004), and the diminishing returns associated with further development of many of the currently extant grasslands (Maczko et al. 2004), a 35% reduction in total grasslands may be a more realistic estimate of what will actually occur over the next 70 years. The maximum amount of grassland land cover the M-CA

was allowed to remove was 35% of the total area originally identified as grasslands in the starting land cover data.

We used putative future land cover and climate variables in the previously described ecological niche modeling to create a probabilistic map of future habitat distribution for prairie-chickens. For the purposes of comparisons between maps, any pixel with a probability of lek occurrence >80% was indicative of high probability of containing suitable prairie-chicken habitat, any pixels with a likelihood of lek occurrence 60% - 79% was described as having a moderate probability of containing suitable prairie-chicken habitat, and pixels with <60% probability of lek occurrence were of low probability of containing suitable prairie-chicken habitat (Gregory et al. *Chapter 4*). We compared current and future distribution maps to calculate potential changes in range and number of habitat areas predicted by each model. We used the mean center tool in Arc Info to calculate the potential shift in the distribution of highly probably prairie-chicken habitat areas across the GPLCC as a function of likely anthropogenic induced habitat modifications and climate change.

## **Results**

### ***Critical Breeding and Nesting Habitat Distribution***

Our analysis indicated that at each spatial scale, different combinations of environmental variables were important in predicting the observed distribution of detected prairie-chicken versus randomly generated pseudo-absence leks. At the broadest spatial scale, which characterized the landscape in 5 Km neighborhoods surrounding leks, a single model received greatest support (Table 5.3). The minimum BIC model, which received ~93% of the model support included a negative effect of the percent of the landscape within 5 km of the lek being classed as human land use (% Urban) and a positive relationship between the proportion of the landscape within 5 Km of the lek point that was classified as grassland habitat:  $\text{lek} = 0.67 + 1.93 \times \% \text{ Grass at 5 Km} - 116.4 \times \% \text{ Urban at 5 km}$ .

At a spatial scale of 500 m, model selection indicated three models with  $\Delta\text{BIC} < 3$  (Table 5.3). Of these three models, one model accounted for >50% of the BIC model weight. This model included effects from a single variable, the percent of the landscape within 500 meters of

the lek that was human impacted:  $\text{lek} = 0.476 - 54.88 \times \% \text{ Urban } 500 \text{ meters}$ . The other potentially good models included negative effects of the amount of forested lands and row crop agriculture within 500 meters of the lek.

At the spatial scale which included only the point location of the lek, two models were found to be equally parsimonious. These models included effects of latitude, weighted elevation, distance to the nearest road, habitat fragmentation within 5 km of the lek, and distance to the nearest urban center (Table 5.3). The top performing model, which received 51% of the model weight, included effects of latitude, weighted elevation, distance to road, and distance to city:  $\text{lek} = -17.6 + 0.51 \times \text{weighted elevation} - 12.9 \times \text{latitude} + 0.32 \times \text{distance to road} + 2.34 \times \text{distance to city}$ .

The top performing combined multi-scale model included effects of latitude, contagion, weighted elevation, % grassland, and % human impacted land cover within 5 km of lek sites:  $\text{lek} = 2665.2 + 2637 \times \text{weighted elevation} + 0.9329 \times \% \text{ Grass } 5\text{Km} - 89.8 \times \% \text{ Urban } 5 \text{ km} + 0.663 \times \text{latitude} + 37.3 \times \text{contagion}$ .

Ecological niche modeling yielded a predictive map of suitable lek habitat based on landscape variables (Figure 5.2). Our validation data set with 10% of the lek locations that were held back were all predicted to be located in moderate or highly suitable lek habitat, suggesting that our ecological niche model had robust predictive power.

Regression analysis of the three climatic variables indicated >90% support for a single two-variable model which included effects of minimum temperature and average annual precipitation:  $\text{leks} = 3.61 - 0.157 \times \text{precipitation} + 0.07 \times \text{minimum temperature}$  (Table 5.3). Landscape and climatic variables were combined as a new global multi-scale model, which included effects from the combined multi-scale environmental model and the top performing climate model (Table 5.3). The final BIC model selection procedure indicated >95% support for a single model, including effects of fragmentation of Grass at 500 m, % Urban areas at 5 Km, minimum temperature, and average precipitation:  $\text{leks} = 7.17 + 1.73 \times \text{contagion} + 4.76 \times \% \text{ Grass at } 500 \text{ meters} - 156.5 \times \% \text{ Urban at } 5\text{Km} + 0.28 \times \text{minimum temperature} - 0.13 \times \text{average precipitation}$ . These four variables were included in the model of critical habitat (Figure 5.5).

### ***Variance in Habitat Estimates and Model Validation***

Overall across all 1,000 model replicates 90.1% of the withheld points were located in areas that had  $\geq 80\%$  likelihood of containing prairie-chicken habitat or what we refer to in this manuscript as potentially high habitat probability areas. In general areas of omission were greater than errors of commission in that on average 7.81% of our validation points each run were located in areas that were predicted to be in what we refer to as relatively low habitat probability areas, or those areas with  $\leq 60\%$  probability of lek habitat presence. The variance in niche model predictions across all model replicates was between 0.001% - 9%. In general, high habitat probability areas had lower variance than did areas that were predicted to be of low habitat probability (Figure 5.6). Finally, the majority of our omission errors occurred in the north central portion of the GPLCC, a region in Nebraska referred to as the Sand Hills (Figure 5.6). This was also an area of the map with the greatest uncertainty in the estimated likelihood of suitable habitat presence.

### ***Critical Dispersal Habitat Distribution***

Excluding samples taken from the same individual, we successfully obtained DNA from 235 unique individuals from the six population foci and genotyped the birds with six microsatellite markers (Table 5.4). Using these six markers, we identified 51 unique alleles which provided a probability of identity of  $PI = 0.0001$ . Tests for Hardy-Weinberg Equilibrium (HWE) indicated that the smaller populations (Western KS and Central KS) were not at equilibrium. We found relatively high estimates of genetic diversity within each population and large effective population sizes (Table 5.5). Populations of Greater Prairie-Chickens were spatially structured across GPLCC with isolation and a lack of genetic exchange among populations indicated by relatively large pairwise population  $F_{ST}$  values (Table 5.6).

Of our six landscape resistance models, the *Isolation by Resistance* and *Contagion Models* lacked explanatory power, and the confidence intervals of their parameter estimates overlapped with zero (Table 5.7). Based on recommendations of Arnold (2010), these models were excluded as potential models prior to the application of model selection procedures. Of the four remaining models, the *Habitat Suitability Model* received ~60% of the overall model weight and explained ~46% of the overall variance in genetic distance between population foci, and so was considered to be the best approximating model (Table 5.7). This model predicted relatively

high resistance among relatively close population foci, indicating that local landscape conditions perturbed gene flow (Table 5.6). The map of least resistance identified areas critical for maintaining genetic connectivity. Kansas and Colorado populations appear to be still connected, but restricted gene flow is occurring between the Nebraska population and other populations in the GPLCC (Figure 5.3).

In a last step, we overlaid critical nesting habitat model with the critical dispersal habitat model to create a map delineating areas of conservation priority for Greater Prairie-Chickens across the GPLCC (Figure 5.7).

### ***Critical Future Habitat Distribution***

Comparing future and contemporary predictions of high habitat probability landscapes indicated a 4% reduction in landscape quality and a 27% reduction in total area identified as being highly-to moderately-probable for containing GPC lek habitat (Figure 5.8). We also detected a 40% reduction in the number of suitable ‘patches’ for lek habitat from 200 to 120. Here, a habitat patch is not meant to be a biological entity, but simply a discrete area or region of the landscape identified by our model as having a high to moderately high probability of containing suitable lekking habitat; however, given the resolution of our model, each patch will be at minimum 100 ha in size. Finally, based on our analysis, a 137 km shift of the center of GPC habitat distribution of Greater Prairie-Chickens is predicted the southeast (Figure 5.9).

## **Discussion**

Our modeling efforts delineated areas having high, moderate, and low Greater Prairie-Chicken conservation priority across the GPLCC. Our final model of critical nesting and breeding habitat distribution included both environmental and climate data and was well supported with >90% of our cross validation points being located in areas predicted by our model to be of high probability for containing lek habitat. Our model predicted that of the ~657,000 km<sup>2</sup> encompassed by the GPLCC, only ~11,000 km<sup>2</sup> (1.5%) was high probability nesting and breeding habitat and an additional 13,000 km<sup>2</sup> (2%) was moderate probability nesting and lekking habitat.



The addition of climatic data in our model forced us to reduce the spatial resolution of our analysis by 10-fold to accommodate a coarser resolution for regional climatic data (Fisher 1997, Hijman 2005). Was inclusion of climate data informative enough to justify loss of model resolution? Two climate variables were included in the top performing multi-scale climate model (Table 5.3), indicating that climate variables do enhance our ability to predict the distribution of reproductive habitats of prairie-chickens. The  $\beta$  slope coefficients for the climatic variables included in the top performing multi-scale climate model were among the lowest  $\beta$ -values indicated that the climate data were 20-1,200 times less influential than other habitat or landscape characteristic variables in the model. Thus, inclusion of effects of climate data, were dwarfed by more critical aspects of the vegetative and geo-physical landscape characteristics. However, inclusion of climate data was attributable to a 2.7% decline in the area of high probability prairie-chicken habitat, but accounted for a 4.2% increase in moderate probability habitat areas (Figure 5.4). Thus, the influence of climatic data may be less important to statistical model development, but is still biologically relevant at the landscape scale.

If the ecological niche of a particular species remains relatively stable over short to intermediate time periods (Soberón 2007, Walls and Stigall 2011), then subtle climatic changes with regard to temperature and precipitation may pose tolerance thresholds for many species (Jackson et al. 2009). Moreover, models of climate variables take temperature and precipitation to be static and ignore any synergistic effects that changing the temperature range or precipitation in an area may have on the biotic community which could exacerbate other anthropogenic changes to the landscape (Williams and Jackson 2007, Jackson et al. 2009). A future application of this model could be to include the effects of climate change indirectly by modeling changes to the vegetative structure of the landscape which prairie-chickens use as a function of climate change.

Our model predicted a 137 km shift in the center of the distribution of prairie-chicken habitat to the southeast. This result was somewhat unexpected, because climate change usually causes pole-ward shifts in the distribution of most species (Root et al. 2003). It could be argued that the reason for the observed southeastern shift in the center of prairie-chicken distribution is because habitat and geo-physical attributes of the landscape are more influential in determining the distribution of high quality habitat than is climate.

Our model also predicted that high probability nesting and breeding habitats were characterized as having lower grassland fragmentation (higher contagion values) than the GPLCC in general (contagion values for critical habitat =  $0.32 \pm 0.09$ , contagion value averaged over the GPLCC =  $0.25 \pm 0.13$ ). In addition, high probability areas were found at higher relative elevations than the GPLCC (weighted elevation of critical habitat =  $1.29 \pm 0.007$ ; range = 1.1 – 1.39, average weighted elevation for GPLCC =  $1.0 \pm 0.006$ ). High weighted elevation means that the habitat occurs at the crest and ridges of upland habitat. High probability critical habitat also had higher proportion of grassland land cover and a lower proportion of row crop agricultural fields within 5 km of a lek than the average land cover for the GPLCC (high probability habitat =  $62 \pm 20\%$  grass and  $10 \pm 30\%$  row crop agriculture compared to GPLCC =  $30 \pm 30\%$  grassland and  $60 \pm 40\%$  row crop agriculture). High probability habitat areas were also located further from cities than average distances within the GPLCC (leks =  $71.62 \pm 13.89$  Km, GPLCC =  $41.7 \pm 75$  km). Last, areas of high probability habitat were found to receive greater and less variant rainfall and also had slightly warmer with less variant minimum annual temperatures than the GPLCC region as a whole (lek precipitation =  $58.6 \text{ cm} \pm 6.8 \text{ cm}$ , GPLCC precipitation =  $37.3 \text{ cm} \pm 15.7 \text{ cm}$ ).

To provide a comprehensive summary of habitat needs for prairie-chickens, we included both critical nesting and dispersal habitat in our final model (Figure 5.6). Areas in green represent areas where high probability habitat conditions are found for Greater Prairie-Chickens, while areas in yellow represent moderate probability habitat areas. Moderate probability habitat areas are where habitat improvement efforts would likely be beneficial and could increase the amount of critical habitat for prairie-chickens. Habitat identified in orange and red are areas with a low probability of encountering suitable habitat conditions for prairie-chickens. In low probability areas habitat conditions are likely of poor quality for the species and thus in these areas intensive management for the species would not likely provide substantial benefit. Areas outlined in black should be given higher conservation priority because these are areas responsible for maintaining population genetic connectivity throughout the GPLCC. As can be seen from Figure 5.3, prairie-chicken populations in Nebraska are at a higher risk of becoming isolated from the rest of the GPLCC prairie-chicken populations.

However, one caveat to our data analysis is the notion of a lag time to observable effect of landscape alterations to Greater Prairie-Chicken presence in an area. Such affects have been

observed for other grouse species such as the Greater Sage-Grouse (*Centrocercus urophasianus*) as sage-grouse were observed to continue to occupy leks in an area heavily impacted by oil and natural gas development for up to ten years after development had occurred (Harju et al. 2010). Holloran (2005) noticed similar lag to effect trends of between five to seven years for sage-grouse leks in coal-ball natural gas developments in western Wyoming. Such observations highlight the importance of assessing the reliability of presence observations with estimates of demographic performance, particularly for species such as prairie-chickens which are known to be philopatric (Pidgeon et al. 2003).

At this time we lack any site specific demographic data for the areas where our model predicts lek habitat to be present, but an interesting future application of our analysis would be to check for lag effects with regards to prairie-chicken lek presence as a function of contemporary or historic landscape alterations. However, one attribute of our analysis which would complicate such an analysis is that the scale at which our habitat assessment is performed is orders of magnitude larger than the scale at which most, even landscape level assessments of demographic performance are collected at (Pidgeon et al. 2003, Harju et al. 2010, McNew 2010). Consequently, the scale at which we conducted this analysis likely encompasses the full suite of localized demographic source-sink-metapopulation dynamics within a region (Hanski and Gaggiotti 2004). In addition this model is specifically focused on breeding season dynamics. For most populations of prairie-chickens breeding season distribution completely overlaps with winter distribution (Schroeder and Robb et al. 1993), prairie-chicken populations in western Nebraska and Colorado are somewhat migratory (Svedarsky et al. 1999). Thus in those areas additional migratory habitat characteristics may need to be incorporated to fully capture the conservation habitat requirements for those populations.

Our spatial modeling approach used regional to landscape scale and we were unable to include micro-habitat features within management areas, which may be important for sustaining viable populations. Factors important for local management might include vegetation structure, vegetative species composition, arthropod abundance, grazing regime, and fire frequency. The fact that this is a regional model cannot be stressed enough, and while we are relatively confident in model performance for the region as a whole, localized model performance may be poor. For example, Figure 5.5 indicates that north central Nebraska, an area referred to as the Sand Hills, contains relatively unsuitable lek habitat for Greater Prairie-Chickens, despite lek location data

from this portion of the GPLCC being included in regional niche model development. Indeed, this portion of the region proved to be the most variable area in the assigned probability of the occurrence of lek habitat (Figure 5.6), and accounted for most of our commission errors. Moreover, based on local assessments of greater prairie-chicken demographic performance in this area, the Sand hills area is known to contain relatively large and stable populations of Greater Prairie-Chickens (*personal communication L. Powell, University of Nebraska Lincoln, and G. White, Colorado State University*). We conducted a localized niche model for the Sand Hills area by buffering the 16 leks for which we have lek location data from this region at 20 Km and then applied the same set of landscape and climate data used for Figure 5.5. The resulting niche model using variables deemed important at predicting the distribution of this species across the GPLCC region when applied at the local scale still performed poorly, ( $P(\text{lek habitat}) = 0.01\text{-}52\%$ ). The poor performance of the regional model at the local scale of the Sand Hills highlights the importance of local variation across the region, and that due to the hierarchical nature of animal use of space, for some localities a regional model predicting the distribution of potential suitable habitat may be inappropriate (Garshelis 1999).

Regardless, our approach and mapping tool should provide a first step towards setting conservation priorities and guidelines. Understanding the characteristics of high probability habitat may allow us to set regional habitat management goals for moderate to low probability areas. In addition, the methods we define here can be readily adapted for use with any number of species or habitat types of conservation concern across the GPLCC. Our approach would be particularly informative in defining critical and dispersal habitat for Sand Dune Lizards (*Sceloporus arenicolus*), Lesser Prairie-Chickens, Snowy Plovers (*Charadrius alexandrinus*), Burrowing Owls (*Athene cunicularia*), and Black-tailed Prairie Dogs (*Cynomys ludovicianus*). In conclusion, our mapping approach provides GPLCC region managers and conservationists a powerful tool to aid in identification of regions of critical conservation concern across the GPLCC. Our results will help to delineate areas for targeted management actions and direct financial resources to critical areas where benefits are greatest for implementation of management actions.

## Literature Cited

- Ahlburg, D.A., and J.W. Vaupel. 1990. Alternative projections of the U.S. population. *Demography* 27:639-652.
- 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 Service Professional Paper 964.
- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175-1178.
- Beaumont, L.J., A.J. Pitman, M. Poulson, and L. Hughes. 2007. Where will species go? Incorporating new advances in climate modeling into projections of species distributions. *Global Change Biology* 13:1368-1385.
- Beier, P., D.R. Majka, and S.L. Newell. 2009. Uncertainty analysis of least-cost modeling for designing wildlife linkages. *Ecological Applications* 19:2067-2077.
- Balkenhol, N. 2009. Evaluating and improving analytical approaches in landscape genetics through simulations and wildlife case studies. PhD. Thesis, University of Idaho.
- Briggs, J.M., A.K. Knapp, J.M. Blair, J.L. Heisler, G.R. Hoch, M.S. Lett, and J.K. McCaron. 2005. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *Bioscience* 3:243-254.
- Burnham, K.P., and D.R. Anderson. 2004. Understanding AIC and BIC model selection. *Sociological Methods and Research* 33:261-304.
- Cheng, H.H., I. Levin, R.L. Vallejo, H. Khatib, J. B. Dodgson, L. B. Crittenden, and J. Hillel. 1995. Development of a genetic map of the chicken with markers of high utility. *Poultry Science*: 74: 1855-1874.
- Collinge, S.K. 2009. Ecology of fragmented landscapes. Johns Hopkins University Press, Baltimore, MA, USA.
- Coulon, A., J. F. Cosson, J. M. Angibault. 2004. Landscape connectivity influences gene flow

- in a roe deer population inhabiting a fragmented landscape: an individual based approach. *Molecular Ecology* 13:2841-2850.
- Fisher, P. 1997. The pixel: a snare and a delusion. *International Journal of Remote Sensing* 18:679-685.
- Flato, G.M., and G.J. Boer. 2001. Warming asymmetry in climate change simulations. *Geophysical Research Letters*. 28:195-198.
- Garshelis, D.L. 1999. Delusions in habitat evaluation: measuring use and selection importance, In L. Boitana and T.K. Fuller editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, NY, USA. 280p.
- Gregory, A.J., L.B. McNew, T.J. Prebyl, B.K. Sandercock, and S.M. Wisely. *Chapter 3. A multi-scale hierarchical modeling approach to mapping Greater Prairie-Chicken (*Tympanuchuscupido*) lekking habitat across central Kansas*. *Studies in Avian Biology*.
- Guthrey, F.S., L.A. Brennan, M.J. Peterson, and J.J. Lusk. 2005. Information theory in wildlife science: critique and viewpoint. *Journal of Wildlife Management* 69:457-465.
- Hagan, C.A., and K.M. Giesen.[ONLINE] 2005. Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*), no. 364. In A. Poole [ED.], *The birds of North America*. Cornell Lab of Ornithology, Ithica, NY.<[http//bna.birds.cornell.edu/species/364](http://bna.birds.cornell.edu/species/364)>
- Hanski, I., and O.E. Gaggiotti. 2004. *Ecology, genetics, and the evolution of metapopulations*. Elsevier Academic Press Inc., Burlington, MA, USA.
- Hardy, O.J., and X. Vekemans. 2002. SPAGEDi: a versatile computer program to analyze spatialgenetic structure at the individual or population levels. *Molecular Ecology Notes* 2, 618-620.
- Harju, S., M.R. Dzialak, R.C. Taylor, L.D. Hayden-Wing, and J.B. Winstead. 2010. Thresholds and time lags in effects of energy development on Greater Sag-Grouse populations. *Journal of Wildlife Management* 74:437-448.
- Hijman, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965-1978.
- Hilty, J.A., W.Z. Lidicker Jr., and A.M. Merenlender. *Corridor Ecology: the science and practice of linking landscapes for conservation*. Island Press, Washington D.C.

- Hollaran, M.J. 2005. Greater Sage-Grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. PhD. Dissertation, University of Wyoming, Laramie, WY, USA.
- Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerrow, J.N. VanDriel, and J. Wickham. 2007. Completion of the 2001 National Land Cover database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73:337-341.
- 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.
- Howard S.M., and J.M. Lagrasse. 2004. An evaluation of gap filled Landsat SLC-off imagery For wildland fire burn severity, *Photogrammetric Engineering and Remote Sensing*, 70:877-880.
- Hulme, M. 2010. Validation required. *Nature* 463:849.
- Jackson, S.T., J.L. Betancourt, R.K. Booth, and S.T. Gray. 2009. Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *PNAS* 106:19685-19692.
- Johnson, J.B., and K.S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19:101-108.
- Keating, K.A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat selection studies. *Journal of Wildlife Management* 68:774-789.
- Li, H., and J.F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75:2446-2455.
- Lowe, W.H., and F.W. Allendorf. 2010. What can genetics tell us about population connectivity. *Molecular Ecology* 19:3038-3051.
- Maczko, K.A., L.D. Bryant, D.W. Thompson, and S.J. Borchard. 2004. Putting the pieces together: Assessing social, ecological and economic rangeland sustainability. *Rangelands* 3:3-15.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. Springer-Verlag Inc., NY, USA.
- McLaughlin, J.F., J.J. Hellmann, C.L. Boggs, and P.R. Ehrlich. 2002. Climate change hastens

- population extinction. PNAS 99: 6070-6094.
- McNew, L.B. 2010. An analysis of Greater Prairie-chicken demography in Kansas: The effect of human land use on the population ecology of an obligate grassland species. Manhattan, KS: Kansas State University; 2010. 149p.
- McRae, B.H. 2006. Isolation by resistance. *Evolution* 60:1551-1561.
- Noss, R.R., E.T. LaRoe III, and J.M. Scott. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. In: Biological Report 28.USDI National Biological Service, Washington D.C.
- Peakall, R., and P.E. Smouse. 2006. GENEALEX 6 Genetic analysis in Excel: population genetic software for teaching and research. *Molecular Ecology Notes* 6:288-295.
- Pidgeon, A.M., V.C. Radeloff, and N.E. Mathews. 2003. Landscape-scale patterns of Black Throated Sparrow (*Amphispiza bilineata*) abundance and nest success. *Ecological Applications* 13:530-542.
- Piertney, S.B., and J.F. Dallas. 1997. Isolation and characterization of hypervariable microsatellites in the Red Grouse (*Lagopus lagopus scoticus*). *Molecular Ecology* 6:93-95.
- Phillips, S.J., M. Dudik, and R.E. Scharpire. 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.
- Pitman, J.C., C.A. Hagan, R.J. Robel, T.M. Loughin, and R.D. Applegate. 2005. Location and success of Lesser Prairie-Chicken nests in relation to vegetation and human disturbance. *Journal of Wildlife Management* 69: 1259-1269.
- McGarigal, K., S. Cushman, and S. Stafford. 2001. Multivariate statistics for wildlife research and ecology research. Springer-Verlag Inc. New York, NY, USA.
- Mitchell, J.E. 2000. Rangeland resource trends in the United States. Fort Collins (CO): USDA Forest Service Rocky Mountain Research Station. General Technical Report RMSR-GTR-68.
- Renqiang, L.I., T. Huidong, and L. Xinhai. 2010. Climate change induces range shifts in Galliformes in China. *Integrative Zoology* 5:154-163.



- Robel, R.J., J.N. Briggs, J.J. Cebul, N.J. Silvy, and P.G. Watt. 1970. Greater Prairie-Chicken ranges, movement, and habitat usage in Kansas. *Journal of Wildlife Management* 34:286-306.
- Rogers, R. 2008. Prairie-chicken lek surveys—2008. Performance Report Statewide Wildlife Research Surveys. Kansas Department of Wildlife and Parks, Pratt, KS, USA.
- Root, T.L. J.T. Price, K.R. Hall. 2003. ‘Fingerprints’ of global warming on animals and plants. *Nature* 421:161-167.
- Rousset, F., 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources* 8: 103-106.
- Ryan, M. R. L. W. Burger, Jr., 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.
- Salazar, K. 2009. Addressing the impacts of climate change on America’s water, land, and other natural and cultural resources. Department of the Interior, Order No. 3289. September 14, 2009.
- Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44:418-421.
- Sauer, J.R., J.E. Hines, and J. Fallon. 2004. The North American Breeding Bird Survey, Results and Analysis 1966-2003. Version 2004.1. USGS Pauxent Wildlife Research Center, Laurel, MD.
- 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*). *The Birds of North America*, Issue No. 36.
- Schwarz, G. 1978. Estimating the dimension of a model. *Annals of Statistics* 6:461-464.
- Schwartz, M.W., L.R. Iverson, A.M. Prasad, S.N. Mathews, and R.J. O’Coonor. 2006. Predicting extinctions as a result of climate change. *Ecology* 87:1611-1615.
- Slatkin, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* 47:264-279.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of

- species. *Ecology Letters* 10: 1115–1123.
- Soares-Filho, B.S., D. Nepstad, L. Curran, E. Voll, G. Cerqueira, R.A. Garcia, C.A. Ramos, A. McDonald, P. Lefebvre, and P. Schlesinger. 2006. Modeling conservation in the Amazon basin. *Nature London* 440:520-523.
- Svedarsky, D. W., 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.
- Taylor, S.E., S.J. Oyler-McCance, and T.W. Quinn. 2003. Isolation and characterization of microsatellite loci in Greater Sage-Grouse (*Centrocercus urophasianus*). *Molecular Ecology Notes* 3:262-264.
- Thomas, C.D., A. Cameron, and R.E. Green. 2004. Extinction risk from climate change. *Nature* 427:145-148.
- Wahlberg, N. A. Moilanen, and I. Hanski. 1996. Predicting the occurrence of endangered species in fragmented landscapes. *Science* 273:1536-1538.
- Walls, B.J., and A.L. Stigall. 2011. Analyzing niche stability and biogeography of late Ordovician brachiopod species using ecological niche modeling. *Palaeogeography, Palaeoclimatology, and Palaeoecology* 299:15-29.
- Wang, G., N. T. Hobbs, K. M. Giesen, H. Galbraith, D. S. Ojima, and C. E. Braun. 2002. Relationships between climate and population dynamics of white-tailed ptarmigan *Lagopus leucurus* in Rocky Mountain National Park, Colorado, USA. *Climate Research* 23:81-87.
- Waples, R.S. 2007. LDNE: a program for estimating effective population size from data on linkage disequilibrium. *Molecular Ecology Notes* 7:167-184.
- Westemeier, R.L., J.D. Braun, S.A. Simpson, T.L. Esker, R.W. Jansen, J.W. Walk, E.I. Kershner, J.L. Bouzat, and K.N. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282:1695-1698.
- Wiens, J.A., D. Stralberg, D. Jongsomjit, C.A. Howell, and M.A. Snyder. 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. *PNAS* 106:19729-19736.
- Williams, J.W., and S.T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475-482.

With, K.A., and T.O. Crist. 1995. Critical thresholds in species responses to landscape structure. *Ecology* 76:2446-2459.

Young, A.G., and G.M. Clarke. 2000. *Genetics, demography, and viability of fragmented populations*. Cambridge University Press, New York, NY, USA.

Table 5.1. Cooperating organizations and number of tissue samples provided for the analysis of critical and dispersal habitat within the Great Plains Landscape Conservation Cooperative. All samples were collected in 2009-2010.

<b>State</b>	<b>Cooperating Organization</b>	<b>Number of Samples</b>
Colorado	Colorado Division of Wildlife (CDW)	61
Kansas	Kansas Department of Wildlife and Parks (KDWP)	44
	Kansas State University	
	Wisely Conservation Genetics Laboratory (KSU)	124
Nebraska	Nebraska Game and Parks Commission (NGPC)	41
South Dakota	USDA Forest Service (USDA)	49
<b>TOTAL</b>		<b>319</b>

Table 5.2. Landscape and climate variables collected at each spatial scale of the hierarchical analysis approach.

Model Scale	Variables	Variable Abbreviation
<b><u>Lek Point</u></b>	1) Latitude	Lat
<i>Data are collected from pixels occupying the same space as the lek location</i>	2) Longitude	Long
	3) Contagion	Cont
	4) Elevation	Elev
	5) Weighted Elevation	WtElev
	6) Population Density	Pop Den
	7) Distance to Roads	Dist Rd
	8) Distance to Cities	Dist City
	9) Distance to Riparian Areas	Dist Rip
	10) Land Cover	Land Cover
	<b><u>500 meter neighborhoods</u></b>	1) % of the landscape in the buffer classified as urban
Data are collected for a region identified from a 500 m buffer surrounding the lek site	2) % of the landscape within the buffer classified as row crop agriculture	% Ag 500m
	3) % of the landscape in the buffer classified as forest	% Tree 500m
	4) % of the landscape within the buffer classified as grasslands	% Grass 500m
<b><u>5 Km Neighborhoods</u></b>	1) % of the landscape in the buffer classified as urban	% Urban 5 km
Data are collected for a region identified from a 5 Km buffer surrounding the lek site	2) % of the landscape within the buffer classified as row	% Ag 5 km

---

	crop agriculture	
	3) % of the landscape in the buffer classified as forest	% Tree 5 km
	4) % of the landscape within the buffer classified as grasslands	% Grass km
<b><u>Climate Models</u></b>	1) Maximum temperature value from WorldClim data set	Max Temp
<i>Data are collected from the WorldClim data set from the centroid of 1Km pixels encompassing the lek location</i>	2) Minimum temperature from the WorldClim data set	Min Temp
	3) Average precipitation value from the WorldClim data set	Avg. Precipitation

---

Table 5.3. Description of and model parameters for the hierarchical model selection procedure.

<b>Model</b>	<b><math>\leq P</math></b>	<b><math>r^2</math></b>	<b>LN(K)</b>	<b>K</b>	<b><math>\Delta BIC</math></b>	<b><math>\leq w_i</math></b>
<b><u>Point models</u></b>						
<b>Global</b> ( <i>Lat., Long., Cont., Elev., WtElev., Pop.Den., Dist. Rd., Dist. City, Dist. Rip., &amp; Land cover</i> ).	<b>0.01</b>	<b>0.598</b>	<b>121.01</b>	<b>10</b>	<b>20.81</b>	<b>0.01</b>
Lat., WtElev., Dist. Rd., & Dist. City	0.01	0.589	123.37	5	0.00	0.51
Lat., Cont., WtElev., & Dist. City	0.01	0.570	128.11	4	0.05	0.49
<b><u>500 m neighborhood Models</u></b>						
<b>Global</b> ( <i>%Urban.500m, %Ag 500m, %Tree 500m, &amp; %Grass 500m</i> )	<b>0.01</b>	<b>0.210</b>	<b>228.92</b>	<b>4</b>	<b>11.73</b>	<b>0.01</b>
%Urban 500m	0.02	0.177	232.80	1	0.00	0.56
%Ag 500 & %Urban 500	0.02	0.210	299.47	2	1.85	0.22
%Tree 500 & % Urban 500	0.01	0.200	230.01	2	2.43	0.17
<b><u>5 Km neighborhood Models</u></b>						
<b>Global</b> ( <i>%Urban 5Km, %Ag 5Km, %Tree 5Km, &amp; %Grass 5Km</i> )	<b>0.03</b>	<b>0.360</b>	<b>197.24</b>	<b>4</b>	<b>8.45</b>	<b>0.01</b>
%Urban 5Km & %Grass 5Km	0.007	0.342	199.30	2	0.00	0.93
%Urban 5Km	0.01	0.253	209.77	1	5.26	0.07
<b><u>Multi-Scale Models</u></b>						
<b>Global</b> ( <i>Lat., Cont., WtElev., Pop. Den., Dist. Rd., Dist. City, %Urban 500m, %Ag 500m, %Tree 500m, %Grass 500m, %Gr 5Km, &amp; %Urban 5Km.</i> )	<b>0.01</b>	<b>0.688</b>	<b>130.80</b>	<b>12</b>	<b>22.55</b>	<b>0.01</b>
Lat., Cont., WtElev., %Grass 5Km, & %Urban 5Km	0.01	0.483	144.68	5	0.00	0.65
Lat., WtElev., %Grass 5Km, Dist. Rd., %Grass 500m, & %Urban 5Km,	0.01	0.588	135.92	6	1.65	0.29
Lat., Cont, WtElev., %Urban 500m, & %Urban 5Km	0.01	0.483	144.01	5	4.53	0.07
<b><u>Climate Models</u></b>						
<b>Global</b> ( <i>Max Temp, Min Temp, &amp; Avg. Precipitation</i> )	<b>0.06</b>	<b>0.230</b>	<b>178.19</b>	<b>3</b>	<b>5.06</b>	<b>0.08</b>
Min. Temp, Avg. Precipitation	0.01	0.220	178.39	2	0.00	0.92
<b><u>Multi-Scale Models Climate Models</u></b>						
<b>Global</b> ( <i>Lat., Cont., WtElev., Dist. Road, %Urban 5Km, Min. Temp., &amp; Precipitation</i> )	<b>0.01</b>	<b>0.867</b>	<b>116.87</b>	<b>8</b>	<b>17.24</b>	<b>0.01</b>
Cont., %Grass 500 m, %Urban 5Km, Min. Temp., & Precipitation	0.01	0.847	110.04	5	0.00	0.99

Table 5.4. Descriptive statistics for the six microsatellite markers used for genetic analysis of Greater Prairie-Chickens (n = 235) in the Great Plains LCC.

<b>Marker</b>	<b>NA</b>	<b>NA Expected</b>	<b>HWE</b>	<b>Marker Citation</b>
ADL146	6.83	3.82	0.062	A
LLST1	7.00	3.72	0.667	B
LSD3	7.33	3.89	0.353	B
LSD4	13.17	8.57	0.526	B
ADL230	6.67	4.41	0.050	A
SGCA6	10.83	6.50	0.100	C

HWE = Hardy Weinberg Equilibrium, A = Domestic chicken (*Gallus gallus*), Cheng et al. 1995, B = Red Grouse (*Lagopus lagopus scoticus*), Piertney and Dallas 1997, and C = Greater Sage-Grouse (*Centrocercus urophasianus*), Taylor et al. 2003.



Table 5.5. Population genetic characteristics of each population focus used in isolation by resistance analysis.

<b>Population ID</b>	<b>Location (°N, °W)</b>	<b>State</b>	<b>Organization</b>	<b><i>N</i></b>	<b><i>N<sub>e</sub></i></b>	<b><i>AR</i></b>	<b><i>H<sub>E</sub></i></b>
East CO	40.1, -102.1	CO	CDOW	55	281.4	7.7	0.85
Central CO	40.1, -103.3	CO	CDOW	10	42.1	4.9	0.76
Nebraska	42.4, -99.7	NE	NGPC	29	26.9	5.9	0.82
Western KS	39.5, -101.6	KS	KDWP	5	NA	2.7	0.47
Central KS	39.6, -99.9	KS	KDWP	4	3.5	3.8	0.72
Eastern KS	38.9, -97.8	KS	KSU	132	158.3	6.5	0.72
<b>Pooled Estimates</b>	-	-	-	<b>235</b>	<b>NA</b>	<b>5.1</b>	<b>0.72</b>

*N*= number of individuals analyzed per population (sample size), *N<sub>e</sub>* = the effective population size based on estimates of linkage disequilibrium (Waples 2007), *AR* = allelic richness or average number of alleles per population adjusted for sample size bias, *H<sub>E</sub>*= expected heterozygosity within each population adjusted for sample size bias.

Table 5.6. Population pairwise genetic and resistance variables for Greater Prairie-Chickens sampled across the GPLCC in 2010.

<b>Population Pair</b>	<b>Pairwise</b> <i>F<sub>ST</sub></i>	<b>Pairwise Genetic</b> <b>Distance</b>	<b>Pairwise Euclidean</b> <b>Distance (km)</b>	<b>Pairwise</b> <b>Resistance</b>
East CO – Central CO	0.088	0.240	95	123.4
East CO – Nebraska	0.018	0.203	323	3,527.8
East CO – Western KS	0.147	0.611	87	371.2
East CO – Central KS	0.048	0.419	204	437.6
East CO – Eastern KS	0.056	0.504	402	675.3
Central CO – Nebraska	0.024	0.205	391	1,814.9
Central CO – Western KS	0.178	0.790	164	773.7
Central CO – Central KS	0.086	0.783	295	374.6
Central CO – Eastern KS	0.088	0.796	492	437.9
Nebraska – Western KS	0.168	0.823	365	2,527.7
Nebraska – Central KS	0.063	0.588	310	2,112.2
Nebraska – Eastern KS	0.082	0.875	418	2,169.6
Western KS – Central KS	0.214	1.158	157	868.8
Western KS – Eastern KS	0.227	1.340	337	936.6
Central KS – Eastern KS	0.118	1.123	191	166.8

Pairwise resistance values are based on the top performing AIC<sub>c</sub> model of landscape resistance based on the habitat model.

Table 5.7. Model description and parameter values for the models used in the isolation by resistance analysis for 5 Greater Prairie-Chicken populations in the GPLCC.

<b>Model</b>	<b><math>r^2</math></b>	<b><math>P</math></b>	<b>MLE</b>	<b>AIC<sub>C</sub></b>	<b><math>\Delta</math>AIC<sub>C</sub></b>	<b><math>w_i</math></b>
Habitat Suitability Model	0.457	0.017	790.1	35.36	0.00	0.60
High Low Habitat Resistance	0.124	0.028	1,235.7	37.60	2.32	0.19
Five Habitat Resistance	0.420	0.019	1,376.0	38.13	2.86	0.14
Habitat Suitability x Contagion Model	0.453	0.016	1,832.6	39.57	4.29	0.07
Isolation By Distance**	0.097	0.202	191.6	28.27	-	-
Contagion**	0.067	0.043	520.7	35.28	-	-

\*\*Models with low  $\Delta$ AIC<sub>C</sub> scores which were excluded from model selection ranking because they had poor explanatory power and/or marginal statistical significance. R-square = the resultant correlation coefficient from Mantel tests of IBR, P = the associated P-value from Mantel tests of IBR, MLE = is the maximum likelihood estimator, AIC<sub>C</sub> = the Akaike Information Criterion statistic adjusted for small sample size bias.

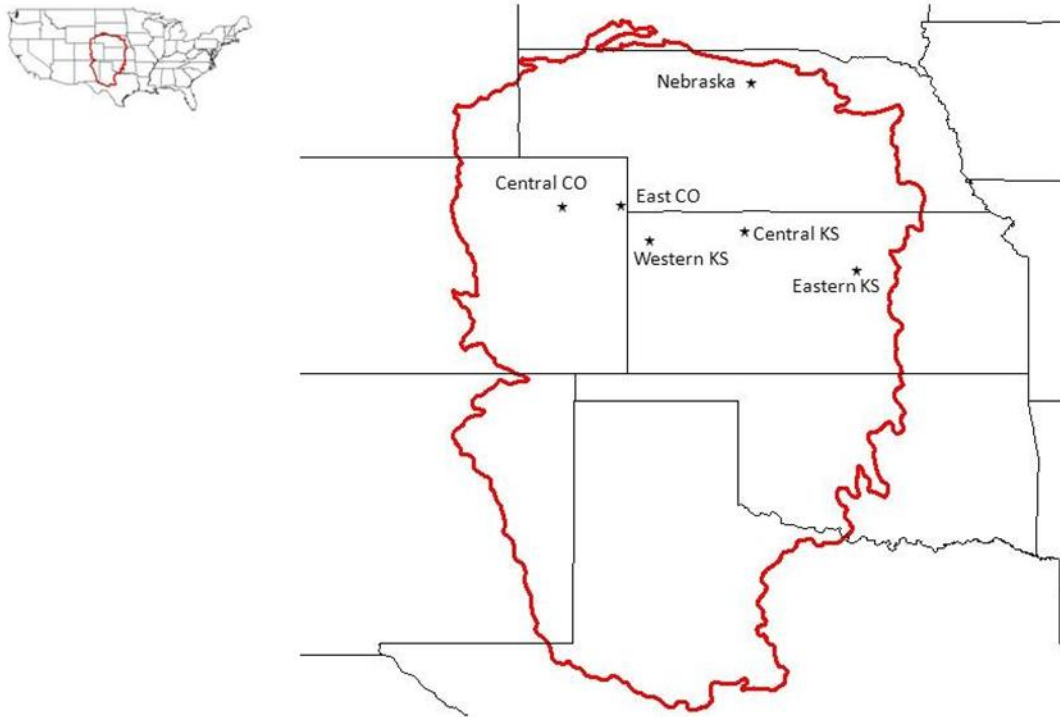


Figure 5.1. Great Plains Landscape Conservation Cooperative study area

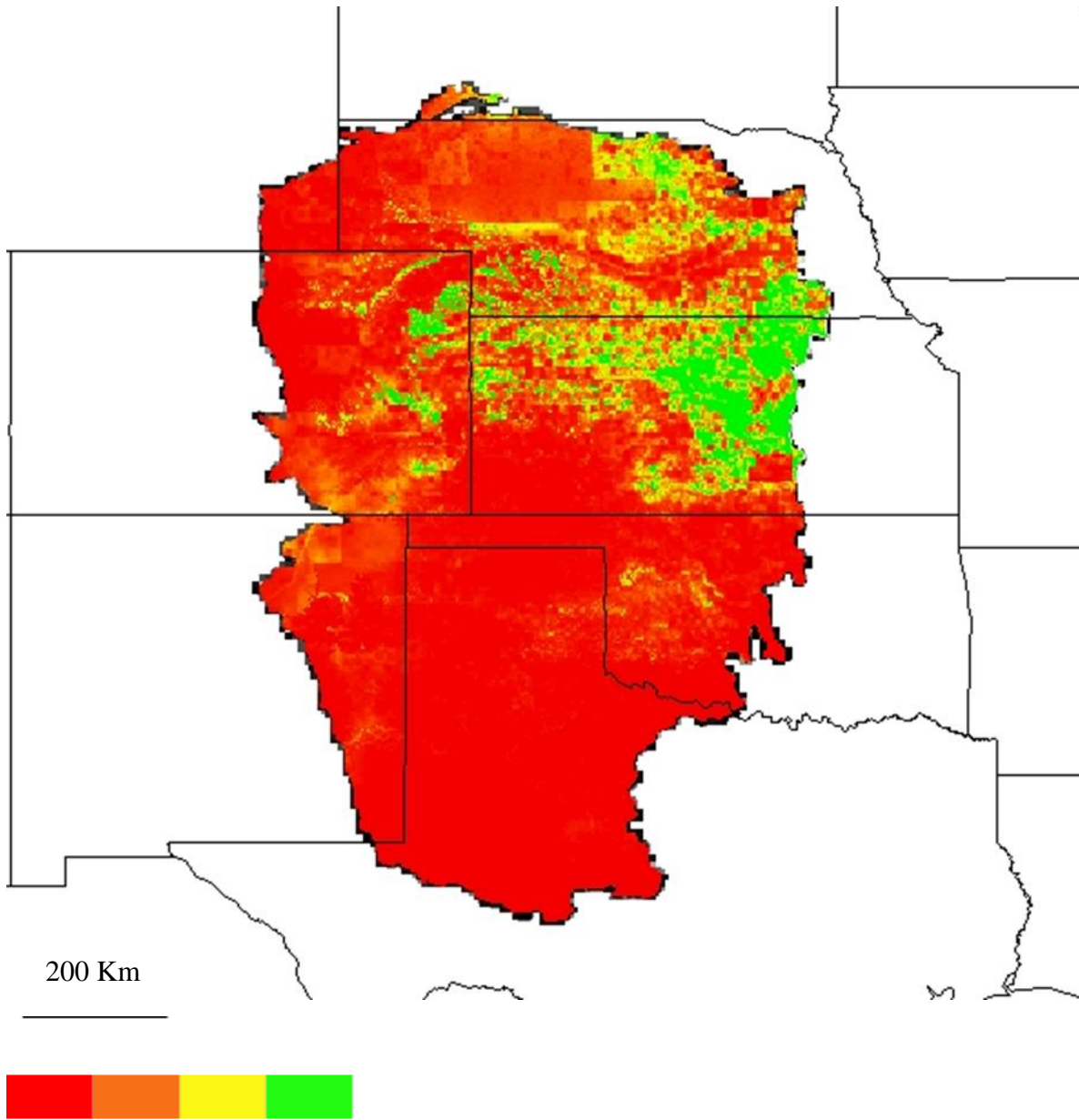


Figure 5.2. Predicted habitat probability of detecting prairie-chicken habitat from ecological niche modeling of lek locations map depicts the likelihood of finding suitable habitat conditions for Greater Prairie-Chicken breeding habitat at a given area. The map ranges  $< 0.001\%$  (red) – 98.4% (green) likelihood.

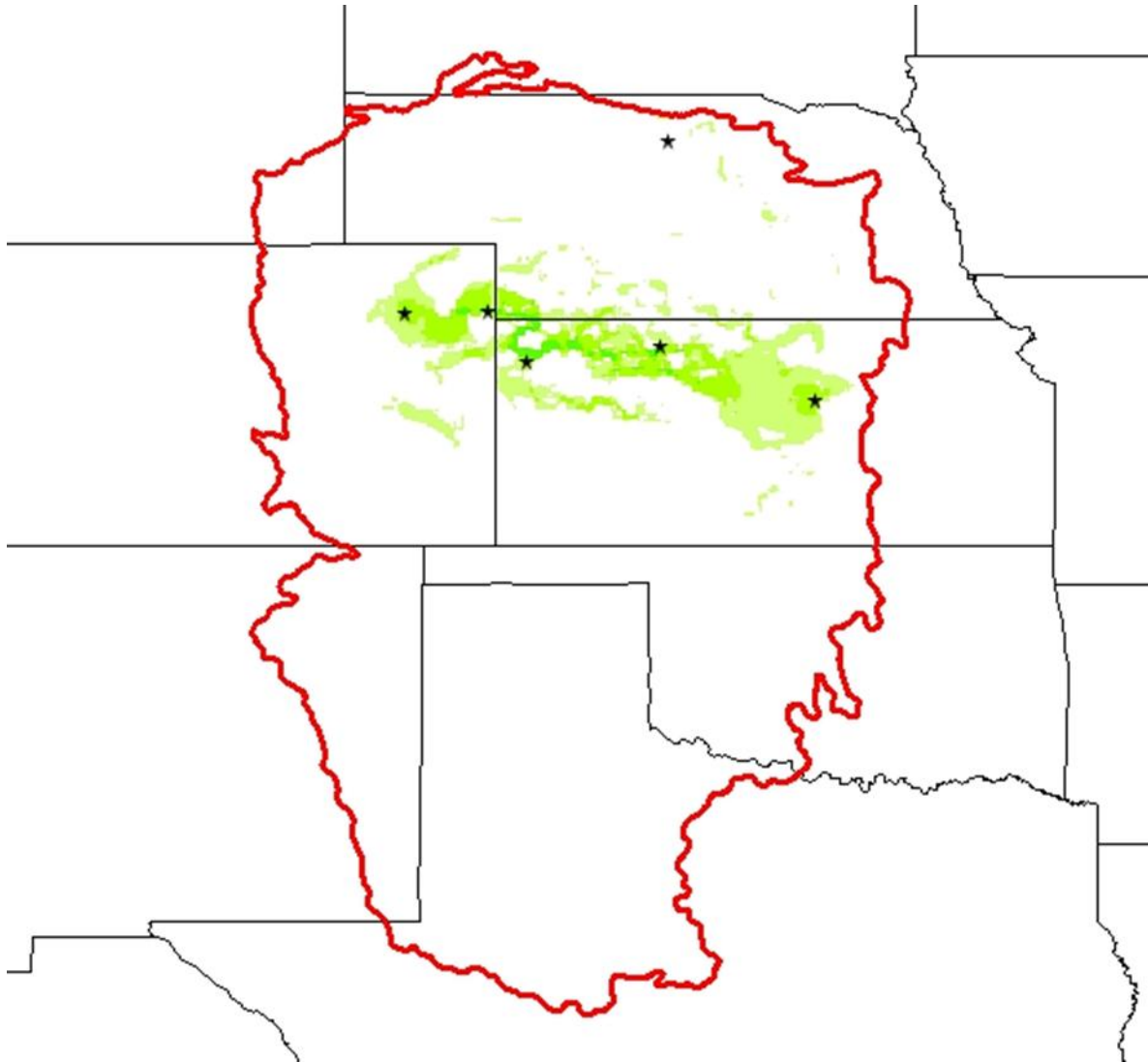


Figure 5.3. Predicted critical connectivity habitat based on isolation by resistance model. Areas in dark green are considered high priority areas for conservation to maintain genetic connectivity and areas of lighter green indicate areas of lesser priority. Black stars represent areas where genetic data were collected.

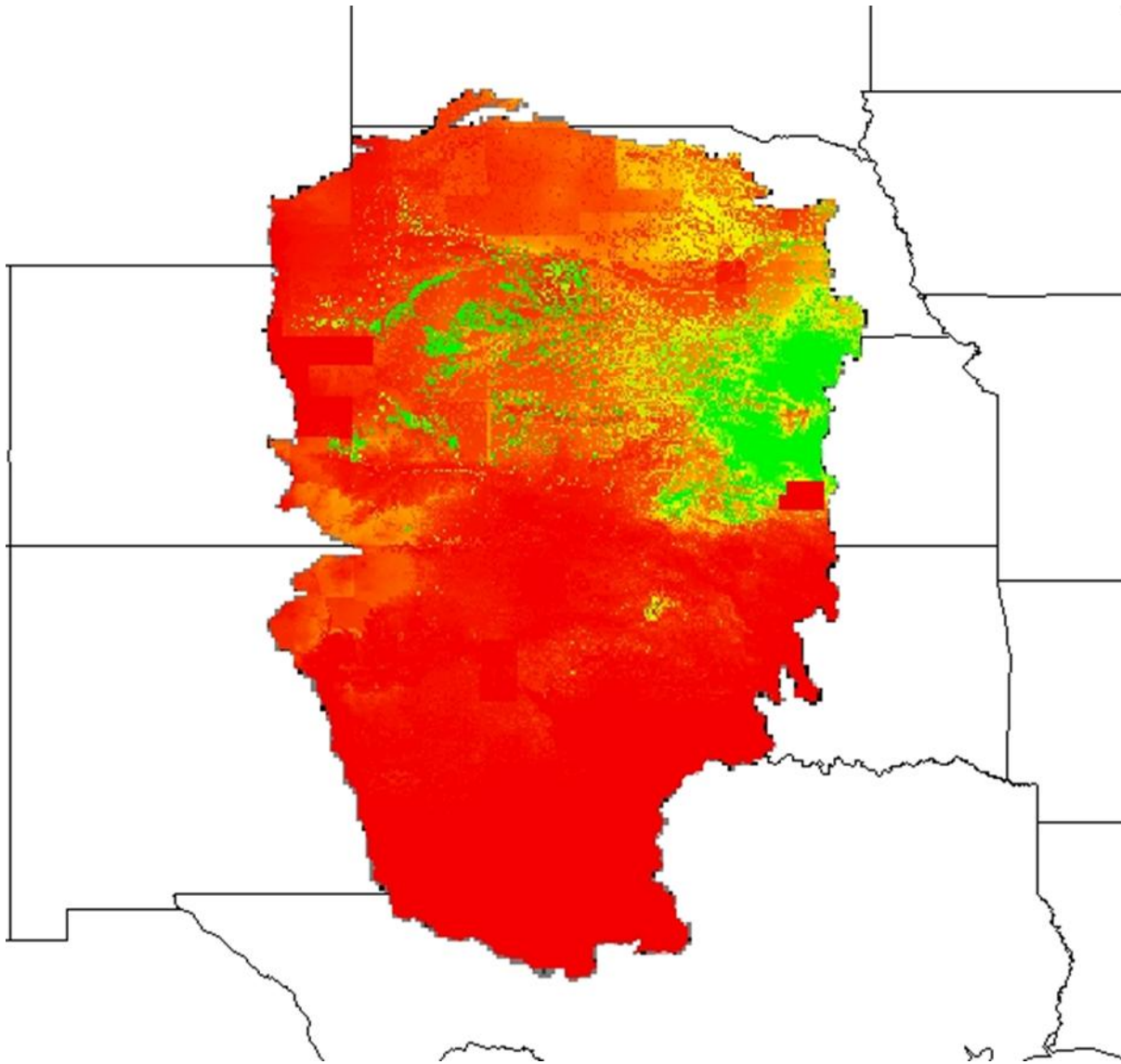


Figure 5.4. Predicted probability of detecting prairie-chicken habitat based on ecological niche modeling excluding climate data. The probability of encountering suitable Greater Prairie-Chicken breeding habitat across the landscape ranges from 0.2% - 94.4%.

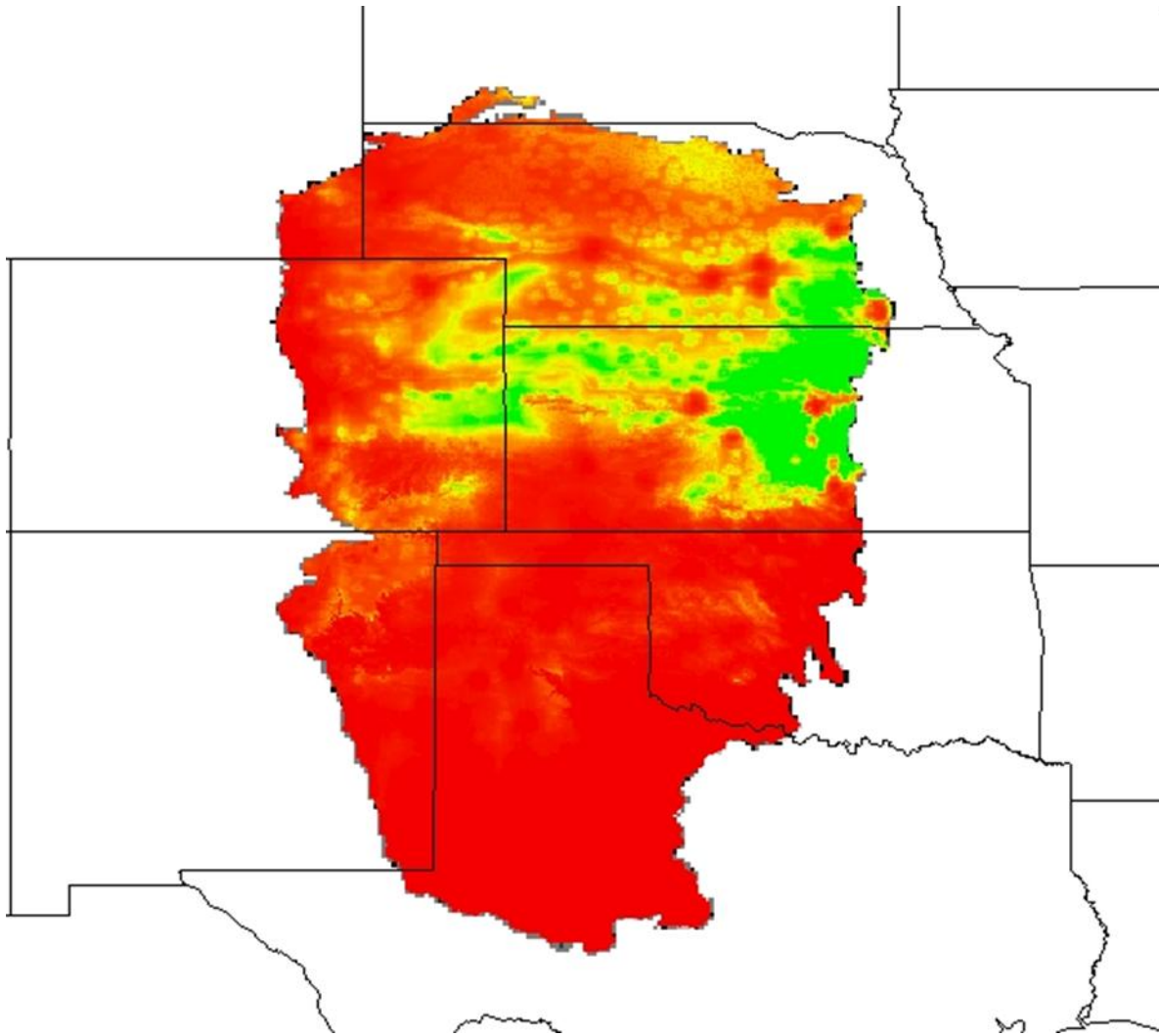


Figure 5.5. Predicted probability of detecting prairie-chicken habitat based on ecological niche modeling using landscape and climatic data. The probability of encountering suitable Greater Prairie-Chicken breeding habitat across the landscape ranges from 1.0% - 98.5%.



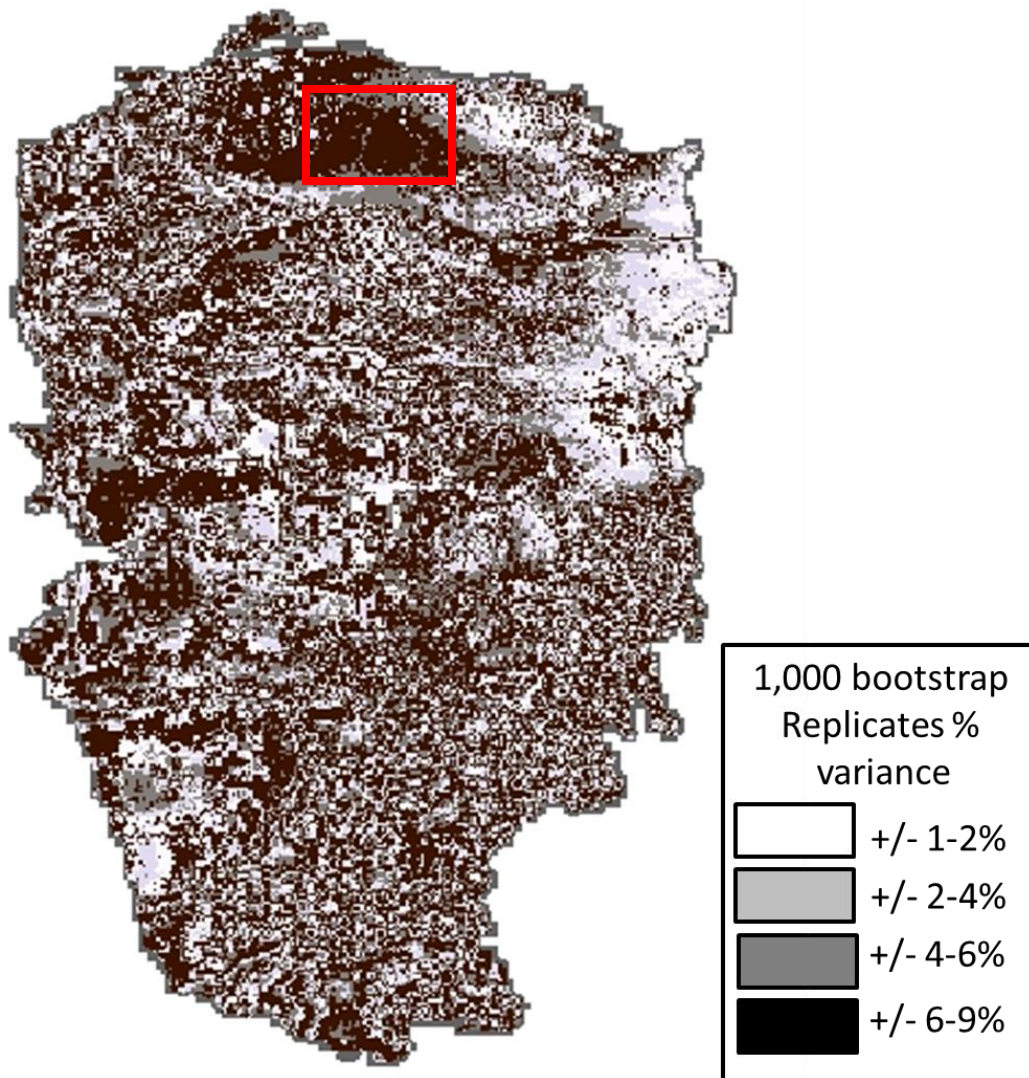


Figure 5.6 Variance in the probability of finding prairie-chicken habitat across the GPLCC region. Red outlined area is the Sand Hills region of Nebraska, where most of our omission errors occurred.

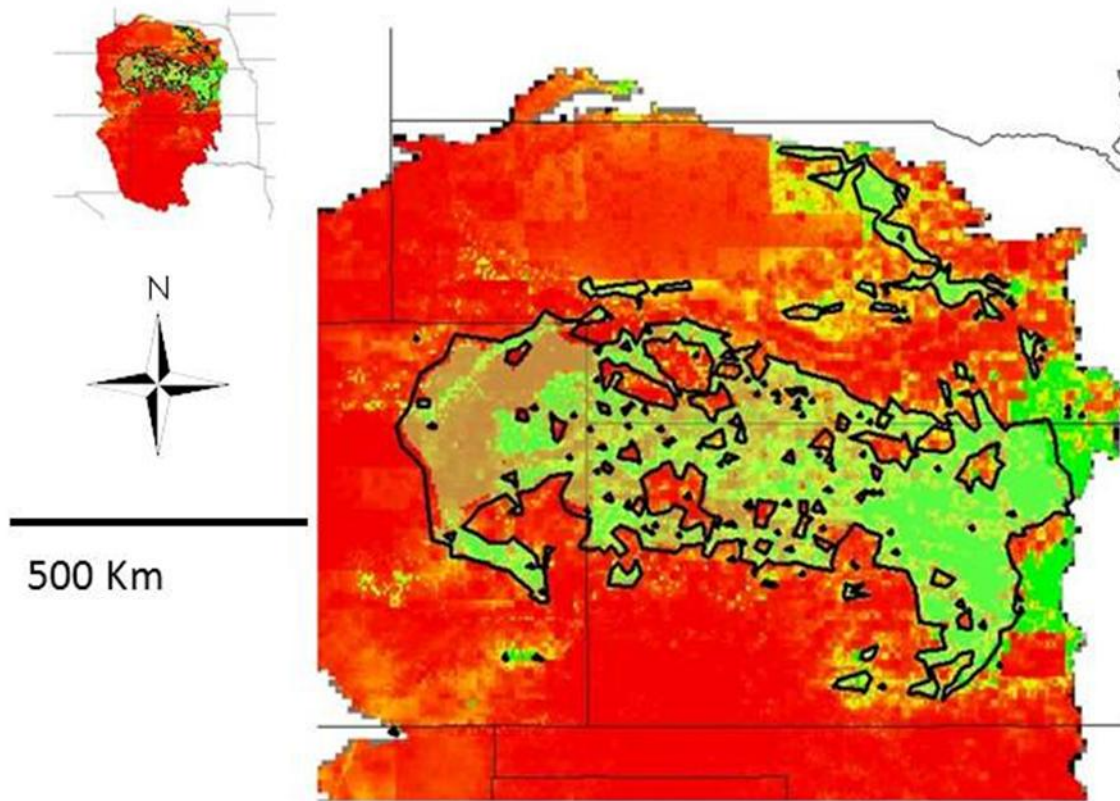


Figure 5.7. Critical breeding and dispersal habitat regions based on combining ecological niche model output with results from the isolation by resistance model.

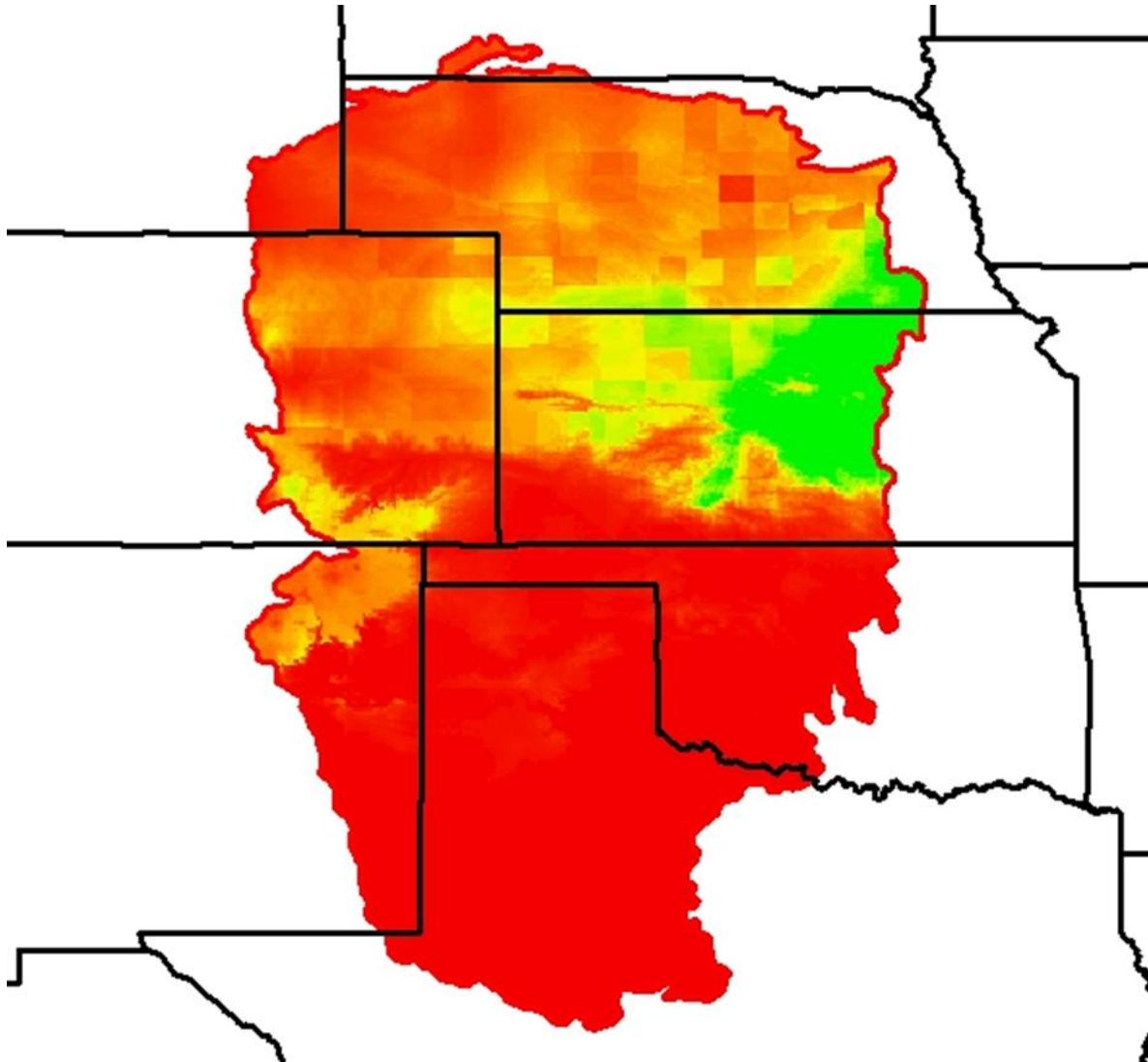


Figure 5.8. Predicted future distribution of Greater Prairie-Chicken breeding habitat across the GPLCC. Probability of finding lek habitat across the region ranges from <0.001% – 94.6%.

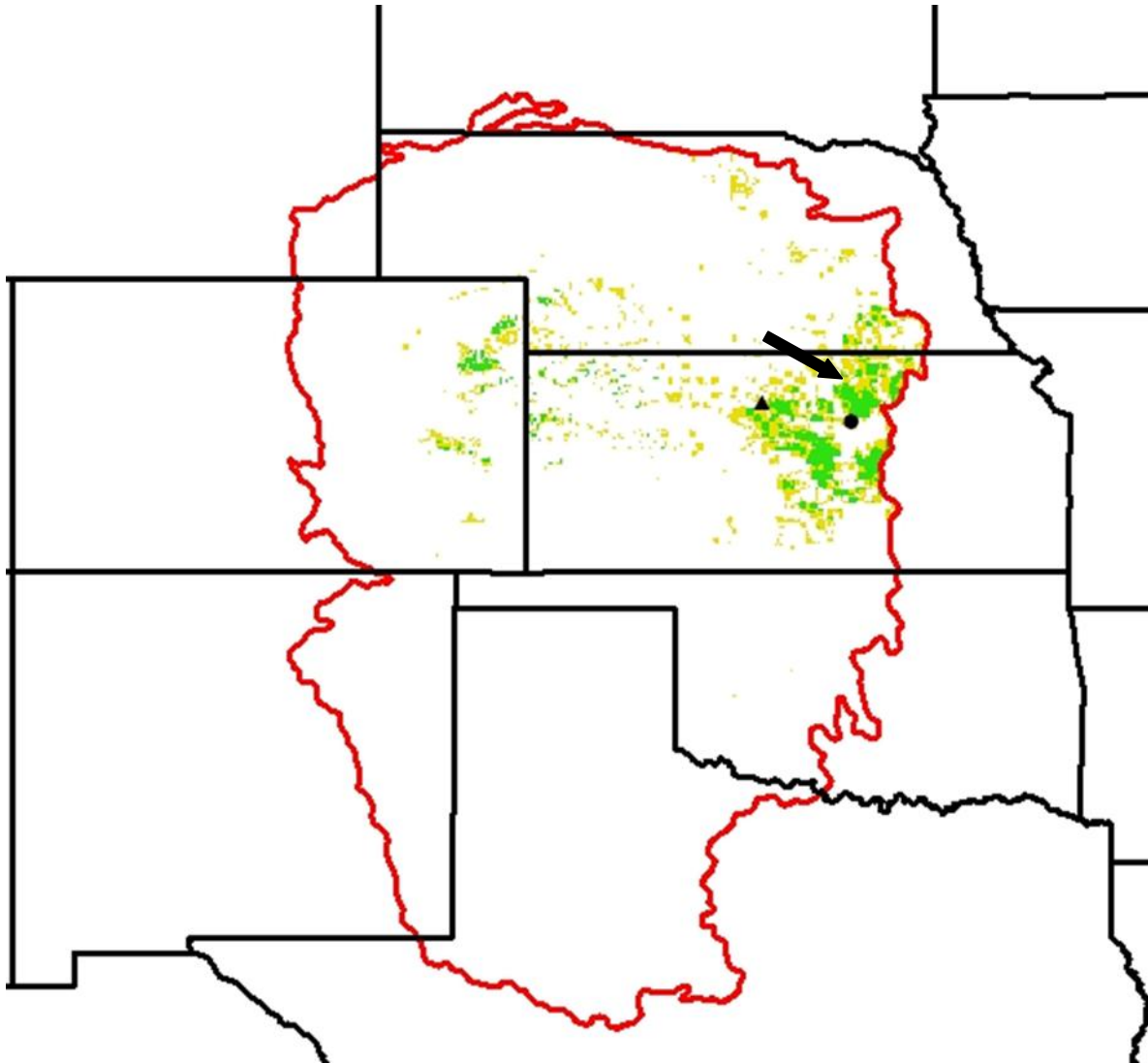


Figure 5.9. Predicted change in distribution map from 2010 ecological niche model compared to the predictions of the putative future habitat areas. Areas in yellow and green are contemporary high probability of occurrence habitats, whereas the subsets of areas in green are the predicted future distribution of high probability of occurrence habitats. Also depicted is the calculated shift in the center of distribution of high probability of occurrence habitats from the contemporary center (triangle) to the future center (circle).

## Chapter 6 - Conclusion

My dissertation work has expanded upon what was previously known about how landscape conformation impacts prairie-chickens and the role of prairie-chicken breeding ecology in species conservation. Most notably this research has delineated areas critical for the long term conservation of this species across both Kansas and the larger GPLCC region. Due to landscape alterations it may be difficult for natural dispersal to sustain high levels of genetic exchange among prairie-chicken populations in Kansas (See Chapter 3), and thus some populations are becoming increasingly isolated. Our habitat models (Chapter 2 and 4) suggest that increased CRP enrollment or reduction in woody plants along the I-70 corridor and around Ft. Riley, Kansas may partially enhance gene flow by increasing the quality of the habitat between disjunct prairie-chicken populations. Many might suggest that conservation efforts focused on the conservation of critical dispersal habitat to maintain panmixia, when breeding and nesting habitat are often considered a more immediate conservation concern (Caughley 1994). Indeed, declining populations through the Flint Hills have been largely attributed to poor nesting success due to predation as a result of a lack of adequate nesting cover (McNew 2010). However, failing to account for the effects of population genetics on species breeding ecology and survival overlooks the interaction of population genetics and population demographics on species ecology and persistence (Hedrick et al. 1996). Moreover, given the proclivity of Greater Prairie-Chickens for inbreeding depression (Westemeier et al. 1998), and links among genetic diversity, male reproductive success, and longevity (Chapter 1), conservation efforts targeted at maintaining panmixia are essential for long-term Greater Prairie-Chicken conservation.

My work described in this dissertation should prove useful in identifying both critical dispersal habitat and critical breeding and nesting habitat for Greater Prairie-Chickens. Specifically, Chapters 2 and 4 of my dissertation work identifies critical prairie-chicken habitat where focused management to improve nesting cover ought to be targeted at both the local scale (within and across Kansas) and the regional scale (across the GPLCC). Moreover, by specifically targeting management to areas identified in Chapter 3 as being important linkages for maintaining genetic connectivity between populations as well as within populations, we can accomplish conservation management for both increased nesting success (the more immediate threat) and increased connectivity (the more pervasive threat) simultaneously.

Last, the use of network and circuit analyses for analyzing landscape genetic patterns is becoming increasingly common in the ecological sciences. These new techniques rely on the parameterization of land cover data to a cost surface relating the perceived quality of the landscape as habitat. The cost surface is then paired with population genetics data as a surrogate measure of functional landscape connectivity (Spear et al. 2010). Most landscapes are parameterized using expert opinion. Expert opinion however, has been shown in many cases to be unreliable, if not inaccurate (Murray et al. 2009). One of the greatest benefits of my dissertation work is that it provides a set of standard methods to be used in parameterizing landscape resistance surfaces for isolation by resistance modeling (Chapter 2). My work in Chapter 2 provides much needed guidelines to researchers using these methodologies and could easily be adopted for other study systems. I feel these methodologies will be useful in parameterizing landscape resistance surfaces for use with many species of conservation concern. Aside from identifying critical portions of the landscape for necessary for conserving nesting, breeding, and dispersal habitats, I can also foresee uses of these methodologies in disease ecology modeling disease spread and identifying critical regions of the landscape important in disease spread. In addition, these methods should also prove useful in planning conservation corridors for species of conservation concern. Once habitat conservation corridors or disease corridors are identified, management actions can be taken to either enhance connectivity for conservation corridors or to restrict connectivity for disease ecology applications. These methodologies might also be useful in aquatic systems, modeling the ability of aquatic species to move along stream channels based on the attributes of the channel such as substrate, depth, oxygen level, acidity, temperature or other geophysical attributes of the stream. In addition, similar types of analyses could also be applied to more pelagic species inhabiting lakes and oceans to model their dispersal ability, or to subterranean species, such as earthworms, based on soil types or other attributes of the subterranean world such as acidity or moisture content. Overall, application of circuit-based network analyses has broad applications in ecology, and the methodologies described in my research will likely provide much needed structure for their application.

## Literature Cited

- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- Hedrick, P.W., R.C. Lacey, F.W. Allendorf, and M.E. Soule. 1996. Directions in conservation biology: a response to Caughley. *Conservation Biology* 10:1312-1320.
- McNew, L.B. 2010. An analysis of Greater Prairie-Chicken demography in Kansas: The effect of human land use on the population ecology of an obligate grassland species. Manhattan, KS: Kansas State University; 2010. 149p.
- Murray, J.V., A.W. Goldizen, R.A. O'Leary, C.A. McAlpine, H.P. Possingham, and S.L. Choy. 2009. How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. *Journal of Applied Ecology* 46:842-851.
- Nunney, L. 1993. The influence of mating system and overlapping generations on effective population size. *Evolution* 47:1329-1341.
- Spear, S.F., N. Balkenhol, M.J. Fortin, B.S. McRae, and K. Scribner. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology* 19:3576-3591.
- Westemeier, R.L., J.D. Braun, S.A. Simpson, T.L. Esker, R.W. Jansen, J.W. Walk, E.I. Kershner, J.L. Bouzat, and K.N. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282:1695-1698.



# **APPENDIX A - FIELD NOTES: OFF-LEK SOLICITATION AND MULTIPLE ON LEK COPULATIONS AMONG GREATER PRAIRIE-CHICKENS (*TYMPANUCHUS CUPIDO*) IN KANSAS**

## **Description**

The field notes data provided in this section of my dissertation are a collection of anecdotal observation collected by myself and my field technicians while gathering data for this project. As these data were obtained without any rigorous field protocols governing their collection, it is unlikely that they would ever be deemed publishable in a peer reviewed journal. Never-the-less, I have elected to include them here as I feel these observations are interesting and may be useful to other researchers, if for no other reason than to generate questions and a starting point for more rigorous investigations into some of the phenomena highlighted in this appendix.

## **Off-Lek Solicitation of Females by Males**

From 2006-2009, ss part of this research female prairie-chickens were captured at lek sites throughout Kansas (Figure 4.1), using drop nets and walk in box traps (Chapter 2). Females were fitted with 11-g necklace-style VHF radio transmitters with an expected battery life of 12 months (Model RI-2B, Holohil Systems Ltd., Ontario, Canada). We located females  $\geq 3$  times per week during the breeding and brood-rearing seasons (March–August), and daily once females began nesting. Once a female had localized in an area for three consecutive days, we used a portable radio receiver and handheld Yagi antenna to locate and flush the bird. Nest sites were visited  $\leq 2$  times during laying and early incubation. During our initial nest flush we counted the number of eggs contained in the clutch, measured each the length and width of each egg, estimated stage of incubation using standard egg float curves developed for greater prairie-chickens as part of this study, and checked for nest parasitism by other gallinaceous species. Nests were not visited again until females had departed and were located away from the nest for  $> 2$  consecutive days. Once a female departed, we classified nest fate as either successful because  $\geq 1$  eggs successfully hatched chicks, or failed because the clutch was depredated, abandoned or destroyed for other reasons. Date of hatching was the last day the female was estimated to be incubating at a successful nest by triangulation with radio-telemetry. Field methods were



approved by Kansas State University's Institutional Animal Care and Use Committee (Protocol numbers 2474 and 2781). While collecting telemetry and nest data technicians were instructed to record any observations which they made, that they felt warranted documentation.

Over the course of this project we collected ~3,720 female Greater Prairie-Chicken telemetry locations. The average number of bearings taken/location was 3.21 bearings and the average time between bearings was 9.2 minutes. Thus our field protocols amounted to 1,833.5 hours of field observations in Kansas across 4 years.

During field and telemetry observations technicians recorded the occurrence of males booming and displaying for nesting females off-lek 11 times. We also recorded two possible pheasant nest parasitism of Greater Prairie-Chicken nests in Cloud County, Kansas (one nest with two pheasant eggs and a second nest with one pheasant egg). Both nests were depredated prior to hatching any chicks.

Finally, while collecting telemetry through the winter technicians observed Greater Prairie-Chicken groups roosting in tress and gallery forests six times. All occurrences of tree roosting prairie-chickens occurred between 12-December and 2-February. The average number of prairie-chickens in a tree roosting group was eight.

### **Multiple on Lek Copulations**

From 2006-2009 Greater Prairie-Chicken leks across Kansas (Figure 4.5), were observed during morning trapping. During morning lek observations technicians were instructed to record the number of copulations observed each morning. Over the four years of this study we made 1,262 lek observations, each observation was ~2.6 hours, thus we have ~3,281.2 hours of lek observations.

During lek observations we observed 113 copulations of 96 hens. Seven hens were observed to successfully copulate with more than one male in a single visit to a lek, as determined by behavioral observations of females post copulation (Nooker and Sandercock 2008). Multiple on-lek copulations occurred from 28-March thru 5-May, with the majority of the multiple on-lek multiple copulations coinciding with peak female lek visiting during the second and third weeks of April (McNew 2010).

## Literature Cited

McNew, L.B. 2010. An analysis of Greater Prairie-Chicken demography in Kansas: The effect of human land use on the population ecology of an obligate grassland species.

Manhattan, KS: Kansas State University; 2010. 149p.

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.

## **Appendix B - MANUSCRIPTS AND DATA SETS**

This appendix lists the title and authorship of manuscripts resulting from each chapter of this dissertation, and provides additional information on the source of the data sets used in the data analysis for each manuscript including a description of the years over which the data were collected.

### **Chapter II**

#### ***GENETIC DIVERSITY DRIVES SURVIVORSHIP AND MATING PREFERENCE IN A LEK-MATING GROUSE***

Andrew J. Gregory, Jacqueline K. Augustine, Brett K. Sandercock, and Samantha M. Wisely

Corresponding Author: Dr. Samantha M. Wisely

At time of publication of this dissertation this manuscript is submitted and in review for publication in *Evolution*.

Data were collected from five leks located south of Manhattan Kansas from 2003-2006. Data include observational data collected by Dr. Jackie Augustine as part of her doctoral work at Kansas State University. During trapping and marking of birds for her behavioral analysis Dr. Augustine collected blood samples for possible future genetic analysis. In 2006 when A. Gregory began his dissertation work with prairie-chickens at Kansas State University he performed the genetic analysis of these samples.

## Chapter III

### *A multi-scale hierarchical modeling approach to mapping lek habitats of Greater Prairie-chickens in EASTERN Kansas*

Andrew J. Gregory, Lance B. McNew, Thomas J. Prebyl, Brett K. Sandercock, and Samantha M. Wisely

Corresponding Author: Dr. Samantha M. Wisely

At time of publication of this dissertation this manuscript is *in press* in Studies of Avian Biology.

The data set used for this analysis consists of the publically available Kansas Department of Wildlife and Parks Greater Prairie-Chicken lek survey route data. We restricted the leks used for these analyzes to only those leks known to be active during the time period form 2006-2008. We also included lek locations from known active leks over this time period collected as part of a 3-year population study of prairie-chickens in eastern Kansas (McNew et al. 2010 cited in each chapter of this dissertation). Collectively this gave us geographic locations for 166 active leks.

For land cover data analysis we used the 2005 land cover data collected by the Kansas Applied Remote Sensing Program, housed at the University of Kansas at Lawrence, for National Land Cover database. The database was created using imagery from the Landsat 5 satellite, which orbits the earth at an altitude of 438 miles. Multi-date images from spring, summer, and fall of 2005 were used, with some 2004 images where 2005 images were not available. In total, over 50 Landsat images were used. Employing data from the red, near-infrared, and shortwave infrared parts of the spectrum (Landsat bands 3, 4, 5, and 7) an 'unsupervised' or statistical clustering, approach was used to identify 11 land cover types. Refinement of field boundaries and the addition of Conservation Reserve Program (CRP) lands were performed using additional data provided by USDA.

The land cover map is based on an Anderson Modified Level I classification scheme and a minimum mapping unit that varies by class type. The classification scheme was designed to be comparable to the 1990 Kansas Land Cover Patterns database, and contains the same ten classes as the 1990 map, with the addition of lands enrolled in the Conservation Reserve Program (CRP).

Ground truthing can be cost and time prohibitive when dealing with large geographic extents. Rather than conducting independent field efforts for the accuracy assessment, two existing databases were used to assess the accuracy of the 2005 land cover map. The 2005 Common Land Unit (CLU) dataset was used to assess the accuracy of mapped grassland and cropland and the Kansas GAP vegetation database was used to assess the accuracy of mapped woodlands. More than 30,000 control points were established to assess the accuracy of the 2005 land cover database based on a stratified random sampling design. An overall error matrix was created to delineate rates of errors of omission and commission along with an overall accuracy assessment statistic, Kappa. The overall accuracy of the map was 90.72% (Kappa = 83.54%). Most common errors were of land cover classes classified as being grassland being crop land (8%) and areas classified as unknown actually being forests (4%). The Final report, including the full accuracy assessment, for the 2005 land cover data base can be found at:

*[http://kars.ku.edu/media/uploads/work/KLCP2005\\_Final\\_Report.pdf](http://kars.ku.edu/media/uploads/work/KLCP2005_Final_Report.pdf)*

Our analysis presented in this chapter is likely robust to the rate of error reported for the 2005 land cover database. The original map was created at 30 m accuracy. However, for our analysis we coarsened this accuracy to 100 m cell sizes using majority filtering in Arc Info. 9.3. By coarsening the land cover data used in the analysis we limit the impact which producer defined errors may have on our analysis.

## Chapter IV

### *Optimizing Landscape Resistance Surfaces to Increase Inferences about Gene Flow: A Case Study for a Grassland Obligate Species, the Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*)*

Andrew J. Gregory, Samantha M. Wisely, Lance B. McNew, and Brett K. Sandercock

Corresponding Author: Dr. Samantha M. Wisely

At time of publication of this dissertation this manuscript is in the final stages of preparation for submission for publication in *Molecular Ecology*.

Genetics data was obtained via live trapping Greater Prairie-Chickens from leks distributed across three sampling locations across the Flint Hills and Smoky Hills of Kansas from 2006 – 2010 (Figure 4.5, and study site maps in McNew 2010 cited in each chapter of this dissertation). Additional genetic samples from Kansas (Saline County and Fort Riley Populations in Figure 4.5), were provided by the Missouri Department of Conservation (MDC). Nebraska samples were provided by Dr. Tye Mathews and Dr. Larkin Powell from the University of Nebraska at Lincoln. MDC samples were collected from wild captured prairie-chickens, captured from 2008-2009 as part of a planned Greater Prairie-Chicken translocation from Kansas to Missouri. Nebraska samples were collected from birds captured in 2008 as part of Dr. Mathews dissertation work (See Mathews et al. *in press* *Studies of Avian Biology*, for a full description of study sites and capture methods).

The land cover data used for spatial modeling with these analyzes was the 2005 land cover data base for Kansas and Nebraska. For discussion on the accuracy of this database and how this level of accuracy is likely to impact the spatial context of our analyzes please see the Chapter III section above.

## Chapter V

### *Modeling habitat suitability change for a grassland specialist as a function of increasing human land use and global climate change across the U.S. Great Plains*

Andrew J. Gregory, Theresa Schneider, Brett K. Sandercock, and Samantha M. Wisely

Corresponding Author: Dr. Samantha M. Wisely

Manuscript is being prepared for submission to Global Change Biology.

Lek location coordinate data were provided by cooperating State Agency personnel, Federal Agency personnel, and NGO's from greater prairie-chicken surveys conducted from 2009-2010. Feather samples were collected for molecular analysis from active leks over the same time interval. We also have feather samples and lek location samples from North Dakota, Minnesota, and Illinois. However, as these states were not part of the GPLCC management unit we do not present data for these locations in this dissertation.

We used the USGS National Land Cover database and National Digital Elevation Model seamless server data set for all land cover and elevation data. Full accuracy assessments and data descriptions for these data sets are available at: <http://seamless.usgs.gov/index.php>