

SPATIO-TEMPORAL PATTERNS OF INFECTIOUS DISEASE VECTORS IN THE  
EASTERN SMOKY HILLS, KANSAS

by

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B.S., Kansas State University, 2012

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Division of Biology  
College of Arts and Sciences

KANSAS STATE UNIVERSITY  
Manhattan, Kansas

2012

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## Abstract

Nearly 30% of emerging infectious diseases are caused by vector-borne pathogens with wildlife origins, posing a risk for public health, livestock, and wildlife species of conservation concern. Understanding the spatial patterns of exposure to dipteran vectors and their associated pathogens is critical for epidemiological research to target prevention and control of vector-borne infectious diseases. In recent years, Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis and avian malaria have not only been a public health concern but also a conservation concern, specifically the conservation of grassland nesting birds. Although the central Great Plains is the most speciose region for grassland nesting birds, their role in the enzootic (primary) amplification cycle of infectious diseases may lead to further population depressions, and could potentially result in spill-over events to humans and livestock. The goals of my thesis were 1) to identify the underlying causes of spatio-temporal abundance patterns of mosquito vectors within the grasslands of the eastern Smoky Hills, and 2) to create probabilistic distributions of functional disease vectors, to evaluate disease risk in Greater Prairie-chicken (*Tympanuchus cupido*, surrogate species for other grassland nesting birds). First, I found that temporal dynamics in mosquito abundances were explained by maximum and minimum temperature indices. Spatial dynamics in mosquito abundances were best explained by environmental variables, such as curvature, TWI (Topographic Wetness Index), distance to woodland and distance to road. Second, the overall predictive power of the ecological niche models of important vector species in the grasslands of the Smoky Hills was better than random predictions, indicating that the most important predictor variables in their distribution were: distance to water, TWI, AASHTO (soil particle size distribution), and mean temperature during the coldest quarter. Furthermore, the spatial analysis indicated that Greater Prairie-chicken nest in areas with a higher probability of vector occurrence than other potentially available habitats within the grasslands. However, I failed to detect a significant difference in the probability of vector occurrence at nest of infected versus uninfected females. Understanding the distribution and abundance patterns of vectors of infectious diseases can provide important insights for wildlife conservation as well as public health management.

## Table of Contents

List of Figures .....	vi
List of Tables .....	xiii
Acknowledgements .....	xvi
Chapter 1 - INTRODUCTION .....	1
Cited Literature .....	4
Chapter 2 - PATTERNS OF SPATIO-TEMPORAL DISTRIBUTION, ABUNDANCE, AND DIVERSITY IN A MOSQUITO COMMUNITY FROM THE EASTERN SMOKY HILLS	9
Abstract .....	9
Introduction .....	10
Methods .....	11
Study Site .....	11
Mosquito Surveillance .....	11
Meteorological Data .....	12
Environmental Data .....	13
Statistical Analysis .....	13
Results .....	15
Community Description .....	15
Temporal Dynamics .....	16
Association between Meteorological/Environmental Variables and Mosquito Abundance/Diversity .....	17
Discussion .....	18
Cited Literature .....	23
Figures and Tables .....	29
Chapter 3 - ECOLOGICAL NICHE MODELING OF DISEASE VECTORS IN THE EASTERN SMOKY HILLS OF KANSAS .....	41
Abstract .....	41
Introduction .....	42
Methods .....	44



Study Site .....	44
Disease Vectors and Occurrence Data .....	44
Environmental Data .....	46
Bioclimatic Data .....	48
Ecological Niche Modeling .....	48
Model Validation .....	49
Evaluation: Comparison to Greater Prairie-chicken Nest locations and Plasmodium Incidence .....	50
Results.....	51
Ecological Niche Modeling of Important Vector Species .....	51
Evaluation: Comparison to Greater Prairie-chicken Nest Location and Plasmodium Incidence .....	52
Discussion.....	52
Ecological niche modeling of important vector species .....	54
Comparison to Disease Incidence .....	55
Assumptions and Limitations .....	56
Conclusion .....	57
Cited Literature .....	59
Figures and Tables .....	66
Appendix A - SUPPLEMENTAL FIGURES AND TABLES FOR CHAPTER 2 .....	101
Appendix B - BLOOD COLLECTION AND HAEMOSPORIDIAN SURVEILLANCE METHODS .....	116
Appendix C - ECOLOGICAL NICHE MODELS OF VECTORS SPECIES WITH LOW ABUNDANCES .....	118

## List of Figures

Figure 2.1. Location and landscape composition of the eastern Smoky Hills study site, Cloud County, Kansas. Locations of CDC CO <sub>2</sub> mosquito traps operated during the study period are shown as red points the map. ....	38
Figure 2.2. Seasonal distribution of the dominant mosquito species found in the eastern Smoky Hills study site in 2010. Counts are standardized by the number of traps operated per week. ....	39
Figure 2.3. Seasonal distribution of mosquito species found at lower abundances in the eastern Smoky Hills study site in 2010. Counts are standardized by the number of traps operated per week. ....	40
Figure 3.1. Study site location. Kansas landcover data were developed by the Kanas Applied Remote Sensing Laboratory at University of Kansas, Lawrence. ....	75
Figure 3.2. Elevation map of the eastern Smoky Hills study site, located in Cloud County, Kansas. The elevation data were used to derive the following topographic maps: aspect, slope, curvature, and TWI (Topographic Wetness Index). ....	76
Figure 3.3. Landcover map of the eastern Smoky Hills study site, located in Cloud County, Kansas. The landcover data were used to derive the following distance measures: distance to woodland, distance to water, distance to edge, and distance to road. Distance measures are in meters. ....	77
Figure 3.4. Soil map of the eastern Smoky Hills study site, located in Cloud County, Kansas. The soil data were retrieved from the Soil Geographic Database, I selected the following soil indices: AASHTO (describes the particle-size distribution), drainage class (describes the frequency and duration of wet periods), and hydrologic soil groups (estimates of runoff potential). ....	78
Figure 3.5. Greater Prairie-chicken nest distribution across the eastern Smoky Hill study site, Cloud County, Kansas. The inset provides a detailed view of the nest locations within the landcover map. ....	79
Figure 3.6. Jackknife test of training gain for <i>Culex tarsalis</i> , <i>Aedes sollicitans</i> and <i>Aedes nigromaculis</i> , which are competent vectors of West Nile virus and <i>Plasmodium</i> species (avian malaria disease agents). The environmental predictor variables included (from the	

top): AASHTO, distance to edge, distance to water, distance to woodland, aspect, curvature, TWI (Topographic Wetness Index), mean temperature of the coldest quarter of the year, and mean precipitation of the driest quarter of the year. ....	80
Figure 3.7. Jackknife test of training gain for <i>Culex salinarius</i> , a competent vector of West Nile Virus and <i>Plasmodium</i> species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to water, distance to woodland, aspect, slope, TWI (Topographic Wetness Index), maximum temperature in July, mean temperature of the coldest quarter of the year, and mean precipitation of the driest quarter of the year. ....	81
Figure 3.8. Jackknife test of training gain for <i>Aedes vexans</i> , a competent vector of West Nile Virus and <i>Plasmodium</i> species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to road, distance to water, aspect, TWI (Topographic Wetness Index), maximum temperature of the coldest quarter of the year, mean temperature of May, mean temperature during the sampling season and mean precipitation of the driest quarter of the year. ....	82
Figure 3.9. Jackknife test of training gain for <i>Aedes taeniorhynchus</i> , a competent vector of West Nile Virus and potential vector of <i>Plasmodium</i> species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to road, distance to water, distance to woodland, aspect, TWI (Topographic Wetness Index), mean temperature of April, mean temperature of the coldest quarter of the year, and mean precipitation of the driest quarter of the year. ....	83
Figure 3.10. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Culex tarsalis</i> , <i>Aedes sollicitans</i> , and <i>Aedes nigromaculis</i> in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	84
Figure 3.11. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Culex salinarius</i> in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	85
Figure 3.12. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Aedes vexans</i> in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	86

Figure 3.13. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Aedes taeniorhynchus* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols..... 87

Figure 3.14. Presence-absence predicted distribution of *Culex tarsalis*, *Aedes sollicitans*, and *Aedes nigromaculis* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10. .... 88

Figure 3.15. Presence-absence predicted distribution of *Culex salinarius* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10..... 89

Figure 3.16. Presence-absence predicted distribution of *Aedes vexans* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10..... 90

Figure 3.17. Presence-absence predicted distribution of *Aedes taeniorhynchus* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10. .... 91

Figure 3.18. Predicted distribution of *Culex tarsalis*. This is the most abundant avian malaria vector with primarily ornithophilic feeding preferences during the avian nesting season. The map was created by importing the Maxent cumulative output of this species into Arc Info 10, and overlaid with Greater Prairie-chicken nests. .... 92

Figure 3.19. Predicted distribution of *Culex salinarius*. This is the second most abundant avian malaria vector with primarily ornithophilic feeding preferences during the avian nesting season. The map was created by importing the Maxent cumulative output of this species into Arc Info 10, and overlaid with Greater Prairie-chicken nests. .... 93

Figure 3.20. The predicted avian malaria vector distribution was created by importing the Maxent cumulative outputs of *Culex tarsalis* and *Culex salinarius* into Arc Info 10, and averaging their values via Spatial Analyst tools. This distribution was overlaid with Greater Prairie-chicken nests. .... 94

Figure 3.21. Comparison of the probability of *Culex tarsalis* occurrence at random points and nest locations of Greater Prairie-chicken in the grasslands of the Smoky Hills, Cloud County, Kansas. .... 95

Figure 3.22. Comparison of the probability of *Culex salinarius* occurrence at random points and nest locations of Greater Prairie-chicken in the grasslands of the Smoky Hills, Cloud County, Kansas. .... 96

Figure 3.23. Comparison of the probability of avian malaria vector (combined: *Culex tarsalis* and *Culex salinarius*) occurrence at random points and nest locations of Greater Prairie-chicken in the grasslands of the Smoky Hills, Cloud County, Kansas. .... 97

Figure 3.24. The simulated sampling distribution of the probability of *Culex tarsalis* occurrence at nest locations of uninfected female Greater Prairie-chicken was created with 10,000 sample means (sample size: n=8). The 95% confidence interval is indicated in the dashed-green line. The mean probability of *Culex tarsalis* occurrence at nests of infected females is indicated with the solid red line. .... 98

Figure 3.25. The simulated sampling distribution of the probability of *Culex salinarius* occurrence at nest locations of uninfected female Greater Prairie-chicken was created with 10,000 sample means (sample size: n=8). The 95% confidence interval is indicated in the dashed-green line. The mean probability of *Culex salinarius* occurrence at nests of infected females is indicated with the solid red line. .... 99

Figure 3.26. The simulated sampling distribution of the probability of avian malaria vector (combined: *Culex tarsalis*, *Culex salinarius*) occurrence at nest locations of uninfected female Greater Prairie-chicken was created with 10,000 sample means (sample size: n=8). The 95% confidence interval is indicated in the dashed-green line. The mean probability of avian malaria vectors occurrence at nests of infected females is indicated with the solid red line. .... 100

Figure A.1. Center for Disease Control and Prevention (CDC) miniature light trap baited with dry ice, used for mosquito collections in this study. .... 109

Figure A.2. Human case incident reports of infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, and West Nile Virus encephalitis) in Kansas from 1964 to 2010 (Kansas Department of Health 2012). .... 110

Figure A.3. Temperature and precipitation data from NOAA (National Oceanic and Atmospheric Administration) during the study period. Mean weekly minimum and maximum temperatures (°C) are represented by the lines with square and diamond markers,

respectively. Precipitation (mm) is represented by vertical bars (National Oceanic and Atmospheric Administration 2012). .....	111
Figure A.4. Seasonal abundance (diamond symbols)/diversity (square symbols) (measured using Shannon-Wiener diversity index) of mosquito species in Cloud County, located within the Smoky Hill eco-region in 2010. Counts for abundance were standardized by the number of traps operated. ....	112
Figure A.5. Seasonal abundance of mosquito genera in Cloud County, located within the Smoky Hill eco-region in 2010. Counts were standardized by the number of traps operated. ....	113
Figure A.6. Changes in the mosquito community composition from May - July, in the Smoky Hills of Cloud County, Kansas. ....	114
Figure C.1. Jackknife test of training gain for <i>Culex pipiens</i> , a competent vector of arboviruses (St. Louis and West Nile Virus disease agents) and <i>Plasmodium</i> species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to road, distance to water, distance to woodland, TWI (Topographic Wetness Index), mean temperature of the coldest quarter of the year, minimum temperature during the sampling season, mean annual precipitation, and mean precipitation of the driest quarter of the year. ....	122
Figure C.2. Jackknife test of training gain for <i>Culex restuans</i> , a competent vector of arboviruses (St. Louis and West Nile Virus encephalitis disease agents) and <i>Plasmodium</i> species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to road, distance to water, curvature, slope, TWI (Topographic Wetness Index), annual temperature seasonality, mean temperature of May, mean precipitation of the driest quarter of the year, and mean precipitation of July. ....	123
Figure C.3. Jackknife test of training gain for <i>Aedes dorsalis</i> , a competent vector of arboviruses (Western equine, St. Louis and West Nile Virus encephalitis disease agents) .The environmental predictor variables included (from the top): AASHTO, distance to road, distance to water, annual temperature seasonality, mean temperature of May, mean precipitation of the driest quarter of the year, and mean precipitation of July. ....	124
Figure C.4. Jackknife test of training gain for <i>Aedes stimulans</i> , a competent vector <i>Plasmodium</i> species (avian malaria disease agents).The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to water, aspect, TWI, maximum temperature	

of the coldest quarter of the year, mean temperature during the sample season, mean annual precipitation, and mean precipitation of the driest quarter of the year. ....	125
Figure C.5. Jackknife test of training gain for <i>Anopheles</i> species. The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to water, distance to woodland, aspect, curvature, TWI, minimum temperature of June, mean precipitation of the driest quarter of the year, mean precipitation of July, and annual precipitation seasonality. ....	126
Figure C.6. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Culex pipiens</i> in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	127
Figure C.7. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Culex restuans</i> in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	128
Figure C.8. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Aedes dorsalis</i> in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	129
Figure C.9. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Aedes stimulans</i> in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	130
Figure C.10. Maximum entropy probability distribution (red = high probability, blue = low probability) of <i>Anopheles</i> species in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols. ....	131
Figure C.11. Presence-absence predicted distribution of <i>Culex pipiens</i> based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10. ....	132
Figure C.12. Presence-absence predicted distribution of <i>Culex restuans</i> based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10. ....	133
Figure C.13. Presence-absence predicted distribution <i>Aedes dorsalis</i> based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10. ....	134

Figure C.14. Presence-absence predicted distribution *Aedes stimulans* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10..... 135

Figure C.15. Presence-absence predicted distribution *Anopheles* species based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10..... 136



## List of Tables

Table 2.1. Number and percent of mosquito species collected during the sample season (May - July 2010) in the Smoky Hills of Cloud County, Kansas. ....	29
Table 2.2. Number of mosquito species collected during the sample season (May - July, 2010) at 20 sites in Cloud County of the Smoky Hill eco-region, Kansas. Location of the sites can be found in Figure 2.1.....	30
Table 2.3. Mosquito taxa correlation according to Pearson’s correlation matrix, indicating a linear association between occurrence records of taxa. ....	31
Table 2.4. Candidate models used to fit the dependent variable, mosquito abundance, to independent meteorological variables.....	32
Table 2.5. Multiple linear regression results of the top performing models between the dependent variable, mosquito abundance, to the independent meteorological variables.....	33
Table 2.6. Cumulative AICc weights for all 6 meteorological variables hypothesized to influence mosquito abundance in the Smoky Hills of Cloud County, Kansas, 2010. ....	34
Table 2.7. Candidate models used to fit the dependent variable, mosquito abundance, to independent environmental variables.....	35
Table 2.8. Multiple linear regression results of the top performing models between the dependent variable, mosquito abundance, to the independent environmental variables.....	36
Table 2.9. Cumulative AICc weights for all 7 environmental variables hypothesized to influence mosquito abundance in the Smoky Hills of Cloud County, Kansas, 2010. ....	37
Table 3.1. Most abundant vector species collected during the sample season (May - July, 2010) at 20 sites in in the grasslands of the eastern Smoky Hill eco-region, Kansas. ....	66
Table 3.2. Occurrence records of mosquito species collected during the sample season (May – July, 2010) at 20 sites in the grasslands of the eastern Smoky Hill eco-region, Kansas. ....	67
Table 3.3. Description of parameters used to construct ecological niche models of vectors species with the grasslands of Cloud County, Kansas. ....	68
Table 3.4. Highly correlated variables ( $r \geq 0.90$ ). I generated 100 random points across the study site, extracted data from the bioclimatic variables and performed a Pearson’s correlation analysis.....	69

Table 3.5. Variable contributions and permutations of ecological niche models developed for vector species in the grassland of the Smoky Hills, Cloud County, Kansas. ....	70
Table 3.6. Training gain without and with predictor variables of ecological niche models developed for vector species in the grassland of the Smoky Hills, Cloud County, Kansas. ....	71
Table 3.7. Jackknife tests of distribution models (LTP, Lowest Presence Threshold) for the six most abundant disease vectors in the Smoky Hills of Cloud County, Kansas .....	72
Table 3.8. Vector probability of <i>Culex tarsalis</i> , <i>Culex salinarius</i> , and cumulative avian malaria vectors associated with Greater Prairie-chicken nests of females that tested positive for <i>Plasmodium</i> species. ....	73
Table 3.9. Results of the 2-sample t-tests, to assess the differences in the probability of vector occurrence at nest locations versus potentially available grassland habitat.....	74
Table A.1. Mosquito taxa encountered in the Smoky Hill eco-region, including their host feeding preferences and susceptibility to zoonotic pathogens. Feeding preferences, susceptibility to disease agents of encephalitides and role as enzootic/bridge vector reported in Turell <i>et al.</i> 2005. Susceptibility to disease agents of avian malaria ( <i>Plasmodium</i> species) was reported in Valkiunas 2005, unless otherwise noted.....	102
Table A.2. Average weekly meteorological variables (precipitation, wind speed, maximum temperature, and minimum temperature) retrieved from National Oceanic and Atmospheric Administration (NOAA) during the sample season, and mosquito abundance/diversity ( $H'$ ). ....	103
Table A.3. Site specific environmental variables (elevation, curvature, aspect, TWI, distance to agriculture, distance to woodland, distance to water, distance to road and distance to edge) of twenty sample locations within a radius of 30 m of mosquito traps and mosquito abundance/diversity ( $H'$ ) within the Smoky Hill eco-region using ArcInfo 10 (Environmental Systems Research Institute, Redlands, CA). Elevation and distance measures are in meters. ....	104
Table A.4. Pearson's correlation coefficients between environmental variables. ....	105
Table A.5. Pearson's correlation coefficients between meteorological variables. ....	106
Table A.6. Candidate models used to fit the dependent variable, mosquito diversity, to independent meteorological variables.....	107

Table A.7. Candidate models used to fit the dependent variable, mosquito diversity, to independent environmental variables.....	108
Table B.1. Primer pairs used for the amplification of haemosporidian RNA and DNA. ....	117
Table C.1. Variable contributions and permutations of ecological niche models developed for low abundance vector species in the grassland of the Smoky Hills, Cloud County, Kansas. ....	119
Table C.2. Training gain without and with predictor variables of ecological niche models developed for low abundance vector species in the grassland of the Smoky Hills, Cloud County, Kansas. ....	120
Table C.3. Jackknife tests of distribution models (LTP, Lowest Presence Threshold) for low abundance vector species ( <i>Culex pipiens</i> , <i>Culex restuans</i> , <i>Aedes dorsalis</i> , <i>Aedes stimulans</i> , and <i>Anopheles</i> species) in the Smoky Hills of Cloud County, Kansas.....	121

## **Acknowledgements**

I wish to thank my adviser Dr. Samantha Wisely for her guidance, support, and encouragement. Dr. Wisely, I appreciate your calm, free-spirited nature, and your confidence to let me embark on a research project that took me out to the dirt roads of the Smoky Hills. “Every mile a memory”.

I would also like to thank my committee members Drs. Kirstin Michel and Ludek Zurek for their input and encouraging words. Thank you, Dr. Brett Sandercock for being an excellent professor, your compassion and contributions to my professional development. Thank you, to the many professors and students I have had the privilege of working with while at Kansas State University; especially, Cody Simmons, Paige Berry, and Rachel Pigg for sharing my love for country music and tolerating my sense of humor. To Lyla Hunt for your kind nature, and pulling me out of the mud; without you Chapter 3 would not have been possible. Thank you, Andy Gregory for your genuine interest in my research and helping with many aspects of this research.

I would also like to thank Kansas State University and the Division of Biology for their support of this research; the National Wind Coordinating Collaborative, Kansas IDeA Network of Biomedical Research Excellence, and the Johnson Center for Basic Cancer Research for funding for this research.

I wish to thank my parents, Ingeborg and Franz Ganser, for their encouragement. Lastly, I thank my husband Rod, I will never be more proud of myself than you are of me.

# Chapter 1 - INTRODUCTION

Monitoring vector communities has been an integral part of disease surveillance and control programs (Center for Disease Control and Prevention 1994). However, merely a century ago the role of mosquitoes as disease agents in the spread of infectious diseases could not be fathomed (Spielman *et al.* 2001). Discoveries of the causative disease agents/vectors of malaria by Charles Laveran and Sir Ronald Ross, as well as Patrick Manson on filarial encephalitis, and the Yellow Fever Commission largely contributed to today's awareness of the importance of dipteran vectors. The Yellow Fever Commission was formed to investigate the causative agents of yellow fever of deployed U.S. soldiers in Cuba, which resulted in one of the earliest vector control programs. Today, mosquito control and eradication programs have eliminated vector-borne diseases (yellow fever, filarial encephalitis, malaria) from most developed countries (World Health Organization 2001).

Despite the diversity of Diptera (100,000 – 120,000 species; Arnett 1985, Evenhuis 1989, Southwood 1978, Gaston 1991) only a few of today's 3,500 described mosquito species are implicated in the spread of infectious diseases (Foley *et al.* 2010, Reither 2001). Important properties of vector species in the spread of disease are: 1) survival and reproduction rate, 2) activity (i.e. biting rate), and 3) rate of development and reproduction of pathogens within the vector itself (Kovats *et al.* 2001). *Anopheles gambiae* and *Aedes aegypti* are amongst today's most important vectors of emerging infectious diseases. The arrival of *Anopheles gambiae* to northeastern Brazil in 1930 triggered a malaria epidemic, which resulted in an estimated 16,000 deaths before the vector could be eradicated (Coggeshall 1944, Tatem *et al.* 2006a). Similarly, the 19<sup>th</sup> and early 20<sup>th</sup> century epidemics of yellow fever were facilitated by the introduction of *Aedes aegypti* to North America (Bryant *et al.* 2007, Rogers *et al.* 2006, Tatem *et al.* 2006b).

Nearly 30 % of the infectious disease events can be attributed to vector-borne pathogens, whose transmission is strongly influenced by the abundance and distribution of vector species (Gratz 1999). Rigorous surveillance programs are an essential component of effective vector control, and suppression of infectious disease spread (Center for Disease Control and Prevention 2011). In the United States, this role is taken on by local health departments and state health agencies. Agencies, particularly the Center for Disease Control and Prevention, coordinate surveillance efforts of infectious disease vectors on a national level. In recent years, the most

rigorous national mosquito surveillance program was a result of the 1999 emergence of West Nile Virus, which led to budget allocations towards vector control programs and disease surveillance. Since then, annual 'West Nile Virus Activity Reports' have been published indicating positive mosquito pools (involving 64 species) across the United States (Center for Disease Control and Prevention 2011, United States Geological Survey 2012). Similar national surveillance and control programs have been put in place for: other arboviral encephalitides (Eastern Equine encephalitis, Western Equine encephalitis, St. Louis encephalitis), and Dengue hemorrhagic fever (Center for Disease Control and Prevention 2008).

Disease transmission is a dynamic process that depends on: host and vector ecology, pathogen properties, and landscape features. In the case of West Nile Virus encephalitis, enzootic transmission cycles between mosquitoes and avian species are responsible for the amplification of the virus in the environment (Turell *et al.* 2001); when West Nile Virus enzootic activity is most intense (Lothrop *et al.* 2008) it results in increased spill-over events to humans. Thus, understanding the infectious cycles of vector-borne pathogens in wildlife can lead to a better understanding of disease in humans. Indeed, the majority of infectious disease events are caused by pathogens with wildlife origin and/or exhibit enzootic cycles (Brown 2004, Jones *et al.* 2008, Taylor *et al.* 2001).

In addition to the threat to public health, vector-borne pathogens can also pose a significant risk to wildlife species. Vector-borne pathogens are implicated in the decline of wildlife species worldwide, and may lead to extinction events when virulent pathogens encounter naïve host populations (Daszak 2000, Daszak *et al.* 2001, Dobson *et al.* 2001, Marra *et al.* 2004, Smith *et al.* 2009). The introduction of avian malaria to the Hawaiian Islands has been implicated in the extinction of the endemic avifauna (van Riper *et al.* 1986, Warner 1968) and continues to be a threat to the highly susceptible Laysan Finch (van Riper *et al.* 1986) and honey creepers (Depanidinae; Atkinson *et al.* 2000). Similarly, the introduction of West Nile Virus in Europe and North America resulted in high mortality events in domestic birds (Europe: domestic geese; North America: American Crow and 22 other bird species; Komar 2003).

Infectious disease threat is of particular concern in the Great Plains, because this region represents the largest North American grassland habitat (Samson *et al.* 2004), and is among the most speciose region for grassland nesting birds (United States Department of Agriculture 1999). The transmission of infectious diseases in the grassland bird community is likely to occur during

the nesting season, and has the potential to exacerbate the decline of resident birds (West Nile Virus in Greater Sage-grouse, *Centrocercus urophasianus*, Naugle *et al.* 2004; avian malaria in Greater Sage-grouse, Boyce 1990), and summer breeding migrants. During the breeding season (early summer) local residents, Greater Prairie-chicken (*Tympanuchus cupido*), Eastern Meadowlark (*Sturnella magna*), and Western Meadowlark (*Sturnella neglecta*) nest sympatrically with summer breeding migrants, Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus savannarum*), and Upland Sandpiper (*Bartramia longicauda*) in the Kansas grasslands. Resident species have been experiencing declines throughout their range due to the conversion of grasslands and changes in land management practices. As a result, Greater Prairie-chicken have been listed as ‘vulnerable’ (Schroeder *et al.* 1993), and although Eastern Meadowlark and Western Meadowlark are considered to be of ‘least concern’, their breeding populations have declined by as much as 70% since the 1970 (Lanyon 1995). Comparable effects due to the loss of continuous grasslands have been observed in summer breeding migrant species; Grasshopper Sparrows have decline throughout their range (Vickery 1996), Upland Sandpipers continue to experience alarming population declines (Houston *et al.* 2001), and Dickcissel after drastic population reductions between 1966 – 1978 have finally stabilized at lower numbers (Temple 2002).

The grasslands of North America represent a unique situation in which public health and wildlife conservation concerns intertwine. The grasslands serve as interface for the disease transmission within the enzootic mosquito-avian cycle (involving grassland bird species), and can pose a significant risk to livestock and public health when enzootic activity is most intense (Petersen *et al.* 2008). In Kansas, infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis) cases in livestock and humans are preceded by epidemics in the local avian fauna. In 2002, there were 794 reports of equine and 22 reports of human West Nile Virus encephalitis across the state (Kansas Department of Health and Environment 2002). The following year, Kansas experienced a sharp increase in human West Nile Virus encephalitis cases (n=91).

Accurate information on the spatio-temporal dynamics of mosquito communities in a region is necessary for the development of efficient control measures of infectious diseases (Alten *et al.* 2002), because vector demography is closely associated with biophysical variables. Variations in spatial abundance and diversity of mosquito communities have been observed as a

result of local topography and vegetation (Johnson *et al.* 2008, Lothrop *et al.* 2001, Zyzak *et al.* 2002), which define habitat and resources for mosquitoes. For instance, fine-scale topographic depression may provide ephemeral breeding sites under suitable meteorological conditions (Fisher *et al.* 2004). In addition, temperature and precipitation are responsible for the seasonal dynamics of mosquito communities (Jones *et al.* 2004). Consequently, disease incidence of pathogens occurs in well-defined seasonal periods that are associated with fluctuations in vector abundances. In the Midwest, the onset of West Nile Virus has been linked to the seasonal shift in mosquito populations of *Culex pipiens* and *Culex restuans* (Westcott *et al.* 2011). However, very little is published on the mosquito community dynamics in grassland communities, where public health and wildlife conservation are both affected by these vector dynamics (Meade *et al.* 2000).

The goal of this study was to investigate the pattern of abundance and distribution of vector mosquito species in the grasslands of the eastern Smoky Hills, its implication on disease transmission to humans, and to sensitive grassland bird species. My thesis is divided into three chapters. Here, I review the history of vector control as it relates to emerging infectious diseases and its importance for public health, and wildlife species of conservation concern. In chapter two, I examine the spatio-temporal distribution of potential vector species of arboviruses and *Plasmodium* species, as well as the underlying meteorological and environmental variables that give rise to peaks in vector abundance. In chapter three, I utilized ecological niche modeling to determine the potential distribution of the most abundant vectors of these disease agents, assess the probability of avian malaria vector occurrence (*Culex* species) at Greater Prairie-chicken nest locations versus potentially available grassland habitat, and finally determine if the probability of vector occurrence relates to disease agent incidence in nesting females.

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# **Chapter 2 - PATTERNS OF SPATIO-TEMPORAL DISTRIBUTION, ABUNDANCE, AND DIVERSITY IN A MOSQUITO COMMUNITY FROM THE EASTERN SMOKY HILLS**

## **Abstract**

Nearly 30% of the emerging infectious disease events are caused by vector-borne pathogens with wildlife origins, posing a risk for public health, livestock and wildlife species of conservation concern. Effective control measures for infectious diseases can only be developed if habitat associations are quantified, and spatio-temporal dynamics of mosquito vector communities are examined. In recent years, Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis and avian malaria have been not only a concern for public health but also a conservation concern, specifically the conservation of grassland nesting birds. Although the central Great Plains is the most specious region for grassland nesting birds, their role in the enzootic (primary) amplification cycle of infectious diseases may lead to further population depressions, and could potentially result in spill-over events to humans and livestock. Previous studies have reported the occurrence and distribution of mosquito vectors in Kansas but little is known about infectious disease vectors in a grassland context. Combining mosquito surveillance data with meteorological and environmental variables, I examined the underlying causes of spatio-temporal abundance patterns of vector species within the grasslands of the eastern Smoky Hills. Using multiple linear regression I found evidence that mosquito abundances are explained by meteorological and environmental variables. Temporal dynamics in mosquito abundances were explained by maximum and minimum temperature indices, both with an adjusted  $R^2$  of 0.73. Spatial dynamics in mosquito abundances were best explained by a model containing the following environmental variables (adjusted  $R^2$  of 0.37): curvature, TWI (Topographic Wetness Index), distance to woodland, and distance to road. My research results address the underlying causes of the spatio-temporal dynamics of mosquito species across a grassland ecosystem, and add to the existing survey of mosquito communities in the central Great Plains, especially Kansas.

## Introduction

Monitoring vector communities has been an integral part of disease surveillance and control programs (Center for Disease Control and Prevention 2011). Nearly 30% of the emerging infectious disease events are caused by vector-borne pathogens with wildlife origins (Jones *et al.* 2008), which pose a risk for public health, livestock and wildlife species of conservation concern. Effective control measures for emerging infectious diseases can only be developed if habitat associations are quantified and spatio-temporal distributions of vector species are examined, because mosquito vector demography is closely associated with biophysical variables. For instance, seasonal rainfalls provide ephemeral breeding sites (Norris 2004) and availability of breeding sites is closely tied to mosquito abundance. In addition, elevated temperatures during summer lead to reduced developmental time for pupal/larval life stages, increased mosquito abundances, and shortened extrinsic incubation periods of pathogens they carry, thus creating conditions for rapid disease emergence.

In recent years multiple mosquito-borne infectious diseases have been of public health and conservation concern in the central Great Plains, including: Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis (Kansas Department of Health and Environment 2012) and avian malaria. In grassland nesting birds, infectious encephalitides and avian malaria exhibit an enzootic avian cycle, which has been shown to result in large scale population declines (West Nile Virus in Greater Sage-grouse, *Centrocercus urophasianus*, Naugle *et al.* 2004), and compromised fitness (avian malaria in Greater Sage-grouse, Boyce 1990). Grassland nesting birds, particularly in the central Great Plains are of conservation concern due to marked population reductions (Brennan *et al.* 2005, Jones *et al.* 1997, Knopf 1994). Infectious encephalitides also exhibit a zoonotic cycle involving human and livestock hosts, and the emergence in humans and livestock is often preceded by avian epidemics, which serve as mechanisms of amplification of the viruses in the environment (Burkett-Cedena *et al.* 2011, Turell *et al.* 2001).

Although the occurrence and distribution of mosquito-borne infectious diseases (Kansas Department of Health and Environment 2012) and their vectors (DeMoss Hill 1939, Edman *et al.* 1964, Janovy 1966, Lungstrom 1954, Lungstrom *et al.* 1961) has been reported for multiple counties in Kansas, little is known about infectious disease vectors in a grassland context. Grasslands along with agricultural fields represent one of the world's largest biomes (Foley *et al.*

2005), and provide a unique interface for the transmission from the enzootic mosquito-avian cycle (involving grassland nesting birds) to mammalian spill-over hosts such as humans and livestock.

This study focused on the seasonal distribution of mosquitoes in the grassland of the Smoky Hills, Cloud County, Kansas. The objectives were to, 1) examine the spatio-temporal distribution of potential vectors of infectious encephalitides, and avian malaria, and 2) determine the underlying meteorological and environmental variables that give rise to peaks in vector abundance.

## **Methods**

### ***Study Site***

The study site was located in north-central Kansas, in the Smoky Hills eco-region of Cloud County, Kansas (Fig. 2.1.). The Smoky Hills are tillable, with native prairies characterized by moderate to high fragmentation, row crop agriculture, and low intensity cattle stocking. The study area encompassed 283 km<sup>2</sup> of fragmented prairie landscape; consisting of 73% grassland, 25% cropland, and a road density of 1.4 km/km<sup>2</sup>. Cultivated croplands included wheat, sorghum, soybeans, and corn. The climate was temperate, with moderate rainfall and annual precipitation during the sample year of 883 mm, of which nearly half could be attributed to precipitation from May through July 2010.

Since 2001 there have been two outbreaks of mosquito-borne infectious disease within 10 counties surrounding the study site (Appendix A: Fig. A.2.; Kansas Department of Health and Environment 2012). Human cases of infectious encephalitides occurred both in 2003 and 2008. The last human incident report in Cloud County occurred in 2003 (West Nile Virus encephalitis, Kansas Department of Health and Environment 2003).

### ***Mosquito Surveillance***

Twenty sites were randomly selected within grassland habitat (Fig 2.1). I chose to sample only grasslands to better understand the vector ecology in this habitat. Adult mosquitoes were collected in Center for Disease Control and Prevention (CDC) miniature light traps (J.W. Hock, Gainesville, FL) weekly from May through July 2010. These light traps are considered the

industry standard for collecting host-seeking mosquitoes (Meeraus 2008). Light traps were baited with 1 kg dry ice, powered by 6-V lantern batteries and hung 1.5 m above the ground. The traps were deployed before dusk and retrieved the following morning (Appendix A: Fig. A.1.).

Collected mosquitoes were transported to the laboratory in ice chests filled with dry ice and subsequently stored at -20 °C until identification. Adults were identified to species level using dichotomous keys (Pratt and Stojanovich 1961). Field collected specimens of *Culex* species were often difficult to differentiate due to missing morphological characters. Differentiation between *Culex restuans* and *Culex pipiens* was achieved by the presence of two small white-scaled rounds spots on the scutum (80% success rate, Apperson *et al.* 2002). Mosquito abundance was estimated by standardizing mosquito counts by the number of traps operated weekly or among locations. The co-occurrence between mosquito taxa was determined using a Pearson's correlation matrix. Correlation coefficients greater than 0.5 may imply habitat similarities or temporal coincidence between mosquito taxa. Species diversity was estimated using the Shannon index, designated  $H'$  (Krebs, 1989):

$$H' = - \sum_{i=1}^R p_i \log p_i$$

where  $p_i$  is the proportion of individuals belonging to the  $i^{\text{th}}$  species within the community of interest.

### ***Meteorological Data***

Daily weather data, including precipitation, wind speed, minimum and maximum temperatures were recorded by the National Oceanic and Atmospheric Administration (NOAA) at Concordia Blosser Municipal Airport (N 39°32.949' W 097.39.133'), 12 km north of the study site. I calculated mean weekly precipitation, temperature (minimum, maximum), wind speed, and accounted for lagged responses to precipitation and temperature by including conditions one, and two weeks prior from May 5<sup>th</sup> (two weeks before sample season) to August 2<sup>nd</sup>, 2010 (Appendix A: Table A.3., Fig. A.3.).



## ***Environmental Data***

I used Arc Info 10 (Environmental Systems Research Institute, Radlands, CA) for geospatial analysis and data extraction. All data sets were acquired from Kansas Geospatial Community Commons ([www.kansasgis.org](http://www.kansasgis.org)). Landcover analysis was conducted using the 30 m resolution of the 2005 landcover map of Kansas (Kansas Applied Remote Sensing Program 2005; Whistler *et al.* 2006) depicting the following landcover classes: urban industrial/commercial, urban residential, urban open land, urban woodland, urban water, cropland, grassland, CRP (Conservation Reserve Program), woodland and water. I used the 1999 National Elevation Dataset (U.S. Geological Survey, EROS Data Center) and roadway dataset that combined the 2006 Kansas State, and Non-State Road System dataset (Kansas Department of Transportation: Bureau of Transportation Planning). Each landcover data set was aggregated to 30 m grain size prior to geospatial analysis. Using this dataset, we estimated five variables at each mosquito trapping location: distance to agriculture, distance to woodland, distance to water, distance to road, and distance to edge.

Characteristics used to evaluate the area surrounding the trapping locations were: curvature, and topographic wetness index (TWI), which were analyzed using the 1999 National Elevation Dataset and Spatial Analyst tools. TWI describes the predicted soil moisture pattern, and is calculated as the natural logarithm of the ratio between local upslope contributing area, and slope (Pathak, 2010). These landscape characteristics were evaluated at the attractiveness range of CO<sub>2</sub> baited mosquito traps, by applying a 30 m radius buffer to each trapping location. The attractiveness range of CDC CO<sub>2</sub> baited light traps is somewhat ambiguous, however it has been shown that CO<sub>2</sub> attracts mosquitoes from distances of <30 m, and is species dependent (Service, 1993). Thus, a 30 m buffer was selected to encompass mosquito habitat around trapping locations.

## ***Statistical Analysis***

Several steps were taken to avoid overparameterizing biophysical models of mosquito abundance and diversity (Appendix A: Table A.4., A.5.). Meteorological and environmental variables were examined for colinearity using Pearson's correlation matrices and redundant or highly correlated variables ( $r > 0.90$ ) were excluded from further analyses. Prior to model

construction, variables were tested for normality using Kolmogorov-Smirnov tests. Relative abundance, and TWI showed significant departures from normality, and were arcsin and  $\log_{10}$  transformed, respectively.

To investigate the relationship of mosquito abundance/diversity with meteorological /environmental variables, I performed multiple linear regression analysis to fit the dependent variable, mosquito abundance/diversity, to the independent meteorological/environmental variables. The effects of meteorological variables (independent variables) on mosquito abundance/diversity (dependent variables) were examined using weekly averages of precipitation, wind speed, maximum temperature and minimum temperature. To account for lagged responses to precipitation, and temperature, conditions one and two weeks prior were included. I sampled mosquitoes weekly for a total of 9 weeks. Each week, mosquito abundance/diversity was averaged over the 20 sampling locations. Due to the small sample size I chose not to split data for cross-validation. The full models included 6 weather variables, and an intercept for a total of 7 parameters. Candidate models for mosquito abundance/diversity included all possible combination of weather variables ( $2^6 = 64$  models). All 6 weather variables had been previously shown to be linked to mosquito abundance/diversity; hence I chose to include each possible combination of these variables. Furthermore, I included combinations of binary interaction terms for all 6 weather variables.

The effects of environmental variables (independent variables) on mosquito abundance/diversity (dependent variables) were examined using curvature, TWI, distance to agriculture, distance to water, distance to woodland, distance to road, and distance to edge. I sampled 20 locations across my study area, and averaged the abundance and diversity of mosquitoes over time (the 9 sample occasions). Due to the small sample size I chose not to split data for cross-validation. The full models included 7 environmental variables, and an intercept for a total of 8 parameters. Candidate models included all possible combinations of environmental variables ( $2^7 = 128$  models). I also included combinations of binary interaction terms for all 7 environmental variables.

I used Akaike's Information Criterion with small sample size bias adjustment (AICc) to select the most parsimonious model(s) (Burnham and Anderson 1998).

$$AICc = AIC + \frac{2k(k + 1)}{N - k - 1}$$

Where  $k$  is the number of model parameters and  $N$  is the number of sample points, AICc has been shown to be superior to AIC. All models within 2 units of the minimum AICc value have substantial support, and should be considered for inferences (Burnham and Anderson 1998).

To determine biologically significant variables I calculated the cumulative AICc weights (Flanders-Wanner *et al.* 2004) of  $2^n$  models created for the analysis of mosquito abundance versus meteorological/environmental variables. The cumulative weight of a variable is calculated by summing up the AICc model weights of model ( $2^n$ ) containing that variable.

$$w_i = \frac{\exp(-0.5*\Delta_i)}{\sum_{r=1}^R \exp(-0.5*\Delta_r)}$$

Where  $w_i$  are Akaike weights for model  $i$ ,  $\Delta_i$  is the difference between best fitting model, and model  $i$ . The denominator is the sum of the relative likelihoods for all candidate models.

## Results

### *Community Description*

The data collected in this study provide a description of the grassland mosquito community in the Smoky Hills eco-system in Cloud County, Kansas. Mosquito samples were collected for 9 weeks (once per week) at 20 sample sites from May through July (Table 2.1, 2.2.). I collected 12,861 individual mosquitoes, of which 11,223 (87.3%) could be identified to species level. The remaining 12.7% could not be identified to due missing or damaged morphological characteristics of field collected samples. The mosquitoes captured in this study belonged to three genera: *Aedes*, *Culex* and *Anopheles*, representing 11 taxa (Table 2.1). *Aedes* was the most abundant genus, comprising 87.6% of the total collection, followed by *Culex* (12.1%), and *Anopheles* (0.3%). Of all taxa, *Aedes sollicitans* was the most abundant species

collected during this study, at 49.7%. *Aedes nigromaculis* (21.5%) was also very abundant throughout the study. Other common species included *Aedes vexans* (9.0%), *Culex tarsalis* (7.4%), *Aedes taeniorhynchus* (6.6%), and *Culex salinarius* (3.6%). Species encountered at lower abundances were *Culex pipiens*, *Culex restuans*, *Aedes dorsalis*, *Aedes stimulans*, and *Anopheles* species. Of the previously 35 (DeMoss Hill 1939, Edman *et al.* 1964, Janovy 1966, Lungstrom 1954, Lungstrom *et al.* 1961) mosquito taxa reported in Kansas, 9 were collected in this study. My collections include two previously unreported species in Kansas: *Aedes stimulans* and *Aedes taeniorhynchus*.

Species abundances were used to calculate a Pearson's correlation matrix. This analysis provided a measure of co-occurrence between mosquito species. Twenty pairs of mosquito taxa with a correlation coefficient greater than 0.5 co-occurred (Table 2.3.). The following pairs of mosquito taxa exhibited correlations greater than 0.9: *Culex restuans/Aedes stimulans* ( $r=0.93$ ), *Culex restuans/Aedes vexans* ( $r=0.93$ ), *Aedes dorsalis/Aedes vexans* ( $r=0.93$ ), and *Culex salinarius/Aedes taeniorhynchus* ( $r=0.95$ ).

### ***Temporal Dynamics***

Temporal analysis revealed similar population fluctuation in all 3 genera. Standardized mosquito abundances indicated early season peaks in May and June followed by a decline in the last quarter of June and resurgence during July (Fig. 2.2., 2.3., Appendix A: Fig. A.5.). *Aedes* species exhibited small peaks in abundance mid-June, and reached their highest numbers in July, with the exception of *Aedes vexans*. *Aedes vexans* reached peak abundances in mid-June, and exhibited a minor peak in July. *Aedes sollicitans* was the most abundant species from June through the end of July, and exhibited a small peak in abundance in the middle of June, and achieved a major peak in the middle of July. *Aedes nigromaculis*, the second most abundant species, was similar to *Aedes sollicitans*; this species reached a small peak in the middle of June, and a maximum in July. *Aedes taeniorhynchus* abundances were low throughout May, and June. In July population numbers increased, reached maximum abundances in the third quarter of July, and remained stable until the end of the sample season. *Culex* species were encountered at lower abundances than *Aedes* species: however, *Culex tarsalis* was the most abundant species collected in May. Abundances of *Culex tarsalis* decreased in June and collection numbers remained small

throughout the sample period. *Culex salinarius* abundances remained low until the end of June and increased until July.

### ***Association between Meteorological/Environmental Variables and Mosquito Abundance/Diversity***

Multiple linear regression models testing the association between meteorological variables, and mosquito abundance/diversity, were reduced from 10 to 6 weather variables, due to the high correlation between sample week temperature indices, and lagged temperature indices (a priori significant threshold,  $r > 0.80$ ; Appendix A: Table A.5.). The analysis between meteorological variables, and mosquito abundance produced 2 plausible models based on their AICc values (Table 2.4., 2.5.). None of the most plausible models contained precipitation, and wind variables. Temperature variables explained the temporal variation in observed mosquito abundances. The two best-fit models had an adjusted  $R^2$  of 0.73 and included one temperature variable. Minimum temperature ( $t=4.71$ ,  $p=0.00$ ), and maximum temperature ( $t=4.47$ ,  $p=0.00$ ) were positively correlated with mosquito abundance. The cumulative AICc weights analysis indicated that minimum and maximum temperature were biologically significant variables, accounting for 69%, and 30% of the AICc weights, respectively (Table 2.6.). Contrary to the abundance data, I found no best supported model with mosquito diversity data (Appendix A: Table A.6.). None of the meteorological variables used in this study explained the spatial variation in observed mosquito diversity.

Multiple linear regression models testing the association between environmental variables, and mosquito abundance/diversity, were constructed with the full set of environmental variables ( $n=7$ ). The Pearson's correlation matrix did not indicate significant correlation between these variables (a priori significant threshold,  $r > 0.80$ ; Appendix A: Table A.4.). All plausible models contained TWI but excluded the following distance variables: distance to agriculture, distance to water, distance to edge habitat. The top model had an adjusted  $R^2$  of 0.37, and included the following variables: TWI, distance to road, distance to woodland, and curvature. TWI, and distance to road were significantly correlated with mosquito abundance; TWI, and distance to road showed a positive ( $t=3.51$ ,  $p=0.00$ ), and negative ( $t=-2.28$ ,  $p=0.04$ ) correlation, respectively. Distance to woodland, and curvature showed a weak correlation with mosquito

abundance. The cumulative AICc weights analysis indicated that TWI, distance to road, distance to woodland, and curvature were biologically significant variables, accounting for 81%, 52%, 45% and 41% of the AICc weights, respectively (Table 2.9.). Unlike the abundance data, I found no best supported model for the association between environmental variables and mosquito diversity (Appendix A: Fig. A.7.). None of the environmental variables used in this study explained the spatial variation in observed mosquito diversity.

## Discussion

The most recent literature on mosquito surveillance in Kansas was published between the 1940s and 1960s (DeMoss Hill 1939, Edman *et al.* 1964, Janovy 1966, Lungstrom 1954, Lungstrom *et al.* 1961), and documented 35 mosquito taxa. Mosquito community surveillance was conducted in south-eastern Kansas (Allen, Anderson, Bourbon and Neosho Counties, Lungstrom *et al.* 1964), Riley County (DeMoss Hill 1939, Edman *et al.* 1964), Barton County (Cheyenne Bottoms, Janovy 1966). These studies were conducted at a broader spatial scale (regional scale) than the present study (local scale). Hence, of the previously documented taxa, only a subset (9 species) was encountered in the study area, along with two previously unreported species in Kansas: *Aedes stimulans* and *Aedes taeniorhynchus*. *Aedes stimulans* occurs predominately in the north-eastern United States, and eastern Kansas is considered to be at the western range boundary of this species (Crans 2010). This species is likely an uncommon but regular part of the mosquito community in northeast Kansas. *Aedes taeniorhynchus* is associated with coastal plains adjacent to the Atlantic and Gulf coasts (Center for Disease Control and Prevention 2012, Harrison *et al.* 1973). However, this species has been shown to occur in inland areas rich in fossil fuels and has first been reported in the central Great Plains in 1973 (Oklahoma, Harrison *et al.* 1973). Collectively, the mosquitoes I encountered in the grasslands of the Smoky Hills in Cloud County, Kansas, serve as vectors for a variety of infectious diseases of public health and/or conservation interest, including: Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis, and avian malaria.

The variation of overall mosquito abundance showed a clear seasonal pattern that was explained by meteorological data. Multiple linear regression suggested a positive association with temperature indices (minimum/maximum temperature). Increased environmental

temperatures likely drive mosquito abundance, by increasing the metabolic rates, reproductive output, and increased host seeking of these vectors (Shone *et al.* 2006), which has previously been shown in laboratory, and field studies (Chuang *et al.* 2011).

In addition to the seasonal pattern observed in this study, I found indication for spatial variation of mosquito abundances across sample sites. Among the environmental variables considered, only TWI showed a strong positive association with mosquito abundances across sites. TWI, is a wetness index that estimates a surface's potential to accumulate water based on the ratio between upslope contributing area, and slope. Hence, the positive correlation with mosquito abundance may be due to the increased availability of larval habitats in areas with a higher TWI. This index has been widely used in hydrological studies, and has previously been shown to predict spatial variation in mosquito communities (Clennon *et al.* 2010, Cohen *et al.* 2008, Shaman *et al.* 2006); hence it is an important variable to include in future habitat models.

In order to be a functional vector of infectious diseases, capable of transmitting a pathogen from one host to the next, a mosquito vector must feed readily on multiple vertebrate hosts, be capable of acquiring the pathogen, and be abundant in the environment (Bates 1949, Russell 1959). On the study site, the following mosquito species fulfill the requirements of functional disease vectors: *Aedes sollicitans*, *Aedes nigromaculis*, *Aedes vexans*, *Culex tarsalis*, *Aedes taeniorhynchus*, and *Culex salinarius*. These taxa accounted for 98% of the collected specimens. Other, more rare taxa which I encountered during this research accounted for less than 2% of the collected specimens. Due to their low abundances, *Culex pipiens*, *Aedes stimulans*, *Culex restuans* and *Aedes dorsalis* were not considered functional disease vectors in my study site.

It has been suggested that vector species play specific roles in transmission of disease. Enzootic vectors (*Culex* species; Hammer *et al.* 2008, Kilpatrick *et al.* 2005, Marra *et al.* 2004, Turell *et al.* 2005) are responsible for amplification of pathogens in birds, due to their primarily ornithophilic, or bird-biting, feeding preferences. Instead, mosquito taxa, that consume a larger portion of their blood meals from mammals (*Aedes* species; Kilpatrick *et al.* 2005, Turell *et al.* 2005) can be considered bridge vectors. However, it has been suggested that *Culex* species (*Culex tarsalis*, *Culex salinarius*, *Culex pipiens*, *Culex restuans*) serve as both, enzootic and epidemic, (e.g. bridge) vectors (Apperson *et al.* 2004, Kilpatrick *et al.* 2005, Turell *et al.* 2005). This has been attributed to seasonal shifts in feeding preferences; in early summer blood meals are

primarily acquired from avian species during their nesting season, as the season progresses, and nesting birds become less available, a shift towards mammalian feeding is observed (Tempelis *et al.* 1975).

The most abundant mosquito collected during the sample season was *Aedes sollicitans*, the eastern salt marsh mosquito, making up nearly 50% of the collected specimens. *Aedes sollicitans*, a known vector of West Nile Virus encephalitis and avian malaria is typically found in moist substrate or depression in grassland habitats, and prefers to feed on mammalian host species (Turell *et al.* 2005) but avian blood meals occur at a high enough frequency to support the transmission of these pathogens (Crans *et al.* 1996) both within the grassland bird community, and in the case of West Nile Virus encephalitis to horses and humans. These mosquitoes exhibited low abundances until June, achieved a small peak in the third quarter of June, and a major peak in the middle of July. Both peaks in abundance occurred when maximum temperatures exceeded 30°C.

*Aedes nigromaculis*, the pasture mosquito (Miura 1969), was the second most abundant mosquito collected (21.5%), and clearly parallels the local biology of *Aedes sollicitans* (Janovy, 1966). *Aedes nigromaculis* prefers mammalian blood meals, but has been shown to feed on avian species in Kansas (Janovy, 1966) at frequencies high enough to support vector competence for avian malaria. Throughout the sampling season, peaks in abundances occurred concurrently with *Aedes sollicitans*. While population abundances of *Aedes sollicitans* decreased in the last quarter of July, *Aedes nigromaculis* abundances continued to increase.

The third most abundant species detected was the inland floodwater mosquito, *Aedes vexans* (9.0%). *Aedes vexans* is commonly encountered in transient water, such as rain pools located in grasslands or roadside ditches. In previous collection efforts, this species has been shown to be one of the most abundant mosquitoes in Kansas (DeMoss Hill 1939, Edman *et al.* 1964, Lungstrom *et al.* 1961), preferentially feeding on mammalian hosts, but feeds on birds as well (Apperson *et al.* 2002, Molaei *et al.* 2006, Turell *et al.* 2005). *Aedes vexans* has been recognized as vector of Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis, and avian malaria. High population abundances of this mosquito have been shown to occur after increased rainfall accumulating in grassland pastures of the Midwest (Janousek *et al.* 1999). In this study, increases abundances seem to follow precipitation events with a one week lag period.



The most abundant species in genus *Culex*, was the standing water mosquito (*Culex tarsalis*) making up 7.4% of the collections. This species utilizes different habitat types, but shows a preference for grasslands and croplands with high primary productivity that provide larval habitats (Reisen, 2002). *Culex tarsalis* was the most abundant species in May (28%), but population numbers collapsed at the end of the month, and remained low (<60 individuals/week) throughout the rest of the study period. *Culex tarsalis* is considered an important vector for the following diseases: Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis and avian malaria. St. Louis encephalitis virus has previously been isolated from this species in the Midwest (Nebraska, Hammon *et al.* 1945, Nebraska Department of Health and Human Services 2012); and West Nile Virus surveillance programs conducted in Kansas confirmed the presence of this virus in *Culex tarsalis* (Kansas State University 2009). *Culex tarsalis* feeds predominately on Passeriformes in early summer and increases its host-breadth to other birds, mammals (livestock and wildlife species) and humans (Tempelis *et al.* 1957). Due to its opportunistic feeding preferences, ability to serve as a functional vector to a variety of pathogens and its high relative abundance, this mosquito may play an integral role in infectious disease transmission as both enzootic and bridge vector (Reisen *et al.* 2006) in the grasslands of the central Great Plains.

*Aedes taeniorhynchus*, also known as the salt-marsh mosquito, has undergone local adaptations to tolerate a variety of freshwater habitats (Nayar, 1974). This species accounted for 6.6% of the collected specimens in this study. Mammalian blood meals are preferred by *Aedes taeniorhynchus* but occasional blood meals of avian species have been reported (Galliformes, Barrera *et al.* 2011; Passeriformes, Suom *et al.* 2010). *Aedes taeniorhynchus* serves as a vector for West Nile Virus encephalitis, and may have vector competence for avian malaria (Carlson *et al.* 2011). Abundances remained low until July (< 20 individuals/week). In July as weekly maximum temperatures exceeded 30°C and precipitation decreased, this species experience a peak in abundance in the third quarter of July, throughout the remainder of the study period population numbers remained stable.

*Culex salinarius* is the second most abundant species in the *Culex* genus, comprising 3.6% of all identified mosquitoes. Abundances remained low until the second quarter of July when weekly maximum temperatures continuously exceeded 33°C. The continued increase in abundance may be a result of increasing temperature. Peaks in seasonal abundances of *Culex*

*salinarius* have previously been shown to occur during the summer, when temperatures are greatest (Eldridge *et al.* 1972, Slaff *et al.* 1981). This species is a vector for St. Louis encephalitis, West Nile Virus encephalitis, and avian malaria. Due to this species opportunistic feeding preferences, including both avian and mammalian hosts (Turell *et al.* 2005), vector competence, and seasonal overlap with West Nile Virus encephalitis cases, it may serve as enzootic and bridge vector (Bolling *et al.* 2005) during the months of June to August. In Kansas West Nile Virus was isolated from *Culex salinarius* in 2009 (Kansas State University, 2009).

These characteristic fluctuations in mosquito abundances produce peaks of variable amplitude, which are linked to increased risk of disease transmission (Yang *et al.* 2009). Specifically, early season mosquito population fluctuations have been shown to be associated with increased human and livestock encephalitis cases (Lothrop *et al.* 2008). Infectious encephalitis (Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis) have the highest number of incidence reports all mosquito-borne zoonotic diseases and hence are of particular importance to public health in North America. In Kansas, West Nile Virus encephalitis in humans and horses are predominately observed in late summer and fall, particularly after incidence reports in birds early in the season (Kansas Department of Health and Environment 2012).

Understanding vector biology can be important to wildlife conservation efforts as well as public health management. Grassland birds are of particular concern due to their conservation status and their role in the principal amplification cycle. Infectious encephalitis are maintained through an enzootic cycle between ornithophilic mosquitoes and viremic birds. Transmission of infectious diseases in the Kansas grasslands is likely to occur during the nesting season (early summer) of grassland nesting birds such as: Greater Prairie-chicken (*Tympanuchus cupido*), Upland Sandpiper (*Bertramia longicauda*), Eastern Meadowlark (*Sturnella magna*), Western Meadowlark (*Sturnella neglecta*), Dickcissel (*Spiza americana*) and Grasshopper Sparrow (*Ammodramus savannarum*). During nesting, females spend extended periods of time in a brooding position which reduces defensive behavior towards mosquito attacks and increases disease transmission, while nestlings lack behavioral and morphological defenses to ward off mosquito parasitism, resulting in peak parasitemia during nesting season (Burkett-Cadena *et al.* 2011, Valkiunas, 2005). The dominant mosquito species during this period was *Culex tarsalis*, with a peak in abundance in the last quarter of May, during which this mosquito species exhibits

an ornithophilic feeding preference. The peak in abundance may increase transmission of infectious encephalitides, particularly West Nile Virus encephalitis and avian malaria in Cloud County, Kansas. Hence, *Culex tarsalis* may be the primary enzootic vector of these pathogens. As the season progressed, I observed a shift in the mosquito community composition, towards opportunistically and mammalian feeding species. The shift in host feeding pattern has been implicated in the increased intensity of human and livestock epidemics of encephalitides particularly following high early season abundances of ornithophilic feeders. Likely bridge vectors in Cloud County are *Aedes sollicitans*, *Aedes nigromaculis* and *Aedes vexans*. During the sample year, no human cases of infectious encephalitides were reported in Cloud County; this may be due to the observed low amplitude peak of early-season ornithophilic mosquito species. Low abundances of these species have been shown to result in decrease tangential transmission to humans (Weaver *et al.* 2010).

The underlying dynamics of seasonality in vector-borne infectious diseases have long been of interest to epidemiologists. Examining the temporal, and spatial dynamics of mosquito communities, when disease transmission is likely to occur, is integral for implementing surveillance programs and control measures. The purpose of this study was to establish general seasonal distributions and population patterns across a grassland ecosystem of various mosquito species that might be implicated as vectors of encephalitides and avian malaria. The information presented here contributes to the existing survey of mosquito communities in the central Great Plains, especially Kansas.

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## Figures and Tables

Table 2.1. Number and percent of mosquito species collected during the sample season (May - July 2010) in the Smoky Hills of Cloud County, Kansas.

<b>Date</b>	<i>Aedes sollicitans</i>	<i>Aedes nigromaculis</i>	<i>Aedes vexans</i>	<i>Culex tarsalis</i>	<i>Aedes taeniorhynchus</i>	<i>Culex salinarius</i>	<i>Culex pipiens</i>	<i>Aedes stimulans</i>	<i>Culex restuans</i>	<i>Anopheles</i>	<i>Aedes dorsalis</i>	<b>Total</b>	<b>% Total</b>
17-May	1	2	0	10	0	0	11	0	0	0	1	25	0.22
24-May	70	64	78	73	0	4	8	0	1	2	1	301	2.68
30-May	28	22	5	574	1	0	17	0	1	0	2	650	5.79
7-Jun	125	87	4	4	4	1	0	0	1	1	0	227	2.02
21-Jun	934	543	565	46	16	15	3	30	30	3	9	2,194	19.55
28-Jun	55	77	38	10	0	7	6	1	5	0	0	199	1.77
12-Jul	1,578	242	52	23	85	75	8	10	4	4	3	2,084	18.57
19-Jul	1,528	463	230	56	281	95	10	6	5	15	6	2,695	24.01
26-Jul	1,261	913	40	32	353	206	14	16	8	4	1	2,848	25.38
<b>Total</b>	5,580	2,413	1,012	828	740	403	77	63	55	29	23	11,223	100
<b>% Total</b>	49.72	21.50	9.02	7.38	6.59	3.59	0.69	0.56	0.49	0.26	0.20	100	

Table 2.2. Number of mosquito species collected during the sample season (May - July, 2010) at 20 sites in Cloud County of the Smoky Hill eco-region, Kansas. Location of the sites can be found in Figure 2.1.

Species	BS1	BS2	BS3	BS4	BS6	BS7	BS8	BS9	BS10	BS11	BS12	BS13	BS14	BS15	BS16	W1	W2	W3	W4	W5	Total	%
																						Total
<i>Culex pipiens</i>	2	0	3	9	5	6	4	1	7	4	8	0	1	3	6	2	2	11	0	3	77	0.69
<i>Culex tarsalis</i>	41	31	30	16	3	53	72	101	65	9	25	5	38	71	33	103	34	92	3	3	828	7.38
<i>Culex restuans</i>	6	18	0	2	0	5	1	2	2	0	6	0	1	1	0	0	0	4	1	6	55	0.49
<i>Culex salinarius</i>	10	16	4	2	13	81	12	11	9	6	18	0	8	11	0	16	12	154	1	19	403	3.59
<i>Aedes dorsalis</i>	3	3	2	2	0	1	1	0	7	0	3	0	0	1	0	0	0	0	0	0	23	0.20
<i>Aedes nigromaculis</i>	43	25	47	80	57	566	246	32	305	93	40	120	36	305	222	24	19	142	4	7	2,413	21.50
<i>Aedes sollicitans</i>	39	84	108	201	113	504	410	246	2,402	123	88	220	87	311	340	80	25	187	6	6	5,580	49.72
<i>Aedes stimulans</i>	3	1	3	0	4	2	5	5	18	1	4	1	4	2	8	0	0	2	0	0	63	0.56
<i>Aedes taeniorhynchus</i>	9	4	25	4	1	170	47	25	195	26	43	0	40	40	12	1	1	95	2	0	740	6.59
<i>Aedes vexans</i>	13	243	256	14	3	6	29	2	113	3	101	18	22	4	172	0	2	11	0	0	1012	9.02
<i>Anopheles</i>	4	10	2	1	1	0	0	1	1	2	4	0	0	0	0	0	1	0	2	0	29	0.26
<b>Total</b>	173	435	480	331	200	1,394	827	426	3,124	267	340	364	237	749	793	226	96	698	19	44	11,223	100
<b>%Total</b>	1.54	3.88	4.28	2.95	1.78	12.42	7.37	3.80	27.84	2.38	3.03	3.24	2.11	6.67	7.07	2.01	0.86	6.22	0.17	0.39	100	

Table 2.3. Mosquito taxa correlation according to Pearson's correlation matrix, indicating a linear association between occurrence records of taxa.

	<i>Culex pipiens</i>	<i>Culex tarsalis</i>	<i>Culex restuans</i>	<i>Culex salinarius</i>	<i>Aedes dorsalis</i>	<i>Aedes nigromaculis</i>	<i>Aedes sollicitans</i>	<i>Aedes stimulans</i>	<i>Aedes taeniorhynchus</i>	<i>Aedes vexans</i>
<i>Culex tarsalis</i>	<b>0.62</b>									
<i>Culex restuans</i>	-0.34	-0.17								
<i>Culex salinarius</i>	0.38	-0.22	0.09							
<i>Aedes dorsalis</i>	-0.15	-0.01	<b>0.80</b>	0.06						
<i>Aedes nigromaculis</i>	0.13	-0.26	0.55	<b>0.87</b>	0.43					
<i>Aedes sollicitans</i>	0.07	-0.28	0.36	<b>0.74</b>	<b>0.56</b>	<b>0.74</b>				
<i>Aedes stimulans</i>	-0.18	-0.22	<b>0.93</b>	0.39	<b>0.76</b>	<b>0.75</b>	<b>0.60</b>			
<i>Aedes taeniorhynchus</i>	0.32	-0.19	0.05	<b>0.95</b>	0.16	<b>0.83</b>	<b>0.74</b>	0.31		
<i>Aedes vexans</i>	0.35	-0.16	<b>0.93</b>	-0.02	<b>0.93</b>	0.44	0.39	<b>0.82</b>	0.05	
<i>Anopheles</i>	<b>0.85</b>	-0.19	0.11	0.49	<b>0.53</b>	0.48	<b>0.74</b>	0.21	<b>0.70</b>	0.35

Correlation coefficients greater than 0.5 are indicated in bold.

Table 2.4. Candidate models used to fit the dependent variable, mosquito abundance, to independent meteorological variables.

Variables in the model	No. of parameter	AICc <sup>a</sup>	Delta AICc	AICc weight <sup>b</sup>	R <sup>2</sup>	Adjusted R <sup>2</sup>	p
T <sub>min</sub> <sup>c</sup>	2	-48.50	0.00	0.58	0.76	0.73	0.00
T <sub>max</sub> <sup>d</sup>	2	-46.88	1.62	0.26	0.76	0.73	0.00
T <sub>min</sub> , P <sub>mean</sub> <sup>e</sup>	3	-42.40	4.11	0.07	0.99	0.88	0.00
T <sub>min</sub> , P <sub>mean</sub> , P <sub>mean</sub> (2) <sup>f</sup>	4	-39.64	6.86	0.02	0.95	0.91	0.00
T <sub>max</sub> , P <sub>mean</sub>	2	-39.12	7.38	0.01	0.87	0.83	0.00
P <sub>mean</sub>	1	-38.80	7.70	0.01	0.30	0.21	0.12

<sup>a</sup> AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

<sup>b</sup> AICc weight = percent of total weight from 128 models that can be attributed to the specified model.

<sup>c</sup> T<sub>min</sub> = minimum temperature during the sample week.

<sup>d</sup> T<sub>max</sub> = maximum temperature during the sample week.

<sup>e</sup> P<sub>mean</sub> = precipitation during the sample week.

<sup>f</sup> P<sub>mean</sub>(2) = precipitation two weeks prior to sample week, to account for lagged responses.

Table 2.5. Multiple linear regression results of the top performing models between the dependent variable, mosquito abundance, to the independent meteorological variables.

<b>Variables in the model</b>	<b>No. of parameters</b>	<b>Slope</b>	<b>(SE)</b>	<b><i>t</i></b>	<b><i>p</i></b>
$T_{\min}^a$	2	0.2057	0.0113	4.7067	0.0022
$T_{\max}^b$	2	0.0392	0.0083	4.7461	0.0021

<sup>a</sup>  $T_{\min}$  = minimum temperature during the sample week.

<sup>b</sup>  $T_{\max}$  = maximum temperature during the sample week.

Table 2.6. Cumulative AICc weights for all 6 meteorological variables hypothesized to influence mosquito abundance in the Smoky Hills of Cloud County, Kansas, 2010.

Variable	Cumulative AICc <sup>a</sup> weight <sup>b</sup>
minimum temperature	0.69
maximum temperature	0.30
precipitation	0.13
precipitation two weeks prior	0.04
wind speed	0.01
precipitation one week prior	0.01

<sup>a</sup> AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

<sup>b</sup> Cumulative AICc weight of a variable = the percent weight attributed to models containing that particular variable. Cumulative AICc weight is calculated as the sum of AICc model weights containing that variable.

Table 2.7. Candidate models used to fit the dependent variable, mosquito abundance, to independent environmental variables.

Variables in model	No. of parameters	AICc <sup>a</sup>	Delta AICc	AICc Weight	R <sup>2</sup>	Adjusted R <sup>2</sup>	P
Curv <sup>c</sup> , TWI <sup>d</sup> , Dist <sub>wl</sub> <sup>e</sup> , Dist <sub>r</sub> <sup>f</sup>	5	-87.73	0.00	0.10	0.50	0.37	0.03
TWI, Dist <sub>wl</sub> , Dist <sub>r</sub>	4	-87.58	0.14	0.09	0.40	0.29	0.04
TWI	2	-86.62	1.11	0.06	0.15	0.10	0.09
Curv, TWI	3	-86.31	1.42	0.05	0.25	0.16	0.09
TWI, Dist <sub>wl</sub>	3	-86.02	1.70	0.04	0.24	0.15	0.10
TWI, Dist <sub>r</sub>	3	-85.83	1.89	0.04	0.23	0.14	0.11
Curv, TWI, Dist <sub>r</sub>	4	-85.79	1.93	0.04	0.34	0.22	0.07

<sup>a</sup> AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

<sup>b</sup> AICc weight = percent of total weight from 128 models that can be attributed to the specified model.

<sup>c</sup> Curvature = is a measurement of rate-change of the slope per unit distance and may be an indicator for of aquatic habitat stability.

<sup>d</sup> TWI = Topographic Wetness Index, calculated as the natural logarithm of the ratio between local upslope contributing area and slope, and describes the predicted soil moisture pattern (ESRI, 2010).

<sup>e</sup> Dist<sub>wl</sub> = distance to the closest woodland, calculated using Euclidean distance (Arc Info 10).

<sup>f</sup> Dist<sub>r</sub> = distance to the closest road, calculated using Euclidean distance (Arc Info 10).

Table 2.8. Multiple linear regression results of the top performing models between the dependent variable, mosquito abundance, to the independent environmental variables.

Variables in the Model	No. of parameters	$p^a$	Independent variable	Slope	(SE)	$t$	$p^b$
curv, TWI,	5	0.0250	curv	0.2456	0.1393	1.7623	0.0980
dist_wl, dist_r			TWI	0.6738	0.1921	3.5071	0.0030
			dist_wl	-0.0001	0.0001	-2.1908	0.0540
			dist_r	-0.0002	0.0001	-2.2803	0.0380

<sup>a</sup>  $p$  = p-value of the overall regression model.

<sup>b</sup>  $p$  = p-value of the independent variables.

<sup>c</sup> curvature = is a measurement of rate-change of the slope per unit distance and may be an indicator for of aquatic habitat stability.

<sup>d</sup> TWI = Topographic Wetness Index, calculated as the natural logarithm of the ratio between local upslope contributing area and slope, and describes the predicted soil moisture pattern (ESRI, 2010)

<sup>e</sup> dist\_wl = distance to the closest woodland, calculated using Euclidean distance (Arc Info 10).

<sup>f</sup> dist\_r = distance to the closest road, calculated using Euclidean distance (Arc Info 10).



Table 2.9. Cumulative AICc weights for all 7 environmental variables hypothesized to influence mosquito abundance in the Smoky Hills of Cloud County, Kansas, 2010.

Variable	Cumulative AICc <sup>a</sup> weight <sup>b</sup>
TWI <sup>c</sup>	0.81
distance to road	0.52
distance to woodland	0.45
curvature <sup>d</sup>	0.41
distance to edge habitat	0.21
distance to agricultural field	0.20
distance to water source	0.18

<sup>a</sup> AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

<sup>b</sup> Cumulative AICc weight of a variable = the percent weight attributed to models containing that particular variable. Cumulative AICc weight is calculated as the sum of AICc model weights containing that variable.

<sup>c</sup> TWI = Topographic Wetness Index, calculated as the natural logarithm of the ratio between local upslope contributing area and slope, and describes the predicted soil moisture pattern (ESRI, 2010)

<sup>d</sup> curvature = is a measurement of rate-change of the slope per unit distance and may be an indicator for of aquatic habitat stability.

Figure 2.1. Location and landscape composition of the eastern Smoky Hills study site, Cloud County, Kansas. Locations of CDC CO<sub>2</sub> mosquito traps operated during the study period are shown as red points the map.

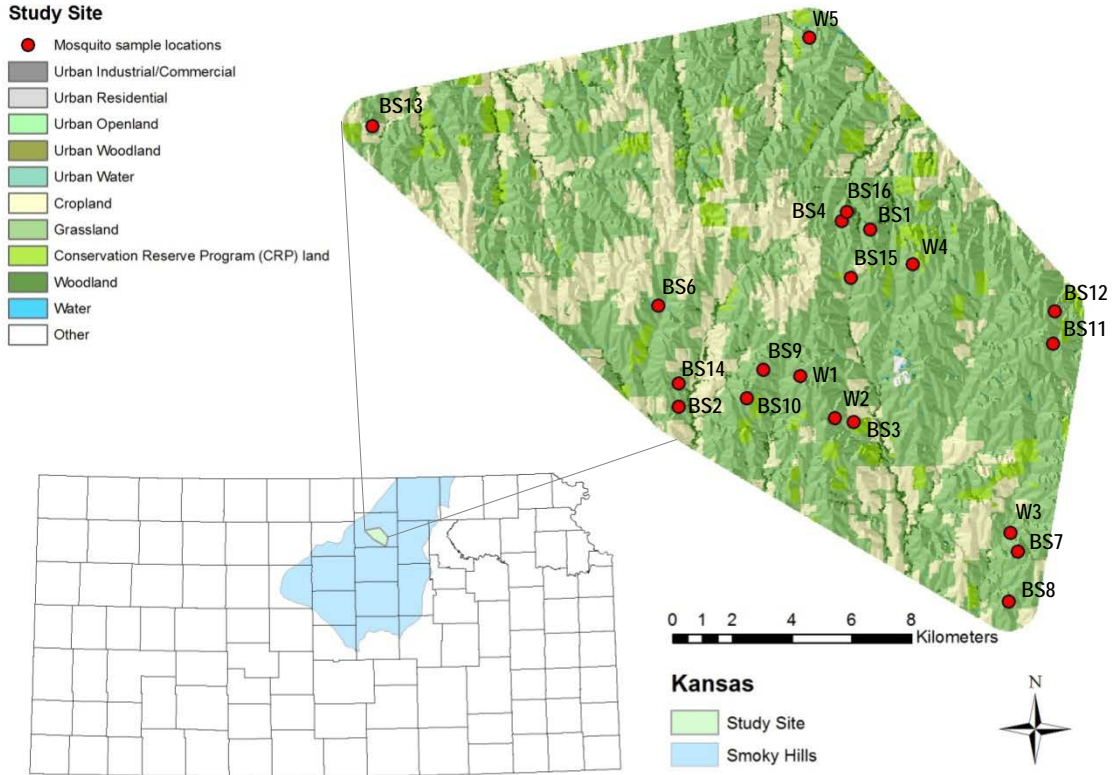


Figure 2.2. Seasonal distribution of the dominant mosquito species found in the eastern Smoky Hills study site in 2010. Counts are standardized by the number of traps operated per week.

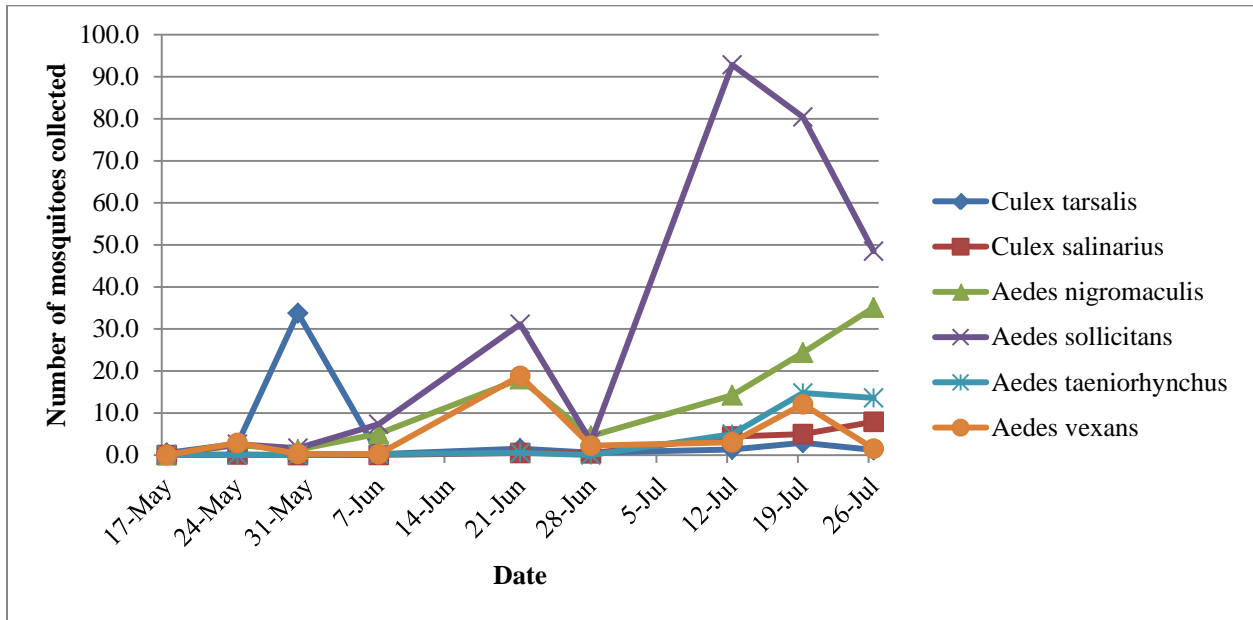
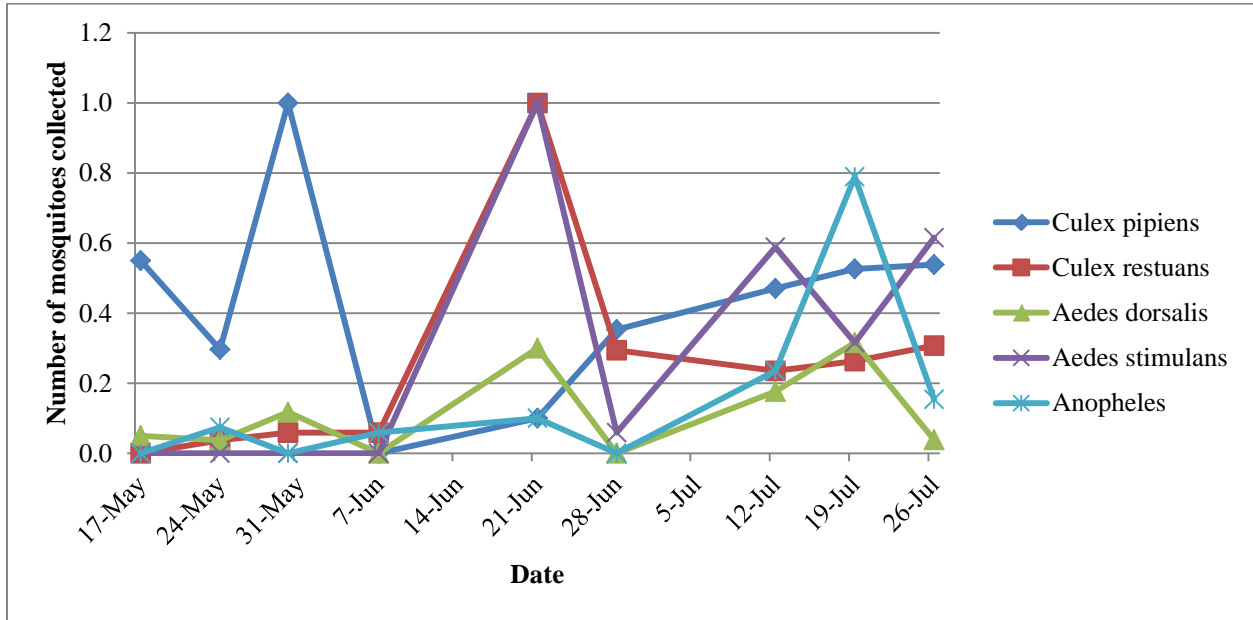


Figure 2.3. Seasonal distribution of mosquito species found at lower abundances in the eastern Smoky Hills study site in 2010. Counts are standardized by the number of traps operated per week.



# Chapter 3 - ECOLOGICAL NICHE MODELING OF DISEASE VECTORS IN THE EASTERN SMOKY HILLS OF KANSAS

## Abstract

Ecological niche modeling techniques have been effectively utilized to address the underlying environmental and climatic factors associated with vector distributions, and have found broad applications in epidemiological studies, due to the fine spatial resolution of vector collection data compared to disease incidence data, which is often only available at a county-level. In the Great Plains, mosquito vectors of arboviruses (disease agents of: Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis) and *Plasmodium* species (disease agents of avian malaria) are of particular concern to public health, livestock and wildlife species. Here, I used the Pearson's jackknife approach to develop ecological niche models for important vector species of these pathogens within the grasslands of the eastern Smoky Hills, Kansas. Both *Culex* and *Aedes* species are susceptible to disease agents of infectious encephalitides and avian malaria. *Culex* species are of primary interest due to their ornithophilic feeding preferences and role in the primary amplification cycle of infectious encephalitides. Although most *Aedes* species prefer mammalian blood meals, they have been implicated in the transmission of avian malaria, and play an important role as bridge vectors of infectious encephalitides to humans and livestock. Occurrence data of *Culex tarsalis*, *Culex salinarius*, *Aedes sollicitans*, *Aedes nigromaculis*, *Aedes vexans*, and *Aedes taeniorhynchus* were collected from May to July 2010 and combined with 48 ecologically relevant environmental and bioclimatic layers. Based on the internal jackknife procedure which measures variable importance, models were reduced to 10 variables explaining at least 85% of the variation in the species' occurrence data. The probabilistic distribution maps of *Culex* vectors (potential vector species of *Plasmodium* species) were used to evaluate if Greater Prairie-chicken (*Tympanuchus cupido*) females nest in areas associated with a higher probability of vector occurrence than other potentially available habitats within the grasslands. I also used the distribution maps to determine if there was a significantly higher probability of vector occurrence at nest locations of *Plasmodium* infected female Greater Prairie-chicken than at nests of uninfected females. The results show that the probability of avian malaria vectors at nest locations was significantly higher than other available grassland habitats within the study area. However, I failed to detect a

significant difference in the probability of vector occurrence at nest of infected versus uninfected females.

## Introduction

The discovery of the link between mosquitoes and the spread of infectious diseases has led to the prevention of disease spread through the control of mosquito vector populations (Medlock *et al.* 2006). The technological advances over the past two decades (remote sensing, geographic information system approaches, statistical modeling techniques) provide new opportunities to prevent and control vector-borne diseases by transforming point-based data into smooth surfaces that predict vector probability across geographical areas (Eisen *et al.* 2011). Ecological niche modeling techniques are a result of these recent developments; and establish the relationship between mapped species occurrences and ecologically relevant predictor variables. Resulting predictions are then utilized to create probabilistic distribution maps of species' occurrences across the landscape (Eisen *et al.* 2011). These models have been effectively utilized to address the underlying environmental and climatic factors associated with vector distributions (Benedict *et al.* 2007, Foley *et al.* 2008, Larson *et al.* 2010, Levine *et al.* 2004, Moffet *et al.* 2007, Peterson *et al.* 2005, Sweeney *et al.* 2007) and to identify patterns across the landscape. Niche models of arthropod vector distributions have found applications in epidemiological studies (Eisen *et al.* 2011) due to the fine spatial resolution of vector collection data compared to disease incidence data, which is often only available at a county-level. Furthermore, vector data can be advantageous because many species transmit multiple pathogens, and many vector-borne diseases are not 'notifiable', resulting in a lack of available epidemiological data (Eisen *et al.* 2011).

Mosquitoes in the central Great Plains can harbor a variety of infectious disease agents of public health and conservation concern, including: arboviruses (disease agent of Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis) and *Plasmodium* species (disease agent of avian malaria). Infectious encephalitides are considered notifiable, and epidemiological data on human disease cases have been available in Kansas since 1964. Humans and livestock are considered incidental hosts of these pathogens; the primary amplification cycle (enzootic) involves mosquitoes and avian species.

In contrast, avian malaria exhibits a strictly enzootic avian cycle and is implicated in the extinction of the Hawaiian avifauna (Warner 1986), and continues to be a threat to the highly susceptible Laysan Finch (van Riper *et al.* 1986) and honey creepers (Depanidinae; Atkinson *et al.* 2001). The disease agent has also been detected in wild and captive penguin species, including: African black-footed penguins (*Spheniscus demersus*; Stoskopf *et al.* 1979), and Magellanic penguins (*Spheniscus magellanicus*; Fix *et al.* 1988). In penguin species, infection often results in clinical symptoms (depression, anorexia, respiratory distress), and intense mortality events. In the Great Plains, the decline of grouse species (Greater Sage grouse, *Centrocercus urophasianus*; Boyce 1990) has been attributed to *Plasmodium* infections. Vector-borne infectious diseases are hence of particular concern across the central Great-Plains, the most speciose region for grassland nesting birds in North America, because of the presence of all the components of disease emergence: host and vector ecology, pathogen properties, and landscape features. Here, I investigate how mosquito abundance and diversity could both influence the decline of the grassland avifauna, and facilitate the primary amplification cycle of encephalitides important to public health.

Previous studies using ecological niche modeling approaches to predict vector species' distributions have commonly used coarse resolution datasets and have rarely been conducted at a local scale. Here, I develop high resolution ecological niche models of potentially relevant disease vectors of infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis) and avian malaria: *Aedes sollicitans*, *Aedes nigromaculis*, *Culex tarsalis*, *Aedes vexans*, *Aedes taeniorhynchus*, *Culex salinarius*. In grassland ecosystems the enzootic cycle of these diseases is maintained through the transmission between grassland nesting birds and *Culex* species. Disease transmission in the grasslands of the eastern Smoky Hills is likely to occur during the nesting season (early summer) of resident grassland birds: Greater Prairie-chicken (*Tympanuchus cupido*), Eastern Meadowlark (*Sturnella magna*), Western Meadowlark (*Sturnella neglecta*) and summer breeding migrants: Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus savannarum*), Upland Sandpipers (*Bartramia longicauda*). Greater Prairie-chicken are a good choice to model the grassland bird community because, 1) they share habitat and nesting requirements with other grassland bird species, and 2) infectious disease agents (*Plasmodium*) have been detected in this species across the eastern Smoky Hills. During the nesting season, grassland species are at risk of being infected with vector-borne

disease agents, due to the extended periods of time spent brooding, which increases their exposure to feeding mosquitoes. Since the nest ecology of Greater Prairie-chicken increases its risk of parasitism by mosquitoes, I compared the probability of vector occurrence (*Culex tarsalis*, *Culex salinarius*) at nest locations versus potentially available habitat to evaluate if females nest in areas that potentially increases their vulnerability to mosquito parasitism, which may result in increased disease transmission. Furthermore, to determine if there is a significant connection between mosquito habitat and incidence of avian malaria disease agents in nesting female Greater Prairie-chicken, I compared the probability of occurrence of *Culex* mosquitoes between nests of infected versus uninfected females.

## **Methods**

### ***Study Site***

The study site was located in north-central Kansas, in the Smoky Hills eco-region of Cloud County, Kansas (Fig. 3.1). The Smoky Hills are tillable, with native prairies characterized by moderate to high fragmentation by row crop agriculture, and low intensity cattle stocking. The study area encompassed 283 km<sup>2</sup> of fragmented prairie landscape; consisting of 73% grassland, 25 % cropland and a road density of 1.4 km/km<sup>2</sup>. Cultivated croplands included wheat, sorghum, soybeans, and corn. The climate was temperate, with moderate rainfall and annual precipitation during the sample year of 883 mm, of which nearly half could be attributed to precipitation from May through July 2010.

### ***Disease Vectors and Occurrence Data***

Mosquitoes were sampled weekly for a total of 9 weeks (May through July 2010) over 20 georeferenced sampling locations using CDC miniature light traps (J. W. Hock, Gainesville, FL; Table 3.1.). I averaged species abundance data over time (the 9 sample occasions) and converted the dataset into presence/absence records for the most abundant vector species in the grassland of the Smoky Hills, Kansas (Table 3.2.). For a detailed methodology of mosquito surveillance in the eastern Smoky Hills refer to “Mosquito Surveillance” in Chapter 2. I chose to sample only grasslands because they represent an interface for the transmission of infectious disease between



livestock and wildlife species. Infectious disease vectors of avian malaria and infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis) were selected based on, 1) capability of acquiring the pathogen and transmitting it from one host to the next, 2) feeding preferences that include multiple vertebrate hosts, and 3) abundance in the environment (Bates 1949, Russell 1959). *Culex tarsalis* and *Culex salinarius* are likely the most significant enzootic vectors of avian malaria and infectious encephalitides (Turell *et al.* 2005, Valkiunas 2005), but also play a significant role as bridge vectors of the latter (Turell *et al.* 2005). Other potential bridge vectors included: *Aedes sollicitans*, *Aedes nigromaculis*, *Aedes vexans*, *Aedes taeniorhynchus*.

*Culex tarsalis* is a vector of many infectious diseases throughout its range, including avian malaria and infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, West Nile Virus Encephalitis; Turell *et al.* 2005). This species has tested positive for avian malaria pathogens (*Plasmodium*; Janovy 1966) and WNV (Kansas State University 2009) in Kansas. *Culex tarsalis* utilizes different habitat types including road side ditches near grasslands that provide larval habitats with high primary productivity (Edmunds 1955, Rapp 1985, Reisen, 2002). This species was encountered at all sample locations, hence 20 occurrence records were used for the construction of species probability distribution (Table 3.2.).

*Culex salinarius* populations peak immediately after flooding because rotten vegetation acts as an oviposition attractant. This species can be found in freshwater habitats with moderate pollution levels, and roadside ditches (Crans 2010). The opportunistic and generalist feeding preferences, including both avian and mammalian hosts (Turell *et al.* 2005), the competence of *Culex salinarius* to transmit arboviruses, and the seasonal overlap with West Nile Virus encephalitis cases, suggest that this mosquito species may serve a enzootic and bridge vector (Bolling *et al.* 2005) during the months of June to August. In Kansas, West Nile Virus was isolated from *Culex salinarius* in 2009 (Kansas State University, 2009). In addition, this species has been shown to exhibit vector competence for avian malaria parasites (Valkiunas, 2005, Burkett-Cadena *et al.* 2011). *Culex salinarius* occurred in 18 out of 20 trapping locations, which were used to construct the species probability distribution within the study area (Table 3.2.).

*Aedes sollicitans* and *Aedes nigromaculis* were the most abundant vector species within the study area and exhibited similarities in their local biology (Janovy 1966). Their larvae are typically found on moist substrate or depressions in grassland habitats. Both species are

susceptible to avian malaria and infectious encephalitis disease agents. *Aedes sollicitans* and *Aedes nigromaculis* are known vectors of West Nile Virus encephalitis and St. Louis encephalitis (Turell *et al.* 2005). They predominately feed on mammalian host species but avian blood meals occur at high enough frequency to support the transmission of these pathogens (Crans *et al.* 1996, Janovy 1996). These species occurred at all 20 trapping locations (Table 3.2.).

*Aedes vexans*, the inland floodwater mosquito, is one of the most abundant mosquitoes in Kansas (DeMoss Hill 1939, Edman *et al.* 1964, Lungstrom *et al.* 1961). *Aedes vexans* is commonly encountered in transient water, such as rain pools located in grassland/woodland pools, vehicle ruts and roadside ditches (Siverly 1972). This species preferentially feeds on mammalian hosts, but feeds on avian hosts as well (Apperson *et al.* 2002, Molaei *et al.* 2006, Turell *et al.* 2005), and is a potential enzootic and bridge vector of infectious disease. *Aedes vexans* has been recognized as a vector of Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis, and avian malaria. This species occurred at 17 out of 20 trapping locations (Table 3.2.).

*Aedes taeniorhynchus*, also known as the salt-marsh mosquito, prefers temporary brackish pools of water for ovipositioning (O'Meara 1986). This species has an affinity for mammalian blood meals (Turell *et al.* 2005) but occasional blood meals of avian species have been reported (Galliformes, Barrera *et al.* 2011; Passeriformes, Suom *et al.* 2010). *Aedes taeniorhynchus* serves as vector for West Nile Virus, and may have vector competence for avian malaria pathogens (Carlson *et al.* 2011). *Aedes taeniorhynchus* specimens have tested positive for West Nile Virus every year in North America from 2001-2009 (Center for Disease Control and Prevention 2009). Eighteen occurrence records of this species were used to create a probability distribution within the study area (Table 3.2.).

### ***Environmental Data***

Environmental variables were selected based on an assessment of the ecology of vector mosquitoes in Cloud County. Ecological niche models were constructed with 12 environmental variables (Table 3.3.), which included spatially explicit features of topography, land-cover and soil. I used Arc Info 10 (Environmental Systems Research Institute, Redlands, CA) for geospatial analysis and data extraction. All data sets were acquired from Kansas Geospatial Community

Commons (topography, land-cover; [www.kansasgis.org](http://www.kansasgis.org)) and National Resources Conservation Service (soil; [soils.usda.gov/survey/geography/ssurgo](http://soils.usda.gov/survey/geography/ssurgo)). Data sets were standardized to finest spatial resolution available (30 m), creating grids that were 829 by 698 cells (578,642 individual cells). This resolution was selected based on the attractiveness range of CDC CO<sub>2</sub> baited mosquito traps. The attractiveness range of CDC CO<sub>2</sub> baited light traps is somewhat ambiguous, however it has been shown that CO<sub>2</sub> attracts mosquitoes from distances of <30 m and is species dependent (Service 1993).

Topographic variables were derived from the USGS national elevation model OCG Map seamless server (U.S. Geological Survey, EROS Data Center) at a 30 m resolution, and edited to the extent of the study site (Fig. 3.2.). I used the elevation dataset to calculate slope, aspect, curvature and Topographic Wetness Index (TWI). Slope identifies the gradient of a surface, calculated as the rate of change in elevation while aspect is the slope direction, with zero degrees at north and increasing clockwise. Both curvature, and TWI have been used to assess soil moisture patterns. Curvature has been used as a proxy for potential of water accumulation and is a function of the second derivative of the surface. TWI describes the predicted soil moisture pattern based on the natural logarithm of the ratio between local upslope contributing area and slope (Pathak, 2010). These variables have been shown to be associated with larval habitats and have been listed in recent literature to significantly contribute to ecological niche models of a variety of species (Ayala *et al.* 2009, Khatchikian *et al.* 2011, Larson *et al.* 2010, Peterson *et al.* 2005, Sweeney *et al.* 2007).

Land-cover variables were derived from the 2005 land cover map of Kansas (Kansas Applied Remote Sensing Program 2005; Whistler *et al.* 2006) and the roadway dataset that combined the 2006 Kansas State and Non-State Road System dataset (Kansas Department of Transportation: Bureau of Transportation and Planning) at a resolution of 30 m, and edited to the extent of the study site (Fig. 3.3.). I measured five variables at each mosquito trapping location: distance to agriculture, distance to woodland, distance to water, distance to road and distance to edge. To identify distance variables, I extracted the respective land-cover class as distinct data layer and then calculated the distance from each trapping location to the nearest land-cover class using Arc Info 10.

Soil variables were derived from the Soil Survey Geographic Database (Natural Resources Conservation Service), converted to raster datasets with a 30 m resolution and edited

to the extent of the study site (Fig. 3.4.). I selected hydrologic soil variables describing the potential of soil to aggregate water based on a variety of soil indices: AASTHO (describes the particle-size distribution), drainage class (describes the frequency and duration of wet periods) and hydrologic soil groups (estimates of runoff potential). These variables have recently been used to characterize vector species distributions via ecological niche models (Larson *et al.* 2010).

### ***Bioclimatic Data***

Thirty-six bioclimatic variables for the year 2010 were obtained from the WorldClim database (Hijmans *et al.* 2005; [www.worldclim.org/bioclim](http://www.worldclim.org/bioclim)). The naïve resolution of WorldClim data is 1 km; due to this coarser resolution I resampled the data to a 30 m resolution, using Bilinear Interpolation in the Resample tool in Arc Info 10, and edited each layer to the constraints of the study site (Table 3.3.). To account for extreme climatic conditions I included both temperature and seasonality of precipitation. I used these variables because they have been previously shown to be important in the spatial distribution of multiple mosquito species (Kulkarni *et al.* 2010, Moffett *et al.* 2007). I used temperature indices (minimum, mean, and maximum) averaged across year, coldest/warmest quarter, coldest/warmest month, sample season, each sample season month and month prior to sample season. Similarly, I used mean precipitation indices averaged across year, the driest and wettest quarters, the driest and wettest months, sample season, each sample season month and month prior to sample season. Because hyper-dimensional spaces can lead to overfitted models (Peterson *et al.* 2007), I determined multicollinearity among the 37 bioclimatic variables using correlation tests. Bioclimatic data from 100 randomly generated points across the study site was extracted to generate a correlation matrix between the variables. Highly correlated variables ( $r \geq 0.90$ ) were identified using a Pearson's correlation matrix, and excluded from the final niche models (Table 3.4.).

### ***Ecological Niche Modeling***

I used a maximum entropy approach to characterize probabilistic distribution of vector species across the study area based on incomplete occurrence data using the software program, Maxent (Phillips *et al.* 2004, Phillips *et al.* 2006b). This program uses a machine-learning approach based on the probability distribution of maximum entropy, a distribution close to

random, which is subjected to constraints imposed by the observed environmental and bioclimatic variables at the locations where the species was observed (Elith *et al.* 2009; Table 3.2.). A probabilistic distribution map is created based on the biophysical characteristics of the occurrence data of a training dataset. The Maxent software version 3.1.0., developed by S. Phillips and colleagues (download at: <http://www.csprinceton.edu/~schapire/maxent/>) shows superior performance with small sample sizes (Pearson *et al.* 2007), spatial errors in occurrence records (Phillips *et al.* 2006a), and tests of model performance (Elith *et al.* 2006, Phillips *et al.* 2006a). Recommended default settings were used for convergence thresholds ( $10^{-5}$ ) and maximum number of iterations (500). Probabilistic distributions maps were created for the most abundant vector species: *Culex tarsalis*, *Culex salinarius*, *Aedes sollicitans*, *Aedes nigromaculis*, *Aedes vexans*, and *Aedes taeniorhynchus*. Occurrence records of each species and the full set (n=48) of environmental and bioclimatic variables were entered as model parameters. Variable importance was determined with jackknife tests. I produced 3 model types using the jackknife procedure, 1) models created excluding one variable at a time, 2) models created with only one variable at a time, and 3) models created with the full set of variables (Phillips *et al.* 2006a, Phillips *et al.* 2008). Variables most important in model development decreased the training gain of the model when the variable was removed and increased the training gain when the model was developed with only that variable. Final models were reduced to less than 10 variables by excluding highly correlated variables ( $r \geq 0.90$ ) with low importance in model development.

I used a cumulative probability distribution to interpret the suitable conditions for a species within a threshold range of 0-100% (Phillips 2006a). To distinguish between absence and presence I created binary maps, selecting a decision threshold, which enabled me to validate model performance (Pearson *et al.* 2007). I applied a Lowest Presence Threshold (LPT; Pearson *et al.* 2007) because I wanted areas to be represented that were at least as suitable as those where the species were observed while maintaining a high predictive success of occurrence records (Hernandez *et al.* 2006, Pearson *et al.* 2007).

### ***Model Validation***

Since the datasets of potential vector species in the Smoky Hills of Cloud County, Kansas included  $\leq 20$  occurrence records, I followed the jackknife validation methodology developed by Pearson *et al.* (2007), which has been shown to be effective for sample sizes of 25 or less; as few

as 5 occurrence records produce an accurate prediction of a species distribution. Briefly, one occurrence record was removed from the data set, and the model was built using  $n-1$  occurrences. Thus, for a species with  $n$  records,  $n$  individual models were built. Model accuracy and significance were tested based on the ability of each model to predict the excluded occurrence record when a Lowest Presence Threshold was used to differentiate between suitable versus unsuitable habitat (LPT; Pearson *et al.* 2007). Models developed with this approach can be interpreted as identifying areas that are at least as suitable as known occurrence localities.

### ***Evaluation: Comparison to Greater Prairie-chicken Nest locations and Plasmodium Incidence***

To determine if grassland birds nest in locations with high probability of occurrence of mosquito vectors, I assessed the probability of occurrence of individual vector species (*Culex tarsalis*, *Culex salinarius*) known to transmit *Plasmodium* and a combined model (created by averaging the models of both vector species into a single probability distribution) at 111 Greater Prairie-chicken nest locations (Fig. 3.5.). I compared the probability of vector occurrence at nests versus randomly selected grassland sites considered to be available nesting habitat for grassland birds with 2-sample t-tests combined with classical descriptive statistics. One hundred eleven random points were generated within the same spatial extent as the sampling area using Arc Info 10. Probabilities of vector occurrence of individual/combined models were extracted from the probabilistic distribution maps for both nest locations and random points. Prior to testing, Kolmogorov-Smirnov tests for goodness of fit were used to verify the normality of the data. To mitigate the effects of inequality of population variances, I applied the Satterthwaite approximation:

$$SE_S = \sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}$$

where  $s_i^2$  and  $n_i$  are the sample variances and sample sizes of both populations. This equation applies a weighted average of the standard errors instead of the pooled variance procedure.

To assess the difference in the probabilities of *Culex* species occurrence at nests of *Plasmodium* infected females (n=8; infection status was determined with previously published primer pairs by Fallon *et al.* 2003 and Beadell *et al.* 2005; Appendix B.) versus all nest locations within the study area (n=111), I applied a Monte Carlo resampling procedure (Gotelli *et al.*

2004). I calculated the mean probability of vector occurrence at nest locations based on the individual and combined vector models of *Culex tarsalis* and *Culex salinarius*. Nest locations were drawn randomly in a group size of n=8; this process was repeated 10,000 times to achieve a representative random datasets that allowed for the comparison between nest of infected female Greater Prairie-chicken and uninfected females. The 2.5% and 97.5% confidence limits of the 10,000 iterations were determined and used to determine significant differences between the datasets.

## Results

Of the resulting four niche models, all possessed a training AUC greater than 0.85 indicating a high predictive success for the fit of the model to the training dataset (Table 3.6.). Predictions of the potential distribution of the six vector species as measured by the Pearson's jackknife-based test procedure, applying the Lowest Presence Threshold (LTP), were significantly better than random expectations ( $p < 0.01$ , Table 3.7.).

### *Ecological Niche Modeling of Important Vector Species*

*Culex tarsalis*, *Aedes sollicitans*, and *Aedes nigromaculis* were encountered at all trapping locations; hence I constructed one model of their potential distribution in the grasslands of the eastern Smoky Hills (Fig. 3.10, 3.14.). The model was created with the full set of occurrence records (n=20), and possessed a training AUC of 0.86 (Table 3.6.), indicating a good model fit. The estimated habitat suitability at occurrence points based on the generated probability distribution for these species was  $59.73 \pm 26.95$  (range: 6.66 – 100). Model validation using the Pearson's jackknife method indicated a high statistical significance ( $p = 2.44e^{-3}$ ) at a success rate of 75% (Table 3.7.). The internal jackknife test of variable importance showed that distance to water, Topographic Wetness Index (TWI), precipitation of the driest quarter, and distance to woodland were the four most important predictors of habitat suitability. These variables contained the most information compared to other variables (Table 3.5., Fig. 3.6.).

Ecological niche models for *Culex salinarius*, *Aedes vexans*, and *Aedes taeniorhynchus* were constructed with 17, 18 and 18 occurrence localities, respectively (Fig. 3.11 – 3.13., 3.15 – 3.17.). All models possessed a training AUC of  $\geq 0.85$  (Table 3.6.), indicating that the

data fit the models well. The average estimated habitat suitability at occurrence points was  $63.71 \pm 26.91$  (range: 6.65 – 100). The jackknife validation indicated high statistical significance ( $p < 0.005$ ) at a success rate ranging from 65 – 95% for the vector models when the Lower Presence Threshold was applied (Table 3.7.). Variable importance was measured via the internal jackknife test, and showed that distance to water, mean temperature of the coldest quarter, and AASHTO contained the most information compared to other variables, and were the most important predictors of habitat suitability within the grasslands of the study area (Fig. 3.7. – 3.9.).

### ***Evaluation: Comparison to Greater Prairie-chicken Nest Location and Plasmodium Incidence***

The individual models of *Culex tarsalis* ( $p = 0.000$ , two-tailed  $t$  test; Table 3.9., Fig. 3.21.), *Culex salinarius* ( $p = 0.000$ , two-tailed  $t$  test; Table 3.9., Fig. 2.22.) and the combined model ( $0.000$ , two-tailed  $t$  test; Table 3.9., Fig. 2.23.) indicated a significantly higher probability of vector occurrence at Greater Prairie-chicken nest locations than randomly selected grassland sites. The Monte Carlo resampled nest locations of uninfected Greater Prairie-chicken had a probability of vector occurrence for *Culex tarsalis* of 36.78 (95% CI 20.57 - 54.25), *Culex salinarius* 34.34 (95% CI 15.99 - 51.26), and combined *Culex* model of 35.41 (95% CI 19.84 - 55.41). The mean probability of vector occurrence at infected nests of the individual models (*Culex tarsalis*,  $\bar{x}=50.31$ ; *Culex salinarius*,  $\bar{x}=45.51$ , Table 3.8.) and combined model ( $\bar{x}=47.91$ , Table 3.8.) did not fall outside the confidence interval for uninfected nest locations; hence I found no significant difference between nest of infected versus uninfected females (Fig. 3.24 – 3.26.).

## **Discussion**

Ecological niche models of medically important vectors species have predominately been developed at broad spatial scales (continental and country-wide distributions) with ( $\geq 1$  km resolutions; Abdel-Dayem *et al.* 2012, Ayala *et al.* 2009, Foley *et al.* 2008, Foley *et al.* 2009, Laporta *et al.* 2012, Levine *et al.* 2004, Masuoka *et al.* 2009, Moffett *et al.* 2007, Sweeney *et al.* 2007). Spatial resolutions  $\geq 1$  km are often too coarse to adequately identify small mosquito habitats (Foley *et al.* 2009), hence there is a need to develop of high resolution maps identifying



areas potentially habitable to vector species. Accurate, high resolution niche models in combination with epidemiological data can help determine where disease transmission is likely to occur (Foley *et al.* 2008). Here, I constructed high resolution ecological niche models at a local scale (extent of the study site, 283 km<sup>2</sup>), focusing on multiple vector species within the grassland habitat that are potentially involved in the transmission cycle of infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, and West Nile Virus encephalitis) and avian malaria. Although the species' identity of infectious encephalitides, and avian malaria vectors within the study area have not been confirmed, there is evidence for *Culex* species, particularly *Culex tarsalis*, *Culex salinarius* to be vectors of infectious encephalitides (Flock 2012, Kansas State University 2009) and avian malaria disease agents (*Plasmodium*, Janovy 1966) in Kansas. Furthermore, *Aedes* species have been implicated as important bridge vectors of infectious encephalitis to humans and livestock (Center for Disease Control and Prevention 2012). *Aedes sollicitans*, *Aedes nigromaculis*, *Aedes vexans* and *Aedes taeniorhynchus* were included in the analysis because they are amongst the most abundant potential vector species within the genus *Aedes*.

The niche models were developed with a suite of predictor variables (n=48) based on the ecology of mosquito species encountered within the study site. In particular bioclimatic variables (temperature, precipitation) are biologically significant (Peterson 2001), because they address factors that potentially limit mosquito distribution (De Barros *et al.* 2007, Foley *et al.* 2008, Foley *et al.* 2009). For example, differences in precipitation during the sampling season or driest quarter of the year may lead to heterogeneity in the distribution of breeding sites, giving rise to the observed presence/absence of mosquito vectors at sample locations. Nonetheless, not all potential environmental variables were used in the construction of the niche models. For example, I excluded elevation, since it represents an indirect gradient, which rarely directly affects species' distributions; instead it has a strong correlation to other predictors, such as temperature and precipitation (Elith *et al.* 2009). I also excluded variables for which sampling was insufficient. Although distance to agriculture has been shown to be ecologically relevant for species within the study area (*Culex tarsalis*, Edmunds 1955), the sample locations within the study area were located at a distance of 711.23±416.83 m (range: 150-1530 m), which would have introduced a bias in the model since locations at close proximity to agricultural fields remained unsampled.

### ***Ecological niche modeling of important vector species***

Overall, the predictive power of 4 ecological niche models: 1) a combined model for *Culex tarsalis*/*Aedes sollicitans*/*Aedes nigromaculis*, 2) *Culex salinarius*, 3) *Aedes vexans*, and 4) *Aedes taeniorhynchus* within the study area was better than random based on the training AUC and jackknife validation tests. All models possessed a training AUC of  $\geq 0.85$  (Table 3.6.), which indicated good model fit. Furthermore, the jackknife validation tests of the models created for the vector species of interest were highly significant ( $p < 0.0005$ ). The most important predictor variables shared by all 4 ecological niche models were: distance to water, Topographic Wetness Index (TWI), AASHTO (soil particle size distribution), and mean temperature during the coldest quarter.

The ecological niche model created for *Culex tarsalis*, *Aedes sollicitans*, and *Aedes nigromaculis* described highly suitable areas which were in close proximity to water sources, had a high TWI, and high levels of precipitation during the driest quarter of the year. This model is in accordance with the biology of *Aedes sollicitans*, *Aedes nigromaculis*, and *Culex tarsalis*, because TWI and distance to water source include the attributes important to larval habitats, from small sources of standing water to large ponds (*Aedes sollicitans*, Crains 2010; *Aedes nigromaculis*, Janovy, 1966; *Culex tarsalis*, Crans 2010). Areas with increased precipitation during the driest quarter of the year provide ephemeral larval habitats when water resources are limited.

*Culex salinarius*, the salt marsh *Culex*, has a wide range of salt tolerance, and is commonly observed in grassland habitats. This species is particularly associated with rotting vegetation around large bodies of water because they create an infusum which acts as oviposition attractant (Crans 2010). It has also been shown that *Culex salinarius* prefers densely vegetated larval habitats, which are commonly encountered near riparian areas (Slaff 1990). The model for *Culex salinarius* was dominated by variables that are in accordance with the ecology of this species, such as distance to water and distance to woodland. Also prevalent in the maximum entropy model was mean temperature during the coldest quarter; *Culex salinarius* has been identified as vector species sensitive to extreme temperatures below freezing (Crans 2010), hence in the absence of shelters (e.g. human dwellings) minimum temperatures during the coldest quarter of the year may influence the species' distribution across the study area.

*Aedes vexans*, the inland floodwater mosquito, is one of the most abundant vector species within the continental United States, and can be found at high population densities in Kansas (DeMoss Hill 1939, Edman *et al.* 1964, Lungstrom *et al.* 1961). The species' seasonal distribution is influenced by precipitation patterns, which give rise to ephemeral larval habitats (Crans 2010, Schafer *et al.* 2006, Shaman *et al.* 2002). The model generated for *Aedes vexans* revealed that a combination of layers including distance to water, TWI and AASHTO (describes the particle size distribution) were associated with suitable environmental conditions. Although this species can be found in numerous habitats, it is predominantly found in transient water pools (Crans 2010) located in grassland habitats, where an increased TWI (Shaman *et al.* 2002) and clay soils provide suitable larval habitats.

*Aedes taeniorhynchus*, also known as the salt-marsh mosquito, has undergone recent adaptation to tolerate habitats with a wide range of salinities (Nayar, 1974). In inland areas it has been shown to be associated with areas rich in fossil fuels, and was first reported in the central Great Plains in 1973 (Oklahoma, Harrison *et al.* 1973). *Aedes taeniorhynchus* prefers to lay eggs in moist or dry soil at the periphery of large bodies of water, particularly ponds and marshes that are associated with decaying vegetation (Lancaster *et al.* 2007, Nielsen *et al.* 1953). The model created for *Aedes taeniorhynchus* was dominated by the distance to water variable, which is in accordance to the species requirement for large bodies of standing water. In addition this species was strongly influenced by mean temperature during the coldest quarter and mean precipitation during the driest quarter. The overwintering egg stage of *Aedes taeniorhynchus* has been shown to be more sensitive to low temperatures experienced during the winter months than other *Aedes* species within the study area (*Aedes sollicitans*, Knight 1967). Since the proliferation of this species is strongly correlated with precipitation patterns (Carlson *et al.* 1985, Wilson *et al.* 2002), their distribution within the study area may be explained by differences in precipitation patterns during the driest quarter of the year, when water resources are limited.

### ***Comparison to Disease Incidence***

In the United States ecological niche maps of vector species have predominately been developed from a public health perspective to evaluate the link between probability of vector occurrence and human incidence of infectious diseases. However, epidemiological data based on

human incidence reports often obscures the spatial dimension of pathogen transmission because the location of pathogen exposure is often not investigated; instead the location of residence is used as a surrogate (Eisen *et al.* 2010). In contrast to these previous studies, I focused on multiple vector species solely within the grassland habitat that are potentially involved in the transmission cycle of infectious encephalitides and avian malaria. The grassland ecosystem is of particular interest because, 1) it represents an interface of the transmission of infectious diseases between mammals and birds (livestock and grassland nesting birds), 2) grassland nesting birds are involved in the principal amplification cycle of these diseases in the Great Plains, and 3) disease transmission to grassland bird species can be assumed to occur within a narrow spatial and temporal range of the nesting season that contributes to the incidence of human exposure later in the summer or early fall. Using the Greater Prairie-chicken as a surrogate species for other grassland nesting birds, I found that nest locations were associated with a higher probability of vector occurrence than other potentially available grassland habitats. This overlap between high probability vector habitat and nest locations is an indicator of increased risk of mosquito parasitism and could potentially serve as an indicator of disease amplification risk. Unexpectedly, I did not find a significant difference in the probability of vector occurrence at nests of infected female Greater Prairie-chicken versus uninfected females. Although few studies have successfully demonstrated the correlation with increased probability of vector occurrence and disease incidence (Carlson *et al.* 2011), vector abundance models rather than presence-only models may be better predictors of disease incidence (Eisen *et al.* 2008).

### ***Assumptions and Limitations***

Despite the predictive power of the ecological niche models created for important vector species, this study has several assumptions and limitations that should be noted. First, I assumed that adult mosquito occurrence is an indicator of suitable habitat conditions. I feel this is a valid assumption given adult mosquitoes are located within close proximity of breeding sites and the small attractiveness range of CDC CO<sub>2</sub> traps (< 30 m, Service 1993). It is, therefore, unlikely that the use of adult mosquito occurrence compared to larval occurrence data affects the accuracy of the model predictions. A second assumption was that that 20 occurrence records were sufficient to predict the distribution of vector species within the study area. As established by

Pearson *et al.* 2007, as few as 5 occurrence records produce accurate predictions of species' distributions. Third, the most abundant vector species, *Culex tarsalis*, *Aedes sollicitans*, and *Aedes nigromaculis* were encountered at all 20 sample locations. While it may be argued that the combined model used to describe the distribution of these species instead reflects the distribution of trap locations; it is important to emphasize that ecological niche models identify suitable habitat conditions based on presence data only, not absence data. Hence, I believe that these models adequately describe the distribution of these species within the study area. Fourth, the analysis was conducted at a small spatial scale (283 km<sup>2</sup>), which can lead to the selection of ecologically irrelevant variables. Although ecological niche models have been performed at smaller spatial scales (< 54 km<sup>2</sup>, Khatchikian *et al.* 2011), I chose to only use potentially ecologically relevant variables for the construction of ecological niche models to limit the effects of the sample area. Lastly, the realism of ecological niche models is strongly dependent the variables used for their construction. I recognize that the Normalized Difference Vegetation Index (NDVI) is an important predictor variable in the distribution of mosquito species, however its available resolution of 1 km was too coarse for the construction of the high resolution niche models for this study.

### ***Conclusion***

The grasslands of the central Great Plains represent an interface for complex transmission dynamics between humans, livestock, and wildlife species, particularly grassland nesting birds. In the grassland ecosystem the enzootic cycle of infectious encephalitides and avian malaria are maintained through the transmission between *Culex* species and grassland nesting birds. My results of the Greater Prairie-chicken nesting habitat analysis confirmed, that nest locations were located in highly suitable habitat of *Culex* species. This overlap in the local distribution of vectors and hosts not only demonstrates that grassland nesting birds are at risk of being parasitized by mosquitoes and associated pathogens, but also strongly supports the mechanism of transmission and amplification involved in the primary enzootic cycle of arboviruses and haemosporidians (*Plasmodium* species). While this poses a significant risk to the conservation of grassland nesting birds, other wildlife species as well as, livestock and humans are at risk. For example, suitable environmental conditions can exacerbate West Nile Virus amplification in the

environment, due to the early emergence of *Culex* vector species, and lead to an increased risk of exposure in humans. My maps highlight habitat suitability and amenable climatic conditions that influence the probability of occurrence of the vector species (*Culex tarsalis*, *Culex salinarius* and *Aedes vexans* have high bridge vector competence) associated with West Nile Virus encephalitis. These maps and predictive models developed from their content could be used by local public health officials to notify the public health of increased disease risk on the neighborhood scale.

Vectors distributions can be modeled with high predictive accuracy due to the strong association with biophysical (environmental and climatic) variables. The knowledge of these associations has been utilized to construct predictive distribution maps identifying suitable habitats, where exposure to vector species is likely to occur. Understanding the spatial patterns of exposure to dipteran vectors and their associated pathogens is critical for epidemiological research to target limited surveillance, prevention, control, and reduce the incidence of vector-borne infectious diseases (Eisen *et al.* 2008). The probabilistic distribution maps created here for medically important vectors species of infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, West Nile Virus encephalitis) and avian malaria are the initial step in understanding the disease transmission dynamics in the grassland of the central Great Plains.

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## Figures and Tables

Table 3.1. Most abundant vector species collected during the sample season (May - July, 2010) at 20 sites in in the grasslands of the eastern Smoky Hill eco-region, Kansas.

Species	BS1	BS2	BS3	BS4	BS6	BS7	BS8	BS9	BS10	BS11	BS12	BS13	BS14	BS15	BS16	W1	W2	W3	W4	W5	Total	%
<i>Aedes sollicitans</i>	39	84	108	201	113	504	410	246	2,402	123	88	220	87	311	340	80	25	187	6	6	5,580	50.84
<i>Aedes nigromaculis</i>	43	25	47	80	57	566	246	32	305	93	40	120	36	305	222	24	19	142	4	7	2,413	21.98
<i>Culex tarsalis</i>	41	31	30	16	3	53	72	101	65	9	25	5	38	71	33	103	34	92	3	3	828	7.54
<i>Aedes vexans</i>	13	243	256	14	3	6	29	2	113	3	101	18	22	4	172	0	2	11	0	0	1,012	9.22
<i>Aedes taeniorhynchus</i>	9	4	25	4	1	170	47	25	195	26	43	0	40	40	12	1	1	95	2	0	740	6.74
<i>Culex salinarius</i>	10	16	4	2	13	81	12	11	9	6	18	0	8	11	0	16	12	154	1	19	403	3.67
<b>Total</b>	155	403	470	317	190	1,380	816	417	3,089	260	315	363	231	742	779	224	93	681	16	35	10,976	100
<b>%Total</b>	1.41	3.67	4.28	2.89	1.73	12.57	7.43	3.80	28.14	2.37	2.87	3.31	2.10	6.76	7.10	2.04	0.85	6.20	0.15	0.32	100.00	

Table 3.2. Occurrence records of mosquito species collected during the sample season (May – July, 2010) at 20 sites in the grasslands of the eastern Smoky Hill eco-region, Kansas.

Site ID	Geographic reference		Species occurrence records					
	Northing	Easting	<i>Aedes sollicitans</i>	<i>Aedes nigromaculis</i>	<i>Culex tarsalis</i>	<i>Aedes vexans</i>	<i>Aedes taeniorhynchus</i>	<i>Culex salinarius</i>
BS1	622056	4366146	1	1	1	1	1	1
BS2	615644	4360203	1	1	1	1	1	1
BS3	621509	4359691	1	1	1	1	1	1
BS4	621101	4366440	1	1	1	1	1	1
BS6	614953	4363595	1	1	1	1	1	1
BS7	627011	4355338	1	1	1	1	1	1
BS8	626702	4353664	1	1	1	1	1	1
BS9	618475	4361437	1	1	1	1	1	1
BS10	617920	4360485	1	1	1	1	1	1
BS11	628193	4362326	1	1	1	1	1	1
BS12	628242	4363409	1	1	1	1	1	1
BS13	605370	4369611	1	1	1	1	0	0
BS14	615638	4360980	1	1	1	1	1	1
BS15	621412	4364537	1	1	1	1	1	1
BS16	621275	4366746	1	1	1	1	1	0
W1	619707	4361234	1	1	1	0	1	1
W2	620866	4359818	1	1	1	1	1	1
W3	626760	4355978	1	1	1	1	1	1
W4	623481	4364995	1	1	1	0	1	1
W5	620011	4372589	1	1	1	0	0	1
<b>Sum of Occurrences</b>			<b>20</b>	<b>20</b>	<b>20</b>	<b>17</b>	<b>18</b>	<b>18</b>

Table 3.3. Description of parameters used to construct ecological niche models of vectors species with the grasslands of Cloud County, Kansas.

Parameter	Description	Parameter	Description
Aspect	Aspect	$T_{max}(wq)$	Current average maximum temperature of the warmest quarter
Slope	Slope	$T_{max}(ss)$	Current average maximum temperature of the sample season
Curv	Curvature of the terrain	$T_{max}(jan)$	Current average maximum temperature of January
TWI	Topographic Wetness Index	$T_{max}(apr)$	Current average maximum temperature of April
$T_{min}(ave)$	Current average minimum annual temperature	$T_{max}(may)$	Current average maximum temperature of May
$T_{min}(cq)$	Current average minimum temperature of the coldest quarter	$T_{max}(jun)$	Current average maximum temperature of June
$T_{min}(wq)$	Current average minimum temperature of the warmest quarter	$T_{max}(jul)$	Current average maximum temperature of July
$T_{min}(ss)$	Current average minimum temperature of the sample season (May – July)	$T_{seas}$	Annual temperature seasonality
$T_{min}(jan)$	Current average minimum temperature of January (coldest month)	$P_{mean}(ave)$	Current average mean annual precipitation
$T_{min}(apr)$	Current average minimum temperature of April	$P_{mean}(dq)$	Current average mean precipitation of the driest quarter
$T_{min}(may)$	Current average minimum temperature of May	$P_{mean}(wq)$	Current average mean precipitation of the wettest quarter
$T_{min}(jun)$	Current average minimum temperature of June	$P_{mean}(ss)$	Current average mean precipitation of the sample season
$T_{min}(jul)$	Current average minimum temperature of July	$P_{mean}(apr)$	Current average mean precipitation of April
$T_{mean}(ave)$	Current average mean annual temperature	$P_{mean}(may)$	Current average mean precipitation of May
$T_{mean}(cq)$	Current average mean temperature of the coldest quarter	$P_{mean}(jun)$	Current average mean precipitation of June
$T_{mean}(wq)$	Current average mean temperature of the warmest quarter	$P_{mean}(jul)$	Current average mean precipitation of July
$T_{mean}(ss)$	Current average mean temperature of the sample season	$P_{seas}$	Annual precipitation seasonality
$T_{mean}(jan)$	Current average mean temperature of January	AASHTO	AASHTO group
$T_{mean}(apr)$	Current average mean temperature of April	HYSOIL	Hydrologic group
$T_{mean}(may)$	Current average mean temperature of May	DRACLA	Drainage class
$T_{mean}(jun)$	Current average mean temperature of June	$Dist_{edge}$	Distance to edge
$T_{mean}(jul)$	Current average mean temperature of July	$Dist_w$	Distance to water
$T_{max}(ave)$	Current average maximum annual temperature	$Dist_{wl}$	Distance to woodland
$T_{max}(cq)$	Current average maximum temperature of the coldest quarter	$Dist_r$	Distance to road



Table 3.4. Highly correlated variables ( $r \geq 0.90$ ). I generated 100 random points across the study site, extracted data from the bioclimatic variables and performed a Pearson's correlation analysis.

<b>Correlated variables</b>	<b>r</b>	<b>Correlated variables</b>	<b>r</b>
T <sub>min</sub> (ave) x T <sub>min</sub> (cq)	0.97	T <sub>mean</sub> (cq) x T <sub>max</sub> (ave)	0.93
T <sub>min</sub> (ave) x T <sub>min</sub> (wq)	0.95	T <sub>mean</sub> (cq) x T <sub>max</sub> (cq)	0.94
T <sub>min</sub> (ave) x T <sub>min</sub> (ss)	0.96	T <sub>mean</sub> (cq) x T <sub>max</sub> (jan)	0.91
T <sub>min</sub> (ave) x T <sub>min</sub> (may)	0.91	T <sub>mean</sub> (cq) x T <sub>max</sub> (may)	0.92
T <sub>min</sub> (ave) x T <sub>mean</sub> (ave)	0.93	T <sub>mean</sub> (wq) x T <sub>max</sub> (apr)	0.90
T <sub>min</sub> (ave) x T <sub>mean</sub> (cq)	0.92	T <sub>mean</sub> (wq) x T <sub>max</sub> (may)	0.90
T <sub>min</sub> (ave) x T <sub>mean</sub> (wq)	0.95	T <sub>mean</sub> (ss) x T <sub>mean</sub> (wq)	0.98
T <sub>min</sub> (ave) x T <sub>mean</sub> (ss)	0.96	T <sub>mean</sub> (may) x T <sub>mean</sub> (ss)	0.91
T <sub>min</sub> (cq) x T <sub>mean</sub> (cq)	0.91	T <sub>mean</sub> (may) x T <sub>max</sub> (may)	0.93
T <sub>min</sub> (wq) x T <sub>mean</sub> (ave)	0.97	T <sub>mean</sub> (jun) x T <sub>max</sub> (ss)	0.90
T <sub>min</sub> (wq) x T <sub>mean</sub> (cq)	0.93	T <sub>mean</sub> (jun) x T <sub>max</sub> (jun)	0.90
T <sub>min</sub> (wq) x T <sub>mean</sub> (wq)	1.00	T <sub>mean</sub> (jul) x T <sub>max</sub> (jul)	0.91
T <sub>min</sub> (wq) x T <sub>mean</sub> (ss)	0.98	T <sub>max</sub> (ave) x T <sub>max</sub> (cq)	0.99
T <sub>min</sub> (wq) x T <sub>max</sub> (apr)	0.90	T <sub>max</sub> (ave) x T <sub>max</sub> (wq)	0.98
T <sub>min</sub> (wq) x T <sub>max</sub> (may)	0.90	T <sub>max</sub> (ave) x T <sub>max</sub> (ss)	0.99
T <sub>min</sub> (ss) x T <sub>min</sub> (wq)	0.99	T <sub>max</sub> (ave) x T <sub>max</sub> (jan)	0.94
T <sub>min</sub> (ss) x T <sub>mean</sub> (ave)	0.94	T <sub>max</sub> (ave) x T <sub>max</sub> (may)	0.95
T <sub>min</sub> (ss) x T <sub>mean</sub> (wq)	0.98	T <sub>max</sub> (ave) x T <sub>max</sub> (jun)	0.93
T <sub>min</sub> (ss) x T <sub>mean</sub> (ss)	1.00	T <sub>max</sub> (cq) x T <sub>max</sub> (wq)	0.96
T <sub>min</sub> (ss) x T <sub>mean</sub> (may)	0.91	T <sub>max</sub> (cq) x T <sub>max</sub> (ss)	0.96
T <sub>min</sub> (jan) x T <sub>mean</sub> (jan)	1.00	T <sub>max</sub> (cq) x T <sub>max</sub> (jan)	0.96
T <sub>min</sub> (may) x T <sub>min</sub> (ss)	0.93	T <sub>max</sub> (cq) x T <sub>max</sub> (may)	0.92
T <sub>min</sub> (may) x T <sub>mean</sub> (ss)	0.93	T <sub>max</sub> (ss) x T <sub>max</sub> (wq)	0.99
T <sub>min</sub> (may) x T <sub>mean</sub> (may)	0.94	T <sub>max</sub> (jan) x T <sub>max</sub> (ss)	0.91
T <sub>min</sub> (jun) x T <sub>min</sub> (wq)	0.93	T <sub>max</sub> (jan) x T <sub>max</sub> (may)	0.91
T <sub>min</sub> (jun) x T <sub>min</sub> (ss)	0.95	T <sub>max</sub> (apr) x T <sub>max</sub> (cq)	0.92
T <sub>min</sub> (jun) x T <sub>mean</sub> (wq)	0.93	T <sub>max</sub> (apr) x T <sub>max</sub> (ss)	0.92
T <sub>min</sub> (jun) x T <sub>mean</sub> (ss)	0.95	T <sub>max</sub> (apr) x T <sub>max</sub> (may)	0.93
T <sub>min</sub> (jul) x T <sub>min</sub> (wq)	0.92	T <sub>max</sub> (may) x T <sub>max</sub> (ss)	0.94
T <sub>min</sub> (jul) x T <sub>min</sub> (ss)	0.91	T <sub>max</sub> (jun) x T <sub>max</sub> (wq)	0.95
T <sub>min</sub> (jul) x T <sub>mean</sub> (wq)	0.92	T <sub>max</sub> (jun) x T <sub>max</sub> (ss)	0.95
T <sub>min</sub> (jul) x T <sub>mean</sub> (ss)	0.91	T <sub>max</sub> (jul) x T <sub>max</sub> (wq)	0.93
T <sub>mean</sub> (ave) x T <sub>mean</sub> (cq)	0.97	T <sub>max</sub> (jul) x T <sub>max</sub> (ss)	0.90
T <sub>mean</sub> (ave) x T <sub>mean</sub> (wq)	0.97	P <sub>mean</sub> (ave) x P <sub>mean</sub> (wq)	0.93
T <sub>mean</sub> (ave) x T <sub>mean</sub> (ss)	0.94	P <sub>mean</sub> (ave) x P <sub>mean</sub> (may)	0.90
T <sub>mean</sub> (ave) x T <sub>mean</sub> (may)	0.91	P <sub>mean</sub> (ave) x P <sub>mean</sub> (jun)	0.90
T <sub>mean</sub> (ave) x T <sub>max</sub> (ave)	0.95	P <sub>mean</sub> (apr) x P <sub>mean</sub> (ave)	0.90
T <sub>mean</sub> (ave) x T <sub>max</sub> (cq)	0.92	P <sub>mean</sub> (apr) x P <sub>mean</sub> (wq)	0.90
T <sub>mean</sub> (ave) x T <sub>max</sub> (ss)	0.91	P <sub>mean</sub> (apr) x P <sub>mean</sub> (jun)	0.90
T <sub>mean</sub> (ave) x T <sub>max</sub> (apr)	0.94	P <sub>mean</sub> (may) x P <sub>mean</sub> (wq)	0.95
T <sub>mean</sub> (ave) x T <sub>max</sub> (may)	0.94	P <sub>mean</sub> (jun) x P <sub>mean</sub> (wq)	0.95
T <sub>mean</sub> (cq) x T <sub>mean</sub> (wq)	0.93		

Table 3.5. Variable contributions and permutations of ecological niche models developed for vector species in the grassland of the Smoky Hills, Cloud County, Kansas.

Species	Variable contributions (permutations)										
<i>Culex tarsalis</i> , <i>Aedes sollicitans</i> , <i>Aedes nigromaculis</i>	Dist <sub>w</sub> , 0.31 (0.07)	TWI, 0.16 (0.37)	P <sub>mean</sub> (dq), 0.14 (0.11)	Dist <sub>wl</sub> , 0.13 (0.11)	AASHTO, 0.07 (0.16)	Dist <sub>edge</sub> , 0.06 (0.05)	T <sub>mean</sub> (cq), 0.05 (0.05)	Aspect, 0.05 (0.03)	Curv, 0.04 (0.06)		
<i>Aedes vexans</i>	Dist <sub>w</sub> , 0.25 (0.00)	TWI, 0.14 (0.27)	AASHTO, 0.12 (0.03)	Aspect, 0.11 (0.20)	P <sub>mean</sub> (dq), 0.09 (0.11)	T <sub>max</sub> (cq), 0.09 (0.09)	T <sub>mean</sub> (apr), 0.07 (0.15)	T <sub>mean</sub> (ss), 0.07 (0.09)	Dist <sub>r</sub> , 0.03 (0.00)	Dist <sub>edge</sub> , 0.03 (0.05)	
<i>Aedes taeniorhynchus</i>	Dist <sub>w</sub> , 0.24 (0.14)	T <sub>mean</sub> (cq), 0.18 (0.32)	P <sub>mean</sub> (dq), 0.16 (0.17)	AASHTO, 0.12 (0.10)	Aspect, 0.09 (0.05)	TWI, 0.06 (0.05)	Dist <sub>r</sub> , 0.05 (0.02)	Dist <sub>wl</sub> , 0.05 (0.02)	Dist <sub>edge</sub> , 0.04 (0.09)	T <sub>mean</sub> (apr), 0.01 (0.04)	
<i>Culex salinarius</i>	Dist <sub>w</sub> , 0.27 (0.07)	T <sub>mean</sub> (cq), 0.24 (0.34)	Dist <sub>wl</sub> , 0.16 (0.16)	AASHTO, 0.07 (0.03)	Aspect, 0.07 (0.11)	TWI, 0.07 (0.09)	P <sub>mean</sub> (dq), 0.06 (0.02)	Dist <sub>edge</sub> , 0.04 (0.08)	T <sub>max</sub> (jul), 0.01 (0.04)		

Table 3.6. Training gain without and with predictor variables of ecological niche models developed for vector species in the grassland of the Smoky Hills, Cloud County, Kansas.

Model	Variable, Training gain without variable (Training gain with variable)									
(Training AUC)										
<i>Culex tarsalis</i> ,										
<i>Aedes sollicitans</i>	Dist <sub>w</sub> , 0.36	TWI, 0.41	Dist <sub>wl</sub> , 0.47	P <sub>mean</sub> (dq),	AASHTO,	Dist <sub>edge</sub> , 0.48	T <sub>mean</sub> (cq),	Aspect, 0.50	Curv, 0.50	
<i>Aedes nigromaculis</i>	(0.18)	(0.07)	(0.08)	0.48 (0.08)	0.48 (0.03)	(0.01)	0.49 (0.07)	(0.05)	(0.01)	
<b>(0.86)</b>										
<i>Aedes vexans</i> <b>(0.88)</b>	Dist <sub>w</sub> , 0.43	TWI, 0.48	AASHTO,	Aspect, 0.50	P <sub>mean</sub> (dq),	T <sub>max</sub> (cq), 0.54	T <sub>mean</sub> (apr),	T <sub>mean</sub> (ss),	Dist <sub>r</sub> , 0.55	Dist <sub>edge</sub> , 0.55
	(0.15)	(0.07)	0.50 (0.07)	(0.07)	0.52 (0.08)	(0.06)	0.53 (0.04)	0.52 (0.05)	(0.01)	(0.02)
<i>Aedes taeniorhynchus</i>	Dist <sub>w</sub> , 0.58	AASHTO,	P <sub>mean</sub> (dq),	Aspect, 0.69	TWI, 0.70	T <sub>mean</sub> (cq),	dist <sub>edge</sub> , 0.71	dist <sub>wl</sub> , 0.72	T <sub>mean</sub> (apr),	Dist <sub>r</sub> , 0.74
<b>(0.90)</b>	(0.19)	0.66 (0.09)	0.68 (0.21)	(0.09)	(0.04)	0.71 (0.17)	(0.02)	(0.06)	0.74 (0.03)	(0.02)
<i>Culex salinarius</i> <b>(0.88)</b>	Dist <sub>w</sub> , 0.49	Dist <sub>wl</sub> , 0.57	T <sub>mean</sub> (cq),	AASHTO,	Aspect, 0.62	TWI, 0.62	Dist <sub>edge</sub> , 0.62	P <sub>mean</sub> (dq),	T <sub>max</sub> (jul),	
	(0.21)	(0.13)	0.58 (0.17)	0.62 (0.04)	(0.04)	(0.03)	(0.01)	0.65 (0.13)	0.65 (0.00)	

Table 3.7. Jackknife tests of distribution models (LTP, Lowest Presence Threshold) for the six most abundant disease vectors in the Smoky Hills of Cloud County, Kansas

Species	Maxent, LPT			
	Locality sample size	Threshold	Success	<i>p</i>
<i>Culex tarsalis</i> ,	20	6.657	15	2.44e <sup>-3</sup>
<i>Aedes sollicitans</i> ,				
<i>Aedes nigromaculis</i>				
<i>Aedes vexans</i>	17	10.699	11	4.32e <sup>-3</sup>
<i>Aedes taeniorhynchus</i>	18	4.523	17	3.50e <sup>-4</sup>
<i>Culex salinarius</i>	18	5.176	14	1.24e <sup>-3</sup>

Table 3.8. Vector probability of *Culex tarsalis*, *Culex salinarius*, and cumulative avian malaria vectors associated with Greater Prairie-chicken nests of females that tested positive for *Plasmodium* species.

Positive Females		Vector Probability	
Nest ID	<i>Culex tarsalis</i>	<i>Culex salinarius</i>	Combined avian malaria vectors
20076801	9.54	5.13	7.33
20076830	80.71	84.83	82.77
20076886	94.15	83.50	88.82
20090788	62.40	56.94	59.67
20097093	66.54	68.59	67.56
20097099	32.85	29.72	31.29
20100788	53.38	32.63	43.00
20110855	2.97	2.73	2.85
<b>Mean</b>	<b>50.31</b>	<b>45.51</b>	<b>47.91</b>

Table 3.9. Results of the 2-sample t-tests, to assess the differences in the probability of vector occurrence at nest locations versus potentially available grassland habitat.

<b>Vector</b>	<b>Group</b>	<b><i>n</i></b>	<b>Mean</b>	<b>SD</b>	<b>SE</b>	<b>DF</b>	<b><i>t</i></b>	<b><i>P</i> (two-tailed)</b>
<i>Culex tarsalis</i>	Random	111	23.3	22.9	2.2	217	-4.05	0.000
	Nest locations	111	36.5	25.5	2.4			
<i>Culex salinarius</i>	Random	111	19.6	21.7	2.1	217	-4.78	0.000
	Nest locations	111	34.4	24.2	2.3			
<i>Avian malaria vectors</i>	Random	111	21.9	21.1	2.0	217	-4.43	0.000
	Nest locations	111	35.4	24.3	2.3	217		

Figure 3.1. Study site location. Kansas landcover data were developed by the Kanas Applied Remote Sensing Laboratory at University of Kansas, Lawrence.

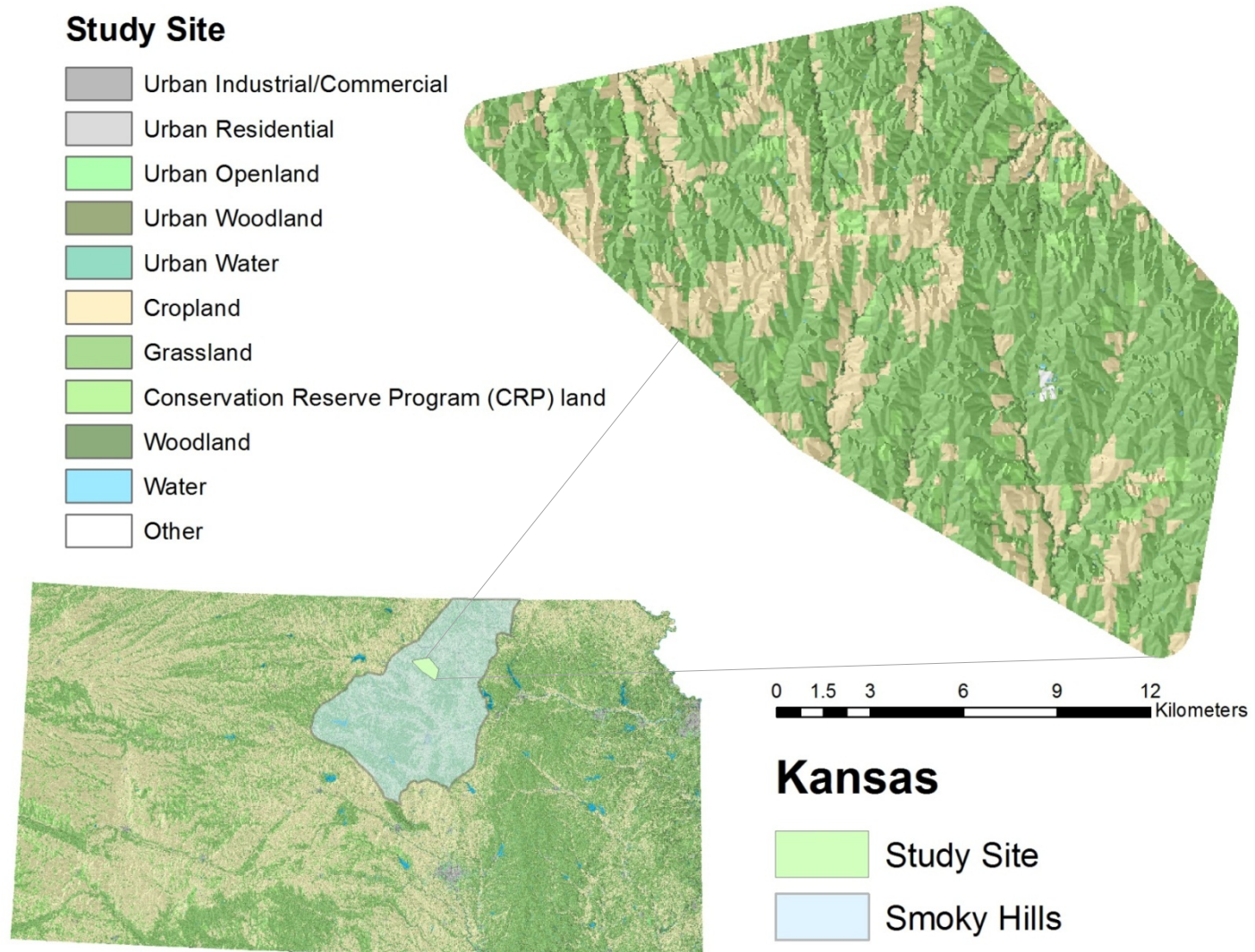


Figure 3.2. Elevation map of the eastern Smoky Hills study site, located in Cloud County, Kansas. The elevation data were used to derive the following topographic maps: aspect, slope, curvature, and TWI (Topographic Wetness Index).

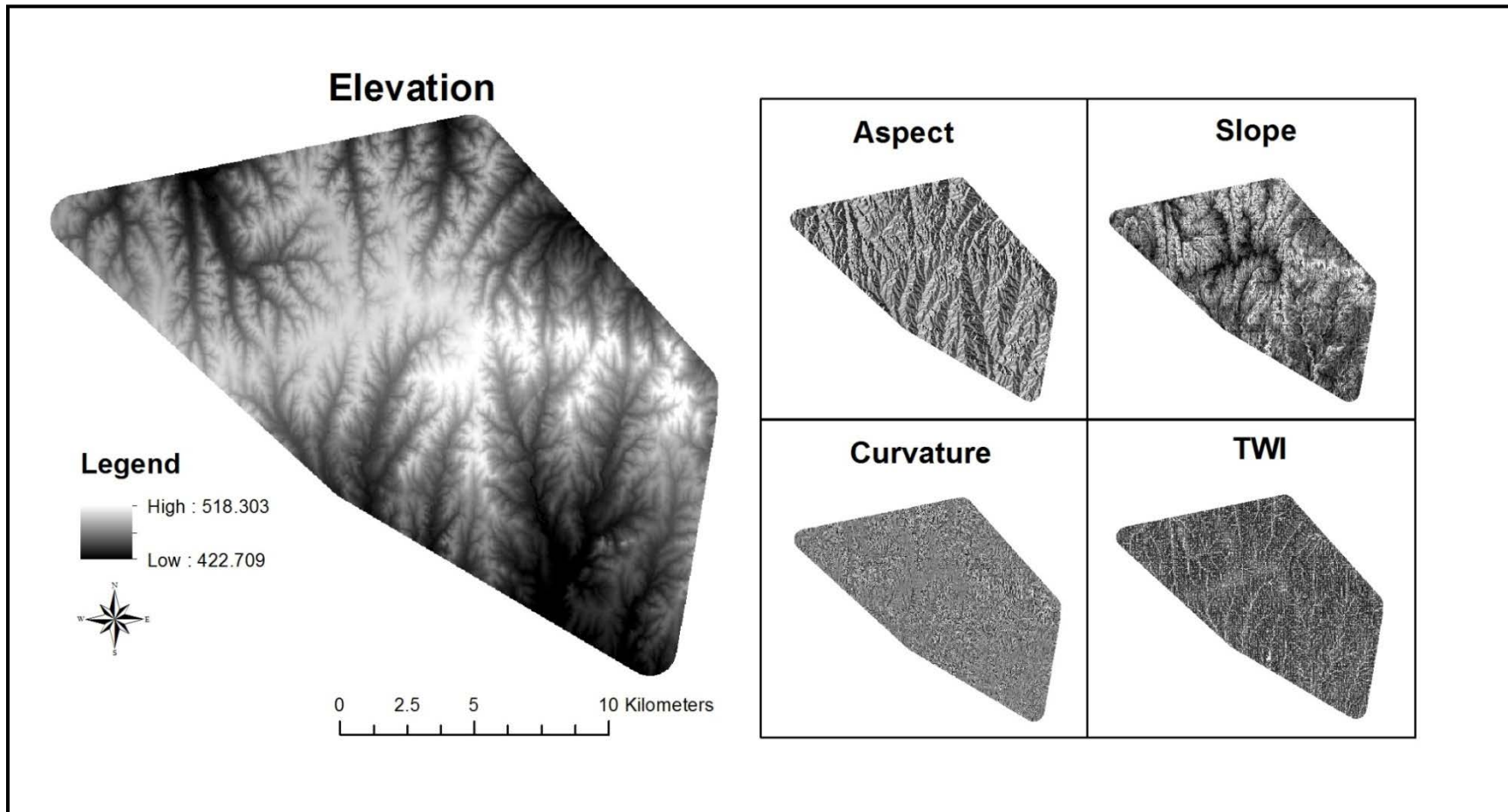




Figure 3.3. Landcover map of the eastern Smoky Hills study site, located in Cloud County, Kansas. The landcover data were used to derive the following distance measures: distance to woodland, distance to water, distance to edge, and distance to road. Distance measures are in meters.

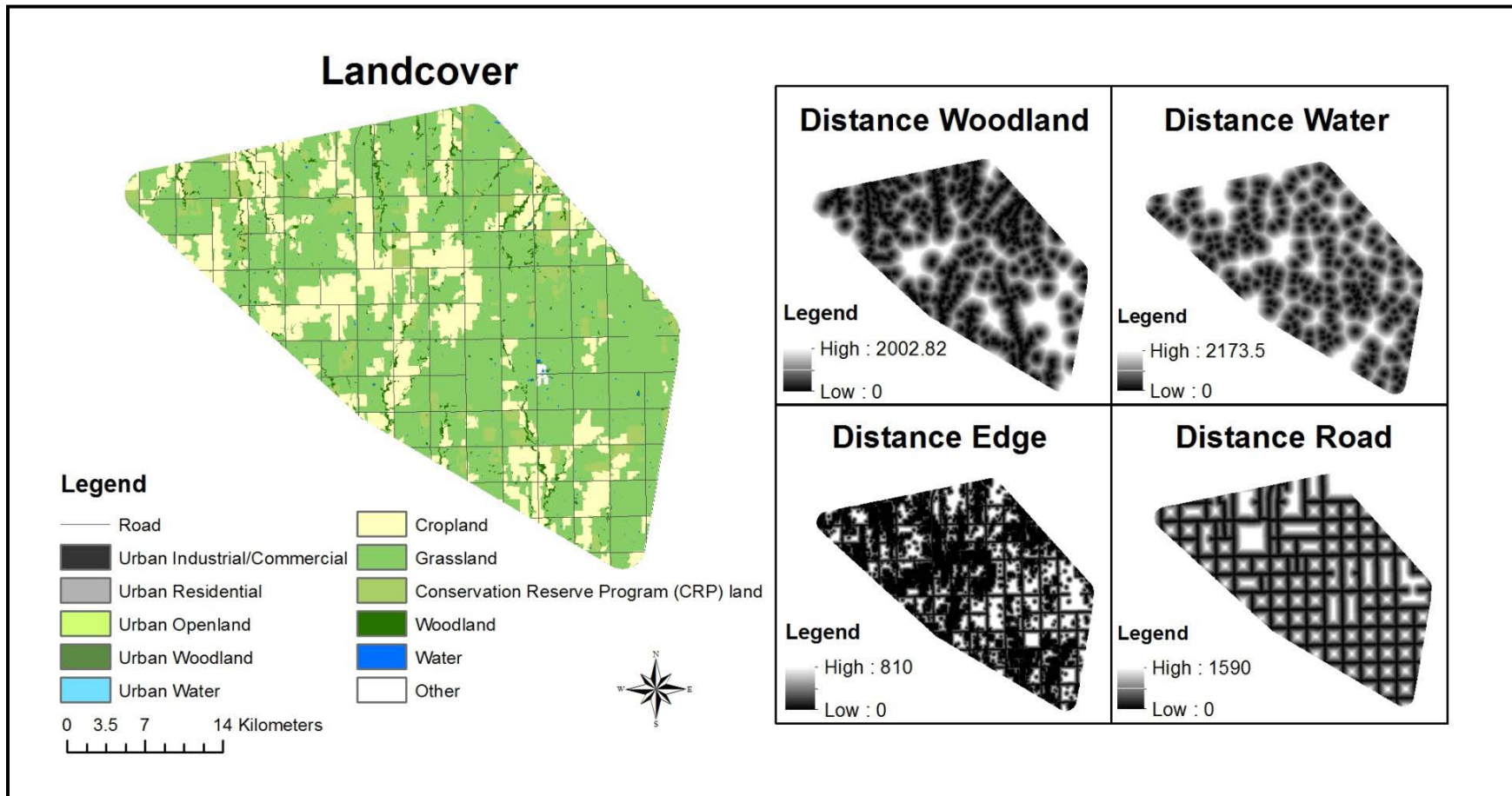


Figure 3.4. Soil map of the eastern Smoky Hills study site, located in Cloud County, Kansas. The soil data were retrieved from the Soil Geographic Database, I selected the following soil indices: AASHTO (describes the particle-size distribution), drainage class (describes the frequency and duration of wet periods), and hydrologic soil groups (estimates of runoff potential).

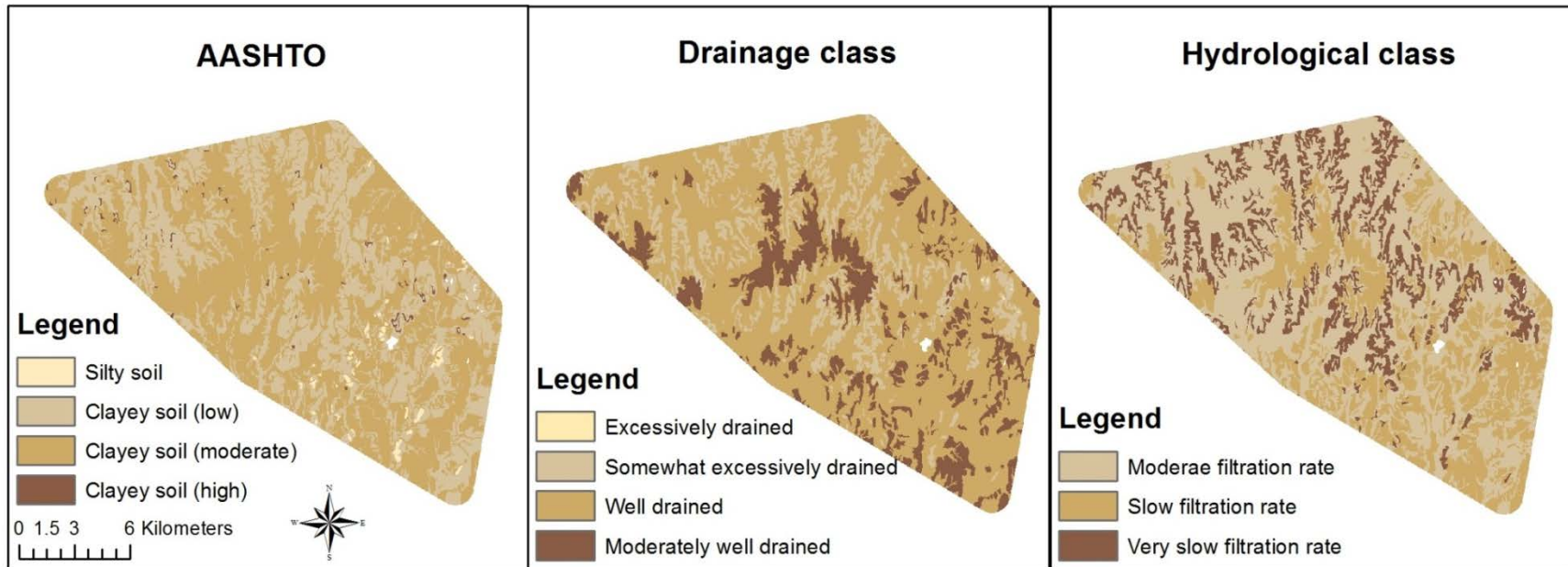


Figure 3.5. Greater Prairie-chicken nest distribution across the eastern Smoky Hill study site, Cloud County, Kansas. The inset provides a detailed view of the nest locations within the landcover map.

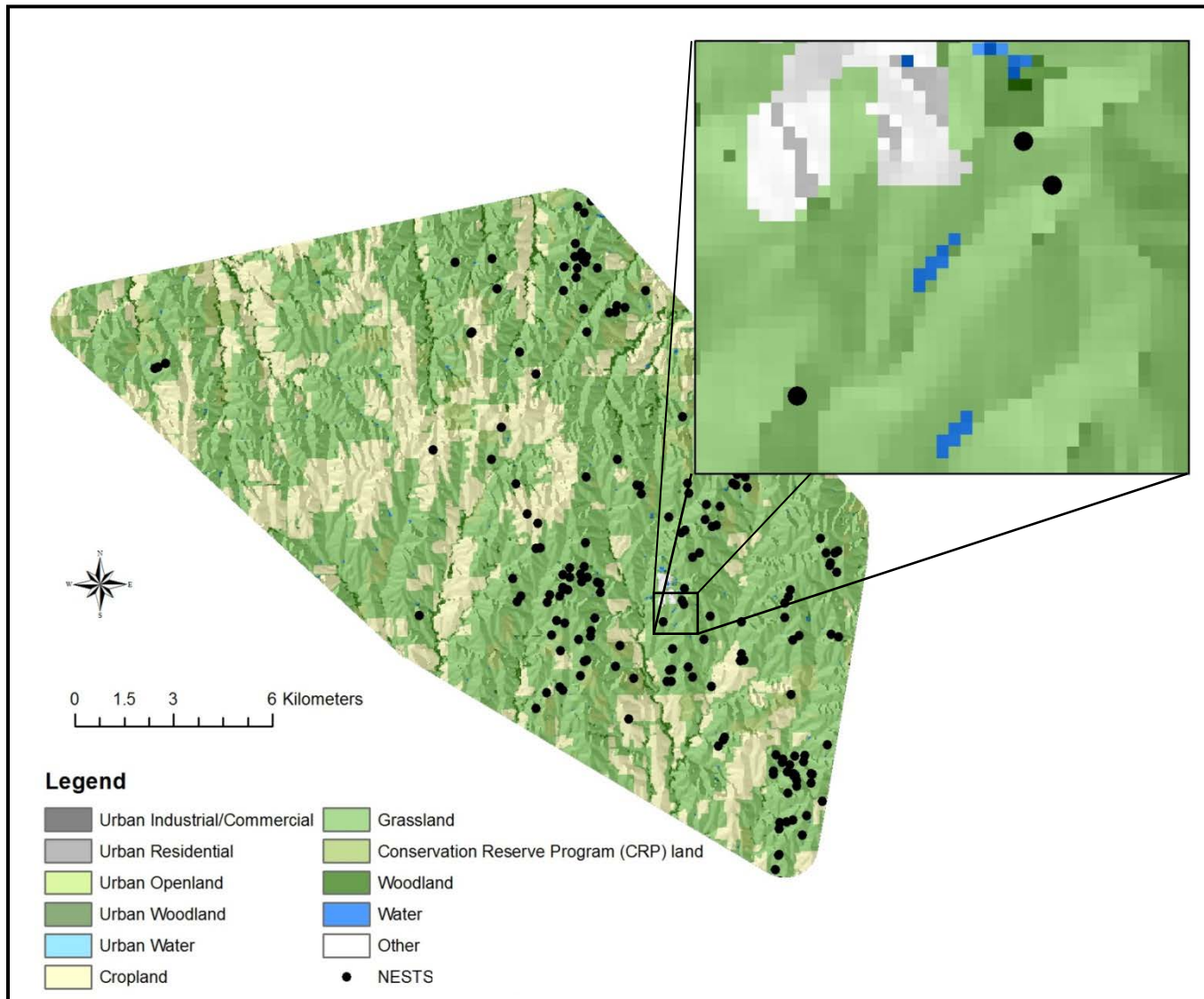


Figure 3.6. Jackknife test of training gain for *Culex tarsalis*, *Aedes sollicitans* and *Aedes nigromaculis*, which are competent vectors of West Nile virus and *Plasmodium* species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to water, distance to woodland, aspect, curvature, TWI (Topographic Wetness Index), mean temperature of the coldest quarter of the year, and mean precipitation of the driest quarter of the year.

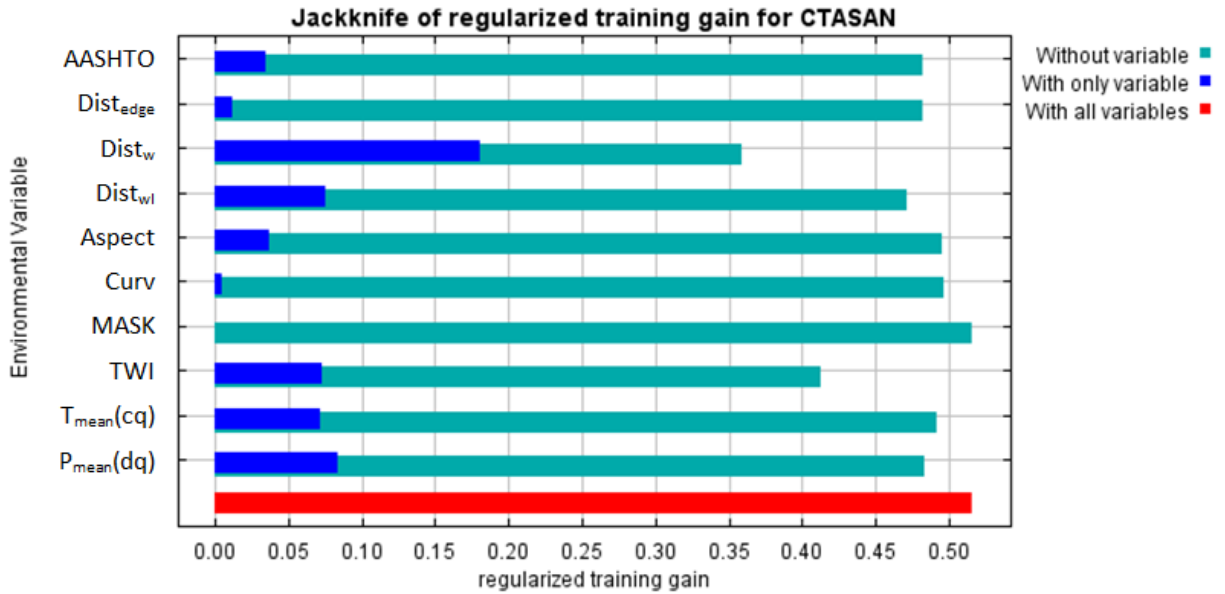


Figure 3.7. Jackknife test of training gain for *Culex salinarius*, a competent vector of West Nile Virus and *Plasmodium* species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to water, distance to woodland, aspect, slope, TWI (Topographic Wetness Index), maximum temperature in July, mean temperature of the coldest quarter of the year, and mean precipitation of the driest quarter of the year.

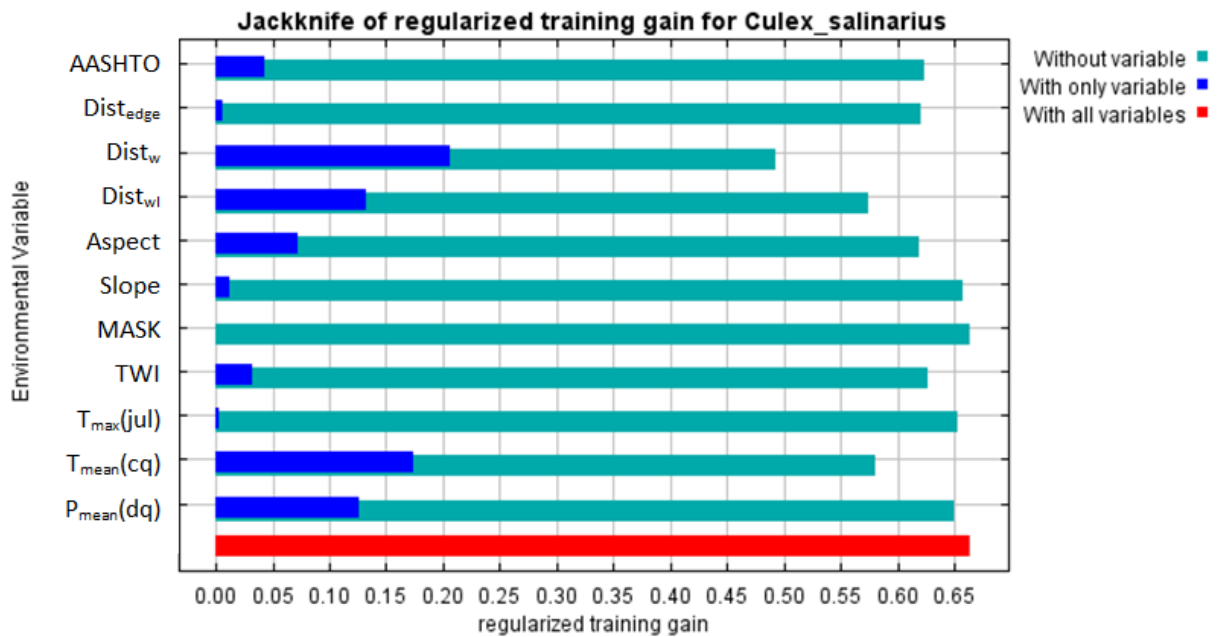


Figure 3.8. Jackknife test of training gain for *Aedes vexans*, a competent vector of West Nile Virus and *Plasmodium* species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to road, distance to water, aspect, TWI (Topographic Wetness Index), maximum temperature of the coldest quarter of the year, mean temperature of May, mean temperature during the sampling season and mean precipitation of the driest quarter of the year.

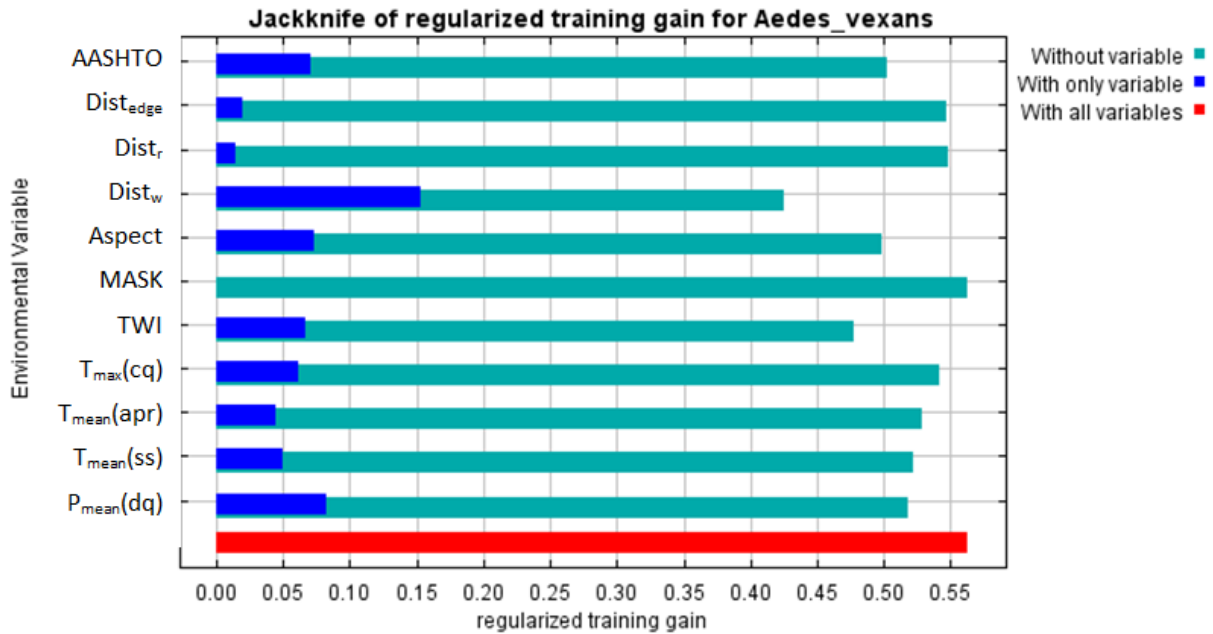


Figure 3.9. Jackknife test of training gain for *Aedes taeniorhynchus*, a competent vector of West Nile Virus and potential vector of *Plasmodium* species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to road, distance to water, distance to woodland, aspect, TWI (Topographic Wetness Index), mean temperature of April, mean temperature of the coldest quarter of the year, and mean precipitation of the driest quarter of the year.

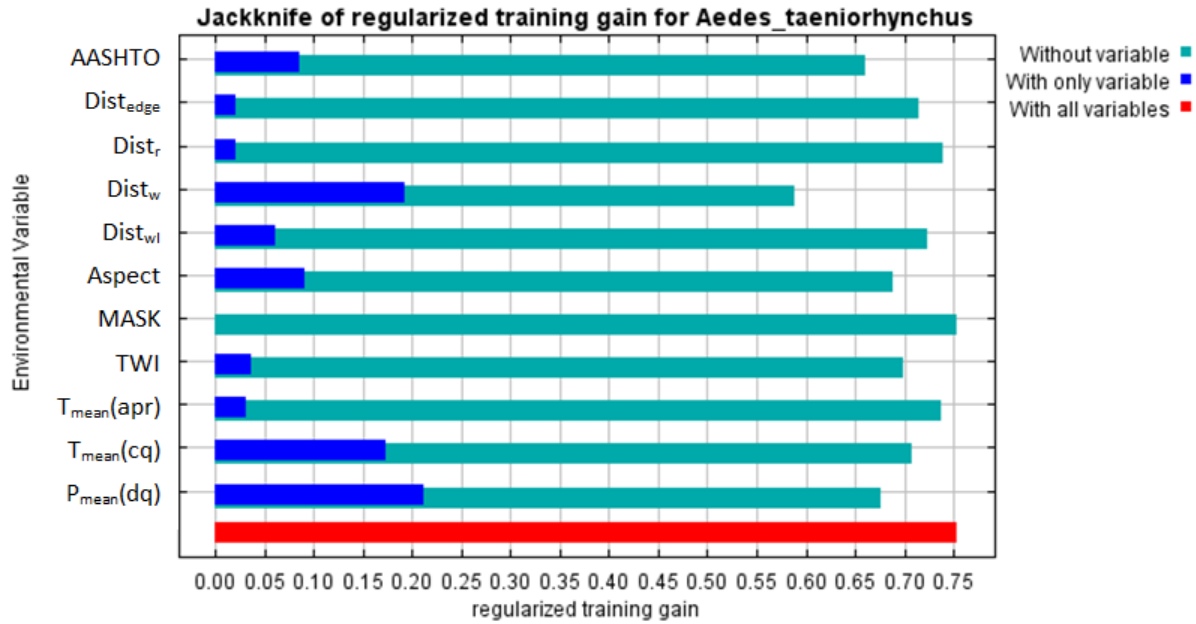




Figure 3.10. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Culex tarsalis*, *Aedes sollicitans*, and *Aedes nigromaculis* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

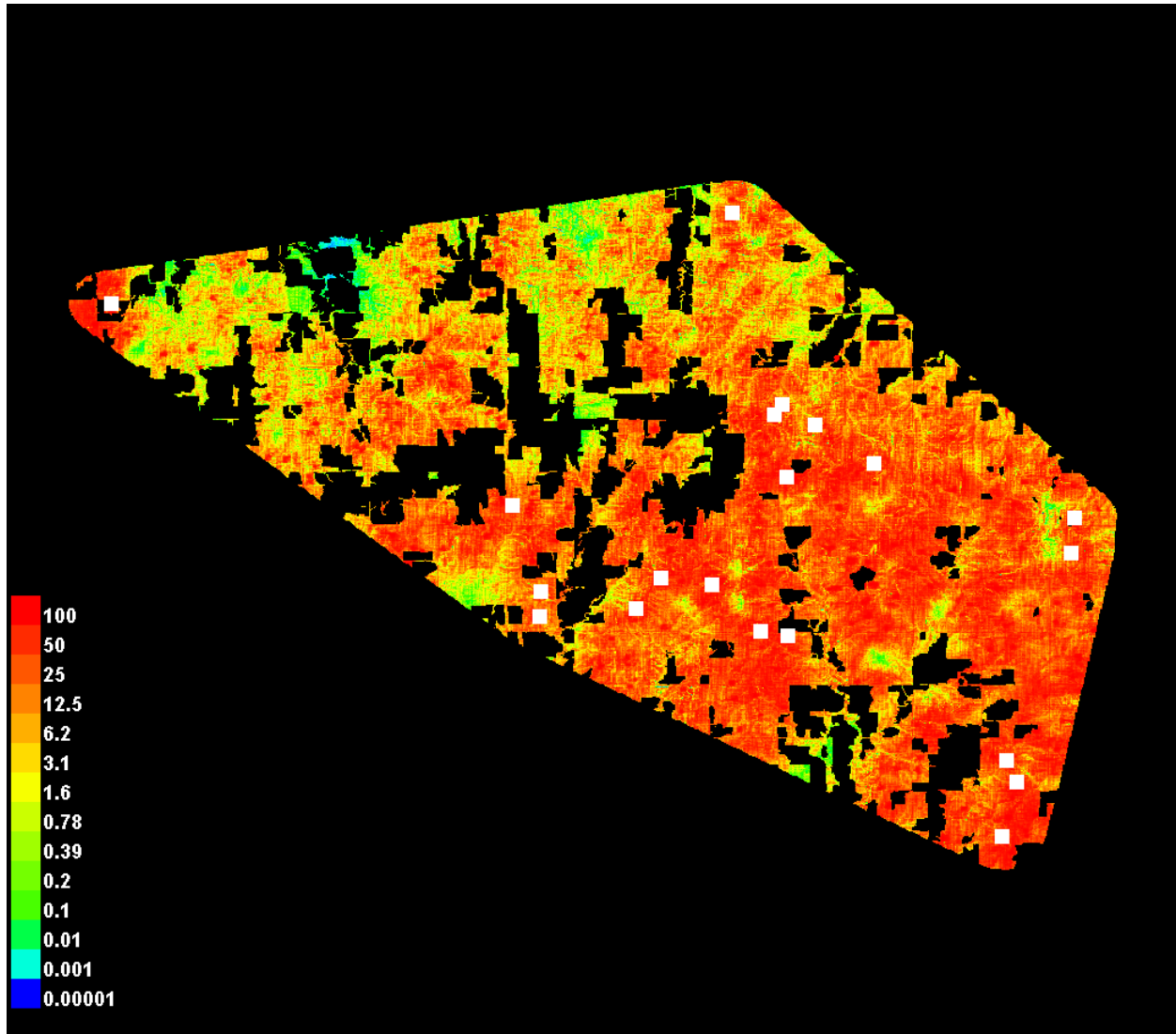




Figure 3.11. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Culex salinarius* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

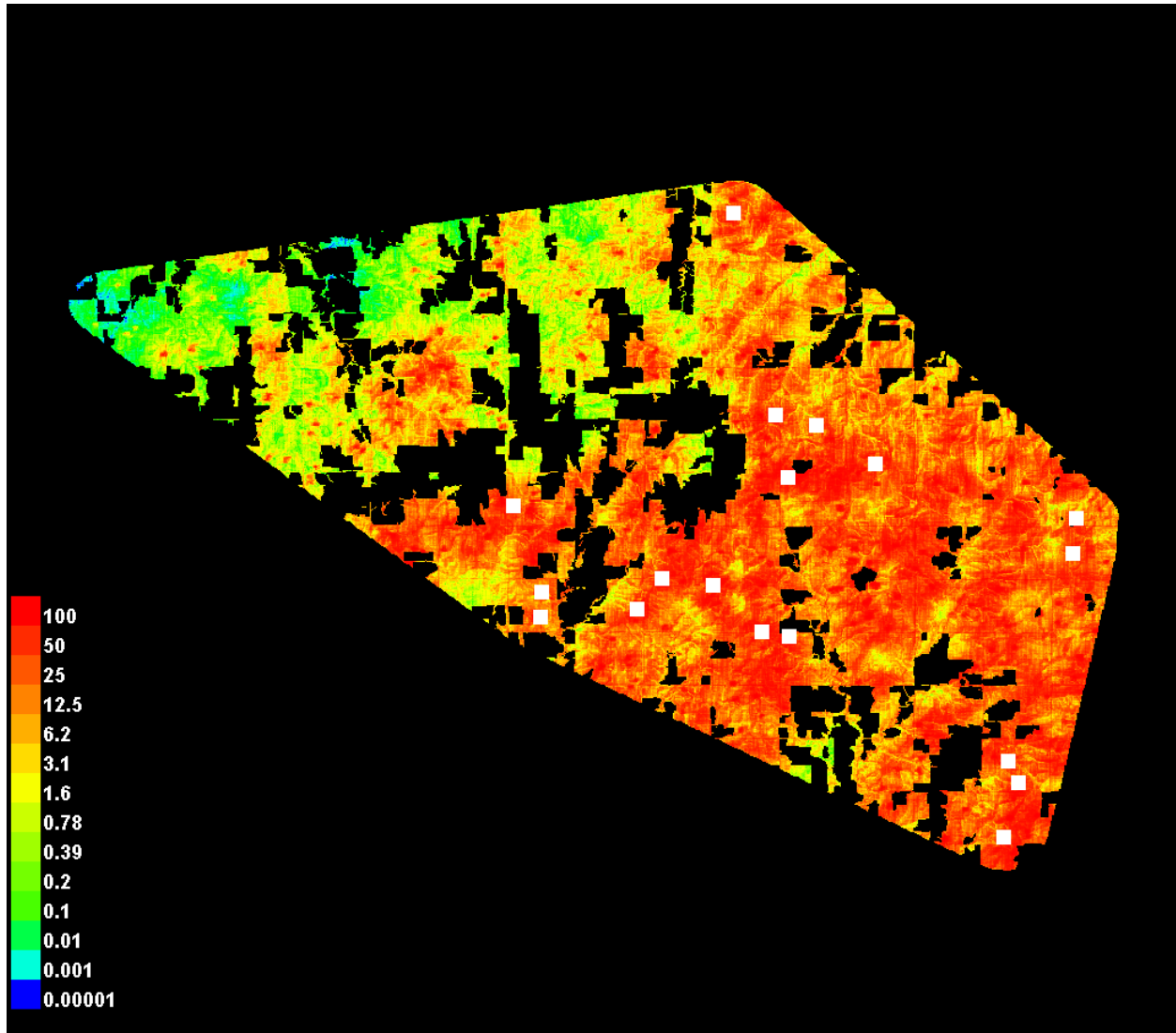


Figure 3.12. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Aedes vexans* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

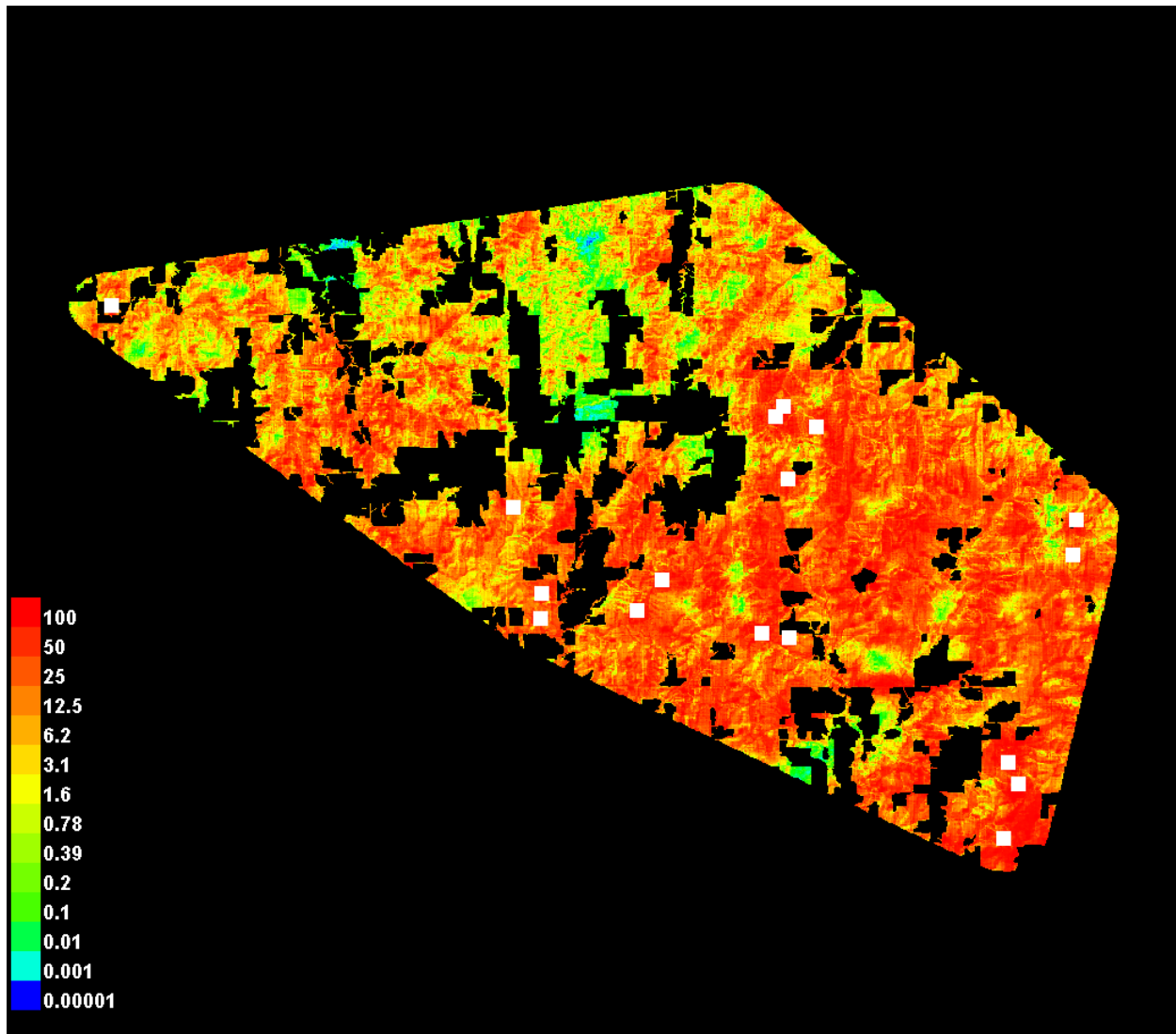


Figure 3.13. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Aedes taeniorhynchus* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

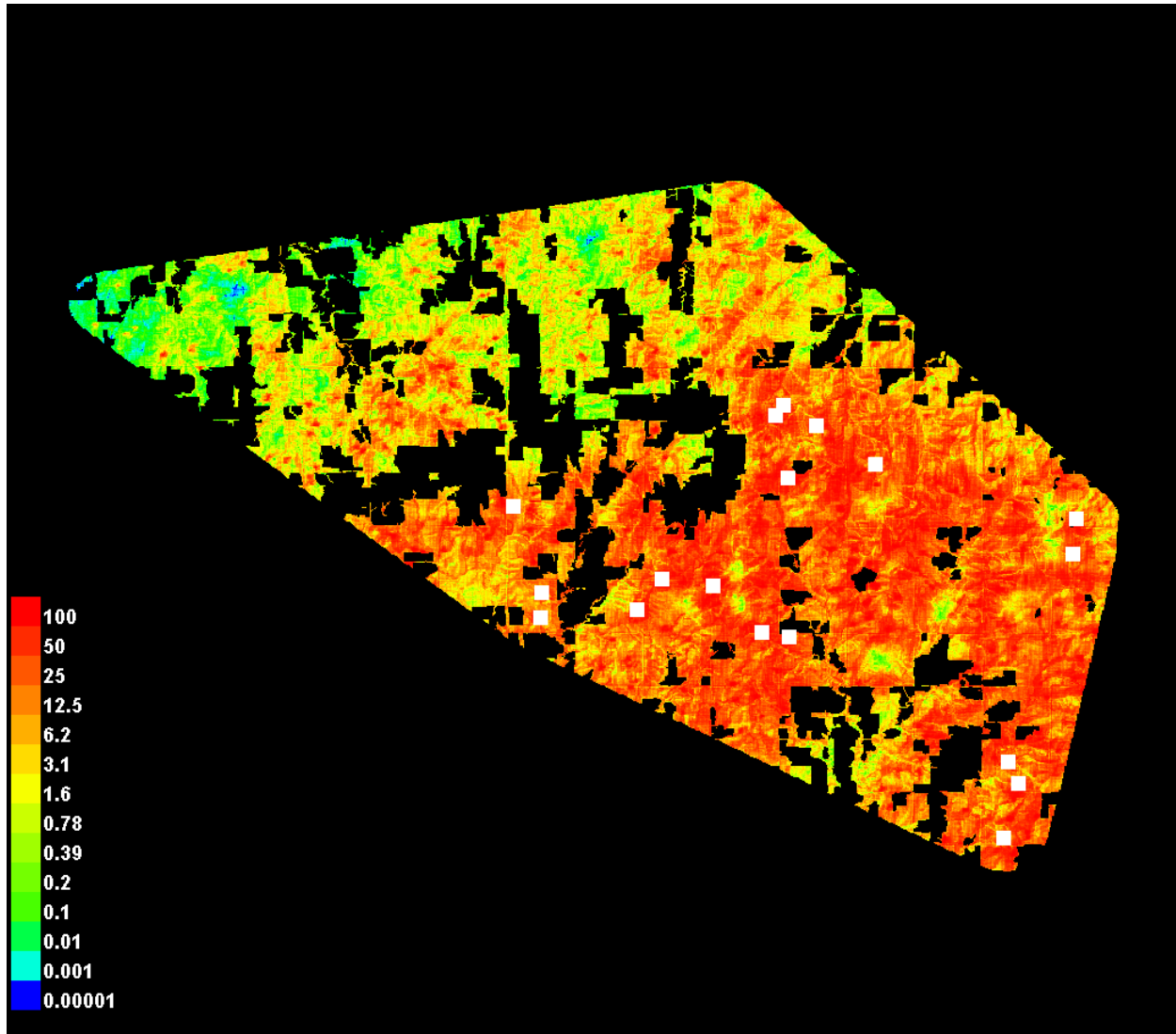


Figure 3.14. Presence-absence predicted distribution of *Culex tarsalis*, *Aedes sollicitans*, and *Aedes nigromaculis* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10.

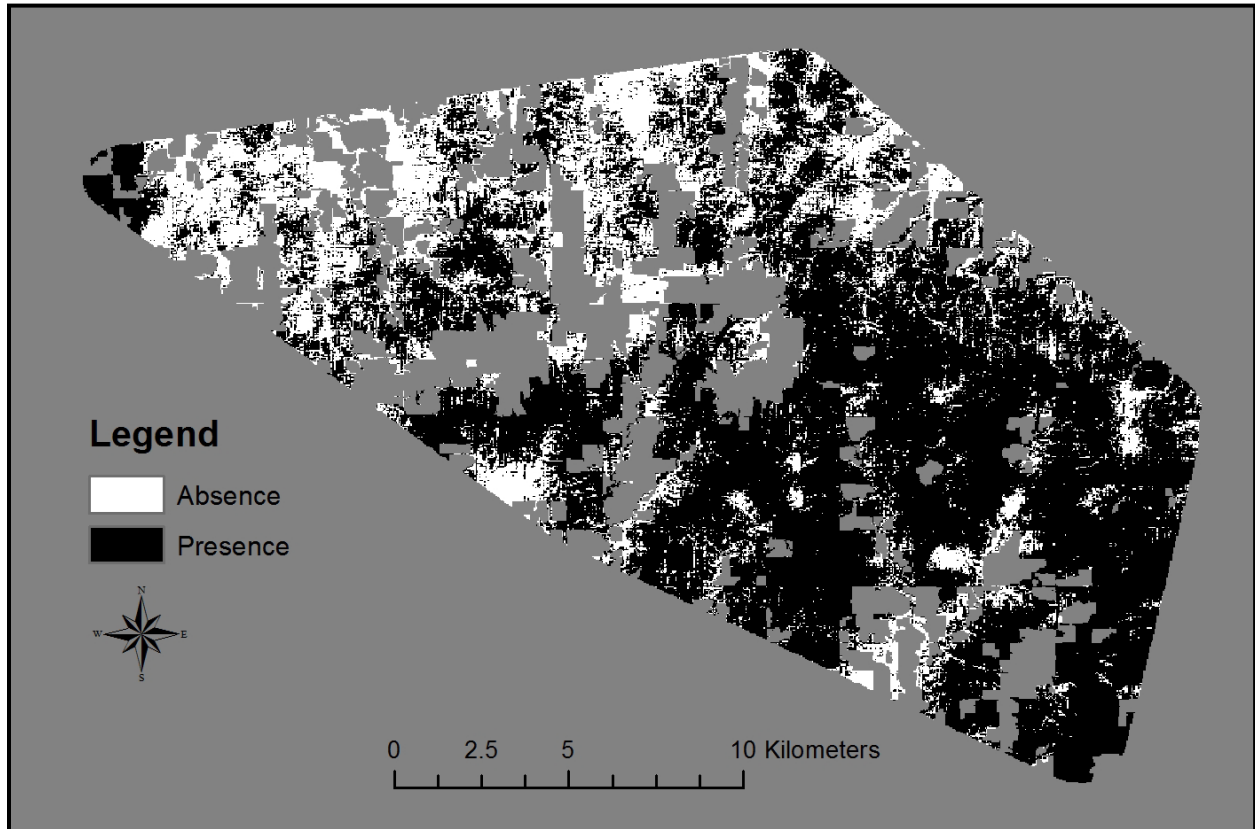


Figure 3.15. Presence-absence predicted distribution of *Culex salinarius* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10.

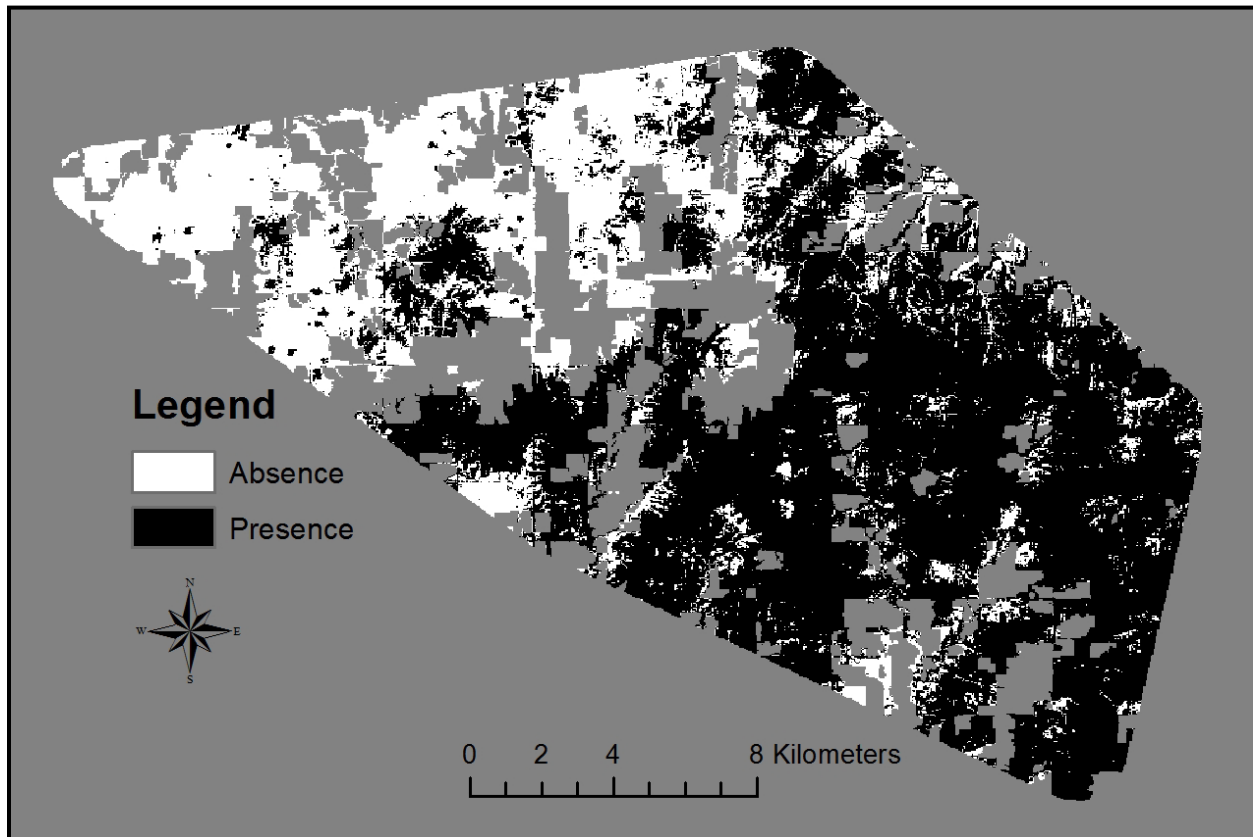


Figure 3.16. Presence-absence predicted distribution of *Aedes vexans* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10.

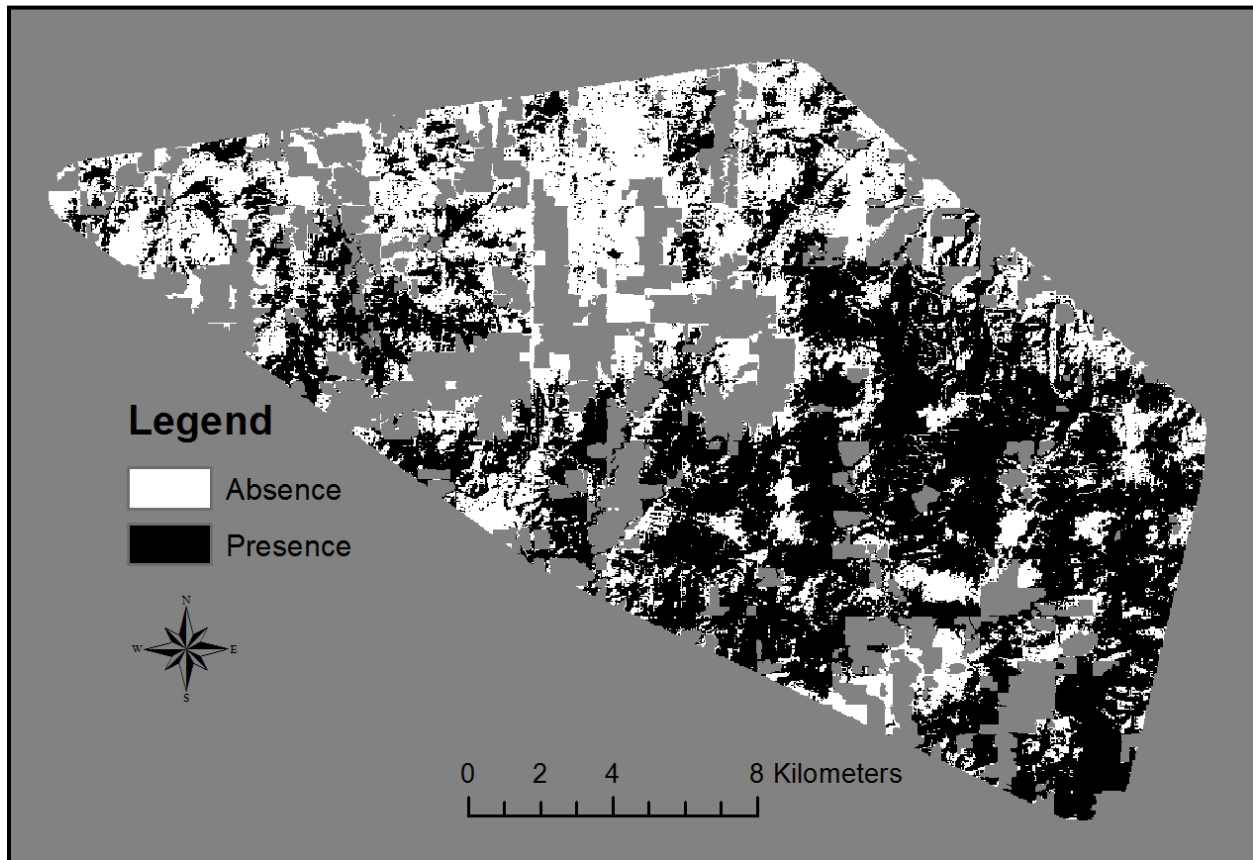


Figure 3.17. Presence-absence predicted distribution of *Aedes taeniorhynchus* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into Arc Info 10.

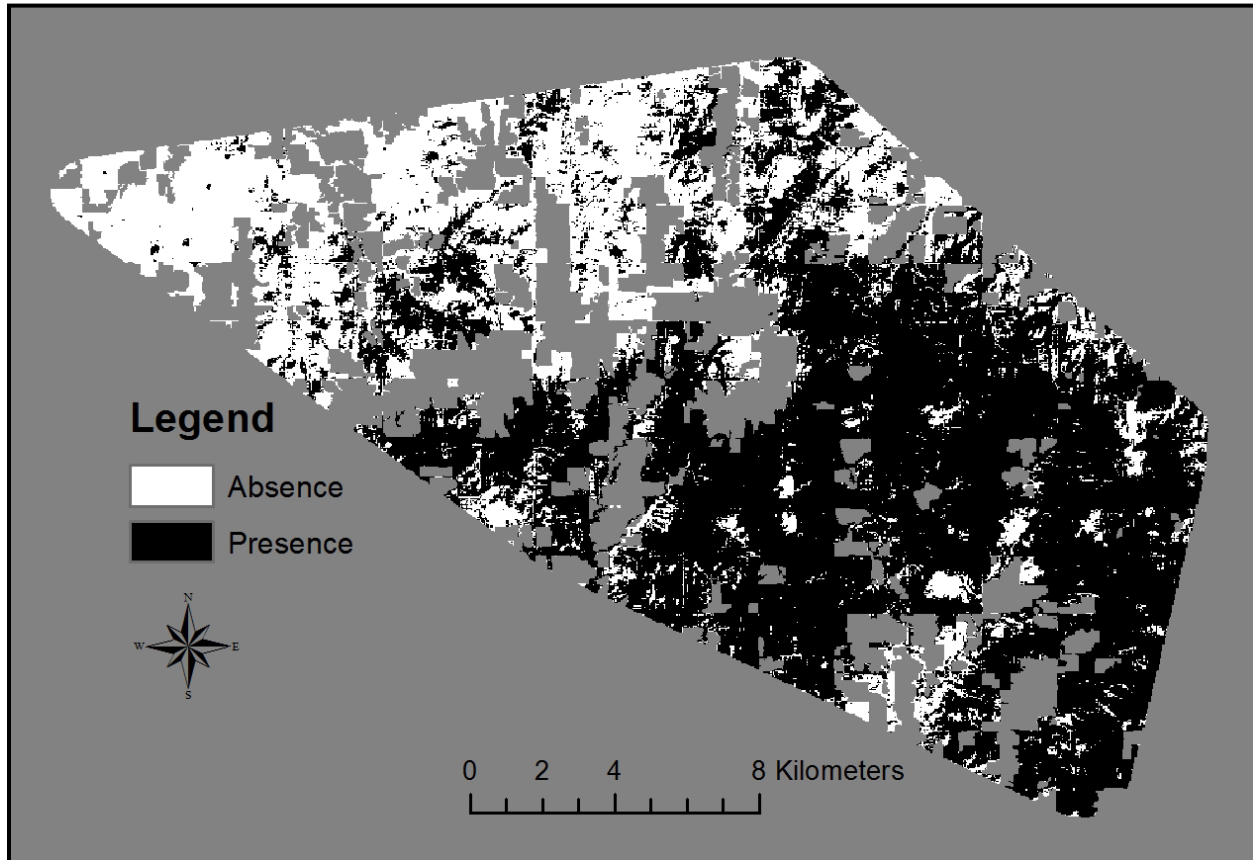




Figure 3.18. Predicted distribution of *Culex tarsalis*. This is the most abundant avian malaria vector with primarily ornithophilic feeding preferences during the avian nesting season. The map was created by importing the Maxent cumulative output of this species into Arc Info 10, and overlaid with Greater Prairie-chicken nests.

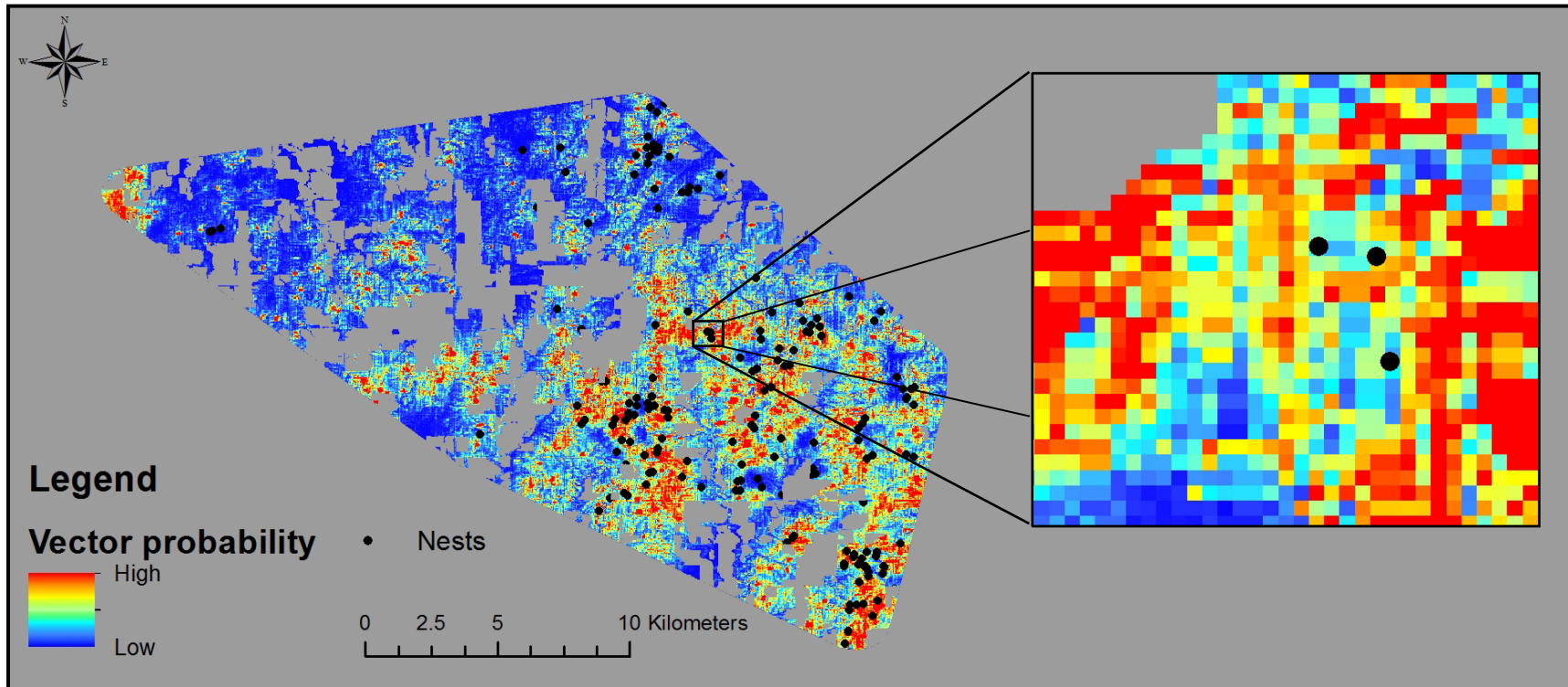




Figure 3.19. Predicted distribution of *Culex salinarius*. This is the second most abundant avian malaria vector with primarily ornithophilic feeding preferences during the avian nesting season. The map was created by importing the Maxent cumulative output of this species into Arc Info 10, and overlaid with Greater Prairie-chicken nests.

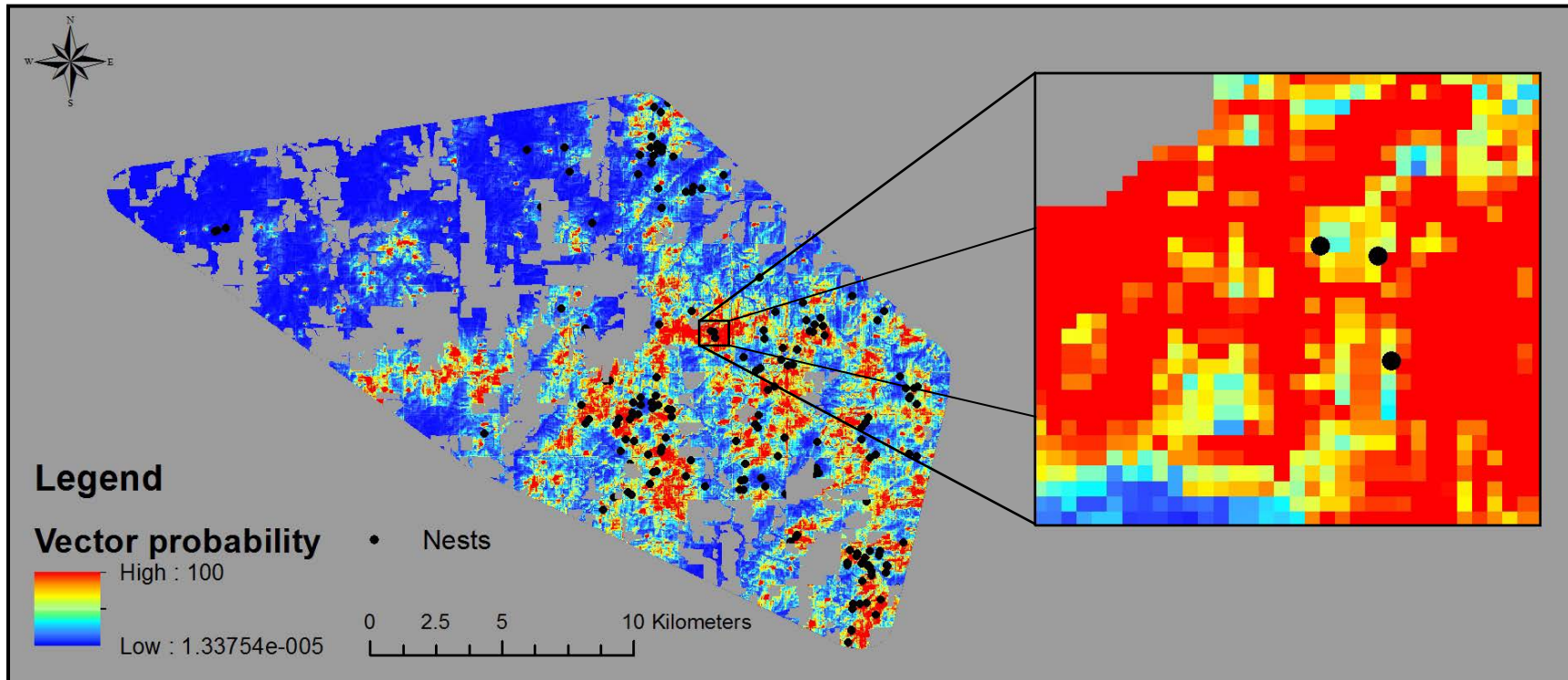


Figure 3.20. The predicted avian malaria vector distribution was created by importing the Maxent cumulative outputs of *Culex tarsalis* and *Culex salinarius* into Arc Info 10, and averaging their values via Spatial Analyst tools. This distribution was overlaid with Greater Prairie-chicken nests.

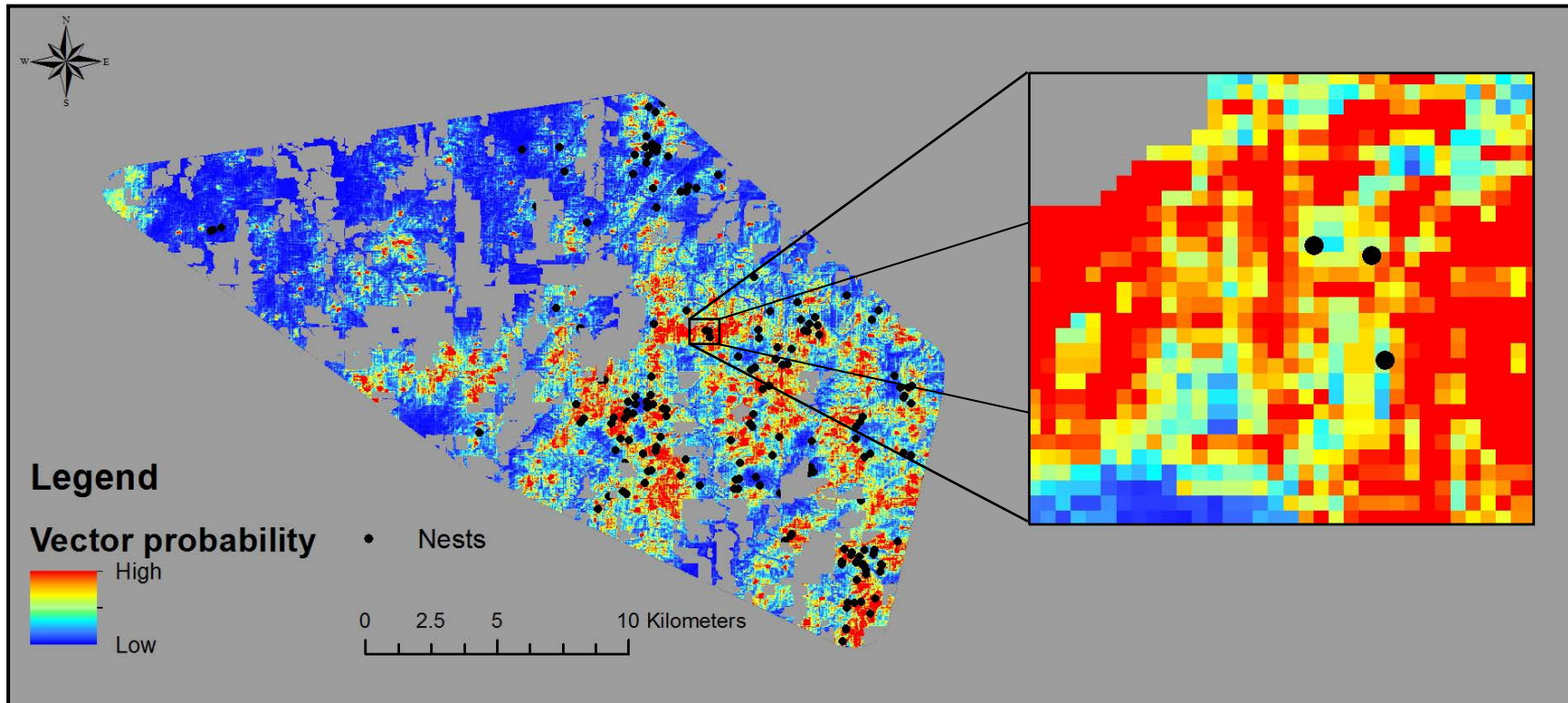


Figure 3.21. Comparison of the probability of *Culex tarsalis* occurrence at random points and nest locations of Greater Prairie-chicken in the grasslands of the Smoky Hills, Cloud County, Kansas.

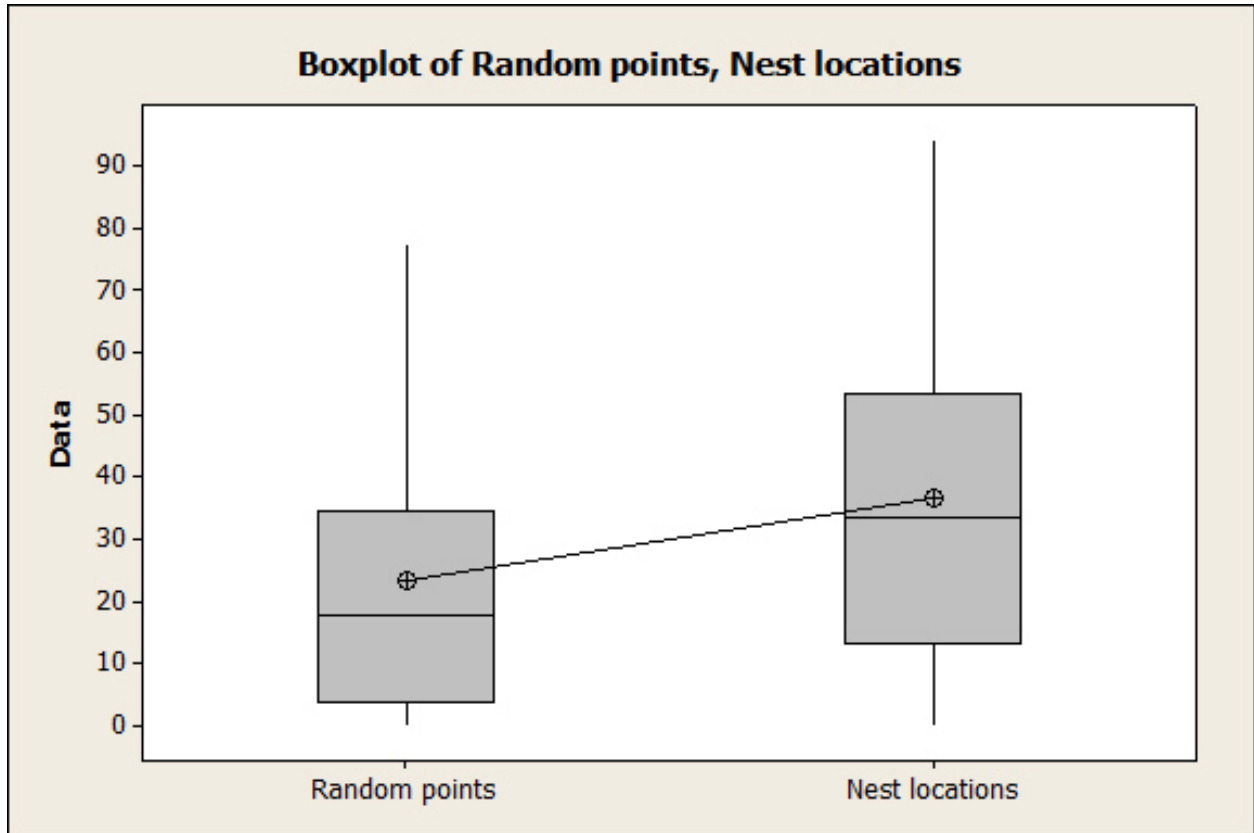


Figure 3.22. Comparison of the probability of *Culex salinarius* occurrence at random points and nest locations of Greater Prairie-chicken in the grasslands of the Smoky Hills, Cloud County, Kansas.

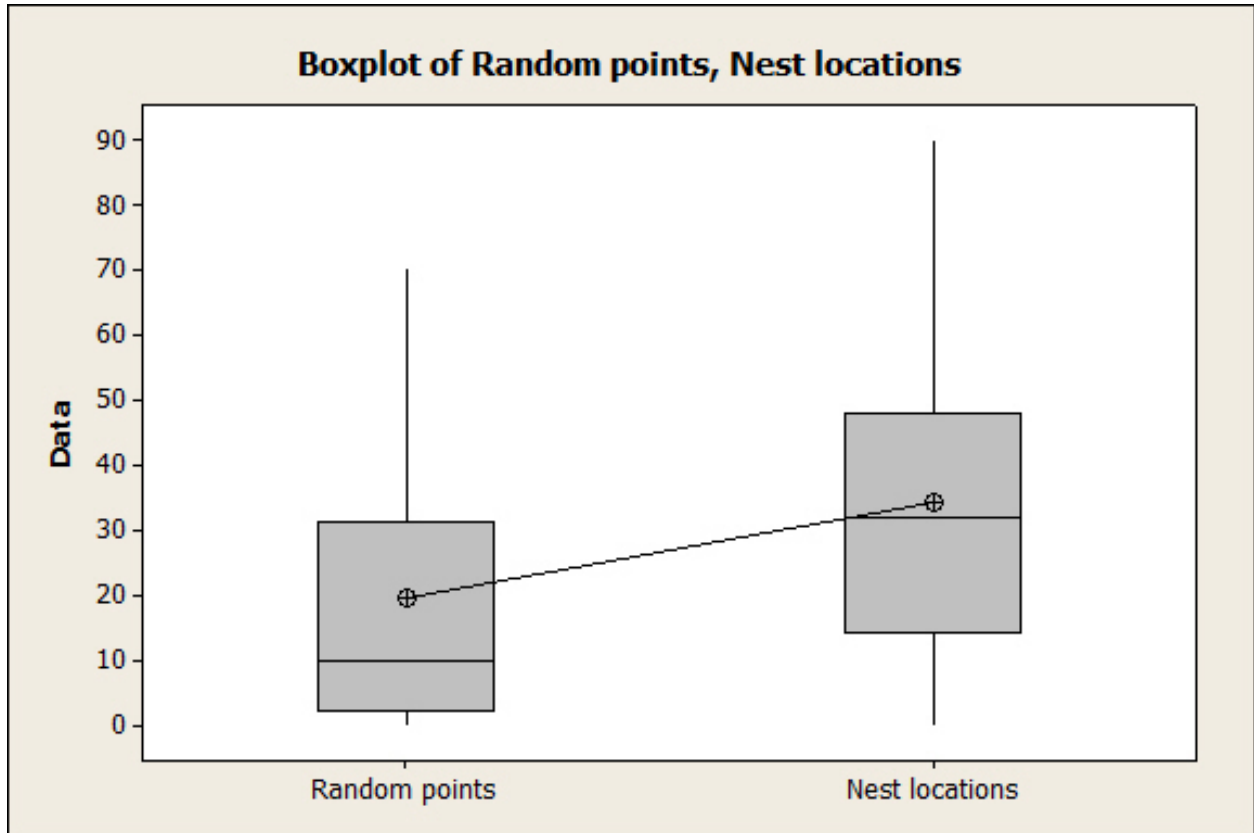


Figure 3.23. Comparison of the probability of avian malaria vector (combined: *Culex tarsalis* and *Culex salinarius*) occurrence at random points and nest locations of Greater Prairie-chicken in the grasslands of the Smoky Hills, Cloud County, Kansas.

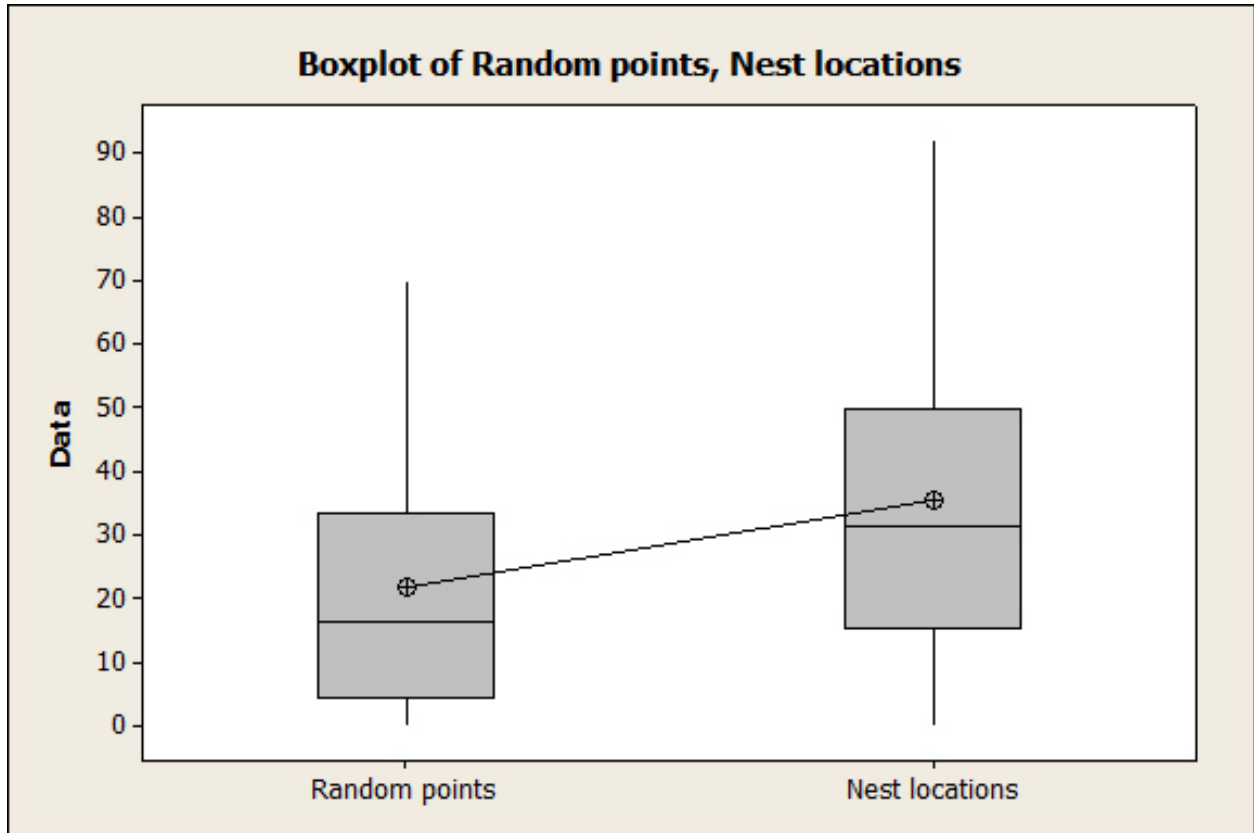


Figure 3.24. The simulated sampling distribution of the probability of *Culex tarsalis* occurrence at nest locations of uninfected female Greater Prairie-chicken was created with 10,000 sample means (sample size:  $n=8$ ). The 95% confidence interval is indicated in the dashed-green line. The mean probability of *Culex tarsalis* occurrence at nests of infected females is indicated with the solid red line.

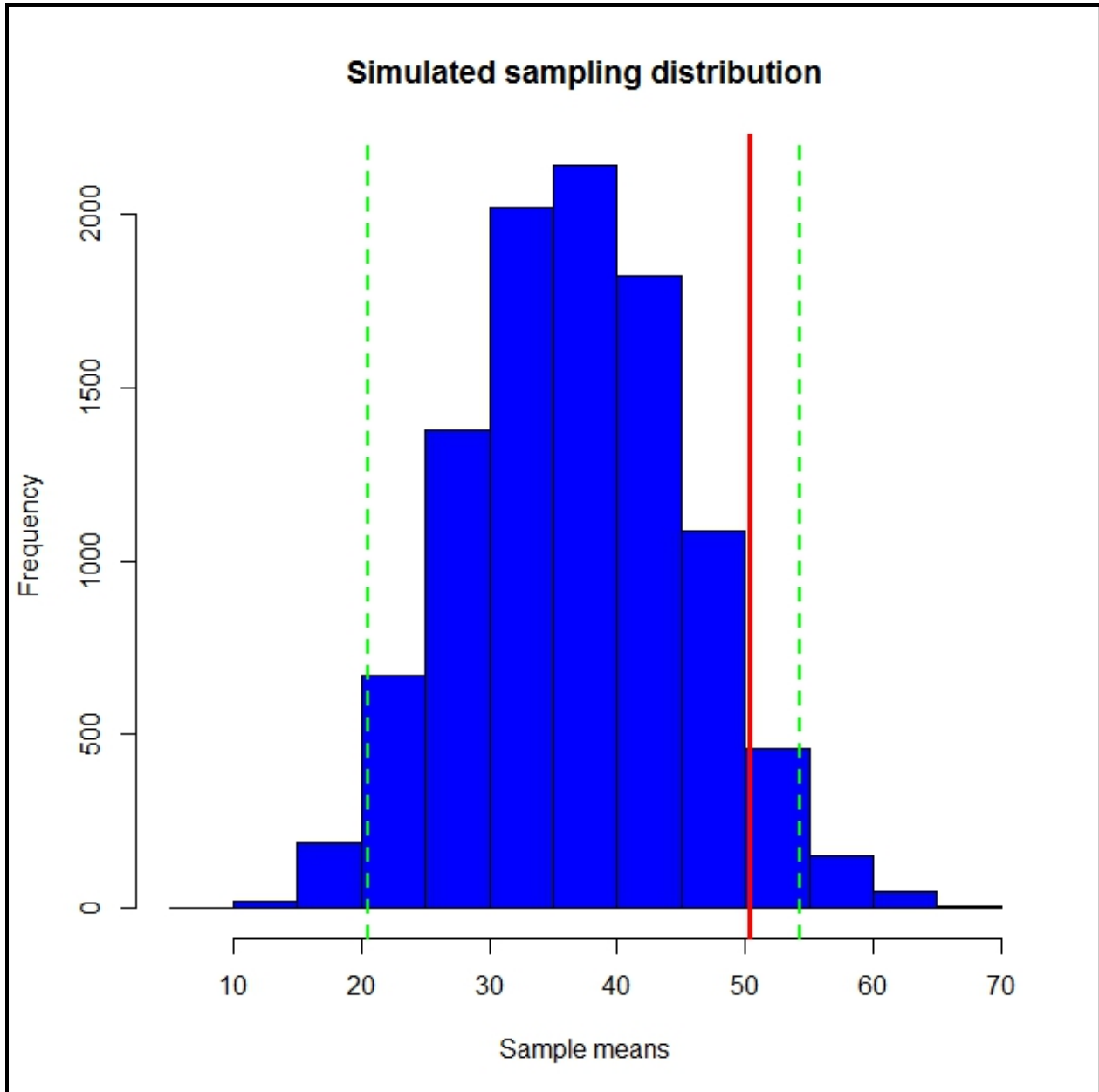


Figure 3.25. The simulated sampling distribution of the probability of *Culex salinarius* occurrence at nest locations of uninfected female Greater Prairie-chicken was created with 10,000 sample means (sample size:  $n=8$ ). The 95% confidence interval is indicated in the dashed-green line. The mean probability of *Culex salinarius* occurrence at nests of infected females is indicated with the solid red line.

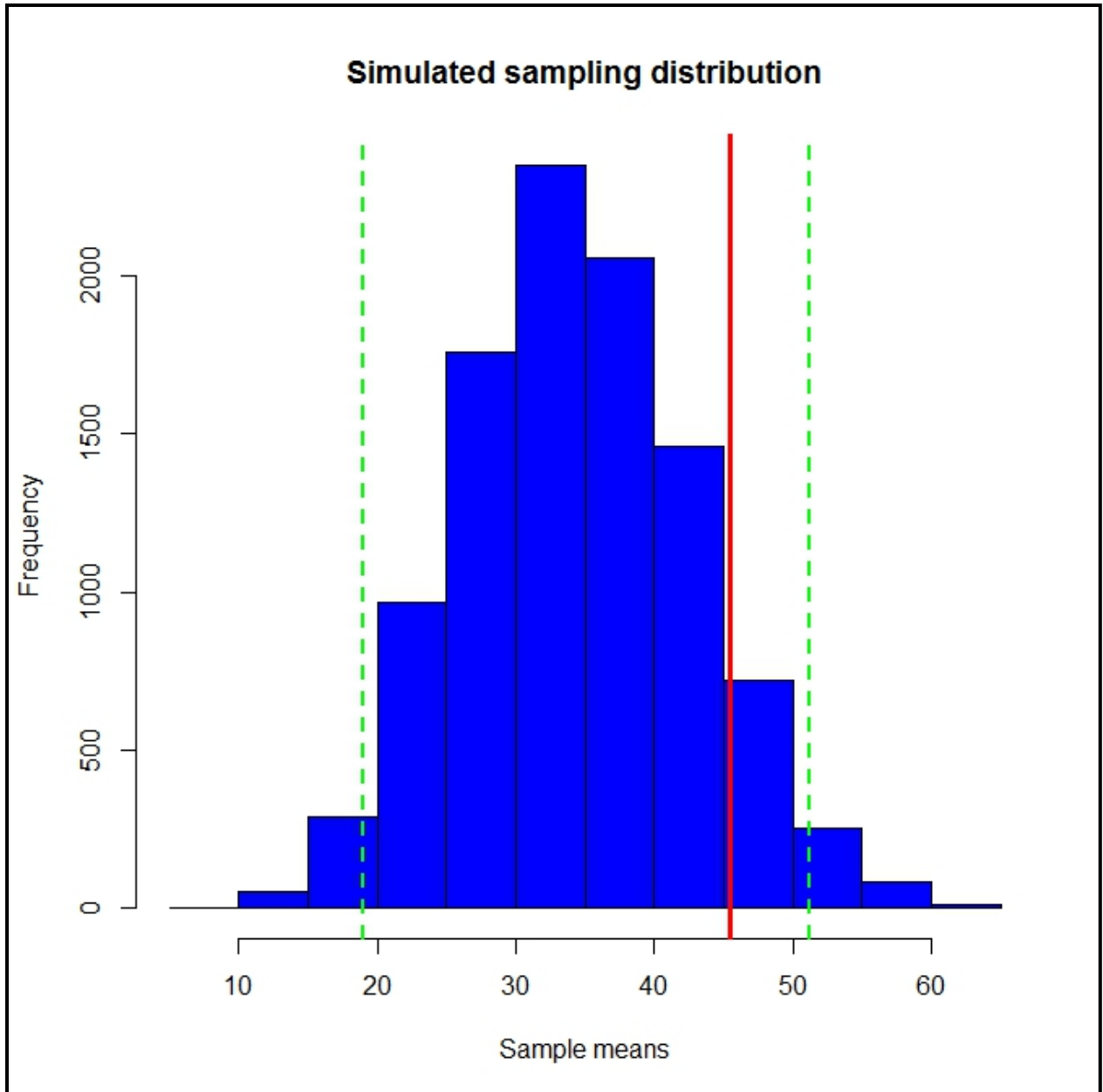
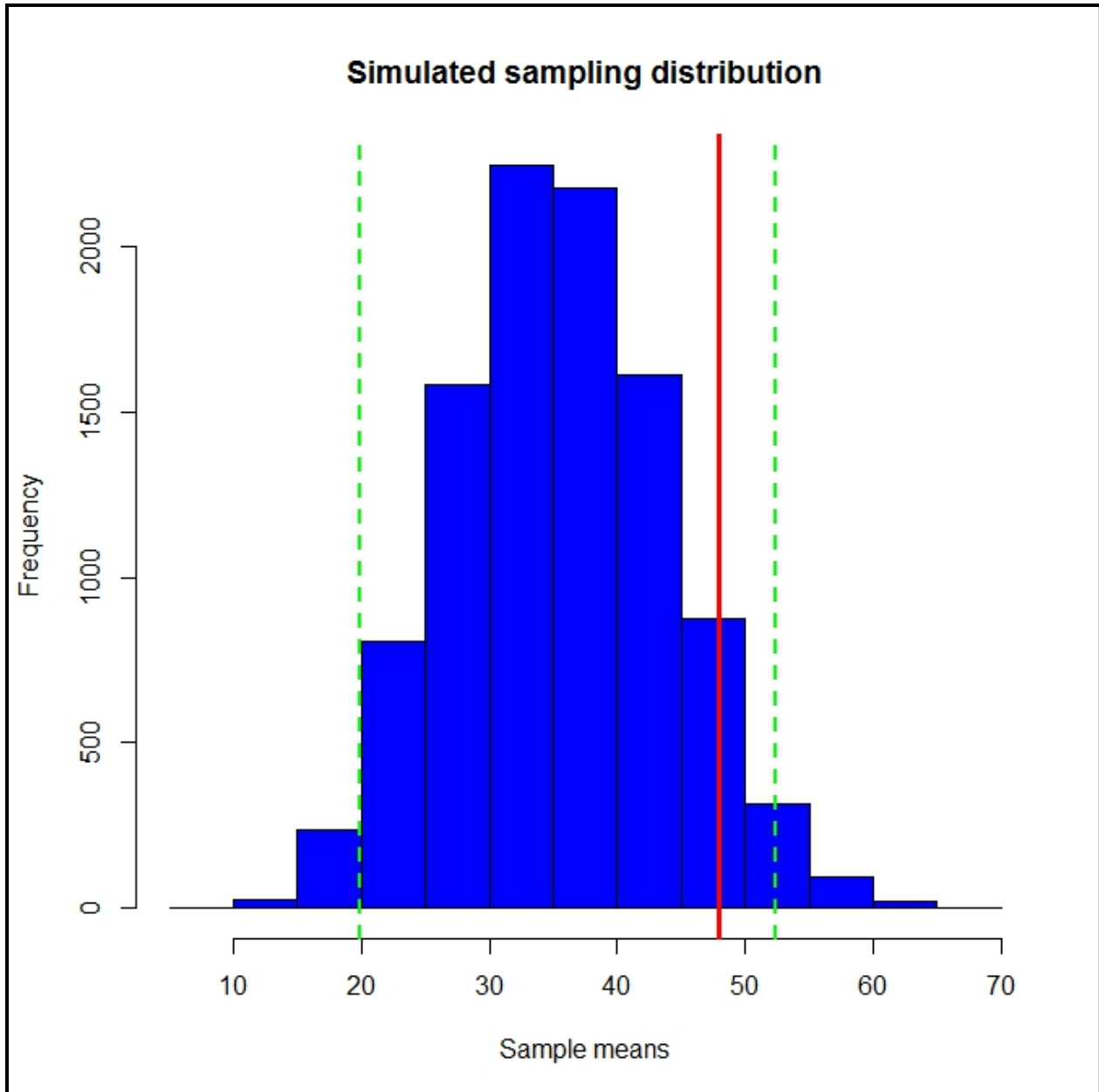


Figure 3.26. The simulated sampling distribution of the probability of avian malaria vector (combined: *Culex tarsalis*, *Culex salinarius*) occurrence at nest locations of uninfected female Greater Prairie-chicken was created with 10,000 sample means (sample size:  $n=8$ ). The 95% confidence interval is indicated in the dashed-green line. The mean probability of avian malaria vectors occurrence at nests of infected females is indicated with the solid red line.





**Appendix A - SUPPLEMENTAL FIGURES AND TABLES FOR  
CHAPTER 2**

Table A.1. Mosquito taxa encountered in the Smoky Hill eco-region, including their host feeding preferences and susceptibility to zoonotic pathogens. Feeding preferences, susceptibility to disease agents of encephalitides and role as enzootic/bridge vector reported in Turell *et al.* 2005. Susceptibility to disease agents of avian malaria (*Plasmodium* species) was reported in Valkiunas 2005, unless otherwise noted.

Mosquito Taxa (most recent report)	Host feeding preference	Susceptible to disease agents of				Potential to serve as (infectious encephalitis)	
		WEE	SLE	WNVE	AM	Enzootic vector <sup>e</sup>	Bridge vector <sup>f</sup>
<i>Aedes</i>							
<i>sollicitans</i> (Janovy 1966)	mammals			S	S	0	+
<i>nigromaculis</i> (Janovy 1966)	mammals		S			0	+
<i>vexans</i> (Janovy 1966)	mammals	S	S	S	S	0	++
<i>taeniorhynchus</i> *	mammals			S	<sup>d</sup>	0	+
<i>stimulans</i> *	mammals <sup>a</sup>				S	0	0
<i>dorsalis</i> (Janovy 1966)	mammals	S		S		0	++
<i>Culex</i>							
<i>tarsalis</i> (Janovy 1966)	opportunistic <sup>b</sup>	S	S	S	S	++++	+++
<i>salinarius</i> (Lungstrom <i>et al.</i> 1961)	opportunistic		S	S	S	+++	++++
<i>pipiens</i> (Janovy 1966)	birds		S	S	S	++++	+++++
<i>restuans</i> (Lungstrom <i>et al.</i> 1961)	birds		S	S	S	+++++	++

\* previously unreported in published literature to occur in Kansas.

<sup>a</sup> host feeding pattern of *Aedes stimulans* reported in Molaei *et al.* 2008.

<sup>b</sup> avian host feeding in spring and early summer with seasonal shift to mammalian hosts in late summer and fall.

<sup>c</sup> Detection of SLE in *Aedes nigromaculis* reported in Hammon *et al.* 1943.

<sup>d</sup> Detection of AM in head/thorax pool of *Aedes nigromaculis*.

<sup>e</sup> Potential for species to serve as enzootic vector from little to no risk 0, to high risk +++++

<sup>f</sup> Potential for species to serve as bridge vector from little to no risk 0, to high risk +++++

Table A.2. Average weekly meteorological variables (precipitation, wind speed, maximum temperature, and minimum temperature) retrieved from National Oceanic and Atmospheric Administration (NOAA) during the sample season, and mosquito abundance/diversity ( $H'$ ).

Date	Precipitation	Wind speed	Maximum Temperature	Minimum Temperature	Abundance	$H'$
5/3/2010	26.57	53.86	19.37	6.41	*	*
5/10/2010	34.57	41.43	15.49	7.30	*	*
5/17/2010	35.29	48.29	21.99	12.79	25	1.19
5/24/2010	30.86	40.00	27.20	15.81	301	1.59
5/31/2010	4.43	38.86	29.86	16.43	650	0.53
6/7/2010	63.43	46.43	28.01	19.20	227	0.98
6/14/2010	124.86	50.86	31.20	18.96	+	+
6/21/2010	21.71	49.71	33.57	19.27	2194	1.37
6/28/2010	87.14	46.71	30.87	17.69	199	1.53
7/5/2010	26.57	29.00	29.91	18.73	+	+
7/12/2010	40.57	39.29	34.06	21.34	2084	0.93
7/19/2010	7.71	48.00	33.03	21.51	2695	1.36
7/26/2010	0.00	37.14	34.51	21.59	2848	1.37

\* Meteorological data prior to the sample season.

+ Mosquitoes samples were not obtained due the effects of excessive precipitation.

Table A.3. Site specific environmental variables (elevation, curvature, aspect, TWI, distance to agriculture, distance to woodland, distance to water, distance to road and distance to edge) of twenty sample locations within a radius of 30 m of mosquito traps and mosquito abundance/diversity (H') within the Smoky Hill eco-region using ArcInfo 10 (Environmental Systems Research Institute, Radlands, CA). Elevation and distance measures are in meters.

Site ID	Latitude	Longitude	Elevation	Curvature	TWI	Distance to agriculture	Distance to woodland	Distance to water	Distance to road	Distance to edge	Abundance	H'
BS1	N 39°26.173'	W097°34.903'	499.58	0.09	3.91	1083.74	60.00	595.48	120.00	60.00	173	1.931986
BS2	N 39°23.014'	W097°39.434'	454.00	-0.04	7.68	420.00	301.50	150.00	480.00	180.00	435	1.426649
BS3	N 39°22.689'	W097°35.355'	466.35	0.17	4.40	120.00	646.22	573.15	120.00	0.00	480	1.374599
BS4	N 39°26.340'	W097°35.566'	495.86	0.30	3.75	937.23	445.98	361.25	90.00	90.00	331	1.187878
BS6	N 39°24.853'	W097°39.881'	487.81	0.18	4.46	366.20	607.45	182.48	150.00	120.00	200	1.207432
BS7	N 39°20.289'	W097°31.573'	457.76	0.35	5.88	658.64	902.50	517.88	300.00	270.00	1394	1.361727
BS8	N 39°19.387'	W097°31.807'	452.06	0.08	7.63	403.61	657.95	523.93	240.00	210.00	827	1.335851
BS9	N 39°23.658'	W097°37.449'	493.77	0.19	4.21	566.04	818.84	494.77	60.00	30.00	426	1.244555
BS10	N 39°23.148'	W097°37.846'	482.38	0.00	9.22	789.18	745.19	361.25	150.00	150.00	3124	0.884195
BS11	N 39°24.055'	W097°30.670'	493.59	0.28	5.05	1266.06	758.95	816.09	810.00	276.59	267	1.321729
BS12	N 39°24.640'	W097°30.623'	495.69	0.22	3.81	1015.14	174.93	630.71	270.00	174.93	340	1.876915
BS13	N 39°28.178'	W097°46.501'	476.20	0.26	3.58	152.97	391.15	240.00	300.00	152.97	364	0.893937
BS14	N 39°23.434'	W097°39.430'	459.92	0.28	4.30	390.00	30.00	30.00	360.00	30.00	237	1.697985
BS15	N 39°25.309'	W097°35.370'	502.34	0.15	4.00	254.56	660.00	174.93	210.00	150.00	749	1.256148
BS16	N 39°26.504'	W097°35.441'	490.80	0.22	4.29	1146.30	150.00	632.85	90.00	90.00	793	1.330054
W1	N 39°23.538'	W097°36.593'	480.98	0.03	8.51	1499.40	967.47	42.43	60.00	30.00	226	1.217171
W2	N 39°22.763'	W097°35.801'	471.39	-0.24	4.59	450.00	1008.46	30.00	30.00	0.00	96	1.554932
W3	N 39°20.637'	W097°31.740'	445.19	0.17	5.84	660.00	852.76	30.00	630.00	60.00	698	1.725951
W4	N 39°25.539'	W097°33.923'	506.68	-0.19	4.63	1530.00	570.79	534.14	720.00	108.17	19	1.767378
W5	N 39°29.673'	W097°36.259'	461.04	0.18	7.34	540.00	785.17	361.25	510.88	313.21	44	1.564678

Table A.4. Pearson's correlation coefficients between environmental variables.

Variable	Curv <sup>a</sup>	TWI	Dist <sub>ag</sub>	Dist <sub>wl</sub>	Dist <sub>w</sub>	Dist <sub>r</sub>
TWI <sup>b</sup>	-0.31					
Dist <sub>ag</sub> <sup>c</sup>	-0.17	0.11				
Dist <sub>wl</sub> <sup>d</sup>	-0.18	0.44	0.41			
Dist <sub>w</sub> <sup>e</sup>	0.28	-0.20	0.36	-0.35		
Dist <sub>r</sub> <sup>f</sup>	0.01	0.16	0.22	-0.21	0.15	
Dist <sub>edge</sub> <sup>g</sup>	0.29	0.35	0.01	-0.21	0.36	0.52

<sup>a</sup> Curvature = is a measurement of rate-change of the slope per unit distance and may be an indicator for of aquatic habitat stability.

<sup>b</sup> TWI = Topographic Wetness Index, calculated as the natural logarithm of the ratio between local upslope contributing area and slope, and describes the predicted soil moisture pattern (ESRI, 2010)

<sup>c</sup> Dist<sub>ag</sub> = distance to the closest agricultural field, calculated using Euclidean distance (Arc Info 10).

<sup>d</sup> Dist<sub>wl</sub> = distance to the closest woodland, calculated using Euclidean distance (Arc Info 10).

<sup>e</sup> Dist<sub>w</sub> = distance to the closest water source, calculated using Euclidean distance (Arc Info 10).

<sup>f</sup> Dist<sub>r</sub> = distance to the closest road, calculated using Euclidean distance (Arc Info 10).

<sup>g</sup> Dist<sub>edge</sub> = distance to the closest habitat edge, calculated using Euclidean distance (Arc Info 10).

Table A.5. Pearson's correlation coefficients between meteorological variables.

	$P_{\text{mean}}^a$	$P_{\text{mean}(1)}$	$P_{\text{mean}(2)}$	Wind	$T_{\text{max}}$	$T_{\text{max}(1)}$	$T_{\text{max}(2)}$	$T_{\text{min}}$	$T_{\text{min}(1)}$
$P_{\text{mean}(1)}^b$	-0.23								
$P_{\text{mean}(2)}^c$	0.63	0.07							
Wind <sup>d</sup>	0.37	0.49	0.05						
$T_{\text{max}}^e$	-0.70	0.20	0.37	-0.26					
$T_{\text{max}(1)}^f$	0.00	0.02	0.42	-0.03	0.88*				
$T_{\text{max}(2)}^g$	0.07	-0.09	0.46	0.00	0.79*	0.85*			
$T_{\text{min}}^h$	-0.20	0.18	0.18	-0.19	0.80	0.87*	0.83*		
$T_{\text{min}(1)}^i$	-0.14	0.64	0.36	-0.14	0.95*	0.98*	0.85*	0.92*	
$T_{\text{min}(2)}^j$	-0.02	0.44	0.44	0.01	0.89*	0.95*	0.96*	0.88*	0.95*

<sup>a</sup>  $P_{\text{mean}}$  = precipitation during the sample week.

<sup>b</sup>  $P_{\text{mean}(1)}$  = precipitation one week prior to sample week.

<sup>c</sup>  $P_{\text{mean}(2)}$  = precipitation two weeks prior to sample week.

<sup>d</sup> Wind = wind speed during the sample week.

<sup>e</sup>  $T_{\text{max}}$  = maximum temperature during the sample week

<sup>f</sup>  $T_{\text{max}(1)}$  = maximum temperature one week prior to sample week.

<sup>g</sup>  $T_{\text{max}(2)}$  = maximum temperature two weeks prior to sample week.

<sup>h</sup>  $T_{\text{min}}$  = minimum temperature during the sample week.

<sup>i</sup>  $T_{\text{min}(1)}$  = minimum temperature one week prior to sample week.

<sup>j</sup>  $T_{\text{min}(2)}$  = minimum temperature two weeks prior to sample week.

\* $P < 0.05$

Table A.6. Candidate models used to fit the dependent variable, mosquito diversity, to independent meteorological variables.

Variables in the Model	No. of parameters	AICc <sup>a</sup>	Delta AICc	AICc weight <sup>b</sup>	R <sup>2</sup>	adjusted R <sup>2</sup>	<i>p</i>
Wind <sup>c</sup>	2.00	-15.46	0.00	0.13	0.09	-0.04	0.44
P <sub>mean</sub> (2) <sup>d</sup>	2.00	-15.09	0.37	0.11	5.00	-0.09	0.57
P <sub>mean</sub>	2.00	-15.04	0.42	0.11	0.04	-0.09	0.59
P <sub>mean</sub> (1) <sup>f</sup>	2.00	-14.99	0.47	0.10	0.04	-0.10	0.61
T <sub>max</sub> <sup>g</sup>	2.00	-14.66	0.80	0.09	0.00	-0.13	0.89
T <sub>min</sub> <sup>h</sup>	2.00	-14.66	0.81	0.09	0.00	-0.14	0.91

<sup>a</sup> AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

<sup>b</sup> AICc weight = percent of total weight from 128 models that can be attributed to the specified model.

<sup>c</sup> Wind = wind speed during the sample week.

<sup>d</sup> P<sub>mean</sub>(2) = precipitation two weeks prior to sample week, to account for lagged responses.

<sup>e</sup> P<sub>mean</sub> = precipitation during the sample week.

<sup>f</sup> P<sub>mean</sub>(1) = precipitation one week prior to sample week, to account for lagged responses.

<sup>g</sup> T<sub>max</sub> = maximum temperature during the sample week.

<sup>h</sup> T<sub>min</sub> = minimum temperature during the sample week.

Table A.7. Candidate models used to fit the dependent variable, mosquito diversity, to independent environmental variables.

Variables in model	No. of parameters	AICc <sup>a</sup>	Delta AICc	AICc Weight	R <sup>2</sup>	Adjusted R <sup>2</sup>	<i>p</i>
Dist <sub>r</sub> <sup>c</sup> , Dist <sub>edge</sub> <sup>d</sup>	3	-48.22	0.00	0.07	0.22	0.13	0.12
Dist <sub>r</sub>	2	-47.98	0.25	0.06	0.10	0.05	0.18
Dist <sub>ag</sub> <sup>e</sup>	2	-47.38	0.84	0.04	0.07	0.02	0.26
Dist <sub>ag</sub> , Dist <sub>wl</sub> <sup>f</sup>	3	-47.07	1.15	0.04	0.18	0.08	0.19
TWI <sup>g</sup>	2	-46.84	1.39	0.03	0.05	-0.01	0.37
TWI, Dist <sub>r</sub>	3	-46.78	1.45	0.03	0.17	0.07	0.21
Dist <sub>wl</sub>	2	-46.69	1.53	0.03	0.04	-0.02	0.41
Curv <sup>h</sup>	2	-46.58	1.65	0.03	0.03	-0.02	0.45
Dist <sub>edge</sub>	2	-46.35	1.88	0.03	0.02	-0.03	0.54

<sup>a</sup> AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

<sup>b</sup> AICc weight = percent of total weight from 128 models that can be attributed to the specified model.

<sup>c</sup> Dist<sub>r</sub> = distance to the closest road, calculated using Euclidean distance (Arc Info 10).

<sup>d</sup> Dist<sub>edge</sub> = distance to the closest habitat edge, calculated using Euclidean distance (Arc Info 10).

<sup>e</sup> Dist<sub>ag</sub> = distance to the closest agricultural field, calculated using Euclidean distance (Arc Info 10).

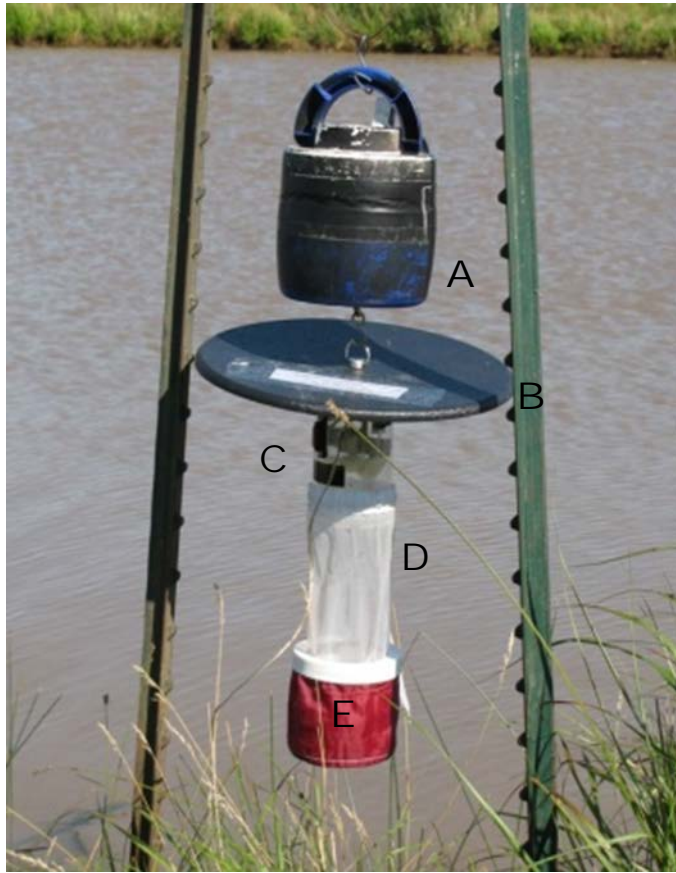
<sup>f</sup> Dist<sub>wl</sub> = distance to the closest woodland, calculated using Euclidean distance (Arc Info 10).

<sup>g</sup> TWI = Topographic Wetness Index, calculated as the natural logarithm of the ratio between local upslope contributing area and slope, and describes the predicted soil moisture pattern (ESRI, 2010)

<sup>h</sup> curvature = is a measurement of rate-change of the slope per unit distance and may be an indicator for of aquatic habitat stability.



Figure A.1. Center for Disease Control and Prevention (CDC) miniature light trap baited with dry ice, used for mosquito collections in this study.



A – Dry ice baited thermos

B - Weather guard

C – Light and fan

D – Trap funnel

E – Catch basin

Figure A.2. Human case incident reports of infectious encephalitides (Western Equine encephalitis, St. Louis encephalitis, and West Nile Virus encephalitis) in Kansas from 1964 to 2010 (Kansas Department of Health 2012).

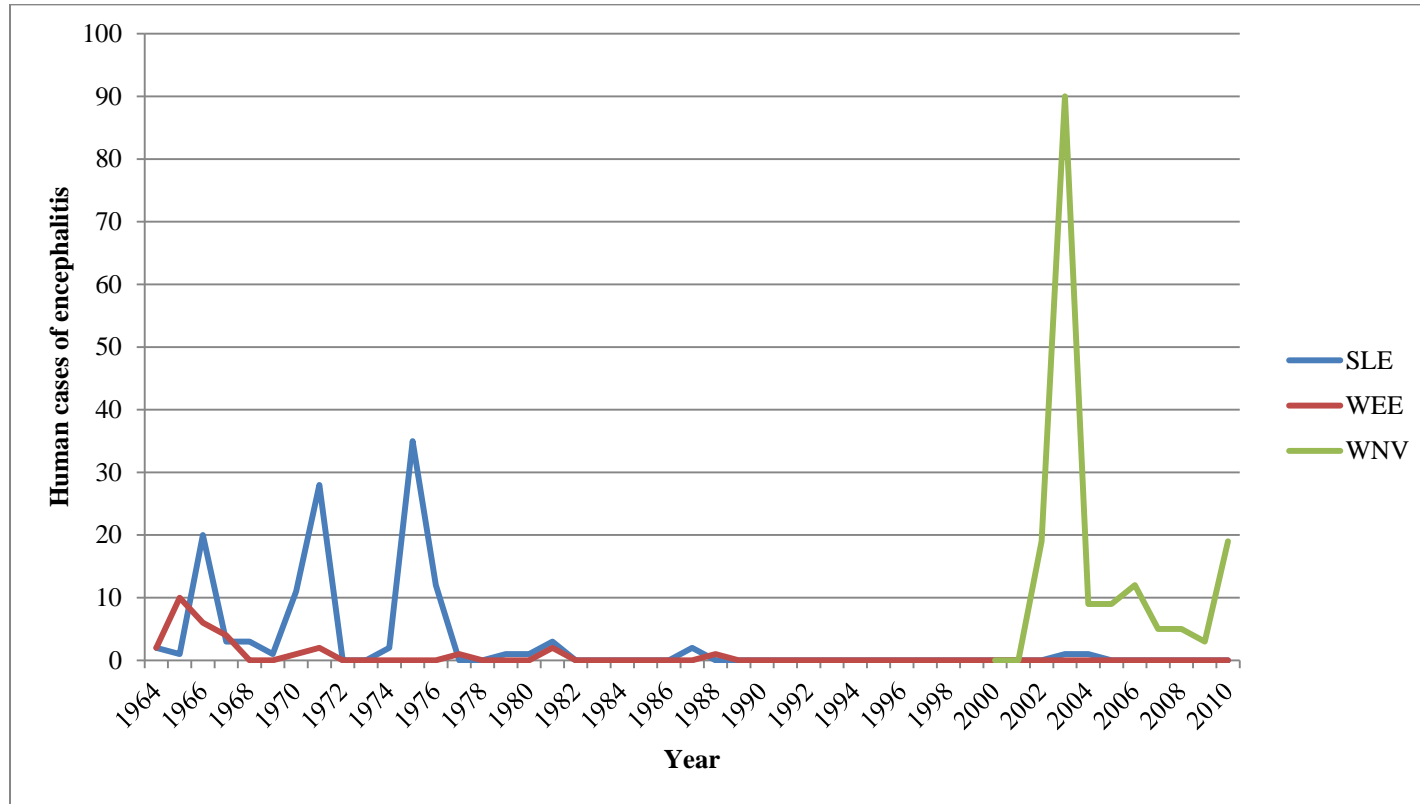


Figure A.3. Temperature and precipitation data from NOAA (National Oceanic and Atmospheric Administration) during the study period. Mean weekly minimum and maximum temperatures ( $^{\circ}\text{C}$ ) are represented by the lines with square and diamond markers, respectively. Precipitation (mm) is represented by vertical bars (National Oceanic and Atmospheric Administration 2012).

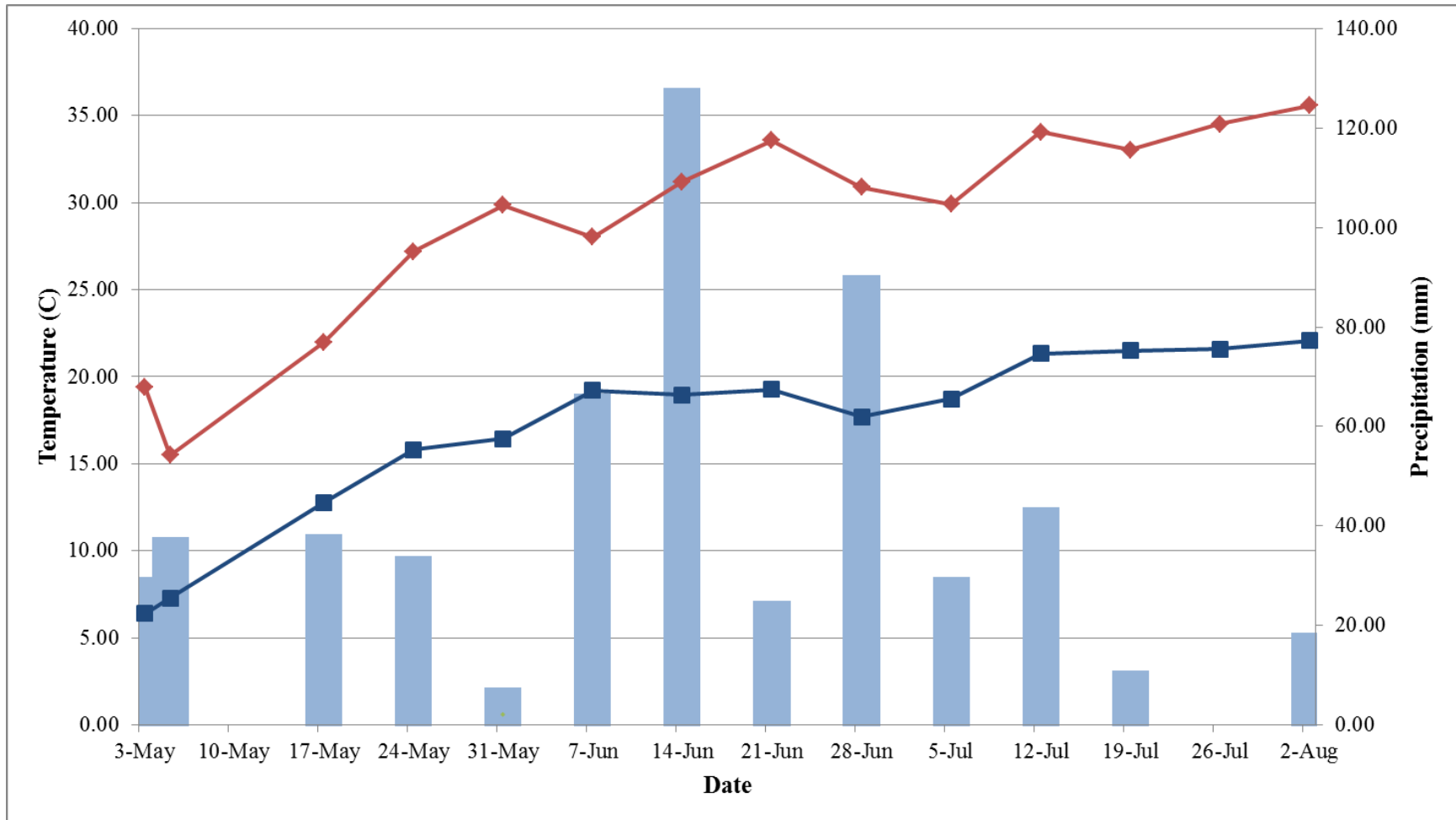


Figure A.4. Seasonal abundance (diamond symbols)/diversity (square symbols) (measured using Shannon-Wiener diversity index) of mosquito species in Cloud County, located within the Smoky Hill eco-region in 2010. Counts for abundance were standardized by the number of traps operated.

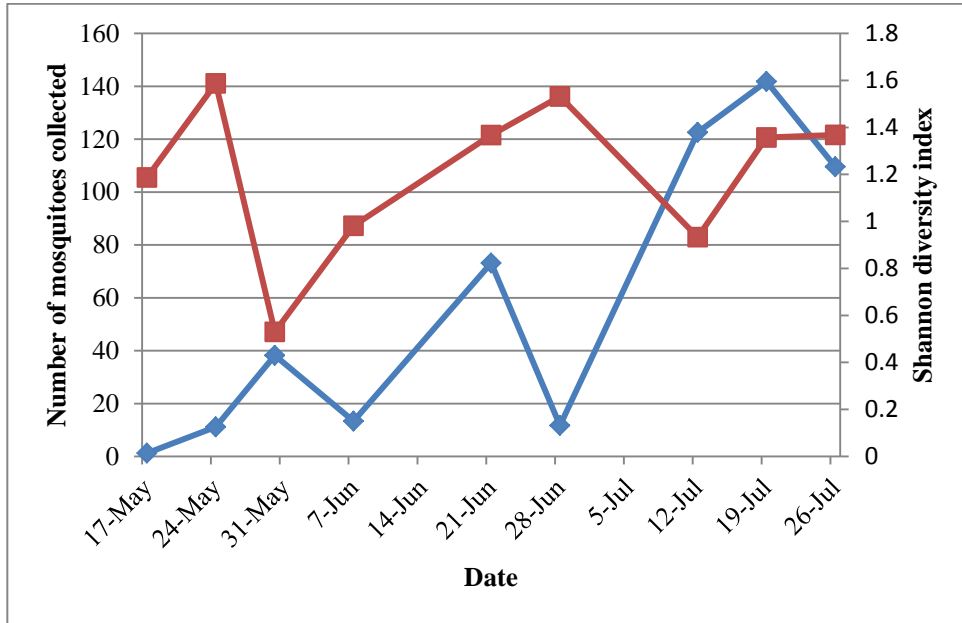


Figure A.5. Seasonal abundance of mosquito genera in Cloud County, located within the Smoky Hill eco-region in 2010. Counts were standardized by the number of traps operated.

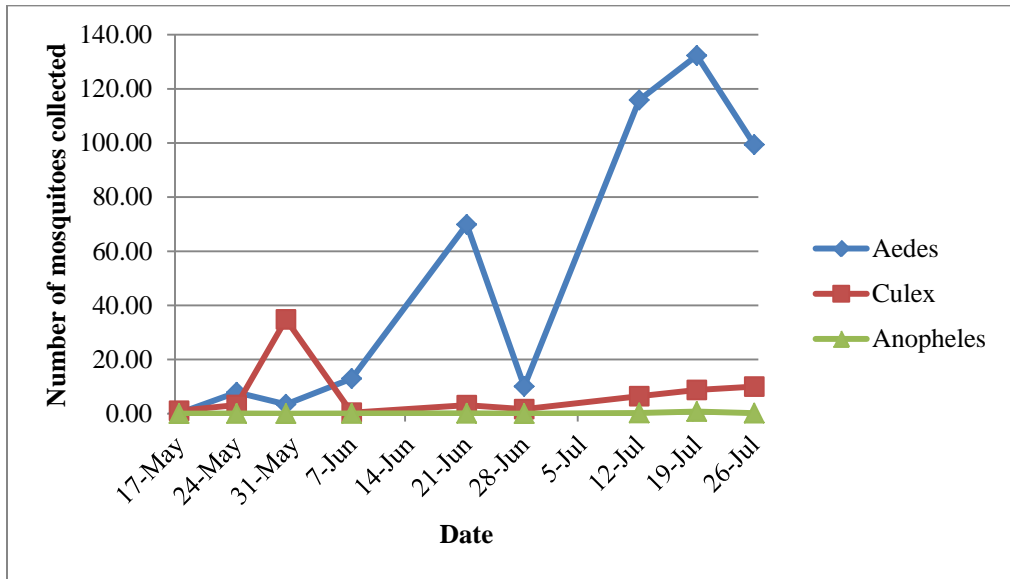
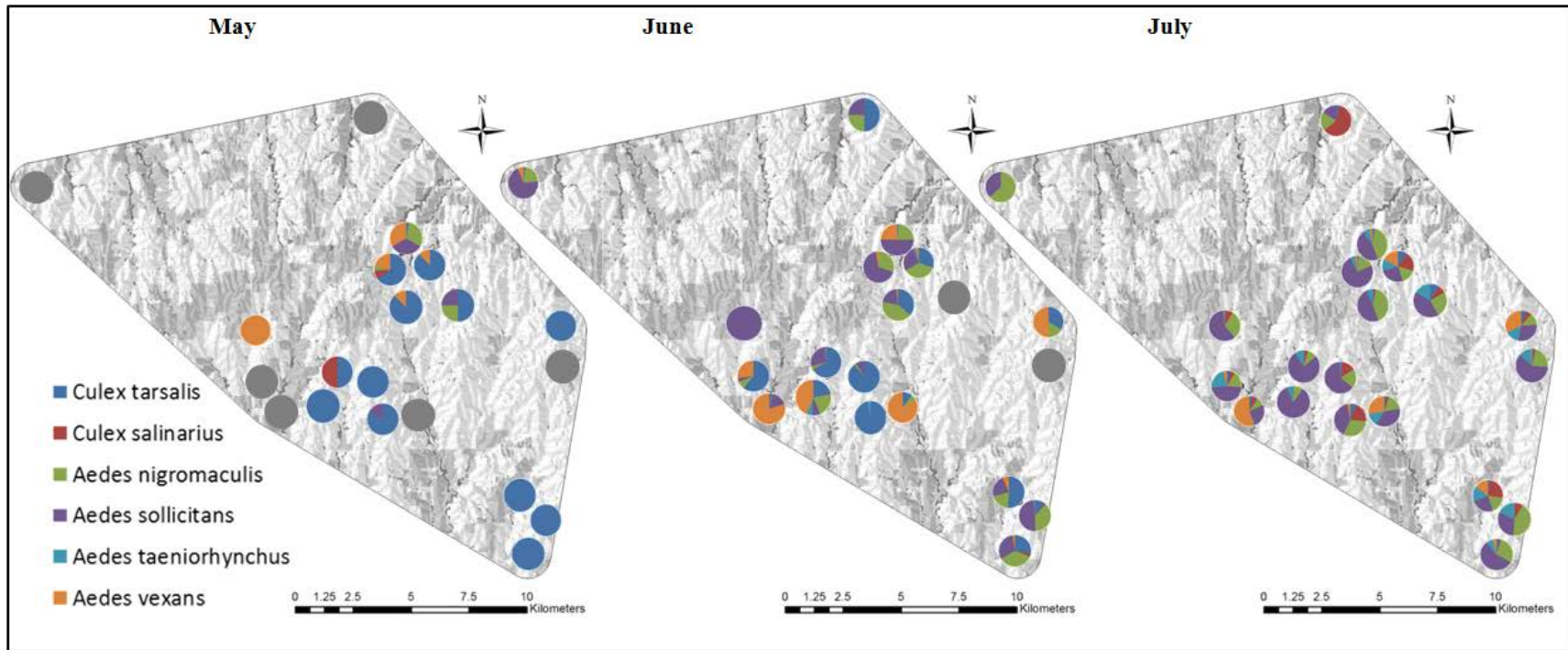


Figure A.6. Changes in the mosquito community composition from May - July, in the Smoky Hills of Cloud County, Kansas.



\* Gray symbol indicate that no species were encountered at a particular site/month.

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## **Appendix B - BLOOD COLLECTION AND HAEMOSPORIDIAN SURVEILLANCE METHODS**

### ***Greater Prairie-chicken Blood Sampling and Nest Monitoring***

Greater Prairie-chicken females were captured during the breeding season from 2007-2011 using walk-in funnel traps and drop-nets (Silvy *et al.* 1990, Schroeder *et al.* 1991). Field methods were approved by the Kansas State University Institutional Animal Care and Use Committee (Protocol Nos. 2474 and 2781). At capture a 40 µl blood sample was collected via toenail clipping and subsequently stored in 1000µl of either Longmire's solution (Longmire *et al.* 1997) or Queen's lysis buffer (Seutin *et al.* 1991) until DNA extraction could be carried out. Females were fitted with 11-g necklace style VHF radio transmitters (Model RI-2B, Holohil Systems Ltd., Ontario, Canada) and numbered metal leg band. During the breeding and nesting season females were located  $\geq 3$  times per week. Once a female was observed in an area for three consecutive days, a portable radio receiver and handheld Yagi antenna was used to locate the nest and flush the bird. Nest locations were georeferenced using portable GPS units.

### ***Avian malaria disease agent surveillance in Greater Prairie-chicken***

DNA extraction was performed on female Greater Prairie-chicken blood samples (n=111) using commercially available Qiagen DNEasy tissue extraction kits (Qiagen Inc. Valencia, CA, USA). All samples were screened using two primer pairs to determine the infection status. Fragments of the parasites ribosomal RNA LSU genes and mitochondrial cytochrome b were amplified using primer pairs 343F/496R (Fallon *et al.* 2003) and 213F/372R (Beadell *et al.* 2005), respectively. Positive and negative controls were included in every Polymerase Chain Reaction (PCR) to reduce the risk of false negatives and increase accuracy in determining infection status (Durrant *et al.* 2007). Amplification of fragments via PCR, was conducted in an Eppendorf epigradient thermocycler (Brinkman Inc. Westbury, NY, USA) in: 20 µl PCR cocktails containing: 30 ng of DNA, 2.5 mM MgCl, 0.2 mM dNTP's, 10 µM of each forward and reverse primer, 0.2 units of Taq polymerase and 30ng of DNA, 2.0 MgCl, 0.2 mM dNTP's, 0.8 µg/µl BSA, 0.6 µM of each forward and revers primer, 0.2 units of Taq polymerase,



respectively for primer set 343F/496R and 213F/372R. Resulting products were visualized on a 3% high resolution 3:1 agarose gel, formulated for the separation of small DNA fragments (Fisher Scientific, Waltham, MA).

## Figures and Tables

Table B.1. Primer pairs used for the amplification of haemosporidian RNA and DNA.

Primer Pair	Haemosporidian	Location	Expected amplicon size
343F/496R	<i>Plasmodium, Haemoproteus,</i>	LSU rRNA genes	154 bp
213F/372R	<i>Plasmodium, Haemoproteus,</i> <i>Leucocytozoon</i>	cyt b mDNA genes	160 bp

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## **Appendix C - ECOLOGICAL NICHE MODELS OF VECTORS SPECIES WITH LOW ABUNDANCES**

This appendix contains the ecological niche modeling results of vector species found at lower abundances in the Smoky Hill study site in 2010: *Culex pipiens*, *Culex restuans*, *Aedes dorsalis*, *Aedes stimulans*, and *Anopheles* species (*Anopheles* species were grouped due to low abundances).

Table C.1. Variable contributions and permutations of ecological niche models developed for low abundance vector species in the grassland of the Smoky Hills, Cloud County, Kansas.

Species	Variable, Variable contributions (permutations)									
<i>Culex pipiens</i>	Dist <sub>w</sub> , 0.25 (0.09)	T <sub>mean</sub> (cq), 0.16 (0.30)	TWI, 0.14 (0.28)	Dist <sub>wl</sub> , 0.13 (0.19)	AASHTO, 0.09 (0.000)	P <sub>mean</sub> (dq), 0.08 (0.08)	Dist <sub>r</sub> , 0.07 (0.01)	T <sub>min</sub> (ss), 0.04 (0.01)	Dist <sub>edge</sub> , 0.03 (0.00)	P <sub>mean</sub> (ave), 0.02 (0.04)
<i>Culex restuans</i>	AASHTO, 0.37 (0.03)	Dist <sub>w</sub> , 0.30 (0.45)	T <sub>mean</sub> (may), 0.13 (0.40)	T <sub>seas</sub> , 0.06 (0.00)	P <sub>mean</sub> (jul), 0.05 (0.00)	P <sub>mean</sub> (dq), 0.04 (0.04)	Slope, 0.03 (0.07)	Dist <sub>edge</sub> , 0.02 (0.02)	TWI, 0.01 (0.00)	
<i>Aedes dorsalis</i>	AASHTO, 0.35 (0.11)	P <sub>mean</sub> (dq), 0.26 (0.73)	P <sub>mean</sub> (jul), 0.25 (0.00)	Dist <sub>r</sub> , 0.09 (0.06)	T <sub>mean</sub> (may), 0.05 (0.09)					
<i>Aedes stimulans</i>	Aspect, 0.17 (0.18)	Dist <sub>w</sub> , 0.16 (0.12)	T <sub>mean</sub> (ss), 0.14 (0.09)	TWI, 0.13 (0.37)	T <sub>max</sub> (cq), 0.10 (0.22)	AASHTO, 0.10 (0.01)	P <sub>mean</sub> (dq), 0.07 (0.02)	Dist <sub>edge</sub> , 0.07 (0.00)	P <sub>mean</sub> (ave), 0.06 (0.03)	
<i>Anopheles</i> species	Aspect, 0.26 (0.04)	AASHTO, 0.24 (0.28)	P <sub>mean</sub> (jul), 0.19 (0.00)	P <sub>mean</sub> (dq), 0.11 (0.37)	Dist <sub>edge</sub> , 0.07 (0.26)	T <sub>min</sub> (jun), 0.07 (0.05)	P <sub>seas</sub> , 0.02 (0.00)	Dist <sub>w</sub> , 0.02 (0.02)	Dist <sub>wl</sub> , 0.01 (0.01)	

Table C.2. Training gain without and with predictor variables of ecological niche models developed for low abundance vector species in the grassland of the Smoky Hills, Cloud County, Kansas.

Model	Variable, Training gain without variable (Training gain with variable)									
(Training AUC)										
<i>Culex pipiens</i>	Dist <sub>w</sub> , 0.57	TWI, 0.66	Dist <sub>wl</sub> , 0.70	T <sub>mean</sub> (cq), 0.72	AASHTO,	dist <sub>r</sub> , 0.74	P <sub>mean</sub> (dq), 0.75	T <sub>min</sub> (ss), 0.76	dist <sub>edge</sub> , 0.76	P <sub>mean</sub> (ave),
<b>(0.92)</b>	(0.20)	(0.08)	(0.13)	(0.17)	0.73 (0.07)	(0.04)	(0.16)	(0.09)	(0.01)	0.77 (0.09)
<i>Culex restuans</i>	AASHTO,	Dist <sub>w</sub> , 0.23	T <sub>mean</sub> (may),	T <sub>seas</sub> , 0.30	Slope, 0.31	Dist <sub>edge</sub> , 0.31	P <sub>mean</sub> (dq), 0.32	P <sub>mean</sub> (jul), 0.32	TWI, 0.32	
<b>(0.82)</b>	0.23 (0.11)	(0.11)	0.28 (0.05)	(0.05)	(0.01)	(0.00)	(0.07)	(0.04)	(0.00)	
<i>Aedes dorsalis</i>	AASHTO,	P <sub>mean</sub> (dq), 0.24	P <sub>mean</sub> (jul), 0.29	Dist <sub>r</sub> , 0.26	T <sub>mean</sub> (may),					
<b>(0.82)</b>	0.19 (0.09)	(0.15)	(0.09)	(0.03)	0.27 (0.06)					
<i>Aedes stimulans</i>	Aspect, 0.32	Dist <sub>w</sub> , 0.32	TWI, 0.34	T <sub>mean</sub> (ss), 0.36	T <sub>max</sub> (cq), 0.36	AASHTO,	P <sub>mean</sub> (ave),	Dist <sub>edge</sub> , 0.36	P <sub>mean</sub> (dq),	T <sub>mean</sub> (cq), 0.39
<b>(0.84)</b>	(0.08)	(0.12)	(0.05)	(0.06)	(0.06)	0.36 (0.04)	0.36 (0.03)	(0.02)	0.38 (0.05)	(0.06)
<i>Anopheles spp.</i>	Aspect, 0.20	AASHTO,	P <sub>mean</sub> (jul), 0.27	P <sub>mean</sub> (dq), 0.23	Dist <sub>edge</sub> , 0.25	T <sub>min</sub> (jun), 0.26	P <sub>seas</sub> , 0.27	Dist <sub>w</sub> , 0.27	Dist <sub>wl</sub> , 0.27	
<b>(0.79)</b>	(0.06)	0.21 (0.06)	(0.05)	(0.10)	(0.01)	(0.00)	(0.02)	(0.02)	(0.00)	

Table C.3. Jackknife tests of distribution models (LTP, Lowest Presence Threshold) for low abundance vector species (*Culex pipiens*, *Culex restuans*, *Aedes dorsalis*, *Aedes stimulans*, and *Anopheles* species) in the Smoky Hills of Cloud County, Kansas.

Species	Maxent, LPT			
	Locality sample size	Threshold	Success	<i>p</i>
<i>Culex pipiens</i>	17	19.203	13	4.32e <sup>-3</sup>
<i>Culex restuans</i>	13	15.583	11	1.00e <sup>-6</sup>
<i>Aedes dorsalis</i>	9	7.788	8	4.47e <sup>-2</sup>
<i>Aedes stimulans</i>	15	16.814	10	9.77e <sup>-3</sup>
<i>Anopheles</i> species	11	4.504	7	1.22e <sup>-1</sup>

Figure C.1. Jackknife test of training gain for *Culex pipiens*, a competent vector of arboviruses (St. Louis and West Nile Virus disease agents) and *Plasmodium* species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to road, distance to water, distance to woodland, TWI (Topographic Wetness Index), mean temperature of the coldest quarter of the year, minimum temperature during the sampling season, mean annual precipitation, and mean precipitation of the driest quarter of the year.

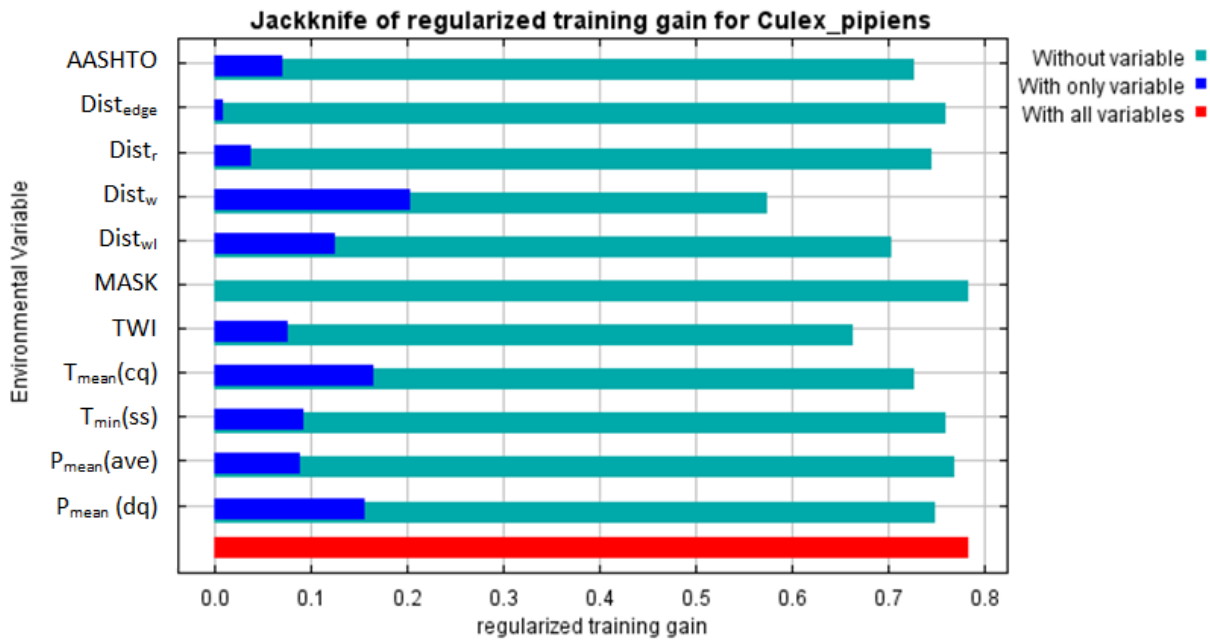


Figure C.2. Jackknife test of training gain for *Culex restuans*, a competent vector of arboviruses (St. Louis and West Nile Virus encephalitis disease agents) and *Plasmodium* species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to road, distance to water, curvature, slope, TWI (Topographic Wetness Index), annual temperature seasonality, mean temperature of May, mean precipitation of the driest quarter of the year, and mean precipitation of July.

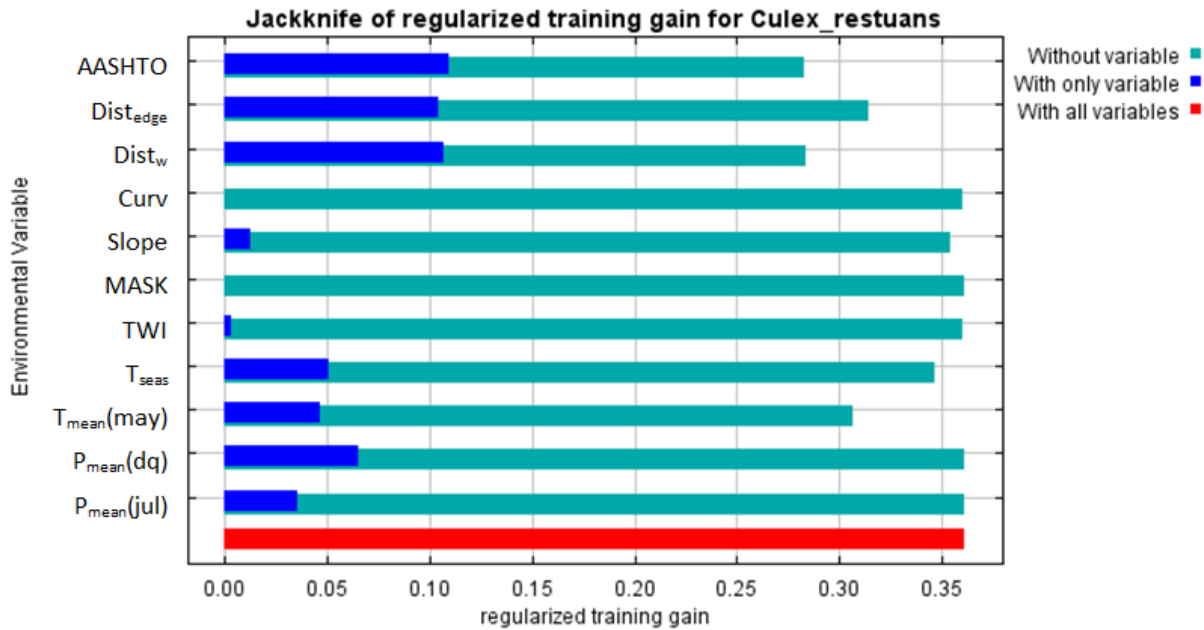


Figure C.3. Jackknife test of training gain for *Aedes dorsalis*, a competent vector of arboviruses (Western equine, St. Louis and West Nile Virus encephalitis disease agents). The environmental predictor variables included (from the top): AASHTO, distance to road, distance to water, annual temperature seasonality, mean temperature of May, mean precipitation of the driest quarter of the year, and mean precipitation of July.

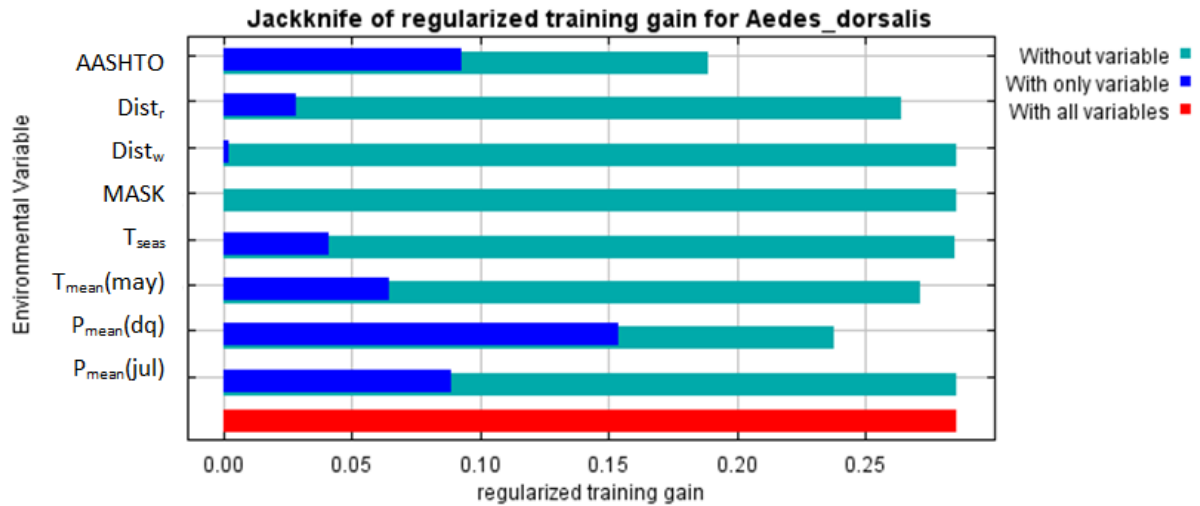




Figure C.4. Jackknife test of training gain for *Aedes stimulans*, a competent vector *Plasmodium* species (avian malaria disease agents). The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to water, aspect, TWI, maximum temperature of the coldest quarter of the year, mean temperature during the sample season, mean annual precipitation, and mean precipitation of the driest quarter of the year.

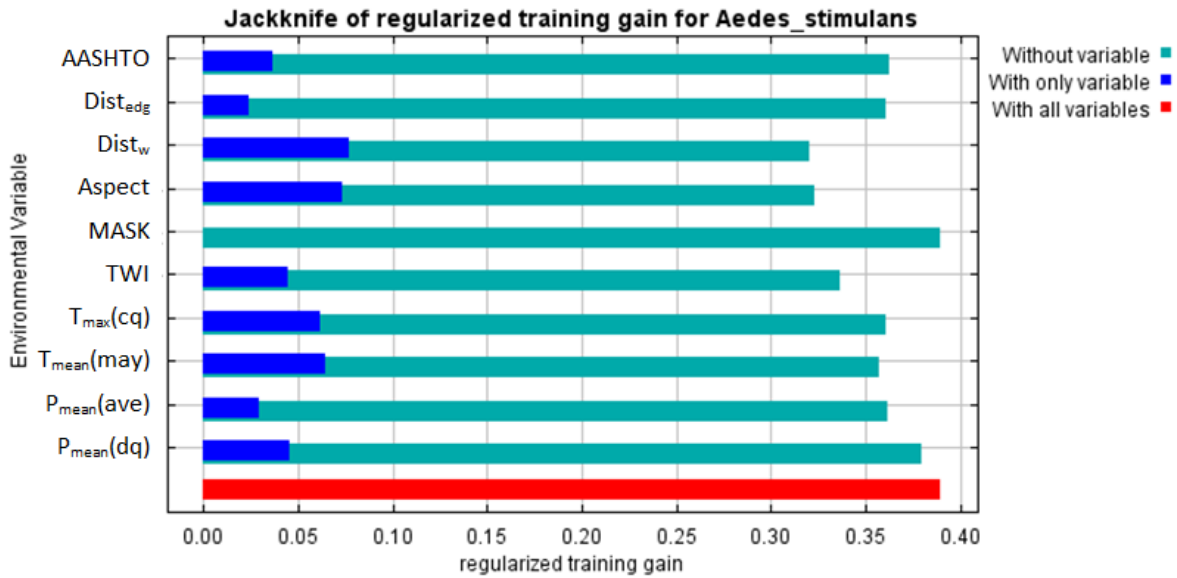


Figure C.5. Jackknife test of training gain for *Anopheles* species. The environmental predictor variables included (from the top): AASHTO, distance to edge, distance to water, distance to woodland, aspect, curvature, TWI, minimum temperature of June, mean precipitation of the driest quarter of the year, mean precipitation of July, and annual precipitation seasonality.

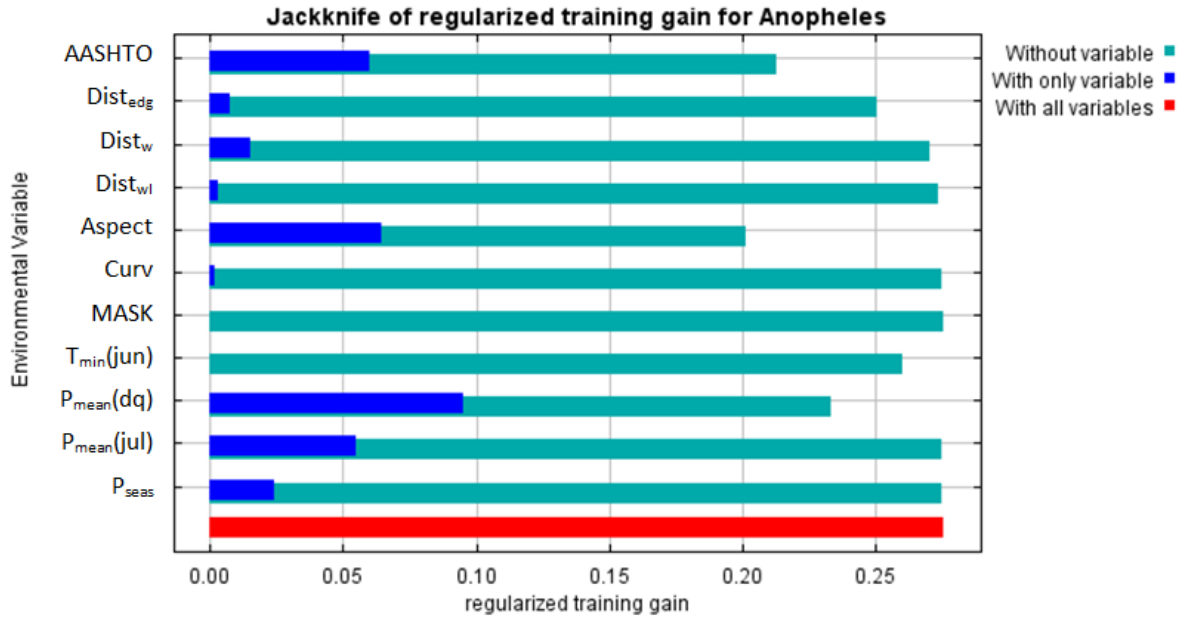


Figure C.6. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Culex pipiens* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

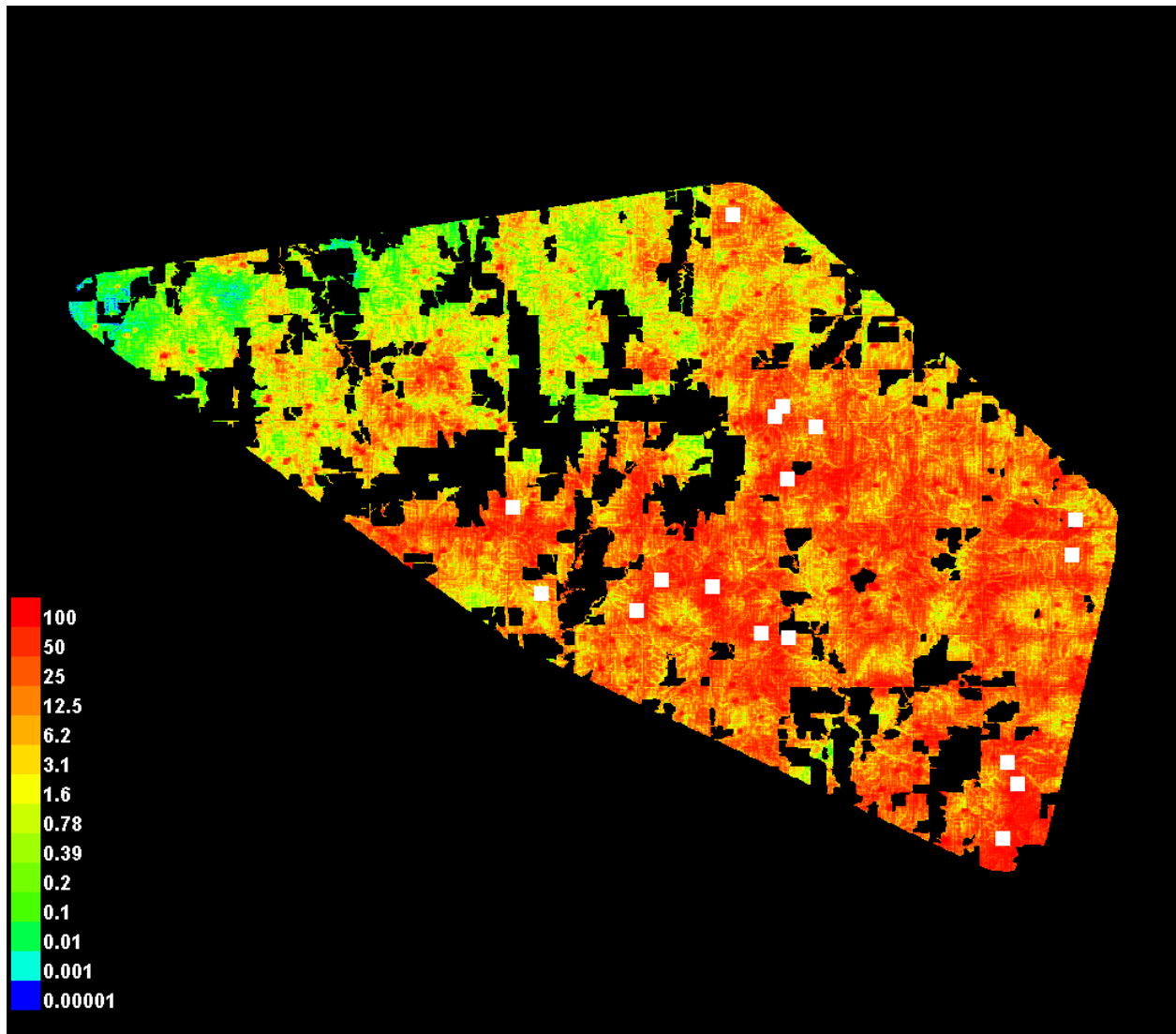


Figure C.7. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Culex restuans* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

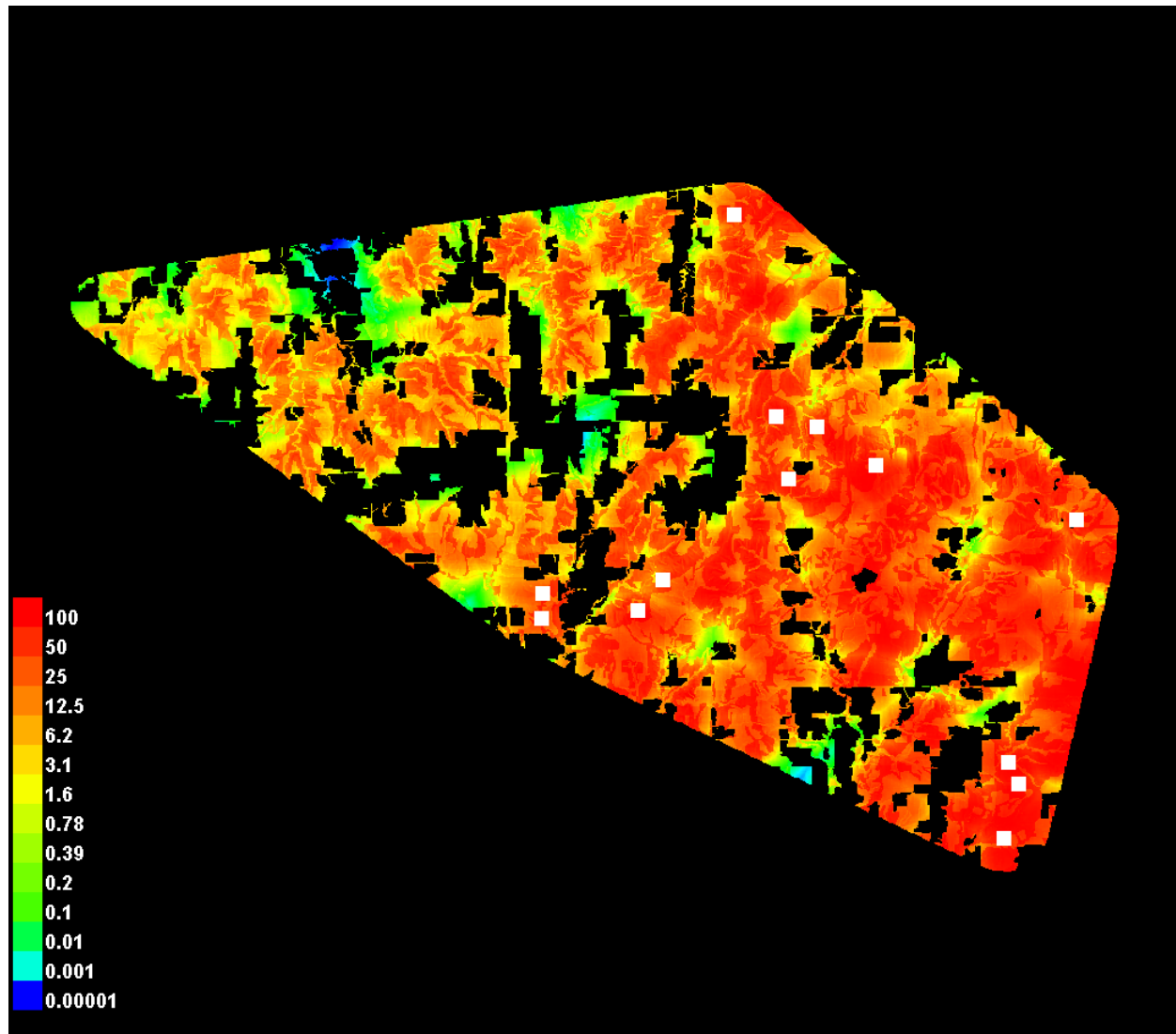


Figure C.8. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Aedes dorsalis* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

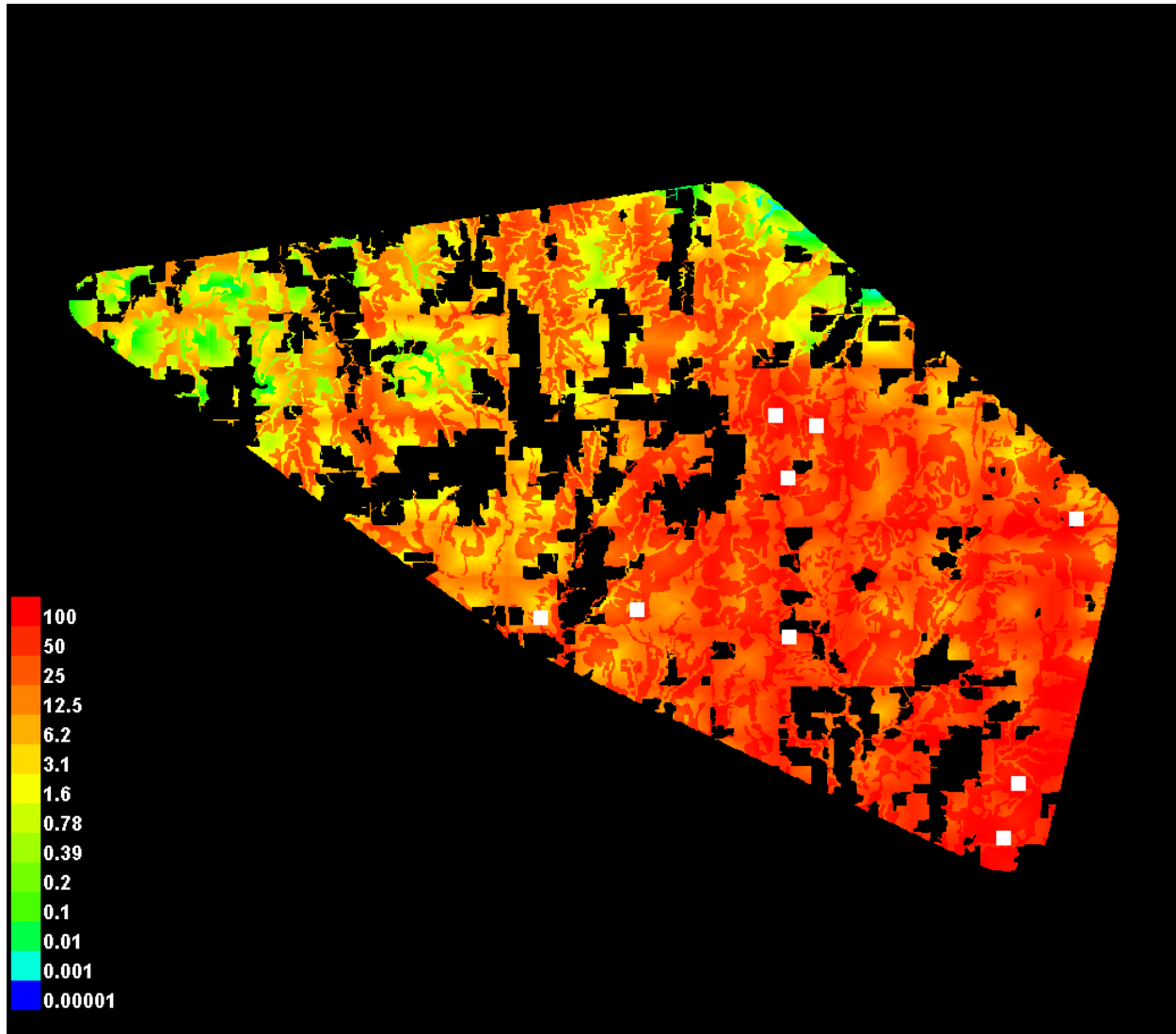


Figure C.9. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Aedes stimulans* in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

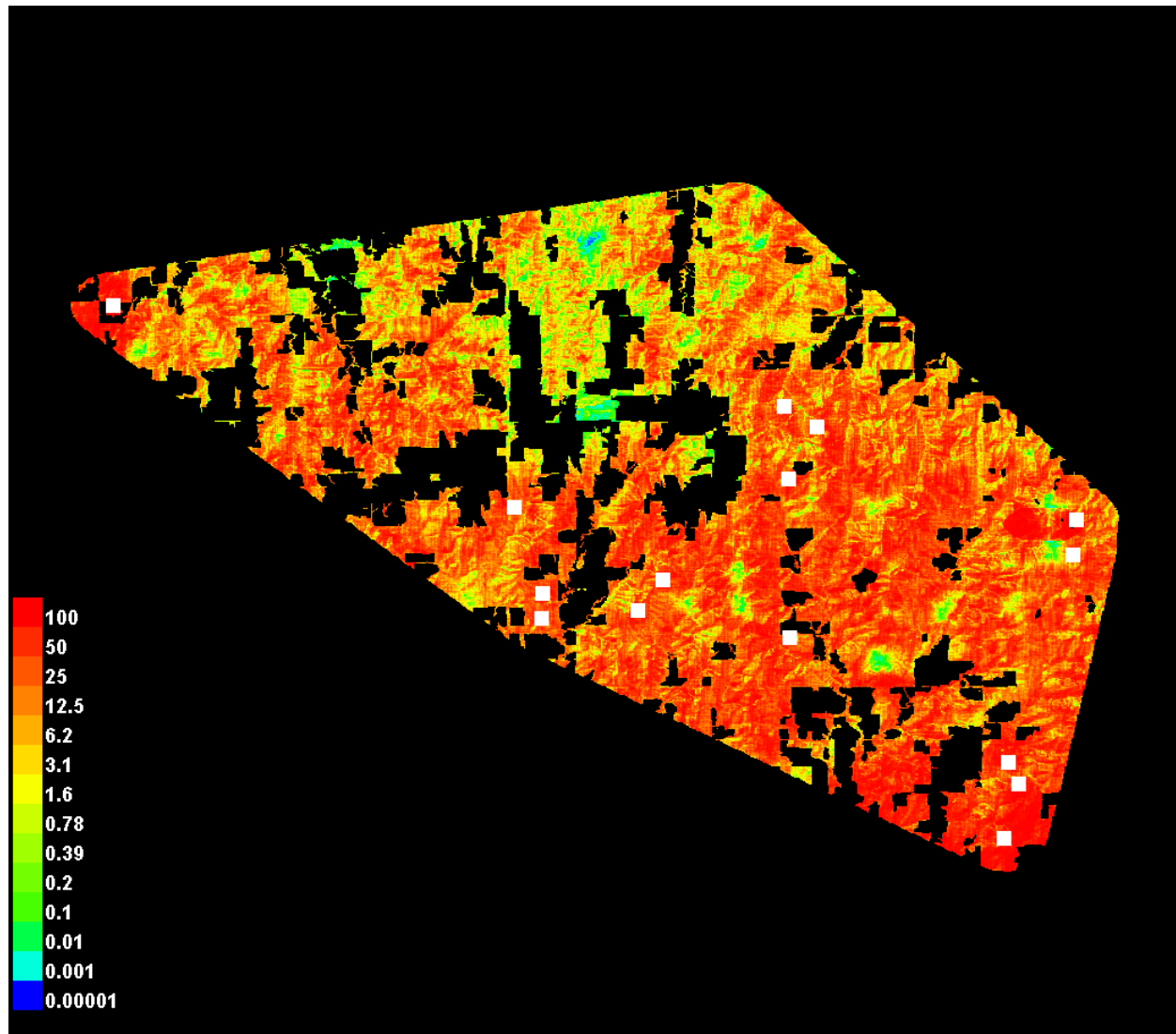


Figure C.10. Maximum entropy probability distribution (red = high probability, blue = low probability) of *Anopheles* species in the grasslands of the Smoky Hill eco-region, Cloud County, Kansas. Species occurrences are indicated with white square symbols.

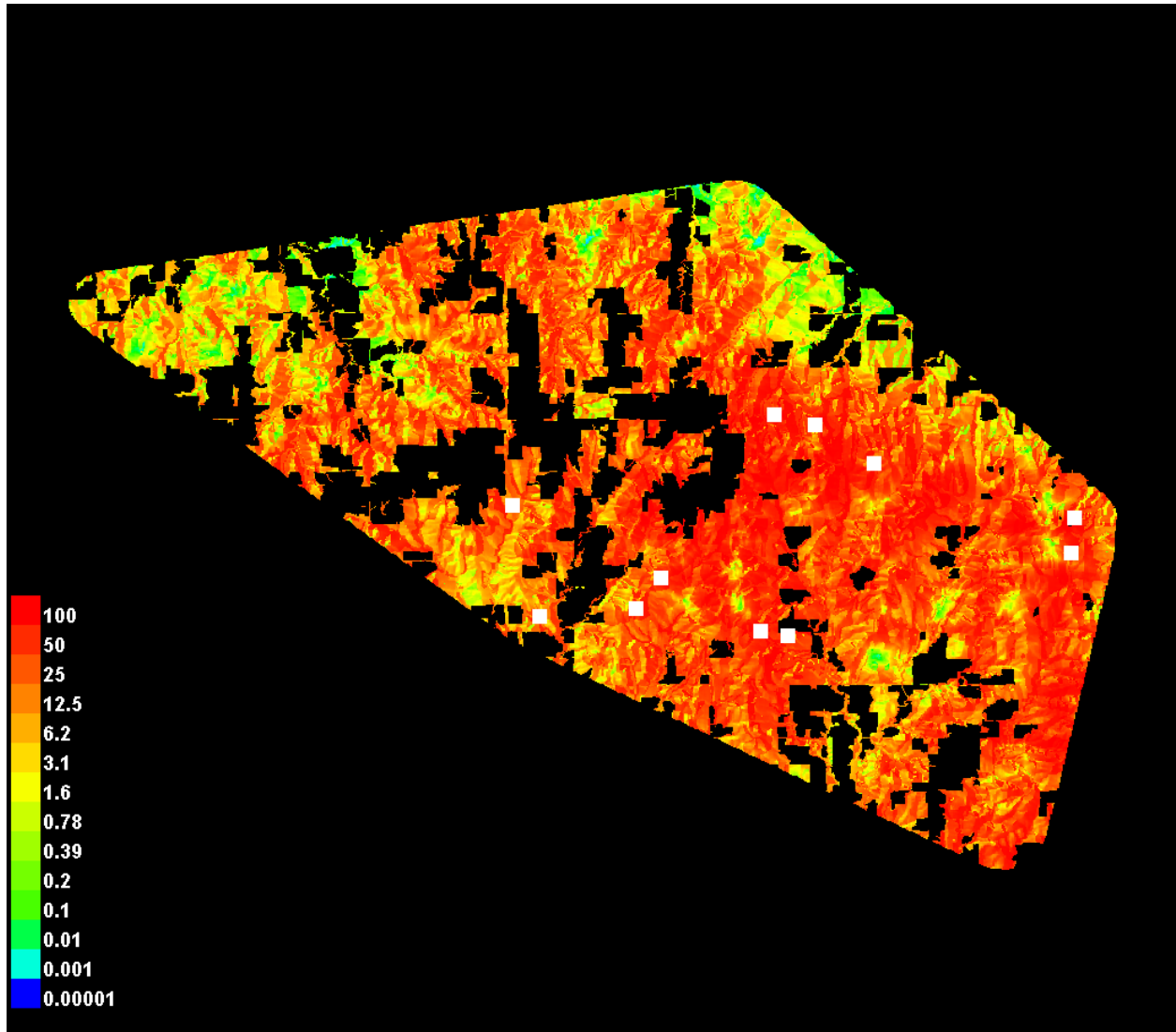


Figure C.11. Presence-absence predicted distribution of *Culex pipiens* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10.

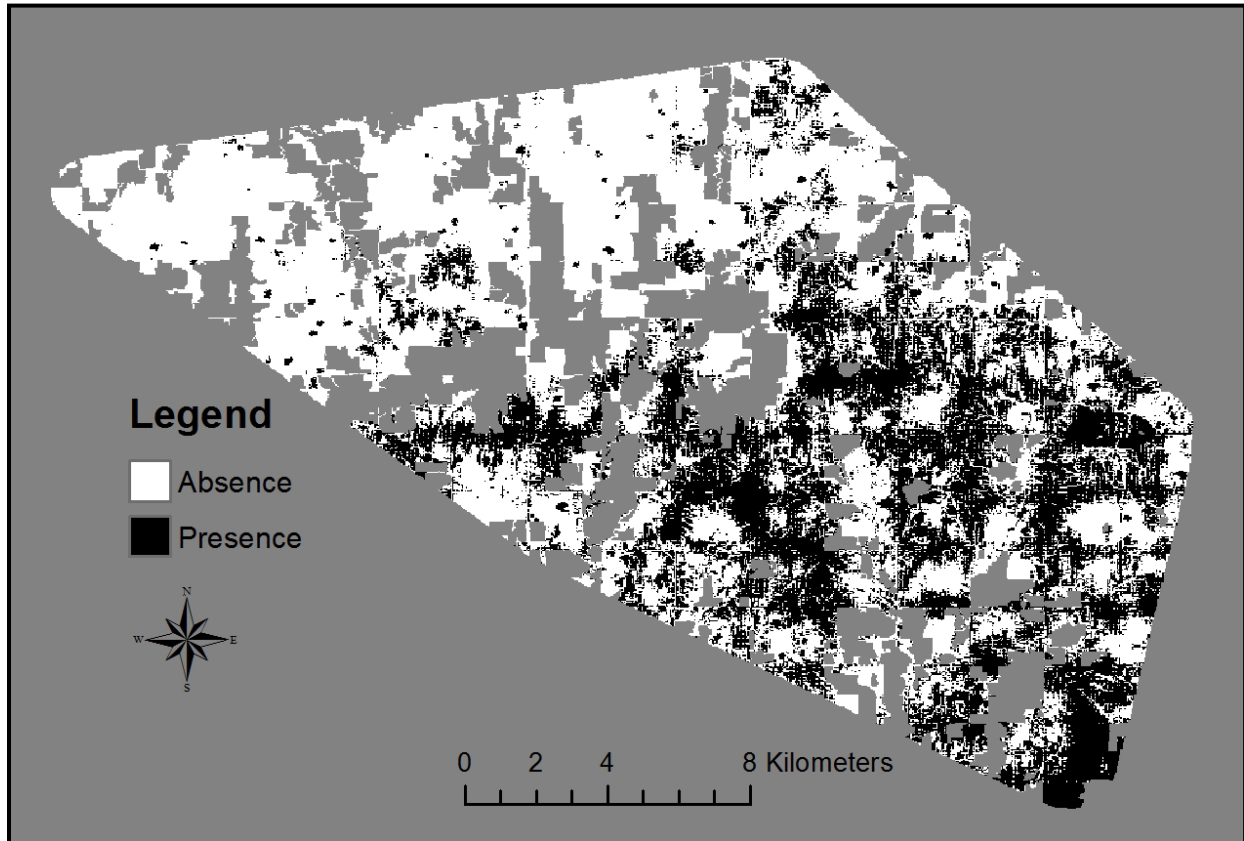




Figure C.12. Presence-absence predicted distribution of *Culex restuans* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10.

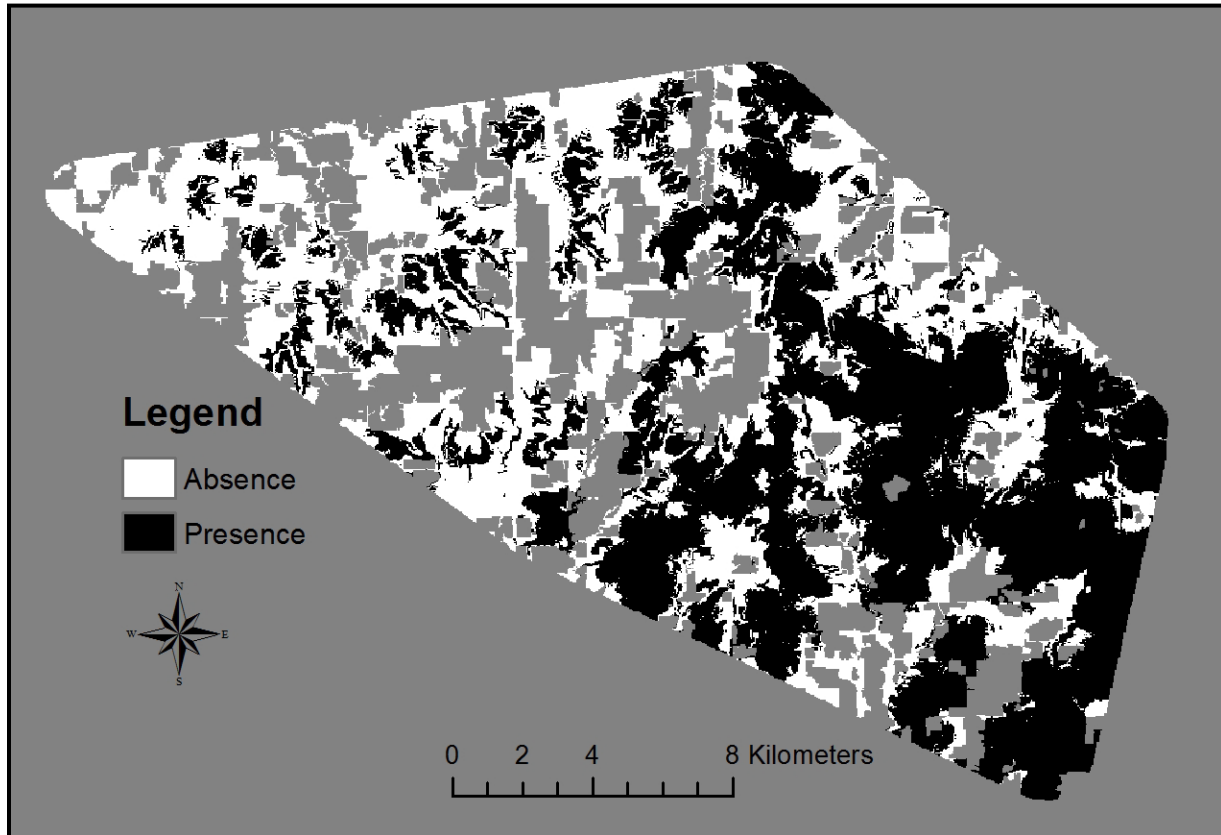


Figure C.13. Presence-absence predicted distribution *Aedes dorsalis* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10.

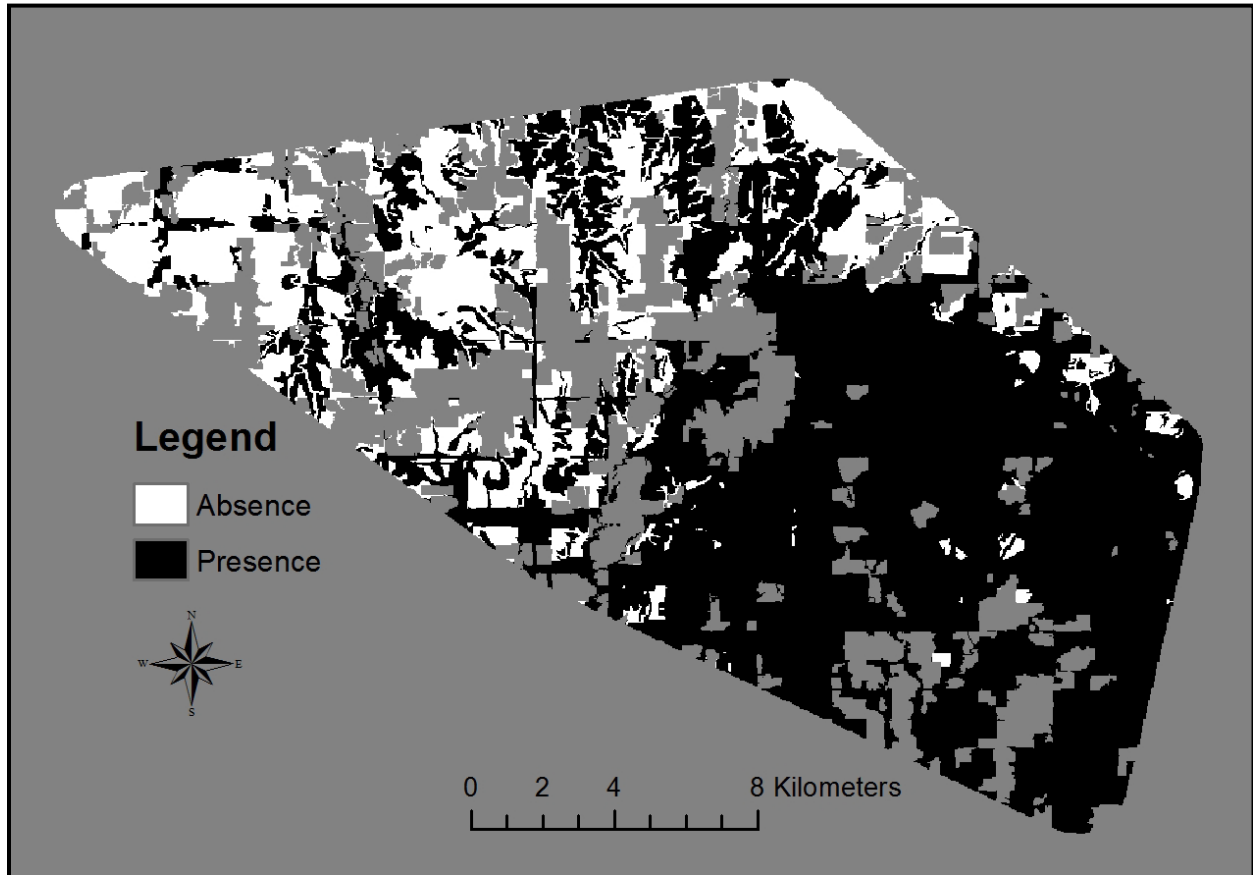


Figure C.14. Presence-absence predicted distribution *Aedes stimulans* based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10.

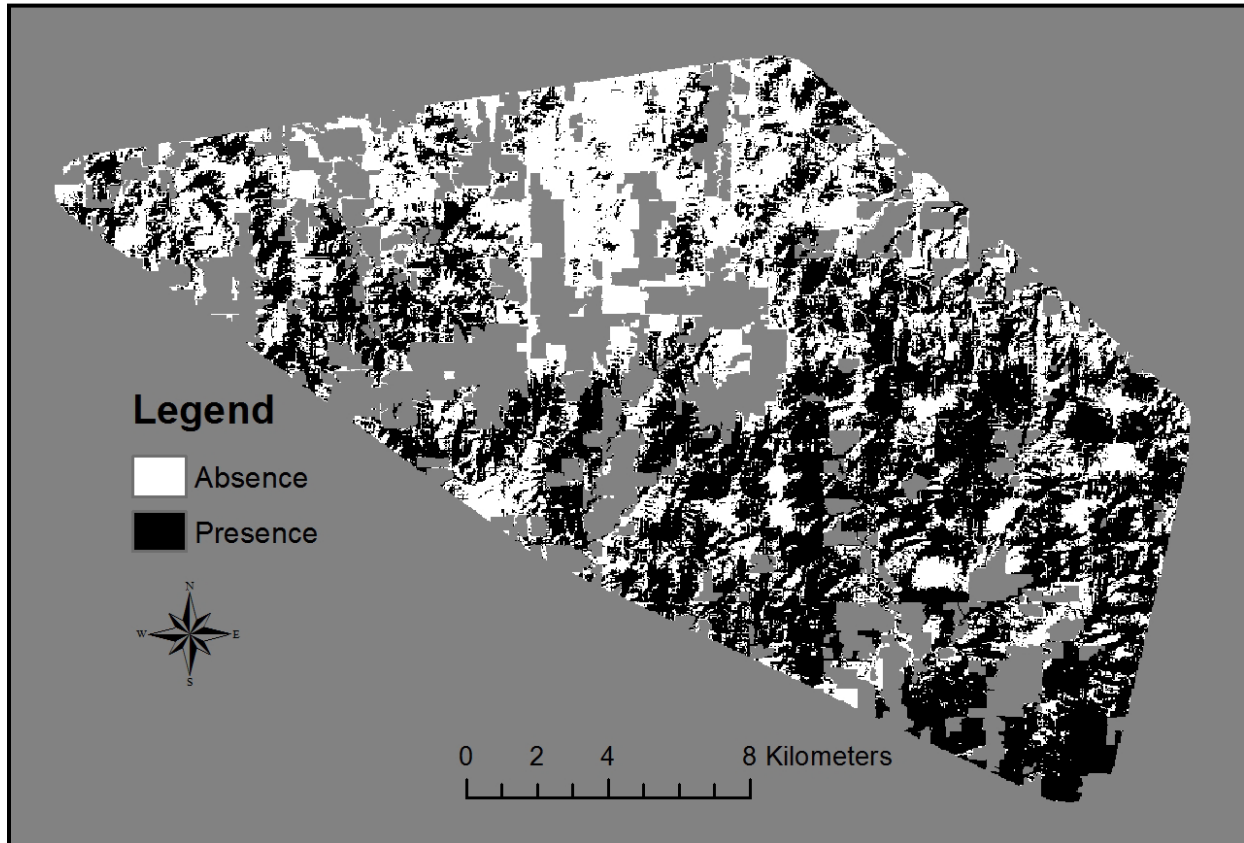


Figure C.15. Presence-absence predicted distribution *Anopheles* species based on the Lowest Presence Threshold (LPT). The distribution map was created by importing the Maxent cumulative output into ArcGIS 10.

