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Impacts of Energy Development on the Lesser Prairie-Chicken Ecology and Management

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Impacts of Energy Development on the Lesser Prairie-Chicken Ecology and Management

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DEPARTMENT OF ZOOLOGY

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Abstract:

Habitat management of the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) has been ongoing throughout its range for many decades. In recent decades the focus of that management has been conservation. Habitat fragmentation caused by anthropogenic sources has reduced the area of suitable habitat throughout the species prehistoric range by greater than 90%. I used MaxEnt to generate models for four habitats used by the species. The predicted suitable habitat tended to be centered on local breeding grounds. In those models, minimum January temperature and annual precipitation were the factors that contributed most to model predictions. In addition, this species avoids anthropogenic structures. I used the MaxEnt habitat models to estimate potential loss of habitat resulting from avoidance of these structures. Of the four habitats examined, nesting habitat was impacted most severely by avoidance of man-made structures.

Introduction:

Global climate change and wildlife management

Global climate change is happening, and is due in large part to human activity, which continues to increase the levels of greenhouse gases present in our atmosphere (Karl and Trenberth 2003). Global climate fluctuations have happened in the past (Broecker 2001), but it is theorized that increased levels of carbon dioxide in the atmosphere are the cause of the current shift (Karl and Trenberth 2003). The increased amount of CO_2 in the atmosphere has created a situation where light (and in turn heat) from the sun that would be reflected back into space is being trapped in the atmosphere, as in a greenhouse. This trapped heat is slowly increasing the mean temperature of the surface of the planet (Karl and Trenberth 2003). It has been shown that daily minimum temperatures increase at a much more rapid rate than daily maximum temperatures (Karl et al. 1993).

If climate in an area shifts, the natural communities in that area are forced to shift as well. Temperatures may increase past the maximum tolerable range of a species, or precipitation patterns may change, altering a species ability to survive in existing habitat (Walther et al. 2002). When plant and animal species are faced with these changes, they have three potential ways a species can react to these changes: (i) adapt to the new changes; (ii) follow their current habitat needs as they may shift geographically, or (iii) die out in areas that have changed due to climate shifts (Heller and Zavaleta 2009).

In some cases it is literally impossible for a species to adapt to changes in habitat quickly enough or be able to follow the geographic shifts of their current habitat (Jump and Penuelas 2005). For the process of adaptation a species that is being affected by climate change must have sufficient genetic variability within its gene pool to adapt to the changes (Hoffman et al. 2003). The process of adaptation generally takes many generations even when genetic variation does exist in a population. Offspring that express the adaptations to changes in climate must not only be born, but then produce offspring of their own to spread the adaptation (Jump and Penuelas 2005). Combined with these genetic constraints, a population must also produce these changes rapidly enough to outpace the changes in climate, a task which may not be possible with the predicted speed of climate change (Billington and Pelham 1991, Savolainen et al. 2004).

A species shifting its range to follow its current habitat may be relatively simpler than adapting to climate change, but it is not without its own problems. A species may not be able to shift their range quickly enough to follow the geographic shifts caused by climate change (Davis and Shaw 2001). Certain habitat requirements for a species may simply not be available in different geographic areas (Thomas et al. 2004). Animal species which require very specific vegetation or prey items to survive may not be able to find those needs if they change location. These habitat specialists will have an especially difficult time dealing with climate change as they will need their required community to either adapt with or move ahead of them to compensate for the shift in climate (Travis 2003).

In the U.S., wildlife management has been a major area of research for the past century (Peek 1986). For most species, the practice of management by humans began because those plants and animals held some inherent value, normally for sport (Macnab 1983). Active management came too late for species like the, now extinct, Passenger Pigeon (*Ectopistes migratorius*) and just in time for others like the White-tailed Deer (*Odocoilius virginianus*) (VerCauteren 2003). Management has become a major contributor in the survival of some species, such as the California Condor (*Gymnogypscalifornianus*) (Woods et al. 2007), and has taken many forms over the years (Peek 1986).

Recent developments with climate change have brought many minds to bear on the ideas of managing species with shifting climates (Heller and Zavaleta 2009). The biggest concern for any wildlife manager is keeping your chosen species or population from going extinct. Unfortunately, it is not a simple task to assist species as they adapt to changing conditions (Heller and Zavaleta 2009). Thus, when faced with climate change, managers need to understand how and where their populations may move in response to the changes. It has been shown that species will generally move northward in latitude or higher in elevation to follow their shifting habitat needs (Parmesan and Yohe 2003, Root et al. 2003). Managers have used this information to begin preparations and research to protect their populations in the future (Heller and Zavaleta 2009). If we know where a population is likely to move to, then we can attempt to protect those new habitats. Managers can also create habitat corridors for individuals to use for travel between old and new (Halpin 1997).

Human development can be a major problem for managers attempting to protect a species in the face of global climate change (Heller and Zavaleta 2009). Man-made structures (e.g., houses, roads, power lines, etc.) tend to reduce and fragment natural habitat. They can become barriers for individuals of a species that may need to travel to new habitat areas (Dixon et al. 2007, Riley et al. 2006, Epps et al. 2007). Even if anthropogenic structures or settlements do not severely impact habitat quality per se, they may still alter the habitat by their mere existence. Species shifting geographic ranges into human developed land has been an issue in previous and on-going studies (Boone and Hunter 1996, Plumb et al. 2009).

Green energy as the enemy?

Our energy needs and acquisition have been evolving for generations and with them, so has our use of the environment. Until our recent use of renewable energy sources, we have had to exploit the environment around us to generate the kind of energy our societies require. This exploitation began as simply harvesting trees, but with new technology we began consuming entire ecosystems with techniques such as strip mining (Brenner et al. 1984). Thus, these newly developing ways of harnessing energy can give us hope for the future existence of the environment. These new technologies come at a cost to the environment, however. Hydroelectric power requires dams to be built, which heavily impact rivers, streams, and the riparian zones they create (Gup 1994). Similarly, wind energy requires large tracts of land where the wind turbines stand. This requirement gives wind energy the potential to cause the same kinds of damage as any other form of energy production.

Wind energy can have multiple effects on many species of wildlife (Kunz et al. 2007a). The most direct effect, being death, has been well documented for birds (Erickson et al. 2001) and bats (Kunz et al. 2007b). Wind fields, large tracts of land containing hundreds of wind turbines, also produce several forms of habitat destruction (Kunz et al. 2007a). The fields can be placed directly on top of existing habitat (where habitat is directly altered for turbine construction), they can create divides between populations (by creating openings that certain species will not cross), or they may alter the habitat in a subtle way (causing certain species to generally avoid habitat around the structures) (National Research Council 2007).

Wind energy and the Great Plains

The Great Plains is a prime area to consider for the impacts of wind energy. There are many wind farms scattered throughout the plains currently, with many more in production or pre-production (Krauss 2008). These areas of energy development have been shown to increase habitat fragmentation and change land use of grassland species (Robel et al. 2004, Pruett et al. 2009b). One species in particular, which is predicted to be greatly affected by wind energy development, is the lesser prairie-chicken (*Tympanuchus pallidicinctus*) (Robel et al. 2004, Pruett et al. 2009b). This bird has been described as an “umbrella species” for the Great Plains (Pruett et al. 2009a). This means that management efforts to protect the lesser prairie-chicken will help to protect other native species of the Great Plains.

With regard to lesser prairie-chickens the most relevant aspect of the wind fields is the physical structure of the turbines. In wooded areas, the insertion of these tall man-made structures may not have much impact on the local community, outside possible avoidance of corridors by local species (National Research Council 2007). It is hypothesized that, in a grassland habitat, the towers stimulate avoidance behavior due to their height and potentially the level of noise they emit (Robel et al. 2004). Many species native to grassland biomes have a natural aversion to trees, lesser prairie-chicken included (Grant et al. 2004, Hagen and Giesen 2005), perhaps because the trees are associated with predator roosts or perches (Hagen et al. 2011).

Proper management of the species has been a concern for decades (Davison 1936, Etheredge 1943, Copelin 1958, Gibson 1973, Applegate and Riley 1998, Hagen et al. 2004). Historically, this management concern was regulating harvest as the species was hunted throughout its range. Hunting has ceased throughout four of the five states that constitute its remaining range (Hagen et al. 2004) and the focus of research has changed to better understanding population trends and habitat requirements (Hagen et al 2004).

This quest for understanding has led to many empirical studies over the past decade, including; habitat use (Fuhlendorf 2002, Salter et al. 2005), nesting ecology (Pitman et al. 2006b, Davis 2009), brooding success (Hagen et al. 2005, Fields et al. 2006, Pitman et al. 2006a), microclimate (Patten et al. 2005a, Bell et al. 2010), community interactions (Jamison et al. 2002, Hagen et al. 2005, Silvy 2006, Hagen et al. 2007b, Derner et al. 2009), species survival (Pitman et al. 2006c, Hagen et al. 2007a, Lyons et al. 2009), interactions with anthropogenic structures (Pitman et al. 2005, Pruett et al. 2009a, Jarnevich and Laubhan 2011) and effects of fire regime (Boyd and Bidwell 2001). These studies have given insight into specific areas of ecology and habitat use, although with the exception of the work of Patten et al. (2005) and Bell et al. (2010), little has been done to quantify the abiotic factors that make habitat suitable for lesser prairie-chickens.

Thirty years ago it was estimated that species' habitat had declined 92% throughout its native range. This loss of land was accompanied by an estimated 97% reduction in total population size (Taylor and Guthery 1980b). Studies have continued to monitor the species since then (Hagen et al. 2004, 2005, 2009). Hagen et al. (2004) suggested that habitat quality may have become the limiting factor in the past two decades, as rate of habitat loss has slowed, but populations continue to decline.

There are several relevant causes for the reduction in habitat quality. Wolfe et al. (2007) described collisions with fences as a major cause of mortality for lesser prairie-chickens in Oklahoma. When flushed, individuals can hit flight speeds high enough to incur serious injury and death when they collide with an object (Wolfe et al. 2007). This, coupled with the fact that old and unused fences tend to become overgrown by prairie-grasses, creates a serious concern for managers of the birds. Guidelines for proper marking and removal of unused and dangerous fences have been published (Wolfe et al. 2009), but fences are only part of the problems accumulating for the species.

Habitat fragmentation is a major concern for lesser prairie-chickens (Fuhlendorf et al. 2002, Patten et al. 2005b, Pruett et al. 2009a). Lesser prairie-chickens prefer large open tracts of prairie habitat as their annual range (Hagen et al. 2004). Individuals and groups of individuals (leks) have been shown to avoid power lines and well-traveled roads (Robel et al. 2004, Pruett et al. 2009b). The birds avoid crossing these structures with such fervor that the authors predict otherwise viable habitat to be rendered unsuitable by their presence. This information leads to a disturbing set of potential problems in the near future. A recent addition to this set of problems is that energy development companies have found areas within and adjacent to occupied prairie-chicken habitat in Oklahoma to be suitable for wind farm installations.

The goal of this study is to create a set of habitat suitability models based on lesser prairie-chicken habitat use throughout the year. The creation of these models will allow me to test several hypotheses relevant to lesser prairie-chicken habitat. (1) Breeding habitat dictates overall habitat. Individuals have been shown to remain close to their lekking grounds year-round (Hagen et al. 2004), thus habitat used should be centralized on lekking and nesting habitats. (2) Different environmental factors will define nest and lek habitat. Lekking grounds are typically of sparse vegetation and on a slightly raised elevation (Hagen and Giesen 2005), while nesting success is dictated by vegetative cover (Pitman et al. 2006). (3) Elevation will impact leks more than nesting, or any other model. Standard deviation of elevation was recently shown to be an important factor in lesser prairie-chicken habitat suitability models (Jarnevich and Laubhan 2011). (4) Normalized Difference Vegetation Index (NDVI) will have the greatest impact on nesting habitat, as that use requires the most specific vegetation requirements. Vegetation requirements are the strictest for nesting habitat (Hagen et al. 2004).

Methods:

Study species and habitat uses

The lesser prairie-chicken is a species of grouse native to south-western North America. It is a diurnal, terrestrial, non-migratory species, which inhabits sand-sagebrush, short and mixed-grass prairie, and sand-shinnery oak habitat (Taylor and Guthery 1980b). It exists only in parts of five states in the U.S.: Colorado, Kansas, New Mexico, Oklahoma, and Texas (figure 1).

There are three important seasonal components of habitat use for lesser prairie-chickens; Lekking (mating season), nesting/brooding, and non-breeding (Taylor and Guthery 1980b). Each of these "phases" uses slightly different habitat. Lekking is the term used for the breeding system employed by genus *Tympanuchus* (as well as several other avian species). A lek is a gathering of individuals for competitive mating display. Local populations of prairie-chickens tend to use the same lekking grounds from year to year (Hagen et al. 2005). Prairie chicken leks also tend to have the same vegetation characteristics from one local population to the next (Hagen and Giesen 2005). A prairie-chicken lek tends to be on open ground surrounded by taller plant species (sand sagebrush (*Artemisia filifolia*) or shinnery-oak (*Quercus havardii*) depending on location, with a much higher proportion of oak in the western part of the prairie-chicken's range and a much higher proportion of sagebrush in the eastern part (Hagen and Giesen 2005). Leks have been recorded on areas of short-grass, abandoned oil platforms, recently burned areas, unimproved roads, heavily grazed areas, cultivated fields, and areas treated with herbicide for shrub removal (Jamison et al. 2002).

After mating, females leave the lekking grounds, either to find a suitable nesting area or to visit another lek. Males remain on the lek after copulation for further chances at mating and have been documented to remain on or around their attended lekking grounds throughout the year (Hagen et al. 2004). Nesting habitat is chosen by the nesting female (Copelin 1963). A nest site is chosen with visible obstruction (Robel et al. 1970) and horizontal cover (Hagen and Giesen 2005) as the most important factors. Nest success has been positively correlated with proximity to and density of tall bunch grasses and shrubs (Riley et al. 1992, Pitman et al. 2005). Nests are often located within 3.5 km of the closest lek (Hagen et al. 2004). Brooding habitat is characterized as bare ground with overhead cover (Hagen et al. 2004, Bell et al. 2010). It has also been shown that high forb density is an important aspect of brooding habitat (Jones 1963, Fields et al. 2006).

Non-breeding habitat encompasses any area used by individuals of the species when not breeding, nesting, or brooding, but is typically near lekking grounds (Taylor and Guthery 1980). These areas contain several types of cover; sand sagebrush, sand shinnery oak, short and mixed grass prairie, riparian areas, and cultivated fields (Taylor and Guthery 1980b). In terms of habitat use, sagebrush and shinnery-oak are mostly equivalent habitat types. Lesser prairie-chickens use both plants for overhead cover, primarily for nesting and roosting (Hagen and Giesen 2005). Sagebrush occurs in the northern parts of the range, while shinnery-oak occupies the southern parts (Hagen et al. 2004). Mixed grasses areas are used for year-round feeding, including brood rearing. A diverse community of forbs is a crucial component to raising chicks (Jones 1963). Riparian areas have been used historically for winter feeding in areas dominated by sand sagebrush, while acorns form a majority of the winter diet in shinnery-oak habitat (Hagen et al. 2004). That behavior has given way in recent decades to the use of monoculture crop fields. Post-harvest fields now contribute heavily to winter feeding where suitable habitat is adjacent (Jamison 2000, Jamison et al. 2002).

Lesser prairie-chickens use these different land cover types at various times of the year, usually based on food needs/preferences. Individuals tend to feed heavily on insects from May to October and on plant materials from November to April (Jones 1963). Their predominant use for agricultural fields is as supplements to winter diet, beginning to forage in these fields soon after fall harvests each year, and as a source of high quality food for pre-nesting females and lekking males (Jamison 2000, Jamison et al. 2002).

Study area

Figure 1 outlines the study area and describes its position in North America. I selected this area because it encompasses current well-known lesser prairie-chicken habitat in Oklahoma, as well as previous documented habitat in the western pan-handle of the state. There is an abundance of locality data for the populations of prairie-chickens at the base of the pan-handle in Harper, Ellis, and Beaver Counties. I wanted to include areas of heavily used current habitat as well as currently unused previous habitat to test the predictive models. I used ArcMap (ESRI) to create a rectangular area which included the previously used habitat in the western pan-handle as well as the habitat used by current populations.

Habitat Modeling

Niche modeling began as habitat suitability modeling, done by either global information system (GIS) or multivariate analysis (Donovan et al. 1987, Clark et al. 1993). In either system, a number of variables, associated with habitat quality for the given species, are used to produce a graphical analysis of a given geographic area. These variables have historically been abiotic factors (temperature trends, precipitation, elevation, etc.), but recent studies have begun using biotic relationships as a means to increase the resolution of the results (Preston et al. 2008, Jarnevich and Laubhan 2011).

The use of niche modeling in ecology has become widespread (Guisan and Zimmerman 2000**,** Raxworthy et al. 2007**,** Ortega-Huerta and Peterson 2008). As the use of these techniques has increased, so has the range of their uses. Today's modeling programs can be used to estimate habitat area (Phillips et al. 2006), predict the effects of global climate change on species (Preston et al. 2008), and illustrate speciation (Graham et al. 2004).

Habitat suitability modeling is still in flux. There are several aspects of model creation and interpretation with are still debated in the current literature (Elith et al. 2006, Peterson et al. 2008). There are now several methods for creating these models, but a consensus on the best available methods is starting to emerge (Elith et al. 2006). Since mapping and modeling software are not perfectly integrated at this juncture, this often leads to problems with transference of data from one to the other (Peterson et al. 2007). This has led to different opinions on validity of model output between programs (Elith et al. 2006, Peterson et al. 2007, 2008). This has also led to debates and further research into what output values are important to model interpretation (Elith et al. 2006, Peterson et al. 2008). Many of these questions cannot be appropriately answered at this time, but as this discipline continues to see use, our view on these issues should become clearer.

Even with these inherent faults, niche modeling has proven itself to be a powerful tool for ecological studies and species management (Peterson 2003, Phillips et al. 2006, Preston et al. 2008). For lesser prairie-chickens, specifically, this technique could provide major insight for habitat managers. With both habitat area and habitat quality dwindling in Oklahoma, having a visual outline of existing and potential habitat would be useful. Maps of prairie-chicken habitat in the state have been constructed using accumulated species knowledge (Horton et al. 2010). Niche modeling may provide us with a way of “double checking” what has already been produced. This would provide a clearer picture of the current situation for decision makers in the process.

This study is centered on ecological niche models created using locality data of individuals, nests, and leks from Oklahoma. At present, the birds are only located in the northwest portion of the state, within and at the base of the pan-handle (Horton et al. 2010). To create the models, I have chosen to use the program MaxEnt, which has been shown to produce models with lower errors of commission than other commonly used software (Phillips et al. 2006, Phillips and Dudik 2008).

The models were created using both biotic and abiotic factors to ensure a high level of accuracy. I created independent models using localities of all individual birds, leks, nests, and individual localities collected outside the nesting/breeding season. I chose to use nests apart from individual localities simply to observe any differences between the two, as far as habitat predictions are concerned. To avoid auto-correlation in this comparison between the nest and individual, the 4th data set of non-breeding/nesting individuals was created. This allows for any actual difference between habitat used for nesting and habitat used during the rest of the year to be identified. This same principle works for lek data as well, thus the non-breeding/nesting individual data set is used for that comparison also.

The next goal of this study is to quantify how much of the habitat proposed by the models, is actually used by the birds. To accomplish this, I imported the maps created by MaxEnt into ArcGis 10 (ESRI). The ArcMap software allowed me to manipulate the models in such a way as to remove the areas around man-made structures, which the species has been shown to avoid. After removing the potentially unusable predicted area, I was able to calculate the amount of acreage left in each model at the various grades of habitat quality. This combination of methods should provide a highly accurate picture for managers and researchers to use and build upon as time goes on.

Data set

I obtained geo-referenced locality data from the data bases of the Sutton Avian Research Center (21,824 points for individual birds, 128 points for nests, and 62 points for leks). All three of these data sets were collected between the years of 1999 and 2010. Individual localities were collected by radio-tracking birds throughout the entire year. Nest locations were collected by tracking females during May and June of each year. Leks were located using both prior knowledge and new surveys during the spring of 1999-2010.

To create a more encompassing set of predictive models, male and female locality data were not separated when creating year-round and non-breeding season models, with non-breeding defined as locations collected between July and December of each year. The intent of this study was to predict and assess habitat suitability for the entire species and splitting the overall population models would likely complicate my ability to do just that. If the data had been split into male and female habitat use, then two separate models would have to be created and compared to assess any trends that are shown by the entire Oklahoma population. For the purposes of this study, the fact that only males display on leks and only females nest is ignored in order to focus on lekking and nesting as important life-history traits. The habitat use for these life-history traits was then compared to habitat use of the overall population, both including and excluding those traits. Models which were created using the entire population contain the entire non-breeding data set as well as individual localities collected during breeding/nesting. To avoid potential bias from possible differential habitat use between sexes, no conclusions were made using sex as a factor when assessing the models based on the entire population.

For the modeling of these data, I chose to use MaxEnt because it requires only presence data and environmental variables. The program generates predictive models of a species' fundamental niche by assigning values to pixels on a grid. These values are derived from combining and comparing the values of each environmental layer in the pixels where the species was present. Those pixels where the species was present are then used as a metric to grade every other pixel in the grid. The pixels on the grid are then color coded, resulting in a gradient map.

When creating habitat suitability models, spatial autocorrelation of the data can be an issue (Phillips et al. 2009, Veloz 2009, Merckx et al. 2011). Further, spatial autocorrelation can be a confounding factor when using radio-tracking data for individual organisms (Otis and White 1999). MaxEnt safeguards against this problem to a certain degree. When creating model parameters, MaxEnt individually grades each pixel, and uses the environmental factor values from pixels where presence of the species is recorded (Phillips et al. 2006, Phillips and Dudik 2008). During the creation of these parameters, pixels are marked in a binary fashion (i.e. pixels where an individual is present are marked 1, while pixels where no individuals are present are marked 0) and a pixel cannot be marked as “present” more than once. This ensures that pixels, which include more than a single individual presence record, are not weighted more heavily than those where fewer records occurred. This reduces some of the strain of autocorrelation caused by radio-tracking, if the pixel size is large enough to contain an individual’s daily movements. For this study, pixels were 0.925 km on a side, or 0.856 km^2 (85.6 ha). This pixel area encompasses recorded daily movement of lesser prairie-chickens (Taylor and Guthery 1980a).

Another way that MaxEnt protects against autocorrelation is through model creation options available to the user. The program allows users to use subsets of data to test model parameters. I used a random 50% of each data set as training data and the other 50% as test data. This division allowed the program to run one half of the data set to make a prediction, and then test that prediction using the other half of the data set. I also chose to run five permutations of each model with bootstrapping enabled. These settings allowed me to see any potential warping of the model caused by outliers in the data set.

I chose to use jackknifing to measure variable importance. This setting creates multiple models which contain different combinations of the environmental layers. The program creates a model using each layer alone, as well as models using every layer but one. The program then compares the extra models created this way to the model, which includes all the variables to determine how important each variable is individually.

The environmental variables that I chose as the layers for these models consist of abiotic and biotic characteristics. For abiotic factors, there is a suite of environmental indicators which have become commonplace in niche models.

These variables are maximum temperature of the warmest month, minimum temperature of the coolest month, annual precipitation, elevation, slope, and aspect. For these models, all of these variables, except slope and aspect, were attained from the Worldclim database (Hijmans et al. 2005, www.worldclim.org). This data were downloaded in the form of raster files with a resolution of 1 km^2 per pixel. Slope and aspect were derived in ArcGIS (ESRI 2008) using the elevation data file. Figure 1 shows the area chosen as the geographic boundary for the output models.

For the biotic component of these models, I decided to use Normalized Difference Vegetation Index (NDVI). For this study, I used NDVI values captured at, or as close to, 12:00pm Central Standard Time for the months of April and January from 1999 to 2010. I obtained NDVI measurements in raster format for the study area from the Goddard Space Flight Center (NASA,http://ladsweb.nascom.nasa.gov/data/search.html). The NDVI values used for the models were created by using ArcGIS to create a mean value raster file for each month.

I have chosen to use NDVI values from two different times of the year, spring and winter. I chose spring as it is a very important time for the species, encompassing both breeding and nesting. During this time-frame, specific plants (large bunch grasses in Oklahoma) are important to nesting females (Pitman et al. 2005). Unfortunately, prairie grasses cannot be easily differentiated from seasonal crops during this growing season, as both produce similar reflectance measurements. This is why I also chose to use winter NDVI values. During the winter months, farm land should be bare or partially green, from winter wheat. This should be seen as a difference between winter fields and the over-wintering prairie species, whether the prairie species are evergreen or have shoots which die during the winter. Prairie land, on the other hand, should retain both species which go dormant during the winter and those species which remain active. This remaining ground cover should be enough to differentiate between bare farm land and existing prairie.

MaxEnt produces AUC (Area Under Curve) values, which estimate how good the model is at predicting where individuals of the species would occur. The program also produces a percentage of contribution to model fit for each variable layer used. Values for both AUC and contribution percentage for all six models can be found in Table 1. Note that it has been argued that simply reporting the raw AUC is not enough when comparing model strength (Peterson et al. 2008). It is not my intent to compare the strength of the models created in the study. Thus, I have avoided needless manipulations of MaxEnt output and am simply reporting the raw AUC for these models.

Once the models were created, I imported the raster files, created by MaxEnt alongside the maps, into ArcMap to extract the areas that the birds are likely to avoid. To do this, I first created a new layer in ArcMap using the Buffer tool. This tool allows the user to create a zone around any object on the map, the user simply has to input the object and the distance they would like the zone to extend from the object. I obtained a GIS layer from The Nature Conservancy, which contained location data for oil wells, major power lines (115 kV or larger transmission lines), existing wind turbines, and building site locations for future wind turbines. These data are current as of May 26, 2011 and were created using information from the Oklahoma Corporation Commission (gas/oil) and the Federal Aviation Administration (current and proposed turbines). Power line data came from Ventyx Corporation and is current as of April 28, 2011. I created buffer zones around energy development structures using avoidance distances based on previous studies and expert opinion (Table 1). Lek locations seem to avoid anthropogenic structures at approximately the same distances as non-nesting individual birds (Pruett et al. 2009b). Once the buffer zones were created, I used the Clip tool to extract the area of the buffer zones from the

MaxEnt model. The program accomplished this by overlaying the buffer zones on the MaxEnt model and removing the area of the buffer zone from the MaxEnt model output. To ensure that the Geographic Coordinate Systems of the buffer zones and the MaxEnt output maps aligned, both were created and imported, respectively, in the same GIS map file. These file layers were then transformed to match the coordinate system of the GIS map. The area of the MaxEnt model that remains is then turned into a new layer, which can be viewed and manipulated individually from the original model layer. To determine how much suitable habitat was lost to the buffer zones, I used the Raster Calculator tool to total up the area of habitat (in hectares) with a non-zero habitat suitability score both before and after the removal of the buffer zones. I then used those values to determine how much suitable habitat from the MaxEnt models was lost to the avoidance buffers. This approach allows me to show just how much of an impact, energy development structures may have on projected habitat.

Results:

Table 2 contains AUC values, standard deviation for those values, and the percent of model contribution for each environmental variable. Minimum temperature in the coolest month of the year (January) was a consistently important variable contributing to 32.9-49.3% of model fit. Annual precipitation was another important variable to each model (36.9-41.3%) except that of Leks, where it had a low to moderate impact (13.9%). Elevation was consistently the second or third most relevant variable (6.1-31.6%). Maximum temperature of the warmest month (July) had little effect on year-round individual or nest localities, but hovered around 10% of contribution for non-breeding/lekking individuals and Leks. Aspect and slope showed little to no contribution (0-2.2%).

Viewing the results for individual variables via jackknifing showed similar results to the percentage contribution data above; minimum temperature and annual precipitation had the largest effects on model fit when removed. The only exception was for the lek model; minimum temperature had a major effect on model fit when removed, and was the only variable that did so (removal of several variables had no impact on the lek model at all).

Figures 2-5 show the predicted habitat area of the four model types. Figures 6-9 show those modeled areas with energy development structures overlaid. MaxEnt predicted a total range area (in hectares) of 1,806,481 for year-round individuals, 2,506,554 for non-spring individuals, 4,834,087 for leks, and 2,207,225 for nesting. These areas included parts of Texas, which were not included in the avoidance calculations. The estimated area of habitat loss (in hectares) due to avoidance of energy development structures was 119,254 for year-round habitat, 120,301 for non-spring habitat, 251,112 for lekking habitat, and 960,917 of nesting habitat (table 3).

Discussion:

Hypotheses

I evaluated a series of specific hypotheses for this study. First, I hypothesized that breeding habitat dictates overall habitat. The models created for this study support this hypothesis. The models for individuals (during both time-frames) fell almost entirely within the overlap of the lekking and nesting habitat models. Next, I hypothesized that different environmental factors would define nest and lek habitat. The models partially supported this hypothesis. Both models shared minimum temperature of the coolest month as the most important environmental factor, but they differed greatly on other important factors. The only other relevant factor for lekking habitat was elevation, while annual precipitation was a large contributor for nesting habitat. I also hypothesized that elevation would impact leks more than nesting, or any other model. This hypothesis was supported by the models. Elevation had the most impact on lekking habitat, but both models for individual habitat included elevation as a notable contributor. Finally, I hypothesized that NDVI would have the greatest impact on nesting habitat, as that use of habitat requires the most specific vegetation requirements. This hypothesis was not supported by the models. NDVI played a very small role for all models, contributing 0-1% to model fit for each model.

Niche Model Breakdown

The geographic extent of predicted suitable habitats for individuals (both year-round and outside of the breeding season), nesting, and lekking was limited (Fig 2-5). The degree of overlap among models concurs with the findings of previous studies; leks are a focal point of lesser prairie-chicken habitat, individuals do not disperse or travel far from their attended leks, and nesting habitat and roosting/loafing habitat are often concurrent geographic areas (Hagen et al. 2004).

The most important predictors of habitat suitability were minimum temperature of the coldest month, annual precipitation, elevation, and maximum temperature of the warmest month. Habitat suitability can and has been graded at a local level by surveying areas (Horton et al. 2010), but these four factors may be the abiotic factors that determine the underpinnings of what makes for suitable prairie-chicken habitat. Three of these factors are weather/climate related, which has not been studied extensively for this species (Hagen et al.

2004). I hope my findings will generate more interest in their impacts on the species.

Minimum temperature of the coldest month (January) made the greatest overall contribution to habitat models, explaining as much as 49.3% of model fit. It has been hypothesized that minimum temperature is a major factor delineating the northern boundary of North American bird home ranges (Root 1988). But further studies have shown that, while minimum temperature may play a role in shaping the northern boundary of North American birds, effects of temperature on birds appears to be indirect (Casto 1989, Repasky 1991, Lennon et al. 2000). Repasky (1991) hypothesized that minimum temperature's impact may more likely be an artifact of the range-extent of plant species which are important to the birds.

The importance of minimum temperature may be of great importance to the future of the species when climate change is considered. Daily minimum temperatures have been shown to be increasing at a more rapid rate than daily maximum temperatures (Karl et al. 1993). This phenomenon has already been shown to impact anurans inhabiting Costa Rican mountains (Pounds et al. 1999, 2006). Kansas populations of lesser prairie-chicken have been recorded as shifting northward (Pitman, unpublished data), and minimum temperature may be a major cause of that shift.

Annual precipitation was the second biggest contributing factor to model prediction. Effects of precipitation on the species have not been studied directly, but correlations have been made between precipitation variation and harvest counts (Brown 1978, Giesen 2000). Brown (1978) illustrated that New Mexico harvest rates were positively correlated with levels of rainfall from the year before. Similarly, Giesen (2000) demonstrated that there was a two-year time lag on a positive correlation between lek attendance and annual rainfall. This correlation is likely due to increased rainfall improving primary productivity of the local plant community. This productivity would create more cover for nesting females as well as support larger invertebrate populations, which are the primary source of food for brooding chicks (Hagen et al. 2004). I believe that the exact relationship between precipitation and lesser prairie-chicken habitat warrants further study.

Elevation was consistently the third highest contributing factor of model prediction. The relevance of elevation on individual activity or even in the context of landscape ecology has not been expressly studied for the species, though elevational ranges for populations have been reported (Bell 2005, Fields

2006). The only relevant instances of elevation being mentioned are in references to leks. Hagen et al. (2004) posited that leks may be positioned on areas of slightly raised topography than surrounding areas**.** My results did not show mean elevation values to contribute as much to model fit as standard deviation of elevation did for lesser prairie-chicken in Kansas (Jarnevich and Laubhan2011). Comparing these findings suggest that variance in elevation may be more important to habitat suitability than mean values.

I believe that total elevation (meters above sea level) played a role in limiting the outcome of these habitat suitability models. All samples for this study were taken from a single population in Oklahoma, whose habitat elevation ranges from 670-716m (Google Earth, 2011). These numbers are comparable to other reported elevations for populations in Kansas (Fields et al. 2006). Parts of the species total range in New Mexico have been reported at elevations of 1080-1300m (Bell 2005). Potential habitat in the Oklahoma panhandle farther west of the sampled population exceeds elevations of 1300m (Google Earth, 2011). Should location data from New Mexico populations be included in later studies, more potential habitat would be predicted in the western parts of the panhandle. It is not unthinkable that the model predictions were limited by the input data, as the lesser prairie-chicken occurred historically throughout Texas and Cimarron Counties, Oklahoma (Taylor and Guthery 1980b). It could be that populations recorded in those counties were “sink populations” to begin with. By “sink population”, I mean populations which inhabit habitat which is not suitable to sustain any kind of population growth (Pulliam 1988). If this were the case, then those populations depended heavily on immigration to sustain population size (Pulliam 1988). Then, as habitat became more fragmented and local metapopulations dwindled in size and become more isolated, those populations in the panhandle declined.

Maximum temperature of the warmest month (July) was the final factor of note for these models. While not contributing nearly as much to model prediction (3.5-5.6%) as the three previous factors, this factor will likely be important for future consideration. Global climate change is something that every habitat manager should be mindful of and preparing for (Halpin 1997, Hulme 2005). Climate change may have more of an effect on daily minimum temperatures, but daily maximum temperatures are also projected to rise (Karl et al. 1993. Lesser prairie-chickens react to temperatures above a certain threshold by seeking taller and thicker overhead vegetation (Patten et al. 2005a, Bell et al. 2010). Survivorship was also shown to increase in microhabitat which was cooler and more humid (Patten et al. 2005a). As maximum temperatures increase, these cooler and more humid microhabitat conditions may cease to exist. This could create a need for populations to seek more acceptable habitat, should survivorship start to decline. In this scenario, the Oklahoma populations would have two potential courses of action: move northward into existing habitat in Kansas (effectively extirpating the species from the state) or move westward along the elevation gradient in the panhandle. Both of these possible migrations will be stymied by anthropogenic features such as well traveled roads, power lines, and buildings, all of which individuals of the species are reluctant to cross or go near (Robel et al. 2004, Pitman et al. 2005, Pruett et al. 2009b).

Potential problems of habitat suitability modeling

As useful as habitat suitability modeling is, it is not perfect. The technique has the potential for serious errors of commission (Elith et al. 2006), which was a driving force behind the creation of MaxEnt (Phillips et al. 2006). Elith et al. (2006) determined MaxEnt to be the best suited modeling technique available for habitat suitability modeling.

Models are only as good as the information we put into them, and we cannot account for every aspect of any given habitat. Thus, if we have no way of accounting for it in the model, the output will not incorporate geographic barriers (manmade or natural), range limitations based on biotic interactions, and future shifts in habitat parameters (Phillips et al. 2006)**.**The models created in this study in no way attempt to predict the interaction of lesser prairie-chickens and climate change. The creation of these models also did not explicitly take geographic barriers to the species (mainly anthropogenic structures) into account. Future studies should attempt both of these feats, preferably in conjunction. Models created for the purpose of possible range shifts with existing anthropogenic structures as a variable would be a boon to current research efforts.

Energy development and habitat loss

Each model generated a different amount of predicted habitat, yielding a different amount of predicted habitat lost to energy development (Table 3). Different forms of energy development also have varied impacts on lesser prairie-chicken habitat uses (Table 2). These estimates of habitat exclusion are for Oklahoma alone, though the output extends into Texas for most models. The energy development layer used for these estimates includes current major power lines, active oil well, and current and future wind turbines. The estimates do not include the power lines that would connect the new turbines to the also required power stations, which the birds will avoid at even greater distances (Pitman et al. 2005). Previous studies have hypothesized that these new power lines will have further fragmentation effects on current lesser prairie-chicken habitat (Robel et al. 2004, Patten et al. 2005b, Pruett et al. 2009a). Nevertheless, power line placement, and likely tall wind turbines as well (Pruett et al. 2009a,b), will be crucial given that prairie grouse avoid power lines much more than roads, wells, or buildings (Hagen 2011).

These predictions of increased habitat fragmentation fit previous assessments of wind energy development for multiple species (Robel et al. 2004, Kunz et al. 2007, NRC 2007). The National Research Council (2007) posited that wind energy has both direct and indirect impacts on a natural community, including; increased mortality, alterations in the availability of food, roost and nest resources, increased risk of predation, and potentially altered demographics, genetic structure, and population viability. All of these aspects have been studied in recent years for the species (Hagen et al. 2004, Horton et al. 2010) and, with the coming changes to the landscape, should continue to be monitored.

Further habitat degradation will likely have serious negative impacts on Oklahoma populations, as habitat quality has become the chief concern for what habitat remains (Hagen et al. 2004). Prairie-chickens in Oklahoma already have a higher mortality rate than populations in New Mexico (Wolfe et al. 2007), as a result of historical patterns of land tenure (Patten et al. 2005b). The lesser prairie-chicken could, in principle, adapt to elevated mortality by increasing reproductive output, but the potential for appreciable evolutionary response to this elevated mortality, in terms of life-history tradeoffs, is limited (Patten et al. 2005b, Pruett et al. 2011). Hence, it would appear that reducing mortality is the only realistic option (Pruett et al. 2011). The major causes of this mortality are avian predators, fence collisions, and mammalian predation (Wolfe et al. 2007). All three of these factors can potentially be caused in part by habitat fragmentation. Raptors require perches for both vantage points and as resting spots after patrolling their territory for food (Reinert 1984). Adding structures, such as power lines, turbines, and power stations, to existing prairie-chicken habitat only increases the likelihood of the presence of raptors in that habitat. Human division of land via fencing is an age-old tradition to delineate ownership. Old and forgotten fences pose a threat to prairie-chickens due to the fact that prairie grasses grow around and over them, making them difficult for the birds to see, which increases the likelihood of collision and injury (Wolfe et al. 2007). Mammalian scavengers, such as striped skunk (*Mephitis mephitis*) and coyotes (*Canis latrans*) have shown increased population density and activity around anthropogenic structures (Bergin et al. 2000, Atwood et al. 2004). Increasing the number of man-made objects inside of current habitat would likely bring more mammalian predators as well.

One recent study has shown that acclimation of the birds to energy structures may be happening (Hagen et al. 2011). The authors described the rate at which an energy development structure (the same kind described in this study) happened to lie within a prairie-chickens monthly home range. The rate at which those structures happened to lie within individual prairie-chicken home ranges increased between the years of 1997 and 2002. Even if acclimation is happening, the birds still tend to avoid energy structures. Similar avoidance distances to those used here were recorded by Hagen et al. (2011). Another interesting finding of this study was the fluctuation of proximity to energy structures by month. April was shown to be the month with the lowest rate of energy development structure occurrence within home ranges. This coincides with nesting for lesser prairie-chickens, the habitat use shown to include the most avoidance of energy structures (Pitman et al. 2006b).

Management recommendations

Managers have the ability to be proactive about this situation. There is still time to take precautions to prevent this unfortunate set of circumstances from becoming a disaster. Further study should attempt to predict which route the birds are more likely to take, north or west. Using these results, managers can then make informed decisions about where to acquire or modify habitat to better serve and protect the species. This could mean creating new protected areas of habitat for populations to move into, creating corridors for the birds to move through on their way to their final destination, or translocating founding populations ahead of the migration to have pre-established leks and nesting grounds for the newcomers to use. Translocation has been used successfully on different species of grouse before (Westemeier et al. 1998), including the greater prairie-chicken (*Tympanuchus c. cupido*) which has been genetically identified as a sister species to lesser prairie-chickens (Johnson 2008).

When these new changes cause more habitat fragmentation, what happens to the lesser prairie-chicken? Habitat quality will continue to degrade as it has (Hagen et al. 2004, Patten et al. 2005b, Wolfe et al. 2007) and the birds will be left with few options. These anthropogenic causes of habitat depletion could jump-start the possible migration discussed earlier. The species has been shrinking back from human expansion for the past century (Taylor and Guthery 1980b) and may continue to do so. Another option may be for the species to simply adapt to what is left. Small adaptations have been seen in prairie-chicken behavior, especially resource use, as human influence has spread throughout their natural range (Jamison 2000, Jamison et al. 2002, Salter 2005).

One way that populations in Oklahoma have begun to respond to degraded habitat is by increasing clutch size (Patten et al. 2005b). Assuming no other cause for this increase, this can be viewed, from a life-history standpoint, as a response to the increased mortality rates among these populations (Stibor 1992, Riessen 1999, Wolfe et al. 2007). If these responses are not enough to help the species adapt to these changing conditions, extirpation from the state may actually occur, as it has for so many other species when faced with human expansion (Steadman 1997).

There may still be time for managers of the species to make a difference. Two management practices stand out for this current situation, the Conservation Reserve Program, and proper construction of wind energy structures. The Conservation Reserve Program was instituted by the USDA in 1985 (USDA, 2011). Since then, it has helped to convert 33.9 million acres of unused/unfit farm land into habitat for a multitude of species in the United States (USDA, 2011). The program has even been shown to provide suitable habitat for lesser prairie-chicken use (Hagen et al. 2004). This effect could be expected since most existing habitat lies within agricultural land which is not tilled (range land) or on land that is low quality for agriculture, but adjacent to tilled agricultural fields (Hagen et al. 2004, Horton et al. 2010). Jarnevich and Laubhan (2011) reported that in habitat suitability models in which Conservation Reserve Program land was included as a variable, it was a substantial contributor to these models.

One potential way to avoid habitat fragmentation is to bury the power lines needed to connect the planned wind turbines to their power stations. As shown in figures 5-9, the turbines themselves do not overlap a large amount of the predicted habitat for the species. These figures are incomplete though, as the power lines will be the true threat to lesser prairie-chicken habitat (Robel et al. 2004, Pruett et al. 2009a).

Proper habitat management has long been a concern for the lesser prairie-chicken (Davison 1936, Etheredge 1943, Copelin 1958, Gibson 1973, Applegate and Riley 1998, Hagen et al. 2004,). Given the current circumstances facing this species in the state of Oklahoma, and elsewhere in its range, management will continue to be a driving force for research on the species. As technology moves forward so will our abilities as researchers, but we must be cognizant of the changes to both.

Habitat suitability modeling is a tool that has been developing over the past two decades and can provide cost-effective results for managers. Nothing can compare to decades of research and expert knowledge, but for some species those approaches are not an option. For predicting potential habitat, modeling programs such as MaxEnt, can provide substantial information at a fraction of the total cost. Fortunately, for the lesser prairie-chicken in Oklahoma we have the opportunity to directly compare MaxEnt created models to a model built using decades of research and expert knowledge rather than the techniques of a modeling program.

An analysis of habitat suitability was recently created by Horton et al. (2010) for the Oklahoma Department of Wildlife Conservation (ODWC). The models created for this study match up favorably with the model created by ODWC within the bounds of my study area. Their model was created using several layers that were based on habitat type, proximity to existing leks, avoidance zones, and historical and current range. The ODWC model was created through a major collaborative effort, using many years of collective data from multiple disciplines. The correspondence of these MaxEnt models to that effort (Figure 10) suggests that, with the proper tuning and in the correct context, habitat suitability modeling programs can be an effective, and less costly, tool for habitat management.

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Table 1: Information on buffer zones used, distances represent radii created around anthropogenic structures.

Anthropogenic Feature	Buffer Distance (m)	Source
Individual Birds		
Powerlines	100	Pruett et al. 2009
Wind Turbine	200	Not measured, projected from Pruett et al. (2009b)
Wellheads	100	Not measured, projected from Pitman et al. (2005)
Leks		
Powerlines	100	Pruett et al. 2009
Wind Turbine	200	Not measured, projected from Pruett et al. (2009b)
Wellheads	100	Not measured, projected from Pitman et al. (2005)
Nests		
Powerlines	1319	Pitman et al. 2005
Wellheads	563	Pitman et al. 2005
Wind Turbine	2638	Not measured, projected from Robel et al. 2005)

Table 2: MaxEnt output values. Values for each variable represent percentage of contribution to the model for that factor.

	Year-round Individuals	Non-Spring Individuals	Nests	Leks
AUC	0.996	0.996	0.995	0.974
Standard Deviation	<0.001	<0.001	0.001	0.005
Annual Precipitation	41.3	36.9	37.8	13.9
Minimum Temperature	32.9	33.9	49.3	45.7
Maximum Temperature	5.3	3.5	3.8	5.6
Elevation	17.9	22.6	6.1	31.6
Slope	0.5	0.8	1.1	1.7
Aspect	0.9	0.7	0.8	0
January NDVI	0.6	0.9	0	0.5
April NDVI	0.6	0.8	0.9	1

Table 3: Total amount of habitat predicted by MaxEnt models with amount of habitat in Oklahoma potentially lost to species avoidance of anthropogenic structures.

Model Focus	Total Predicted Habitat (Ha)	Est. Habitat Lost in OK (Ha)
Full Individuals	1,806,481	119,254
Non-Spring Indiv.	2,506,554	120,301
Lek	4,834,087	251,112
Nest	2,207,225	960,917

Figure 1: The outline represents the boundaries of the area used to create the visual maps for the models.

Figure 2: Habitat suitability model made using the full set of individual localities. “Warmer” colors represent higher predicted values of species occurrence.

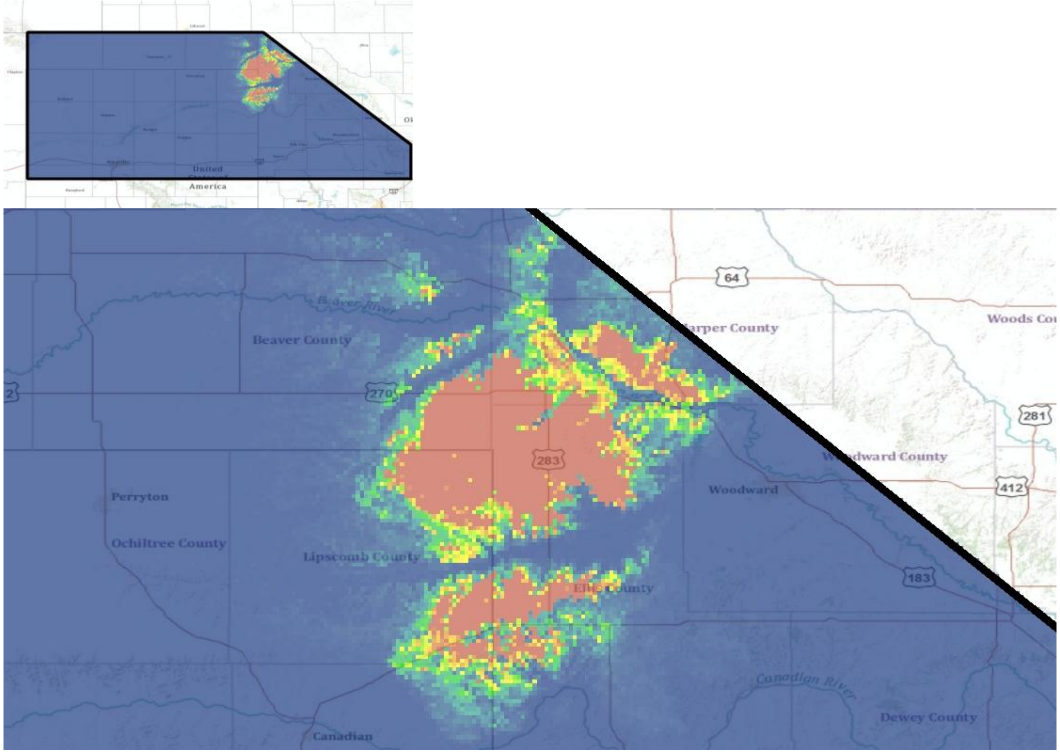


Figure 3: Habitat suitability model made using individual localities from outside the breeding season. “Warmer” colors represent higher predicted values of species occurrence.

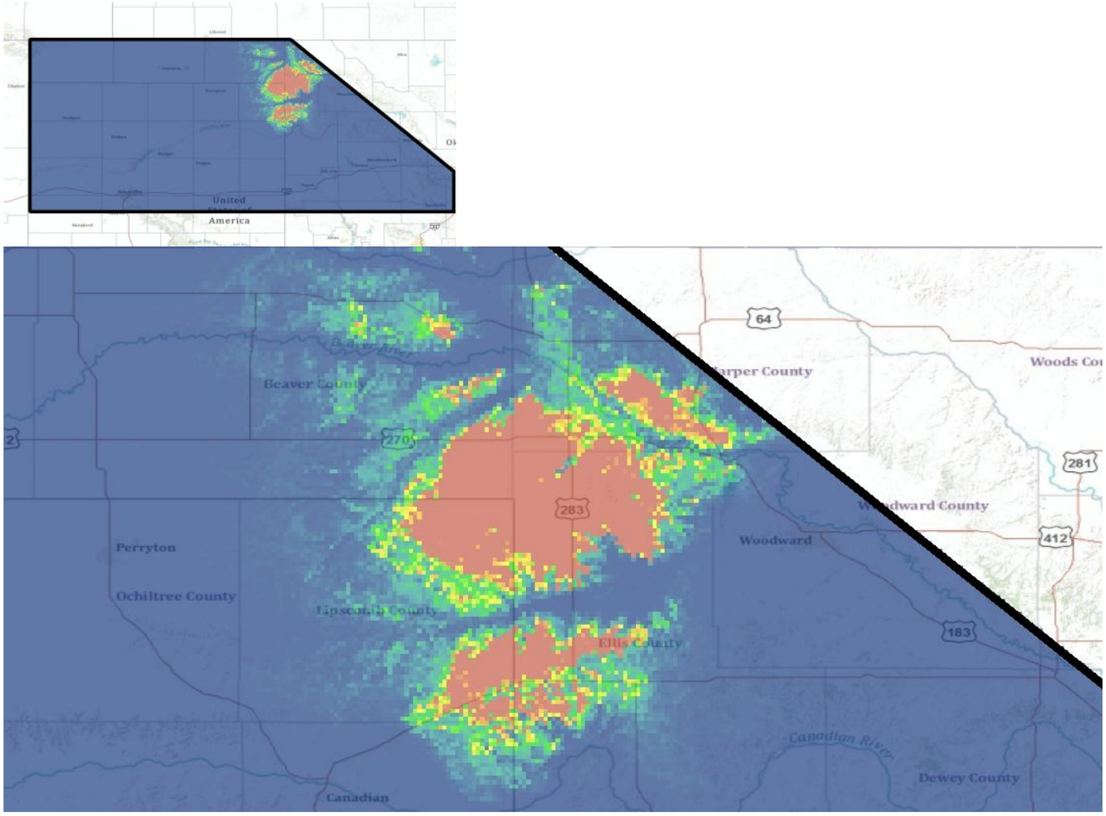


Figure 4: Habitat suitability model made using nest localities. "Warmer" colors represent higher predicted values of species occurrence.

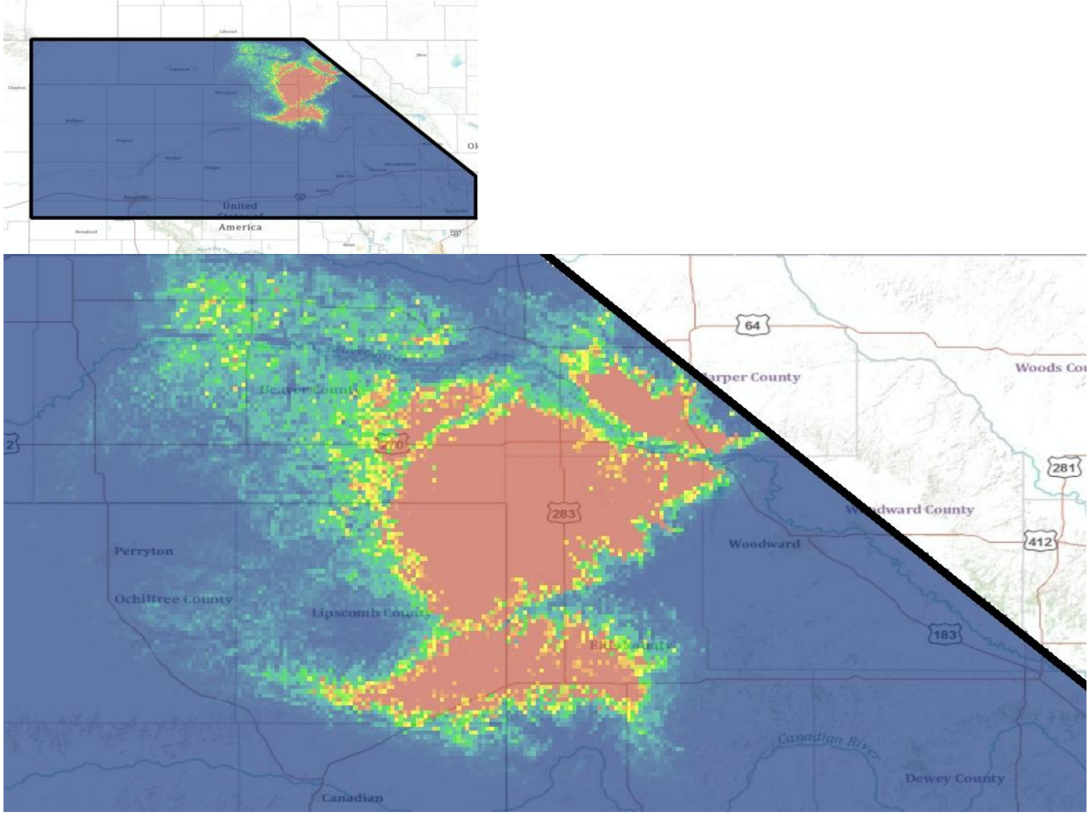


Figure 5: Habitat suitability model made using the lek localities. “Warmer” colors represent higher predicted values of species occurrence.

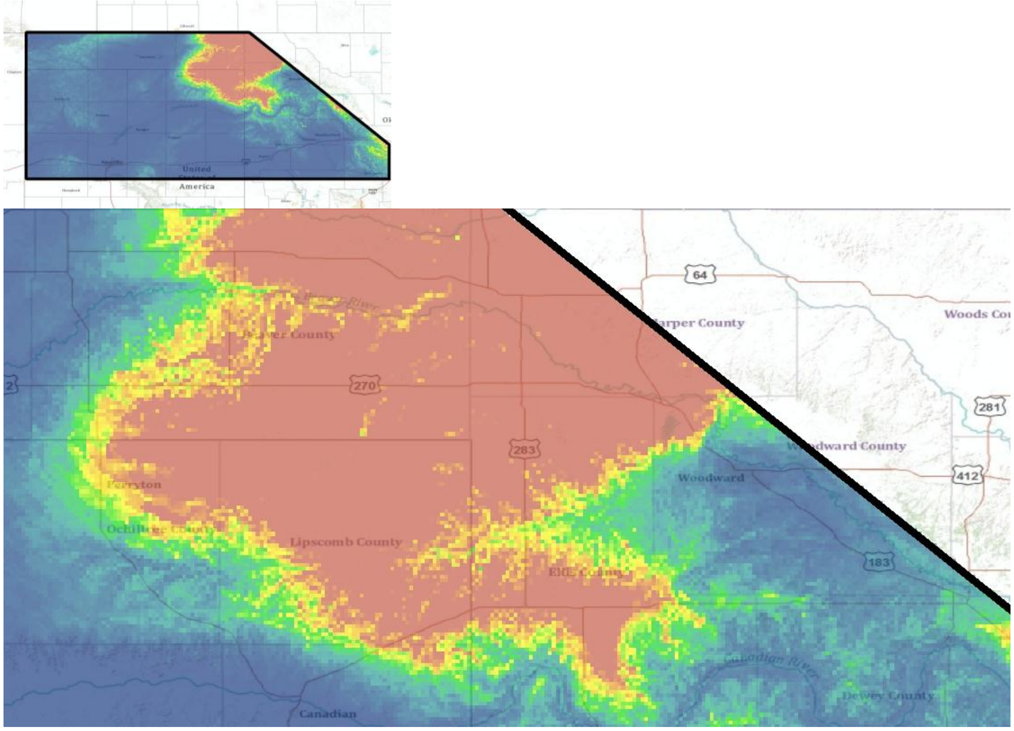


Figure 6: Habitat suitability model made using the full set of individual localities. “Warmer” colors represent higher predicted values of species occurrence. Buffer zones around avoided anthropogenic structures have been added. Smaller circles represent active oil wells while larger circles represent current and planned wind turbines, blue lines represent major power lines.

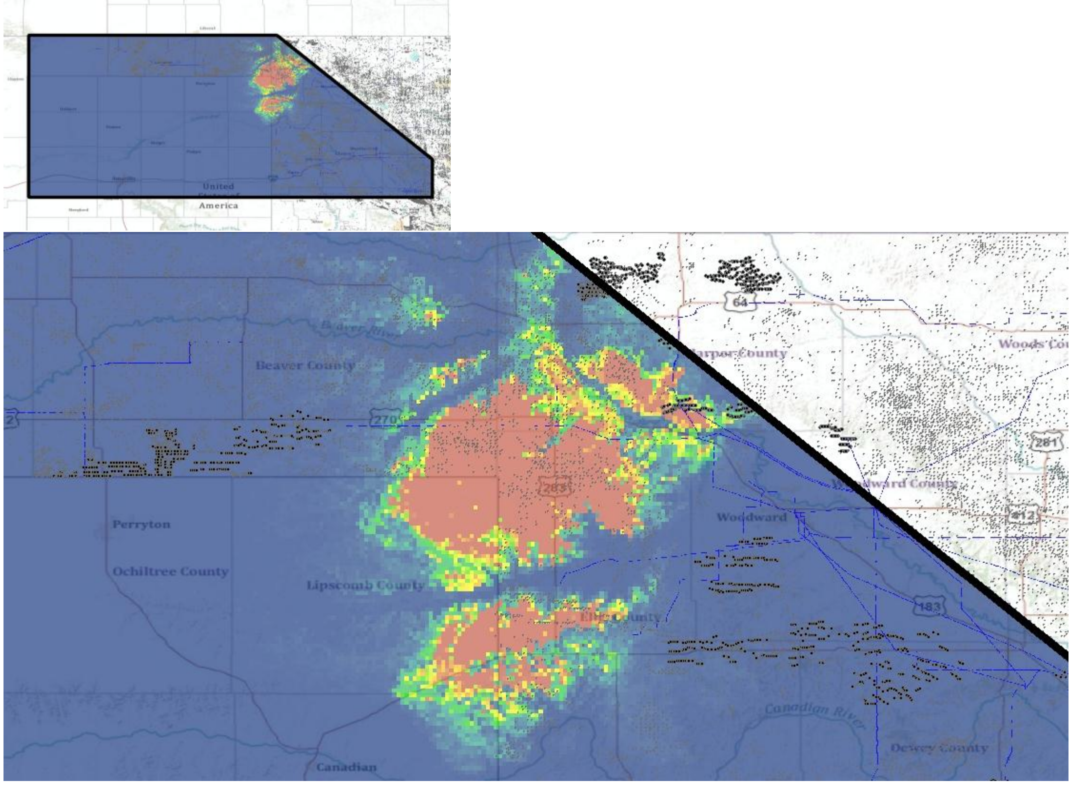


Figure 7: Habitat suitability model made using individual localities from outside the breeding season. "Warmer" colors represent higher predicted values of species occurrence. Buffer zones around avoided anthropogenic structures have been added. Smaller circles represent active oil wells, larger circles represent current and planned wind turbines, and blue lines represent major power lines.

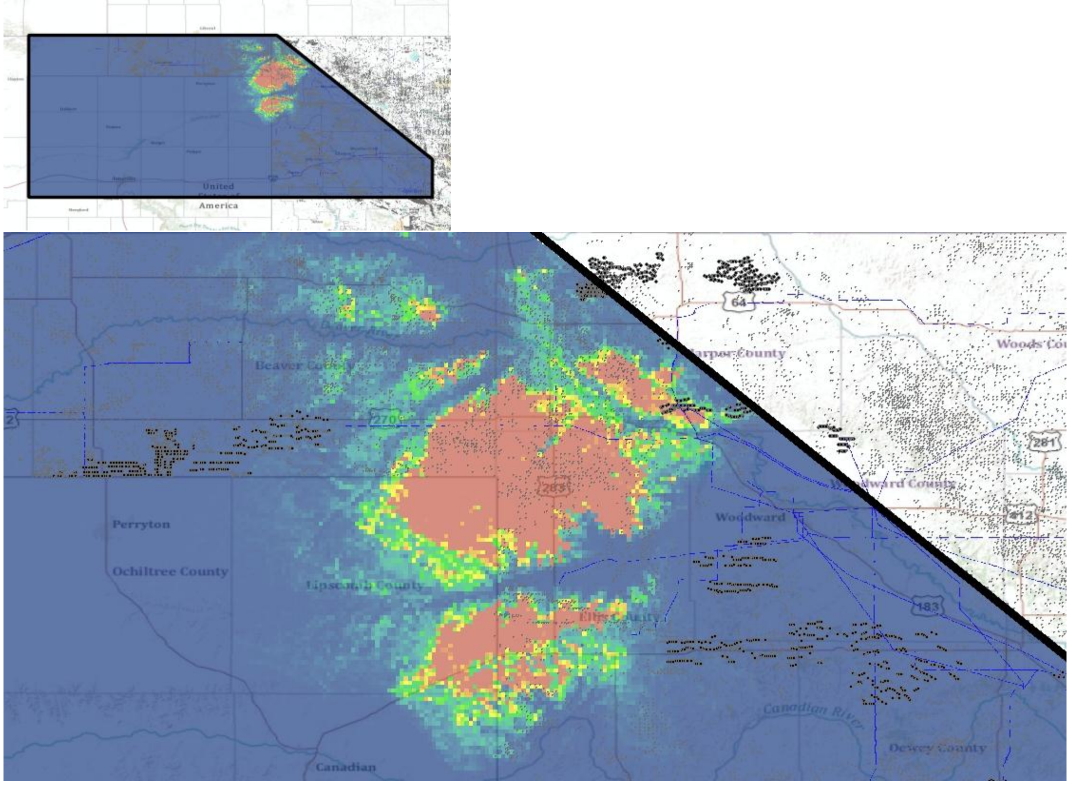


Figure 8: Habitat suitability model made using nest localities. “Warmer” colors represent higher predicted values of species occurrence. Buffer zones around avoided anthropogenic structures have been added. Smaller circles represent active oil wells while larger circles represent current and planned wind turbines, thick lines represent major power lines.

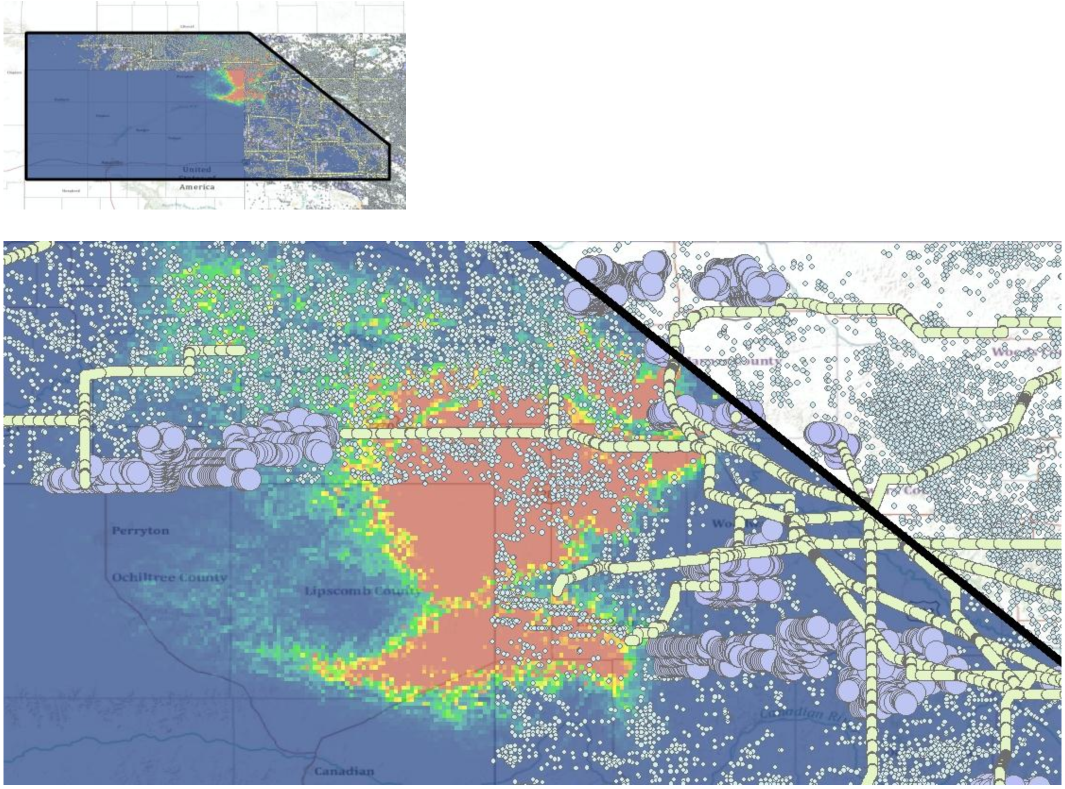
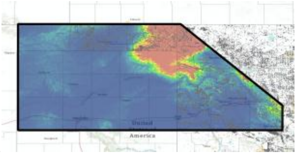


Figure 9: Habitat suitability model made using lek localities. "Warmer" colors represent higher predicted values of species occurrence. Buffer zones around avoided anthropogenic structures have been added. Smaller circles represent active oil wells, larger circles represent current and planned wind turbines, and blue lines represent major power lines.



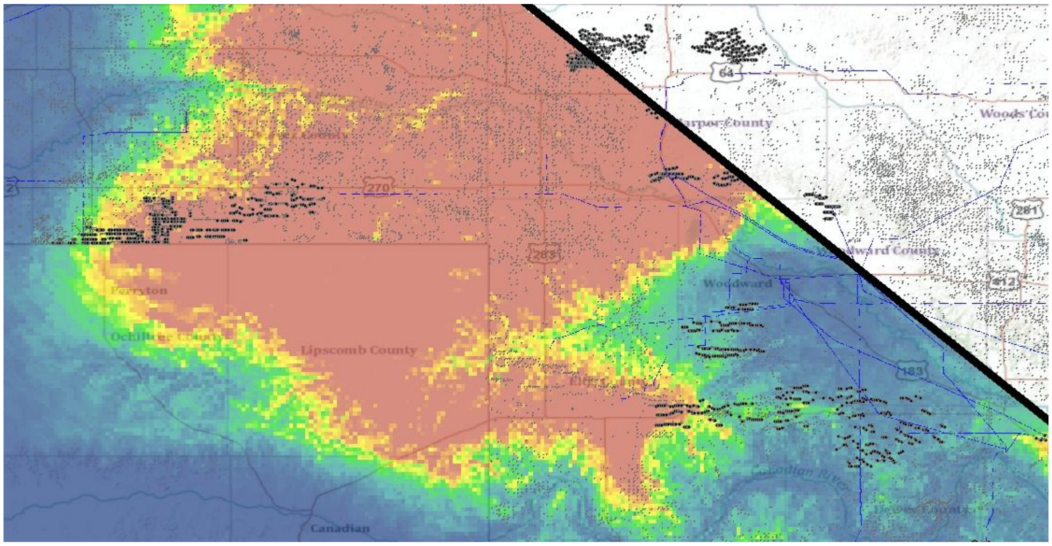


Figure 10: A side-by-side comparison of the Year-round Individual habitat model from this study (a) with the habitat map created for Horton et al. (2010) (b)