PLAYING CHICKEN:

AT THE INTERSECTION OF ANTHROPOGENIC DEVELOPMENT AND LESSER PRAIRIE-CHICKENS

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Abstract: Ecology and natural history have long documented the spatial arrangement of organisms over time. Our definition of space and time, or scale, will determine what ecological relationships we are able to detect between organisms and their environment. No one scale is capable of fully capturing the complexities of these relationships; therefore it is critical that research is conducted at multiple scales. We assessed the relationship between the imperiled lesser prairie-chicken (hereafter LPC; *Tympanuchus pallidicinctus*) and its environment at scales ranging from their distribution to the space an animal could encounter in 1 hours' time. Distribution-wide studies require data of sufficient quantity and quality that is geographically representative of the species' space use; however these data are often expensive to collect. Freely available citizen science observations of LPCs from eBird and professionally collected observations from an aerial survey produced potential species distributions that were supported (test omission rate ≤ 15.6%) and had a high degree of similarity to one another ($I = 0.956$), indicating that citizen science data from eBird could be used as a low-cost supplement to species distribution modeling efforts. Environmental variables that are important and consistent in the direction of their relationship to the animal across scales are indicators of primary drivers of animal space use. Birds responded negatively to cropland and positively to land enrolled in the conservation reserve program (CRP) across their distribution, and in weekly, daily, 4 hourly, and hourly movements and habitat selection. Moreover, the CRP facilitated LPC movement across roads, which were found to be a significant barrier to movement. Birds minimized time spent crossing roads and power lines, but did not respond to the proximity of residential areas or an oil or gas wells. LPCs were strongly tied to their breeding grounds across all scales, which could be used as a basis for conservation planning. Our results indicate that humans have significantly impacted the landscape for LPCs across a range of spatial and temporal scales. LPC conservation efforts should engage with policy and focus on understanding the human role in shaping the arrangement of anthropogenic features and vegetation on the landscape.

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CHAPTER I

USING AERIAL SURVEYS AND CITIZEN SCIENCE TO MODEL HABITAT SUITABILITY FOR AN IMPERILED GROUSE

ABSTRACT Estimating potential species distributions requires species presence data of sufficient quantity, from reputable sources, and that are geographically representative of the species' space use. Collecting presence data that meets these standards can be costly and is often complicated by limited land access. Given these challenges, citizen science projects are an appealing source of presence data as these data are freely collected by a global network of volunteers. Online observation reporting websites, such as eBird, have become increasingly large repositories of citizen science data. The vulnerable lesser prairie-chicken (LPC; *Tympanuchus pallidicinctus*), is a species well-represented in the eBird database, with presence observations from 140 unique locations from 2012-2014. During that same time period, a distribution-wide, intensive state and federally supported aerial survey recorded 106 LPC detections. Our objective was to compare site suitability models made with freely available eBird data to models made with rigorously collected aerial survey data to determine the potential for eBird data, or similar citizen science data, to contribute to conservation planning. We used maximum entropy modeling (Maxent) to create distribution models based on eBird data, aerial survey data, and a combination of both data sets using variables of biological significance to LPCs as reported in the literature. We obtained comparable model performance using aerial survey data only (test omission rate: 15.4%, AUC: 0.773) and with eBird data only (test omission rate: 15.6%, AUC: 0.737). The I-statistic confirmed a very high degree of similarity between the outputs of the two models (I = 0.956). We obtained the lowest test omission when we combined eBird data and aerial survey data (test omission rate: 14.4%). Our results indicated that eBird data could be used as a low-cost source for, or supplement to, existing species occurrence data to create suitability models and inform distribution-wide conservation plans.

INTRODUCTION

The creation of a species distribution model requires species presence data of sufficient quantity and quality (Wisz et al. 2008, Feeley and Silman 2011). Ideally these data: are geographically representative of the species' space use, collected by experienced observers using well-documented methods, exist in quantities large enough to meet minimum modeling requirements ($\geq$30 spatially explicit locations), and capture the variability in environmental conditions (Wisz et al. 2008). However data meeting those specifications can be costly to obtain across a species' distribution. For example, western North American wildlife agencies spent between $440,000 and $1,700,000 per state in 1998 to survey big game species alone (Rabe et al. 2002). Grouse surveys have also been shown to be costly, with sharp-tailed grouse (*Tympanuchus phasianellus*) lek surveys costing between $74 and $177 per observation (Gillette et al. 2015).

Over the past decade, citizen science projects have created a global network of volunteers collecting scientific data that is often available to researchers at little to no cost (Miller-Rushing et al. 2012). It has therefore become an increasingly popular and consistent source of data for a range of research purposes, including calibration of species distribution models (Hochachka et al. 2012). In fact, citizen science projects are among the fastest-growing contributors to observational data (Theobald et al. 2015), even for rare species (Dickinson et al. 2010). Though an appealing source of data, citizen science data is not without challenges, including road bias, variations in observer experience (Dickinson et al. 2010), weekend bias (Courter et al. 2013), and a bias towards monitoring more charismatic species (Clark and May 2002, Clark et al. 2002). However, for some species, such as the 12 species of North American grouse, a charismatic bias can be beneficial. These species are highly sought-after by bird enthusiasts from around the world, and are subsequently well reported within eBird, a popular citizen science tool that serves as a repository for bird observation data (Sullivan et al. 2009, Table 1). Even the rarest species of North American grouse, the Gunnison sage grouse (*Centrocercus minimus*, 2015 IUCN Red List Status: Endangered), have enough eBird records within the past 10 years to potentially create a species distribution model (76 records, Table 1, Wisz et al. 2008). These grouse are also the basis for which many critical natural resource management decisions are being made across large portions of North America, including when and where to develop energy infrastructure (Naugle et al. 2010, Kiesecker et al. 2010, Jarnevich and Laubhan 2011, Hovick et al. 2015). As the data quality of programs such as eBird continue to improve (Sullivan et al. 2014), comparisons between rigorously collected survey data and citizen science data are important for determining the potential for citizen science to contribute to conservation efforts (Dickinson et al. 2010).

The lesser prairie-chicken (hereafter LPC; *Tympanuchus pallidicinctus*) is a North American prairie grouse that has experienced distribution-wide population declines and distribution reduction for many years (Taylor and Guthery 1980a, Silvy 2006). In response to the long-term decline of the LPC, the five states within the current LPC distribution created the LPC Range-Wide Conservation Plan in 2013 (Van Pelt 2013). To monitor the population, the states instituted an annual, distribution-wide, aerial survey starting in 2012 to record lek locations and number of birds at each location (McDonald et al. 2014). The LPC locations recorded in the distribution-wide, aerial survey are ideal for creating a species distribution model for LPCs. These data were collected following rigorous and consistent methodology across the entirety of the LPC's distribution, which created a rare dataset whereby sampling method differences between states was eliminated (see Van Pelt 2013 for state sampling protocols), road bias was eliminated, and geographic area sampled was maximized and random (McDonald et al. 2014). Additionally, the LPC is also well represented in the citizen science database eBird (338 locations between 2000 and 2015, Table 1). Therefore, the LPC aerial survey dataset and citizen science dataset create a unique opportunity to compare species distribution models based on calibrated citizen science data versus models based on more rigorously collected, aerial survey data. Consequently, the objective of our study was to assess the potential for citizen science data to contribute to LPC species distribution modeling. We compared LPC estimated distributions created with 3 different sets of input data: data from a range-wide, aerial lek survey, observations from citizen scientists using eBird, and a combination of those 2 data sources. Results from this work can serve as a case study of how citizen science data can supplement and/or replace other collection methods to maximize conservation resources.

METHODS

Location Data

Our aerial survey LPC lek location data were compiled by the Western Association of Fish and Wildlife Agencies (WAFWA) from 2012 – 2014 (McDonald et al. 2014). These data were collected by West Ecosystems Technology, Incorporated (Laramie, WY) using transect, helicopter-based surveys to locate leks across the LPC distribution. Two observers sat in the rear left and right seats and a third observer in the front left seat of the helicopter during surveys. Transects were flown 25m above ground at 60km per hour from sunrise until approximately 2.5 hours after sunrise from March 15 to May 15 during each year. In total, 283, 15 x 15km cells were sampled. Observations of 5 birds or less were ground-truthed to confirm the actual presence of a lek. Observations with more than 5 birds were considered lek sites. From 2012 to 2014, a total of 106 LPC leks were detected in aerial surveys (Figure 1). Of the 106 locations, 12 also contained greater prairie-chickens (*Tympanuchus cupido*) and were recorded as “mixed” leks. We included these leks in our analysis as they were representative of LPC site occupation.

We acquired LPC observations from citizen scientists from 2012 through 2014 using data compiled by eBird (eBird Basic Dataset February 2015). eBird is a freely-available website that gathers, organizes, maintains, and disseminates information about bird observations from the public(Sullivan et al. 2009). Data submission requires the observer to report the date, time, location, distance traveled, effort (time), species observed, and number of individuals observed and any relevant comments or images. Observations of species that are rare for the location, time of year, or number observed are flagged for review by a regional editor (Sullivan et al. 2009). Because multiple observers can report LPCs at the exact same location, we filtered our data to include only observations that were spatially independent. We also omitted observations where the observer reported "moving" the location in the interest of the privacy of the landowner, or that were flagged for review but not verified by a regional editor. From January 2012 to December 2014, 522 observations of LPCs were reported to eBird by 215 different observers (Figure 1). Most (78.6%) LPC observations were reported in March and April, and approximately half (49.8%) of the observations were made by 6 observers. The 522 eBird observations were made at 140 different sites.

We used the spatial rarefication tool in SDMtoolbox (Brown 2014) to reduce spatial auto-correlation of our lek location data in ArcGIS 10.1(ESRI 2011). Although lesser prairie-chicken home ranges are typically less than 800 ha (Taylor and Guthery 1980a, Giesen 1998, Toole 2005), home ranges have been reported up to 1,944 ha (Taylor and Guthery 1980b). In Texas, 98% of locations of radio-marked birds were within 5km of the lek where they were captured (Kukal 2010). Therefore, we spatially rarefied our lek location data by 5km. We only included eBird observations where the distance traveled by the eBird user was ≤5km or effort area was ≤25km^2 (2,500ha) to match the grain of our environmental data (see below).

Environmental Data

LPC occupation of an area is often determined by the vegetation types present, amount of the landscape covered by those vegetation types (Jarnevich and Laubhan 2011, Timmer et al. 2014, Hagen et al. 2016), and associated vegetation heights. We used the 2013 existing vegetation cover (EVC) and existing vegetation height (EVH) layers (LANDFIRE 2013) as environmental layers in our analysis. These layers were created using combination of field-based data and geospatial data layers under the direction of the Wildland Fire Leadership Council. Both layers had a cell size of 30m, but were resampled using the majority classification to a cell size of 5km. The EVC layer represented percent cover of the live canopy layer of the dominant vegetation type from 0 to 100% and was divided into in three major classes: tree, shrub, and herbaceous. The layer was presented as categorical data where each cover class is separated into 10% cover categories (e.g., herbaceous cover >20 and <30%). Cropland and developed vegetation types (areas with anthropogenic structures and infrastructure) were also included in the EVC layer. The EVH represented the average height of the dominant vegetation and included four classes: tree, shrub, herbaceous, and forest. Heights were recorded by class in at least 0.5m intervals and up to 10m intervals for the forest class. Cropland and developed vegetation types were also included as part of the EVH layer.

Worldwide, anthropogenic development has had a negative effect on survival and caused displacement of grouse (Hovick et al. 2014), and LPCs are no exception (Pitman et al. 2005, Wolfe et al. 2007, Hagen 2010). To measure anthropogenic impacts, we used the global human footprint dataset available through the Socioeconomic Data and Applications Center and compiled by the Wildlife Conservation Society and Center for International Earth Science Information Network (Columbia University 2005). This layer incorporates human population pressure, land use, infrastructure, and access into one continuous data set ranging from 0 – 100 where 0 is no impact and 100 is maximum impact. The cell size is 1km, however we resampled the layer by averaging to 5km.

The global human footprint dataset does not specifically incorporate oil and gas wells, which can impact LPC site occupation (Hunt and Best 2010) and has been important to predicting LPC lek density (Timmer et al. 2014). The critical habitat assessment tool (CHAT) provides a measure of oil and gas well density within a 1km grid that is available for download through the Kansas Biological Survey (kars.ku.edu/maps/sgpchat). We downloaded the oil and gas well density layer from the CHAT and resampled the layer to 5 km resolution.

The amount of land enrolled in the Conservation Reserve Program (CRP) has also been found to be important in predicting LPC occupation (Jarnevich and Laubhan 2011, Hagen et al. 2016). CRP provides annual rental payments for a period of 10-15 years to landowners enrolled in exchange for "retiring" and establishing grass cover on former cropland (Stubbs 2014), and has been determined critical to past and current LPC conservation efforts (Spencer et al. 2017). The CHAT contains a CRP layer as well detailing the number of acres enrolled in the program in a1km grid. We resampled both layers by sum to a 5km cell size.

The environmental layers were clipped to the extent of the counties within the LPC distribution as defined by the crucial habitat assessment tool (CHAT). The LPC distribution included 105 counties located in New Mexico, Texas, Oklahoma, Kansas, and Colorado. All layers were projected to WGS 1984 , including the location data. We were most interested in examining the impact of using location data from different sources on our modeling efforts; therefore, we limited our environmental layers to those most likely to impact LPC potential distribution based on our knowledge of prairie grouse and existing literature.

Data Analysis

We used maximum entropy modeling to generate LPC probability of distribution models with MaxEnt modeling software version 3.3.3k (Phillips et al. 2006, Elith et al. 2010).

MaxEnt has proven capable of accurately modeling probability of distribution for a variety of species over a range of environmental conditions (Phillips and Dudik 2008), including grouse (Hovick et al. 2015, Jackson et al. 2015). MaxEnt compares environment conditions at known LPC locations to all available conditions within the study extent (the counties within the LPC distribution), and then estimates the probability distribution of maximum entropy for the focal species.

To assess the potential of citizen science data for use in LPC habitat suitability modeling, we created 3 different models: an aerial survey model, an eBird model, and a joint model where the aerial survey and eBird location data were combined. Each model included all 5 environmental layers: EVC, EVH, global human footprint, number of wells (from CHAT), and acres of CRP (from CHAT). We withheld 30% of the location data in each model for accuracy testing . Each model was replicated 100 times using a bootstrapping method in MaxEnt. The average percent contribution from these 100 replicates was reported for all variables and used to assess variable importance. Variables that were found to have negligible contribution (<5%) were omitted (Sahlean et al. 2014). As metrics of model performance, we reported the average test omission rate (or false negative rate) and area under the curve (AUC) of the receiver operating characteristic (ROC) for model evaluation. The AUC measures the discriminatory capacity of the model such that a value of 0.5 is no better than random and a value of 1.0 would indicate a perfect prediction of site suitability by the model. Models with an AUC value >0.7 are generally considered informative (Swets 1988, Fielding and Bell 1997), though evaluating models with AUC alone may be misleading or violate AUC theory when modeling efforts use background data in place of true absence data, as our models do

(Jiménez-Valverde 2012). Test omission rates can also be misleading as they are threshold dependent whereby they represent the proportion of presence records predicted absent, or “omitted” by the model based on a suitability threshold value (Fielding and Bell 1997). Here we used 10% training omission error as threshold to reclassify the Maxent continuous suitability values to binary (presence above the threshold and absence at or below the threshold), Considering the limitations of AUC and test omission rates, we opted to use both the threshold independent AUC values and threshold dependent test omission rates to evaluate models.

Our objective was to compare the effect of location data between the 3 models; therefore we needed to remove the potential for our environmental data to add to differences between the 3 models. To remove the variability contribution of background data, we created a background bias file by randomly selecting 50% of the pixels within our study extent (10,219 pixels). Using this bias file ensured that the background cells used for all 3 models were identical. We then specified that 10,219 background points were to be used by MaxEnt, which is > 10,000 and therefore sufficient to represent the environment available (Phillips and Dudik 2008). We compared outputs of the 3 models to one another using the I statistic , a measure of niche similarity, in ENMTools (Version 1.4.4, Warren et al. 2010). The I statistic directly compares model estimates of habitat suitability for each cell between models, thus making the I statistic a threshold-independent method of comparing model output (Warren et al. 2008, Warren et al. 2010). A null distribution of the I statistic was created in ENMTools, using a background similarity test, from 100 MaxEnt runs that used random sample of background pixels from eBird and aerial survey data.

RESULTS

From 2012 to 2014, a total of 106 LPC leks were detected by aerial surveys. Spatial rarefication of the aerial survey locations reduced our sample size from 106 to 78 leks. From January 2012 to December 2014, 522 observations of LPCs were reported to eBird at 140 spatially independent sites. Manual filtering and the 5km spatial rarefication of independent eBird locations reduced our sample size from 140 to 101 locations. When the eBird and aerial survey location data were combined, our sample size was 179, which was reduced to 176 LPC locations after spatial rarefication.

The average test AUC was >0.7 for all three models, with the greatest average test AUC reported for the aerial survey model (0.773), Table 2 . The average (±SE) test omission was also greatest in the aerial survey model (15.35 ± 0.98%, Table 2) and least in the joint model (14.42 ± 0.60%), however the difference between the 2 models was minimal (<1%). Average area predicted present increased from 42.17% in the aerial model to 51.27% in the eBird model and finally to 53.78% in the joint model. Probability distributions of site suitability between the aerial survey model and eBird model were found to have a large degree of overlap (I = 0.956). The I statistic did not fall within the null distribution (P < observed = 0.01), indicating that the probability distributions of the eBird model and aerial survey model were significantly different (Figure 2).

The global human footprint variable performed poorly (<5% contribution) in all 3 models and was omitted. The final models included existing vegetation cover (EVC), existing vegetation height (EVH), number of wells, and acreage of CRP (Figure 2). EVC contributed the most to all 3 models (contribution ≥58.36%, Table 2), followed by EVH (contribution ≥14.24%), acreage of CRP (contribution ≥9.04%), and number of wells (contribution ≥5.52%).

Within the categorical variable EVC, 10-20% shrub cover and 40-70% herbaceous cover had a strong, positive association with LPC habitat suitability across models based on coefficients (β ≥ 0.35 ± 0.06 and ≤ 1.97 ± 0.04, Table 3). Row crops, which would mostly include irrigated corn in our study area, had a negative association with habitat suitability across all 3 models (β ≥ -1.12 ± 0.06 and ≤ -0.49 ± 0.07, Table 3). There was a positive relationship with close grown crops and wheat in the eBird (β = 2.42 ± 0.07 and 0.60 ± 0.05, respectively) and joint models (β = 2.04 ± 0.07 and 0.36 ± 0.03, respectively), however, the relationship was non-existent or neutral within the aerial survey model (Table 3). Close grown crops included crops that were drill-seeded or broadcast, such as wheat, oats, rice, barely, and flax, though we expect that the most common crop was wheat. Within EVH, shrub heights 0-0.5m were positively associated with chicken habitat suitability across all models (β ≥ 1.62 ± 0.07 and ≤ 2.55 ± 0.09, Table 3). All herbaceous height coefficients were positive regardless of height category or model, though the relationship was weaker than that of shrub heights 0-0.5m (Table 3). The acreage of CRP had a positive association with LPC probability of habitat suitability across models (β ≥ 0.78 ± 0.09 and ≤ 1.11 ± 0.16, Table 3), while the number of wells had a strong negative association with probability of habitat suitability, particularly within the aerial survey (β = -7.27 ± 0.49) and eBird (β = -4.87 ± 0.49) models (Table 3).

DISCUSSION

Comparison of the species distribution model created with eBird data to the model created with aerial survey data revealed a large degree of overlap in probability distributions (Figure 2) indicating that model outputs are not substantially different from one another. While examination of the null distribution of the I statistic revealed statistically significant differences between the eBird and aerial survey model outputs at the $\alpha = 0.05$ acceptance level, this difference is not likely biologically meaningful. The observed degree of overlap (I = 0.956) indicates extremely very high similarity of model (Warren et al. 2008), thus we concluded that the eBird and aerial survey model outputs are not substantially different from one another.

We also observed minimal differences in average AUC values between the eBird (AUC = 0.737) and aerial survey (AUC = 0.773) models . AUC is calculated based on the model's ability to distinguish between presences and background data, however background data contain both presences and absences, making the interpretation of the AUC value difficult (Merow et al. 2013). Because the calculation of AUC is based on this presence/background comparison, AUC can be interpreted as a measure of how much a species is restricted to an area of modeled environmental variation (Lobo et al. 2008). For example, models for a generalist species would be expected to have a lower AUC value than models for a specialist because generalists occupy a wide range of environmental conditions across their distribution, whereas a specialist may have more limited environmental requirements in a smaller geographic extent (Lobo et al. 2008). Therefore, the specialist's presence locations would be expected to differ greatly from the background, resulting in a high AUC value. Our observed difference in average AUC values (difference = 0.036) between the eBird model and aerial survey model was minimal, therefore we concluded that the models were equally able to distinguish between presence data and the background similarly. While the differences were minimal, they were likely related to the increased presence locations associated with the eBird model (eBird = 101 locations, aerial = 78 locations), which could have increased environmental variability at presence locations, and therefore decreased the ability to distinguish between presence locations and background. Furthermore, we observed no difference between the average test omission in the eBird model (15.63 ± 0.80%) and the average test omission in the aerial survey model (15.35 ± 0.98%), which supports our conclusion that the models performed equally well, regardless of input data used.

Percent contributions of the environmental variables were also comparable between the aerial survey and eBird models, including examinations of the coefficients. The existing vegetation cover (EVC) layer was the best predictor of LPC probability of habitat suitability in models created with eBird data and models created with aerial survey data (Table 2). Within EVC we found a strong, positive relationship with probability of suitability and shrub cover and herbaceous cover. Other large-scale studies have shown a positive association with percent of shrub/grassland and occupation (Jarnevich and Laubhan 2011, Timmer et al. 2014). At smaller spatial scales, successful nests are typically found in areas with more shrub/herbaceous cover than surrounding areas (Pitman et al. 2005, Davis 2009, Hagen at al. 2013). Our results concluded that at a 5km spatial scale, areas with herbaceous cover between 40 and 70% and shrub cover between 50-60% (Table 3) were positively associated with probability of LPC habitat suitability in both eBird and aerial survey models. These areas would likely meet recommendations of > 60% cover for nesting birds at smaller scales (Hagen et al. 2013). There was a positive relationship with habitat suitability and shrub cover between 10 and 20% across models as well, which could meet small scale shrub cover recommendations depending on how shrub cover is distributed. Use of areas with shrub cover <20% have been found to reduce survival rates in sand shinnery oak, which was attributed to the more favorable microclimate provided in higher density shrub areas (Patten et al. 2005). However other studies suggest that grasslands with <15% shrub cover are optimal during the winter (Kukal 2010). A mosaic of vegetation cover classes is likely needed to provide habitat for LPCs throughout the year. Given the similarity between our results for shrub cover and herbaceous cover and the existing literature, we consider that the models created with eBird data and aerial survey data are representative of LPC habitat suitability.

Existing vegetation height (EVH) was also an important predictor for LPC probability of habitat suitability in our model. Barren ground was positively related to probability of habitat suitability for the aerial survey model but not the eBird model, which is expected given the nature of the aerial survey data. Leks are typically located on a knoll or ridge with sparse vegetation (< 10cm) (Copelin 1963, Taylor and Guthery 1980a, Giesen 1991). Chickens lekking on these areas would be particularly exposed from an aerial vantage point. Areas deemed "developed", such as roads or residential areas, were positively related to probability of habitat suitability in the eBird model but not the aerial survey model. This relationship likely represents some amount of road bias in the eBird data, similar to that of a bias towards sparsely vegetated areas in the aerial survey model. Herbaceous height and shrub heights were influential variables within the aerial survey and eBird models, and both are important in nest success and brood rearing. At small spatial scales, height of both shrubs and herbaceous vegetation tends to be higher at successful nests (Patten et al. 2005, Davis 2009, and Hagen et al. 2013). Our results revealed a positive association with herbaceous vegetation of all height classes across all models, leading us to conclude that at the 5km spatial scale, LPCs require herbaceous vegetation structure, regardless of height. There was also a positive association with shrub vegetation height between 0 and 0.5m, which can be used for thermoregulation in the summer (Copelin 1963).

Land enrolled in the Conservation Reserve Program (CRP) has been identified as critical to LPC habitat (Jarnevich and Laubhan 2011, Spencer et al. 2017), but when studying the entire LPC distribution, it was not the best predictor of LPC probability of habitat suitability. However, the relationship was positive, indicating that probability of LPC habitat suitability increased as land enrolled in the CRP increased. LPCs have used CRP land to expand their distribution (Rodgers and Hoffman 2005) and do not appear to be negatively affected by CRP (Garton 2012). The effects of CRP on LPC probability of habitat suitability are likely not uniform across their distribution. This could relate to variation in regional availability of CRP, or to regional variation in quality of CRP.

Oil and gas well density contributed the least to our understanding of probability of LPC habitat suitability. Our results concluded that as oil and gas well density increased, the probability of LPC habitat suitability within an area decreased, which is consistent with the findings of other large-scale studies (Timmer et al. 2014). In Texas, density of oil and gas wells and density of paved roads decreased local lek abundance (Timmer et al. 2014). Other local studies have reported negative effects of oil and gas developments as well (Hagen et al. 2005, Pitman et al. 2006, Beck 2009), and these negative associations are seen across grouse species within the literature (Hovick et al. 2014).

Our results clearly indicate that eBird data could be valuable for supplementing existing species location data. eBird data increased the number of spatially independent presence locations available by nearly 226%. While most LPC observations reported to eBird were from the breeding season, 21.4% of the observations were not made during the breeding season, which can help modeling efforts account for seasonal variation in space use. The MaxEnt model created using both datasets had the lowest average test AUC value (0.727), lowest average test omission (14.42 ± 0.60%), and highest average predicted presence area (53.78%, Table 2). As previously detailed, the low AUC value could be attributed to the increase in environmental variability at presence locations, which is expected as more presence locations were added. This is numerically represented by the increase in average of area predicted present (Table 2), and visually apparent in the resulting models (Figure 2).

Based on the comparable AUC values, test omission rates, and the large degree of similarity (I = 0.956) between the aerial survey model and eBird model, we concluded that citizen science data from eBird can be a reliable source of location data for the creation of species distribution models. We also concluded that eBird data could be valuable for supplementing existing species location data as eBird data increased the number of spatially independent presence locations. Our results were further substantiated by the support for our observed environmental variable performance within existing literature. The model produced with eBird data was not only capable of performing as well as a model created using data from a rigorously conducted aerial survey; it identified the same environmental variables as important to site suitability. The availability of this freely-available location data that can produce a species distribution model comparable to a model made with locations resulting from rigorous, distribution-wide aerial survey is extremely appealing to conservation efforts worldwide. As access to technology increases, citizen science data will become an increasingly important and useful conservation tool .

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Table 1. Number of eBird records for all North American grouse from spatially independent locations reported during 2000-2015.

North American grouse locations recorded on eBird from 2000-2015		IUCN Red List Status[1]
Species	eBird records at independent locations	
Gunnison sage grouse	76	Endangered
Lesser prairie-chicken	338	Vulnerable
White-tailed ptarmigan	680	Least concern
Greater sage grouse	1248	Near threatened
Greater prairie-chicken	1426	Vulnerable
Rock ptarmigan	1709	Least concern
Willow ptarmigan	2573	Least concern
Dusky grouse	2590	Least concern
Spruce grouse	3386	Least concern
Sooty grouse	3469	Least concern
Sharp-tailed grouse	3864	Least concern
Ruffed grouse	28356	Least concern

[1] Statuses determined using the 2015 International Union for Conservation of Nature Red List of Threatened Species at www.iucnredlist.org.

Table 2. Estimates of model performance for 3 different maximum entropy models of lesser prairie-chicken (*Tympanuchus pallidicinctus*) site suitability created using observations from eBird data, recorded in aeriel surveys, and a combination of the two from 2012 – 2014.

Location type	# Locations used	Average test AUC	±SE	Avg. 10th percentile training presence test omission (%)	±SE (%)	Avg. 10th percentile training presence area (%)	Average % contribution			
							CRP[a]	EVC[b]	EVH[c]	WELLS[d]
Aerial survey	78	0.773	0.005	15.35	0.98	42.17	11.17	58.36	24.95	5.52
eBird	101	0.737	0.004	15.63	0.80	51.27	9.04	62.87	19.93	8.17
Both	176	0.727	0.003	14.42	0.60	53.78	11.74	63.86	14.24	10.16

[a] Acreage of conservation reserve program per $25km^2$

[b] Existing vegetation cover

[c] Existing vegetation height

[d] Number of oil and gas wells per $25km^2$

Table 3. Beta coefficients produced by maximum entropy models using 3 different sets of observation data: eBird records, aerial survey locations, and combination of the two. These beta coefficients represent the environmental variables used in our modeling efforts, including existing vegetation cover (EVC), existing vegetation height (EVH), acreage of conservation reserve program land (CRP), and number of oil and gas wells (WELLS).

	Aerial survey			eBird			Both		
Variable	*n*	β	±SE	*n*	β	±SE	*n*	β	±SE
EVC									
Row crop	50	-0.49	0.07	73	-1.03	0.06	87	-1.12	0.06
Close-grown crop	0			95	2.42	0.07	96	2.04	0.07
Wheat	64	-0.05	0.07	88	0.60	0.05	81	0.36	0.03
Shrub cover ≥10% <20%	57	1.80	0.08	70	1.94	0.09	91	1.60	0.07
Shrub cover ≥50% <60%	67	0.80	0.07	28	0.59	0.08	58	0.28	0.05
Herbaceous cover ≥40% <50%	100	1.97	0.04	78	0.35	0.06	100	1.14	0.04
Herbaceous cover ≥50% <60%	100	1.56	0.04	100	1.44	0.04	100	1.39	0.03
Herbaceous cover ≥60% <70%	100	1.36	0.05	99	1.09	0.05	100	1.12	0.03
Herbaceous cover ≥70% <80%	70	0.29	0.06	72	-0.22	0.07	59	-0.03	0.05
Herbaceous cover ≥80% <90%	0			97	1.77	0.06	93	1.07	0.06
EVH									
Developed upland herbaceous	0			39	1.61	0.07	46	1.15	0.06
Developed low intensity	0			55	2.52	0.07	54	1.95	0.07
Barren	42	2.86	0.08	0			50	1.71	0.07
Herbaceous height 0-0.5m	100	0.87	0.05	57	0.18	0.03	82	0.25	0.02
Herbaceous height 0.5-1.0m	74	0.53	0.06	93	0.64	0.05	95	0.47	0.03
Herbaceous height >1.0m	27	0.52	0.10	76	0.49	0.05	78	0.20	0.05
Shrub height 0-0.5m	79	2.55	0.09	74	1.73	0.08	91	1.62	0.07
Shrub height 0.5-1.0m	84	1.14	0.06	39	-0.06	0.05	67	0.02	0.06
Shrub height 1.0-3.0m	0			27	0.70	0.09	50	-0.11	0.06
Forest height 10-25m	0			48	1.12	0.07	47	0.57	0.06
CRP	100	0.78	0.09	100	1.11	0.16	100	0.92	0.09
WELLS	100	-7.27	0.49	100	-4.87	0.49	100	-0.81	0.11

Figure1. Observations of lesser prairie-chickens (*Tympanuchus pallidicintus*) as reported by the Western Association of Fish and Wildlife Agencies from aerial surveys (blue dots) and by citizen scientists as reported on the online bird observation repository, eBird (yellow dots), from 2012-2014.

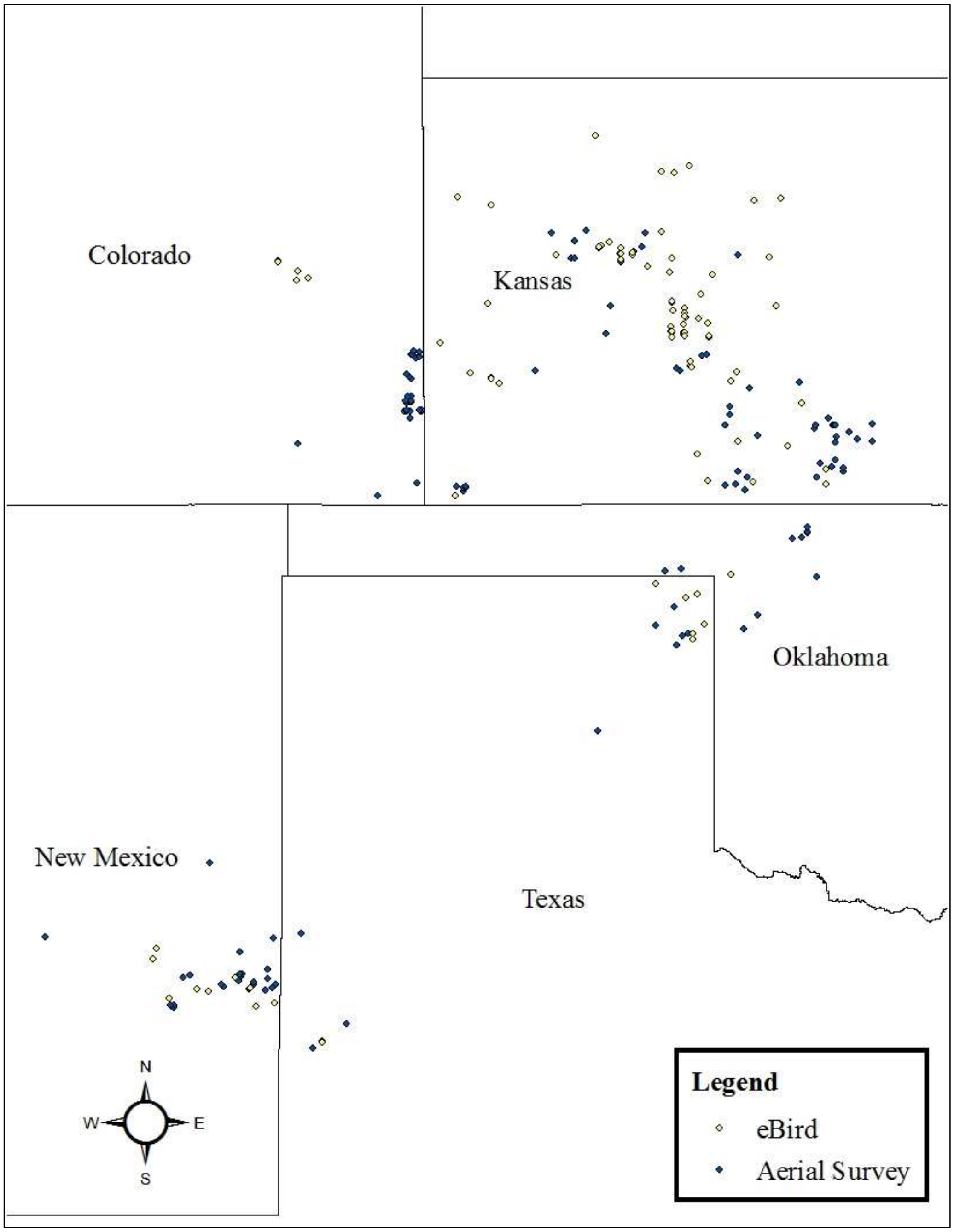


Figure 2. Lesser prairie-chicken (*Tympanuchus pallidicintus*) site suitability and species distribution models created using maximum entropy modeling of lesser prairie-chicken location data from 2 different sources (aerial surveys and eBird observations) from 2012 to 2014.

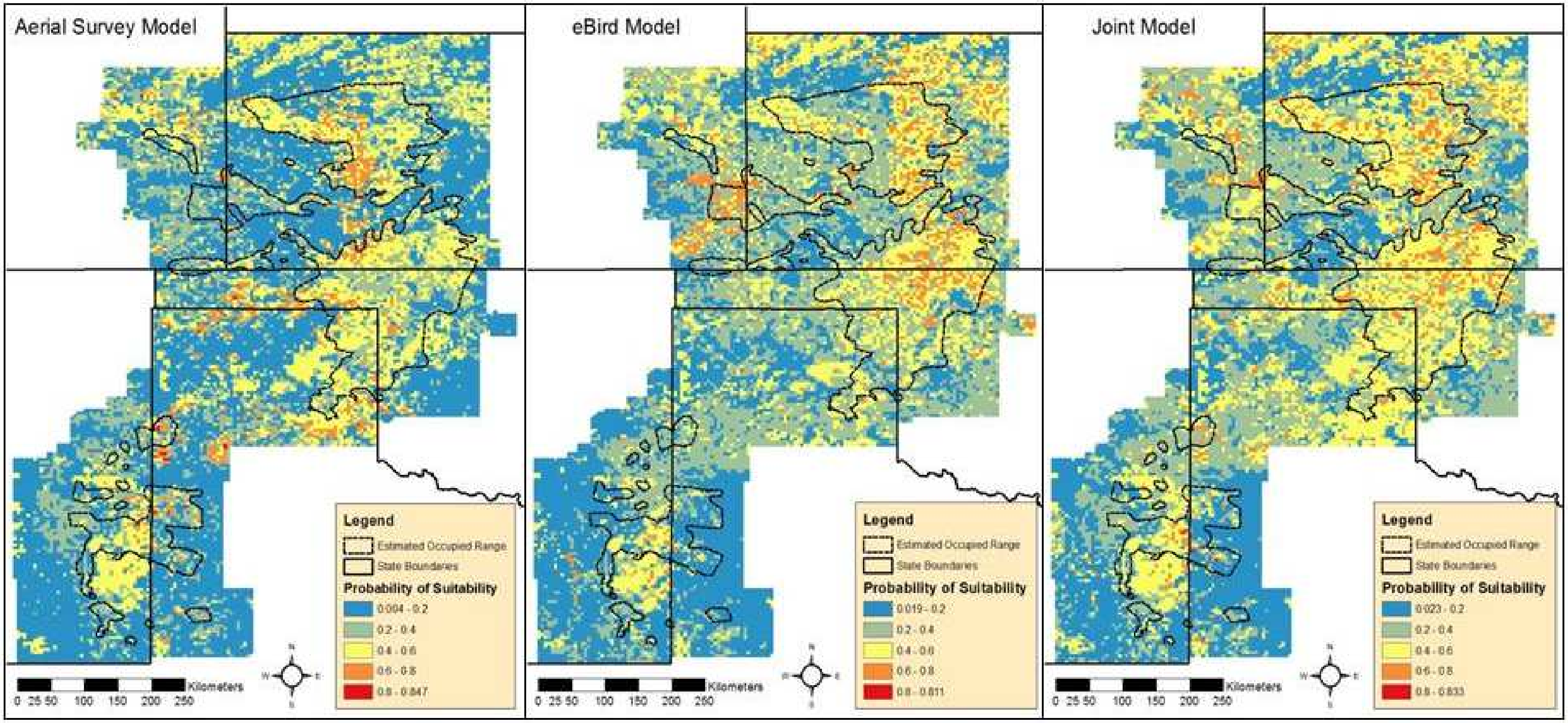
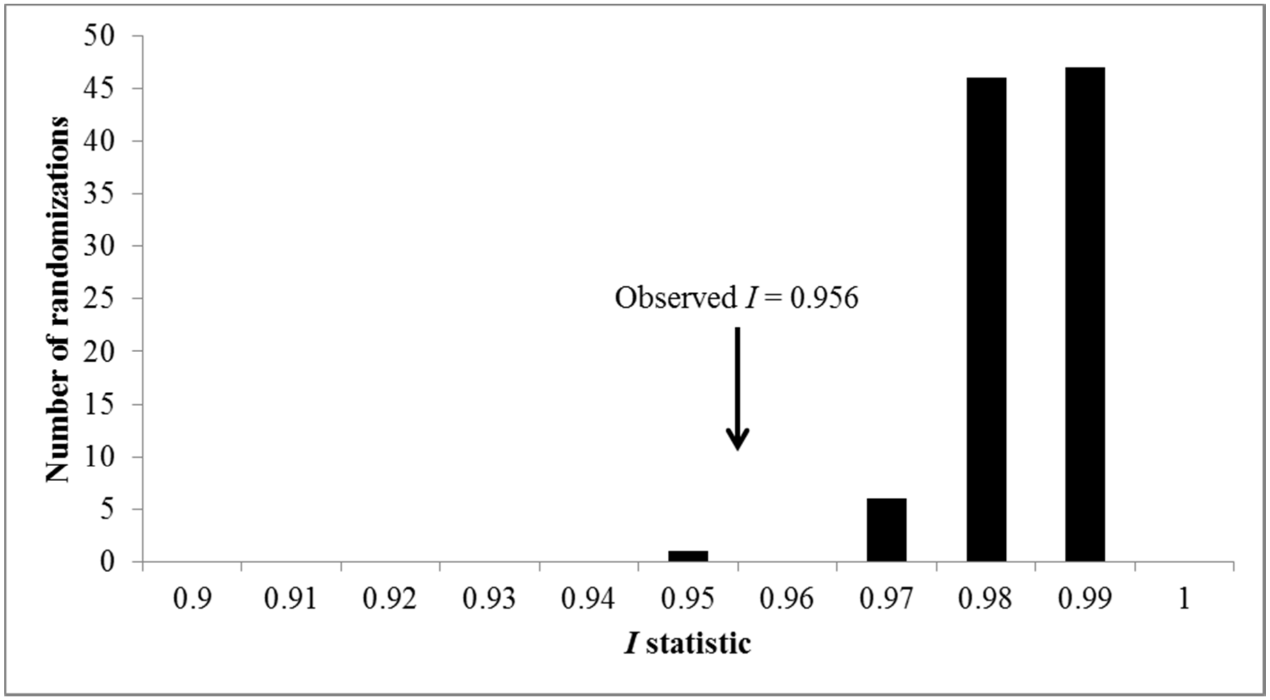


Figure 3. The null distribution of the ecological niche model overlap statistic *I* created from 100 maximum entropy modeling runs that compared randomly selected lesser prairie-chicken (*Tympanuchus pallidicintus*) locations from the aerial survey data to locations recorded in eBird datasets.



CHAPTER II

TEMPORAL SCALING OF MOVEMENT AND HABITAT SELECTION

ABSTRACT Our perception of ecological relationships is dependent on our definition of scale in terms of both time and space. These perceptions can influence policy and management decisions which may have important implications for species that respond to spatio-temporal patterns at multiple scales. Anthropogenic disturbances impact landscape patterns, and animal responses to these disturbances can vary across scales. We assessed spatio-temporal scale dependence in lesser prairie-chicken (LPC, *Tympanuchus pallidicintus*) movement and habitat selection in relation to 4 types of anthropogenic features: roads, power lines, residential areas, and oil and gas wells. We used the integrated step selection function to examine habitat selection and movement at four spatio-temporal scales representing local decision making (1 hour between successive locations) to more broad decision making (168 hours between successive locations). As the temporal grain (time between successive locations) of our analysis increased, the spatial extent (distance moved between successive locations) increased as well, demonstrating that temporal scaling our data inherently alters the spatial extent of our analysis as well. We found that LPC movements were biased, and increasingly so as the spatio-temporal scale increased. Further, birds displayed scale-invariance in the direction

of their relationship to land enrolled in the conservation reserve program (CRP) and cropland. Specifically, the LPC selected for CRP land cover and avoided cropland across all scales. CRP also facilitated LPC in crossing roads as steps that crossed roads contained more CRP land cover than expected across all scales. We did not find evidence that LPCs avoided power lines, residential areas, or oil or gas wells at any scale. However, steps that crossed powerlines or roads were longer than expected across all scales, indicating that LPCs minimized time spent under/crossing these features. The anthropogenic landscape, including human-created vegetation types (CRP and cropland) and anthropogenic features, was a primary driver of LPC habitat selection and movement patterns at local and broad spatio-temporal scales. Human policy and management decisions can greatly affect the anthropogenic landscape for this sensitive species, therefore conservation planning should account for the arrangement of vegetation and anthropogenic features on the landscape.

INTRODUCTION

Natural history and ecology have long documented the arrangement of organisms over space and time. Early studies of plant succession inspired decades of research and debate about the impact of temporal factors and spatial gradients on plant communities (Clements 1916, Gleason 1917). Thirty years later, Watt (1947) would conclude that aggregates of individual plants, termed patches, form a mosaic across a landscape that are dynamically related to one another at any given time. His work effectively linked space and time in ecology. This link would inspire the idea that both spatial and temporal patterns across different scales (extent and grain) influence ecological processes (Turner 1989). The influence of these patterns has since been demonstrated within food webs

(Polis et al. 1997), in research of herbivore grazing patterns (Bailey et al. 1996), and has become a fundamental part of animal movement ecology (Nathan et al. 2008).

Organismal movement is defined as the spatial change in location of an individual over time and is driven by processes acting at multiple scales (Nathan et al. 2008). For example, the mechanisms of seed dispersal (or movement), a relatively short-term event, have broad-scale impacts on the long-term spatial arrangement and persistence of that plant species (Nathan and Muller-Landau 2000, Damschen et al. 2008). Movements can lend insight into how a species or individual may interact with and respond to their environment at different scales (van Moorter et al. 2013), and an animal's decision to move is often a response to changes in the environmental conditions (van Moorter et al. 2013). Therefore movements can directly affect animal space use, and space used can directly impact movement (van Moorter et al. 2016). Species distributions may reflect movement decisions made over a temporal scale of decades while nest site locations may reflect decisions made over a temporal scale as small as a week or even 24 hours (see Figure 1 in Mayor et al. 2009). It is unlikely that any one scale will wholly characterize animal movement and space use decisions (Wiens 1973, Wiens 1989, Johnson 1980), therefore they should be examined at multiple spatio-temporal scales (Wiens 1989, Mayor et al. 2009, McGarigal et al. 2016).

The way in which humans perceive the environment may not be equal to the way an animal perceives the environment, particularly in terms of time and space (Turner et al. 2001). This disparity in views of the world is described by the concept of *Umwelt*, where different organisms at the same location can have different views of the space around them depending on body size, foraging strategy, predators, and more (Von

Uexküll 1926, Manning et al. 2004). Therefore *Umwelt* is not "habitat" as defined by humans, but rather the environment as it exists and is used by the animal. This distinction is important because studies of animal movement and space use are inherently limited by the ability of humans to interpret the world as the animal might, especially at different scales. Despite our best efforts, conservation planning and policy depend on the human interpretation of an animal's Umwelt to determine what management actions to take and where to focus them. Habitat loss and fragmentation are also subject to an animal's perception of each (Betts et al. 2014). Specialist species can be more impacted by habitat loss and fragmentation than generalist species, who may see the landscape as more contiguous despite disturbance (Devictor et al. 2008). An animal's perception will therefore directly influence how it moves and selects space at various spatio-temporal scales of decision making.

Animals may respond to perceived risks in their *Umwelt* by adjusting their movement patterns and/or by altering habitat selection, such as electing to use areas that include vegetation that provides refuge from a perceived risk (Fortin et al. 2005, Laundré et al. 2010, Prokopenko et al. 2016). For example, elk shift their habitat use to include more forest in the presence of wolves despite the better forage quality in other, though more exposed, vegetation types (Hernández and Laundré 2005). Movement patterns may also reveal how animals respond to perceived risks, such as by moving quickly through risky areas so as to reduce time spent there (Berggren et al. 2002, Prokopenko et al. 2016). Human disturbed areas, such as roads, oil and gas wells, and other human constructs, are often perceived as risky space and the impacts of these anthropogenic features on wildlife can vary across time and space (Naugle 2011, Northrup and

Wittemyer 2013). Behavioral responses, such as an alteration in movement patterns or displacement, are the most frequently reported responses to development (Northrup and Wittemyer 2013) rather than direct changes in survival or reproductive output.

Avoidance of energy development and associated infrastructure can fragment habitat for some sensitive species, such as those in the grouse family (Tetraonidae), ultimately resulting in a reduction in distribution and lower survival (Walker et al. 2007, Hovick et al. 2014). Within the Great Plains, lesser (hereafter LPC, *Tympanuchus pallidicinctus*) and greater prairie-chickens (*Tympanuchus cupido*) have both experienced distribution reductions, possibly exacerbated by energy development (Hagen et al. 2004, Hagen and Giesen 2005, Johnson et al. 2011). Roads, power lines, oil and gas wells, and buildings have all been shown to be avoided by prairie-chickens to varying degrees (Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011). For example, prairie-chicken home ranges were placed further than would be expected from all four anthropogenic feature types in Oklahoma and Kansas (Hagen et al. 2011). Another study found that power lines can be a significant barrier to movement (Pruett et al. 2009). At a larger scale (multiple counties), increasing densities of oil and gas wells and paved roads have been associated with a decrease in LPC lek abundance (Timmer et al. 2014).

We used the integrated step selection analysis (iSSA) to examine spatio-temporal habitat selection and movement patterns of the at-risk LPC in relation to 4 different anthropogenic features. We first determined how LPC breeding grounds (lek sites), temperature variation, and vegetation characteristics influenced LPC habitat selection and movement. The results of this analysis were then used to inform our anthropogenic modeling efforts to determine how LPCs responded to residential areas, oil and gas wells, roads, and power lines independently; our second objective. Our anthropogenic analysis tested whether LPCs avoided each anthropogenic feature by electing to be further from it and how proximity to these features affected movement and selection of environmental covariates. Our third objective assessed how crossing power lines and roads affected movement and subsequent selection of environmental covariates. Our final objective explored how LPC movement and habitat selection varied across 4 different temporal scales: 1 hour, 4 hours, 24 hours and 168 hours (1 week). We evaluated our top performing models for each anthropogenic feature type at each time scale at both the population and individual levels.

METHODS

Study Site

We conducted our study in Beaver County, Oklahoma (36° 45' N, 100° 23' W), the easternmost county in the panhandle of Oklahoma. During our study, the Oklahoma Mesonet (Brock et al. 1995, McPherson et al. 2007) weather recording stations in Beaver County recorded temperatures that ranged from -20°C to 42.2°C and annual precipitation varied from a minimum of 39.42cm in 2014 to a maximum 98.20cm in 2015. The county is dominated by sand sagebrush (*Artemisia filifolia*) shrublands (34.6%, Figure 1) and land actively enrolled in the conservation reserve program (CRP, 31.5%, Figure 1), which varied in composition but frequently included the exoticOld world bluestem (*Bothriochloa ischaemum*), sideoats grama (*Bouteloua curtipendula*), western wheatgrass (*Elymus smithii*), and Illinois bundleflower (*Desmanthus illinoensis*). Planted pastures (5.8%, Figure 1) were often areas where the CRP contract had not been renewed or where old world bluestem had been planted and managed for cattle grazing purposes. Shortgrass prairie (17.1%, Figure 1) vegetation included blue grama (*Bouteloua gracilis*), buffalograss (*Bouteloua dactyloides*), sideoats grama, soapweed yucca (*Yucca glauca*), and sand sagebrush. Cropland (10%, Figure 1) was primarily planted to winter wheat (*Triticum* spp.), but also included small amounts of sorghum (*Sorghum bicolor*) and corn (*Zea mays*). The Beaver River flows west to east through Beaver County and most of the county's woodland vegetation (2.0%, Figure 1) can be found along it, consisting primarily of eastern cottonwood (*Populus deltoids*) and non-native, invasive salt cedar (*Tamarix* spp.). Vegetation was classified using the Oklahoma ecosystems map, a 10m resolution map of the vegetation types of Oklahoma created using collected field data and remote sensing classification of satellite imagery (Diamond and Elliot 2015). Active CRP was identified using shapefile data provided by the United States Department of Agriculture Farm Service Agency.

Our study sites in Beaver County contained 4 primary types of anthropogenic features: roads, power lines, oil and gas wells, and residential areas. We used the US Department of Agriculture's (USDA) GeoSpatial Data Gateway website to access the TIGER shapefile (produced by the US Census Bureau) depicting the primary and secondary roads of Beaver County. We did not differentiate between road types (paved/unpaved) in our analysis. Residential areas were mapped by hand in ArcMap 10.1 (ESRI 2011, Redlands, CA) using the 2013 USDA National Agriculture Imagery Program imagery as a guideline for Beaver County. We obtained the location of power lines and active oil and gas wells from the Western Association of Fish and Wildlife Agencies.

Lesser Prairie-Chicken Capture and Monitoring

Our study was centered on 3 LPC breeding grounds, known as leks, which were spaced approximately 32 km apart in the northern, southwestern, and southeastern regions of the county (Figure 2). We trapped 32 female and 72 male LPCs from March to May 2013-2015 on lek sites primarily during the spring using methods approved by Oklahoma State University's Institutional Animal Care and Use Committee under protocol #AG-13-3. We used 20-25 walk-in funnel traps (per lek) arranged strategically around lek sites (Haukos et al. 1990). Captured birds were be sexed, aged (Copelin 1963), and banded with a numbered, aluminum band (Hagen et al. 2007). We fit a 22 gram, solar, GPS transmitter to both male and female LPCs just above the pelvis of the bird (a "rump mount") using a lightweight, Teflon harness (Bedrosian and Craighead 2007). Transmitters were constructed by Microwave Telemetry Inc. (Columbia, MD) and programed to collect as many as 15 locations in a 24 hour period, including at least 2 nocturnal locations. The minimum interval between locations was 1 hour. The horizontal error associated with our transmitters was +/-18m with 85% of locations falling below an 18m circular error (Ted Rollins, Microwave Telemetry, personal communication, Figure 3). We censored locations collected in the first 2 weeks after capture to account for the potential effects of capture myopathy.

Integrated Step Selection Analysis

The iSSA compared the characteristics of observed steps to those of available steps, allowing conclusions to be drawn about animal habitat selection and movement (Avgar et al. 2016). The time between the start point and end point of the step (time interval) is consistent for all steps in the analysis, but can be scaled temporally. We conducted 4 separate analyses where the time intervals or steps (grain) were 1 hour, 4 hours, 24 hours, and 168 hours (1 week) between locations. Preliminary examination of our data revealed significant differences between the step lengths of each of these time intervals, regardless of time of year (Figures 2 and 4). Therefore our approach allowed us to test if and how LPC habitat selection and movement varied across different temporal and spatial scales simultaneously. We omitted all locations from nesting females and locations where the step length was less than our transmitter error (18m). We also removed individuals with less than 350 steps (Avgar et al. 2016).

We randomly generated available steps to represent the steps an individual could have potentially taken using characteristics (step length and bearing) of the observed steps at each temporal scale (Figure 5, Avgar et al. 2016). Random step lengths were generated from the gamma distribution of the observed step lengths using the shape and rate (rate = 1/scale) parameters (Figure 5, R Core Team 2017). The shape and rate parameters differed across temporal scales (Table 1). Strong site fidelity to leks (Giesen 1994, Pirius et al. 2013, Winder et al. 2015) suggests that LPCs would display directional persistence towards the lek site where they were captured. We calculated the deviation of the observed step from the direction of the lek (Lek Angle, Figure 5) and fit these deviations to a von Mises distribution (circular normal distribution, Figure 5). We then used the von Misses concentration parameter, (kappa, Table 1) of the observed steps to generate random bearings for our available steps to account for the site fidelity towards the lek (Figure 5). Biasing available steps towards the lek site allowed us to examine the effect of our environmental covariates on habitat selection and movement while minimizing the potential directional influence of the lek.

We generated 10 available steps for every observed step at each temporal scale (Avgar et al. 2016, Prokopenko et al. 2016). This created a unique set of 11 steps, including one case (observed step) and 10 controls (available steps) for comparison, all with the same start point. The iSSA uses conditional (case-control) logistic regression to compare covariates of observed steps to covariates of available steps (Kleinbaum and Klein 2010, Avgar et al. 2016). We used the clogit function in the survival package in R (R Core Team 2017) to conduct our conditional logistic regression analysis, using the unique ID for each start point (11 step grouping) as the strata. The resulting beta coefficients were then used to draw conclusions about LPC habitat selection and movement patterns.

Our iSSA analysis was conducted in two steps. We first developed core models that included covariates we expected to drive LPC habitat selection and movement regardless of the influence of anthropogenic development (Table 2). We used Akaike Information Criterion (AIC) values produced in the iSSA to identify the best core model for the entire population at each temporal scale. Once a core model was identified, this model was then used as the foundation for our anthropogenic modeling efforts (Figure 5). Anthropogenic models (Table 3) were run for each individual bird at each temporal scale for all 4 types of anthropogenic features: roads, power lines, oil and gas wells, and residential areas. We developed 5 models that examined the relationship of proximity to these anthropogenic features and LPC habitat selection and movement. We developed an additional 4 models for our linear anthropogenic features, roads and power lines, which tested the influence of crossing these features on LPC behavior.

Core Model Covariates

We formulated 15 core models to asses LPC habitat selection and movement (Table 2). The first 4 models examined the influence of temperature variation and the lek site on step lengths and movement direction. Because of previously observed and documented site fidelity (Taylor and Guthery 1980, Pirius et al. 2013, Winder et al. 2015) we calculated the Euclidean distance (m) from the start and end points of a step to the lek for each step at each temporal scale using ArcMap 10.1 (ESRI 2011, Redlands, CA). We transformed step lengths using the natural log (lnStepLenth, Table 4). When included in the iSSA, the coefficient of the natural log transformation of step length is a modifier of the shape parameter (1/rate, Table 1) of the gamma distribution used to create available steps.

We expected that LPCs would not only respond to the lek in terms of distance, but also of directionality of their movements. We calculated two bearings: one from the step start point to the step end point, and the second from the step start point to the lek. We then found the smallest angle between these two bearings (Lek Angle, Figure 5). Taking cosine of this angle resulted in a linear correlation factor between -1 (moving directly away from the lek) and 1 (moving directly towards the lek) where 0 indicates a random walk (cosLek, Table 4, Benhamou 2006, Prokopenko et al. 2016). When the cosine of the lek angle is included in the iSSA, the produced beta coefficient is an unbiased estimator of the von Mises distribution concentration parameter (kappa, Duchesne et al. 2015, Avgar et al. 2016). The generated coefficient of the cosine of the lek angle was used to modify our kappas (Table 1) as necessary to describe LPC directional persistence toward the lek in the context of the model. We expected that directionality would be influenced by how far an individual was from the lek at the start of the step, therefore we included the cosine of the lek angle as an interaction term with the step start distance from the lek. We used temperature data gathered every 5 minutes from the Beaver and Slapout Oklahoma Mesonet stations (Brock et al. 1995, McPherson et al. 2007) to calculate variation in temperature during each step at each temporal scale (VarTemp, Table 4). We then included the variation in temperature as an interaction term with both the natural log of step length and the cosine of the lek angle.

Models 5 – 8 were developed to investigate the influence of vegetation on the end points of LPC steps. We included 4 primary vegetation types in our analysis: shrubland, cropland, CRP, and shortgrass prairie. Woodlands consisted of only a small portion of Beaver County (2.0%, Figure 1), and were very rarely encountered by LPCs, therefore we did not include woodlands. We also excluded planted native and non-native pastures from our study as they comprised a small portion of the county (5.8%) and were sometimes indistinguishable from CRP areas, making it potentially difficult for LPCs to distinguish between these two vegetation types. We expected that vegetation use may vary as temperature varied; therefore we used the variation in temperature as an interaction term with our vegetation variables.

The shrubland (Shrub, Table 4) and shortgrass prairie (Short, Table 4) vegetation types covered 51.7% of Beaver County. Shrublands can provide LPCs with nesting habitat (Pitman et al. 2005), increase adult survival (Patten et al. 2005), provide predator protection and help moderate thermal extremes (Larsson et al. 2013). A mosaic of these two vegetation types is often recommended as part of LPC management guidelines (Hagen et al. 2004, Van Pelt et al. 2013), therefore both were included as vegetation covariates in our iSSA. These variables were binary variables that indicated whether a step ended in that particular vegetation type (1) or not (0).

Croplands can serve as a potential source of food for LPCs after fields are harvested (Salter et al. 2005), however conversion of native grasslands and shrublands to cropland has been cited as a significant factor in the population decline of LPCs (Fuhlendorf et al. 2002, Hagen et al. 2004, Wolfe et al. 2016). We expected that croplands may influence movement patterns and habitat selection by LPCs, and included cropland as a binary variable (Crop, Table 4) that indicated whether a step ended in cropland (1) or not (0).

Land actively enrolled in the conservation reserve program (CRP) was the second largest vegetation type in our study area (31.5%). CRP has been credited with increasing grassland quantity and connectivity in Kansas since the 1950's (Spencer et al. 2017), and was found to be an important predictor of LPC lek occurrence (Jarnevich and Laubhan 2011) and assist LPC distribution expansion (Rodgers and Hoffman 2005). Preliminary viewing of our data also revealed an apparent connection between LPC locations and CRP (Figure 7). We expected that LPC habitat selection and movements would be influenced by whether an area was enrolled in the CRP (1) or not (0), and therefore included this vegetation type in our iSSA (CRP, Table 4).

The normalized difference vegetation index (NDVI) captures differences in vegetation greenness using remotely sensed light reflectance. We used NDVI values to explore additional variation in vegetation condition, likely due to the effects of season and rainfall. Low NDVI values are indicative of sparse vegetation or bare ground, which may be found in areas such as lek sites (Wolfe et al. 2016). High NDVI values are indicative of dense, green vegetation, such as that found within crop fields during peak growth. We obtained NDVI values from the US Geological Survey Earth Resources Observation and Science Center Science Processing Architecture, who processed Landsat 8 OLI-TIRS sensor data to produce NDVI values for our study area (30 m resolution). In order to capture seasonal and yearly variation in vegetation, we obtained NDVI data for February, May, July, and October of each year (12 files total). We then standardized these NDVI values using the raster calculator in ArcMap 10.1 (ESRI 2011, Redlands, CA, Prokopenko et al. 2016). We added the absolute minimum value (10,000) to all cells, then divided by 10,000 plus the maximum value (10,000), and finally multiplied by 100 to obtain values between 0 and 100%. We included this NDVI value as both a linear (endNDVI, Table 4) and quadratic term (endNDVI2, Table 4) in our models. We used the quadratic term to allow for LPCs to selection for intermediate NDVI values. The end point of each step was matched to the NDVI values closest to the date the step was observed. We used the linear NDVI variable as an interaction term with each vegetation type to test for variance in habitat selection within a vegetation type.

Models 9 – 12 assessed the influence of the vegetation along the path of the step on movement and habitat selection. We used the isectlinerst tool in the Geospatial Modeling Environment software (2012) to determine the proportion of each vegetation type along the path of each step. For example, a 30% of a path may have crossed through cropland, and the remaining 70% through CRP. These proportions were recorded for each of the 4 vegetation types: shrub (proportionShrub), crop (proportionCrop), CRP (proportionCRP), and shortgrass prairie (proportionShort, Table 4). LPCs may spend different amounts of time in each of these vegetation types. Step lengths not only describe distance traveled, but can also represent LPC time spent traveling through specific areas or vegetation types (Avgar et al. 2016). We used the natural log of step length as an interaction term with each of our proportion variables to examine how LPCs move through specific vegetation types. We also examined the effects of variance in temperature (VarTemp, Table 4) during the step influence the proportion of each vegetation type in the step.

Models 13 – 15 were developed to determine the influence of two specific vegetation types on LPC movement and habitat selection: shortgrass prairie and CRP. Preliminary visualization of our data revealed an apparent connection between LPC locations, CRP (Figure 7), and shortgrass prairie (Figure 8). Both CRP and shortgrass prairie have been cited as important to LPC conservation (Hagen et al. 2014, Van Pelt 2013), and we determined these specific relationships warranted further examination independently of the other vegetation types. The use of either of these vegetation types may have been influenced by temperature (VarTemp) or vegetation condition (endNDVI), therefore we examined the interaction between these terms and shortgrass prairie and CRP.

Anthropogenic Model Covariates

We developed 9 models to quantify how LPCs responded to roads, power lines, oil and gas wells, and residential areas. The first 5 models focused on the influence of proximity to these features on step length, directionality, and habitat selection. The final 4 models examined the influence of crossing a linear feature (road or power line) on step length, directionality, and habitat selection.

Given the historically negative relationship between anthropogenic features and LPCs (Hagen et al. 2011), we expected LPCs in our study to select for areas further from roads, power lines, oil and gas wells, and buildings than expected. We calculated the Euclidean distance (m) from the start and end points of a step to each of the 4 anthropogenic feature types (start/end[feature type], Table 4) for each step at each temporal scale using ArcMap 10.1 (ESRI 2011, Redlands, CA). We expected that the distance to an anthropogenic feature at the start of a step may influence the resulting length of that step, and we therefore included the natural log of step length and as an interaction term with our proximity to feature variables. We also included vegetation type and NDVI value at the end of the step as interaction terms with our proximity to feature variables as birds may alter their vegetation selection as they near anthropogenic features.

Avoidance of a feature can not only be measured in distance, but also in angular deviations from that feature. For example, birds may respond to oil and gas wells by physically turning and moving away from them. These turns can then be measured in terms of degree of deviation from the direction of the well. We examined LPC angular deviations from our 4 anthropogenic feature types using the same methods used to create the cosine of the lek angle (cosLek, Table 4) variable. The cosine of the anthropogenic feature angle (cos[feature type], Table 4) described whether a movement was directly towards a feature (1), directly away from a feature (-1), or a described a random walk (0, Benhamou 2006, Prokopenko et al. 2016). This turning behavior may be dependent on the proximity of the anthropogenic feature to the bird, therefore we included the cosine of the feature angle as an interaction term with the distance to that feature (start/end[feature type], Table 4).

Linear anthropogenic features, such as roads and power lines, can also serve as barriers to movement (Pruett et al. 2009, Hagen et al. 2011). We developed an additional 4 models to assess how crossing a power line or road would influence LPC habitat selection and movement. We created two binary variables that determined if steps intersected (1) or did not intersect (0) a road (crossRoad) or power line (crossPower, Table 4) using ArcMap 10.1 (ESRI 2011, Redlands, CA). We expected that birds would increase movement rates across power lines and roads in order to reduce time near these features; therefore we included the natural log of step length as an interaction term with our crossing covariates. Crossing a linear feature may also affect vegetation selection along a step and at the end of a step. We included the proportion of each vegetation type along a step and the NDVI value at the end of a step as an interaction terms with our crossing covariates.

Model Interpretation

We identified the proximity model and crossing model with the lowest AIC value for each individual bird at each temporal scale for each anthropogenic feature type. We tallied the number of instances each of the models was found to have the lowest AIC value, and then assessed the covariates of the models with the highest counts. We estimated the population averages and confidence intervals for the estimated beta coefficients by performing a bootstrap with 5,000 iterations using the boot package in R (R Core Team 2017). We then calculated and reported the proportion of individuals whose beta coefficient followed the direction of the population mean.

The bootstrapped coefficient of the natural log of step length (lnStepLength) was a modifier of the shape parameter for the gamma distribution of step lengths at each temporal scale (Avgar et al. 2016). We added this coefficient to the original shape parameter, then multiplied this number by the original scale parameter value (Table 1), resulting in an estimation of movement rate for each time interval. The bootstrapped coefficient confidence intervals were used to modify movement rate confidence intervals.

RESULTS

Core Model Results

Sample size varied from 44 individuals (4 hour analysis) to 67 individuals (168 hour analysis), and the average number of steps per individual ranged from 663 steps (4 hour analysis) to 2,233 steps (24 hour analysis, Table 5). Models 12, 13, and 5 contained the lowest AIC values and carried the majority of the weight for the 1, 4, 24, and 168 hour analyses respectively (Tables 6, 7, 8, and 9). The top performing models for the 1 and 4 hour time intervals included proportions of vegetation along a step while the top performing model for the 24 and 168 hour time intervals included the vegetation type at the end of the step.

Movement and Lek Covariates

Step lengths at the 1, 24, and 168 hour time intervals were longer than expected and increased as temporal scale increased (movement rate = 167.9 m/1 hour, 293.1 m/24 hours, 863.1 m/168 hours, Table 10). LPCs also directed their movements towards the lek significantly more than expected at the 1, 24, and 168 hour temporal scales (cosLek, $P \leq 0.001$, Table 11). The beta coefficients in our 4 hour analysis indicated that step length decreased as variation in temperature increased (beta coefficient = -0.002, $P < 0.001$) and birds directed their movements more towards the lek as distance from the lek increased (beta coefficient = 0.000, $P < 0.001$), however these relationships were weak for both coefficients. LPCs Birds ended their steps closer to the lek than would be expected at random across all temporal scales (endLek). While the beta coefficients were weak (beta coefficient ≤ -0.001, P < 0.001, Table 11), when exponentiated, they revealed that birds were 39.2% less likely to use areas 500m away from the lek site.

Vegetation Covariates

We observed a strong selection for areas actively enrolled in the CRP. A higher proportion of the step consisted of CRP vegetation at the 1 and 4 hour temporal scales (beta coefficients = 1.137 and 0.882, P < 0.001, Table 11), and birds preferred to end their steps in CRP vegetation at the 24 and 168 hour temporal scales (0.772 and 0.862, P < 0.001). Cropland was avoided along the 1 hour interval step paths (beta coefficient = -0.245, P < 0.001), as well as at the end of the 24 and 168 hour interval steps (-0.308 and -0.361, P < 0.001). Shortgrass prairie constituted a higher proportion of the 1 and 4 hour steps that would be expected at random (beta coefficients = 0.680 and 0.326, P < 0.001), however shortgrass prairie was avoided at the end of the 24 and 168 hour steps (-0.214 and -0.424, P < 0.001). Birds were positively associated with shrub vegetation along 1 hour steps (beta coefficient = 0.955, P < 0.001), but avoided shrub vegetation at the end of the 24 and 168 hour steps (-0.333 and -0.622, P < 0.001, Table 11). Using exponentiated beta coefficients, we concluded that birds were at least 116.4% more likely to use CRP than would be expected at random, at least 21.7 % less likely to use cropland than would be expected at random, and responded differently to shortgrass prairie and shrub vegetation depending on the temporal scale examined.

Anthropogenic Model Results

Models 3 and 5 consistently contained the lowest AIC values for the most individuals across all temporal scales and for all 4 types of anthropogenic features (Tables 12-15). These models contained 6 of the same covariates: the interaction between the distance to a feature and the step end point vegetation types (4 covariates), the interaction between distance to a feature and the step end NDVI values, and the distance to an anthropogenic feature. To estimate the population mean and confidence intervals for these variables, we bootstrapped the individual beta coefficients produced by model 3, which typically contained the highest AIC tally (Tables 12-15). We assessed the influence of crossing a linear feature (road or power line) on step length, directionality, and habitat selection using 4 different models (Table 3). Model 9 overwhelmingly contained the highest AIC tally for both anthropogenic feature types across all temporal scales (Tables 16-17). Therefore we report here the bootstrapped population means and confidence intervals for the covariates of model 9 for road and power line crossings.

Residential Covariates

Across all temporal scales, LPC locations were no further than expected from residential areas (endResidential, 95% CIs overlap 0, Table 18). Step lengths increased slightly as LPC distance from a residential areas increased at the 1 and 4 hour temporal scales, however the beta coefficients were weak (mean coefficient value = 0.0001, 95% CI [0.0000, 0.0001], Table 18). At least 59% of birds used more shortgrass prairie when they were closer to residential areas than expected at the 1 hour (mean coefficient value = -0.0025, 95% CI [-0.0067, -0.0003]) and 4 hour (-0.0021, 95% CI [-0.0058, -0.0000] temporal intervals. Birds also used more shrub vegetation than expected as they neared residential areas at the 24 (mean coefficient value = -0.0015, 95% CI [-0.0023, -0.0008]) hour and 168 hour (-0.0012, 95% CI [-0.0018, -0.0005]) temporal scales. As LPCs got closer to residential areas, at least 68% of birds tended to turn away (move backwards), however this relationship was very weak (mean coefficient values ≤ 0.0002, 95% CI [0.0000, 0.0003], Table 18).

Oil and Gas Well Covariates

We did not find evidence of LPC avoidance of oil and gas wells (endWell, 95% CIs overlap 0, Table 19). Birds tended to turn away from wells as they got closer to them at the 4, 24, and 168 hour temporal scales, however this relationship was very weak (mean coefficient values = 0.0001, 95% CI [0.0000, 0.0002], Table 19) and the relationship between step lengths and distance to an oil and gas well was equally weak. At least 69% of birds selected for shrub vegetation near wells at the 1 hour (mean coefficient value = -0.0085, 95% CI [-0.0179, -0.0007], Table 19) and 4 hour (-0.0230, 95% CI [-0.0344, -0.0126], Table 19) temporal scales. Use of cropland increased as distance from a well increased for at least 70% of individuals at the 24 (mean coefficient value = 0.0009, 95% CI [0.0006, 0.0013], Table 19) hour and 168 (0.0013, 95% CI [0.0008, 0.0019], Table 19) hour temporal scales.

Power line Covariates

LPCs were no further than expected from power lines across all temporal scales (endPower, 95% CIs overlap 0, Table 20). Calculated movement rates of at least 61% of LPCs decreased as they got closer to a power line (Table 20). Movement rates were comparable to the estimated movement rates of the population at 1 hour (population mean = 167.925 m, near power line mean = 163.391 m) and 4 hours (293.136 m, 293.919 m), but began to differ at 24 hour (522.178 m, 476.045 m) and 168 hour (863.067 m, 747.487 m) temporal scales (Table 10). Birds used areas with a lower NDVI value as distance to a power line decreased across all temporal scales; however the mean beta coefficients were all less than 0.0001 (Table 20). Use of shrub (mean coefficient value = -1.9060, 95% CI [-5.0673, -0.1770]), cropland (-0.2175, 95% CI [-0.5895, -0.0006]), and shortgrass prairie (-0.0781, 95% CI [-0.2269, -0.0003]) increased as distance to a power line decreased at the 4 hour scale. Use of shrub increased as distance to a power line decreased at the 24 (mean coefficient value = -0.0025, 95% CI [-0.0050, -0.0006]) and 168 hour temporal scales as well (-0.0019, 95% CI [-0.0037, -0.0003]). At the 1 hour temporal scale, shortgrass prairie use increased as distance to a power line decreased (mean coefficient value = -0.0663, 95% CI [-0.1975, -0.0005]).

At least 85% of birds moved significantly further than expected when crossing a power line across all temporal scales (Table 10 and 21). The difference between the average movement rates of the population and birds crossing a power lines ranged from 317.109 m longer at the 1 hour scale to 1,323.430 m longer at the 24 hour temporal scale. When crossing a power line, bird steps ended in areas with a lower NDVI values than would be expected at random across all temporal scales (mean coefficient value range = -0.3498 at to -0.1226l, Table 21). The proportion of a step in shrubland and cropland decreased when crossing a power line at the 4, 24, and 168 hour temporal scales (Table 21); however these estimates were extreme likely due to a few individuals who rarely (if ever) encountered these crossing scenarios. The proportion of shortgrass prairie in 1, 4, and 24 hour steps that crossed a power line was also less than expected, as was the proportion of CRP land at 1 hour (mean coefficient value = -3.3909, 95% CI [-6.2124, -1.2145]).and 168 hour (-1.5106, 95% CI [-3.8852, -0.637]) temporal scales (Table 21).

Road Covariates

Using exponentiated beta coefficients, we found that LPCs were 40.2 – 100.0% less likely to use areas more than 100m away from a road across all temporal scales (mean coefficient value range = -0.0993 to -0.0052, Table 22). Movement rates of at least 65% of LPCs decreased as they got closer to a road. Movement rates while near roads were comparable to the estimated movement rates of the population at 1 hour (population mean = 167.925 m, near road mean = 163.409 m) and 4 hours (293.136 m, 293.942 m), but began to differ at 24 hour (522.178 m, 476.110 m) and 168 hour (863.067 m, 747.625 m) temporal scales (Table 10). As distance from a road increased, use of CRP land increased across all temporal scales (mean coefficient value range = 0.0014 to 0.0987). While this was the observed trend for the majority of birds at the 1, 4, and 168 hour temporal scales, this was not the trend for the majority of birds at the 24 hour scale (48.5%, Table 22).

At least 76% of birds moved significantly further than expected when crossing a road across all temporal scales (Tables 10 and 23). The difference between the average movement rates of the population and birds crossing a road ranged from 168.346 m longer at the 1 hour scale to 312.364 m longer at the 24 hour temporal scale. As birds crossed roads, at least 81% of individuals ended up in areas with significantly lower NDVI values than would be expected at random across all temporal scales (mean coefficient value range = -0.0876 to -0.0623). The proportion of shrub and cropland vegetation decreased as birds moved across roads, however extreme values were observed once again. The proportion of land actively enrolled in the CRP increased as birds moved across roads at the 4 hour (mean coefficient value = 0.6298, 95% CI

[0.0026, 1.2650]), 24 hour (1.3041, 95% CI [0.5918, 2.1068]), and 168 hour (0.9112, 95% CI [0.2674, 1.5991]) time scales, indicating that birds may have crossed roads to get from one patch of CRP land to another.

DISCUSSION

We used two characteristics of movement, step length and direction, to define the available landscape at multiple spatio-temporal scales for LPCs. By doing so, we were able to assess the landscape more as a LPC might perceive it; the LPC *Umwelt*. As the temporal grain of our study increased, the spatial extent increased as well, representing LPC increase in potential space used over time. LPC directional bias toward the lek site also increased as the temporal scale increased, indicating that the lek became more influential to broad-scale decisions. Covariates that exhibited scale-invariance were indicative of primary drivers of habitat selection and all the covariates that displayed scale-invariance were either human constructed vegetation types (CRP and cropland) or related to anthropogenic features. LPC movements and habitat selection are strongly tied to the activities and impacts of humans on these landscapes, and therefore these birds can be significantly impacted by policy and management actions affecting these landscapes.

Temporal and spatial scales are inherently not independent of one another (Mayor et al. 2009). Our data revealed that as the grain of our temporal scale (time between consecutive locations) increased, the extent of our spatial scale (area considered available to a LPC at any one location) increased simultaneously (Figures 3 and 4). Most multi-scale studies of habitat selection alter the spatial extent of availability, using techniques such as outlining a study area or home range to define availability (McGarigal et al. 2016). While these techniques are effective, the temporal scale over which selection decisions are made is unclear or undefined. Spatial scaling of a habitat selection analysis without consideration for the time the animal would require to cover that space would result in a definition of available space that is not truly available to the animal. Our study used observed patterns of movement at different temporal grains to define the available space in which we studied the process of habitat selection. This may be a more empirical and biologically relevant representation of an animal's perception of the landscape (Northrup et al. 2016), and also reduces inferential bias of the habitat selection covariates (Thurfjell et al. 2014). As GPS transmitters become more commonplace in wildlife research (Cagnacci et al. 2010), it becomes increasingly possible to collect data at the resolution needed to improve our definitions of availability and take one step closer to understanding an animal's *Umwelt*.

In his discussion of pattern and scale in ecology, Levin (1992) stated that "The observer imposes a perceptual bias, a filter through which the system is viewed." For LPCs, the filter through which a bird views the world may be the lek. Our study revealed strong directional persistence of LPCs towards the lek site where they were captured, which is not surprising given that most LPCs stay within 5 km of a lek site (Giesen 1994, Pirius et al. 2013, Winder et al. 2015). The strength of this directional persistence increased as temporal scale increased (Table 11), indicating that the lek became more important to how LPCs oriented their movements at larger temporal, and by default, spatial scales. LPCs in our study were also at least 99.3% less likely to use areas 5km from a lek site. Based on our results, we suggest that future habitat selection analyses that employ a used versus availability framework account for the influence of directional bias on an animal's movement. Defining availability based on the directional bias of an animal will allow discernment between the influence of the bias and a covariate of interest. For example, bison and cattle are drawn to water (Allred et al. 2011), and likely bias their movements in favor of the direction of a water source. However, they have other nutritional needs. A habitat selection analysis assuming equal availability may conclude that the vegetation around water was preferred, when in reality the water itself was the attractant.

The nature of our vegetation covariates was different between the finer (1 and 4 hour) scales and the courser (24 and 168 hour) scales assessed. At the 1 and 4 hour temporal scales, the proportion of the step within a vegetation type was included as a covariate in the top performing models, while the vegetation type at the end of the step was included as a covariate in the top performing model for the 24 and 168 hour analyses. This disparity indicates that the straight-line path between locations 1 and 4 hours apart may contain information relevant to the actual path the animal travelled that was not able to be discerned at courser (24 and 168 hour) scales.

Cropland and land enrolled in the CRP (Conservation Reserve Program by USDA) significantly and consistently influenced LPC habitat selection across all temporal scales (Table 11). Responses to covariates that are consistent in direction across all examined scales (scale-invariant) indicate that these covariates are primary drivers of the process of habitat selection (Northrup et al. 2016). The CRP is a cost-share payment program focused on establishing vegetation cover on former crop fields (Stubbs 2014). Therefore it is interesting that LPCs strongly selected for land enrolled in CRP while avoiding croplands, the very vegetation type that enabled the establishment of CRP land. This suggests that management decisions and human policy can directly impact LPCs, even at the relatively small temporal scale of 1 hour movements. Occupancy by LPCs has been shown to increase by 12% for every 1% increase in CRP land cover at the much larger spatial scale of 7.5 km2, suggesting that the importance of CRP land cover extends beyond the scale of our study as well (Hagen et al. 2016). Conversely, increasing coverage of cropland within even larger landscapes (7,238ha, ~72 km2) have been associated with LPC population declines (Fuhlendorf et al. 2002). Conservation planning efforts for the LPC should account for the arrangement of CRP land and crop land when determining where to focus conservation efforts as CRP land cover may be important to connectivity (Spencer et al. 2017), and cropland may contribute to further fragmentation.

The relationship between LPCs and the shrub and shortgrass prairie vegetation types were scale-variant with birds using more shrub and shortgrass prairie vegetation than would be expected at random at finer (1 and 4 hour) time scales, then using less of these vegetation types at courser (24 and 168 hour) time scales (Table 11). These results likely reflect LPC use of small patches or edges of these vegetation types within or near already preferred space, such as land enrolled in the CRP, but avoidance of large patches of shortgrass prairie and shrubland (visible in Figure 8). LPCs typically have a strong association with grass and shrub land vegetation types at both spatially large (Jarnevich and Laubhan 2011, Timmer et al. 2014) and small scales (Pitman et al. 2005, Hagen et al. 2013). Shortgrass prairie and shrub land vegetation types in our study site were largely found in areas with high topographical variation. This is likely due to the fact that Euro-American settlers were encouraged to cultivate as much of the arable land as possible (Engle et al. 2008). Therefore flat areas, which LPCs prefer for lekking (Jarnevich and Laubhan 2011), of native shrub land and shortgrass prairie were among the first areas to be converted to croplands. Avoidance of these vegetation types in our study site could be related to the topography of these areas rather than the characteristics of the vegetation.

The direction of our beta coefficients across temporal scales was very consistent in our assessment of LPC response to anthropogenic features, indicating that anthropogenic features were important drivers in the process of LPC habitat selection at the scales we examined. Relationships may change at scales exceeding our largest time interval, 168 hours. For example, we did not find evidence that LPCs avoided being close to oil or gas wells, residential areas, or power lines despite the strong negative response to these features documented in the literature (Hagen et al. 2011, Hovick et al. 2014). Lek site selection may be the scale at which chickens respond to these anthropogenic features. Habitat suitability for lek sites in Kansas increased as distance from a transmission line, highway, and oil or gas wells increased (Jarnevich and Laubhan 2011) and lek densities in Texas were greatest in areas with lower densities of oil and gas wells and paved roads (Timmer et al. 2014). If LPCs are responding to these anthropogenic features at the scale of lek site selection, then perceptual bias (Levin 1992) may also explain why we observed a lack of response by LPCs to the proximity of an oil or gas well, power line, or residential area. As stated earlier, LPCs view the world through the filter of the lek, and if leks are placed in areas that reduce exposure to anthropogenic features, an analysis that accounts for this filter, such as ours, would reflect that relationship.

LPCs responded differently to crossing a road than to the proximity of a road. Birds were closer to roads than would be expected at random, however when birds crossed roads, they took bigger steps (an average of at least 168.346 m longer, Table 10) and therefore crossed roads more quickly. These results suggest that while birds may choose to use areas near roads, roads are still impacting LPC movements and may act as a barrier to movement (Taylor and Goldingay 2010). The majority of roads in our study site were unpaved, and thus our results may be more representative of LPC response to unpaved roads. However, research on the specific paved highway (Highways 412) that runs through our study area also found that LPCs were no further than expected from this road and birds did not perceive it as a barrier to movement (Pruett et al. 2009).

We expect that the observed relationships between LPCs and roads are tied to vegetation characteristics of the area. When LPCs crossed roads, a greater proportion of their step consisted of land enrolled in the CRP. Moreover, LPC use of CRP increased as distance from a road increased, indicating that birds were using the central parts of a patch of CRP. It would appear that the answer to the question "Why did the chicken cross the road?" is to move between patches of CRP land cover, and more specifically, the central parts of these patches. This kind of relationship between roads and preferred habitat has been documented in elk where highway crossings increased when the highway divided preferred habitat (Gagnon et al. 2007) and elk selected for more open habitat when crossing roads, which was attributed to the need to promote visibility or move quickly (Prokopenko et al. 2016). Similarly, LPCs elected to end their steps when crossing a road in areas with a lower NDVI value. There was also evidence that LPC attraction to roads may be influenced by ditches, which can provide food resources, vegetative cover, and perform connectivity functions in the landscape (Figure 9, Herzon and Helenius 2008). Once again, we conclude that the arrangement of CRP land cover is a critical part of LPC conservation planning.

The average LPC step length when crossing a power line was at least twice as long as the average LPC step length across all temporal scales. This significant departure from normal movement indicates that power lines are not an especially permeable feature on the landscape for LPCs, a conclusion that we are not alone in reaching (Pruett et al. 2009). Given the substantial distance traveled when crossing a power line, it is possible that LPCs are mostly crossing power lines when they are already engaging in specific behaviors that involve large movements, such as dispersal or exploratory movements. These types of large movements are critical to genetic flow, population growth, and overall population persistence (Earl et al. 2016, Oyler-McCance et al. 2016). Power line placement in landscapes occupied by LPCs should be carefully reviewed to avoid inhibiting movement between populations and desirable space.

Similar to LPC response to roads, LPCs ended their steps in areas with lower NDVI values when crossing a power line across all temporal scales (Table 21). We expect that birds select these areas for the increased visibility they afford. All vegetation types were used less than expected by LPCs when crossing a powerline. Though this relationship was not consistently significant across temporal scales, and suffered from extreme covariate values from individuals that did not encounter power lines often, if at all. The distribution of LPC step lengths follows a gamma distribution, where shorter steps taken are taken more frequently than longer steps. Therefore the long movements associated with crossing power lines would have mostly been compared to shorter, available movements that encountered fewer vegetation types, thus explaining our results.

We did not find evidence of LPC avoidance of residential areas or oil and gas wells. The relationships between LPC habitat selection and proximity to these anthropogenic features were mostly insignificant (P > 0.05). What relationships were observed was likely a product of how these features were distributed across the landscape. For example, LPCs were at least 56.9% less likely to be in shrub vegetation at 100 m from an oil or gas well at the 1 and 4 hour temporal scales (Table 19). However, birds used these vegetation types more than expected at these scales (Table 11). The distribution of oil and gas wells favored the shrub vegetation type, resulting in the conclusion that birds use shrub land more when near an oil or gas well.

Human study of an animal's *Umwelt* will always be imperfect as we will never account for all the dynamics that influence animal decision making, however technological advancements have made a more accurate approximation possible. We argue that, when possible, habitat selection and movement analyses should use the characteristics of movement (step lengths and directional bias) to better define true availability. Moreover, these analyses should be conducted at multiple spatio-temporal scales in order to capture scale-dependent relationships. While we did not detect many scale-dependent relationships in our assessment of LPC habitat selection, a lack of dependence is equally informative. Covariates that maintain significance across scales are indicative of drivers of selection, and should consequently be drivers of conservation planning. Ultimately, we hope that by attempting to understand the spatio-temporal landscape through the eyes of the LPC, conservation efforts for this sensitive species can move forward with their biases, movement capabilities, and habitat preferences in mind at local and broader scales.

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Table 1. Parameters used to created random, biased turning angles following a von Mises distribution and random step lengths following a gamma distribution for creation of available steps used in an integrated step selection analysis with lesser prairie-chickens (*Tympanuchus pallidicinctus*).

	Hour Interval	4 Hour Interval	24 Hour Interval	168 Hour Interval
von Mises distribution				
kappa	0.13858	0.33214	0.35359	0.44604
Gamma distribution				
shape	0.69914	0.68462	0.86149	0.79208
rate	0.00428	0.00233	0.00181	0.00106

Table 2. Core models used to assess lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat selection in Beaver County, Oklahoma from April 2013-May2016.

Model Category	Model Number	Covariates[1]
Influence of the lek and temperature models	1	lnStepLength + cosLek + endLek
	2	lnStepLength:VarTemp + cosLek:VarTemp + endLek:VarTemp
	3	lnStepLength:VarTemp + cosLek:startLek + endLek
	4	lnStepLength:startLek + cosLek:startLek + cosLek + endLek
Step end point vegetation models	5	lnStepLength + Shrub + Crop + CRP + Short + endNDVI² + cosLek + endLek
	6	lnStepLength:VarTemp + Shrub:VarTemp + Crop:VarTemp + CRP:VarTemp + Short:VarTemp + endNDVI:VarTemp + cosLek:VarTemp + endLek:VarTemp
	7	lnStepLength:VarTemp + Shrub + Crop + CRP + Short + endNDVI² + cosLek:startLek + endLek
	8	lnStepLength:VarTemp + Shrub:endNDVI + Crop:endNDVI + CRP:endNDVI + Short:endNDVI + cosLek:endNDVI + endLek
Step vegetation models	9	lnStepLength:proportionShrub + lnStepLength:proportionCrop + lnStepLength:proportionCRP + lnStepLength:proportionShort + lnStepLength:VarTemp + endNDVI² + cosLek:startLek + endLek
	10	lnStepLength:VarTemp + proportionShrub + proportionCrop + proportion CRP + proportionShort + endNDVI² + cosLek:startLek + endLek
	11	lnStepLength:VarTemp + proportionShrub:VartTemp + proportionCrop:VarTemp + proportion CRP:VarTemp + proportionShort:VarTemp + endNDVI:VarTemp + cosLek:VarTemp + endLek:VarTemp
	12	lnStepLenth + proportionShrub + proportionCrop + proportion CRP + proportionShort + endNDVI² + cosLek + endLek
Specific vegetation type models	13	lnStepLength:VarTemp + proportionCRP + proportionShort + endNDVI² + cosLek:startLek + endLek
	14	lnStepLength:VarTemp + CRP + Short + endNDVI² + startLek:cosLek + endLek

Table 2 continued. Core models used to assess lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat selection in Beaver County, Oklahoma from April 2013-May2016.

Model Category	Model Number	Covariates[1]
Specific vegetation type models	15	lnStepLength:VarTemp + CRP:endNDVI + Short:endNDVI + startLek:cosLek + endLek

[1] Variable descriptions are available in Table 4

Table 3. Anthropogenic models used to assess lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat selection in Beaver County, Oklahoma from April 2013-May2016.

Model Number	Anthropogenic Models	Covariates[1]
1	Influence of feature on vegetation selection	Core Model + endFeature:Shrub + endFeature:Crop + endFeature:Short + endFeature:CRP + endFeature:endNDVI + endFeature
2	Influence of feature on movement	Core Model + startFeature:lnStepLength + endFeature
3	Influence of feature on vegetation selection and movement	Core Model + endFeature:Shrub + endFeature:Crop + endFeature:Short + endFeature:CRP + endFeature:endNDVI + startFeature:lnStepLength + endFeature
4	Influence of feature on bearing	Core Model + startFeature:cosFeature + endFeature
5	Influence of feature on bearing and vegetation selection	Core Model + startFeature:cosFeature + endFeature:Shrub + endFeature:Crop + endFeature:Short + endFeature:CRP + endFeature:endNDVI + endFeature
Additional Models Included in Road and Power Line Analysis Only		
6	Influence of crossing feature on step length	Core Model + crossFeature:lnStepLength
7	Probability of crossing a feature	Core Model + crossFeature
8	Influence of crossing feature on path vegetation	Core Model + crossFeature:proportionShrub + crossFeature:proportionCrop + crossFeature:proportionShort + crossFeature:proportionCRP + crossFeature:endNDVI
9	Influence of crossing feature on movement and path vegetation	Core Model + crossFeature:lnStepLength + crossFeature:proportionShrub + crossFeature:proportionCrop + crossFeature:proportionShort + crossFeature:proportionCRP + crossFeature:endNDVI

[1] Variable descriptions are available in Table 4.

Table 4. Variables included in the integrated step selection analysis of lesser prairie-chicken (*Tympanuchus pallidicinctus*) locations collected from April 2013-May 2016 in Beaver County, Oklahoma.

Variable	Description
lnStepLength	Natural log of the step length (m)
VarTemp	Variance in temperature between the step start date and step end date
Shrub	Binary variable indicating whether the step ended in the shrub land vegetation type
Crop	Binary variable indicating whether the step ended in the cropland vegetation type
Short	Binary variable indicating whether the step ended in the shortgrass prairie vegetation type
CRP	Binary variable indicating whether the step ended in the conservation reserve program vegetation type
endNDVI	NDVI value at the end point of the step
endNDVI^2	Quadratic NDVI value at the end point of the step
porportionCRP	Proportion of the step that is within the conservation reserve program vegetation type
proportionShortgrass	Proportion of the step that is within the shortgrass prairie vegetation type
proportionShrub	Proportion of the step that is within the shrub vegetation type
proportionCrop	Proportion of the step that is within the crop vegetation type
endLek	Distance (m) from the end point of the step to the lek where captured
endWell	Distance (m) from the end point of the step to an active well
endResidential	Distance (m) from the end point of the step to a residential area
endRoad	Distance (m) from the end point of the step to a road
endPower	Distance (m) from the end point of the step to a power line
startLek	Distance (m) from the start point of the step to the lek where captured
startWell	Distance (m) from the start point of the step to an active well
startResidential	Distance (m) from the start point of the step to a residential area
startRoad	Distance (m) from the start point of the step to a road
startPower	Distance (m) from the start point of the step to a power line
CrossRoad	Bianary variable indicating whether the step crosses a road or not
CrossPower	Bianary variable indicating whether the step crosses a power line or not
cosLek	Cosine of the bearing deviation between the step and the lek where captured
cosWell	Cosine of the bearing deviation between the step and the nearest well
cosResidential	Cosine of the bearing deviation between the step and the nearest residential area
cosRoad	Cosine of the bearing deviation between the step and the nearest road
cosPower	Cosine of the bearing deviation between the step and the nearest power line

Table 5. Sample size of individual lesser prairie-chickens (*Tympanuchus pallidicinctus*) and lesser prairie-chicken steps used in an integrated step selection analysis of data collected between April 2013 and May 2016.

	Hour Interval	4 Hour Interval	24 Hour Interval	168 Hour Interval
Number of individuals	62	44	66	67
Number of steps	70,406	29,195	147,395	133,356
Average number of steps per individual	1,135.581	663.523	2,233.258	1,990.388
Range in number of steps per individual	510-3,639	350-1,803	501-8,534	366-8,120

Table 6. Core model rankings based on the AIC scores for the integrated step selection analysis conducted using a 4 hour time interval between consecutive lesser prairie-chicken (*Tympanuchus pallidicinctus*) locations.

Model	AIC	ΔAIC	AICweights	Parameters
12	333278.318	0.000	0.944	8
13	333334.909	56.592	0.056	6
10	333657.128	378.811	0.000	8
5	333868.299	589.981	0.000	8
8	333892.601	614.283	0.000	7
7	333927.684	649.366	0.000	8
15	333937.507	659.189	0.000	5
14	333962.868	684.551	0.000	6
9	335100.328	1822.010	0.000	8
1	335811.316	2532.999	0.000	3
3	335940.234	2661.916	0.000	3
11	336099.354	2821.036	0.000	8
6	336315.337	3037.020	0.000	8
2	336996.861	3718.544	0.000	3
4	337277.353	3999.035	0.000	4

Table 7. Core model rankings based on the AIC scores for the integrated step selection analysis conducted using a 4 hour time interval between consecutive lesser prairie-chicken (*Tympanuchus pallidicinctus*) locations.

Model	AIC	ΔAIC	AICweights	Parameters
13	135874.436	0.000	0.922	6
7	135931.457	57.021	0.053	8
8	135948.363	73.926	0.023	7
10	136013.833	139.397	0.001	8
14	136026.763	152.327	0.000	6
15	136035.448	161.012	0.000	5
12	136134.263	259.827	0.000	8
5	136160.618	286.182	0.000	8
9	136160.717	286.281	0.000	8
3	136591.051	716.615	0.000	3
1	136865.824	991.388	0.000	3
6	137359.377	1484.941	0.000	8
11	137373.693	1499.257	0.000	8
2	137676.861	1802.424	0.000	3
4	139518.830	3644.394	0.000	4

Table 8. Core model rankings based on the AIC scores for the integrated step selection analysis conducted using a 24 hour time interval between consecutive lesser prairie-chicken (*Tympanuchus pallidicinctus*) locations.

Model	AIC	ΔAIC	AICweights	Parameters
5	675265.700	0.000	1.000	8
10	675508.892	243.192	0.000	8
8	675720.114	454.414	0.000	7
7	675795.184	529.484	0.000	8
15	676186.117	920.417	0.000	5
14	676214.046	948.346	0.000	6
12	682146.632	6880.932	0.000	8
9	682654.540	7388.840	0.000	8
6	682965.904	7700.204	0.000	8
13	683177.610	7911.910	0.000	6
11	688258.043	12992.343	0.000	8
1	691511.605	16245.905	0.000	3
3	691603.916	16338.216	0.000	3
2	695312.268	20046.568	0.000	3
4	704635.881	29370.181	0.000	4

Table 9. Core model rankings based on the AIC scores for the integrated step selection analysis conducted using a 168 hour time interval between consecutive lesser prairie-chicken (*Tympanuchus pallidicinctus*) locations.

Model	AIC	ΔAIC	AICweights	Parameters
5	599079.905	0.000	1.000	8
10	599959.495	879.590	0.000	8
7	600164.193	1084.289	0.000	8
8	600314.372	1234.467	0.000	7
14	600941.213	1861.308	0.000	6
15	601124.768	2044.863	0.000	5
6	602963.366	3883.461	0.000	8
12	609553.277	10473.372	0.000	8
9	610424.260	11344.355	0.000	8
13	611583.422	12503.517	0.000	6
11	612786.660	13706.755	0.000	8
1	623077.058	23997.153	0.000	3
3	624092.799	25012.894	0.000	3
2	624929.010	25849.105	0.000	3
4	640924.191	41844.286	0.000	4

Table 10. Calculated mean movement rates (m/associated hour) of lesser prairie-chickens (*Tympanuchus pallidicinctus*), when near a power line or road, and when crossing a power line or road based on beta coefficients produced in the integrated step selection analysis.

	1 Hour Interval			4 Hour Interval			24 Hour Interval			168 Hour Interval		
Movement Rate (m)	Lower 95%	Mean	Upper 95%	Lower 95%	Mean	Upper 95%	Lower 95%	Mean	Upper 95%	Lower 95%	Mean	Upper 95%
Population	166.722	167.925	169.127	293.035	293.136	293.237	519.836	522.178	524.520	858.886	863.067	867.247
Near power line	163.369	163.391	163.414	293.891	293.919	293.946	475.984	476.045	476.106	747.363	747.487	747.610
Crossing power line	374.089	485.034	637.823	762.576	988.525	1248.288	923.566	1845.608	3633.894	1401.795	1849.723	2548.322
Near Road	163.388	163.409	163.431	293.942	293.989	294.036	476.038	476.110	476.184	747.462	747.625	747.791
Crossing Road	287.691	336.270	389.918	524.390	585.037	646.748	730.331	834.542	957.041	980.416	1142.439	1331.166

Table 11. Population beta coefficients of the top-ranked core model for each temporal scale (time between consecutive lesser prairie-chicken (*Tympanuchus pallidicinctus*) locations) assessed. Arrows indicate significant (P-value < 0.05) positive/negative coefficient values with arrow size representative of the strength of the relationship.

	Hour Interval	4 Hour Interval	24 Hour Interval	168 Hour Interval
Covariates	Beta Coefficient	Beta Coefficient	Beta Coefficient	Beta Coefficient
lnStepLength	↑ 0.020	-	↑ 0.084	⬆ 0.123
lnStepLength:VarTemp	-	↓ -0.002	-	-
Short	-	-	⬇ -0.214	⬇ -0.424
proportionShortgrass	⬆ 0.680	⬆ 0.326	-	-
Crop	-	-	⬇ -0.308	⬇ -0.361
proportionCrop	⬇ -0.245	-	-	-
Shrub	-	-	⬇ -0.333	⬇ -0.622
proportionShrub	⬆ 0.955	-	-	-
CRP	-	-	⬆ 0.772	⬆ 0.862
proportionCRP	⬆ 1.137	⬆ 0.882	-	-
endNDVI^2	↑ 0.000	↓ 0.000	↑ 0.000	0.000
cosLek	↑ 0.023	-	⬆ 0.145	⬆ 0.242
cosLek:startLek	-	↓ 0.000	-	-
endLek	↓ -0.001	↓ -0.001	↓ 0.000	↓ 0.000

Table 12. Count of the number of times a model had the lowest AIC score for an individual lesser prairie-chicken (*Tympanuchus pallidicinctus*) out of all the models run in this analysis of distance to residential areas.

	Minimum AIC talley for residential models			
Model	1 Hour	4 Hour	24 Hour	168 Hour
1	15	6	3	2
2	4	1	1	1
3	27	25	34	27
4	1	2	1	1
5	15	10	27	36
Total	62	44	66	67

Table 13. Count of the number of times a model had the lowest AIC score for an individual lesser prairie-chicken (*Tympanuchus pallidicinctus*) out of all the models run in this analysis of distance to oil and gas wells.

	Minimum AIC talley for well models			
Model	1 Hour	4 Hour	24 Hour	168 Hour
1	23	5	6	6
2	5	1	2	2
3	31	25	35	34
4	0	1	0	3
5	3	12	23	22
Total	62	44	66	67

Table 14. Count of the number of times a model had the lowest AIC score for an individual lesser prairie-chicken (*Tympanuchus pallidicinctus*) out of all the models run in this analysis of distance to power lines.

	Minimum AIC tally for power line models			
Model	1 Hour	4 Hour	24 Hour	168 Hour
1	10	6	2	1
2	2	1	0	0
3	28	29	32	28
4	2	0	0	0
5	19	8	32	37
Total	61[a]	44	66	66[a]

[a] 1 individual did not converge.

Table 15. Count of the number of times a model had the lowest AIC score for an individual lesser prairie-chicken (*Tympanuchus pallidicinctus*) out of all the models run in this analysis of distance to roads.

	Minimum AIC tally for road models			
Model	1 Hour	4 Hour	24 Hour	168 Hour
1	12	5	4	3
2	1	1	0	1
3	29	26	34	35
4	1	2	1	0
5	18	9	27	28
Total	61[a]	43[a]	66	67

[a] 1 individual did not converge.

Table 16. Count of the number of times a model had the lowest AIC score for an individual lesser prairie-chicken (*Tympanuchus pallidicinctus*) out of all the models run in this analysis of power line crossings.

	Minimum AIC talley for power line crossing models			
Model	1 Hour	4 Hour	24 Hour	168 Hour
6	5	3	1	0
7	9	7	4	6
8	8	3	2	5
9	39	30	59	56
Total	61[a]	43[a]	66	67

[a] 1 individual did not converge.

Table 17. Count of the number of times a model had the lowest AIC score for an individual lesser prairie-chicken (*Tympanuchus pallidicinctus*) out of all the models run in this analysis of road crossings.

	Minimum AIC tally for road crossing models			
Model	1 Hour	4 Hour	24 Hour	168 Hour
6	5	1	0	1
7	4	3	1	0
8	6	4	7	5
9	46	35	58	61
Total	61[a]	43[a]	66	67

[a] 1 individual did not converge.

Table 18. Mean beta coefficients for residential area distance models for each temporal scale assessed. Arrows indicate significant (confidence interval not overlapping 0) positive/negative coefficient values with arrow size representative of the strength of the relationship. Percent agreement represents the number of individuals for whom the beta coefficient was in the same direction as the population beta coefficient.

	1 Hour Interval		4 Hour Interval		24 Hour Interval		168 Hour Interval	
Variables	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement
lnStepLength:startResidential	↑ 0.0001	54.10	↑ 0.0001	81.82	0.0000	-	-0.0001	-
endResidential	0.0005	-	-0.0002	-	0.0001	-	-0.0009	-
endResidential:NDVI	0.0000	-	0.0000	-	0.0000	-	0.0000	-
endResidential:Shrub	-0.0310	-	-0.0185	68.18	0.0011	-	0.0007	-
endResidential:Crop	0.0008	-	-0.0033	-	↓ -0.0015	63.64	↓ -0.0012	63.64
endResidential:Short	↓ -0.0025	59.02	↓ -0.0021	61.36	0.0001	-	0.0003	-
endResidential:CRP	-0.0001	-	0.0002	-	-0.0003	-	-0.0002	-
startResidential:cosResidential	↑ 0.0001	72.13	↑ 0.0001	68.18	↑ 0.0001	81.82	↑ 0.0002	71.21

Table 19. Mean beta coefficients for oil and gas well distance models for each temporal scale assessed. Arrows indicate significant (confidence interval not overlapping 0) positive/negative coefficient values with arrow size representative of the strength of the relationship. Percent agreement represents the number of individuals for whom the beta coefficient was in the same direction as the population beta coefficient.

	1 Hour Interval		4 Hour Interval		24 Hour Interval		168 Hour Interval	
Variables	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement
lnStepLength:startWell	↓ -0.0001	62.90	↑ 0.0001	86.36	0.0000	-	0.0000	-
endWell	0.0001	-	-0.0001	-	0.0012	-	0.0000	-
endWelll:NDVI	0.0000	-	0.0000	-	0.0000	-	0.0000	-
endWell:Shrub	↓ -0.0085	69.35	↓ -0.0230	75.00	-0.0004	-	-0.0003	-
endWell:Crop	0.0022	-	-0.0036	-	↑ 0.0009	69.70	↑ 0.0013	71.64
endWell:Short	-0.0021	-	-0.0013	-	-0.0002	-	0.0001	-
endWell:CRP	↑ 0.0009	69.35	↑ 0.0005	65.91	0.0002	-	0.0005	56.72
startWell:cosWell	0.0000	-	↑ 0.0001	65.91	↑ 0.0001	66.67	↑ 0.0001	61.19

Table 20. Mean beta coefficients for power line distance models for each temporal scale assessed. Arrows indicate significant (confidence interval not overlapping 0) positive/negative coefficient values with arrow size representative of the strength of the relationship. Percent agreement represents the number of individuals for whom the beta coefficient was in the same direction as the population beta coefficient.

Powerline Distance Covariates	1 Hour Interval		4 Hour Interval		24 Hour Interval		168 Hour Interval	
	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement
lnStepLength:startPower	↑ 0.0002	67.74	↑ 0.0002	81.82	↑ 0.0002	60.61	↑ 0.0003	66.18
endPower	-0.0083	-	-0.0012	-	0.0009	-	-0.0003	-
endPower:NDVI	↑ 0.0000	75.81	↑ 0.0000	72.73	↑ 0.0000	87.88	↑ 0.0000	80.88
endPower:Shrub	0.6052	-	⬇ -1.9060	65.91	↓ -0.0025	63.64	↓ -0.0019	61.19
endPower:Crop	-0.1333	-	⬇ -0.2175	43.18	-0.0002	-	-0.0004	-
endPower:Short	↓ -0.0663	64.52	↓ -0.0781	61.36	-0.0005	-	-0.0009	-
endPower:CRP	0.0001	-	0.0005	-	↓ -0.0007	56.06	↓ -0.0008	56.72
startPower:cosPower	↑ 0.0000	59.68	0.0000	-	↑ 0.0003	84.85	↑ 0.0003	70.59

Table 21. Mean beta coefficients for power line crossing models for each temporal scale assessed. Arrows indicate significant (confidence interval not overlapping 0) positive/negative coefficient values with arrow size representative of the strength of the relationship. Percent agreement represents the number of individuals for whom the beta coefficient was in the same direction as the population beta coefficient.

Powerline Crossing	1 Hour Interval		4 Hour Interval		24 Hour Interval		168 Hour Interval	
Covariates	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement
lnStepLength:CrossPower	↑ 1.3768	85.48	↑ 1.6186	88.64	↑ 2.4791	90.91	↑ 1.1686	85.29
NDVI:CrossPower	↓ -0.1226	83.87	↓ -0.1700	84.09	↓ -0.3498	95.45	↓ -0.1486	91.04
proportionShrub:CrossPower	511.8625	-	↓ -20312.2082	63.64	↓ -1037.3827	50.00	↓ -519.7069	61.19
proportionCrop:CrossPower	-196.5824	-	↓ -942.3331	81.82	↓ -75.1158	66.67	↓ -897.9588	79.10
proportionShort:CrossPower	↓ -314.3801	74.19	↓ -2.3102	70.45	1.7635	-	↓ -2.3171	65.67
proportionCRP:CrossPower	↓ -3.3909	79.03	-5.5359	-	1.7897	-	↓ -1.5106	67.16

Table 22. Mean beta coefficients for road distance models for each temporal scale assessed. Arrows indicate significant (confidence interval not overlapping 0) positive/negative coefficient values with arrow size representative of the strength of the relationship. Percent agreement represents the number of individuals for whom the beta coefficient was in the same direction as the population beta coefficient.

	1 Hour Interval		4 Hour Interval		24 Hour Interval		168 Hour Interval	
Variables	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement
lnStepLength:startRoad	↑ 0.0002	66.67	↑ 0.0004	83.72	↑ 0.0003	65.15	↑ 0.0004	71.64
endRoad	↓ -0.0993	63.77	↓ -0.0059	67.44	↓ -0.0052	65.15	↓ -0.0095	61.19
endRoad:NDVI	↑ 0.0001	69.57	↑ 0.0001	69.77	↑ 0.0001	71.21	↑ 0.0001	65.67
endRoad:Shrub	0.1362	-	-0.1007	69.77	0.0003	-	0.0022	-
endRoad:Crop	-0.0806	-	-0.0161	-	-0.0008	-	-0.0022	-
endRoad:Short	0.0494	-	-0.0053	-	-0.0013	-	-0.0028	-
endRoad:CRP	↑ 0.0987	62.32	↑ 0.0034	65.12	↑ 0.0014	48.48	↑ 0.0028	53.73
startRoad:cosRoad	↑ 0.0002	76.81	↑ 0.0001	58.14	↑ 0.0001	68.18	↑ 0.0001	-

Table 23. Mean beta coefficients for road crossing models for each temporal scale assessed. Arrows indicate significant (confidence interval not overlapping 0) positive/negative coefficient values with arrow size representative of the strength of the relationship. Percent agreement represents the number of individuals for whom the beta coefficient was in the same direction as the population beta coefficient.

Variables	1 Hour Interval		4 Hour Interval		24 Hour Interval		168 Hour Interval	
	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement	Mean	% Agreement
lnStepLength:CrossRoad	⬆ 0.7401	88.41	⬆ 0.6785	90.70	⬆ 0.6490	87.88	⬆ 0.4189	76.12
NDVI:CrossRoad	↓ -0.0704	81.16	↓ -0.0692	97.67	↓ -0.0876	95.45	↓ -0.0623	91.04
proportionShrub:CrossRoad	⬇ -1584.6716	47.83	⬇ -353.0209	62.79	⬇ -105.8367	56.06	⬇ -138.3209	62.69
proportionCrop:CrossRoad	160.8478	-	⬇ -22.5650	60.47	⬇ -6.6829	51.52	⬇ -36.6514	55.22
proportionShort:CrossRoad	36.3834	-	-1.1126	-	0.5690	-	-0.5691	-
proportionCRP:CrossRoad	0.0420	-	⬆ 0.6298	67.44	⬆ 1.3041	66.67	⬆ 0.9112	67.16

Figure 1. Summary of vegetation cover of Beaver County, Oklahoma calculated using the Oklahoma Ecological System map created in 2015.

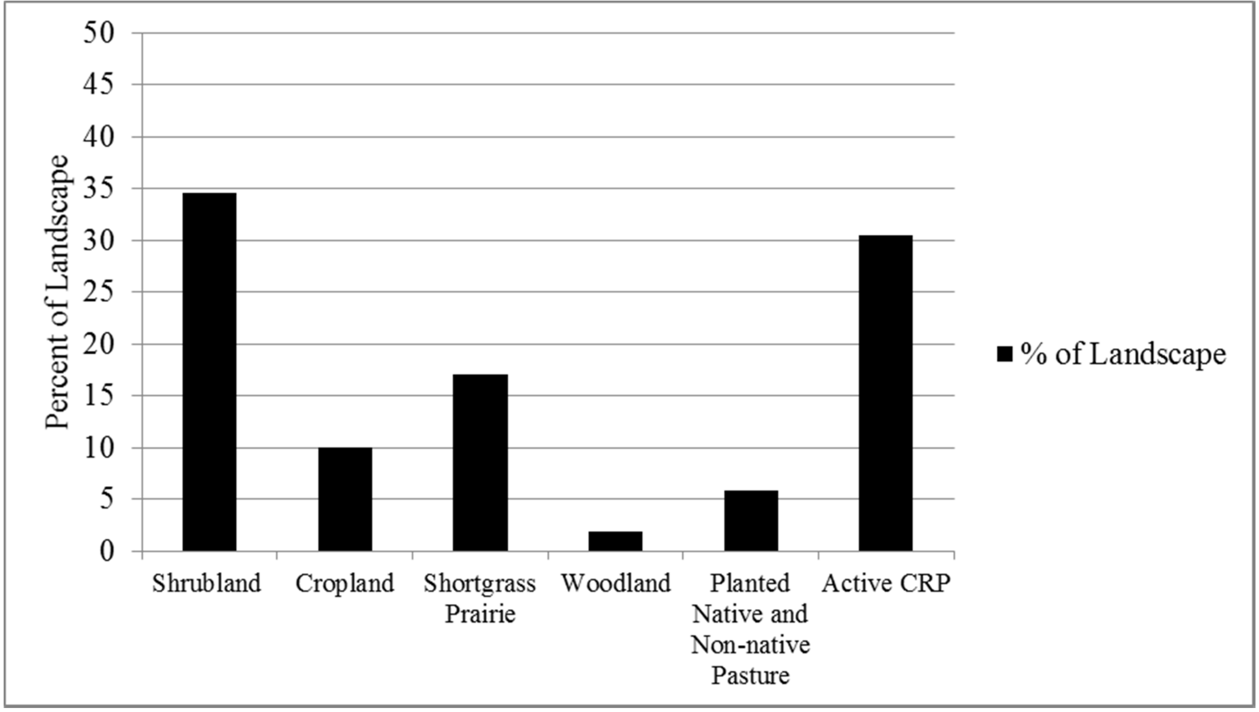


Figure 2. Observed steps (straight line movement between two consecutive locations) and available, but unused steps used to assess lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat selection and movement patterns across 4 different temporal scales (time between consecutive locations) in Beaver County, Oklahoma from April 2013-May 2016.

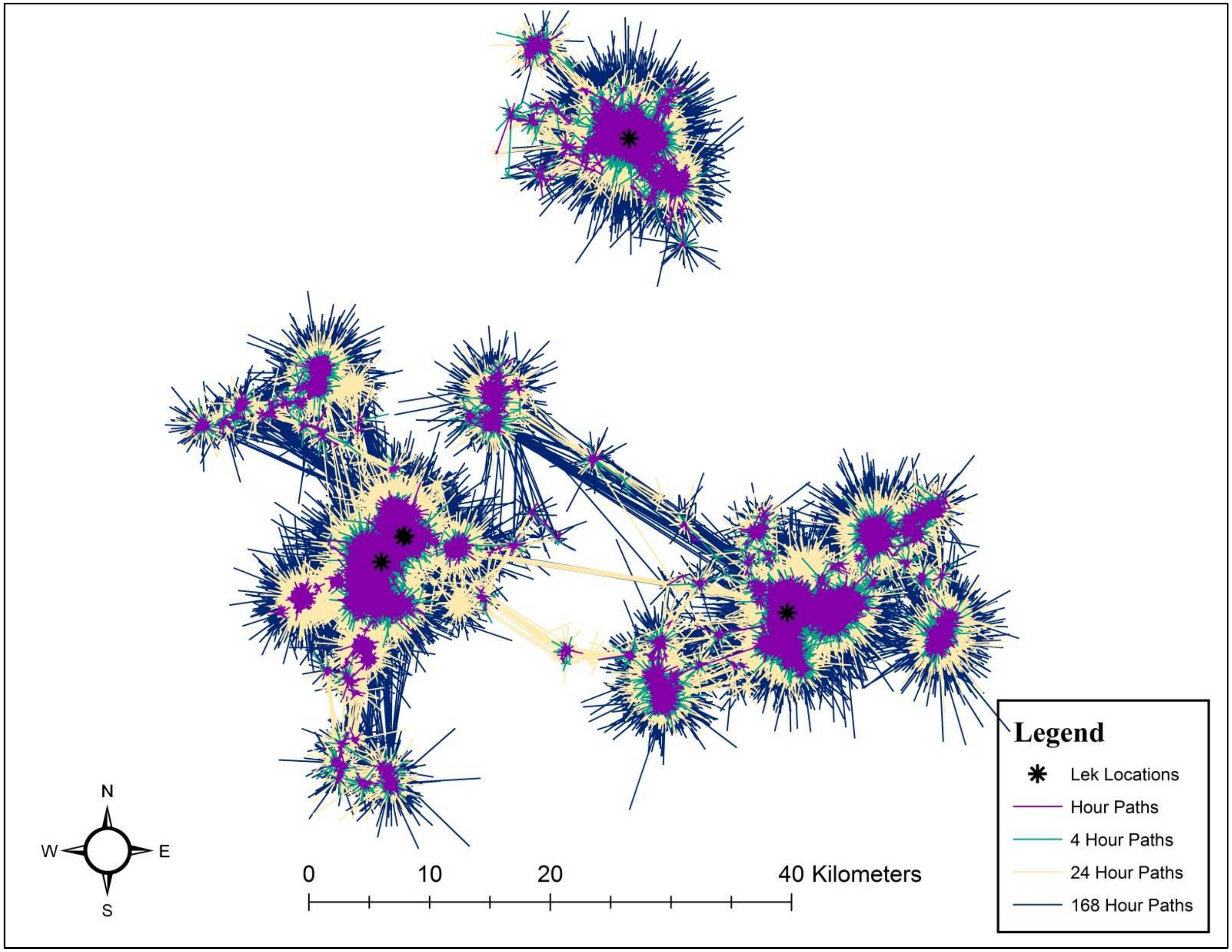
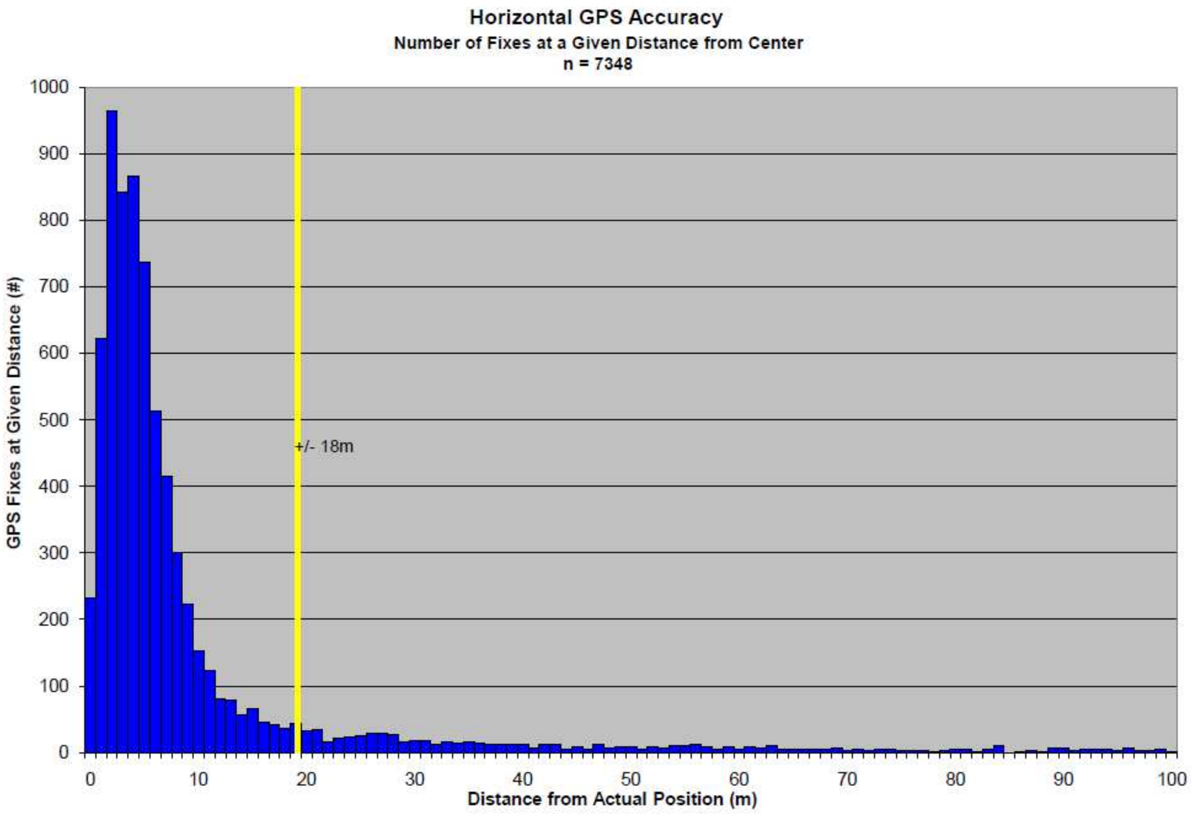


Figure 3. Microwave Telemetry Inc.'s graphical depiction of horizontal errors associated with the 22 gram GPS transmitters used to track lesser prairie-chicken (*Tympanuchus pallidicinctus*) movements in Beaver County, Oklahoma from April 2013-May 2016.



Histogram showing the frequency distribution of GPS fixes based on horizontal accuracy (m) from a known location.

Figure 4. Average distance moved between consecutive GPS locations (step length) across different temporal scales (time between successive locations) and weeks of the year for lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Beaver County, Oklahoma from April 2013-May 2016.

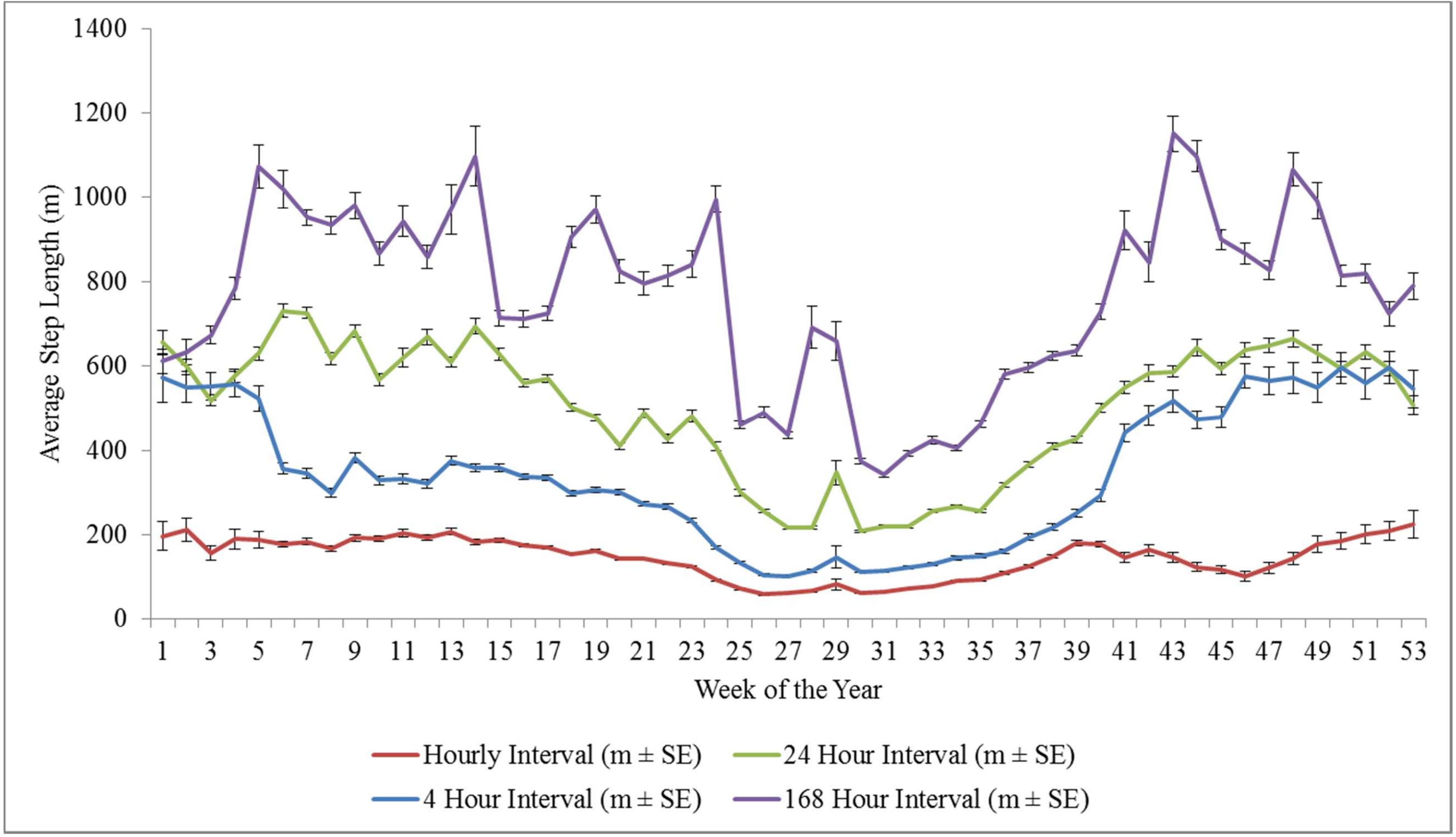
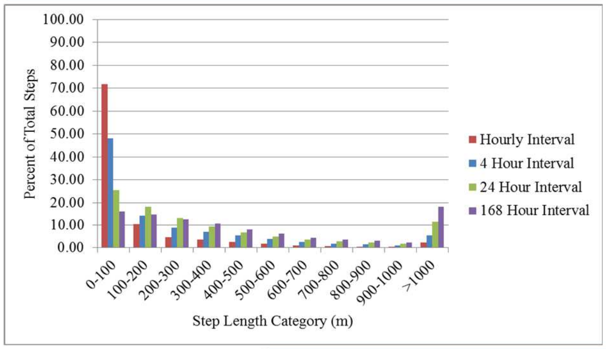
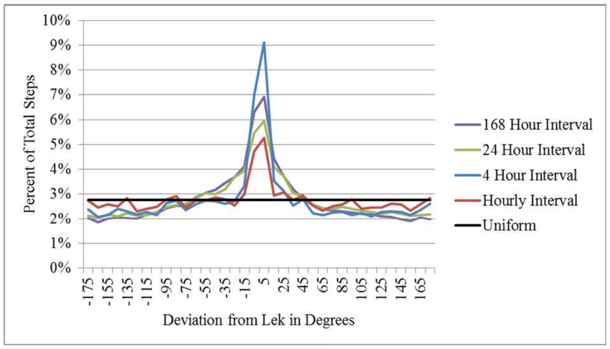


Figure 5. Workflow of our progression through our integrated step selection analysis of lesser prairie-chicken (*Tympanuchus pallidicinctus*) habitat selection and movement. The analysis began with the creation of available, but unused steps using the gamma distribution of step lengths and von Mises distribution of direction persistence towards the breeding grounds (lek). It then progressed to modeling of core covariates, the top model of which served as the base model for all anthropogenic modeling efforts.

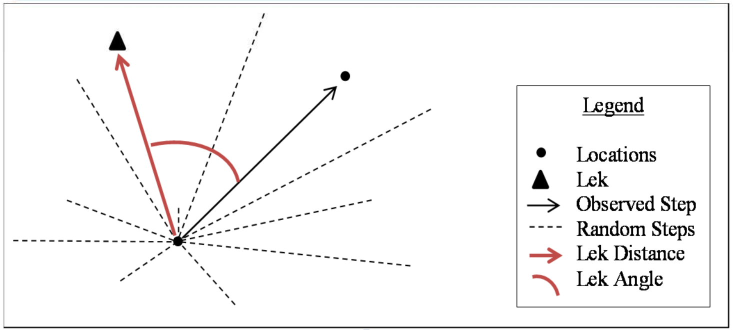
Fit gamma distribution to observed step lengths.



Fit von Mises distribution to deviations from lek.



Create random steps for each time scale using empirical gamma and von Mises distributions.



Core Model Analysis

Analysis was done at each temporal scale on the entire population. Models were built to examine the influence of the lek, temperature, and vegetation on step lengths and habitat selection. The top model for each temporal scale was identified using the minimum AIC score.

Anthropogenic Model Analysis

The top core model for each temporal scale was used as the base model for all anthropogenic analyses. We conducted all anthropogenic analyses by individual bird at each time scale.

Linear Features:
Roads, Powerlines
5 models analyzing the effect of distance to a feature and 4 models analyzing the effect of crossing a feature on selection and movement.

Non-linear Features:
Residential, Oil and Gas Wells
5 models analyzing the effect of distance to a feature on selection and movement.

The top model for each anthropogenic type at each temporal scale for each individual was determined using AIC ranking. Bootstrapping was used to generate beta coefficients and confidence intervals.

Figure 6. Yearly air temperature patterns in Beaver County, Oklahoma from April 2013-May2016 obtained from the Oklahoma Mesonet stations in Beaver and Slapout, Oklahoma.

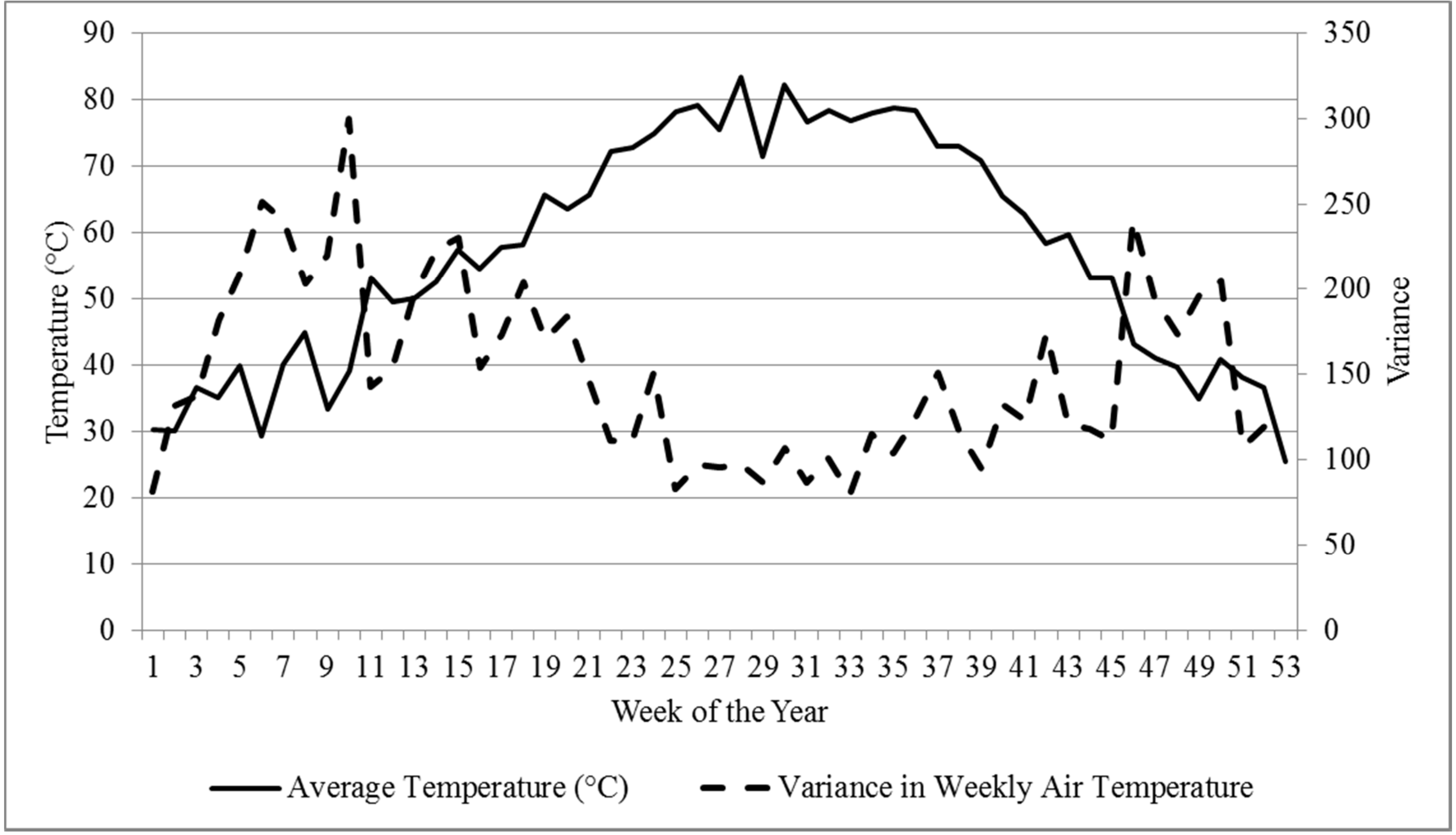


Figure 7. Locations of lesser prairie-chickens (*Tympanuchus pallidicinctus*) in relation to land enrolled in the conservation reserve program (CRP) in Beaver County, Oklahoma from April 2013-May 2016.

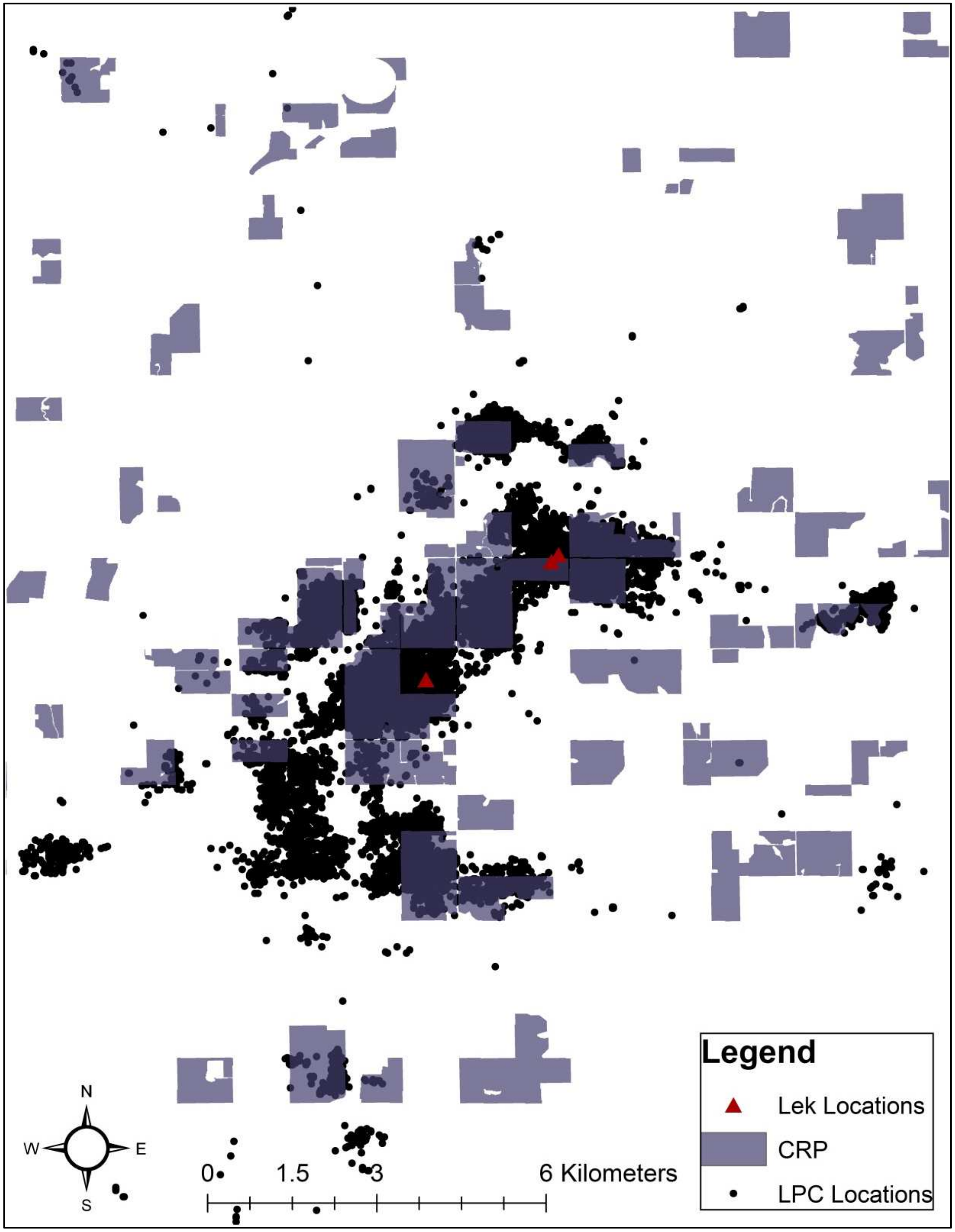


Figure 8. Locations of lesser prairie-chickens (*Tympanuchus pallidicinctus*) in relation to shortgrass prairie vegetation in Beaver County, Oklahoma from April 2013-May 2016.

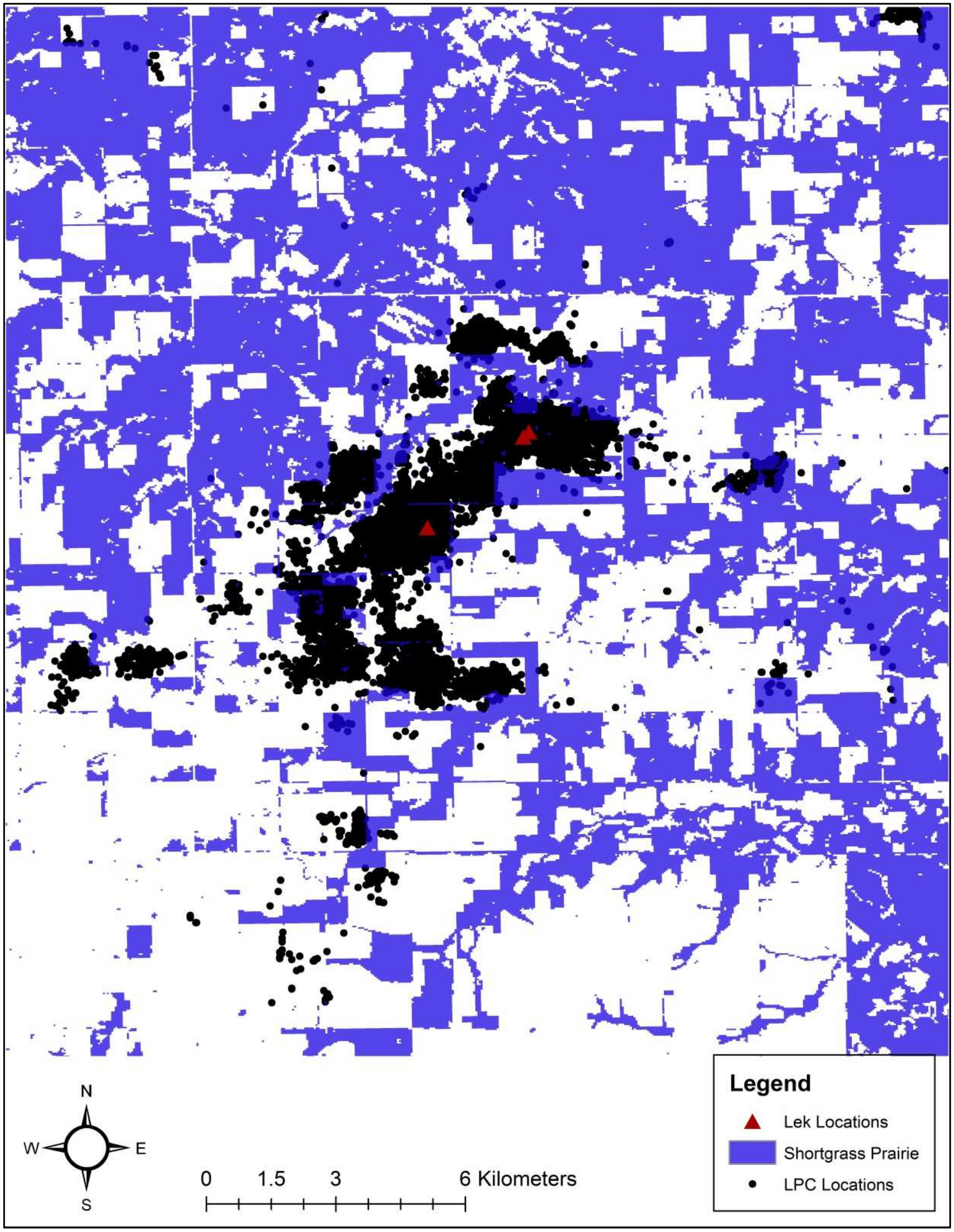
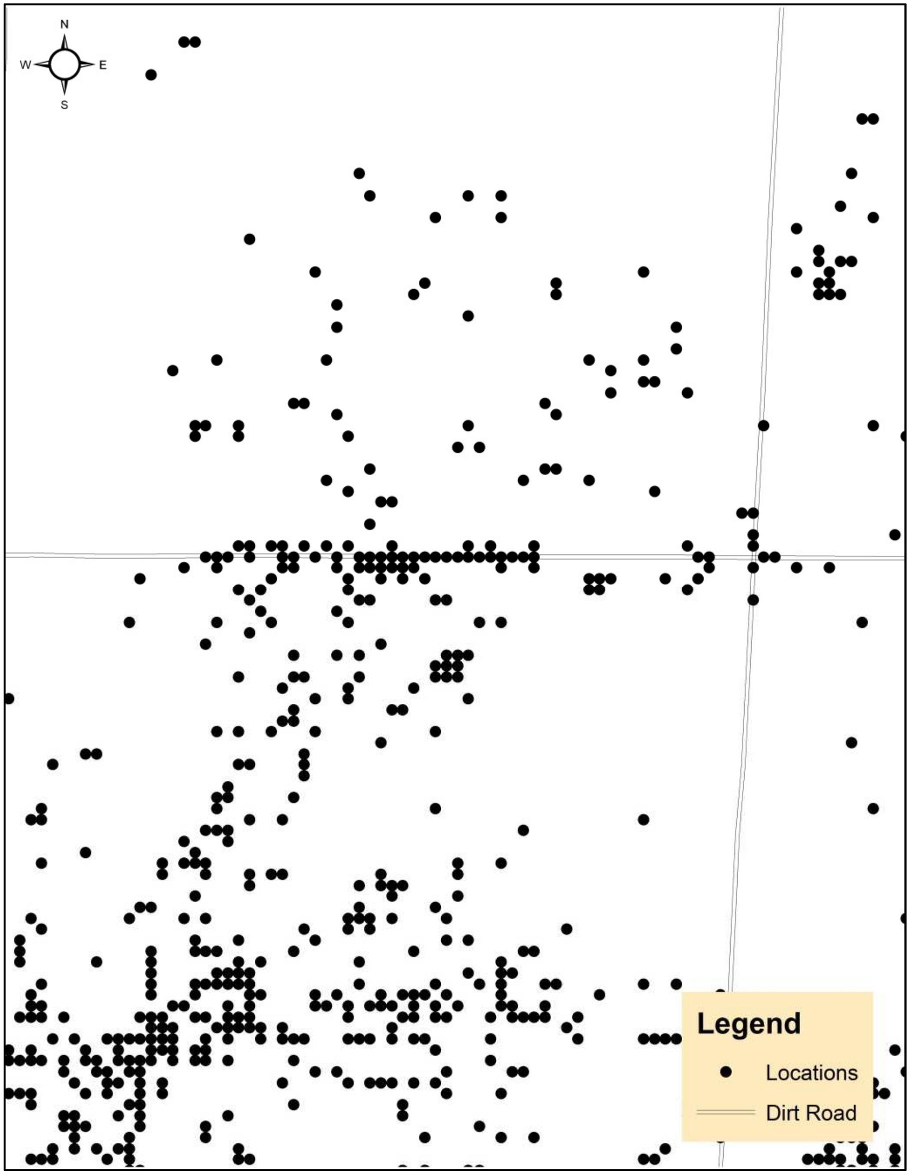


Figure 9. Lesser prairie-chicken (*Tympanuchus pallidicinctus*) locations in relation to 2 unpaved roads in Beaver County, Oklahoma depicting use in/along roads from April 2013-May 2016.



VITA

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