Estimating response distances of lesser prairie-chickens to anthropogenic features during long-distance movements

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Abstract. Spatially distributed populations often rely on large-scale processes for long-term population stability. These processes are driven by individuals moving across the landscape through long-distance dispersal movements. However, as landscapes are continually altered by anthropogenic development, increased fragmentation and avoidance behavior can affect landscape permeability and limit dispersal. Lesser prairie-chickens (Tympanuchus pallidicinctus) are a species of concern that have lost significant portions (>90%) of their historic distribution in the Southern Great Plains of the United States and are currently being impacted by continued anthropogenic development. Using GPS telemetry locations of 346 lesser prairie-chickens across their entire geographic distribution, we identified 184 different long-distance movements that drive population connectivity. We used empirical cumulative distribution functions to create a selection–avoidance–neutral curve and estimated the spatial scale of response to anthropogenic features (i.e., towers and windmills, large transmission and smaller distribution powerlines, oil wells, roads, and fences) during these movements. In addition, we tested for behavioral differences between movement types (e.g., exploratory loops vs. long-distance movements between home ranges) and for regional differences in response among study areas. We found that during long-distance movements, lesser prairie-chickens generally avoided all anthropogenic feature types we tested despite some variation in the reported response distance among study areas. However, they avoided the tallest features (i.e., towers and windmills and transmission powerlines) at much greater distances in comparison with the shorter features in our analysis. Our results show that long-distance movements are likely affected by responses to functional landscape fragmentation through increased development of anthropogenic features in important connectivity zones. As our estimated response distances during long-distance movements varied in comparison with previously reported response distances during other behavioral states (e.g., breeding or nesting), using long-distance or dispersal specific movement data may be more appropriate when asking questions related to connectivity across the landscape.

Key words: anthropogenic disturbance; behavioral fragmentation; connectivity; cumulative distribution function; dispersal; lesser prairie-chicken; selection–neutral–avoidance curve.

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INTRODUCTION

Biotic and abiotic components of the environment affect the distribution and movements of animals across the landscape. Movement allows animals to adjust to changes in their environment (i.e., dispersal, migration, density dependence; Dingle 1996, Clobert et al. 2001), access more resources, and use behavioral trade-offs in habitat selection to maximize fitness (Barten et al. 2001, Zollner and Lima 2005). These processes are complex and occur in multiple spatial and temporal scales but advances in our understanding of animal behavior and technology allow a greater comprehension of the system as a whole.

Land-use change and fragmentation continue to alter landscapes, further confounding management and conservation of species. While fragmentation is often viewed as an explicit change in patch and landscape metrics, such as the edge density or shape complexity of landcover, some features in the environment may cause fragmentation through avoidance behaviors (i.e., avoidance of habitat as a response to a feature in the landscape). Behavioral fragmentation in response to anthropogenic features has been observed as disruptions to normal behavior such as larger step length when crossing features (Panzacchi et al. 2013, Kite et al. 2016), reduced movement across features (Pruett et al. 2009), or avoidance of areas near features (Robel et al. 2004, Hess and Beck 2012, Northrup et al. 2015).

There are several behavioral strategies that animals may use in response to features in the landscape. Beyer et al. (2016) presented the idea that features in the landscape can impede or disrupt movements of individuals in four different ways. They explained that features can be either barriers (i.e., can be crossed but not circumnavigated), obstacles (i.e., can be circumnavigated but not crossed), impedances (i.e., can be crossed or circumnavigated in a trade-off of the behavioral cost of circumnavigating vs. crossing), or constraints (i.e., cannot be crossed or circumnavigated). A feature’s exact classification into one of these categories is species specific but may also be context specific to the presence of other landscape elements. It may also depend on the behavioral state of the individual, as varying states (i.e., breeding vs. nonbreeding) can lead to changes in the response to landscape features (Wilson et al. 2012, Harju et al. 2013, Abrahms et al. 2016). Studying effects of behavioral-dependent responses to landscape features is the first step to understanding the potential these features have for fragmentation. Long-distance movements are useful in studying population connectivity and corridors, as increased fragmentation can disrupt key population-level processes such as gene flow or the stabilization of small populations through immigration and the rescue effect (Hanski 1999, Clobert et al. 2001). A better understanding of long-distance movement behaviors may allow the identification of possible fragmentation sources that could have negative effects on landscape connectivity. Additionally, it may be important to consider specific movement types within this category (i.e., dispersal, migration, or exploratory searching), because selection and response to landscape characteristics could vary among behavioral states.

As a grassland-obligate species distributed in the southern Great Plains, USA, the lesser prairie-chicken (Tympanuchus pallidicinctus) has experienced a loss of >90% of their presumed historic distribution due mainly to loss of habitat and land-use change (Hagen and Giesen 2005). Remaining populations exist in a highly fragmented landscape that was once mostly contiguous grass and shrubland. The lesser prairie-chicken was listed for a short time as threatened under the Endangered Species Act, but a federal court ruling vacated the listing which delisted the species (USFWS 2016). Research suggests grouse species, including lesser prairie-chickens, respond negatively to anthropogenic features in the environment (Hovick et al. 2014). These features can include windmills, oil and gas wells,
power lines, roads, ski resorts, and fences (Pitman et al. 2005, Walker et al. 2007, Pruett et al. 2009, Hagen et al. 2011, Jarnevich and Laubhan 2011, Arlettaz et al. 2013, Winder et al. 2014, Plumb et al. 2018). However, most of these data have been collected at the home range scale, such as nest locations and the area around communal breeding leks. The effect of these anthropogenic features during long-distance movements has not been assessed. Lesser prairie-chicken populations are spatially distributed by the locations of their leks (i.e., home ranges are usually within five km of leks; Taylor and Guthery 1980, Winder et al. 2014). This structure is representative of a spatially structured population, where connectivity can have greater effects on the stability of the population, providing further need to study long-distance movements to prevent continued fragmentation among changing landscapes.

Recent research with lesser prairie-chickens has provided large datasets to study long-distance movements across their distribution (Earl et al. 2016). Using a dataset from multiple study sites spanning the geographic distribution of lesser prairie-chickens, we examined behavioral fragmentation through potential impedances or barriers to connectivity. Our main objective was to assess the response of lesser prairie-chicken locations to anthropogenic features during long-distance movements compared to random locations across the landscape. In particular, we wanted to examine the direction of response (selection vs. avoidance) and obtain conservative estimates for the response distance to anthropogenic features. We expected long-distance movements of lesser prairie-chickens to occur at farther distances from anthropogenic features in the landscape than random as it would follow avoidance trends observed for home range movements (Pitman et al. 2005, Hagen et al. 2011, Plumb et al. 2018). Furthermore, we hypothesized that birds would be found at greater distances from taller features in the landscape during these movements, because taller features can be seen from farther distances. In addition to our primary objective, we explored how the response to anthropogenic features during long-distance movements changes when controlling for some potentially confounding variables. We examined the effects that the geographic region (i.e., study area) and the long-distance movement type (i.e., dispersal vs. migration between home ranges) have on response distance. We hypothesized that lesser prairie-chickens displaying foray movements (i.e., exploratory dispersal movements where an individual returns to its previous home range) are more likely to show a greater avoidance response to features than successful dispersal movements.

**Methods**

**Study area**

GPS telemetry location data were collected from research projects in southeast Colorado (Cheyenne, Prowers, and Baca counties), the panhandle of Oklahoma (Beaver County), east-central New Mexico (Chaves, Lea, and Roosevelt counties), northwest Kansas (Gove and Logan counties), and south-central Kansas (Clark, Comanche, and Kiowa counties; Fig. 1). The New Mexico and Oklahoma study areas included birds with movements that crossed into Texas, and the Colorado study area also had two birds that made long-distance movements in southwest Kansas. Landcover varied in each study area, as they were spread across four different prairie ecoregions (McDonald et al. 2014, Winder et al. 2015). Our New Mexico and Colorado study areas existed in the Sand Shinnery Oak and Sand Sagebrush Ecoregions dominated shinnery oak and sand sagebrush, respectively. The northwest Kansas study area was apart of the Shortgrass/Conservation Reserve Program Ecoregion constituting of a matrix of row-crop agriculture and shortgrass prairie. Both the south-central Kansas and the Oklahoma study areas occurred within the Mixed-Grass Prairie Ecoregion. While these two study areas have similar landcover, the intensity of anthropogenic development varies by study area (see our feature density analysis in Appendix S1).

**Capture methods**

Lesser prairie-chickens were captured in each study area using lek-focused dropnets (Silvy et al. 1990) and walk-in drift funnel traps (Haukos et al. 1990, Schroeder and Braun 1993). At capture, a rump-mounted GPS transmitter (22-g PTT-100, Microwave Telemetry, Columbia, Maryland, USA; Model 22GPS, North Star Science and
Fig. 1. Map of our study areas overlaid on top of the estimated current distribution of lesser prairie-chickens. Current distribution layer is based on Van Pelt et al. (2013) and Davis et al. (2008) and downloaded from the Southern Great Plains Crucial Habitat Assessment Tool (Klute et al. 2013).
Technology, King George, Virginia, USA) was attached. Captures occurred from March 2013 through April 2016, and data were collected through December 2016.

**Movement classifications**

Using GPS telemetry locations, long-distance movements were characterized for every marked individual. Similar to Earl et al. (2016), any consecutive groups of points found >5-km net displacement outside of observed lesser prairie-chicken home ranges were considered a long-distance movement. We defined net displacement as the Euclidean distance between the boundary of the home range to the farthest location in a movement path occurring outside a home range. The 5-km distance was chosen as a cutoff, because it is further than movements related to the daily activity of lesser prairie-chickens (Haukos and Zavaleta 2016). In order to separate long-distance movements from home range movements with this displacement-based method, we needed estimated home range polygons that fit two criteria: (1) The home range polygons do not contain stopover habitat used during long-distance movements, and (2) the home range polygon did not overfit the locations that should be considered home range movements. Home ranges were defined using kernel utilization density-based home range analysis (Worton 1989) with the Program R (R Core Team 2019) package adehabitatHR (Calenge 2006).

Due to the limitations listed above, we did not use a standardized isopleth (e.g., 95% or 50%) when creating home range polygons. Instead, we balanced the trade-offs in the criteria to visually choose an isopleth for each individual that did not contain stopover habitat and encompassed all the points within the main areas of use to represent the home range.

Identified long-distance movements were separated into three categories. First, if an individual made a long-distance movement that went between two separate home range polygons, the movement was considered a home range to home range movement, hereafter “HR to HR.” This type of movement was representative of either a dispersal movement, where an individual moved from an established home range into a new area at least 5 km away and established a new home range, and round-trip movements (e.g., migration or seasonal movements) between two established home ranges. Separating between these two types of movements is difficult without location data for the entire lifespan of the individuals, because it is unclear if an individual had used a home range previously before capture or if it was a true dispersal event. Due to this difficulty, these movements were grouped into one category for our analysis. The second movement classification was characterized when a movement left a home range, ventured at least 5-km net displacement away, and returned to the same home range. We classified these movements as foray loops and were representative of search strategies and long-distance movements that did not end in reaching or establishing a different home range. The final category consisted of the movements that could not be determined to fit the other categories for one of two reasons: (1) The movement began immediately after the capture of the individual or (2) ended with the individual’s death or the permanent malfunction of its satellite transmitter. In either case, only one end of the movement was bounded by a home range polygon, while the other end of the movement was unbounded from an established area of use. These unclassified movements were not distinguishable as one of the other movement types, but still contained information on how individuals use the environment during long-distance movements and were included in analysis.

**Feature description**

We examined effects of roads, powerlines, oil wells, towers, and fences on lesser prairie-chickens space-use during movements. Road data were acquired from the U.S. Census Bureau 2016 TIGER/Line dataset. This included both heavy-traffic, paved roads and rural road networks in our study area. We were unable to obtain traffic data for all roads in such a large study area, so all roads were analyzed together for our study. Powerline data were separated into two categories by size due to a difference in potential response. Transmission powerlines were defined as powerlines transmitting >69 kV and were obtained from the U.S. Department of Homeland Security. Transmission powerlines were taller (>40 m) and more visible from farther distances in comparison with smaller <69 kV powerlines used for local energy distribution. We used
distribution powerline data gathered from the Southern Great Plains Crucial Habitat Assessment Tool (Klute et al. 2013) and from the Kansas Corporation Commission (http://www.kcc.state.ks.us/; Plumb et al. 2019). However, these combined datasets were incomplete for the Colorado and New Mexico study areas and were only used for analysis in the Oklahoma and Kansas study areas. We used active oil and gas well locations identified between 2010 and 2013 from the Southern Great Plains Crucial Habitat Assessment Tool (Klute et al. 2013). The oil well dataset was incomplete in the Colorado study area, and therefore, this feature was not included in the analysis for Colorado. The tower dataset included structures taller than 15 m (i.e., towers, buildings, windmills, stacks, utilities) and was obtained from the Federal Aviation Administration’s Digital Obstacle File. Finally, fence data were collected in portions of the Oklahoma and Kansas study areas’ study sites and digitized into shapefiles using ESRI ArcGIS 10.3 (ESRI 2014). This mapping was focused around the home ranges and capture locations of individuals and did not cover all long-distance movement tracts in the Oklahoma and Kansas study areas.

The distribution of some anthropogenic features (e.g., roads, distribution powerlines, fences) may be correlated as their locations are likely influenced by the historical structure of the utility and access grid within the United States. During western expansion, one square-mile sections were created that influenced property line boundaries and the location of infrastructure. These grid-like sections encompass all study areas with the exception the New Mexico study area that includes large portions of undeveloped state and federal lands. While the distribution and density of anthropogenic features has been identified as potential predictors of space use in grouse studies (Walker et al. 2007, Doherty et al. 2008), estimates for feature density have not been characterized across the geographic distribution of lesser prairie-chickens. We addressed this knowledge gap by estimating the density of anthropogenic features within each of our study areas and among our different movement types. As this analysis did not directly relate to our primary objective of identifying anthropogenic feature response trends and distances, we have included the full description for how the feature density analysis was calculated and its associated results in Appendix S1.

**Cumulative distribution function analysis**

We used empirical cumulative distribution functions (CDFs) to determine the selection–neutral–avoidance responses of lesser prairie-chickens as a function of distance to each anthropogenic feature type (Kopp et al. 1998, Dunkin et al. 2009, Martin et al. 2012, Tanner et al. 2015). Compared to other methods used to obtain estimates of response distance to anthropogenic features (e.g., zone of influence, Polfus et al. 2011; Monte Carlo simulations; Pitman et al. 2005, Hagen et al. 2011), the CDF-based method allows selection–neutral–avoidance behavior in relation to landscape features to be examined on an approximately continuous scale (Dunkin et al. 2009). The CDF-based method uses cumulative frequencies of the observed lesser prairie-chicken relocations (G[x]) and random relocations (F[x]) as functions of the distance to the nearest feature which creates a used-available design. The difference between the cumulative density of used points and random points at a specific distance from a feature (G[x] – F[x]) provides an index of the selection–neutral–avoidance response to anthropogenic features (Dunkin et al. 2009). This creates a function, in relation to a continuous variable (e.g., distance to feature), where a positive slope indicates that the used lesser prairie-chicken locations (G[x]) accumulate faster in relation to distance to nearest feature than random locations (F[x]), signifying selection or attraction to the feature. A negative slope indicates avoidance of a feature at the corresponding distance, and relatively flat slopes (nearing 0) indicate a neutral response. Because CDFs always sum to 1, the selection–neutral–avoidance trend (G[x] – F[x]) always returns to zero. As a result, it is only the initial response trend that has biological relevance.

We generated thirty random points for each lesser prairie-chicken location to create a distribution of available random locations within each study area. The distance to the nearest feature was then estimated for every location. We randomly sampled points from the available random location distribution to create CDFs with bins (i.e., breaks) set every 50 m (Dunkin et al. 2009, Tanner et al. 2015). The number of points
selected for each sample was equal to the number of actual lesser prairie-chicken locations in the study area (a 1:1 ratio of used vs available points). In total, we iterated this process 30 times in order to create a mean random relocation CDF ($F[x]$) and associated standard error using CDFs from each iteration. $G[x]$ was calculated by creating an empirical CDF of the nearest distance between actual relocations and features in the study area by the same distance bins. We then used the data from selection–neutral–avoidance trend index ($G[x] - F[x]$) to estimate the response distance. We defined the response distance as the local maxima (for selection or positive trends) or minima (for avoidance or negative trends) in the initial response trend.

The scale at which lesser prairie-chickens perceive features in their environment and respond to them during long-distance movements has yet to be characterized. However, it is likely that the scale of response is different during long-distance movements compared to movements within home ranges (Harju et al. 2013). We addressed this knowledge gap by buffering all long-distance movement tracts by different distances to simulate the available area that the random locations were selected from. We conducted our CDF-based analysis 20 different availability scales with buffer distances ranging 1 km up to 20 km in 1-km increments. This range was chosen to cover all possible scales of selection up to at least the average net displacement of long-distance movements of lesser prairie-chickens at 16 km (Earl et al. 2016). Our intent was to visually assess whether the scale of availability affected conclusions from the CDF-based analysis. All CDF analyses were conducted in Program R (R Core Team 2019) using the CDF function from the GitHub hosted R package jactpete/jpfxns (Peterson 2019).

RESULTS

We examined location data from 346 lesser prairie-chickens. Of these, 85 (25%) individuals made movements >5 km from their home range and were included in analyses. There were 184 separate long-distance movement tracts (Table 1) that were comprised of 4,757 individual GPS points. The Kansas study areas had the most birds with long-distance movements, while New Mexico had the least. New Mexico only had birds that made HR to HR movements. The most common movement type among all study areas was HR to HR (74.4%) followed by Foray Loops (19.0%). At least four birds from each study area made more than one long-distance movement totaling 39 birds. Of these, 13 birds made movements of different types, with at least one from every study area except for New Mexico (Table 1).

Oklahoma generally had the highest mean density of anthropogenic features among our study areas, including significantly higher mean density for oil wells, roads, fences, and distribution powerline features (Appendix S1: Fig. S1). The tallest anthropogenic features (i.e., towers and transmission powerlines) had the lowest mean densities among our study areas (Appendix S1: Table S1). Unclassified movements generally occurred in areas with higher mean densities of anthropogenic features compared to the other movement types (Appendix S1: Fig. S1).

Cumulative distribution functions

The most common selection–neutral–avoidance trend for long-distance movements of lesser prairie-chickens was avoidance of anthropogenic features (Fig. 2). However, this avoidance trend was not seen in all regions, movement types, or available area buffer sizes. We found similar response distances among movement types (Table 2). Our estimated response distances for movement types were also similar to the estimated distances when all data were combined into a pooled dataset (Table 2). Due to this, we decided to focus the rest of our results and discussion on the CDF results among study areas and the pooled dataset. Our entire CDF results for movement types can be found in the supplementary data (Appendix S2: Fig. S1), as well as the reported response distances (Table 2). In addition, we found that there was little variation in the estimated response distance as the available area buffer changed, especially after 5 km. As a result, we report the average CDF across all buffer sizes to simplify the results from our analyses but include the full results in the supplementary data (Appendix S3).

Lesser prairie-chickens avoided distribution powerlines with the estimated response distance
Table 1. Counts of lesser prairie-chicken long-distance movements by movement type (columns) and study area (rows) including summary information for the number of birds making these movements.

| Region               | Movement type          | No. LPC†  | Multiple LD movements§ | Different types of movements¶ | Total |
|----------------------|------------------------|-----------|-------------------------|-------------------------------|-------|
|                      | HR to HR‡ Foray loop Unclassified |           |                         |                               |       |
| Colorado             | 28 6 0 34              | 6 1 9     |                         |                               |       |
| Kansas Northwest     | 25 9 5 39              | 10 2 25   |                         |                               |       |
| Kansas South-central | 42 13 5 60             | 11 8 33   |                         |                               |       |
| New Mexico           | 21 0 0 21              | 4 0 5     |                         |                               |       |
| Oklahoma             | 21 7 2 30              | 8 2 13    |                         |                               |       |
| Total                | 137 35 12 184          | 39 13 85  |                         |                               |       |

† Number of individual lesser prairie-chickens.
‡ Home range to home range movements.
§ Number of lesser prairie-chickens that made multiple long-distance movements.
¶ Number of lesser prairie-chickens that made long-distance movements of different types.

Fig. 2. Selection–neutral–avoidance summary outputs from CDF analysis of the long-distance movements of lesser prairie-chickens by study area, the pooled movement dataset, and feature type. Each graph displays the mean selection–avoidance–neutral response line (solid) from the 20 available area buffers, along with 95% confidence intervals (dashed), and range of results from all 20 available area buffers (dotted). Positive slope indicates selection, negative slope indicates avoidance, and neutral slope indicates no preference. Dashes depict study areas and feature type combinations that the feature dataset was incomplete for and not included in analysis.
lowest in Oklahoma and highest in the south-central Kansas study area (Table 2). Road CDF results indicated avoidance across most CDF analyses (Fig. 2). However, the south-central Kansas study area results indicated lesser prairie-chickens selected for roads in the first 100 m. We witnessed variation in the avoidance response distances for roads, with the lowest response estimate in the Oklahoma study area and the greatest in the northwest Kansas study area (Table 2). We only had fence data for certain parts of the Oklahoma and Kansas study areas. Fence response distance estimates varied between all study areas with both Kansas study areas and our pooled dataset indicating avoidance (Fig. 2). In Oklahoma, we observed selection for fences in the first 50 m. Lesser prairie-chickens avoided oil wells at similar distances for the both the Kansas and Oklahoma study areas, as well as the pooled dataset (Table 2). However, the estimated avoidance response distance in New Mexico was much higher. Taller anthropogenic structures (i.e., transmission powerlines and towers) generally had larger estimated avoidance response distances in comparison with the other feature types, but also had large regional variation (Fig. 2). For transmission powerlines, the northwest Kansas study area had the largest estimated avoidance response distance at 9 km. The Colorado, south-central Kansas, and New Mexico study areas, and the pooled dataset estimates were intermediate with response distances around 6 km (Table 2). In Oklahoma, the estimate was much lower at about 3 km. Towers in the south-central Kansas region had the greatest avoidance response distance estimate at over 10 km (Table 2). However, the tower response distance estimates varied widely as the response distance estimate in Oklahoma was much lower at less than one km (Table 2).

### DISCUSSION

This study is the first to provide quantitatively derived estimates of behavioral response to anthropogenic features during long-distance movements for lesser prairie-chickens, as well the first to provide these estimates using data from across the entire distribution of a species. We found that lesser prairie-chickens generally exhibit avoidance to all feature types we examined with some variation in the response distance among study areas and feature types. Our study adds further evidence that anthropogenic features have the potential to disrupt movements of wildlife species (e.g., Polfus et al. 2011 and Laberee et al. 2014). Long-distance movements play a crucial role in the persistence of spatially structured populations, and our understanding of them allows us to better manage connectivity across the landscape.

Our estimated avoidance response distances in relation to tall features (i.e. towers and transmission powerlines) were greater in general when compared to other grouse studies (Pitman et al. 2015).

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**Table 2. Summary of response distances (m) of long-distance movements of lesser prairie-chickens for each feature type identified through the CDF analysis.**

| Study area/Movement type | Fences | Oil wells | Transmission powerlines | Distribution powerlines | Roads | Towers |
|-------------------------|--------|----------|-------------------------|-------------------------|-------|--------|
| CO                      | †       | –        | 6550                    | –                       | 600   | 2700   |
| KS NW                   | 100    | 350      | 9000                    | 700                     | 700   | 7700   |
| KS SC                   | 400    | 350      | 6100                    | 1500                    | +100  | 10500  |
| NM                      | –      | 2250     | 5750                    | –                       | 500   | 8950   |
| OK                      | +50‡   | 400      | 2950                    | 250                     | 350   | 900    |
| All                     | 400    | 350      | 5400                    | 500                     | 350   | 900    |
| Foray Loop              | 400    | 350      | 5400                    | 500                     | 350   | 750    |
| HR to HR                | 400    | 350      | 6100                    | 600                     | 450   | 900    |
| Unclassified            | 400    | 400      | 5500                    | 1000                    | 300   | 7500   |

**Notes:**
- Distances estimates were obtained from averaged results across different spatial scales. The distance at which the maximum negative or positive value in the initial trend was reported. All distances represent avoidance behaviors unless otherwise indicated.
- † Dashes indicate areas removed from analysis due to missing feature vectors in the study area.
- ‡ The plus sign indicates a selection preference to the indicated distance.
2005, Walker et al. 2007, Hagen et al. 2011, Winder et al. 2014, Plumb et al. 2018). In contrast, our avoidance distances to roads and oil wells were smaller than previous reports (Pitman et al. 2005, Hagen et al. 2011). This difference in response distance could indicate that lesser prairie-chickens’ response varies during different behavioral states or periods in the life cycle. The majority of studies examining grouse response to anthropogenic features have focused on general home range movements, breeding-season movements, or nest-site selection (Pruett et al. 2009, Hagen 2011, Johnson et al. 2011, Winder et al. 2014). As these behaviors occur at different temporal and spatial scales, it suggests that there is variability in how individuals use their perceptual range to make context- or behavior-specific decisions (Olden et al. 2004, Pé’er and Kramer-Schadt 2008). Adding behavior-specific protocols to species management plans could improve their effectiveness. These additional protocols could be especially important for species of conservation concern or for species that exhibit relatively rare behaviors that could be crucial to their populations’ long-term success.

As we predicted, our greatest response distances were in relation to the tallest features on the landscape (i.e., towers and transmission powerlines). A similar avoidance response to wind turbines has been reported in other bird species (e.g., hen harrier, buzzard, golden plover, snipe; Pearce-Higgins et al. 2009). However, there is difficulty associated with isolating response to these features from other potential casual factors such as habitat structure, predation pressure, or confounding factors from other sources of anthropogenic disturbance (Walters et al. 2014). Despite this, lesser prairie-chickens can likely perceive taller features from farther away and thus may be more likely to avoid them from greater distances than shorter features (Pruett et al. 2009, Hagen et al. 2011).

Our measured response distances are likely relative estimates, as any number of environmental cues may be used by an individual to make navigation decisions (Goodenough et al. 2009, Yahner 2011). This leads to a gradient in the behavioral effect these features may have on movement and permeability of the landscape (i.e., the gradient describing how a feature moves from being a barrier, obstacle, or impedance to a constraint; Beyer et al. 2016). While the presence of anthropogenic structures does not necessarily cause structural fragmentation to the available habitat (i.e., the spatial configuration of the habitat itself remains unchanged), the presence of features may cause fragmentation through behaviors such as displacement or avoidance (Robel et al. 2004). Behavioral changes due to landscape features can lead to functional fragmentation that limits the functional connectivity of populations (Kindlmann and Burel 2008). We need empirical estimates of response to develop management protocols so functional connectivity can be preserved before fragmentation constrains movements in crucial connectivity zones (Fuhlendorf et al. 2017). This study provides evidence that anthropogenic features can affect the functional fragmentation of the landscape during long-distance movements of lesser prairie-chickens. As discrete landscape features such as anthropogenic structures may induce an avoidance response causing functional fragmentation, there is a need for more studies that focus on understanding the possible effects these features have on connective movements.

Habitation is a behavioral and physiological process that results in a decreased responsiveness to stimuli after repeated encounters (Blumstein 2016). This process has been used to describe a reduced avoidance response of wildlife to anthropogenic features in the environment (Madsen and Boertmann 2008, Johnson and Russell 2014). We found evidence of this process as study areas with the greatest densities of anthropogenic features distances tended to have the lowest response distances (e.g., towers in the Oklahoma study area; Appendix S1). In addition, one of the two features examined that had a selective response was fences in Oklahoma, where the fence density was significantly greater than the study areas in Kansas. Despite some support for the process of habituation and tolerance to landscape features, the topic is still debated (Beale 2007, Bejder et al. 2009). This relationship could also be related to the spatial distribution of features across the landscape. For example, if the increased fence density in the Oklahoma study area correlates with more fences built in the interior portion of the generally grid-like distribution of road and distribution powerline distribution common across our...
study areas, then the apparent observed selection to fences could be related to a stronger behavior to avoid those other features.

We also found that there was less variation in the response distances among movement types than among study areas. Response to features during different movements was similar to our pooled population estimates. Exploratory movements such as foray loops are commonly attributed to dispersing individuals. These movements are likely used to better inform their directional decisions and balance the costs associated with leaving their home range (Conradt and Roper 2006). However, dispersers do not seem to follow this pattern in lesser prairie-chickens (Earl et al. 2016). The similarities in the estimated response distances between the movement types may indicate that these observed exploratory loops are abandoned dispersals, where the individual decided to return to their established home range (Conradt et al. 2001).

It is important to consider how CDF response distances change when varying the size of available area. This is related to the scale of selection during long-distance movements and has not been studied previously (Appendix S3). For most CDF combinations of study area, movement type, or the pooled dataset, selection–neutral–avoidance trends generally had the same shape and similar magnitude; albeit the magnitude of response seemed to increase with larger available area buffers. Selection–neutral–avoidance trends strayed from this pattern the most when the available area buffer was <5 km. At these small scales, there may have only been very few features included in the analysis, skewing the distance to nearest feature estimates. However, even if there was variability in the magnitude of the selection–neutral–avoidance trend on the y-axis, the inflection points that describe the response distance varied only slightly. The average selection–neutral–avoidance trends across all buffer sizes were sufficient to draw conclusions from and were used to present our results.

Cumulative distribution functions are useful to measure responses on a continuous scale (Kopp et al. 1998). With the CDF method, the x-axis can be adapted to different continuous metrics (i.e., density or time since fire; e.g., Martin et al. 2012). Our primary objective was to obtain an estimate for the direction and scale of the response to anthropogenic features during long-distance movements and CDF analysis with nearest distance as the explanatory variable allowed us to meet this objective. However, it is important to note that this method does not estimate the magnitude of effect. While the magnitude of effects during long-distance movements still needs to be assessed, this study provides evidence that lesser prairie-chickens, in general, negatively respond to anthropogenic features in the landscape. Unfortunately, there are many potentially confounding factors that our analysis does not control for. Our analysis only accounts for distance to the nearest feature. Configuration of stopover habitat within the landscape matrix, other physical characteristics of anthropogenic features, or different spatial metrics of anthropogenic features (e.g., density, height, or the amount of sound or light produced by them) may influence lesser prairie-chickens’ responses and warrants additional study.

There are many other relevant movement and resource selection-related questions remaining, such as how does lesser prairie-chicken response to anthropogenic features impact fitness or overall permeability of the landscape? This is particularly important given the variation we saw in the avoidance distance between study areas. In future studies, it would be helpful to integrate more detailed individual-level data (e.g., vital rate data) to examine how stress levels relate to regional differences in habitat availability and spatial structure of anthropogenic structures. Without this individual-level data, we cannot assume that the minimum avoidance distances detected can support a stable population just because lesser prairie-chickens exhibited lower avoidance distances in some study areas. Species can tolerate a variety of landscape configurations; however, once a species threshold is crossed, the population may decline. Given increasing empirical evidence that lesser prairie-chickens avoid anthropogenic features during multiple life-history stages or behaviors (e.g., nesting, Pitman et al. 2005, Plumb et al. 2018; within home ranges, Pruett et al. 2009, Hagen et al. 2011), including long-distance movements, future research should evaluate how the avoidance of anthropogenic features affects fitness.
CONCLUSION

With the southern Great Plains already experiencing large amounts of land-use change and fragmentation, it is imperative that we consider management for lesser prairie-chickens at the landscape scale to ensure continued population persistence (Fuhlendorf et al. 2017). We found that lesser prairie-chickens’ locations during long-distance movements were farther than expected from most anthropogenic features we tested. These avoidance responses support the majority of past research on the effects of anthropogenic features on grouse and provide further evidence they can have a negative effect at all life stages and behavioral states (Hagen 2011, Hovick et al. 2014, Plumb et al. 2018). In particular, the tallest features we tested (i.e., large powerlines and towers) tended to have the largest avoidance distance estimates, usually several kilometers. The estimated response distance to these features from previous studies has often been >1.4 km regardless of the behavioral state of the individual (e.g., Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011, Plumb et al. 2018), but our estimated response distance during long-distance movements was typically greater. Our results suggest that these tall features may be the most important when considering landscape connectivity for lesser prairie-chickens. Data from this study can help parameterize connectivity models to define important areas across the distribution of the lesser prairie-chickens to maintain connectivity within the metapopulation and prevent further fragmentation.

Long-distance movements are the mechanism behind gene flow and recolonization in a metapopulation (Hanski 1999, Clobert et al. 2001). Dispersal and migration movements are needed for population persistence in spatially distributed species (Tromeur et al. 2016). Studying large-scale movements is often difficult and not feasible in individual studies due to the rarity of capturing an adequate sample of these events. There is potential in a variety of species for researchers to collaborate or utilize an open database like Movebank (Wikelski and Kays 2019), making large-scale studies such as ours more feasible. Combining data from multiple study areas collected during the same time allowed us to estimate responses to anthropogenic features across the landscape and demonstrate their potential to disrupt long-distance movements in an already fragmented landscape. Results from this study provide a starting point to ensure metapopulation connectivity for lesser prairie chickens, but more information is needed concerning the magnitude of these effects, effects of other physical features of anthropogenic structures such as density or sound production, and how these features affect fitness in order to fully inform connectivity models for this species.

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WWW.ESAJOURNALS.ORG 12

September 2020  Volume 11(9)  Article e03202
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