Characteristics of lesser prairie-chicken (*Tympanuchus pallidicinctus*) long-distance movements across their distribution

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Abstract. Long-distance movements are important adaptive behaviors that contribute to population, community, and ecosystem connectivity. However, researchers have a poor understanding of the characteristics of long-distance movements for most species. Here, we examined long-distance movements for the lesser prairie-chicken (*Tympanuchus pallidicinctus*), a species of conservation concern. We addressed the following questions: (1) At what distances could populations be connected? (2) What are the characteristics and probability of dispersal movements? (3) Do lesser prairie-chickens display exploratory and round-trip movements? (4) Do the characteristics of long-distance movements vary by site? Movements were examined from populations using satellite GPS transmitters across the entire distribution of the species in New Mexico, Oklahoma, Kansas, and Colorado. Dispersal movements were recorded up to 71 km net displacement, much farther than hitherto recorded. These distances suggest that there may be greater potential connectivity among populations than previously thought. Dispersal movements were displayed primarily by females and had a northerly directional bias. Dispersal probabilities ranged from 0.08 to 0.43 movements per year for both sexes combined, although these movements averaged only 16 km net displacement. Lesser prairie-chickens displayed both exploratory foray loops and round-trip movements. Half of round-trip movements appeared seasonal, suggesting a partial migration in some populations. None of the long-distance movements varied by study site. Data presented here will be important in parameterizing models assessing population viability and informing conservation planning, although further work is needed to identify landscape features that may reduce connectivity among populations.

Key words: dispersal; foray loop; migration; Southern Great Plains; tortuosity.

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INTRODUCTION

Long-distance movements are a key aspect of the ecology of species, communities, and ecosystems. Long-distance movements are adaptive behaviors that allow individuals to utilize resources in disjunct areas (Clobert et al. 2001, Milner-Gulland et al. 2011) and search the landscape to locate resources (Zollner and Lima 1999, 2005, Conradt et al. 2003). The result of long-distance movements is that individuals and their genetic material are redistributed among populations. The redistribution of individuals is one key driver of the dynamics of spatially structured populations, including the rescue of sink populations (Hanski 1999), gene flow (Clobert

et al. 2001), and geographic distributional shifts (Knowlton and Graham 2010). Additionally, as individuals move, they transport nutrients and energy that can affect the recipient communities (Holyoak et al. 2005) and ecosystems (Polis et al. 2004, Earl and Zollner 2014).

Many of the ecological processes shaped by long-distance movements are key to maintaining the viability of species and conserving ecosystem function. However, researchers have limited information about long-distance movements for most species. A greater understanding of long-distance movements would inform conservation and management decisions and modeling efforts that may guide those decisions (Pittman et al. 2014). Enhanced knowledge of long-distance movements would include the suite of movement types used by a species, which could include dispersal (Clobert et al. 2001), migration (Milner-Gulland et al. 2011), and exploratory searching (e.g., foray loops; Conradt et al. 2003). It would also include the probability and characteristics of those movements, context under which individuals choose to make those movements, and variability of those factors among sexes, life stages, and populations (Holyoak et al. 2008).

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a lekking, grouse species inhabiting the Southern Great Plains of the central United States. Lesser prairie-chickens have experienced an estimated reduction in geographic distribution by greater than 90% over the last century and represent a species of conservation concern (Hagen and Giesen 2005). While recent research has improved our understanding of lesser prairie-chicken habitat requirements (Hagen et al. 2013, Jarnevich et al. 2016) and population dynamics (McDonald et al. 2014, Ross et al. 2016), there is still limited information about connectivity among populations. Previous work demonstrated that most individuals remain within a few kilometers during their lifetime and that long-distance movements are fairly rare (e.g., Campbell 1972, Pitman et al. 2006), although some have suggested that conservation of the species may require larger landscapes (Fuhlendorf et al. 2002).

Our goal in this study was to determine the types, probability, and characteristics of the long-distance movements of the lesser prairie-chicken. Information on long-distance movements is vital for accurately parameterizing models on lesser prairie-chicken metapopulations to determine population viability, assess the most effective locations for habitat restoration, and estimate the species ability to move to new areas under a changing climate. Specifically, we aimed to answer the following questions: (1) At what distances could populations be connected? (2) What are the characteristics and probability of dispersal movements? (3) Do lesser prairie-chickens display exploratory or round-trip movements? (4) Do the characteristics of long-distance movements vary by site?

Methods

Our study utilized GPS satellite transmitters, which permitted tracking individuals at fixed time points at any location. Most previous studies rely on either mark–recapture analysis based on lek capture or very high-frequency radio-transmitter data, which rarely is capable of detecting when individuals leave the tracking area, limiting their utility for investigating long-distance movements. We deployed GPS transmitters on individuals throughout the species' geographic distribution from New Mexico, Oklahoma, Kansas, and Colorado. Movements greater than 5 km net displacement outside of the home range were considered long-distance movements (i.e., further than movements related to daily activity; Haukos and Zavaleta 2016). We classified movements into four types: dispersal, possible dispersal, round-trip movements between two or more home ranges, and exploratory foray loops.

Study areas (Fig. 1) included east-central New Mexico (Chaves, Lea, and Roosevelt Counties), Oklahoma (Beaver County), southeastern Colorado (Cheyenne, Prowers, and Baca Counties), and four sites across western and southern Kansas, including Gove County and Smoky Valley Ranch (Logan County) in northwest Kansas and Clark County and Red Hills (Kiowa and Comanche Counties) in south-central Kansas. Some individuals from the New Mexico study area moved into adjacent areas in Texas (Cochran County). Lesser prairie-chickens were captured on leks using walk-in drift traps (Haukos et al. 1990, Schroeder and Braun 1991), magnetic dropnets, and rope-trigger dropnets
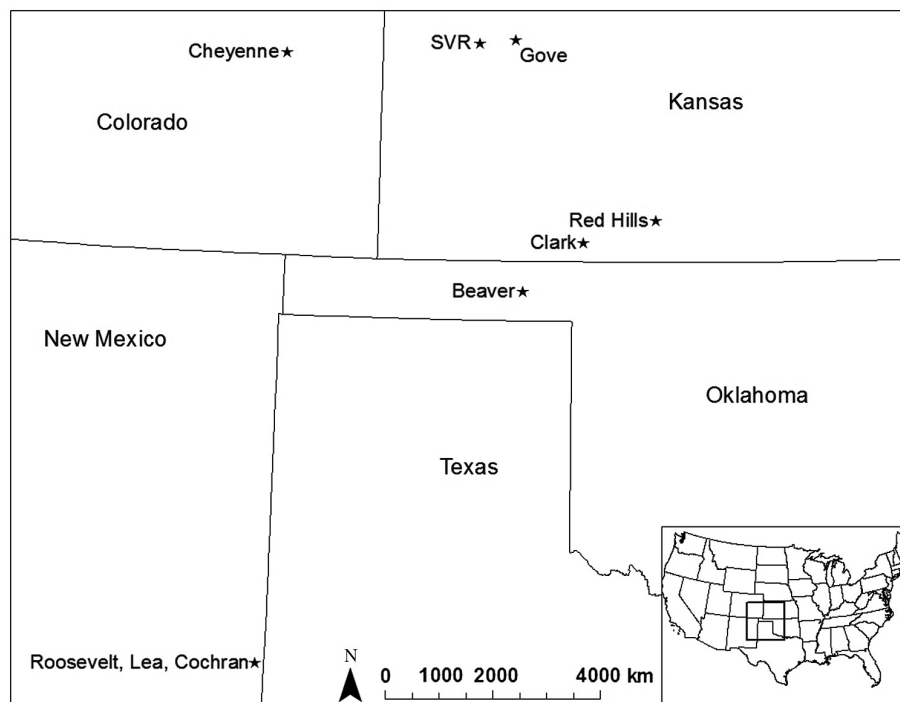
Fig. 1. Locations of study sites for lesser prairie-chickens tracking using GPS transmitters in Colorado, Kansas, Oklahoma, Texas, and New Mexico during 2013–2015. Stars indicate the centroid of each study site. SVR, Smoky Valley Ranch.

(Silvy et al. 1990). Similar methods were used on all sites. These capture methods do not decrease survival probabilities of individuals (Grisham et al. 2015). Individual birds were aged and sexed based on plumage characteristics (Copelin 1963). Males and females were fitted with rump-mounted GPS transmitters (22 g PTT-100, Microwave Telemetry Inc., Columbia, Maryland, USA; Model 22GPS, North Star Science and Technology, King George, Virginia,

USA) in 2013, 2014, and 2015 at sites across their geographic range (Table 1). Transmitters collected a minimum of seven locations per individual per day at all study sites. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (IACUC) protocol 3241; the Oklahoma State University IACUC protocol AG133; New Mexico State University IACUC protocol 2014-015; Kansas Department

Table 1. Number of lesser prairie-chickens tracked (*n*) using GPS transmitters during 2013–2015 and characteristics of the location data collected for these individuals in Colorado, Kansas, Oklahoma, Texas, and New Mexico.

| Site	*n*	Average days tracked per individual (SD)	Start date	End date
Beaver County, Oklahoma	106	138 (166)	2 April 2013	1 July 2015
Eastern New Mexico/Western Texas	25	226 (187)	6 April 2014	29 June 2015
Southeastern Colorado	28	144 (155)	24 March 2013	15 March 2015
Clark County, Kansas	20	220 (123)	1 April 2014	15 March 2015
Gove County, Kansas	57	179 (163)	2 April 2013	15 March 2015
Red Hills, Kansas	41	192 (150)	27 March 2013	15 March 2015
Smoky Valley Ranch, Kansas	13	182 (150)	2 April 2013	15 March 2015
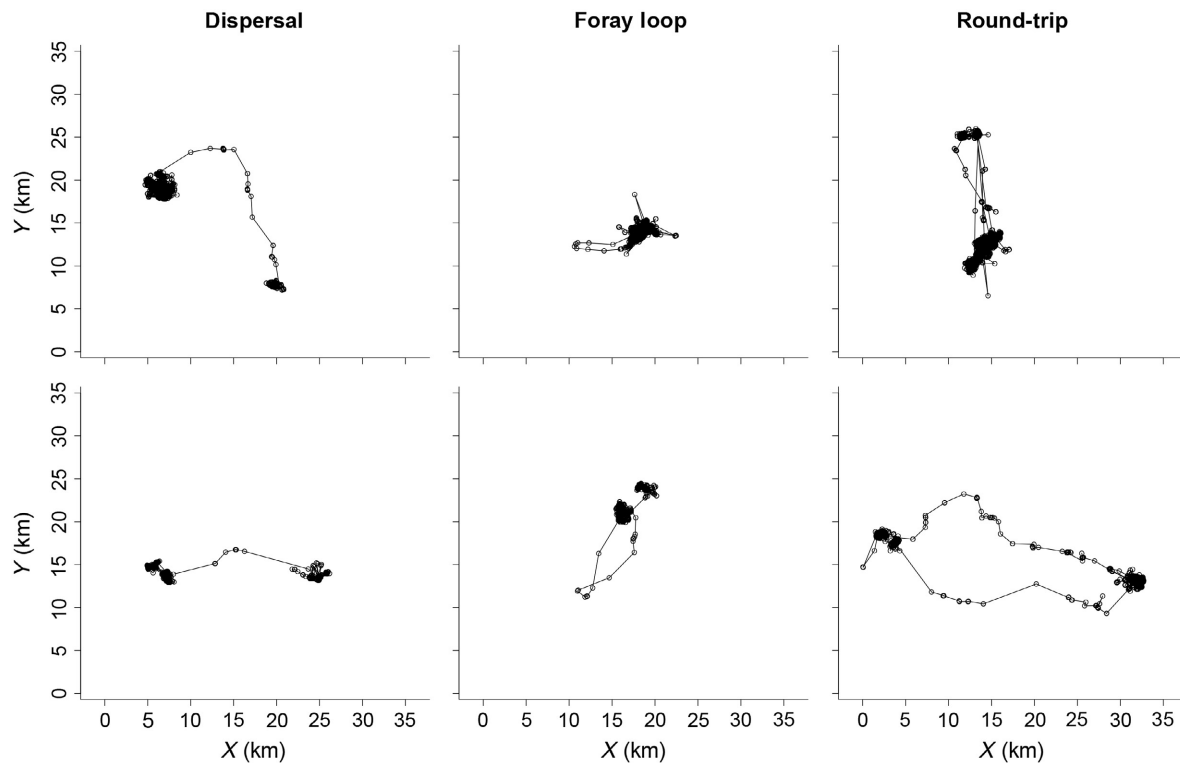
Fig. 2. Examples of dispersal movements (Clark County, Kansas, USA), foray loops (top: Gove County; bottom: Red Hills, Kansas, USA), and round-trip movements (top: Colorado; bottom: Red Hills, Kansas, USA) from adult female lesser prairie-chickens tracked in Colorado, Kansas, Oklahoma, Texas, and New Mexico during 2013–2015.

of Wildlife, Parks and Tourism scientific collection permit numbers SC-042-2013 and SC-079-2014; Colorado Parks and Wildlife scientific collection license numbers 13TRb2053 and 14TRb2053; Oklahoma Department of Wildlife Conservation scientific collecting permit 6230; and New Mexico Department of Game and Fish permit 3535.

We examined long-distance movements, where individuals deviated from their typical movements by leaving their established home range by at least 5 km net displacement (Haukos and Zavaleta 2016). We chose 5 km as the threshold, which is greater than twice typical or expected movements for individuals staying within their home range (Haukos and Zavaleta 2016). Home ranges were not explicitly estimated, but delineated as the outside border of clustered, short-distance, overlapping movements (see Fig. 2 for example movement paths). We placed each movement into one of four categories: dispersal,

possible dispersal, round-trip movements, and foray loops. Dispersal was defined as a one-way movement, where individuals did not return to their initially established home range during the tracking period. For movements to be classified as dispersal, individuals had to display normal short-distance home range movements for a 30-d period before and after the long-range movement. Movements were classified as possible dispersal if data on the initial or final home range movement spanned fewer than 30 d or if subsequent dispersal-like movements were observed. Round-trip movements were sets of movements linking two or three home range areas (i.e., at least two movements were observed going back and forth between two home range areas). Round-trip movements were further classified as seasonal if movements in one direction tended to occur in spring (March to June) and the other direction occurred in fall (September to November). We defined foray loops as movements starting and

ending in the same home range area, where the location farthest from the edge of the home range resulted in at least a 5 km net displacement.

For each movement, we identified the path by starting with the first movement leaving a home range and ending with the first movement entering a home range. We then calculated net displacement (km), total distance moved (km), tortuosity (total distance moved divided by the net displacement), heading in degrees (0° was due east with degrees increasing counterclockwise), number of days in transit, day of the year the movement was initiated, and number of days in the ending home range until the end of the tracking period, the individual's death, or a subsequent long-range movement. If the movement had only two locations, we recorded the total distance moved and tortuosity as missing values. For foray loops, we split the movement into two phases (leaving and returning) by examining the movement to and from the farthest point from the home range. We additionally calculated the net displacement between the start and end of the foray loop.

We analyzed movements in program R (R Core Team 2015) by comparing the characteristics of each type of movement among study sites. For each movement type, we first examined the correlation between the net displacement, total distance moved, tortuosity, days in transit, and the day of the year the movement was initiated. Because net displacement and total distance moved were always highly correlated ($r > 0.9$), we only included net displacement in the further analyses. We examined each movement type separately and used ANOVA to assess differences among study sites. For dispersal, we also tested for differences between true dispersal events and possible dispersal events. If ANOVAs had significant effects ($\alpha = 0.05$), we used Tukey's test to determine which pairs of factor levels differed. We used regression to determine whether the net displacement varied with the time of year of the movement. For round-trip movements, we averaged the response variables for each individual and used the individual as the replicate. In these analyses, we combined movements made by both males and females, because there were typically very few movements made by males and the number of movements made by each sex was dependent on the study site. Net displacement was log-transformed to meet

assumptions of normality and homoscedasticity. No other response variables were transformed. To assess directionality, we tested whether the movements' headings differed from a random distribution using Rayleigh's test of uniformity using the CircStats package in program R (Jammalamadaka and SenGupta 2001). We further tested whether foray loops, dispersal, and spring seasonal round-trip movements were directed north and whether fall seasonal round-trip movements were directed south using the V test (Jammalamadaka and SenGupta 2001).

We estimated the probability of dispersal (including both dispersal and possible dispersal) for each site using a Kaplan–Meier estimate (Bennetts et al. 2001) using Proc Lifetest in SAS (SAS 2004). We excluded individuals tracked less than 1 week and made estimates for each sex when the number of individuals tracked was 10 or greater per site. We repeated the analysis to examine the probability of a movement resulting in a potential reproductive connection between two areas. Males were considered to have a potential reproductive connection between two areas, if they were located in two different home range areas within a single breeding season (February to May) or in subsequent breeding seasons. Females were considered to have potential reproductive connections based on the same criteria as males, but also if they were located in one home range area during the breeding season and another during nesting (May to June). For sites with no dispersers or potential reproductive connections, we estimated the maximum potential dispersal probability for the sample by adding one disperser to the sample at the mean number of days that individuals were tracked at that site. This gave us an upper dispersal probability threshold for comparison with other sites.

Results

Long-distance movements were found at all sites although events were fairly uncommon (Tables 2 and 3). Several individuals in Kansas and one in New Mexico displayed more than one type of long-distance movement. Three individuals (Clark County, Red Hills, Kansas, and New Mexico) displayed a foray loop and round-trip movements, and two individuals (Clark County and Red Hills) displayed a round-trip movement

Table 2. Characteristics of lesser prairie-chicken long-distance movements (> 5 km net displacement) collected using GPS transmitters in Colorado, Kansas, Oklahoma, Texas, and New Mexico during 2013–2015.

Movement characteristic	Dispersal	Foray loops	Round-trip movements
Number detected	30	13	20 individuals
States detected	Kansas, Oklahoma, New Mexico	Kansas, Oklahoma, New Mexico	Colorado, Kansas, Oklahoma, New Mexico
Net displacement (km)	16.18 ± 2.77 (5.00–71.43)	8.84 ± 0.75 (5.92–13.94)	13.03 ± 1.47 (5.24–29.99)
Total distance moved (km)	22.09 ± 3.74 (7.27–85.91)	21.72 ± 1.93 (13.63–36.96)	19.03 ± 1.88 (6.34–37.68)
Tortuosity	1.41 ± 0.07 (1.01–2.34)	1.23 ± 0.03 (1.03–1.36)	1.48 ± 0.09 (1.06–2.40)
Time in transit (d)	4.4 ± 0.7 (1–20)	3.9 ± 0.6 (1–8)	3.56 ± 0.37 (1–7)
Day of year	2 April–27 November	6 April–23 November	All year

Note: Means and SE are presented with the range of values in parentheses.

Table 3. Counts of lesser prairie-chicken long-distance movements by type, site, and sex for GPS tracking data in Colorado, Kansas, Oklahoma, Texas, and New Mexico during 2013–2015.

Site	Sex	n	Dispersal	Foray loops	Round-trip movements
Beaver County, Oklahoma	Female	34	5†	1	1
	Male	72	1	1	3
Eastern New Mexico/Western Texas	Female	6	0	0	0
	Male	19	1	1	3
Southeastern Colorado	Female	20	0	0	1
	Male	8	0	0	0
Clark County, Kansas	Female	17	6	1	4
	Male	3	0	0	0
Gove County, Kansas	Female	51	8†	1	4
	Male	6	0	0	0
Red Hills, Kansas	Female	30	5	8†	3
	Male	11	0	0	0
Smoky Valley Ranch, Kansas	Female	11	3	0	0
	Male	2	1	0	0

Notes: Note that round-trip movements represent the number of individuals, not number of movements.
† This count includes two movements from a single individual.

and possible dispersal to a new area. In the Red Hills, one individual also performed two dispersal events and a foray loop, and another had two foray loops and one possible dispersal movement. Only females displayed long-distance movements in Kansas (except one individual in Smoky Valley Ranch) and Colorado, but only males displayed long-distance movements in New Mexico (Table 3). Both males and females displayed long-distance movements in Oklahoma. Overall, 9% of males (n = 124) displayed at least one long-distance movement, while 28% of females (n = 153) did, excluding individuals tracked for less than 1 week.

Dispersal (e.g., Fig. 2) and possible dispersal movements occurred in Kansas, Oklahoma, and New Mexico with none detected in Colorado. We detected 13 dispersal and 17 possible dispersal movements (Tables 2 and 3). We found no evidence that the characteristics of movements (e.g., net displacement, tortuosity) categorized as dispersal and possible dispersal were different (all $P > 0.69$). As such, we pooled data on dispersal and possible dispersal events for further analysis. There was a strong correlation between net displacement, total distance moved, and the number of days in transit, but not tortuosity, indicating that longer movements
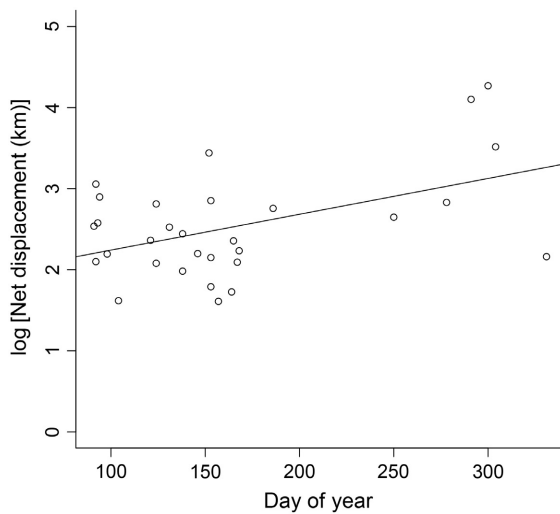
Fig. 3. Relationship between lesser prairie-chicken dispersal net displacement and the day of the year (Julian date; $n = 30$, $r^2 = 0.42$) in Colorado, Kansas, Oklahoma, Texas, and New Mexico during 2013–2015.

required more days to complete but were not more linear. Dispersal movements also had significantly longer net displacements later in the year ($F_{1,28} = 12.05$, $P = 0.002$; Fig. 3). There was no difference among sites in dispersal net displacement, tortuosity, or the day of year dispersal was initiated (all $P > 0.05$; Table 4). Overall, the average net displacement was 16.18 ± 2.77 km (±SE; Table 2, Fig. 4). Dispersal movements were directed significantly toward north ($n = 30$; r-bar = 0.36, $P = 0.002$) with a mean direction of 69.43° (north northeast; Fig. 5).

Foray loops (e.g., Fig. 2) occurred in Kansas, Oklahoma, and New Mexico (Table 3). The average net displacement of a foray loop from the home range was 8.84 ± 0.75 km (Table 2, Fig. 4). Foray loops were directed significantly toward north ($n = 13$, r-bar = 0.40, $P = 0.02$) with a mean direction of 150.49° (northwest; Fig. 5). Foray loops occurred from 6 April to 5 July with two outliers occurring in November.

Round-trip movements (e.g., Fig. 2) were detected in all states at all sites, except for the Smoky Valley Ranch in Kansas. Most individuals went back and forth between home ranges only once ($n = 14$; Oklahoma and Gove County, Clark County, and Red Hills, Kansas). Two individuals made three movements (New Mexico and Clark County, Kansas), two made four

movements (Oklahoma, New Mexico), one made five movements (New Mexico), and two made six (Colorado and New Mexico). There were no differences among sites in round-trip movement net displacement or the number of days in transit (all $P > 0.78$; Table 4). There was a difference among sites in tortuosity ($F_{5,14} = 3.50$, $P = 0.03$), but Tukey's pairwise comparison showed no differences between any two sites. Individual average net displacement between home ranges was 13.03 ± 1.47 km (Table 2, Fig. 4). First movements between home ranges were not different from second movements in total distance or tortuosity (all $P > 0.29$).

Of the 20 round-trip movements observed (Table 2), 10 were seasonal with movements in one direction in March to June and movements back in late September to November. This movement seasonality was found in the individual in Colorado, in one of three individuals in New Mexico, and in eight of 11 individuals in Kansas. For most individuals, the range of data only captured one movement in each direction, so it is unclear whether this pattern is repeated over multiple years. However, the individual in Colorado spent three breeding seasons in the same home range and two winters in a home range approximately 12 km away, all movements in March and October/November. Additionally, one individual from New Mexico spent two breeding seasons in the same home

Table 4. Results from analysis of variance on the effect of site on characteristics of lesser prairie-chicken long-distance movements from across their geographic distribution in Colorado, Kansas, Oklahoma, Texas, and New Mexico during 2013–2015.

Movement type	Characteristic	df	F	P
Dispersal	Net displacement	5, 24	1.38	0.27
	Tortuosity	5, 23	1.71	0.17
	Day of year	5, 24	0.97	0.46
Foray loop	Net displacement	4, 8	0.55	0.70
	Tortuosity	4, 8	1.28	0.35
	Day of year	4, 8	13.70	0.001†
Round-trip	Net displacement	5, 14	0.23	0.94
	Tortuosity	5, 13	3.50	0.03‡

† The only significant difference was between Clark County, Kansas, and all other sites, but there was only one movement from Clark County, so this result lacks sufficient replication.
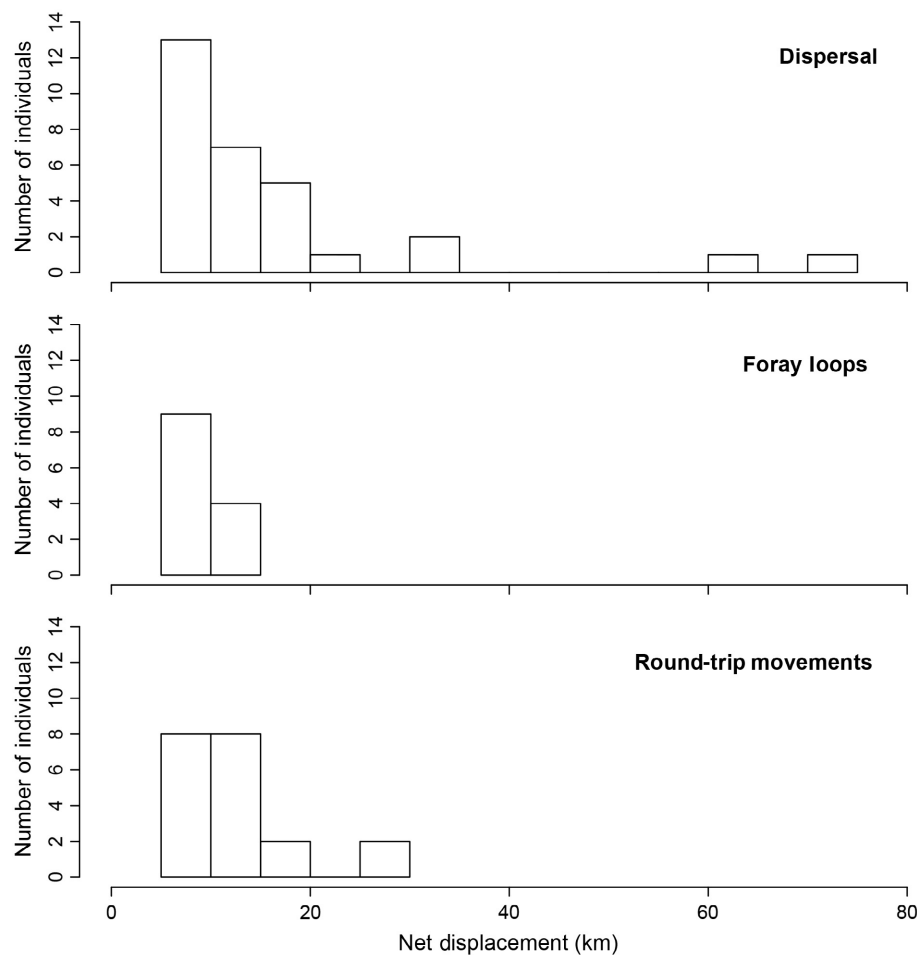‡ The Tukey pairwise test revealed no significant differences between pairs of sites.

Fig. 4. Histograms of the net displacement for dispersal, foray loops, and round-trip movements for lesser prairie-chickens in Colorado, Kansas, Oklahoma, Texas, and New Mexico 2013–2015.

range and two winters in a home range 16.6 km away. For seasonal movements, spring movements were directed northwest (mean heading of 136.1°), which was not significantly north (r-bar = 0.33, P = 0.07). Fall movements were directed southeast (mean heading of 313.8°), which was not significantly south (r-bar = 0.33, P = 0.07; Fig. 5).

Dispersal probability of all individuals ranged from 0.076 in Oklahoma to 0.430 per year in Clark County, Kansas (Table 5). Female dispersal probability ranged from 0.131 in Red Hills, Kansas, to 0.484 per year in Clark County, Kansas. Male dispersal was only recorded in Oklahoma and New Mexico with a probability of 0.021 and 0.059 per year, respectively (Table 5). Only in Oklahoma were dispersal events recorded for both sexes,

and females had a dispersal probability that was almost nine times greater than males. Several round-trip movements were timed such that it was possible that an individual could have had reproductive events in different areas, but the addition of these would only increase dispersal probability by 0.01–0.03 in most cases, well within the confidence intervals of the probability without those movements (Table 5).

DISCUSSION

We found that long-distance movements by lesser prairie-chickens were much farther than previously recorded, suggesting potential connectivity between populations up to 71 km apart through dispersal movements. The dispersal

Dispersal (*N* = 30)

Foray loops (*N* = 13)

Spring round-trip movements (*N* = 10)

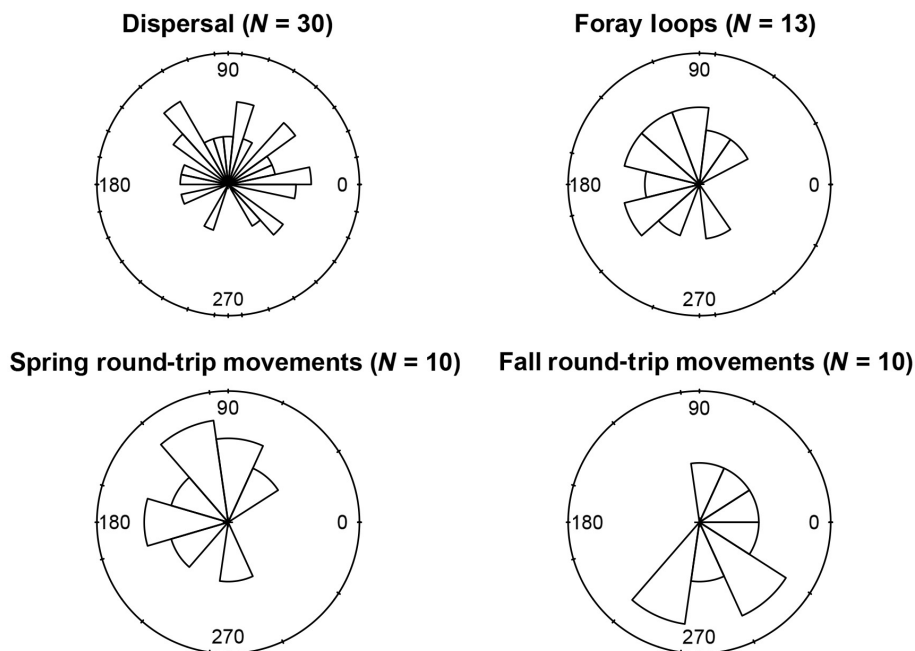**Fall round-trip movements (*N* = 10)**

Fig. 5. Rose diagrams depicting the directionality of lesser prairie-chicken long-distance movements across their distribution in Colorado, Kansas, Oklahoma, Texas, and New Mexico during 2013–2015.

Table 5. Lesser prairie-chicken dispersal probability (d ± SE) per year by site and sex for movements classified as dispersal or possible dispersal events and movements that could potentially result in reproduction in two different areas are shown in parentheses.

Site	Females		Males		All individuals	
	n	d	*n*	d	*n*	d
Beaver County, Oklahoma	30	0.185 ± 0.084 (0.214 ± 0.086)	65	0.021 ± 0.021 (0.021 ± 0.021)	95	0.076 ± 0.033 (0.086 ± 0.034)
Eastern New Mexico/Western Texas	6†		17	0.059 ± 0.057 (0.338 ± 0.147)	23	0.044 ± 0.043 (0.271 ± 0.125)
Southeastern Colorado	8†		20	<0.125‡	28	<0.10‡
Clark County, Kansas	17	0.484 ± 0.149	3†		20	0.430 ± 0.140
Gove County, Kansas	51	0.202 ± 0.074 (0.235 ± 0.079)	6†		57	0.172 ± 0.063 (0.200 ± 0.067)
Red Hills, Kansas	30	0.131 ± 0.072 (0.166 ± 0.078)	11	<0.167‡	41	0.100 ± 0.056 (0.125 ± 0.060)
Smoky Valley Ranch, Kansas	11	0.377 ± 0.180	2†		13	0.383 ± 0.158

Notes: Data were collected in Colorado, Kansas, New Mexico, and Oklahoma during 2013–2015.
† Dispersal estimates were not made for samples of <10 individuals.
‡ Estimates marked as < are maximum potential probabilities and had no actual dispersal events or potential reproductive connections. Maximum potential probabilities were estimated by adding one disperser at the mean tracking time to the sample.

probability was greater than expected, up to 0.43 per year for a site in southern Kansas. Lesser prairie-chickens displayed both exploratory movements through foray loops and round-trip movements, which suggests a partial migration in some populations. Finally, none of the movement characteristics varied by study site, although some sites had low numbers of long-distance movements, which likely limited our ability to detect differences.

The farthest movements in net displacement were dispersal, or one-way movements from one home range to a second home range. The farthest recorded dispersal movement was 71.4 km net displacement by a female in Kansas. Previously, the farthest recorded movement for male and female lesser prairie-chickens was 44 and 26 km, respectively, both from Kansas (Jamison 2000, Pitman et al. 2006). The farthest male movements we detected were round-trip movements between home ranges about 16 km apart in New Mexico. These data suggest that there is the potential for greater connectivity among populations than previously thought, primarily through the movement of females. This is supported by distribution-wide genetic data consistent with persistent gene flow among populations within ecoregions despite fragmented landscapes and population declines (Hagen et al. 2010, Oyler-McCance et al. 2016). Populations can be grouped into four main ecoregions (McDonald et al. 2014). The Sand Shinnery Oak Prairie Ecoregion in eastern New Mexico/western Texas is spatially separated from other ecoregions. The distance between the Sand Shinnery Oak Prairie Ecoregion and the rest of the geographic distribution is more than two times farther than the longest movement we recorded, making population connectivity between the two areas unlikely. This separation is also supported by genetic data showing no gene flow between the two areas (Van Den Bussche et al. 2003, Johnson 2008, Hagen et al. 2010, Oyler-McCance et al. 2016).

Our data also suggest that the probability of dispersal per year is relatively high, ranging from about 0.08 to 0.43 for both sexes combined. However, the average net displacement for a single dispersal event was 16 km, which would not span the distance between many habitat patches due to high levels of habitat fragmentation (Fuhlendorf et al. 2002, Patten et al. 2005). Landscape-level modeling efforts will be necessary to estimate the connectivity among currently occupied patches and the probability of colonization for other suitable or recently restored patches. Most dispersal movements were made by females, indicating that they are likely responsible for most of the connectivity among populations. Most long-distance movements in general were made by females, which is supported by genetic data showing that males have higher site

fidelity than females (Bouzat and Johnson 2004). This is also consistent with evidence across bird species, including grouse, showing a general trend for female-biased dispersal (Clarke et al. 1997).

Dispersal movements were found to be significantly oriented north. Recent evidence has shown that the lesser prairie-chicken is expanding its distribution northward in Kansas due to the Conservation Reserve Program (CRP; Rodgers and Hoffman 2005, Dahlgren et al. 2016, Rodgers 2016). Recent genetic data show movement of genes from the Mixed Grass Ecoregion and Sand Sagebrush Prairie Ecoregion northward to the Short-Grass Prairie/CRP Mosaic Ecoregion but negligible movement of genes southward (Oyler-McCance et al. 2016), consistent with our results. Climate change is expected to reduce vital rates below that required for population persistence in the Southern High Plains of Texas and New Mexico (Grisham et al. 2013). Further distribution shifts northward may be necessary to avoid a reduction in the species' distribution size. Directed dispersal has a greater fitness advantage than random dispersal for species moving to escape climate change (Buckley et al. 2013), and the lesser prairie-chicken's northerly dispersal bias will likely make any northerly range expansions occur more rapidly than if they had randomly directed dispersal. Of course, this assumes that both sexes are able to colonize new areas and establish a sustainable lek structure for mating; habitat is available north of the current distribution; and interactions with other taxa would not preclude the establishment of new populations. There is currently a narrow range of sympatry between lesser and greater prairie-chickens (*Tympanuchus cupido*) with low rates of hybridization in northwest Kansas (Bain and Farley 2002, Oyler-McCance et al. 2016). It is unclear whether interactions between the two species will affect further northward movements by lesser prairie-chickens or lead to introgression.

Twenty individuals were found to display round-trip movements, 10 of which were seasonal. For seasonal movements, individuals tended to go northeast in spring and southwest in fall, although these directional tendencies were not significant, which is not surprising given the small sample size. These data suggest that some lesser prairie-chicken individuals

exhibit short-distance migration behavior, previously found in about 5% of individuals in southwest Kansas (Hagen 2003). Partial migration has also been shown for greater prairie-chickens (Schroeder and Braun 1993). There is anecdotal evidence that historical populations of lesser prairie-chickens were migratory, breeding in the north and spending the winter in southern portions of the distribution (Sharpe 1968). However, Taylor and Guthery (1980) note that it is unclear whether this behavior actually occurred or was yearly or an occasional response to certain weather conditions, food availability, or intraspecific competition. Rodgers (2016) suggests that it may actually have been dispersal during a historic period of abundance.

Lesser prairie-chickens were also found to display foray loop exploratory movements. Foray loops are behavioral movements that are very effective for locating habitat patches or other resources (Conradt et al. 2003) and are typically thought to precede dispersal (Conradt and Roper 2006). These movements require some directional memory but allow individuals to return to their home range to access resources and rest for further exploration or dispersal. Foray loops have been described in insects (e.g., Seymour et al. 2003, Conradt and Roper 2006), mammals (e.g., Doncaster et al. 2001, Roper et al. 2003), and woodland birds (e.g., Walters et al. 1992, Doerr and Doerr 2005). In some taxa, foray loops make up a high proportion (>70%) of long-distance movements (e.g., Conradt and Roper 2006), but our data show that foray loops only make up about 10% of all long-distance movements in lesser prairie-chickens. Also, lesser prairie-chickens clearly do not always exhibit foray loops before dispersing, as looping behavior was found both before and after dispersal and round-trip movements. The movements tended to occur during breeding primarily by females and may be used to search for nesting sites. Greater prairie-chickens have also been shown to exhibit exploratory movements when translocated to other areas, although the movement patterns are consistent with spiral search, not foray loops (Vogel et al. 2015).

This study represents one of the few surveys of different types of long-distance movements for a species across its geographic distribution. The data presented here provide new information on the distances and probability of long-distance movements in lesser prairie-chickens, enhancing our knowledge of potential connectivity between habitat patches and the species' ability to colonize unoccupied patches. This type of information is essential for modeling spatially structured populations, which could enhance population viability estimates and broadscale conservation planning. However, we suggest further investigation of the reasons why individuals make long-distance movements, the landscape features they are willing to traverse, and the factors they use to determine where to establish a new home range. This type of detailed information could inform management by revealing barriers to dispersal and colonization, potential source–sink dynamics, and gene flow.

Acknowledgments

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