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Research Article

Nonbreeding Home-Range Size and Survival of Lesser Prairie-Chickens

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ABSTRACT The lesser prairie-chicken (*Tympanuchus pallidicinctus*), a species of conservation concern with uncertain regulatory status, has experienced population declines over the past century. Most research on lesser prairie-chickens has focused on the breeding season, with little research conducted during the nonbreeding season, a period that exerts a strong influence on demography in other upland game birds. We trapped lesser prairie-chickens on leks and marked them with either global positioning system (GPS) satellite or very high frequency (VHF) transmitters to estimate survival and home-range size during the nonbreeding season. We monitored 119 marked lesser prairie-chickens in 3 study areas in Kansas, USA, from 16 September to 14 March in 2013, 2014, and 2015. We estimated home-range size using Brownian Bridge movement models (GPS transmitters) and fixed kernel density estimators (VHF transmitters), and female survival using Kaplan–Meier known-fate models. Average home-range size did not differ between sexes. Estimated home-range size was 3 times greater for individuals fitted with GPS satellite transmitters ($\bar{x} = 997$ ha) than those with VHF transmitters ($\bar{x} = 286$ ha), likely a result of the temporal resolution of the different transmitters. Home-range size of GPS-marked birds increased 2.8 times relative to the breeding season and varied by study area and year. Home-range size was smaller in the 2013–2014 nonbreeding season ($\bar{x} = 495$ ha) than the following 2 nonbreeding seasons ($\bar{x} = 1{,}290$ ha and $\bar{x} = 1{,}158$ ha), corresponding with drought conditions of 2013, which were alleviated in following years. Female survival ($\hat{S}$) was high relative to breeding season estimates, and did not differ by study area or year ($\hat{S} = 0.73 \pm 0.04$ [SE]). Future management could remain focused on the breeding season because nonbreeding survival was 39–44% greater than the previous breeding season; however, considerations of total space needs would benefit lesser prairie-chickens by accounting for the greater spatial requirements during the nonbreeding season.

KEY WORDS drought, home range, Kansas, known-fate, management, survival, *Tympanuchus pallidicinctus*.

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a species of prairie grouse in the southern Great Plains in Colorado, Kansas, New Mexico, Oklahoma, and Texas, USA. Lesser prairie-chicken abundance, occupied range, and population densities have declined during the past century, making the bird a species of conservation concern (Garton et al. 2016). The population decline has been attributed to conversion of native grassland to cropland, increasing energy infrastructure, encroachment of invasive species, and unmanaged grazing by livestock (Woodward et al. 2001, Hagen and Giesen 2005). Because of ongoing declines, the lesser prairie-chicken was listed as threatened in May 2014, under the 1973 United States Endangered Species Act, as amended (U.S. Fish and Wildlife Service 2014). Although the listing was vacated by a federal judge in September of 2015 (Permian Basin Petroleum Association et al. v. Department of Interior, U.S. Fish and Wildlife Service,

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[Case 7:14-cv-00050-RAJ, U.S. District Court, Western District of Texas, Midland-Odessa Division]) and the species was removed from the threatened list in July 2016, lesser prairie-chicken population abundance and occupied range remains historically low and effective conservation strategies will be necessary to expand their numbers and range (Hagen and Giesen 2005, Hagen et al. 2016, Ross et al. 2016).

Despite knowledge that decline and degradation of grasslands have reduced habitat quantity and quality for lesser prairie-chickens, a better understanding of each portion of their life-cycle, including nonbreeding ecology, is needed to develop successful conservation strategies (Haukos and Boal 2016, Haukos and Zavaleta 2016). Uniform management prescriptions are currently being applied range wide, but lesser prairie-chickens occupy 4 distinct ecoregions across their range (Sand Shinnery Oak Prairie, Sand Sagebrush Prairie, Mixed-Grass Prairie, and Short-Grass Prairie-Conservation Reserve Program [CRP] Mosaic), which differ in vegetation composition and structure because of differing soil types and climatic conditions (Van Pelt et al. 2013, McDonald et al. 2014). An increased understanding of the differences and similarities of lesser prairie-chicken ecology among ecoregions and across the annual life-cycle of the species will contribute to the conservation effort to stem the decline of lesser prairie-chicken populations.

Overall grassland area has not changed substantially throughout the northern portion of the lesser prairie-chicken range since the 1950s; thus, factors influencing recent declines of lesser prairie-chicken populations remain unclear (Spencer et al. 2017). Ecological studies of a declining species need to determine target areas for conservation, and whether those areas remain consistent spatially and temporally across inhabited ecoregions (Sanderson et al. 2002, Pressey et al. 2007). Relatively little information is available for lesser prairie-chicken ecology during the nonbreeding season (i.e., when females are not attending leks, nests, or broods; Lyons et al. 2009, Robinson 2015). If habitat requirements during the nonbreeding season are not included in conservation strategies, then a life stage critical to population demography may be overlooked. For example, management of nonbreeding season needs can have an effect on breeding ecology by cross-seasonal effects, such as providing quality habitat to maintain body condition, thus improving individual survival and fitness rates (Norris and Marra 2007). Additionally, additive mortality during the nonbreeding season can effectively reduce the reproductive potential of an entire population during the breeding season (Norris and Marra 2007). Cross-seasonal interactions are not well understood and their potential importance has largely been overlooked in nonmigratory avian species such as lesser prairie-chickens.

One of the gaps in nonbreeding season ecology of lesser prairie-chickens is home-range size, especially in the northern portion of their range (Table 1). Nonbreeding season studies, which are generally limited to the southern portions of the lesser prairie-chicken range, reported larger home ranges and greater movements than during the breeding season (Candelaria 1979, Jones 2009, Lyons et al. 2009, Kukal 2010, Pirius et al. 2013). Estimates of home-range size during the nonbreeding season vary between 62 ha and 1,946 ha; however, most estimates are hampered by small sample size of radio-marked individuals (Haukos and Zavaleta 2016). Addressing this knowledge gap is important in understanding spatial needs for lesser prairie-chicken populations. Space use in the nonbreeding season may be fundamentally different than the breeding season because of differences in activity relative to available resources and lack of limitations in space use that are implicit during the breeding season.

Regional estimates of nonbreeding season survival for lesser prairie-chickens are lacking (Hagen et al. 2009, Lyons et al. 2009). Conditions experienced during the nonbreeding season may affect future reproductive potential of lesser prairie-chickens because females in poor body condition entering the breeding season may be less physically fit to mate, incubate eggs, and brood chicks, leading to intermittent breeding success (Norris and Marra 2007). Low survival of breeding age females during the nonbreeding season would also affect the overall number of individuals that can reproduce. Historically, having an adequate sample size to estimate space use and survival for nonbreeding season studies has been problematic. Although females can be captured and marked on leks and marked during the spring, capture outside of this period is challenging because of their cryptic and secretive nature while not attending leks (Salter

Table 1. Seasonal estimates of home-range size (ha) for nonbreeding lesser prairie-chickens in the United States, including method of estimation.

Source	State	*n*	Season	Home range (ha)	Method[a]
Candelaria (1979)	NM	2 M 2 F	Fall and winter	298, both sexes	Grid maps
Jamison (2000)	KS	23 M	Oct	229–409, M	KDE
Pirius et al. (2013)	TX	6 F 17 M	Nonbreeding	503, F 489, M	KDE
Taylor (1978)	TX	12 M 7 F	Nov Dec Jan Feb	160–789, both sexes 1,946, both sexes 331, both sexes 62, both sexes	MCP
Toole (2005)	TX	7 individuals	Seasonal	207, both sexes	MCP

[a] KDE, kernel density estimate; MCP, minimum convex polygon.

and Robel 2000). In most instances, assessing female survival during the nonbreeding period is dependent on a reasonable sample of individuals first surviving the breeding season and transmitters functioning properly after already being deployed for approximately 6 months. However, knowledge should not be limited to periods that are easy to research, and survival during the nonbreeding season is an important factor in their overall life cycle.

Available estimates of female nonbreeding season survival are consistently greater than breeding season survival rates. When standardized to 6-month intervals using weekly or monthly reported estimates, reported nonbreeding survival for female lesser prairie-chickens are variable, with a range from 0.43 to 1 (Lusk 2016; Table 2). Similarly, studies on nonbreeding season survivability for prairie-grouse are generally sparse and influences are poorly understood (Winder et al. 2014*a*). The strong variation in nonbreeding survival studies suggests regional, landscape, and weather-related effects, but factors influencing nonbreeding season survival have not been investigated and comparing ecoregions with a consistent temporal extent and method can be useful.

A study of female lesser prairie-chicken space use and survival requires the use of radio-transmitters to track these secretive birds with large space requirements through space and time. Past studies have primarily used very high frequency (VHF) transmitters to locate lesser prairie-chickens on the landscape. However, this method is limited by the amount of effort to find individual birds and variation in transmitter range because of transmitter design and topography. Recent technological advances allow for the use of global positioning system (GPS) satellite platform transmitting terminal (SAT-PTT) tags small enough ($\leq$5% of mass) to attach to birds such as lesser prairie-chickens (Plumb 2015, Lautenbach et al. 2016). These transmitters provide a finer scale of location data, spatially and temporally, and can be used to answer fine-scale space and habitat use questions. However, the standard method of estimating home range with these 2 transmitter types differs. Location data from VHF transmitters are typically analyzed using fixed kernel density estimators, whereas GPS location data are typically analyzed using models that account for temporal autocorrelation, such as Brownian Bridge movement models (Bullard 1991, Horne et al. 2007, Walter et al. 2015). Because of the different temporal scales of the data used with these methods, different home range sizes are likely.

Table 2. Reported 6-month survival estimates of lesser prairie-chickens during the nonbreeding season in the United States. We converted estimates from reported estimates to 6-month rates for direct comparisons.

Study	State	Survival rate	*n*
Hagen et al. (2007)	KS	0.68	220 F
Jamison (2000)	KS	0.74	160 both sexes
Kukal (2010)	TX	0.63	41 both sexes
Pirius et al. (2013)	TX	0.72	53 both sexes
Hagen et al. (2006)	KS	0.65	216 M
Lyons et al. (2009)	TX	0.72	187 both sexes
Lusk (2016)	NM	0.43–1.0	63 both sexes

We studied lesser prairie-chickens for 3 nonbreeding seasons in Kansas to gain a better understanding of the required spatial extents and survival of nonbreeding lesser prairie-chickens. Our objectives were to compare home-range size between lesser prairie-chickens with different transmitter types and sexes, compare home-range size among seasons and ecoregions, and compare survival among seasons and ecoregions. We hypothesized that home-range size of lesser prairie-chickens would vary between sexes and transmitter types estimated with different estimators. We also hypothesized that home-range size and survival would vary among ecoregions and years because of different landscape and climatic conditions.

STUDY AREA

Within the current 5-state occupied range of lesser prairie-chickens, the species occupies 4 different ecoregions. Portions of 3 ecoregions (Sand Sagebrush Prairie, Mixed-Grass Prairie, and Short-Grass Prairie/CRP Mosaic ecoregions) occur in Kansas, with the fourth (Sand Shinnery Oak) occurring at the southwest extent of the range (McDonald et al. 2014). We established 3 study areas that represented each of the 3 ecoregions in Kansas, which supported >60% of extant lesser prairie-chickens (Van Pelt et al. 2013, McDonald et al. 2014; Fig. 1). We delineated boundaries for study areas by creating a minimum convex polygon around all VHF and SAT-PTT bird points for each area, excluding dispersal events (unidirectional movements >5 km), using the Minimum Bounding Geometry tool in ArcGIS 10.2 (ESRI, Redlands, CA, USA).

The northwestern Kansas study area (Northwest) included 2 sites within the Short-Grass Prairie/CRP Mosaic Ecoregion dominated by native short-grass prairie, CRP grasslands, and row-crop agriculture on silt-loam soils (McDonald et al. 2014). The Northwest study area was 1,714.4 km^2 located in Gove and Logan counties, on private land and the Smoky Valley Ranch, and was owned and managed by The Nature Conservancy. Primary land uses in this area were livestock grazing, energy extraction, and row-crop agriculture. Temperatures ranged between -8.5°C and 33.1°C (High Plains Regional Climate Center [HPRCC] 2017). Elevation in the area ranged from 733 m to 961 m (U.S. Geological Survey [USGS] 2015). Dominant plants included blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), sand dropseed (*Sporobolus cryptandrus*), little bluestem (*Schizacyrim scoparium*), broom snakeweed (*Gutierrezia sarothrae*), and purple three-awn (*Aristida purpurea*). Dominant fauna include coyote (*Canis latrans*), swift fox (*Vulpes velox*), northern harrier (*Circus cyaneus*), and Swainson's hawk (*Buteo swainsoni*).

The Red Hills, Kansas, study area was 491.1 km^2 and centered on private lands in Kiowa and Comanche counties within the Mixed-Grass Prairie Ecoregion (McDonald et al. 2014). This area consisted of mixed-grass prairie on loamy soils, with primary land uses of livestock grazing, oil and gas extraction, and limited row-crop agriculture in bottomlands. Temperatures ranged between -7.5°C and 33.8°C (HPRCC 2017). Elevation in the area ranged from 515 m

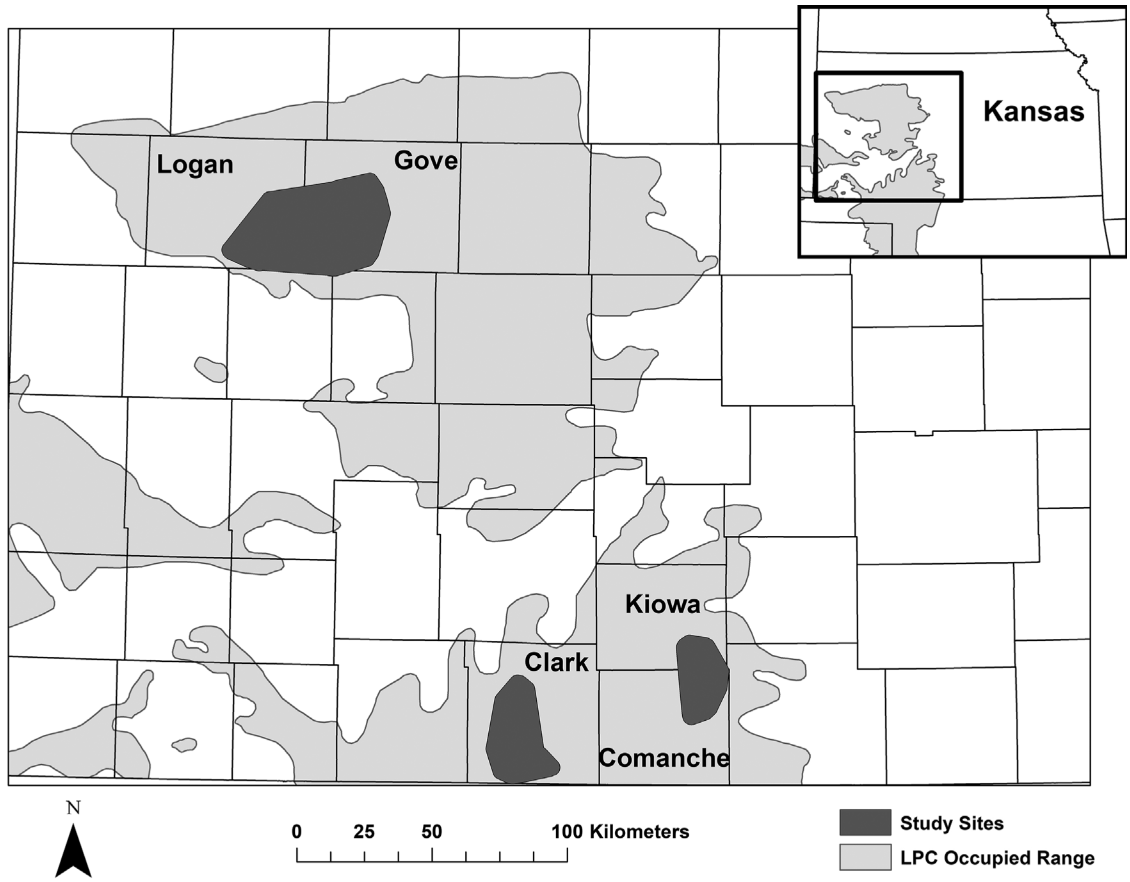

Figure 1. Location of 3 Kansas, USA, study areas where were estimated nonbreeding survival and home range for lesser prairie-chickens (LPC) across the northern portion of their range, 2013–2016. Study areas are represented in dark grey, with the estimated contemporary lesser prairie-chicken range in light grey. The Northwest site was in Logan and Gove counties in the Short-Grass Prairie/Conservation Reserve Program [CRP] Mosaic Ecoregion, the Clark County site was in Clark County in the Sand Sagebrush Prairie and Mixed-Grass Prairie ecoregions, and Red Hills site was in Kiowa and Comanche counties in the Mixed-Grass Prairie Ecoregion.

to 669 m (USGS 2015). Dominant plant species in the Red Hills study area included little bluestem, Louisiana sagewort (*Artemisia ludoviciana*), sideoats grama, western ragweed (*Ambrosia psilostachya*), sand dropseed, cheatgrass (*Bromus tectorum*), and blue grama. Dominant fauna include coyote, red-tailed hawk (*Buteo jamaicensis*), and northern harrier.

The Clark County study area within south-central Kansas was 712.1 km^2 and located in the transition between the Mixed-Grass Prairie and Sand Sagebrush ecoregions (McDonald et al. 2014). Land use was dominated by livestock grazing with interspersed extraction of fossil fuels and row-crop agriculture. Temperatures ranged between -7.7°C and 34.6°C (HPRCC 2017). Elevation in the area ranged from 551 m to 703 m (USGS 2015). Dominant plants included sand dropseed, western ragweed, blue grama, Russian thistle *(Salsola tragus*), little bluestem, alkalai sacaton (*Sporobolus airoides*), and sand sagebrush (*Artemisia filifolia*). Dominant fauna include coyote, American badger (*Taxidea taxus*), red-tailed hawk, and northern harrier. The Clark County area also had considerable alkali flats along drainages.

The 3 study areas varied by spatial configuration and composition. We used program FRAGSTATS (McGarigal and Marks 1995) to quantify landscape configuration and composition of the 3 study areas, using a landcover classification developed by Spencer et al. (2017) with landcover classes of grassland, cropland, water, and urban, merged with the 2014 CRP layer from the United States Department of Agriculture, Farm Services Agency. We used the contagion metric, for which a smaller value corresponds to a less aggregated landscape, and mean patch size to describe the landscape context. The Northwest study area was the most fragmented of the 3 study areas, with the smallest mean patch size ($\bar{x} = 33.3 \pm 8.8$ ha [SE]) and smallest contagion value (61.5). The Northwest study area was also comprised of less grassland (54%) than the other sites. In comparison, the Red Hills and Clark County study areas had larger mean patch sizes of 63.5 ± 45.5 ha and 50.4 ± 23.3 ha, respectively, and larger contagion values of 69.5 and 79.3, respectively. The Red Hills and Clark County study areas were comprised of 86.7% and 76.6% grassland, respectively.

Precipitation varied among the 3 years of the study in relation to the long-term average. For all study areas, the 2013 growing season produced 27–54% less precipitation (3.27–7.2 cm) than the long-term average (7.2–10 cm). Whereas, the 2014 and 2015 growing seasons produced 16–76% (11.4–12.6 cm) and 23–66% (8.8–15.2 cm) more precipitation relative to the long-term average, respectively (Kansas State University 2017).

METHODS

Capture

We used walk-in traps and dropnets to capture lesser prairie-chickens at leks during spring (Mar–May) in 2013, 2014, and 2015 in Northwest and Red Hills study areas and during 2014 and 2015 in the Clark County study area (Haukos et al. 1990, Silvy et al. 1990). We aged and sexed captured individuals following techniques of Copelin (1963).

We fitted female lesser prairie-chickens with a 12- or 15-g bib-style VHF transmitter (A3960, Advanced Telemetry System, Isanti, MN, USA), or a rump-mounted 22-g SAT-PTT (Solar Argos/GPS PTT 100, Microwave Telemetry, Columbia, MD, USA). We attached SAT-PTTs on the rump using leg harnesses made of Teflon® ribbon, with elastic at the front of the harness for flexibility (Dzialak et al. 2011). We also opportunistically fit male lesser prairie-chickens with remaining SAT-PTTs after females stopped attending leks in May.

We defined the nonbreeding season as the 6-month period between 16 September and the 14 March, for an even comparison with breeding season survival and home range during the same study. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee under protocol number 3241, and Kansas Department of Wildlife, Parks and Tourism scientific collection permits (SC-042-2013 SC-079-2014, SC-001-2015).

Tracking

We located lesser prairie-chickens outfitted with VHF transmitters 3 to 4 times/week during the nonbreeding season. We collected locations during all times of day by varying routes through the study area on each day we conducted telemetry. We triangulated individuals from 3 to 5 locations using a 3-piece hand-held Yagi antenna and an Advanced Telemetry Systems receiver (R4000, R4500) or a Communications Specialists receiver (R1000, Communications Specialists, Orange, CA, USA). Bearings of locations were ≥15 degrees apart and taken within 20 minutes to decrease error from bird movement. We entered bearings and Universal Transverse Mercator (UTM) positions for birds with VHF radios into the program Location of a Signal (LOAS; Ecological Software Solutions, Hegymagas, Hungary) to determine the estimated UTM location of the individual and estimate an error polygon around the point. We attempted to limit error polygons to 0.1 ha but used locations with error polygons ≤1 ha for birds with a limited number of locations (<20% of all locations). If we could no longer locate individuals because of long distance movements from the focal study area, we attempted to locate individuals from a fixed-wing Cessna aircraft.

Birds outfitted with an SAT-PTT recorded up to 8 GPS positions a day, with ±18 m accuracy, every 2 hours between 0600 and 2200 during the nonbreeding season. Locations were uploaded to an Argos satellite, downloaded every 3 days into the Argos System, and compiled bi-weekly.

Home Range

We estimated lesser prairie-chicken home ranges for individuals marked with SAT-PTTs by calculating a utilization distribution using Brownian Bridge movement models (Horne et al. 2007) and the kernelbb function in the package adehabitatHR in Program R (Calenge 2006, R Version 3.3.1, https://www.r-project.org/, accessed 21 June 2016). Brownian Bridge movement models account for the time lag between successive locations, path between the 2 successive locations, transmitter error, and temporal autocorrelation, which represents a refinement over the use of fixed kernel density estimators for this type of data (Bullard 1991, Walter et al. 2011). We estimated home ranges for the entire nonbreeding season for individuals fitted with SAT-PTTs that had ≥100 points for 1 nonbreeding season (Plumb 2015).

We estimated home ranges for VHF-marked individuals using a fixed kernel density estimator and least squares cross validation (LSCV) for smoothing with the function kernelUD within package adehabitatHR in Program R (Calenge 2006). We estimated home ranges for birds that had ≥30 locations for 1 nonbreeding season (Seaman et al. 1999). Because of the tendency for about half of the VHF-marked individuals during the nonbreeding season to establish discontinuous use areas from the area surrounding their capture site (D. A. Haukos, U.S. Geological Survey, unpublished data), LSCV could not converge across the gap between the last detection prior to movement from the focal study area and where individuals were subsequently located from aircraft. We used the average smoothing parameter from all individuals for which LSCV converged to calculate the kernel density estimate of individuals with a large spatial gap in locations. These home ranges ended up as ≥2 discontinuous use areas with intervening spatial gaps when no information was collected about the movement between established use areas.

We used nonparametric Mann–Whitney U tests in Program R to test for differences in average home-range size between home-range estimators used for different transmitter types (VHF and SAT-PTT) and sexes. For birds marked with SAT-PTTs, if a difference existed between home-range size for males and females, we separated the sexes for the remainder of the analyses, and if a difference did not exist, we grouped sexes. If a difference existed between home-range sizes for birds with VHF and SAT-PTTs, we tested for differences in home-range size among areas and years by transmitter type. We used a Kruskal–Wallis (K–W) test to compare home-range size among study area and years. Following a significant main effect ($P < 0.05$), we used Mann–Whitney U tests to determine differences in mean home-range sizes between study areas or years. We used nonparametric statistical tests because the data were not normally distributed.

Survival

We used Kaplan–Meier known fate functions within the survival package to model survival of nonbreeding female lesser prairie-chickens (Therneau 2014) in Program R. We used Cox proportional hazard functions to test for differences among years, between ages, and among study areas to determine if these categorical effects had a significant influence on nonbreeding survival. We tested model diagnostics with the cox.zph function to determine if these data met assumptions of proportional hazards (Fox and Weisberg 2011). We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c). We considered models with $\Delta AIC_c \leq 2$ to be competing candidate models (Burnham and Anderson 2002). We did not consider survival estimates with overlapping 95% confidence intervals as statistically different.

RESULTS

Home-Range Size

We estimated nonbreeding home ranges for 100 individual lesser prairie-chickens (86 F, 14 M; Table 3). Twelve SAT-PTTs malfunctioned during the study. We censored 6 individuals with malfunctioned transmitters that did not have enough consecutive points to calculate utilization distributions with Brownian Bridge movement models correctly. Additionally, 14 individuals marked with SAT-PTTs dispersed outside of our defined study area. We did not include the 95% isopleth home ranges for these individuals in the home-range comparisons because we considered these movements to be dispersal events and not within-season home-range movements.

Estimated average home-range size for male and female lesser prairie-chickens outfitted with SAT-PTTs differed from those outfitted with VHF transmitters (Mann–Whitney $U = 1{,}641$, $P \leq 0.001$). Estimated home range for lesser prairie-chickens with SAT-PTTs ($\bar{x} = 997 \pm 145$ ha; Table 4) was >3 times greater than those for lesser prairie-chickens outfitted with VHF transmitters ($\bar{x} = 286 \pm 21$ ha; Table 5). Estimated home ranges for individuals marked with VHF transmitters did not differ among study areas (K–W = 2.79, $P = 0.25$) or seasons (K–W = 3.79, $P = 0.15$). Male lesser prairie-chickens were outfitted only with SAT-PTTs (Table 3). Average home-range sizes did not differ between female ($\bar{x} = 959 \pm 150$ ha) and male lesser prairie-chickens ($\bar{x} = 1{,}181$ ha, SE = 437; Mann–Whitney $U = 10.5$, $P = 0.61$). Therefore, we combined sexes for comparisons of home-range estimates among study areas and years. For birds marked with SAT-PTTs, estimated home-range size differed among years (K–W = 10.85, $P = 0.004$). Average home-range size was 61% and 57% smaller during the 2013–2014 nonbreeding season than the 2014–2015 and 2015–2016 seasons, respectively (Table 4). Within years, we found that estimated home-range size differed among study areas in the 2013–2014 (K–W = 5.47, $P = 0.02$) and 2014–2015 (K–W = 7.22, $P = 0.03$) nonbreeding seasons but not the 2015–2016 nonbreeding season (K–W = 0.30, $P = 0.86$). Home-range size for the Red Hills study area was double that of the Northwest study area during 2013–2014 nonbreeding season. During the 2014–2015 nonbreeding season, estimated home-range size was 2.5 times greater in Clark County than the Northwest study area. Across years, estimated home-range size differed among study areas (K–W = 12.07, $P = 0.002$). Lesser prairie-chickens in Clark

Table 3. Distribution of 100 lesser prairie-chickens among 3 study areas and sex by transmitter type, satellite (SAT) or very high frequency (VHF), used to estimate nonbreeding home-range size in Kansas, USA, during 2013–2016. Nonbreeding season was 16 September to 14 March.

		Study area					
		Clark		Northwest		Red Hills	
Year	Sex	SAT	VHF	SAT	VHF	SAT	VHF
2013–2014	F			10	5	8	3
	M			2		3	
2014–2015	F	9	4	7	4	6	3
	M	1		3		2	
2015–2016	F	7	3	7	2	4	4
	M	1		1		1	
Total		18	7	30	11	24	10

Table 4. Average 95% isopleth home range (ha) of lesser prairie-chickens marked with satellite transmitters in 3 study areas in Kansas, USA, during the nonbreeding seasons of 2013–2014, 2014–2015, and 2015–2016. Estimates include both male and female lesser prairie-chickens. All satellite marked individuals had ≥100 points with which to estimate home ranges.

Season	Site	*n*	$\bar{x}$	SE	Range
2013–2014	Season (all sites)	23	495	75	62–1,392
	Northwest	12	337	70	62–706
	Red Hills	11	667	119	211–1,391
2014–2015	Season (all sites)	28	1,290	276	227–7,474
	Northwest	10	684	104	227–1,168
	Clark County	10	1,730	311	539–3,412
	Red Hills	8	1,498	867	260–7,473
2015–2016	Season (all sites)	21	1,158	302	131–6,707
	Northwest	8	1,477	776	131–6,707
	Clark County	8	924	182	178–1,640
	Red Hills	5	1,023	262	460–1,891
All years	Northwest	30	757	219	62–6,707
	Clark County	18	1,372	210	178–3,412
	Red Hills	24	1,018	295	211–7,474
All sites, years	Total	72	997	145	62–7,474

Table 5. Mean 95% kernel density estimates (ha) of 95% volume contour home range for nonbreeding female lesser prairie-chickens marked with very high frequency (VHF) radio-transmitters, Kansas, USA, 2013–2016. The nonbreeding season was the 6-month period between 16 September and 14 March. We estimated home-range size for individuals that had ≥30 points throughout the entire nonbreeding season.

Year	Site	*n*	$\bar{x}$	SE	Range
2013–2014	All	8	305	22	235–417
	Northwest	5	293	25	235–388
	Red Hills	3	324	47	268–417
2014–2015	All	11	303	40	57–549
	Clark County	4	287	56	131–369
	Northwest	4	372	64	249–549
	Red Hills	3	231	92	57–367
2015–2016	All	9	248	38	95–488
	Clark County	3	274	39	231–353
	Northwest	2	329	159	170–488
	Red Hills	4	188	36	95–245
All years	Clark County	7	282	33	131–369
	Northwest	11	328	34	170–549
	Red Hills	10	242	35	57–417
All sites, years		28	286	21	57–549

County had 81% and 34% greater home-range size than lesser prairie-chickens in the Northwest and Red Hills study areas, respectively (Table 4).

Survival

Of the 119 individual female lesser prairie-chickens that survived the 2013, 2014, and 2015 breeding seasons prior to being included as part of the nonbreeding season analyses, 16 individuals survived 2 consecutive breeding seasons, resulting in 135 bird-years (Table 6). Of these, 67 individuals were outfitted with SAT-PTTs and 52 individuals were outfitted with VHF transmitters. We recorded 33 mortalities during the nonbreeding season across the 3 years of the study. Of these mortalities, 6 were due to avian predation (18%), 13 to mammalian predation (39%), and 14 (42%) were unknown events.

There was no single top ranked model in the model set (Table 7). Therefore, we made inference based on the top 4 models, all of which had a $\Delta AIC_c \leq 2$ and a cumulative model weight of 0.87. The top 4 models were study area (site), the null model, site + year, and year (Table 7). Coefficients for site and year in all models were nonsignificant (i.e., 95% CI overlapped 0), indicating that site and year were spurious terms in the models. The null model resulted in an overall 6-month nonbreeding survival estimate of 0.73 (95% CI = 0.65–0.81), which represents the overall nonbreeding survival rate across the 3 study areas in Kansas. Despite overlapping confidence intervals among study areas, point estimates of survival were 25% greater in the Red Hills than in the other study areas (Table 8). Estimates of nonbreeding survival for each season also had overlapping confidence intervals, although point estimates for the first and second seasons were greater than the third season of the study (Table 8).

DISCUSSION

We found support for our hypothesis that home-range size of lesser prairie-chickens would vary by transmitter types estimated with different estimators (home-range sizes estimated from VHF transmitters were smaller than those estimated from SAT-PTTs), but our data did not support our hypothesis that home-range size would vary by sex. For our study of 6-month nonbreeding survival, we also found no support for our hypothesis that survival would vary among years and ecoregions, despite differences in weather, vegetation, and landscape composition.

Table 7. Model results for a known-fate survival model set for nonbreeding female lesser prairie-chickens for 3 seasons (2013–2014, 2014–2015, and 2015–2016) in Kansas, USA, including site, year, and age effects.

	K[a]	Deviance	ΔAIC_c[b]	w_i[c]
Site	2	303.42	0.00	0.31
Constant	1	307.65	0.15	0.29
Site + year	3	302.78	1.46	0.15
Year	1	307.20	1.72	0.13
Site × year	5	300.11	3.07	0.07
Age	2	307.64	4.22	0.04
Age + year	3	307.13	5.80	0.02
Age × year	5	303.99	6.95	0.01

[a] Number of parameters.
[b] Difference in Akaike's Information Criterion corrected for small sample size.
[c] Model weights.

Home Range

Differences in home-range estimates between transmitter types is likely a result of differences in the temporal resolution of locations. Methods for home-range estimation of lesser prairie-chickens in the past have typically used either minimum convex polygon or fixed kernel density estimators with location data from VHF transmitters (Table 1). Use of VHF transmitters results in a coarser temporal resolution of location data compared to SAT-PTTs (3–4 points/week vs. >50 points/week). Such a large difference in home-range size between transmitter and estimator types does not allow for comparison of our estimates of home-range size for lesser prairie-chickens fitted with SAT-PTTs to past studies, which all used VHF technology.

The estimated home-range size of nonbreeding lesser prairie-chickens marked with VHF transmitters in this study is within the range of estimates from past studies. The single study that reported nonbreeding home-range size in Kansas reported a range of 229–409 ha for October (Jamison 2000). Pirius et al. (2013) reported nonbreeding home-range

Table 6. Number of female lesser prairie-chickens for 3 study sites that survived the breeding season prior to be included in the nonbreeding survival study, Kansas, USA, 2013–2016. Number of individuals are separated by year, study site, and transmitter type, global positioning system satellite platform transmitting terminal (SAT-PTT) and very high frequency (VHF).

Season	Site	n	n SAT-PTT	n VHF
2013–2014	Northwest	25	12	13
	Red Hills	17	8	9
2014–2015	Clark County	15	11	4
	Northwest	22	13	9
	Red Hills	15	8	7
2015–2016	Clark County	17	12	5
	Northwest	11	8	3
	Red Hills	13	7	6

Table 8. Known-fate survival ($\hat{S}$) estimates for nonbreeding female lesser prairie-chickens for 3 study areas in Kansas, USA, over 3 seasons (16 Sep–14 Mar, 2013–2014, 2014–2015, 2015–2016). Our Northwest study area was in Logan and Gove counties, the Clark County study area was in Clark County, and the Red Hills study area was in Kiowa and Comanche counties. Within each season, study areas (Northwest, Clark County, Red Hills) are pooled. Estimates are derived from year and site models.

	Survival estimate		
Group	$\hat{S}$	SE	95% CI
Season			
2013–2014	0.75	0.069	0.62–0.90
2014–2015	0.74	0.064	0.63–0.88
2015–2016	0.68	0.081	0.54–0.86
Study area			
Northwest	0.66	0.066	0.54–0.80
Clark	0.68	0.090	0.52–0.88
Red Hills	0.86	0.055	0.76–0.97

estimates for VHF birds in Texas that were 200 ha greater than our study. Taylor (1978), using minimum convex polygons, reported a wide array of home-range sizes across months in Texas (62–1,946 ha). With home-range estimates for VHF individuals similar to past studies, but much larger estimates for SAT-PTT individuals, it is likely that previous VHF studies underestimated the spatial extent of lesser prairie-chicken use during the nonbreeding season. As SAT-PTTs continue to decrease in cost and size, future studies interested in space use of prairie-grouse should consider use of SAT-PTT to better understand space use more clearly over broad spatial scales.

Contrary to our prediction, nonbreeding home-range size of individuals marked with SAT-PTTs did not differ between males and females. Lesser prairie-chickens congregate into mixed-sex wintering flocks after the breeding season, which likely leads to males and females moving in a similar fashion (Riley et al. 1993). With males and females combined, nonbreeding season home ranges were 3 times larger than the breeding season home ranges reported for the counterpart to this study. Plumb (2015) reported an average home-range size of breeding female lesser prairie-chickens in Kansas and Colorado to be 340 ha (±53), using the same methods with SAT-PTT tags and Brownian Bridge movement models. The increased size of home ranges during the nonbreeding season indicates that estimates obtained for the breeding season do not accurately represent the amount of space required for individual lesser prairie-chickens on an annual basis. Given these findings, it is unlikely that available habitat is limiting home-range size during the breeding season because during the nonbreeding season, lesser prairie-chicken populations can use a greater amount of space without affecting survival rates. Home-range size constraints during the breeding season are more likely explained by reproductive activities that limit the extent of movement from a central location, such as lek visitation and tending nests and broods (Plumb 2015). These constraints are lacking during the nonbreeding season. Combining the breeding and nonbreeding locations for these birds to estimate annual home ranges could indicate whether the amount of annual space used increases or remains consistent in comparison to the nonbreeding season.

For lesser prairie-chickens marked with SAT-PTTs, home-range size varied among study areas in the first and second nonbreeding seasons but did not statistically differ among study areas for the 2015–2016 nonbreeding season. Although there were no detectable statistical differences between the Northwest and Red Hills study areas in 2 of the 3 years, mean home-range sizes exhibited different patterns. Some differences may not be detected statistically because of substantial variability among individuals within study areas, observable as large standard errors and wide ranges for average home-range estimates, especially in the Red Hills and Clark County study areas. The next step to understanding the individual variation could be to separate birds that exhibit different movement strategies, such as extensive versus limited movement, and try to understand why birds are behaving in different ways, such as genetic differentiation (DeYoung and Williford 2016, Earl et al. 2016). A possible reason for differential space use between the Northwest study area and the Red Hills and Clark County study areas is the different proportions of landcover composition between the Northwest site and the southern sites, with the Northwest study area being comprised of considerably less grassland distributed in a patchier configuration. Differences in landcover characteristics that resist movement could be perceived by individuals and result in smaller home ranges (Zeller et al. 2012).

Mean home-range size during the 2013–2014 nonbreeding season was 61% and 57% smaller than the 2014–2015 and 2015–2016 nonbreeding seasons, respectively. During the 2013 growing season, the entire Southern Great Plains region remained in a severe drought, but increased precipitation occurred in 2014 across all study areas and persisted into the 2015 breeding season (Kansas State University 2017). Increased precipitation during the growing season altered the landscape by increasing residual vegetation, which lesser prairie-chickens use in the nonbreeding season (Haukos and Zavaleta 2016, Kraft 2016). This increased availability of residual cover could foster greater movement and prospecting of resources by increasing functional connectivity (Hodgson et al. 2011). If more of the landscape can be perceived as available by lesser prairie-chickens, they may be likely to move greater distances to acquire available resources, resulting in suppressed home-range sizes during the height of the drought and subsequent increases in home-range sizes the following 2 years after increases in precipitation from 2013 to 2014.

Nonbreeding season space use is understudied in other species of prairie-grouse, with few published studies that explicitly estimated nonbreeding home-range size (Pirius et al. 2013, Winder et al. 2014*b*). The estimated nonbreeding season home ranges derived from VHF transmitter data for greater prairie-chickens (*Tympanuchus cupido*) in eastern Kansas were 7.1–7.8 km^2 (710–780 ha; Winder et al. 2014*b*). These home-range estimates are 2.5 times larger than our VHF estimates of lesser prairie-chicken home-range size. They reported that home-range size increased with increasing levels of fragmentation; however, we did not find that home-range differences corresponded well with differences among fragmentation levels among study areas (S. G. Robinson, Kansas State University, unpublished data).

Survival

Our overall estimate of nonbreeding female survival ($\hat{S} = 0.73$) was within the range of past studies of nonbreeding lesser prairie-chickens; although reported estimates were wide ranging ($\hat{S} = 0.43$–1.0; Table 1, Haukos and Zavaleta 2016). Hagen et al. (2007) estimated a survival rate of 0.77 for female lesser prairie-chickens in Kansas from November to February, which over 6 months equates to 0.68; their estimate is slightly lower than our nonbreeding estimate but within the range of survival estimates spanned by our 3 study areas. The evidence for a consistent overwinter survival across the lesser prairie-chicken range suggests that this period is not contributing to differences in persistence among populations across the species' range and possibly not contributing to long-term declines given positive population trends in areas surrounding the Northwest study area (Dahlgren et al. 2016).

The 6-month survival estimates did not differ among the 3 years across all study areas. Mortality events were relatively evenly spaced across the nonbreeding seasons of each site and year (0–2 mortalities/week) except for a single week in 2014 (17–23 Nov) with 3 mortality events. We hypothesized an increase in survival from the first year of the study (2013–2014) to the second year of the study (2014–2015) because of the alleviation of extreme drought that occurred across much of the Southern Great Plains from 2011 to 2013, including the 2013 breeding season. Decreased precipitation, coupled with increased grazing pressure (Kraft 2016), should have left less residual vegetation for lesser prairie-chicken cover during the 2013–2014 nonbreeding season compared to 2014–2015 and 2015–2016 seasons. During 2014, breeding season rain started in late May in all study areas and continued consistently across the remainder of the growing season, resulting in an increase in residual vegetation for the 2014–2015 and 2015–2016 nonbreeding season across all study areas in Kansas (S. G. Robinson, unpublished data). However, with differences not evident in survival among years, nonbreeding survival does not appear to be related to precipitation characteristics of the preceding growing season. The effects of precipitation on available cover and subsequent survival may be modulated by resource selection of cover types having differing vegetative structure (D. S. Sullins, Kansas State University, unpublished data).

Additionally, survival rates did not statistically differ among study areas. However, a lower point estimate of survival was evident for the Northwest study area compared to the Red Hills study area. Several differences between these sites may explain the observed variance in survival. The southern study areas had a mixed-grass vegetation community, which includes increased shrub cover relative to the Northwest study area (S. G. Robinson, personal observation). Shrubs provide increased cover for improved thermoregulation and predator avoidance during the nonbreeding period (Patten et al. 2005*a*). The southern study areas were also centered on more intact grasslands. Intact grasslands with low fence, road, and power-line densities could correspond to less potential hazards for lesser prairie-chickens. Power lines, fences, and roads act as areas for avian perching and predator corridors; an absence of these could correspond to a decrease in mortality risk (Patten et al. 2005*b*). We would expect lesser prairie-chicken survival to be greater in areas with greater habitat quality and lower population density. However, we conducted our study on some of the best remaining lesser prairie-chicken habitat in Kansas, which could explain why survival rates were not significantly different among populations.

Our prediction that survival during the nonbreeding season would be greater than that for the breeding season of the preceding year was supported. Seasonal survival rates estimated for the breeding season (15 Mar–14 Sep) were 0.42 (95% CI = 0.31–0.52) in 2013 and 0.48 (95% CI = 0.38–0.58) in 2014 (Plumb 2015). The estimates were 39–44% lower than the corresponding nonbreeding survival rate from this study. Reduced survival during the breeding season relative to the nonbreeding season is intuitive; adult female lesser prairie-chickens should have reduced predation risk during the nonbreeding season because they do not have to exert extra energy or risk exposure to visit leks, locate nesting sites, incubate eggs, or protect broods (Hagen et al. 2007, 2009; Pirius et al. 2013). Additionally, over the years of this study, no extreme weather events (blizzards or ice storms) occurred at our study sites, which would have had the potential to increase mortality risk to nonbreeding lesser prairie-chickens.

Nonbreeding season estimates of survival of greater prairie-chickens are nearly double that of the breeding season (Augustine and Sandercock 2011, Winder et al. 2014*a*). Populations of greater sage-grouse (*Centrocercus urophasianus*) generally have high survival rates during the winter, but these can be greatly reduced by harsh and extreme winters (Wik 2002, Connelly et al. 2004, Moynahan et al. 2006). Severe weather events affecting overwinter mortality is also likely the case for lesser prairie-chickens; a severe blizzard in Colorado in 2006 greatly reduced populations of lesser prairie-chickens (J. Reitz, Colorado Parks and Wildlife, personal communication). Many species of grouse are experiencing population declines (Storch 2007), but for lesser prairie-chickens, barring catastrophic events, survival rates for the nonbreeding season do not seem to be as influential on population growth as breeding season survival and recruitment. Our conclusion regarding nonbreeding survival is additionally corroborated by a sensitivity analysis for lesser prairie-chickens in southwest Kansas, where simulated management to increase nest and brood survival was more influential than management for female survival for lesser prairie-chicken population growth rates (Hagen et al. 2009).

Although home-range size appears to be related to precipitation amount during the growing season and landscape characteristics, yearly differences in home-range size did not relate to survival of nonbreeding lesser prairie-chickens. In other species of grouse, the inverse has been found to be true, with increased movements resulting in lower survival (Thompson and Fritzell 1989, Beck et al. 2006). Because increased home-range size during the nonbreeding season in our study did not correspond with decreases in survival or with differences in survival among ecoregions in the northern extent of their range, years with more movement by lesser prairie-chickens could allow for the potential colonization of new habitat, thus increasing occupied range.

MANAGEMENT IMPLICATIONS

Our data fill knowledge gaps in relation to space use and survival for nonbreeding lesser prairie-chickens in Kansas, which can be used to inform managers when assimilating nonbreeding ecology into overall management objectives. Management strategies could be improved by considering nonbreeding or annual home-range size estimates, rather than only breeding season space use, when trying to determine the proper amount of space required for a sustainable lesser prairie-chicken population. Our results suggest nonbreeding survival rates are not substantively influencing lesser prairie-chicken population size in Kansas, relative to the breeding season. Management focused on improving survival rates of adults, nests, and broods during the breeding season rather than concerns with nonbreeding season survival would be most beneficial to population growth.

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