



Assessment of lesser prairie-chicken translocation through survival and lek surveys

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Abstract

Translocation is a management tool used to restore or augment wildlife populations, but outcomes of translocations are often poorly documented and can have varying levels of success for improving wildlife population declines. The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a prairie grouse endemic to the southern Great Plains. In response to declining abundance and distribution, in 2023 lesser prairie-chickens were listed as threatened or endangered under the Endangered Species Act in different states. Translocation is a potential management response to population declines when there is an availability of unoccupied habitats, but translocation efficacy has not been evaluated for lesser prairie-chickens. We translocated 411 lesser prairie-chickens seasonally from 2016–2019 and monitored the translocated lesser prairie-chicken population from 2017–2022. To assess translocation as a management tool for lesser prairie-chickens, we estimated survival for 2017–2020 and conducted lek surveys during 2017–2022. Over a fifth (22.8%, $n = 94$) of translocated birds either died or went missing within the first 2 weeks following release. Survival rates of translocated birds during the breeding (0.44 ± 0.02 [SE]) and nonbreeding (0.55 ± 0.03 [SE]) seasons were relatively low compared to nontranslocated lesser prairie-chickens in other studies (0.63–0.93 for breeding season;

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0.43–0.87 for non-breeding season). Twenty-seven percent of translocated birds survived to the breeding season after release (i.e., >1 year). Translocated lesser prairie-chickens initiated 28 lekking sites over the study period. We estimated 77% of males available >2 weeks post release participated in lekking activity. The number of leks and male high counts on leks in the study area increased after translocation, peaking one year post-translocation (an overall increase of 250% and 340%, respectively). However, both the number of leks and male high counts decreased (48% and 39%, respectively) within 3 years after translocation cessation. Establishment of leks and increasing lek attendance directly following translocation initially suggested that translocation could be a viable management tool. However, survival rates after translocation and declining lek counts following translocation indicates that the increased population abundance and occupied range from this translocation effort may be unsustainable. Our results highlight the necessity of monitoring to determine outcomes of a large lesser prairie-chicken translocation. Other management strategies, such as targeted grassland restoration and management in areas of greatest lesser prairie-chicken density, could be more beneficial for conservation of lesser prairie-chicken populations.

KEYWORDS

Colorado, Kansas, known fate, lesser prairie-chicken, public land, sand sagebrush prairie, translocation, *Tympanuchus pallidicinctus*

Translocation is defined as the deliberate movement of organisms from one site to another for conservation benefit (IUCN/SSC 2013). As a management tool, translocations are frequently used to restore or augment wildlife populations (Scott and Carpenter 1987). Broadly, translocation success can be evaluated using several factors, including a local population becoming established, increases in abundance and occupied range, and a self-sustaining local population. Translocations have a long history in wildlife conservation and have been implemented for a large number of species with varying degrees of success (Griffith et al. 1989, Seddon et al. 2014, Hoffmann et al. 2015). Generally, translocation efforts are poorly evaluated and existing documentation may be biased toward prolific and successful translocation projects (Scargle 2000, Schooler 2011).

The absence of evaluating translocation success is concerning as translocations are expensive and often involve sensitive, threatened, or endangered species. Determining translocation success can be difficult as the definition of success is specific to the species being translocated and individual translocation objectives. Limited evaluations and bias toward reporting successful translocations may be due to lack of subsequent monitoring to assess short- and long-term success. Due to uncertainty surrounding outcomes of translocations, extensive posttranslocation information, including estimating survival and population metrics for translocated species, is critical for assessing the viability of translocation as a conservation tool (Griffith et al. 1989).

Several prairie grouse (e.g., *Tympanuchus* spp.) of the Great Plains states have undergone translocations, including greater prairie-chicken (*Tympanuchus cupido*), sharp-tailed grouse (*T. phasianellus*), and Attwater's prairie-chicken (*T. c. attwateri*); however, little information is known about fate and distribution of individuals following release, with few translocations reported as successful (Snyder et al. 1999). Translocation is often considered to be one of many management tools for prairie grouse because it can provide immediate positive effects of increased population abundance and occupied range, especially when other management strategies (e.g., prairie restoration) require long periods to have similar outcomes. Unfortunately, prairie grouse from the Great Plains have been among the most difficult groups to successfully translocate, whether for restoration into historic range or to augment low population abundance. Lack of success may be attributed to the large numbers of birds (possibly >1,000) necessary to successfully restore or supplement populations due to inherent low survival and recruitment for many translocated populations (Toepfer et al. 1990). Therefore, estimating survival and distribution of translocated individuals is imperative to effectively evaluate translocation success.

The lesser prairie-chicken (*T. pallidicinctus*) is a prairie grouse currently listed as either threatened or endangered based on distinct population segments under the 1973 Endangered Species Act and found in the southwestern Great Plains of the United States (Van Pelt et al. 2013, McDonald et al. 2014, U.S. Fish and Wildlife Service 2022). Lesser prairie-chickens breed on leks where males gather from March through May to display and defend territories to attract females for mating. Conducting counts of birds, generally males, on leks from either an aerial or ground survey is commonly used as a reliable index to estimate lesser prairie-chicken population trends (Garton et al. 2016, Hagen et al. 2017, Ross et al. 2018, Nasman et al. 2022). Lesser prairie-chicken population estimates have declined from 150,000 birds in the mid-1980s to ~27,000 birds in 2022 and current estimates suggest that the lesser prairie-chicken occupies only ~15% of its pre-European settlement historical range (Hagen et al. 2017, Nasman et al. 2022).

Drivers contributing to lesser prairie-chicken declines included loss of habitat quantity and quality through anthropogenic development, extensive conversion of native prairie to row-crop agriculture, encroachment of woody vegetation, energy extraction and development, incompatible grazing practices, invasive plant species, and increasing frequency of severe droughts and extreme weather events (Van Pelt et al. 2013, Haukos and Boal 2016, Ross et al. 2016). Effects of these drivers are evident in the Sand Sagebrush Prairie Ecoregion where an estimated population of 25,000 birds in the 2000s declined to ~2,000 birds by 2022 (Garton et al. 2016, McDonald et al. 2016, Hagen et al. 2017, Nasman et al. 2022). Nearly 20% of the ecoregion area is comprised of the U.S. Forest Service Cimarron and Comanche National Grasslands in Kansas and Colorado, respectively, which combined is the largest area of publicly managed lands throughout the lesser prairie-chicken range (Elmore and Dahlgren 2016). However, in 2016, lek surveys indicated <10 lesser prairie-chickens remained in Baca County, Colorado, and that lesser prairie-chickens were locally extirpated from Morton County, Kansas, where the majority of the Comanche and Cimarron National Grasslands are located, respectively (Berigan et al. 2022). With the combined implementation of a lesser prairie-chicken management plan by the Comanche and Cimarron National Grasslands in 2014 and increased precipitation following the 2010–2014 intensive drought, habitat quality was thought to have improved sufficiently to support a lesser prairie-chicken translocation to the study area (U.S. Forest Service 2014).

Population declines and lack of immigration from other ecoregions make translocation one of the few remaining management tools available to prevent extirpation of lesser prairie-chickens in the Sand Sagebrush Prairie Ecoregion. Although previous translocations have been attempted for the species (Snyder et al. 1999), vital rates of translocated populations are not well documented; therefore, extensive monitoring is imperative to understand translocation success. We evaluated translocation as a management strategy for lesser prairie-chicken populations in the Sand Sagebrush Prairie Ecoregion by translocating birds from the Short-Grass Prairie/CRP Mosaic Ecoregion in northwest Kansas, which supports >75% of the current lesser prairie-chicken population (Nasman et al. 2022). We released translocated birds on sand sagebrush prairie landscapes of the U.S. Forest Service Cimarron and Comanche National Grasslands in southwestern Kansas and southeastern Colorado,

respectively. In our study we used potential metrics of translocation success for lesser prairie-chickens as 1) the translocated population remaining near the release area, 2) an initial increase in population abundance and occupied range, 3) translocated populations achieving comparable demographic vital rates to resident populations, and 4) maintaining an increased population after translocation ceases. Our goal was twofold: 1) evaluating the outcomes of the translocation effort, and 2) assessing translocation as a conservation tool for lesser prairie-chickens. Our first objective was to estimate survival rates of lesser prairie-chickens translocated to the Sand Sagebrush Prairie Ecoregion throughout the annual life cycle (breeding or nonbreeding) and explore possible drivers of survival, including week within breeding and nonbreeding seasons, sex (male or female), release site (KS, CO), and transmitter type (very-high-frequency [VHF], satellite-platform transmitter terminals [SAT-PTT]). These phenological periods and other variables listed previously have been shown to be important for lesser prairie-chicken survival with previous nontranslocated lesser prairie-chicken studies (Hagen et al. 2007, Plumb 2015, Robinson et al. 2018b). Our second objective was to determine the change in maximum male counts (i.e., monitoring index) from lek surveys during and following translocation.

STUDY AREA

Capture area

We captured lesser prairie-chickens during fall 2016 and spring 2017–2019 in the Short-Grass Prairie/CRP Mosaic Ecoregion, which had the greatest contemporary density of lesser prairie-chickens across their range (Nasman et al. 2022). We captured lesser prairie-chickens on short- and mixed-grass prairie and cropland landscapes in Gove, Lane, Ness, and Finney counties in Kansas, USA (1,357,189 ha). The landscape had limited topography with rolling hills and shallow ravines; elevation ranged from 628–942 m (U.S. Geological Survey [USGS] 2018). Land cover in these counties was a mixture of row-crop agriculture, U.S. Department of Agriculture Conservation Reserve Program (CRP) grassland, and native short-grass prairie intermixed with remnant mixed-grass prairie (McDonald et al. 2014, Dahlgren et al. 2016, Robinson et al. 2018a, Berigan et al. 2022). Historical (1901 to 2015) mean monthly temperatures ranged from -10.8°C to 29.9°C , and annual precipitation ranged from 23.0 to 84.3 cm ($\bar{x} = 50.1$ cm) in Lane County, Kansas. From 2016 to 2022, mean monthly temperatures ranged from -3.5°C to 27.6°C , and annual precipitation ranged from 20.3 to 60.6 cm (Lane County, Kansas; National Oceanic and Atmospheric Administration [NOAA] 2023).

Vegetation at capture sites primarily reflected the composition of the native short-grass prairie, but also contained species from mixed-grass prairie and CRP (Sullins 2017, Berigan 2019). Common grass species included little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), composite dropseed (*Sporobolus compositus*), western wheatgrass (*Pascopyrum smithii*), sideoats grama (*Bouteloua curtipendula*), buffalograss (*B. dactyloides*), blue grama (*B. gracilis*), hairy grama (*B. hirsuta*), sand dropseed (*Sporobolus cryptandrus*), and inland saltgrass (*Distichlis spicata*). Forb species included slimflower scurfpea (*Psoralidium tenuiflorum*), winterfat (*Krascheninnikovia lanata*), western ragweed (*Ambrosia psilostachya*), broom snakeweed (*Gutierrezia sarothrae*), white heath aster (*Symphyotrichum ericoides*), common prickly pear (*Opuntia monacantha*), and field sagewort (*Artemisia campestris*; McGregor and Barkley 1986). The dominant shrub species was sand sagebrush (*Artemisia filifolia*; Fields et al. 2006, Berigan et al. 2022). Planted CRP grasslands in Kansas were seeded with a native grass-forb mixture since 1986. These grass species included little bluestem, sideoats grama, big bluestem, switchgrass, western wheatgrass, blue grama, buffalograss, and indiangrass (*Sorghastrum nutans*). Forb species planted since 1996 included alfalfa (*Medicago sativa*), Maximillian sunflower (*Helianthus maximiliani*), white sweet clover (*Melilotus alba*), yellow sweet clover (*M. officinalis*), purple prairie clover (*Dalea purpurea*), upright prairie coneflower (*Ratibida columnifera*), and prairie bundleflower (*Desmanthus illinoensis*; Fields et al. 2006, Berigan et al. 2022).

Release area

We released lesser prairie-chickens on either historic lek locations or areas of grassland capable of providing nesting habitat on the Comanche and Cimarron National Grasslands in Baca County, Colorado, and Morton County, Kansas, USA, respectively (Figure 1). We delineated study area boundaries by creating a minimum convex polygon around all locations from released birds marked with transmitters once initial dispersal following release ended and birds had established a stable home range (Teige 2021). The study area was 913,320 ha and comprised of 13% CRP, 10% National Grasslands, 29% private native grass or shrubland, 46% cropland, and 2% other land cover type (roads, water, etc.; Teige 2021). Greater than 25% of the Sand Sagebrush Prairie Ecoregion was encompassed by the study area. Generally, the landscape was characterized by rolling sand dunes covered with a gradient of shrubby vegetation at elevations that ranged from 942 to 1,474 m (USGS 2018, Locklear 2021). Vegetation on Comanche and Cimarron National Grasslands was sand sagebrush prairie, with patches ranging from sparse to abundant densities of sand sagebrush. Vegetation composition and structure on the National Grasslands was largely dependent on grazing intensity and soil type (Berigan et al. 2022). Composition included both short- and mixed-grass prairie interspersed with tall grasses and sand sagebrush. Common grass species included sand dropseed, sand love grass (*Eragrostis trichodes*), little bluestem, blue grama, buffalograss, western wheatgrass, and sand bluestem (*Andropogon hallii*). Forb species included evening primrose (*Calylophus serrulatus*), buffalo bur (*Solanum rostratum*), buffalo gourd (*Cucurbita foetidissima*), yucca (*Yucca glauca*), blazing star (*Liatris* spp.), western ragweed, prairie sunflower (*Helianthus petiolaris*), annual sunflower (*H. annuus*), camphorweed (*Heterotheca subaxillaris*), Indian blanket flower (*Gaillardia pulchella*), Russian thistle (*Salsola tragus*), pigweed (*Amaranthus hybridus*), tansy aster (*Machaeranthera tanacetifolia*), bush morning glory (*Ipomoea leptophylla*), fumewort (*Corydalis solida*), and toothed spurge (*Euphorbia dentate*; Teige 2021, Berigan et al. 2022). The shrub community was dominated by sand sagebrush (Haukos and Zavaleta 2016). Vegetation in CRP fields surrounding the National Grasslands was similar to vegetation in CRP fields of the capture study area. Historical (1901 to 2015) mean monthly temperatures ranged from -7.3 to 29.6°C , and annual precipitation ranged from 21.9 to 70.5 cm ($\bar{x} = 42.8$ cm) in Morton County, Kansas. During 2016 to 2022, mean monthly temperatures ranged from -2.3 to 27.7°C , and mean annual precipitation was

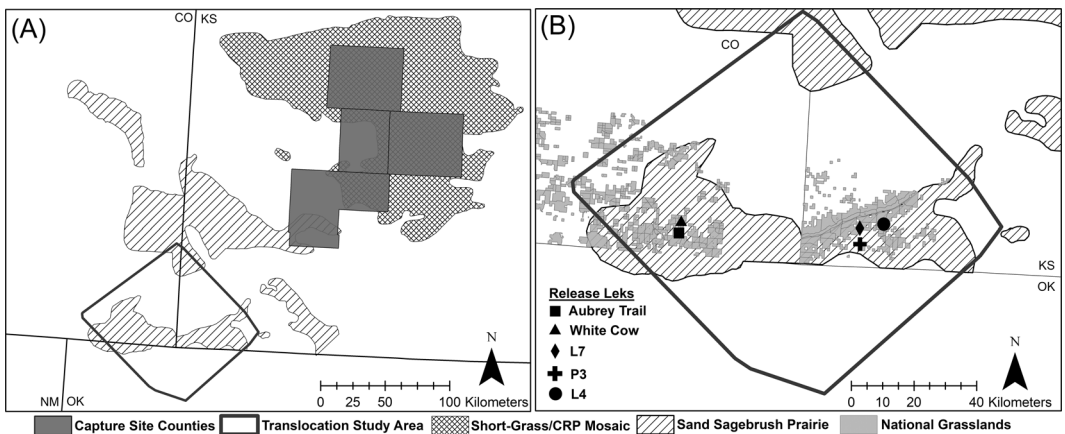


FIGURE 1 (A) Lesser prairie-chickens (*Tympanuchus pallidicinctus*) were captured in the Short-Grass Prairie/CRP Mosaic Ecoregion Kansas, USA, counties of Gove, Finney, Lane, and Ness during 2016–2019. (B) Lesser prairie-chickens were released at either active or historic leks on the U.S. Forest Service, Cimarron or Comanche National Grasslands, in Kansas (KS) and Colorado (CO), USA, respectively, during 2016–2019 in the Sand Sagebrush Prairie Ecoregion. (B) Release sites used were as follows: Aubrey Trail (2016–2017) and White Cow (2018–2019) in Colorado; P3 (2016–2018), L7 (2018) and L4 (2019) in Kansas. The study area polygon was made by encompassing translocated lesser prairie-chicken settled home ranges.

59.4 cm in 2017, 50.1 cm in 2018, 41.3 cm in 2019, 29.9 cm in 2020, 35.3 cm in 2021, and 28.8 cm in 2022 (Morton County, Kansas, and Baca County, Colorado; NOAA 2023).

METHODS

Capture

We captured lesser prairie-chickens on leks during September–October (2016) and March–April (2017–2019) in 4 northwestern Kansas counties within the Short-Grass Prairie/CRP Mosaic Ecoregion using walk-in funnel traps and tension or magnetic drop nets (Haukos et al. 1990, Silvy et al. 1990; Figure 1). Fall lekking is not well described in recent peer-reviewed literature but is well-known local management knowledge and described historically (Copelin 1963, Smith 1979, Ahlborn 1980, Taylor and Guthery 1980). The reason lesser prairie-chickens display in the fall is largely unknown (Haukos and Boal 2016). The abundance of males and overall fall lekking activity is reduced compared to spring, with rare attendance by females making fall capture efforts more difficult than spring (Haukos and Boal 2016). The goal of translocating males during fall 2016 was to augment the number of males associated with leks at the release site prior to the larger translocation effort starting spring 2017, which would potentially increase the likelihood for attraction to local conspecifics and settling near release locations (Rogers 1992). We fit male and female lesser prairie-chickens with either a 12- or 15-g, bib-style very-high-frequency (VHF) transmitter (RI-2B Holohil Systems Ltd., Carp, Ontario, Canada, or Series A3960, Advanced Telemetry System, Isanti, MN, USA) or a rump-mounted 22-g, Satellite Platform Transmitting Terminal GPS (SAT-PTT) transmitter (PTT-100, Microwave Telemetry, Columbia, MD, USA). All transmitters were <5% of an individual bird's body mass (Fair et al. 2010, Berigan et al. 2022). We attached SAT-PTT transmitters using leg harnesses made of tubular Teflon® ribbon for durability and sewn in elastic for maneuverability (Bedrosian and Craighead 2010, Dzialak et al. 2011, Sullins 2017, Lautenbach et al. 2021). We determined sex of each bird from plumage and behavior on lek, and aged birds as second-year (SY) or after-second-year (ASY) via the molt characteristics of the outer primary feathers (Ammann 1944). We marked individuals with a numbered aluminum leg band and a unique combination of plastic color bands for identification and resighting (Copelin 1963).

We released birds within 11 hours of capture on the Cimarron or Comanche National Grasslands. During transportation to release sites we minimized unnecessary noise and stops, and kept vehicle temperatures cool to reduce bird stress. Chosen release sites were reviewed annually and consisted of either historic lek locations or landscapes containing quality nesting habitat based on visual assessment of robust residual vegetation (Figure 1).

Monitoring

We monitored male and female lesser prairie-chickens during the breeding (Mar 15–Sep 15) and nonbreeding (Sep 16–Mar 14) seasons during April 2017–August 2020 (Robinson et al. 2018b, Lautenbach et al. 2021). Birds fitted with a VHF transmitter were located ≥ 3 times per week using triangulation from 3–5 observer locations via handheld Yagi antennas and radio receivers (R4000, R410—Advanced Telemetry System, Isanti, MN, USA, or R1000—Communications Specialists, Orange, CA, USA). Triangulation consisted of ≥ 3 compass bearings ≥ 15 degrees apart and within 20 minutes to decrease error from bird movement. We estimated locations and associated error with Location Of A Signal software (LOAS; Ecological Software Solutions, Hegymagas, Hungary). A fixed-wing aircraft was used approximately monthly to locate individuals with VHF transmitters that had dispersed and could not be found by ground scanning. Birds fitted with SAT-PTT transmitters had 8 to 10 GPS locations recorded per day in 2-hour intervals between 0600 and 2200 (18-m accuracy). Locations were uploaded to the Argos satellite system every 3 days and downloaded weekly (Sullins et al. 2018, Robinson et al. 2018b).

Survival

We confirmed adult mortality events by either a signal change for VHF transmitters (within 2 days) or activity and movement data from SAT-PTT transmitters (within 7 days). We investigated mortalities immediately after seeking landowner permission to access carcasses. Once the mortality site or transmitter was located, we classified cause of death as mammalian predator, avian predator, weather related, collision, or unknown causes following Hagen et al. (2007). We concluded a mammalian predator based on bite marks on transmitters and leg bands, feathers matted with saliva, cached carcasses, and nearby tracks or scat. Avian predators were identified via piles of plucked feathers, decapitated carcasses, removal of breast tissue, and transmitters without tooth marks (especially with transmitter straps intact). Evidence of a weather mortality (i.e., hail) were apparent injuries to the back and neck immediately following a large storm event. Mortalities with conflicting evidence, deficient evidence, or on properties where we were denied permission to access were labeled as unknown.

We used known-fate models to estimate weekly adult survival for both male and female translocated lesser prairie-chickens using Program MARK as it allows for staggered entry (White and Burnham 1999). We did not evaluate birds translocated in fall 2016 that died before 15 March 2017 due to infrequent monitoring. Following Hagen et al. (2007), we censored birds that did not survive 2 weeks post release as those mortalities were likely due to capture, handling, and translocation stress. Due to large dispersal movements following release (\bar{x} = 144 km, min–max = 1–374 km; Berigan 2019), some VHF-marked birds were not found each week. At times, we were unable to locate VHF-marked birds for extended periods. Translocated individuals that went missing or slipped collars and were not confirmed mortalities were included as alive until their last known alive week and then right censored from the model. When birds were missing for several weeks and then found as a mortality, we estimated mortality date by determining the median week between the last known alive week and the week the mortality was found (n = 67; Mayfield 1961, Musil et al. 1993).

We investigated several *a priori* selected variables that may influence lesser prairie-chicken survival including the following: release site (KS, CO), transmitter type (VHF, SAT-PTT), sex (male, female), week of mortality, and additive and interactive combinations of these variables. Release site was grouped into broader categories of state due to differences between frequency of use and number of individual release sites between states. We evaluated year and bird age in an exploratory analysis and determined them not to be influential and removed them from consideration (Teige 2021). We developed 2 model sets—the breeding season (Mar 15–Sep 15) and nonbreeding season (Sep 16–Mar 14). For both model sets, we fit candidate models (n = 15 for each) for adult survival and ranked them using Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002). Model weight (w_i), beta coefficients (β), and 95% confidence intervals (CI) were evaluated from competitive models where $\Delta AIC_c \leq 2$.

Lek surveys

We monitored lekking activity during March 15–May 31 (lekking season) from 2017 to 2022 and report maximum male high count as an index of population trends in our study area. A lek is often defined as having 3 or more males displaying (Haukos and Boal 2016), but due to dispersal behavior of released birds after translocation, leks were defined as locations where at least one male displaying was observed. We surveyed for leks on the ground throughout the study area by listening for calls between sunrise and 1000 Central Daylight Savings Time, during favorable weather conditions (e.g., wind <24 km/h; no concurrent precipitation; Parker et al. 2022). Leks were also located using marked female and male birds and concentrations of telemetry locations. When needed, we flushed individuals to determine a count of male attendance and reported the maximum male count for each year it was surveyed. Each year, we conducted lek surveys in the study area after spring translocation effort ceased. We expected relatively greater maximum male counts and number of leks during 2017–2019 as surveys occurred

following translocation releases. Leks were visited ≥ 2 times during the season to derive an accurate maximum count of male attendance. If leks were active for multiple years, we revisited them annually to assess trends in maximum male counts. We attempted fall lek surveys opportunistically, but birds were rarely heard displaying and flushes in the fall were avoided to reduce stress on translocated and young lesser prairie-chickens.

RESULTS

Capture

We translocated 411 lesser prairie-chickens, generally distributed evenly between Cimarron and Comanche National Grasslands with the majority (73%) released during 2018 and 2019 (Table 1). Twenty-six males and one female were captured and translocated in the fall of 2016, with the primary objective to establish leks on which to release lesser prairie-chickens and minimize dispersal of birds translocated during the following spring. Of the 411 birds translocated, 394 were marked with transmitters (279 VHF and 115 SAT-PTT) and 17 males were banded only due to all transmitters being deployed near the end of the trapping effort in 2019. Females received 54% of the SAT-PTT transmitters due to their reproductive importance; however, SAT-PTT transmitters were only deployed in 2018 and 2019. Range-wide aerial population surveys indicated that our translocation effort did not negatively affect the source population (Nasman et al. 2022).

Adult survival

Of the 394 birds with transmitters, 27% ($n = 106$; 46 females, 60 males) survived one-year post-translocation to the following breeding season and 5% ($n = 19$; 5 females, 14 males) survived to the breeding season 2 years post translocation. Only one male, which was translocated in fall 2016, survived to a second nonbreeding season.

For the adult survival analysis, 126 birds were censored from analysis because they died within 2 weeks of release ($n = 54$; 28 SAT-PTT, 26 VHF); were not found after release ($n = 40$; 1 SAT-PTT, 39 VHF); were determined to have a slipped transmitter within 2 weeks of release ($n = 9$; 2 SAT-PTT, 7 VHF); were released in the fall 2016 and did not survive to 15 March 2017 ($n = 6$; all VHF); or did not have transmitters when released and could not be monitored ($n = 17$). A total of 285 translocated lesser prairie-chickens were used for the known-fate survival analyses. Of those birds, 200 (70.2%) were equipped with VHF transmitters and 85 (29.8%) with SAT-PTT transmitters.

TABLE 1 Total number of lesser prairie-chickens (*Tympanuchus pallidicinctus*) translocated to the U.S. Forest Service Cimarron and Comanche National Grasslands (NG) in Kansas and Colorado, USA, respectively, during 2016–2019. Birds are categorized by release site (Cimarron, Comanche), sex (Male, Female), and year (2016, 2017, 2018, 2019).

	Cimarron NG		Comanche NG		Annual total
	Male	Female	Male	Female	
Fall 2016	13	0	13	1	27
Spring 2017	16	19	29	19	83
Spring 2018	32	37	39	36	144
Spring 2019	40	49	22	46	157
Release site total	101	105	103	102	411

The most-supported breeding season model was the effect of week on survival, suggesting that weekly survival varied throughout the breeding season (Table 2, Figure 2). The weekly survival model was 1.41 times more likely than the next ranked model that suggested survival varied by release site and week. The second ranked model ($\Delta AIC_c < 2.0$) suggested that birds released in Colorado had greater survival during the breeding season than birds released in Kansas; however, the beta coefficient for release site did not differ from zero and was not informative ($\beta = -0.27$, $SE = 0.15$, $95\% CI = -0.56-0.023$). We report the derived survival estimates based on sex for comparison with other studies even though the model was not supported. Females and males had a breeding season survival rate of 0.44 ± 0.03 ($95\% CI = 0.38-0.50$) and 0.45 ± 0.04 ($95\% CI = 0.37-0.53$), respectively; breeding season survival rate for both sexes combined was 0.44 ± 0.02 ($95\% CI = 0.42-0.46$).

The most supported and only competitive model for the nonbreeding season suggested survival varied by week (Table 3, Figure 3). The competitive model was 5.15 times more likely than the next model, which suggested survival varied by release site and week. Although not the most supported model, we report the derived survival estimates based on sex for comparison with other studies. Females and males had a nonbreeding season survival rate of 0.55 ± 0.04 ($95\% CI = 0.47-0.63$) and 0.56 ± 0.06 ($95\% CI = 0.44-0.68$), respectively and nonbreeding survival rate of both sexes combined was 0.55 ± 0.03 ($95\% CI = 0.52-0.58$).

TABLE 2 *A priori* candidate models used to estimate breeding season (Mar 15–Sep 15) survival for translocated adult lesser prairie-chickens (*Tympanuchus pallidicinctus*) translocated to U.S. Forest Service, Cimarron and Comanche National Grasslands, in Kansas and Colorado, USA, respectively, during 2017–2020. Models include variable combinations of release site (KS, CO), transmitter type (VHF, SAT-PTT), sex (male, female), week, and null (intercept only).

Model	K^a	ΔAIC_c^c	AIC_c^b	w_i^d	Deviance ^e
Week	26	0.00	2,038.53	0.41	137.13
Release site + Week	28	0.66	2,039.19	0.29	133.76
Sex * Transmitter * Release site + Week	34	2.58	2,041.11	0.11	123.58
Transmitter + Week	28	2.99	2,041.52	0.09	136.08
Sex + Week	28	3.94	2,042.46	0.06	137.03
Sex * Transmitter + Week	30	4.65	2,043.18	0.04	133.72
Transmitter * Week	52	35.35	2,073.88	0.00	119.94
Sex * Transmitter * Week	104	99.62	2,138.15	0.00	78.07
Sex * Transmitter * Release site	8	103.69	2,142.22	0.00	276.98
Release site	2	107.01	2,145.54	0.00	292.32
Transmitter	2	109.51	2,148.04	0.00	294.82
Sex * Transmitter	4	109.66	2,148.19	0.00	290.97
Null	1	109.93	2,148.46	0.00	297.24
Sex	2	111.85	2,150.38	0.00	297.16
Transmitter * Release site * Sex * Week	208	238.24	2,276.77	0.00	0.00

^aNumber of parameters.

^bAkaike's Information Criterion, corrected for small sample size.

^cDifference in Akaike's Information Criterion, corrected for small sample size.

^dAkaike weights.

^eDeviance or $-2 \times \log$ likelihood.

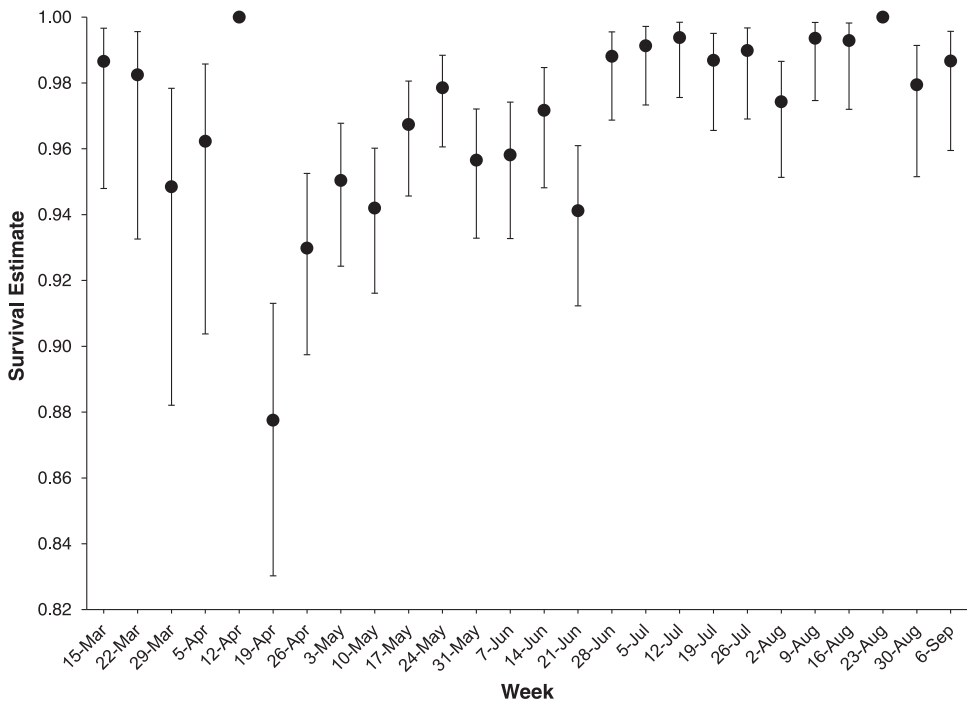


FIGURE 2 Estimated weekly survival estimates with 95% confidence intervals during the breeding season (15 Mar–15 Sep) for male and female lesser prairie-chickens (*Tympanuchus pallidicinctus*) translocated to the U.S. Forest Service, Cimarron and Comanche National Grasslands, in Kansas and Colorado, USA, respectively, during 2017–2020 in the Sand Sagebrush Prairie Ecoregion.

We investigated cause of mortality for 177 translocated lesser prairie-chickens during 2017–2020. During the breeding season, mammalian predation dominated mortality for both male and female lesser prairie-chickens (Table 4). In the nonbreeding season, avian predation dominated for females and mammalian predation dominated for males. For sexes combined over the duration of the study, 41.2% of mortalities were mammalian, 27.1% were avian, 1.6% were weather-related, 0.5% were from vehicle collision, and 29.3% were unknown (Table 4).

Lek surveys

All known leks within our study area developed after translocation with the exception of a single lek, which was on average $70 \text{ km} \pm 2$ (SE) from any release site (min–max = 65–77 km; Table 5). Of all translocated males, 53% were known to be near or displaying on leks. Of the males available to be detected lekking ($n = 126$), ~77% participated in lekking activity. Total number of leks and maximum male counts in the study area increased by 250% and 340%, respectively, by 2020. However, by 2022 the number of active leks had decreased by 48% and maximum male counts decreased 39% from the 2020 peak. The greatest maximum male count was 122 males at 21 leks across the study area in 2020. In 2022, there were only 48 males and 10 active leks detected in the study area (Table 5). Average maximum male counts on leks peaked at 6.42 ± 1.01 (SE; min–max = 2–11) males per occupied lek in 2019 during on-going translocation but decreased to 4.80 ± 3.22 (SE) by 2022 (min–max = 2–10), 3 years post translocation. Generally, leks with consistently more males persisted longer than leks with lower maximum male counts. Leks were established by translocated lesser prairie-chickens on average $39.2 \text{ km} \pm 2$ (SE; min–max = 0.0–77.0 km) from any of the release sites. Over the study period, 7 of the 29 total leks established were on the Comanche and Cimarron National Grasslands.

TABLE 3 *A priori* candidate models used to estimate nonbreeding season (Sep 16–Mar 14) survival for translocated adult lesser prairie-chickens (*Tympanuchus pallidicinctus*) translocated to U.S. Forest Service, Cimarron and Comanche National Grasslands, in Kansas and Colorado, USA, respectively, during 2017–2020. Models include variable combinations of release site (KS, CO), transmitter type (VHF, SAT-PTT), sex (male, female), week, and null (intercept only).

Model	K^a	ΔAIC_c^c	AIC_c^b	w_i^d	Deviance ^e
Week	26	0.00	1,031.42	0.67	124.03
Release site + Week	28	3.28	1,034.70	0.13	123.26
Transmitter + Week	28	3.83	1,035.25	0.10	123.81
Sex + Week	28	4.02	1,035.44	0.09	124.00
Sex * Transmitter + Week	30	7.87	1,039.29	0.01	123.80
Null	1	12.46	1,043.88	0.00	186.78
Transmitter * Release site * Sex + Week	34	12.55	1,043.97	0.00	120.37
Release site	2	13.78	1,045.20	0.00	186.10
Transmitter	2	14.14	1,045.56	0.00	186.46
Sex	2	14.43	1,045.85	0.00	186.74
Sex * Transmitter	4	18.09	1,049.51	0.00	186.40
Sex * Transmitter * Release site	8	23.23	1,054.65	0.00	183.52
Transmitter * Week	52	41.38	1,072.80	0.00	112.54
Sex * Transmitter * Week	104	97.42	1,128.84	0.00	61.11
Transmitter * Release site * Sex * Week	208	258.51	1,289.93	0.00	0.00

^aNumber of parameters.

^bAkaike's Information Criterion, corrected for small sample size.

^cDifference in Akaike's Information Criterion, corrected for small sample size.

^dAkaike weights.

^eDeviance or $-2 \times \log$ likelihood.

DISCUSSION

Determining success of translocation as a conservation strategy for prairie grouse is challenging. Long-term success of translocation or reintroduction of prairie grouse may take as long as 5–20 years following release to evaluate if a population became established and self-sustaining, and if abundance and occupied range increased (Toepfer et al. 1990). Our study included intensive marking and monitoring of released lesser prairie-chickens, which allowed for an initial assessment of the success of the translocation through survival and lek counts. We recognize that ultimate determination of success will be decided by continued intensive monitoring of annual lek counts within the study area for at least 3–5 more years. However, initial intensive monitoring has allowed more precise insight into lekking behavior and survival of translocated birds, which is vital information to evaluate translocation as a management tool for lesser prairie-chickens.

We documented reduced survival rates for translocated prairie-chickens relative to nontranslocated conspecifics in the Sand Sagebrush Prairie Ecoregion and throughout the lesser prairie-chicken range. Nearly 23% of birds died or were not re-located shortly after release because of large dispersal movements (Berigan 2019). Less than one-third of translocated birds survived to a following breeding season after release and few survived to a second breeding season after release. Survival rates of the translocated population were at the low end of what was

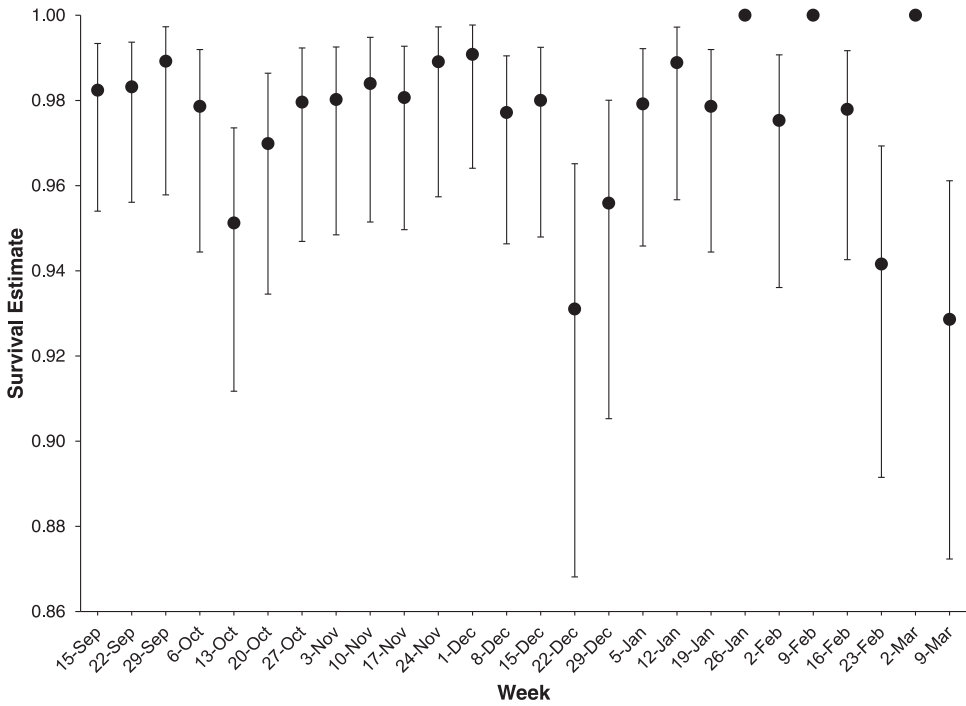


FIGURE 3 Estimated weekly survival estimates with 95% confidence intervals during the nonbreeding season (16 Sep–14 Mar) for male and female lesser prairie-chickens (*Tympanuchus pallidicinctus*) translocated to the U.S. Forest Service, Cimarron and Comanche National Grasslands, in Kansas and Colorado, USA, respectively, during 2017–2020 in the Sand Sagebrush Prairie Ecoregion.

TABLE 4 Cause-specific mortality of lesser prairie-chickens (*Tympanuchus pallidicinctus*; %, n = 177) translocated to U.S. Forest Service, Cimarron and Comanche National Grasslands, in Kansas and Colorado, USA, respectively, by season (Breeding, Nonbreeding) and sex (Female, Male) during 2017–2020. Breeding season was defined as March 15–September 15 and nonbreeding season was September 16–March 14.

	Mammal	Avian	Unknown	Weather	Collison
Breeding season					
Female (n = 72)	48.6	26.4	22.2	1.4	1.4 ^a
Male (n = 47)	40.4	25.5	29.8	4.3	-
Nonbreeding season					
Female (n = 31)	25.8	35.5	38.7	-	-
Male (n = 27)	40.7	22.2	37.1	-	-

^aVehicle collision—found on road.

expected during years of favorable environmental conditions. The stress of capture, transportation, and dispersal following release on lesser prairie-chickens produces challenges for creating a self-sustaining population through translocation (Ross et al. 2016, 2018). These difficulties may be further exacerbated by the initial low abundance and scattered occurrence of lesser prairie-chickens within the Sand Sagebrush Prairie Ecoregion.

Estimating adult survival throughout the translocation process provides valuable information on translocation success. The largest initial obstacle of our targeted translocation was mortality and dispersal of lesser prairie-chickens

following release. The total loss of over a fifth of translocated birds within the first 2 weeks following release was most likely caused by the large initial dispersal movements (≥5 km). Movements averaged 144 km from release sites over a period of 1-2 months and were undertaken by nearly all birds equipped with SAT-PTT (Berigan 2019). It is likely that a similar dispersal pattern occurred with VHF-marked birds but is unconfirmed due to the difficulty locating VHF-marked

TABLE 5 Maximum counts of male lesser prairie-chickens (*Tympanuchus pallidicinctus*) in attendance at occupied leks following translocation in Baca and Prowers counties, Colorado, USA, and Morton and Stanton counties, Kansas, USA, surveyed within the study area from 2017–2022. Leks were surveyed from 15 March–15 May.

State	Lek ID	During Translocation			After Translocation		
		2017	2018	2019	2020	2021	2022
CO	Chihuahua ^a	3	11	11	17	12	7
	Red Roof ^b	4	4	8	9	5	4
	Little Silo	– ^a	– ^a	3	8	5	4
	White Cow ⁺	– ^a	3	8	7	5	0
	Buffalo Point [*]	– ^a	– ^a	– ^a	3	4	2
	Big Bird	– ^a	– ^a	– ^a	– ^a	1	0
	Boston ⁺	– ^a	5	7	8	1	1
	Crossroads	– ^a	– ^a	– ^a	3	0	0
	Vilas Top [*]	– ^a	2	2	0	0	0
	Santa Fe ⁺	– ^a	4	0	0	0	0
	Loamy Plains	3	0	0	0	0	0
KS	Broken Windmill	6	7	12	12	11	10
	Yukon [*]	7	– ^a	– ^a	8	8	10
	Wheaties [*]	– ^a	– ^a	9	8	3	5
	L48 ⁺	– ^a	– ^a	– ^a	2	0	3
	L4 ^{*,+}	– ^a	– ^a	2	0	3	2
	Circus	5	9	6	5	0	0
	Lost	3	4	0	0	0	0
	Kanorado	– ^a	3	2	0	0	0
	T3	– ^a	3	– ^a	5	2	0
	Conestoga	– ^a	– ^a	7	4	0	0
	Connie48 ^c	– ^a	– ^a	– ^a	– ^a	3	0
	Bluestem [*]	– ^a	– ^a	– ^a	2	2	0
	Llama	– ^a	– ^a	– ^a	2	– ^a	0
	Stanton	– ^a	– ^a	– ^a	4	0	0
	Hail	– ^a	– ^a	– ^a	5	0	0
X	– ^a	– ^a	– ^a	2	0	0	
L47 ⁺	– ^a	– ^a	– ^a	3	2	0	

(Continues)

TABLE 5 (Continued)

State	Lek ID	During Translocation			After Translocation		
		2017	2018	2019	2020	2021	2022
	Saunders ^a	- ^a	- ^a	- ^a	5	3	0
Total		31	55	77	122	70	48

^aLek location shifted (<800 m) throughout the duration of the study.

[†]Lek present on U.S. Forest Service Comanche and Cimarron National Grasslands.

^aLek not surveyed, not currently found, or not possibly formed yet.

^bActive native bird lek prior to translocation (confirmed translocated birds attended).

^cConnie48 is a merged lek of Conestoga and L48.

birds after release. It is important to note, however, that the overall proportion of VHF and SAT-PTT transmitters used in our study (71% VHF; 29% SAT-PTT) corresponded with the proportion of marked birds that died or went missing during the 2 weeks after release (69% VHF; 31% SAT-PTT), and we did not find that transmitter type affected adult survival. Work on nontranslocated lesser prairie-chickens and translocated Gunnison sage-grouse (*Centrocercus minimus*) also did not find a difference in survival between transmitter types (Plumb 2015, Robinson et al. 2018a, Lawrence et al. 2021, Apa et al. 2022).

Comparing our findings to other lesser prairie-chicken translocations is difficult because little information is known about survival estimates from previous translocation efforts (Snyder et al. 1999, Giesen 2000). However, translocations of other prairie grouse have reported similar responses following release. Greater sage-grouse (*Centrocercus urophasianus*) translocations with a similar methodology to our study have shown a range of mortality (4–9%; Musil et al. 1993, Baxter et al. 2008, Gruber-Hadden et al. 2016) and the inability to relocate released birds (13–18.2%; Gruber-Hadden et al. 2016, Musil et al. 1993, respectively) 2 to 3 weeks post release. Greater prairie-chickens translocated to Iowa and Missouri, USA, showed similar initial mortality patterns to translocated lesser prairie-chickens, with 24% of translocated birds dying during initial dispersal movements following release and a single bird moving >4,000 km before settling (Kemink and Kesler 2013, Vogel et al. 2015). Similarly, 13% of translocated greater prairie-chickens in Missouri were not found after release (Carrlson et al. 2014). A translocation effort of >200 Columbian sharp-tail grouse (*T. phasianellus columbianus*) in Nevada, USA, reported survival rates were lowest initially after release (Mathews et al. 2016). Considerable loss of translocated prairie grouse to dispersal and mortality immediately following release appears unavoidable and makes the success of translocation efforts uncertain.

We did not find a difference in survival between male and female translocated birds during the breeding and nonbreeding season. However, differences in survival between sexes during the breeding season is common among nontranslocated lesser prairie-chickens (Patten et al. 2005, Hagen et al. 2007, Grisham and Boal 2015, Plumb 2015, Lawrence et al. 2021). Our study's lack of difference in survival between male and female translocated lesser prairie-chickens may be caused by several factors, including the uniform stressor of adapting to a novel landscape, limited quality vegetation surrounding release sites (Berigan et al. 2022), and density of anthropogenic structures on the landscape (Vhay 2022), all of which may have short- and long-term effects on survival (Robinson et al. 2018a, Lawrence et al. 2021).

Our results indicate that translocated lesser-prairie chickens have lower breeding season survival rates than nontranslocated birds, which has been reported for other translocated prairie grouse. Breeding season survival for translocated lesser prairie-chickens in our study was considerably lower than nontranslocated lesser prairie-chicken breeding season survival estimates from the Sand Sagebrush Prairie Ecoregion (0.63–0.93; Haukos and Zavaleta 2016). In other grouse translocation studies, translocated greater prairie-chickens in Missouri had a breeding season survival rate of 48% compared to 69% for nontranslocated birds (Kemink 2012). Spring

translocated Gunnison sage-grouse had lower survival during the first 75 days following release than during the remainder of the first year (Apa et al. 2022). Similarly, translocated Columbian sharp-tail grouse had a survival rate of 42% for adults and 67% for yearlings during the breeding season, with substantially greater mortality for the 40-50 days after release (Mathews et al. 2016, 2022). Within the breeding season, we found adult survival was lowest the third week of April, and was lower than survival estimates for females during that week in nontranslocated birds (~0.92; Plumb 2015). Survival is often lower during this time period due to females transitioning from lek visitation to nest site identification and initiation, but translocated survival may be further reduced due to individuals that perished shortly after release. The overall lowered breeding season survival of translocated lesser prairie-chickens could lead to reduced population recruitment, but more work monitoring specific reproductive demographic rates, such as nest and brood survival, is needed to understand which life stages are affecting dynamics of the translocated population most. Furthermore, connecting vital rates and habitat use (Sullins et al. 2018) and comparing different habitat use between nontranslocated and translocated birds (see Berigan et al. 2022), will help to elucidate whether translocation can be effective for establishment and growth of lesser prairie-chicken populations.

Nonbreeding season survival is not well documented for lesser prairie-chickens. Studies throughout the species occupied range have shown nonbreeding survival to range 0.43–0.87 for the 6-month period (Haukos and Zavaleta 2016). Using similar survival estimate methods to our study, Robinson et al. (2018b) estimated an average nonbreeding survival rate for females of 0.73 across the northern extent of the lesser prairie-chicken range. The nonbreeding season survival rate for translocated males and females combined was on the lower end of previous estimates, but not substantially lower than survival for resident populations. It is unlikely that slightly lower nonbreeding survival for translocated birds affected translocation success as nonbreeding survival is not considered a limiting factor for lesser prairie-chicken population persistence (Dahlgren et al. 2016, Robinson et al. 2018b). Nonbreeding season survival was lowest during the fourth week of December and the last week of the nonbreeding season. Survival typically declines at the end of the nonbreeding season due to movement related to initially finding and displaying at leks by males as the breeding season approaches (Haukos and Boal 2016). Overall, these results suggest that high mortality immediately following release and lowered survival in the breeding season likely had stronger effects on translocation success than nonbreeding survival.

Annual maximum counts of male attendance at leks are an index of overall population trends, and when coupled with lek distribution, persistence, and abundance, can be important to understanding translocation success. All known leks within our study area developed after translocation with the exception of a single lek. Translocated males occupied leks nearly 40 km away from the release sites. Throughout the study, males shifted lek locations up to 800 m and many leks were ephemeral, with over a third of total leks becoming unoccupied within one year. The large distance between the release sites and lek sites and the ephemeral nature of lek sites are likely due to a combination of initial dispersal following release (Berigan 2019), female space use and nest site selection influencing lek placement (Aulicky 2020), and potential lack of quality nesting habitat surrounding release sites (Gehrt et al. 2020, Berigan et al. 2022). Lek surveys in the study area were conducted after spring translocation effort ceased and, therefore, relatively greater maximum male counts and number of leks during years of ongoing translocation were expected. Although male counts peaked the year after translocation ceased, this may be due to increased lek search effort in spring 2020 because the translocation effort ended the year before. Up to 10 leks found in 2020 may have been established in previous years, potentially inflating the number of new leks in 2020. However, leks first reported in 2020 only supported ~25% of all males counted in 2020 with an average of 3 birds/lek, and many were likely ephemeral leks as only 2 remained active in 2022.

By 2022, >50% of the leks in the study area became inactive and remaining leks had reduced male maximum counts. Lek count fluctuations could be a result of the boom-bust nature of lesser prairie-chicken population response to annual precipitation (Ross et al. 2018). Environmental conditions for survival and recruitment were optimal for the Sand Sagebrush Prairie Ecoregion from 2016–2019, but decreased precipitation during 2020 and 2021 may have reduced reproductive success. However, lesser prairie-chicken population trends based on aerial

surveys in the Sand Sagebrush Prairie Ecoregion from 2017–2022 were opposite of our translocation lek count trends over the same time period, suggesting translocation population declines were not from environmental factors alone (Nasman et al. 2022). Although information on demographic vital rates including lek counts is difficult to obtain for unsuccessful translocations, a translocation of greater prairie-chickens to northeast North Dakota found leks and number of males on leks declined 10 years after a 6-year, 360 bird effort (Huschle and Toepfer 2020). Similarly, our study's lek counts in 2023 have continued to decline although exact numbers have not been released.

It has been previously suggested that translocations releasing ≥ 100 birds could be more successful for prairie grouse (Snyder et al. 1999). However, our results show that >400 birds may be necessary, especially for areas with little to no resident population or existing leks. Alternative procedures to our study could be considered for future translocations (e.g., soft release or brood translocation; Rodgers 1992, Snyder et al. 1999, Ruzicka et al. 2017, Meyerpeter et al. 2021), but in using these methods it may be difficult to obtain a sufficient number of birds for a successful translocation and such efforts are costly and time consuming. Further, as low overall population estimates of lesser prairie-chickens and effects from climate change (e.g., increasing frequency and duration of intensive drought) are expected to increase, a continued translocation effort may eventually reach a threshold that is detrimental to source populations.

MANAGEMENT IMPLICATIONS

Our large-scale translocation effort showed initial promise by increasing lek and male high counts, but abundance of lesser prairie-chickens in the study area decreased quickly after translocation ceased, suggesting uncertainty about the long-term success of translocation as a management strategy. Before translocation, managers may benefit by considering other management strategies, including habitat restoration targeted in areas with the greatest lesser prairie-chicken densities and scaling up habitat restoration to appropriate scales in those areas. Definitive evidence for ecological causes and limiting factors resulting in declines of lesser prairie-chickens in the Sand Sagebrush Prairie Ecoregion remains elusive. Until factors known to limit lesser prairie-chicken populations in this ecoregion are determined and addressed through conservation actions, we would expect similar results for future translocations intended to increase population abundance and occupied range in the ecoregion.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Our research was conducted in accordance with guidelines on the use of wild birds in research and in compliance with state and federal regulations (Fair et al. 2010). All handling and capture protocols were completed and approved by the Kansas State University Institutional Animal Care and Use Committee Permit #3703, Kansas Scientific Wildlife Permits SC-024-2018 and SC-015-2019, and Colorado Scientific Wildlife Permits SC-128-2016, SC-079-2017, SC-076-2018, and SC-077-2019. All capture and intensive monitoring happened during 2017–2020, before the lesser prairie-chicken was listed as endangered or threatened under the Endangered Species Act.

DATA AVAILABILITY STATEMENT

Data available on reasonable request from the authors.

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