Dispersal, reproductive success, and habitat use by translocated lesser prairie-chickens

by

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Abstract

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations in the Sand Sagebrush Prairie Ecoregion have reached historic lows in the last decade. Former core areas of the ecoregion, such as the U.S. Forest Service Cimarron and Comanche National Grasslands in southwestern Kansas and southeastern Colorado, have reached population densities so low that populations will not be able to recover without a new source of birds. In an attempt to recolonize previously occupied areas in the region, Colorado Parks and Wildlife and Kansas Department of Wildlife, Parks, and Tourism translocated 411 lesser prairie-chickens to the National Grasslands between fall 2016 and spring 2019. For a translocation project to be successful, translocated birds need to stay near the release site, find habitat that meets their survival requirements, and successfully reproduce. I assessed the success of the translocation project to determine which of these requirements were met following release to meet the goal of increasing lesser prairie-chicken density on the National Grasslands and define potential obstacles for future translocation projects. I estimated nest success of lesser prairie-chickens translocated to the National Grasslands using Program MARK and determined those factors important in predicting nest success. I found that the number of years that had elapsed since the bird's release was the best predictor of its nesting success in any given year. This fits with existing literature on grouse translocations, which state that translocation effects dissipate in years following release. Unfortunately, only 10.3% of translocated birds survived into the second year to take advantage of the increased nest success rate. My analysis of lesser prairie-chicken movement after release showed extensive dispersal away from the release site, with 99% of birds undergoing a dispersal movement >5 km from the release site. I conducted a behavioral change point analysis on translocated birds as they dispersed to determine where they settled down and how long their

dispersal lasted. Birds moved an average of 144 km during their 1-2 month dispersal movement following release. Despite the presence of leks and habitat at the release sites, 69% of released birds settled >5 km from their release site after their movements. These results indicate that dispersal is an innate response to translocation, and release site placement will not be sufficient to minimize the dispersal movement.

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Chapter 1 - Influence of habitat, dispersal, and adjusting effects on the nest survival of lesser prairie-chickens after translocation

Introduction

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations are in a rapid decline throughout most of their range. The current status of the species has attracted considerable attention from state and federal authorities. Despite being a species of conservation concern, significant doubt remains regarding the efficacy of some management techniques for lesser prairie-chicken populations. Of interest is the potential for translocation to increase population densities or re-establish populations in previously occupied range, which has had mixed success for lesser prairie-chickens despite evidence of success in other prairie grouse species (Giesen 1994, Snyder et al. 1999). Past lesser prairie-chicken translocation efforts have not monitored the introduced population beyond lek counts at the release site in subsequent years, so reasons for the failure of translocations for this species are poorly understood. As lesser prairie-chicken populations across their range continue to decline and local extirpations occur, significant interest exists in determining if translocation of this at-risk species might be a valid management option, and, if so, how to maximize the probability of success (Hagen et al. 2004).

Nest survival is important to the success of lesser prairie-chicken translocations due to the species' short lifespan. Lesser prairie-chickens live to a mean age of 1.95 years (Van Pelt et al. 2013). Therefore, annual reproductive success of individual birds is of special significance to a population's persistence and a measure of translocation success. Translocated hens will likely only have one or two nesting seasons to reproductively contribute to the supplemented population before mortality. Therefore, reproductive success of female lesser prairie-chickens during those one or two years following release will be critical to the success of any translocation strategy. Factors affecting reproductive success following release include increased mortality risk in a novel environment, uncertain capacity for locating quality nesting and brooding habitat, and dispersal from the release area. Specifically, habitat selection, dispersal following release, and a first-year adjusting effect to a novel environment might reduce lesser prairie-chicken reproductive success following release, jeopardizing translocation success.

Nesting habitat is presumed to be a limiting factor for most lesser prairie-chicken populations (Hagen et al. 2004). Management of nesting habitat at the release site is crucial to the success of a translocation (Moehrenschlager and Lloyd 2016). Habitat quality can be broadly generalized by habitat type, reflecting the difference in vegetation communities and characteristics between U.S. Department of Agriculture Conservation Reserve Program (CRP) grassland and native prairies, including sand sagebrush, short-grass, and mixed-grass prairies (Chapter 2). As some of the habitat types at the release site may not have been present at the capture site, it's important to test if lesser prairie-chickens can nest successfully in habitat types for which they have had no prior exposure. Adaptable plasticity in habitat use is a critical attribute for successful translocations across long distances, making it important to test how well lesser prairie-chickens respond to translocation and adapt to a novel release environment.

Dispersal behavior following release is believed to have contributed to the failure of past lesser prairie-chicken translocations (Jonathan Reitz, pers. comm). Dispersal primarily affects mortality and diffusion of translocated birds away from the release site, but it is also a potentially prominent factor influencing nest site selection and affecting nest success of translocated lesser prairie-chickens. Dispersal is a natural, if infrequent, occurrence in native lesser prairie-chicken populations, which usually consists of female movements typically as a several kilometer exploratory loop or displacement before establishing a new home range (Earl et al. 2016). In translocated birds, however, dispersal following release is ubiquitous, and frequently results in 100-200 km movements before settlement (Chapter 3). This dispersal is accompanied by significant mortality (Chapter 3). Several aspects of dispersal behavior following release have the potential to impede nest success once the movement ends. First, energy expenditures during this dispersal period are considerable, and may impede a hen's ability to undergo the energetically-demanding process of egg development and subsequent incubation. Second, this dispersal movement delays nesting by 10-14 days (Chapter 3), which pushes nesting further into the more extreme heat of June when nest survival greatly declines (Grisham et al. 2014, Lautenbach 2019). These effects of dispersal are likely to result in decreased nest success, and could be a mechanism by which dispersal undermines the success of a translocated population.

A first-year adjusting effect could negatively affect the reproductive success of translocated lesser prairie-chickens. The lesser prairie-chicken range spans several ecoregions with distinctly different plant communities and environmental conditions (Boal and Haukos 2016). Translocation efforts will move females to areas with unfamiliar landscape composition and configuration of potential habitat types. Some adjustment time is presumed to be necessary for released females to determine relative quality of available nesting and brooding habitat as translocated birds gain familiarity with the release area and establish a new home range, referred to as a first-year adjusting effect. Past studies of greater sage grouse (*Centrocercus urophasianus*) and sharp-tailed grouse (*Tympanuchus phasianellus*) have noted that movement patterns of translocated birds follow a first-year adjusting effect (Coates 2001, Ebenhoch et al. 2019). This would be the first documentation of a first-year adjusting effect on nesting success in a grouse species. As lesser prairie-chickens have a mean lifespan of two years, reproductive consequences of a first-year adjusting effect could have severe implications for lesser prairie-chicken translocation.

I tested for the influence of habitat type, post-release dispersal, and first-year adjustment effects on nest survival during a lesser prairie-chicken translocation conducted by Colorado Parks and Wildlife and Kansas Department of Wildlife, Parks, and Tourism. The objective of translocation was to increase lesser prairie-chicken populations in the Sand Sagebrush Prairie Ecoregion, where lesser prairie-chicken populations have been historically strong but have been nearly extirpated in the last decade (Haukos et al. 2016). Greater than 400 lesser prairie-chickens were translocated during 2016-2019 from the Short-Grass Prairie/CRP Mosaic Ecoregion of northwest Kansas to the Sand Sagebrush Prairie Ecoregion – specifically the U.S. Forest Service Cimarron and Comanche National Grasslands in southwestern Kansas and southeastern Colorado, respectively. This effort provided an opportunity to study the nesting ecology of translocated lesser prairie-chickens and determine potential effects of post-released dispersal and acclimation to a novel landscape on the reproductive success of released birds. My hypotheses are that i) nest success will be greater in habitat types which were present at the capture site (e.g. CRP grassland, shortgrass prairie), ii) increased dispersal (measured as both distance moved and displacement) will result in lower nest success, and iii) nest success will be greater in the year after translocation.

Study Area

Lesser prairie-chickens were translocated from the Short-Grass Prairie/CRP Mosaic Ecoregion in northwestern Kansas to the Sand Sagebrush Prairie Ecoregion – specifically the U.S. Forest Service Cimarron and Comanche National Grasslands in southwestern Kansas and southeastern Colorado (Figure 1-1). The Short-Grass Prairie/CRP Mosaic Ecoregion has the highest density of lesser prairie-chickens throughout their range (est. 22,700 individuals in 2018), and this population has been stable over the last decade. The Sand Sagebrush Prairie Ecoregion, to which the lesser prairie-chickens were translocated, has the lowest contemporary density of lesser prairie-chickens throughout their range (est. 3,000 individuals in 2018); the ecoregion's estimated population declined below 500 birds in 2014 (Nasman et al. 2018). The probability of quasi-extinction (below 50 individuals) by 2037 in the Short-Grass Prairie/CRP Mosaic Ecoregion has been estimated at 1%, while the probability of quasi-extinction in the Sand Sagebrush Prairie Ecoregion was estimated at 47% (Hagen et al. 2017). These two regions have distinct climates and plant communities.

Capture Site: Short-Grass Prairie/CRP Mosaic Ecoregion

Lesser prairie-chickens were captured 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 (McDonald et al. 2017). With landowners' permission, lesser prairie-chickens were captured on short- and mid-grass prairie and cropland in Gove, Logan, Lane, Ness, and Finney counties in Kansas (1,357,189 ha). Land use in these counties was a mixture of row-crop agriculture, oil and gas extraction, 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. 2018). Historical (1960 to 2015) mean monthly temperatures ranged from -8.9º C to 28.8º C, and annual precipitation ranged from 29.4 to 83.3 cm ($\bar{x}$ = 53.3 cm) in Healy, Kansas. During the study period (2016 to 2018) mean monthly temperatures ranged from -2.9 º C to 26.6º C, and annual precipitation ranged from 58.3 to 65.0 cm (High Plains Regional Climate Center 2019).

Vegetation in the source population area primarily reflects the composition of the native short-grass prairie, but also contains species of mixed-grass prairie (Sullins 2017). Common grass species include little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), composite dropseed (*Sporobolus compositus*), western wheatgrass (*Pascopyrum smithii*), buffalograss (*Bouteloua dactyloides*), blue grama (*Bouteloua gracilis*), hairy grama (*Bouteloua hirsuta*), sand dropseed (*Sporobolus cryptandrus*), and inland saltgrass (*Distichlis spicata*). Forb species include 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). Dominant shrub species are sand sagebrush (*Artemisia filifolia*) and four-wing saltbush (*Atriplex canescens*; Fields et al. 2006). Planted CRP grasslands in Kansas have been initially seeded with a native grass-forb mixture since 1986. Grass species include little bluestem, sideoats grama, big bluestem, switchgrass, western wheatgrass, blue grama, buffalograss, and indiangrass (*Sorghastrum nutans*). Forb species include alfalfa (*Medicago sativa*), white sweet clover (*Melilotus alba*), yellow sweet clover (*Melilotus officinalis*), Maximillian sunflower (*Helianthus maximiliani*), prairie bundleflower (*Desmanthus illinoensis*), purple prairie clover (*Dalea purpurea*), and upright prairie coneflower (*Ratibida columnifera*; Fields et al. 2006).

Release site: Cimarron and Comanche National Grasslands, Sand Sagebrush Prairie Ecoregion

The area surrounding the release sites was composed of row-crop agriculture, CRP grasslands, and a combination of sand sagebrush and short-grass prairies in Morton County, Kansas, and Baca County, Colorado. The U.S. Forest Service manages 45,300 ha of this region as a part of the Cimarron and Comanche National Grasslands, with a focus on providing multi-use opportunities for grazing, energy exploitation, and wildlife recreation. The National Grasslands provides the majority of grazed rangelands in the area and is the largest parcel of public land in the lesser prairie-chicken's range. Vegetation on the National Grasslands is largely dependent on soil type and grazing intensity and includes both short- and mid-grass prairie interspersed with tall grasses, and sand sagebrush prairie. Short-grass prairie species match those found at the capture site, especially blue grama and buffalograss. In the sand sagebrush prairie, grass species include sand dropseed, blue grama, needle and thread (*Stipa comate*), and sand bluestem (*Andropogon hallii*). Forb species include annual buckwheat (*Eriogonum annuum*), blazing star (*Liatris* spp.), western ragweed, prairie sunflower (*Helianthus petiolaris*), annual sunflower (*Helianthus annuus*), camphorweed (*Heterotheca* subaxillaris), fumewort (*Corydalis solida*), Indian blanket flower (*Gaillardia pulchella*), Russian thistle (*Salsola tragus*), pigweed (*Amaranthus hybridus*), tansy aster (*Machaeranthera tanacetifolia*), bush morning glory (*Ipomoea leptophylla*), evening primrose (*Calylophus serrulatus*), buffalo bur (*Solanum rostratum*), buffalo gourd (*Cucurbita foetidissima*), Texas croton (*Croton texensis*), and toothed spurge (*Euphorbia dentata*). The shrub community is dominated by sand sagebrush, although yucca (*Yucca glauca*) and prickly pear cactus (*Opuntia macrorhiza*) are also abundant. Historical (1960 to 2015) mean monthly temperatures ranged from -4.6º C to 29.7º C, and annual precipitation ranged from 28.4 to 74.1 cm ($\bar{x}$ = 46.0 cm) in Elkhart, Kansas. During the study period (2016 to 2018) mean monthly temperatures ranged from 0.3º C to 27.3º C, and annual precipitation ranged from 53.7 to 67.0 cm (High Plains Regional Climate Center 2019).

Methods

From fall 2016 to spring 2019, 411 lesser prairie-chickens were translocated to the Cimarron and Comanche National Grasslands. The initial fall 2016 release was male-only to facilitate lek establishment; all subsequent releases were in spring and included both males and females (Table 1). Birds translocated during fall 2016 and spring 2017 were equipped with 11-g bib-style very-high-frequency (VHF) transmitters (RI-2B Holohil Systems Ltd., Carp, Ontario, Canada). In 2018 and 2019, rump-mounted 22-g Satellite Platform Transmitting Terminal (PTT) GPS transmitters (PTT-100, Microwave Telemetry, Columbia, MD, USA) and 12-g VHF transmitters (A3950, Advanced Telemetry System, Isanti, MN, USA) were deployed on translocated birds (total 115 birds with GPS transmitters, 279 birds with VHF transmitters). Birds were initially released on either the Cimarron or the Comanche National Grasslands in areas chosen for their proximity to high quality nesting habitat and historical leks (Figure 1-2). Release sites were adjusted once translocated birds began lekking to ensure that birds were released near active lekking sites. All capture and handling was completed under Institutional Animal Care and Use Committee Permit #3703 and Kansas Scientific Wildlife Permits SC-024-2018 and SC-015-2019 in compliance with state and federal regulations.

Birds equipped with VHF transmitters were monitored at least three times per week until nesting began. Due to the breadth of dispersal, many VHF birds went missing for extended periods of time during their dispersal movement following release. A fixed wing aircraft was used once a month (May-July) to relocate missing VHF birds using aerial telemetry. Due to operational issues fewer flights occurred in 2018, which resulted in a lower proportion of VHF hens with confirmed nests (54.8% VHF, 76.4% satellite females initiated nests in 2018). Birds equipped with satellite transmitters were monitored remotely, with a GPS location collected every two hours between 0500 and 2300 and uploaded into the Argos system every three days.

I monitored the nesting effort of translocated female lesser prairie-chickens during summer 2017, 2018, and 2019. I determined nest initiation, location, and fate of satellite birds using weekly GPS updates to determine when nesting patterns began and ended. Satellite birds were never intentionally flushed and nests were checked only after location and sensor data indicated the female either had permanently left the nest or experienced mortality while on the nest. I monitored nesting of VHF birds using daily checks once birds were determined to have ended their dispersal movement and localized movements. I flushed VHF birds once to locate the exact nesting site, and then monitored daily using radiotelemetry from an observation point ~100 m away. The VHF nests were checked for fate after the bird was detected off nest for three days in a row or a mortality signal was detected.

Habitat types were classified in the field using vegetation community measurements during the summer (June 21st to September 23rd) of 2018 and 2019 on the National Grasslands and adjacent CRP grasslands. These areas were divided into patches based on dominant plant species for sampling using property, allotment, and soil type boundaries. Composition of plant communities in these patches were measured using two 250-m step-point transects per patch, with the observer recording the plant species encountered at each step-point. These vegetation surveys were then used to determine the habitat type of the patch. As I found these habitat types to be relatively uniform within allotments (the unit of grazing management on the National

Grasslands, or of habitat management on the CRP grasslands), I extrapolated these habitat type designations out from a patch to an allotment scale. Additionally, CRP grasslands had relatively uniform vegetation communities within the study site, so I classified CRP as a single habitat type. I broke out the National Grasslands into separate habitat types by allotment based on the vegetation communities present. These included “Sand Sagebrush Only” (large component of Sand Sagebrush, low occurrence of grasses), “Sand Sagebrush & Short-Grass” (large component of Sand Sagebrush, high occurrence of blue grama and buffalograss), “Sand Sagebrush & Mixed-Grass” (large component of Sand Sagebrush, high occurrence of sand dropseed and sideoats grama), “Short-Grass” (high occurrence of blue grama and buffalograss), and “Mixed-Grass” (high occurrence of sand dropseed and sideoats grama). Each habitat type except for Sand Sagebrush & Shortgrass was present on both the Cimarron and Comanche National Grasslands. Nests only occurred in the CRP, Mixed-Grass, Sand Sagebrush & Mixed-Grass, and Short-Grass habitat types.

For each nest, I measured the distance to the nearest known lek and the bird’s original release site using package ‘sf’ in Program R (Pebesma 2018, R Core Team 2019). To test the distance moved before nesting, I subsampled the locations of each satellite bird down to a single location per day to reduce the impact of daily foraging movements and created a trajectory from those locations using package ‘adehabitatLT’ in Program R (Calenge 2006). I then calculated the total distance moved during each bird’s trajectory. This analysis was only run on satellite birds in their year of release, as only satellite birds could be tracked throughout the duration of their dispersal movement.

I estimated daily nest survival using package ‘RMark’ as an interface for Program MARK to determine the comparative influence of habitat type, year of release, and dispersal factors on nest survival. (White and Burnham 1999, Laake 2013). I also tested for the effect of the state in which nesting occurred to detect differences between the release site populations. All continuous covariates were converted to *z*-scores before they were used in the nest survival analysis to ensure that beta estimates were comparable among models. I compared models using two model sets. The first model set was run for all nests with known fates (n = 120) and included all models except for distance moved before nesting, as this model required data about the complete dispersal movement which was only available for satellite birds. These 17 models included combinations of the following variables: encounter occasion (time), nest age, nest initiation date, nesting attempt, nesting year, number of years since release, habitat type, state, distance from the release site, and distance from the nearest lek. The second model set included only nests incubated by satellite birds in their release year (n = 39). It included all prior variables except for years since release, and additionally included distance moved before nesting as a variable.

I ranked all models within model sets using Akaike Information Criterion corrected for small sample sizes (AIC_c) scores. I calculated derived nest survival estimates by extrapolating daily nest survival out over a 34-day period (the expected length of lesser prairie-chicken incubation and egg laying; Lautenbach et al. 2019) and then used the Delta method (Ver Hoef 2012) to calculate 95% confidence intervals for the period survival estimate.

Results

Of the 411 lesser prairie-chickens translocated to the Cimarron and Comanche National Grasslands, 207 were females. 105 of these females were released in Kansas and 102 released in Colorado; 69.5% of these females were second-year (juvenile) birds, and 79.3% (78.5% year of release, 100% year after release) of satellite-equipped females had a detected nesting attempt in any given year. I monitored and determined fate for 15, 37, and 68 nests from 2017, 2018, and 2019, respectively. Most birds did not get the opportunity to nest in a second year; only 7 (18.9%) nests in 2018 and 13 (19.1%) of nests in 2019 were from birds released before that year. Nests were primarily concentrated in CRP (76 nests, 63.3%), nests on the National Grasslands occurred in mixed-grass (8 nests, 6.7%), sand sagebrush & mixed-grass (17 nests, 14.2%), and shortgrass (4 nests, 3.3%). Only 12 nests (10%) occurred in areas off the National Grasslands and CRP; 3 nests (2.5%) were in areas of the National Grasslands where habitat type was not quantified due to their remote location. Observed nest success among all years was 48.3%. Estimated nest success using the best model in the first model set was 41.7%, and estimated nest success using the best model in the second model set was 44.9%.

Dispersal prior to nesting was observed in almost all nesting females (92.5%), with only three nests occurring before a bird had dispersed at least 15 km. Mean and median distances moved prior to nesting were 144 km and 135 km respectively, with a maximum dispersal distance of 374 km and a minimum dispersal distance of 1 km (Figure 1-3).

Nest survival in the first model set was explained primarily by a single variable (Table 2): years since release (one-year post release β = 1.26, SE = 0.52, 95% CI = 0.25, 2.28). Estimated nest success increased by 38% in the year after translocation (Figure 1-4). This model held 49.6% of the model weight, with the next highest model (nest age) holding only 14.8% of the model weight. Habitat type ($\beta_{\text{Mixed-Grass}}$ = 0.24, SE = 0.61, 95% CI = -0.96, 1.44; $\beta_{\text{Sand Sagebrush \& Mixed-Grass}}$ = -0.66, SE = 0.35, 95% CI = -1.34, 0.02; $\beta_{\text{Short-Grass}}$ = -1.55, SE = 0.55, 95% CI = -2.64, -0.47) tested 4.42 AIC_c units below the top model, although it outperformed the null model. Only the CRP and short-grass habitat types had significantly different estimates of nest survival; there was no statistical difference between habitat types that were or were not present at the capture site (Figure 1-5). Distance from the release site (β = 0.01, SE = 0.14, 95% CI = -0.26, 0.28) tested 8.52 AIC_c units below the top model and underperformed the null model, showing that distance from release site did not have a significant effect on nest survival. Time and nest age models tested above the null model (β_{Time} = -0.02, SE = 0.01, 95% CI = -0.04, -0.002; ($\beta_{NestAge}$ = -0.03, SE = 0.01, 95% CI = -0.06, -0.01), showing declines in daily nest survival later in the nesting season. However, nest initiation date did not test above the null model ($\beta_{Nest\ Initiation\ Date}$ = 0.01, SE = 0.01, 95% CI = -0.02, 0.03), failing to conclusively show that delays in nest initiation due to dispersal influenced nest survival.

Nest survival in the second model set was explained primarily by variables unrelated to the translocation (Table 3). Three models held a combined 69% of the model weight: nest age, nest age + time, and time. No other models tested above the null model. Distance moved before nesting (β = -0.01, SE = 0.20, 95% CI = -0.40, 0.38) tested 5.63 AIC_c units below the top model and underperformed the null model, indicating that dispersal distance did not have a statistically significant impact on nest success.

Discussion

By monitoring nest success of translocated lesser prairie-chickens, I was able to test hypotheses regarding their nest success in a novel landscape with unfamiliar habitat types, after dispersal movements, and the presence of a first-year adjusting effect. I hypothesized that nest success would be greater in habitat types that were present at the capture site, increased dispersal would result in lower nest success, and nest success would be greater in the year after translocation. These factors all posed potential dangers to lesser prairie-chickens' reproductive success after translocation, and this study was intended to test whether they would be potential roadblocks to translocation success.

To determine whether lesser prairie-chickens were capable of nesting in habitat types that they were not familiar with, I tested whether habitat type affected nest survival. The release sites included a wide variety of habitat types, of which only two (CRP grassland and short-grass prairie) were present in landscapes at capture sites. I found that nest success did not differ between habitat types available and not available at the capture site. However, the vast majority (63%) of nests occurred in CRP grassland, which was selected at greater rates than the National Grasslands (Chapter 2). Strong selection for CRP grasslands for nesting and overall use indicates that translocated lesser prairie-chickens are selecting to nest in this habitat type over the habitat types previously used by resident hens despite the lack of difference in nesting success among habitat types. This could be due to natal habitat preference induction (adult preference for vegetation characteristics similar to natal habitat, Stamps and Swaisgood 2007) or perhaps because sites with quality nesting cover were more abundant in CRP than other habitat types. Despite this preference, my results show that lesser prairie-chickens can still nest successfully in these habitat types when necessary and possess the ability to use novel habitat types after translocation.

I tested for the presence of a first-year adjusting effect on lesser prairie-chicken nest success to determine if the difficulties of adjusting to a novel habitat would decrease nesting success in the year of release. Nesting propensity is low in the year of release, with 21.5% of living hens forgoing nesting in the year of release, and nest success in the year of release is 38% lower than it is in the year after release. These results show that a first-year adjusting effect is indeed present. This has the potential to cause problems for a successful lesser prairie-chicken translocation; survival past the first year is low for translocated birds (8 satellite birds alive by following May, 10.3%), so only a few birds will live long enough to take advantage of the increased nest success in the second nesting year. One notable aspect of these results was that, despite the presence of such a strong first-year adjusting effect, nest success was still high enough in the first year to result in a reasonable rate of reproductive success. Estimated nest success in the year of release was 38% in this study, which is comparable to studies from native populations (Cummings et al. 2017). Estimated nest success in the year after release was 76%, which is exceptional for lesser prairie-chickens. These results suggest that the baseline nest success rate at the release site was sufficient to accommodate a high magnitude first-year adjusting effect. However, studies from native populations suggest that most baseline nest success rates throughout the lesser prairie-chicken's range are relatively low, and future lesser prairie-chicken translocations will likely not have a high enough baseline nest success rate to accommodate a first-year adjusting effect of this magnitude. Such an effect could easily be a roadblock for future translocation projects, especially when combined with other factors reducing reproductive success, recruitment, and overall fitness.

After translocation, most females underwent a lengthy dispersal movement that did not seem to be mitigated by encountering available nesting or brooding habitat or conspecifics (Chapter 3). Despite this, distance from the nest to the release site and dispersal distance both lacked an effect on nest survival. Translocated female lesser prairie-chickens seem to be able to nest successfully once they settle in available nesting habitat, despite the energetic cost of their dispersal movements. This may be due in large part to the fat stores that female lesser prairie-chickens accumulate prior to nesting (C. Aulicky, Kansas State University, pers. comm.), which would allow females to sustain this increased rate of energy expenditure. Dispersal delayed nesting by 10-14 days in 2018 (but not 2019; Chapter 3), and time and nest age models show that daily nest survival declines over time. However, nest initiation date did not affect nest survival, so there is not a clear impact of dispersal-induced nesting delay on nest success. Dispersal likely has myriad effects on translocation success, including increased mortality and displacement from conspecifics. However, my results do not show any concrete evidence that dispersal affects nest success should a female initiate a nest.

Our results show that nest success in the year of release is significantly impaired relative to years following release. This decline in nest success is not well explained by dispersal and is likely the result of other processes involved in recovering from translocation. These might include a lack of familiarity with local predators and landscape features or an inability to effectively stockpile fat before incubation. Significant research has gone into finding ways to moderate the effect of translocation on grouse, specifically attempting to reduce dispersal (Meyerpeter et al. 2019). These results suggest that reducing the effect of translocation on nest success should also be treated with importance in short-lived birds such as the lesser prairie-chicken, as even a moderate first-year adjusting effect has the potential to reduce the reproductive output of the translocated population. It is currently unclear how this effect might be moderated, as lesser prairie-chicken translocation protocols leave little time for translocated birds to adjust to the release site prior to nesting. The best available options may be to translocate large numbers of birds to compensate for the low post-release survival and decreased nesting success, or in some circumstances, focus resources on restoring native populations instead. In circumstances where translocations are determined to be the best method of restoring lesser prairie-chicken populations, managers should plan for substantially reduced nesting success during the year of release and have a strategy to counteract it.

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Table 1-1: Number of lesser prairie-chickens translocated from the Short-Grass Prairie/CRP Mosaic Ecoregion of northwest Kansas to the Cimarron and Comanche National Grasslands in southwest Kansas and southeast Colorado between Fall 2016 and Spring 2019.

	Release Site				
	Cimarron		Comanche		
	Males	Females	Males	Females	Total
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
Total	101	105	103	102	411

Table 1-2: Model rankings estimating daily nest survival for 120 nests for female lesser prairie-chickens translocated from the Short-Grass Prairie/CRP Mosaic Ecoregion of northwest Kansas to the Sand Sagebrush Prairie Ecoregion of southwest Kansas and southeast Colorado during 2017-2019 (model set one).

Model[1]	***K***[2]	**AICc**[3]	**ΔAICc**[4]	w_i[5]
Years Since Release	2	557.39	0	0.50
Nest Age	2	559.81	2.42	0.15
Time + Nest Age	3	560.90	3.51	0.09
Time	2	561.39	4.00	0.07
Habitat Type	6	561.81	4.42	0.05
Nest Attempt	2	562.84	5.45	0.03
Distance from lek	2	562.91	5.52	0.03
Null Model	1	563.92	6.53	0.02

Models used in model set one, displaying only models ranked above the null model

[2] Number of parameters in the model

[3] Akaike Information Criterion, corrected for small sample sizes

[4] Number of AIC_c units between the top and current model

[5] Model weight

Table 1-3: Model rankings estimating the comparative influence of dispersal distance on daily nest survival for 40 nests for female lesser prairie-chickens equipped with SAT-PTT transmitters during 2018-2019 translocated from the Short-Grass Prairie/CRP Mosaic Ecoregion of northwest Kansas to the Sand Sagebrush Prairie Ecoregion of southwest Kansas and southeast Colorado (model set two).

Model[1]	***K***[2]	**AICc**[3]	**ΔAICc**[4]	w_i[5]
Nest Age	2	259.02	0	0.60
Null Model	1	262.64	3.62	0.07
Dispersal Distance	2	264.65	5.63	0.02

Models used in model set two, displaying only models ranked above the null model as well as dispersal distance

[2] Number of parameters in the model

[3] Akaike Information Criterion, corrected for small sample sizes

[4] Number of AIC_c units between the top and current model

[5] Model weight

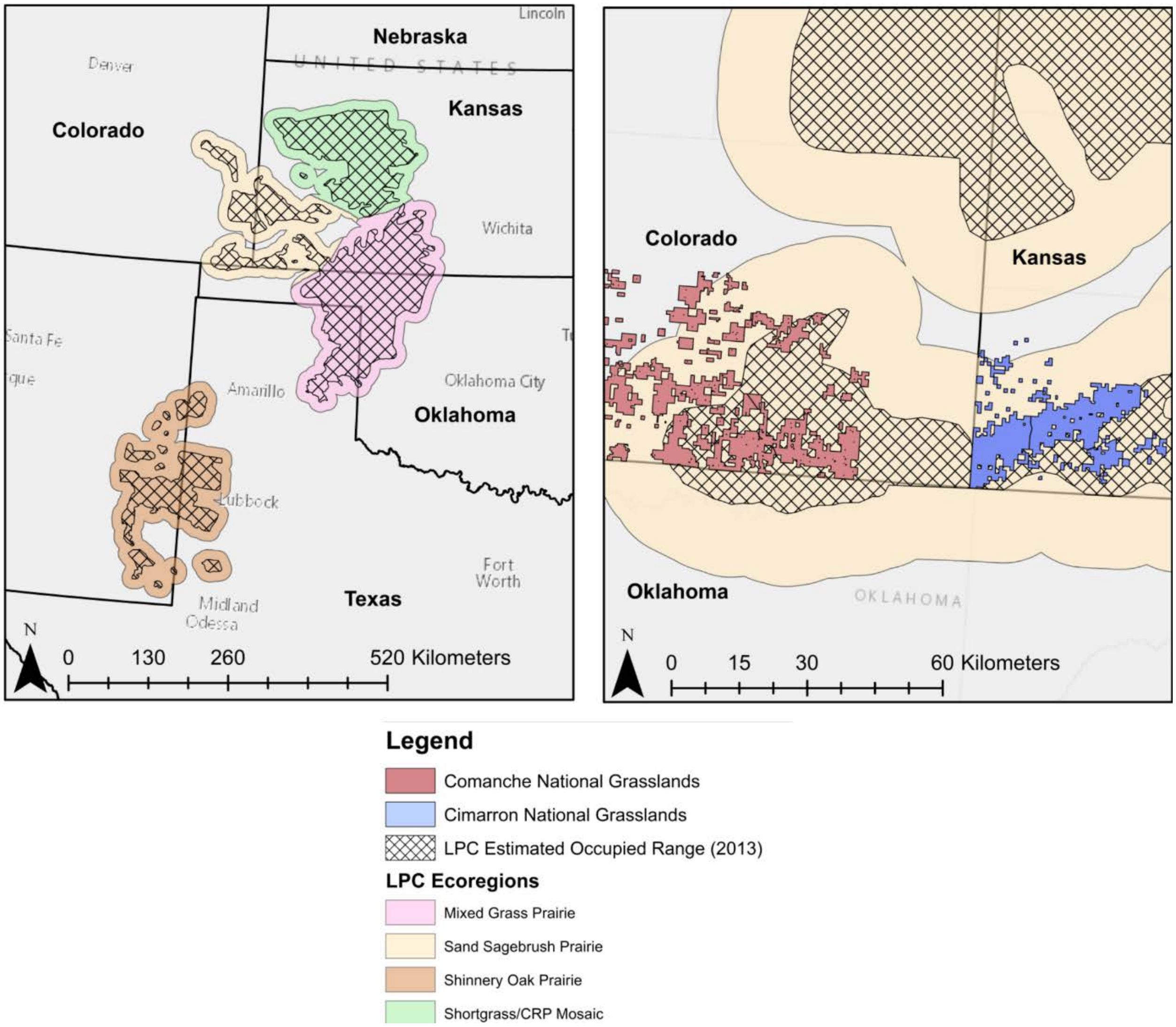

Figure 1-1: Lesser prairie-chicken ecoregions and locations of the Cimarron and Comanche National Grasslands

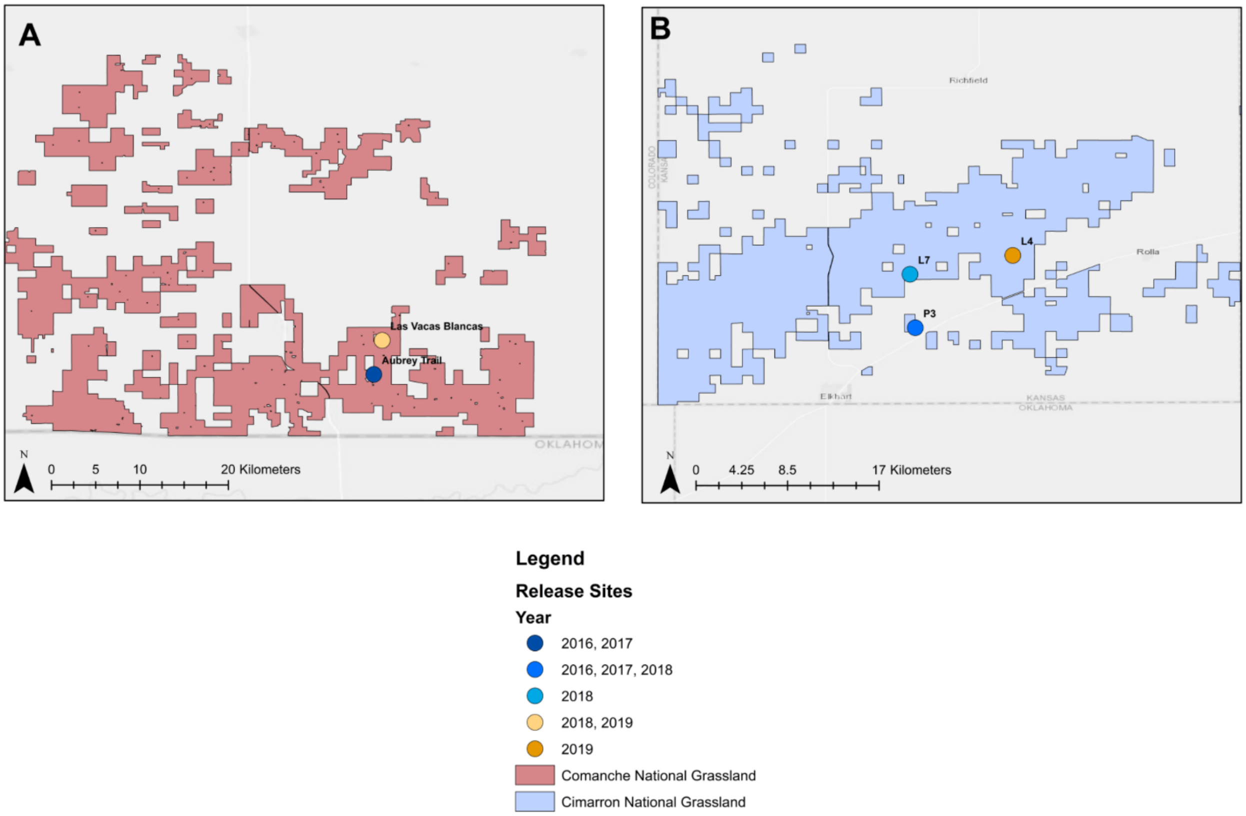

Figure 1-2: Locations of release sites on the Comanche (A) and Cimarron (B) National Grasslands in Colorado and Kansas, respectively, during 2016-2019.

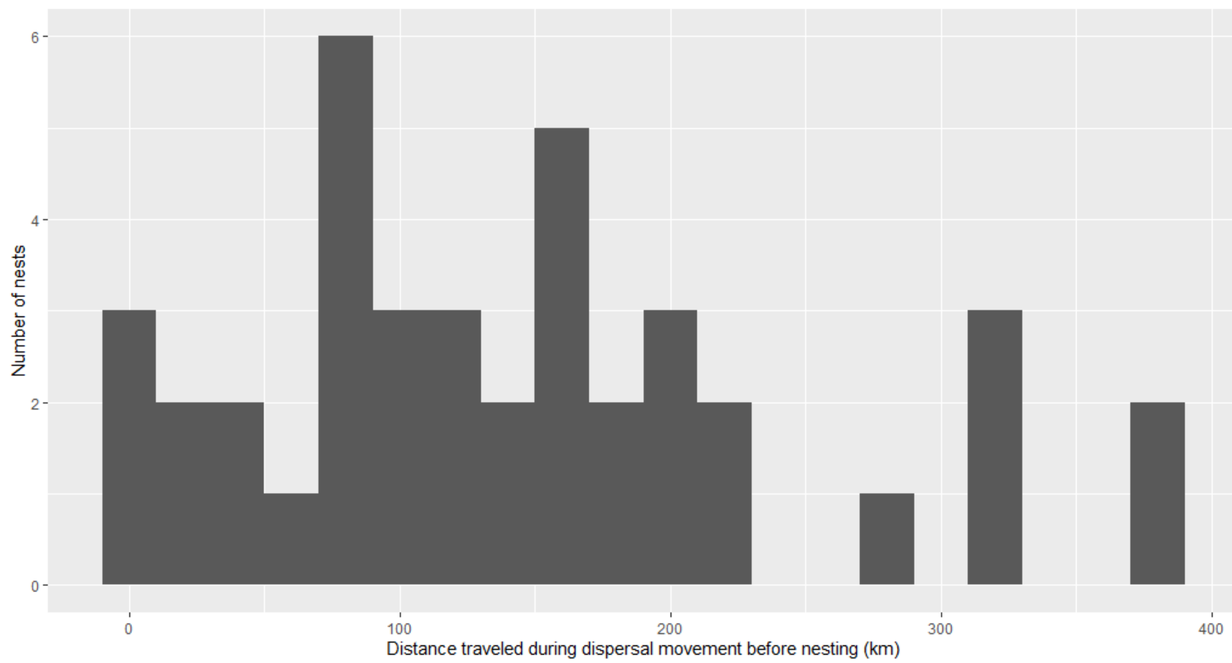

Figure 1-3: Distance moved before nesting in 2018-2019 by SAT-PTT equipped female lesser prairie-chickens translocated to the Sand Sagebrush Ecoregion.

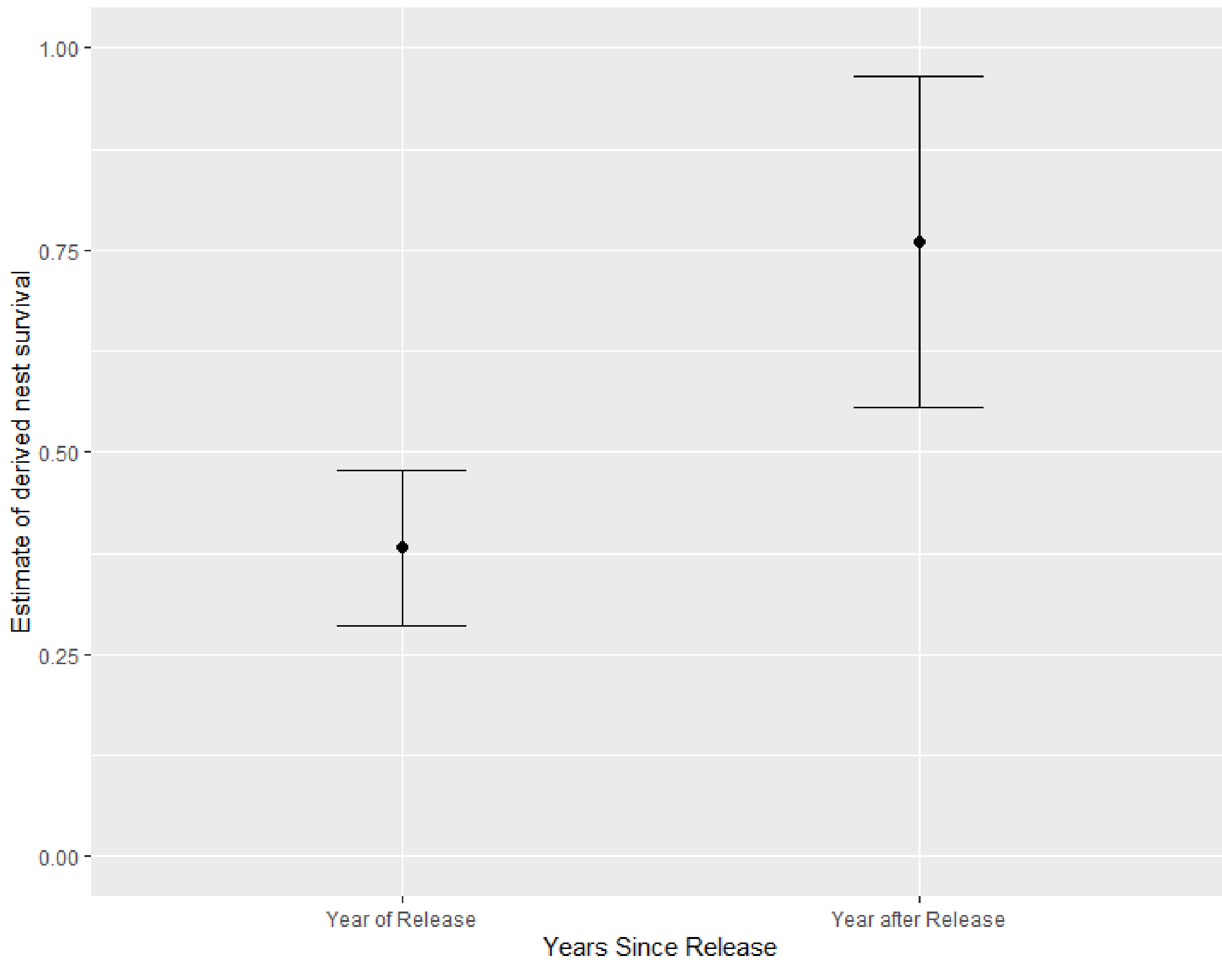

Figure 1-4: Effect of the number of years since the release of a translocated lesser prairie-chicken on estimates of derived nest survival in the Sand Sagebrush Prairie Ecoregion, specifically southeastern Colorado and southwestern Kansas during 2017-2019. 95% confidence intervals are displayed by error bars (model set one).

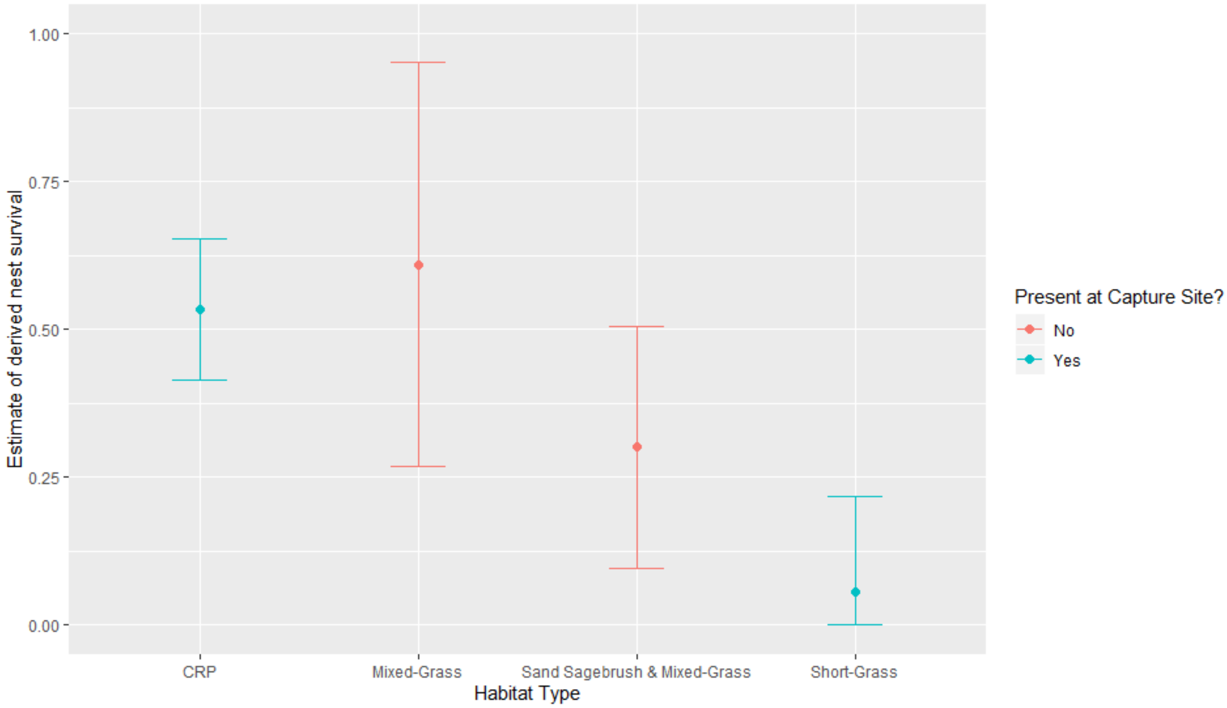

Figure 1-5: Effect of novel habitat types on estimates of derived nest survival for translocated lesser prairie-chickens in the Sand Sagebrush Prairie Ecoregion, specifically southeastern Colorado and southwestern Kansas during 2017-2019. 95% confidence intervals are displayed by error bars (model set one).

Chapter 2 - Dispersal of lesser prairie-chickens translocated to the Sand Sagebrush Ecoregion in relation to lek sites and nesting habitat

Introduction

Lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations are undergoing steep declines in areas where they have had historically strong populations. These declines, fueled by habitat loss, tree encroachment, and drought, have driven lesser prairie-chickens to extirpation in large portions of their former range. Even with effective habitat management and grassland restoration, restoring lesser prairie-chickens to the parts of their range from which they have been extirpated will require human intervention.

Translocation is a frequently used technique for the managed restoration of wildlife species (Griffith et al. 1989) and has been frequently utilized in prairie grouse management (Snyder et al. 1999). Translocation has been attempted to restore lesser prairie-chickens to unoccupied portions of their range. While this technique has had mixed success in other prairie grouse species (Snyder et al. 1999), there is no indication of success for lesser prairie-chickens to date (Giesen 2000). One presumed reason for this lack of success is the high rates of dispersal following release, which have been noted in at least one instance following a lesser prairie-chicken translocation (translocated bird harvested 200 miles from release site, Jonathan Reitz pers. comm.). Furthermore, lesser prairie-chickens in prior translocations have been unmonitored, so the extent of translocated lesser prairie-chicken dispersal after release (and its effects on translocation success) has not been quantified.

High rates of dispersal following release in translocation efforts have been noted in other prairie grouse species. Kemnick and Kesler (2013) observed a 54% rate of emigration of female greater prairie-chickens after release, and Vogel et al. (2015) found mean movement distances of 336 km for translocated greater prairie-chickens, with one individual moving 4000 km after release. Studies of prairie grouse have yielded some hypotheses regarding the potential reasons for dispersal behavior following translocation. Coates et al. (2006) observed decreased dispersal when sharp-tailed grouse (*Tympanuchus phasianellus*) were released closer to a site where recently translocated birds had begun lekking and nesting. It was unclear in this case whether the proximity to quality habitat or conspecifics was causing the decreased dispersal. However, there is substantial reason to believe that either or both factors could lead to decreased dispersal in translocated lesser prairie-chickens.

Lesser prairie-chicken translocation primarily occurs during lekking season from late March through the end of April. Female lesser prairie-chickens are presumed to select quality nesting habitat, which is usually characterized by prairie with a high density of tall bunch grasses, as lekking season ends (Haukos and Zavaleta 2016). When female lesser prairie-chickens are translocated, they lose the benefit of experience in finding a quality nesting site on a familiar landscape. It is possible that dispersal of female lesser prairie-chickens is geared towards finding a quality nesting site and releasing birds near high quality nesting habitat could lessen the dispersal movement.

Lesser prairie-chickens are a lek-centric species during the breeding season, and finding a nearby lek is another potential motivator for dispersal after translocation. Much of the species' life history is defined by proximity to a lek; lesser prairie-chickens typically nest and raise young within 3.2 km of a lek site and remain within the immediate area outside of the breeding season

(Boal and Haukos 2016). Some theories of lek formation (e.g., female choice hypothesis; Bradbury 1981) hypothesize that female lesser prairie-chickens deliberately place their home ranges within the vicinity of leks to facilitate mate choice. If this theory is correct, translocated female lesser prairie-chickens may use leks as cues to stop dispersing and establish a home range.

Testing how the proximity of nesting habitat and leks relate to the likelihood and extent of dispersal by translocated lesser prairie-chickens could provide insight for managers to moderate the effect of dispersal following release. To answer questions related to these factors, I monitored the likelihood, extent, and role of available habitat and active leks on characteristics of dispersal by lesser prairie-chickens translocated from the Short-Grass Prairie/CRP Mosaic Ecoregion in northwestern Kansas to the Sand Sagebrush Prairie Ecoregion in southwestern Kansas and southeastern Colorado. Release sites were on the Cimarron and Comanche National Grasslands, which represent the largest extent of public land in the lesser prairie-chicken's range (Elmore and Dahlgren 2016). The National Grasslands had thriving lesser prairie-chicken populations peaking in the late 1980s, but these populations have been on a steady decline since then (Giesen 2000, Kraig Schultz pers. comm.). The last native lesser prairie-chickens lekking on the National Grasslands were observed in spring 2016.

From fall 2016 through spring 2019, Colorado Parks and Wildlife and Kansas Department of Wildlife, Parks, and Tourism translocated >400 lesser prairie-chickens to the National Grasslands to restore populations on the National Grasslands. Translocated birds were equipped with transmitters and released at one of several sites, with varying distances from active leks and nesting habitat. I tracked these birds as they dispersed after release and quantified their interaction with lek sites and nesting habitat during dispersal events. My objectives were to quantify the dispersal and survival of translocated lesser prairie-chickens after release and determine if positioning release sites near leks and presumed quality nesting habitat would moderate dispersal movements.

Study Area

Lesser prairie-chickens were translocated from the Short-Grass Prairie/CRP Mosaic Ecoregion in northwestern Kansas to the U.S. Forest Service Cimarron and Comanche National Grasslands in southwestern Kansas and southeastern Colorado (Figure 3-1). The Short-Grass Prairie/CRP Mosaic Ecoregion has the highest density of lesser prairie-chickens throughout their range (est. 22,700 individuals in 2018); this population has been relatively stable over the last decade. The Sand Sagebrush Prairie Ecoregion, to which the lesser prairie-chickens were translocated, has the lowest density of lesser prairie-chickens throughout their range (est. 3,000 individuals in 2018), with the ecoregion's estimated population below 500 birds in 2014 (Nasman et al. 2018). The probability of quasi-extinction (below 50 individuals) by 2037 in the Short-Grass Prairie/CRP Mosaic Ecoregion has been estimated at 1%, while the probability of quasi-extinction in the Sand Sagebrush Prairie Ecoregion was estimated at 47% (Hagen et al. 2017). These two regions have distinct climates and plant communities.

Capture Site: Short-Grass Prairie/CRP Mosaic Ecoregion

Lesser prairie-chickens were captured 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. 2018). With the permission of private landowners, lesser prairie-chickens were captured on short- and mid-grass prairie and cropland in Gove, Logan, Lane, Ness, and Finney counties in Kansas (1,357,189 ha). Land use in these counties was a mix of row-crop agriculture, oil and gas extraction, Conservation Reserve Program (CRP) grassland, and grazing on native short-grass prairie intermixed with remnant mixed-grass prairie (McDonald et al. 2014, Dahlgren et al. 2016, Robinson et al. 2018). Historical (1960 to 2015) mean monthly temperatures ranged from -8.9º C to 28.8º C, and annual precipitation ranged from 29.4 to 83.3 cm ($\bar{x}$ = 53.3 cm) in Healy, Kansas. During the study period (2016 to 2018) mean monthly temperatures ranged from -2.9º C to 26.6º C, and annual precipitation ranged from 58.3 to 65.0 cm (High Plains Regional Climate Center 2019).

Vegetation in the source population area primarily reflects the composition of the native short-grass prairie, but also contains species of mixed-grass prairie (Sullins 2017). Common grass species include little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), composite dropseed (*Sporobolus compositus*), western wheatgrass (*Pascopyrum smithii*), buffalograss (*Bouteloua dactyloides*), blue grama (*Bouteloua gracilis*), hairy grama (*Bouteloua hirsuta*), sand dropseed (*Sporobolus cryptandrus*), and inland saltgrass (*Distichlis spicata*). Forb species include 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). Dominant shrub species are sand sagebrush (*Artemisia filifolia*) and four-wing saltbush (*Atriplex canescens*; Fields et al. 2006). The CRP grassland in Kansas has been seeded with a native grass-forb mixture since 1986. Grass species include little bluestem, sideoats grama, big bluestem, switchgrass, western wheatgrass, blue grama, buffalograss, and indiangrass (*Sorghastrum nutans*). Forb species include alfalfa

(*Medicago sativa*), white sweet clover (*Melilotus alba*), yellow sweet clover (*Melilotus officinalis*), Maximillian sunflower (*Helianthus maximiliani*), prairie bundleflower (*Desmanthus illinoensis*), purple prairie clover (*Dalea purpurea*), and upright prairie coneflower (*Ratibida columnifera*; Fields et al. 2006).

Release site: Cimarron and Comanche National Grasslands, Sand Sagebrush Prairie Ecoregion

The area surrounding the release sites was composed of row-crop agriculture, CRP grasslands, and a combination of sand sagebrush and short- and mid-grass prairies in Morton County, Kansas, and Baca County, Colorado. The U.S. Forest Service manages 45,300 ha of this region as a part of the Cimarron and Comanche National Grasslands, with a focus on providing multi-use opportunities for grazing, energy exploitation, and wildlife recreation. The National Grasslands provides the majority of grazed rangelands in the area and is the largest parcel of public land in the lesser prairie-chicken's range. Vegetation on the National Grasslands is largely dependent on soil type and grazing intensity and includes both short- and mid-grass prairie interspersed with tall grasses, and sand sagebrush prairie. Short-grass prairie species match those found at the capture site, especially blue grama and buffalograss. In the sand sagebrush prairie, grass species include sand dropseed, blue grama, needle and thread (*Stipa comate*), and sand bluestem (*Andropogon hallii*). Forb species include annual buckwheat (*Eriogonum annuum*), blazing star (*Liatris* spp.), western ragweed, prairie sunflower (*Helianthus petiolaris*), annual sunflower (*Helianthus annuus*), camphorweed (*Heterotheca* subaxillaris), fumewort (*Corydalis solida*), Indian blanket flower (*Gaillardia pulchella*), Russian thistle (*Salsola tragus*), pigweed (*Amaranthus hybridus*), tansy aster (*Machaeranthera tanacetifolia*), bush morning glory

(*Ipomoea leptophylla*), evening primrose (*Calylophus serrulatus*), buffalo bur (*Solanum rostratum*), buffalo gourd (*Cucurbita foetidissima*), Texas croton (*Croton texensis*), and toothed spurge (*Euphorbia dentata*). The shrub community is dominated by sand sagebrush, although yucca (*Yucca glauca*) and prickly pear cactus (*Opuntia macrorhiza*) are also abundant. Historical (1960 to 2015) mean monthly temperatures ranged from -4.6º C to 29.7º C, and annual precipitation ranged from 28.4 to 74.1 cm ($\bar{x}$ = 46.0 cm) in Elkhart, Kansas. During the study period (2016 to 2018) mean monthly temperatures ranged from 0.3º C to 27.3º C, and annual precipitation ranged from 53.7 to 67.0 cm (High Plains Regional Climate Center 2019).

Methods

From fall 2016 to spring 2019, 411 lesser prairie-chickens were translocated to the Cimarron and Comanche National Grasslands. The initial fall 2016 release was male-only to facilitate lek establishment; all subsequent releases were in spring and included both males and females (Table 1). Birds translocated during fall 2016 and spring 2017 were equipped with 11-g bib-style very-high-frequency (VHF) transmitters (RI-2B Holohil Systems Ltd., Carp, Ontario, Canada). In 2018 and 2019, rump-mounted 22-g Satellite Platform Transmitting Terminal (PTT) GPS transmitters (PTT-100, Microwave Telemetry, Columbia, MD, USA) and 12-g VHF transmitters (A3950, Advanced Telemetry System, Isanti, MN, USA) were deployed on translocated birds (total 115 birds with GPS transmitters, and 279 birds with VHF transmitters; Table 2). All capture and handling was completed under Institutional Animal Care and Use Committee Permit #3703 and Kansas Scientific Wildlife Permits SC-024-2018 and SC-015-2019 in compliance with state and federal regulations.

Birds were initially released on either the Cimarron or the Comanche National Grasslands in 2016 and 2017 in areas chosen for their proximity to presumed high quality nesting habitat and historical leks (Figure 3-2). Release sites after initial releases were adjusted in 2018 and 2019 once translocated birds began lekking to ensure that birds were released near active lekking or previous nesting sites. The initial release site on the Comanche National Grasslands was at the Aubrey Trail lek, which was active through spring 2016. This release site was used in fall 2016 and spring 2017, but active lekking was not present at the Aubrey Trail site in 2017. In spring 2018 and 2019, the release site on the Comanche National Grassland was moved to the Las Vacas Blancas allotment, which was re-established as a lekking site in 2019. The initial release site for the Cimarron National Grassland was at the P3 lek, a small active lek on private land to the south of the Cimarron river. This release site was used exclusively in fall 2016 and spring 2017, but lekking was not observed at the site in 2018 and 2019. In 2018, birds translocated to the Cimarron National Grasslands were released jointly at P3 and a new release site at the inactive historical L7 lek. L7, chosen because of its proximity to presumed quality nesting habitat on the Cimarron National Grassland, was only used to release birds during 2018. In 2019, all translocated birds were released at the inactive historical L4 lek, around which 2 females nested during 2018.

Birds equipped with VHF transmitters were monitored three or more times per week. Due to the breadth of dispersal movements following release, many VHF birds went missing for extended periods. A fixed-wing aircraft was used once a month (May-July) to relocate missing VHF birds via aerial telemetry. Birds equipped with satellite transmitters were monitored remotely, with a GPS location collected every two hours between 0500 and 2300 and uploaded into the Argos system every three days.

Because of uncertainties in the date of mortality of dispersing VHF-transmittered birds, only satellite-transmittered birds were used when quantifying survival through the end of the dispersal period. I estimated the survival of all birds through July 31st in the year of release, by which most birds had finished their dispersal movements. I was unable to distinguish between mortality from dispersal and unrelated causes during this evaluation, so instead I use this estimate as a measure of cumulative mortality in the summer after release.

When transmittered birds congregated in an area, that area was surveyed at sunrise to determine if lekking was taking place. All active and historic leks on the Cimarron and Comanche National Grasslands, as well as leks established or visited by translocated birds off the National Grasslands, were surveyed at least once per season for both translocated and native lekking males. Known lek locations were used to quantify the number of leks which satellite-transmittered birds visited during their dispersal movement and identify whether nesting patterns near leks deviated from patterns expected for native populations (i.e., within 3.2 km).

Because of missing data on the dispersal movements of VHF-equipped lesser prairie-chickens, only satellite birds could be used for analyses that defined the length of the dispersal movement. Dispersal is here defined to mean an exploratory movement that takes the bird >5 km from its release site, following the definition of Earl et al. (2016). I used these satellite locations to conduct a behavioral change point analysis in Program R using package 'adehabitatLT' (Calenge 2006, R Core Team 2019). This analysis was intended to determine the point at which the dispersing lesser prairie-chicken transitioned from a 'dispersing' movement state to a 'settled' (localized within a set area) movement state based on the lesser prairie-chicken's daily step lengths. This analysis was limited to birds equipped with satellite transmitters and survived their dispersal movement (43 birds). Of these birds, three did not have a clear difference in step lengths that would indicate a transition between a dispersing and settled state, and three more failed to converge on a single behavioral change point. These six birds were excluded from the analysis. The remaining 37 behavioral change points were used to determine distance travelled, displacement from the release site, and time elapsed during the dispersal movement for each bird.

To determine the effect of dispersal on nesting, I monitored the nesting effort of translocated female lesser prairie-chickens during 2017, 2018, and 2019. I determined nest initiation, location, and fate of satellite birds using weekly GPS updates to determine when nesting patterns began and ended. Satellite birds were never intentionally flushed and nests were checked only after location and sensor data indicated the female either had permanently left the nest or experienced mortality while on the nest. I monitored nesting of VHF birds using daily checks once birds were determined to have ended their dispersal movement and localized movements. I flushed VHF birds once to locate the exact nesting site, and then monitored daily using radiotelemetry from an observation point ~100 m away. The VHF nests were checked for fate after the bird was detected off nest for three days in a row or a mortality signal was detected. I compared the nest initiation dates of translocated birds to those of native lesser prairie-chickens in Ashland, Kansas (210 km away from the Cimarron National Grassland and similar latitude), which were being monitored as a part of a separate project. This comparison allowed me to determine whether nest initiation date was being delayed by post-translocation dispersal movements.

Results

From 2016-2019, 411 birds were translocated to the Cimarron and Comanche National Grasslands, 394 of them with transmitters. Of these, 115 of these birds were equipped with satellite transmitters, which allowed me to examine the full dispersal movement after release. Almost all satellite-transmittered birds (100% in 2018, 95% in 2019) underwent an extensive dispersal movement (venturing > 5 km from the release site) after translocation. No birds survived until June without initiating a dispersal movement in 2018, and only two satellite birds survived that long without making a dispersal movement in 2019. Following dispersal, 69% of all released birds settled ≥5 km from the release site. Dispersal movements started a few days after release ($\bar{x}$ = 2.3 days, range = 0 – 7 days, excluding two dispersals post-nesting), and were 1-2 months long (female $\bar{x}$ = 52 days, SD = 24 days, range = 15 – 100 days; male $\bar{x}$ = 46 days, SD = 17 days, range = 15 – 75 days; Figure 3-3). Nesting was delayed by an average of 15 days in 2018. This dispersal-induced delay was not evident in 2019 (Figure 3-4). Lesser prairie-chickens traveled hundreds of kilometers during their dispersal movements (female $\bar{x}$ = 175 km, SD = 108 km, range 15 – 474 km; male $\bar{x}$ = 103 km, SD = 73 km, range = 26 – 279 km), with individuals birds demonstrating more extensive movements (Figure 3-5). Sites where birds ceased their dispersal movement were usually some distance from the release site (net displacement - female $\bar{x}$ = 23 km, SD = 20 km, range = 0.7 – 69 km; male $\bar{x}$ = 13 km, SD = 21 km, range = 0.5 – 64 km; Figure 3-6), but not representative of the total dispersal distance. Although I was unable to determine which mortalities were directly related to the dispersal of translocated birds, lesser prairie-chicken survival in the year of release (40% survival through July 31st in 2018 and 34% in 2019) was below summer survival rates from other studies in the

Sand Sagebrush Prairie Ecoregion (median survival = 74%, range = 0 – 1.00; Cummings et al. 2017).

Although males and females moved comparable distances during their dispersal following release (Figure 3-7), movement patterns differed between sexes. Male lesser prairie-chickens usually moved directly from lek to lek during their dispersal movement. Males usually settled near one of these leks at the conclusion of their dispersal, typically with a net displacement of less than 20 km from their release site. Females, however, dispersed regardless of nearby leks or available quality habitat. Females and males encountered similar numbers of leks during their dispersal, but females did not halt their dispersal when encountering a lek (Figure 3-8). Instead, they continued dispersing until eventually nesting at sites some distance from the release site ($\bar{x}$ = 19.2 km, SD = 18.8 km) and frequently greater than twice as far as expected (<3.2 km) from known leks ($\bar{x}$ = 7.9 km, SD = 8.9 km; Figure 3-9).

Lesser prairie-chickens did not nest in the immediate vicinity (within 2 km) of the P3, L7, or Aubrey Trail release sites while these leks were active. However, both the Las Vacas Blancas and L4 release sites resulted in (3 and 9 nests, respectively, within 2 km while they were active. Both of these release sites were in the 'Sand Sagebrush & Mixed-Grass' habitat type, which was one of the few habitat types on the National Grasslands selected by lesser prairie-chickens (Chapter 2). Despite the clear presence of quality lesser prairie-chicken nesting habitat at these sites, the distance of lesser prairie-chicken dispersal from these release sites was similar to prior release sites not used for nesting (Figure 3-10).

Of the five release sites, L4 had the largest rate of nesting in the immediate vicinity of the release site (Figure 3-11). Five of the 24 satellite birds (21%) released at L4 in 2019 nested within 2 km of the site (in addition to 4 VHF birds with unknown dispersal movements). Most of the satellite birds that nested at the L4 release site still dispersed at some point following release. One bird dispersed up to 10 km from the release site to the east, west, and south, and then returned to nest. Two more attempted to nest and then dispersed to locations 35 and 45 km away after their nests failed, dying shortly after their dispersal movements. One of these satellite birds did not disperse but died in mid-June during its nesting attempt. The final bird stayed near the L4 release site after its nest was predated in mid-June, and survived in the area through the summer. While these nesting attempts indicate that release sites in high quality nesting habitat may help increase site fidelity, the large rate of dispersal both before and after the nesting attempt by 96% of released females demonstrate a drive to disperse that adjacent nesting habitat was unable to moderate.

Discussion

My objectives were to quantify patterns of dispersal of translocated lesser prairie-chickens after release to determine if positioning release sites near leks and quality nesting habitat would moderate these dispersal movements. Dispersal is an occasional occurrence for lesser prairie-chickens in established populations, with one study observing that only 9% of males and 28% of females attempted a long-distance movement in a given summer (Earl et al. 2016). During this translocation, however, dispersal was nearly universal among released birds. This was true for both males and females, with only two of 114 satellite-transmittered birds not undergoing a dispersal movement in 2018 - 2019. The universal nature of this dispersal suggests that the initiation of the dispersal movement is an innate response to encountering an unfamiliar landscape. While most lesser prairie-chickens initiated the movement shortly (3-4 days) after release, two females released at L4 initiated 35 km and 45 km dispersal movements after failed nests in June (~2 months after release). These movements demonstrate that the propensity to initiate a dispersal movement can last several months into the summer after release. This is particularly concerning because most methods to reduce prairie grouse dispersal (brood translocation, Meyerpeter et al. 2019; soft releases, Snyder et al. 1999) focus on reducing the ability of prairie grouse to disperse in the 1-2 weeks immediately after translocation. As some hens initiated dispersal movements long after that period had concluded, it is likely that conservation techniques to keep prairie grouse from initiating dispersal movements will not work for the lesser prairie-chicken.

Once these dispersal movements began, translocated lesser prairie-chickens moved incredible distances. Total movement distance during dispersal averaged 145 km, with a few birds moving as much as 474 km. These movements are extensive compared to past literature for established populations in a familiar landscape (Earl et al. 2016). Movements of this magnitude have only been measured before in prairie grouse during a few isolated instances, and only during translocation (Vogel et al. 2015). These movements resulted in considerable diffusion of birds throughout the landscape, and while some came back to the vicinity of the release sites on the National Grasslands, 69% of all released birds settled ≥5 km from the release site. This dispersal also resulted in a more diffused pattern of nesting than traditionally expected in a lesser prairie-chicken population, with many nests outside the 3.2 km limit from active leks normally expected for lesser prairie-chicken nests (Boal and Haukos 2016). This pattern made the restoration of populations in specific areas, such as near reestablished leks or managed habitat areas, difficult to accomplish. Although this translocation initially aimed to reestablish populations in the vicinity of the National Grasslands, it more broadly resulted in a supplementation of populations throughout the southern portion of the Sand Sagebrush

Ecoregion. Managing for habitat at this scale is difficult, and the diffusion of birds across the landscape means that newly established leks in some areas may not reach population sizes large enough to persist (i.e., Allee effect). Diffusion poses a significant barrier to the success of translocation, and if dispersal is indeed an innate response to release in a novel landscape, it may not be possible to mitigate the negative effects of diffusion on translocated populations.

Even when birds returned to areas near the release sites, dispersal likely contributed to high rates of mortality during the first few months after release; 40% and 34% of newly released birds survived through the end of July 2018 and 2019, respectively. While I was not able to distinguish between mortality as the result of a dispersal movement and other causes, the gap between these results and summer survival rates from native Sand Sagebrush populations indicate that translocation is reducing survival rates in the summer after release. This suggests that, even in the 31% of cases where translocated lesser prairie-chickens do settle within 5 km of their release site, these dispersal movements may still have considerable effects on the success of lesser prairie-chickens in re-establishing these populations.

Prior studies have suggested that positioning release sites near leks or nesting habitat may decrease dispersal for translocated female prairie grouse (Coates et al. 2006). While this may be true for other species of prairie grouse, I found little evidence of this during a translocation of lesser prairie-chickens. While males moved among lek sites during their dispersal movement, females tended to visit leks and then continue dispersing. Their eventual settlement and nesting sites were frequently considerable distances from known lek sites, which suggests that lek sites do not play the primary role in stopping the dispersal movement. Nesting habitat also did not play a large role in retaining dispersing lesser prairie-chickens. The release sites were chosen based on their proximity to historic lesser prairie-chicken habitat, and surrounding areas were associated with large patches of CRP grassland, which has provided uniformly high nest success rates for the translocated population (Chapter 1). However, translocated lesser prairie-chickens did not appear to consider this nesting habitat while dispersing from the release site. The only release site that resulted in large numbers of translocated females nesting in the immediate vicinity (L4) still had three of its five satellite-equipped nesting females disperse at some point that summer. Release site placement near leks or nesting habitat is therefore unlikely to resolve this issue for lesser prairie-chickens.

Translocation of lesser prairie-chickens appears to present significantly more obstacles to success than the translocation of other grouse species. Dispersal movements that lesser prairie-chickens undergo appear to be innate, and these movements are not easily constrained by nearby leks or habitat. While translocation is likely to be raised as an option by state and federal agencies as the debate over the species' conservation status continues, some caution should be exercised when initiating new translocation projects. Mortality and diffusion caused by dispersal movements are likely to result in the rapid failure of lesser prairie-chicken translocations that use fewer than several hundred birds. Managers should also consider if alternatives to translocation might be more effective ways to increase lesser prairie-chicken populations. Habitat conservation, including the establishment of CRP grasslands and improvements to rangeland management, is a proven technique for conserving lesser prairie-chickens (Hagen et al. 2004), and there may be circumstances where funding would be better spent on conserving habitat within the range of preexisting populations than on translocating birds to habitat outside their current range.

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Table 2-1: Number of lesser prairie-chickens translocated from the Short-Grass Prairie/CRP Mosaic Ecoregion of northwest Kansas to the Cimarron and Comanche National Grasslands in the Sand Sagebrush Prairie Ecoregion in southwest Kansas and southeast Colorado between fall 2016 and spring 2019.

	Release Site				
	Cimarron		Comanche		
	Males	Females	Males	Females	Total
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
Total	101	105	103	102	411

Table 2-2: Transmittered lesser prairie-chickens released at each site on the Comanche and Cimarron National Grasslands in southeast Colorado and southwest Kansas between fall 2016 and spring 2019.

	Comanche Release Sites		Cimarron Release Sites		
	Aubrey Trail	Las Vacas Blancas	P3	L7	L4
Fall 2016	14 (VHF)		13 (VHF)		
Spring 2017	48 (VHF)		35 (VHF)		
Spring 2018		66 (32 VHF, 34 SAT-PTT)	17 (3 VHF, 14 SAT-PTT)	51 (29 VHF, 22 SAT-PTT)	
Spring 2019		68 (47 VHF, 21 SAT-PTT)			82 (58 VHF, 24 SAT-PTT)

VHF: Translocated lesser prairie-chickens equipped with bib-style Very High Frequency radiotransmitters

SAT-PTT: Translocated lesser prairie-chickens equipped with backpack-style satellite platform transmitter terminal GPS transmitters

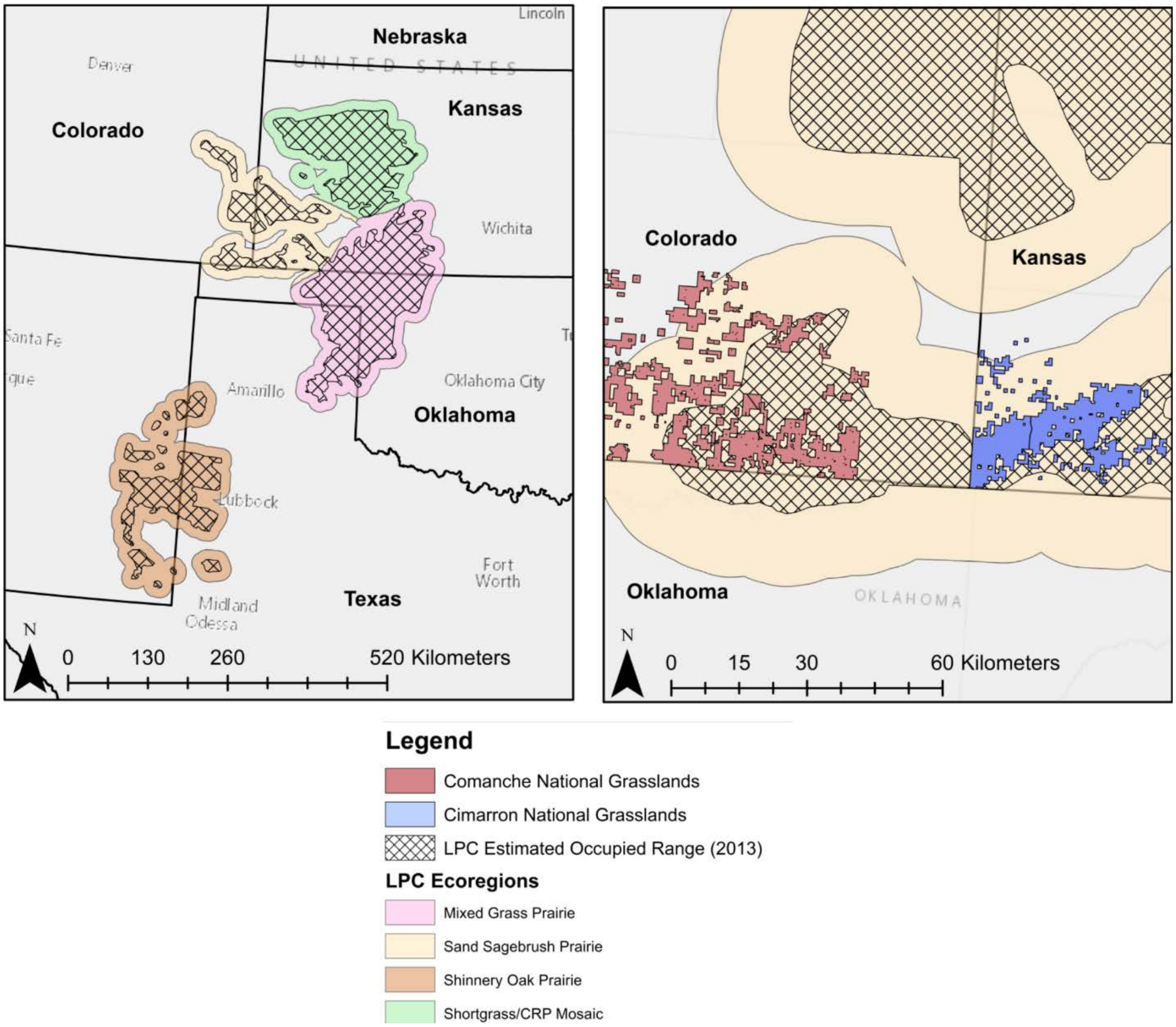

Figure 2-1: Lesser prairie-chicken ecoregions and locations of the Cimarron and Comanche National Grasslands within the Sand Sagebrush Ecoregion

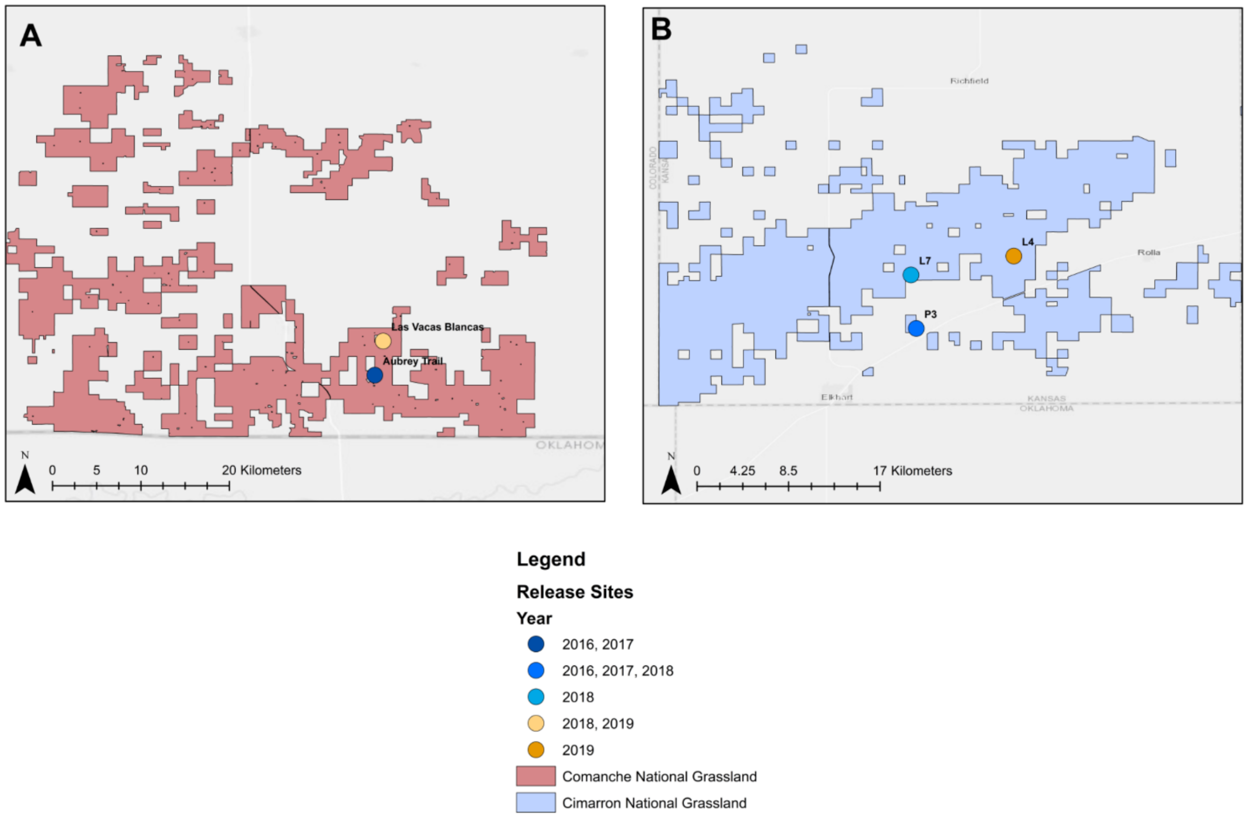

Figure 2-2: Locations of release sites on the Comanche (A) and Cimarron (B) National Grasslands in Colorado and Kansas, respectively, during 2016-2019.

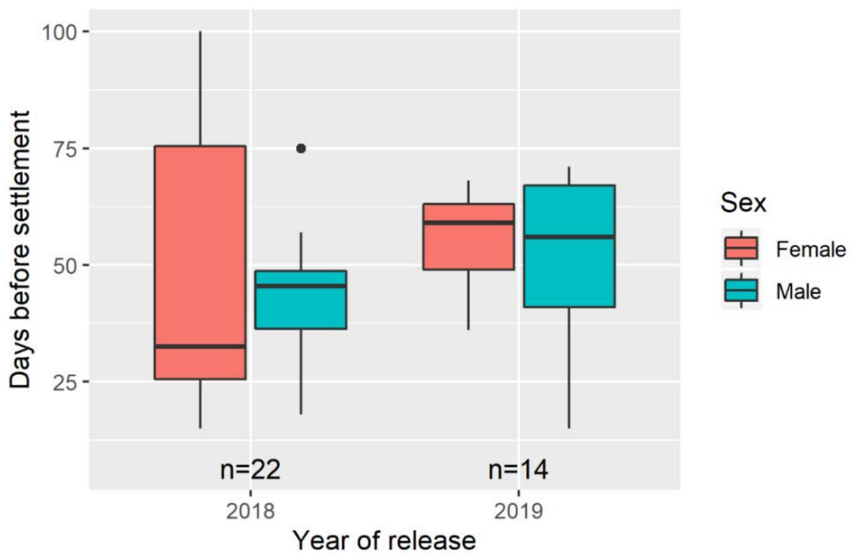

Figure 2-3: Number of days between the release and settlement of satellite-equipped translocated lesser prairie chickens in southwestern Kansas and southeastern Colorado in 2018 and 2019, representing the amount of time each lesser prairie-chicken spent dispersing.

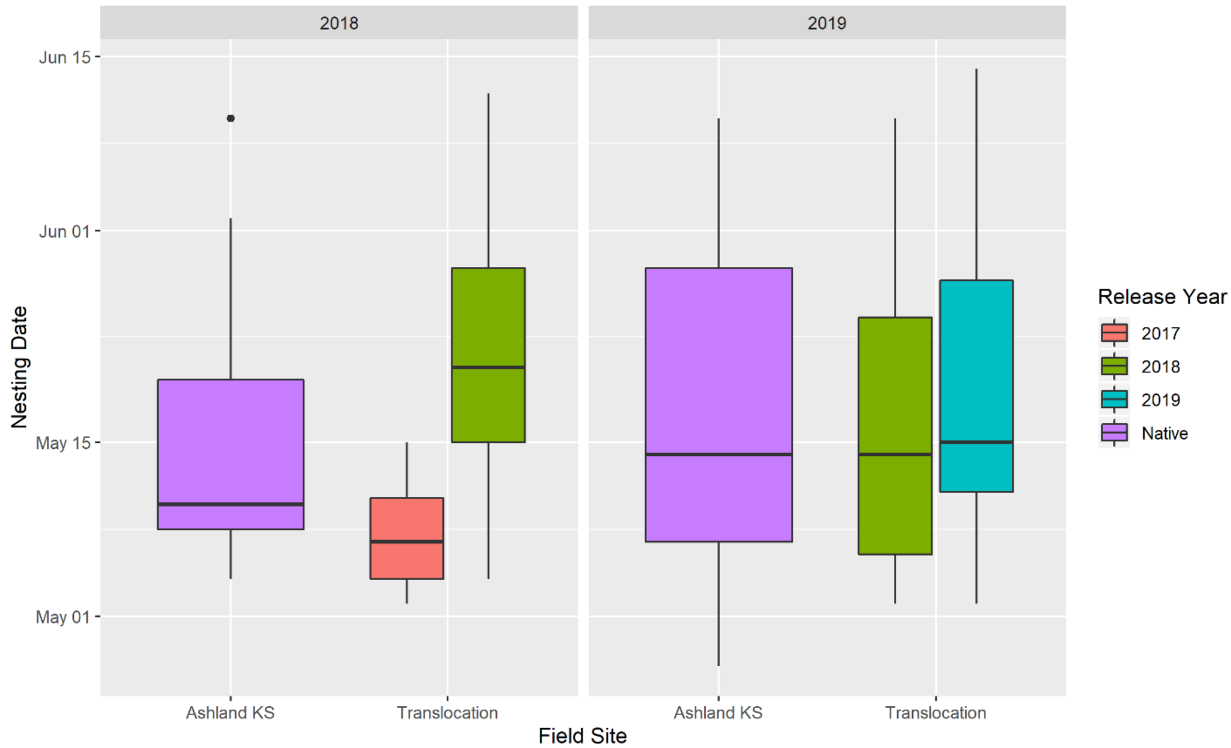

Figure 2-4: Nest initiation dates for translocated lesser prairie-chickens that were released in 2017, 2018, and 2019 in southwestern Kansas and southeastern Colorado compared to the nest initiation dates of a neighboring, native lesser prairie-chicken population in Ashland, Kansas.

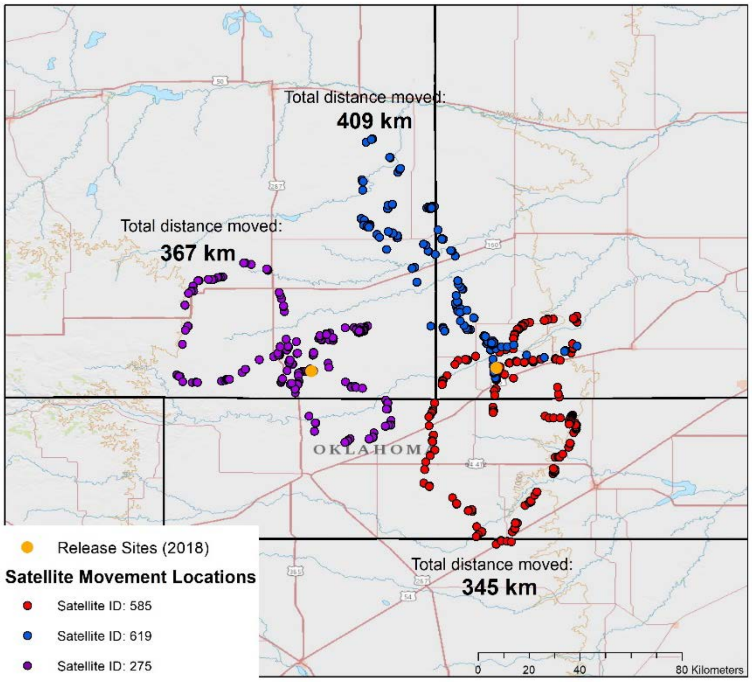

Figure 2-5: Distance moved by the three lesser prairie-chickens translocated to southwestern Kansas and southeastern Colorado with the longest recorded dispersal movements in the summer of 2018, displaying the extent and breadth of exploratory movements made by translocated lesser prairie-chickens.

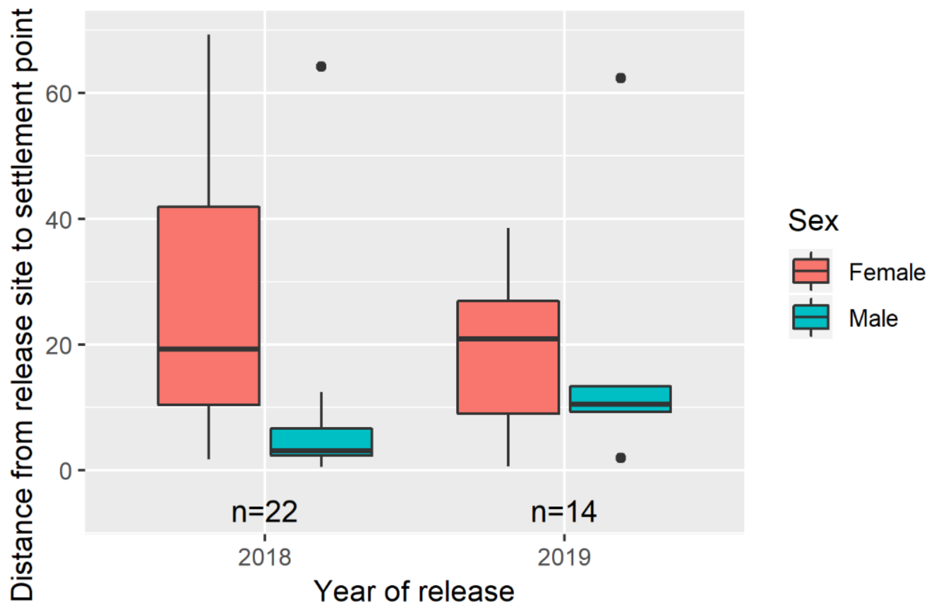

Figure 2-6: Distance from the release site to the settlement site (km) of satellite-equipped lesser prairie-chickens translocated to southwestern Kansas and southeastern Colorado in 2018 and 2019, representing displacement from the release site at the conclusion of the dispersal movement. Boxplots represent variation in displacement from the release site among individuals.

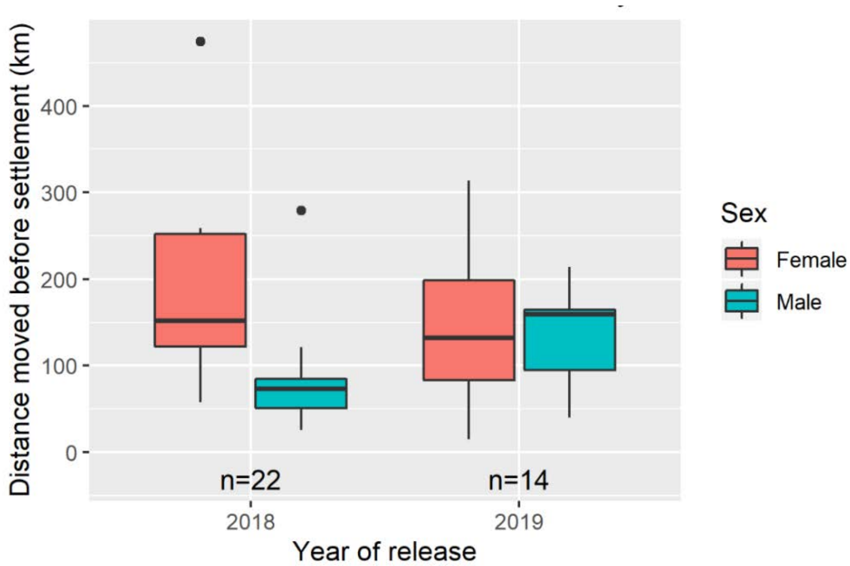

Figure 2-7: Total distance moved between release and settlement for each satellite-equipped lesser prairie-chicken translocated to southwestern Kansas and southeastern Colorado in 2018 and 2019, representing the distance traveled during the dispersal period. Boxplots represent variation in dispersal distance among individuals.

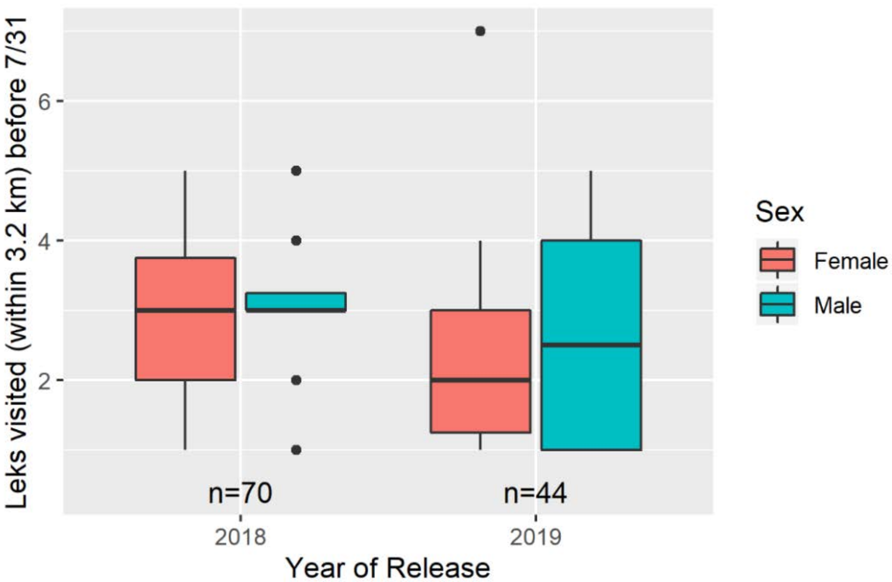

Figure 2-8: Number of known leks visited by each newly translocated lesser prairie-chicken (VHF and SAT-PTT transmitters) before July in the summer of release, for birds moved to southwestern Kansas and southeastern Colorado in 2018 and 2019. Boxplots represent variation in the number of leks visited among individuals.

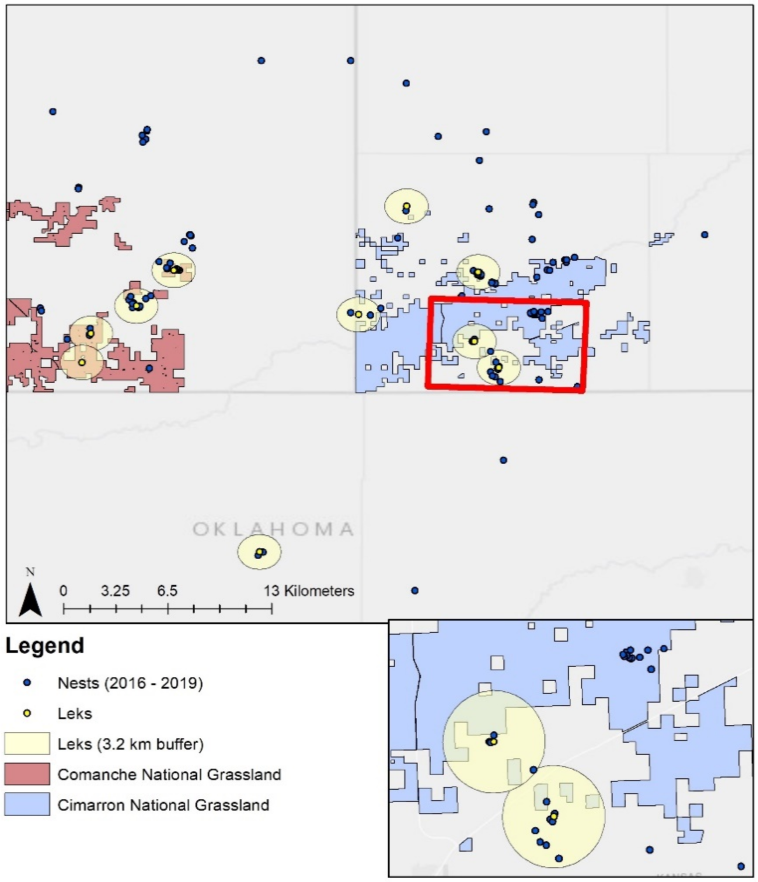

Figure 2-9: Distribution of nests laid by translocated lesser prairie-chickens from 2017 and 2019 in southwestern Kansas and southeastern Colorado, in relation to the locations of leks and their immediate surroundings (3.2 km radius). Almost all nests would fall within 3.2 km of a lek in a native population (Boal and Haukos 2016).

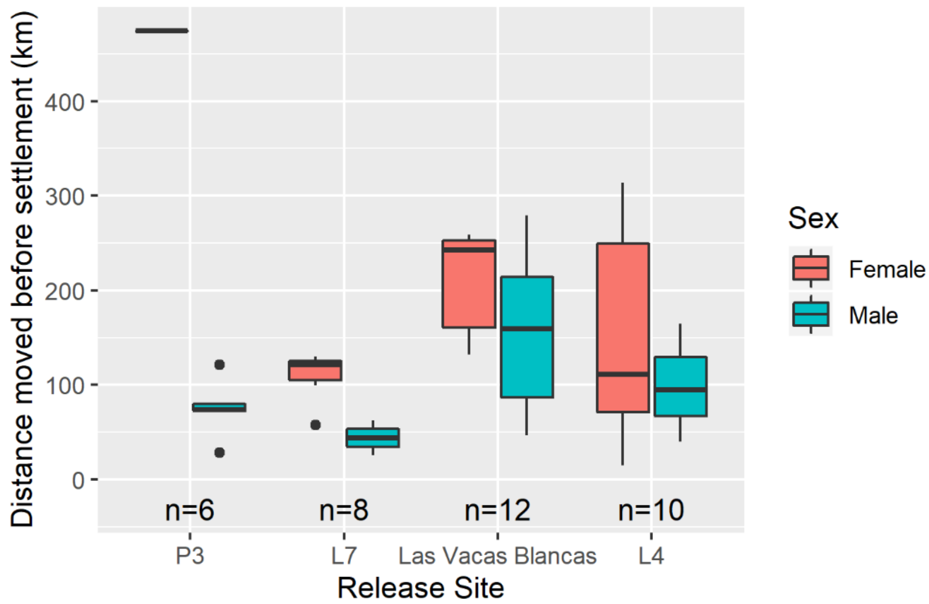

Figure 2-10: Distance traveled during the dispersal period for each satellite-equipped lesser prairie-chicken translocated to southwestern Kansas and southeastern Colorado in 2018 and 2019, broken out by the sites at which these lesser prairie-chickens were released. Boxplots represent variation in dispersal distance among individuals.

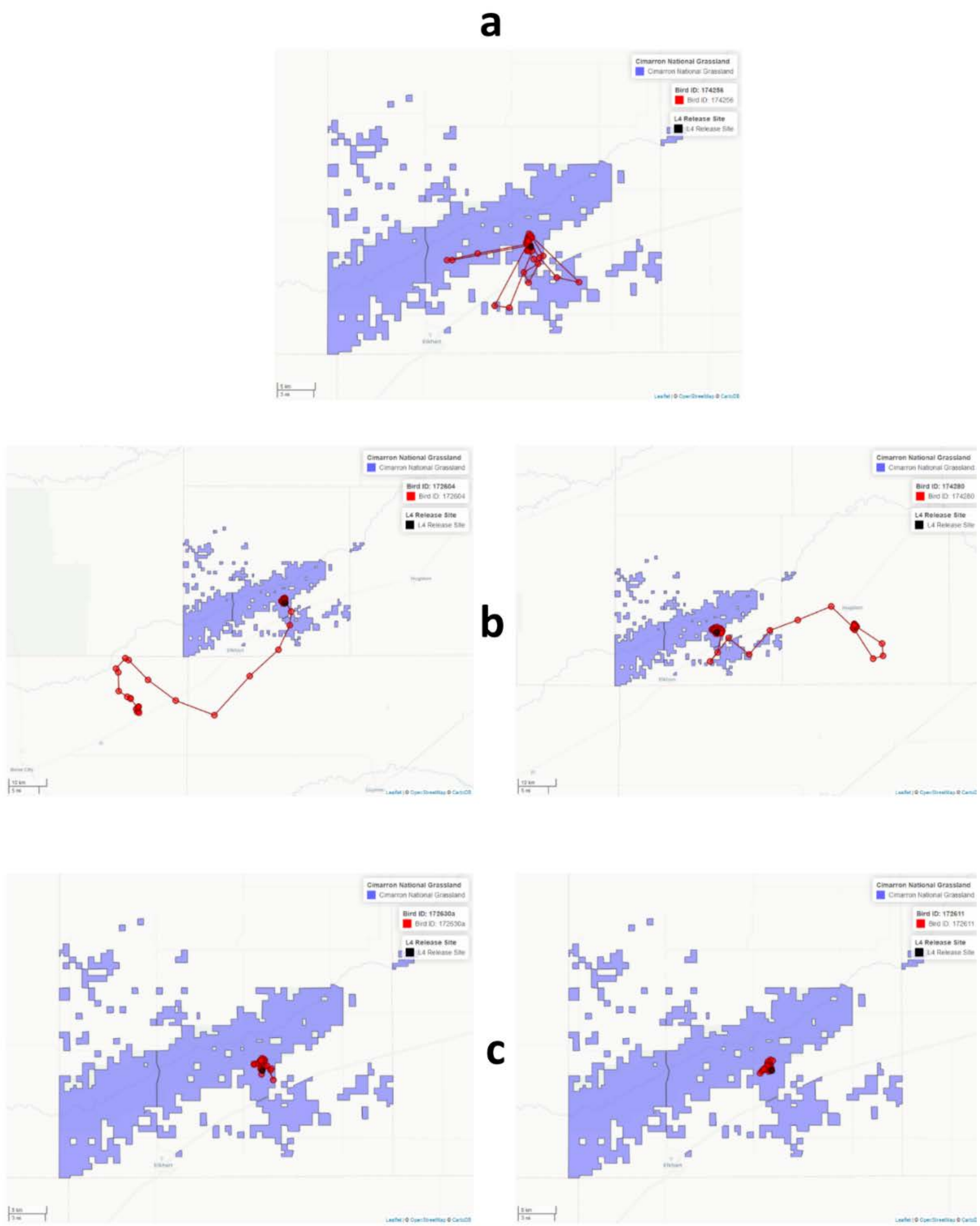

Figure 2-11: Movements of satellite-equipped translocated lesser prairie-chicken females which nested at the site where they were released (L4 on the Cimarron National Grassland in southwestern Kansas) in 2019. One bird (a) underwent a dispersal before nesting, moving 10 km to the east, south, and west before returning to the release site. Two birds (b) dispersed after failed nesting attempts, one (left) moving 45 km west and the other (right) moving 35 km east. Both died after these dispersal movements. The final two (c) females did not disperse from the release site, with one (right) dying before the end of nesting and the other (left) remaining at the release site through the end of the summer.