Response of greater prairie-chickens to natural and anthropogenic disturbance on Fort Riley

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Abstract

Greater Prairie-chickens (*Tympanuchus cupido*) historically occupied 20 states within the contiguous United States and four Canadian provinces; however, due to habitat degradation and loss, they are currently found in 11 states; only four of which have a stable population. Kansas supports a relatively large abundance of Greater Prairie-chickens, where the Flint Hills ecoregion historically supported the largest population of all ecoregions. In the past decade, however, the Flint Hills population has declined to an estimated 8,334 individuals in 2021 from 34,180 individuals in 2015 due to changes and intensification of grassland management practices. The Fort Riley Military Reservation in the northeast portion of the Flint Hills ecoregion is one of a few areas within the ecoregion that does not implement grazing or vast annual burning. The Greater Prairie-chicken population within Fort Riley has remained stable over the past 25 years despite being constrained by surrounding landscape features and development. To understand why this population is doing relatively well compared to populations in surrounding areas, I trapped, collared, and tracked 46 female Greater Prairie-chickens from March-April 2019-2020 on Fort Riley. My goals with this project were to assess female survival, nest survival, resource selection, and space use during the breeding season (Apr-Aug) on the military reservation. Despite being free from grazing and annual burning, Fort Riley experiences fairly constant military activity, which may elicit responses from Greater Prairie-chickens. I used known-fate and nest survival models in Program MARK to estimate female survival and nest success of Greater Prairie-chickens. I estimated breeding season survival as 0.275 ± 0.065 (SE) and nest survival as 0.2643 ± 0.0689 (SE), which are average and high for the Flint Hills, respectively. I used logistic regression models to assess resource selection by Greater Prairie-chicken females. I analyzed landscape features, vegetation variables, and burn mosaics to understand which features had the most influence on resource selection and found landscape features to impact resource selection. Females avoided trees within Fort Riley (probability of use greatest at 2,000 m from nearest tree) at a greater margin than any other study in Kansas. Lastly I calculated home ranges, net, and total daily displacement across the lekking, nesting, and post-nesting stages of the breeding season to understand how Greater Prairie-chickens responded to military activity. Home ranges were slightly smaller than those in surrounding areas yet breeding stage trends remained constant (lekking: 238 ± 43 ha, nesting: 115 ± 20 ha, post-nesting: 113 ± 11 ha) when compared to past literature. Lastly, total daily movements did not differ significantly between days where activity was occurring versus when it was not (training occurring: 1,121 ± 127m, training not occurring: 1,309 ± 63m). My findings suggest that despite being in a constrained environment, Greater Prairie-chickens on Fort Riley are doing well demographically and are not showing signs of being affected by military activity. Because of the constrained environment, however, it is important for land managers to monitor woody encroachment and other tall vertical features as this may lead to loss of habitat and cause potential negative effects on the Fort Riley population.

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Chapter 1 - Nest Success and Breeding Season Survival of Female Greater Prairie Chickens on Fort Riley Military Reservation

Introduction

Natural areas within North America are continually being degraded, transformed, exploited, and ultimately lost despite conservation and monitoring efforts. Grasslands of North America comprise one of the most endangered biomes in the world with 70%-99% of historic grassland areas lost to land conversion (Sampson and Knopf 1994). These losses in turn affect all biodiversity within grasslands, and one group in particular, avifauna, have undergone sharp declines with >74% of all grassland bird species experiencing significant population declines since 1970 (Rosenberg et al. 2019). To continue to monitor the health of grasslands and other declining ecosystems, many biologists have turned to birds to serve as indicator species of ecosystem health and function (Browder et al. 2002, Carnigan and Villard 2002, Mekonen 2017). One particular bird species that may serve as an excellent indicator species of grassland health and function is the Greater Prairie-chicken (*Tympanuchus cupido*) due to its diverse habitat requirements throughout its life.

Greater Prairie-chickens typically live 2-3 years and during that time have diverse habitat requirements depending on the stage of their life cycle. During mating, which is a lek-style system, these birds require short vegetation at relatively high elevation, but females require taller vegetation to provide concealment and thermal refugia during nesting (Jones 1963, Niemuth 2000, Matthews et al. 2013, McNew et al. 2013, Anderson et al. 2015, Hovick et al. 2015). Following egg hatch, females with broods travel to areas with more bare ground and greater forb density than nesting sites or sites available to them on the landscape (Horak 1985, Matthews et al. 2011). Following the breeding season, these birds require different areas for fall and wintering grounds as well as different habitat types for loafing, foraging, and roosting sites (Toepfer and Eng 1988). Because these birds require such large area to incorporate all required habitat types (up to 4,898 ha; Matthews et al. 2011), the Greater Prairie-chicken is an appropriate indicator of grassland health (Winder et al. 2017).

Greater Prairie-chickens historically occupied 20 states within the contiguous United States and four Canadian provinces; however, due to habitat degradation and loss from conversion of grassland to row-crop agriculture, increased urbanization, intensification of grazing, increased presence of woody vegetation, and alteration of natural burning patterns, they are currently found in 11 states, only four of which have a stable population, and no Canadian provinces (Svedarsky et al. 2000; Niemuth 2001; Robbins et al. 2002; Fuhlendorf et al. 2006, 2017; Ross et al. 2006; Hovick et al. 2014a; Winder et al. 2015). This drastic decrease in occupied range has been accompanied by a 75-80% decrease of the original Greater Prairie-chicken population abundance in North America, once numbering in the millions but now down to an estimated 360,000 (Johnsgard 2002, Partners in Flight 2020).

Present-day strongholds for Greater Prairie-chickens include Nebraska and Kansas, USA. In Kansas, the Flint Hills ecoregion historically supported the largest Greater Prairie-chicken population of all ecoregions in Kansas, but the Flint Hills population has declined over the past 30 years (Haukos and Church 1996, Applegate and Horak 1999, Rodgers 2009, Nasman et al. 2021. These declines may be in part due to changes and intensification of grassland management practices to enhance livestock production, reducing the population in the Flint Hills ecoregion to 8,334 in 2021 (Nasman et al. 2021; Figure 1.1a). Current grassland management in >90% of the Flint Hills ecoregion includes prescribed burning and livestock grazing of various intensities and frequencies (Robb and Schroeder 2005, Patten et al. 2007, With et al. 2008, McNew et al. 2015), but these management strategies are often too intense (e.g., double-stock grazing) or too frequent (i.e., annual burning) to maintain adequate vegetation cover and heterogeneity for Greater Prairie-chickens. Many studies have documented implementation of these strategies and associated deleterious effects of current land management practices on Greater Prairie-chicken populations in the Flint Hills ecoregion; but despite this knowledge, nearly 40% of land in the Flint Hills ecoregion is burned annually and intensive early stocking remains a common practice (Collins 1992; Svedarsky et al. 2000; Fuhlendorf and Engle 2001; Fuhlendorf et al. 2006, 2017; Patten et al. 2007; McNew et al. 2015; Winder et al. 2018; Baker et al. 2019).

The Fort Riley Military Reservation is a 41,000-ha parcel of land within the northwest region of the Flint Hills, Kansas, that may serve as refuge from the intense land management practices that occur in surrounding areas for Greater Prairie-chickens and other grassland birds. Fort Riley does not allow grazing on its lands and implements a mosaic style of burning to maintain vegetation heterogeneity on the landscape. Heterogeneity may play an important role in maintaining a stable Greater Prairie-chicken population on Fort Riley Military Reservation since environmental staff started conducting surveys in 1998 (Figure 1.1b). This heterogeneity is especially important to Greater Prairie-chickens that require vastly different habitat types throughout their life cycle. Breeding season habitat, particularly nesting and chick-rearing habitat, is especially important to maintain populations of short-lived species such as the Greater Prairie-chicken where low nesting success coupled with low brood survival is the demographic parameter that limits population viability and most critical vital rate for population growth and persistence due to having the highest elasticity (Wisdom and Mills 1997, Augustine and Sandercock 2011, McNew et al. 2012). To have high nest success and high fecundity, there has to also be high female survival, so understanding female survival is of great importance in addition to estimating the rates vital to population growth. Estimation of nest success and adult breeding season survival in a landscape free of intense management practices common to the Flint Hills, while also comparing these parameters to areas shaped by these intense practices, will enhance understanding of the effects that these practices may have on vegetation structure and habitat quality, but also demography of a declining grassland bird species (Figure 1.1*a, b*). In making these comparisons, I estimated those demographic parameters responsible for maintaining a stable population on Fort Riley Military Reservation and which factors drive these demographics.

Factors such as bird age, time during the breeding season, precipitation, body mass, and annual variation in weather could affect estimates of female breeding season survival. Older females have already survived a breeding season, which should increase their probability of surviving subsequent breeding seasons. Female survival should increase throughout the breeding season because most predation on adults occurs during peak breeding (April-June) when females are initiating and attending nests and at greater risk of predation (Augustine and Sandercock 2011). Regarding precipitation, up to a point this factor would benefit breeding season survival (more vegetation growth and more food availability), but with extreme or frequent precipitation events, females may become more detectable by olfactory predators (Conover 2007, Webb et al. 2012, McNew et al. 2011). Greater body mass equates to better bird condition, which means birds will not have to take as many or as long foraging breaks, reducing their mortality risk (Cresswell 2008).

Environmental factors such as precipitation that may affect female survival can also influence nest success. In addition to environmental factors, nest success can also depend on nest attempt, grass height and cover surrounding the nest, and management strategies such as burn interval. Daily nest survival would be expected to decrease with nest age because of the increasing amount of scent emitted by the female surrounding the nest site as incubation progresses (Lehman 2008). Nest success is expected to decrease with nest attempt. With each subsequent nest attempt, female condition declines (i.e., decreased clutch sizes), ambient temperatures increase, and there are fewer nests on the landscape for predators (McNew et al. 2012, Hovick et al. 2014*b*). Nest survival should increase with increased vegetation surrounding the nest to a point because vegetation serves as cover from predators as well as extreme thermal conditions, but too much cover may hinder a hen's ability to escape a predator. This same relationship should be observed with fire frequency as fire frequency, in the absence of grazing, can be a proxy for vegetation height (Matthews et al. 2013, Grisham et al. 2016). Lastly, due to the negative effects of extreme precipitation events such as exposure, female abandonment, and increased predation following extreme precipitation, nest survival should decrease with increased precipitation (McNew et al. 2014, Londe et al. 2021).

Because many studies focusing on Greater Prairie-chickens in the Flint Hills occur in areas with intense grazing and burning, resultant management recommendations are tailored to mitigating the effects of such land management practices (McNew et al. 2012, 2015; Winder et al. 2017, 2018). Therefore, understanding factors affecting female breeding season survival and nest success in the absence of intense grazing and burning could help inform alternative management practices, provide high-quality habitat, and maximize female survival and nest success rates in these unique areas within the Flint Hills. Therefore, my objectives were to 1) estimate breeding season survival and nest success for female Greater Prairie-chickens across the 24-week breeding season (22 Mar-30 Aug) on Fort Riley Military Reservation, and 2) assess the relative influence of innate and environmental factors on Greater Prairie-chicken female survival and nest success throughout the breeding season on Fort Riley Military Reservation.

Methods

Study Area

Fort Riley Military Reservation (hereafter, Fort Riley) located between Manhattan and Junction City, Kansas, in the northern Flint Hills ecoregion contains ~41,000 contiguous ha, making it one of the largest Military Reservations in the United States (Figure 1.2). About 31,000 of the 41,000 ha are used for military training, wildlife management, hunting, conservation, and other outdoor recreational activities. Unlike other areas surrounding the reservation, Fort Riley does not allow cattle grazing. Within these 31,000 ha, there are 87 training areas that receive various military training activity, burn frequencies, and haying treatments. The average size of training areas is 302 ha (range: 118–642 ha). In addition to training, burning, and haying, Fort Riley environmental staff manage food plots as a wildlife management tool. Within the 31,000 ha area, there are 192 food plots comprising a total area of 289 ha planted with Korean lespedeza (*Kummerowia stipulacea*), corn, soybeans, alfalfa, sunflowers, and wheat, which are grown individually, in combination, and in rotations. Of all active food plots, 70.8% are alfalfa, 7.8% are sunflower-soybean mixture, 7.3% are Korean lespedeza, 6.8% are corn-soybean mixture, 6.8% are wheat, and 0.5% are corn-soybeans-alfalfa mixture.

In addition to wildlife management activities and food plot implementation, the 87 training areas are assigned to various burn regimes. Prescribed burn management typically starts in late winter and continues through fall with most fires occurring in early spring. Prescribed fire is primarily used to control the initiation and spread of woody vegetation, but can be used as a management tool to maintain vegetation heterogeneity on the landscape. The amount of area burned varies annually, but averages 3,943 ha each year. Prescribed burns range in frequency with some areas being burned multiple times within a year to areas not being burned for >20 years; there are occasional wildfires that occur throughout the year in training areas due to lightning strikes and more frequently from detonation of munitions during military training exercises. Overall, 17% of Fort Riley is burned at high fire frequency (≤2 years), 70% is burned at high to mid fire frequency (>2 to 4 years), 6% is burned at mid fire frequency (>4 years to 8 years), and 7% is burned at low fire frequency (>8 years to 16 years).

Haying also occurs in training areas during late summer. These areas are leased by Fort Riley Environmental Division for haying by private landowners. Leases specify harvest time and type, which can be even years, odd years, or annual harvest and for warm season or cool season grasses based on the type of grasses that dominate leased areas. No matter the type of lease, prairie hay is cut and removed mechanically from 15 July - 15 August. The amount of area available for haying varies annually but averages around 11,717 ha within 41 training areas within the area used for military training and wildlife management. Despite being available for cutting, not all of this area is cut each year (Fort Riley Integrated Natural Resources Management Plan 2015).

The climate at Fort Riley is temperate. Maximum daily average temperatures range from a low of 4.2° C in January, to a high of 33.7° C in July. Precipitation averages 85 cm per year, with 75% of that falling in the 6-month period from April through September. In 2019, precipitation events were extreme during the summer months, with the annual average of 85 cm falling in just 3.5 months from late April to August (116 cm total yearly precipitation in 2019), while 2020 experienced approximately average amounts of precipitation (79.5 cm).

Dominant vegetation within the area include grasses such as big bluestem (*Andropogon geradii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), Scribner's panicum (*Dichanthelium oligosanthes*), grama grasses (*Bouteloua* spp.), and smooth brome (*Bromus inermis*); forbs such as false indigo (*Amorpha fruticose*), milkweeds (*Asclepias* spp.), wild indigo (*Baptisia bracteata*), indian blanket (*Gaillardia pulchella*), sunflowers (*Helianthus* spp.), ironweeds (*Vernonia* spp.), wooly verbena (*Verbea stricta*), heath aster (*Symphyotrichum ericoides*), round-head bush clover (*Lespedeza capitate*), Chinese bushclover (*Sericea lespedeza*), and goldenrods (*Solidago* spp.); and woody plants/shrubs such as sumac species (*Rhus* spp.), eastern redcedar (*Juniperus virginiana*), bur oak (*Quercus macrocarpa*), rough-leaf dogwood (*Cornus drummondii*), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*).

Capture

I captured Greater Prairie-chickens at leks, the mating grounds, in the spring (Mar-Apr) during 2019 and 2020. Birds were trapped using walk-in funnel traps and drop-nets (Silvy et al. 1990, Schroeder and Braun 1991). I sexed and aged captured individuals based on morphometric traits (mass and pinnae length) and plumage characteristics (sex by tail color patterns; age by coloration, shape, and wear of outermost primary feathers (P9 and P10; Ammann 1944), respectively, as yearling (second-year [SY]) or adults (after-second-year [ASY]). Females were fitted with a rump-mounted 22-g solar-powered Argos GPS satellite transmitter (Model PTT-100, Microwave Telemetry, Columbia, MD, USA) using small loops of Teflon ribbon fitted around the legs of the birds (Rappole and Tipton 1991, Bedrosian and Craighead 2007, Humphry and Avery 2014, Streby et al. 2015). I also recorded morphometric measurements including mass, tail length, tarsus length, tarsus + toe, wing length, total head length, pinnae length, comb length, comb height, and culmen; mass was measured in grams using a spring scale, all others were measured in mm using digital calipers (Table 1.1). Lastly, each bird was given a unique combination of colored plastic leg bands based on lek of capture, along with one uniquely numbered metal band. Capture and handling procedures were approved under Kansas State University IACUC protocol 4193, and Kansas Department of Wildlife, Parks, and Tourism scientific collection permits SC-015-2019 and SC-032-2020.

Monitoring

Satellite transmitters recorded bird locations via GPS satellite transmitters every 2 hours from 0400-2200 during the breeding season for a total of 10 locations per day with an accuracy of ±18 m. I downloaded locations weekly for movement and mortality assessment. Transmitters also had temperature and activity sensors, which helped detect mortality events. When an event was indicated, I visited the indicated location of mortality and searched until the transmitter was located and signs of mortality were found (carcass or other remains). I attempted to determine cause of mortality based on feather and transmitter condition (Dumke and Pils 1973).

I determined nest site locations once GPS locations indicated a female had started incubating (females continuously in the same location >2 days in a row). I approached the indicated nest location and searched until the nest was found. I spent little time at the nest location (<5 min) and would not return to the nest location again until transmitter data indicated that the female permanently left the nest site or experienced a mortality event. Using clutch size at the time of nest discovery as well as time of incubation onset based on satellite data, I estimated hatch date for each nest. Once the female left the nest site, I returned and determined whether the nest had hatched (≥1 egg hatched) or failed based on egg break patterns (presence of pipping), predator sign at the nest site (scat, hair, feces), and day of fate determination (compared to the estimated hatch date; Hagen et al. 2007). Due to the low number of successful nests, we did not track broods and therefore did not assess brood survival.

Nest Vegetation Surveys

I conducted vegetation sampling at each nest site within a week of known or estimated hatch date. I recorded vegetation measurements at the nest bowl and in each cardinal direction 4 m from the nest bowl (Lautenbach et al. 2019). At each point, I recorded percent cover of forbs, grass, shrub, bare ground, and litter within a 60 x 60 cm Daubenmire frame (Daubenmire 1959). I used a Robel pole to estimate vegetation density at the nest site by taking visual obstruction readings (VOR; Robel 1970). Readings were taken 1 m above ground at 0%, 25%, 50%, 75%, and 100% obstruction where 0% obstruction was the measurement of the highest dm on the Robel pole that was completely uncovered by vegetation and 100% obstruction was the highest dm on the Robel pole completely covered by vegetation.

Survival Analysis

Adult survival

I used the known-fate survival model type in Program MARK to test factors of precipitation, mass, age, year, and time as predictors for breeding-season survival of female Greater Prairie-chickens (White and Burnham 1999). I modeled weekly survival over a 24-week time span (22 Mar – 30 Aug). Precipitation data were retrieved from the US Climate Data website (usclimatedata.com) at the weather station closest to the field site (Milford, Kansas). I differentiated weeks during the breeding season based on precipitation received each week. Weeks receiving ≥5 cm of precipitation were categorized as wet compared to weeks that received less precipitation. I developed 17 *a priori* models based on my hypotheses and ranked the models using Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and

Anderson 2002). Models within 2 ΔAIC_c of the top-ranked model were considered competing models and model averaging was considered based on the number of parameters within the competing models. The estimated weekly survival from my top model was derived over the 24-week breeding season and I used the delta method to calculate the standard error of the derived estimate (Powell 2007).

Nest survival

I used the nest survival model in Program MARK to estimate daily nest survival. I tested the relative effects of combinations of burn frequency of the nest site, age of the hen, grass cover at the nest site, grass height at the nest site, nest attempt, and average precipitation during nesting on daily nest survival. Precipitation data were the same as described for hen survival models. I developed 15 *a priori* models based on my hypotheses. All models were ranked within an AIC_c framework; models within 2 ΔAIC_c of the top-ranked model were considered competing models and model averaging was considered based on the number of parameters within the model. Estimated nest survival was derived from the constant time model over the 35-day average nesting period (egg laying and incubation) and I used the delta method to calculate standard error.

Results

Adult Survival

I captured and fitted transmitters on 20 females in 2019 and 16 in 2020. Of the 36 birds outfitted with transmitters only 34 were included in survival analyses. I excluded 2 birds that died within 1 week of release post-capture likely due to capture and handling. Thirteen birds were known to survive either breeding season of 2019 or 2020. In 2019, 10 of the 20 birds captured died during the breeding season and 4 birds were right censored. Of the 16 birds captured in 2020, 7 died during the breeding season and 2 were right censored due to battery failure (1) and a slipped transmitter (1). Finally, of the 19 total mortalities that occurred during the breeding season, 11 (58%) were due to raptors, 4 (21%) were due to mammals, and 4 (21%) were due to unknown causes.

There were 5 models within 2 ΔAIC_c of the top-ranked model, but only the model with mass did not include spurious variables (variables where 95% confidence intervals did not overlap 0; β_{mass} = 0.0069, SE = 0.0026, 95% CI = 0.0017, 0.0121; Table 1.2); therefore, I used this model to estimate breeding season survival. Survival increased as mass at capture increased; from the lightest bird (700 g) to the heaviest bird (1050 g), there was a 17.7% increase in weekly survival probability throughout the breeding season. From the lightest bird to the median bird mass (884 g), there was a 13.6% increase in survival probability, whereas from the median mass to the heaviest bird there was only a 3.7% increase in survival probability (Figure 1.3). The weekly survival rate based on mass was 0.9477 (95% CI = 0.9260-0.9632) and when extrapolated out to the 24-week breeding season, the survival estimate was 0.275 ± 0.065 (SE).

Nest Survival

I located and monitored 34 nests during 2019 and 2020 (16 in 2019 and 18 in 2020). Of those nests, 4 were successful in 2019 for an apparent nest success rate of 25% and 4 were successful in 2020 for an apparent nest success rate of 22%. The average distance from lek of capture to the nest was 1,569 m ± 272 (SE; range = 496 – 5,488 m) while the average distance from nearest lek to nest was 982 m ± 155 (SE; range = 215–5,534 m). Among the 15 models tested, 7 were competitive in that they had a $\Delta AIC_c \leq 2$ but the top ranked model was the constant model (β = 3.251, SE = 0.199, 95% CI = 2.859, 3.642; Table 1.3). The daily nest survival rate based on the constant model was estimated as 0.9627 (95% CI = 0.9457 - 0.9745).

Overall nest survival was estimated as 0.2643 ± 0.0689 (SE) extrapolated out to the 35-day nesting period. Despite not being the top-ranked model, the potential year effect on nest survival was of interest to me as my study area received vastly different amounts of precipitation between 2019 and 2020 (see *Study Area* above). I estimated daily nest survival rates for both 2019 (0.9709 [95% CI = 0.9495-0.9834]) and 2020 (0.9507 [95% CI = 0.9185-0.9706]), which extrapolated to an estimated nest survival rate of 0.3563 ± 0.1061 (SE) and 0.1704 ± 0.0806 (SE) over the entire 35-day nesting period for 2019 and 2020, respectively (Figure 1.4).

Discussion

Adult Survival

Interestingly, female body mass at capture was the most influential innate factor for female survival during the breeding season. Several other competing models included year, precipitation, and age, but the betas for these covariates were not significant at the 95% confidence interval, and the model with the most weight was purely driven by body mass. The most beneficial strategy in terms of increasing survival seems to be increasing over-winter body mass of birds with below-average mass. These results highlight the importance of forage availability and carry-over effects on female survival where fall and winter conditions may ultimately influence female survival during the breeding season.

Carry-over effects are those events or processes that occur in one season but have lasting effects on an animal in subsequent seasons (Harrison et al. 2011). Some examples of carry-over effects affecting birds include forage quality during the previous season (Heffron 1989, Sorensen et al. 2009), habitat quality during the previous season (Gunnarsson et al. 2006, McNew et al. 2015, Winder et al. 2018), and weather conditions (i.e., drought) the previous season (Duriez et al. 2012, Londe et al. 2021). For grouse species, forage quality during winter comes in the form of seeds, leaves, and agricultural waste. Therefore, there needs to be readily available forage, primarily in the form of native sunflowers and other forbs, Korean lespedeza, or crops such as soybeans, wheat, corn, or sorghum for birds to maintain mass over-winter (Heffron 1989). Coincidentally, Fort Riley implements food plots as supplemental food for wildlife, so examining the use of these food plots by Greater Prairie-chickens in fall and winter of their lifecycle would be of interest from a land management perspective as well as a wildlife sustainability standpoint. Habitat quality during the previous year is also important for annual survival in the next year. Winder et al. (2018) found annual survival to be greater and mortality risk to be lower for female Greater Prairie-chickens in areas that implemented patch-burn grazing due to the heterogeneous habitat created and residual vegetation cover left over from patch-burn grazing practices as opposed to annual burning and intensive grazing that would typically be used in these landscapes. Finally, weather can influence nesting phenology of Greater Prairie-chickens in subsequent years. Londe et al. (2021) found that birds experiencing drought conditions in the previous year would delay incubation initiation the next year. Such carry-over effects often affect survival and reproductive success of the species of interest, as found in female Greater Prairie-chicken survival in my study.

My result of mass as the main indicator of female breeding season survival among tested covariates is surprising as other studies identified age, site, place of origin (resident versus translocated bird), or constant models to be most explanatory for female breeding season survival (Augustine and Sandercock 2011, McNew et al. 2012, Carrlson et al. 2014). The only other Greater Prairie-chicken study to test mass at time of capture found mass to have a positive yet nonsignificant effect on survival ($\beta = 0.27 \pm 0.32$; 95% CI: -0.36, 0.90; Augustine and Sandercock 2011). Augustine and Sandercock (2011) estimated constant breeding season survival to be 0.122 ± 0.049 (SE) over a 26-week breeding season (compared to my estimate of 0.25 for 26-week survival), while McNew et al. (2012) found age to be the biggest factor in determining survival. Outside of Kansas, Carrlson et al. 2014 found breeding season survival of resident birds in Missouri, USA, to be much higher than those translocated (0.65 ± 0.09 (SE) and 0.42 ± 0.13 (SE) respectively). My estimates were significantly greater when compared to the Augustine and Sandercock (2011) estimate from a study area within 15 km of Fort Riley. Their study area incorporated grazing by cattle and bison (*Bison bison*) but had a burn regime similar to Fort Riley, where the area was divided into different experimental units that received varying burning and grazing regimes. Unlike Fort Riley, however, these units averaged 66 ha as opposed to the average 302 ha on Fort Riley, which increases edge habitat and limits contiguous area available within each habitat type. Both of these factors could limit survival of Greater Prairie-chickens. Augustine and Sandercock (2011) cited intensive predation as the main reason for low breeding season survival. Predators have been cited to use more edge habitat and have greater abundance in smaller patch sizes, so differences in patch size between the two sites may partially explain the increased predation in Augustine and Sandercock (2011) study as opposed to mine (Chalfoun et al. 2002). The presence of cattle could also affect survival in this area as foraging cattle will inevitable decrease visual obstruction, a proxy for the amount of cover available on the landscape to nesting hens.

Nest Survival

Overall, nest success was relatively high at Fort Riley compared to previous studies on surrounding areas and did not show much variation because of environmental factors like precipitation or differences in micro-habitat. Previous studies have cited the detrimental effects of extreme precipitation on nest success of several upland game bird species (Palmer et al. 1993, Roberts et al. 1995, Moynahan et al. 2007, Londe et al. 2021), but nest success in my study was two times greater in the year of extreme precipitation, most of which fell during the laying and incubation period, than the year of average precipitation. The amount of residual vegetation and therefore high-quality nesting habitat available to nesting hens on the landscape on Fort Riley may have contributed to the lack of detrimental effects of extreme precipitation had on nests. Additionally, studies in similar landscapes to my study area have found there to be significant differences in vegetation between what is used by and available to Greater Prairie-chickens, but there was not a significant difference between used and available vegetation on Fort Riley, (Chapter 2). My findings suggest that Fort Riley has sufficient vegetation structure and cover to provide high quality nesting habitat for Greater Prairie-chickens at the landscape scale relative to estimates from previous studies in surrounding areas.

Augustine and Sandercock (2011) estimated nest success on Konza Prairie Biological Station (Manhattan, KS; 35-d) at 0.074. In the north-central Nebraska, Harrison et al. (2017) estimated nest survival during incubation (25-d) at 0.37. Matthews et al. (2013) estimated nest survival (25-d) of nests placed in cool-season grasses as 0.44 and nests placed in warm-season grasses as 0.54 study in Johnson County, Nebraska. If extrapolated to 25-d nesting period, my nest success estimates would be 0.46 and 0.28 for 2019 and 2020, respectively, which are similar or greater than estimates in Nebraska. Finally, across the southern Flint Hills, the northern Flint Hills, and the Smoky Hills of Kansas, McNew (2010) estimated an overall nest success rate over a 37-day period to be 0.12 ± 0.04 (mine would be 0.32 and 0.14 for 2019 and 2020, respectively). Given the variation in estimates of nest success between Fort Riley and other study areas in the Flint Hills, it begs the question of how variation in vegetation and grazing influences regional differences in nest success.

Many studies have documented the importance of vegetation height to nest success of prairie grouse species (Webb et al. 2012, Matthews et al. 2013, McNew et al. 2013, Grisham et al. 2016, Harrison et al. 2017, Lautenbach et al. 2019). For example, McNew et al. (2013) found daily nest survival increased from 0.85 to 0.97 when nesting cover increased from <2 dm to >5 dm and determined that overall nest success could increase from 0.17 to 0.52 if 100% visual obstruction at the nest increased from 25 to 50 cm. Despite the number of studies documenting the importance of vegetation height and cover to nest success, I did not find these to be contributing factors to nest success in my study. This could be due to the lack of cropland on Fort Riley, and therefore more area for high-quality grassland, as opposed to other study areas that had more cropland on the landscape (46% Matthews et al. 2013; 3%, 10%, and 38% McNew et al. 2012; 7% Harrison et al. 2017) and thus less area available for nesting cover. Alternatively, the lack of intense management practices that are found elsewhere in the Flint Hills that reduces vegetation heterogeneity and decreases the amount of high-quality nesting habitat available for Greater Prairie-chickens could explain difference in vegetation selection. Based on my findings, I would draw the conclusion that high-quality nesting habitat is not limiting on Fort Riley; therefore, there may not be sufficient variation of vegetation structure and composition at nest sites for some features of vegetation to be considered influential in nest success.

In conclusion, it appears that the vegetation structure on Fort Riley meets the needs of Greater Prairie-chickens during the breeding season. There is enough high-quality forage during the fall and winter months to maintain high fitness levels (as determined by mass) that would in turn lead to relatively high adult survival rates during the breeding season. There is also enough vegetation cover to provide good nesting habitat, which would lead to better than normal nest success for the Flint Hills ecoregion. Despite the seemingly high-quality forage during the fall and winter months, adult survival rates are relatively similar or greater comparing Fort Riley and surrounding areas (Augustine and Sandercock 2011, McNew et al. 2012). This similarity does not hold for nest survival rates, as Fort Riley has greater nest success than surrounding areas (McNew 2010, Augustine and Sandercock 2011). The lack of differences in adult survival but fairly large difference in nest success between Fort Riley and surrounding private lands in the Flint Hills ecoregion leads me to conclude that nest success is what may be driving the population on Fort Riley and therefore, maintaining the stable population on Fort Riley (Wisdom and Mills 1997, Sullins et al. 2018, Ross et al. 2018).

Management Implications

My results highlight the importance of focusing on year-round habitat quality rather than just breeding season habitat quality. By doing so, enough over-winter cover and food resources will be available to increase Greater Prairie-chicken fitness for the subsequent breeding season and possibly lead to greater survival and reproductive output. Cover can be maintained on Fort Riley through application of fire in the proper fire return intervals. Fortunately, a majority of area on Fort Riley is burned every 2-4 years, leaving abundant vegetation structure to conceal nesting hens and nests while maintaining a burn frequency that controls woody vegetation. This is in stark contrast to many private lands in surrounding areas that burn on an annual basis followed by intensive stocking of livestock, leaving little residual cover for nesting the next year. In addition to burning at the proper intervals, sparse haying could mimic grazing and therefore increase grass abundance while burning at different times of the year (late growing season) could increase forb growth by minimizing grass competition. Forb growth would be important as forbs are a main food source for adults both during the late breeding season as well as during fall and winter months. In addition, forbs attract arthropods, which are the main food source for chicks during the first several months of their life. Maintaining cover and food resources is the key to maintaining Greater Prairie-chicken populations, so by implementing these strategies, populations across the range could see stability instead declines that are currently being faced.

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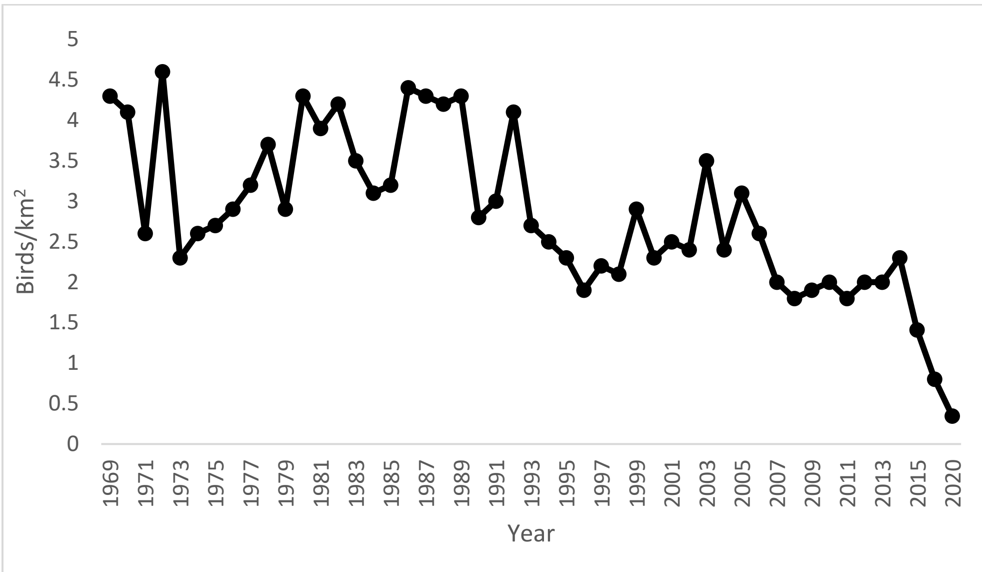
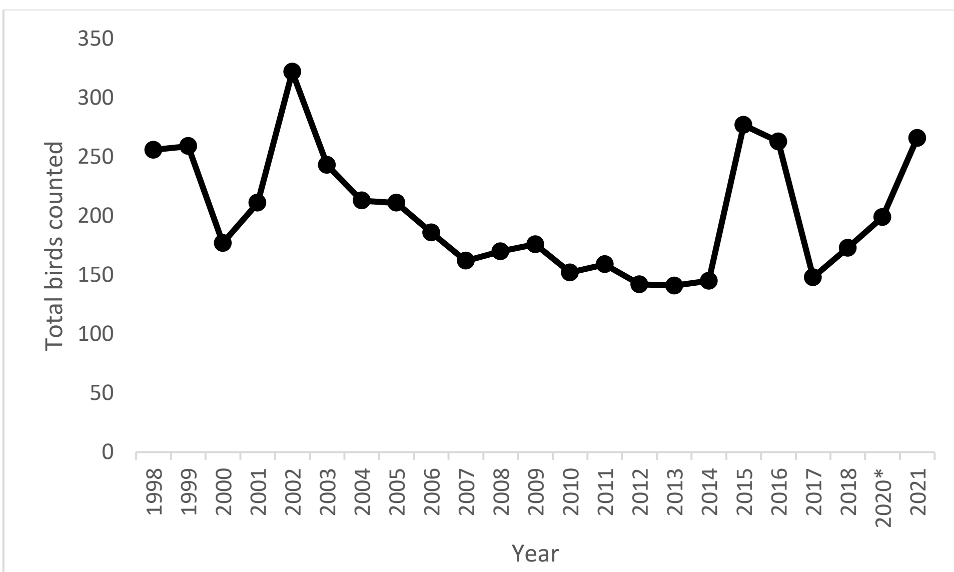
Figures





b)

Figure 1.1. Population trends of Greater Prairie-chickens in the Flint Hills ecoregion of Kansas, USA. Data were derived from annual and semi-annual lek counts conducted by Kansas Department of Wildlife, Parks, and Tourism from 1969–2018. b) Counts of annual lek surveys conducted on Fort Riley Military Reservation, Kansas. Numbers represent total birds flushed from leks during the lekking season. * = complete survey set not conducted due to COVID-19

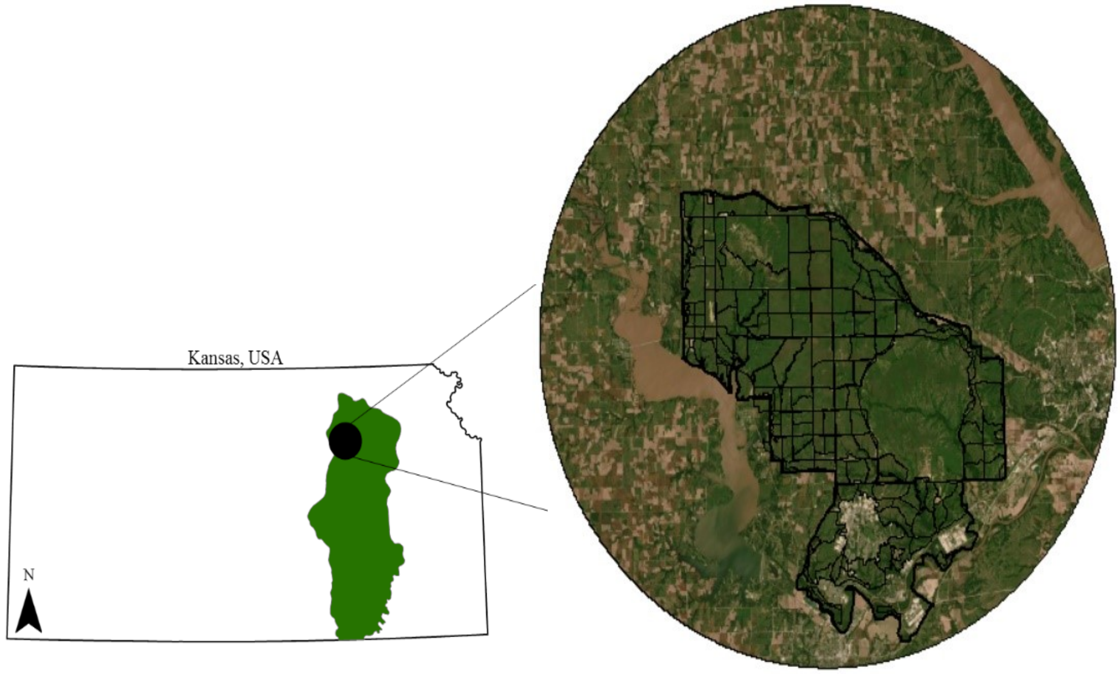


Figure 1.2. Location of Fort Riley Military Reservation within the Flint Hills ecoregion of Kansas, USA (outlined in green). Training units within Fort Riley Military Reservation are delineated (figure adapted from McCullough et al. 2021).

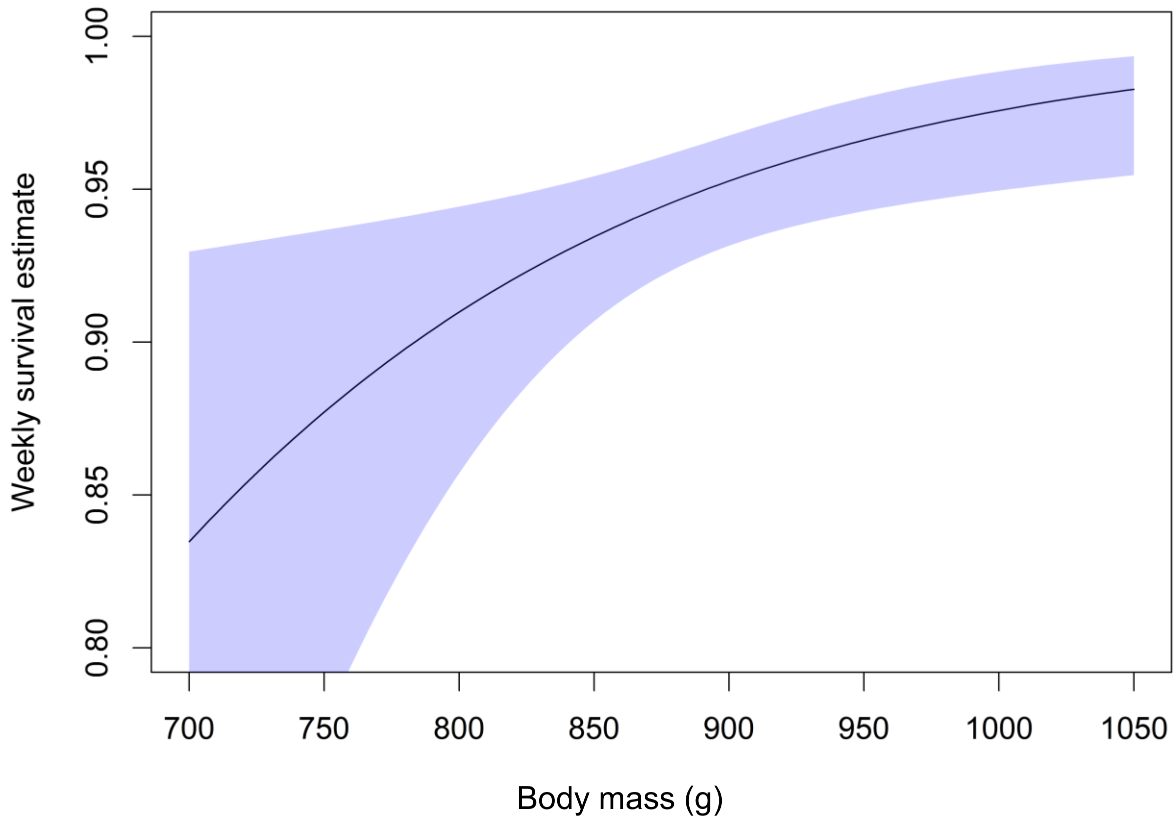


Figure 1.3. Estimate of adult female weekly survival of Greater Prairie-chickens as a function of mass over the 24-week breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019–2020.

Tables

Table 1.1. Average (± standard error) of morphometric measurements of female Greater Prairie-chickens captured during 2019-2020 on Fort Riley Military Reservation, Kansas, USA.

Morphometric measure	$\bar{x} \pm SE$
Bird mass (g)	888.88 ± 10.63
Tail length (cm)	9.89 ± 0.15
Diagonal tarsus (cm)	5.74 ± 0.08
Wing length (cm)	21.72 ± 0.08
Head (cm)	6.09 ± 0.05
Pinnae length (cm)	3.24 ± 0.09
Comb length (cm)	2.30 ± 0.17
Comb height (cm)	0.38 ± 0.04
Culmen (cm)	1.65 ± 0.05

Table 1.2. Model rankings using known-fate analyses in Program MARK to estimate the 24-week breeding season survival of adult female Greater Prairie-chickens on Fort Riley Military Reservation, Riley, Kansas, USA, 2019–2020.

Model[1]	*K*	*AICc*	*Δ AICc*	ω_i	*Deviance*
S mass	2	241.13	0.00	0.29	237.10
S year+mass	3	242.83	1.70	0.12	236.79
S precipitation+mass	3	243.01	1.88	0.11	236.97
S age+mass	3	243.04	1.91	0.11	237.00
S mass^2	3	243.12	1.99	0.11	237.08
S year+mass^2	4	244.82	3.69	0.05	236.75
S mass+precipitation+year	4	244.82	3.70	0.05	236.75
S mass^2 +precipitation	4	245.01	3.88	0.04	236.94
S age+mass^2	4	245.02	3.90	0.04	236.95
S constant	1	245.97	4.85	0.03	243.97
S age	2	247.18	6.06	0.01	243.16
S year	2	247.65	6.53	0.01	243.63
S precipitation	2	247.82	6.70	0.01	243.80
S year+age	3	248.93	7.81	0.01	242.89
S time	24	249.32	8.19	0.01	199.23
S precipitation+year	3	249.63	8.50	0.00	243.59
S year*time	48	300.49	59.36	0.00	195.93

[1] K = no. of parameters, AIC_c = Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i = AIC_c weight, Deviance = model fit.

Table 1.3. Model rankings for nest survival analyses in Program MARK to estimate nest survival over the 35-day laying and incubation period of Greater Prairie-chickens on Fort Riley Military Reservation, Riley, Kansas, USA, 2019–2020.

Model[1]	*K*	*AICc*	*Δ AICc*	ω_i	*Deviance*
S constant	1	224.04	0.00	0.23	222.03
S year	2	224.17	0.13	0.21	220.15
S year+age	3	225.58	1.55	0.10	219.55
S year+grass cover	3	225.63	1.59	0.10	219.60
S year+grass height	3	225.76	1.72	0.10	219.72
S year+precipitation	3	225.82	1.79	0.09	219.79
S year+burn frequency	3	225.94	1.91	0.09	219.91
S year+attempt	3	226.05	2.02	0.08	220.02
S year+time+grass height	96	383.19	159.15	0.00	160.15
S year+time+burn frequency	96	386.31	162.27	0.00	163.27
S year+time+grass cover	96	387.07	163.04	0.00	164.03
S year+time+attempt	96	387.69	163.65	0.00	164.65
S year+time+precipitation	96	399.34	175.31	0.00	176.30
S year+time+age	96	402.85	178.81	0.00	179.81
S year*time	190	650.29	426.26	0.00	126.85

[1] K = no. of parameters, AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i = AIC_c weight, Deviance = model fit.

Chapter 2 - Resource Selection by Female Greater Prairie-chickens on Fort Riley Military Reservation during the Breeding Season

Introduction

Despite conservation and monitoring efforts, many ecosystems are facing significant decreases in area due to landscape degradation, transformation, and exploitation. Grasslands of North America are considered one of the most endangered biomes in the world with 70-99% of historic grassland areas lost to land conversion (Samson and Knopf 1994). These losses in turn affect biodiversity within remaining grasslands, with avifauna in particular experiencing steep population declines (>74% of species in decline since 1970; Rosenberg et al. 2019). To continue to monitor the health of grasslands, and other declining ecosystems, many biologists have turned to birds as indicator species of ecosystem health and function (Browder et al. 2002, Carnigan and Villard 2002, Mekonen 2017). Grouse may serve as excellent indicator species of ecosystem health and function due to their relatively short lifespans and diverse habitat requirements throughout their life (Coates et al. 2016); populations of Greater Prairie-chickens (*Tympanuchus cupido*) are considered indicators for overall grassland health (Winder et al. 2017).

Over their average 2-3 year lifespan, Greater Prairie-chickens require diverse habitat types based on the state of their life stage. During mating, which is a lek-style system, these birds require short vegetation on relatively high elevation, but females select taller and thicker vegetation to provide concealment and thermal refugia during nesting (Jones 1963, Niemuth 2000, Matthews et al. 2013, McNew et al. 2013, Anderson et al. 2015, Hovick et al. 2015a). Once eggs hatch, females travel with broods to areas with more bare ground but greater forb density than nesting sites (Horak 1985, Matthews et al. 2011). Following the breeding season, Greater Prairie-chickens prioritize areas that have readily available forage to survive over winter (Toepfer and Eng 1988). Because these birds require large landscapes to incorporate all required habitat types (up to 4,898 ha; Matthews et al. 2011), the Greater Prairie-chicken is an appropriate indicator species for monitoring grassland ecosystems (Winder et al. 2017).

Resource selection is measured by comparing use by a species relative to availability of that resource on the landscape. Selection can occur at multiple spatial scales (Johnson 1980). The more a resource is used relative to available, the more influential that selection is on the ecology of the focal species. Measuring resource selection is necessary for species because it identifies potential limiting factors and prioritizes management strategies developed during conservation planning for species of conservation concern, such as the Greater Prairie-chicken. In addition, due to their vast range of habitats needed during the breeding season, identifying resources important for Greater Prairie-chickens across their life cycle can ensure grasslands have the heterogeneity necessary to meet the needs of many other species as well (Hovick et al. 2015).

Contemporary strongholds for Greater Prairie-chickens include Nebraska and Kansas, USA. In Kansas, the estimated Greater Prairie-chicken population declined from 880,000 in 1979 to 58,569 in 2021 (Robb and Schroeder 2005, Nasman et al. 2021). Of increasing concern, populations in the Flint Hills ecoregion, which historically supported the largest Greater Prairie-chicken population of all ecoregions in Kansas, have declined at a greater rate over the past 30 years (Haukos and Church 1996, Applegate and Horak 1999, Rodgers 2009, Nasman et al. 2018). Declines may be due in part to changing and intensification of grassland management practices to enhance livestock production and increasing encroachment of invasive woody vegetation, causing an apparent decline in the Flint Hills' ecoregion population to an estimated 8,334 in 2021 based on aerial surveys (Nasman et al. 2021). Current management in >90% of the Flint Hills ecoregion includes prescribed burning and livestock grazing of various intensities and frequencies (Robb and Schroeder 2005, Patten et al. 2007, With et al. 2008, McNew et al. 2015), but these management strategies are often too intense (e.g., intensive double-stocking grazing systems), improperly timed (grazing March-May coincides with bird nesting seasons), or too frequent (i.e., annual burning) to maintain adequate vegetation cover and heterogeneity (Mohler et al. 2012). Many studies have documented implementation of these strategies and associated deleterious effects of current land management practices on Greater Prairie-chicken populations in the Flint Hills ecoregion; but despite this knowledge, nearly 40% of land in the Flint Hills ecoregion is burned annually and intensive early stocking remains a common practice due to the benefits for cattle (Smith and Owensby 1978, Collins 1992; Svedarsky et al. 2000; Fuhlendorf and Engle 2001; Fuhlendorf et al. 2006, 2017; Patten et al. 2007; McNew et al. 2015; Winder et al. 2018; Baker et al. 2019).

The U.S. Department of Defense Fort Riley Military Reservation is a 41,000-ha parcel of land within the northwest region of the Flint Hills that may serve as refuge for Greater Prairie-chickens and other grassland birds from the intense land management practices occurring in surrounding areas. Fort Riley does not allow grazing on its lands and implements a mosaic style of prescribed burning to maintain heterogeneity of vegetation composition and structure on the landscape that likely benefits Greater Prairie-chickens. Breeding season habitat, particularly nesting habitat, is crucial to maintain populations of short-lived species such as the Greater Prairie-chicken where low nesting success coupled with brood survival are the demographic parameters that limit population viability and are most critical vital rate for population growth and persistence (Wisdom and Mills 1997, Augustine and Sandercock 2011, McNew et al. 2012). Understanding factors influencing nest-site selection as well as overall breeding season resource selection by Greater Prairie-chickens on Fort Riley is crucial to the development of conservation strategies for maintaining a robust population on the reservation.

Factors that may influence selection of resources and nest sites on the reservation include both vegetation and landscape variables. As previously mentioned, Greater Prairie-chickens may use different vegetation structure for different life stages, so understanding which vegetation characteristics (e.g., grass density, percent cover, amount of litter) influence resource selection, especially in such a heterogeneous landscape as Fort Riley, is informative to managers. Despite the abundance of intact grassland on the reservation, Fort Riley is fairly developed in comparison to many private lands in Kansas and has a number of landscape features that may prevent Greater Prairie-chickens from fully utilizing land available on the reservation. These manmade landscape features include electric poles and roads, but in addition Fort Riley has an expanse of riparian areas (forests; 24% of the wildlife management area is riparian; J. Gehrt unpublished data) that can contribute to woody encroachment. All of these factors have been previously cited to deter prairie-chicken movement (Pruett et al. 2009, Lautenbach et al. 2017, Raynor et al. 2019, Plumb et al. 2019). In particular, avoidance of trees could lead to the biggest loss of potentially usable habitat due to rapid encroachment into otherwise pristine Greater Prairie-chicken habitat if left unmanaged (Fuhlendorf et al. 2017). Additionally, I examined the effects of fences on Greater Prairie-chicken movement and resource use as fences have been cited as a cause of mortality in Greater Sage-grouse (*Centrocercus urophasianus*) due to collisions, but no study has examined the effects of fences on Greater Prairie-chicken space use (Wolfe et al. 2007; Blomberg et al. 2013; Patten et al. 2021 (all Lesser Prairie-chicken (*Tympanuchus pallidicinctus)* citations)).

Along with manmade landscape features, Fort Riley itself is surrounded by moderate expanses of urban development (Junction City, Ogden, and Manhattan, KS, and Milford Reservoir- the largest manmade lake in Kansas with 15,700 acres of water immediately surround the reservation on the east, south, and west sides). These features, combined with the extensive cropland north of the reservation, create a landscape resistant to movement of Greater Prairie-chickens away from the boundaries of Fort Riley. Because of this constrained environment, Greater Prairie-chickens are limited in their resource selection to what is available on Fort Riley. Due to the number of landscape features on Fort Riley that may influence resource use by grouse, I assessed the relative effect of factors potentially influencing Greater Prairie-chicken resource use and compared how landscape versus vegetation features affected resource use on Fort Riley.

In addition to identifying factors affecting resource selection, I investigated the scale at which Greater Prairie-chickens select resources on the landscape. Johnson (1980) describes multiple scales of selection (i.e., Orders 1-4); although these scales are nested within one another, animals may differentially select resources among spatial scales to fulfill different habitat requirements. Acknowledging different scales of selection is important for managers because at a coarse scale, a landscape may provide high-quality habitat for a species, but testing at finer scales of selection may reveal a landscape that does not provide proper heterogeneity for the species and can reveal limiting factors for population use. Therefore, I compared resource selection at the landscape scale and at the within-patch scale to understand specific resources sought by Greater Prairie-chickens on Fort Riley.

My overall objective was to evaluate resource selection by female Greater Prairie-chickens on Fort Riley at multiple scales. Specifically, I tested for 1) breeding season resource selection at the landscape scale; 2) nest-site selection at the landscape scale; 3) breeding season resource selection at the within-patch scale; and 4) nest-site selection at the within-patch scale. I hypothesized landscape variables will be the most influential factors when evaluating resource selection at the landscape scale, but vegetation variables will be most influential at the within-patch scale.

Methods

Study Area

Fort Riley Military Reservation (hereafter, Fort Riley; 39.0883, -96.8139), located between Manhattan and Junction City, Kansas, in the northern Flint Hills ecoregion, contains ~41,000 contiguous ha, making it one of the largest Military Reservations in the United States (Figure 2.1). About 31,000 of the 41,000 ha are used for military training, wildlife management, hunting, conservation, and other outdoor recreational activities. Landcover composition of these 31,000 ha is about 24% riparian area (7,440 ha) and 76% grassland (23,560 ha). There are 84 training areas ($\bar{x}$: 316 ha, range: 100–1,189 ha) within these 31,000 ha that receive various burn frequencies, military training activity, and haying treatments. Unlike areas surrounding the reservation, Fort Riley does not allow cattle grazing.

Prescribed burn management typically starts in late winter and continues through fall with most fires occurring in early spring. Prescribed fire is primarily used to control the initiation and spread of woody vegetation, but can be used as a management tool to create and maintain vegetation heterogeneity on the landscape. The amount of area burned varies annually, but averages 3,943 ha. Prescribed burns range in frequency with some areas being burned multiple times within a year to areas not being burned for >20 years; there are occasional wildfires that occur throughout the year in training areas due to lightning strikes and, more frequently, from detonation of munitions during military training exercises. Overall, 17% of Fort Riley is burned at high fire frequency (1– 2 years); 70% is burned at high to mid fire frequency (>2–4 years); 6% is burned at mid fire frequency (>4–8 years); and 7% is burned at low fire frequency (>8–16 years).

The Fort Riley Environmental Division maintains food plots and leases plots for haying as additional management activities on the reservation. Within the 31,000 ha, there are 192 food plots comprising a total area of 289 ha planted with Korean lespedeza (*Kummerowia stipulacea*), corn, soybeans, alfalfa, sunflowers, and wheat, which are grown individually, in combination, and in rotations. Of all active food plots, 70.8% are alfalfa, 7.8% are sunflower-soybean mixture, 7.3% are Korean lespedeza, 6.8% are corn-soybean mixture, 6.8% are wheat, and 0.5% are corn-soybeans-alfalfa mixture. Private landowners cut hay in prescribed training areas during late summer. Leases specify harvest time and type, which can be even years, odd years, or annual harvest and for warm season or cool season grasses based on the type of grasses that dominate each leased-out area. No matter the type of lease, prairie hay is cut and removed mechanically from 15 July -15 August. The amount of area available for haying varies annually but averages approximately 11,717 ha within 41 training areas within the area used for military training and wildlife management (Fort Riley Integrated Natural Resources Management Plan 2015).

The climate at Fort Riley is temperate. Maximum daily average temperatures range from a low of 4.2° C in January, to a high of 33.7° C in July. Precipitation averages 85 cm per year, with 75% of that falling in the 6-month period from April through September. In 2019 precipitation was extreme during the summer months, with the annual average of 85 cm in just 3.5 months from late April to August (116 cm total yearly precipitation in 2019), while 2020 experienced approximately average amount of precipitation (79.5 cm). Dominant vegetation within Fort Riley include grasses such as big bluestem (*Andropogon gerardii*), indiangrass

(*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), Scribner's panicum (*Dichanthelium oligosanthes*), grama grasses (*Bouteloua* spp.), and smooth brome (*Bromus inermis*); forbs such as false indigo (*Amorpha fruticose*), milkweeds (*Asclepias* spp.), wild indigo (*Baptisia bracteata*), indian blanket (*Gaillardia pulchella*), sunflowers (*Helianthus* spp.), ironweeds (*Vernonia* spp.), wooly verbena (*Verbea stricta*), heath aster (*Symphyotrichum ericoides*), round-head bush clover (*Lespedeza capitate*), Chinese bushclover (*Sericea lespedeza*), and goldenrods (*Solidago* spp.); and woody plants/shrubs such as sumac species (*Rhus* spp.), eastern redcedar (*Juniperus virginiana*), bur oak (*Quercus macrocarpa*), rough-leaf dogwood (*Cornus drummondii*), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*). Potential predators of Greater Prairie-chickens and their nests include racoon (*Procyon lotor*), coyote (*Canis latrans*), opossum (*Didelphis virginianus*), badger (*Taxidea taxus*), snakes, and raptor species.

Capture

I captured Greater Prairie-chickens at leks in the spring (Mar-Apr) of 2019 and 2020 using walk-in funnel traps or drop-nets (Silvy et al. 1990, Schroeder and Braun 1991). I sexed captured individuals based on neck feather (pinnae) length and tail feather coloration (Henderson et al. 1967). Females were fitted with a rump-mounted 22-g solar-powered Argos GPS satellite transmitter (Model PTT-100, Microwave Telemetry, Columbia, MD, USA) using small loops of Teflon ribbon fitted around their thighs (Rappole and Tipton 1991, Bedrosian and Craighead 2007, Humphry and Avery 2014, Streby et al. 2015). I aged birds as either second-year (SY) or after-second-year (ASY) based on wear and coloration of primary flight feathers (Ammann 1944). Capture and handling procedures were approved under Kansas State University IACUC protocol 4193, and Kansas Department of Wildlife, Parks, and Tourism scientific collection permits SC-015-2019 and SC-032-2020.

Locations of tagged Greater Prairie-chickens were recorded every 2 hours from 0400-2200 for a total of 10 locations per day with an accuracy of ±18 m. I downloaded points weekly from the Argos satellite system (CLS America, Lanham, MD, USA) for locations and mortality assessments. In addition to female locations and movements throughout the season, I determined nest site locations. Nest sites were determined once GPS locations indicated a female had started incubating (females continuously in the same location >2 days in a row). I approached the perceived nest location and searched until the nest was found. I spent minimal time at the nest location (<5 min) and would not return to the nest location again until transmitter data indicated that the female permanently left the nest site or experienced a mortality event. Using clutch size at the time of nest discovery as well as time of incubation onset based on satellite data, I calculated an estimated hatch date for each nest.

Vegetation Surveys

I conducted vegetation surveys to test for different scales of selection, landscape scale and within-patch scale. For testing landscape scale selection, I conducted surveys at used and random points. For used points, I randomly selected 4 non-nesting locations used by each bird each week based on satellite locations. In addition to used points, I created random points on the landscape. These random points served as available locations on the landscape and were stratified based on the 84 training areas located within Fort Riley, soil types derived from the U.S. Department of Agriculture soil survey, and burn intervals specific to Fort Riley. In total, there were 124 patches with unique training area/soil type/burn frequency combinations and 38 patch types with unique soil type/burn frequency combinations (Figure 2.2; Table 2.1). Within each unique patch, I generated 10 random points, separated by at least 50 m between points. Ultimately, I compared used and random data to assess home range selection.

To assess within-patch scale selection, I sampled vegetation at used, used paired, nest, and nest paired points. Used points were the same as described above, while nest points were points where birds nested; these vegetation surveys were conducted within one week of the hatch date or estimated hatch date. Associated with used and nest points, I generated paired points (termed used-paired and nest-paired) within 300 m of the used or nest point within the same patch using ArcGIS 10.6 (ESRI Inc., 2013, Redlands, USA). I then conducted vegetation samples at these locations to compare used and used paired and nest and nest paired data in each patch.

For each vegetation survey, I estimated percent horizontal cover of shrubs, forbs, grasses, and bare ground using a 60 x 60-cm Daubenmire frame at the point center and 4-m radius in each cardinal direction (Daubenmire 1959). To estimate vertical density of standing vegetation, I estimated a visual obstruction reading (VOR) using Robel pole at the point center from a distance of 4 m and a height of 1 m (Robel et al. 1970). Visual obstruction readings were recorded at 75% obstruction to the nearest decimeter (Lautenbach et al. 2019). I also recorded the 3 most dominant plant species within the 4-m radius around the nest location. Once all data were collected, I averaged all recorded measurements for each point and used these values for subsequent analyses.

Patch Features

I assessed overall patch use within Fort Riley by placing each used and random location sampled within a unique soil type and burn interval category. This allowed me to determine which specific patches Greater Prairie-chickens used on the landscape and where to prioritize management strategies on the landscape

Landscape Features

Because landscape and anthropogenic features influence space and resource use by prairie grouse (Pruett et al. 2009, Winder et al. 2014, Lautenbach et al. 2017, Plumb et al. 2019, Raynor et al. 2019), I evaluated the role of landscape features on resource selection by Greater Prairie-chickens. For each vegetation survey location, I measured the distance from the point to a number of landscape features including nearest fence, electric pole, road, and trees from spatial layers generated by Fort Riley Environmental Division staff and myself using ArcGIS. In addition to landscape features, I calculated time since last burn (in months) of the patch where I conducted each vegetation survey based on burn schedules provided by the Fort Riley Environmental Division staff.

Statistical Analyses

Landscape scale

I used logistic regression to evaluate resource selection and nest-site selection at the landscape scale. To represent the home range, I compared data collected at locations used by birds, which were represented with a 1, versus random points sampled on the landscape, which were represented with a 0 (representing presence/available resource units in Boyce et al. 2002). I evaluated how probability of use varied (between 0 and 1) among vegetation variables, landscape features, and burn mosaics throughout the breeding season. I then used a hierarchical model selection approach within an information-theoretic framework to evaluate model parsimony. To account for the latest bird captured each year and 1-week censor period following tagging to account for any mortalities due to capture and handling, I subset locations used in the analyses to span from late April (19, 2019 /20, 2020) to early August (2, 2019/4, 2020).

Within my vegetation variable model suite, I tested visual obstruction, percent cover grass, percent cover forb, percent cover bare, and percent cover shrub. I tested single variable and quadratic models as well as a constant (i.e., intercept only) model for a total of 11 models in the model suite. For the landscape variable model suite, I tested the effect of distance to tree, electric pole, utility pole, fence, and road in both single variable and quadratic models for a total of 11 models (including the intercept-only model) tested. My final model suite for home-range scale analyses was based on months since burn, where I evaluated the effect of year as a covariate because burn patterns within the wildlife management area of Fort Riley differed among years. I tested months since burn as a single and quadratic variable and used year as a main effect for both. Additionally, I used year as an interactive effect with the quadratic variable of months since burn. Finally, I tested a constant model for a total of 6 models in the suite.

For each model suite, I ranked all models using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). If the intercept-only model was ranked highest, I declared that none of the variables tested influenced female resource selection in that particular model suite. Models within 2 AIC_c units were considered to be competing models, so I assessed the beta values to determine if they were significant (95% confidence intervals did not overlap zero). I ultimately combined all top ranked models into a final model suite to determine the most influential variable across vegetation variables, landscape variables, and burn frequency.

Within-patch scale

To test for within-patch selection during the breeding season, I used the multivariate Hotelling's T^2 test to compare used and used-paired locations and nest and nest-paired locations. I specifically tested for differences among visual obstruction, percent grass cover, percent forb cover, percent bare ground, and percent shrub cover for vegetation characteristics; distance to fences, roads, electric poles, and trees for distance to landscape variables; and lastly, time since last burn. If the Hotelling's T^2 test indicated differences between used and paired points in multivariate space ($P < 0.05$), I independently tested each variable between used and paired points using a paired *t*-test.

Results

Overall, I conducted vegetation surveys at 2,081 random points, 683 used points, 683 used-paired points, 18 nest points, and 18 nest-paired points (Table 2.2). Although 16 more nests were found, military activity prevented me from conducting vegetation surveys within the required 1 week of nest fate at these nest sites.

Patch Use

Among all soil types and burn intervals, Greater Prairie-chickens selected for areas in the uplands (Clay Upland, Upland Hills, Clayey Upland) of Fort Riley and within areas that were burned every 2-4 years based on percent use (Table 2.1). Used points in these areas (uplands burned every 2-4 years) comprised roughly 40% of used points compared to all other soil types and burn intervals that comprised roughly 60% of points throughout the breeding season and 43% of nest locations across 2019 and 2020 while all other soil types and burn intervals comprised 57% of nest locations.

Landscape Scale-Overall Use

Among all vegetation variables, shrub cover at the landscape scale had the greatest influence on Greater Prairie-chicken resource selection ($\beta_{shrub(standardized)} = -0.83 \pm 0.12$, $\beta_{shrub^2(standardized)} = 0.06 \pm 0.03$, $\omega_i = 0.55$; Table 2.2; Figure 2.3). Probability of use was greatest when shrub cover was 0%, with probability of use decreasing 63.65% as shrub cover increased to 10%, and when shrub cover increased from 0% to 20%, probability of use decreased nearly 83%. Regarding distance to landscape features, birds selected areas away from trees more so than any other landscape feature ($\beta_{tree(standardized)} = 1.91 \pm 0.09$, $\beta_{tree^2(standardized)} = -0.49 \pm 0.05$, $\omega_i = 1.0$; Figure 2.4; Table 2.3). Probability of use was greatest when distance to tree was approximately 2,000 m, with probability of use increasing 316% as distance to tree increased from 500 m to 2,000 m. Lastly, in response to time-since-burn, female use was most influenced by the year interaction with time-since-burn ($\beta_{msb(standardized)} = -0.01 \pm 0.06$, $\beta_{year(standardized)} = -0.26 \pm 0.13$, $\beta_{msb^2 * year(standardized)} = -0.30 \pm 0.10$, $\omega_i = 0.97$; Figure 2.5; Table 2.4). Probability of use was greatest in 2019 when areas were burned about 29 months prior, with probability of use increasing 17.50% when time-since-burn increased from 12 months to 29 months and increasing 53.40% when time-since-burn decreased from 48 months to 29 months. In 2020, probability of use was greatest for areas burned 14 months prior, with probability of use decreasing 16.32% when time since burn increased from 14 to 24 months and decreasing 90.90% when time since burn increased from 14 to 48 months. Among all top models combined, distance to tree had the most support (Table 2.5).

Landscape Scale-Nest Site Selection

Among tested vegetation variables, landscape variables, and months since burn, the only factor significant in nest-site selection was distance to tree ($\beta_{tree(standardized)} = 0.97 \pm 0.16$, Figure 2.6; Table 2.6). Time since burn did not affect nest placement as the constant model received the most support out of all models testing this variable ($\omega = 0.48$; Table 2.7). The most supported vegetation variable (% cover bare ground) had 95% confidence intervals that overlapped 0 (Figure 2.8). The most supported model of all top models was distance to tree (Table 2.9).

Within-Patch Selection

According to the Hotelling's T^2 test, there was a difference in used and used-paired point characteristics ($F_{16,\,1349} = 2.35$, $P = 0.002$). Specific characteristics that differed were only vegetation variables and included visual obstruction reading at 75% obstruction ($t_{682} = -3.12$, $P = 0.002$), percent cover grass ($t_{682} = -3.21$, $P = 0.001$), percent cover forb ($t_{682} = 3.13$, $P = 0.002$), and percent cover bare ground ($t_{682} = 3.01$, $P = 0.003$). Although statistically significant, these differences did not appear to present ecologically relevant differences (Figure 2.7). I did not find a difference in vegetation characteristics, landscape variables, or time-since-burn between nest and nest-paired locations ($F_{16,\,19} = 0.37$, $P = 0.98$; Table 2.10).

Discussion

Contrary to other populations of Greater Prairie-chickens in Kansas, the population on Fort Riley is quite constrained by surrounding landscape features. Despite this constrained environment, population levels are stable based on lek counts (Figure 2.8). My findings show that current management on Fort Riley appears to promote grassland habitat and provide high-quality habitat as we found limited differences between used and available locations. Therefore, these conditions may be enabling populations to persist at stable levels on Fort Riley which contrasts with the significant declines in Greater Prairie-chicken populations across Kansas. However, landscape-scale characteristics appeared to drive resource selection at both the home range and within-patch scales; therefore, landscape-scale changes may eventually affect population persistence because of the inability for birds to disperse from Fort Riley. These landscape- scale changes may disproportionately affect Greater Prairie-chickens if they occur in patches of high use by birds such as those within Clayey Upland soils or those burned at high to mid fire frequency. Therefore, any changes that may be happening at the landscape-level within these areas must be monitored closely.

The most influential landscape-scale characteristic regarding Greater Prairie-chicken movement and space use is the proximity to trees as my study population avoided trees out to 2,000-m. Avoidance of trees is common for many prairie grouse species and supported by other studies, many of which describe the detrimental effects of trees to lek attendance, lek persistence, resource use, and overall occupancy of Greater Prairie-chickens (Gregory et al. 2011, McNew et al. 2012b, Hovick et al. 2015, Londe et al. 2019, Raynor et al. 2019). In the Sandhills ecoregion of Nebraska, Greater Prairie-chickens were found to use areas 1,000 m from trees most frequently (Raynor et al. 2019). Likewise, the Greater Prairie-chicken's close relative, the Lesser Prairie-chicken (*Tympanuchus pallidicinctus*) exhibited similar response to distance from tree, where probability of use was greatest around 1,000 m from the closest tree within their range in the Red Hills of south-central Kansas (Lautenbach et al. 2017). Surprisingly, despite Fort Riley having more riparian areas than the Sandhills (Raynor et al. 2019) and Red Hills regions, my findings indicate that Greater Prairie-chickens on Fort Riley are sensitive to tree presence at a greater distance than those in the sandhills of Nebraska and the Red Hills of Kansas.

Beyond having an effect on general resource use, tree encroachment also affects where a female selects to place her nest on the landscape. Greater Prairie-chickens on Fort Riley placed their nests on average at distances 7 times farther from trees than at random locations (1,500m versus ~200m, respectively) on the landscape. Greater Prairie-chickens in Nebraska and Lesser Prairie-chickens in Kansas followed similar trends (Matthews et al. 2013, Lautenbach et al. 2017). In Nebraska, probability of use for nesting Greater Prairie-chickens increased 20% for every 100 m increase in distance from trees. Lesser Prairie-chickens in the Red Hills ecoregion had the greatest probability of use for nesting when distance from trees was at least 800 m and tree density was <2 trees · ha^{-1}.

Avoidance of trees to the extent described above when choosing where to forage or place nests can have direct consequences for availability of functional habitat supporting reproductive capacity, reproductive success, carrying capacity, and future population growth on Fort Riley. In addition, because Fort Riley population may be more constrained and unable to emigrate compared to other populations of Greater Prairie-chickens, the consequences that can arise if tree encroachment is not dealt with promptly are potentially devastating to the Fort Riley prairie chicken population. As is, Greater Prairie-chickens on Fort Riley have about 10,000 ha of treeless space (i.e., functional habitat) available within the management area; if trees encroach beyond their current extent by even a kilometer, the area available to Greater Prairie-chickens on Fort Riley would decreased by more than 3-fold (Table 2.11). To address the issue of tree encroachment, tree removal has been found to have a positive correlation with prairie grouse occupancy: Greater sage grouse used restored habitats within one year after removing juniper trees (Frey et al. 2013); Greater Prairie-chicken occupancy increases further from woody encroachment (McNew et al. 2012). Therefore, targeted tree removal on Fort Riley would be an effective strategy to keep tree encroachment in check and potentially expand usable breeding season habitat for Greater Prairie-chickens. Currently, tree cutting has been an ongoing process within Fort Riley but tree removal efforts have not caught up to the cutting process and therefore should be prioritized in the future.

Response by Greater Prairie-chickens to shrubs is similar to trees on Fort Riley. Probability of use by Greater Prairie-chickens during the breeding season rapidly decreases with even minor shrub cover, which contrasts with other studies where the presence of shrubs does not appear to be as detrimental and are even beneficial in some cases by providing overhead cover for nesting grouse (Niemuth 2000, McNew et al. 2014). Shrubs on Fort Riley, when not including the semi-shrub leadplant (*Amorpha canescens),* often occur in larger patches or islands of smooth sumac (*Rhus glabra*), roughleaf dogwood (*Cornus drummondii*), or buckbrush (*Ceanothus cuneatus*) and average around 1.05-m tall. Therefore, unlike areas that may be more arid with shorter vegetation where shrubs are the only dense cover, Greater Prairie-chickens may perceive shrubs on Fort Riley similar to trees where predators may perch or hide and subsequently avoid them. Similar to trees, it would be beneficial to Greater Prairie-chickens for these shrub islands to be controlled and not encroach far into prairie habitat as that could render these areas unusable by Greater Prairie-chickens on Fort Riley.

Within the larger landscape, it is critical to understand within-patch resource selection by Greater Prairie-chickens to inform their management based on small-scale requirements. However, I found that resource selection was not dictated by within-patch vegetation (i.e. at the used vs used-paired and nest vs nest-paired level). Although there were several statistically significant vegetation differences between used and used-paired locations, these were not ecologically relevant to land managers and therefore these differences are likely to be negligible when Greater Prairie-chickens select for cover within Fort Riley. Additionally, there were no statistical differences between nest and nest-paired locations. These findings contrast with previous studies in the Flint Hills and Smoky Hills ecoregion of Kansas and Loess and Glacial Drift ecoregion of Nebraska (Matthews et al. 2013, McNew et al. 2013). Coarse variables (percent grassland cover) were important at the 300-m scale, but specific vegetation variables were important at the micro-scale selection (within 6-m of nests; McNew et al. 2013). At nest sites, McNew et al. (2013) found Greater Prairie-chickens selected nest sites where 100% VOR was taller than at random points (28-30 cm vs 15-16 cm averages, respectively) and bare ground was more sparse (9-12% vs 19-21% averaged, respectively). Comparatively, I found nest sites at Fort Riley to have 100% VOR readings of 22 cm, while random sites had 100% VOR readings of 20 cm and percent cover of bare ground to be 6% versus 12%, respectively. McNew et al. (2013) findings are similar to other findings where land use practices consist of intense management regimes such as annual fire and intensive grazing or increased development on the landscape (Jones 1963, Patten et al. 2007, Harrison et al. 2017). The differences in my findings show the contrast between available cover on Fort Riley versus other areas in the Flint Hills as well as the lack of difference between used and available habitat on Fort Riley, likely due to the lack of such intense land use practices found elsewhere (Table 2.10). These more intensive practices may cause finer scale selection by birds as they seek out habitat structure that fulfills their needs in a landscape that is more heterogeneous in habitat quality versus that of Fort Riley, which has little variation in available habitat quality and is therefore not a limiting factor for Greater Prairie-chicken use.

Understanding Greater Prairie-chickens' responses to vegetation on the landscape as well as at fine scales is important in addressing their needs and adjusting management strategies to tailor to them, but relating selection to current management practices (i.e., burning) is also critical. Greater Prairie-chickens during the breeding season had the greatest selection for areas burned between every 1.5-2.5 years, which corresponds with previous findings (Patten et al. 2007, Fuhlendorf et al. 2017). Unexpectedly, the difference in burn selection between years was drastic (29 months prior in 2019 and 14 months prior in 2020). The breeding season of 2019 received exceptional rainfall, so perhaps that additional precipitation stimulated vegetation growth sufficiently to generate cover available for Greater Prairie-chicken use despite being burned more recently. This drastic difference in selection of time-since-burn patches due to precipitation fluctuations will become more of an issue in future years due to changing climate and precipitation cycles; therefore, time-since-burn selection by this population should be monitored closely and burn schedules should be flexible to continue to provide enough heterogeneity on the landscape to provide all necessary habitat types for Greater Prairie-chickens throughout their lifecycles.

Based on selection against landscape-scale features and indifference towards fine-scale vegetation features, it is clear that vegetation resources used by Greater Prairie-chickens on Fort Riley are plentiful and not limiting. It also appears that despite the differing burn regimes between years, Greater Prairie-chickens are content to stay in similar areas from year to year, away from landscape-scale disturbances, even if that means adapting to varying vegetation height due to these contrasting burn frequencies. This exemplifies the need for close monitoring of landscape changes as these will be detrimental to Greater Prairie-chicken populations, particularly if they occur in patches of high use by these birds.

Management Implications

My findings indicate that suppression of woody encroachment through the use of prescribed fire along with tree removal on Fort Riley could effectively expand habitat availability for Greater Prairie-chickens. Once established on the landscape, woody encroachment is difficult to reverse even with burning and should therefore be addressed before encroachment becomes so prevalent that it crosses a threshold where reversal is unlikely (Fahrig 2001; Fuhlendorf et al. 2008, 2017). Woody encroachment can be suppressed if prescribed fire is applied in regular intervals (every 2-3 years; Collins 1987, Briggs et al. 2005, Fuhlendorf et al. 2006). If trees are already established, prescribed fire, chemical application, and mechanical removal efforts should be applied to restore grassland, and once an area is cleared of trees, a regime of routine prescribed fire should be established to prevent any new trees from appearing on the landscape (Lautenbach et al. 2017).

These suppression and removal efforts should first be focused in areas used by Greater Prairie-chickens most frequently based on lek surveys or tracking methods throughout the year. I found the patches in Clay and Clayey Upland soils that are historically burned every 2-4 years to have the greatest amount of use, so these would be good starting points for targeted tree removal. Efforts to expand areas providing high-quality habitat to Greater Prairie-chickens on Fort Riley should be the next focus; fire application in proper intervals combined with targeted woody removal will aid in these efforts. If land managers at Fort Riley consider the probability of use by Greater Prairie-chickens at varying distances to trees and assess available land based on these probabilities, they can make a targeted management plan for clearing out trees and maintaining treeless areas on the landscape for Greater Prairie-chickens.

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Figures

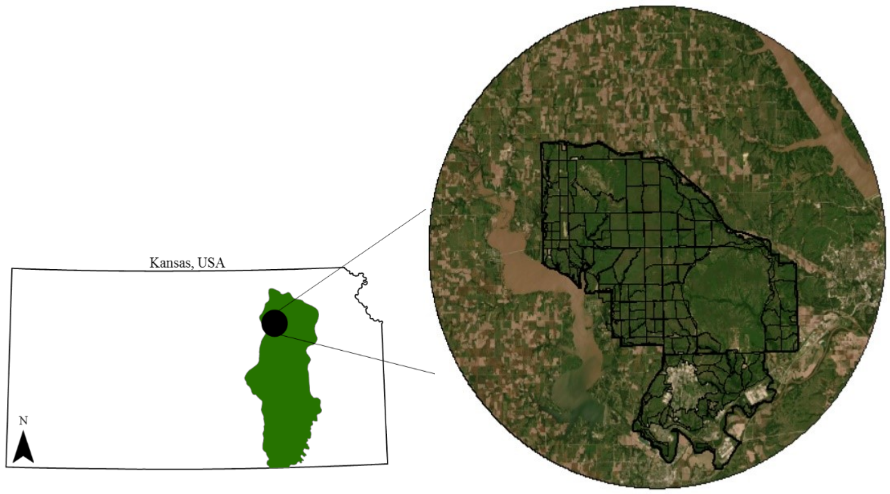

Figure 2.1. Location of Fort Riley Military Reservation within the Flint Hills ecoregion of Kansas, USA (outlined in green). Training units within Fort Riley Military Reservation are delineated (figure adapted from McCullough et al. 2021).

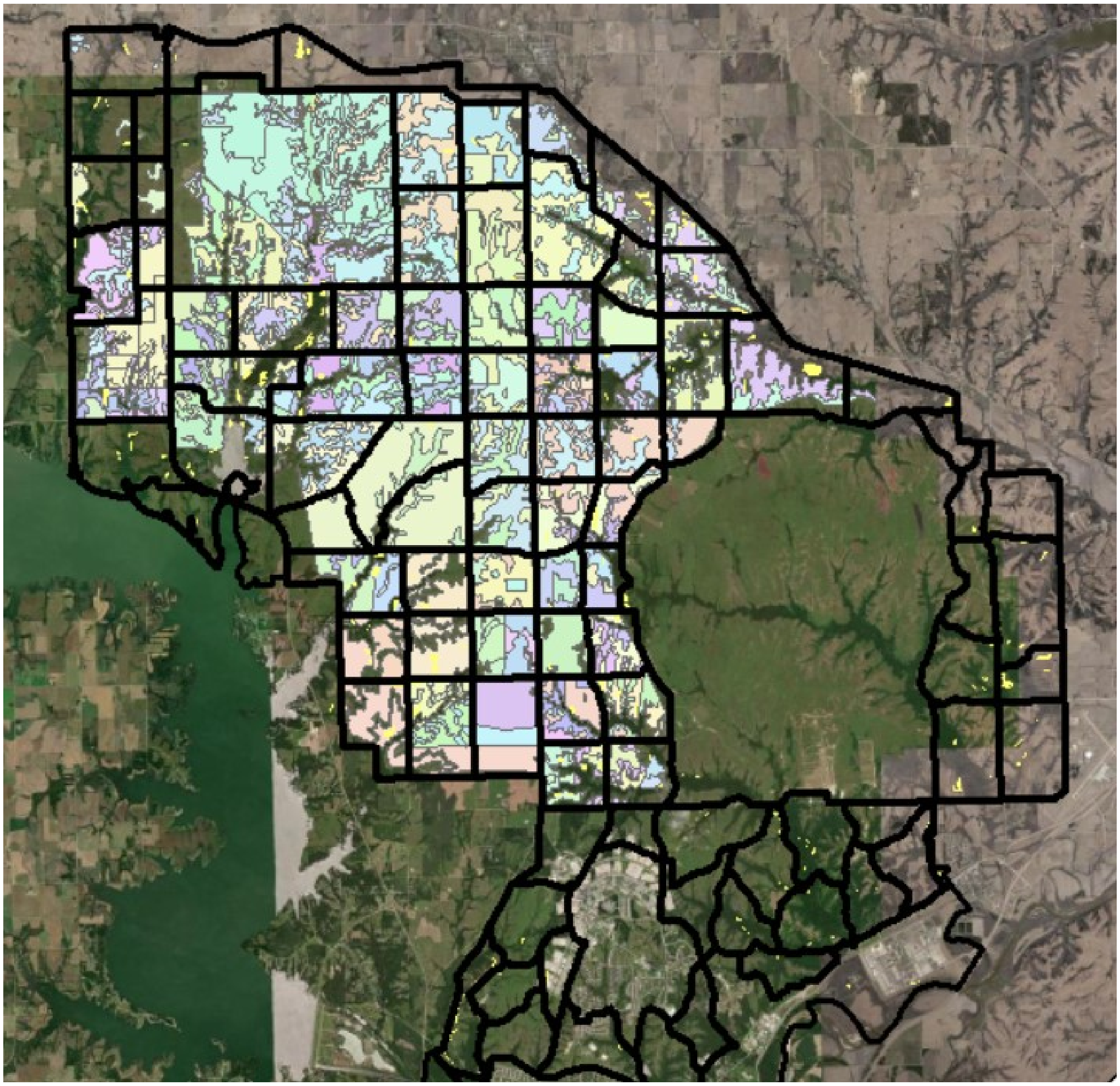

Figure 2.2. Fort Riley Military Reservation in Kansas, USA, with unique patches delineated based on color. Each color within individual training areas —outlined in black— represent a unique combination of soil type, burn frequency, and training area. Random vegetation surveys were recorded within each unique patch to identify available locations to female Greater Prairie-chickens during the breeding season, 2019-2020.

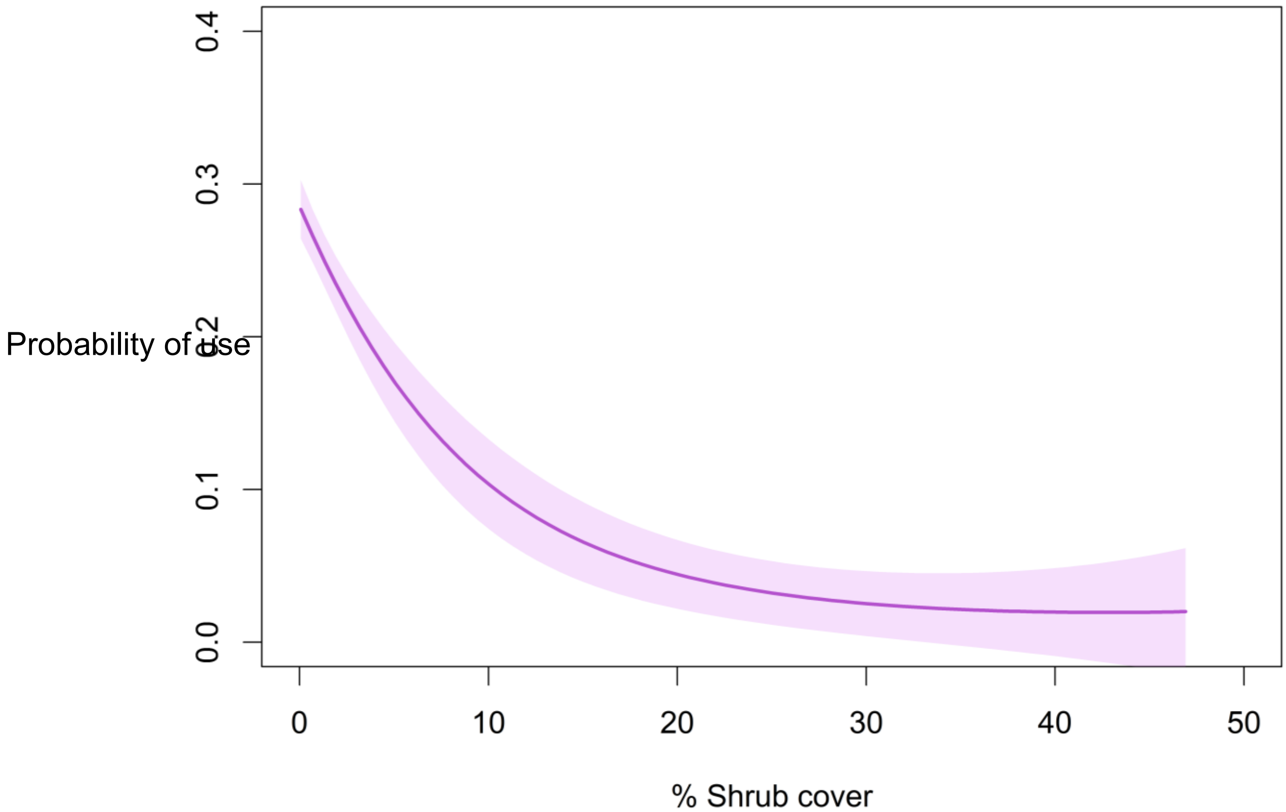

Figure 2.3. Relationship between percent cover shrub (±95% confidence interval) and probability of use by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

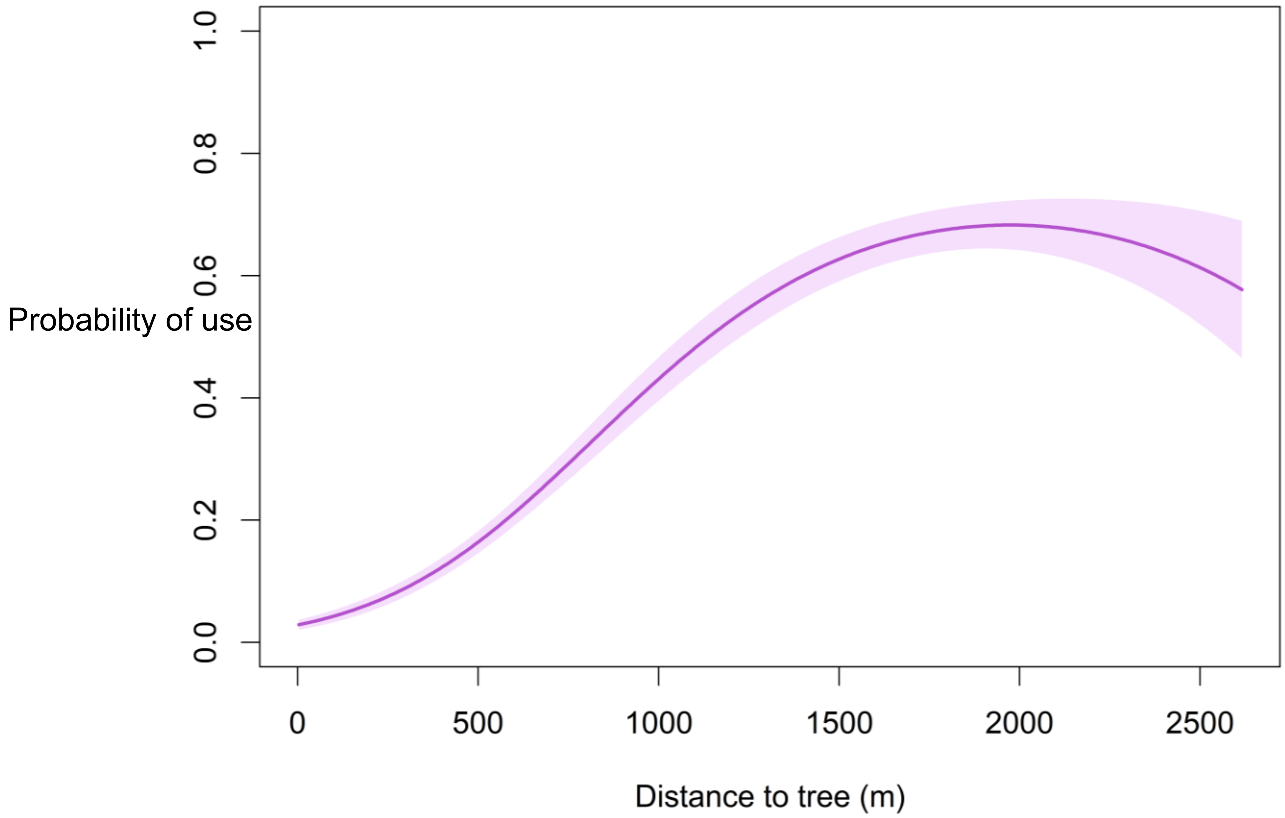

Figure 2.4. Relationship between distance to tree (±95% confidence interval) and probability of use by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

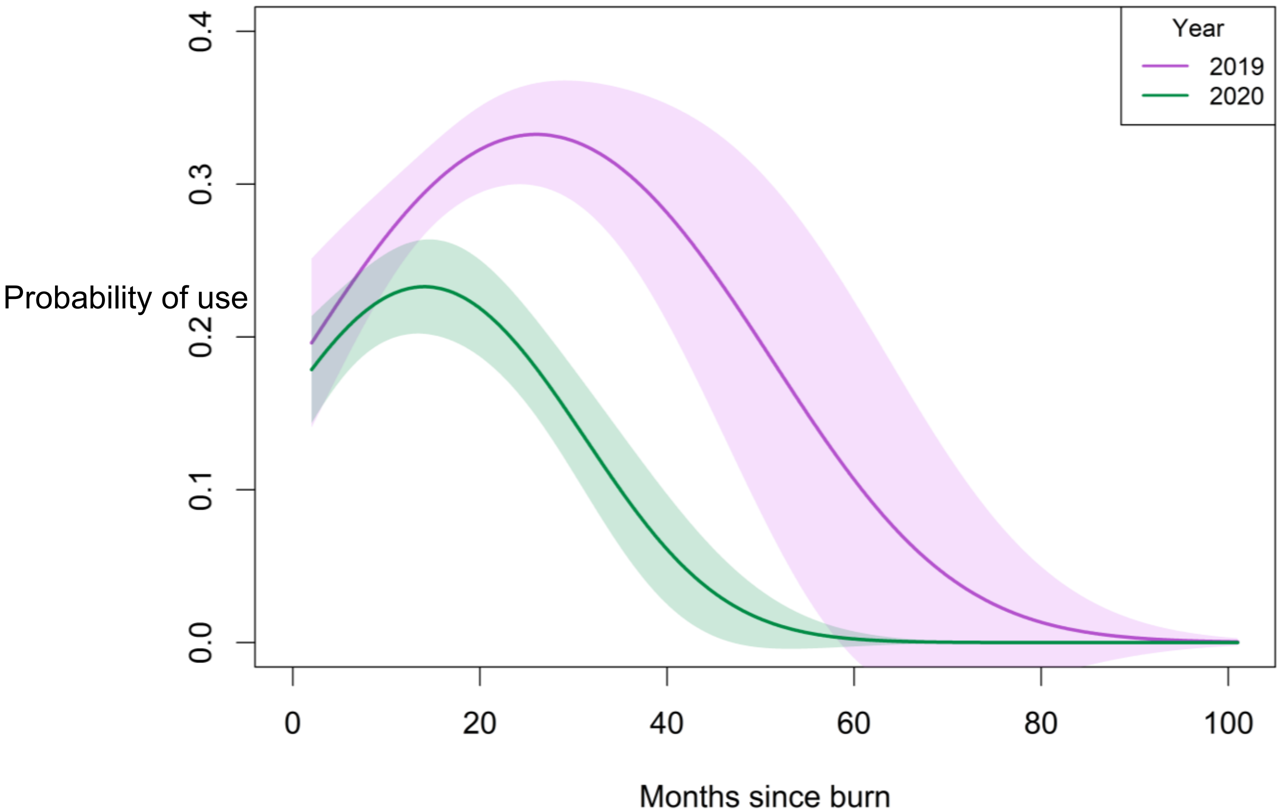

Figure 2.5. Relationship between months since burn by year (±95% confidence interval) and probability of use by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

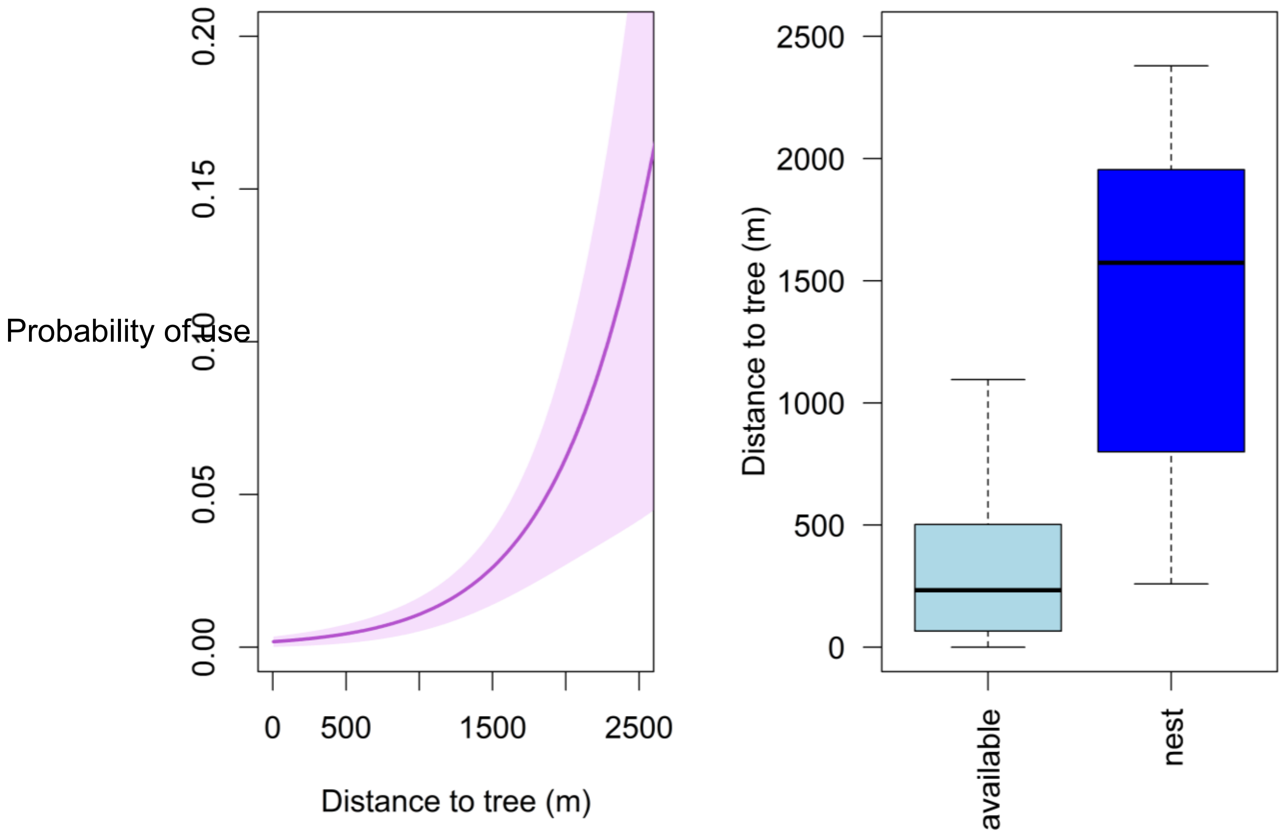

Figure 2.6. ***Left:*** **Relationship between nest-site selection and distance to tree (±95% confidence interval) of Greater Prairie-chicken nests.** ***Right:*** **Box plot depicting differences in distance to tree between nest sites and available locations. Both plots represent data collected on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.**

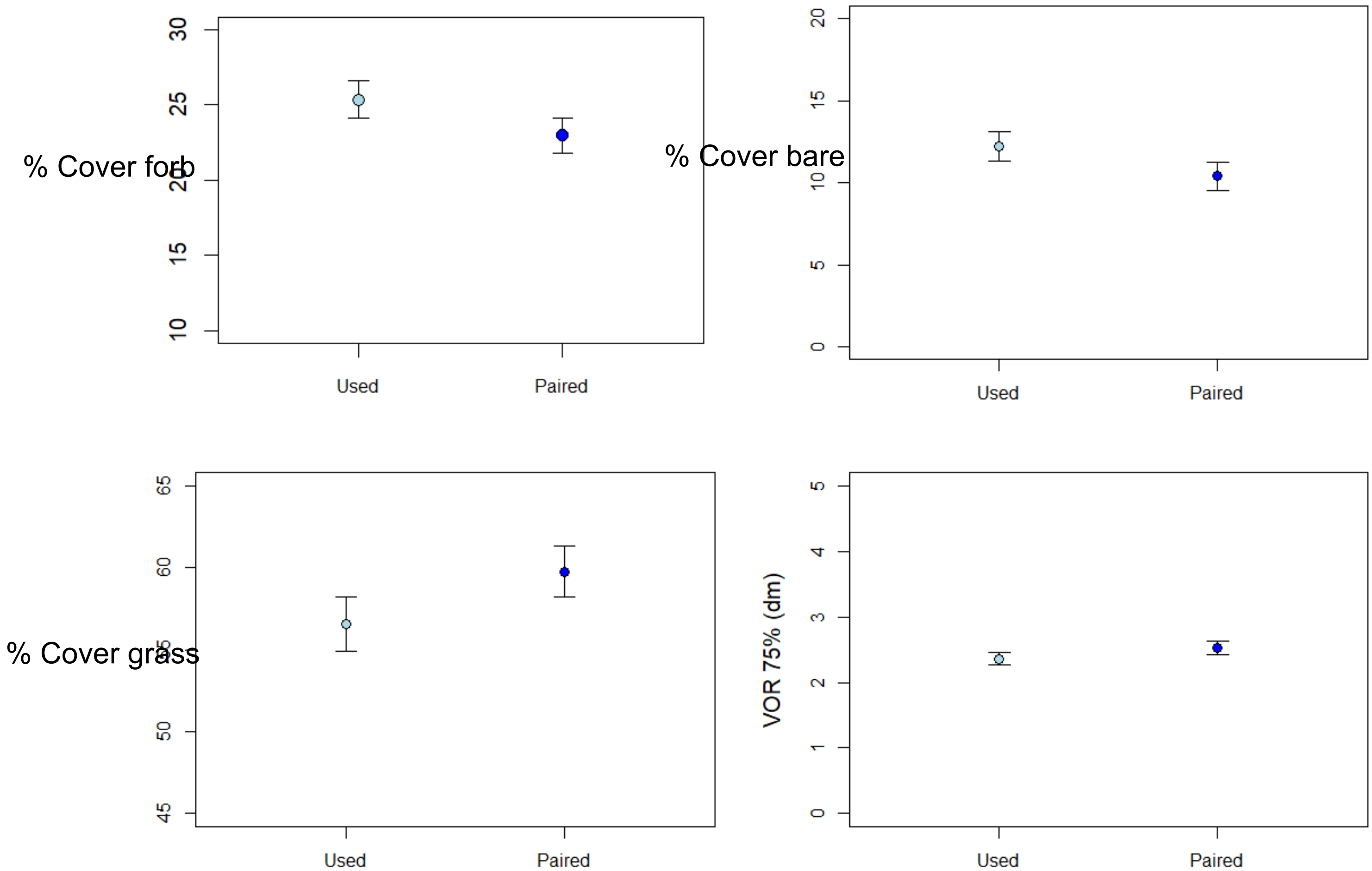

Figure 2.7. Comparisons of the mean (±95% CI) vegetation variables that differed (*P* < 0.05) between used and paired-random points during the 2019 and 2020 breeding seasons between used and paired points for vegetation variables on Fort Riley Military Reservation in Kansas, USA.

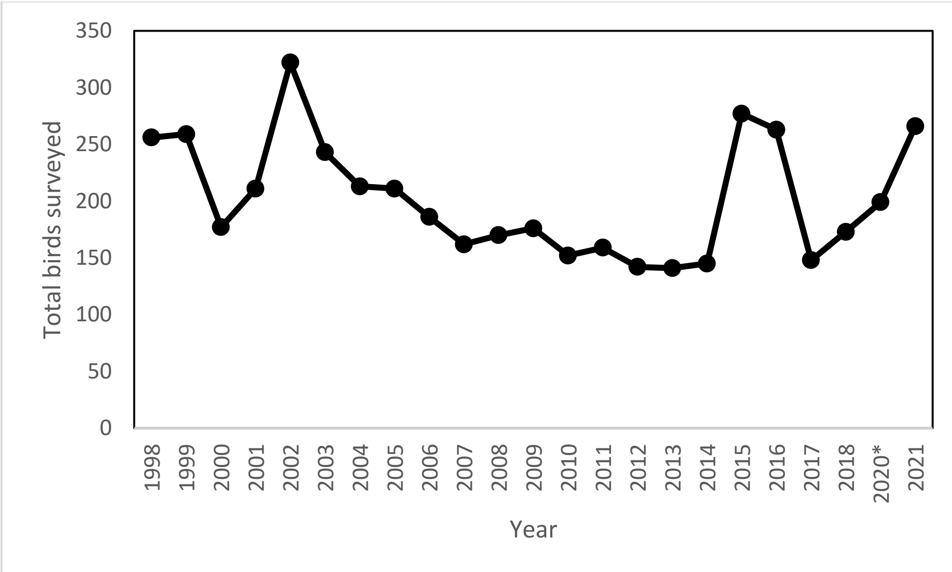

Figure 2.8. Counts of annual lek surveys conducted for Greater Prairie-chickens on Fort Riley Military Reservation from 1998-2021. Numbers represent total birds flushed from leks during the lekking season. * = complete survey not conducted due to COVID-19.

Tables

Table 2.1. Patch-types created for vegetation sampling grouped by soil type and burn interval unique to each patch type along with amount of area included in each type, number of used locations, and number of nest locations within each type. The total amount of area surveyed was 14,935 ha, comprised of 38 patch types; 706 used locations were sampled, and 21 nests were surveyed. Locations were recorded during 2019-2020 on Fort Riley Military Reservation in Kansas, USA.

Soil Type	*Burn interval*	*Burn Frequency*	*Total area (ha)*	*Percent total area*	*Used locations (#)*	*Percent used locations*	*Nest locations (#)*	*Percent nest locations*
Clay Lowland	0.56	>1-2	69	0.46	0	0.00	0	0.00
Clay Lowland	annually	1 yr	113	0.76	8	1.14	0	0.00
Clay Upland	0.25	>2-4	626	4.19	0	0.00	0	0.00
Clay Upland	0.31	>2-4	467	3.13	0	0.00	0	0.00
Clay Upland	0.38	>2-4	2114	14.15	55	7.82	4	19.05
Clay Upland	0.44	>2-4	615	4.12	26	3.70	0	0.00
Clay Upland	0.50	>1-2	670	4.49	40	5.69	1	4.76
Clay Upland	0.56	>1-2	480	3.21	59	8.39	2	9.52
Clay Upland	0.69	>1-2	167	1.12	0	0.00	0	0.00
Clay Upland	annually	1 yr	641	4.29	24	3.41	0	0.00
SLH*	0.25	>2-4	369	2.47	0	0.00	0	0.00
SLH	0.31	>2-4	333	2.23	9	1.28	0	0.00
SLH	0.38	>2-4	287	1.92	14	1.99	0	0.00
SLH	0.44	>2-4	26	0.17	2	0.28	0	0.00
SLH	0.50	>1-2	114	0.76	19	2.70	2	9.52
SLH	0.56	>1-2	30	0.20	0	0.00	0	0.00
SLH	annually	1 yr	94	0.63	5	0.71	0	0.00
Upland Hills	0.25	>2-4	245	1.64	0	0.00	0	0.00
Upland Hills	0.31	>2-4	174	1.17	0	0.00	0	0.00
Upland Hills	0.38	>2-4	423	2.83	7	1.00	0	0.00
Upland Hills	0.50	>1-2	252	1.69	10	1.42	0	0.00
Upland Hills	0.56	>1-2	136	0.91	32	4.55	0	0.00
Upland Hills	0.69	>1-2	28	0.19	0	0.00	0	0.00
Upland Hills	annually	1 yr	93	0.62	1	0.14	0	0.00
Clayey Plains	0.19	>4-8	75	0.50	0	0.00	0	0.00
Clayey Plains	0.25	>2-4	191	1.28	0	0.00	0	0.00
Clayey Plains	0.31	>2-4	2138	14.32	73	10.38	2	9.52
Clayey Plains	0.38	>2-4	252	1.69	16	2.28	0	0.00
Clayey Plains	0.44	>2-4	256	1.71	8	1.14	0	0.00

Clayey Plains	0.50	>1-2	178	1.19	29	4.13	0	0.00
Clayey Upland	0.25	>2-4	283	1.89	0	0.00	0	0.00
Clayey Upland	0.31	>2-4	103	0.69	1	0.14	1	4.76
Clayey Upland	0.38	>2-4	1133	7.59	145	20.63	3	14.29
Clayey Upland	0.44	>2-4	285	1.91	34	4.84	1	4.76
Clayey Upland	0.50	>1-2	377	2.52	34	4.84	2	9.52
Clayey Upland	0.56	>1-2	391	2.62	25	3.56	3	14.29
Clayey Upland	0.69	>1-2	210	1.41	0	0.00	0	0.00
Clayey Upland	annually	1 yr	497	3.33	27	3.84	0	0.00

*SLH=Shallow Limestone Hills, burn interval= proportion of times burned over 16 years (i.e. 0.5 was burned 8/16 years, or every other year)

Table 2.2. Models tested to evaluate vegetation variables that influence resource selection at the home-range scale by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	*ω_i*	*K*	*Deviance*
% cover $shrub^2$	3007.80	0.00	0.55	3	-1500.89
% cover shrub	3008.22	0.42	0.44	2	-1502.11
VOR 75^2	3058.16	50.36	0	3	-1526.07
VOR 75	3059.02	51.22	0	2	-1527.51
% cover $grass^2$	3069.20	61.40	0	3	-1531.59
% cover $bare^2$	3070.96	63.16	0	3	-1532.48
% cover grass	3077.21	69.41	0	2	-1536.6
Constant	3092.89	85.09	0	1	-1545.44
% cover forb	3093.47	85.68	0	2	-1544.73
% cover bare	3094.84	87.04	0	2	-1545.42
% cover $forb^2$	3095.06	87.26	0	3	-1544.52

[1] AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit, VOR=visual obstruction reading

Table 2.3. Models tested to evaluate landscape variables that influence resource selection at the home-range scale by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	ω_i	*K*	*Deviance*
Distance to tree^2	2285.19	0.00	1.00	3	-1139.59
Distance to tree	2368.63	83.44	0	2	-1182.31
Distance to electric pole^2	2609.10	323.91	0	3	-1301.55
Distance to electric pole	2726.54	441.35	0	2	-1361.27
Distance to fence^2	2845.83	560.64	0	3	-1419.91
Distance to fence	2846.05	560.85	0	2	-1421.02
Distance to road^2	3078.23	793.04	0	3	-1536.11
Distance to road	3085.53	800.33	0	2	-1540.76
Constant	3092.89	807.70	0	1	-1545.44

[1] AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit

Table 2.4. Models tested to evaluate how timing of burning influences resource selection at the home-range scale by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	ω_i	*K*	*Deviance*
msb^2*year	3035.62	0.00	0.97	5	-1512.80
msb^2+year	3042.46	6.84	0.03	4	-1517.22
msb+year	3051.28	15.66	0	3	-1522.64
msb^2	3073.20	37.57	0	3	-1533.60
constant	3092.89	57.26	0	1	-1545.44
msb	3094.22	58.60	0	2	-1545.11

[1] msb= months since burn, AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit

Table 2.5. Comparison of top-ranked models from the 3 tested model suites to evaluate home- range resource selection by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	ω_i	*K*	*Deviance*
Distance to tree^2	2291.09	0.00	1.00	3	-1142.54
% cover shrub^2	3012.83	721.74	0	3	-1503.41
msb^2*year	3040.47	749.38	0	5	-1515.23
Constant	3098.48	807.38	0	1	-1548.24

[1] msb= months since burn, AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit

Table 2.6. Models tested to evaluate landscape variables for influence on nest-site selection at the home-range scale by female Greater Prairie-chickens on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	ω_i	*K*	*Deviance*
Distance to tree[2]	176.69	0.00	0.58	3	-85.34
Distance to tree	177.33	0.64	0.42	2	-86.66
Distance to electric pole[2]	191.38	14.69	0	3	-92.68
Distance to electric pole	195.71	19.02	0	2	-95.85
Distance to fence	208.12	31.43	0	2	-102.06
Constant	209.17	32.47	0	1	-103.58
Distance to fence[2]	209.84	33.15	0	3	-101.92
Distance to road	210.69	34.00	0	2	-103.34
Distance to road[2]	211.58	34.89	0	3	-102.78

[1] AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit

Table 2.7. Models tested to evaluate the effect of timing of burning on nest-site selection at the home-range scale by female Greater Prairie-chickens on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	ω_i	*K*	*Deviance*
constant	209.17	0.00	0.48	1	-103.58
msb	211.14	1.98	0.18	2	-103.57
msb^2	211.83	2.66	0.13	3	-102.91
msb+year	212.07	2.90	0.11	3	-103.03
msb^2+year	213.23	4.07	0.06	4	-102.61
msb^2*year	214.66	5.49	0.03	5	-102.31

[1] msb=months since burn, AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit

Table 2.8. Models tested to evaluate effects of vegetation variables on nest-site selection at the home-range scale by female Greater Prairie-chickens on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	*ω_i*	*K*	*Deviance*
% cover bare	205.40	0.00	0.45	2	-100.70
% cover bare^2	207.32	1.91	0.17	3	-100.65
VOR 75^2	207.93	2.53	0.13	3	-100.96
Constant	209.17	3.76	0.07	1	-103.58
% cover shrub	210.48	5.08	0.04	2	-103.24
% cover forb	210.51	5.11	0.04	2	-103.25
% cover grass	210.59	5.19	0.03	2	-103.29
VOR75	210.85	5.45	0.03	2	-103.42
% cover forb^2	212.40	7.00	0.01	3	-103.19
% cover shrub^2	212.48	7.08	0.01	3	-103.23
% cover grass^2	212.60	7.20	0.01	3	-103.29

[1] AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit, VOR=visual obstruction reading

Table 2.9. Comparison of top-ranked models from the 3 tested model suites to evaluate nest-site selection by female Greater Prairie-chickens during the breeding season on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Model[1]	*AICc*	*Δ AICc*	ω_i	*K*	*Deviance*
Distance to tree[2]	184.73	0.00	1	3	-89.36
% cover bare	215.46	30.73	0	2	-105.73
Constant	218.63	33.90	0	1	-108.31

[1] AIC_c= Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value, ω_i= AIC_c weight, K= no. of parameters, Deviance = model fit

Table 2.10. Average ± SE of vegetation and landscape characteristics of points used in 4th order analyses. Nest and used locations are those used by female Greater Prairie-chickens while the paired points are those taken within a 300-m radius of each used location. Random points are those sampled using randomly selected points across Fort Riley Military Reservation. Data were collected from 2019-2020 on Fort Riley Military Reservation in Kansas, USA. All distances were measured in meters, statistically significant differences are denoted with a * between Used and Used-Paired points; no other comparisons differed ($P > 0.05$).

	Nest	*Nest Paired*	*Used*	*Used Paired*	*Random*
75% VOR (dm)	2.92 ± 0.24	2.53 ± 0.22	2.36 ± 0.05*	2.53 ± 0.05*	2.72 ± 0.03
% Grass cover	56.35 ± 5.02	57.86 ± 4.12	56.54 ± 0.85*	59.76 ± 0.78*	52.61 ± 0.46
% Shrub cover	1.83 ± 1.11	0.06 ± 0.05	0.91 ± 0.12	0.98 ± 0.12	3.09 ± 0.16
% Forb cover	27.70 ± 4.58	26.84 ± 3.82	25.31 ± 0.63*	22.95 ± 0.59*	24.45 ± 0.36
% Bare ground cover	5.30 ± 1.71	7.73 ± 1.90	12.21 ± 0.47*	10.42 ± 0.44*	12.07 ± 0.31
Distance to fence	3804.08 ± 343.25	4556.80 ± 308.63	4236.72 ± 52.81	4311.67 ± 52.92	3163.28 ± 34.04
Distance to road	383.71 ± 63.86	487.79 ± 92.87	373.31 ± 10.95	361.36 ± 10.58	333.28 ± 6.42
Distance to electric pole	4998.72 ± 324.36	4976.16 ± 321.83	4743.99 ± 53.01	4713.67 ± 53.14	3165.69 ± 41.65
Distance to tree	1404.04 ± 164.67	1413.63 ± 161.73	1276.33 ± 25.63	1253.59 ± 26.15	468.51 ± 11.57

Table 2.11. Approximate area remaining on Fort Riley Military Reservation, Kansas, USA (in hectares), based on the buffered distances from trees outlined and buffered using ArcMap 10.6. Trees were the biggest deterrents to female Greater Prairie-chicken space use during the breeding season.

Buffer distance from tree (m)	*Area remaining on Fort Riley (ha)*
2,000	694
1,500	1,446
1,000	3,242
500	8,379

Chapter 3 - Female home ranges and daily space use in response to military activity on Fort Riley Military Reservation during the breeding season

Introduction

Historically, grasslands of North America once stretched from Texas, USA, to Canada with mixed- and tall-grass prairies covering >340 million acres (Dixon et al. 2014). These expanses provided ample area for grassland species to find forage, reproductive opportunities, and cover from predators – all resources necessary to support the ecological needs of individual species (Powell and Mitchell 2012). However, due to the enactment of the Homestead Act of 1862 and Canada Dominion Land Act of 1872 as well as the high propensity for these lands to be cultivable, these previously pristine grasslands started to disappear (Ostlie et al. 1997). Today, approximately 76% of the mixed-grass prairie and 98% of the tallgrass prairie have disappeared, making these areas among the most threatened biomes in North America and limiting their ability to support the number and abundance of species dependent on grassland systems (Samson and Knopf 1994, Comer et al. 2018).

Prairie grouse are especially vulnerable to loss and degradation of prairie due to their sensitivity to land conversions (i.e., grassland to cropland; Greater Sage Grouse [*Centrocercus urophasianus*], Lesser Prairie-chickens [*Tympanuchus pallidicinctus*], and Greater Prairie-chickens [*T. cupido*]; Svedarsky et al. 2000, Smith et al. 2016, Ross et al. 2016). Requiring multiple, specialized habitat types, in conjunction with a requirement for large expanses of grassland cover to meet their ecological needs, prairie grouse are good indicator species of surrounding land health and ecosystem function (McNew 2010, Matthews et al. 2013, McNew et al. 2013, Coates et al. 2016, Fuhlendorf et al. 2017). Greater Prairie-chickens are an obligate species of tall and mixed-grass prairies and considered an indicator species for the tallgrass prairie among all prairie grouse species.

The Greater Prairie-chicken is a species of conservation concern due to habitat loss, but also habitat degradation and disturbance leading to unsuitable conditions for these birds to live, resulting in drastic population declines throughout much of the species' occupied range. The Flint Hills ecoregion alone experienced a 76% population decline from 34,180 in 2015 to 8,334 in 2021 (Nasman et al. 2018; 2021; Figure 3.1). A short-lived prairie-obligate grouse found only in mixed- and tall-grass prairies, Greater Prairie-chickens are subjected to multiple types of intense land use practices include frequent burning and intensive grazing, where burning occurs on an annual basis and grazing pastures are often double-stocked and intensively grazed (Robb and Schroeder 2005, Patten et al. 2007, McNew et al. 2015). These practices may deem otherwise unfragmented grasslands unusable by Greater Prairie-chickens due to the resulting decreased vegetation heterogeneity and habitat quality on the landscape. Greater Prairie-chicken population numbers respond negatively to these land use practices as the decrease in habitat quality could make it difficult for these birds to find enough forage or adequate cover on the landscape (Svedarsky et al. 2000, Patten et al. 2007, McNew et al. 2015, Fuhlendorf et al. 2017, Winder et al. 2017).

Estimating movements and space use by prairie grouse are vital as these metrics are tied to an individual's ability to successfully find resources on the landscape that may affect breeding season survival and reproductive success (i.e., habitat quality); thereby, affecting these species on a population level (Chapter 1). Space use by female Greater Prairie-chickens can be quite variable with home ranges ranging from 190 - 5,400 ha (Robel et al. 1970, Augustine and Sandercock 2011, Winder et al. 2014), but with a fairly constant trend of larger home ranges during the lekking months, when males congregate to display for females and females visit many different leks to breed, and smaller during the nesting and brood-rearing months, when females must incubate nests or movements are constrained due to chicks. Fewer studies have reported daily movements (range: 220-709 m/day; Toepfer and Eng 1987), but temporal variation in daily movements are similar to that reported for home ranges. Understanding what drives variations in movement is important for recognizing how Greater Prairie-chickens differentially use space throughout various life stages, especially during the breeding season.

Assessing drivers of differential space use is critical for all Greater Prairie-chicken populations as continued loss and degradation of grasslands are decreasing area and quality of available habitat across the species range. Many populations are becoming constrained to isolated areas of grasslands, which likely influences movements and space use differently than for populations in larger, more connected grassland landscapes. Greater Prairie-chickens on the U.S. Department of Defense's Fort Riley Military Reservation are constrained by urban development (Junction City, Ogden, and Manhattan, KS), a large water body (Milford Reservoir- the largest manmade lake in Kansas with 6,353 ha of water) immediately surrounding the Reservation on the east, south, and west sides. Further constraining the population is the extensive cropland north of the Reservation. Previous studies have examined home ranges and movements in less constrained populations (Toepfer and Eng 1987, Augustine and Sandercock 2011, Matthews et al. 2011, and Winder et al. 2014), but none have examined populations as potentially constrained as that within Fort Riley Military Reservation. The constraint seen on Fort Riley will become more common in the future due to continued grassland conversions, and the amount of pristine grasslands with minimal disturbance could become virtually non-existent (Lark et al. 2020). Therefore, understanding how a population that has been constrained for generations uses space and responds to disturbances will be important for future populations that will face such constraint.

In addition to living within a potentially constrained environment, Greater Prairie-chickens are subject to various types of disturbances not experienced by populations in surrounding areas including military activity and reservation-wide management activities such as mosaic-style prescribed burning, where patches on the landscape are burned at different frequencies, food-plot establishment, and haying. Previous studies have examined avian species' immediate behavioral responses to military training and other noises and increase in movement and flushing (Cadwell et al. 1994, Stalmaster and Kaiser 1997, Grubb et al. 2010, McLaughlin and Kunc 2013), but few have dealt with season-long responses to these effects or how responses to training could vary by day or breeding stage (Barron et al. 2012). Few areas within the Flint Hills ecoregion outside of Fort Riley use different burn frequencies within contiguous land, so understanding the response of Greater Prairie-chickens to the juxtaposition of burns will be important, particularly during the breeding season where habitat needs vary greatly (Fuhlendorf et al. 2017). Finally, management practices not directly intended for the benefit of Greater Prairie-chickens such as food plots may affect Greater Prairie-chicken space use. Understanding if and when these areas are used for acquiring food or as cover may guide managers in crop-rotation decisions and prioritization of food plot composition. It is important to measure Greater Prairie-chicken response to hayed areas because birds may find recently hayed areas provide easier access to food, but perhaps avoid them due to lack of residual cover for predator protection. Understanding how these management activities are utilized by Greater Prairie-chickens may aid land managers in the enhancement of these already existing programs unique to Fort Riley.

My goal therefore, was to quantify Greater Prairie-chicken space use and movements on Fort Riley Military Reservation in response to patch types and various disturbances throughout each stage of the breeding season in an isolated, constrained landscape. My objectives were to 1) estimate home range area for each breeding season stage (lekking, nesting, and post-nesting) and entire breeding season; 2) measure total and net daily displacement in response to military activity; and 3) identify responses of Greater Prairie-chickens to haying, food plot implementation, native and invasive grasses, and various burning regimes based on home-range overlap with these management activities. I hypothesized the lekking season would have the largest home ranges and largest daily movements, but overall home ranges would be smaller than those for Greater Prairie-chicken hens in unconstrained landscapes. I hypothesized birds would respond to military activity by moving more to try and escape the increased disturbance. Lastly, I hypothesized that food plots would be used most during the lekking season as sites for leks as well as foraging areas, but avoided during nesting and post-nesting due to some food plots having too dense of vegetation for females to detect incoming predators or chicks to navigate through while others would provide too sparse of cover for either activity. Hayed areas I predicted would be used more during post-nesting as haying does not occur until late summer when most of the nests would be finished for the season. Using these findings, I recommend concrete actions for land managers at Fort Riley to enhance management regimes in accordance with the responses of Greater Prairie-chickens to current management practices.

Methods

Study Area

Fort Riley Military Reservation (herafter, Fort Riley) located between Manhattan and Junction City, Kansas, in the northern Flint Hills ecoregion contains ~41,000 contiguous ha, making it one of the largest Military Reservations in the United States (Figure 3.2). About 31,000 of the 41,000 ha are used for military training, wildlife management, hunting, conservation, and other outdoor recreational activities. Unlike other areas surrounding the reservation, Fort Riley does not allow cattle grazing. Within these 31,000 ha, there are 87 training areas that receive various military training activity, burn frequencies, and haying treatments. The average size of training areas is 302 ha (range: 118–642 ha). In addition to training, burning, and haying, Fort Riley environmental staff manage food plots as a wildlife management tool. There are 192 food plots comprising a total area of 289 ha planted with Korean lespedeza, corn, soybeans, alfalfa, sunflowers, and wheat, which are grown individually, in combination, and in rotation. Of all active food plots, 70.8% are alfalfa, 7.8% are sunflower-soybean mixture, 7.3% are Korean lespedeza (*Kummerowia stipulacea*), 6.8% are corn-soybean mixture, 6.8% are wheat, and 0.5% are corn-soybeans-alfalfa mixture.

Various burn frequencies are also assigned to the 87 training areas. Prescribed burn management typically starts in late winter and continues through fall with most fires occurring in early spring. Prescribed fire is primarily used to control the initiation and spread of woody vegetation, but can be used as a management tool to maintain vegetation heterogeneity on the landscape. The amount of area burned varies annually, but averages 3,943 ha each year. Prescribed burns range in frequency with some areas being burned multiple times within a year to areas not being burned for >20 years; there are occasional wildfires that occur throughout the year in training areas due to lightning strikes and more frequently from detonation of munitions during military training exercises. Overall, 17% of Fort Riley is burned at high fire frequency (≤2 years), 70% is burned at high to mid fire frequency (>2 to 4 years), 6% is burned at mid fire frequency (>4 years to 8 years), and 7% is burned at low fire frequency (>8 years to 16 years).

Haying also occurs in training areas during late summer. These areas are leased by Fort Riley Environmental Division for haying by private landowners. Leases specify harvest time, which can be even years, odd years, or annual harvest, and for warm season or cool season grasses based on the type of grasses that dominate leased areas. No matter the type of lease, prairie hay is cut and removed mechanically from 15 July -15 August. The amount of area available for haying varies but averages around 11,717 ha within 41 training areas within the area used for military training and wildlife management. Despite being available for cutting, not all of this area is cut each year (Fort Riley Integrated Natural Resources Management Plan 2015).

Military activity is another large disturbance that takes place on Fort Riley. Within the management area, the majority of training events take place within 38 training areas. When trainings occur, there is increased noise due to munition firings as well as tank and helicopter activity. There are also increased vegetation disturbances with vehicles and troops traversing through the landscape. Some training activities also include troops camping for weeks at a time in the training areas causing localized disturbances on the landscape.

The climate at Fort Riley is temperate. Maximum daily average temperatures range from a low of 4.2° C in January, to a high of 33.7° C in July. Precipitation averages 85 cm per year, with 75% of that falling in the 6-month period from April through September. In 2019, precipitation averages were extreme during the summer months, with the 85 cm in just 3.5

months from late April to August (116 cm total yearly precipitation in 2019), while 2020 experienced relatively average amounts of precipitation (79.5 cm). Dominant vegetation within the Reservation include grasses such as big bluestem (*Andropogon geradii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), Scribner's panicum (*Dichanthelium oligosanthes*), grama grasses (*Bouteloua* spp.), and smooth brome (*Bromus inermis*); forbs such as false indigo (*Amorpha fruticose*), milkweeds (*Asclepias* spp.), wild indigo (*Baptisia bracteata*), indian blanket (*Gaillardia pulchella*), sunflowers (*Helianthus* spp.), ironweeds (*Vernonia* spp.), wooly verbena (*Verbea stricta*), heath aster (*Symphyotrichum ericoides*), round-head bush clover (*Lespedeza capitate*), Chinese bushclover (*Sericea lespedeza*), and goldenrods (*Solidago* spp.); and woody plants/shrubs such as sumac species (*Rhus* spp.), eastern redcedar (*Juniperus virginiana*), bur oak (*Quercus macrocarpa*), rough-leaf dogwood (*Cornus drummondii*), American elm (*Ulmus americana*), and honey locust (*Gleditsia triacanthos*).

Capture

I captured Greater Prairie-chickens at leks in the spring (Mar-Apr) of 2019 and 2020 using walk-in funnel traps or drop-nets (Silvy et al. 1990, Schroeder and Braun 1991). Once captured, I sexed individuals based on neck feather (pinnae) length and tail feather coloration (Henderson et al. 1967). Females were fitted with a rump-mounted 22-g solar-powered Argos GPS satellite transmitter (Model PTT-100, Microwave Telemetry, Columbia, MD, USA) using small loops of Teflon ribbon fitted around their thighs (Rappole and Tipton 1991, Bedrosian and Craighead 2007, Humphry and Avery 2014, Streby et al. 2015). I aged birds as either second-year (SY) or after-second-year (ASY) based on wear and coloration of primary flight feathers (Ammann 1944). Capture and handling procedures were approved under Kansas State University

IACUC protocol 4193, and Kansas Department of Wildlife, Parks, and Tourism scientific collection permits SC-015-2019 and SC-032-2020.

Locations of tagged Greater Prairie-chickens were recorded every 2 hours from 0400-2200 for a total of 10 locations per day with an accuracy of ±18 m. Nest sites were determined once GPS locations indicated a female had started incubating (females continuously in the same location >2 days in a row). I approached the perceived nest location and searched until the nest was found. I spent little time at the nest location (<5 min) and did not return to the nest location again until transmitter data indicated that the female permanently left the nest site or experienced a mortality event.

At the end of the season, in addition to determining overall breeding season home ranges, I examined the progress of each individual bird through the breeding season to obtain ranges for individual breeding stages. Based on their stage, I assigned each bird location as "lekking" from March 1 to the time they first started a nest, "nesting" as any time they were on a nest no matter what attempt, and "post-nesting" as any time between nesting or after nesting was fully complete until August 31. I did not monitor broods on the ground as to not disturb them due to the lack of access because of military training, and low sample size of nests and nest success during the study.

Estimating Home Range Area

I estimated the 95% isopleth home range area of female Greater Prairie-chickens during the breeding season using biased random bridge movement models using Program R (*adehabitat;* R Core Team 2021). I excluded any bird that had <100 locations at any stage in the breeding season for stage in which we were interested in (Robinson et al. 2018, Plumb et al. 2019). I used biased random bridge movement models because they are more appropriate for spatially and temporally autocorrelated data; they account for time lag as well as temporal autocorrelation between locations, the path traveled between two successive locations, and transmitter error (Behnamou 2011). In addition to spatial and temporal autocorrelation, biased random bridge movements account for animals reorienting within their home ranges as they adjust to landscape composition. These models are a good trade-off between being too simplistic and unrealistic and too complex to be functionally useful (Behnamou 2011). I then used analysis of variance (ANOVA) to compare average home range area among the different breeding stages.

Once I generated home ranges, I overlaid polygons of various management activities (food plots, hayed areas, and burn frequencies) onto the home ranges in ArcGIS 10.6 (ESRI Inc., 2013, Redlands, USA) to understand how birds used these areas and if they were used differentially during various breeding stages. Food plot and burn frequency layers were developed by Fort Riley Environmental Division staff; burn frequencies were based off of burn intervals within Fort Riley (developed by K. McCullough and D. Goodin) and then grouped based on frequency of burn as mentioned above. I generated the hayed layers by outlining and ground truthing each area. For each bird during each stage of the breeding season, I used the tabulate intersection tool in ArcGIS 10.6 to calculate the proportion of each management activity and grass type that intersected with the bird’s 95% isopleth home range. I then calculated averages of proportions of all birds based on each breeding stage and compared these averages between breeding stages.

Estimating Daily Displacement

I estimated total and net daily displacement by each female during the breeding season. I categorized each day as military training or not based on days when there were training area closures due to scheduled military activity and associated activities (maintenance days, range sweeps, etc.). Total daily displacement was the difference in Euclidian distance between each successive point summed over the 10 points collected per day while net daily displacement was the distance displaced during daily movement, derived as the difference between the first and last point of the day. I estimated both measures of distances to test if military activity caused birds to move differently than during days of no military activity or if they actually dispersed from the area they were at when points were first collected at the beginning of the day to the area where they chose to roost at the end of the day. I conducted paired *t*-tests to test for significant differences in movement overall between days where activity occurred versus when activity did not occur and I used ANOVA to compare differences in movement between breeding stages.

Results

Home Range Area

I captured 20 females in 2019 and 16 in 2020 for 36 total Greater Prairie-chickens in my analyses. The overall home range area for transmittered birds on Fort Riley during the breeding season was 232 ± 31 ha ($\bar{x}$ ± SE range 46-761 ha). I estimated lekking home range area for 26 birds, nesting home range area for 23 birds, and post-nesting home range area for 20 birds due to some birds not meeting the 100-point criteria/breeding stage. Home range differed significantly based on breeding stage ($F_{2,66} = 5.60$, $P = 0.005$). Home range area during the lekking season was 238 ± 43 ha (range 32-761 ha), 115 ± 20 ha for nesting (range 24-443 ha), and 113 ± 11 ha for post-nesting (range 14-209 ha) making the home range area for the lekking season 2 times greater than nesting and 2.1 times greater than post-nesting home ranges (Table 3.1).

Food plot and hayed area use varied by breeding stage. Percent area of food plots within these home ranges did not vary much among breeding stages and was low for all breeding stages (*lekking*: 0.8%, range 0-4.5%; *nesting*: 0.9%, range 0-5.5%, *post-nesting*: 0.7% range 0-4.3%;

Table 3.1). The type of food plot used most was alfalfa, and this trend was true across all breeding stages. Korean lespedeza, soybeans, and sunflower food plots were also used by breeding Greater Prairie-chickens, but not extensively nor across all breeding stages (Table 3.2). Use of hayed area cut in the current year increased three-fold from lekking season to post-nesting despite the amount of hayed area staying constant across the breeding season. During the lekking stage, the amount of hayed area within home ranges averaged 0.8% (range 0-10.7%), increased to 1.9% (range 0-36.4%) during the nesting stage, and increased even more during the post-nesting stage to 3.2% (range 0-53.1%; Table 3.2).

Finally, the proportion of burn frequencies making up home ranges followed similar trends among all breeding stages. During the lekking stage, areas burned every 2-4 years encompassed the most home range area and were visited the most by birds, followed by areas burned every 1-2 years, then areas annually burned, and finally areas burned every 4-8 years made up the least amount of home range among all burn frequencies. The same trend was followed in the nesting stage, but during the post-nesting stage the frequency encompassing the most home range area was area burned every 1-2 years followed by areas burned 2-4 years, then areas burned every 4-8 years. No post-nesting home ranges included areas burned annually and no bird locations were recorded in areas burned annually or every 4-8 years (Table 3.3).

Daily Movements

Of the 36 females captured in 2019 and 2020, I calculated total daily displacement for 31 because 5 birds did not have the 10 points needed each day to calculate total daily displacement. In addition, when comparing total daily displacement between days where there was training and days where there was not, I limited those analyses to 27 birds because 4 birds did not have locations for any days where military activity occurred (i.e., died beforehand). Regarding breeding stages, total daily displacement differed between lekking, nesting, and post-nesting stages ($F_{2,\ 2614}$ = 124.67, P < 0.001). However, relative to military activity schedules, mean total daily displacement on days where activity occurred did not differ from days when activity did not occur (t_{27} = 1.37, P = 0.18). Total daily displacement did not differ during the lekking (t_{276} = -1.34, P = 0.09), but did during nesting (t_{595} = 2.39, P = 0.008), and post-nesting (t_{603} = 2.78, P = 0.002) breeding stages between days when training occurred and days when they did not (Table 3.4).

I included 27 birds in my analysis comparing net daily displacement. Net daily displacement differed between lekking, nesting, and post-nesting stages ($F_{2,\ 1844}$ = 34.11, P < 0.001), but did not differ on days when military activity occurred versus when it did not (t_{27} = -0.51, P = 0.62). Net daily displacement did not differ between lekking (t_{285} = -1.10, P = 0.14), and post-nesting stages (t_{567} = 1.37, P = 0.09), but did differ during the nesting stage (t_{404} = 2.79, P < 0.01; Table 3.5) with birds moving less during military activity than on days without. Although overall daily displacement means were not found to be statistically significant, patterns among individuals for distances moved on days with and without military activity was not constant. Eleven birds had greater net daily displacements when military training was not occurring, while 16 had lower net daily displacements when military training was not occurring (Figure 3.3).

Discussion

The Greater Prairie-chicken population on Fort Riley is unique given a relatively stable population while persisting in a constrained landscape subject to multiple disturbances including fire, munition firings, increased on-the-ground activity, and other military related activity. Despite these conditions, birds appear to use space normally, occupy areas with adequate resources (not limited to low-quality habitat i.e. burned too frequently or not enough), and are not reliant on supplemental management activities during the breeding season (food plots, haying). Area and composition of home ranges of female Greater Prairie-chickens during the breeding season reflects the high-quality habitat available within the native prairie on Fort Riley, where birds are able to acquire all the resources they need within an area comparable to other Greater Prairie-chicken populations that are not as confined as the Fort Riley population. In addition to bird responses to and use of management activities, Greater Prairie-chickens used space differently depending on the breeding stage they were in. This space use also differed at certain stages depending on if military activity was ongoing or not, leading to the conclusion that the breeding stage of a Greater Prairie-chicken as well as outside influences such as military training affects site fidelity and resource use.

Regarding space use, my overall estimate of 232 ha during the breeding season is one of the smaller estimates for Greater Prairie-chicken populations in Kansas and surrounding states. Using very-high-frequency (VHF) transmitters, Augustine and Sandercock (2011) estimated breeding season space use (95% isopleth) to be 575±65 ha; Patten et al. (2011) found summer movements by females to be 272±55 ha; and Winder et al. (2014) determined 99% breeding season home ranges to be 5400±1310 ha before wind farm construction and 9680±2450 ha post wind farm construction. These results are interesting because normally using VHF telemetry produces smaller home ranges because of the coarse temporal resolution of locations (3-7 locations/week as opposed to 70/week for GPS transmitters; Robinson et al. 2018, Verheijen et al. 2021). This contrast may be due to high fidelity for certain areas on Fort Riley by Greater Prairie-chickens during the breeding season due to an abundance of food resources and required habitat types within that area, or may be a byproduct of the constrained environment that Fort Riley presents.

Despite Fort Riley's constrained environment, there is little infrastructure or intensive land use practices that would deter Greater Prairie-chickens from using space (Chapter 2). In Winder et al. (2014), Greater Prairie-chickens had to initially deal with navigating high road densities and after wind farm construction had to navigate closely spaced wind turbines with even greater road density and urbanization due to newly erected power substations. Further contrasting my findings to previous studies, unlike surrounding areas that use annual burning for most of their land, Fort Riley only annually burns areas needed for continuous military activity. This type of annual burning is not conducive to resource acquisition for Greater Prairie-chickens and therefore, birds would have to travel further distances and subsequently, home ranges would become larger. Grazing is also common practice in areas surrounding Fort Riley; intensive stocking leaves little residual cover for arthropod forage or Greater Prairie-chickens to find cover for nesting, foraging, or escape cover (van Klink et al. 2014, McNew et al. 2015, Winder et al. 2017).

Although landscape-level variables appear to disproportionately affect overall home ranges of Greater Prairie-chicken populations outside of Fort Riley more than on Fort Riley, individual breeding stage movements seem to follow similar trends between populations on and off Fort Riley. I determined that lekking movements were the largest followed by nesting and post-breeding. My findings corroborate previous findings, citing that during the lekking season, females will visit many different leks to scout for the best possible mate; whereas they are constrained by being on the nest during nesting season and by broods and the molting process during the late summer (Robel 1970, Schroeder and Braun 1992, Patten et al. 2011, Verheijen et al. 2021). Studies have shown mixed trends in the post-breeding stage based on whether birds were constrained by broods or not (Schroeder and Braun 1992), but for this analysis I did not differentiate females based on whether they still had broods or not.

Understanding differences in overall movement by breeding stage and how land use practices affect movements at different stages is important, particularly if these practices have the capacity to influence space use across seasons (i.e., lag effect), which could be seen with haying practices on Fort Riley. Haying on Fort Riley occurs between mid-July and mid-August, so although it did not occur during nesting season, it may still affect habitat use when tending broods and during fall and winter use of the same year or nest placement the following year due to the vegetation disturbance. Haying is thought to stimulate forb growth that is used as fall and winter food of grouse (Kobriger 1965, Begay et al. 2011); if there is residual cover left over from some strips left unhayed, or haying only occurs every other year, that may be even more attractive for grouse when foraging (Kirsch et al. 1973, Dale 1992). On Fort Riley, my findings suggest that birds are not readily using hayed areas from the previous year during the lekking months, but use increases as the breeding season progresses. This may be due to the progression of vegetation growth throughout the growing season, where, by the time post-breeding comes around, birds are using the taller vegetation more until it is hayed. However, the total lack of cover after haying may influence use at times during post-breeding until cool-season grasses regrow. Hayed areas used by birds on Fort Riley are warm-season hay permits that can and were hayed each year. Such yearly haying did not seem to disturb or deter birds from using these areas during the post-breeding season especially. It will be necessary to understand how these same hayed areas are used by Greater Prairie-chickens during the fall and winter seasons as these hayed areas could prove to be invaluable food sources that aid in non-breeding season survival and increase fitness leading up to subsequent breeding seasons (Chapter 1).

In addition to hayed areas, food plots could also be a valuable food source linked to increased non-breeding survival and subsequent breeding season survival, although not directly intended for the benefit of Greater Prairie-chickens. Food plots were used at similar intensities during the lekking and nesting seasons. During the lekking season, birds used food plots as lekking grounds while staying on these grounds to forage after lekking was completed for the day (J. Gehrt, *personal observation*). During the nesting season, food plots may have been used as convenient forage sites for females taking incubation breaks, as food plots were typically surrounded by taller vegetation suitable for nesting sites. Jones and Sullivan (1962) conducted a study of food plot utilization by Greater Prairie-chickens on Fort Riley during the spring months and found birds to use plots with corn the most, and overall utilization of food plots to be 65%. This study was conducted at a time when there were fewer crop fields surrounding Fort Riley, so perhaps these food plots acted as a substantial source of food during spring. They did note that due to excellent weather conditions the year before the study, birds may have not needed these supplemental resources. These food plots may have been used more if the study incorporated drought conditions where much of the typical food sources such as native forbs and grasses would not be as plentiful to foraging Greater Prairie-chickens on Fort Riley. Like hayed areas, it is important to assess use of food plots during the fall and winter months to understand how these supplemental food sources may be used during times where food is less plentiful.

The final land use practice I examined was burning. Fort Riley, with their mosaic-style burning, is quite different from surrounding landscapes that implement annual burning. The fact that nesting birds use areas burned every 2-4 years coincides with previous literature (Fuhlendorf et al. 2017) where females are seeking out areas with enough residual vegetation to conceal nests. It is interesting, however, that birds use areas burned every 2-4 years for lekking. This is typically thought of as too dense of vegetation for males to display, but on Fort Riley, many food plots are within these 2-4 year since burn areas, and food plots served display sites for many of these birds. Finally, the result that post-nesting birds use areas burned every 1-2 years the most may suggest that there are more forbs in these areas to provide food for post-nesting birds (e.g., with broods), or that these areas provide enough cover yet are easily navigable by females with broods. The final surprising result is that post-nesting birds did not use areas burned annually or every 4-8 years. Perhaps these burn frequencies are too frequent to promote high-quality forb growth for Greater Prairie-chicken forage or not frequent enough to where warm-season grasses outcompete forbs for nutrients and sunlight. My results show the importance of heterogeneity of burn frequencies on the landscape, which is seldom implemented within the Flint Hills. Previous studies have cited many benefits of heterogeneous burning through regimes such as patch-burn grazing for both landscape health as well as wildlife health, and with this strategy Greater Prairie-chickens may be able to acquire all needed resources from the landscape (McNew et al. 2015, Winder et al. 2017).

Perhaps the largest, most frequent disturbance on Fort Riley is the military activity. Previous studies have examined responses of birds to military training and found birds of a wide range of species, life history strategies, and size to only slightly react to military activity (Cadwell et al. 1994, Stalmaster and Kaiser 1997, Grubb et al. 2010, Barron et al. 2012). The only direct comparison made to my findings is that Cadwell et al. (2014) found that mean daily distance moved by Greater Sage grouse (*Centrocercus urophasianus)* during training was 1,031 m compared to 832 m/day after training. These findings were statistically significant whereas my findings that Greater Prairie-chickens moved 1,121 m per day with military activity and 1,309 m per day without activity were not statistically significant (i.e., greater variation among individual birds). More specific than overall movement, only the nesting stage differed significantly in both net and total daily displacement where females moved less during military activity than days without activity. This suggests that the nesting stage, already a time where birds are vigilant to nest predation, may be a particularly vulnerable time where females are weary of outside threats and the presence of military training may pose the most threat.

Overall, disturbances on Fort Riley seemingly are not causing many differences in movement compared to other studies despite the constrained environment. I hypothesize the abundance of high-quality habitat on the landscape may be reason for such findings. Greater Prairie-chickens are able to acquire all needed resources in a relatively small area and therefore, need not to make large movements (Chapter 2). It also appears these birds have adapted to military activities and are not significantly affected by these activities. Management of Fort Riley is providing necessary resources for a persistent Greater Prairie-chicken population meeting their physiological needs with a variety of management activities that enable birds to succeed in each stage of the breeding season.

Management Implications

To provide for Greater Prairie-chickens throughout the breeding season, it is necessary to have sufficient vegetation heterogeneity on the landscape juxtapositioning forage, cover, and specific habitat types for lekking, nesting, and brood rearing. To do so, land managers must burn at various frequencies and cease annual burning of lands. In addition, fires should not encompass more than 100ha because this area would allow for proper heterogeneity based on the home range of Greater Prairie-chickens during their different breeding stages. Heterogeneous burning will provide a variety of cover and forage types needed by Greater Prairie-chickens throughout the breeding season. My findings indicate that waiting to burn past every 4 years will significantly decrease use by Greater Prairie-chickens at any stage in the breeding season, and annual burns will not be useful at some stages of the breeding season. Burning less frequently than every 4 years will invite woody encroachment onto the landscape, which greatly deters Greater Prairie-chickens from using areas in close proximity to such encroachment, but burning annually produces landscapes that do not provide adequate cover for many stages during the breeding season.

In addition to proper burning regimes, hayed areas do not seem to be used by Greater Prairie-chickens in the early stages of the breeding season, although some studies cite the usefulness for creating lekking areas for males by haying. Haying too early in the season may be detrimental to nesting birds, so delayed haying (starting around mid-July) would be a good option to stimulate forb growth that may be used as food during the fall months while still giving grasses an opportunity to grow during the cool season and ensure adequate cover is available for over-wintering birds.

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Figures

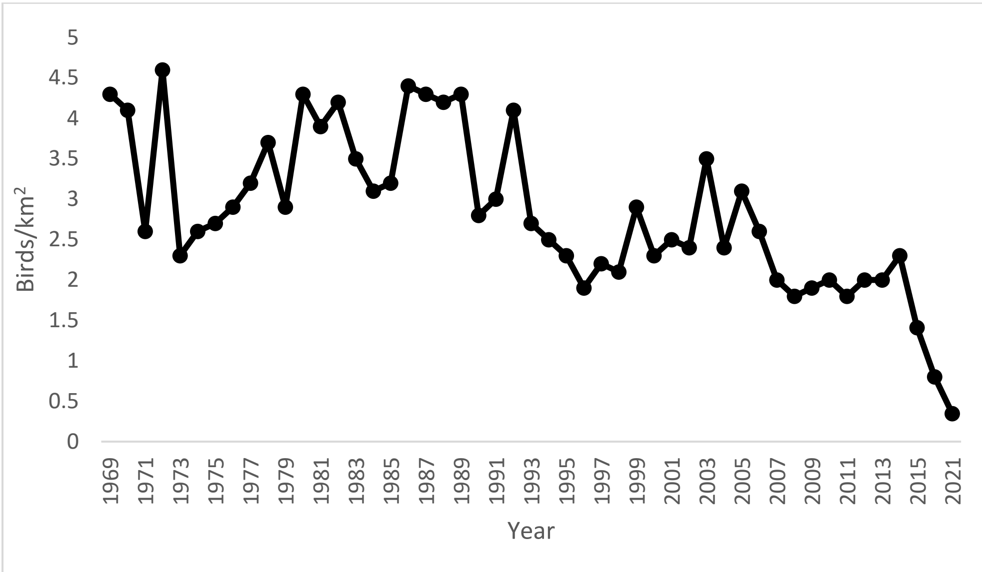

Figure 3.1. Population trends of Greater Prairie-chickens in the Flint Hills ecoregion of Kansas, USA. Data were derived from annual and semi-annual lek counts conducted by Kansas Department of Wildlife, Parks, and Tourism from 1969–2021.

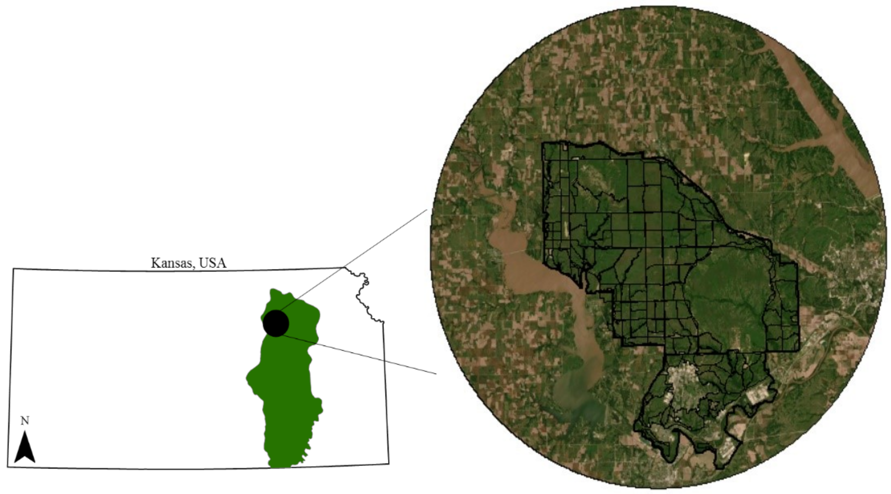

Figure 3.2. Location of Fort Riley Military Reservation within the Flint Hills ecoregion of Kansas, USA (outlined in green). Training units within Fort Riley Military Reservation are delineated (figure adapted from McCullough et al. 2021).

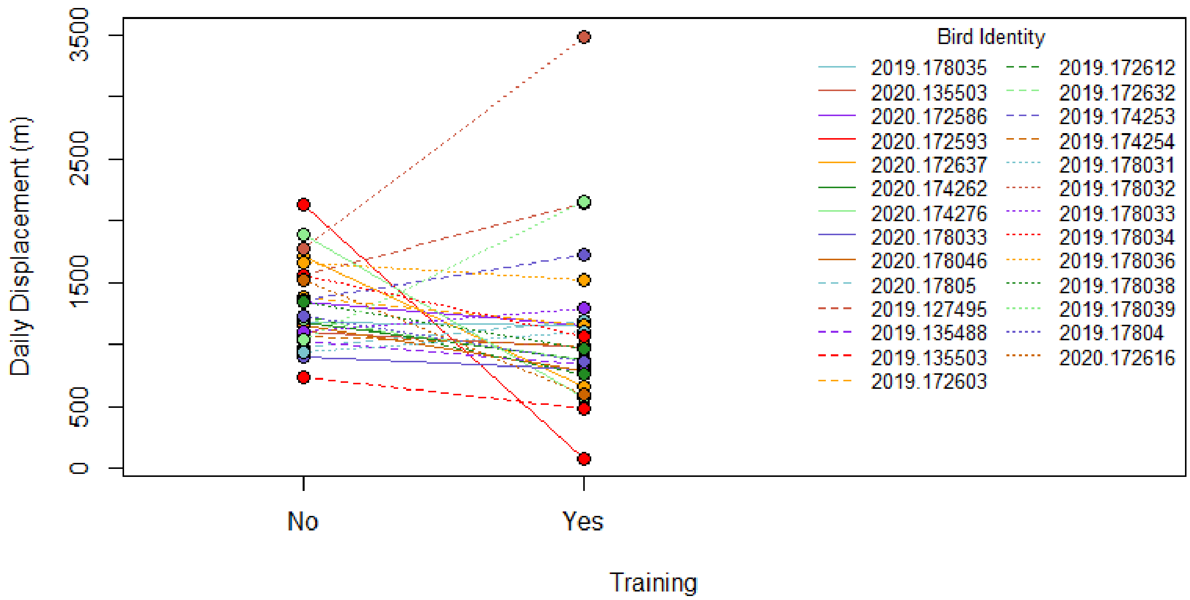

Figure 3.3. Individual variation in net daily displacement of female Greater Prairie-chickens based on days when training occurs versus when training does not occur on Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

Tables

Table 3.1. Descriptive statistics ($\bar{x}$ ± SE) of cover types within home ranges of female Greater Prairie-chickens on Fort Riley Military Reservation in Kansas, USA, during 2019-2020. These are based on breeding stage of the breeding season and cover types are broken into percent of home range encompassed by food plots and hayed area*, total amount of area represented by each on Fort Riley. Overall home range mean and standard error are also included for each breeding stage.

	% of home range		*overall home range(ha)*
Breeding stage	*food plot*	*hayed area*	$\bar{x}$ ± *SE*
Lekking	0.81±0.23%	0.78±0.46%	238±43
Nesting	0.87±0.33%	1.87±1.58%	115±20
Post-nesting	0.66±0.27%	3.17±2.65%	113±11
% area on Ft. Riley	0.93%	4.99%	

*hayed areas are those cut during the same year as when birds are using the area

Table 3.2. Relative use of food-plot type by female Greater Prairie-chickens based on composition of home range by stages during the breeding season on the Fort Riley Military Reservation in Kansas, USA, during 2019-2020.

	Percent food plot type in home range			*Percent of used points in food plots*		
Breeding stage	*Korean Lespedeza*	*Alfalfa*	*Sunflowers-soybeans*	*Korean Lespedeza*	*Alfalfa*	*Sunflowers-soybeans*
Lekking	0.02	17.64	1.32	0.00	2.53	0.09
Nesting	0.03	28.67	0.00	0.00	2.12	0.00
Post-nesting	0.00	10.38	0.00	0.00	4.30	0.00

Table 3.3. Descriptive statistics ($\bar{x}$ ± SE) of the percentage of burn frequencies within home ranges of female Greater Prairie-chickens on Fort Riley Military Reservation in Kansas, USA, during 2019-2020. Statistics are broken down by breeding stage of the breeding season and also include the total amount of area represented by each on Fort Riley as well as percent of used points within each burn frequency.

	Percent home range by time since burn				*Percent of used points in burn interval*			
Breeding stage	*1 year*	*≥1-2 year*	*≥2-4 year*	*≥4-8 year*	*1 year*	*≥1-2 year*	*≥2-4 year*	*≥4-8 year*
Lekking	2.38±2.09	31.90±6.50	65.50±6.73	0.12±0.08	1.65	38.20	60.08	0.05
Nesting	4.35±4.34	34.37±8.72	61.15±8.13	0.21±0.15	2.63	45.81	51.16	0.39
Post-nesting	0.00±0.00	49.85±9.73	50.22±9.72	0.01±0.01	0.00	51.43	48.56	0.00
% area on Ft. Riley	9.00%	8.00%	70.00%	6.00%				

Table 3.4. Total daily displacement (m) by female Greater Prairie-chickens on Fort Riley Military Reservation in Kansas, USA from 2019-2020. Distances are broken up by breeding stage and whether or not military training was occurring. Asterisks denote statistical significance between days where training occurred versus when training did not occur (*P* ≤ 0.05).

	Breeding stage			
Military training occurring?	Lekking	Nesting*	Post-nesting*	Overall
Yes	1,673±102m	1,048±53m	860±20m	1,121±127m
No	1,521±46m	1,223±51m	983±39m	1,309±63m

Table 3.5. Net daily displacement by female Greater Prairie-chickens on Fort Riley Military Reservation in Kansas, USA from 2019-2020. Distances are broken up by breeding stage and whether or not military training was occurring. Asterisks denote statistical significance between days where training occurred versus when training did not occur ($P \leq 0.05$).

	Breeding stage			
Military training occurring?	Lekking	Nesting*	Post-nesting	Overall
Yes	545±66m	198±24m	317±12m	392±61m
No	466±29m	287±20m	351±24m	357±35m