

Lesser prairie-chicken demography, resource selection, and habitat response following megafire
in the mixed-grass prairie

by

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Abstract

Fire is an ecological driver that historically interacted with grazing and periodic drought throughout large portions of the Great Plains to maintain grasslands used by several wildlife species. More recently, fire suppression, coupled with changing climate and landscapes, has led to altered grassland ecosystems that may be more likely to experience massive wildfire events known as megafires. Megafires (>40,000 ha) have extreme socioeconomic impacts and may also affect grassland-dependent wildlife including lesser prairie-chickens (*Tympanuchus pallidicinctus*). The lesser prairie-chicken is a grouse species of the southern Great Plains that has experienced population declines since the 1980s, primarily as a result of grassland habitat degradation and loss. While fire has long functioned as an ecological driver to shape grassland habitat, knowledge about the influence of megafires on lesser prairie-chickens and their habitat is lacking. To better understand how remaining grasslands and lesser prairie-chickens may be impacted by megafire, I hierarchically evaluated lesser prairie-chicken survival, reproduction, resource selection, and habitat response to a 2017 megafire at a site inhabited by lesser prairie-chickens in the mixed-grass prairie of Kansas, USA (Starbuck fire, ~254,000 ha). I captured lesser prairie-chickens on leks during the spring before (2014–2015) and after (2018–2019) the fire, attached VHF radio and GPS satellite transmitters, and tracked individuals to evaluate survival, reproduction, and habitat selection. To estimate population trends, I conducted counts of male attendance on leks before and after the fire. There was a 67% decline in the number of attending males on leks post-fire and a 46% decline in the number of occupied leks post-fire. Despite the population decline indicated by lek counts, female breeding season adult survival remained similar before (0.63 ± 0.08) and after the fire (0.64 ± 0.08), as did chick survival

(before: 0.27 ± 0.03 ; after: 0.32 ± 0.11), while nest survival trended lower post-fire (before: 0.42 ± 0.06 ; after: 0.27 ± 0.07). Individual space use was evaluated using 95% isopleth Brownian Bridge home ranges, and did not differ before (828 ± 110 ha) and after (719 ± 101 ha) the fire. However, home ranges included 5 times more percent cover of Conservation Reserve Program (CRP) fields after the fire compared to before, suggesting CRP/cropland landscapes with disjointed fire fuel availability can provide refugia during extreme events. An analysis of lek attendance corroborated home range results, with greatest male lek attendance in areas with more surrounding cropland post-fire, opposite of trends seen before the fire and lesser prairie-chicken literature. Step selection revealed lesser prairie-chickens strongly avoided wooded areas before and after the fire, indicating that although I did see mortality of woody species, burned woodlands did not become available for use by lesser prairie-chickens. Furthermore, lesser prairie-chickens avoided burned areas post-fire, suggesting limited habitat availability up to 3 years post-fire and emigration from the study site. My analysis of fine-scale habitat and grassland vegetation characteristics response supported a decrease in available cover, with a 32% decrease in 100% visual obstruction, 17% decrease in litter depth, and a 16% increase in bare ground. Based on vegetation criteria, abundance of nest habitat decreased 34% one year post-fire; however, nest habitat and many vegetation characteristics returned to pre-fire levels within two years post-fire, thanks in part to substantial growing season precipitation received in the years following the fire (>70 cm/year). The large size and intense nature of the fire affected lek attendance, habitat abundance, and nest survival, but had no lasting (>2 year) detrimental impacts for grasslands or lesser prairie-chicken habitat. Post-fire recovery of grasslands did not correspond with a rebounding population and it will likely take >3 years for lesser prairie-chickens to fully recolonize burned grasslands. My results indicate that multiple management

strategies (e.g., CRP enrollment, post-fire removal of snags, prescribed fire) are needed to manage lesser prairie-chicken habitat and limit future megafires.

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Dedication

To my parents and sister, for inspiring a love of nature and for supporting me in everything that I do. Thank you Elli Teige, for being with me every step of the way. I could not have done it without you.

Chapter 1 - Introduction

Grasslands in the Great Plains have declined roughly 70% since European settlement and are one of the most imperiled ecosystems worldwide (Samson et al. 2004, Augustine et al. 2019, Lark 2020). Grasslands have been lost through conversion to row-crop agriculture, energy exploration, and other anthropogenic development (Brennan and Kuvlesky 2005). Remaining grasslands have been largely degraded due to altered ecological drivers including poor grazing management in some areas and a decoupling of fire from the system (Samson and Knopf 1994, Fuhlendorf and Engle 2001, Briggs et al. 2005). Fire was a key ecological driver in shaping large portions of the Great Plains of North America and helped maintain treeless landscapes (Axelrod 1985, Askins et al. 2007, Engle et al. 2008). Fire and grazing by bison (*Bison bison*) interacted with the continental climate of the Great Plains to create heterogeneous landscapes needed by a variety of grassland-dependent wildlife (Fuhlendorf and Engle 2001, Askins et al. 2007, Fuhlendorf et al. 2009). The dominant practice of fire suppression since European settlement has led to homogeneity in grassland composition and structure, leading to a loss of biodiversity in grasslands across the Great Plains (Fuhlendorf and Engle 2004). Consequently, grassland birds have experienced the greatest declines of any guild in North America since the 1970s (Rosenberg et al. 2019).

One such threatened species is the lesser prairie-chicken (*Tympanuchus pallidicinctus*), a grassland-obligate grouse species of the southern Great Plains that has declined since the 1980s (Haukos and Boal 2016). Much of their decline has been attributed to habitat loss concurrent with loss and degradation of grasslands throughout their distribution (Haukos and Zaveleta 2016). Lesser prairie-chickens now occupy only an estimated 14% of their estimated historic distribution and are restricted to four increasingly isolated ecoregions in Kansas, Colorado, New

Mexico, Oklahoma, and Texas, USA (Van Pelt et al. 2013, Garton et al. 2016). Concerns about populations have led to a dynamic legal status including listing as threatened under the Endangered Species Act of 1973 (2014), subsequent de-listing (2016), and a 2021 proposed listing of the species as two distinct populations (USFWS 2014, USFWS 2021). Under the proposed listing, the northern population segment population in Kansas, Colorado, Oklahoma, and the eastern panhandle of Texas would be considered threatened while the southern population segment in western Texas and New Mexico would be considered endangered. The uncertain future of the lesser prairie-chicken highlights the need for science that can guide conservation efforts and planning in light of continued habitat loss and climate change.

Coupling of climate change and years of fire suppression has led to a rise of massive wildfires in the Great Plains, which are often referred to as megafires (Lindley et al. 2013, Donovan et al. 2017, Lindley et al. 2019). Megafires are generally defined by their immense size (>40,000 ha), but are also characterized by their extreme and lasting social, economic, and environmental impacts (Williams et al. 2011, Stephens et al. 2014). Increased megafire events are not limited to the Great Plains or North America, but are escalating worldwide (Williams et al. 2011). While the most destructive and high profile megafires in the United States have occurred in the forests of North America, the southern Great Plains has experienced an increase of large and destructive fires over the last 30 years (Donovan et al. 2017, Lindley et al. 2019). This trend is predicted to continue (Barbero et al. 2015, Cao et al. 2015). Fire suppression in the Great Plains has led to the buildup of fuel, the invasion of nonnative species, and woody encroachment that all contribute to megafires of unprecedented size in recent history (Lindley et al. 2013, Donovan et al. 2020).

The negative results of fire suppression that led to increased megafire risk have also contributed to a decline in habitat availability and quality for lesser prairie-chickens. Historically, lesser prairie-chickens relied on disturbance from fire and grazing by bison to maintain heterogeneous grasslands needed to provide distinct habitat patches for different life stages (Fuhlendorf and Engle 2001, Hagen and Giesen 2005, Haukos and Zaveleta 2016, Fuhlendorf et al. 2017). Recently burned and grazed areas can provide lekking grounds for male displays in the breeding season, along with forbs and open areas for chicks (Cannon and Knopf 1979, Boyd and Bidwell 2001, Hagen and Giesen 2005). Areas not recently burned can provide grass cover necessary for nesting and adult lesser prairie-chicken concealment from predators (Haukos and Zaveleta 2016). Lesser prairie-chickens avoid trees and other tall features, therefore, woody encroachment due to lack of fire has reduced habitat across their distribution (Van Pelt et al. 2013, Lautenbach et al. 2017, Sullins et al. 2019). As such, megafires may benefit lesser prairie-chickens if they remove trees and return a vital disturbance to the landscape, potentially improving overall grassland health and biodiversity (Ratajczak et al. 2012, Twidwell et al. 2013). Alternatively, megafires may negatively affect lesser prairie-chicken populations as they temporarily remove vast swaths of residual herbaceous cover that provide nesting, brooding, roosting, and nonbreeding habitat. Residual herbaceous cover can be limiting for lesser prairie-chickens, and even temporary loss of grasslands could result in local extinction if there is no nearby habitat in which to disperse following megafire (Simberloff 1994, Fuhlendorf et al. 2002, Ross et al. 2016). While lesser prairie-chickens evolved with fire, and historically relied on it to maintain habitat, lesser prairie-chicken response to fires of this magnitude in contemporary fragmented and altered grasslands is unknown.

I conducted a comprehensive and multi-scaled analysis of lesser prairie-chicken demography, resource selection, space use, and habitat in order to understand lesser prairie-chicken response to megafire. I monitored lesser prairie-chickens and their habitat before and after the largest fire in Kansas history (Starbuck fire; ~254,000 ha). To monitor population trends and assess lesser prairie-chicken survival and reproductive success, I conducted lek surveys (population level) and monitored individual lesser prairie-chickens outfitted with VHF and GPS transmitters. I examined how megafire influenced lesser prairie-chicken space use, resource selection, and lek attendance using high-resolution GPS data from marked individuals. I collected and analyzed vegetation data to examine megafire effects on fine-scale vegetation and lesser prairie-chicken habitat. With this work, I hope to inform conservation efforts by stakeholders managing lesser prairie-chicken populations and grasslands in response to the growing megafire reality in the Great Plains.

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Chapter 2 - Lesser prairie-chicken demographic response to megafire

Introduction

Increases in the frequency and magnitude of massive wildfires, known as megafires, are a predicted result of climate change (Barbero et al. 2015, Cao et al. 2015). Megafires are generally defined as a wildfire covering >40,000 ha (100,000 acres; USFS 2018, Lindley et al. 2019), but this size definition often fails to capture the increasingly large social and economic effects of megafires (Williams et al. 2011, Stephens et al. 2014). Although the impacts of megafires on human life and property are well known, effects on wildlife are difficult to quantify due to the limited opportunity for planning before and after impact studies. Following the 2019–2020 megafires in Australia, nearly 3 billion individual vertebrates were affected and >800 vertebrate species lost critical habitat (Van Eeden et al. 2020, Ward et al. 2020). In the United States, the frequency of megafires has been increasing, particularly in the American West, and negatively affecting threatened species in the region, such as spotted owls (*Strix occidentalis*; Stephens et al. 2014; Jones et al. 2016, 2021). In contrast to smaller wildfires, megafires can also negatively affect fire-adapted species, such as black-backed woodpeckers (*Picoides arcticus*) that use a mosaic of burned and unburned forest (Stillman et al. 2019). Outside of a forest ecosystem, wildfire can reduce adult and nest survival rates of greater sage-grouse (*Centrocercus urophasianus*; Foster et al. 2019). Recent research suggests that wildfires, when coupled with invasion of non-native grasses, are one of the greatest threats to greater sage-grouse and their habitats in the western part of their range (Nelle et al. 2000, USFWS 2015, Coates et al. 2016).

The lesser prairie-chicken (*Tympanuchus pallidicinctus*), an imperiled prairie grouse species endemic to the southern Great Plains, has experienced multiple megafires throughout its

distribution in recent years (Hagen and Giesen 2005, Donovan et al. 2017, Lindley et al. 2019). Lesser prairie-chickens currently occupy only 14% of their estimated historic range and rely heavily on the few remaining grassland-dominated landscapes within its distribution (Garton et al. 2016). Grasslands within the historic lesser prairie-chicken range have been converted to row-crop agriculture, energy production infrastructure, and other anthropogenic development (Van Pelt et al. 2013, Haukos and Zaveleta 2016). Habitat in remaining grasslands has also been degraded by alteration in the frequency and intensity of fire, grazing, drought, and invasion of woody plants (Haukos and Zaveleta 2016). Lesser prairie-chickens were listed as threatened in 2014 under the 1973 Endangered Species Act, and despite the listing status being revoked in 2016, a 2021 proposed listing indicates lesser prairie-chickens are still a species of concern requiring conservation efforts (USFWS 2014, USFWS 2021).

Fire regimes largely shaped grassland systems in the Great Plains of North America and play an important role in lesser prairie-chicken ecology (Samson et al. 2004, Thacker and Twidwell 2014). The interaction of fire, grazing, and climate formed the grasslands in North America, establishing landscape heterogeneity and diversity in plant communities (Axelrod 1985, Fuhlendorf and Engle 2001, Samson et al. 2004, Askins et al. 2007). In the mixed-grass prairie, an estimated historic fire return interval of 5–10 years (Wright and Bailey 1982, Brockway et al. 2002, Samson et al. 2004) helped maintain treeless landscapes required by a number of grassland biota (Axelrod 1985, Engle et al. 2008). Landscapes have been substantially altered by human expansion and contemporary land and fire management practices (Twidwell et al. 2013). Perhaps most importantly, fire was suppressed in many areas, allowing trees and other woody species to invade grasslands (Briggs et al. 2005). In the mixed-grass prairie of Kansas,

USA, lesser prairie-chickens have lost 21% of otherwise available habitat as they avoid areas with >2 trees/ha (Lautenbach et al. 2017, Sullins et al. 2019).

Lesser prairie-chickens require grasslands that are heterogeneous in herbaceous cover and composition, which can be maintained by fire (Haukos and Zavelata 2016, Lautenbach 2017). Habitats used during lekking, nesting, brooding, and nonbreeding seasons all differ, and without each component the populations may decline or experience local extinction (Simberloff 1994, Haukos and Zaveleta 2016). Small patchy fires on the landscape are ideal for creating and sustaining such a variety of habitat types, by inter-mixing different successional stages of vegetation communities (Elmore et al. 2009). For example, quality foraging and brood habitat can be created by prescribed fire in the spring, but can negatively affect nesting habitat for several years (Boyd and Bidwell 2001). This highlights the importance of implementing fire at appropriate spatiotemporal scales, with recommendations to only burn 20–30% of a management area in a year to mimic a 3–5 year fire-return interval (Elmore et al. 2009). Patch-burn grazing can benefit lesser prairie-chickens by recoupling the historic fire-grazing interaction (Fuhlendorf and Engle 2001). In this system, lesser prairie-chickens can select patches that will best meet life-stage specific needs based on time since fire (e.g., using >2 years since fire patches for nesting and 1–2 years post fire for brooding; Lautenbach 2017). While effects of wildfire on lesser prairie-chicken populations are largely unknown, one study in Texas, USA, documented use of burned areas by lekking and brooding lesser prairie-chickens following small wildfires (45–63 ha; Jones 2009).

The importance of fire for lesser prairie-chicken habitat is clear, but population effects likely depend on the size and severity of the fire. Large-scale, higher intensity fire could set back woody encroachment, opening areas of habitat previously lost (Twidwell et al. 2016).

Furthermore, it could improve habitat quality through removal of invasive herbaceous species and while promoting plant diversity (Ratajczak et al. 2012, Twidwell et al. 2013). Alternatively, large-scale megafires could create grasslands more homogeneous in cover compared to a shifting mosaic of small fires. Loss of heterogeneity in vegetation structure and composition in remaining grasslands, even for a brief time, may negatively affect populations as lesser prairie-chickens are already restricted to limited, isolated grassland patches (Fuhlendorf et al. 2002, Ross et al. 2016). Given the increasing number of megafires across the lesser prairie-chicken range in recent years, with the prediction these will only increase in frequency and severity (Barbero et al. 2015, Donovan et al. 2017, Lindley et al. 2019), it is important to evaluate the short-term population response to megafires.

Vital rates of lesser prairie-chickens are influenced by disturbances found in the Great Plains, such as anthropogenic expansion, fragmentation, grazing, and fire. Annual survival of adult lesser prairie-chickens can increase in areas with more grassland and that have more diverse landscapes, indicating that the homogenizing effects of large fires on the landscape and temporary loss of grasslands may negatively affect adult survival (Robinson et al. 2018a). Within grasslands, intensive grazing can reduce herbaceous cover and decrease lesser prairie-chicken nest survival rates (Kraft et al. 2021). Reduction in herbaceous cover from a megafire may similarly influence adult and nest survival. In contrast to grazing pressure, which is confined to relatively small pastures, I would expect demographic effects of a megafire to operate on broader landscape scales. Use of annual intensive burning and grazing practices, compared to patch-burn grazing systems, can reduce adult and nest survival in greater prairie-chickens (*Tympanuchus cupido*; McNew et al. 2015, Winder et al. 2018) and may have influenced the estimated 75% decline of this species in the Flint Hills from 2015–2021 (Nasman et al. 2021).

Even though only 25% of a grassland landscape may need to provide cover for nesting habitat, grasslands burned in entirety every year will likely fall substantially below this threshold of cover available for *Tympanuchus* spp. (Gehrt et al. 2020). A megafire would potentially mimic the annual intensive burning and grazing commonly practiced in the Flint Hills of Kansas on an even larger scale, leaving less habitat available at a landscape scale for lesser prairie-chickens. In contrast to adult and nest survival, brooding is one life stage that may benefit from recent fire. Broods generally use areas with more open areas and forbs, allowing for easy movement of chicks and increased forage (e.g., forbs and invertebrates; Hagen and Giesen 2005). Increased chick survival has been linked to increased percentage of forbs on the landscape (Fields et al. 2006). Given these factors, a megafire may increase brood survival by increasing annual forbs and open space on the landscape. Patten et al. (2007) noted reduced greater prairie-chicken brood success further from burns, lending some support to this hypothesis.

I evaluated the influence of a 2017 megafire (Starbuck fire, ~254,000 ha) on lesser prairie-chickens using a before-and-after-impact design. My objective was to assess the effects of the Starbuck fire on key lesser prairie-chicken population growth parameters. Using data collected before (2014–2016) and after (2018–2020) the 2017 Starbuck fire, I compared pre- and post-fire adult, nest, and chick survival rates. I predicted that adult and nest survival would decrease immediately following the fire due to loss of cover and habitat. However, I predicted chick survival would improve post-fire, as the fire could have created areas of quality brood habitat (i.e., increased forbs and open areas). Overall, I predicted that the extreme nature of the megafire would result in decreased lesser prairie-chicken survival and reduction of the lesser prairie-chicken population in the area.

Study Area

In March 2017, the Starbuck fire burned approximately 253,810 ha (627,178 acres) in Kansas and Oklahoma, USA (Kansas Forest Service 2019). This was the largest fire in recorded Kansas history, killing between 5,000–9,000 cattle (*Bos taurus*) and resulting in an estimated \$44 million (USD) in damage (Bickel 2018). The spatial extent of the Starbuck fire was entirely within the Mixed-Grass Prairie Ecoregion, one of four ecoregions inhabited by lesser prairie-chickens (Figure 2.1; Van Pelt et al. 2013). The Mixed-Grass Prairie Ecoregion contained some of the largest tracts of contiguous grassland and available habitat in the entire lesser prairie-chicken range (Spencer et al. 2017, Sullins 2017) and was estimated to support 14% of the entire lesser prairie-chicken population in 2020 (Nasman et al. 2020).

My study area was at the western edge of the mixed-grass prairie, in Clark County, Kansas, USA. The 50-year (1970–2020) average annual precipitation is 58.3 cm, with the majority of rainfall occurring from April–July (NOAA 2020; Figure 2.2). Through the duration of the study (2014–2019), average annual precipitation was 66.7 cm, and was similar before (2014–2015; 69.7 cm) and after (2018–2019; 71.6 cm) the fire (NOAA 2020). The average annual high temperature was 21.2° C and the average annual low was 6.1° C (NOAA 2020). Dominant plant species in the area were sand dropseed (*Sporobolus cryptandrus*), western ragweed (*Ambrosia psilostachya*), little bluestem (*Schizocyrim scoparium*), Russian thistle (*Salsola tragus*), alkali sacaton (*Sporobolus airoides*), sand sagebrush (*Artemisia filifolia*), and blue grama (*Bouteloua gracilis*). Common animal species within the region included coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), thirteen-lined ground-squirrel (*Ictidomys tridecemlineatus*), Ord's kangaroo rat (*Dipodomys ordii*), northern harrier (*Circus hudsonius*), meadowlarks (*Sturnella* spp.), grasshopper sparrow (*Ammodramus savannarum*),

dickcissel (*Spiza americana*), gopher snake (*Pituophis catenifer*), and prairie rattlesnake (*Crotalus viridis*). Soils were composed of fine loamy sands, fine sandy loams, and fine sands (Soil Survey Staff 2020). The majority of the area was used for cattle ranching and livestock production. Other land-use types in the area included row-crop agriculture, energy exploration, and properties enrolled in USDA, Conservation Reserve Program (CRP). The study site was composed of 76.6% grassland, 14.2% cropland, and 5.5% CRP (Robinson et al. 2018a). Prior to the fire, the study was conducted primarily in the southern half of Clark County along the Cimarron river floodplain. This study area was characterized by alkali flats in drainages, sandy rolling hills, and mixed-grass and sand sagebrush prairies. The northern portion of the study site was at higher elevation and consisted of rolling hills made up of silty clay, clay loam, and silt loam (Soil Survey Staff 2020). A low-intensity long-duration rotational grazing system among large pastures was used for both cow/calf and yearling herds, designed to take half of the available forage each growing season. Post-fire, grazing pressure varied following the loss of many cattle and variable restocking as ranches recovered from the fire. There was no use of prescribed fire in the study area.

Methods

I evaluated lesser prairie-chicken demographic response to the megafire hierarchically based on overall counts of males attending leks and nest density surrounding leks. I also estimated vital rates specific to nest, chick, and adult survival during the breeding and nonbreeding season to understand the effects of megafire on key lesser prairie-chicken life stages with differing requirements.

Lek Counts

I conducted counts of leks and male attendance at leks before and after the megafire to examine an index to changes in population size and distribution across my study area. I visited the same lek locations before and after the fire, and each year surveyed for newly developed leks. I only included counts from leks that were surveyed both before and after the fire, as I have no pre-fire information on leks found only post-fire. Lek surveys occurred during peak lekking time from 15 March–1 May in 2014 and 2015 before the fire and in 2018 and 2019 after the fire. I surveyed each lek twice during this period, between sunrise and 1000 during favorable weather conditions (wind <24 km/h) to increase likelihood of detecting all individuals. Prior to cessation of displays at each lek, I observed and flushed birds to determine sex ratio and recorded high counts of male attendance.

Capture

I captured lesser prairie-chickens on leks in the spring of 2014 and 2015 before the fire, and in the spring of 2018 and 2019 after the fire using walk-in funnel traps and tension drop nets (Haukos et al. 1990, Silvy et al. 1990). I sexed captured birds based on pinnae length and tail feather coloration (Copelin 1963). I aged birds as either second-year (SY) or after-second-year (ASY) based on wear and coloration of primary flight feathers (Ammann 1944). Each bird received 3 color bands as well as a unique numbered aluminum band for identification and resighting. All females captured were given either a 22-g Argos Satellite PTT transmitter (SAT-PTT; PTT-100, Microwave Technology, Columbia, MD, USA) or a 15-g bib style VHF transmitter (Advanced Telemetry Systems, Isanti, MN, USA; Robinson et al. 2018b, Kraft et al. 2021). Satellite transmitters were rump mounted using Teflon ribbon (4-mm width) with elastic inserted at the front for flexibility (Bedrosian and Craighead 2010, Dzialak et al. 2011). I marked

all captured females with transmitters because I was primarily interested in female survival and reproductive success as these contribute most to overall demographic rates of populations. All methods were approved by Kansas State University Institutional Animal Care and Use Committee (protocol numbers 3241, 3703, and 4193) and the Kansas Department of Wildlife, Parks, and Tourism (scientific collection permit numbers (SC-079-2014, SC-001-2015, SC-024-2018, and SC-015-2019).

Adult Survival

I located VHF-radiomarked lesser prairie-chickens 2–3 times per week via triangulation using a 3-element handheld Yagi antenna and radio receiver (Advanced Telemetry Systems, Isanti, MN, USA and Communication Specialists, Inc. Orange, CA, USA). A minimum of 3 bearings were taken, within a 20-minute timeframe to minimize location error. I used the software Location of a Signal (Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate UTM coordinates of each bird's location from VHF triangulation data. Satellite transmitters gave locations every 2 hours from 0400–2200 resulting in ~8–10 locations per day. Locations were uploaded to the Argos satellite system every 3 days and downloaded weekly. Each satellite GPS location has an associated potential error of <18 m.

I searched for, and investigated, mortalities as soon as possible following the activation of a mortality switch for VHF transmitters (within 2 days) and activity sensor data for satellite transmitters (within 7 days). Once the kill site or transmitter was located, I classified the cause of death as mammalian predator, avian predator, or unknown. Mammalian predation was identified based on bite marks on transmitters, chewed leg bands, feathers matted with saliva, cached carcasses, and/or nearby tracks/scat. American badger (*Taxidea taxus*), coyote, and swift fox (*Vulpes velox*) were all potential mammalian predators. Piles of plucked feathers, decapitated

carcasses, removal of breast tissue, transmitters without tooth marks, and/or presence of avian scat were classified as avian predation. Potential avian predators in the area were red-tailed hawk (*Buteo jamaicensis*), ferruginous hawk (*B. regalis*), rough-legged hawk (*B. lagopus*), northern harrier (*Circus cyaneus*), prairie falcon (*Falco mexicanus*), and great-horned owl (*Bubo virginianus*). Those with conflicting or lacking evidence and mortalities on properties where I was denied permission were labeled as unknown. I only used these three categories as there was no evidence of other known causes of lesser prairie-chicken mortality (e.g., collision with anthropogenic features, precipitation event, snake predation; Hagen et al. 2007).

I used known-fate Kaplan-Meier models to estimate weekly adult female lesser prairie-chicken survival before and after the fire in program R (R Core Development Team 2021) using the “survival” package (Therneau 2015). I then estimated overall survival separately for the 27-week breeding season (15 Mar–15 Sep) and the 25-week nonbreeding season (16 Sep–14 Mar). I did not consider survival estimates with overlapping 95% confidence intervals as statistically different.

Nest Survival

I closely monitored marked hens for nesting behavior and identified nesting hens based on females remaining at one location for >3 days (Lautenbach et al. 2019). I approached nests wearing rubber boots and moving in a serpentine manner to avoid leaving a scent trail to the nest. Once the nest was located, I recorded UTM coordinates of the exact nest location. I counted eggs to determine clutch size and floated eggs to estimate nest age (McNew et al. 2009, Lautenbach et al. 2019). I monitored nests remotely and returned to estimate nest fate once the hen moved off the nest or was killed. I considered nests successful if ≥ 1 egg hatched, based on pipped eggshells. If eggs were intact, the nest was considered abandoned.

For unsuccessful nests, I examined remaining eggshells and the nest bowl for signs of trampling or specific nest predators. I broadly classified nest predators as mammalian, snake, or unknown based on patterns of eggshells in or nearby the nest, cached eggs, or signs of disturbance to the nest bowl (Sargeant et al. 1998, Pitman et al. 2006). Potential mammalian nest predators included coyote, badger, raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), thirteen-lined ground squirrels, and other rodent and small mammal species. I classified nest bowls that were empty and undisturbed as snake predation. Common species include gopher snakes, prairie rattlesnakes, and eastern yellowbelly racers (*Coluber constrictor flaviventris*). I categorized the predation type on unsuccessful nests with lacking or conflicting evidence as unknown.

I estimated daily nest survival rates using the nest survival procedure in the RMark package in R (Dinsmore et al. 2002, Laake 2013). I used a 38-day exposure period with an average laying period of 10 days and incubation of 28 days to estimate survival over the entire nesting period, then applied the delta method to calculate variance around the estimate (Powell 2007, Lautenbach et al. 2019). I fit candidate models ($n = 16$) for nest survival and ranked them using an Akaike's Information Criterion corrected for small sample size (AICc) using *a priori* selected variables (Burnham and Anderson 2002). Variables tested in the models included nesting attempt (first or re-nest), hen age (second year or after second year), fire status (before or after), burn (nest in a burned or unburned area), year, and additive and interactive combinations of these variables. I included *a posteriori* models of precipitation received during the entire nesting season (April–July) and for the primary months of nesting (May–June) after experiencing severe weather that I suspected to have a major effect on survival (NOAA 2020). Models with $\Delta\text{AICc} \leq 2$ were considered competitive.

To evaluate reproductive influences at the population level, I included nest densities in my assessment (Pidgeon et al. 2006, Sullins et al. 2018*b*). To investigate this, I calculated nest densities within a 5-km radius surrounding each active lek, then averaged among leks. Within these 5-km buffers I derived overall nest densities, nest densities in burned and unburned areas, and nest densities in native working grasslands (grasslands managed for grazing) and CRP fields (Sullins et al. 2018*b*). I used the 2011 National Land Cover Database to identify all areas of grassland, and within those a 2014 CRP layer provided by the USDA Farm Service Agency to identify CRP fields. Burned areas were identified using a map of the Starbuck fire compiled by the Monitoring Trends in Burn Severity program (MTBS 2019). Analyses were conducted using ArcMAP 10.7 (ESRI, Inc., Redlands, CA, USA).

Chick Survival

Once I identified a successful nest, I performed weekly flushes of the female and her brood to estimate survival of chicks. I flushed broods at approximately 7, 14, 21, 28, and 35 days post-hatch, dependent on weather conditions, and availability of a GPS point from satellite transmitters. I performed flushes at or before sunrise when the female was brooding to increase likelihood of detecting her and the chicks. At each brood flush location, I captured and counted the number of chicks accompanying the female and recorded their location. If I did not encounter chicks on two consecutive flush attempts I identified the brood as failed and stopped flushes. After 35 days, chick survival approximates adult survival and I stopped flushing broods (Hagen et al. 2009). I used Lukacs young survival from a marked adult model to estimate weekly chick survival in Program MARK (White and Burnham 1999, Lukacs et al. 2004). I derived survival over the 35-day period as a product of the weekly estimates with error calculated using the delta method assuming independence (Powell 2007).

Results

Lek Counts

The average high count of males on leks surveyed decreased 67% after the wildfire from an average high count of 10.74 ± 6.51 ($\bar{x} \pm SD$) males before to an average of 3.17 ± 5.06 males after at all leks (occupied and unoccupied; Table 2.1). Average male attendance at occupied leks was 6.79 ± 5.54 males post-fire. From the 14 active leks in 2015, six were vacated in 2018, and two more leks disappeared in 2019, representing a 46% decrease in the total number of occupied leks.

Capture

Prior to the fire, I marked 46 females (26 in 2014, 20 in 2015) with VHF ($n = 18$) or GPS transmitters ($n = 28$). Post-fire, I marked 31 females (9 in 2018, 22 in 2019) with transmitters (VHF = 4, GPS = 27). The majority were second-year females both before ($n = 34$) and after ($n = 25$) the fire.

Adult Survival

Breeding season and nonbreeding season survival rates of female lesser prairie-chickens were similar before and after the megafire (Figure 2.3). Breeding season survival for female lesser prairie-chickens pre-fire was 0.63 ± 0.08 ($\bar{x} \pm SE$, 95% CI = 0.49–0.81) and post-fire was 0.64 ± 0.08 (95% CI = 0.50–0.83). The pre-fire nonbreeding season survival for females (0.68 ± 0.09 ; 95% CI = 0.50–0.85) was slightly lower than post-fire survival (0.79 ± 0.09 ; 95% CI = 0.63–0.99), but 95% confidence intervals for these estimates overlapped.

Probable causes of mortality and number of predations in the breeding season were similar before and after the fire, with a nearly equal split between mammalian and avian predators (Table 2.2). In the nonbreeding season, the majority (81%) of pre-fire mortality events

were attributed to mammals; whereas, all post-fire mortality events in the nonbreeding season were attributed to avian predators.

Nest Survival

A total of 52 nests were monitored prior to the fire (27 in 2014, 25 in 2015) with 42 first attempts and 10 renests documented. Pre-fire first nest attempts had a median initiation date of 12 May, ranging from 13 April–10 June. Post-fire, I monitored 35 nests (9 in 2018, 26 in 2019) with 6 renesting attempts. First nests after the fire had a median initiation date of 8 May (range: 15 Apr–31 May). Before the fire, 34.6% of nests were successful, 34.6% were depredated by mammals, 15.4% were depredated by snakes, with the remainder either experiencing hen mortality (3.8%), abandonment (3.8%), or unknown causes (7.7%; Table 2.3). After the fire, only 20% of nests were successful, 17% were depredated by mammals, 42.8% were depredated by snakes, 8.6% had hen mortality, and 11.4% were unknown.

The single variable model of fire status ($\beta_{\text{fire}} = 0.41$, SE = 0.26, 95% CI = -0.09–0.93) was the top ranked model of nest survival ($w_i = 0.14$, Table 2.4). The additive model of nesting attempt ($\beta_{\text{attempt}} = -0.43$, SE = 0.31, 95% CI = -1.04–0.18) and fire status was the second most-supported based on AIC_c ($w_i = 0.12$) and was the only other model that outcompeted the null. Ten of my 16 models were $\Delta\text{AIC}_c \leq 2$ indicating high model uncertainty, and suggesting little influence of tested variables on nest survival. Furthermore beta estimates for top models overlapped zero at the 95% confidence level, indicating these parameters were spurious. Nest survival rates were 0.42 ± 0.06 (95% CI = 0.30–0.55) before the fire and 0.27 ± 0.07 (95% CI = 0.14–0.40) after the fire (Figure 2.4).

Overall nest density of marked females in the 5-km-radius surrounding leks before the fire was $0.74/10 \text{ km}^2 \pm 0.09$ ($\bar{x} \pm \text{SD}$), falling to $0.31/10 \text{ km}^2 \pm 0.06$ after the fire. The majority

(79%) of the landscape in the 5-km buffers surrounding active leks burned in the fire, and 96% of nests before the fire were in the burned area. Following the fire, only 54% of the land in the 5-km buffers surrounding active leks had burned, indicating a shift in lek activity to overall more unburned areas (Chapter 3). In 2018, only 22% of nests were in burned areas, but in 2019 increased to 73% of nests in burned areas. Nest densities in burned areas declined from $0.84/10 \text{ km}^2 \pm 0.10$ before the fire to $0.23/10 \text{ km}^2 \pm 0.08$ after the fire.

After the fire, nest densities were greater in CRP fields ($0.50/10 \text{ km}^2 \pm 0.19$) than in native working grassland ($0.34/10 \text{ km}^2 \pm 0.08$). This is in strong contrast to before the fire, when nest density in native working grassland was $0.85/10 \text{ km}^2 \pm 0.10$ and no nests were in CRP fields. CRP fields made up only a very small portion of the landscape surrounding active leks both before (3.8%) and after (8.5%) the fire, but the percentage more than doubled post-fire. This may partially explain the increased CRP nest density post-fire, and overall points to increased importance of CRP post-fire.

Chick Survival

Before the fire, 14 broods (5 in 2014, 9 in 2015) were monitored for survival, and after the fire 7 (1 in 2018 and 6 in 2019) were monitored. Apparent survival of broods (number of broods with ≥ 1 chick surviving 35 days/total number of broods) was low before the fire (36%) with 5 broods consisting of 25 total chicks surviving to 35 days. After the fire, apparent survival was greater (71%), but broods were smaller, with 5 broods and 14 total chicks surviving to 35 days. Overall, estimated chick survival over 35 days was similar before (0.27 ± 0.03 ; 95% CI = 0.21–0.33) and after (0.32 ± 0.11 ; 95% CI = 0.11–0.53) the fire (Figure 2.5).

Discussion

I found evidence that, while resilient, lesser prairie-chicken populations can be negatively affected by megafire in the short term. Lek counts indicated reduced population numbers in the area, but adult, nest, and chick survival rates did not drastically differ after the fire. The biggest effects appear to be in the form of short-term, widespread, habitat loss as lesser prairie-chickens abandoned historic lek sites and previously inhabited areas. Most of these lek shifts were related to movements to unburned areas (Chapter 3), corroborating the importance of unburned islands as refugia for wildlife following wildfire (Steenvoorden et al. 2019). The large amount of high quality native working grassland in the area and ample presence of CRP likely allowed for the persistence of this population and high survival rates (Ross et al. 2016, Robinson et al. 2018a). Had the fire occurred in an area with more limited habitat, lesser prairie-chickens may have been forced to utilize lesser quality habitat in burned areas or embark on larger dispersal movements outside the study area, potentially leading to lowered survival (Johnson and Gaines 1990, Yoder et al. 2004, Gulick 2019). Unlike species such as sage-grouse, that can experience directly reduced survival as a result of wildfire (Foster et al. 2019, Dudley et al. 2021), it appears lesser prairie-chickens may be resilient to megafire disturbance, likely in part due to their historic interactions with fire.

Adult Survival

Despite the extreme size and severity of the Starbuck fire, I did not detect a significant change in survival of adult lesser prairie-chickens following the fire, in either the breeding or nonbreeding season. In addition, while nonbreeding season survival trended higher, I found no significant difference in survival between seasons. Female lesser prairie-chicken survival during the breeding season is generally lower than during the nonbreeding season and considered more

important for overall population stability, often because female breeding survival is related to nest success (Hagen et al. 2007, 2009; Plumb 2015). Despite superficially lower nest survival post-fire, I did not observe a similar effect on breeding season survival rates. Previous estimates for breeding season survival in Kansas have been variable (0.39–0.76) depending on the year and site (Fields 2004, Hagen et al. 2007, Plumb 2015), but my estimates were within and on the upper end of those bounds, even following megafire. Prior to the fire, my study area had greater breeding season survival relative to five other study sites across Kansas and Colorado during the same time (Plumb 2015), presumably due to the large stretches of grasslands and well-managed grazing within the study area that created quality habitat (Sullins 2017). It is surprising that survival did not decrease post fire as I predicted reduced cover and heterogeneity would negatively affect survival (Plumb 2015, Robinson et al. 2018a, Winder et al. 2018). Indeed, use of these native working grasslands declined post-fire, but was augmented by increased use of CRP fields. This resulted in pre- and post-fire home ranges containing the same amount of grassland overall (Chapter 3), potentially explaining why I saw no change in survival (Robinson et al. 2018a).

Nonbreeding season survival estimates were also not different after the fire, but trended higher post-fire. Estimates for nonbreeding survival are generally greater than the breeding season and can range from 0.66–0.86 in Kansas (Hagen et al. 2007, Robinson et al. 2018b). My post-fire estimate was on the higher edge of this range of estimates, and was linked to the relatively few predations observed in the nonbreeding season post-fire. Predation is the primary cause of mortality for lesser prairie-chickens (Boal 2016); therefore, effects of the fire on predator communities may have top-down effects on lesser prairie-chickens. Interestingly, I saw no mammalian predations in the nonbreeding season post-fire, but were the main source of

predation before the fire, and in other areas of Kansas (Hagen et al. 2007, Plumb 2015, Robinson et al. 2018*b*). This was surprising, as coyote and other mammalian populations generally have a positive response to fire (Ream 1981, Crabtree and Sheldon 1999, Thompson et al. 2008). In the tallgrass prairie, coyotes selected for more recently burned areas from November–March (Ricketts 2016). If they behaved similarly in my study area, this may have lowered lesser prairie-chicken predation risk as lesser prairie-chickens decreased use of burned areas post-fire. As lesser prairie-chickens avoided burned grasslands, they increased use of cropland and CRP post-fire (Chapter 3). In such cropland landscapes, coyotes can experience greater mortality in the fall and winter months (Van Deelen and Gosselink 2006). While overall predation decreased, I did observe increased raptor predation in the nonbreeding season post-fire. Increased raptor presence can occur following fire and is likely due to ease of detecting prey in more open areas (Bock and Bock 1978). In the tallgrass prairie, greater prairie-chickens in recently burned and intensively grazed areas can have increased risk of avian predation (Winder et al. 2018). Shifts in predation patterns highlight the potential widespread effects of megafire and the need for further research on the effects of megafire on grassland wildlife communities.

Nest Survival

Of all demographic rates, nest survival appeared to be most negatively affected by megafire (decreasing 36%), but also displayed no difference in estimated survival rates at the 95% confidence interval. Overall nest densities following the fire were 58% lower than before the fire, which is not surprising given that the fire likely reduced available nest habitat across the landscape. I documented an increased use of CRP for nesting post-fire, likely because many of these fields did not burn as they were surrounded by a matrix of cropland (Donovan et al. 2020) and can provide nest habitat (Sullins et al. 2018*b*). The use of CRP following the fire may be

responsible for the lack of difference in nest survival, and suggests that it may play an important role as a refuge for lesser prairie-chickens following megafire, similar to the increased use of CRP during drought (Sullins et al. 2018*b*). Post-fire nest densities in areas that burned were low compared to pre-fire nest densities in the same areas, likely due to the large loss of nest habitat immediately following the fire (Chapter 4). This is not surprising, as reduced nest habitat and nest success in recently burned areas has been documented for prairie-chickens in other studies (Boyd and Bidwell 2001, Patten et al. 2007, McNew et al. 2015). Within the mixed-grass prairie, lesser prairie-chickens in a patch-burn grazing system selected for nest sites in areas with the longest time since burn (>2 years post-fire; Lautenbach 2017). Given such effects from small scale fire, it may be longer before nest habitat fully recovers following megafire. While my estimates of nest habitat indicated recovery by 2019 (Chapter 4) and nest density increased in burned areas in 2019, continued low survival of nests suggests habitat quality may not be comparable to before the fire (Hagen et al. 2004, Lautenbach et al. 2019). My results highlight the importance of interpreting both habitat use and vital rates when evaluating habitat (Van Horne 1983).

Although precipitation models were not significant, severe weather may have played a role in influencing nest survival, potentially confounding the effects of the fire. The 2019 nesting season experienced record precipitation in my study area, with >27 cm of rain received in May, compared to an average of 8.6 cm (NOAA 2020). May is the month when the majority of females initiate and incubate nests, and when they are particularly vulnerable to disturbance and predation (Pitman et al. 2006). During their study of greater prairie-chickens in Oklahoma over the same time period, Londe et al. (2020) documented several female deaths on nest due to hail, as well as decreased nest success and an overall reproductive failure of their marked population

for 2019 due to extreme precipitation. While I did not document any deaths attributed to hail for nesting hens, it is possible strong rain and hail forced hens to abandon nests that were later depredated.

Following the fire, I documented a 2.8x increase in the number of nest snake depredations. Increased snake depredation could be due to a myriad of factors, including increased snake populations after the fire, a reduction in snake prey populations, or a decrease in other nest predator populations post-fire. Small mammal response to burning varies greatly by species and site (Bock and Bock 1978, Ream 1981, Kaufman et al. 1990, Yarnell et al. 2006), but if small mammal populations were negatively affected by the intensity of the fire, snakes may have increased predation of nests as a result of reduced availability of other prey. Snakes can avoid fire through burrowing, and some studies have found increased population numbers several months post-fire, but overall population response to fire is variable (Russell et al. 1999, Cavitt 2000, Setser and Cavitt 2003, Wilgers and Horne 2006). In the tallgrass prairie, increased risk of snake predation of grassland bird nests was linked to areas with increased vegetative cover (Jackrel and Reinart 2009). Therefore, areas with more vegetation cover and concealment selected by nesting hens may be the same areas selected by snakes in the post-fire landscape.

Chick Survival

I found no difference in estimated chick survival before and after the fire. More broods survived post-fire, but with less chicks overall. I had hypothesized that chick survival may improve following the fire, as the fire had the potential to create bare patches and increase forb cover, leading to quality brood habitat (Boyd and Bidwell 2001). Instead I recorded reduced forb cover and overall less brood habitat (Chapter 4), likely contributing to the lack of change in chick survival and small brood sizes. As lowered brood survival has been linked to increased

precipitation events during the primary brooding period from June–July, I expected lower survival given the high amounts of summer precipitation post-fire (Fields et al. 2006). This was certainly the case in 2018, when the only brood was killed in a hailstorm, but in 2019 the concentration of rain in May (before the brooding period) with average amounts of precipitation the rest of the season may have aided brood survival. When properly timed, large precipitation events have the potential to increase grasshopper and other arthropod populations necessary for chick nutrition (Branson 2008, Sullins et al. 2018a). High chick and juvenile survival is key for lesser prairie-chicken populations, particularly during periods of stress such as drought, and therefore is likely essential for post-fire recovery (Hagen et al 2009, Ross et al. 2018). However, negative effects of the megafire on nesting habitat at a landscape scale likely outweigh any potential for benefits to brood survival, as documented in smaller burns (Boyd and Bidwell 2001, Patten et al. 2007). This was the case in 2018, as the complete reproductive failure of my marked birds highlights that potential for increased brood survival is inconsequential without successful nests.

Conclusions

I documented no major changes in the survival parameters of lesser prairie-chickens, but megafire did reduce the population in this area (as evidenced by lek counts) and lowered reproductive output. While I do not have data for 2017, reproductive output was likely low to non-existent given the fire's occurrence just a month before the breeding season. This, followed by a complete reproductive failure in 2018 for my marked birds, makes it remarkable that lesser prairie-chickens still occur in the area. Population persistence indicates lesser prairie-chickens are resilient to megafire, as they have remained in the area and maintained relatively high adult and juvenile survival rates. Much of this is likely due to the large stretches of grassland in the

area, and quality patches of CRP nearby that provided refuge (Ross et al. 2016, Sullins et al. 2018b, Steenvoorden et al. 2019). Ample precipitation immediately, and in the years following the fire likely helped sustain the population, as vegetation was able to recover relatively quickly following three growing seasons (Chapter 4). Despite this, lowered recruitment and lek counts indicate it will take longer for lesser prairie-chicken populations to recover to pre-fire conditions. Even with the return of habitat, recovery will continue to depend on local weather conditions, grazing regimes, and other factors that contribute to the boom-or-bust population ecology of this species that fluctuates even when not affected by megafire (Hovick et al. 2015, Ross et al. 2018). If drought conditions had occurred following the fire, this already reduced population may not have survived, as lesser prairie-chickens can be negatively affected by drought (Grisham et al. 2013, Ross et al. 2016). Longer term monitoring of populations following megafire are necessary to gauge the total effect and determine how long it may take for a population to recover. If megafires remain infrequent, there may be positive long-term effects for lesser prairie-chickens in the form of increased plant diversity and reduction of invasive woody species (Twidwell et al. 2013, 2016). Given the importance of fire in the Great Plains and the unstable nature of lesser prairie-chicken populations and habitat, working to control the size and frequency of fires will be key in future lesser prairie-chicken management.

Management Implications

While megafires may have negative short-term consequences, fire is still beneficial for lesser prairie-chickens. I suggest implementation of smaller scaled prescribed burning and patch burn grazing to improve grassland health as well as lesser prairie-chicken habitat (Fuhlendorf and Engle 2001, Twidwell et al. 2013, Starns et al. 2020). Fire suppression will no longer be a viable option to prevent megafire, particularly when woody encroachment and climate change

exacerbate the intensity of wildfires in the region. More frequent prescribed burning can help to prevent future megafires by reducing fuel loads, as documented in other fire-prone systems (Stephens et al. 2014). Prescribed burns should be implemented at reasonable spatial (pasture-level) and temporal scales (every 5–10 years) to preserve patches of key nesting habitat, while also creating quality forage and brood habitat. Furthermore, CRP enrollment should be maintained or targeted in areas with existing lesser prairie-chicken populations inhabiting grasslands with higher fire risk. Following fire, careful grazing management should be implemented to ensure healthy grasslands return and lesser prairie-chickens have the best shot at recovery (Starns et al. 2020, Kraft et al. 2021).

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Tables

Table 2.1 High counts of male attendance at leks in Clark County, Kansas, USA, surveyed before (2014–2015) and after (2018–2019) the Starbuck fire in March 2017. Leks were surveyed from 15 March–1 May before 1000 and under favorable weather conditions.

Lek	2014	2015	2018	2019	Within Burned Area
1	3	0	0	0	Yes
2	24	19	0	0	Yes
3	3	4	0	0	Yes
4	7	4	4	2	Yes
5	15	15	0	0	Yes
6	14	10	2	1	Yes
7	3	8	2	0	Yes
8	13	13	0	0	Yes
9	14	9	0	0	Yes
10	15	20	19	12	Yes
11	12	17	9	5	Yes
12	5	11	11	12	No
13	NA ^a	22	4	11	Yes
14	NA ^a	7	1	0	Yes
15	NA ^a	3	0	0	Yes
Total	128	162	52	43	

^aLek not surveyed or found until 2015.

Table 2.2 Cause-specific mortality of adult female lesser prairie-chickens in Clark County, Kansas, USA before (2014–2016) and after (2018–2020) the Starbuck fire in March 2017. Breeding season was defined as 15 March–15 September and nonbreeding season was 16 September–14 March

	Mammal	Avian	Unknown	Total
<i>Breeding Season</i>				
Before	9	7	0	16
After	5	7	2	14
<i>Nonbreeding Season</i>				
Before	9	1	1	11
After	0	4	0	4

Table 2.3 Lesser prairie-chicken nest fates in Clark County, Kansas, USA before (2014–2015) and after (2018–2019) the Starbuck fire in March 2017.

Year	Nest Depredated			Hen Depredated	Abandoned	Unknown	Total
	Successful	Mammal	Snake				
<i>Before</i>							
2014	7	15	3	0	0	2	27
2015	11	3	5	2	2	2	25
Total	18	18	8	2	2	4	52
<i>After</i>							
2018	1	2	4	0	0	2	9
2019	6	4	11	3	0	2	26
Total	7	6	15	3	0	4	35

Table 2.4 *A priori* candidate models used to estimate nest survival rates for lesser prairie-chickens in Clark County, Kansas, USA. Models include variable combinations of fire (before, after), attempt (first, reneat), burn (nest in burned or unburned area), age (second year, after second year), year (2014–2019), total precipitation (Precip) during nesting periods (April–July, May–June) and quadratic relationship with precipitation, and null (intercept only).

Model	K ^a	Δ AICc ^c	AICc ^b	w_i ^d	Deviance ^e
Fire	2	0.00	564.99	0.14	560.98
Fire + Attempt	3	0.21	565.20	0.12	559.19
Null	1	0.48	565.47	0.11	563.47
Attempt	2	0.77	565.76	0.09	561.76
Precip _{April–July} ²	3	1.20	566.19	0.08	560.18
Precip _{May–June} ²	3	1.29	566.28	0.07	560.27
Precip _{April–July}	2	1.68	566.67	0.06	562.66
Precip _{May–June}	2	1.84	566.83	0.05	562.82
Age	2	1.93	566.92	0.05	562.92
Fire + Attempt + Precip _{April–July}	4	1.99	566.98	0.05	558.96
Fire * Attempt	4	2.21	567.20	0.05	559.18
Burn	2	2.37	567.35	0.04	563.35
Year	4	3.20	568.19	0.03	560.17
Fire + Attempt + Precip _{April–July} ²	5	3.70	568.69	0.02	558.66
Fire * Burn	4	3.71	568.70	0.02	560.68
Attempt * Age	4	4.10	569.09	0.02	561.07

^aNumber of parameters.

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

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

^dAkaike weights.

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

Figures

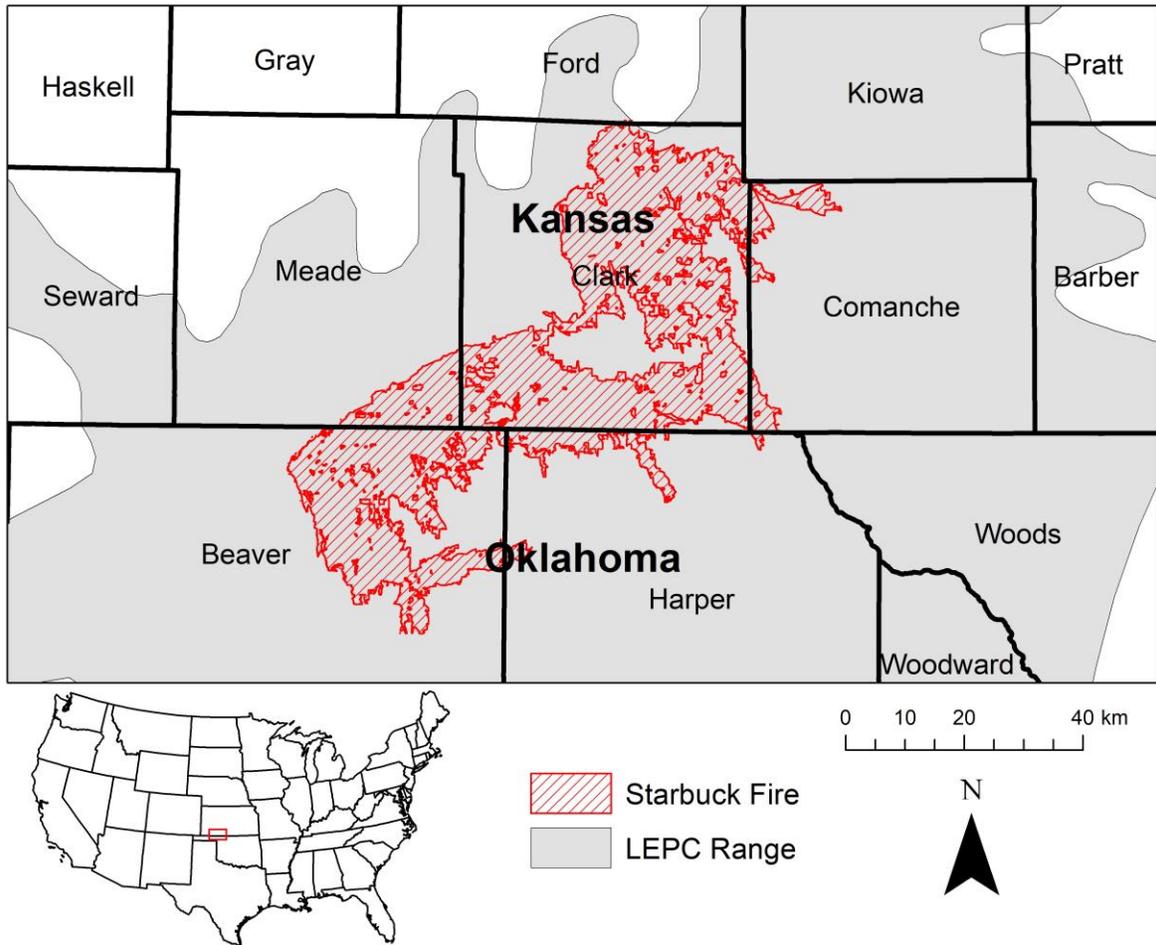


Figure 2.1 Map of the study area in Clark County, Kansas, USA detailing the extent of the 2017 Starbuck fire in Kansas and Oklahoma in the Mixed-Grass Prairie Ecoregion of the lesser prairie-chicken range.

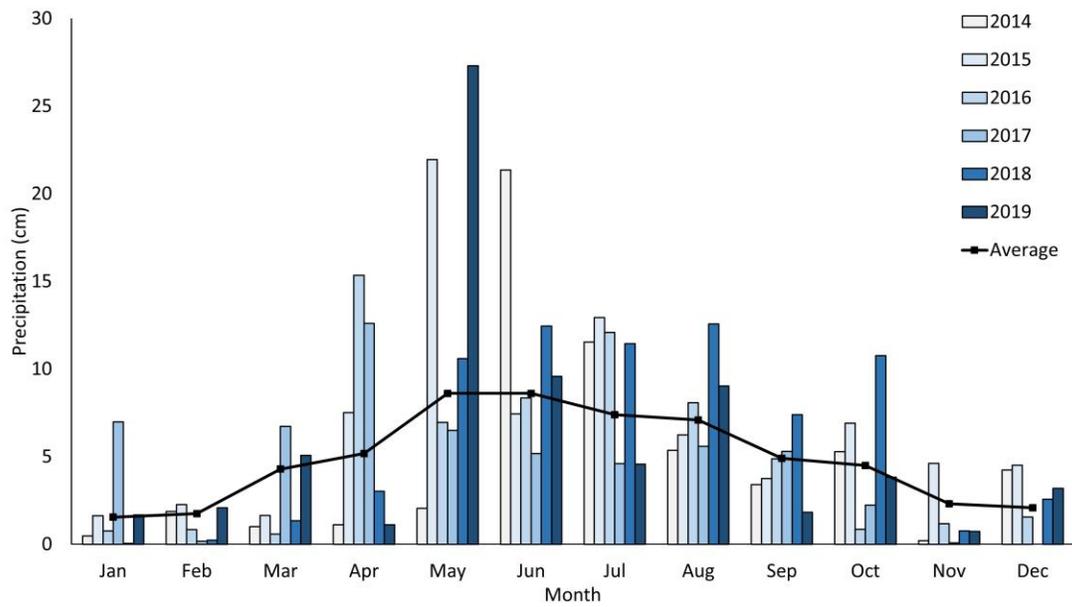


Figure 2.2 Monthly precipitation (cm) totals and 50-year (1970–2020) averages for Clark County, Kansas, USA (NOAA 2020).

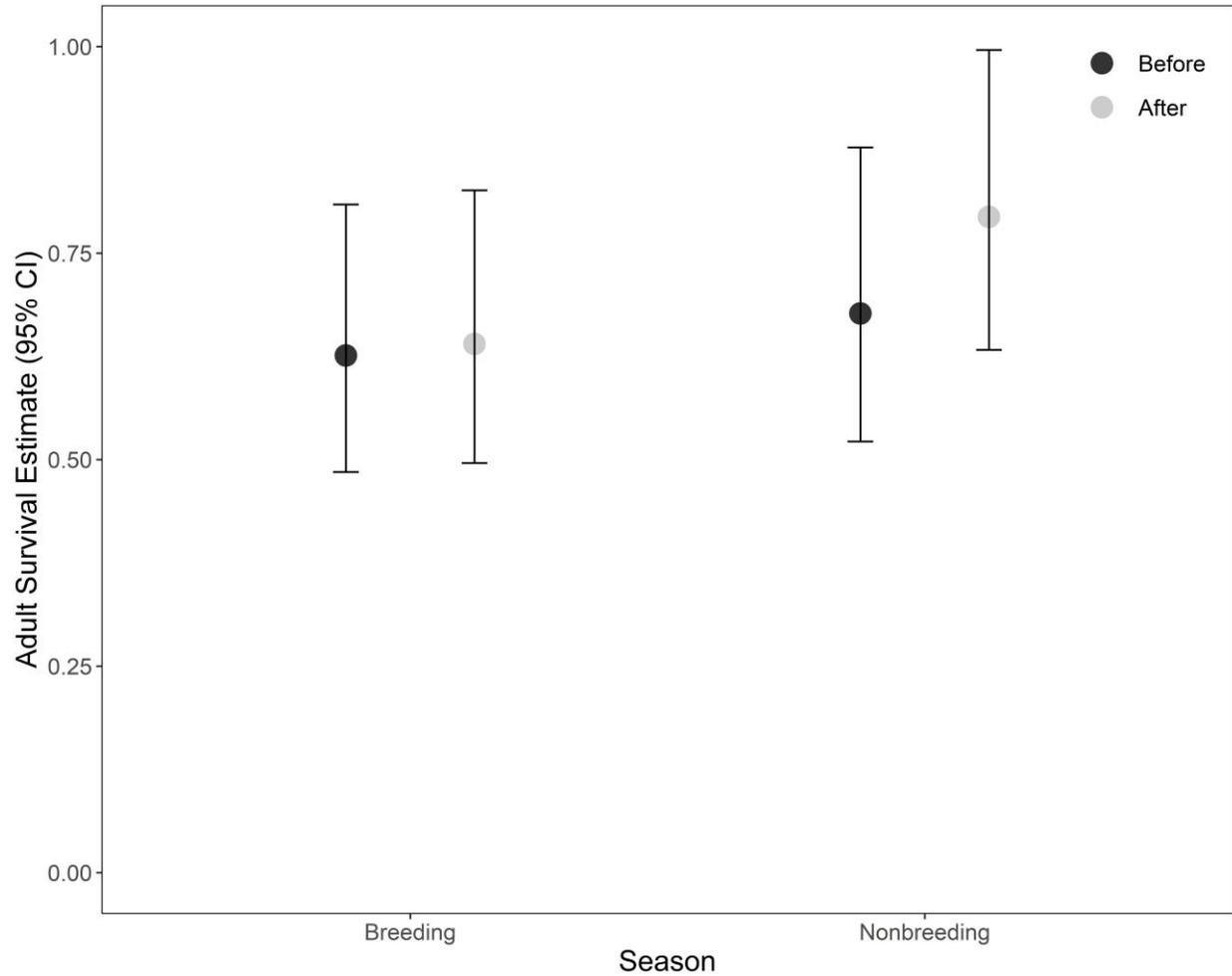


Figure 2.3 Kaplan-Meier survival estimates and 95% confidence intervals for female adult lesser prairie-chickens in the breeding (15 Mar–15 Sep) and nonbreeding (16 Sep–14 Mar) seasons in Clark County, Kansas, USA before (2014–2016) and after (2018–2020) the 2017 Starbuck fire.

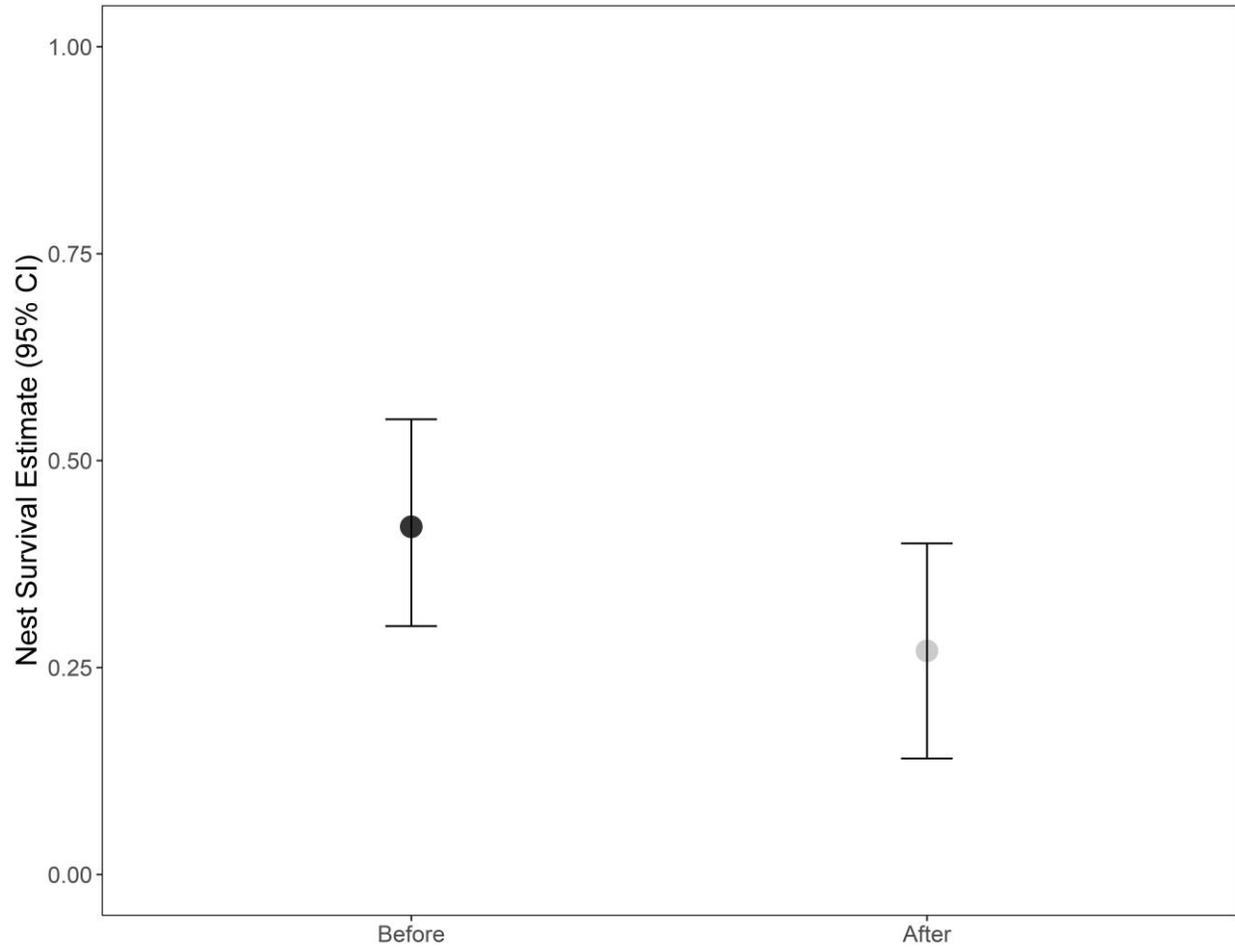


Figure 2.4 Nest survival estimates and 95% confidence intervals for a 38-day exposure of lesser prairie-chickens in Clark County, Kansas, USA before (2014–2015) and after (2018–2019) the 2017 Starbuck fire.

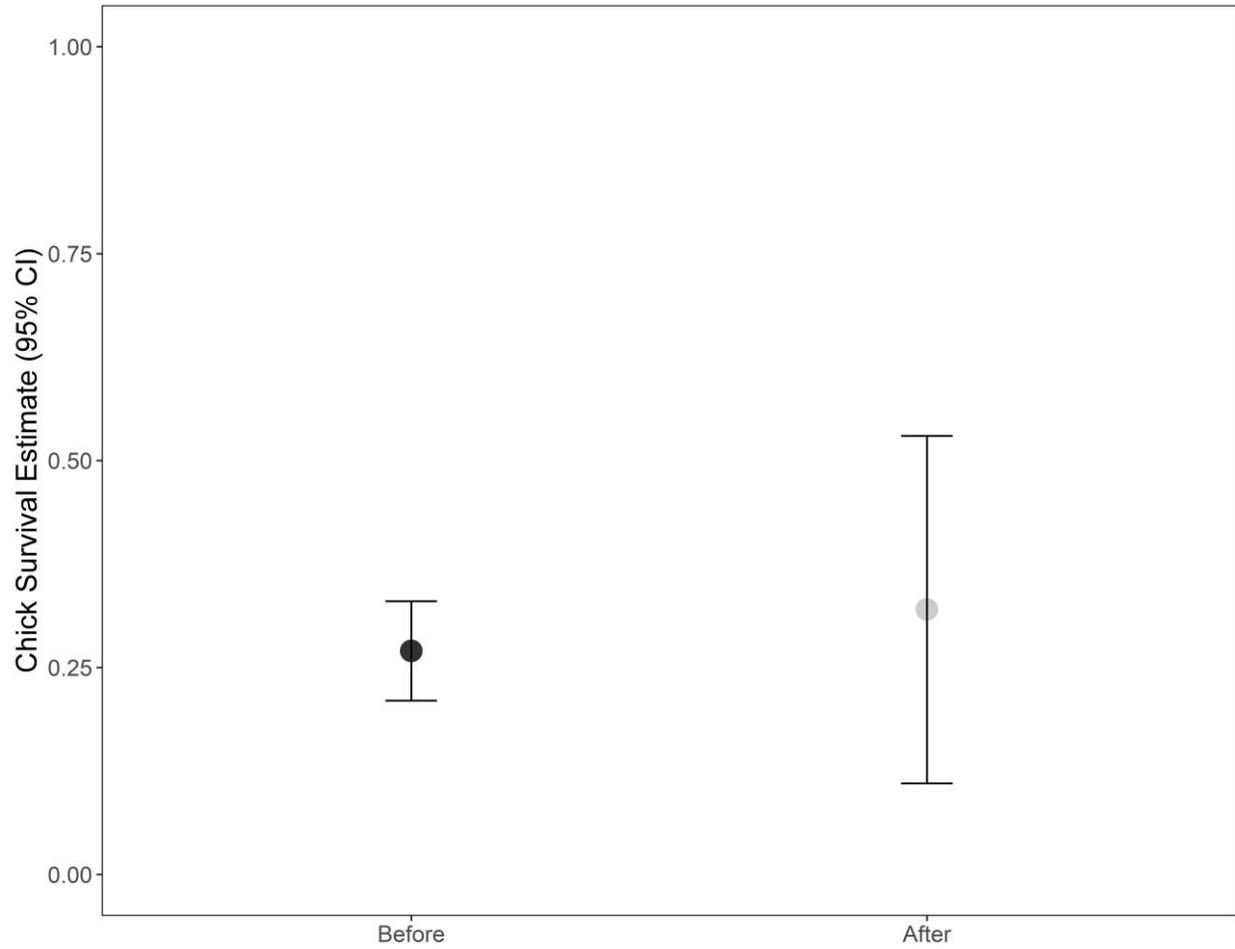


Figure 2.5 Chick survival estimates and 95% confidence intervals over 35 days of lesser prairie-chicken chicks in Clark County, Kansas, USA before (2014–2015) and after (2018–2019) the 2017 Starbuck fire.

Chapter 3 - Landscape influences lesser prairie-chicken space use, resource selection, and lek attendance following megafire

Introduction

Space use and habitat selection by animals is a hierarchical process, driven by individuals' needs and behavior, and partially bounded by regional and landscape scale disturbances of past and present that shape range-wide population distribution (Johnson 1980, Jones 2001, Boyce et al. 2016). Population-level responses to ecological disturbance, such as wildfire, emerges from individuals selecting for a variety of competing needs (food, reproduction, predator avoidance, etc.) in context of landscape pattern and therefore should be evaluated at multiple scales before and after disturbance (Fretwell and Lucas 1970, Guthery 1997, Brawn et al. 2001, Hodson et al. 2010, Rodewald 2015). Evaluating habitat selection at multiple scales is especially important for species of conservation concern to ensure detection of population response, to inform targeted conservation efforts, and because populations occurring in highly fragmented habitat may be less predictable (Morris 1992, Caughley 1994, Fuhlendorf et al. 2002, Duchardt et al. 2020). Recent megafire events within the Great Plains present an opportunity to evaluate the effect of a substantial natural disturbance on an at-risk prairie grouse species living in fragmented grasslands where ecological drivers have been altered (Brawn et al. 2001, Fuhlendorf et al. 2017, Driscoll et al. 2021).

Loss and degradation of grasslands in the Great Plains through agriculture conversion, anthropogenic development, and woody encroachment have reduced lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations and their available habitat since the 1980s (Fuhlendorf and Engle 2001, Van Pelt et al. 2013, Haukos and Zaveleta 2016, Lautenbach et al. 2017). Lesser prairie-chickens are estimated to occupy only 14% of their estimated historic range and occupy

remnant grasslands where ecological drivers, including periodic fire events, have been altered (Hagen and Giesen 2005, Garton et al. 2016). Fire, and its interactions with grazing, maintained grasslands heterogeneous in structure and composition that provided habitat for different lesser prairie-chicken life stages (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2017). Such ecological drivers maintained areas of thicker grass and vegetation for nesting and adult cover adjacent to more open areas for lekking and brood rearing (Hagen and Giesen 2005, Haukos and Zaveleta 2016).

Within the occupied distribution of lesser prairie-chickens, intensive and very large fire (>40,000 ha) events known as “megafires” are increasing and effects on habitat use by lesser prairie-chicken are unknown (Williams et al. 2011, Stephens et al. 2014, Lindley et al. 2019). Fire suppression over the last century has led to a buildup of fuels, woody encroachment, and other vegetation changes that may promote megafire in conjunction with climate change (Frost 1998; Fuhlendorf and Engle 2001; Brockway et al. 2002; Briggs et al. 2005; Engle et al. 2008; Donovan et al. 2017, 2020; Lindley et al. 2019). Although fire historically played a role in maintaining grassland habitat, the extent to which lesser prairie-chickens evolved with such large-scale fire events remains unclear. We know that Native Americans used fire extensively in portions of the Great Plains and some historical fires are thought to have been quite massive, spanning vast areas of prairie (Pyne 1982, 2012; Axelrod 1985; Roos et al. 2018). In other areas extensive bison grazing and numerous prairie dog towns may have limited the scale and frequency of historical burns (both natural and human caused; Seton 1929, Hart 2001). While the exact size and frequency of historic fire regimes are unknown, megafires are a recent phenomenon in contemporary fragmented and altered grasslands, and their effects on wildlife species are unknown.

To understand the influence of a large disturbance such as a megafire on lesser prairie-chickens, an evaluation of habitat selection at multiple scales is needed. Habitat selection must be evaluated at multiple scales to ensure detection of any change in habitat use and understand how individual life-stage specific habitat use emerges as a population-level response (Whitham 1980, Rodewald 2015). For example, the addition of wind turbines can have limited effects on within-home range habitat selection for greater prairie-chickens (*Tympanuchus cupido*); however, home range size doubled and lek occupancy decreased in areas in closer proximity to wind turbines (Winder et al. 2014). Home range and resource selection analyses are beneficial for understanding how monitored individuals select and use the landscape over short time periods; however, they are not designed to account for previous local extinction and colonization events that also affect habitat use at broader scales of time and space. Analysis of lek attendance can illicit broader population trends and information about larger landscapes that are not apparent at smaller scale analysis (Hovick et al. 2015*a, b*; Aulicky 2020; Gehrt et al. 2020). Therefore, an evaluation of prairie-grouse habitat use should consider an evaluation of the full hierarchy of habitat selection including home-range space use, individual habitat selection, and lek attendance to evaluate the response to a disturbance such as a megafire.

At the individual level, home range size and space use of lesser prairie-chickens may differ following a megafire due to limited availability of cover in burned grasslands. Following drought disturbance, lesser prairie-chicken home ranges can increase in area due to limited availability of food and cover (Merchant 1982, Hagen and Giesen 2005). In the tallgrass prairie, home ranges of nonbreeding female greater prairie-chickens were larger in more frequently burned areas (Winder et al. 2017). Similarly, I expect lesser prairie-chicken home range area to increase following megafire. Space use following megafire will also depend on landscape

composition of the area, as lesser prairie-chickens need an abundance of grassland within annual home ranges to maximize survival (~57% grassland; Robinson et al. 2018a). If lesser prairie-chickens are forced to occupy areas of reduced grassland and increased cropland post-fire, it may result in decreased fitness. In these scenarios, patches of habitat such as U.S. Department of Agriculture Conservation Reserve Program (CRP) fields may become important as these fields of planted grasses are often near cropland that can function as a fire barrier and reduce likelihood of ignition in CRP fields (Donovan et al. 2020). The CRP has been key in maintaining grassland within the lesser prairie-chicken distribution, can provide refugia during drought, and may be equally important in providing quality habitat following megafire (Spencer et al. 2017, Sullins et al. 2018, Harryman et al. 2019).

Along with alterations in space use, habitat selection by individual lesser prairie-chickens may additionally change in response to megafire. Accounting for individual selection when evaluating habitat selection is increasingly important, as individuals within populations may react differently to features and can provide a more mechanistic understanding from which broader scale patterns emerge (Hebblewhite and Merrill 2008, Duchesne et al. 2010, McLoughlin et al. 2010, Milligan et al. 2020). High-resolution GPS location data and new modeling techniques allow for a more accurate assessment of individual habitat selection at multiple scales (Avgar et al. 2016, Muff et al. 2020). Studies documenting individual response to megafire include an examination of within home range selection of spotted owls (*Strix occidentalis*) in a post-megafire landscape. Resource selection functions suggested that spotted owls avoid high severity areas and selected for low severity patches, but only as the amount of area burned at high severity increased within home ranges (Kramer et al. 2021). In grassland systems, female prairie-chickens avoid recently burned areas following low severity prescribed

fire (especially for nesting), but following much larger fires may be forced to select for low severity burned areas (Lautenbach 2017, Winder et al. 2017). Although megafire could reduce nesting habitat for lesser prairie-chickens, it could open areas unusable to lesser prairie-chickens by reducing woody cover, where an estimated 21% of their habitat in the mixed-grass prairie is lost to woody encroachment (Lautenbach et al. 2017, Sullins et al. 2019). Tree removal can have immediate positive response by other grouse species, such greater sage-grouse (*Centrocercus urophasianus*), that shift selection following removal of juniper to use treated areas, with increasing use as time since treatment increased (Severson et al. 2017, Olsen 2019). Such results suggest lesser prairie-chickens may be able to recolonize formerly wooded areas following megafire, if trees are removed and nearby habitat recovers from the fire.

Enough space and life-stage specific habitat for multiple individuals must be available following a megafire disturbance for a lek to persist. Lesser prairie-chickens leks emerge based on the properties of their surrounding landscape (Gehrt et al. 2020). Although fire can create patches of shorter vegetation used by lekking males (Cannon and Knopf 1979, Hagen and Giesen 2005, Jones 2009), leks are more than a patch of short grass (Gehrt et al. 2020). Most females nest and raise young in grassland within 5 km of a lek, and adult lesser prairie-chickens stay nearby leks throughout the nonbreeding season (Taylor and Guthery 1980, Giesen 1994, Pitman et al. 2006, Bell et al. 2010, Winder et al. 2015). The landscape surrounding leks must provide heterogeneous habitat to fulfill needs of all life stages, and lek attendance can increase in grassland-dominated landscapes with optimal visual obstruction for nests and adults (Niemuth 2000, Woodward et al. 2001, Aulicky 2020, Gehrt et al. 2020). In tallgrass prairie managed with patch burn grazing, greater prairie-chickens leks were dynamic and shifted in response to disturbance, with leks in burned areas placed closer to unburned habitat (Hovick et al. 2015a).

Therefore, megafires may result in abandonment of historic leks when surrounded by burned habitat, with use shifting to landscapes with more unburned habitat. As lesser prairie-chickens are already restricted to isolated areas of remaining grassland, quality unburned habitat following megafire may be limited, potentially leading to local extinction (Fuhlendorf et al. 2002; Winder et al. 2014, 2017; Ross et al. 2016).

A synthesis of habitat selection from the individual to population will be most likely to shed light on lesser prairie-chicken response to a megafire. Therefore, the objective of my study was to explore differences in lesser prairie-chicken space use, resource selection, and lek attendance before (2014–2016) and after (2018–2020) a 2017 megafire (Starbuck fire; ~254,000 ha) in the mixed-grass prairie of Kansas. As potentially limited habitat and resources post-fire may necessitate use of larger areas to access quality habitat, I predicted home range area would be larger post-fire. I predicted lesser prairie-chickens would avoid burned areas and increase use of CRP fields as many of these did not burn in the fire and provide quality lesser prairie-chicken habitat. I predicted lesser prairie-chickens would move closer to areas of formerly dense woody cover, as the fire reduced woody encroachment and potentially opened areas of previously unavailable habitat. Finally, I predicted that lesser prairie-chicken lek attendance post-fire would be largest in areas with greater amounts of nesting habitat in the surrounding area. My purpose was to evaluate the landscape-scale effects of this fire on lesser prairie-chickens to limit potential negative effects of future megafires on other lesser prairie-chicken populations.

Study Area

In March 2017, the Starbuck fire burned approximately 253,810 ha (627,178 acres) in Kansas and Oklahoma, USA (Kansas Forest Service 2019). This was the largest recorded fire in Kansas history, killing between 5,000–9,000 cattle and resulting in an estimated \$44 million

(USD) in damage (Bickel 2018). The spatial extent of the Starbuck fire was entirely within the Mixed-Grass Prairie Ecoregion, one of four ecoregions inhabited by lesser prairie-chickens (Van Pelt et al. 2013). The Mixed-Grass Prairie Ecoregion contains some of the largest tracts of contiguous grassland and available habitat in the entire lesser prairie-chicken range (Spencer et al. 2017, Sullins et al. 2019) and was estimated to support 14% of the entire lesser prairie-chicken population in 2020 (Nasman et al. 2020).

My study area was at the western edge of the Mixed-Grass Prairie, in Clark County, Kansas (Figure 3.1). The 50-year (1970–2020) average annual precipitation is 58.3 cm, with the majority of rainfall occurring from April–July (NOAA 2020). The average annual high temperature is 21.2° C and the average annual low is 6.1° C (NOAA 2020). The dominant plant species in the area were sand dropseed (*Sporobolus cryptandrus*), western ragweed (*Ambrosia psilostachya*), little bluestem (*Schizocyrim scoparium*), Russian thistle (*Salsola tragus*), alkali sacaton (*Sporobolus airoides*), sand sagebrush (*Artemisia filifolia*), and blue grama (*Bouteloua gracilis*). Common animal species within the region included coyote (*Canis latrans*), white-tailed deer (*Odocoileus virginianus*), thirteen-lined ground-squirrel (*Ictidomys tridecemlineatus*), Ord’s kangaroo rat (*Dipodomys ordii*), northern harrier (*Circus hudsonius*), meadowlarks (*Sturnella sp.*), grasshopper sparrow (*Ammodramus savannarum*), dickcissel (*Spiza americana*), gopher snake (*Pituophis catenifer*), and prairie rattlesnake (*Crotalus viridis*). The majority of the area was used for cattle ranching and livestock production; other major uses in the area included row crop agriculture, energy exploration, and properties enrolled in CRP. The study site was composed of 76.6% grassland, 14.2% cropland, and 5.5% CRP (Robinson et al. 2018a). Research before the fire was primarily focused on a ranch within the southern half of the study area along the Cimarron river floodplain. Here, the soils were composed of fine loamy sands,

fine sandy loams, and fine sands (Soil Survey Staff 2020). This area was characterized by alkali flats in drainages, sandy rolling hills, and mixed-grass and sand sagebrush prairies. The northern portion of the study site was at higher elevation and consisted of rolling hills made up of silty clay, clay loam, and silt loam (Soil Survey Staff 2020). Before the fire, a low-intensity long-duration rotational grazing system among large pastures was used for both cow/calf and yearling herds, set to take half of the available forage each growing season. Post-fire, grazing pressure varied following the loss of many cattle and variable restocking as ranches recovered from the fire. There was no use of prescribed fire in the study area.

Methods

Capture and Tracking

I captured lesser prairie-chickens on leks in the spring of 2014 and 2015 before the fire, and spring of 2018 and 2019 after the fire using walk-in funnel traps and tension drop nets (Haukos et al. 1990, Silvy et al. 1990). Once caught, I sexed birds based on pinnae length and tail feather coloration (Copelin 1963). I aged birds as either second-year (SY) or after-second-year (ASY) based on wear and coloration of primary flight feathers (Ammann 1944). Each bird received 3 color bands as well as a unique numbered aluminum band. All females captured were marked with a 22-g Argos Satellite PTT transmitter (SAT-PTT; PTT-100, Microwave Technology, Columbia, MD, USA). Satellite transmitters were rump mounted using tubular Teflon ribbon (4-mm width) with elastic inserted at the front for flexibility (Bedrosian and Craighead 2010, Dzialak et al. 2011). I marked all captured females with transmitters because I was primarily interested in habitat selection by females, which independently care for young in this species. I marked males with transmitters when female attendance at leks was low making it not possible to deploy all transmitters on females. Satellite transmitters gave locations every 2

hours from 0400–2200 resulting in ~8–10 locations per day. Locations were uploaded to the Argos satellite system every 3 days and downloaded weekly. Each satellite GPS location has an associated potential error of 18 m or less.

All methods were approved by Kansas State University Institutional Animal Care and Use Committee (protocol numbers 3241, 3703, and 4193) and the Kansas Department of Wildlife, Parks, and Tourism (scientific collection permit numbers SC-079-2014, SC-001-2015, SC-024-2018, and SC-015-2019).

Home Range Estimation

To first screen for changes in space use before and after the fire, I estimated breeding (15 Mar–15 Sep) and nonbreeding (16 Sep–14 Mar) season home ranges for male and female lesser prairie-chickens marked with GPS transmitters before (2014–2016) and after (2018–2020) the Starbuck fire. I used Brownian Bridge Movement Models to estimate 95% isopleth home ranges using the “adehabitatHR” package in R (Calenge 2006, R Core Development Team 2021). Home ranges were estimated for birds with ≥ 100 locations in that season.

To assess differences in home range area, I first log-transformed home range area to normalize residuals, then used a one way analysis of variance (ANOVA, $\alpha = 0.05$) to assess differences between male and female lesser prairie-chickens. If there was a difference ($P < 0.05$), sexes were analyzed separately, otherwise I pooled sexes. I used a post-hoc Tukey’s Honest Significant Difference (HSD) test following a significant ($P < 0.05$) ANOVA to test for differences in home range area among multiple groups, including combinations of breeding season (breeding and nonbreeding) and fire status (before and after). Within home ranges, I calculated the proportion of different land cover types (native working grassland, CRP, cropland) and percent burned area. I used the 2011 National Land Cover Database land cover classification

map to identify areas of grassland, cropland, and other (forest, urban, wetland, etc.). Within the grassland, I identified CRP fields using a 2014 CRP layer provided by the United States Department of Agriculture Farm Service Agency. Burned area was calculated using a map of the Starbuck fire compiled by the Monitoring Trends in Burn Severity program (MTBS 2019). I then used Kruskal-Wallis tests to compare proportion of each land cover type between seasons and before and after the fire. If a main effect was identified ($P < 0.05$), I used Mann-Whitney U tests to identify differences in land cover use before and after the fire and between seasons. I used nonparametric tests for land cover analysis of home ranges as data were not normally distributed.

Step Selection

To understand selection decisions by lesser prairie-chickens as they moved through the landscape before and after the megafire, I used a step-selection analysis to estimate individual level (Design III, Manly et al. 2002) lesser prairie-chicken resource selection. I used GPS locations from two years before the fire (15 March 2014–15 March 2016), and two years after (15 March 2018–15 March 2020). I removed locations of nesting hens when incubating as they remained fixed in a specific location, leading to potential bias. Step-selection analysis categorizes locations as bursts, representing periods of continuous movement. Bursts were periods of continuous movement that consisted of steps with two hours between locations, as this was the finest temporal frequency of my data. Steps incorporated the starting and ending location, step length, and turning angle; which were then used to create 10 random available points associated with each true step. I used package “amt” in program R for step selection (Avgar et al. 2016, Signer et al. 2019, R Core Development Team 2021). At the endpoint of each true and random step, I extracted landscape covariates for analysis.

First, I extracted values of land cover type as described above (native working grassland, CRP, cropland, other) and used a binomial response (0, 1) to examine selection of CRP and cropland. To examine use of native working grassland, I used focal statistics to calculate the percentage of native working grassland within a 5-km radius around each raster cell from the 2011 NLCD land cover map, as the amount of grassland at this scale has been shown to be most important for lesser prairie-chickens (Sullins et al. 2019). To investigate selection for wooded areas, I used a map of conifer and mesquite tree canopy cover generated by Falkowski et al. (2017), which provided percent tree canopy estimates using 30 x 30-m pixels. I then used focal statistics to calculate average tree canopy within a 226-m radius (16 ha) of each cell in my study area, the scale most important for lesser prairie-chicken nest selection in relation to tree cover (Lautenbach et al. 2017). As I was interested in determining if lesser prairie-chickens occupied formerly wooded areas, I used the same map of tree cover before and after the fire. To examine how the extent and severity of the Starbuck fire may have affected lesser prairie chicken selection, I extracted difference in normalized burn ratio (dNBR) values of burn severity for the Starbuck fire from the Monitoring Trends in Burn Severity project (MTBS 2019). Finally, I used a 30-m resolution digital elevation model (DEM) obtained from the Kansas GIS Data Access and Support Center (<http://www.kansasgis.org/>) to explore potential relationships with elevation. All geospatial analyses were conducted in ArcMAP version 10.7 (ESRI, Inc., Redlands, CA, USA).

After extracting landscape covariates to my steps, I created models including all landscape covariates for lesser prairie-chicken selection before and after the fire. I also included step length to reduce bias in parameter estimates (Forester et al. 2009, Muff et al. 2020). I used mixed conditional Poisson regression using the “glmmTMB” package in R following Muff et al. (2020; R Core Development Team 2021). This included use of a large fixed variance to estimate

random intercepts for each stratum (collection of used and available points per step) as well as random slopes for each individual for every parameter estimated except step length. This was done to account for unbalanced sampling among individuals and spatial autocorrelation between points (Hebblewhite and Merrill 2008, Duchesne et al. 2010). I z -scaled all continuous variables to obtain standardized coefficients of selection and tested to ensure no variables used in the same model were highly correlated ($r > |0.60|$; Milligan et al. 2020, Kramer et al. 2021). Coefficients that did not overlap zero with 95% confidence intervals were considered to be informative.

Landscape Scale Predictors of Lek Attendance

I evaluated patterns of male lek attendance to gain an understanding of population level changes in resource availability before and after the fire that may go undetected in more fine-scale home range and step-selection analyses. To understand what influenced lek attendance and occupancy following the fire, I examined characteristics of the landscape surrounding leks within a 5-km buffer in relation to male abundance on leks. I investigated three different categories of covariates that may influence lek attendance: landscape composition, reproductive habitat, and fire effects. My response variable was the high count of male abundance at each lek surveyed before and after the fire (Chapter 2). Leks that were vacated before or after the fire were included with a male count of zero.

To test the influence of landscape composition, I calculated the percent composition of the same land cover types examined in home ranges and the step-selection function (native working grassland, CRP, cropland, and other) within 5 km of each lek. Reproductive habitat and female attendance are also thought to drive lek formation and attendance (Gehrt et al. 2020, Aulicky 2020), so I estimated abundance of reproductive habitat and the number of female locations within 5 km of each lek. Nesting and brood habitat abundance were estimated as the

proportion of random vegetation points within 5 km of each lek that met requirements of nesting and brooding habitat (Chapter 4). Because lesser prairie-chickens primarily nest in grassland, I also evaluated an adjusted amount of reproductive habitat based on the amount of total grassland (native working grassland + CRP) within 5 km. I calculated the proportion of female GPS locations occurring within 5 km of the lek during peak lek time (15 Mar–31 May) to test if female presence near leks influenced male attendance. To evaluate the effects of the fire, I calculated the proportion of area burned and an average measure of burn severity within 5 km of each lek. I used spatially explicit burn severity estimates (difference in normalized burn ratio [dNBR]) from the Monitoring Trends in Burn Severity project (MTBS 2019).

From these three categories, I developed three different model suites (landscape composition, reproductive habitat, fire effects) and fit Poisson regressions in an information theoretic framework to test for relationships with lek attendance using generalized linear models in Program R. Each set included single and quadratic variables, with and without an interaction term for “before/after” the fire, and a null model. Within the fire effects suite, I also included a year model. I ranked models using Akaike’s Information Criterion adjusted for small sample size (AICc), and combined competitive models from each set (model weight ≥ 0.10) into a final model set, consisting of models with all combinations of uncorrelated ($r \geq |0.60|$) variables (Burnham and Anderson 2002, Baxter et al. 2017). Models with $\Delta\text{AICc} \leq 2$ were considered competitive; variables with slope coefficients that overlapped zero at the 95% confidence interval were considered spurious.

Results

Capture and Tracking

Prior to the fire, I marked 32 adult lesser prairie-chickens with GPS transmitters, 5 of which were male. Post-fire, I marked 43 individuals with GPS transmitters. More males (17) were given transmitters post-fire, with the majority (13) in 2018. Two females pre-fire and two males post-fire each lived less than two weeks following marking, generating less than 100 locations and were not included in the analysis. This resulted in 30 and 41 individuals used for analysis before and after the fire, respectively. There were 48,434 locations before the fire, with an average of $1,615 \pm 1,228$ ($\bar{x} \pm \text{SD}$) locations per individual. After the fire, there were 63,425 total locations with an average of $1,547 \pm 1,259$ locations per individual.

Home Range Estimation

I estimated 57 home ranges from 30 individuals before the fire and 65 home ranges from 40 individuals after the fire. Average home range size over both seasons for males (606 ± 142 ha; $\bar{x} \pm \text{SE}$) was not different from females (822 ± 87 ha; $F_{1,120} = 3.55$, $P = 0.06$), so I pooled sexes for further analysis. There was a significant interaction for fire status and season ($F_{3,118} = 4.71$, $P = 0.03$), so I proceeded with Tukey's HSD to identify differences in home range area between breeding seasons and before and after the fire. Home range area did not differ before and after the fire for either the breeding or nonbreeding season (Table 3.1). However, relative home range area when comparing breeding and nonbreeding home ranges changed after the fire. Before the fire, breeding season home ranges were 69% smaller than nonbreeding home ranges. After the fire, breeding and nonbreeding season home range size did not differ.

Land cover composition within home ranges differed by fire status and season. I identified a difference in percent cover of cropland in home ranges between fire status and

season (K-W = 17.07, $P < 0.001$; Table 3.2), with more cropland used in the breeding season after the fire than before. Greatest percent of cropland occurred in the nonbreeding season, although there was no difference in nonbreeding percent of cropland before and after the fire. Percent cover of CRP in home ranges increased 5 times after the fire compared to before, but did not differ between breeding and nonbreeding seasons (K-W = 23.16, $P < 0.001$). Pre-fire, breeding season home ranges had greater cover of native working grassland than nonbreeding home ranges and breeding season home ranges post-fire (K-W = 18.41, $P < 0.001$). There was no difference in percent cover of native working grassland between seasons post-fire. The percent area burned within home ranges followed a similar trend as percent cover of native working grassland and was greatest in the breeding season pre-fire, and was overall greater pre-fire (K-W = 16.95, $P < 0.001$).

Step Selection

Before the fire, lesser prairie-chickens avoided areas with woody cover within 16 ha ($\beta = -0.28$, 95% CI = -0.36 – -0.20; Figure 3.2), but did not select habitat based on any other variables examined. In areas with >40% tree canopy cover, lesser prairie-chicken probability of use decreased to almost zero (Figure 3.4). After the fire, lesser prairie-chickens continued to avoid areas with greater tree canopy cover ($\beta = -0.69$, 95% CI = -0.91 – -0.48), but an even greater rate than before, with zero probability of use in areas with >20% tree canopy cover (Figure 3.4). Post-fire, lesser prairie-chickens selected for unburned areas, displaying a negative relationship with dNBR burn severity ($\beta = -0.11$, 95% CI = -0.22 – -0.01, Figure 3.5) and strongly selected for areas of higher elevation ($\beta = 3.56$, 95% CI = 2.62–4.50; Figures 3.3, 3.6). Similar to before the fire, lesser prairie-chickens did not select for CRP or cropland cover types, or percent grassland within 5 km.

Landscape Scale Predictors of Lek Attendance

Average high counts of males at monitored leks before the fire was 10.5 ± 6.5 ($\bar{x} \pm SD$) males, falling to an average count of 3.8 ± 5.0 males at all monitored leks (both occupied and unoccupied) after the fire. Occupied leks post-fire had an average count of 6.8 ± 4.9 males.

In my landscape composition suite, the best supported model was an interactive model of percent cropland and fire status, which carried 59% of AICc model weight and no other models were competitive ($\Delta AICc \leq 2$, Table 3.3). This model indicated a negative association of lek attendance with proportion of cropland before the fire and a positive relationship with cropland post-fire (Table 3.4; Figure 3.7). Among reproductive models, the quadratic relationship of brood habitat with a fire interaction was best supported and carried 99% of the weight; however, beta coefficients overlapped zero (Table 3.4). Within the fire effects model group, the top-ranked model was a quadratic relationship of dNBR with a fire interaction; beta coefficients were significant at 95% CI (Table 3.4; Figure 3.8). Two other models had weight ≥ 0.10 , the interactive model of dNBR and fire, and the interactive model of fire and percent burned.

My combined model set had 19 models with a before/after fire variable in each one except the null. Percent cover of grass and cropland, percent burned, and dNBR were all correlated ($r \geq 0.84$), unsurprising as the landscape was dominated by grass cover, which largely burned in the fire. Areas that were not grass are primarily cropland, which did not burn in the fire. Therefore, land cover composition and fire effects were not included in the same model. Two models had $\Delta AICc \leq 2$, both including the percent cropland and fire interaction, one including the quadratic effect of brood habitat. Coefficients for brood habitat overlapped zero at 95% CI and was considered to be uninformative, indicating percent cover of cropland best predicted male lek attendance before and after the fire.

Discussion

My study provides evidence that megafire in the mixed-grass prairie can influence lesser prairie-chicken space use and resource selection at multiple scales. Lesser prairie-chickens displayed a direct response to this fire's effects, avoiding burned areas at the expense of increasing use of areas fragmented by cropland, generally thought to be lower quality habitat. Habitat previously lost to woody encroachment did not become available to lesser prairie-chickens post-fire, suggesting the need for post-fire management of snags to make formerly wooded areas usable. However, temporary loss of habitat was augmented by the increased use of CRP, further re-enforcing the importance of this conservation practice for lesser prairie-chickens (Sullins et al. 2018, Harryman et al. 2019). Despite changes in resource selection, lesser prairie-chickens exhibited no change in home range area and demonstrated resilience to disturbance by remaining in the area. Overall, responses to megafire became apparent at different scales of evaluation and highlight the need to examine the full hierarchy of habitat selection when investigating wildlife-habitat relationships. Many of the factors that influenced lek attendance and home range composition, such as cropland and CRP, were not evident at an individual level. My results suggest that multiple management strategies (e.g., CRP enrollment, post-fire removal of snags) should be used before and after megafire to reduce effects of megafire on limiting lesser prairie-chicken habitat (primarily nest habitat) in a post-megafire landscape.

Overall space use by individual lesser prairie-chickens did not change post-fire, suggesting lesser prairie-chickens did not require increased space to obtain resources. However, placement of home ranges did change, as evidenced by different land cover composition within home ranges after the fire. There was greater use of cropland post-fire during the breeding season, likely due to increased use of unburned areas for lekking. The increase during the

breeding season was unexpected as cropland use by lesser prairie-chickens is typically more prevalent during the nonbreeding season, during which we observed no difference in use (Haukos and Zaveleta 2016). Proportion of cropland in the nonbreeding season home ranges pre-fire was relatively high (19%), and may be explained by fall and winter use of a few alfalfa fields before the fire that were later planted to wheat following the fire (D. S. Sullins, Kansas State University, personal communication). The reduced proportion of cropland in nonbreeding home ranges post-fire (9%) may highlight the importance of crop type diversity and planting wildlife friendly crops such as alfalfa in treeless landscapes that provide food for a variety of wildlife species (Hartman and Kyle 2010, Quinn et al. 2012). A study on lesser prairie-chickens across their range in Kansas and Colorado found that annual survival was optimized at 31% percent composition of cropland within annual home ranges (Robinson et al. 2018a). This suggests some cropland is necessary for lesser prairie-chicken survival, or is at least tolerable, given the high amount of cropland within the lesser prairie-chicken distribution. This threshold is much higher than the relatively low overall amounts of cropland (< 20%) I observed within home ranges, but may reflect the relatively small amount of cropland within the study site as a whole.

Concurrent with increased cropland in home ranges post-fire, I saw a large increase in the amount of CRP within home ranges. This matched predictions, as I expected lesser prairie-chickens to use CRP fields that can provide quality nest habitat and were largely unburned in the fire. Fields enrolled in CRP can be viewed as a refuge for lesser prairie-chickens following drought (Sullins et al. 2018) and can be a major factor in population persistence in portions of the lesser prairie-chicken distribution (Spencer et al. 2017, Harryman et al. 2019). Despite a 5-fold increase in the proportion of CRP in home ranges post-fire, I did not find significant selection for CRP in my step-selection analysis. Selection may not be apparent at this scale as CRP provides

quality nesting habitat, but outside of intensive use for that purpose may not be used as heavily the rest of the year (Sullins et al. 2018). In the breeding season, home ranges before the fire averaged 94% total grassland (native working grassland + CRP), 90% of which was native working grassland. Post-fire, home ranges were similar in composition of total grassland (93%), but only 75% was native working grassland, with CRP making up the other 18%, compared to 4% pre-fire. My estimates suggest a threshold of >90% grassland to sustain a breeding season home range in my study area in the mixed-grass prairie, with lesser prairie-chickens actively shifting use to CRP post-fire to fulfill this requirement. My estimated 90% threshold is much higher than some estimates that pointed to optimized annual survival at a composition of 57% grassland in a home range (Robinson et al. 2018a). However, this estimate was for annual home ranges across multiple study sites in Kansas (including areas with far less native working grassland) and may reflect a minimum threshold for lesser prairie-chicken survival in an area. While I did observe decreased total grassland use in nonbreeding season home ranges, it was still well above the 57% annual threshold for persistence and closer to the estimates of 77% grassland that is an important predictor of lesser prairie-chicken occupancy (Sullins et al. 2019) and the 91% grassland threshold linked to stable or increasing lesser prairie-chicken populations (Ross et al. 2016). Possibly as a result of these high proportions of grasslands within home ranges at my study site, lesser prairie-chicken survival was high before the fire and continued to be high following the fire (Chapter 2). Lesser prairie-chickens displayed resilience to disturbance by maintaining high proportions of total grassland within home ranges, highlighting the continued importance of ample native working grasslands and CRP to sustain lesser prairie-chicken populations with ongoing fragmentation and disturbance (Ross et al. 2016, Spencer et al. 2017, Sullins et al. 2018, Harryman et al. 2019).

Despite the importance of grasslands, my step selection did not document selection for grasslands at the 5-km radius scale, both before and after the fire. This lack of relationship was surprising, particularly before the fire, given the high amount of grassland in home ranges. Furthermore, the amount of grassland at this scale has been considered one of the most important factors for predicting lesser prairie-chicken population level distribution (Sullins et al. 2019). This lack of selection may be linked to the high amounts of grassland already on the landscape and suggests that my selection analysis is hierarchically constrained within already grassland dominated landscapes, for it is impossible to measure step selection where populations are locally extinct. Pre-fire, 89% of all used and available points had $\geq 70\%$ grassland within 5 km, likely explaining the lack of selection and high survival rates of lesser prairie-chicken in the area prior to the fire (Robinson et al. 2018a). Post-fire, 67% of all points were in areas with $\geq 70\%$ grassland within 5 km, indicating overall movement to areas with less surrounding grassland after the fire. While there is still majority use of areas with a high percentage of grassland after the fire, I observed lesser prairie-chickens moving out of areas that were normally selected, as they increased use of CRP and avoided burned areas.

Burn severity based on dNBR had a negative influence on lesser prairie-chicken distribution post-fire, with lower lek attendance (population level) in areas with more surrounding burned area and individual level selection for unburned areas post-fire. Post-fire burned areas had reduced visual obstruction and more bare ground, and it took three growing seasons during which we monitored birds for vegetation characteristics to return to pre-fire conditions (Chapter 4). Based on the limited relationship of vegetation characteristics with burn severity (Chapter 4), lesser prairie-chickens are likely avoiding burned and selecting for unburned areas, rather than identifying differences in severity. Following prescribed fire,

Tympanuchus spp. generally avoid recently burned areas and can select for areas with a longer time since fire, especially during nesting (Boyd and Bidwell 2001, Lautenbach 2017, Winder et al 2017). Therefore, in this grassland system, the effects of megafires for lesser prairie-chickens may be more apparent in their size, rather than traditional measures of burn severity. Preventing megafire then becomes important as habitat is lost over the entire burned area and even if only for a relatively short time (≤ 3 years), may result in reduced lesser prairie-chicken populations or emigration.

Strong selection for elevation post-fire points to some lesser prairie-chicken emigration out of major areas of lesser prairie-chicken use pre-fire. My study area encompassed a natural elevation gradient from lowlands along the Cimarron River to upland areas that are ~250 m higher in elevation ~40 km to the north. Lower elevations along the Cimarron River floodplain in the southern part of the study area were most heavily used prior to the fire. Moving north, the study site increases in elevation, and consists of steep rolling hills and grasslands, which were not used extensively before the fire. Post-fire, lesser prairie-chickens spent less time in the lowland floodplain as it was almost entirely burned, and moved north into higher elevation areas, likely leading to the strong relationship with elevation. This matches with fire dynamics in grasslands, where lower elevations can better facilitate the spread of wildfire than higher elevations (Cao et al. 2013). Such knowledge of grassland wildfire and lesser prairie-chicken response may facilitate predictions of areas and lesser prairie-chicken populations at higher risk for megafire, and highlights the importance of conserving heterogeneous landscapes at even larger scales than previously suggested.

The Starbuck fire had the greatest potential to benefit lesser prairie-chickens by reducing woody encroachment, but this was not the case, at least in the period of my study, as avoidance

of trees increased following fire. This may be because woody areas that burned were surrounded by burned grasslands, which lesser prairie-chickens largely avoided post-fire. Lack of overhead vegetation and cover in burned areas can increase raptor predation risk for *Tympanuchus* spp. (Bock and Bock 1978, Winder et al. 2018) potentially explaining the increased avoidance of woody areas with ideal raptor perches following the fire. Furthermore, many trees killed by the fire remained standing as snags post-fire (M. W. Sirch, Kansas State University, unpublished data). As lesser prairie-chickens avoid any tall features and trees likely due to perceived predation risk from raptors, it makes sense that standing snags make areas unusable for lesser prairie-chickens (Lautenbach et al. 2017). I noted lesser prairie-chicken use and nesting in several pastures where snags had been mechanically removed after the fire, whereas before the fire those area was unoccupied by marked lesser prairie-chickens (N. J. Parker, unpublished data). This highlights the need for post-fire management and mechanical removal of snags following fire to open areas of lesser prairie-chicken habitat, as well as improve overall grassland health (Ortmann et al. 1998, Twidwell et al. 2013). The need for mechanical removal of snags following fire makes this megafire appear similar to prescribed fire, but this fire did result in greater mortality of eastern redcedar (*Juniperus virginiana*) and other invasive tree species compared to results from prescribed fire (Ortmann et al. 1998; M. W. Sirch, unpublished data). As such, megafires provide a unique conservation opportunity to more easily remove invasive woody species that would typically be prohibitively costly. Such data corroborate the need for increased use of prescribed fire, as well as higher intensity prescribed fire, to help prevent further woody encroachment (Twidwell et al. 2016).

Following the megafire, I observed a decline in male lek attendance and a change in landscape use at the population level, with male lek attendance best predicted by the amount of

cropland within 5 km of leks. Prior to the fire, lek attendance decreased as the amount of crop increased, but post-fire the trend reversed, in direct opposition to most literature on lesser prairie-chickens (Woodward et al. 2001, Fuhlendorf et al. 2002, Aulicky 2020, Gehrt et al. 2020). For lesser prairie-chickens, and other imperiled grouse species, relatively large areas of cropland (and threat of conversion) remain a major impediment to lek and population persistence (Ross et al. 2016, Smith et al. 2016). In my study, areas that were not native working grassland were primarily cropland, interspersed with CRP fields that did not burn in the fire. Leks in the crop/CRP matrix post-fire likely had greater male attendance because they were close to remaining unburned quality adult cover and nest habitat in nearby CRP fields. It was surprising then, that I did not find a stronger influence of nest habitat abundance or female presence on lek attendance, as these are thought to be key for lek persistence and formation (Schroeder and White 1993, Aulicky 2020). Part of this may be tied to the fast recovery of nest habitat by 2019 (Chapter 4), resulting in some unoccupied historic leks having nest habitat in the surrounding area, but no actual use of those areas for lekking or nesting. In addition, I did not account for lag effects of nest success and female presence around leks in the preceding year, which may be more influential than current year nest habitat and female presence (Aulicky 2020). Overall, grassland-dominated landscapes are important for lesser prairie-chicken population persistence, but my work indicates a limited amount of fragmentation and landscape diversity may also provide resilience to disturbance (Fuhlendorf et al. 2002, Ross et al. 2016, Robinson et al. 2018a, Fahrig et al. 2019, Sullins et al. 2019).

Following the Starbuck fire in the mixed-grass prairie, lesser prairie-chickens were forced out of their formerly high quality habitat, moving out of burned areas with more grassland to areas of unburned, fragmented grasslands. Large stretches of connected, high quality grasslands

are key for lesser prairie-chicken population persistence, and in this area of the mixed-grass prairie provided quality lesser prairie-chicken habitat prior to the fire (Fuhlendorf et al. 2002, 2017; Ross et al. 2016; Robinson et al. 2018*a, b*). Ironically, features that made this area ideal lesser prairie-chicken habitat likely contributed to the vast size and intensity of this fire and lesser prairie-chicken avoidance post-fire. Despite reduced habitat, lesser prairie-chicken populations have persisted in this area, demonstrating resilience to megafire. Key patches of unburned CRP likely facilitated lesser prairie-chicken survival in this area, and suggest that some structural fragmentation and landscape diversity can also provide population resilience (Ross et al. 2016, Spencer et al. 2017, Sullins et al. 2018, Fahrig et al. 2019). This is supported by the fact that 71% of the estimated lesser prairie-chicken population is in the Short-Grass Prairie/CRP Mosaic Ecoregion; historically, the ecoregion most structurally fragmented by agriculture and containing the greatest proportion of CRP (Spencer et al. 2017, Sullins et al. 2018, Nasman et al. 2020). However, even in these areas, CRP use increased in local landscapes (~50 km²) with >70% grassland, re-enforcing the importance of preserving intact grasslands and preventing fragmentation and habitat loss across the lesser prairie-chicken range (Fuhlendorf et al. 2017, Sullins et al. 2018). As climate change is predicted to increase the frequency of extreme drought and fire throughout the Great Plains (Grisham et al. 2013, Barbero et al. 2015, Ross et al. 2016), it becomes imperative to conserve CRP and remaining native grasslands to strengthen lesser prairie-chicken populations and resilience to disturbance.

Management Implications

Targeted enrollment of CRP near areas of quality grassland, and reduced anthropogenic development of cropland/CRP mosaic landscapes on the edges of large grasslands, will strengthen lesser prairie-chicken resilience to disturbance such as megafire, as well as increase

connectivity between populations (Spencer et al. 2017; Sullins et al. 2018, 2019). Preventing loss of CRP grassland following contract expiration is also important, as are conservation easements and other practices that conserve grasslands (Morefield et al. 2016, Claassen et al. 2017, Barnes et al. 2020, Sullins et al. 2021). Emergency grazing or haying should be rotated or minimized on CRP patches near leks and nearby edges of grasslands to ensure patches of quality habitat remain as a refuge for lesser prairie-chickens following drought or fire (Luttschwager et al 1994, Twidwell et al. 2018). Implementing prescribed fire in remaining grasslands is key to preserve grassland health, manage habitat, and prevent future megafire and woody encroachment (Twidwell et al. 2013; Starns et al. 2019, 2020). To ensure that opportunities for conservation are not lost following future fires, removal of snags and other killed trees following both prescribed fire and megafire is crucial. Chaining is an affordable option to remove standing dead trees (Steven and Monsen 2004, Miller et al. 2005), that would provide benefits not only for lesser prairie-chickens and other wildlife, but also cattle producers and overall grassland health.

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Tables

Table 3.1 Average 95% isopleth home range (ha) of male and female lesser prairie-chickens in the breeding (15 Mar–15 Sep) and nonbreeding (16 Sep–14 Mar) seasons before (2014–2016) and after (2018–2020) the March 2017 Starbuck fire in Clark County, Kansas, USA.

Season	Fire Status	<i>n</i>	\bar{x}^*	SE	Range
Breeding	Before	36	452 ^a	63	49–1577
	After	41	608 ^{a,b}	132	59–4070
Nonbreeding	Before	21	1474 ^c	217	110–3317
	After	24	911 ^{b,c}	152	89–2604

*Means with matching superscripts do not differ.

Table 3.2 Average percent cover and standard error of cropland, Conservation Reserve Program (CRP), native working grassland, and burned area within home ranges (ha) of male and female lesser prairie-chickens in the breeding (15 Mar–15 Sep) and nonbreeding (16 Sep–14 Mar) seasons before (2014–2016) and after (2018–2020) the March 2017 Starbuck fire in Clark County, Kansas, USA. Means with matching superscripts do not differ within land cover types.

Season	Fire Status	<i>n</i>	% Crop	% CRP	% Grassland	% Burned
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
Breeding	Before	36	3.35 ± 1.12	3.94 ± 1.41 ^a	90.20 ± 2.33	78.18 ± 5.86
	After	41	5.84 ± 1.25 ^a	17.81 ± 3.40 ^b	74.76 ± 4.14 ^a	51.21 ± 6.69 ^a
Nonbreeding	Before	21	18.88 ± 4.24 ^b	3.53 ± 1.69 ^a	74.40 ± 4.37 ^a	58.47 ± 7.79 ^a
	After	24	8.89 ± 1.98 ^{a,b}	11.38 ± 2.68 ^b	77.47 ± 3.89 ^a	46.09 ± 8.63 ^a

Table 3.3 Ranking of Poisson regression models used to predict male lesser prairie-chicken attendance at leks at a 5-km scale before (2014–2016) and after (2018–2020) the March 2017 Starbuck fire in Clark County, Kansas, USA. Variables investigated included before/after fire status (Fire), percent cropland (Crop), percent native working grassland (Grass), amount of brood habitat (Brood), average burn severity (dNBR), percent area burned (Burn), and an intercept only model (Null).

Model	K^a	ΔAICc^b	AICc^c	w_i^d	Deviance^e
Land Cover					
Crop * Fire	4	0.00	457.26	0.59	448.58
Grass * Fire	4	2.06	459.33	0.21	450.64
Crop ² * Fire	6	2.56	459.82	0.16	446.34
Null	1	175.34	632.61	0.00	630.54
Reproductive Habitat					
Brood ² * Fire	6	0.00	475.74	0.99	462.28
Null	1	156.86	632.61	0.00	630.54
Fire Effects					
dNBR ² * Fire	6	0.00	462.31	0.62	448.84
dNBR * Fire	4	2.64	464.95	0.16	456.28
Burn * Fire	4	3.13	465.44	0.13	456.76
Null	1	170.3	632.61	0.00	630.54
Combined Model Set					
(Brood ² +Crop) * Fire	8	0.00	455.72	0.46	437.10
Crop * Fire	4	1.54	457.26	0.21	448.58
Null	1	176.88	632.61	0.00	630.54

^aNumber of parameters.

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

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

^dAkaike weights.

^eDeviance or -2*loglikelihood.

Table 3.4 Summary of beta coefficients (β) and 95% lower (LCI) and upper (UCI) confidence intervals of top ranked Poisson regression models used to predict male lesser prairie-chicken attendance at leks at a 5-km scale before (2014–2016) and after (2018–2020) the March 2017 Starbuck fire in Clark County, Kansas, USA. Variables investigated included before/after fire status (Fire), percent cropland (Crop), amount of brood habitat (Brood), and average burn severity (dNBR).

Model Set	Variables	β	95% LCI	95% UCI
Land Cover	Fire	2.3692	1.9649	2.7735
	Crop	5.7569	4.3643	7.1495
	Crop * Fire	-8.1106	-10.0702	-6.1510
Reproductive Habitat	Fire	-1.0105	-2.4424	0.4213
	Brood	0.0129	-0.1371	0.1629
	Brood ²	-0.0027	-0.0068	0.0014
	Brood * Fire	0.0722	-0.0867	0.2311
	Brood ² * Fire	0.0012	-0.0030	0.0055
Fire Effects	Fire	0.5291	-1.4738	0.4156
	dNBR	0.0052	-0.0066	0.0171
	dNBR ²	-0.000093	-0.000161	-0.000025
	dNBR * Fire	0.000096	-0.017642	0.017834
	dNBR ² * Fire	0.000091	0.000004	0.000178

Figures

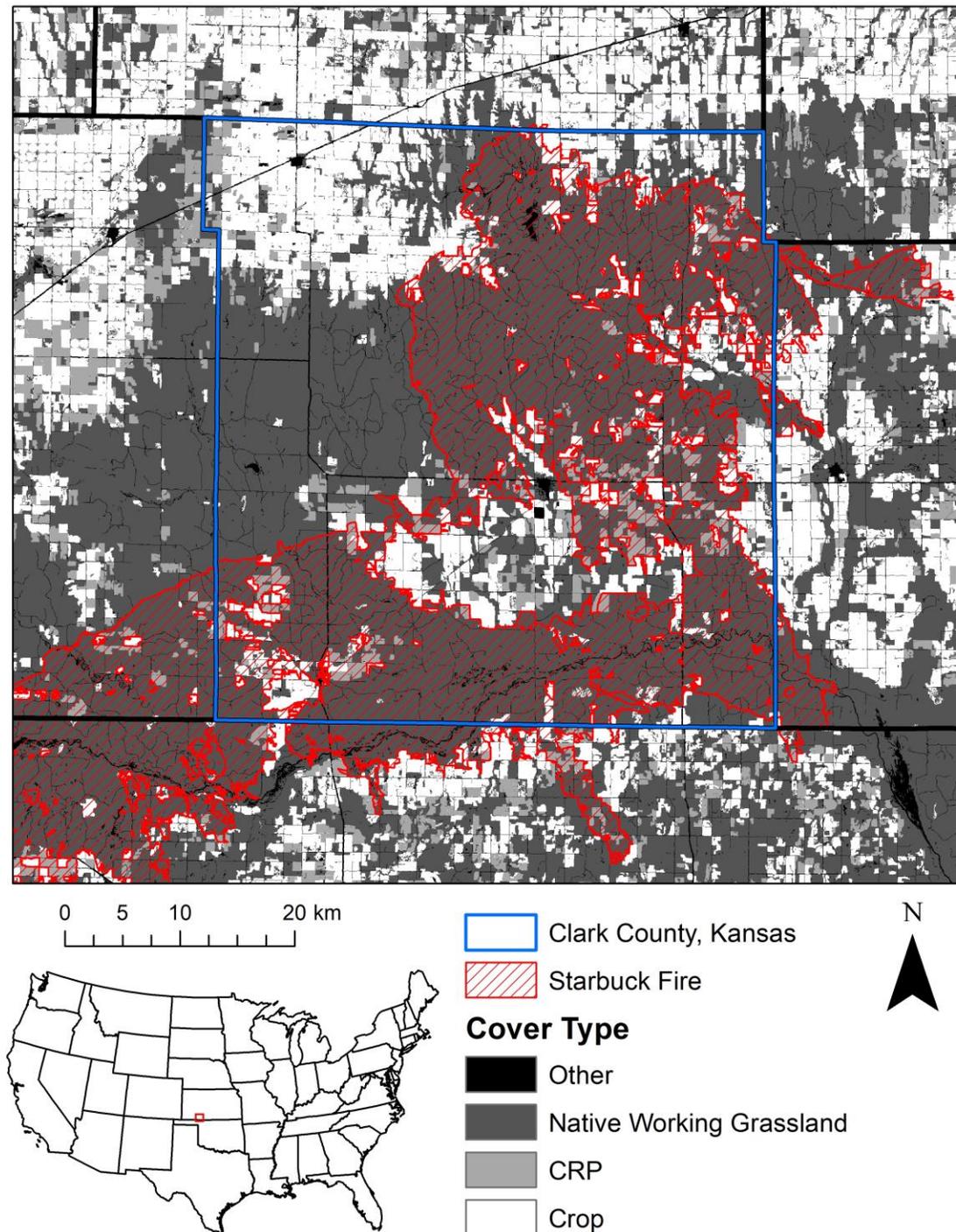


Figure 3.1 Study area in Clark County, Kansas, USA, detailing the 2017 Starbuck fire and dominant land cover types. Cover types include native working grassland, CRP (Conservation Reserve Program), crop, and other (urban, water, wooded, etc.).

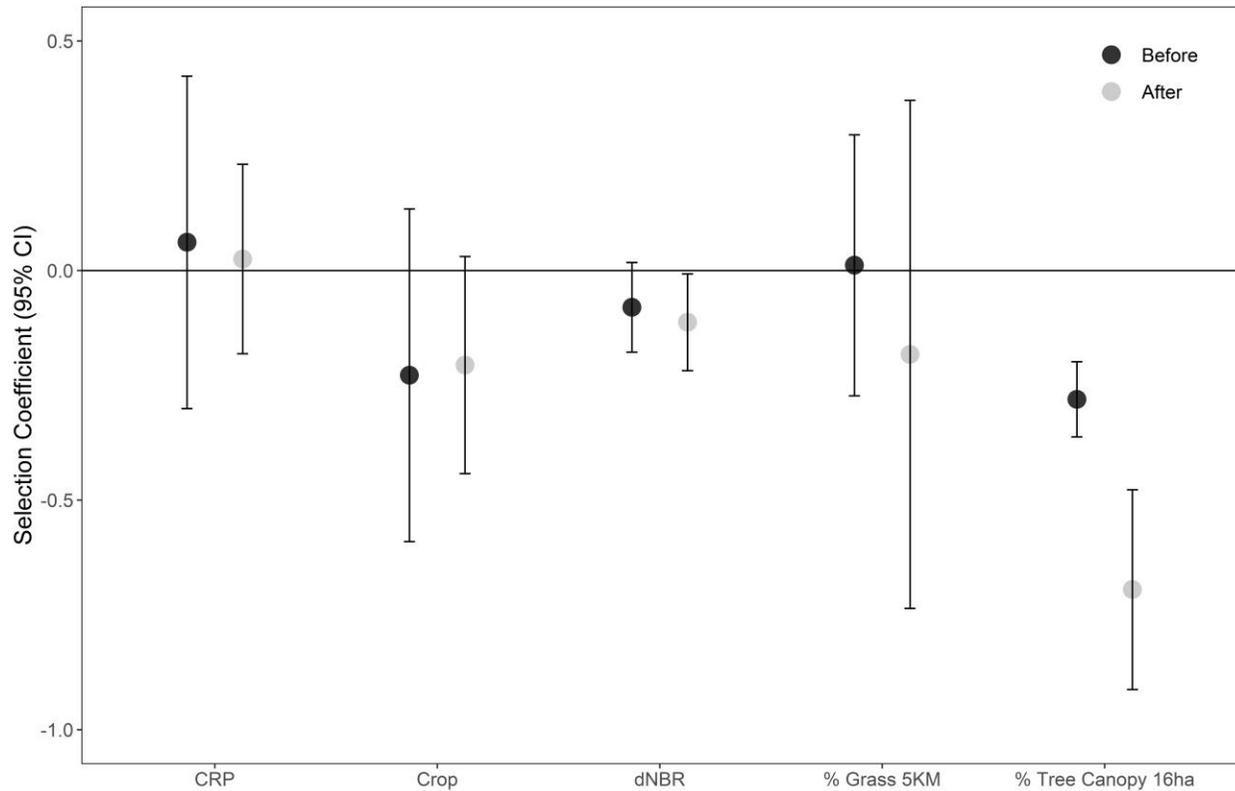


Figure 3.2 Standardized selection coefficients for fixed effects representing lesser prairie chicken landscape scale selection before (2014–2016) and after (2018–2020) the 2017 Starbuck fire in Clark County, Kansas, USA. CRP and crop were binomial (0,1) selection for Conservation Reserve Program (CRP) fields and agriculture fields (crop). The rest of the covariates were continuous and included difference in normalized burn ratio (dNBR), percent native working grassland within a 5 km radius (% Grass 5KM), and percent tree canopy cover within 16 ha (% Tree Canopy 16ha).

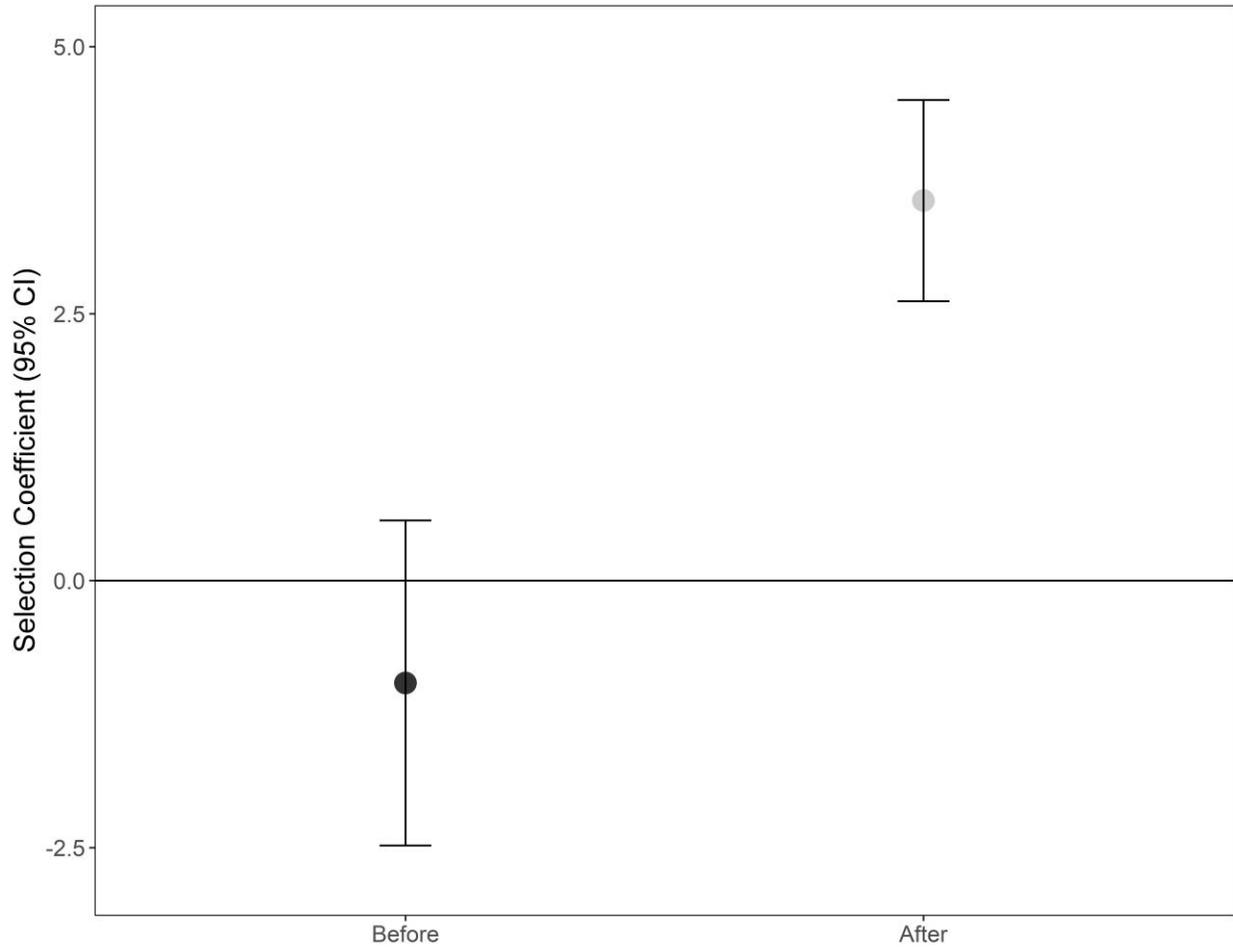


Figure 3.3 Standardized selection coefficients for fixed effects representing lesser prairie-chicken selection for elevation (m) before (2014–2016) and after (2018–2020) the 2017 Starbuck fire in Clark County, Kansas, USA. While tested in the same models as covariates in Figure 3.2, these were displayed separately due to the high strength of selection for elevation post-fire.

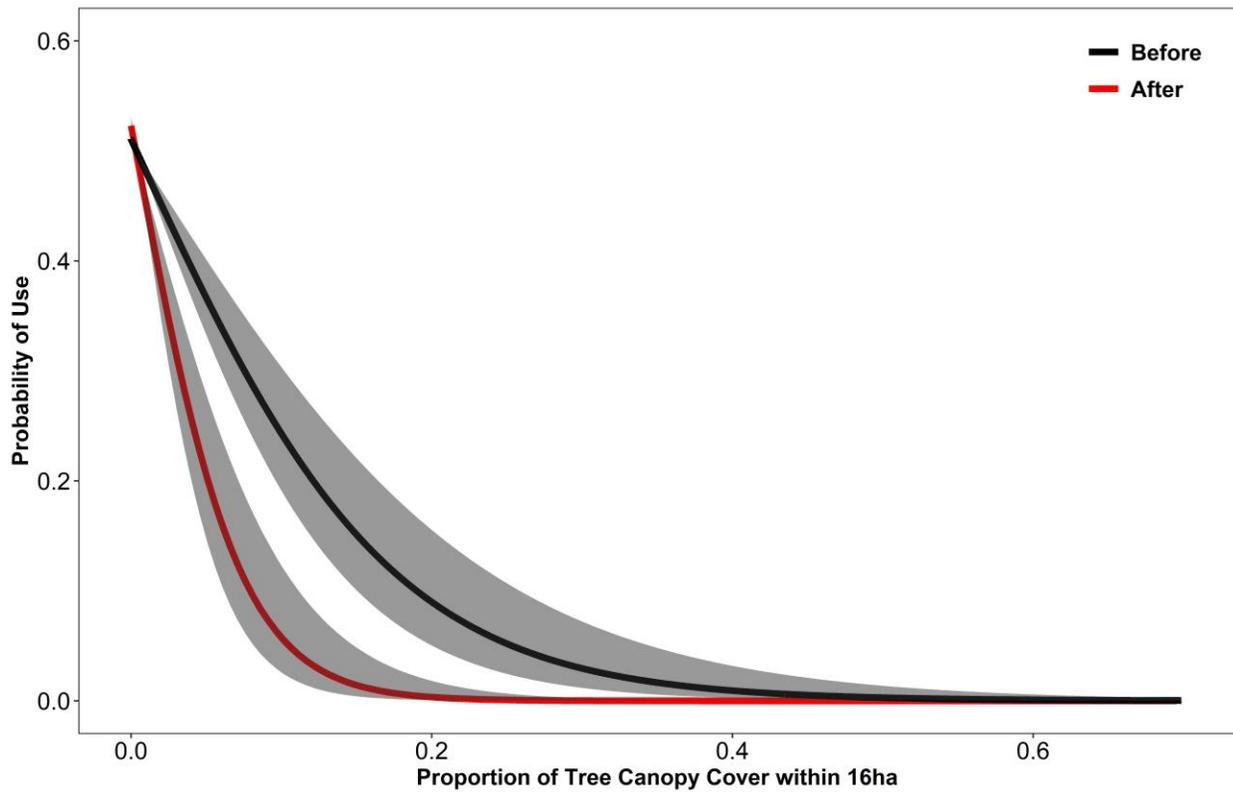


Figure 3.4 Probability of lesser prairie-chicken use based on proportion of tree canopy cover within 16 ha in Clark County, Kansas, USA before (2014–2016) and after (2018–2020) the 2017 Starbuck fire. Shaded areas represent 95% confidence intervals.

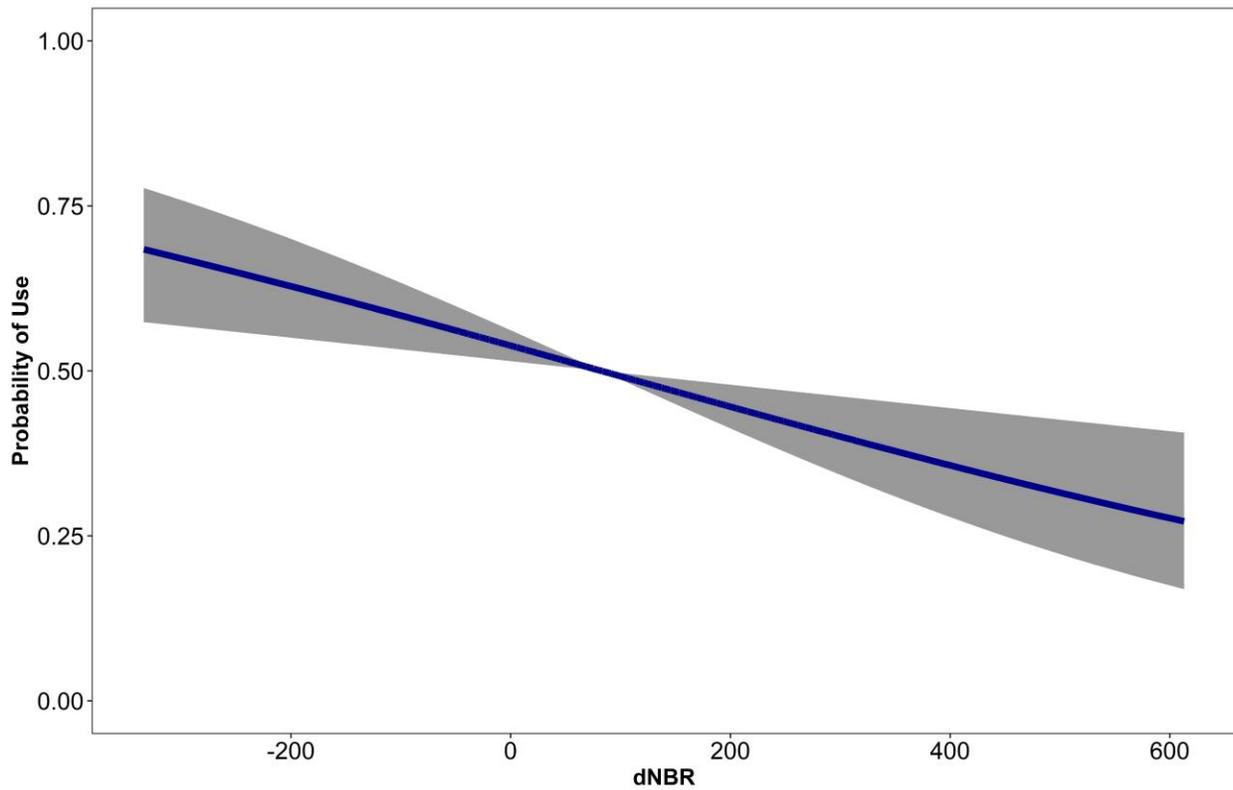


Figure 3.5 Probability of lesser prairie-chicken use based on observed values of differenced Normalized Burn Ratio (dNBR) calculated by Monitoring Trends in Burn Severity (MTBS 2019) in Clark County, Kansas, USA after (2018–2020) the 2017 Starbuck fire. Areas are categorized as regrowth (-400 – -101), unburned (-0.100–99), low severity (100–269), moderate-low severity (270–439) and moderate-high severity (440–659) according to USGS classifications (USGS 2004). Shaded areas represent 95% confidence intervals.

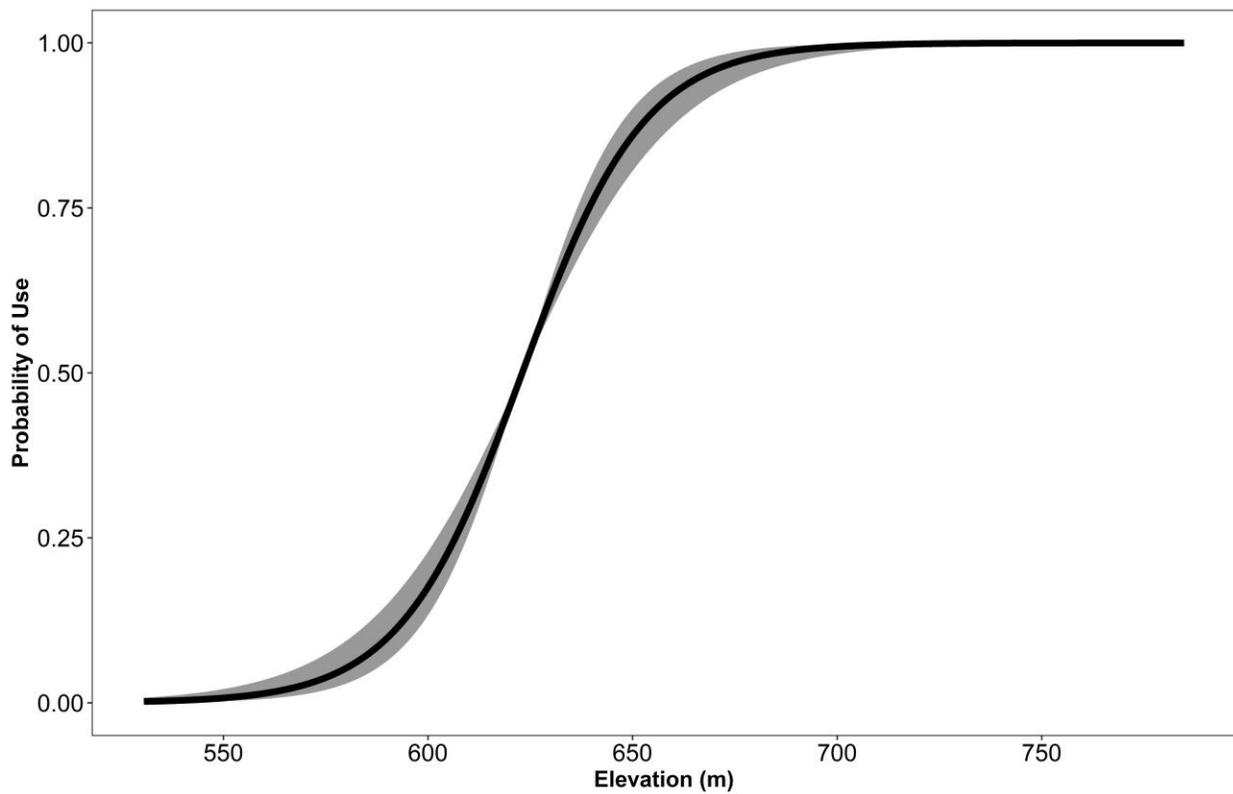


Figure 3.6 Relationship of elevation and probability of lesser prairie-chicken use in Clark County, Kansas, USA after (2018–2020) the 2017 Starbuck fire. Shaded areas represent 95% confidence intervals.

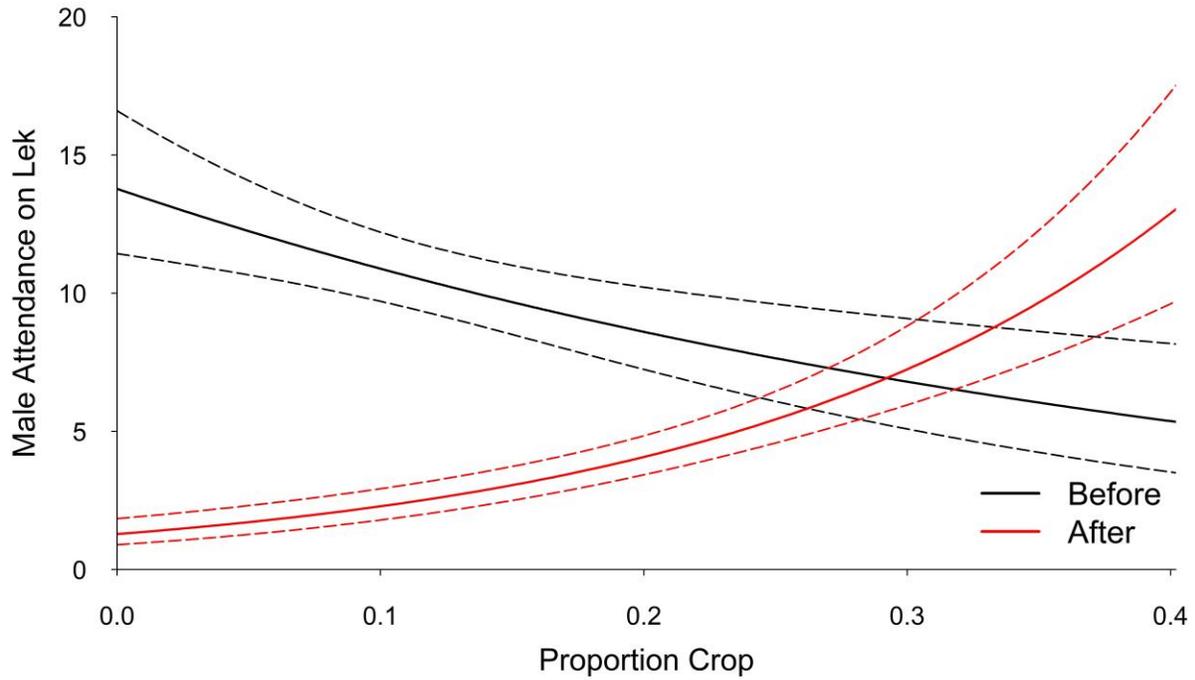


Figure 3.7 Poisson regression of the relationship between male lesser prairie-chicken attendance at leks and the proportion of cropland within a 5-km radius of leks before (2014–2015; black) and after (2018–2019; red) the 2017 Starbuck fire in Clark County, Kansas, USA. Dashed lines represent 95% confidence intervals. No leks were observed in areas with >40% cropland.

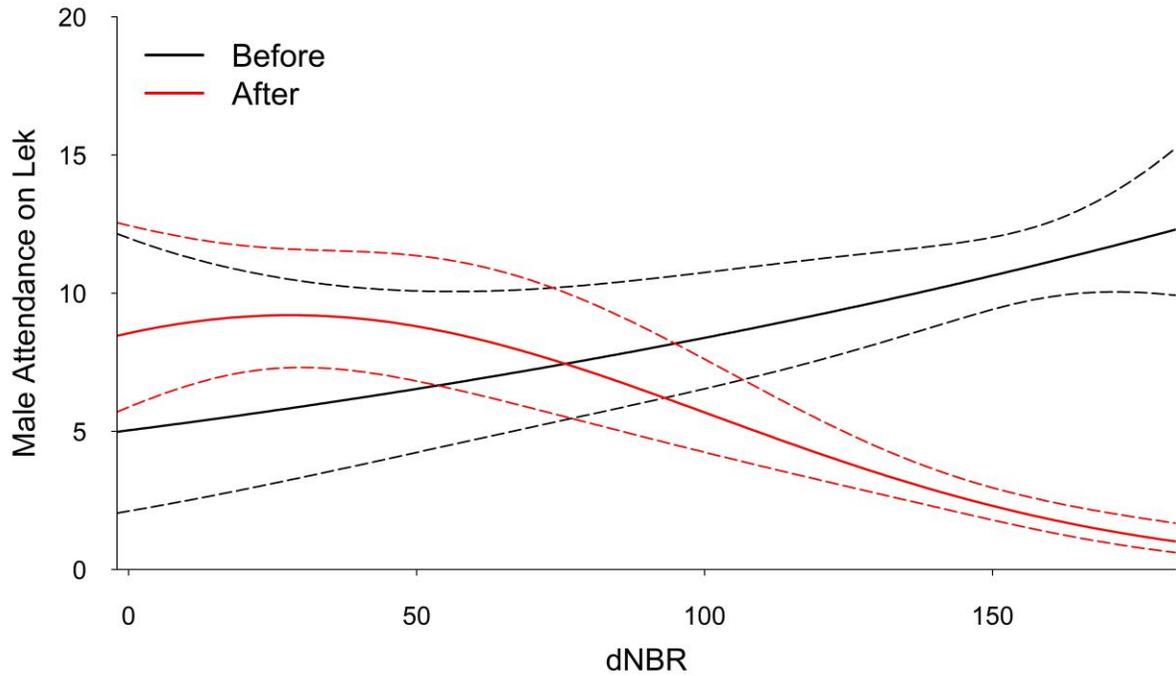


Figure 3.8 Poisson regression of the relationship between male lesser prairie-chicken attendance at leks and the mean value of the difference in normalized burn ratio (dNBR) within 5 km of leks before (2014–2015) and after (2018–2019) the 2017 Starbuck fire in Clark County, Kansas, USA. Dashed lines represent 95% confidence intervals. Higher values of dNBR indicate a greater amount of area burned or area burned at higher severity.

Chapter 4 - Vegetation and lesser prairie-chicken habitat response to megafire in the mixed-grass prairie

Introduction

Fire was a key force in the formation of North American grasslands (Axelrod 1985) and plays a vital role in maintaining remaining grasslands (Wright and Bailey 1982, Anderson 2006). While long excluded from grassland ecosystems following European settlement, fire is now commonly prescribed for a variety of benefits, including increasing forage yields for cattle producers (McMurphy and Anderson 1965, Smith and Owensby 1978, Towne and Craine 2016), increased grassland biodiversity (Collins and Barber 1986, Howe 1994*a*), and control of invasive species (DiTomaso et al. 2006, Twidwell et al. 2013). The use of prescribed fire (and its effects) varies geographically, with annual prescribed fire long a widespread practice within the cattle-producing Flint Hills region of eastern Kansas and Oklahoma, USA; as such, much of the research on prescribed fire and grasslands have focused in this area and tallgrass prairie (Aldous 1934, Anderson et al. 1970, Briggs et al. 2005, Towne and Craine 2016). In contrast, the more arid mixed-grass prairie of the central Great Plains have relatively low use of prescribed fire, for several reasons including reduced and less reliable precipitation, vegetation composition, and wildfire fears (Wright 1974*a*, Wright and Bailey 1982, Harr et al. 2014). As a result, grasslands in this region have experienced a loss of biodiversity, reduced heterogeneity, and increased wildfire risk (Wright and Bailey 1982, Collins and Barber 1986, Lindley et al. 2013, Twidwell et al. 2013).

Although fire has been removed from large portions of the Great Plains as a natural disturbance, the size and severity of the wildfires occurring within the Great Plains have increased in recent years as a result of climate change and fire suppression (Lindley et al. 2013,

2019; Donovan et al. 2017), and are predicted to increase in the future (Barbero et al. 2015, Cao et al. 2015). The increase of wildfires in the Great Plains is concurrent with global increases in large fires, often termed “megafires” for their large size and intensity, as well as their social and economic impacts (Williams et al. 2011, Stephens et al. 2014). Megafires within the Great Plains are a recent phenomenon in the last 30-40 years, largely unseen since record keeping began in the early 20th century (Lindley et al. 2013, 2019; Donovan et al. 2017). Megafires have major effects on human lives, infrastructure, and cattle production in the region, resulting in fears that megafires will have similar catastrophic effects for ecological systems (e.g., desertification, vegetation community shifts) and wildlife (Turner 2010; Donovan et al. 2017, 2020; Lindley et al. 2019). Remote sensing of grasslands indicates fears of catastrophic ecological effects to be largely unfounded, with limited lasting effects on grasslands, highlighting the resiliency of grasslands to such disturbance from which they evolved (Donovan et al. 2020, Steiner et al. 2020). Field studies of grassland response to wildfire are limited, but corroborate remotely sensed research that grasslands are resilient to wildfire, and respond in a similar manner to prescribed fire (Rideout-Hanzak et al. 2011, Arteburn et al. 2017, Kral-O’Brien et al. 2020). However, due to the unpredictable nature of wildfire many field studies lack before/after fire data, and often focus on effects to broad scale functional groups and biomass, not fine-scale composition and structure (Rideout-Hanzak et al. 2011, Arteburn et al. 2017, Donovan et al. 2020). Rideout-Hanzak et al. (2011) found that effects of wildfire to grassland biomass in the short- and mixed-grass prairies largely dissipated 2–3 years post-fire; however, a follow-up study revealed changes in species diversity and community composition only became apparent 2–3 years after the fire (Wester et al. 2014). Experimental work has corroborated the potential for long-term effects on grasslands from fire, with combined effects of wildfire and climate change

leading to lasting changes in plant composition and diversity (Ratajczak et al. 2019). Such studies emphasize the need for in-depth and on-the-ground assessments in addition to remotely sensed work (Ludwig et al. 2007) and highlight the complex interplay that variability in climate, disturbance, and vegetation has on grassland ecosystems.

Wildfire effects on grasslands can scale up to affect wildlife that inhabit them. Of particular concern are grassland birds, which have experienced the largest declines of any avian guild in North America (Rosenberg et al. 2019). Like the grasslands they inhabit, grassland birds evolved with fire and historically relied on it to maintain habitat, with studies confirming benefits from prescribed fire and grazing that mimic historic disturbance (Bock and Block 2005, Fuhlendorf et al. 2006, Hovick et al. 2014). Response to fire is species specific, with some species preferring short, recently burned prairie, and others using unburned areas with dense vegetation (Knopf 1996, Johnson 1997, Askins et al. 2007, Fuhlendorf et al. 2009). Variability in use highlights the need for heterogeneity within grassland landscapes that promotes avian diversity when areas of differing time since fire are available (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Hovick et al. 2014). Grassland bird response to wildfire is generally analogous to response to prescribed fire, with no major changes in abundance or diversity following fire (Bock and Bock 1978, 1992; Roberts et al. 2012). Roberts et al. (2012) monitored birds at the same study site as the grassland research conducted by Rideout-Hanzak et al. (2011) and Wester et al. (2014) in the short- and mixed-grass prairies, and noted temporary shifts in avian communities, but communities recovered to an unburned state within 3 years following fire, consistent with the measured grassland vegetation response.

One grassland bird species that has seen an increase of wildfires throughout its distribution is the lesser prairie-chicken (*Tympanuchus pallidicinctus*; Donovan et al. 2017,

Lindley et al. 2019, USFWS 2021). The lesser prairie-chicken is a grassland-obligate grouse of the southern Great Plains that has faced population declines primarily due to habitat loss since the 1980s and now occupies only an estimated 14% of its estimated historical range (Garton et al. 2016, Haukos and Zaveleta 2016). Like many grassland bird species, lesser prairie-chickens require a heterogeneous landscape that was formerly provided by fire and bison (*Bison bison*) grazing to fulfill habitat needs for different life stages (Fuhlendorf and Engle 2001, Hagen and Giesen 2005, Haukos and Zaveleta 2016, Fuhlendorf et al. 2017). Historically, an estimated fire return interval of 5–10 years in the mixed-grass prairie and bison selectively grazing in recently burned areas created a shifting mosaic of habitat types used by lesser prairie-chickens (Wright and Bailey 1982, Brockway et al. 2002, Fuhlendorf and Engle 2004, Samson et al. 2004).

Current management recommendations for lesser prairie-chickens call for an attempt to create heterogeneity through managed grazing and prescribed fire, including patch-burn grazing (Fuhlendorf and Engle 2001, Elmore et al. 2009, Lautenbach 2017). Patch-burn grazing systems use rotational burning to establish a mosaic of different time since burn patches and grazing pressures (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009) that can provide different habitats for wildlife, with beneficial results for *Tympanuchus* spp. (McNew et al. 2015, Lautenbach 2017, Winder et al. 2018, Starns et al. 2020). Lesser prairie-chickens avoid trees and other tall features on the landscape, so use of prescribed fire to control woody encroachment benefits lesser prairie-chickens, as well as overall grassland ecosystems (Twidwell et al. 2013, Lautenbach et al. 2017).

Based on the importance of fire for lesser prairie-chicken ecology, the increasing prevalence of megafires may benefit lesser prairie-chickens. Megafire presents the opportunity for vegetation regrowth, increased plant biodiversity, and removal of invasive species, which may increase and improve lek and brood habitat for lesser prairie-chickens (Collins and Barber

1986, Howe 1994*a*, Twidwell et al. 2013). For lekking, lesser prairie-chickens require areas with bare ground and short vegetation for their displays to be seen (Hagen et al. 2004, Haukos and Zaveleta 2016). In Oklahoma and Texas, recently burned pastures attracted lesser prairie-chickens to form new leks, indicating fire would be ideal for creating lek habitat (Cannon and Knopf 1979, Jones 2009). However, lek habitat is not currently considered a limiting factor for lesser prairie-chickens, with lek persistence and formation more influenced by reproductive habitat and female presence at landscape scales (Aulicky 2020, Gehrt et al. 2020). Therefore, despite an abundance of lek habitat on the landscape following a megafire, it may not be occupied post-fire if there is no nest habitat within close proximity (<5 km). Such negative consequences of fire may not be an issue when fires are implemented at pasture scales, but may be problematic when burns span >40,000 ha.

Unlike lek habitat, brood habitat is one factor thought to be limiting for lesser prairie-chicken populations and typically consists of areas of reduced grass cover and greater forb cover that make arthropods more accessible for chicks (Hagen et al. 2004, Sullins et al. 2018*a*). Recently burned areas often provide brood habitat for several years following fire (Boyd and Bidwell 2001, Doxon et al. 2011, Winter et al. 2012), indicating megafire may increase vital brood habitat in grassland landscapes. In Texas, USA, forb density increased in areas burned by a small wildfire (45–63 ha), and lesser prairie-chicken broods used burned areas one and two years following the fire (Jones 2009). However, chicks have limited dispersal ability and even if megafire is successful at creating brood habitat, these areas may be unusable for lesser prairie-chickens if there is reduced or no nest habitat in close proximity (Guthery 1997, Hagen et al. 2013, Lautenbach 2015). Only along the edges of megafire would there be opportunity for brood habitat adjacent to optimal nest habitat. The size and scale of the fire may be just as important as

the fire itself when providing heterogeneity necessary to support lesser prairie-chicken reproduction (Fuhlendorf and Engle 2001, Elmore et al. 2009).

While reintroducing fire to the landscape is important, the scale and intensity of a megafire could have homogenizing negative effects for lesser prairie-chicken habitat. Adult lesser prairie-chickens need adequate herbaceous cover for predator concealment and thermal regulation and often remain close to quality nest habitat even outside of the nesting period (Haukos and Zaveleta 2016). Loss of vertical cover and visual obstruction following fire may increase predation risk for *Tympanuchus* spp., particularly by raptors (Bock and Bock 1978, Winder et al. 2018). In the Flint Hills Ecoregion, intensive annual prescribed burning and grazing practices at the pasture scale can reduce nesting habitat for greater prairie-chickens (McNew et al. 2015). Within the mixed-grass prairie, I expect to see similar negative effects for lesser prairie-chickens, but at the landscape scale following megafire. Nest habitat for lesser prairie-chickens consists of moderately tall (>30–50 cm) cover from grasses or shrubs, relatively high visual obstruction at 75% (2–4 dm), minimal bare ground, and increased litter (Hagen et al. 2013, Haukos and Zavelata 2016, Lautenbach et al. 2019). I expect increased bare ground and decreased grass cover, visual obstruction, and litter cover following a megafire, ultimately reducing available nest habitat for several years post-fire (Boyd and Bidwell 2001, Winter et al. 2012, McNew et al. 2015). Quality nesting habitat is essential for lesser prairie-chicken nest success and persistence in an area (Lautenbach et al. 2019, Gehrt et al. 2020) and, therefore, megafires may result in lowered nest survival and emigration from burned areas.

My objective in this study was to evaluate short-term (<3 year) effects of a 2017 megafire (Starbuck fire; ~254,000 ha) in the mixed-grass prairie of Kansas, USA, on vegetation composition and structure, lesser prairie-chicken fine-scale habitat use, lesser prairie-chicken

reproductive habitat abundance, and to explore correlations of burn severity with vegetation characteristics. I measured vegetation characteristics important to lesser prairie-chickens before the fire (2014–2016) and returned to the same areas after the fire (2018–2020) to evaluate grassland response. I predicted increased bare ground and forb cover, and decreased litter depth and visual obstruction immediately following the fire, and hypothesized that these effects would last longer than those seen from smaller prescribed fire. I predicted lesser prairie-chicken fine-scale habitat use may change post-fire if they are forced to use areas of poorer quality (e.g., reduced visual obstruction, increased bare ground) due to changes in available vegetation and loss of quality habitat. Overall, I predicted that lesser prairie-chicken reproductive habitat would be greatly reduced and degraded up to three years following the fire. I predicted burn severity would be greater in areas with more litter, shrubs, and higher visual obstruction pre-fire, as these areas would have more fuel. Post-fire, I anticipated areas that burned with highest severity to have less litter, reduced visual obstruction, and more bare ground as they would have lost the most vegetation and residual cover. With this work, I aim to provide insights into the effects of the largest fire in Kansas history on both lesser prairie-chickens and the threatened grasslands they inhabit to help land managers, ranchers, conservationists, and other stakeholders manage and prepare for future megafires.

Study Area

In March 2017, the Starbuck fire burned approximately 253,810 ha (627,178 acres) of mostly grasslands managed for cattle production in Kansas and Oklahoma (Kansas Forest Service 2019). This was the largest recorded fire in Kansas history, killing between 5,000–9,000 cattle and resulting in an estimated \$44 million (USD) in damage (Bickel 2018). The spatial extent of the Starbuck fire was entirely within the Mixed-Grass Prairie Ecoregion, one of four

ecoregions inhabited by lesser prairie-chickens (Van Pelt et al. 2013). The Mixed-Grass Prairie Ecoregion contains some of the largest tracts of contiguous grassland and available habitat in the entire lesser prairie-chicken range (Spencer et al. 2017, Sullins et al. 2019) and was estimated to support 14% of the entire lesser prairie-chicken population in 2020 (Nasman et al. 2020).

The study area sits at the western edge of the mixed-grass prairie, in Clark County, Kansas. The 50-year (1970–2020) average annual precipitation is 58.3 cm, with the majority of rainfall occurring from April–July (NOAA 2020; Figure 4.1). Through the duration of the study (2014–2019), average annual precipitation was 66.7 cm, and was similar before (2014–2015; 69.7 cm) and after (2018–2019; 71.6 cm) the fire (NOAA 2020). The average annual high temperature was 21.2° C and the average annual low was 6.1° C (NOAA 2020). The soils are composed of fine loamy sands, fine sandy loams, and fine sands (Soil Survey Staff 2020). The dominant plant species in the area were sand dropseed (*Sporobolus cryptandrus*), western ragweed (*Ambrosia psilostachya*), little bluestem (*Schizacyrim scoparium*), Russian thistle (*Salsola tragus*), alkali sacaton (*Sporobolus airoides*), sand sagebrush (*Artemisia filifolia*), and blue grama (*Bouteloua gracilis*). The majority of the area was used for cattle ranching and livestock production. Other major uses in the area included row crop agriculture, energy exploration, and properties enrolled in Conservation Reserve Program (CRP). The study site was composed of 76.6% grassland, 14.2% cropland, and 5.5% CRP (Robinson et al. 2018). The study was conducted primarily in the southern half of Clark County along the Cimarron River floodplain. This area was characterized by alkali flats and subirrigated soils covered by patches of small and large sand dunes that promote a heterogeneous mix of mixed-grass and sand sagebrush prairies. Before the fire, a low-intensity long-duration rotational grazing system among large pastures was used for both cow/calf and yearling herds, set to take half of the

available forage each growing season. Post-fire, grazing pressure varied following the loss of many cattle and variable restocking as ranches recovered from the fire. There was no use of prescribed fire in the study area.

Methods

To examine changes in grassland vegetation and lesser prairie-chicken habitat following megafire, I conducted a comprehensive analysis of vegetation measurements collected before and after the 2017 Starbuck fire. First, I quantified overall effects to vegetation structure and composition by comparing measurements at points randomly distributed across the study area before and after the fire. Next, to examine potential changes in the habitat and vegetation used by lesser prairie-chickens, I compared points used by birds to randomly distributed points. I was most interested in vegetation during the breeding season, as it is most important for lesser prairie-chicken population persistence, so I used a subset of data from the breeding season for a more in-depth analysis of the fire's effects on vegetation and habitat. To track grassland recovery over time and estimate when grasslands returned to a pre-fire state, I compared measurements taken during the breeding season at the exact same random locations before and after the fire. To test if vegetation characteristics were influenced by the severity of the fire, I explored linkages between breeding season vegetation measurements and a remotely sensed index of burn severity. Finally, to quantify effects of the megafire on key reproductive habitat essential for lesser prairie-chickens, I used criteria previously established in the literature to estimate the amount of available nest and brood habitat before and after the fire.

Vegetation Surveys

I conducted vegetation surveys two years before the fire during 2014–2016 and two years after, during 2018–2020. Before the fire, I surveyed vegetation at random points within patches

across the study area in the spring (Mar–May), summer (Jun–Aug), and fall/winter (Oct–Feb). Patches were defined as areas >2 ha in area that consisted of homogenous vegetation and land use, identified using aerial imagery using basemaps in ArcMap 10.2 (ESRI, Inc., Redlands, CA, USA) and confirmed on the ground (Figure 4.2). Within each patch, points were randomly generated before the fire at a rate of 1 per 4 ha, with a maximum of 10 points in a patch (Sullins et al. 2018b, Lautenbach et al. 2019, Kraft et al. 2021). Following the fire, I conducted vegetation surveys at the same random points within patches surveyed before the fire where I had reliable location data. I surveyed all randomly selected points in the spring, and at a stratified random sample of those points in the summer and fall/winter each year. Vegetation data collected in spring and summer were classified as breeding season (defined as 15 Mar–15 Sep), and points surveyed in the fall/winter were classified as nonbreeding (16 Sep–14 Mar).

I also conducted vegetation surveys at points used by female lesser prairie-chickens in the breeding and nonbreeding seasons. I limited my analysis to females as the majority of captured birds were female because I was interested lesser prairie-chicken reproductive success. I randomly selected two locations per week for each female lesser prairie-chicken captured and outfitted with a transmitter (Chapter 2) and collected vegetation data at those locations. I also conducted vegetation surveys at nest sites, located as described in Chapter 2.

At each point (random, used, nest) before and after the fire, I measured vegetation following protocols established in the lesser prairie-chicken literature (Sullins et al. 2018b, Lautenbach et al. 2019, Gehrt et al. 2020). I measured 100%, 75%, 50%, 25%, and 0% visual obstruction in each cardinal direction using a Robel pole placed at point center (Robel et al. 1970). I used a modified Daubenmire frame (60 x 60 cm) to estimate percent cover of grass, forbs, litter, bare ground, shrub, and annual bromes (*Bromus* spp., primarily *B. tectorum* and *B.*

japonicus) at the point center, as well as at locations 4 m from the point center in each cardinal direction. I also measured vegetation height at each of these five locations where I estimated percent cover. Litter depth (cm) was measured every 0.5 m along 4-m transects in each cardinal direction from point center. As litter depth heterogeneity can be important for nesting lesser prairie-chickens (Lautenbach 2015, Sullins 2017), I also considered the standard deviation of litter depth measurements as a metric of this heterogeneity. I visually estimated percentage of the top three most abundant plant species within the 4-m radius circle surrounding each point.

Change in Vegetation Structure and Composition

To examine overall patterns in grassland structure and composition before and after the fire, I conducted a principal components analysis (PCA) on z -scaled vegetation data from used and random points. Next, I used a multivariate analysis of variance (MANOVA) to test for differences in vegetation characteristics between seasons (breeding or nonbreeding) in random points. Following a significant difference (Wilks' λ $P < 0.05$), I proceeded with separate analyses for each season. For the breeding season, I used MANOVA to test for differences between burned and unburned areas before and after the fire. When a significant difference was identified (Wilks' λ $P < 0.05$), I used analysis of variance (ANOVA) with a Tukey post hoc analysis to identify significant differences ($P < 0.05$) in each vegetation characteristic between burned and unburned areas before and after the fire. From these same random breeding season points, I also estimated the change in plant species composition by summing percentages of the top 3 most abundant plant species, then estimated the overall percent abundance of each plant species and ranked the top 10 most abundant species in burned and unburned areas before and after the fire.

Because almost all points collected in the nonbreeding season before the fire were burned, I was unable to compare burned and unburned areas in the nonbreeding season.

Therefore, I limited analysis to only burned areas and used MANOVA to test for significant differences (Wilks' λ $P < 0.05$) in vegetation characteristics before and after the fire in the nonbreeding season. Once a significant effect was detected, I proceeded with ANOVA to identify significant differences ($P < 0.05$) in each characteristic before and after the fire.

Change in Lesser Prairie-Chicken Vegetation Use

To assess potential changes in vegetation use by lesser prairie-chickens, I compared points used by lesser prairie-chickens with those available (random points). I first used MANOVA to test for differences in vegetation characteristics between fire status (before or after), use (used or available), and season (breeding or nonbreeding). If there was a significant interaction (Wilks' λ $P < 0.05$), I conducted separate MANOVA for each season before and after the fire. If this was also significant (Wilks' λ $P < 0.05$), I used ANOVA to identify significant differences ($P < 0.05$) in each vegetation characteristic between used and available points. Finally, I used MANOVA to assess differences in vegetation characteristics between nest points and those available (breeding season random points) before and after the fire. Upon finding a significant interaction (Wilks' λ $P < 0.05$), I compared nest and available points separately before and after the fire, and used ANOVA to identify differences ($P < 0.05$) in each vegetation characteristic between nest and available points.

Vegetation Recovery Following Megafire

In addition to examining overall changes before and after the fire, I evaluated vegetative recovery over time at static locations in burned areas up to 2.5 years post fire. I used a paired Hotelling T^2 test to examine multivariate differences in vegetation characteristics at the exact same points before and after the fire. Points sampled in the spring or summer of 2014 or 2015 were compared to their matching point that was sampled in the corresponding season in both

2018 and 2019, resulting in four comparisons (Spring Before and Spring 2018, Summer Before and Summer 2018, Spring Before and Spring 2019, Summer Before and Summer 2019). As I was primarily interested in vegetation characteristics during the breeding season, I selected post-fire points from those conducted in the spring and summer before the fire, which resulted in no matching points in the fall post-fire. Once a multivariate difference was detected from the Hotelling T^2 test ($P < 0.05$) I used paired t -tests with a Bonferroni correction ($P < 0.0036$; $0.05/14$ vegetation characteristics) to examine changes in the mean of each vegetation characteristic before and after the fire and see when there were no longer differences in vegetation characteristics after the fire.

Linking Burn Severity to Vegetation Characteristics

To evaluate how vegetation characteristics affect burn severity and how grassland recovery may be influenced by the severity of the fire, I examined correlations between vegetation characteristics and a metric of burn severity. I used the difference in normalized burn ratio (dNBR) calculated for the Starbuck fire by the Monitoring Trends in Burn Severity project (MTBS 2019) using satellite imagery from before (20 February 2017) and after (17 March 2017) the fire. I limited analysis to vegetation data collected at random points during the breeding season in burned areas as we expected breeding habitat, specifically nesting habitat, to be most affected by the fire.

Effect of Megafire on Abundance of Reproduction Habitat

Using criteria established in previous literature, I estimated nesting and brooding habitat abundance to evaluate the effects of the fire on available reproductive habitat (Lautenbach 2015, Sullins et al. 2018b, Lautenbach et al. 2019, Gehrt et al. 2020). Random locations having an average 75% visual obstruction between 1.5–3.5 dm and $\leq 10\%$ bare ground were identified as

nest habitat. Brood habitat was classified as locations with an average 50% visual obstruction between 2–5 dm and forb cover between 7–37%. I estimated the proportion of points meeting nest and brood habitat requirements from random points surveyed in the breeding season within 5 km of known leks, as most females nest and raise their brood within this area (Winder et al. 2015, Sullins et al. 2018*b*, Lautenbach et al. 2019, Gehrt 2020). I then averaged estimates among all leks to get an overall estimate of available nesting and brooding habitat before and after the fire.

Results

Vegetation Surveys

I collected vegetation measurements at a total of 1,978 random points before the fire, 1,768 of which burned in the Starbuck fire in March 2017. Of the 1,978 random points used for analysis, 1,587 were surveyed in the breeding season and 391 were surveyed in the nonbreeding season. Following the fire, I surveyed 2,803 random points, of which 2,266 were in burned areas. Of the total 2,803 random points, 2,197 were surveyed in the breeding season and 606 were surveyed in the nonbreeding season.

I collected vegetation measurements at 1,067 points used by female lesser prairie-chickens before the fire, 690 in the breeding season and 377 in the nonbreeding season. Following the fire, I surveyed 1,212 used points, of which 803 were surveyed in the breeding season and 409 were surveyed in the nonbreeding season. I collected vegetation data at 43 nests before the fire and 31 nests after the fire.

Change in Vegetation Structure and Composition

PCA analysis of vegetation characteristics revealed an overall loss of heterogeneity following the fire in both vegetation structure and composition (Figure 4.3). Principal

components axes 1 and 2 had eigenvalues of 4.58 and 2.23, explaining 32.72% and 15.91% of variation in the data, respectively. Visual obstruction was associated with PCA axis 1, with top ranked loadings of 50% VOR (0.43), 75% VOR (0.43), 25% VOR (0.41), and 100% VOR (0.39). Axis 2 consisted of grassland composition, with the most important variables being percent cover of grass (0.52), litter depth (0.47), and percent cover of bare ground (-0.45). I detected a difference between breeding and nonbreeding seasons (Wilks' $\lambda = 0.90$, $F_{14, 4,760} = 37.63$, $P < 0.001$) for overall vegetation characteristics at random points, so I conducted separate MANOVA analyses by season. There was a significant interaction between fire and burn status during the breeding season (Wilks $\lambda = 0.96$, $F_{14, 3,767} = 10.59$, $P < 0.001$), so I conducted ANOVAs for each vegetation characteristic followed by a Tukey post-hoc analysis.

In the breeding season (15 Mar–15 Sep), there was little difference in average vegetation height between burned and unburned areas before and after the fire ($F_{3, 3,780} = 3.69$, $P = 0.01$; Table 4.1). Visual obstruction at 0% (analogous to vegetation height) was higher in burned areas post-fire ($F_{3, 3,780} = 24.03$, $P < 0.001$). Visual obstruction at 25% was lower in both burned and unburned areas following the fire, but there was no difference between these areas post-fire ($F_{3, 3,767} = 20.02$, $P < 0.001$). Visual obstruction at 50% ($F_{3, 3,780} = 12.80$, $P < 0.001$) and 75% ($F_{3, 3,780} = 9.53$, $P < 0.001$) decreased in burned areas post-fire, but were not different from unburned areas after the fire. Visual obstruction at 100% was reduced in burned areas post-fire, and lower than unburned areas post-fire ($F_{3, 3,780} = 28.98$, $P < 0.001$). Percent cover of litter ($F_{3, 3,780} = 15.53$, $P < 0.001$) and grass ($F_{3, 3,780} = 83.53$, $P < 0.001$) were greatest in unburned areas post-fire. In burned areas, percent cover of grass increased following the fire. There was a greater percent cover of shrubs in burned areas before the fire, which decreased after the fire ($F_{3, 3,780} = 19.97$, $P < 0.001$). However, percent cover of shrubs in burned areas post-fire was still greater

than unburned areas post-fire. Percent cover of forbs was reduced overall after the fire, but with more forbs in burned areas than unburned post-fire ($F_{3, 3,780} = 44.86, P < 0.001$). This was the opposite of trends before the fire, when areas that burned had less forbs than unburned. Before the fire, there was no difference in percent cover of bare ground between burned and unburned areas ($F_{3, 3,780} = 81.57, P < 0.001$). Post-fire burned areas had greater percent cover of bare ground and post-fire unburned areas had less percent cover of bare ground. Percent cover of annual bromes was greater in burned areas than unburned areas before the fire ($F_{3, 3,780} = 24.91, P < 0.001$). Following the fire, that trend reversed, with burned areas having less annual bromes than unburned areas. Litter depth was lower in burned areas both before and after the fire ($F_{3, 3,780} = 53.13, P < 0.001$). Within these burned areas, litter depth was reduced post-fire. Litter depth heterogeneity (as estimated by litter depth standard deviation) was lowest in burned areas post-fire ($F_{3, 3,767} = 59.97, P < 0.001$).

Overall occurrence of species in the top 10 most abundant plant species before and after the fire remained similar, but there were some shifts in abundance (Table 4.2). Burned areas before the fire were dominated by sand dropseed (18%), followed by blue grama (8%), western ragweed (7%), Russian thistle (7%), and little bluestem (7%). Post-fire, burned areas contained similar species, with blue grama (12%), little bluestem (11%), and sand dropseed (10%) as the most dominant species. Forb species declined, with western ragweed falling from 3rd to 8th (5%) and Russian thistle falling from 4th to 14th (2%). Unburned areas were dominated by little bluestem both before (25%) and after (28%) the fire, and also had a high prevalence of sideoats grama (*Bouteloua curtipendula*) before (15%) and after (9%). Similar to burned areas, sand dropseed (10%), Russian thistle (8%), and blue grama (6%) were common in unburned areas before the fire. After the fire, Indiangrass (*Sorghastrum nutans*) was a dominant species in

unburned areas (11%), along with blue grama (10%) and sand dropseed (8%). Russian thistle remained abundant in unburned areas post-fire (5%), while western ragweed declined from 7th (4%) to 14th (1%). Overall, burned areas were more diverse, with the top 10 species making up approximately 69% and 73% of total percent abundance of the most abundant species before and after the fire, respectively, compared to 81% and 83% in unburned areas before and after the fire, respectively.

In the nonbreeding season (16 Sep–14 Mar), there was a significant difference in overall vegetation characteristics before and after the fire (Wilks $\lambda = 0.53$, $F_{14, 814} = 52.21$, $P < 0.001$), so I conducted one-way ANOVAs for each vegetation characteristic. Vegetation height was higher after the fire ($F_{1, 827} = 13.39$, $P < 0.001$), as was visual obstruction at 0% ($F_{1, 827} = 146.61$, $P < 0.001$; Table 4.3). The only other measure of visual obstruction that differed in the nonbreeding season post-fire was 75%, which decreased ($F_{1, 827} = 4.38$, $P = 0.04$). All measures of composition except percent cover of shrub ($F_{1, 827} = 1.76$, $P = 0.18$) and annual bromes ($F_{1, 827} = 2.84$, $P = 0.09$) differed post-fire. Percent cover of litter ($F_{1, 827} = 84.11$, $P < 0.001$) and bare ground ($F_{1, 827} = 19.61$, $P < 0.001$) increased, while percent cover of grass ($F_{1, 827} = 8.03$, $P = 0.005$) and forb ($F_{1, 827} = 36.28$, $P < 0.001$) decreased. Litter depth ($F_{1, 827} = 69.78$, $P < 0.001$) and litter depth heterogeneity ($F_{1, 827} = 214.67$, $P < 0.001$) were both lowered post-fire.

Change in Lesser Prairie-Chicken Vegetation Use

Overall comparison of used and available points revealed lesser prairie-chicken use of areas with reduced visual obstruction post-fire, increased grass cover, and less bare ground. There was a significant interaction between season, fire status, and use (Wilks $\lambda = 0.99$, $F_{14, 7,576} = 4.42$, $P < 0.001$) so I compared used and available points by breeding and nonbreeding seasons separately before and after the fire. There was a significant interaction between nest and

available points and fire status (Wilks $\lambda = 0.99$, $F_{14, 4,244} = 2.32$, $P = 0.004$), so I compared vegetation characteristics of nest and available points separately before and after the fire.

Before the fire, female lesser prairie-chickens in the breeding season showed no selection for visual obstruction at any level except 100%, which they used at a slightly lower level than available ($F_{1, 2,588} = 5.87$, $P = 0.02$; Figure 4.4). Conversely, for nests they used consistently greater visual obstruction at every level. After the fire, visual obstruction was used at lower levels than available at every level except 100% ($F_{1, 3,088} = 0.15$, $P = 0.70$). For nests, only 100% visual obstruction differed among nest and random points; nest locations had greater visual obstruction than available ($F_{1, 2,316} = 3.91$, $P = 0.05$). Points used by lesser prairie-chickens in the breeding season before the fire had lower percent cover of litter ($F_{1, 2,588} = 5.33$, $P = 0.02$) and shrub ($F_{1, 2,588} = 8.42$, $P = 0.004$) than available. They also used points with slightly higher vegetation height ($F_{1, 2,588} = 8.48$, $P = 0.004$) and less litter depth than available ($F_{1, 2,588} = 7.62$, $P = 0.006$). Nest points before the fire had a greater percent cover of grass ($F_{1, 1,941} = 7.34$, $P = 0.007$), lower percent cover of bare ground ($F_{1, 1,941} = 7.26$, $P = 0.007$), and greater litter depth values than available ($F_{1, 1,941} = 29.93$, $P < 0.001$). Post-fire, breeding season used points had more grass cover ($F_{1, 3,088} = 58.90$, $P < 0.001$) and less bare ground ($F_{1, 3,088} = 77.21$, $P < 0.001$), shrub cover ($F_{1, 3,088} = 27.62$, $P < 0.001$), and litter cover ($F_{1, 3,088} = 5.41$, $P = 0.02$) than available. However, they used points with increased litter depth ($F_{1, 3,088} = 10.62$, $P = 0.001$). Similar to pre-fire, post-fire nests had more grass cover ($F_{1, 2,316} = 9.40$, $P = 0.002$), less bare ground ($F_{1, 2,316} = 12.78$, $P < 0.001$), and greater litter depth ($F_{1, 2,316} = 5.34$, $P = 0.02$) when compared to available.

During the nonbreeding season before the fire (Figure 4.5), female lesser prairie-chickens consistently selected for lower visual obstruction at every level. The same trend occurred at

every level of visual obstruction post-fire, but at even further reduced values of visual obstruction. Before the fire, used points in the nonbreeding season were characterized by lower vegetation height ($F_{1, 810} = 17.91, P < 0.001$), more forb ($F_{1, 810} = 5.53, P = 0.02$) and bare ground cover ($F_{1, 810} = 4.13, P = 0.04$), less shrub cover ($F_{1, 810} = 19.35, P < 0.001$), lower litter depth ($F_{1, 810} = 19.86, P < 0.001$) and litter depth heterogeneity ($F_{1, 810} = 21.86, P < 0.001$) compared to available. After the fire, lesser prairie-chickens also selected for reduced vegetation height ($F_{1, 1,103} = 39.04, P < 0.001$) and less shrub cover than available ($F_{1, 1,103} = 19.48, P < 0.001$). Used points post-fire also had greater percent cover of litter ($F_{1, 1,103} = 8.24, P = 0.004$) and greater litter depth than available ($F_{1, 1,103} = 36.27, P < 0.001$). While the direction of selection for litter depth switched before and after the fire, the mean value of litter depth at used points before and after remained similar.

Vegetation Recovery Following Megafire

Of the vegetation characteristics measured, few (5/14) had recovered or showed no difference from pre-fire measurements in spring 2018, one year post-fire. By spring 2019, two years post-fire, half (7/14) had recovered, and by summer 2019 (2.5 years post-fire) the majority (11/14) had recovered or surpassed pre-fire measurements. Hotelling's T^2 paired test revealed an overall negative difference in vegetation characteristics measured at the same locations before and after the fire in spring 2018 (Hotelling's $T^2 = 21.77, P < 0.001$), summer 2018 (Hotelling's $T^2 = 45.45, P < 0.001$), and spring 2019 (Hotelling's $T^2 = 34.05, P < 0.001$), indicating vegetation characteristics remained reduced overall 2 years post-fire. By summer 2019, there was an overall positive difference between vegetation characteristics before and after the fire (Hotelling's $T^2 = 23.23, P < 0.001$), suggesting overall recovery of vegetation 2.5 years post-fire.

Vegetation height had recovered one year post fire in spring 2018, as did visual obstruction at 0%, and both had larger values by summer 2019 than before the fire (Tables 4.4, 4.5). Visual obstruction at every level except 0% (analogous to vegetation height) remained lowered through the summer of 2018 (Figure 4.6). In spring 2019, visual obstruction at 75% had returned to pre-fire levels, and by summer 2019 all measures of visual obstruction had returned to pre-fire levels, except visual obstruction at 25%. Percent cover of grass remained similar to pre-fire measurements throughout 2018, increased in the spring of 2019, and remained high through summer 2019. There was an increase in percent cover of bare ground throughout 2018, but it recovered by spring 2019 and was lower than pre-fire levels by summer 2019. Percent cover of forbs decreased in the spring of 2018, and further still in the summer of 2018. In spring 2019, forb cover was still much lower than before the fire, but remained similar to spring 2018 cover. However, by summer 2019 forb cover increased, returning to pre-fire levels. Percent cover of shrubs followed a similar trend, with reduced shrub cover through spring 2019, but returning to pre-fire levels by summer 2019. Before the fire, percent cover of annual bromes was low in the spring and high in the summer. After the fire, percent cover of annual bromes remained low throughout the two years of my study and was reduced from pre-fire measurements in the summer of both 2018 and 2019. Percent cover of litter did not differ post-fire and by the summer of 2019 had increased from pre-fire levels. Measurements of litter depth differed from this trend, with reduced litter depth and litter depth heterogeneity through the spring and summer of 2018. By spring 2019, litter depth had surpassed pre-fire levels while litter depth heterogeneity remained similar. In the summer of 2019, litter depth remained at pre-fire levels, while heterogeneity decreased slightly.

Linking Burn Severity to Vegetation Characteristics

Overall, burn severity (dNBR) did not exhibit strong correlation with vegetation characteristics measured before or after the fire ($r \leq 0.46$; Figure 4.7). Burn severity was weakly positively correlated with percent grass cover ($r = 0.46$) and negatively correlated with percent cover of bare ground ($r = -0.40$) before the fire, suggesting that areas with more grass and less bare ground burned at higher severity. After the fire, the relationships of dNBR and grass cover ($r = -0.45$) and dNBR and bare ground cover ($r = -0.43$) remained similar. Shrub cover was also weakly correlated with dNBR before ($r = -0.28$) and after ($r = -0.29$), suggesting that areas with more shrubs burned at lower severity. Before the fire, dNBR was weakly correlated with litter depth ($r = 0.25$) that reduced post-fire ($r = 0.12$), indicating increased litter depth also contributed to greater burn severity. Overall, this suggests minor effects of vegetation composition on burn severity and little effect of burn severity on grassland composition post-fire.

Effect of Megafire on Abundance of Reproduction Habitat

There was far less nesting habitat available in 2018 ($10.78\% \pm 12.84$ of points) compared to 2019 ($22.07\% \pm 8.63$) after the fire. However, the overall abundance of available nesting habitat did not differ before and after the fire, with $16.41\% \pm 3.50$ of points before and $16.54\% \pm 10.41$ of points after meeting nesting habitat requirements (Table 4.6). There was more variability in the proportion of nest habitat around leks post-fire, ranging from 7.31–48.53% post-fire, compared to 13.02–24.54% pre-fire. Similar to the abundance of nest habitat, there was slightly less brood habitat available in 2018 ($20.41 \pm 6.75\%$) compared to 2019 ($24.17 \pm 5.95\%$). The overall abundance of available brood habitat decreased slightly following fire, from $27.32 \pm 6.18\%$ before to $22.29 \pm 5.82\%$ after.

Decreased nest habitat abundance in 2018 was a result of reduced values of visual obstruction and increased amounts of bare ground (Table 4.6). In 2019, the percent of points meeting optimal VOR returned to pre-fire amounts, and the percent of points with optimal bare ground increased from pre-fire measurements. Decreased brood habitat after the fire was primarily limited by the reduction of forbs that lasted through both 2018 and 2019. Percent of points with optimal brood VOR were reduced in 2018, but returned by 2019.

Discussion

My study provides evidence of short-term effects (<3 years post-fire) on grassland vegetation structure and composition following megafire in the mixed-grass prairie. Although the grassland flora appeared resilient to the megafire and mostly recovered 2.5 years post-fire, the loss of heterogeneity within grasslands at a landscape scale had emergent effects on useable space for lesser prairie-chickens. As lesser prairie-chickens require complex, heterogeneous grasslands, the broad-scale homogenization of grasslands following the megafire degraded lesser prairie-chicken habitat in the short term. Specifically, decreased visual obstruction and nest habitat abundance in first year after the fire highlight potential detrimental effects of such a large fire. Native grassland flora demonstrated resilience to this extreme disturbance and effects to grassland vegetation from this megafire were not drastically different from other wildfires and prescribed burns (Collins and Barber 1986, Engle and Bidwell 2001, Wester et al. 2014). Despite relatively quick grassland recovery, lesser prairie-chicken populations remain diminished in the area. Grasslands must be heterogeneous at optimal scales of patchiness to provide habitat for lesser prairie-chickens, and my research enforces the idea that fire disturbance must be applied at the appropriate size and scale for it to be useable (Guthery 1997).

Following megafire, I observed a homogenizing effect on grassland structure and composition overall. PCA analysis revealed that vegetation characteristics at points after the fire were far less variable and diverse than before the fire. Values of visual obstruction and litter depth were overall decreased, and grassland composition was dominated by two main functional groups (grass and bare ground). The loss of heterogeneity is likely explained in part by the timing of the fire in early March, prior to the start of the growing season, as the use of early spring prescribed burning can result in reduced diversity and heterogeneity in grasslands compared to summer season burns (Howe 1994*b*, Towne and Kemp 2008, Weir and Scasta 2017). Dormant season fires under other conditions generally remove close to 100% of above ground biomass, as compared to growing season burns where some vegetation remains (Bragg 1982, Howe 1994*b*, Copeland et al. 2002, Ruthven et al. 2008, Knapp et al. 2009). Therefore, the megafire likely consumed herbaceous vegetation across the majority of the study area, leading to a homogenous vegetative recovery. The scale of the fire was detrimental for lesser prairie-chickens as vast areas of homogenous recovering habitat allows for limited useable space (Guthery 1997). Useable space for lesser prairie-chickens requires lek, nest, and brood habitats to all be relatively close. Nests and broods are generally located within 5 km of a lek (Gehrt et al. 2020), with the majority of nests occurring even closer (within 1.6 km of a lek [Hagen et al. 2013]) and brood habitat needs to be within ~1 km of nest habitat based on limited chick dispersal ability (Lautenbach 2015, Plumb 2015). Therefore, only areas along edges of the burn with both burned and unburned areas in close proximity (nearby leks) would provide the necessary heterogeneity for overall reproductive habitat. While our study area was largely in the interior of the burn and I was unable to directly examine habitat use and vegetation along the fire perimeter, the limited interspersion of burned and unburned patches from such a large fire likely

restricted available habitat. In addition, areas burned by the megafire was primarily limited by cropland and roads, precluding an increase of desirable within grassland heterogeneity and limiting lesser prairie-chicken population size and recovery potential.

Following the fire, grassland recovery appeared swift. One year after the fire, grasslands looked superficially similar to pre-fire conditions, with average vegetation height similar to pre-fire values. While we do not have vegetation data immediately following the fire, a study by Steiner et al. (2020) on the Starbuck fire found indices of remotely sensed vegetation greenness (MODIS imagery) returned to pre-fire levels months after the fire following the 2017 summer growing season and enhanced primary productivity in burned grasslands, suggesting a rapid recovery. Ample precipitation was received in the spring of 2017 immediately following the fire, which likely contributed to grasses reaching pre-fire heights within a year, as precipitation can strongly influence grassland recovery following fire (Jackson 1965, Wright 1974*b*, Anderson 2006). Furthermore, there was likely a reduced amount of grazing on regrowth immediately following the fire, as somewhere between 5,000–9,000 cattle died and millions of dollars in fencing infrastructure were lost in the fire (Bickel 2018, Rethorst et al. 2018). By February 2018, it was estimated that 90% of fences had been rebuilt (Bickel 2018) and grazing had largely been re-established a year after the fire, although likely still in a reduced intensity. While we did not have grazing data, and grazing effects are hard to quantify due to moving windows during restocking, the lack of immediate grazing in the year after the fire (and potentially reduced grazing pressure in the following years) likely contributed to fast recovery and high vegetation heights post-fire, as grazing can substantially reduce grass and vegetation height following burning (Vermeire et al. 2004, Starns et al. 2020). While grasslands burned by the Starbuck fire

appeared superficially similar to pre-fire conditions within a year, fire can have less obvious and longer lasting effects on vegetation composition and structure.

Despite quick recovery of vegetation height, visual obstruction decreased at almost every level, particularly one year post-fire, and did not improve until summer 2019, three growing seasons post-fire. Fire's effects on visual obstruction are likely linked to the removal of residual vegetation, litter, and thatch that provide most of the fuels for dormant season fire (Wright 1974a, Vermeire and Gillen 2001, Knapp et al. 2009). Unfortunately, even with enhanced regrowth post-fire visual obstruction cannot quickly return, as it depends on interacting factors including years of vegetation growth, precipitation patterns, and grazing (Robel 1970, McNew et al. 2015, Kraft et al. 2021). Visual obstruction is a critically selected feature for nesting prairie-chickens (McNew et al. 2014, Lautenbach et al. 2019), important for lek persistence (Gehrt et al. 2020), and key for nonbreeding habitat (Kraft et al. 2021). As a result, the megafire limited areas available to lesser prairie-chickens post-fire and likely contributed to reduced nest survival and overall population (Chapter 2). Nest sites pre-fire had greater visual obstruction compared to available at every level, while post-fire nests had visual obstruction that matched the low measures of visual obstruction available post-fire. Conversely, during the breeding season after the fire, female lesser prairie-chickens that were not actively nesting used areas with even lower visual obstruction than available. Assuming that lesser prairie-chickens are selecting the best habitat available (Fretwell and Lucas 1970), use of areas with reduced visual obstruction may be linked to habitat requirements for brood rearing and use of more open areas (Fields et al. 2006, Bell et al. 2010, Lautenbach 2015) or to evade mammalian predators (Winder et al. 2018). In patch-burn grazing systems, female lesser prairie-chickens overall selected 2-year post-fire patches in the summer, within which they selected for lower visual obstruction than available

(Lautenbach 2017). Therefore, megafire may have improved post-nesting habitat for adult lesser prairie-chickens, which was not available before the fire when visual obstruction was overall high. Differences in selection between nests and used points in the breeding season pre- and post-fire underscore the need for heterogeneity in vegetation structure across areas used by lesser prairie-chickens. With smaller prescribed burns and patch-burn grazing systems it is possible to achieve such heterogeneity and provide areas of differing visual obstruction in close proximity (Lautenbach 2017), but that is not the case following megafire.

While vegetation structure was altered following the megafire, I also observed changes in the composition of functional groups including increased grass and bare ground cover, and reduced forb and shrub cover. The most consistent change occurred in percent cover of forbs, which decreased ~40% after the fire in both burned and unburned areas. This was contrary to my predictions, as forbs generally increase in recently burned and grazed areas (Boyd and Bidwell 2001, Fuhlendorf and Engle 2004, Vermeire et al. 2004, Winter et al. 2012). The decrease in forbs may partially be due to the aforementioned lack of immediate grazing on regrowth due to cattle and fencing losses from the fire, potentially limiting the post-fire grazing disturbance that can help promote forbs (Starns et al. 2020). Following fire, cattle selectively graze regrowth of dominant warm-season grasses, usually allowing for an increase in forbs and overall diversity (Collins and Barber 1986, Drewa and Havstad 2001). Furthermore, the timing of the fire during the dormant season in early March likely favored an increase in grass cover and reduced forb cover, as documented within the southern Great Plains and in other systems (Peoples et al. 1994, Engle and Bidwell 2001, Howe 2011, Weir and Scasta 2017). Early spring fires will kill early blooming forbs, whereas warm-season grasses are still dormant and not harmed by fire, and may experience increased growth post-fire (Lovell et al. 1982, Howe 1994a, Copeland et al. 2002,

Russell et al. 2015). Particular forb species declined, such as Russian thistle, which was extensive at the field site before the fire, but decreased after. This was opposite my predictions, as Russian thistle often colonizes disturbed areas and increases following fire, but may be related to the strong response of grass to this fire and the poor competitive ability of Russian thistle (Bernau and Eldredge 2018). The megafire greatly reduced the prevalence of invasive Russian thistle in burned areas, while its presence remained high in unburned areas. Other forb species remained common following fire, such as western ragweed, which has variable response to fire and whose abundance can vary without influence of grass dominance (Peoples et al. 1994, Vermeire 1997, Engle and Bidwell 2001). Contrary to many fears, it does not appear that megafire will result in a widespread takeover of invasive forbs in the mixed-grass prairie and may help reduce invasive species under the right conditions (Harr et al. 2014).

While the presence of invasive annual brome grass species was low at my study site, I did document reduced percent cover of these troublesome grass species. While not a major issue in the mixed-grass prairie, invasion of annual bromes and cheatgrass is a major problem in many other North American grasslands and an issue for greater sage-grouse (*Centrocercus urophasianus*) in the Great Basin, where large wildfires promote the invasion of cheatgrass and loss of native sagebrush habitat (Nelle et al. 2000, USFWS 2015, Coates et al. 2016). I found the opposite, with reduced cover of annual bromes two years after the fire. Because precipitation patterns in the Great Plains are already a major limiting factor for annual brome invasion, the pronounced concentration of rainfall in the warm season post-fire likely also contributed to reduced presence of annual bromes post-fire (Bradley 2009). If future wildfires occur during years with a dry summer and wet early spring, annual brome invasion may be a potential issue. However, my results provide further evidence that fire does not promote the invasion of annual

bromes in the Great Plains, and may be an effective form of control (Harmony 2007, Porensky and Blumenthal 2016). Fire also provides an opportunity to follow up with herbicide control of invasive annual bromes in areas where they are problematic (Bahm et al. 2011). Most encouraging is the evidence that even with increased size and severity of fire, invasive annual bromes seem to be ineffective at outcompeting native perennial grass species that respond well to fire.

I observed an increase in percent cover of grass and bare ground post-fire. As previously mentioned, the increase in grass cover was likely linked to reduced grazing, allowing for dominant warm season grasses to proliferate without reduction from selective grazing, and fire timing, as early spring, dormant season burns tend to favor grasses (Howe 1994*b*, Vermeire et al. 2004, Weir and Scasta 2017, Starns et al. 2020). Several tallgrass species such as little bluestem, big bluestem, and Indiangrass benefitted from the fire and increased in abundance, not surprising as many of these species are fire adapted (McMurphy and Anderson 1965, Wright 1974*a*). Indiangrass increased greatly in not only burned areas, but also unburned areas post-fire, likely due to its strong positive response to fire (Hadley and Kieckhefer 1963, Stilleti and Knapp 2002, Towne and Kemp 2008). The increase in certain tallgrass species likely provided some benefit, as many of these grasses provide excellent cover and are associated with lesser prairie-chicken nests (Lautenbach et al. 2019). The overall increase in grass should have benefitted lesser prairie-chickens as they consistently selected for increased grass cover during the breeding season and for nesting post-fire.

Unfortunately, increased grass cover was accompanied by an increase in percent cover of bare ground, likely negating any potential benefits from increased grass cover. Lesser prairie-chickens select areas with minimal bare ground for nesting (Hagen et al. 2013, Lautenbach et al.

2019), so the overall increase in bare ground post-fire, particularly the ~10% increase in bare ground observed in 2018, likely contributed to reduced nest success (Chapter 2) and nest habitat availability post-fire. Lesser prairie-chicken nest sites before and after the fire had less bare ground than available. While pre-fire breeding season points used by female lesser prairie-chickens had similar amounts of bare ground as available, post-fire used points had less bare ground than available. This shift in habitat use shows a strong avoidance of bare ground post-fire, and is likely related to increased use of unburned areas post-fire (i.e., CRP fields; Chapter 3), which had a much lower percent cover of bare ground. Use of these unburned areas (particularly for nesting) post-fire, likely helped maintain the relatively high adult survival post-fire (Chapter 2) and provided areas with higher quality nest sites post-fire, analogous to lesser prairie-chicken use of CRP during drought (Sullins et al. 2018*b*). While increased bare ground may benefit broods, facilitating easier chick movement, too much bare ground can expose them to predators and severe weather, lowering survival as young chicks are unable to thermoregulate (Bell et al. 2010, Lautenbach 2015). Given little change in chick survival (Chapter 2), it is unlikely that the increase in bare ground provided much benefit for broods, with negative effects to nest habitat outweighing any potential benefits for broods.

Percent cover of litter did not differ following the fire, but litter depths were reduced, particularly in the first year post-fire. Because thinned grass cover post-fire exposes more ground and areas of litter than before the fire, litter depth provides a better estimate of litter as it accounts for all litter on the ground, both seen and unseen from an overhead view. I predicted the abundance of litter to be greatly reduced post-fire, as litter provides excellent fuel and is quickly consumed by grassland fire (Wright 1974*a*, Knapp et al. 2009, Winter et al. 2012). Litter can take several years to build up following fire and is dependent on residual vegetation from

previous growing seasons and grazing practices (Hadley and Kieckhefer 1963, Winter et al. 2012, Kraft et al. 2021), but we noted a fairly fast recovery, with increased litter depths two years post-fire. Litter is key for grassland recovery, as it can help to insulate soil, preventing drying and temperature fluctuations that can affect plant growth (Vermeire et al. 2011). It is also important for lesser prairie-chickens, as litter is consistently selected by nesting hens (Hagen et al. 2013, Lautenbach et al. 2019). Pre-fire nest sites had litter depths double what was available and post-fire nests had greater than available litter depth. However, litter depth at nest sites post-fire was reduced 43% compared to pre-fire, indicating the loss of litter post-fire likely contributed to reduced nest survival (Chapter 2).

Linking Burn Severity to Vegetation Characteristics

Burn severity had weak relationships with both pre- and post-fire vegetation characteristics, suggesting limited application of dNBR in predicting future fire severity or vegetation recovery following megafire. I chose the dNBR index as it is commonly used and an easily accessible index of burn severity, but it may be better suited for forest fires with greater fuel loads compared to grassland fires, potentially explaining why I observed minimal relationships with vegetation characteristics (Epting et al. 2005, Schepers et al. 2014). Even in areas with greater fuel loads, there can be limited ability of such indices to predict ecosystem response to burn severity (Keeley et al. 2008), highlighting the continued importance of on-the-ground measurements to assess landscape health (Ludwig et al. 2007). In my study, the strongest relationship noted was between dNBR and grass cover both before and after the fire, which is not surprising as dNBR relies on remotely sensed indices that respond strongly to vegetation (Keeley 2009). Areas dominated by grass cover pre-fire often had nearly ubiquitous vegetation cover that were then entirely consumed by the fire and became bare ground, resulting in a large change in

reflectance of satellite imagery one-week post-fire. By the time I returned to sample vegetation a year later, those same areas were once again dominated by grass, leading to a similar relationship between burn severity and grass cover post-fire. Areas of bare ground had a negative relationship with burn severity, as these areas went from a bare state pre-fire to a bare state post-fire, representing little change in reflectance (i.e., low burn severity). This relationship also did not change post-fire, indicating that bare areas and vegetation composition may be constrained by soil type, water, and other topographic factors outside of fire and grassland management (Winter et al. 2011, Gates et al. 2017). Similarly, following drought and fire in the Sandhills grasslands of Nebraska, bare areas stayed bare and grassland biomass returned within two years following fire, highlighting resilience of grasslands to disturbance (Arterburn et al. 2017, Donovan et al. 2020). I found burn severity was correlated with increased litter depth before the fire, likely because litter and dead vegetation provide major sources of fuel for grassland wildfire (Wright 1974a, Knapp et al. 2009). This relationship diminished post-fire, indicating the fire substantially reduced litter and fuel from the landscape, highlighting benefits of prescribed fire, as reduction of litter and other fine fuels from the landscape reduces risk of future megafires (Wright 1974a, Steuter 1986, Stephens et al. 2014, Starns et al. 2019). Overall, vegetation metrics showed only a weak correlation with burn severity, and these results do not suggest that managing for lesser prairie-chicken nest habitat results in increased fire danger or burn severity. Rather, they suggest that megafire's influence on grasslands is similar to small-scale fire, and will not result in any major shifts in grassland functional group composition.

Effect of Megafire on Abundance of Reproduction Habitat

I predicted greatly decreased nest habitat post-fire, which was the case in 2018. As discussed above, increased bare ground, reduced visual obstruction and reduced litter depth

contributed to the overall reduction in nest habitat in 2018, but reversed by 2019, resulting in increased availability of nest habitat in 2019. Return of nest habitat within two years post-fire was surprising, as lesser prairie-chicken nest habitat within Sand Shinnery Oak Prairie and Sand Sagebrush Prairie ecoregions takes approximately 3–4 years to return following fire (Boyd and Bidwell 2001, Vermiere et al. 2004, Winter et al. 2012, Thacker and Twidwell 2014). This slower recovery is linked to reduced precipitation in these more arid regions and the slower recovery of shrubs from fire, which dominate vegetation in these areas. While we did see reduced cover of shrubs at our study site post-fire, they play a relatively small role for nesting at our study site in the mixed-grass prairie, composing only an observed 2% percent cover at nest sites before the fire, compared to 15–20% in other ecoregions (Hagen et al. 2013). In the mixed grass-prairie, nesting hens in a patch-burn system selected for >2 years post-fire patches, indicating that even in grassland areas with faster recovery, more time is needed for quality nest habitat to return following fire (Lautenbach 2017). Therefore, even with abundance of available nest habitat returning two years following megafire, it may still not be of the highest quality. This is supported by the demographic data, where the majority of nests were in burned areas in 2019 (73%), but nest success was the lowest seen throughout the project (Chapter 2). Therefore, it may take longer than two years for nest habitat to recover completely.

Brood habitat declined slightly post-fire, opposite of my predictions that the fire would increase brood habitat by increasing forbs and creating open areas. The decrease in brood habitat was due to the ~40% decrease in percent cover of forbs across the study area post-fire that may indicate a decrease in available food for broods post-fire. Forbs are an important food source for broods and closely linked to invertebrate abundance, another important food source for broods (Hagen et al. 2004, Sullins et al. 2018a). Generally, invertebrate populations are not negatively

affected by fire, suggesting that grassland recovery will dictate invertebrate response (Swengel 2001, Doxon et al. 2011). As a result, invertebrate populations may have decreased concurrent with the decrease in forbs, but we did not directly measure invertebrate populations.

Furthermore, the large size of the fire likely limited the number of invertebrate that could successfully recolonize burned areas from unburned refugia given the limited dispersal ability of some species (Uys et al. 2006, Doxon et al. 2011). The overall loss of food resources is highly detrimental, as brood survival is essential for lesser prairie-chicken populations and likely for recovery following fire (Hagen et al. 2009, Ross et al. 2018, Sullins et al. 2018*b*). In the Sand Shinnery Oak Prairie Ecoregion, forb and invertebrate abundance was greatest in burned areas 1–2 years post-fire, and in the Sand Sagebrush Prairie Ecoregion, brood habitat was identified in areas 2–3 years post-fire (Boyd and Bidwell 2001, Vermiere et al. 2004, Winter et al. 2012, Thacker and Twidwell 2014). In the Mixed-Grass Prairie Ecoregion, Lautenbach (2017) did not directly measure brood use, but during the summer brooding period hens selected for 1- and 2-year post-fire patches in a patch-burn grazing system. Across the lesser prairie-chicken range, it appears that brood habitat is limited to a relatively short window of time following fire. As such, the lack of increased brood habitat 1- and 2-years post-fire in my study indicates limited benefit from the fire for brood habitat, corroborated by no change in observed chick survival (Chapter 2). Unlike nest habitat, which has potential to continue to improve and increase with greater time since fire, brood habitat is unlikely to increase with greater time since fire, and future availability will depend on management, grazing, and precipitation.

Conclusions

The relatively fast recovery of grasslands following megafire in the mixed-grass prairie indicates that beyond the immense area burned, megafires appear to affect mixed-prairie

grasslands similarly to smaller scale fires. Other megafires may act differently as these are a relatively new phenomenon and depend on a variety of conditions such as fire timing, available fuel, climate, and topography (Stephens et al. 2014, Donovan et al. 2017, Lindley et al. 2019); these same features will also dictate grassland response to megafire. In this study, return of visual obstruction, litter depth, bare ground, and grass cover to pre-fire levels within two years post-fire is congruent with recovery time following prescribed fire and patch-burn grazing within the lesser prairie-chicken distribution (Boyd and Bidwell 2001, Winter et al. 2012, Lautenbach 2017, Starns et al. 2020) and corroborates resilience of grasslands to large fires (Rideout-Hanzak et al. 2011, Arteburn et al. 2017, Donovan et al. 2020, Steiner et al. 2020). While short-term effects appear similar to small-scale fire, this megafire was large enough to cause mortality of fully grown invasive woody species and established trees, such as eastern red cedar (*Juniperus virginiana*), that are not always killed in smaller, less intense, prescribed fire (Ortmann et al. 1998; M. W. Sirch, Kansas State University, unpublished data). Widespread mortality of woody species highlight the size and severity of this fire, and point to potential need for higher intensity prescribed fire to control woody encroachment (Twidwell et al. 2016).

Unfortunately, the quick recovery of grassland flora cannot erase the immediate negative effects of this fire on the lesser prairie-chickens in this area, as evidenced by greatly reduced lek counts and poor reproductive success in the years post-fire (Chapter 2). While I did not collect data in 2017, reproductive success was likely low to non-existent, which was then followed by two additional years of low reproductive success. Therefore, despite habitat recovery two years post-fire, lesser prairie-chicken populations remained reduced in the short term. If favorable land management is continued in the coming years, there is high potential for the lesser prairie-chicken population to return in this area as the habitat recovers and may continue to improve in

quality. However, this will rely on high reproductive success (variable in this boom-bust species) and dispersing lesser prairie-chickens from the surrounding matrix (constrained due to limited connectivity of populations; Haukos and Boal 2016, Gulick 2019). The effects of megafire on grasslands appear to be relatively short-lived, but with extended consequences for lesser prairie-chicken populations.

Management Implications

Megafires may pose a short-term threat to lesser prairie-chickens as they remove thousands of hectares of habitat, but grasslands appear to be resilient to megafire effects. If precipitation is limited immediately following megafire, grazing should be deferred or limited to ensure healthy recovery of grasslands. However, the longer lasting effects to lesser prairie-chicken populations make preventing megafires equally important. Using patch-burn grazing and prescribed fire can help reduce available fuels and dead vegetation, preventing larger fires in the future (Steuter 1986, Twidwell et al. 2013, Starns et al. 2019). Implementing prescribed fire practices at the pasture scale, with a burn interval of 4–6 years in the mixed-grass prairie, would allow for a maximization of gains for producers and a wealth of available habitat for the different lesser prairie-chicken life stages (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009, Scasta et al. 2016, Lautenbach 2017). Increased knowledge of both grassland and lesser prairie-chicken response to prescribed fire practices make controlled fire an effective way to manage grasslands and avoid future megafires.

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Tables

Table 4.1 Breeding season (15 Mar–15 Sep) mean vegetation values and standard deviation measured at random locations in burned and unburned areas before (2014–2015) and after (2018–2019) the March 2017 Starbuck fire in Clark County, Kansas, USA. Means followed by the same superscript do not differ for each vegetation characteristic.

Variable	Burned		Unburned	
	Before	After	Before	After
Vegetation Height	62.71 ± 20.92 ^a	61.48 ± 24.96 ^{a,b}	63.56 ± 18.75 ^{a,b}	58.67 ± 21.48 ^b
Visual Obstruction				
100%	0.99 ± 1.18 ^a	0.67 ± 0.89	1.04 ± 0.82 ^{a,b}	0.82 ± 0.92 ^b
75%	1.76 ± 1.62 ^a	1.50 ± 1.29 ^b	1.71 ± 1.04 ^{a,b}	1.56 ± 1.20 ^b
50%	2.39 ± 1.85 ^a	2.04 ± 1.55 ^b	2.25 ± 1.22 ^{a,b}	2.04 ± 1.70 ^b
25%	3.49 ± 2.26 ^a	3.02 ± 2.10 ^{b,c}	3.21 ± 1.41 ^{a,b}	2.73 ± 1.62 ^c
0%	6.63 ± 2.76 ^a	7.58 ± 4.01	6.49 ± 1.97 ^a	6.74 ± 2.96 ^a
Percent Cover				
Litter	10.16 ± 9.79 ^a	10.73 ± 8.03 ^a	8.84 ± 10.63 ^a	13.43 ± 11.63
Grass	45.43 ± 26.23 ^a	50.02 ± 23.28 ^b	49.91 ± 25.18 ^{a,b}	66.26 ± 26.47
Shrub	3.48 ± 9.29	2.48 ± 6.53 ^a	1.14 ± 4.61 ^{a,b}	0.48 ± 3.11 ^b
Forb	17.79 ± 15.60	13.07 ± 12.90	19.88 ± 24.57	10.27 ± 14.99
Bare	22.76 ± 17.56 ^a	26.34 ± 18.85	20.04 ± 13.38 ^a	10.82 ± 13.26
Annual Bromes	1.44 ± 6.50 ^a	0.07 ± 0.71 ^b	0.12 ± 0.59 ^{b,c}	1.09 ± 6.07 ^{a,c}
Litter Depth	1.23 ± 1.40	1.02 ± 0.69	1.68 ± 1.76 ^a	1.71 ± 1.28 ^a
Litter Depth SD	1.35 ± 1.52	0.85 ± 0.99	1.73 ± 1.40	1.13 ± 0.92

Table 4.2 Relative rankings (#1 being the most abundant) and percent abundance of plant species found in the top three most abundant species recorded at random locations in burned and unburned areas before (2014–2015) and after (2018–2019) the March 2017 Starbuck fire in Clark County, Kansas, USA during the breeding season (15 Mar– 15 Sep). Rankings in bold represent the top 10 most abundant species in that category.

Species	Burned		Unburned	
	Before	After	Before	After
Sand Dropseed	1 (18%)	3 (10%)	3 (10%)	5 (8%)
Blue Grama	2 (8%)	1 (12%)	5 (6%)	3 (10%)
Western Ragweed	3 (7%)	8 (5%)	7 (4%)	14 (1%)
Russian Thistle	4 (7%)	14 (2%)	4 (8%)	6 (5%)
Little Bluestem	5 (7%)	2 (11%)	1 (25%)	1 (28%)
Alkali Sacaton	6 (6%)	5 (7%)	12 (2%)	34 (0.1%)
Sand Sagebrush	7 (6%)	9 (5%)	13 (2%)	16 (1%)
Big/Sand Bluestem	8 (5%)	4 (8%)	8 (3%)	9 (3%)
Tall Dropseed	9 (4%)	19 (1%)	20 (1%)	18 (1%)
Switchgrass	10 (3%)	6 (6%)	14 (1%)	17 (1%)
Western Wheatgrass	11 (3%)	7 (6%)	9 (3%)	7 (4%)
Sideoats Grama	13 (2%)	11 (3%)	2 (15%)	4 (9%)
Kochia	14 (2%)	16 (2%)	6 (5%)	8 (4%)
Silver Bluestem	25 (1%)	26 (0.5%)	10 (3%)	10 (3%)
Indiangrass	58 (0.1%)	10 (3%)	26 (0.4%)	2 (11%)
Total Percent from Top 10 Species	69%	73%	81%	84%

Table 4.3 Nonbreeding season (16 Sep–14 Mar) mean vegetation values and standard deviation measured at random locations in burned areas before (2014–2016) and after (2018–2020) the March 2017 Starbuck fire in Clark County, Kansas, USA. Unburned areas were not included as sample size was limited before the fire.

Variable	Before	After
Vegetation Height	73.41 ± 22.61	80.09 ± 28.40*
Visual Obstruction		
100%	0.95 ± 0.93	0.95 ± 1.02
75%	2.13 ± 1.45	1.92 ± 1.47*
50%	2.99 ± 1.82	2.76 ± 1.86
25%	4.33 ± 2.20	4.01 ± 2.50
0%	7.25 ± 2.93	10.85 ± 5.01*
Percent Cover		
Litter	6.57 ± 7.01	11.87 ± 8.88*
Grass	58.77 ± 27.68	55.64 ± 22.32*
Shrub	3.35 ± 9.16	2.68 ± 5.88
Forb	12.82 ± 14.60	7.44 ± 10.18*
Bare	19.15 ± 18.96	25.06 ± 16.54*
Annual Bromes	0.15 ± 1.21	0.05 ± 0.34
Litter Depth	1.61 ± 1.81	0.89 ± 0.40*
Litter Depth SD	1.68 ± 1.61	0.57 ± 0.32*

*Indicates a significant ($P < 0.05$) difference in mean value from before the fire.

Table 4.4 Recovery of spring (Mar–May) vegetation characteristics based on mean vegetation values and standard deviation (SD) measured at the same points ($n = 375$) before (2014 or 2015) and after (2018 & 2019) the March 2017 Starbuck fire in Clark County, Kansas, USA. Values in bold recovered or surpassed pre-fire measurements.

Variable	Before		2018				2019			
	Mean	SD	Mean	SD	<i>t</i>	<i>P</i>	Mean	SD	<i>t</i>	<i>P</i>
Veg Height	64.03	23.14	59.80	27.33	-2.86	0.004	58.89*	21.38	-4.11	<0.001
Visual										
Obstruction										
100%	0.79	0.94	0.48*	0.63	-5.35	<0.001	0.56*	0.76	-3.64	<0.001
75%	1.58	1.25	1.28*	1.10	-4.03	<0.001	1.39	0.99	-2.46	0.015
50%	2.36	1.59	1.96*	1.51	-4.06	<0.001	1.88*	1.20	-5.06	<0.001
25%	3.93	2.43	3.37*	2.59	-3.40	0.001	2.74*	1.60	-9.16	<0.001
0%	7.14	3.24	7.21	4.29	0.31	0.756	7.72*	3.86	2.97	0.003
Percent Cover										
Litter	10.65	9.37	10.26	8.34	-0.68	0.497	12.12	7.38	2.44	0.015
Grass	43.12	25.75	42.89	20.75	-0.86	0.389	52.17*	21.22	6.23	<0.001
Shrub	4.15	10.12	2.72*	7.73	-3.42	<0.001	1.87*	5.33	-5.37	<0.001
Forb	21.21	17.46	13.67*	10.62	-7.92	<0.001	13.29*	13.34	-7.67	<0.001
Bare	20.71	17.19	33.22*	16.59	11.38	<0.001	21.72	16.23	0.80	0.424
Annual Bromes	0.53	4.09	0.00	0.07	-2.44	0.015	0.06	1.04	-2.11	0.036
Litter Depth	1.02	1.00	0.70*	0.49	-5.74	<0.001	1.35*	0.62	5.85	<0.001
Litter Depth SD	1.22	1.59	0.78*	0.78	-4.79	<0.001	1.11	0.64	-1.21	0.227

*Indicates a significant ($P < 0.0036$) difference in mean value from before the fire based on a paired t -test ($df = 374$) with Bonferroni correction.

Table 4.5 Recovery of summer (Jun–Aug) vegetation characteristics based on mean vegetation values and standard deviation (SD) measured at the same points ($n = 228$) in the before (2014 or 2015) and after (2018 & 2019) the March 2017 Starbuck fire in Clark County, Kansas, USA. Values in bold recovered or surpassed pre-fire measurements.

Variable	Before		2018				2019			
	Mean	SD	Mean	SD	t	P	Mean	SD	t	P
Veg Height	67.94	20.37	62.97	25.51	-2.75	0.007	72.69	18.21	2.93	0.004
Visual Obstruction										
100%	1.44	1.36	0.80*	0.97	-5.84	<0.001	1.39	1.20	-0.42	0.673
75%	2.54	1.87	1.43*	1.35	-8.99	<0.001	2.28	1.59	-1.87	0.062
50%	3.20	2.06	1.78*	1.53	-10.41	<0.001	2.76	1.75	-2.89	0.004
25%	4.27	2.32	2.41*	1.72	-12.06	<0.001	3.50*	1.98	-4.51	<0.001
0%	6.84	2.59	7.35	4.28	1.83	0.068	8.47*	3.13	6.94	<0.001
Percent Cover										
Litter	7.95	7.75	6.53	7.21	-1.97	0.050	11.48*	8.21	5.56	<0.001
Grass	48.03	26.75	50.14	27.51	1.45	0.147	53.20	23.33	2.81	0.005
Shrub	4.21	9.90	2.18*	5.89	-3.65	<0.001	3.67	7.90	-1.21	0.227
Forb	17.67	14.22	9.08*	11.96	-8.87	<0.001	16.88	15.10	-0.58	0.562
Bare	22.79	17.90	35.74*	24.38	8.52	<0.001	19.14*	16.44	-3.13	0.002
Annual Bromes	2.08	8.17	0.01*	0.20	-3.49	<0.001	0.28*	1.15	-3.07	0.002
Litter Depth	1.35	1.49	0.72*	0.37	-6.73	<0.001	1.21	0.93	-1.26	0.211
Litter Depth SD	1.41	1.21	0.43*	0.25	-12.00	<0.001	0.84*	2.05	-3.56	<0.001

*Indicates a significant ($P < 0.0036$) difference in mean value from before the fire based on a paired t -test ($df = 227$) with Bonferroni correction.

Table 4.6 Percent of points meeting nest and brood habitat criteria from Lautenbach (2015) and Lautenbach et al. (2019), following Gehrt et al. (2020). Nest habitat was defined as points with $\leq 10\%$ cover of bare ground and 75% visual obstruction (VOR) from 1.5–3.5 dm. Brood habitat was defined as points with 7–37% cover of forbs and 50% visual obstruction from 2–5 dm. Vegetation measurements were collected at random points within 5km of leks during the breeding season (15 Mar–15 Sep) before (2014–2015) and after (2018–2019) the March 2017 Starbuck fire in Clark County, Kansas, USA.

Category	Before	2018	2019	After
Nest Habitat				
Meets all requirements	16.41%	10.78%	22.07%	16.54%
Optimal VOR	43.21%	34.67%	46.28%	40.79%
Too short VOR	48.00%	59.44%	48.20%	53.51%
Too tall VOR	8.79%	5.89%	5.52%	5.70%
Optimal bare	28.92%	21.12%	37.99%	30.02%
Too bare	71.08%	78.88%	62.01%	69.98%
Brood Habitat				
Meets all requirements	27.32%	20.41%	24.17%	22.29%
Optimal VOR	46.94%	37.20%	46.61%	42.16%
Too short VOR	46.83%	58.22%	50.21%	54.00%
Too tall VOR	6.23%	4.58%	3.18%	3.84%
Optimal forbs	58.29%	49.91%	50.88%	50.42%
Too few forbs	28.98%	45.51%	42.34%	43.84%
Too many forbs	12.74%	4.58%	6.78%	5.74%

Figures

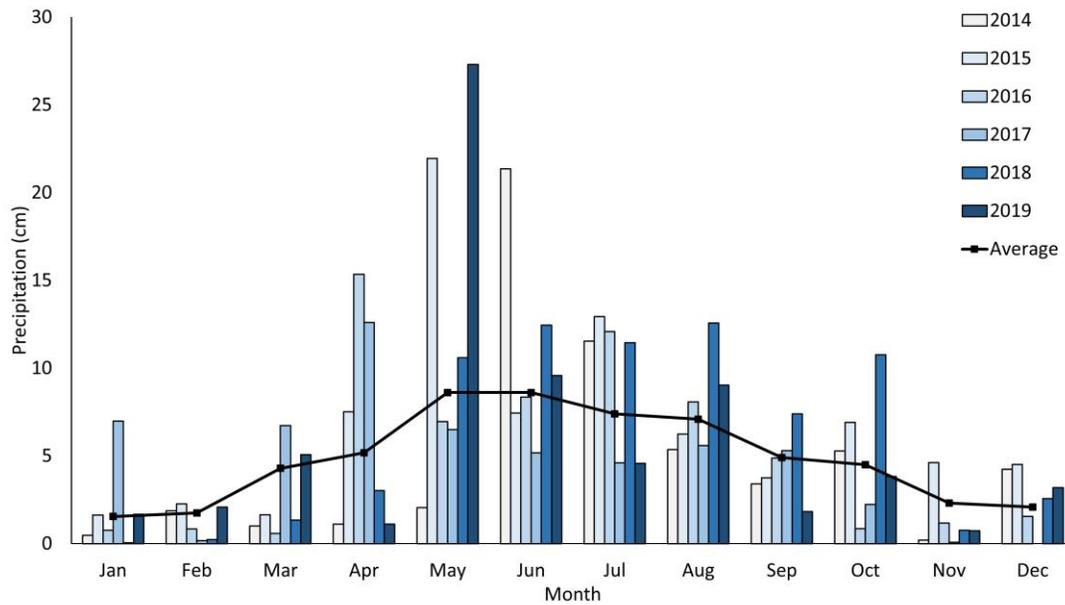


Figure 4.1 Monthly precipitation (cm) totals (2014-2019) and 50-year (1970–2020) averages for Clark County, Kansas, USA (NOAA 2020).

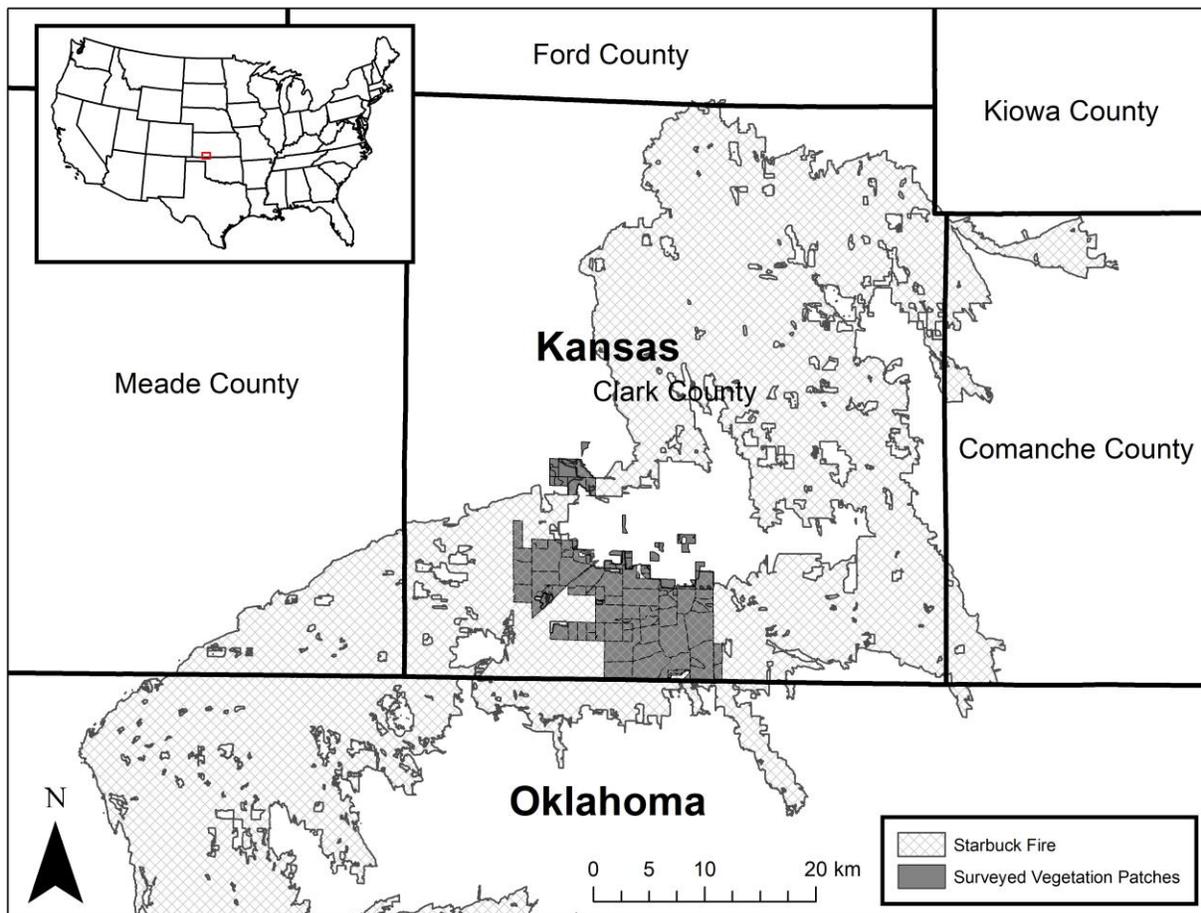


Figure 4.2 Study area map detailing vegetation patches surveyed before (2014–2016) and after (2018–2020) the March 2017 Starbuck fire in Clark County, Kansas, USA.

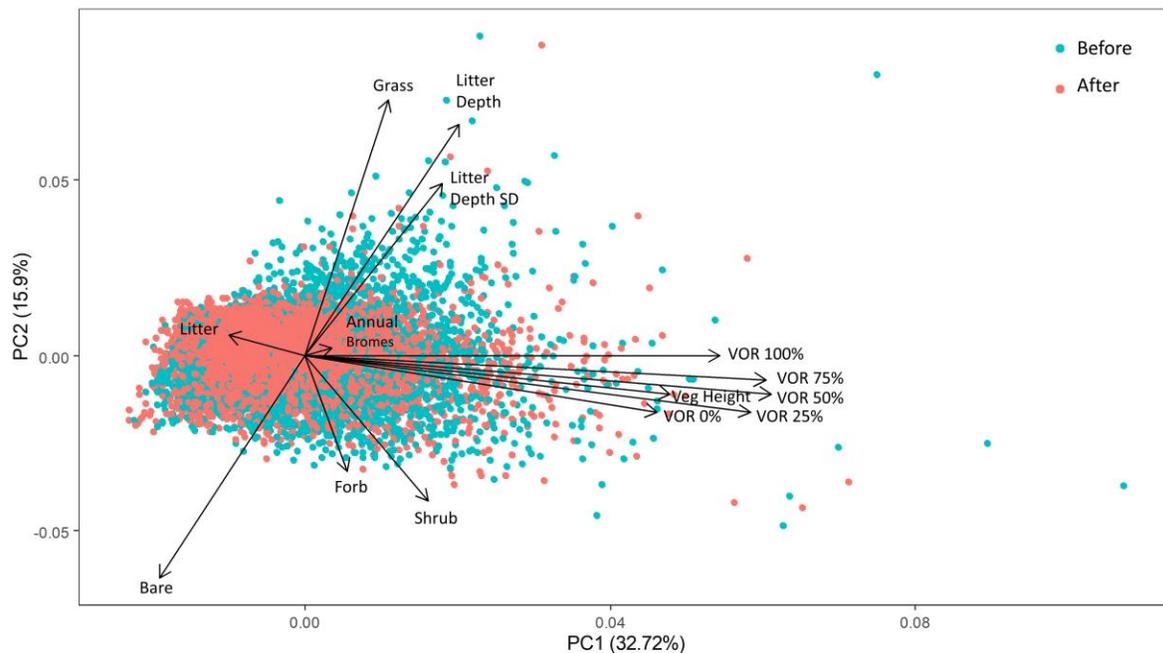


Figure 4.3 First two axes (PC1 and PC2) and percent of variation (in parentheses) from principal components analysis (PCA) of vegetation characteristics measured at all points before (2014–2016) and after (2018–2020) the March 2017 Starbuck fire in Clark County, Kansas, USA. Black arrows indicate loadings for percent cover of key functional groups and visual obstruction readings (VOR) at different percentages of obstruction.

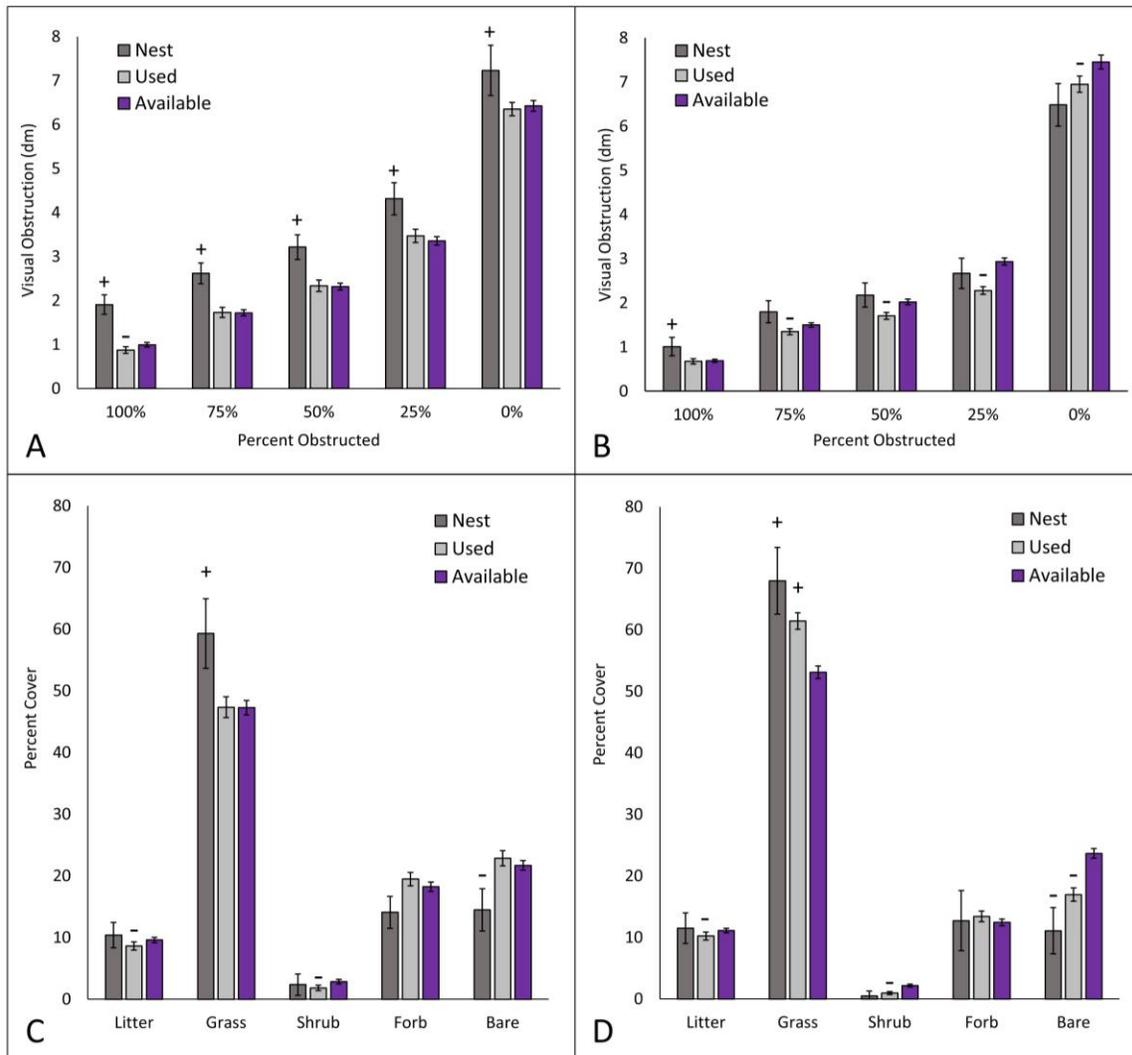


Figure 4.4 Mean values of breeding season (15 Mar–15 Sep) visual obstruction before (2014–2015; A) and after (2018–2019; B) and mean values of percent cover composition of key functional groups before (2014–2015; C) and after (2018–2019; D) the March 2017 Starbucks fire in Clark County, Kansas, USA, measured at nest sites, points used by female lesser prairie-chickens, and available locations. Error bars represent 95% confidence intervals and “+” or “-” indicates a significant use at a greater or lower level than available based ($\alpha = 0.05$).

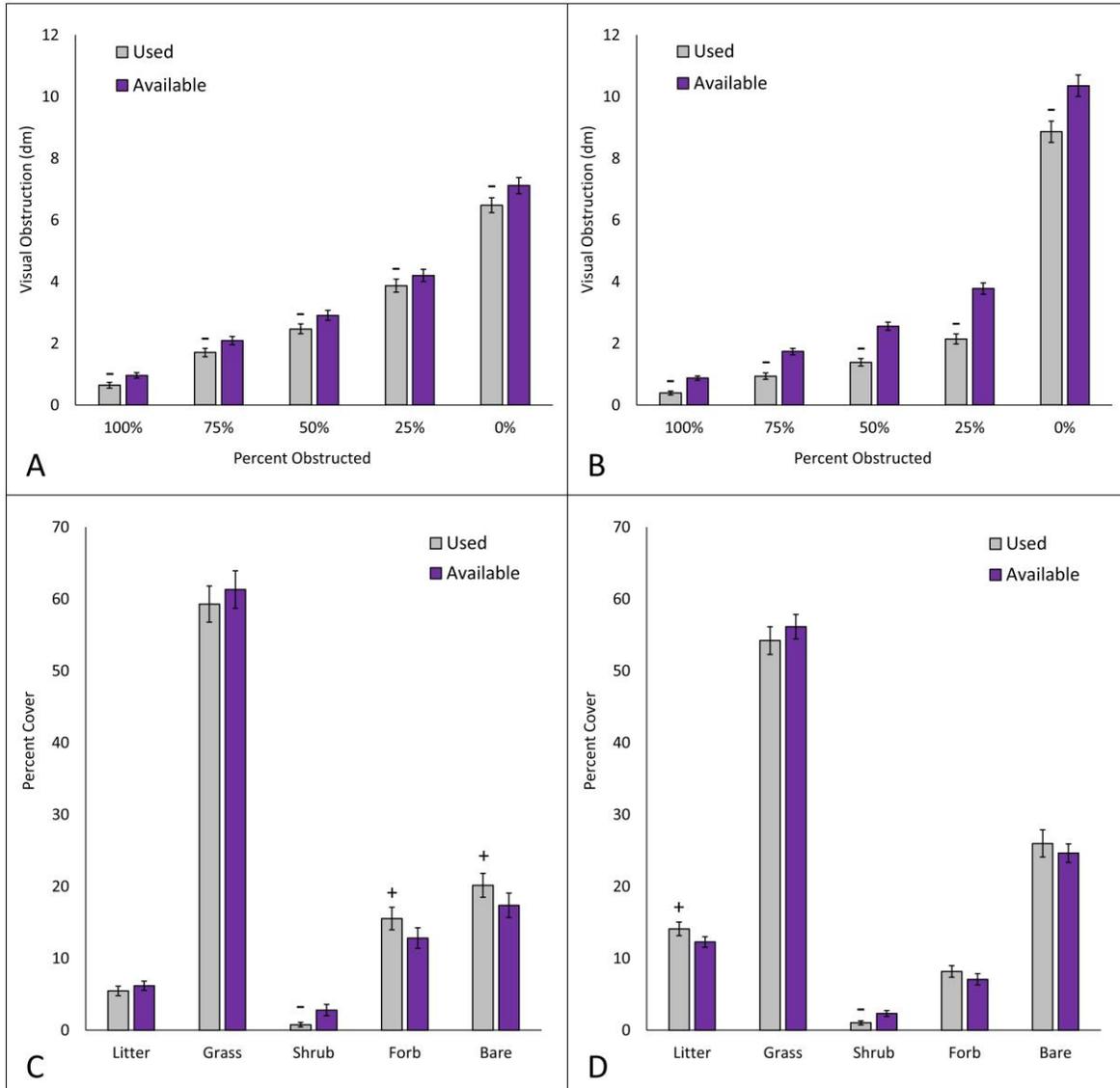


Figure 4.5 Mean values of nonbreeding season (16 Sep–14 Mar) visual obstruction before (2014–2016; A) and after (2018–2020; B) and mean values of percent cover composition of key functional groups before (2014–2016; C) and after (2018–2020; D) the March 2017 Starbucks fire in Clark County, Kansas, USA, measured at points used by female lesser prairie-chickens and available locations. Error bars represent 95% confidence intervals and “+” or “-” indicates a significant use at a greater or lower level than available ($\alpha = 0.05$).

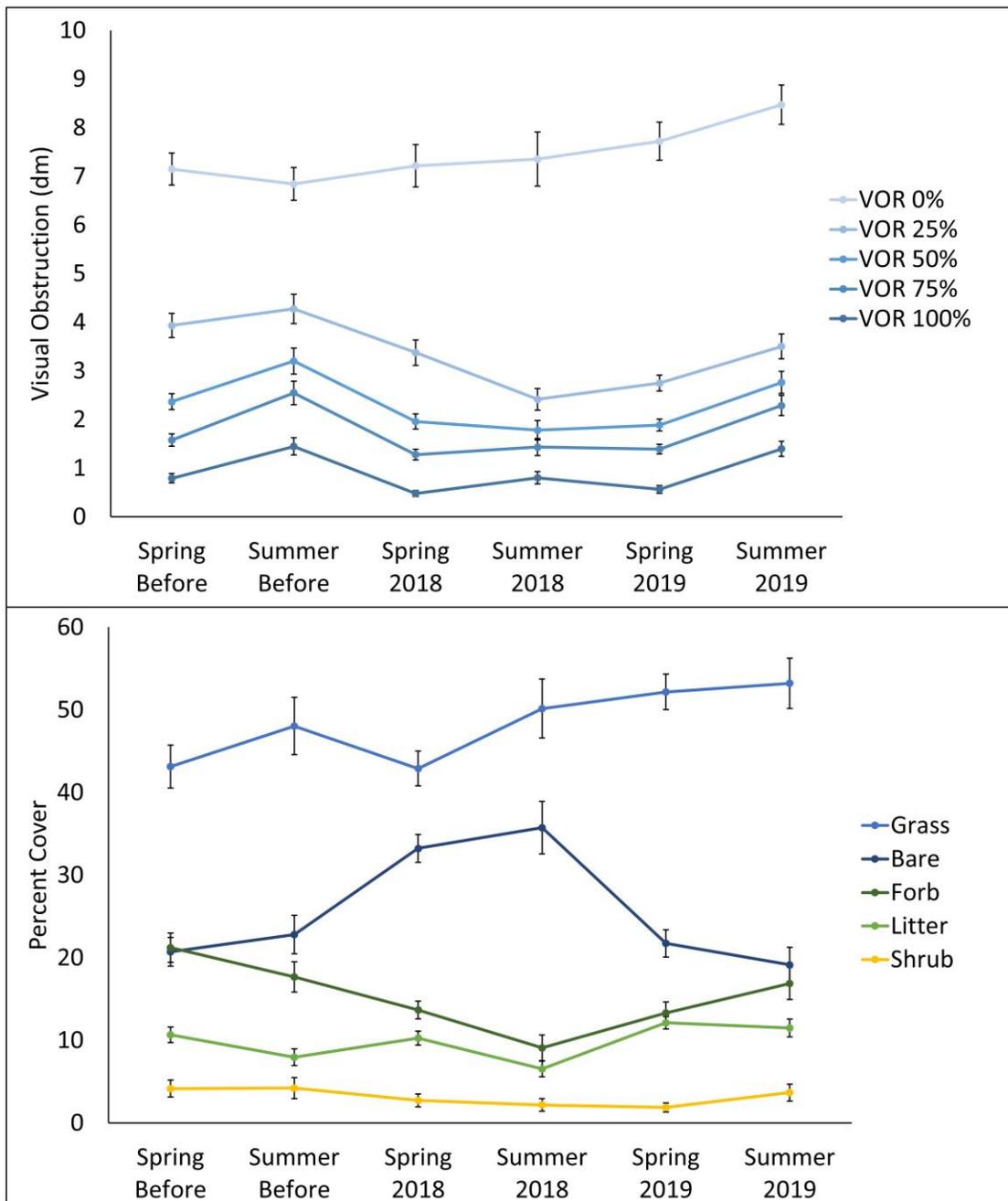


Figure 4.6 Mean values and 95% confidence intervals of visual obstruction (VOR; top) and percent cover (bottom) of vegetation measured at the same locations in the spring (Mar–May) and summer (Jun–Aug) before (2014 or 2015) and after (2018 and 2019) the March 2017 Starbuck fire in Clark County, Kansas, USA.

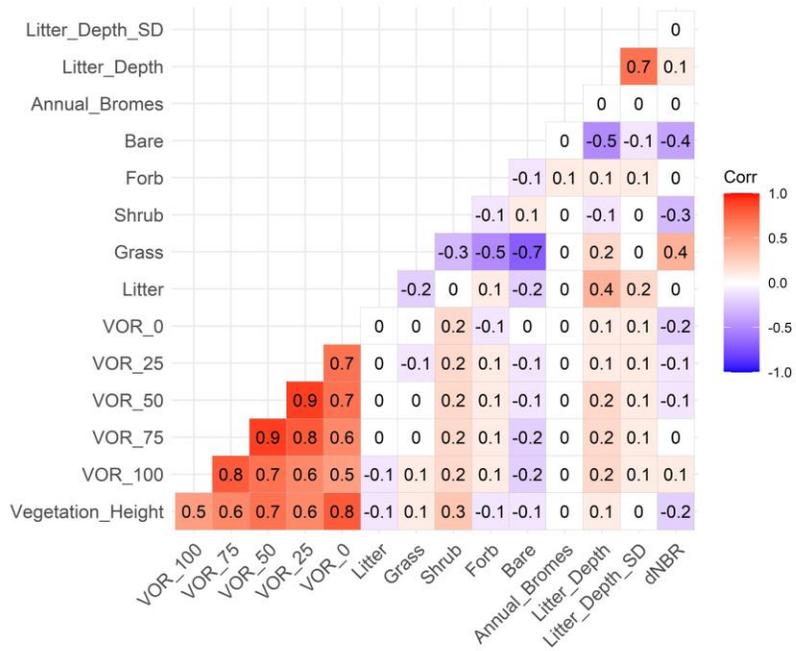
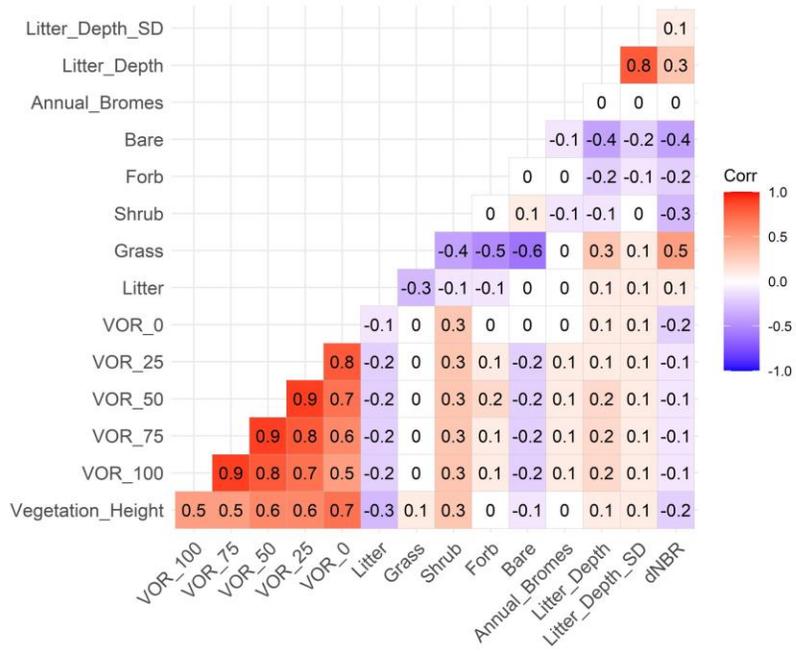


Figure 4.7 Correlation matrix of vegetation characteristics and a measure of burn severity (dNBR) before (2014–2015; top) and after (2018–2019; bottom) the March 2017 Starbuck fire measured at random points (before: $n = 1,410$, after: $n = 1,795$) in burned areas during the breeding season (15 Mar–15 Sep) in Clark County, Kansas, USA. Vegetation characteristics include vegetation height, visual obstruction (VOR) at multiple scales (100%, 75%, 50%, 25%, 0%), percent horizontal cover of functional groups (litter, grass, shrub, forb, bare ground, annual bromes), litter depth, and litter depth standard deviation.