Research Article

Effects of Rangeland Management on Survival of Female Greater Prairie-Chickens

VIRGINIA L. WINDER,1 Department of Biology, Benedictine College, Atchison, KS 66002, USA
LANCE B. MCNEW, Department of Animal and Range Sciences, Montana State University, Bozeman, MT 59717, USA
JAMES C. PITMAN,2 Kansas Department of Wildlife, Parks & Tourism, Emporia, KS 66801, USA
BRETT K. SANDERCOCK, Division of Biology, Kansas State University, Manhattan, KS 66506, USA

ABSTRACT Identifying relationships between habitat selection and population processes is important for habitat management and wildlife conservation. For prairie-obligate species, space use and demography in extant grasslands are influenced by habitat conditions caused by rangeland management practices associated with livestock production. Greater prairie-chickens (Tympanuchus cupido) are an indicator species for native tallgrass prairie ecosystems, but populations have declined in the Flint Hills ecoregion of eastern Kansas, USA because of intensification of rangeland management practices, including annual prescribed fire and high stocking densities. Patch-burn grazing is a rotational system that provides heterogeneous habitats and can improve productivity of grassland birds, but the effects of grazing systems on habitat use or survival of greater prairie-chickens are unknown. We used 3 types of survival analyses to investigate impacts of rangeland management on female greater prairie-chickens in the central Flint Hills during 2011–2013: Kaplan–Meier models and Cox proportional hazards to examine factors affecting annual survival rates, hazard functions to assess seasonal patterns of mortality, and Andersen–Gill models to explore the links between habitat selection and cause-specific mortality risk. Females captured at properties managed with patch-burn grazing had annual survival rates (0.61 ± 0.07 SE) that were 35% higher than females on properties managed with annual burning and intensive early cattle stocking (0.45 ± 0.06). Moreover, females that selected habitats associated with intensive management had increased mortality risk and were particularly vulnerable to avian predators, whereas females that selected habitats created by patch-burn grazing experienced lower overall mortality risk but were more vulnerable to mammalian predators. Overall mortality risk was significantly reduced under patch-burn grazing management, and widespread implementation of annual spring burning and intensive early stocking is likely depressing survival of greater prairie-chickens in the Flint Hills ecoregion. Our results join a growing body of evidence that patch-burn grazing can provide higher quality grassland habitats for native wildlife species than current rangeland management associated with intensive cattle production.

Landscape ecologists emphasize relationships between pattern and process when investigating organismal responses to environmental conditions (Turner 1989, Benton et al. 2006, Frederiksen et al. 2014). Resource availability and predation risk vary across natural landscapes, and the tradeoff between the 2 ecological factors can be an important influence on habitat selection and, in turn, population dynamics (Verdolin 2006; Aldridge and Boyce 2007; Cresswell 2008; Dinkins et al. 2014a,b). For many animals, habitat selection is a hierarchical process, with interactions among behavior, predation risk, and fitness acting at different spatial and temporal scales (Southwood 1977; Boyce and McDonald 1999; Cagnacci et al. 2010; Dinkins et al. 2014a,b). Linking habitat selection to demographic performance is important for effective conservation of wildlife populations because a basic understanding of mechanistic links is needed to identify important influences on vital rates, and source and sink habitats (Aldridge and Boyce 2007, Frederiksen et al. 2014, Furrer and Pasinelli 2015, Sandercock et al. 2015).

Grassland ecosystems in North America are a high conservation priority, largely because of extensive conversion of grassland habitats to cropland over the past century (Vitousek et al. 1997, White et al. 2000, Fuhlendorf et al. 2012). Only 5% of the historical extant of tallgrass prairie remains, and 80% of the remaining area is located in the Flint Hills ecoregion of eastern Kansas and northern Oklahoma (Samson and Knopf 1994, Samson et al. 2004, Hoekstra...
et al. 2005). Over 90% of the 2 million ha of grasslands in the Flint Hills are private lands used to support an economically valuable cattle industry (With et al. 2008). For the past 40 years, annual burning in the spring combined with double stocking of steers for the first half of the growing season (intensive early stocking and burning) has been the widespread rangeland management practice in the Flint Hills (Smith and Owensby 1978). The goal of intensive early stocking and burning is to maximize livestock production by generating homogenous grazing distribution and forage use across the landscape (Hart 1978, Fuhlendorf and Engle 2001, Holecheck et al. 2004, Rahmig et al. 2009, Allred et al. 2014). Widespread implementation of intensive early stocking and annual burning has disrupted the historical dynamics between fire and grazing in most of the remaining tallgrass prairie in North America, and has coincided with population declines for many grassland vertebrates (Zimmerman 1997, Brennan and Kuvelsky 2005, Reinking 2005, With et al. 2008, Sauer et al. 2014).

Patch-burn grazing is an alternative rangeland management strategy that restores ecological pattern and process in grassland ecosystems, and aims to promote habitat heterogeneity and biodiversity while maintaining agricultural productivity (Christensen 1997, Ostfeld et al. 1997, Wiens 1997, Tews et al. 2004, Fuhlendorf et al. 2006). In patch-burn grazing, a pasture is subdivided into 3–5 patches using firebreaks but without cross fencing. One of 3–5 patches is burned on a rotational basis each year, and cattle are allowed unrestricted movement among patches within a pasture. The most recently burned patch usually receives the heaviest grazing pressure because cattle prefer to forage in recently burned areas with high-quality food plants and no detritus from previous growing seasons (Coppege and Shaw 1998, Allred et al. 2011). Patch-burn grazing mimics historical fire-grazing interactions (pyric herbivory), which were the keystone processes that shaped the evolution of grassland ecosystems (Milchunas et al. 1988, Knapp et al. 1999, Askins 2000, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006). Patch-burn grazing creates temporal and spatial heterogeneity within a shifting mosaic that includes patches at different stages of disturbance and recovery (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001). Recent studies have provided growing evidence that patch-burn grazing can benefit native species of grassland animals, without loss of revenue from cattle production (Churchwell et al. 2008, Powell 2008, Limb et al. 2011, Sandercock et al. 2015, Ricketts and Sandercock 2016).

Greater prairie-chickens (\textit{Tympanuchus cupido}; prairie chickens) are an umbrella species in the tallgrass prairie ecosystem, and their populations in the Flint Hills have declined by as much as 50% over the last 30 years (Poiani et al. 2001, Johnson et al. 2011, Pitman et al. 2012). Prairie chickens have large seasonal home ranges (10–25 km$^2$), and require a range of habitats including open sites on hilltops for leks, tall vegetative cover for nesting, and areas of intermediate vegetative structure for brood-rearing (Gregory et al. 2011; Matthews et al. 2013; Winder et al. 2014\textit{b}, 2015; Hovick et al. 2015). Adult female survival rates often have a strong influence on the finite rate of population change for declining populations of prairie chickens and other species of prairie grouse (Aldridge and Boyce 2007, McNew et al. 2012, Blomberg et al. 2013, Dinkins et al. 2014\textit{a}).

The objective of our 3-year field study was to examine the impacts of intensive early stocking and burning versus patch-burn grazing on seasonal survival, annual survival, and cause-specific mortality risk of adult female greater prairie-chickens. First, we predicted that annual survival rates of adult females would benefit from increased habitat heterogeneity and residual cover in areas managed with patch-burn grazing (Fuhlendorf and Engle 2004, Coppedge et al. 2008, McNew et al. 2015). Second, we predicted that mortality risk to sight-based avian predators would be greater in pastures with heavy stocking rates and recently burned areas with little residual vegetative cover, or in areas with greater availability of perches for raptors, such as near roads (Aldridge and Boyce 2007; Dinkins et al. 2012, 2014\textit{a}, \textit{b}; McNew et al. 2015). Last, we predicted that mortality risk to scent-based mammalian predators would be greatest in lightly grazed or unburned areas with tall vegetative cover, which might limit the ability of prairie chickens to detect approaching predators, and in areas near patch edges, which provide corridors and focal areas of predator activity (Kuehl and Clark 2002, McNew et al. 2015).

**STUDY AREA**

We conducted our 3-year field study during 2011–2013 at a 3,000-km$^2$ site in portions of Butler, Chase, Greenwood, Lyon, and Morris counties, 5 of the most intensively burned counties in the Flint Hills ecoregion (Fig. 1; Mohler and Goodin 2012). Land cover in our study area was dominated by grasslands (90%), which are primarily used for cattle production. Grasslands in the ecoregion are composed of native species of perennial, warm-season grasses such as big bluestem (\textit{Andropogon gerardii}), little bluestem (\textit{A. scoparius}), Indian grass (\textit{Sorghastrum nutans}), and switchgrass (\textit{Panicum virgatum}), in addition to a diverse mixture of other warm- and cool-season grasses, composites, legumes, and broad-leaf forbs. The Flint Hills ecoregion experiences 4 distinct seasons and receives an average of 70–90 cm of precipitation annually, with most precipitation occurring in spring and early summer. Elevation ranges from approximately 400 m to 500 m across the Flint Hills. Road density within our study area was relatively low at 0.58 km of road/km. Within our field site, we had permission to access 1,100 km$^2$ of land: 1,000 km$^2$ of privately owned ranch lands primarily managed with intensive early stocking and burning, 50 km$^2$ of public grasslands (Tallgrass Prairie National Preserve) managed with patch-burn grazing, and 45 km$^2$ of privately owned properties managed with patch-burn grazing (Browning Ranch: 30 km$^2$, Koger Ranch: 15 km$^2$; Fig. 1).

Management strategies of private land owners for intensive early stocking properties were dependent upon annual weather conditions. In years following growing seasons with typical rainfall, properties managed with intensive early stocking received prescribed burns in spring and were grazed by steers for 90 days (3 animal unit months, [AUM]) during April–July. Drought conditions during 2012 and 2013...
caused managers of intensive early stocking and burning properties to reduce or postpone prescribed burns or reduce stocking rates. Average stocking rate during the study on intensive early stocking and burning properties was 2.33 ± 1.03 SD AUM/ha. Of rangelands managed with intensive early stocking, >90% were burned in spring 2011, 10% were burned in spring 2012, but only 1% of the study area was burned in spring 2013 because of drought conditions. Management strategies for patch-burn grazing properties were consistent over the 3-year field effort, and spanned one complete fire and grazing rotation. Patch-burn grazing properties were stocked with domestic cattle at 1.5–2 AUM/ha on private lands, or with bison (Bison bison) at 0.45 AUM/ha at the national preserve. Despite drought conditions which led to modified management practices on properties managed with intensive early stocking during 2 of the 3 years of our study, we observed significant differences in vegetation structure and composition between properties managed with intensive early stocking and those managed with patch-burn grazing during all 3 years of our study. Properties managed with intensive early stocking had less residual cover and more homogenous composition, resulting in habitat conditions on unburned sites in a drought year being comparable to conditions after a spring burn (McNew et al. 2015).

**METHODS**

**Prairie Chicken Capture and Monitoring**

Our study adhered to relevant regulations and guidelines regarding the ethics of animal welfare approved by Kansas State University Institutional Animal Care and Use Protocol. We captured prairie chickens with walk-in traps and drop-nets at lek sites during March to May 2011–2013 (Silvy et al. 1990). At first capture, we marked all birds with a unique numbered metal leg band and 3 colored leg bands. We aged birds as yearlings or adults based on the shape and coloration of the outer 2 primary feathers versus the rest of the wing (Henderson et al. 1967). Females were outfitted with 11-g very high-frequency (VHF) radio-transmitters attached with a wire necklace harness (Model A3950, Advanced Telemetry Systems [ATS], Isanti, MN, USA). Radios had an expected battery life of 18 months and were equipped with mortality switches that changed pulse rate when the transmitter was stationary for >6 hours.

Radio-marked females were located by triangulation or homing with portable radio receivers and handheld Yagi antennas (Model R2000, ATS). We relocated birds ≥3 times per week during the 6-month breeding season (1 Mar–31 Aug), and ≥2 times per week during the 6-month nonbreeding season (1 Sep–28 Feb). Observers rotated check schedules among monitored females within each week to obtain bird locations at different times of the day. The double-checked the area of triangulated locations in the field to ensure that all sides of the triangle encompassing the bird’s location were <200 m in length (~1 ha), minimizing estimation errors for our point locations. We estimated coordinates for locations using Program Locate III (version 3.34, Tatamagouche, Nova Scotia, Canada) with Universal Transverse Mercator projection (North American Datum 1983, Zone 14N).

If the pulse rate from a mortality switch indicated that a female had died, observers relocated the carcass within 1–2 days and attempted to determine cause of death from evidence at the mortality location. We considered radios with broken or stretched harnesses but no other damage and no sign of bird remains to be dropped collars and treated the associated prairie chickens as surviving birds. We considered bird carcasses with evidence of tooth marks or scat to be the result of mammalian predation by coyotes (Canis latrans), badgers (Taxidea taxus) or other mesocarnivores. We considered carcasses that were plucked at a perch site, decapitated remains where breast muscles were removed, carcasses lacking tooth marks, and presence of white fecal matter to be signs of avian predation by raptors or owls. We considered carcasses that had broken necks or wings, long open gashes, and no other evidence of predator activity that were found <200 m from fence, road, or power lines to be due to collision mortality. We considered birds shot by hunters where leg bands or radios were reported to our field team or to the Kansas Department of Wildlife, Parks and

**Figure 1.** Study site (3,000 km²) in the central Flint Hills of Kansas, USA, 2011–2013. Dark black lines are state highways; gray lines are secondary or gravel roads. Pastures with light gray were managed with intensive early stocking and annual burning. Pastures with dark gray were managed with patch-burn grazing. Greater prairie-chicken leks are represented by black triangles. Female mortality locations are represented by white circles (mammalian predation), gray circles (avian predation), and black circles (hunter, collision, and unknown causes of mortality). Inset: light gray polygon = Flint Hills, black polygon = field study site.
Tourism to be harvest mortality. We recovered most carcasses within 1–2 days of death, but causes of mortality are tentative because we cannot discount the possible effects of scavenging of dead birds (Bumann and Stauffer 2002, Larsen et al. 2008). If we were unable to determine cause of mortality because carcasses were too degraded when recovered, or if multiple signs of evidence were present, we considered the mortality event to be of unknown cause.

Statistical Analyses

**Kaplan–Meier models and Cox proportional hazards.**—We calculated cumulative survival rates of radio-marked females with staggered entry Kaplan–Meier models with package survival in Program R (Therneau 2015, accessed 1 Mar 2015; version 2.13.11, R Foundation for Statistical Computing, Vienna, Austria). To match the timing of our spring capture effort, we created encounter histories for each female for an annual period from 1 March to 28 February of the following year (i.e., Mar 1–7 = week 1; bird-year). Encounter histories consisted of: week of entry, week of exit, and event (1 = mortality, 0 = survived). We opted not to left-censor encounter histories to buffer for potential effects of capture stress because deaths within 1–2 weeks of capture were rare (<4% of the marked population). Moreover, our objective in this study was to compare survival rates between 2 types of rangeland management, and any potential bias that might have arisen because of capture stress would have been similar between management types. Our data were both left- and right-censored to accommodate staggered entry of birds into the sample, and loss of birds due to harness failure or battery failure of the radio transmitter. We monitored some females in multiple years and modeled individual identity as a random effect with the cluster function to control for lack of independence. As a first step, we tested whether the assumption of proportional hazards was met by our survival data with model diagnostics based on scaled Schoenfeld residuals (cox.zph function; Fox 2002). We used Cox proportional hazards models to test for differences in survival among years, rangeland management at lek of capture (intensive early stocking vs. patch-burn grazing), and female age-class (yearlings vs. adults; we censored 14 individuals of unknown age class from this analysis). Elsewhere, we have shown that space use by female prairie chickens is tightly linked to lek locations (Winder et al. 2014b, 2015, 2017). Therefore, rangeland management practices in the pastures near the lek of capture should be a good indication of habitats available to females during the breeding season.

We ranked models using Akaike’s Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). We excluded models with ΔAICc < 2.0 that differed from the minimum AICc model by a single parameter from the set of candidate models if covariates were uninformative parameters (Arnold 2010). We report the effects of year, rangeland management, and other factors as hazard ratios ($\hat{\beta}$), where the hazard ratio (HR) is expected to equal 1 if there is no difference in the risk of mortality between groups.

**Hazard functions.**—To examine seasonal patterns of mortality, we calculated hazard functions based on weekly survival data using smoothing spline functions in package gss in Program R (DelGiudice et al. 2006). Hazard functions assess the instantaneous risk of mortality per week, given that an individual has survived until that point. Hazard functions are rates and not probabilities, and are well suited for calculation of seasonal patterns of mortality risk. We used the default value of 1 for the smoothing parameter to avoid over-fitting splines. We generated separate hazard functions for females captured at leks on properties managed with patch-burn grazing versus intensive early stocking to explore the effects of rangeland management on seasonal patterns of mortality risk.

**Andersen–Gill models.**—We used Andersen–Gill models for survival to incorporate spatial covariates associated with an animal’s location on the landscape, and to model the effects of habitat selection on cause-specific mortality risk to avian versus mammalian predation (Andersen and Gill 1982, Fleming and Harrington 1991, Johnson et al. 2004, Murray and Patterson 2006). We created a separate set of encounter histories for each female for an annual period from 1 March to 28 February the following year (i.e., Mar 1–7 = week 1). Encounter histories for Andersen–Gill models are structured so that each entry represents an interval between successive pairs of relocations, and individual animals contribute multiple encounter histories to the dataset. Encounter histories contain day of entry, day of exit, length of the interval in days, the animal’s fate at the end of a monitoring interval (1 = mortality, 0 = right-censored), and the continuous and categorical covariates that represented habitat features associated with each relocation event (e.g., stocking rate). Mortality events likely occur close to the end of an interval, so we used habitat covariates corresponding to the detections at the end of an interval (Johnson et al. 2004). We left-censored individuals entering the monitored population at different times, and right-censored data from individuals with dropped or failed collars or individuals that remained alive at the end of the monitoring period (Dinkins et al. 2014a). Female age-class had little effect on estimates of survival in our Kaplan–Meier analysis, and we pooled all females in our Andersen–Gill models.

We used the coxph function in package survival in Program R to fit the Andersen–Gill formulation of the Cox proportional hazards model to our encounter data. We examined the spatial variation in risk factors for female prairie chickens across levels of anthropogenic disturbance and rangeland management treatments (Andersen and Gill 1982, Dinkins et al. 2014a, Appendix A, available online in Supporting Information). One important assumption of Andersen–Gill models is that hazards vary linearly across predictor variables. We used the cox.zph function in package survival for Program R to check the fit of Schoenfeld residuals for our global model and for individual predictor variables (Therneau and Grambsch 2000, Fox 2002, Johnson et al. 2004, Murray et al. 2010).

To conduct a cause-specific mortality analysis, we duplicated the encounter histories in our dataset to account for both mammalian and avian mortality and recorded fate as a failure type variable to distinguish between 2 causes of
death (failure type = avian or mammalian). We used a fail variable to indicate whether an individual died because of a specific cause (fail = 1), or otherwise (fail = 0). For example, the fate of an individual that died as a result of avian predation was coded as fail = 1 in the failure type = avian dataset but as fail = 0 in the failure type = mammalian dataset. Including cause of death as a covariate allowed us to model factors affecting cause-specific mortality (Murray et al. 2010; Appendix A).

We used the Spatial Analyst Extraction tool in ArcMap 9.3 (ESRI, Redlands, CA, USA) to extract landscape covariates related to rangeland management, anthropogenic disturbance, and proximity to lek for each location of all birds included in our analyses. Each year of our study, we surveyed landowners to obtain stocking and burning data specific to each of the nearly 500 pastures in the accessible area of our study site. We used the spatial data to create rasters with 30-m resolution for stocking rates and fire histories to assess the effects of rangeland management practices on mortality risk of female prairie chickens. We used landscape data from publicly available geographic information system (GIS) layers for land cover classes, paved and gravel roads, and elevation from the Kansas Data Access and Support Center at a 30-m resolution with a 30 × 30-m pixel size (2005; www.kansasgis.org, accessed 1 Feb 2015). We estimated distance to patch edge using land cover class grids, the Extract Raster Edge function in Hawth’s Tools, and the Spatial Analyst Distance tool in ArcMap 9.3 (spatialecology.com/htools, accessed 01 Feb 2015; Beyer 2004). We derived raster grids with 30-m resolution for distance to nearest paved or gravel road, lek, and land cover patch edge using the Spatial Analyst Euclidian Distance tool. We also examined cumulative fire frequency as an indicator of potential legacy effects of prescribed fire as the number of years burned from 2000 to 2011 based on satellite imagery and a GIS layer prepared by Mohler and Goodin (2012).

We compared alternative Andersen–Gill models in an information-theoretic framework (Anderson 2008). We based model selection on differences in AIC, (ΔAICc) and evidence ratios from Akaike weights (\( \omega_i \)) with function aictab from the aicmodavg package in Program R (Burnham and Anderson 2002). We discarded models with ΔAICc ≤ 2 that differed from the top model by a single parameter if predictors were uninformative (Burnham and Anderson 2002, Arnold 2010).

Our model set included 34 models that estimated the additive and interactive effects of 7 variables that were predicted a priori to influence mortality risk of female prairie chickens. Three variables were related to rangeland management: cumulative fire frequency, years since last prescribed fire, and stocking rate of cattle or bison (AUM/ha). Four predictor variables described anthropogenic disturbance and landscape features affecting prairie chicken social behavior: distance to nearest land cover patch edge, distance to nearest road, distance to nearest lek, and elevation. Prairie chickens are open country birds and may avoid habitats fragmented by small forest patches or row-crop agriculture (Patten et al. 2011). We used distance to land cover patch edge as an index of the patchiness of land cover. Prairie chickens may be sensitive to anthropogenic disturbance, and we used distance to nearest paved or gravel road as an index of proximity to traffic and vehicle noise (Pitman et al. 2005; Pruett et al. 2009; Hagen et al. 2011; Winder et al. 2014a,b, 2015). Gregory et al. (2011) reported that lek sites are often located at high points on the landscape. We modeled absolute elevation and distance to nearest monitored lek as 2 landscape features that might affect space use by female prairie chickens.

RESULTS

We monitored 133 female prairie chickens over 170 bird-years (2011: \( n = 48 \); 2012: \( n = 55 \); 2013: \( n = 67 \)). Of our 170 bird-years, 84 represented females captured at leks on properties managed with patch-burn grazing, and 86 represented females captured at leks on properties managed with intensive early stocking. The assumption of proportional hazards was met for a global model with factorial effects of management at lek of capture and female age-class (\( \rho = -0.07, \chi^2 = 0.53, P = 0.91 \)). Overall annual survival for female prairie chickens across all years and sites was 0.52 ± 0.05 (SE; 95% CI = 0.44–0.62). Despite considerable annual variation in environmental conditions, annual survival of females did not differ significantly among the 3 years of our field study (Cox proportional hazards HR = 1.21, 95% CI = 0.89–1.64, \( Z = 1.20, P = 0.23 \)) or between female age-classes (Cox proportional hazards HR = 0.65, 95% CI = 0.37–1.13, \( Z = -1.54, P = 0.12 \)). Our model set contained 4 models with AICc ≤ 2 (Table 1). The best-supported model showed that annual survival was a function of rangeland management at lek of capture (\( \omega_i = 0.36 \); Table 1). Annual survival was 35% higher among females captured at leks on properties managed with patch-burn grazing (0.61 ± 0.07, 95% CI = 0.49–0.76) versus females captured at leks on properties managed with intensive early stocking (0.45 ± 0.06, 95% CI = 0.34–0.59; Cox proportional hazards HR = 0.60, 95% CI = 0.36–1.00, \( Z = -1.96, P = 0.05 \); Fig. 2).

Table 1. Model selection results for annual survival of female greater prairie-chickens in the central Flint Hills of Kansas, USA, 2011–2013 (\( n = 170 \) bird-years for 133 individuals of known age class). Treatment describes rangeland management practices at the lek of capture (patch-burn grazing vs. intensive early stocking with annual burning).

<table>
<thead>
<tr>
<th>Models for survivala</th>
<th>Kc</th>
<th>Deviance</th>
<th>ΔAICc</th>
<th>wi/d</th>
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<td>Treatment</td>
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<td>557.32</td>
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<td>1.09</td>
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<tr>
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<td>1.87</td>
<td>0.14</td>
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<tr>
<td>Age × treatment</td>
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<td>2.78</td>
<td>0.09</td>
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<tr>
<td>Year</td>
<td>3</td>
<td>559.80</td>
<td>4.55</td>
<td>0.04</td>
</tr>
</tbody>
</table>

a Model notation: year = 2011, 2012, 2013; treatment = patch-burn grazing vs. intensive early stocking with annual burning; age = female age-class as yearlings (SY) vs. adults (ASY), where + = main effects models and × = factorial model with interactions; constant = intercept only model.

b K = number of parameters, deviance = −2lnL.

c Minimum corrected Akaike’s Information Criterion (AICc) = 561.39.
d Akaike weight.
To investigate the seasonal patterns leading to lower risk of mortality for female prairie chickens on properties managed with patch-burn grazing, we calculated hazard functions for females captured at leks on properties managed with patch-burn grazing versus intensive early stocking and burning. During the early nesting period of late-April through early-July (weeks 7–18), the instantaneous risk of mortality for females captured at leks on properties managed with intensive early stocking and burning (0.033) was approximately 2 times higher than for females captured at leks on properties managed with patch-burn grazing (0.016; Fig. 3). Unexpectedly, we observed a second peak in risk of mortality for females captured at leks on properties managed with intensive early stocking during the midwinter period of late-December through late-January (weeks 43–47; hazard rates = 0.016–0.043; Fig. 3). The weekly risk of mortality for females captured at leks on properties managed with patch-burn grazing during the same period was approximately 4 times lower and ranged from 0.004 to 0.005 (Fig. 3).

For females captured at leks on properties managed with patch-burn grazing, we observed an overall low mortality risk that steadily decreased from the beginning of the breeding season to the end of the bird-year (Fig. 3).

Overall, 84% of mortality events (58 of 69) were due to avian or mammalian predation. The remaining 16% (11 of 69) of mortality events were due to collisions, harvest, or unknown causes. Because other causes of mortality were relatively rare, we focused on competing risks from mammalian and avian predators and censored females that were killed by other causes. We pooled yearlings, adults, and females of unknown age, and our Andersen–Gill analyses included data from 136 females across 173 bird-years, and included 9,213 individual locations. During our 3-year field study, 78 females survived and 58 radio-tagged females (43%) were killed by avian (n = 41) or mammalian predators (n = 17; Table 2). The assumption of proportional hazards was met for all covariates in all models (P ≥ 0.07). We found that the 3 best-fit models included effects of stocking rate (Σwi = 0.66 across all 34 models) and years since burn (Σwi = 0.36 across all 34 models) on the predator-specific mortality risk for female prairie chickens (Table 3, Appendix A). Mortality risk was generally higher from avian than mammalian predation but covaried with habitat conditions. Mortality risk from avian predation was highest in pastures with high stocking rates or recent prescribed fire, whereas mortality risk from mammalian predation was highest in pastures with low stocking rates or at least one year since prescribed fire (Table 4 and Fig. 4).

DISCUSSION

Our 3-year field study provides new evidence that rangeland management practices influence survival rates and mortality risk of female greater prairie-chickens. Females captured at properties managed with patch-burn grazing had annual survival rates that were approximately 35% higher than females captured at properties managed with intensive early stocking and burning. In previous work, we reported that females selected habitats created by patch-burn grazing for nesting and seasonal home ranges, leading to higher nest survival compared to intensive early stocking management practices (McNew et al. 2015, Winder et al. 2017). Integration of landscape characteristics and demographic performance are vital to providing a mechanistic understanding of the ecological processes that drive variation in fitness across a landscape (Aldridge and Boyce 2007, Dzialak et al. 2011, Blomberg et al 2013, Frederiksen et al. 2014).

Habitat-specific analyses of mortality risk are relatively rare (Johnson et al. 2004, Aldridge and Boyce 2007), and results from our Andersen–Gill models provided new insights into the spatial ecology and population dynamics of prairie chickens. We found that females selecting habitats in pastures with high stocking rates and recently burned areas experienced increased mortality risk, and were more vulnerable to avian predators. On the other hand, females that selected habitats with lower grazing pressure or...
unburned areas experienced lower overall mortality risk but were more vulnerable to mammalian predators. Our results support the hypothesis that intensive early stocking and burning practices increase the exposure and mortality risk of female prairie chickens by decreasing the amount of vegetative cover available for concealment, making it more difficult for females to avoid sight-based avian predators. Widespread implementation of intensive early stocking and burning practices across the Flint Hills is likely depressing 2 key demographic parameters with high elasticity, nest survival and annual survival rates of female prairie chickens, and contributing to population declines (McNew et al. 2012, 2015; this study). It follows that cost-sharing incentives or programs aimed at increasing the implementation of patch-burn grazing and other practices that leave more residual cover on private lands could aid the recovery of greater prairie-chicken populations in the Flint Hills (Fuhlendorf and Engle 2001, Rahmig et al. 2009, Allred et al. 2014).

The tradeoff we observed between habitat management and predator-specific mortality risk illustrates the complexity of habitat requirements for female prairie chickens. Adequate vegetative cover is necessary for concealment, but an area that goes unburned for >2 growing seasons may accumulate residual vegetation that prevents females from detecting approaching scent-based mammalian predators. Patch-burn grazing uses a fire regime that creates a mosaic of habitat patches that match the changing seasonal habitat needs of prairie chickens (Coppedge and Shaw 1998; Fuhlendorf and Engle 2001, 2004). In our study system, habitat conditions generated by patch-burn grazing were related to higher annual survival and lower mortality risk from avian predators. Thus, pastures managed with intensive early stocking may serve as ecological sinks.

Seasonal patterns of mortality have not been well studied in prairie chickens or other species of prairie grouse, but available studies usually report high mortality rates during nesting and brood-rearing (Hagen et al. 2007, Lyons et al. 2009, Augustine and Sandercock 2011, Dinkins et al. 2014a, Winder et al. 2014a). Our hazard rates indicated that breeding season mortality risk from late-April through early-July for females captured at leks on properties managed with patch-burn grazing was roughly half that of females captured

Table 2. Causes of mortality for radio-marked female greater prairie-chickens in the central Flint Hills of Kansas, USA, 2011–2013 (n [%]).

<table>
<thead>
<tr>
<th>Yr</th>
<th>Avian predation</th>
<th>Mammalian predation</th>
<th>Collision mortality</th>
<th>Hunter harvest</th>
<th>Unknown cause</th>
<th>Total birds</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>17 (65%)</td>
<td>6 (23%)</td>
<td>0 (0%)</td>
<td>1 (4%)</td>
<td>2 (8%)</td>
<td>26</td>
</tr>
<tr>
<td>2012</td>
<td>10 (59%)</td>
<td>4 (24%)</td>
<td>2 (12%)</td>
<td>0 (0%)</td>
<td>1 (6%)</td>
<td>17</td>
</tr>
<tr>
<td>2013</td>
<td>14 (54%)</td>
<td>7 (27%)</td>
<td>1 (4%)</td>
<td>0 (0%)</td>
<td>4 (15%)</td>
<td>26</td>
</tr>
<tr>
<td>All</td>
<td>41 (59%)</td>
<td>17 (25%)</td>
<td>3 (4%)</td>
<td>1 (1%)</td>
<td>7 (10%)</td>
<td>69</td>
</tr>
</tbody>
</table>

a Bird-year begins 1 March and ends 28 February.


<table>
<thead>
<tr>
<th>Model factorsa</th>
<th>Kb</th>
<th>Deviance</th>
<th>ΔAICc</th>
<th>ωd</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stocking rate</td>
<td>3</td>
<td>595.99</td>
<td>0.00</td>
<td>0.22</td>
</tr>
<tr>
<td>Years since burn + stocking rate</td>
<td>5</td>
<td>593.84</td>
<td>1.85</td>
<td>0.09</td>
</tr>
<tr>
<td>Stocking rate × years since burn</td>
<td>7</td>
<td>589.92</td>
<td>1.93</td>
<td>0.08</td>
</tr>
<tr>
<td>Years since burn</td>
<td>3</td>
<td>598.71</td>
<td>2.72</td>
<td>0.06</td>
</tr>
<tr>
<td>Stocking rate + distance to road</td>
<td>5</td>
<td>594.84</td>
<td>2.85</td>
<td>0.05</td>
</tr>
<tr>
<td>Stocking rate + distance to patch edge</td>
<td>5</td>
<td>595.13</td>
<td>3.14</td>
<td>0.05</td>
</tr>
<tr>
<td>Constant</td>
<td>1</td>
<td>611.57</td>
<td>9.58</td>
<td>0.00</td>
</tr>
</tbody>
</table>

a All models included cause of death (avian or mammalian) as an interactive term.
b $K = $ number of parameters, deviance $=-2\ln\hat{L}$.
c Minimum corrected Akaike’s Information Criterion (AICc) = 601.99.
d All other models with Akaike weights ($\omega$) <0.05 culled for space; all culled models performed better than the constant model.

Table 4. Parameter estimates for greater prairie-chicken mortality risk in the central Flint Hills of Kansas, USA, 2011–2013 estimated from an Andersen–Gill formulation of Cox proportional hazards model including the additive effects of years since burn and stocking rate, with an interaction term describing cause of mortality. Results indicate the probability of predator-specific mortality risk (avian vs. mammalian) as related to spatial variation in habitat conditions.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Effect on mortality risk from</th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>P</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yr since burn</td>
<td>Avian predation</td>
<td>0.80</td>
<td>0.19</td>
<td>-1.20</td>
<td>0.23</td>
<td>0.55</td>
<td>1.15</td>
</tr>
<tr>
<td>Stocking rate</td>
<td>Avian predation</td>
<td>1.62</td>
<td>0.43</td>
<td>1.12</td>
<td>0.26</td>
<td>0.69</td>
<td>3.79</td>
</tr>
<tr>
<td>Avian vs. mammalian predation</td>
<td></td>
<td>1.13</td>
<td>0.64</td>
<td>0.19</td>
<td>0.85</td>
<td>0.32</td>
<td>3.97</td>
</tr>
<tr>
<td>Yr since burn</td>
<td>Mammalian predation</td>
<td>1.42</td>
<td>0.26</td>
<td>1.36</td>
<td>0.17</td>
<td>0.86</td>
<td>2.36</td>
</tr>
<tr>
<td>Stocking rate</td>
<td>Mammalian predation</td>
<td>0.20</td>
<td>0.73</td>
<td>-2.23</td>
<td>0.03</td>
<td>0.05</td>
<td>0.82</td>
</tr>
</tbody>
</table>
prairie-chickens provides strong evidence that habitat conditions generated by patch-burn grazing provide improved concealment for female greater prairie-chickens, resulting in lower mortality risk compared to intensive early stocking. The links we have demonstrated between fire and grazing practices, habitat quality and quantity, habitat selection, and demographic rates provide new information on the spatial ecology of prairie chickens for policy makers. Incentives for private landowners to use patch-burn grazing or similar practices that increase habitat heterogeneity to rebuild a tallgrass prairie mosaic in the Flint Hills will aid the recovery of populations of greater prairie-chickens and other grassland vertebrates.

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Our study was made possible by the generous cooperation of private landowners who allowed access to their lands, by the Tallgrass Prairie National Preserve, and by many dedicated field technicians who helped to collect field data. We extend special thanks to W. Browning and J. Koger for allowing access to their private ranches and for their dedication to prairie chicken research and conservation. K. Hase and B. Obermeyer provided helpful advice and logistical support. Funding and equipment were provided by the Kansas Department of Wildlife, Parks and Tourism, Kansas State University, the National Park Service, and Sportfish and Wildlife Restoration Program of the United States Fish and Wildlife Service.

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LITERATURE CITED


Winder et al. • Prairie-Chicken Survival and Rangeland Management


