IMPACTS OF ALTERNATIVE GRASSLAND MANAGEMENT REGIMES ON THE POPULATION ECOLOGY OF GRASSLAND BIRDS

Brett K. Sandercock, Kansas State University, Manhattan, KS
Virginia L. Winder, Benedictine College, Atchison, KS
Amy E. Erickson, Kansas State University, Manhattan, KS
Lance B. McNew, Montana State University, Bozeman, MT

KDWPT Award No. KDWP-W-67-R
30 November 2014

Summary:

1. We investigated the impacts of rangeland management practices on the *diversity*, *density*, and *nest survival* of grassland songbirds and on the *demography*, *habitat selection*, and *population viability* of Greater Prairie-Chickens (*Tympanuchus cupido*). Our study site was located in eastcentral Kansas and included portions of Chase, Greenwood, Lyon, and Morris Counties. We had access to ~1,100 km^2 of private and public lands. Over 95% of the land was privately owned (~1040 km^2), and the remaining ~5% was the Tallgrass Prairie National Preserve. Our final project report is based on data collected during a 3-year period from Feb. 2011 through Feb. 2014. Our study focused on grassland songbirds and Greater Prairie-Chickens as indicators of ecosystem response. Our analyses are based on direct comparisons between monitoring efforts in pastures managed with patch-burn grazing (PBG) and pastures managed with traditional intensive early stocking and annual burning (IESB).

2. We addressed *three potential impacts* of rangeland management practices on grassland songbirds: *species diversity*, *density*, and *nest survival*. We used line transects to estimate abundance and diversity of grassland songbirds within grazed pastures managed with PBG and IESB. Our data for grassland birds included 463 surveys on a total of 156 different 300-m line transects (12 each in 13 pastures) and monitoring of 340 nests (4 pastures). In addition, we surveyed vegetative structure along a subset of 26 primary transects at a total of 130 sampling points across the study area. We estimated percent cover, litter depth, and visual obstruction at two time points during the field season – once in mid-June (mid-season vegetation) and again in late July (late-season vegetation).

3. We detected a total of 74 species of birds with our line transect surveys, but 52% of our 10,311 detections were from five common species: Dickcissels (*Spiza americana*), Eastern Meadowlarks (*Sturnella magna*), Grasshopper Sparrows (*Ammodramus savannarum*), Brown-headed Cowbirds (*Molothrus ater*), and Upland Sandpipers (*Bartramia longicauda*), and one sensitive species, Henslow's Sparrows (*A. henslowii*). We calculated *bird densities* with distance sampling models for line transect data. Grassland birds had heterogeneous responses to rangeland management: meadowlarks and Henslow's Sparrows had the highest densities in patch-burn grazing units, whereas Dickcissels and Brown-headed Cowbirds had high densities in pastures with season-long stocking and cow-calf grazing. *Nest survival* of grassland songbirds was not habitat-

specific and did not differ among different treatments. Grassland songbirds differ in ecological requirements and patch-burn grazing can help to create a heterogeneous environment with a mixture of different habitat types.

4. We addressed *six potential impacts* of rangeland management practices on Greater Prairie-Chickens: *nest site selection*, *fecundity*, *seasonal home ranges*, *space use*, adult female *survival*, and *population growth and viability*. Our monitoring efforts during the 3-year study period included 34 lek sites, 147 radio-marked females monitored for 179 bird-years, >10,000 individual locations of radio-marked females, 143 nesting attempts (109 first nests, 34 renesting attempts), and 36 broods that were monitored until they failed or the young reached independence at 30 days.

5. We located 143 prairie-chicken nests and surveyed vegetation structure at nest sites, as well as at 47 brood locations and 286 random points within the study area to investigate the effects of rangeland management practices on *nest site selection*. Our results indicated that nest site selection was directly related to vertical nesting cover determined by fire return interval on patches. Overall, the quantity and quality of nesting sites was improved under patch-burn grazing management when compared with more intensive grazing regimes for cattle production.

6. We monitored the fate of 143 prairie-chicken nests to investigate the effects of rangeland management practices on *fecundity*. Nest survival for prairie-chickens in the unfragmented grasslands of our study areas was largely determined by vertical nesting cover, which was affected by rangeland management. Mean nest survival (± SE) on patch-burn grazing properties (0.21 ± 0.05) was twice as high as nests on intensive properties (0.10 ± 0.03), suggesting a direct benefit of patch-burn grazing to prairie-chicken populations. We found no effects of rangeland management on the date of clutch initiation, clutch size, egg hatchability, or renesting following nest failure.

7. We used kernel density methods to estimate *seasonal home ranges* for 102 radio-marked female prairie-chickens for 112 bird-seasons during the breeding season (Mar.–Aug.) and 45 individuals for 45 bird-seasons during the nonbreeding season (Sep.–Feb.). We investigated *space use* within breeding and nonbreeding home ranges using resource utilization functions (RUFs). The RUF analyses allowed us to identify individual and population level drivers of space use based on a set of landscape characteristics, including stocking density, prescribed fire frequency, and years since fire. Space use decisions can affect survival and productivity of prairie-chickens through interactions with predators and energy costs. The strongest predictor of female prairie-chicken space use within home ranges during both breeding and nonbreeding seasons was distance to lek. Our results also showed that the interaction between fire application and stocking rates influences the space use decisions of female prairie-chickens. Moreover, we found evidence that PBG management practices create mosaic of burned and unburned patches that are preferred habitats for female prairie-chickens.

8. We calculated *survival* rates of radio-marked female prairie-chickens with staggered entry Kaplan-Meier models. We tested for effects of year, rangeland management

practices at the lek of capture and nest site, home range size, proximity to road, lek, and patch edge, and individual habitat selection for landscape-level drivers of space use (β coefficients from RUF models). We found that PBG practices provide habitat conditions that increase female survival during both breeding and nonbreeding seasons, indicating that widespread implementation of PBG has the potential to greatly improve prairie-chicken population dynamics at a large spatial scale. We also found that areas near roads may act as ecological sinks for female prairie-chickens because females are at increased risk of predation from raptors in these areas.

9. In our analysis of *population growth and viability*, we used eight demographic parameters in a matrix population model: probability of breeding, fecundity as the product of four parameters (number of reproductive attempts per female, clutch size per reproductive attempt, number of young surviving to 25-d post-hatch per egg, and proportion of females at hatching), and annual survival estimates for yearling and adult females. Prairie-chicken populations were not viable with observed demographic rates and were predicted to decline without immigration under different rangeland management treatments, but the rate of decline was steeper under IESB ($\lambda = 0.436$) compared to PBG ($\lambda = 0.727$). Data from our field study suggest that widespread implementation of PBG would slow the rate of population decline, simultaneously improving the two most influential rates to population viability at our study site – fecundity and annual survival of adult females. PBG management could help improve population viability and would allow for additional time for further studies and experimental implementation of management practices.

10. Our results provide multiple lines of evidence that PBG benefits native prairie wildlife and ecosystem health (**Figure 0.1)**. More than 90% of the extant distribution of prairie-chickens occurs on managed rangelands. Therefore habitat conditions and ultimately the conservation of prairie-chickens are largely determined by the management decisions of private landowners and livestock producers. Fire and grazing are keystone ecological processes that created and continue to maintain grassland ecosystems. Therefore, the primary goals of range and wildlife managers to maintain grassland habitats are complimentary. Our results indicate that patch-burn grazing regimes have the potential to mitigate ongoing population declines of prairie-chickens. Conservation easements that provide cost-shared support or technical assistance for implementing patch-burn grazing management programs on private ranches should reduce obstacles and facilitate adoption by land owners. Conservation and educational programs that facilitate a transition from homogenous grassland management to regimes that provide a shifting mosaic in herbaceous plant composition and structure are required to maintain the integrity of tallgrass prairie ecosystems (Fuhlendorf and Engle 2004).

11. Research funding for this project included a State Wildlife Grant from the Kansas Department of Wildlife, Parks & Tourism (*this final report*) and support from Kansas State University for Master's student A. Erickson and faculty member B.K. Sandercock. Research products from data collected during this project have included *two research articles* (one accepted for publication at Rangeland Ecology & Management with minor

revisions, and a second under review at Biological Conservation). A. Erickson is scheduled to complete her *Master's Thesis* at Kansas State University in 2015.

Background

Tallgrass prairie is the most intensively altered biome in North America with more than 95% of the former area lost to rowcrop agriculture or other development during the last century (Hoekstra et al. 2005, Samson et al. 2004). Marked declines in grassland bird populations across a wide spatial scale have corresponded to loss and degradation of habitat (Knapp et al. 1998, Brennan and Kuvlesky 2005). The Flint Hills region of eastern Kansas and Oklahoma contains the largest remaining tracts of tallgrass prairie and is ecologically important because the region supports populations of many sensitive species (Powell 2006, With et al. 2008). Many conservationists consider the Flint Hills to be vital to the long-term persistence of many obligate grassland birds (Svedarsky et al. 2000, Reinking 2005). The Flint Hills is generally unsuitable for cultivated crops but the area supports an economically important cattle grazing industry occupying >90% of its prairies (With et al. 2008). During the last 30 years, rangeland management has shifted from periodic prescribed burning and year-round grazing to annual spring burning combined with intensive early stocking of steers during April–July (**IESB**; Smith and Owensby 1978). IESB benefits cattle production by promoting the growth of high quality forage and allowing ranchers to stock ranges with cattle early in the growing season. IESB may negatively affect grassland birds by reducing structural heterogeneity of grassland habitats, and implementation of IESB has coincided with population declines among obligate grassland species (Fuhlendorf et al. 2006, Rahmig et al. 2008, Reinking 2005).

Historically, grazing and fire were natural ecological processes whose interaction shaped grassland ecosystems and their wildlife populations (Askins 2000, Fuhlendorf and Engle 2001). Grazing, when combined with periodic burning, created and maintained shifting mosaics of vegetation that fulfilled many different life-cycle requirements of the grassland bird community (Brennan and Kuvlesky 2005, Fuhlendorf et al. 2006). Modem grazing practices implemented after European settlement, such as IESB, result in homogenized plant communities and habitat structure which, in turn, drove severe declines in the abundance and diversity of grassland wildlife (Zimmerman 1997, Kauffman et al. 1998, Fuhlendorf et al. 2006).

Recently, patch-burn grazing (**PBG**) was introduced as an alternative management technique that increases the heterogeneity of vegetation structure and composition on grazed grasslands while providing viable revenue for cattle producers and landowners (Fuhlendorf and Engle 2001, 2004). Patch-burn grazing is a rotational burning management scheme that mimics presettlement fire-grazing interactions which may benefit many declining prairie species (**Figure 0.2**; Churchwell et al. 2008, Coppedge et al. 2008, Powell 2008). Patch-burn grazing regimes produce a shifting mosaic of vegetation that provides a host of ecosystem benefits. Patch-burn grazing results in an accumulation of fuel on unburned patches which increases the intensity of fire during prescribed burning, aiding in control of noxious species that are unpalatable to cattle and compete with native plants (Steuter 1986, Cummings et al. 2007). Previous research has found that revenues from cattle grazing with PBG practices are comparable to those with IESB in tallgrass prairie systems (Rensink 2009, Limb et al. 2011).

Additionally, increased spatial heterogeneity of vegetation created with PBG practices provides floristic and structural variability that increases grassland wildlife diversity and provides benefits to invertebrate species that service grassland ecosystems (Fuhlendorf et al. 2006, Swinton et al. 2007, Churchwell et al. 2008, Coppedge et al. 2008, Black et al. 2011). Wildlife biologists have speculated that widespread implementation of patch-burn grazing could result in significant improvements in the quality of habitats for grassland wildlife in tallgrass prairie ecosystems (Fuhlendorf et al. 2006). However, studies evaluating the effectiveness of patch-burn grazing as a conservation strategy to impede or reverse population declines of grassland birds in unfragmented tallgrass ecosystems are limited.

The purpose of our 3-year field study was to examine the potential impacts of traditional vs. alternative grassland management regimes on declining species of grassland songbirds and Greater Prairie-Chickens (*Tympanuchus cupido*; hereafter "prairie-chickens") as indicators of ecosystem health in eastcentral Kansas. High levels of homogeneity in pastures managed for cattle production are often associated with lower species diversity and abundance of grassland songbirds (Fuhlendorf et al. 2006). Increasing habitat homogeneity has been suggested to be one of the main drivers of widespread population declines in songbird populations in North America and Europe (Herkert et al. 2002, Sauer et al. 2014). In the tallgrass prairie, steep population declines have been observed in Grasshopper Sparrows (*Ammodramus savannarum*), and Henslow's Sparrows (*A. henslowii*), Eastern Meadowlarks (*Sturnella magna*), and Dickcissels (*Spiza americana*, Sauer et al. 2014). To counter ongoing population declines, rangeland managers often implement management regimes that focus on higher levels of heterogeneity in vegetative structure. Most studies that evaluate how heterogeneity in the landscape influences bird populations focus on species diversity and abundance (Powell 2006). Species diversity and abundance, however, do not reflect whether habitat heterogeneity benefits the demographic performance of bird species that breed on those fields. Garshelis (2000) recommended recording demographic information such as nest survival, to test landscape heterogeneity in the light of ongoing population declines.

The Greater Prairie-Chicken is an obligate grassland bird and umbrella species for tallgrass prairie conservation (Poiani et al. 2001, Johnson et al. 2011). Prairie-chickens are a species of conservation concern because their breeding range has been greatly reduced and the core of their remaining range is located in Kansas, Nebraska, and South Dakota (Busby and Zimmerman 2001). Lek count data from monitoring programs of the Kansas Department of Wildlife, Parks, and Tourism indicate that prairie-chicken numbers have declined in Kansas during the past 30 years (Rodgers 2008, Pitman et al. 2012). Declining population numbers and genetic isolation are of particular concern for Greater Prairie-Chickens because they are one of the few wildlife species where inbreeding depression has been documented in wild populations (Westemeier et al. 1998). Population declines of prairie-chickens have paralleled continental losses of native tallgrass prairie and much of the species' remaining distribution occurs in the relatively unfragmented Flint Hills ecoregion. Prairie-chickens are thought to be sensitive to disturbance because they have large home ranges, and females may move up to 30 km from lek sites to nest (Robel et al. 1970, Schroeder 1991, Augustine and Sandercock 2011, Winder et al. 2014b). Previous studies have provided evidence that female prairie-chickens may avoid disturbance from oil, gas, and wind energy development and power lines (Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011, Winder et al. 2014b).

Prairie-chickens require a diverse mosaic of floristic and structural grassland habitat types for successful reproduction and survival: open sites at relatively high elevations for display arenas or leks, dense vegetative cover for concealment during nesting, and intermediate vegetative structure rich in forbs for foraging and rearing of broods (Johnson et al. 2011, Svedarsky et al. 2000). High predation rates of nests and young resulting from a lack of adequate vegetative cover during nesting is the primary cause of population declines of prairie-chickens in the Flint Hills (McNew et al. 2012a, McNew et al. 2014). However, the direct relationships between prairie-chicken fecundity, nesting cover, and rangeland management practices have not been evaluated.

Our 3-year field study was designed as a direct comparison between PBG and IESB management practices with regard to their impacts on sensitive species of grassland birds. We studied grassland songbirds and prairie-chickens at a ~3,000 km^2 study site including portions of Chase, Greenwood, Lyon, and Morris Counties in eastcentral Kansas. The Flint Hills ecoregion is a landscape of relatively unfragmented tallgrass prairie, and native grassland was the dominant land cover type at our field site (> 90%; **Figure 0.3**). Road density was relatively low at ~0.58 km of road/km^2 at our study site, compared to other study sites in the Flint and Smoky Hills (Winder et al. unpubl. ms). Mean annual precipitation from 1980 to 2010 at our study site was 92.4 cm (ncdc.noaa.gov, station no. 147305).

Within the study area, we had permission from land owners and managers to access pastures covering ~1,100 km^2 (**Figure 0.4**). A majority of accessible lands were privately owned (96%, 1,050 km^2), and the remaining land was managed by the National Park Service at the Tallgrass Prairie National Preserve (4%, 50 km^2). The National Preserve and two additional privately owned properties (Browning and Koger ranches) were managed with PBG while the remaining lands in our study area was managed with intensive early-stocking (IESB), and in a few cases, season-long stocking (SLSB) or cow-calf grazing (CCB, **Figure 0.4**).

Though the management strategies on the PBG properties were consistent over the 3-year field effort, management strategies on the adjacent IESB properties were variable from year to year and dependent upon weather conditions and individual ranch managers. Historically, most IESB properties were managed with annual spring burn and a stocking density of 1 head per 0.8 ha for 90 days during April–July. However, drought conditions resulted in many property managers not burning rangeland in 2012 and 2013 and stocking at lower densities; average (± SD) stocking intensity during the study on reference properties was 2.33 ± 1.03 animal unit months (AUMs)/ha. The majority (>90%) of the remaining grasslands managed with IESB were burned in the spring of 2011, ~10% was burned in 2012, and only ~1% of the study area managed with IESB was burned in the spring of 2013 because of drought conditions in the previous two years. Pastures in patch-burn treatments were divided into thirds and each third was burned rotationally every third year. Cattle were free to move among the patches within a pasture but concentrated their grazing on the most recently burned patches (Fuhlendorf and Engle 2004). PBG properties were stocked with cattle (1.5–2 AUM/ha), or bison (0.45 AUM/ha).

More than 95% of the remaining native tallgrass prairie in the Flint Hills ecoregion is privately owned with the vast majority being managed for cattle production. Thus, information on how alternative rangeland management practices directly affect species diversity, density, space use, and demography are needed to build effective conservation strategies for grassland birds in the region. We had six objectives for testing the potential impacts of alternative grassland management regimes on the population ecology of grassland birds.

Objective 1 *Impacts on grassland songbird diversity, density, and nest survival.* Frequency and intensity of grassland disturbance determines vegetative composition and structure (Vinton et al. 1993, Coppedge et al. 1998). In turn, structural heterogeneity of vegetation drives grassland bird community dynamics (Wiens 1997, Coppedge et al. 2008). We expected densities and nest survival of grassland songbirds to be higher in areas managed with PBG compared to IESB.

Objective 2 *Impacts on breeding habitat selection of Greater Prairie-Chickens*. Prairie-chickens generally have the highest productivity in areas with moderate amounts of residual cover (Bowman and Robel 1977, McKee et al. 1998, Ryan et al. 1998, McNew et al 2013, 2014). IESB limits quality nesting sites because residual cover is eliminated or greatly reduced across a large spatial scale. We expected that implementation of PBG would result in a heterogeneous mosaic of habitat suitable for nesting sites and that female prairie-chickens would actively select PBG sites for their nests.

Objective 3 *Impacts on fecundity of Greater Prairie-Chickens*. Greater Prairie-Chickens are ground-nesting birds, and most reproductive losses are due to depredation of nests and young (Svedarsky 1988, Peterson and Silvy 1996, McNew et al. 2012a). We predicted that the reduction in cover in areas managed with IESB would be result in decreased reproductive success and that increased cover in areas managed with PBG would result in increased reproductive success.

Objective 4 *Impacts on seasonal home ranges and space use by Greater Prairie-Chickens*. The interaction of fire-return intervals and grazing regime influences the long-term occupancy of prairie-chickens (McNew et al. 2012b). PBG has the potential to influence how prairie-chickens select habitats because it results in a mosaic of heterogeneous habitats (Fuhlendorf et al. 2006). We predicted that PBG would result in smaller breeding home ranges and that prairie-chickens would avoid recently burned and heavily grazed areas as well as areas with infrequent fire return intervals.

Objective 5 *Impacts on survival of Greater Prairie-Chickens*. Adult prairie-chicken survival is decreased in heavily fragmented, cultivated, and developed areas (Hagen et al. 2007, McNew et al. 2012a), and survival rates of prairie-chickens in the relatively unfragmented Flint Hills are among the highest reported for prairie grouse (McNew et al. 2012a). Most mortality for adult females occurs during the breeding season because females are vulnerable during incubation and brood-rearing, relying on cryptic coloration to avoid detection by predators (Hagen et al. 2007, Winder et al. 2014a). We predicted that survival rates of adult females would benefit from increased residual cover in areas managed with PBG.

Objective 6 *Impacts on the rate of population change and population viability of Greater Prairie-Chickens*. Rates of prairie-chicken population change are most sensitive to changes in reproductive rates (Wisdom and Mills 1997, Fefferman et al. 2006, Hagen et al. 2009). The overall impact a shift in range management has on population viability may be the result of a combination of impacts on the underlying vital rates rather than a direct effect on the most important vital rate. We predicted that PBG would improve population size and long-term viability of Greater Prairie-Chickens via increases in suitable nesting habitat, nest survival, and adult female survival.

Figure 0.1. Schematic representation of the linked effects of rangeland management practices on Greater Prairie-Chicken demography and space use in the Flint Hills, eastcentral Kansas, 2011–2013. Green = PBG, red = IESB, blue = ecology; Nest S = successful nest; Nest F = failed nest; BHR = breeding home range; NHR = nonbreeding home range; S = survival; VOR = visual obstruction reading; SR = selection ratio.

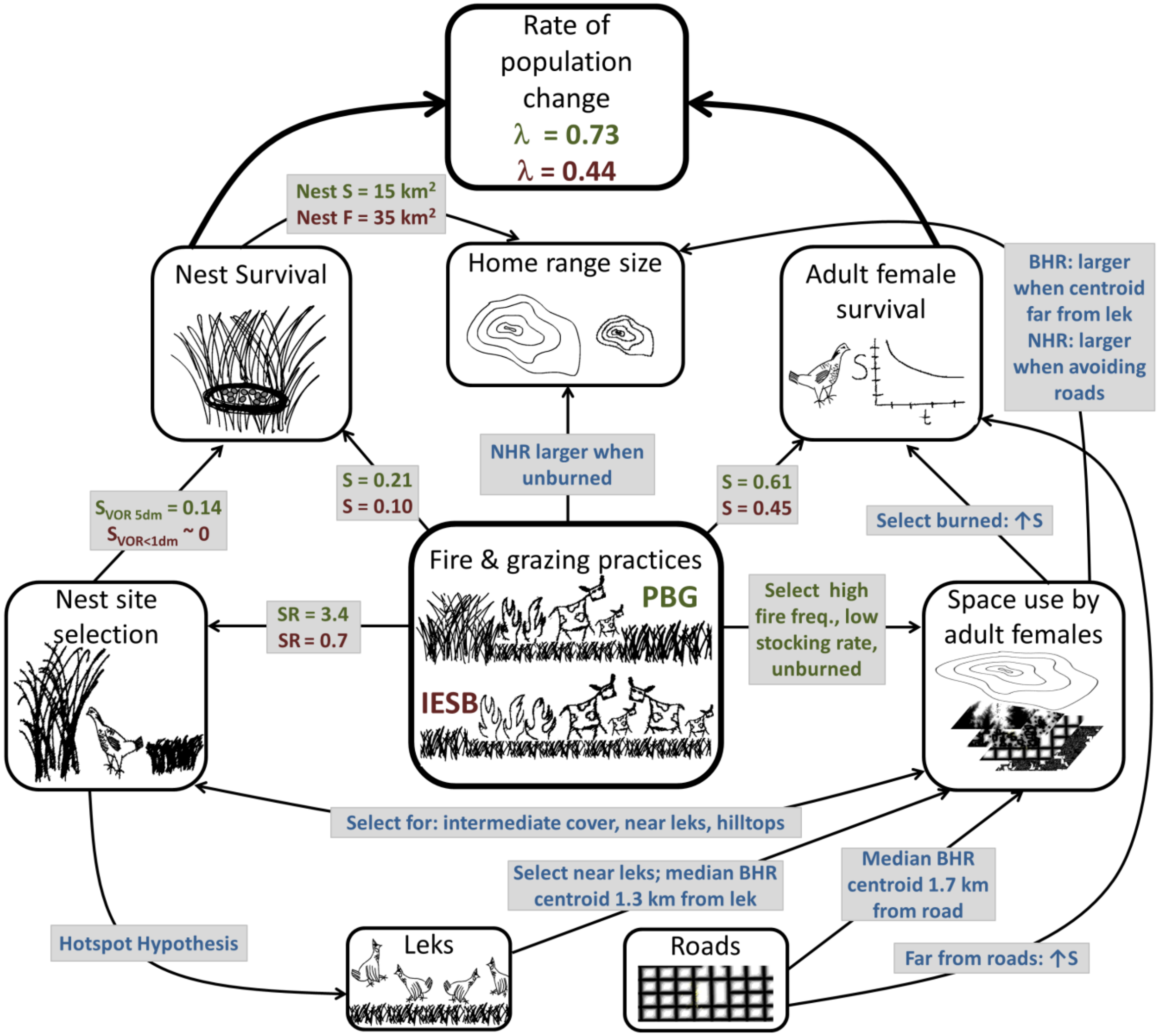


Figure 0.2. Schematic representation of patch-burn grazing regime. Pastures are divided into patches using fire breaks, not fences. Fire is applied to each patch of the pasture on a 3-year rotation. Year of burn is represented by dark green, one year post-fire is represented by light green, and two years post-fire is represented by tan. Cattle concentrate their grazing intensity in the most recently burned patch, allowing for accumulation of vegetative structure and litter, varied vegetative composition, and an overall increase in habitat heterogeneity.

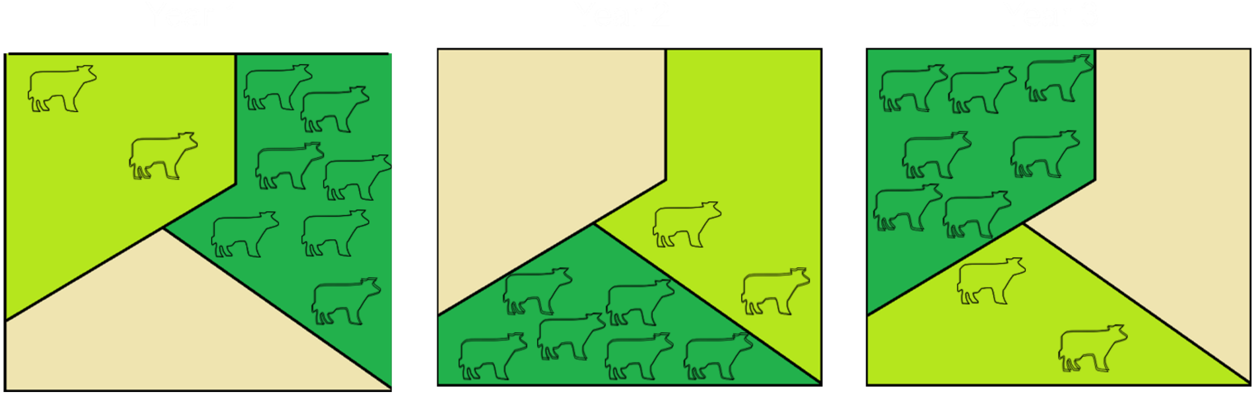


Figure 0.3. Location of field site for study of the impacts of alternative rangeland management regimes on grassland birds in eastcentral Kansas. Dark black lines are state highways, gray lines are county roads, black triangles are Greater Prairie-Chicken leks. Green represents grassland, tan represents row-crop agriculture, and orange represents pastures in the Conservation Reserve Program (CRP).

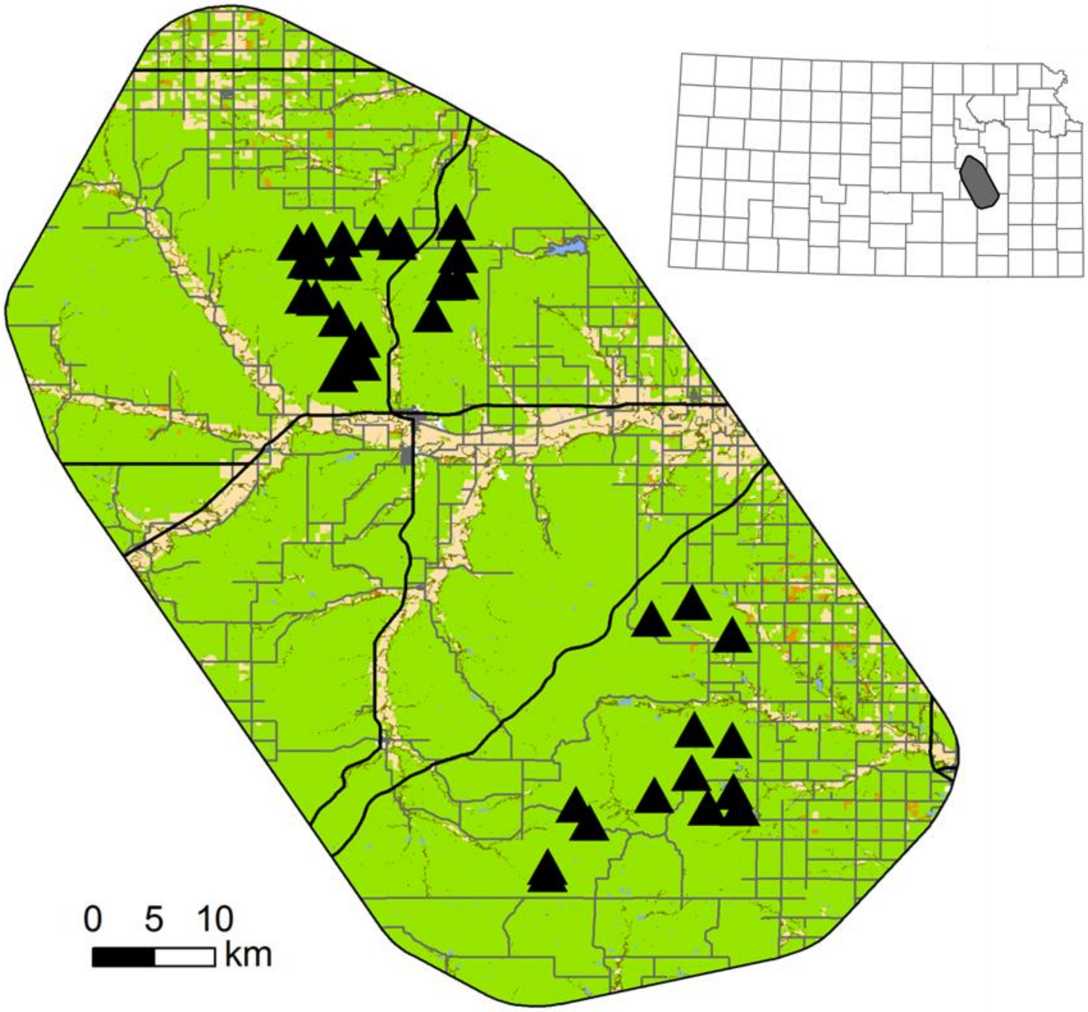
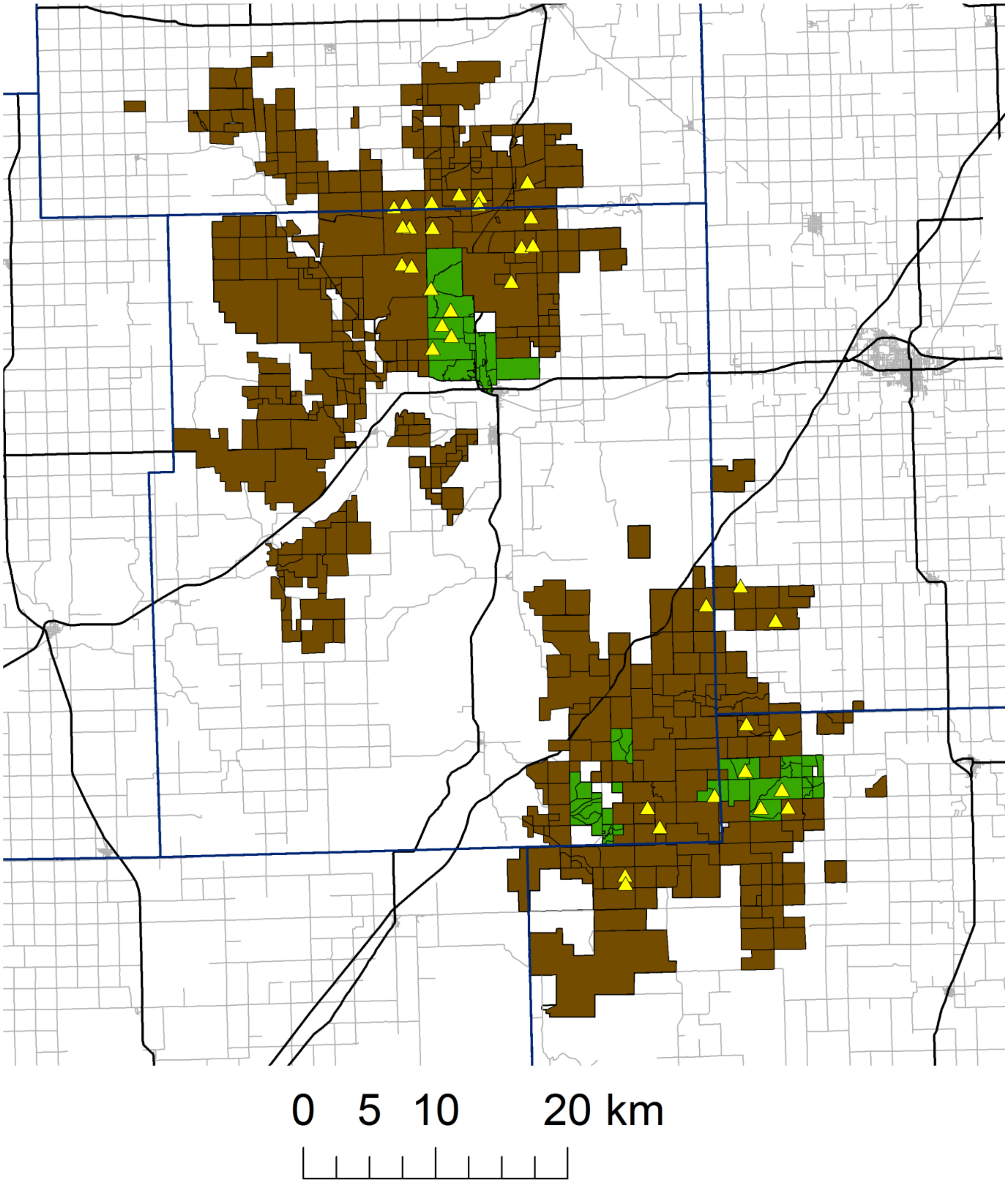


Figure 0.4. Map of properties included in our field study of the impacts of alternative rangeland management regimes on grassland birds in eastcentral Kansas. Dark black lines are state highways, gray lines are county roads, blue lines are County borders. Properties filled in brown were managed with intensive early stocking and annual burning (IESB); properties filled in green were managed with patch-burn grazing (PBG). Greater Prairie-Chicken leks are represented by yellow triangles.



Objective 1. *Impacts on densities and nest survival of grassland birds*

We examined the effects of rangeland management on grassland songbirds with a combination of bird surveys with line transects and intensive nest monitoring. Bird surveys were used to examine species responses in the entire bird community, whereas nest monitoring focused primarily on four species of open-cup nesting species.

Objective 1a. Surveys of grassland birds

Field methods. – Line transects were laid out at random in 13 pastures with different rangeland management. Transects were at least 0.5 km from pasture edges and from each other. All transects were mapped and located with hand held GPS units based on UTM coordinates Two pastures were negative controls with intensive early-stocking and annual burning (IESB, Highland, 419 ha; Nation, 533 ha). Nine pastures were three replicates of a rotational patch-burn grazing treatment that went through a complete rotation in our 3-year study period of 2011-2013 (PBG, Bell, 80-137 ha; Schoolhouse, 142-155 ha; Tower, 57-134 ha). In each year of the study, a third of the total area was newly burned (PBG0), a third was rested from fire for one year (PBG1), and a third was rested for two years (PBG2). Two pastures were positive controls with season-long stocking with annual burning (SLSB, Huber, 587 ha) and cow-calf grazing with annual burning (CCB, Browning West, 337 ha). We surveyed birds in each of the 13 pastures with twelve 300-m line transect lines for a total of 156 transect lines. We conducted three rounds of surveys each summer and rotated observers among transects to avoid possible effects of observer bias. All surveys were conducted with four hours of sunrise on days with low winds and little precipitation. We identified all birds heard or seen to species, and recorded group size, and the perpendicular distance from the line transect with laser rangefinders. Transects were of variable width and we recorded all distances without truncation. If birds were detected as a flock, we treated the sighting as a single cluster and recorded the distance once only. Records of birds that were fly-overs were not included in the analyses.

Statistical Analyses. – We modeled detections of clusters of birds on line survey transects with the unmarked package in Program R. We set the range of possible perpendicular distances to be bounded between 0-400 m with a bin width of 20 m for a total of 20 possible bins. We used the formatDistData function to summarize sightings as a multinomial distribution with counts of clusters in each 20 m bin. The unmarkedFrameDS function was used to combine a reference file with covariates for each transect with a second file with our bird detections. We then used the distsamp function to fit alternative models for the probability of detection and abundance. Modeling proceeded in three steps. First, we fit a model with constant detection and abundance with three different detection functions: exponential, half normal, and hazard that described the decay in detection away from the center of the line transect. In all species, the hazard function was the best fit and received more support than the other two functions (ratio of $w_i/w_j > 50\times$). Second, we tested four possible factors as effects on probability of detection: a null model where detection was a constant, year of study (2011-2013), round of survey (1-3), and stratum (IESB, PBG0-PBG2, SLSB, CCB). Last, we took the best fit model for detection and modeled abundance as a function of year and stratum. The predict function was used to calculate density of clusters of birds per hectare. To calculate the expected strip width (ESW) for our line transects for each species, we used the integrate function to calculate the area under the detection curve, where the curve was defined by parameter estimates for the shape and scale of the hazard function.

Results. – Bird surveys were based on three rounds of sampling for 12 transects in each of 13 pastures for a total of 468 possible transect surveys. Five surveys were omitted and our analyses were based on sample set of 463 surveys. We detected a total of 74 bird species in our sample and recorded a total of 13,944 detections of birds, including 10,113 records where perpendicular distance was recorded. After censoring records of fly-overs, the five most abundant species of birds in our surveys were Dickcissels (n = 3,351 clusters), Eastern Meadowlarks (n = 2,156 clusters), Grasshopper Sparrows (n = 2,103 clusters), Brown-headed Cowbirds (483 clusters), and Upland Sandpipers (391 clusters). Henslow's Sparrows (185 clusters) were relatively rare but we modeled our survey data for this species since it is a grassland bird of conservation concern in Kansas. Detections of these six species accounted for 52.6% of all birds recorded in our line transect surveys (5,318 of 10,113 records).

Point count surveys often show evidence of 'donut effects' where detections at the center of the point count circle are reduced because of observer effects on bird activity, including reductions in singing or display or displacement away from the survey point. We found some evidence for displacement in our line transect surveys because the numbers of detections were reduced in the 0-20 and 20-40 m bins for Eastern Meadowlarks, Grasshopper Sparrows, and Henslow's Sparrows (**Figure 1.1**). On the other hand, detections were highest in the 0-20 or 20-40 m bins for Dickcissels, Brown-headed Cowbirds, and Upland Sandpipers. Donut effects can be addressed by left truncation of the survey data but we opted to retain all detection records so that our modeling approach was consistent for all six study species. Effective strip width of the line transects was shortest for Henslow's and Grasshopper Sparrows (67-71 m) which are small, secretive birds with songs comprised of soft trills. As might be expected, strip width was longer for Brown-head Cowbirds and Eastern Meadowlarks (122-138 m) which are large-bodied, conspicuous birds that are effective at broadcasting loud songs in a prairie environment.

Model selection showed that different factors affected detection for our six study species. The detection function for Dickcissels was affected by the round of surveys with a shorter estimated strip width in round 1 (83.0 m) compared to rounds 2-3 (99.0-100.7 m, **Table 1.1**). The detection function for four other species was affected by year, with different patterns of annual variation in estimated strip variation among these species. The detection function for Upland Sandpipers was affected by stratum with shorter detection distances in open habitats (IESB) compared to pastures with greater vegetative cover (PBG2, SLSB).

In all six study species, the best fit model for abundance contained the effect of stratum (**Table 1.1**). Thus, bird densities of each species differed among the six different treatments for rangeland management: IESB, PBG0-PBG2, SLSB and CCB. Moreover, in all six species, a single model received a majority of support within each candidate set and ratios of model weights between the minimum AIC model and the next best model ranged from 10-100×.

The effects of fire and grazing on densities of grassland birds in managed pastures differed among our six study species (**Figure 1.2**). Dickcissels, Eastern Meadowlarks, and Brown-headed Cowbirds are all generalist species that forage for invertebrates in ground vegetation. Densities of these species were lowest in rangelands managed with IESB and in the year of burn in the patch-burn grazing rotation (PBG0), but higher in the other four treatments. For Dickcissels, densities were low in the patch-burn grazing treatment, and were highest in the SLSB and CCB treatments. Densities of meadowlarks was highest in the PBG2 treatment, whereas cowbirds had the the highest density in the SLSB treatment. Stratum was the top model for abundance of Grasshopper Sparrows but estimates of density were comparable among all six treatments, and were only reduced in the year of burn in the patch-burn grazing rotation (PBG0). Upland Sandpipers are a specialist species that selects disturbed areas for foraging. In contrast to the other five species, Upland Sandpipers had high densities in the year of burn in the patch-burn grazing, and also in the SLSB treatment. Last, Henslow's Sparrows are a specialist species that require undisturbed prairie. Henslow's Sparrows were almost completely absent from all treatments with annual burning. The highest densities of birds were found in the patch-burn grazing treatments that had been rested from fire for two years and had accumulated vegetative litter from two growing seasons.

Objective 1b. Nest survival of grassland songbirds

Field methods. – Nest searching and nest monitoring required an intensive field effort that was not possible to conduct at the same spatial scale as the line transects for the bird surveys. Our field study of nest survival was conducted at one replicate of the patch-burn grazing treatment (Schoolhouse, 142-155 ha) and had one control plot managed with IESB (Highland, 419 ha). We located nests by watching behavior of the attending parents and by opportunistically flushing birds. We focused on nests of four grassland songbirds: Dickcissels, Eastern Meadowlarks, Grasshopper Sparrows, and Lark Sparrows. We used nest architecture, egg coloration, and egg size to identify nests of different songbird species. The four species build nests of woven grass at ground level or on the stem of a forb. Dickcissels and Lark Sparrows are open cup nesters, whereas meadowlarks and Grasshopper Sparrows build a dome nest with a lateral entrance. Dickcissels lay immaculate blue eggs, meadowlarks and Grasshopper Sparrows lay speckled eggs, and Lark Sparrows lay white eggs with black streaking.

At first discovery, we recorded the nest contents including number of eggs or young for the host species and the parasitic young of cowbirds. We marked the nest at ~10-20 m with a small rock cairn and recorded the distance and compass bearing to the nest site. Wherever possible, we used proximity to natural features to relocate and check nests. We visited nests every 2-3 days to determine nest fate and recorded number of young, and age-class of chicks on a 6-point scale. A nest was considered to have *failed* if the nest contents disappeared before the expected fledging date, or if broken eggs, torn nest, a predator, or other sign at the nest site indicated that the nest contents had been destroyed by a predator, rainfall or other causes. A nest was considered to be *successful* if the chicks survived until fledging, and if parents were observed defending or feeding dependent young at the nest or within the vicinity of the nest after fledging.

Statistical Analyses. – We modeled daily nest survival of songbird nests with the Rmark package in Program R as an interface to the nest survival procedure of Program Mark (ver. 7.1, Colorado State University, Ft. Collins, CO). We created encounter histories for all nests monitored in our 3-year field study (2011-2013) where we had complete information for dates of monitoring and nest fate. Encounter histories included the date of initial nest discovery (i), the last date a nest was known to be active (j), the date that the nesting attempt was completed (k), the fate of the nest (f, 0 = successful and 1 = failed), and the number of nests with the encounter history (n). The last two dates were set to be identical if a nest was successful ($j = k$), but bracketed the period of loss if a nest failed ($j < k$).

We modeled daily nest survival with a set of eight *a priori* models that included an intercept-only model, single factor models, additive models with the main effects (+), and factorial models with main effects and their interactions (×). Model factors included year of study (2011-2013), rangeland treatment (intensive early-stocking vs. patch-burn grazing), and rangeland patch (intensive early-stocking vs. year of fire, one year rested or two years rested within the patch-burn grazing treatment). We used daily nest survival model to calculate period survival of a nest for a 24-day exposure period based on 2 days for egg-laying, 13 days for incubation, and 9 days for brood-rearing (e.g., Dickcissels, Sandercock et al. 2008). We used the delta method to derive an expression to calculate the variance of period survival. The estimates of period survival correct for losses prior to nest discovery and are lower than apparent nest survival based on the percentage of nests in the sample that were observed to fledge young.

Results. – We located a total of 340 songbird nests in our 3-year field study in Chase Co., Kansas (**Table 1.2**). Sample sizes improved each year with 90 nests in 2011, 112 nests in 2012, and 138 nests in 2013. The largest sample of nests was found for Dickcissels with 189 nests, but with smaller numbers of nests were monitored for Grasshopper Sparrows with 82 nests, Eastern Meadowlarks with 51 nests, and Lark Sparrows with 18 nests. Apparent nest survival was low overall and among species (23.2%-32.8%) with different patterns of annual variation in each species. Given the small samples in some cases, we opted to pool nests of all four songbird species for analyses of nest survival.

The top model for survival of songbird nests was a model with a constant daily nest survival rate (**Table 1.3**). A model with annual variation was the second best fit and was equally parsimonious (ΔAICc = 0.88) but the constant model received 1.6× more support (i.e., w_i/w_j =

0.38/0.24). Period nest survival was highest in the first year of the study (2011: 19.7%) and lower in the following two years with drought conditions (2012-2013: 11.4-12.4%, **Table 1.4**). The third best model was also parsimonious (ΔAICc = 1.98) and included the effects of treatment comparing nests in intensive early-stocking versus nests in patch-burn grazing units. In both habitats, songbird nests were expected to have a low 13.3-13.8% probability of surviving until fledging. A model with the effect of patch estimated daily survival separately for all strata but received relatively little support (ΔAICc = 4.69). Unexpectedly, the highest rate of daily and period nest survival was found in the year of burn in the patch-burn grazing treatment (PBG0: 25.5% vs. 11.1-13.8% for the other treatments). However, density of songbirds was lowest in this treatment (**Figure 1.2**). Relatively few nests were found in the PBG0 treatment (n = 9) and the high estimate of period survival also had the lowest precision (PBG0: SE(S_n) = 14.2% vs. 2.2-4.4% for the other treatments).

Rangeland management had strong effects on densities of grassland birds but little effect on habitat-specific rates of nest survival. Patch-burn grazing provided breeding habitat for three sensitive species: Eastern Meadowlarks and Henslow's Sparrows had the highest densities in pastures that had not been burned for two years, whereas Upland Sandpipers had high densities in the year of burn. Other species like Dickcissels and Brown-headed Cowbirds had the high densities in rangelands managed with traditional grazing practices such as season-long stocking and cow-calf grazing. Our findings indicate that different species of grassland birds have different ecological requirements and that conservation of the community will require a heterogeneous environment with a mixture of different habitat types. Patch-burn grazing provides critical habitat for specialist species like Henslow's Sparrows, but rangelands managed intensively for cattle production can provide breeding habitat for other generalist species. Despite a large sample of nests, we were unable to detect differences in nest survival among our study strata. Any variation in productivity of songbirds among different habitat strata is likely determined by differences in bird density and not differences in reproductive success. High nest survival in the PBG0 treatment with the lowest density of birds is consistent with negative density-dependence, which could make low or declining populations more resistant to local extirpation.

Table 1.1. Model selection for candidate models for detection and abundance of grassland songbirds on line transects in managed rangelands in Chase Co., Kansas, 2011-2013.

Detection	Abundance	K	AIC	ΔAIC	$w_i \leq$
Dickcissel					
Round	Stratum	10	10115.95	0.00	1.00
Year	Constant	5	10271.98	156.03	0.01
Round	Year	7	10311.12	195.18	0.01
Round	Constant	5	10335.26	219.32	0.01
Stratum	Constant	8	10371.19	255.24	0.01
Constant	Constant	3	10383.00	267.05	0.01
Eastern Meadowlark					
Year	Stratum	10	8624.03	0.00	1.00
Year	Year	7	8664.56	40.53	0.01
Year	Constant	5	8695.91	71.88	0.01
Round	Constant	5	8871.52	247.48	0.01
Constant	Constant	3	8871.81	247.78	0.01
Stratum	Constant	8	8880.24	256.21	0.01
Grasshopper Sparrow					
Year	Stratum	10	5892.94	0.00	0.90
Year	Year	7	5897.44	4.51	0.10
Year	Constant	5	5952.23	59.29	0.01
Stratum	Constant	8	6085.54	192.60	0.01
Round	Constant	5	6091.11	198.17	0.01
Constant	Constant	3	6096.56	203.62	0.01
Brown-headed Cowbird					
Year	Stratum	10	3123.54	0.0	0.99
Year	Year	7	3133.50	9.97	0.01
Year	Constant	5	3151.18	27.64	0.01
Stratum	Constant	8	3167.01	43.47	0.01
Constant	Constant	3	3169.99	46.45	0.01
Round	Constant	5	3172.62	49.09	0.01
Upland Sandpiper					
Stratum	Stratum	13	3052.89	0.00	1.00
Stratum	Constant	8	3086.20	33.31	0.01
Year	Constant	5	3086.93	34.04	0.01
Stratum	Year	10	3087.81	34.92	0.01
Round	Constant	5	3087.85	34.96	0.01
Constant	Constant	3	3088.45	35.56	0.01
Henslow’s Sparrow					
Year	Stratum	10	1036.58	0.00	1.00
Year	Year	7	1197.19	160.61	0.01
Year	Constant	5	1315.83	279.25	0.01
Constant	Constant	3	1402.47	365.89	0.01
Round	Constant	5	1403.23	366.65	0.01

Table 1.2. Sample size of nests monitored for four species of grassland songbirds in Chase Co., Kansas, 2011-2013.

Species	Year	Successful	Unsuccessful	Total	Percent successful
Dickcissel	2011	23	32	55	41.8%
	2012	18	48	66	27.3%
	2013	21	47	68	30.9%
	Total	62	127	189	32.8%
Eastern Meadowlark	2011	6	6	12	50.0%
	2012	2	11	13	15.4%
	2013	6	20	26	23.1%
	Total	14	37	51	27.5%
Grasshopper Sparrow	2011	7	11	18	38.9%
	2012	4	22	26	15.4%
	2013	8	30	38	21.0%
	Total	19	63	82	23.2%
Lark Sparrow	2011	2	3	5	40.0%
	2012	2	5	7	28.6%
	2013	1	5	6	16.7%
	Total	5	13	18	27.8%
Grand Total	Total	100	240	340	29.4%

Table 1.3. Model selection for candidate models for daily nest survival (S_d) of grassland songbirds in managed rangelands in Chase Co., Kansas, 2011-2013.

Model for S	K	Dev	AIC_c	ΔAIC_c	w_i
Constant	1	1240.05	1242.05	0.00	0.38
Year	3	1236.92	1242.93	0.88	0.24
Treatment	2	1240.03	1244.03	1.98	0.14
Year + Treatment	4	1236.70	1244.71	2.66	0.09
Year × Treatment	6	1233.23	1245.26	3.21	0.08
Patch	4	1238.72	1246.74	4.69	0.04
Year + Patch	6	1235.19	1247.22	5.17	0.03
Year × Patch	12	1229.12	1253.24	11.18	0.00

Notes: Model parameters include K = no. of parameters, Dev = model deviance, AIC_c = Akaike's Information Criterion corrected for small sample size, ΔAIC_c = difference in AIC value from model with lowest AIC value, and w_i = model weight within candidate set. Model factors included year of study (2011-2013), rangeland treatment (intensive early-stocking vs. patch-burn grazing), and rangeland patch (intensive early-stocking vs. year of fire, one year rested or two years rested within patch-burn grazing). Factors were combined in main effects or additive models (+) or factorial models with interaction terms (×).

Table 1.4. Estimates of daily survival (S_d) and period survival for a 24-day exposure period for songbird nests in managed rangelands in Chase Co., Kansas, 2011-2013.

Factor	S_d	SE(S)	95%L	95%U	N	S_n	SE(S_n)	95%L	95%U
Output for constant DSR model									
Constant	0.9204	0.0049	0.9101	0.9295	340	13.6%	1.8%	10.4%	17.3%
Output for Year model									
2011	0.9346	0.0088	0.9151	0.9498	90	19.7%	4.5%	11.9%	29.1%
2012	0.9136	0.0089	0.8945	0.9296	112	11.4%	2.7%	6.9%	17.3%
2013	0.9166	0.0079	0.8997	0.9309	138	12.4%	2.6%	7.9%	17.9%
Output for Treatment model									
Annual	0.9209	0.0060	0.9082	0.9319	230	13.8%	2.2%	9.9%	18.4%
PBG	0.9194	0.0087	0.9007	0.9348	110	13.3%	3.0%	8.1%	19.8%
Output for Patch model									
Annual	0.9209	0.0060	0.9082	0.9319	230	13.8%	2.2%	9.9%	18.4%
PBG0	0.9446	0.0220	0.8822	0.9749	9	25.5%	14.2%	4.9%	54.4%
PBG1	0.9198	0.0128	0.8908	0.9417	50	13.5%	4.5%	6.2%	23.6%
PBG2	0.9125	0.0136	0.8820	0.9358	51	11.1%	4.0%	4.9%	20.3%

Notes: Estimates of daily nest survival (S) taken from four of the best fit models (Table 1.3). Period survival for a 24-day exposure period estimated as $S_p = S_d^{24}$ where SE(S_p) was calculated from the delta method as $\mathrm{SE}(S_p) = \sqrt{[\mathrm{SE}(S_d)]^2 \times [24 S_d^{23}]^2}$.

Figure 1.1. Distributions of detection distances for six species of grassland birds in managed rangelands in Chase Co., Kansas, 2011-2013. Survey data were modeled for detections within 400 m of the line transect and in 20 m bins.

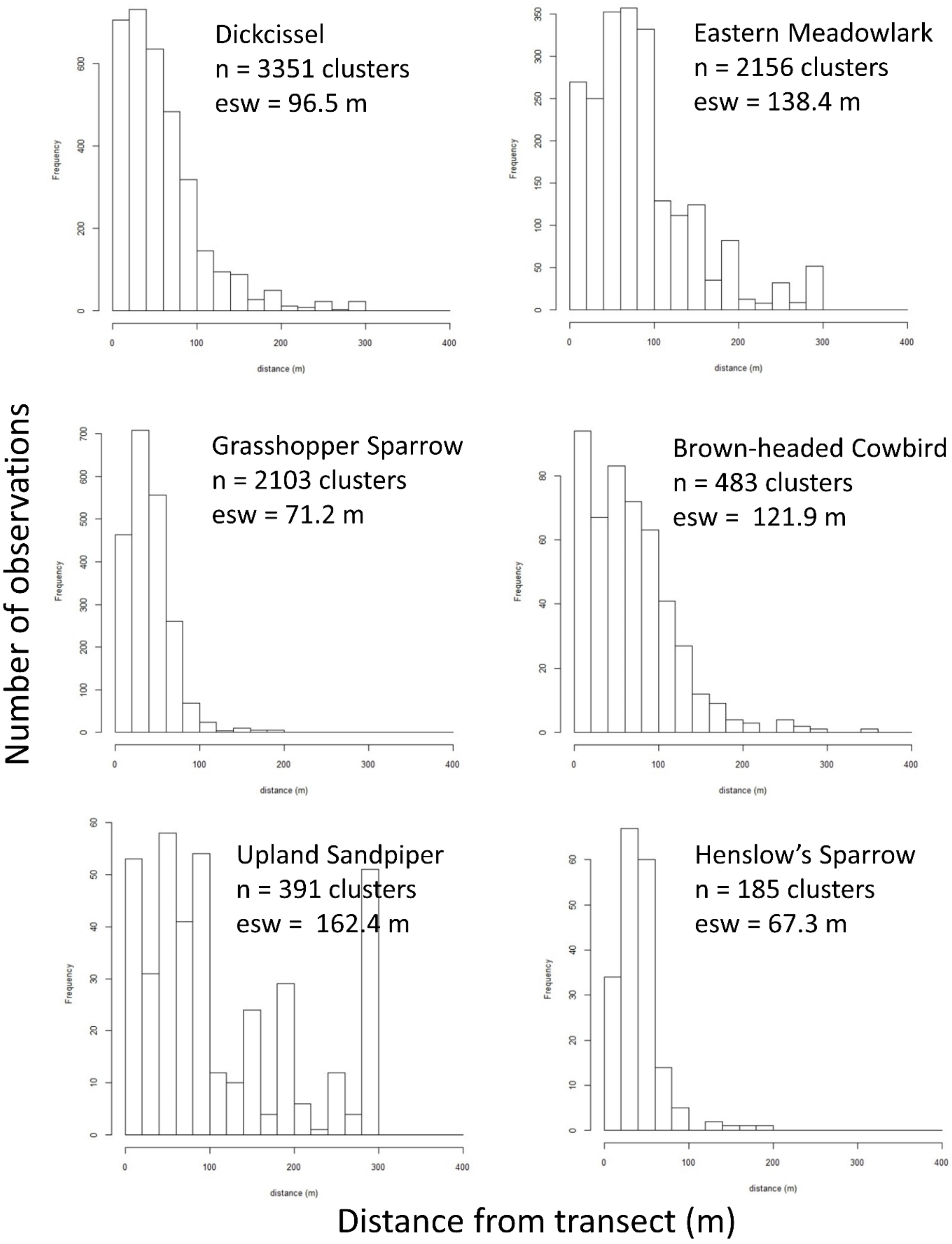
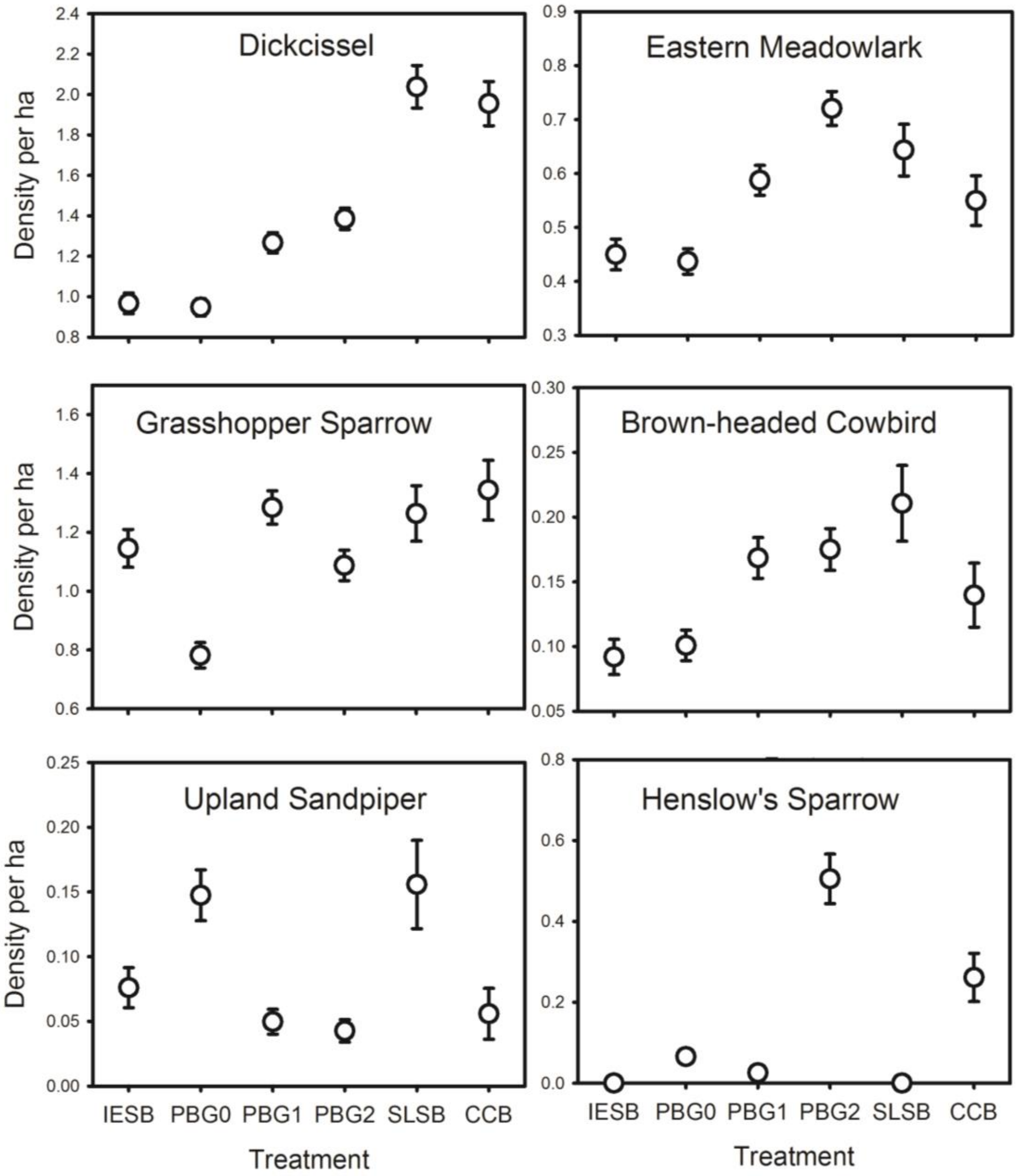


Figure 1.2. Density of six species of grassland birds in managed rangelands in Chase Co., Kansas, 2011-2013. Density calculated from line transect sampling where abundance was corrected for perpendicular detection distances. Treatments included intensive early stocking with annual burning (IESB), rotational patch-burn grazing (PBG0-PBG2), season long stocking with annual burning (SLSB), and cow-calf with annual burning (CCB).



Objective 2. ***Impacts on breeding habitats of Greater Prairie-Chickens***

Our recent research indicates that high predation rates of nests and young resulting from a lack of adequate concealing vegetative cover during nesting is the primary cause of population declines of Greater Prairie-Chickens in the Flint Hills (McNew et al. 2012a, 2014). However, the direct relationships between prairie-chicken fecundity, nesting cover, and rangeland management practices have not been evaluated. Our field efforts focused on live capture and radio-marking of female prairie-chickens to examine the relationships between rangeland management practices, habitat conditions, and nesting ecology of prairie-chickens in the central Flint Hills. We evaluated whether rangeland management factors such as fire return interval and stocking intensity influenced vegetative structure and composition of prairie-chicken habitat, and how management-determined vegetative conditions influenced selection of nest sites of prairie-chickens in areas managed with PBG versus areas managed with more common management regimes like IESB.

Field Methods. – Prairie-chickens were captured with walk-in traps at 34 lek sites during March to May (25 leks on intensive properties; 9 on PBG properties; **Figure 2.1**). Birds were sexed by plumage characteristics and aged by feather patterns on the outer two primary feathers of the wing. Females were equipped with VHF radio transmitters with an elastic necklace harness, a 6–8 hour mortality switch and an expected battery life of 18 months (model A3950, Advanced Telemetry Systems, Minnesota, U.S.A.). Radio-marked prairie-chickens were located ≥3 times/week from project trucks, an ATV, or on foot using portable radio receivers and handheld 3-element yagi antennas. Bird locations were estimated from ≥3 triangulation bearings using a maximum-likelihood estimator in Program Locate (ver. 3.34, Pacer Computing, Tatamagouche, Nova Scotia), or flush locations were recorded with a GPS ±5 m.

To locate nests, females were relocated on foot when females had settled and their locations had not changed for 2–3 days. Nest locations were marked discretely with natural landmarks placed ≥25 m from the nest bowl, and geographic coordinates were recorded with a GPS unit. We sampled habitat conditions within 3 days of hatching or failure at nests and random points within study areas delineated by a convex hull placed 5-km outside of nest locations at each research unit (McNew et al. 2013, 2014). We evaluated an index of vertical nesting cover by estimating the average of 4 visual obstruction readings (VOR) at a distance of 2 m and a height of 0.5 m (Robel et al. 1970) and estimated the proportion of grass, forb, shrub, or bare ground in a 20×50 cm quadrat frame at 12 subsampling locations within 6 m of each nest or random point (Daubenmire 1959). We recorded the distance (m) and height (cm) to nearest shrub in the field and estimated the distance (km) from each nest to nearest state highway, county road, non-grassland habitat edge and water edge using ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA). We gathered information on fire and stocking for every patch or pasture in the study area for each year of study by interviewing property managers to determine years since last prescribed fire and stocking intensity (animal unit months per hectare [AUM/ha]) for each nest or random point. In addition, we considered potential legacy effects of fire by determining the number of years between 2000 and 2011 a nest site or random point burned using a remotely-sensed fire classification map for the study area (Mohler and Goodin 2012a, b).

Statistical Analyses. – We explored the effects of rangeland management practices on habitat conditions using generalized linear models. We previously found that nest site selection and nest survival in intensively managed grasslands were determined primarily by visual obstruction, an index of biomass and vertical nest concealment (McNew et al. 2013, 2014). Therefore, we explicitly tested the relationships between VOR and the predictor variables stocking intensity (AUM/ha), years since last fire, and the frequency of fire over the preceding 11 years. We used linear models with Gaussian error structure to build models and Akaike's Information Criterion adjusted for small sample sizes to evaluate and compare candidate models with a null model (AIC_c; Burnham and Anderson 2002).

To examine nonlinear relationships between nest site selection and habitat conditions, we explored different shapes for responses to each covariate before fitting models with resource selection functions. We evaluated generalized additive models (GAMs) with nests and random points as binary responses and fitted smoothing splines to univariate habitat predictors to model potential nonlinear relationships (Wood 2006). We inspected plots of predicted relationships and partial residuals to transform smoothed variables into polynomials that approximated nonlinear relationships (Crawley 2005). We hypothesized that behavioral responses to some habitat variables, such as distance to edge, may exhibit a threshold pattern so we tested pseudothreshold models by evaluating the natural log of the explanatory variable (i.e., ln[x+0.001]; Dugger et al. 2005).

We evaluated nest site selection using a resource selection function (RSF) where nest sites (use) and random points (available) were independent samples. We used generalized linear models (GLM) with the logistic link function, a binomial error structure, and linear or non-linear responses to fixed effects following patterns from our GAM analyses to evaluate resource selection functions. We included only a single nesting attempt per female per year to reduce autocorrelation among nests in the sample. We used a hierarchical approach based on forward stepwise variable selection and used AIC_c to evaluate candidate models (Burnham and Anderson 2002). We excluded models with $\Delta AIC_c \leq 2$ that differed from the top model by a single parameter if confidence intervals indicated the parameter was non-informative (or $\Delta AIC_c \leq 4$ if $\Delta K = 2$, Burnham and Anderson 2002; Arnold 2010). All statistical analyses were performed in R statistical software (ver. 2.4; R Development Core Team 2011, Vienna, Austria), where GAM models were fit with the "mgcv" package (Wood 2006).

Results. – We located 143 prairie-chicken nests (109 first nests, 34 renesting attempts) belonging to 93 individual females during 2011–2013 (**Figure 2.1**). We located 60 (42%) nests on properties managed with patch-burn grazing and 83 (58%) nests on adjacent properties managed with intensive management. Thirty-eight (27%) of 143 nests successfully produced offspring.

Rangeland Management – Habitat Relationships – We evaluated the relationships between the most important ecological predictor of nest site selection and survival, VOR, and factors associated with rangeland management for 143 points selected randomly within the study areas. Four models were supported by the data and the lack of a single parsimonious model was caused by uncertainty in the interactions of the three rangeland management effects (**Table 2.1**). Models with rangeland management treatment (intensive or PBG), AUM/ha, and years since fire

(YSF) had more than 99% of the support of the data and outperformed a constant model as well as models with just single main effects (Table 2.1). There was no support for a legacy effect of fire frequency over the preceding 10 years. Visual obstruction increased with years since fire for both patch-burn grazing and intensive rangeland management, but decreased with stocking intensity (AUM/ha) only on properties managed with intensive management (**Figure 2.2**).

Nest site selection. – About 6,817 ha (12%) of the area available to nesting female prairie-chickens (i.e., areas within 5-km of a lek of capture) was managed with patch-burn grazing, whereas 88% of available habitat was managed with intensive regimes. Selection ratios (% used : % available) indicated strong selection of patch-burn grazing properties and avoidance of adjacent properties by nesting prairie-chickens (patch-burn grazing = 3.4, intensive management = 0.7). Within patch-burn grazing properties, prairie-chickens preferred patches that were burned 2–3 years prior to nesting (**Figure 2.3**). Compared with random points, nest sites were closer to leks, had greater forb coverage and visual obstruction readings (VOR), and less bare ground (**Table 2.2**).

We randomly selected only one nesting attempt for each female in each year to reduce autocorrelation in nest placement behavior when evaluating resource selection functions, resulting in a reduced sample of 109 nests. A single model that included a quadratic effect of VOR and negative linear effect of distance to lek had the majority of support ($w_i = 0.7$; **Table 2.3**). Models that included the quadratic effect of VOR had virtually all support ($w_i > 0.99$) and indicated that the relative probability of an area being used as a nest site was maximized when VOR was 3–6 dm (**Figure 2.4**). We found relatively little support for a direct effect of years since fire, stocking intensity, or fire frequency during the preceding 10 years (**Table 2.3**). Years since fire and stocking intensity had significant effects on VOR, suggesting an indirect influence of rangeland management on nest site selection.

Implications. – Rangeland management actions directly impacted the quality of nesting habitat and indirectly influenced placement and subsequent survival of prairie-chicken nests at our study site in the Flint Hills. Our results confirm the strong influence of vertical nesting cover on prairie-chicken nesting ecology (McNew et al. 2014) and explain observed patterns of fecundity over gradients of rangeland management intensity (McNew et al. 2012a, Robbins et al. 2002). Our research project is the first study to directly link rangeland management decisions to prairie-chicken demography and we expect the results will be useful to range managers and conservationists.

Nest site selection by prairie-chickens in the unfragmented grasslands of our study areas was largely determined by vertical nesting cover. Nest site selection exhibited a quadratic response to vertical nesting cover, maximized when visual obstruction was 3–6 dm. A quadratic response of nest site selection to vertical nesting cover is consistent with our previous research in more fragmented landscapes and supports a ubiquitous recommendation of fire and grazing regimes that provide herbaceous nesting cover for prairie-chickens between 30 and 60 cm in height (McNew et al. 2014). Nesting habitat on study properties managed intensively with annual spring burning and early stocking of cattle were of low quality; less than 2% of available nest locations had measures of vertical cover of at least 30 cm. Areas with optimal nesting cover were 8 times more prevalent in patch-burn grazing treatments; 16% of random locations had VOR between 30 and 60 cm.

We found a direct relationship between VOR and factors determined by the rangeland management practices, confirming correlational evidence of the negative effects of annual burning and intensive early cattle stocking on the quality of prairie-chicken nesting habitat (McNew et al. 2012a, 2014; Robbins et al. 2002). Interestingly, we observed different influences of stocking intensity on vertical nesting cover between the two rangeland management treatments. Nesting cover decreased with stocking intensity on properties managed with more traditional intensive burning and grazing regimes, but was relatively unaffected by stocking intensity on properties managed with patch-burn grazing. Variable responses among the treatments can be explained by the grazing behavior of cattle. Grazing by cattle tends to be uniform within pastures managed with intensive early stocking and annual burning; the entire pasture is burned and subsequently grazed by cattle. In patch-burn grazing treatments, cattle focused their grazing on patches burned in the current year, effectively resting unburned patches (Fuhlendorf and Engle 2001). Thus, up to two-thirds of a pasture received little to no grazing, and nesting cover on unburned portions was relatively unaffected by stocking intensity within a pasture.

Our results indicate that nest site selection was directly related to vertical nesting cover determined by fire return interval on patches. Nesting habitat was affected little by stocking intensity in patch-burn grazing management regimes because preferred nesting locations that result in the highest nest survival were unburned patches that were relatively unused by cattle. Overall, the quantity and quality of nesting sites was improved under patch-burn grazing management when compared with intensive regimes. Our results are evidence that rangeland management strategies that mimic historical heterogeneous fire and grazing regimes benefit native prairie wildlife and ecosystem health.

Table 2.1. Model selection for models evaluating the effects of rangeland management factors on visual obstruction reading (VOR), the primary habitat condition determining nest site selection and nest survival of prairie-chickens in Kansas, 2011–2013.

Model factors[a]	k^b	AIC$_c$	ΔAIC$_c$	w_i	Σw_i
Treatment + AUM + YSF[c]	4	368.2	0	0.26	0.26
AUM + YSF	3	369.0	0.8	0.18	0.44
Treatment*AUM + YSF	5	369.7	1.5	0.13	0.56
Treatment*YSF + AUM	5	370.1	1.9	0.10	0.67
Treatment + YSF*AUM	5	370.3	2.1	0.09	0.76
YSF + AUM2	4	370.4	2.2	0.09	0.85
YSF*AUM	4	370.7	2.5	0.08	0.92
YSF + ln(AUM)	3	371.7	3.5	0.04	0.97
AUM + ln(YSF)	3	373.8	5.57	0.02	0.98
Treatment*YSF*AUM	8	375.6	7.4	0.01	0.99
Constant (null)	1	385.5	17.3	0.00	1.0

[a] Only models with Akaike weights (w_i) ≥ 0.01 are presented except for the null model.

[b] k= number of parameters

[c] AUM = Animal unit month per hectare; YSF = years since fire

Table 2.2. Mean ± SE habitat measurements assessed at greater prairie-chicken nest locations and random points in the central Flint Hills, Kansas, 2011–2013.

Variable	Nests (*n* = 143)	Random Points (*n* = 143)
Distance to nearest lek (km)	1.37 ± 0.16	2.86 ± 0.22
Distance to local road (km)	2.11 ± 0.14	1.79 ± 0.13
Distance to state highway (km)	6.48 ± 0.36	5.98 ± 0.34
Distance to nearest edge (km)	1.07 ± 0.05	0.93 ± 0.05
Distance to water (km)	0.58 ± 0.03	0.50 ± 0.03
Years since last burn	1.55 ± 0.12	1.28 ± 0.11
AUM / ha [a]	2.12 ± 0.07	2.07 ± 0.1
Proportion unburned [b]	0.82	0.70
Years since last burn	1.27 ± 0.07	1.06 ± 0.07
Grass (%)	45.9 ± 2.03	51.1 ± 2.01
Forb (%)	23.3 ± 1.44	17.9 ± 1.4
Shrub (%)	3.44 ± 0.6	2.53 ± 0.4
Bare ground (%)	3.96 ± 0.64	16.4 ± 1.58
Detritus (%)	21.7 ± 2.28	10.9 ± 1.49
VOR (dm) [c]	2.52 ± 0.09	1.39 ± 0.09
Near shrub height (cm)	39.2 ± 2.33	48.4 ± 5.36
Near shrub distance (m)	12.5 ± 2.4	31.8 ± 4.61
Elevation	437 ± 3.89	416 ± 7.04
Fire frequency	8.24 ± 0.18	8.21 ± 0.21

[a] Animal unit month / hectare.

[b] Proportions of nest and random point locations that were unburned in the current year.

[c] Visual obstruction reading, and index of biomass and nest concealment.

Table 2.3. Model selection results of nest site selection and nest survival of female prairie-chickens in Kansas, 2011–2013.[a]

Model factors	k[b]	Dev	AIC$_c$	ΔAIC$_c$	w_i	Σw_i
Nest site selection						
VOR^2 + Distance to lek	4	203.2	211.4	0.00	0.73	0.73
VOR^2 + % forb + Distance to lek	5	203.1	213.4	1.95	0.27	> 0.99
Constant (null)	1	302.2	304.2	92.80	0.00	1.00

[a] Only models with Akaike weights(w_i) ≥ 0.01 are presented except for null models.

[b] k = number of parameters

Figure 2.1. Location of greater prairie-chicken study areas in the Flint Hills of Kansas, USA 2010–2013. Properties represented with white were managed with patch-burn grazing; properties in gray were managed with more intensive burning and grazing treatments.

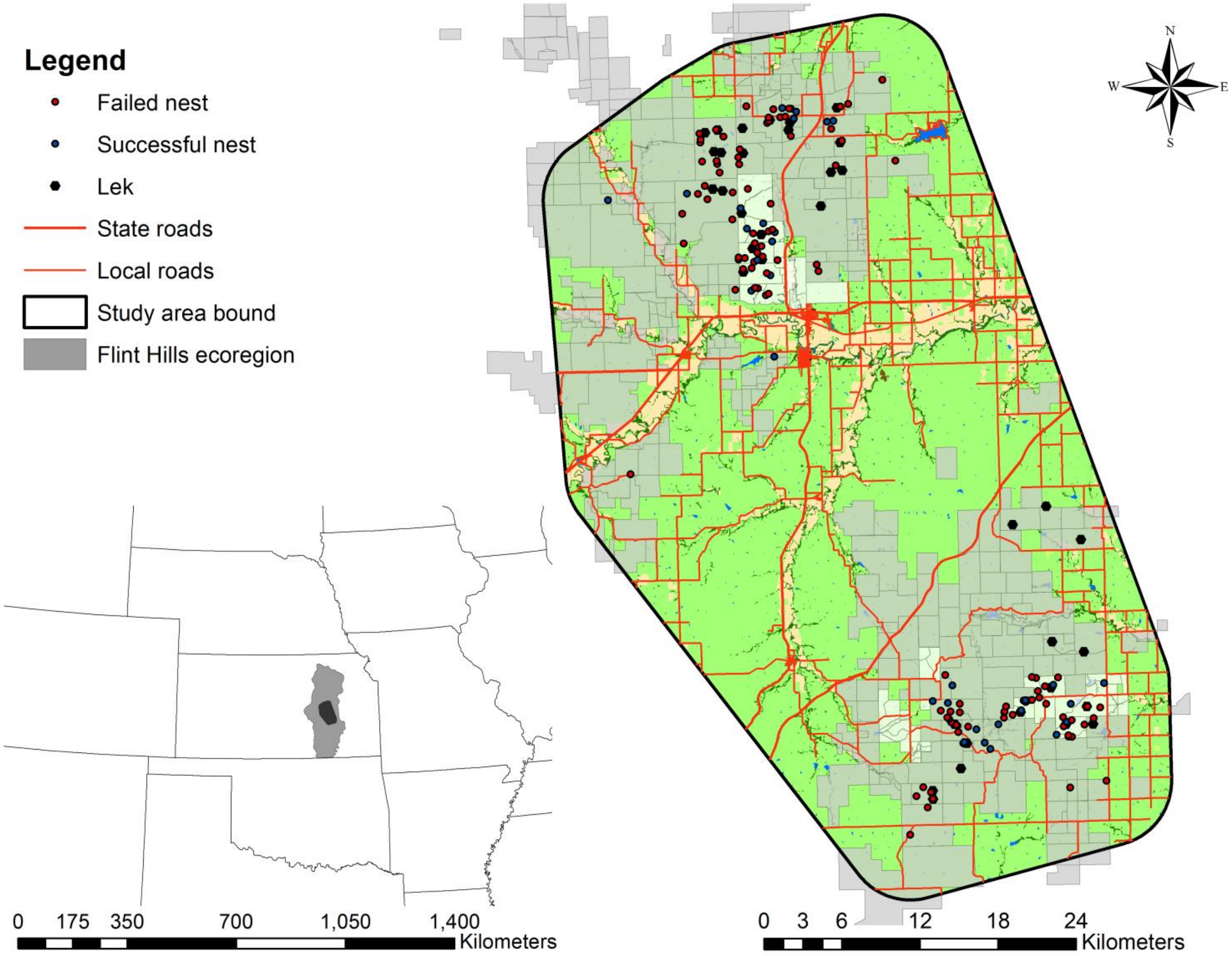


Figure 2.2. Relationships between VOR, years since fire (YSF), and stocking intensity (AUM/ha) for properties managed with (top) intensive management strategies and (bottom) patch-burn grazing in the Flint Hills of Kansas, 2011–2013. Dotted lines represent 95% confidence intervals. Parameter estimates taken from a parsimonious model with interactive effect of treatment and stocking intensity.

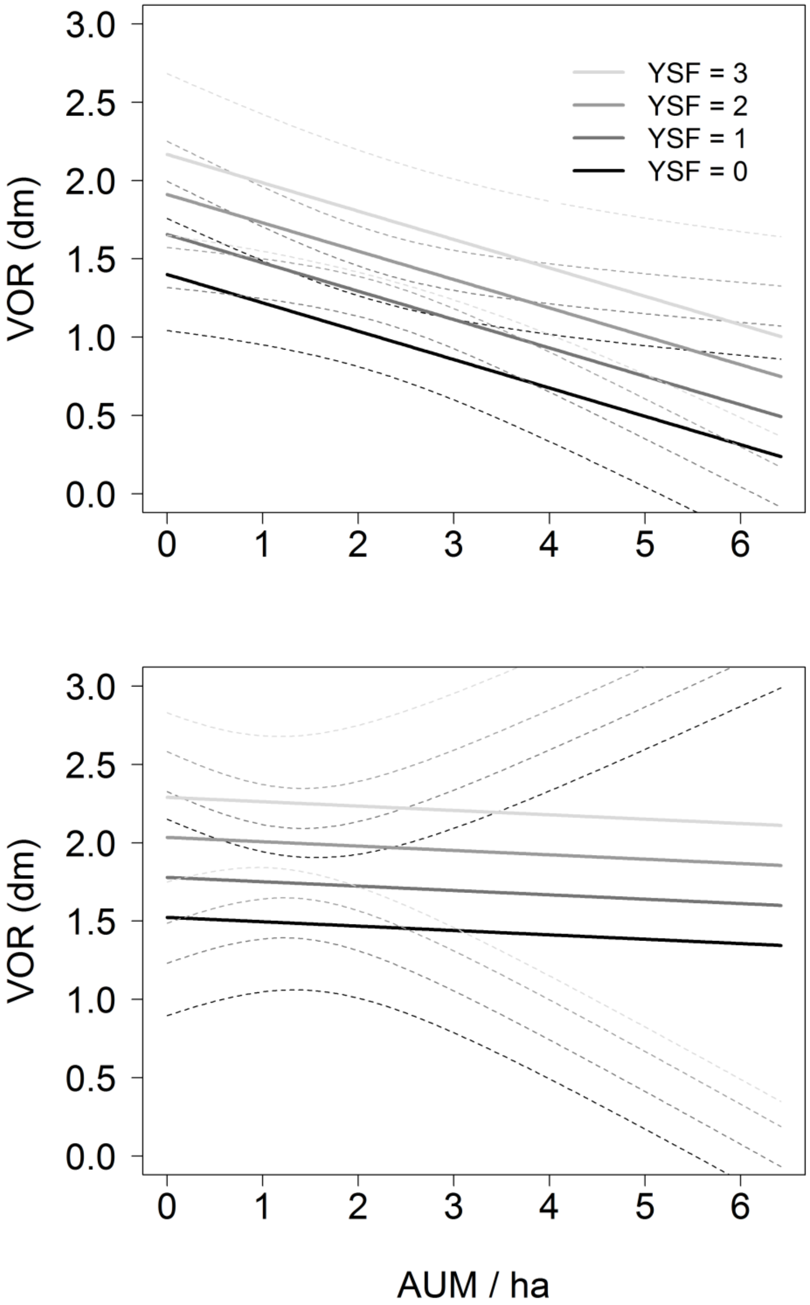


Figure 2.3. Proportion of nests and random points located (top) in intensive (IESB) and patch-burn grazing treatments, and (bottom) within burn treatments on patch-burn grazing properties in the Flint Hills of Kansas, 2011–2013.

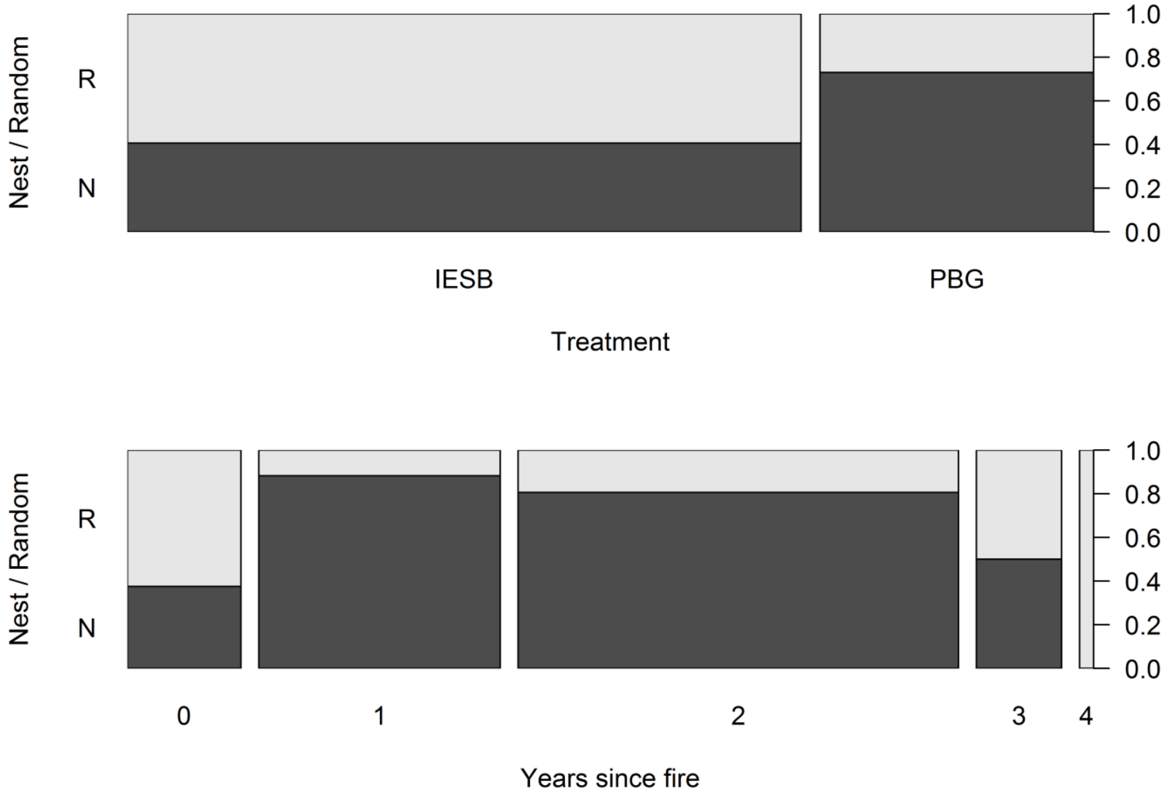
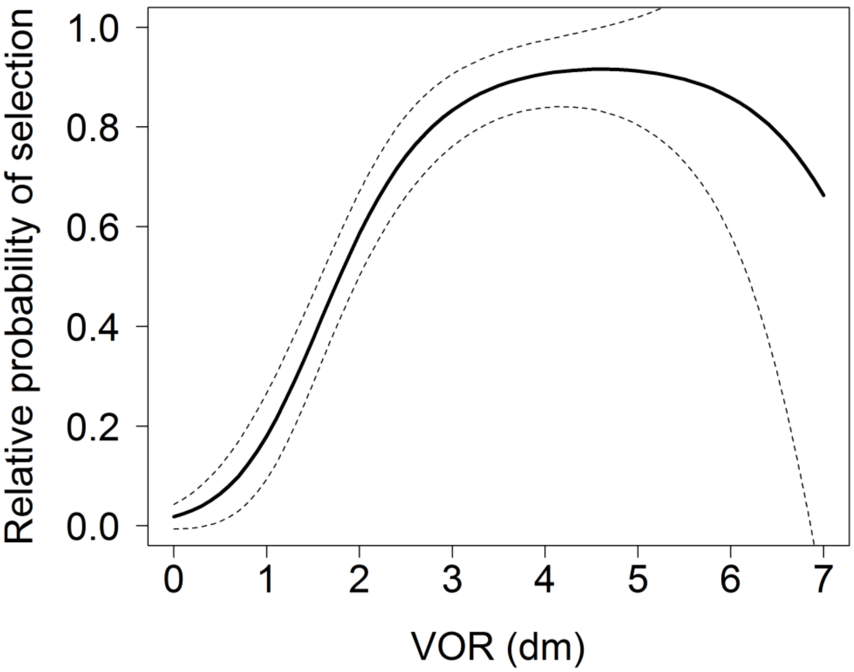


Figure 2.4. Relationships between relative probability (95% CI) of nest site selection and visual obstruction reading (VOR), a measure of nest concealment and index of vegetative biomass in the Flint Hills of Kansas, 2011–2013.



Objective 3. ***Impacts on fecundity of Greater Prairie-Chickens***

Greater Prairie-Chickens are characterized by a life-history strategy with relatively high reproductive effort, early age at maturity, and low annual survival rates. Reduced habitat quality for nesting females could have negative impacts on reproductive performance if females have fewer inadequate for egg-laying, if changes in incubation behavior lead to reduced rates of nest attendance during incubation, or if habitat conditions are related to nest survival rates. If fecundity of prairie-chickens is negatively impacted by IESB practices, we predicted that females might nest later in the breeding season, lay smaller clutches with fewer eggs, or lay lower quality eggs with lower rates of hatchability. Our previous work has shown that nest survival is the main demographic parameter affecting seasonal productivity of prairie-chickens in Kansas (McNew et al. 2012a). We modeled nest survival as a function of nest-site scale habitat covariates that described habitat quality at the local nest site or in the surrounding area. If rangeland management affects nest survival, we predicted lower rates of daily survival for the nests in pastures managed with IESB compared to PBG.

Field Methods. –Prairie-chickens were captured with walk-in traps and drop-nets at lek sites during March to April. A few females were captured at the nest or with broods to replace failing transmitters. Females were outfitted with 10-11 g radio transmitters attached with an elastic or wire necklace harness (model A3950, Advanced Telemetry Systems, Minnesota, U.S.A.). Females were relocated ≥3 times a week during the breeding, nesting, and brood-rearing seasons (Mar. through Aug.) to locate nests and broods. Once a female localized in an area for three successive days, we located the nest by tracking the female with portable radio receivers and handheld antennas. We flushed the female once in early incubation to count eggs, determine stage of incubation by floating the eggs in a cup of lukewarm water, and record nest location with a handheld GPS in UTM coordinates (±5 m). To minimize disturbance, incubating females were monitored by triangulation with radio telemetry at distances ≥100 m until the nest failed or successfully hatched. We considered a nest to have *failed* if movements showed that a female had ceased incubation, and we revisited the nest to determine whether the nest contents were destroyed or removed before the expected hatch date. We continued to monitor females who lost their first nest to locate any renesting attempts during the breeding season. We considered nests to be *successful* if the nestbowl contained pipped eggshells or if at least one egg hatched and produced a chick. For successful nests, we conducted systematic brood flushes within one hour of sunrise at 14, 24, 34, and 60-d post-hatch by radio-tracking the brood female.

Components of Fecundity. – We examined four components of the reproductive effort of female prairie-chickens our field site in eastcentral Kansas. *Date of clutch initiation* was estimated by backdating from stage of egg-laying or incubation, assuming an egg-laying rate of one egg per day. We examined timing of clutch initiation for first nests only because timing of laying for renests is affected by timing and stage of loss of first nests. *Clutch size* of first nests and renests were estimated as the maximum number of eggs observed in the nest at the completion of egg-laying. *Nest survival* was the probability that a nest survived a 38-day period that included egg-laying and incubation, and was estimated with nest survival modeling. Last, we calculated *egg hatchability* as the number of chicks produced per egg for the subset of nests that survived incubation and successfully hatched. Rates of hatchability <1 were primarily due to inviable eggs that failed to hatch. We monitored survival of broods and juveniles but due to high rates of nest mortality, our samples were small and inadequate for testing for potential effects of rangeland management on brood survival.

Ecological Covariates. – We sampled habitat conditions within 3 days of hatching or failure at nests and random points within study areas delineated by a convex hull placed 5-km outside of nest locations at each research unit (McNew et al. 2013; McNew et al. 2014). We evaluated an index of vertical nesting cover by estimating the average of four visual obstruction readings (VOR) at a distance of 2 m and a height of 0.5 m (Robel et al. 1970) and estimated the proportion of grass, forb, shrub, or bare ground in a 20×50 cm quadrat frame at 12 subsampling locations within 6 m of each nest or random point (Daubenmire 1959). We recorded the distance (m) and height (cm) to nearest shrub in the field and estimated the distance (km) from each nest to nearest state highway, county road, non-grassland habitat edge and water edge using ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA). We gathered information on fire and stocking for every patch or pasture in the study area for each year of study by interviewing property managers to determine years since last prescribed fire and stocking intensity (animal unit months per hectare [AUM/ha]) for each nest or random point. In addition, we considered potential legacy effects of fire by determining the number of years between 2000 and 2011 a nest site or random point burned using a remotely-sensed fire classification map for the study area (Mohler and Goodin 2012a, b).

Statistical Analyses. – We used single-factor ANOVAs to test for the effects of rangeland management treatment (PBG vs. IESB) at the nest site on nest initiation date, clutch size, and hatchability (eggs hatched/total eggs laid) for both first nests and renests. We used logistic regression to test for the effects of rangeland management treatment on the propensity to renest following nest failure.

We used the nest survival procedure to test competing models and estimate daily survival rates of nests during a 106-d nesting period between 18 April and 1 August (Dinsmore et al. 2002, White and Burnham 1999). We previously found that variation in nest survival was explained primarily by habitat conditions assessed at the scale of the nest site (McNew et al. 2014). Thus, we modeled nest survival as a function of nest-site scale habitat covariates that may be influenced by fire and grazing, including VOR, proportion grass, and proportion forbs. We also evaluated the direct effects of rangeland management factors: years since fire, AUM/ha, and historical fire frequency. All models were constructed using the logit-link function, and model selection was based on differences in AIC_c (ΔAIC_c) and evidence ratios from Akaike weights (Burnham and Anderson 2002). Model selection started with an intercept-only (constant) model, and variables were added and retained if the led to a reduction in AIC_c. We excluded models with $\Delta AIC_c \leq 2$ that differed from the top model by a single parameter if confidence intervals indicated the parameter was noninformative (Burnham and Anderson 2002). Following our analyses of nest survival for songbirds (Objective 1), we used package RMark in Program R to model nest survival of prairie chickens with the nest survival procedure of Program MARK 7.1 (White and Burnham 1999, Laake and Rexstad 2008, R Development Core Team 2011).

Results. – We collected detailed demographic data on the reproductive performance of female prairie-chickens over a 3-year period (2011–2013). If radio-marked females survived the 2–4 week period from capture at the lek to the onset of egg-laying, almost all females initiated at least one nesting attempt. Early failure of nests before discovery likely accounted for the few females where we did not locate nests (McNew et al. 2012a). We located 143 prairie-chicken nests (109 first nests, 34 renesting attempts) belonging to 93 individual females during 2011–2013. We located 60 (42%) nests on properties managed with patch-burn grazing and 83 (58%) nests on adjacent properties managed with intensive management. Apparent nest survival was 27% and 38 of 143 nests successfully produced offspring.

We detected no effects of rangeland management at the nest site for three key components of reproductive effort for both first nests and renests: nest initiation date, clutch size, and egg hatchability (**Tables 3.1, 3.2**). Rates of renesting following failure were 45% (14 of 31 females) on properties managed with PBG and 35% (16 of 46 females) on properties managed with IESB. We found no effect of rangeland management treatment on the propensity to renest following nest failure ($z = 0.91$, $df = 75$, $P = 0.36$).

Nest Survival. – We included 143 nests in nest survival analyses (83 intensive, 60 patch-burn grazing). Eighteen of 83 (22%) nests located on intensively managed properties successfully produced ≥ 1 chick, compared to 20 of 60 (33%) nests on patch-burn grazing properties (**Figure 3.1**). Apparent nest success pooled across study areas was similar in 2011 (36%) and 2012 (30%), but lower in 2013 (17%). Apparent nest success was higher in patch-burn treatments in all years, especially in 2013 when we observed 4% and 11% nest survival rates in intensive and patch-burn treatments, respectively (**Table 3.3**).

Models with a quadratic effect of VOR received virtually all the support among candidate models evaluating daily nest survival probabilities ($\Sigma w_i > 0.99$; **Table 3.4**). Daily nest survival increased from a low of < 0.75 when VOR was less than 1 dm to 0.95 when VOR exceeded 5 dm (**Figure 3.2**). Models with the effect of grass cover at the nest site were also supported ($\Sigma w_i > 0.99$) and indicated a modest but positive relationship ($\beta = 0.02 \pm 0.005$; **Table 3.4**). There was some support for rangeland management treatment ($\Sigma w_i \approx 0.54$). However, the 95% confidence interval of the effect size (-0.08–0.74) overlapped 0 and treatment did not significantly improve model fit, suggesting that the effect was non-informative (**Table 3.5**). The direct effects of year since fire and stocking intensity on nest survival were not supported ($\Sigma w_i < 0.01$; **Table 3.4**), though VOR was directly related to these rangeland management factors.

Implications. – Rangeland management actions directly affected the quality of nesting habitat and indirectly influenced placement and subsequent survival of prairie-chicken nests at our study site in the Flint Hills. Our results confirm the strong influence of vertical nesting cover on prairie-chicken nesting ecology (McNew et al. 2014) and explain observed patterns of fecundity over gradients of rangeland management intensity (McNew et al. 2012; Robbins et al. 2002). Information on the relationships between nest survival and rangeland management practices is critical for the conservation of prairie-chickens because the species occurs predominantly on private lands.

Nest site survival exhibited a quadratic response to vertical nesting cover, maximized when visual obstruction was 3–6 dm. A quadratic response of nest site selection and survival to vertical nesting cover is consistent with our previous research in more fragmented landscapes and supports a recommendation of fire and grazing regimes that provide herbaceous nesting cover for prairie-chickens between 30 and 60 cm in height (McNew et al. 2014). Nesting habitat on study properties managed intensively with annual spring burning and early stocking of cattle were of low quality; less than 2% of available nest locations had measures of vertical cover of at least 30 cm. Areas with optimal nesting cover were 8 times more prevalent in patch-burn grazing treatments; 16% of random locations had VOR between 30 and 60 cm.

Nest survival at both treatments was well below the threshold of 0.50 recommended to maintain a stable population of prairie-chickens (McNew et al. 2012a, Westemeier 1979). Depressed nest survival may have been caused by drought conditions during the second two years of our study in 2012–2013 (National Weather Service 2013). The growth of herbaceous plants that provide concealment for game bird nests is reduced during drought years and nest survival was likely negatively impacted, especially in burned areas without residual plant growth from the preceding year (Hernández et al. 2005, Leopold 1933). We expect the positive effects of patch-burn grazing to be even more pronounced in years with normal precipitation. However, additional research is needed to evaluate potential interactive effects of weather and rangeland management on habitat quality and to determine long-term effects of patch-burn grazing on productivity and population dynamics.

The quality of nesting habitat has direct influence on productivity in grouse (Bergerud 1988, Pitman et al. 2005), and nest survival is a limiting factor for prairie-chicken populations (Wisdom and Mills 1997, McNew et al. 2012). Nest survival for prairie-chickens in the unfragmented grasslands of our study areas was largely determined by vertical nesting cover, which was, in turn, affected by rangeland management. Mean nest survival (± SE) on patch-burn properties (0.21 ± 0.05) was twice as high as that on intensive properties (0.10 ± 0.03), suggesting a direct benefit of patch-burn grazing to prairie-chicken populations.

Table 3.1. ANOVA results for tests for effects of rangeland management treatment on fecundity components in prairie-chickens in Kansas, 2011–2013.Treatment = patch-burn grazing (PBG) or intensive early stocking and annual burning (IESB)

Model	*df*	*F*	*P*
Nest initiation date ~ Treatment			
First nests	1,107	0.00	1.00
Renests	1,32	0.001	0.97
Clutch size ~ Treatment			
First nests	1,107	0.72	0.40
Renests	1,32	4.01	0.05
Hatchability ~ Treatment			
First nests	1,107	1.30	0.26
Renests	1,32	0.04	0.84

Table 3.2. Components of fecundity for prairie-chicken nests on properties managed with patch-burn grazing (PBG) or intensive early stocking with annual burning (IESB) in in Kansas, 2011–2013.

Component of fecundity	*n*	Mean ± SE	Min.	Max.
Nest initiation date				
First nests				
PBG	50	2 May ± 2 d	13 April	1 July
IESB	59	3 May ± 2 d	4 April	14 Jun
Renests				
PBG	10	31 May ± 4 d	7-May	14-Jun
IESB	24	31 May ± 4 d	2-May	4-Jul
Clutch size				
First nests				
PBG	50	10.5 ± 0.4	2	16
IESB	59	11.1 ± 0.4	1	18
Renests				
PBG	10	7.1 ± 1.1	2	12
IESB	24	8.9 ± 0.4	5	11
Hatchability				
First nests				
PBG	17	0.85 ± 0.05	0.50	1.00
IESB	14	0.86 ± 0.04	0.50	1.00
Renests				
PBG	3	0.50 ± 0.22	0.08	0.80
IESB	4	0.75 ± 0.16	0.27	1.00

Table 3.3. Annual nest survival estimates (SE) extrapolated for a 38-d exposure period for radio-monitored prairie-chickens in Kansas. PBG = patch-burn grazing, a form of alternative rangeland management; IESB = intensive early stocking with annual burning, traditional rangeland management.

Year	PBG	IESB
2011	0.22 (0.07)	0.12 (0.06)
2012	0.24 (0.08)	0.13 (0.05)
2013	0.11 (0.05)	0.04 (0.02)

Table 3.4. Model selection results of nest site selection and nest survival of female prairie-chickens in Kansas, 2011–2013.[a]

Model factors	k[b]	Dev	AIC$_c$	ΔAIC$_c$	w_i	Σw_i
Nest survival						
Treatment + VOR^2 + % grass	5	695.6	705.6	0.00	0.54	0.54
VOR^2 + % grass	4	698.1	706.1	0.48	0.42	0.96
Year + VOR^2 + % grass	7	697.6	711.6	6.03	0.03	0.99
Constant (null)	1	725.6	727.6	21.97	0.00	1.00

[a] Only models with Akaike weights(w_i) ≥ 0.01 are presented except for null models.

[b] k = number of parameters

Table 3.5. Model selection for models evaluating the effects of rangeland management factors on visual obstruction reading (VOR), the primary habitat condition determining nest site selection and nest survival of prairie-chickens in Kansas, 2011–2013.

Model factors[a]	k^b	AIC$_c$	ΔAIC$_c$	w_i	Σw_i
Treatment + AUM + YSF[c]	4	368.2	0	0.26	0.26
AUM + YSF	3	369.0	0.8	0.18	0.44
Treatment*AUM + YSF	5	369.7	1.5	0.13	0.56
Treatment*YSF + AUM	5	370.1	1.9	0.10	0.67
Treatment + YSF*AUM	5	370.3	2.1	0.09	0.76
YSF + AUM2	4	370.4	2.2	0.09	0.85
YSF*AUM	4	370.7	2.5	0.08	0.92
YSF + ln(AUM)	3	371.7	3.5	0.04	0.97
AUM + ln(YSF)	3	373.8	5.57	0.02	0.98
Treatment*YSF*AUM	8	375.6	7.4	0.01	0.99
Constant (null)	1	385.5	17.3	0.00	1.0

[a] Only models with Akaike weights (w_i) ≥ 0.01 are presented except for the null model.

[b] k = number of parameters

[c] AUM = Animal unit month per hectare; YSF = years since fire

Figure 3.1. Location of Greater Prairie-Chicken study areas in the Flint Hills of Kansas, USA 2010–2013. Properties represented with white were managed with patch-burn grazing; properties in gray were managed with more intensive burning and grazing treatments.

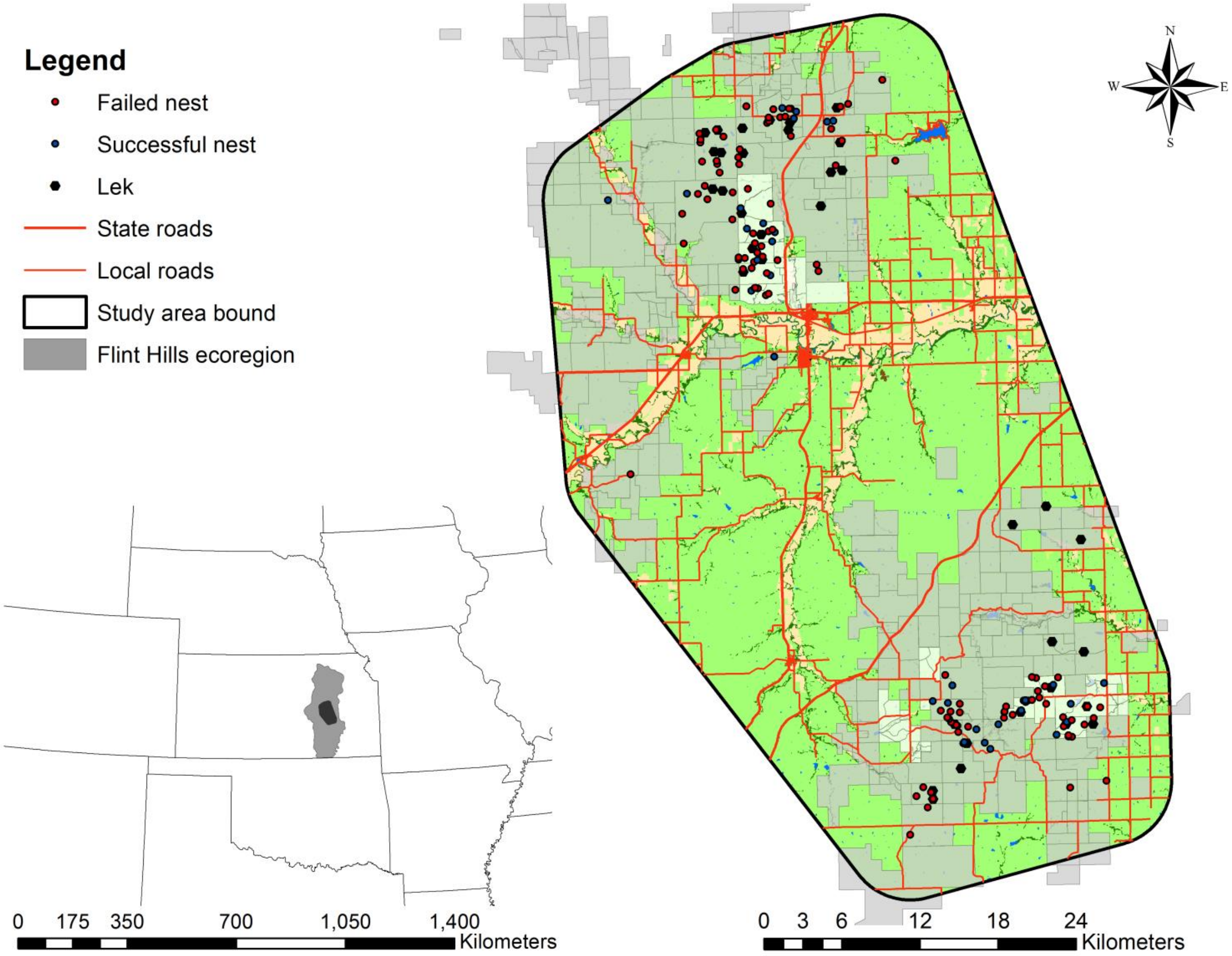
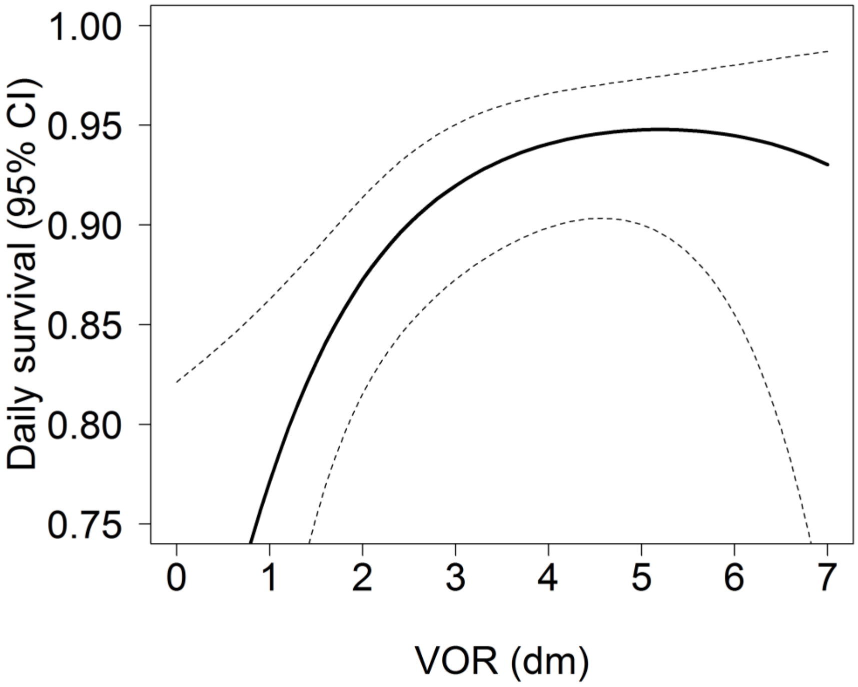


Figure 3.2. Relationship between daily nest survival and visual obstruction reading (VOR), a measure of nest concealment and index of vegetative biomass in the Flint Hills of Kansas, 2011–2013. Solid line = nest survival estimate; dotted lines = upper and lower 95% confidence limits.



Objective 4. *Impacts on seasonal home ranges and space use by Greater Prairie-Chickens*

Quantitative information on the spatial ecology of prairie-chickens is limited, especially with respect to potential responses seasonal differences in habitat use (Niemuth 2011, Patten et al. 2011). Demographic analyses of prairie-chicken populations in Kansas indicate that adult female mortality rates are 3–4 times higher during the 6-month breeding season than the 6-month nonbreeding season (Hagen et al. 2007, Augustine and Sandercock 2011, Winder et al. 2014a). However, analyses of demographic rates alone do not allow us to determine whether space use is a driving factor in mortality risk.

Resource utilization functions (RUFs) calculate a probabilistic measure of non-uniform space use within an animal's home range, and then use a multiple regression framework to relate space use to resource variables, while accounting for spatial autocorrelation among multiple locations from the same individual. Regression coefficients from the RUF can be used to draw inferences about the direction and magnitude of relationships between intensity of space use and values of selected resources at either an individual or a population level (Marzluff et al. 2004, Kertson et al. 2011). The objectives of our field study were to use resource utilization functions as an improved tool for testing for potential effects of wind energy development on resource use, and for quantifying the breeding and nonbreeding spatial ecology of female prairie-chickens.

Our analyses of impacts of rangeland management practices on space use were based on locations of female Greater Prairie-Chickens marked with radio transmitters. We developed individual and population level resource utilization functions separately for breeding and nonbreeding seasons. We used resource utilization functions to investigate the relationships between prairie-chicken space use and a set of seven landscape metrics describing rangeland management practices, patchiness, anthropogenic disturbance, and prairie-chicken social behavior. We used home range estimates and RUFs to test for three hypothetical effects of PBG on space use by prairie-chickens: *i*) selection for unburned areas, *ii*) selection for areas stocked at lower intensities, and *iii*) reductions in home range size.

Field Methods. – Lek sites were located by searching for displaying prairie chickens at sunrise on days with low winds during early spring with the help of local landowners and conservation officers. Lek sites were mapped using portable GPS units (±5 m). Females were captured and marked with transmitters (model A3950, Advanced Telemetry Systems, Minnesota, U.S.A.) at 34 leks from March through May, and battery life of the transmitters allowed monitoring for ~18 months. Radio-marked females were located by triangulation or homing with portable radio receivers and handheld antennas (Model R2000, ATS, Isanti, MN). We relocated birds ≥3 times per week during the 6-month breeding season (1 March–31August) and ≥2 times per week during the 6-month nonbreeding season (1 September–28 February). Observers altered their routes among monitored females within each week to obtain locations at different times of the day. We double-checked area of triangulated locations in the field to ensure that all sides were <200 m in length, minimizing error in location estimates. Coordinates for locations were estimated using Program Locate III (v. 3.34, Tatamagouche, NS; UTMs projected in NAD 1983, Zone 14N).

Statistical Analyses. – We analyzed location and space use data separately for breeding and nonbreeding seasons. If a female prairie chicken was monitored in multiple years, we considered each set of movements to be independent and accepted a modest amount of pseudoreplication to use our complete dataset. For the purposes of our study, we considered the home range to be the amount of space an individual female required to forage, survive, and reproduce (breeding season). We included females in our RUF analysis if we had ≥30 locations within a 6-month season (Seaman et al. 1999). During the breeding season, we further restricted our analysis to females that had ≥20 locations that were not associated with a nest or a brood. We included multiple locations associated with nest or brood attendance because these activities correspond to the periods of greatest mortality risk for female prairie-chickens in our study population, and resource selection during the breeding season is critical for determining demographic performance. Data requirements for spatial modeling introduce potential bias because breeding ranges can only be estimated for females that survive long enough to accumulate an adequate number of locations. On the other hand, females that die early in the breeding season contribute little to population growth, and factors that affect performance of successful birds should be more important for conservation. We accepted a tradeoff between number of locations and survival to investigate space use and associated habitat choices of successful female prairie chickens during the breeding season.

Home Range Estimation and Resource Utilization Functions. – We used utilization distributions to quantify space use as a continuous, probabilistic variable, and then related space use to landscape metrics using multiple regression in an RUF framework (Marzluff et al. 2004, Hepinstall et al. 2005, Millspaugh et al. 2006, Kertson et al. 2011). Resource utilization functions have several advantages over other commonly used methods for resource selection analysis. RUF methods allow for the quantification of inter-animal variation in resource use, and examine space use as a probabilistic and continuous metric, increasing sensitivity for detection of resource selection. Statistical advantages of RUFs include reduction of the effects of error in location estimation or lack of independence among location points. Individual animals (or populations) are treated as the experimental unit, and utilization distributions incorporate the entire distribution of an individual's movements for a specified time period rather than focusing on individual locations. Last, RUFs use a standardized designation of available habitat, not delineated by the arbitrary boundaries of a study area or other subjective measures (Marzluff et al. 2004).

We followed methods of Kertson and Marzluff (2009) to model animal movements, and built utilization distributions, extracted landscape metric values, and developed RUF models using the Ruf.fit package in Program R (ver. 2.13.11, R Foundation for Statistical Computing, Vienna, Austria). The first step in the RUF process was to generate 99% volume contour polygons – defined as the boundary of the area that contains 99% of the volume of the probability density distribution for an individual's movements. Spatial distributions of bird locations differed among individuals, and we used least squares cross validation to calculate a unique bandwidth value or smoothing parameter (*h*) for each female (Worton 1989, Powell 2000). We created a 99% volume contour polygon for the seasonal home range with the Fixed Kernel Density Estimator and Percent Volume Contour options in Hawth's Tools for ArcMap 9.3 (ESRI, Redlands, California). In addition to the 99% volume contour home ranges needed for the RUFs, we calculated the 50% volume contour home range for a more restricted area of primary activity (Patten et al. 2011). To facilitate direct comparisons with previous studies, we also calculated the 95% volume contour home range. We used linear models to test for the effects of year, season, individual selection for landscape metrics, rangeland management, anthropogenic disturbance, and nest outcome on variation in the size of female breeding ranges.

To locate the center, or centroid, of each female's breeding home range, we used Hawth's Tools to identify the 1% volume contour, which represented the smallest core at the most heavily used area within the utilization distribution. We determined the geographic center of the 1% contour and used this location as the centroid for each female's home range. We measured distances (km) from the centroid of each female breeding range to the nearest lek, road, and land cover patch edge. To develop recommendations about management of grassland habitat near leks, we ranked each sample of females by increasing distance from the centroid of the breeding range to nearest lek and found the distance for the individual at the 95th percentile. We added distance to nearest lek to the radius of a circle of equal area to the mean 95% breeding range area at each site to estimate a conservative focal distance for management of habitat around leks.

The second step in the RUF process was to create a raster of the utilization distribution within the 99% volume contour for each female's home range. We assigned a use value bounded from 1 to 99 for each 30 × 30 m cell within the home range, based on the relative volume (height) of the utilization distribution in that cell (Marzluff et al. 2004, Kertson and Marzluff 2010). The RUF framework combines the products of steps 1 and 2, using the 99% volume contour as the extent of available space, and the utilization distribution as the observed differential space use within the home range.

The third step was to determine landscape conditions at each grid cell within the home range for key resources hypothesized to predict space use. We identified seven landscape metrics that were hypothesized *a priori* to be good predictors of prairie-chicken space use. Habitat conditions may influence movement and settlement decisions of female prairie-chickens based on vegetative cover and composition, forage and roosting sites, and predator avoidance. Three variables were indicators of rangeland management: 1) cumulative fire frequency (number of years burned from 2000 to 2011; Mohler and Goodin 2012b), 2) years since fire application, and 3) stocking intensity (AUMs/ha). Prairie-chickens may avoid fragmentation, and one variable described the patchiness of land cover (Patten et al. 2011): 4) distance to land cover patch edge. Prairie grouse may be sensitive to anthropogenic disturbance, and one variable was an indicator of proximity to anthropogenic activity: 5) distance to nearest road. Gregory et al. (2011) showed that leks are often at high points in the landscape, and two variables described the landscape in terms of: 6) absolute elevation and 7) distance to nearest monitored lek.

For the first level of our RUF analysis, we ran models including all seven of the predictor variables described above. Only a small portion of our study area was managed with PBG practices, and many leks were dozens of kilometers away from pastures managed with PBG. This meant that individuals captured far from PBG properties had little chance of selecting for PBG-related landscape characteristics since were not likely to ever encounter a PBG property in their movements. As a second level of analysis, we used a subset of monitored females that had been captured at leks on PBG properties. For these 53 individuals, we ran a second set of RUF models that included only the three predictor variables directly related to rangeland management activities: stocking rate, cumulative fire frequency (2000‒2011), and years since prescribed fire.

We obtained GIS layers developed land cover classes, roads, and elevation from the Kansas Data Access & Support Center (www.kansasgis.org). Distance to patch edge was estimated using the land cover class grid, the Extract Raster Edge function in Hawth's Tools, and the Spatial Analyst Euclidian distance tool. We derived raster grids for distance to nearest road, lek, and landcover patch edge using the Spatial Analyst Euclidian Distance tool. We surveyed landowners across our study area each year to obtain stocking and burning data specific to each pasture on their properties (~500 pastures total). We used these data to create rasters for stocking rates and fire histories to assess the effects of rangeland management practices on prairie-chicken space use (**Figure 4.1A, B**). We used the cumulative fire frequency rasters (2000‒2011) developed from satellite imagery by Mohler and Goodin (2012b) to assess the potential legacy effects of prescribed fire regimes (**Figure 4.1C**). When a female's home range included areas that we were unable to survey for stocking and burning data, we used mean stocking and burning values for that year in areas of unknown history. This allowed us to retain all individuals in our analyses of space use and to analyze other landscape level drivers of space use at their full spatial scale within the home range. We used the Spatial Analyst Extraction tool to create spatially explicit data files as input for the Ruf.fit package (Kertson and Marzluff 2010).

The last step in our RUF analyses was to relate the height of the utilization distribution to resource values on a cell-by-cell basis to obtain coefficients of relative resource use. We $\log_e$-transformed space use data to meet the assumptions of linear multiple regression models. We used the Ruf.fit package for Program R to estimate RUFs with standardized and unstandardized β coefficients to investigate the influence of landscape metrics on prairie-chicken space use within home ranges and the potential for interactions with wind energy development (Marzluff et al. 2004, Kertson et al. 2011).

To develop population level inferences, we calculated mean standardized β coefficients ($\overline{\beta}$) for each landscape metric by treatment period and computed a variance that incorporated inter-individual variation (Marzluff et al. 2004). For both individual and population level inferences, standardized coefficients with 95% confidence intervals that did not overlap zero were significant predictors of space use. If a resource coefficient was significantly different from zero, we inferred that resource use was greater (+) or less (-) than expected based on availability of the resource within the home range (Marzluff et al. 2004). We ranked the relative importance of significant landscape metrics using the absolute value of their mean standardized β coefficients. To assess heterogeneity among individuals, we used individual standardized β coefficients and associated 95% confidence intervals to quantify the number of female prairie-chickens with significant positive or negative relationships with each of the ten landscape metrics.

Results – Home Range Estimation. – We analyzed movement data for a total of 104 females over 157 bird-seasons (112 breeding, 45 nonbreeding). Females had an average of 58 ± 2 locations per bird during the breeding season and 46 ± 1 locations per bird during the nonbreeding season (**Table 4.1**). Breeding home range size was estimated without bias with respect to sampling effort because the 99% breeding range size was not related to number of individual locations (linear model, $t = -1.926$, $df = 155$, adjusted $r^2 = 0.02$, $P = 0.06$).

Breeding home range size (95%) varied >150-fold among individual females, from 2 to 353 km^2, with a median of 21 km^2 (**Table 4.1**). An additive linear model indicated that home range size did not vary by year ($t = 1.6$, $df = 154$, $P = 0.10$) or season ($t = 1.1$, $df = 154$, $P = 0.28$), but median nonbreeding home range sizes tended to be >50% larger than during the breeding season (**Table 4.1**). Area of 95% breeding home ranges was larger when the centroid of the home range was farther from a lek ($F_{1,\,110} = 9.80$, $P = 0.002$; **Figure 4.2**). Nest failure also resulted in larger home range sizes (logistic regression, $z = -2.32$, $df = 88$, $P = 0.02$; **Figure 4.3**). Female prairie-chickens with a *successful* nest had a median 95% breeding home range size of 15 km^2, while females whose nest attempt *failed* had a median home range of 35 km^2.

Area of 95% breeding home range was not related to individual β coefficients from RUF models ($F_{1,\,110}$ <0.001 to 2.70, P = 0.10 to 0.99), fire and grazing metrics at the home range centroid ($F_{1,\,110}$ = 0.44 to 1.09, P = 0.30 to 0.51), distance from home range centroid to nearest road ($F_{1,\,110} = 0.21$, $P = 0.65$) or nearest patch edge ($F_{1,\,110} = 1.19$, $P = 0.27$), or rangeland management treatment (PBG vs. IESB) at the lek of capture ($F_{1,\,110} = 0.72$, $P = 0.40$).

Centroids of breeding home ranges tended to be ~1 km from a lek, >1.5 km from a road, 0.5 km from a patch edge, in an area of moderate stocking intensity, one year post-fire, and in an area that had been burned approximately twice every three years (**Table 4.1**). Over 90% of females had home range centroids <5 km from the nearest lek (**Figure 4.4**). We calculated a conservative radius to serve as a focal distance for management of habitat around leks. The value for the 95th percentile of distance from home range centroid to nearest lek was 5.51 km. The median 95% breeding home range area was 20.93 km^2, and a circle of equal area has a radius of 2.58 km. Adding these two values results in a conservative focal distance around leks of 8.1 km.

Nonbreeding home range size (95%) varied ~50-fold among individual female, from 5 to 241 km^2, with a median of 34 km^2 (**Table 4.1**). Area of 95% nonbreeding home ranges was related to individual β coefficients for distance to lek ($F_{1,\,43} = 7.80$, $P = 0.008$), distance to road ($F_{1,\,43} = 9.67$ $P = 0.003$), and cumulative fire frequency ($F_{1,\,43} = 19.05$, $P < 0.0001$), with larger home ranges when females selected for areas near leks, avoided roads, and when cumulative fire frequency was low (**Figure 4.5A-C**). Females also had larger nonbreeding home ranges when the centroid of their home range was unburned ($F_{1,\,42} = 7.04$, $P = 0.01$), when close to leks ($F_{1,\,43} = 5.56$, $P = 0.02$), and far from roads ($F_{1,\,43} = 13.10$, $P = 0.001$; **Figure 4.5D-F**). We constructed an additive model to explain variation in nonbreeding home range size and included significant predictors from different rangeland management and ecological categories (β distance to lek, β distance to road, β cumulative fire frequency, distance from centroid to nearest lek and road, and years since prescribed fire at the home range centroid; **Table 4.2**). Our additive model explained ~50% of the variation in home range size ($F_{6,\,37} = 8.12$, $P < 0.0001$, adjusted $r^2 = 0.50$).

Area of 95% nonbreeding home range was not related to individual β coefficients for elevation, ($F_{1,\,43}$ = 0.06 to 2.30, P = 0.14 to 0.80), stocking intensity at the home range centroid ($F_{1,\,42} = 0.10$, $P = 0.76$), cumulative fire frequency at the home range centroid ($F_{1,\,43} = 3.61$, $P = 0.06$), or distance from home range centroid to nearest patch edge ($F_{1,\,43} = 0.02$, $P = 0.89$).

Centroids of nonbreeding home ranges tended to be farther from leks at ~2.5 km, >1.5 km from a road, 0.4 km from a patch edge, in an area of moderate stocking intensity, <1 year post-fire, and in an area that had been burned approximately three times every four years (**Table 4.1**).

Drivers of Space Use. – The first level of our resource utilization analysis of space use considered seven factors and found that distance to lek was the strongest predictor of space use during the breeding season and was a significant driver of space use for all three years of our study ($\bar{\beta}$ = -0.59 to -0.35; **Figure 4.6A-C**). Negative coefficients indicated that females selected areas close to leks within their breeding ranges, and 83% (93 of 112) individual females followed this pattern.

In 2011, females avoided intensely stocked areas ($\bar{\beta}$ = -0.10; 65% of individuals, 24 of 37) and selected areas with a high cumulative fire frequency within their breeding home ranges ($\bar{\beta}$ = +0.09, 58% of individuals, 21 of 37; **Figure 4.6A**). In 2012, females' selection for stocked areas changed, and they selected for areas with high stocking intensities ($\bar{\beta}$ = +0.08, 53% of individuals, 18 of 34) and areas on ridges and hilltops ($\bar{\beta}$ = +0.13, 59% of individuals, 20 of 34; **Figure 4.6B**).

RUF models for nonbreeding home ranges indicated that distance to lek was still a driver of space use during two of the three years of our study even when birds were not seeking out mates or nesting habitat ($\bar{\beta}$ = -0.32 [2011] and -0.53 [2012]; **Figure 4.6D, F**). Across all years, 64% of individuals (29 of 45) selected space close to leks within their nonbreeding home ranges. Females also selected for frequently burned areas within nonbreeding home ranges ($\bar{\beta}$ = +0.19 [2012] and +0.08 [2013]; **Figure 4.6 E, F**).

The second level of our resource utilization analysis of space use considered just three factors (stocking rate, cumulative fire frequency, and years since prescribed fire) and included only individuals captured at leks on PBG properties (n = 53). Females selected areas with low stocking rates ($\bar{\beta}$ = -0.11, 55% of individuals, 29 of 53) and high fire frequencies ($\bar{\beta}$ = +0.09, 55% of individuals, 29 of 53; **Figure 4.7**). We also observed a tendency for females to select unburned areas ($\bar{\beta}$ = +0.05, 53% of individuals, 28 of 53), but the magnitude of this relationship suggests it was not as important to space use decisions as stocking rate and fire frequency.

Implications. – Our resource utilization analysis of landscape factors driving differential space use within breeding home ranges revealed that distance to lek was the primary driver of female prairie-chicken space use during both breeding and nonbreeding seasons. Habitats selected by female prairie-chickens were consistently close to leks. We observed a strong relationship between breeding season space use by female Greater and Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) and distance to lek at nine other study sites across five states (NE, MO, KS, OK, and NM; Winder et al. unpubl. ms), but the present study is the first to compare breeding and nonbreeding space use with respect to rangeland management practices. Links between female space use and lek placement are consistent with the hotspot hypothesis, which predicts that males should establish lek sites where female breeding home ranges are relatively dense or at the intersection of dispersed female home ranges (Bradbury et al. 1986). But selection for areas near leks during the nonbreeding season is unexpected. Standardized lek surveys are often used by wildlife managers to monitor trends in grouse populations. Lek surveys have been criticized because bird counts are often treated as population indices, but detection probabilities are imperfect and fail to account for day of season, sex, age, and weather conditions (Walsh et al. 2004, Clifton and Krementz 2006, Blomberg et al. 2013). Even so, female selection for areas near leks during both breeding and nonbreeding seasons suggests that lek surveys of prairie-chickens are effectively sampling habitat features important to females year-round, not just counts of individuals.

The first level of our RUF results indicated that resource selection can vary widely among years and individuals. The switch we observed in female avoidance of high stocking rates in 2011 to selection for highly stocked areas in 2012 may be related to drought conditions that caused many ranchers in our study area to reduce stocking rates and avoid burning. In 2011, when the majority of the landscape in our study area was burned, females avoided intensely stocked areas. In 2012, when only ~10% of the study area was burned and ranchers had reduced stocking rates, female prairie-chickens selected for intensely stocked areas. This switch in the response of female prairie-chickens to stocking rate suggests that interaction between stocking and burning matters to the birds. Recently burned and heavily stocked areas were avoided, while unburned and heavily stocked areas were selected. Managing rangelands with PBG provides annually shifting grazing and burning interactions at a scale that should be meaningful to wildlife such as prairie-chickens.

The second level of our RUF analysis indicated that females captured at leks on PBG-managed properties avoided intensely stocked areas and selected areas with a relatively high cumulative fire frequency. We also observed a tendency toward selection of unburned areas. Simultaneous selection for high fire frequency and unburned patches provides support that a PBG rangeland management strategy provides the type of habitat and resources necessary for female prairie-chickens. Females avoid patches that are rarely burned as well as patches that are recently burned. Under a typical PBG rangeland management regime, no patch would go unburned for longer than three years, and two-thirds of every pasture would be at least one year post-burn. Our analysis of space use within home ranges indicated that a PBG management strategy would provide the habitat diversity and quality selected for by female prairie-chickens.

Space use decisions can affect survival and productivity of prairie-chickens through interactions with predators and energy costs. During the breeding season, home ranges were larger when centroids were farther from a lek and when a female had a failed nest attempt. During the nonbreeding season, home ranges tended to be ~50% larger than during the breeding season. Nonbreeding home ranges were larger when females selected for areas near leks, avoided roads, when cumulative fire frequency was low, and when the centroid of their home range was unburned, close to leks, or far from roads. Our RUF analyses of space use allow us to extend the implications of rangeland management practices to a landscape scale because we directly evaluated the spatial interactions between prairie-chickens and stocking rates, prescribed fire, and anthropogenic influences. The strongest predictor of female prairie-chicken space use within home ranges during both breeding and nonbreeding seasons was distance to lek. Our results also suggest that the interaction between fire application and stocking rates influences the space use decisions of female prairie-chickens. Moreover, we found evidence that PBG management practices create preferred habitats for female prairie-chickens with a 3-year fire return interval and a mosaic of burned and unburned patches.

Table 4.1. Seasonal home range characteristics (mean ± SE [min., max.]) for radio-monitored female prairie-chickens in Kansas, 2011–2013.[a]

						Centroid metrics[3]					
Season	No. of locations	Bandwidth (km) [1]	50% area (km^2)[2]	95% area (km^2)	99% area (km^2)	Distance to lek (km)	Distance to road (km)	Distance to edge (km)	Stocking intensity (AUM/ha)	Years since burn	Fire frequency
Breeding *n* = 112 (1 Mar.–31 Aug.)	58 ± 2 [30, 109]	1.30 ± 0.09 [0.26, 4.50]	5.0 [0.3, 89.0]	20.9 [2.2, 352.6]	32.9 [3.5, 508.4]	1.3 ± 0.1 [0.1, 9.3]	1.7 ± 0.1 [0.03, 5.0]	0.5 ± 0.03 [0.04, 1.7]	0.9 ± 0.03 [0.2, 2.3]	1 ± 0.1 [0, 5]	8.3 ± 0.2 [0, 12]
Nonbreeding *n* =45 (1 Sep.–28 Feb.)	46 ± 1 [30, 70]	1.41 ± 0.12 [0.41, 3.78]	7.7 [1.0, 56,3]	34.1 [5.0, 241,4]	56.9 [7.4, 350.5]	2.5 ± 0.3 [0.5, 7.6]	1.7 ± 0.2 [0.2, 4.9]	0.4 ± 0.05 [0.0, 1.58]	0.9 ± 0.04 [0.1, 1.5]	0.6 ± 0.1 [0, 4]	8.7 ± 0.3 [0, 12]

[1] Bandwidth = smoothing parameter (*h*) used in kernel density estimation, individually determined for each bird using least squares cross validation.

[2] Median estimates of area are given for 50%, 95%, and 99% volume contours of female breeding home ranges.

[3] Centroid metrics include mean distance from breeding range centroids to the nearest lek, road, or edge of land cover patch, and the value for stocking intensity, years since burn, and cumulative fire frequency (2000-2011) at the home range centroid.

Table 4.2. Model results for predictors of 95% nonbreeding home range size for radio-monitored female prairie-chickens in Kansas 2011–2013.

Model factors[a]	t	P	Adj. r^{2b}	Larger home range when…
β distance to lek	-3.22	0.003	0.13	Female selects space near leks
β distance to road	1.86	0.07	0.16	Female avoids roads
β cumulative fire frequency	-2.68	0.01	0.29	Cumulative fire frequency is low
Distance from centroid to lek	1.30	0.20	0.10	Centroid is close to a lek
Distance from centroid to road	1.66	0.11	0.22	Centroid is far from a road
Years since prescribed fire at centroid	1.99	0.05	0.12	Centroid is unburned

[a] Full model: 95% Home Range Size ~ β distance to lek + β distance to road + β cumulative fire frequency + distance from centroid to nearest lek + distance from centroid to nearest road + years since prescribed fire at centroid; $F_{6, 37} = 8.12$, $P < 0.0001$, adjusted $r^2 = 0.50$.

[b] From single factor model.

Figure 4.1. Raster layers for stocking rate (**A**), years since prescribed fire (**B**), and cumulative fire frequency during 2000–2011 (**C**, Mohler and Goodin 2012b) at our field study site in eastcentral Kansas, 2011–2013.

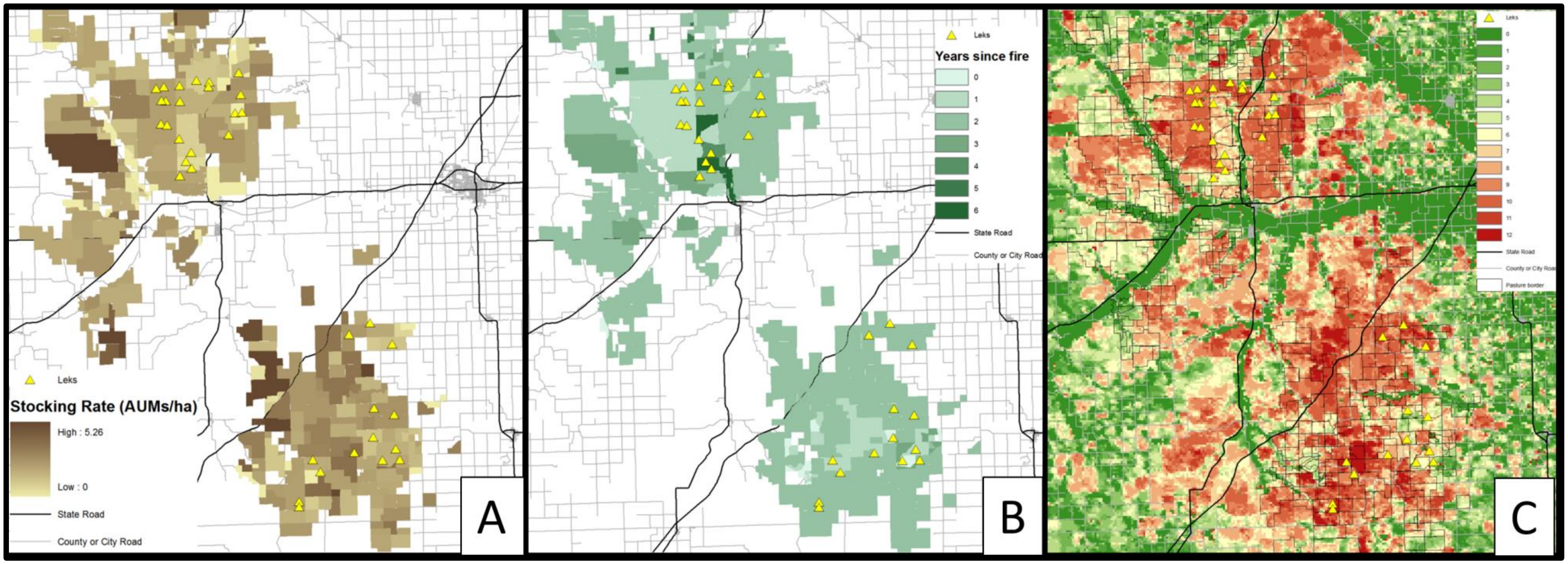


Figure 4.2. Relationship between distance from home range centroid to nearest lek and 95% breeding home range size for radio-monitored female prairie-chickens in Kansas 2011–2013. Untransformed values are shown, but analyses were conducted on natural log transformed data.

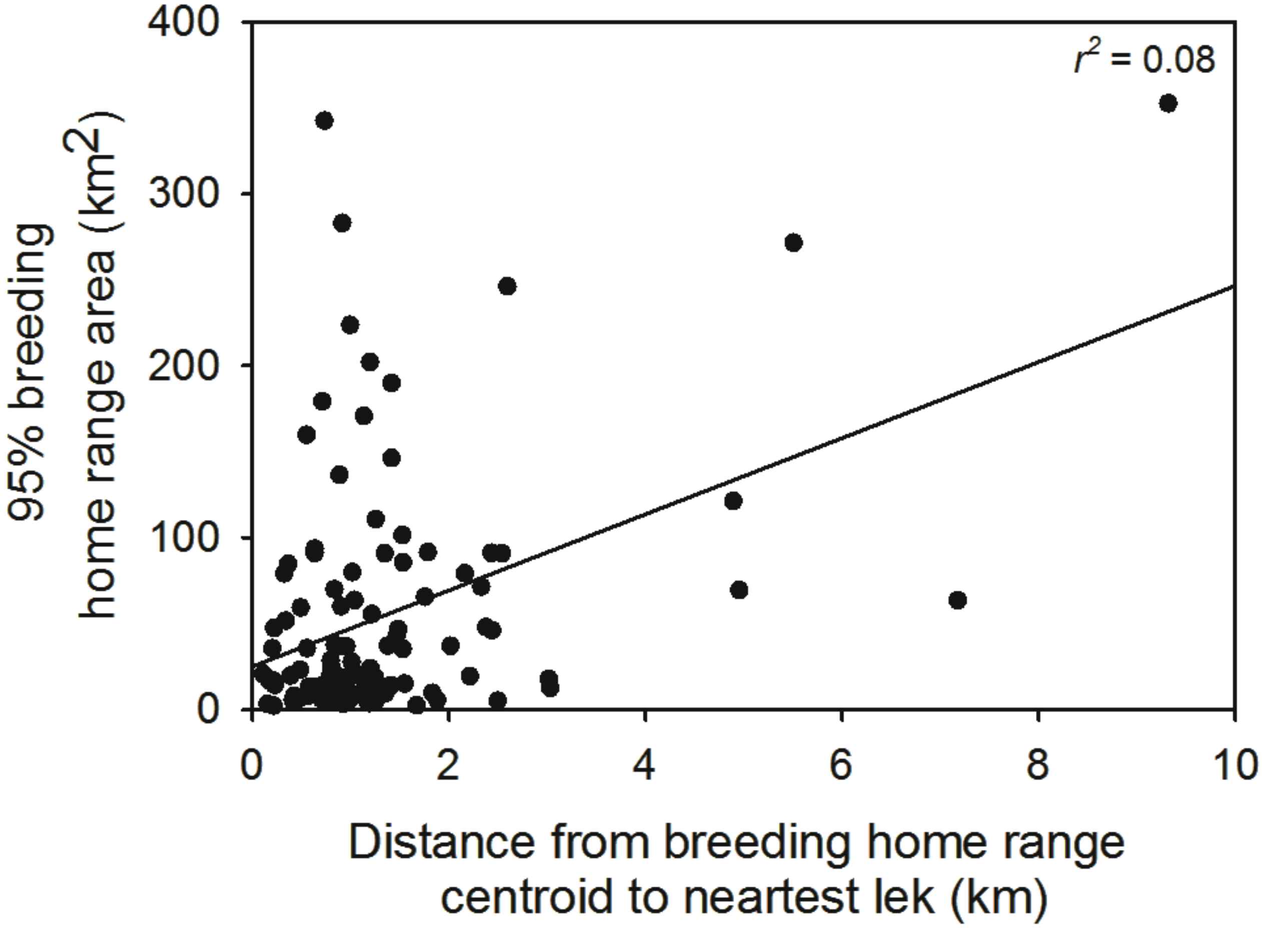


Figure 4.2. Relationship between nest outcome and 95% breeding home range size for radio-monitored female prairie-chickens in Kansas 2011–2013.

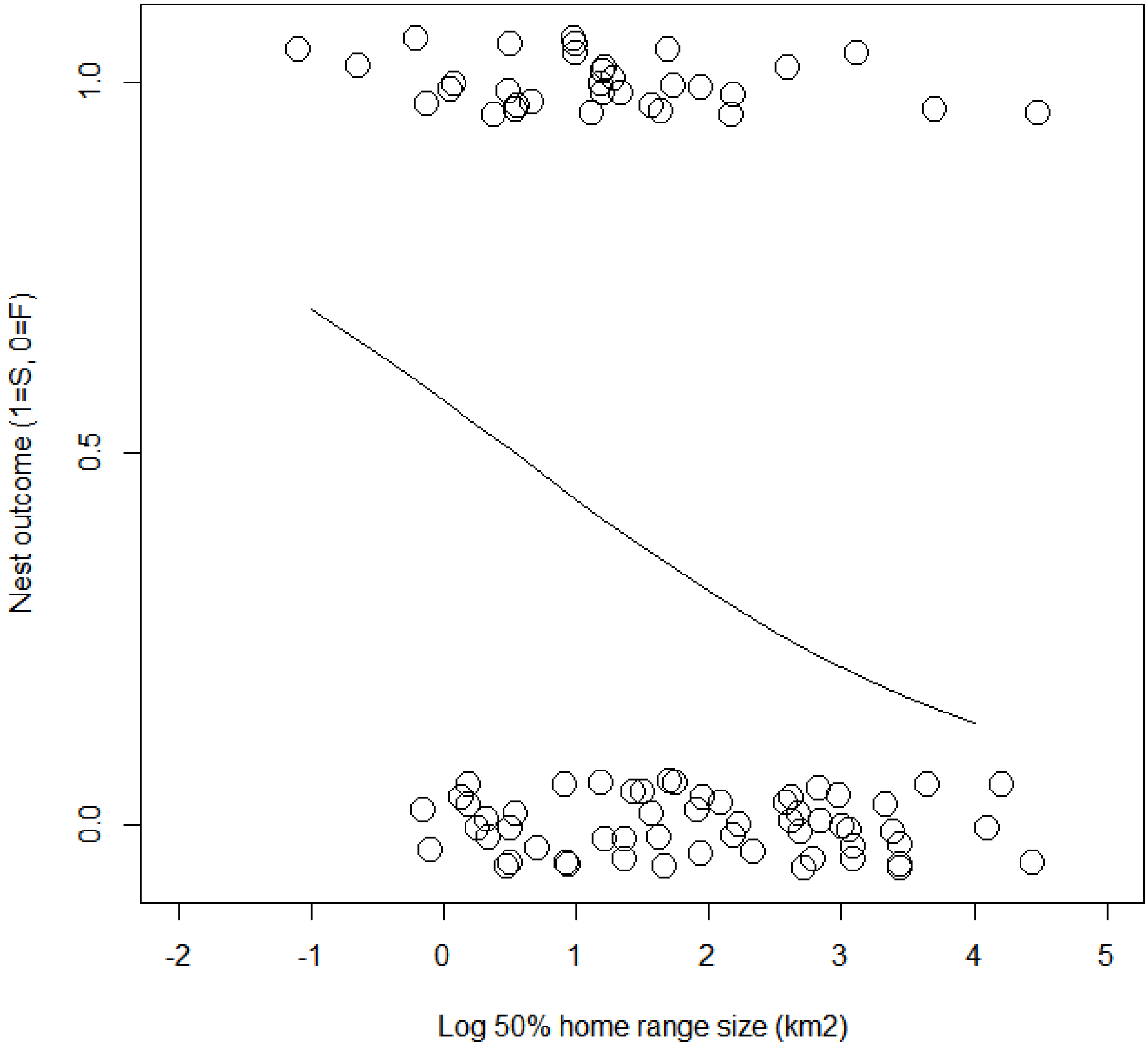


Figure 4.3. Rank order for distance from 95% breeding home range centroid to nearest lek. Over 95% of monitored females had home range centroids <5 km from the nearest lek. Triangles represent individual birds, and the vertical dotted line represents the 95th percentile at 5.5 km.

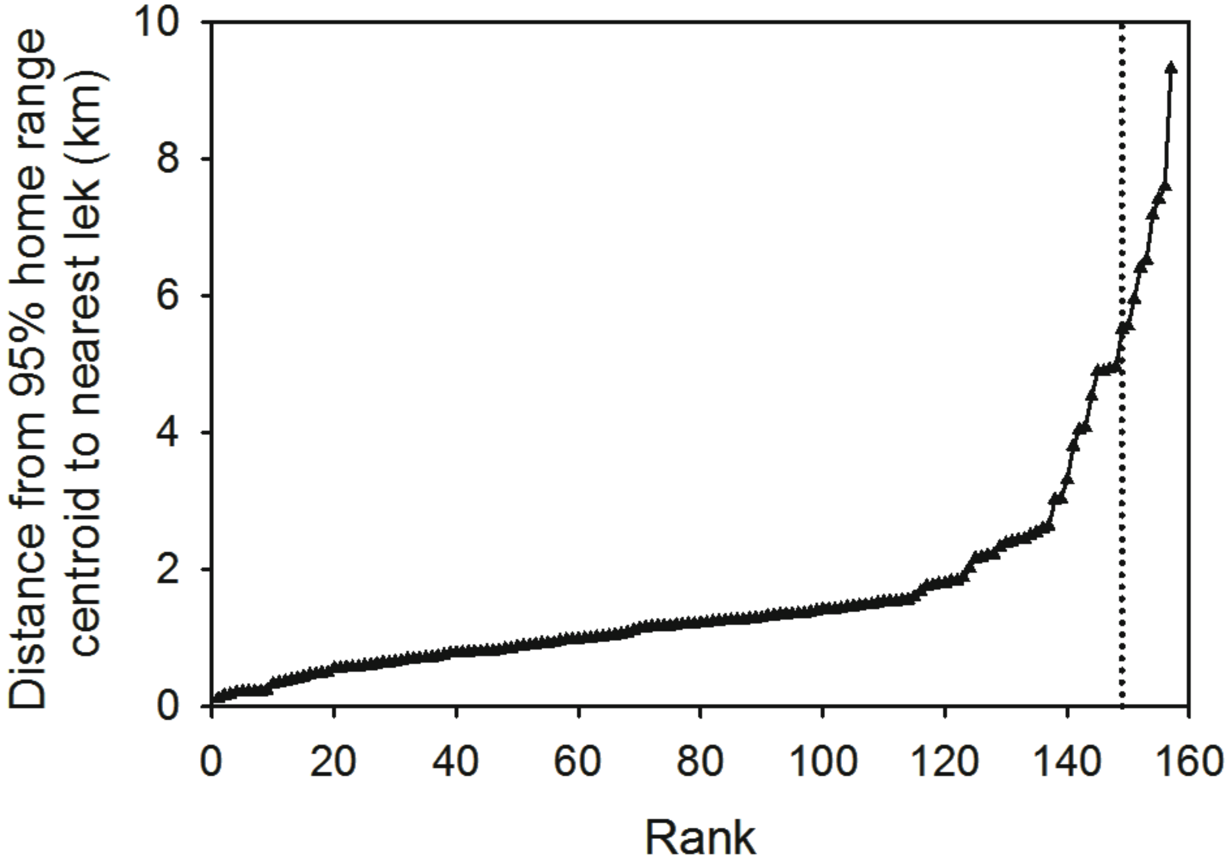


Figure 4.4. Predictors of nonbreeding 95% home range size for radio-monitored female prairie-chickens in Kansas 2011–2013. Untransformed values are shown, but analyses were conducted on natural log transformed data. Values for r^2 are from single factor linear models.

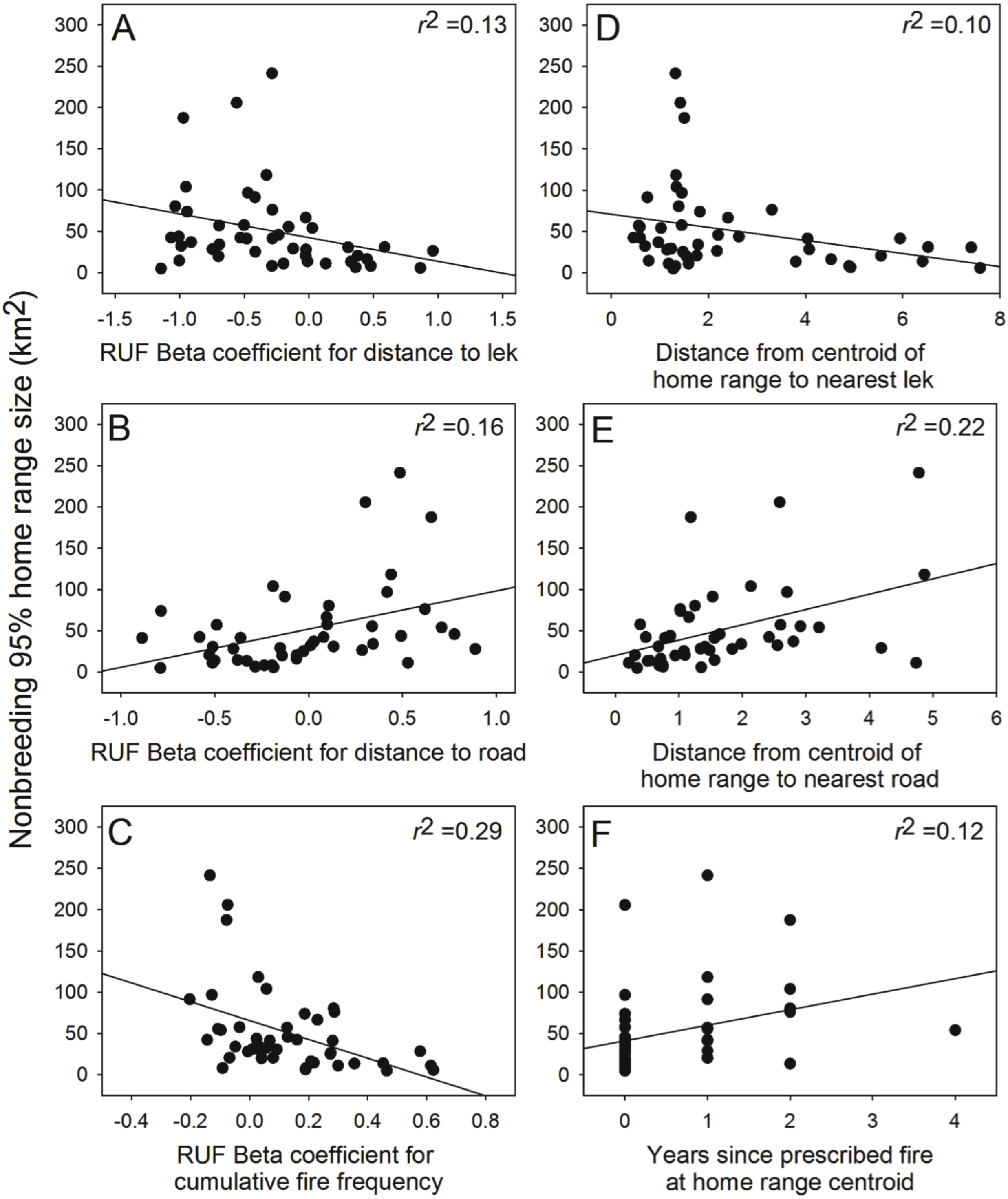


Figure 4.5. Mean standardized resource utilization function coefficients ($\bar{\beta}$) and 95% confidence intervals for seven landscape metrics. Resource utilization functions analyzed space use within seasonal 99% home ranges of radio-marked female prairie-chickens in Kansas 2011–2013.

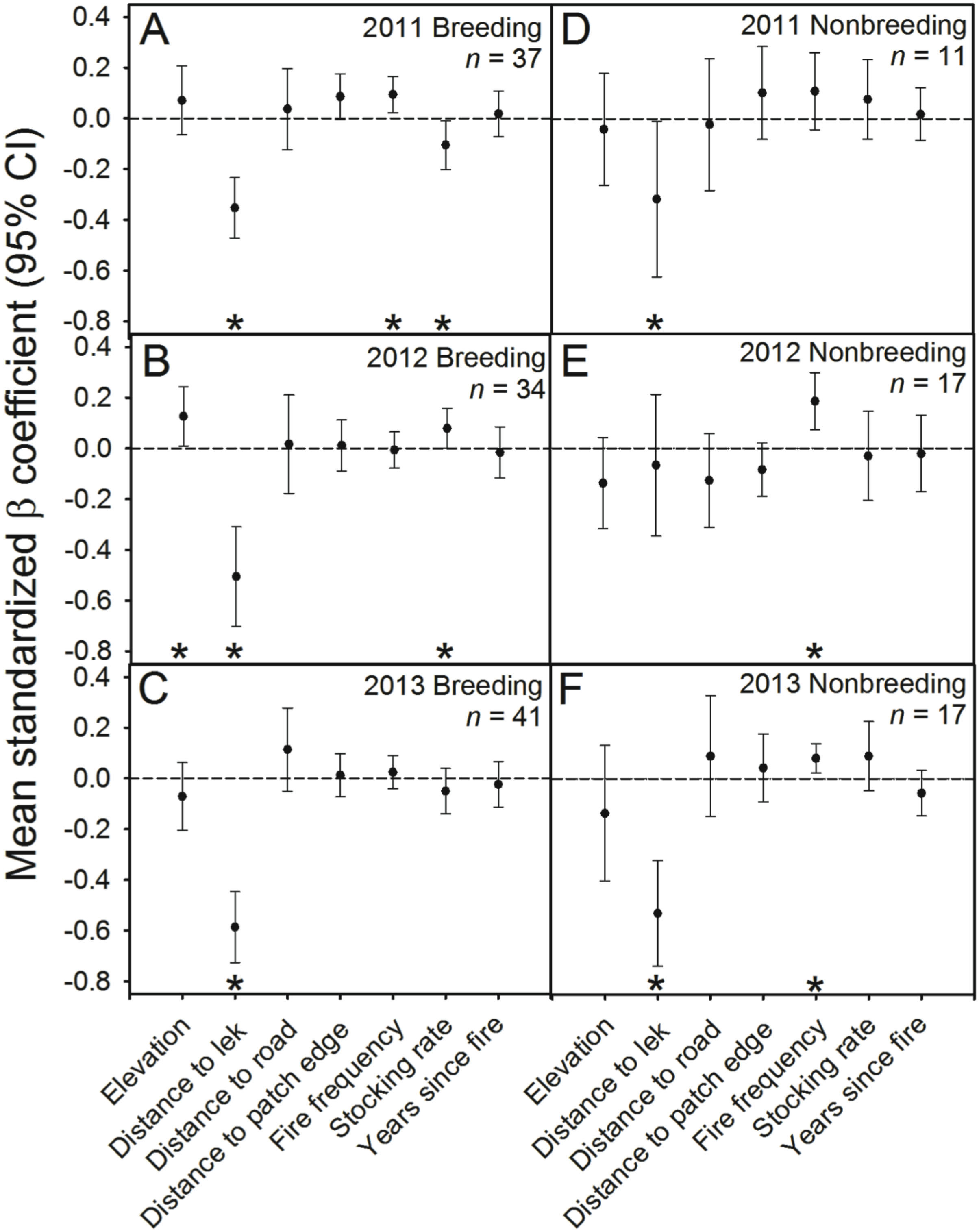
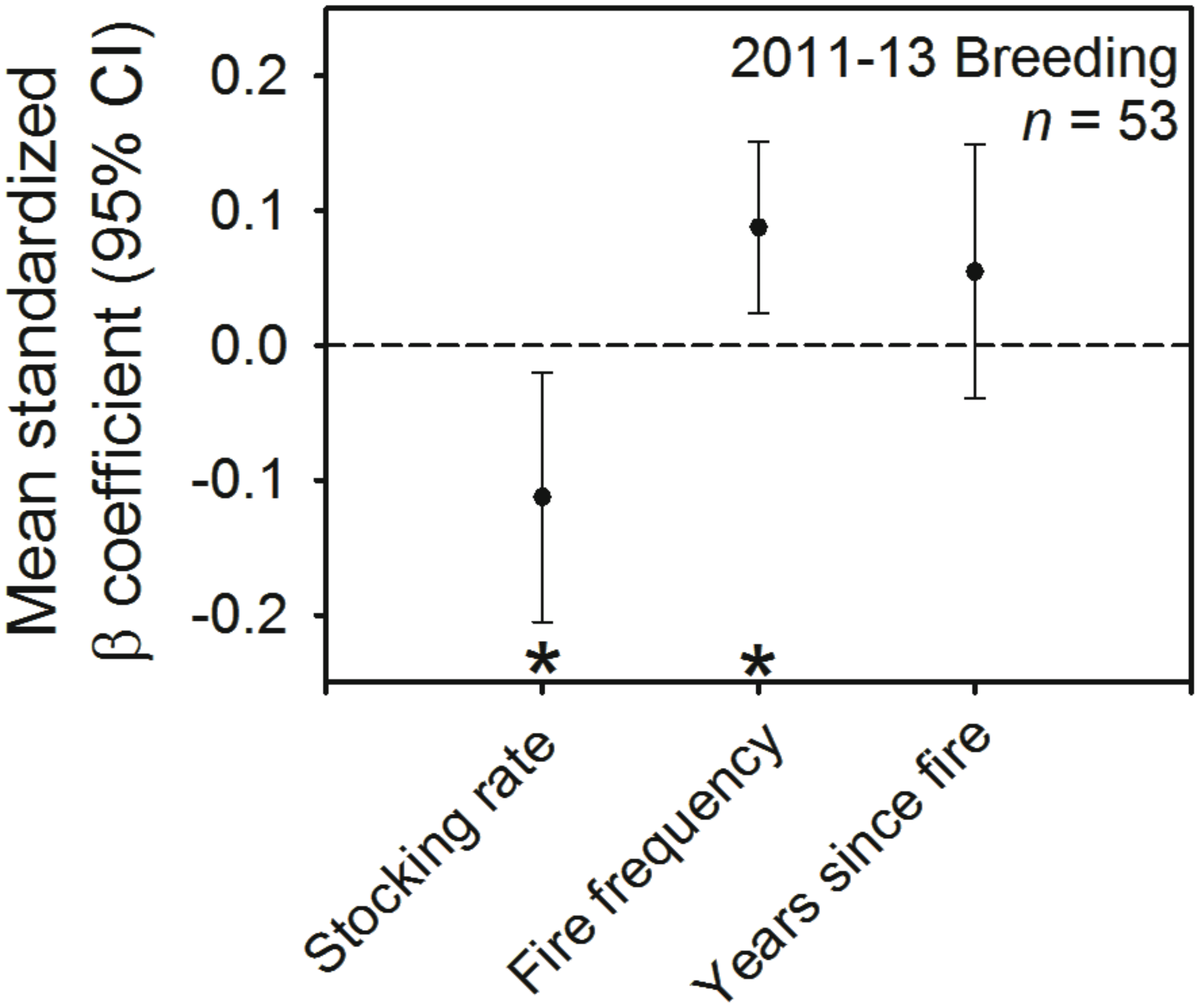


Figure 4.6. Mean standardized resource utilization function coefficients ($\bar{\beta}$) and 95% confidence intervals for four landscape metrics. Resource utilization functions analyzed space use with respect to landscape level predictors related to rangeland management within seasonal 99% home ranges of radio-marked female prairie-chickens captured at leks on properties managed by patch-burn grazing in Kansas 2011–2013.



Objective 5. *Impacts on survival of Greater Prairie-Chickens*

Rangeland management regimes could affect survival of prairie-chickens through several possible mechanisms. Most losses in natural populations of prairie-chickens are due to predation, and rangeland management could affect survival rates if numbers or foraging behavior of key predators is altered.

Seasonal Survival of Females. – Prairie-chickens were captured with walk-in traps and drop-nets at lek sites during March to May. A few females were captured at the nest or with broods to replace failing transmitters. At first capture, we marked all birds with a numbered metal leg band and three colored leg bands and sexed them by plumage. Females were outfitted with 10-11 g radio transmitters attached with an elastic or wire necklace harness (ATS or Holohil). Radios had an expected battery life of 1-2 years and were equipped with mortality switches that changed pulse rate when a bird was killed. Females were relocated 3-4 times a week during the breeding season (1 March through 31 August) and weekly during the nonbreeding season (1 September through 28 February). Following the timing of our capture effort, we created encounter histories for each female per year for an annual period from Mar 1 to Feb 28/29 the following year (i.e., Mar 1-7 = week 1). Encounter histories consisted of: week of entry, week of exit, and event (1 = mortality, 0 = survived). Our data were both left- and right-censored with staggered entry of birds into the sample, and surviving birds which were censored after failure of an attachment harness or battery of the radio transmitter.

If the pulse rate from the 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. Radios with broken harnesses but no other damage, and no sign of bird remains were considered to be *dropped collars* and were treated as surviving birds. Bird carcasses with evidence of tooth marks or scat were considered to be the result of *mammalian* predation by coyotes, badgers or other mesocarnivores. Carcasses that were plucked at a perch site, decapitated remains where breast muscles were removed with no evidence of tooth marks, or presence of white fecal matter were considered to be the result of *avian* predation by raptors or owls. 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 were considered to be the result of *collision* mortality. Birds shot by hunters where leg bands were reported to our field team or to KDWPT were considered to be *harvest* mortality. Most carcasses were recovered within 1-2 days of death, but causes of mortality are tentative because we cannot discount the possible effects of scavenging of dead birds. 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 event to be an *unknown* cause of mortality.

We calculated cumulative survival rates of radio-marked females with staggered entry Kaplan-Meier models with package survival in Program R (ver. 2.13.11, R Foundation for Statistical Computing, Vienna, Austria; Murray 2006, Sandercock et al. 2011). As first step, we checked 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 first examined survival rates for all monitored females. We used Cox proportional hazards models to test for differences in survival among years, capture lek treatments (i.e., rangeland management regime at capture lek, PBG vs. IESB), and age classes (yearlings vs. adults).

Next, we examined survival for a subset of individuals for which we had adequate data to perform analyses of home ranges and space use. For this group, we tested for differences in survival among years, capture lek treatments (i.e., rangeland management regime at capture lek, PBG vs. IESB), age classes (yearlings vs. adults), and as a function of individual space use (β from breeding season resource utilization function models; see **Objective 4**) with respect to elevation, proximity to leks, roads, and land cover patch edges, cumulative fire frequency, stocking rate, and years since prescribed fire. We also tested for the effects of home range area (95%), and landscape characteristics at the centroid of the home range, including stocking rate, years since prescribed fire, cumulative fire frequency, distance to nearest road, lek, and land cover patch edge. Data requirements for spatial modeling introduced potential bias to our analysis of survival for this subset of individuals because breeding ranges can only be estimated for females that survive long enough to accumulate an adequate number of locations. On the other hand, females that die early in the breeding season contribute little to population growth, and factors that affect performance of successful birds should be more important for conservation. We accepted this bias to investigate the effects of space use and associated habitat choices on survival rates. We tested for effects of breeding season space use on survival rates because the majority of mortality events for prairie-chickens occur during the breeding season (Augustine and Sandercock 2011, Winder et al. 2014a), and space use decisions are likely especially important to survival during this period.

For both groups, we ranked models using Akaike's information criterion adjusted for small sample sizes (AIC_c). Models with $\Delta AIC_c < 2.0$ that differed from the minimum AIC_c model by a single parameter were excluded 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 (e^{β}) where a hazard ratio is expected to equal one if there is no difference in the risk of mortality between groups. Some females were monitored in multiple years and we modeled individual identity as a random effect to control for a potential lack of independence among different encounter histories for the same female (with the cluster function).

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 value of 1 for the smoothing parameter to avoid over-fitting splines.

Results. – We monitored 53 females in 2011 (29 mortalities), 58 in 2012 (16 mortalities), and 68 in 2013 (28 mortalities; **Table 5.1**). The assumption of proportional hazards was met for our global model with factorial effects of capture treatment lek and age ($\rho = -0.07$, $\chi^2 = 0.53$, $P = 0.91$, $n = 179$). Regardless of year, age, or rangeland management at capture lek, overall annual survival was 0.52 ± 0.05 (95% CI = 0.44, 0.62, $n = 170$; **Figure 5.3**). Annual survival did not differ among years (Cox proportional hazards HR = 1.20, 95% CI = 0.89, 1.64, *z* = 1.20, *P* = 0.23; **Figure 5.4**).

The best supported model estimated survival as a function of rangeland management at capture lek (w_i = 0.36; **Table 5.2**). Annual survival was ~35% higher for hens captured at leks on properties managed with PBG (0.61 ± 0.07, 95% CI = 0.49, 0.76, *n* = 84) compared to IESB (0.45 ± 0.06, 95% CI = 0.34, 0.59, *n* = 86; Cox proportional hazards HR = 0.60, 95% CI = 0.36, 1.00, *z* = -1.96, *P* = 0.05; **Figure 5.1**).

The second best model in our set included the additive effects of capture lek treatment and age (w_i = 0.21; **Table 5.2**). Annual survival of adult females captured at PBG leks (0.62 ± 0.08, 95% CI = 0.47, 0.81, *n* = 56) was nearly twice as high as adults captured at IESB leks (0.33 ± 0.08, 95% CI = 0.21, 0.53, *n* = 54; Cox proportional hazards HR = 0.62, 95% CI = 0.35, 1.09, *z* = -1.67, *P* = 0.09; **Figure 5.2**). Annual survival of yearlings was similar across capture lek treatments (PBG = 0.62 ± 0.10, 95% CI = 0.45, 0.85, *n* = 28; IESB = 0.63 ± 0.09, 95% CI = 0.47, 0.84, *n* = 32; **Figure 5.2**).

We created 19 candidate models to explore the effects of breeding season space use and rangeland management regime on annual survival of female prairie-chickens with the required ≥30 locations to estimate home ranges and run resource utilization function (RUF) models (*n* = 100, **Table 5.3**). The best supported model in our candidate set received 90% of the model weight and included the additive effects of β coefficients for years since most recent prescribed fire (Cox proportional hazards HR = 4.64, 95% CI = 1.37, 15.64, *z* = 2.47, *P* = 0.01; **Figure 5.5**) and distance from home range centroid to nearest road (Cox proportional hazards HR = 0.60, 95% CI = 0.42, 0.84, *z* = -2.93, *P* = 0.003; **Figure 5.6**). Mortality rates were higher when female prairie-chickens selected for unburned areas within their home ranges and when home range centroids were close to roads (**Figures 5.5-5.6**). There were 28 mortality events in our subset of individuals used in RUF analyses. Of these, 71% selected for unburned areas within their home ranges (+β coefficient). Of the 100 females included in this subset of models, 38 had home range centroids <1 km from a road.

Over 38% of female prairie-chicken carcasses were found <1 km from a road once the mortality switch had been activated on the radio-collar (28 of 73, **Figure 5.7**). Of the 28 carcasses we recovered <1 km of a road, 64% (18 of 28) were attributed to avian predation, 18% (5 of 28) to mammalian predation, and 4% (1 of 28) to collision. Cause of death could not be determined reasonable certainty for 3 carcasses recovered <1 km from a road, and one death was due to harvest mortality.

The second best model in our candidate set received only 4% of the model weight and included the additive effects of β coefficients for years since most recent prescribed fire (Cox proportional hazards HR = 3.96, 95% CI = 1.19, 13.17, *z* = 2.25, *P* = 0.02) and rangeland management treatment at the lek of capture (Cox proportional hazards HR = 0.41, 95% CI = 0.19, 0.89, *z* = -2.26, *P* = 0.02; **Figure 5.8**). Mortality rates were higher when female prairie-chickens selected for unburned areas and for individuals captured at leks on properties managed with IESB.

The single factor model for the effects of rangeland management at capture lek on female prairie-chicken survival received little support in our candidate set but indicated that survival rates were ~30% higher for individuals captured at leks on properties managed with PBG (0.76 ± 0.06, 95% CI = 0.65, 0.90) compared to IESB (0.58 ± 0.07, 95% CI = 0.45, 0.75; Cox proportional hazards HR = 0.50, 95% CI = 0.24, 1.04, $z = -1.86$, $P = 0.06$). We also found that neither age (Cox proportional hazards HR = 0.76, 95% CI = 0.37, 1.56, $z = -0.74$, $P = 0.46$; $S_{\mathrm{ASY}} = 0.65 \pm 0.07$, $S_{\mathrm{SY}} = 0.70 \pm 0.07$) nor 95% home range area had an effect on female prairie-chicken survival (Cox proportional hazards HR = 1.05, 95% CI = 0.75, 1.47, $z = 0.27$, $P = 0.79$; **Figure 5.9**).

We used hazard functions based on weekly survival to investigate patterns of seasonal mortality. Female survival was 0.65 ± 0.04 (95% CI = 0.58, 0.0.74) during the breeding season and ~0.80 during the nonbreeding season (0.525 survival in week 52/0.654 survival in week 26). During the breeding season (March through August, weeks 1–26), the average instantaneous risk of mortality for female prairie-chickens was ~2 times higher than during the nonbreeding season (0.0167 vs. 0.009). Hazard rates began to increase sharply beginning in week 5 (0.012) and peaking in week 11 (0.0337) before falling back to 0.012 by week 20 (**Figure. 5.10**). If a female survived the breeding season, there was limited mortality during the nonbreeding period from September through February (weeks 26 to 52). The cumulative survival in Kaplan-Meier plots was a flat line in fall and winter, and the instantaneous risk of mortality was ~0.01 per week (**Figure 5.10**). We observed this pattern of high risk of mortality during the breeding season followed by relatively little mortality during the fall and winter during all three years of our field study (**Figure 5.11**).

To investigate the mechanisms leading to lower risk of mortality for female prairie-chickens on properties managed with PBG, we calculated hazard functions for females captured at leks on properties managed with PBG vs. IESB. During the early nesting period of late April through early July (~weeks 7–18), the instantaneous risk of mortality for females captured on properties managed with IESB (0.033) was ~2 times higher than for females captured on properties managed with PBG (0.016; **Figure 5.12**). Unexpectedly, we observed a second peak in risk of mortality for females captured at leks on properties managed with IESB during late December through late January (weeks 43–47; hazard rates = 0.016–0.043; **Figure 5.12**). Risk of mortality for females captured at leks on properties managed with PBG during this same period ranged from 0.004 to 0.005 (**Figure 5.12**).

Implications. – We used two sets of models to evaluate the effects of ecological and anthropogenic variables on female prairie-chicken survival. First we modeled weekly survival for all radio-marked females a function of age, year, and rangeland management practices at the lek of capture. Overall annual survival of female prairie-chickens was intermediate (0.52) at our site compared to other recently studied sites in Kansas: 0.34–0.42 in the Smoky Hills, 0.42–0.50 in Geary, Morris, Riley, and Wabaunsee Counties, and 0.64–0.71 in Chautauqua and Cowley Counties (McNew et al. 2012a).

Females captured at leks on properties managed with PBG had higher survival rates (0.61) compared to females at leks on IESB properties (0.45). We have shown that space use by female prairie-chickens is tightly tied to leks (Winder et al. 2014b, Winder unpubl. ms, current study). Therefore, rangeland management practices at the lek of capture should be indicative of habitat selection by the female during the breeding season. Rangeland management practices directly impacted the quantity and quality of vegetative cover on the landscape. Females rely upon cryptic coloration and concealment to avoid predators, and our data support the hypothesis that IESB practices put female prairie-chickens at risk to predators by decreasing the amount of cover available across wide spatial scales.

We also found that rangeland management practices have a greater effect on adult females compared to yearlings. Annual survival of adult females captured at PBG leks (0.62) was almost twice as high as adults captured at IESB leks (0.33), while annual survival rates of yearlings were similar (~0.6) regardless of rangeland management practices. Differences in survival rates among age class are not uncommon in grouse. McNew et al. (2012a) analyzed age-specific female survival at three sites in Kansas and found that adult survival was ~10-25% higher than yearlings. Hagen et al. (2005) reported that survival rates of yearling males (0.60) were consistently high compared to adult males (0.44) in Lesser Prairie-Chickens, and showed that higher survival of yearling males is a general pattern among male grouse. But the mechanisms for these age-specific differences have not been investigated, and our results indicate that rangeland management practices can play a role.

For our second set of models, we modeled annual and seasonal survival as a function of breeding season space use and rangeland management practices. This analysis was limited to females that survived long enough to accumulate ≥30 locations, allowing us to estimate home ranges and analyze space use using resource utilization functions. We acknowledge a bias in these analyses for individuals with inherently higher survival rates, but we accepted this bias to investigate the effects of space use and associated habitat choices on survival rates, an important step in addressing source-sink population dynamics.

Time since fire and distance to road were important drivers of survival for this subset of individuals (n = 100). Lyons et al. (2009) reported habitat-specific annual survival rates for Lesser Prairie-Chickens occupying in shinnery oak *Quercus havardii* (0.31) and sagebrush habitats (0.52). Habitat-specific analyses of survival are rare, and our results provide important new insights into the spatial ecology and population dynamics of prairie-chickens. Collision and hunting mortality were rare in our study (combined, <5% of observed mortality). A majority of the demographic losses in our study were due to predation, and habitat selection choices that put individuals at increased risk to predation have important effects on population dynamics. We observed higher survival rates when females selected for recently burned areas within their home ranges and when home range centroids were far from roads. Higher survival rates in recently burned areas may seem to be at odds with our finding that overall survival rates were higher for individuals captured at PBG leks compared to leks on properties managed with IESB. We believe that this combination of results illustrates the complexity of female prairie-chicken habitat requirements. Adequate vegetative cover is necessary for concealment, but an area that goes unburned for more than ~2 growing seasons may accumulate litter at a depth that prevents females from detecting an approaching predator until it is too late. PBG uses a fire regime that creates habitats that meet these requirements, and the result is female survival rates that are ~35% higher than those on IESB properties.

We also identified distance to road as an important anthropogenic driver of female prairie-chicken survival rates. Females with home range centroids close to roads had lower survival rates than those with home ranges distant from roads. Identifying the cause of death from a recovered carcass cannot be done with complete certainty, and we were unable to discount the possibility that some prairie-chickens were killed by raptors, but scavenged by mammals before we located and inspected the carcasses. Nevertheless, 64% of carcasses recovered <1 km from a road were attributed to *avian predation*. Given the potential bias for coding as *mammalian predation* due to scavenging, we report our observed rate of avian predation near roads as a minimum estimate. The increased incidence of raptor predation we observed near roads indicates that proximity to roads may be confounded with the placement of electric lines which can serve as perch sites for hunting raptors.

Our data support the hypothesis that areas near roads at our study site may serve as ecological sinks. Nearly 40% of the females in this analysis had home range centroids <1 km from a road, and ~50% had individual β coefficients from resource utilization function analyses indicating selection for areas close to roads within their home ranges. Our results show that a large portion of our monitored population was selecting habitat that increased the risk of mortality, specifically to raptor depredation.

Low rates of natural mortality have been reported during the nonbreeding season for prairie-chicken populations in Kansas (0.13–0.25 in the current study; 0.11–0.18 in Winder et al. 2014a; 0.06–0.28 in Augustine and Sandercock 2011). A large-scale experiment on willow ptarmigan *Lagopus lagopus* provided evidence that harvest mortality can be partially compensatory at harvest rates <15% (Sandercock et al. 2011). Based on low natural rates of mortality during the nonbreeding season, partial compensation is possible but would support only low levels of harvest mortality in prairie-chickens at our study site.

Estimates of seasonal survival for grouse are rare, but high mortality rates during nesting and brood rearing are common in greater and lesser prairie-chickens (Hagen et al. 2007; Lyons et al. 2009; Augustine and Sandercock 2011, Winder et al. 2014a). Females may be vulnerable to predators during breeding because they rely on cryptic colouration for concealment and are less likely to flush if attending eggs or young.

Hazard rates indicated that lower annual survival of individuals captured at IESB leks was due to higher rates of mortality during the early nesting period from late April through early July. One possible explanation for the increased instantaneous risk of mortality during the nesting season for individuals captured at IESB leks is the lack of quality nesting habitat that to adequate cover and concealment from predators. Risk of mortality for females captured at PBG leks was roughly half as high as for females captured at IESB leks. We also observed disparity in hazard rates during winter from late December through January for females captured at PBG vs. IESB leks. Our study did not address habitat quality during the nonbreeding season, but one hypothesis for the increase in risk of mortality for females captured at IESB leks is that traditional rangeland management practices may result in reduced quality of foraging and roosting habitats. The cumulative costs of foraging and temperature regulation through the winter may weaken individuals tied to these habitats, ultimately making them easier targets for predators. Additional research on the effects of PBG on nonbreeding season habitat would be necessary to further address this hypothesis.

Habitat-specific analyses of survival are rare, and our results provide important new insights into the spatial ecology and population dynamics of prairie-chickens. We found that areas near roads may act as ecological sinks for female prairie-chickens because females are at increased risk of predation, especially from raptors, in these areas. We also found that areas that are not burned regularly (~once every 2–3 growing seasons) put females at increased risk to mortality. Our analysis of annual and seasonal survival rates and hazard functions showed that PBG practices provide habitat conditions that increase female survival during both breeding and nonbreeding seasons, indicating that widespread implementation of PBG has the potential to greatly improve prairie-chicken population dynamics at a large spatial scale.

Table 5.1. Causes of mortality for radio-marked female prairie-chickens found dead (*n* [percentage]) at our field site in Kansas.

Year[a]	Mammalian Predation	Avian Predation	Collision Mortality	Hunter Harvest	Mortality of Unknown Cause	Total
2011	7 [24]	19 [66]	0 [0]	1 [3]	2 [7]	29
2012	4 [25]	10 [63]	1 [6]	0 [0]	1 [6]	16
2013	9 [32]	15 [54]	1 [4]	0 [0]	3 [11]	28
All	20 [27]	44 [60]	2 [3]	1 [1]	6 [8]	73

[a] Bird year begins 1 March and ends 28 February.

Table 5.2. Model selection results of survival of female prairie-chickens in Kansas, 2011–2013 (*n* = 170 bird years for individuals of known age).

Models for survival[a]	*k*	AIC_c	ΔAIC_c	w_i	Σw_i
Capture lek treatment	2	561.39	0	0.36	0.36
Age + Capture lek treatment	4	562.48	1.09	0.21	0.57
Age	2	562.83	1.44	0.17	0.74
Constant	1	563.26	1.87	0.14	0.88
Age × Capture lek treatment	6	564.18	2.78	0.09	0.97
Year	3	565.94	4.55	0.04	1.00

[a] Model notation: year = 2011, 2012, 2013; capture lek treatment = patch-burn grazing (PBG) vs. intensive early stocking with annual burning (IESB); age = adults (ASY) vs. yearlings (SY), where "+" = main effects models and "×" = factorial model. Model fit was assessed by: k = number of parameters, ΔAIC_c = difference in corrected Akaike's Information Criterion value from the minimum AIC_c model, and w_i = Akaike's weight.

Table 5.3. Model selection results of survival of female prairie-chickens in Kansas, 2011–2013 (n = 100 bird years for individuals of known age with home range and space use results).

Models for survival[a]	k	AIC_c	ΔAIC_c	w_i	Σw_i
β years since prescribed fire + distance from home range centroid to nearest road	3	224.75	0.00	0.90	0.90
β years since prescribed fire + capture lek treatment	4	230.79	6.04	0.04	0.94
β years since prescribed fire	2	231.66	6.90	0.03	0.97
β years since prescribed fire + β stocking rate	3	232.45	7.70	0.02	0.99
β years since prescribed fire + β cumulative fire frequency	3	233.69	8.94	0.01	1.00
β years since prescribed fire + β cumulative fire frequency + 95% home range size	4	235.83	11.08	0.00	1.00
Stocking rate at home range centroid	2	243.70	18.94	0.00	1.00
Distance from home range centroid to nearest road	2	258.6	33.84	0.00	1.00
Capture lek treatment	2	261.54	36.78	0.00	1.00
β distance to road	2	262.64	37.88	0.00	1.00
β distance to patch edge	2	262.84	38.08	0.00	1.00
Constant	1	262.92	38.17	0.00	1.00
β stocking rate	2	263.06	38.30	0.00	1.00
β distance to lek	2	263.64	38.88	0.00	1.00
Distance from home range centroid to nearest patch edge	2	263.86	39.10	0.00	1.00
β elevation	2	264.00	39.24	0.00	1.00
95% home range size	2	264.90	40.14	0.00	1.00
β cumulative fire frequency	2	264.98	40.22	0.00	1.00
Year	3	267.01	42.26	0.00	1.00

[a] Model notation: year = 2011, 2012, 2013; capture lek treatment = patch-burn grazing (PBG) vs. intensive early stocking with annual burning (IESB); individual β coefficients for resource utilization function models of space use, descriptive landscape metrics at 95% home range centroid, where "+" = main effects models. Model fit was assessed by: k = number of parameters, ΔAIC_c = difference in corrected Akaike's Information Criterion value from the minimum AIC_c model, and w_i = Akaike's weight.

Figure 5.1. Kaplan-Meier plots showing annual survival estimates as a function of rangeland management regime at lek of capture for radio-marked female prairie-chickens, 2011–2013. Analyses were based on a weekly time step where Week 1 = 1–7 March. Confidence intervals omitted for clarity. PBG = patch-burn grazing; IESB = intensive early stocking with annual burning.

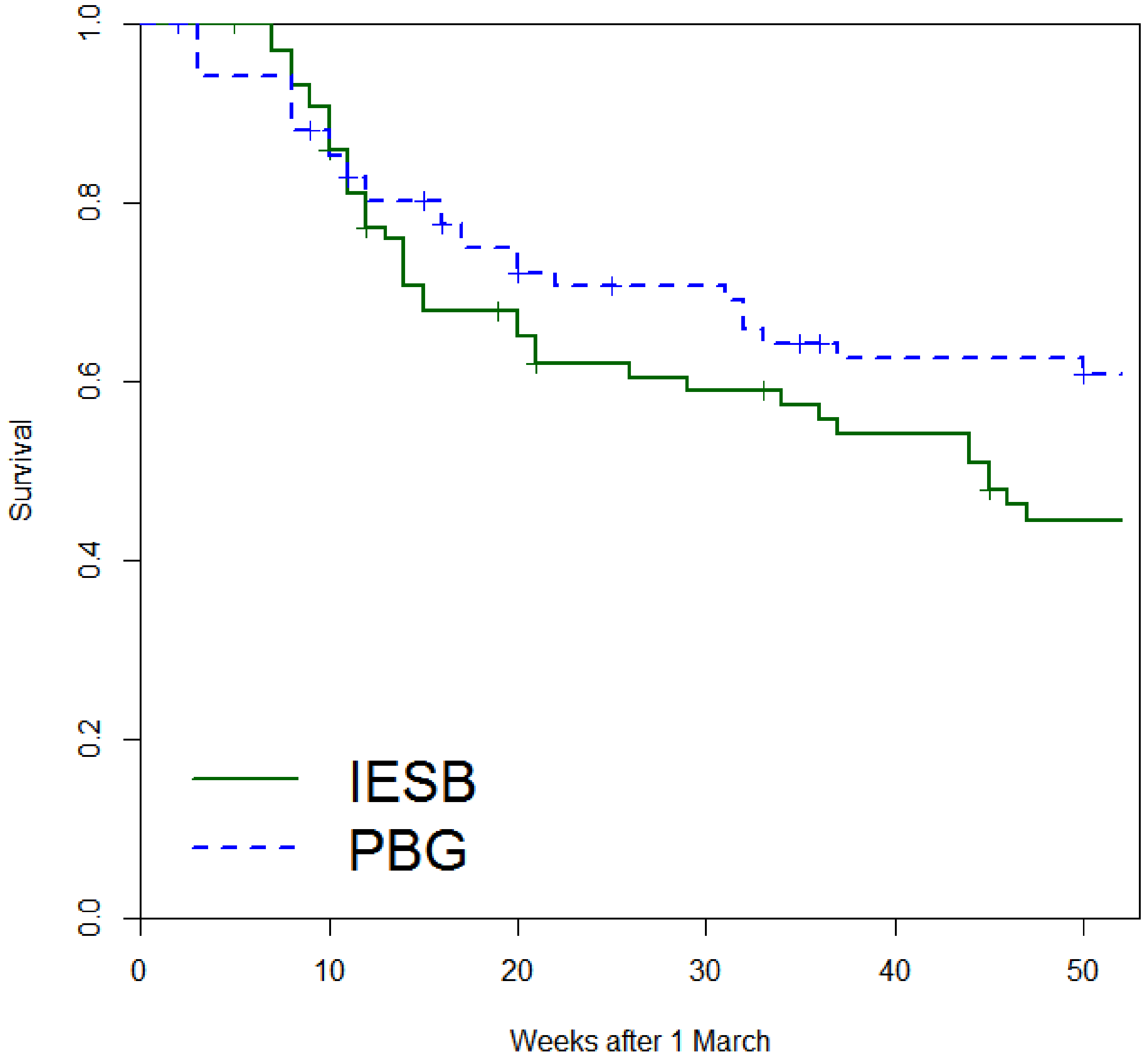


Figure 5.2. Kaplan-Meier plots showing annual survival estimates as a function of age class and rangeland management regime at lek of capture for radio-marked female prairie-chickens, 2011–2013. Analyses were based on a weekly time step where Week 1 = 1–7 March. Confidence intervals omitted for clarity. PBG = patch-burn grazing; IESB = intensive early stocking with annual burning; ASY = after second-year, adult; SY = second-year, yearling.

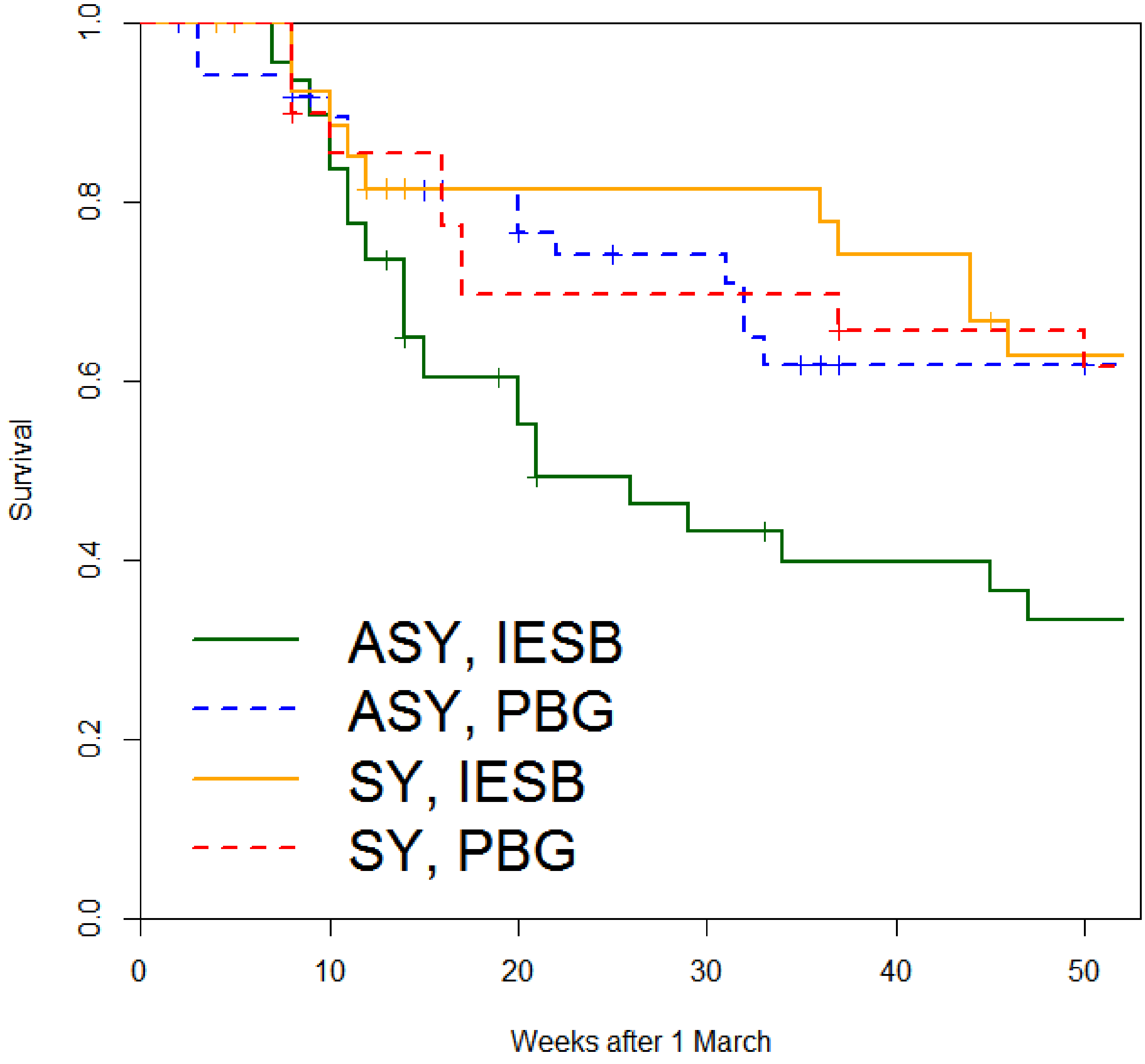


Figure 5.3. Kaplan-Meier plots showing pooled annual survival estimates for radio-marked female prairie-chickens, 2011–2013. Analyses were based on a weekly time step where Week 1 = 1–7 March. Dashed lines represent 95% CIs.

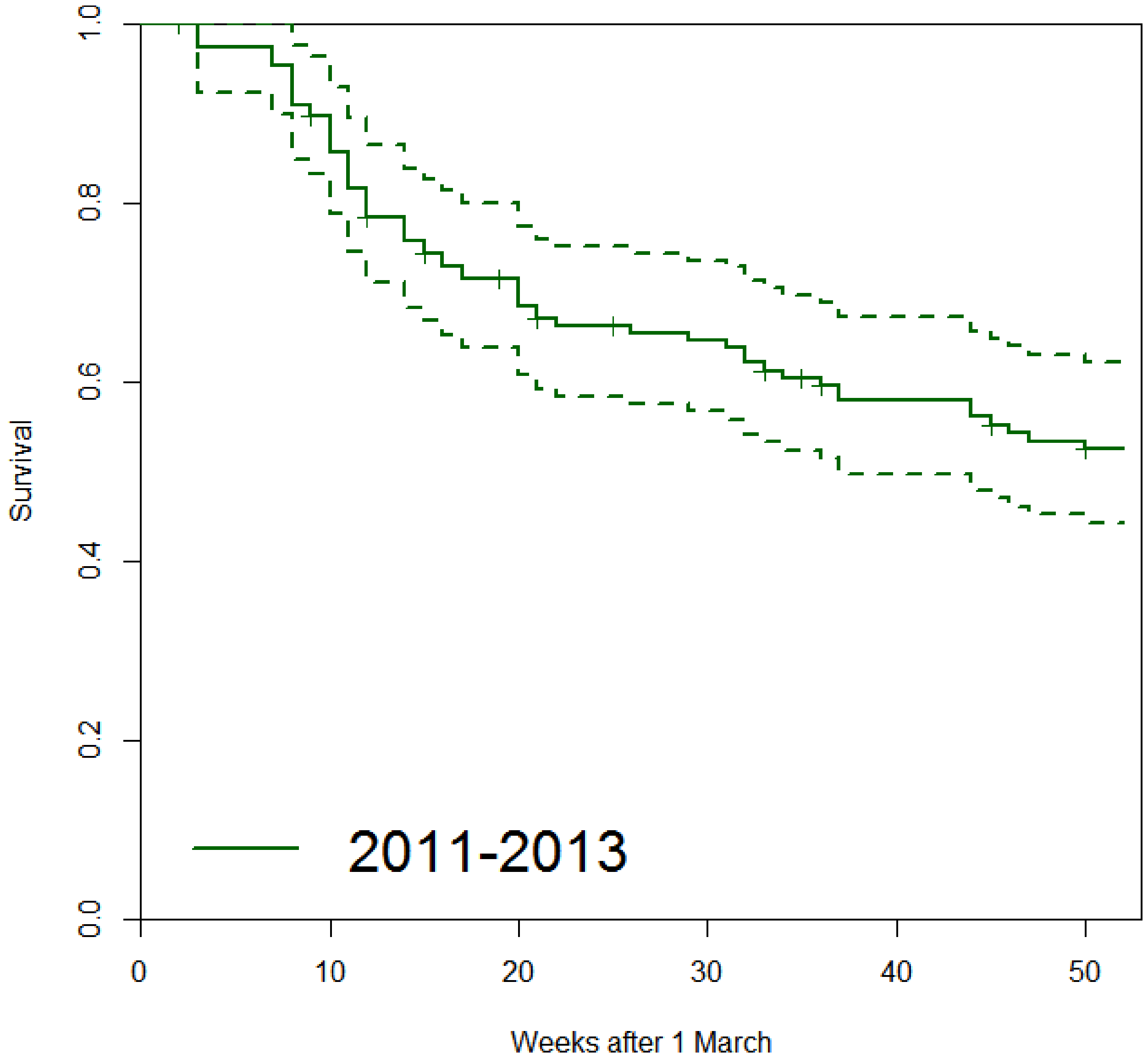


Figure 5.4. Kaplan-Meier plots showing annual survival estimates for radio-marked female prairie-chickens, 2011–2013. Analyses were based on a weekly time step where Week 1 = 1–7 March. Confidence intervals omitted for clarity.

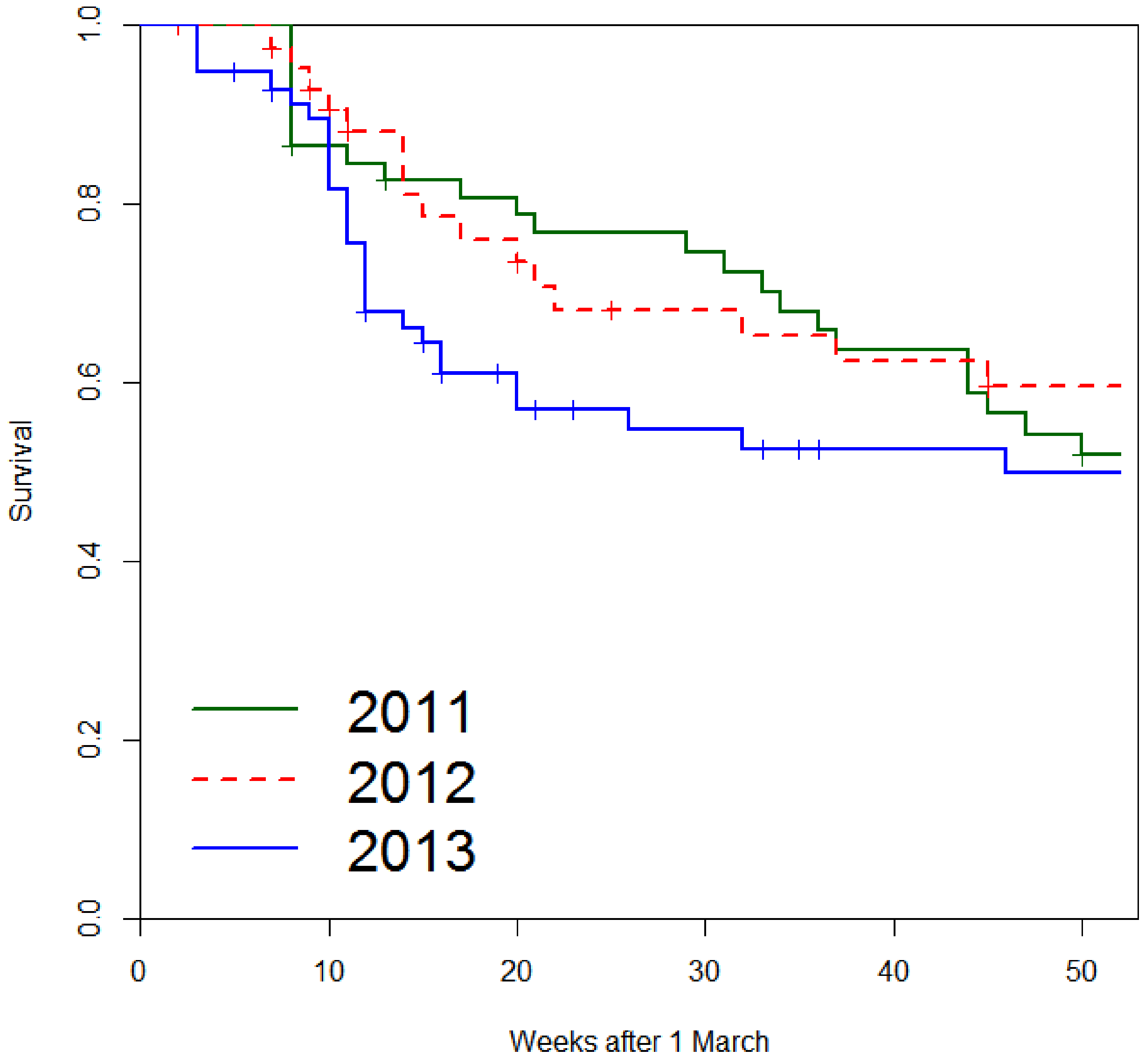


Figure 5.5. Risk of mortality (hazard function, 95% CI) for female Greater Prairie-Chickens in relation to individual β coefficients for years since previous prescribed fire from resource utilization (RUF) models. Negative coefficients indicate selection for recently burned areas while positive coefficients indicate selection for unburned areas. Parameter estimates were taken from a model with additive effects of years since fire and distance from home range centroid to nearest road ($w_i = 0.90$).

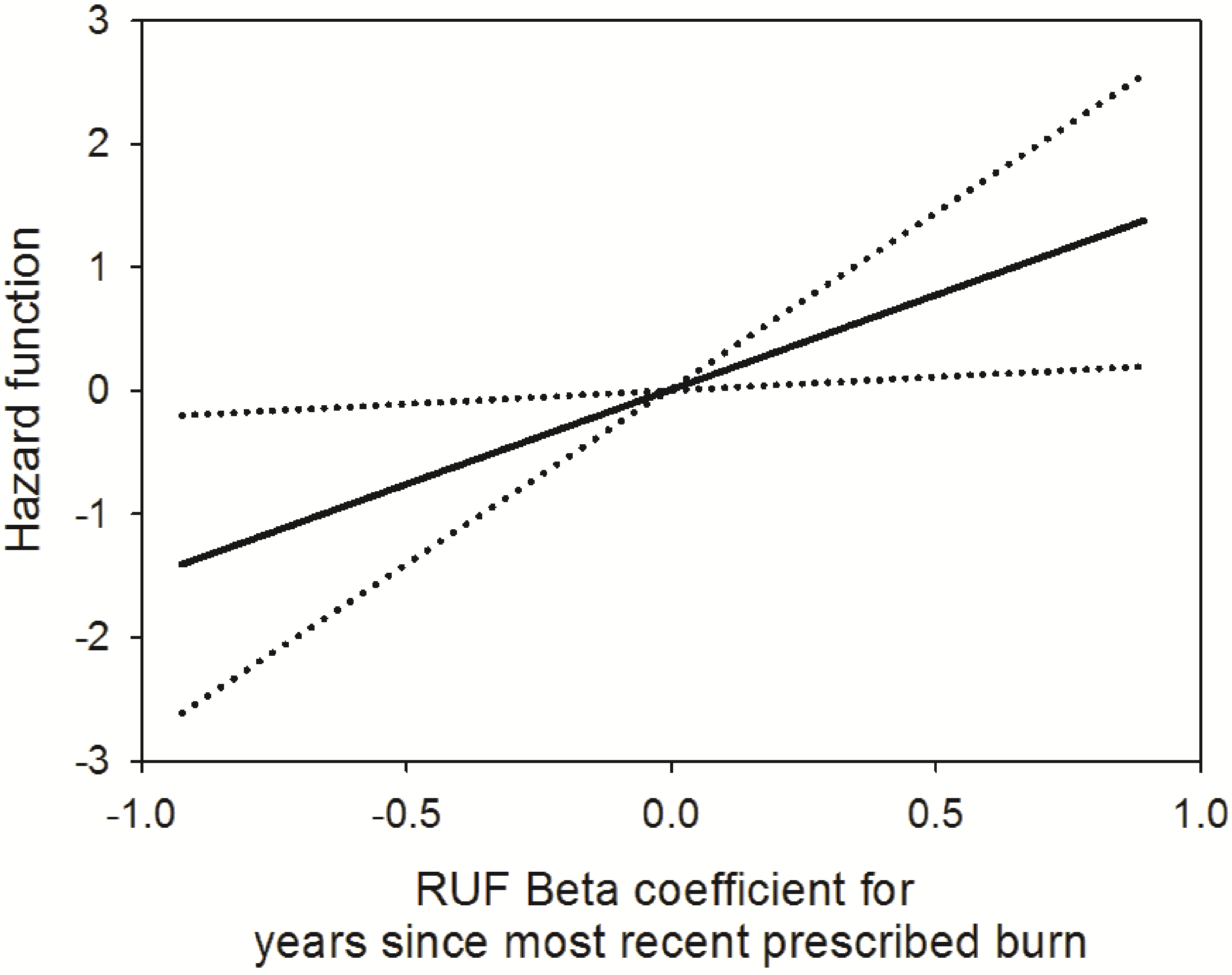


Figure 5.6. Risk of mortality (hazard function, 95% CI) for female Greater Prairie-Chickens in relation to distance from home range (95%) centroid to nearest road (paved or unpaved). Parameter estimates were taken from a model with additive effects of years since fire and distance from home range centroid to nearest road ($w_i = 0.90$).

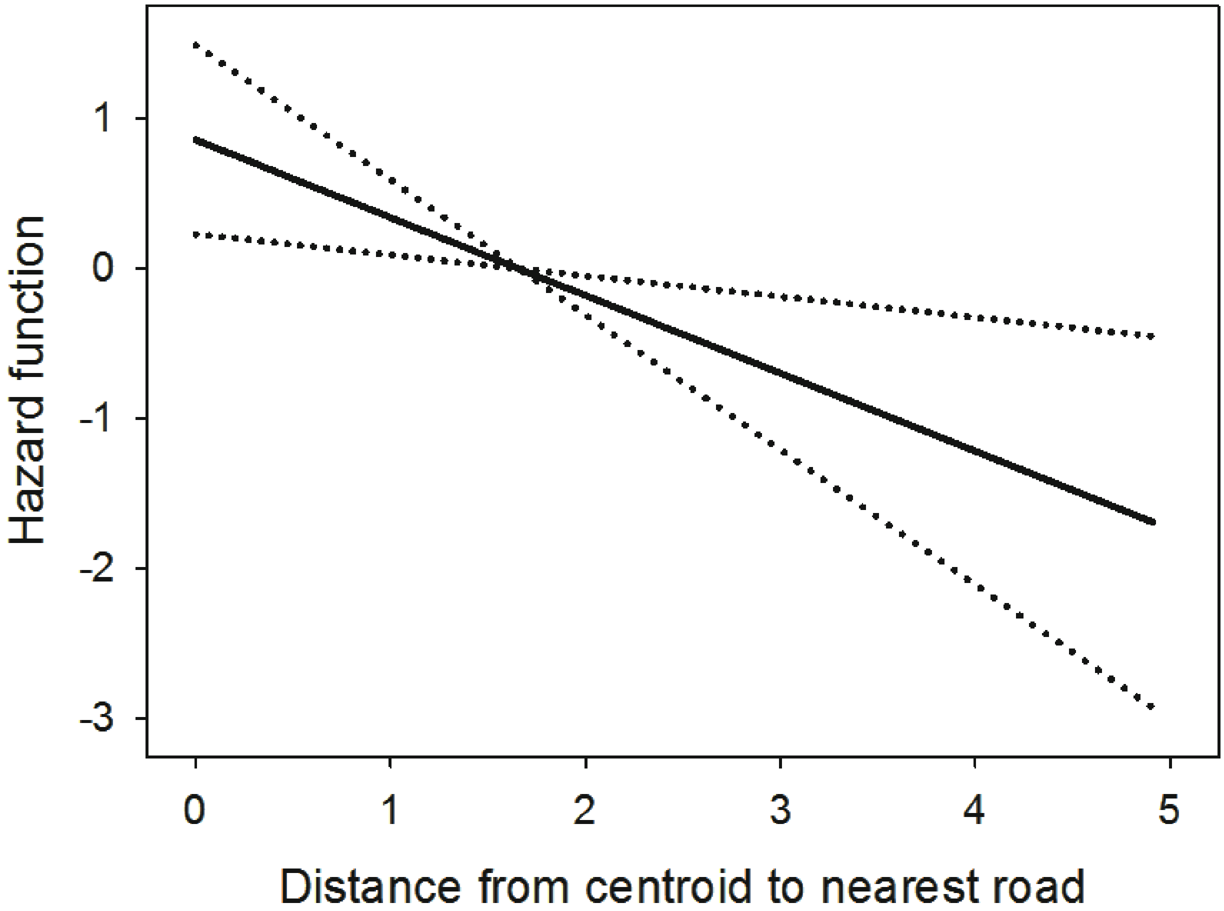


Figure 5.7. Map of carcass recoveries for radio-marked female prairie-chickens, 2011–2013.

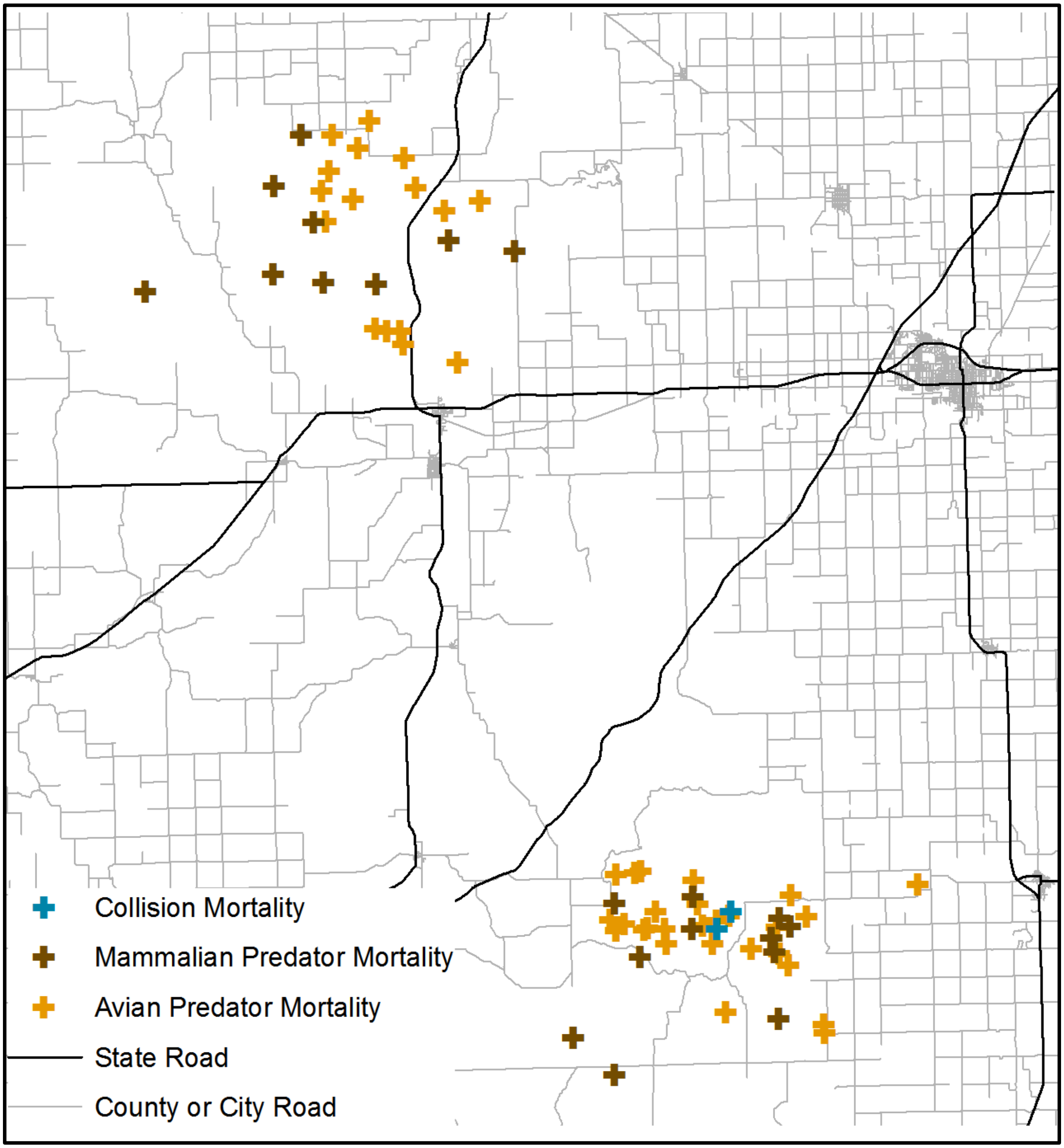


Figure 5.8. Risk of mortality (hazard function, 95% CI) for female Greater Prairie-Chickens in relation to individual β coefficients for years since previous prescribed fire from resource utilization (RUF) models. Parameter estimates were taken from a model with additive effects of years since fire and rangeland management practices at lek of capture ($w_i = 0.04$; black = patch-burn grazing, red = intensive early stocking with annual burning).

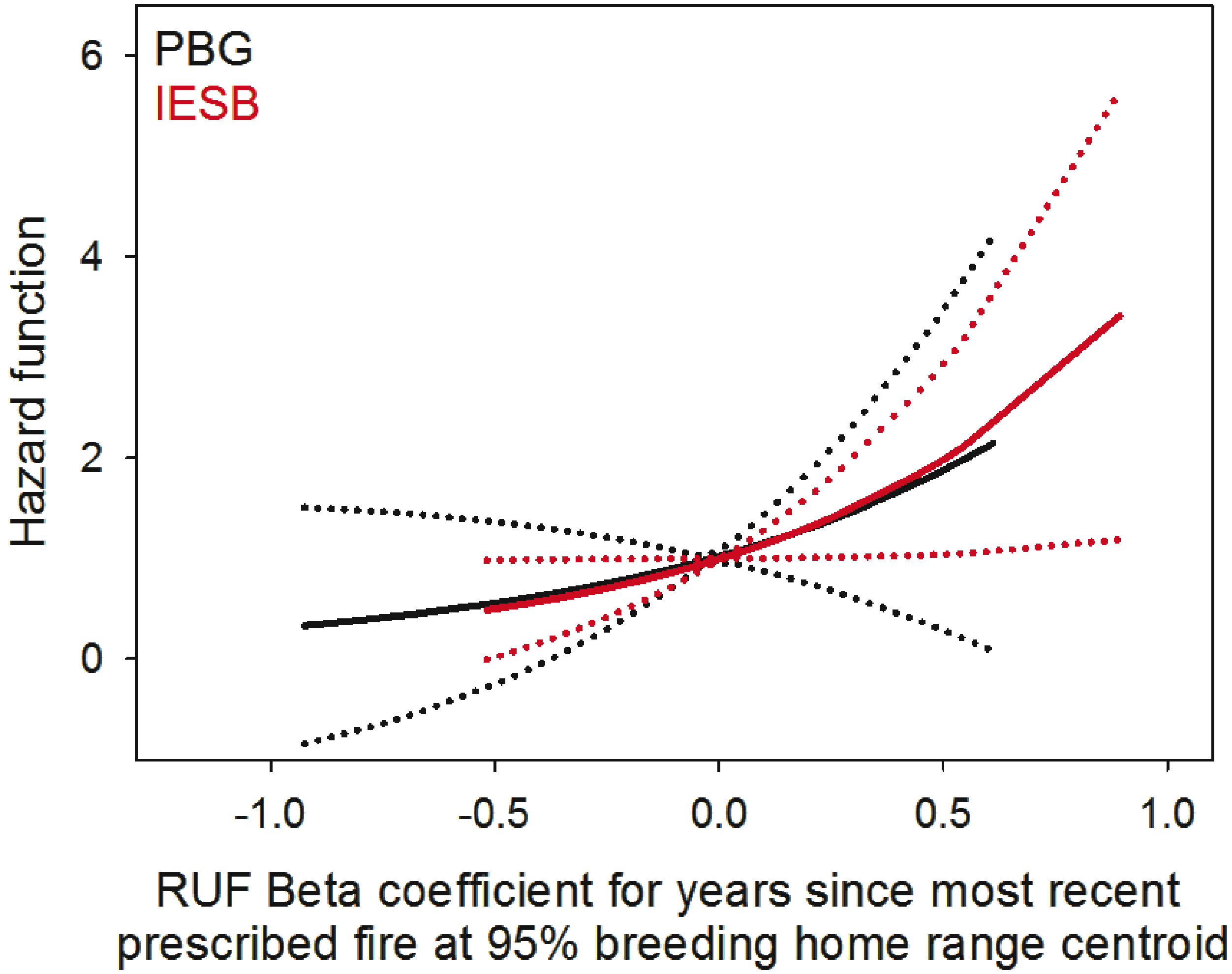


Figure 5.9. Risk of mortality (hazard function, 95% CI) for female Greater Prairie-Chickens in relation to 95% breeding home range size. Parameter estimates were taken from a model with the main effect of home range size (w_i = 0.00).

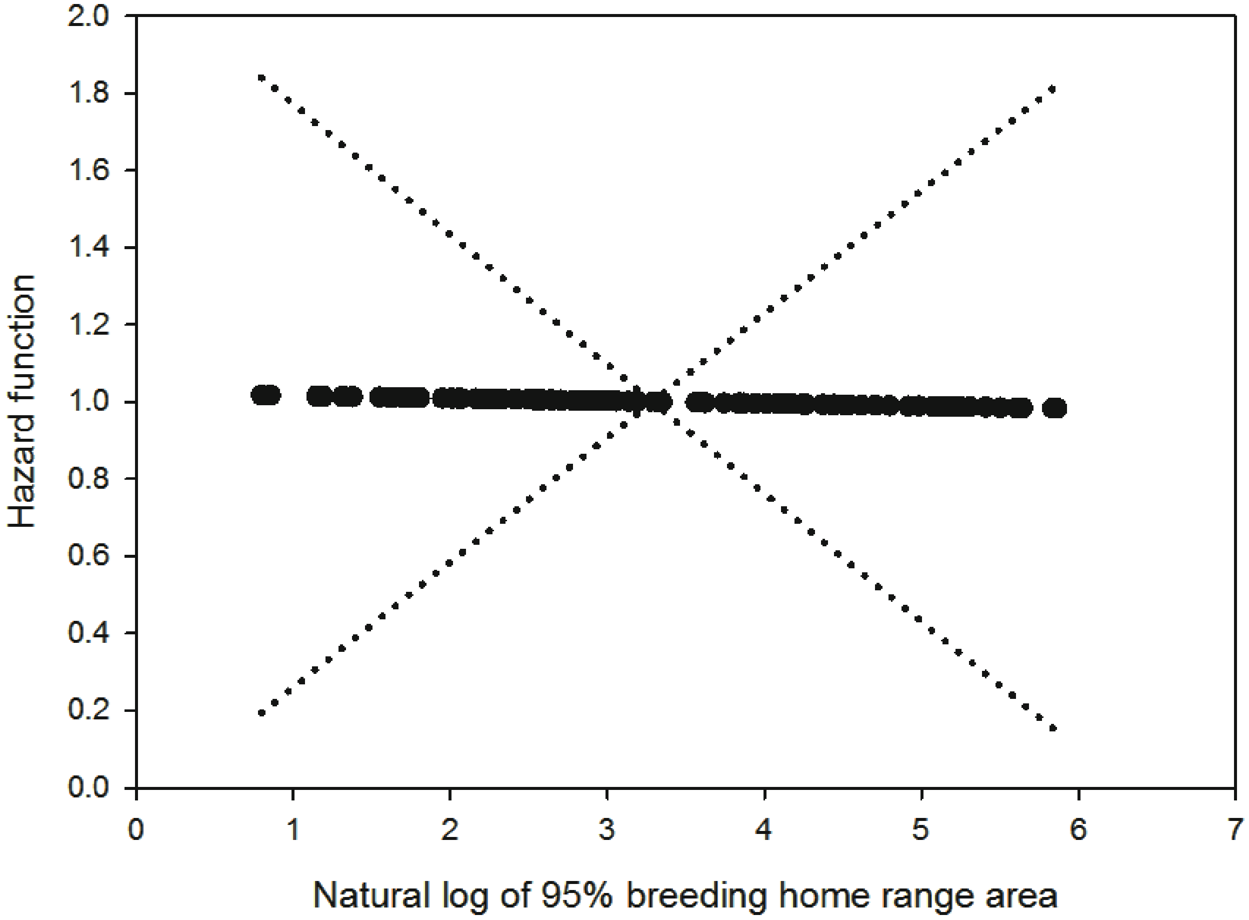


Figure 5.10. Pooled hazard functions for radio-marked female prairie-chickens in eastcentral Kansas, 2011–2013.

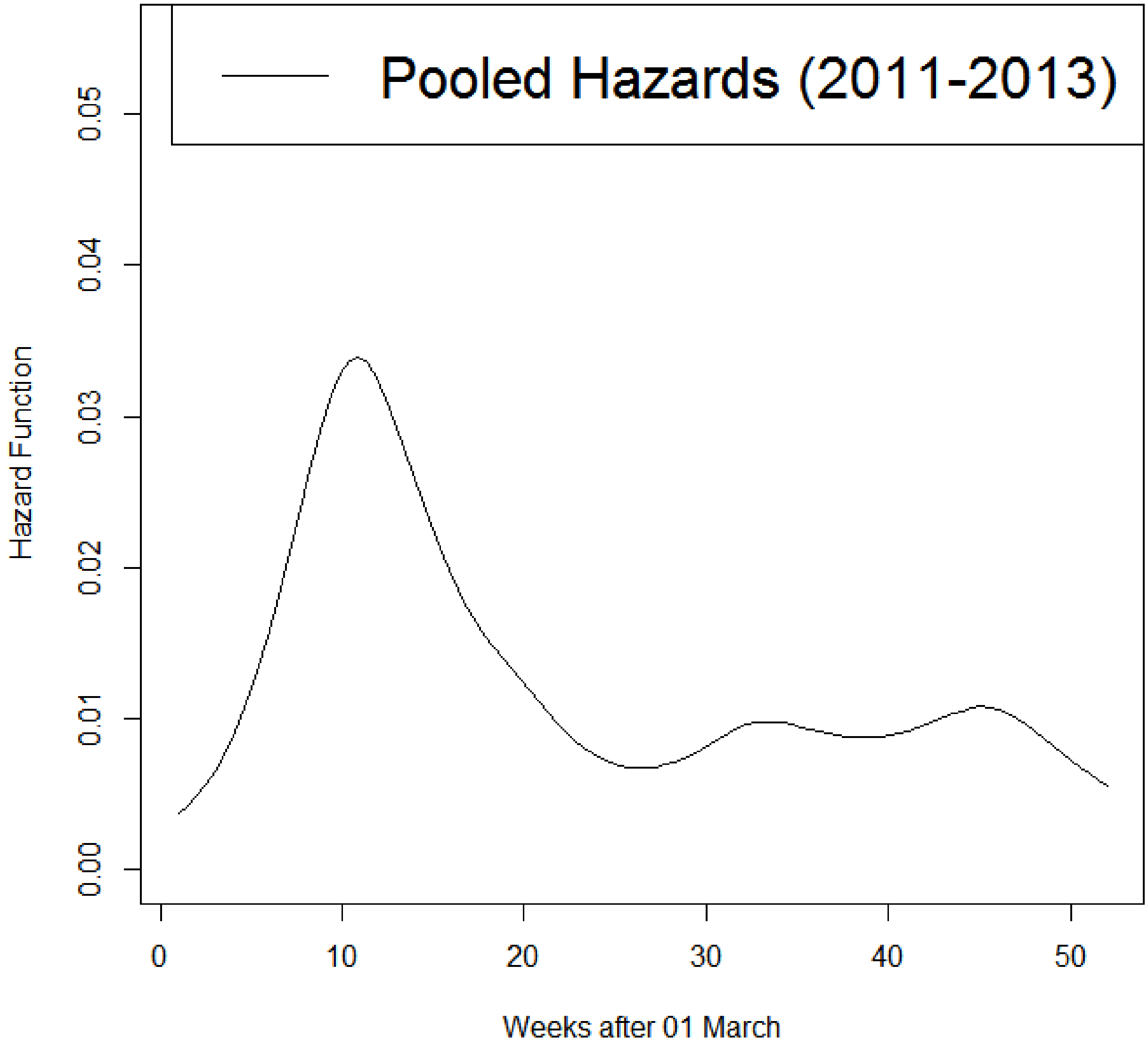


Figure 5.11. Hazard functions for each year of our field study of radio-marked female prairie-chickens in eastcentral Kansas, 2011–2013.

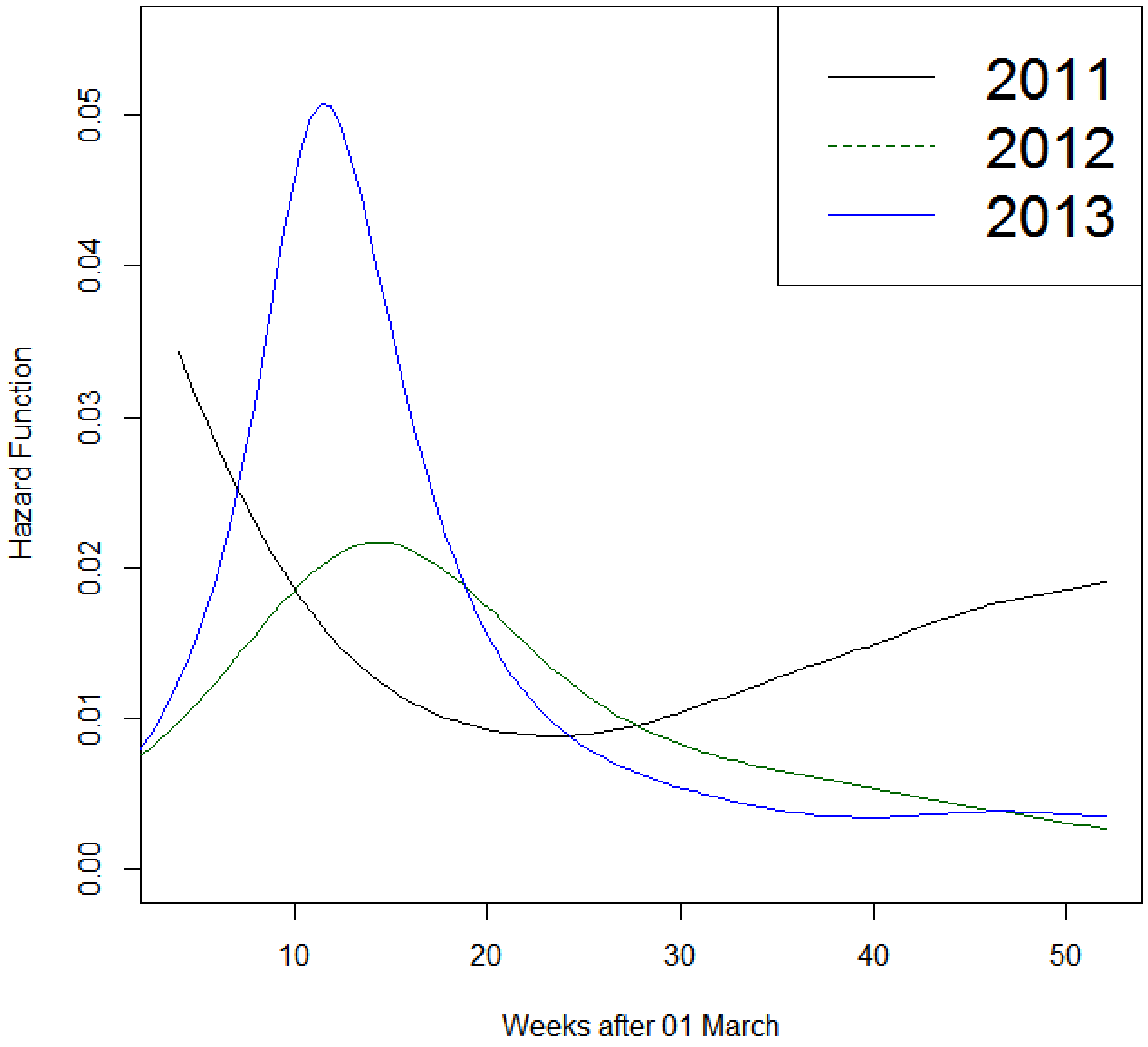
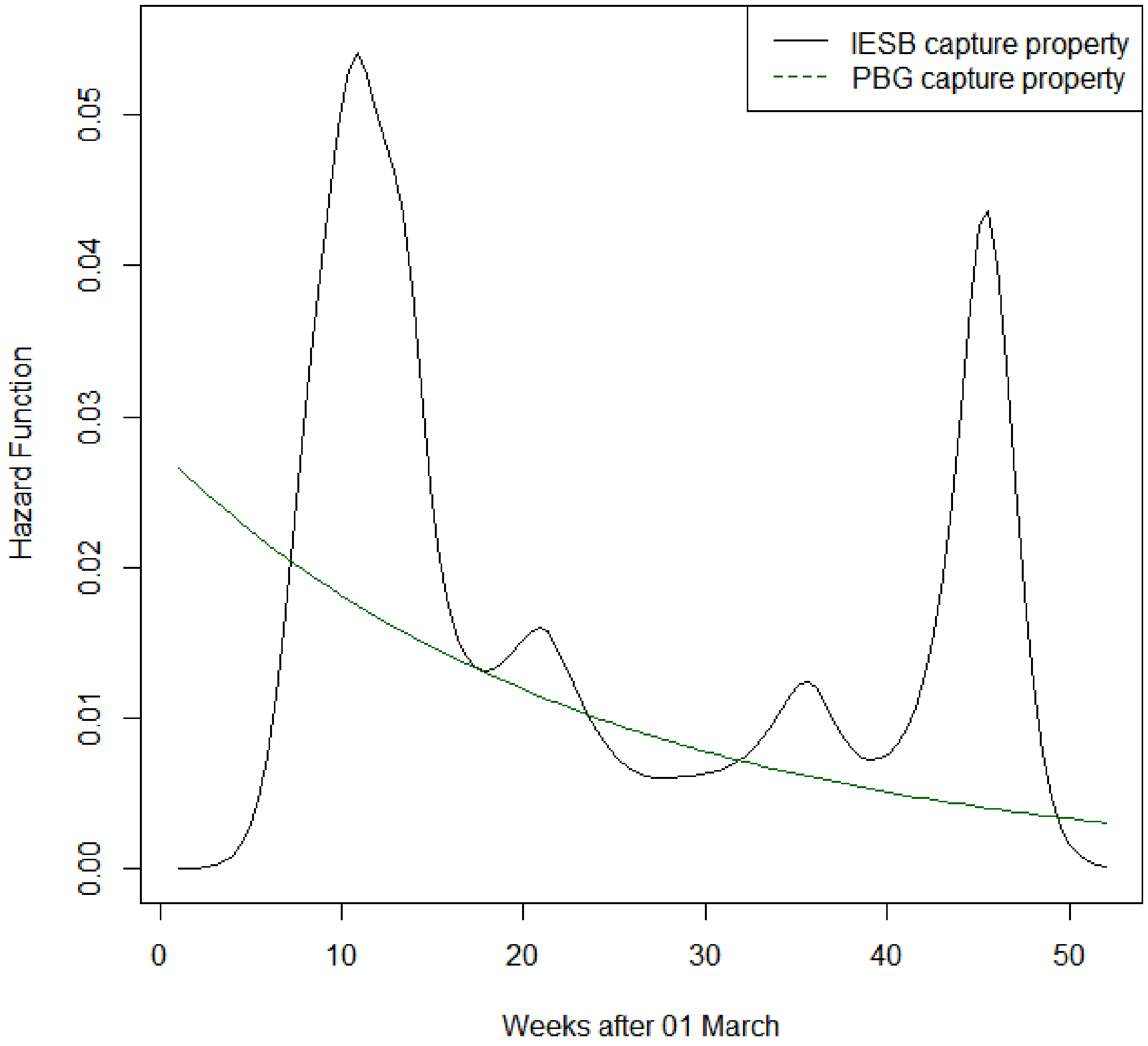


Figure 5.12. Hazard functions for radio-marked female prairie-chickens captured at leks on properties managed with patch-burn grazing (PBG, green) compared to intensive early stocking with annual burning (IESB, black) in eastcentral Kansas, 2011–2013.



Objective 6. ***Impacts on population growth and viability of Greater Prairie-Chickens***

Intensification of rangeland management has coincided with population declines among obligate grassland species in the largest remaining tallgrass prairie in North America, although causes of declines remain unknown. Interactions between grazing and fire frequency on native grasslands influence demography, abundance, diversity, and site occupancy of grassland birds (Powell 2006, 2008, With et al. 2008, McNew et al. 2012b). Rangeland management practices have intensified over the last 30 years, resulting in losses of heterogeneity and residual vegetative cover. These changes represent a reduction in habitat quality for grassland wildlife and have coincided with population declines among obligate grassland species (Robbins et al. 2002, Reinking 2005, Wilgers and Horne 2006, Powell 2008, With et al. 2008).

We modeled population dynamics and conducted sensitivity analyses of demographic data collected for the Greater Prairie-Chickens (*Tympanuchus cupido*), an obligate grassland bird that is an indicator species for tallgrass prairie. Vital rates of prairie-chickens have been studied among populations in fragmented habitats at margins of the extant range of the species (Svedarsky 1988, McKee et al. 1998, Ryan et al. 1998), but few demographic data are available for core populations (Robel 1970, Horak 1985, Augustine and Sandercock 2011, McNew et al. 2012a). Conservation efforts for prairie-chickens require baseline data representing vital rates and their respective influence on population dynamics in native and managed habitats. We estimated demographic rates for prairie-chickens on properties managed with PBG and IESB during our 3-year field study in eastcentral Kansas and synthesized rates in a matrix model to estimate rates of population change specific to rangeland management practices. We used the tools of matrix models to evaluate the influence of vital rates on finite rates of population change.

First, we included components of fecundity and survival based on data from our monitoring effort of radio-marked females. Second, we estimated rangeland management specific rates of population change to assess whether populations were viable ($\lambda \geq 1.0$) or projected to decline ($\lambda \leq 1.0$). Third, we conducted prospective elasticity and variance-scaled sensitivity (VSS) analyses to identify the vital rates predicted to have the greatest influence on λ under different rangeland management regimes. We hypothesized that the finite rate of population change would be negatively affected by reduced cover and habitat quality associated with IESB management regimes.

Demographic Parameters. – We estimated eight demographic parameters for prairie-chickens at our field site. During our 3-year study period, we located nests of 93 of 147 (63%) radio-marked female prairie-chickens. Some nests likely failed before we could find them, and we made a conservative assumption that ≥75% of females made at least one nesting attempt and set *probability of breeding* for both yearlings (c_0) and adults (c) at 0.75 for both PBG and IESB rangeland management treatments.

We modeled the remaining six demographic parameters separately for PBG vs. IESB management regimes. We included four parameters in our calculation of *fecundity* (b), 1) *number of reproductive attempts* per female, 2) *clutch size* per reproductive attempt, 3) *number of fledglings* alive at 25 days post-hatch per reproductive attempt, and 4) *sex ratio* at hatching (assumed to be 1:1). The final two demographic parameters included *yearling* (s_0) and *adult female annual survival* (s) rates estimated from models including the additive effects of age and rangeland management treatment at capture lek.

Population growth and viability. – We synthesized vital rates using two age-classes of female prairie-chickens: yearlings (≥11 months old) and adults (≥22 months old). We created a deterministic matrix model of the form:

$$A = \begin{bmatrix} c_0 b s_0 & c b s_0 \\ s & s \end{bmatrix},$$

where c_0 and c represent the probability of breeding for yearlings and adults, b incorporates four components of fecundity (above), s_0 *and* s represent yearling and adult annual survival estimates. We used separate matrix models for PBG vs. IESB to test for the effects of rangeland management practices on the population dynamics of prairie-chickens.

We used Program R to build matrix models and calculate λ, the finite rate of population change, and the stable age distribution. We also generated a sensitivity matrix to check for effects of absolute changes in matrix elements on λ. We then took the product of the sensitivity matrix and the partial derivatives of the matrix elements with respect to each lower level parameter to calculate elasticity values and check for effects of proportional changes in matrix elements on λ Caswell 2000). We summed lower-level elasticity values across age classes to evaluate the relative effectiveness of management actions for improving λ. Elasticity values can covary with the variance of a vital rate (Pfister 1998), and we used variance-scaled sensitivity (VSS) values to assess vital rate sensitivities (Link and Doherty 2002, McNew et al. 2012a), but we report both standard elasticity values and VSSs for comparison (**Figure 6.1**)

Results. – Regardless of rangeland management practices, rates of productivity were not high enough for female replacement. The finite rate of population change varied by ~40% across rangeland management practices: $\lambda_{PBG} = 0.7270$, $\lambda_{IESB} = 0.4357$ (**Table 6.1**). Population declines were predicted under both sets of rangeland management practices, but PBG dampened the rate of decline compared to IESB. Stable-age distributions were skewed toward adults for under both sets of management practices ($w_Y = 0.15, 0.24$; $w_A = 0.85, 0.76$; **Table 6.1**). Elasticity values and VSSs for lower-level parameters indicated that λ would be most sensitive to future changes in adult survival (s) followed by fecundity (b; **Figure 6.1**).

Implications. – Our study of two types of rangeland management practices showed markedly different demographic rates for PBG compared to IESB. Rangeland management influenced reproductive success and annual survival of adult females, ultimately resulting in a large effect on the predicted rate of population change. Despite high reproductive potential, low rates of adult survival and nest and brood survival resulted in depressed productivity under IESB management practices. Our projections indicated that prairie-chicken populations would decline >50% annually under IESB management practices, a more drastic decline than those reported for other recently studied populations in Kansas (McNew et al. 2012a). Our matrix models are effectively asymmetrical because they include losses to both mortality and emigration, but do not include gains to immigration. Thus, estimates of the finite rate of change < 1 indicate that the prairie chicken populations are not viable with observed demographic rates but could be maintained by immigration from other areas of the Flint Hills.

Our results agree with data from annual lek surveys conducted in the Flint Hills ecoregion by the Kansas Department of Wildlife, Parks & Tourism, which indicate ~50% declines in lek attendance across the Flint Hills over the last three decades (Pitman 2012). Prairie-chicken populations are often found to be most sensitive to changes in fecundity (Wisdom and Mills 1997, Fefferman and Reed 2006, Hagen et al. 2009). However, our results agree with McNew et al. (2012a) that changes in adult survival have the largest influence on rates of population declines regardless of management practices. Management actions aimed at improving adult survival would be most effective at slowing or reversing population declines. In our field study, annual survival of females was highest in recently burned areas away from roads and on properties managed with PBG. Our analyses indicated that both annual survival of adult females and fecundity exerted important influences on the finite rate of population change. In our study, both of these demographic parameters were improved under PBG rangeland management practices.

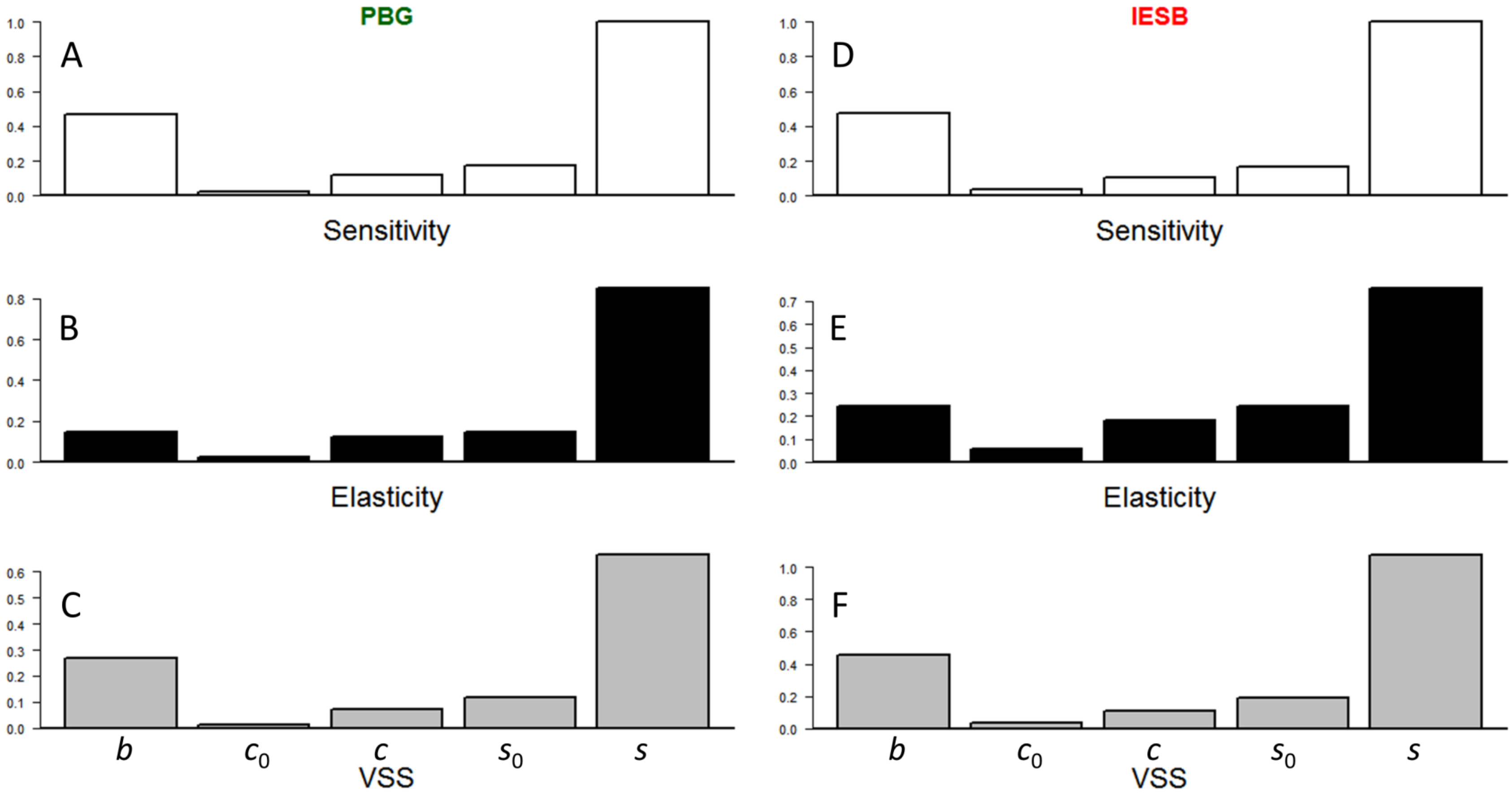
Populations of prairie-chickens at our field study site in eastcentral Kansas were not viable with current rates of population decline, and declines were predicted to be ~40% greater under traditional IESB management compared to PBG. Populations could be maintained by immigration but estimates of this demographic parameter are not currently available. Data from our field study suggest that widespread implementation of PBG and targeted management to improve habitat availability away from roads would slow the rate of population decline, in effect, buying time for further study and management implementation. Our results indicate that PBG management practices have the ability to improve multiple vital rates, simultaneously improving the two most influential rates to population viability at our study site – annual survival of adult females and fecundity.

Table 6.1. Demographic parameters of yearling and adult female Greater Prairie-Chickens from a 3-year study in eastcentral Kansas, 2011–2013. Rangeland management techniques included: PBG = patch-burn grazing, and IESB = intensive early stocking with annual burning.

Parameter	Description	PBG	IESB
c_0	Probability of breeding for yearlings	0.7500	0.7500
c	Probability of breeding for adults	0.7500	0.7500
b	Fecundity = number of female offspring per female*	0.2300	0.2237
	No. reproductive attempts per female	1.2000	1.2388
	Clutch size per reproductive attempt	9.93	10.47
	No. 25-d old young per egg	0.0386	0.0345
	Proportion of females at hatching	0.50	0.50
s_0	Annual survival of yearling females	0.62	0.63
s	Annual survival of adult females	0.62	0.33
w_Y	Proportion of yearlings in stable-age distribution	0.15	0.24
w_A	Proportion of adults in stable-age distribution	0.85	0.76
λ	**Finite rate of population change**	**0.7270**	**0.4357**

*Fecundity = No. reproductive attempts per female × clutch size per reproductive attempt × no. 25-d old young per egg × proportion of females at hatching

Figure 6.1. Sensitivity, elasticity, and variance-scaled sensitivity (VSS) values from a prospective population model based on data from radio-marked yearling and adult female Greater Prairie-Chickens during a 3-year study in eastcentral Kansas, 2011–2013. Values indicate the effect of an absolute (sensitivity) or proportional (elasticity) change in a matrix element on the rate of population change. Parameters included: fecundity (*b*; with four components, number of reproductive attempts per female, clutch size per reproductive attempt, number of 25-d fledglings per egg, and proportion of females at hatch), probability of breeding for yearling (c_0) and adult females (*c*), and annual survival for yearling (s_0) and adult females (*s*). Rangeland management techniques included: PBG = patch-burn grazing (A–C), and IESB (D–F) = intensive early stocking with annual burning.



Literature Cited

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Askins, R. A. 2000. Restoring North America’s birds: lessons from landscape ecology. Yale University Press, New Haven, Connecticut, USA.

Augustine, J.K., and B.K. Sandercock. 2011. Demography of female Greater Prairie-Chickens in unfragmented grasslands in Kansas. Avian Conservation and Ecology-Écologie et Conservation des Oiseaux 6:2.

Bergerud, A. T. 1988. Population ecology of North American grouse. In: A. T. Bergerud and M. W. Gratson, editors, Adaptive strategies and population ecology of northern grouse. University of Minnesota Press Minneaplois, Minnesota, USA. p. 578−648.

Black, S. H., M. Shepherd, and M. Vaughan. 2011. Rangeland Management for Pollinators. Rangelands 33:9-13.

Blomberg, E. J., J. S. Sedinger, D.V. Nonne, and M. T. Atamian. 2013. Annual male lek attendance influences count-based population indices of Greater Sage-Grouse. Journal of Wildlife Management 77:1583–1592.

Bowman, T. J., and R. J. Robel. 1977. Brood break-up, dispersal, mobility, and mortality of juvenile prairie-chickens. Journal of Wildlife Management 41:27–34.

Bradbury, J. W., R. M. Gibson, and I. M. Tsai. 1986. Hotspots and the dispersion of leks. Animal Behaviour 34:1694–1709.

Brennan, L. A., and W. P. Kuvlesky, Jr. 2005. North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management 69: 1-13.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA. p. 1−488.

Busby, W. H., and J. L. Zimmerman. 2001. Kansas breeding bird atlas. University Press of Kansas, Lawrence, Kansas, USA, p. 1−488.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619‒627.

Churchwell, R. T., C. A. Davis, S. D. Fuhlendorf, and D. M. Engle. 2008. Effects of patch burn management on dickcissel nest success in a tallgrass prairie. The Journal of Wildlife Management 72:1596–1604.

Clifton, A. M., and D. G. Krementz. 2006. Estimating numbers of Greater Prairie-Chickens using mark-resight techniques. Journal of Wildlife Management 70:479–484.

Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998. Effects of seasonal fire, bison grazing, and climatic variation on tallgrass prairie vegetation. Plant Ecology 139:235-246.

Coppedge, B. R., S. D. Fuhlendorf, W. C. Harrell, and D. M. Engle. 2008. Avian community response to vegetation and structural features in grasslands managed with fire and grazing. Biological Conservation 141:1196–1203.

Crawley, M. J. 2005. Statistics: an introduction using R. John Wiley & Sons Ltd., Chichester, UK, p. 1−342.

Cummings, D. C., S. D. Fuhlendorf, and D. M. Engle. 2007. Is altering frazing selectivity of invasive forage species with patch burning more effective than herbicide treatments? Rangeland Ecology and Management 60:253−260.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

DelGiudice, G. D., J. Fieberg, M. R. Riggs, M. C. Powell, and W. Pan. 2006. A long-term age-specific survival analysis of female white-tailed deer. Journal of Wildlife Management 70: 1556–1568.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Dugger, K. M., F. Wagner, R. G. Anthony, and G. S. Olson. 2005. The relationship between habitat characteristics and demographic performance of northern spotted owls in southern Oregon. Condor 107:863–878.

Fefferman, N. H., and J. M. Reed. 2006. A vital rate sensitivity analysis for non-stable distributions and short-term planning. Journal of Wildlife Management 70:649−656.

Fox, J. 2002. Cox proportional-hazards regression for survival data. J. Fox, editor, An R and S-plus companion to applied regression, Sage Publications, Inc., Thousand Oaks, California, USA, p. 1−18.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51:625–632.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. L. Jr. 2006. Should heterogeneity be the basis for conservation: Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.

Garshelis, D.L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance, p. 111–164. In L. Boitani and T. K. Fuller (Eds.), Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.

Gregory, A. J., L. B. McNew, T. J. Prebyl, B. K. Sandercock, and S. M. Wisely. 2011. Hierarchical modeling of lek habitats of Greater Prairie-Chickens. Studies in Avian Biology 39:21–32.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2005. Age-specific variation in apparent survival rates of male Lesser Prairie-Chickens. Condor 107:78–86.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2007. Age-specific survival and probable causes of mortality in female Lesser Prairie-Chickens. Journal of Wildlife Management 71:518–525.

Hagen, C. A., Sandercock, B. K., Pitman, J. C., Robel, R. J., and Applegate, R. D. 2009. Spatial variation in Lesser Prairie-Chicken demography: a sensitivity analysis of population dynamics and management alternatives. Journal of Wildlife Management 73:1325–1332.

Hagen, C. A., J. C. Pitman, T. M. Loughin, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2011. Impacts of anthropogenic features on habitat use by Lesser Prairie-Chickens. Studies in Avian Biology 39:63–75.

Herkert, J.R., D.L. Reinking, D.A. Wiedenfield, M. Winter, J.L. Zimmerman, W.E. Jensen, E.J. Finck, R.R. Koford, D.H. Wolfe, S.K. Sherrod, M.A. Jenkins, J. Faaborg and S.K. Robinson. 2002. Effects of prairie fragmentation on the nest success of breeding birds in the Midcontinental United States. Conservation Biology 17: 587-594.

Hepinstall, J. A., J. M. Marzluff, M. S. Handcock, and P. Hurvitz. 2005. Incorporating utilization distributions into the study of resource selection. In: S. Huzurbazar, editor, Resource selection methods and applications. Omnipress, Madison, Wisconsin, USA, p. 2–19.

Hernández, F., F. Hernández, J. A. Arredondo, F. C. Bryant, L. A. Brennan, and R. L. Bingham. 2005. Influence of precipitation on demographics of northern bobwhites in southern Texas. Wildlife Society Bulletin 33:1071–1079.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Robers. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Horak, G. J. 1985. Kansas prairie-chickens. Kansas Fish and Game Commision, Pratt, Kansas, USA.

Johnson, J. A., M. A. Schroeder, and L. A. Robb. 2011. Greater Prairie-Chicken (*Tympanuchus cupido*). In: A. Poole, editor, The Birds of North America Online: Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Kauffman, D. W., G. A. Kauffman, P. A. Fay, J. L. Zimmerman, and E.W. Evans. 1998. Anima l populations and communities. In: A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors, Grass land dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, USA, p. 113–139.

Kertson, B. N., and J. M. Marzluff. 2009. Animal movement, home range, and resource utilization (RUF) analysis in ArcMap 9.3. School of Forest Resources, University of Washington, Seattle, Washington, USA.

Kertson, B. N., and J. M. Marzluff. 2010. Improving studies of resource selection by a greater understanding of resource use. Environmental Conservation 38:391–396.

Kertson, B. N., R. D. Spencer, J. M. Marzluff, J. Hepinstall-Cymerman, and C. E. Grue. 2011. Cougar space use and movements in the wildland-urban landscape of western Washington. Ecological Applications 21:2866–2881.

Knapp A. K., J. M. Briggs, D. C. Harnett, and S. L. Collins. 1998. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, Oxford.

Laake, J. and E. Rexstad. 2008. RMark – an alternative approach to building linear mondels in MARK. In: E. Cooch and G. C. White, editors, Program MARK: A Gentle Introduction, p. C1–C113.

Leopold, A. 1933. Game management. Madison, WI: University of Wisconsin Press, p. 1–520.

Limb, R. F., S. D. Fuhlendorf, D. M. Engle, J. R. Weir, R. D. Elmore, and T. G. Bidwell. 2011. Pyric–Herbivory and Cattle Performance in Grassland Ecosystems. Rangeland Ecology & Management 64:659–663.

Link, W. A. and P. A. Doherty. 2002. Scaling in sensitivity analysis. Ecology 83:3299‒3305.

Lyons, E.K., B. A. Collier, N. J. Silvy, R. R. Lopez, B. E. Toole, R. S. Jones, and S. J. DeMaso. 2009. Breeding and non-breeding survival of Lesser Prairie-Chickens *Tympanuchus pallidicinctus* in Texas, USA. Wildlife Biology 15:89–96.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85:1411–1427.

McKee, G., M. R. Ryan, and L. M.Mechlin. 1998. Predicting Greater Prairie-Chicken nest success from vegetation and landscape characteristics. Journal of Wildlife Management 82:314-321.

McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2012a. Demography of Greater Prairie-Chickens: regional variation in vital rates, sensitivity values, and population dynamics. Journal of Wildlife Management 76:987–1000.

McNew, L. B., T. J. Prebyl, and B. K. Sandercock. 2012b. Effects of rangeland management on the site occupancy dynamics of prairie-chickens in a protected prairie preserve. Journal of Wildlife Management 76:38–47.

McNew, L. B., A. J. Gregory, and B. K. Sandercock. 2013. Spatial heterogeneity in habitat selection: nest site selection by Greater Prairie-Chickens. Journal of Wildlife Management 77:791–801.

McNew, L. B., L. M. Hunt, A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2014. Effects of wind energy development on nesting ecology of Greater Prairie-Chickens in fragmented grasslands. Conservation Biology 28:1089–1099.

Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.

Mohler, R. L., and D. G. Goodin. 2012a. Identifying a suitable combination of classification technique and bandwith(s) for burned area mapping in tallgrass prairie with MODIS imagery. International Journal of Applied Earth Observation and Geoinformation 14:103–111.

Mohler, R. L., and D. G. Goodin. 2012b. Mapping burned areas in the Flint Hills of Kansas and Oklahoma, 2000–2010. Great Plains Research 22:15–25.

Murray, D.L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70:1530–1543.

Niemuth, N. D. 2011. Spatially explicit habitat models for prairie grouse. Studies in Avian Biology 39:3–20.

Patten, M. A., C. L. Pruett, and D. H. Wolfe. 2011. Home range size and movements of Greater Prairie-Chickens. Studies in Avian Biology 39:51–62.

Peterson, M. J., and N. J. Silvy. 1996. Reproductive stages limiting productivity of the endangered Attwater's Prairie-Chicken. Conservation Biology 10:1264–1276.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences of the United States of America 95:213–218.

Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2005. Location and success of Lesser Prairie-Chicken nests in relation to vegetation and human disturbance. Journal of Wildlife Management 69:1259–1269.

Pitman, J. C., J. Kramer, and M. Michener. 2012. Prairie-chicken lek survey – 2012. Pratt, KS: Kansas Department of Wildlife, Parks, and Tourism.

Poiani, K. A., M. D. Merrill, and K. A. Chapman. 2001. Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. Conservation Biology 15:513–522.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. In: L. Boitani, and T. K. Fuller, editors, Research Techniques in Animal Ecology, Columbia University Press, New York, New York, USA, p. 65–110.

Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. Auk 123:183–197.

Powell, A. F. L. A. 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. Journal of Field Ornithology 79:41–52.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. Avoidance behavior by prairie grouse: Implications for wind energy development. Conservation Biology 23:1253–1259.

Rahmig, C. J., W. E. Jensen, and K. A. With. 2008. Grassland bird responses to land management in the largest remaining tallgrass prairie. Conservation Biology 23:420–432.

Reinking, D. L. 2005. Fire regimes and avian responses in the central tallgrass prairie. Studies in Avian Biology 30:116–126.

Rensink, C. B. 2009. Impacts of patch-burn grazing on livestock and vegetation in the tallgrass prairie. Kansas State University, Manhattan, Kansas, USA. p. 1–44.

Robbins, M. B., A. T. Peterson, and M. A. Ortega-Huerta. 2002. Major negative impacts of early intensive cattle stocking on tallgrass prairies: the case of the Greater Prairie-Chicken (*Tympanuchus cupido*). North American Birds 56:239–244.

Robel, R. J., J. N. Briggs, J. J. Cebula, N. J. Silvy, C. E. Viers, and P. G. Watt. 1970. Greater Prairie-Chicken ranges, movements, and habitat usage in Kansas. Journal of Wildlife Management 34:286–306.

Rodgers, R. D. 2008. Prairie-chicken lek survey – 2008. Performance report statewide wildlife research and surveys, May 2008. Kansas Department of Wildlife and Parks, Pratt, KS.

Ryan, M. R., L. W. Burger Jr, and D. P. Jones. 1998. Breeding ecology of Greater Prairie-Chickens (*Tympanuchus cupido*) in relation to prairie landscape configuration. American Midland Naturalist 140:111–121.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6–15.

Sandercock, B. K., E. L. Hewett, K. L. Kosciuch. 2008. Effects of experimental cowbird removals on brood parasitism and nest predation in a grassland songbird. Auk 125:820-830.

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of Willow Ptarmigan. Journal of Animal Ecology 80:244–258.

Sauer, J.R., J.E. Hines, J.E. Fallon, K.L. Pardieck, W.A. Link and D.J. Ziolkowski Jr. 2014. The North American Breeding Bird Survey, Results and Analysis 1966 - 2012. Version 02.19.2014.

Schroeder, M. A. 1991. Movement and lek visitation by female Greater Prairie-Chickens in relation to predictions of Bradburys's female preference hypothesis of lek evolution. Auk 108:896–903.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Smith, E. F., and C. E. Owensby. 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills range. Journal of Range Management 31:14–17.

Steuter, A. A. 1986. Fire behavior and standing crop characteristics on repeated seasonal burns: norhtern mixed prairie. In: A. L. Koonce, editor, Prescribed burning in the Midwest: state of the art. University of Wisonsin, College of Natural Reources, Fire Science Center, Stevens Point, Wisconsin, USA, p. 54–59.

Svedarsky, W. D. 1988. Reproductive ecology of female Greater Prairie-Chickens in Minnesota. In: A. T. Bergerud, and M. W. Gratson, editors, Adapti ve strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, Minnesota, USA, p. 193–239.

Svedarsky, W. D., R. L. Westemeier, R. J. Robel, S. Gough, and J. E. Toepher. 2000. Status and management of the Greater Prairie-Chicken *Tympanuchus cupido pinnatus* in North America. Wildlife Biology 6:277–284.

Swinton, S. M., F. Lupi, G. P. Robertson, and S. K. Hamilton. 2007. Ecosystem services and agriculture: cultivating agricultural ecosystems for diverse benefits. Ecological Economics 64:245–252.

Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. American Midland Naturalist 129:10–18.

Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for Greater Sage-Grouse. Wildlife Society Bulletin 32:56–68.

Westemeier, R. L. 1979. Factors affecting nest success of prairie-chickens in Illinois. Proceedings of the Prairie Grouse Technical Council 13:9–15.

Westemeier, R., J. Braun, S. Simpson, T. Esker, R. Jansen, J. Walk, E. Kershner, J. Bouzat, and K. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. Science 282:1695–1698.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Wiens, J. A. 1997. The emerging role of patchiness in conservation biology. In: S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, editors, The ecological basis for conservation: heterogeneity, ecosystems, and biodiversity. Chapman & Hall, New York, New York, USA, p. 93–107.

Wilgers, D. J. and E. A. Horne. 2006. Effects on different burn regimes on tallgrass prairie herpetofaunal species diversity and community composition in the Flint Hills, Kansas. Journal of Herpetology 40:73–84.

Winder, V. L., McNew, L. B., Gregory, A. J., Hunt, L. M., Wisely, S. M., and Sandercock, B. K. 2014a. Effects of wind energy development on the survival of Greater Prairie-Chickens. Journal of Applied Ecology 51:395–405.

Winder, V. L., McNew, L. B., Gregory, A. J., Hunt, L. M., Wisely, S. M., and Sandercock, B. K. 2014b. Space use by female Greater Prairie-Chickens in response to wind energy development. Ecosphere 5:art3.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management 61:302–312.

With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152–3167.

Wood, S. 2006. Generalized additive models: an introduction with R. London, United Kingdom: Chapman & Hall, p. 1–410.

Worton, B. J. 1989. Kernal methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Zimmerman, J. 1. 1997. Avian community responses to fire, grazing, and drought in the tallgrass prairie. Pages 167-180 In: F. L. Knopf and F. B. Samson, editors, Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York, New York, USA, p. 1–323.