OF MICE AND COYOTES: MAMMALIAN RESPONSES TO RANGELAND
MANAGEMENT PRACTICES IN TALLGRASS PRAIRIE

by

ANDREW MICHAEL RICKETTS

B.S., Kansas State University, 2003

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

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Abstract

Habitat heterogeneity is a key driver of biodiversity in many ecosystems. In native ecosystems, habitat heterogeneity can arise from multiple drivers including nutrients, topoedaphic conditions, and ecological disturbance. Historically, the prairies of North America existed as a heterogeneous mosaic of habitat conditions created by the interaction of fire and grazing by native ungulates. The focus of many grazing systems has been to minimize disturbance caused by grazing by promoting uniform distributions of grazing animals across management units. Patch-burn grazing is an alternative rangeland management practice that has been proposed to restore historical patch dynamics and biodiversity to rangelands by simulating historical disturbance processes. In my dissertation research, I tested the hypothesis that patch-burn grazing restores habitat heterogeneity to rangelands, and that the resulting habitat heterogeneity can promote biodiversity of native wildlife. I focus on responses of small mammals and coyotes to patch-burn grazing to gain a better understanding of wildlife responses to rangeland management, and because grassland mammals are an ecologically important group. My 3.5-year field study of habitat and small mammal responses to rangeland management showed that: 1) patch-burn grazing created greater heterogeneity in vegetative structure and composition of plant functional groups than in positive and negative controls; 2) habitat heterogeneity created by the interaction of fire and grazing increased small mammal richness and diversity compared to a negative control managed for uniform grazing distributions; 3) the interaction of fire and grazing structured small mammal communities in tallgrass prairie; and 4) population dynamic responses of small mammals to fire and grazing disturbance were species-specific. My 3-year study of coyote survival and resource selection revealed that: 1) rangeland management influences resource selection by coyotes in seasons when they depend on small

mammal prey, but not during other seasons; and 2) anthropogenic sources of mortality are important for coyotes at a protected area, even in the absence of harvest. My field results show that restoring the drivers of historical patch dynamics to managed rangelands and publicly held grasslands that are not currently grazed could have profound effects on biodiversity conservation in North America, while continuing to provide ecosystem services to society.

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mammal prey, but not during other seasons; and 2) anthropogenic sources of mortality are important for coyotes at a protected area, even in the absence of harvest. My field results show that restoring the drivers of historical patch dynamics to managed rangelands and publicly held grasslands that are not currently grazed could have profound effects on biodiversity conservation in North America, while continuing to provide ecosystem services to society.

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John Briggs, Doug Goodin, and Aaron Reed have been fantastic committee members, and I am thankful for their patience and support. I must also thank them for encouraging me to halve the number of small mammal trapping grids that I originally proposed… Special thanks go to Aaron who showed me how important it is to provide field opportunities to undergraduate students when I was pursuing my BS at K-State. He and other graduate students at had a large impact on many of us who were fortunate enough to have them as instructors. Although David Haukos was not a committee member, he has been a mentor to me throughout my time as a graduate student at K-State, and I look forward to working with him in the future.

Dedication

To my parents, Mitch and Becky Ricketts, who immersed me in the outdoors and fostered a passion for wildlife in me from a young age; and to my wife Shelly, who has given her time, love, patience, and support to my endeavors.

Thank you

Chapter 1 - Introduction

Habitat heterogeneity is a driver of biodiversity in many ecosystems (Ostfeld et al. 1997; Fuhlendorf et al. 2010). For wildlife to coexist sympatrically, each species may be adapted to take advantage of different niche spaces available in each ecosystem (Hutchinson 1959). In native ecosystems, habitat heterogeneity can arise from multiple drivers including nutrients, topoedaphic conditions, and ecological disturbance (Fuhlendorf and Smiens 1999). In the absence of periodic disturbance, ecosystems tend toward a climax community that will eventually be homogeneous in space and time. Therefore, effects of disturbance from fire, grazing and other ecological processes on habitat structure and composition are often drivers of biodiversity.

Prior to European settlement, the prairies of North America existed as a heterogeneous mosaic of habitat conditions created by the interaction of fire and grazing by native ungulates (Fuhlendorf and Engle 2001). Selective grazing of recently burned areas created intense focal disturbances, while other areas that had not recently burned recovered from previous fire and grazing disturbance. A shifting mosaic of heterogeneous patches at local, regional, and landscape scales provided wildlife inhabiting the prairies a diverse array of habitat conditions. Thus, wildlife native to the prairies have evolved to take advantage of a wide variety of habitat conditions. Vagile animals, such as prairie grouse, require a full spectrum of habitat conditions to complete their annual cycle (Winder et al. 2015), whereas less mobile small mammals have adapted to rely on specific habitat conditions for their entire life (Kaufman et al. 1988).

In the early 20th century, overgrazing for livestock production was a major threat to the integrity of rangeland ecosystems. Accordingly, the focus of the majority of grazing systems has been to minimize the disturbance caused by grazing through promoting uniform grazing distributions within management units (Fuhlendorf et al. 2012). Spatially uniform grazing can be achieved through rotational grazing systems where livestock are moved among different cross-fenced areas of a management unit, or through the even application of prescribed fire to an entire management unit. When similar management strategies that promote uniformity are applied to large spatial areas, habitat conditions in rangeland ecosystems become homogeneous and differ ecologically from the historical patch dynamics that are necessary for the maintenance of biodiversity (Fuhlendorf et al. 2009). The homogenization of rangelands is a critical threat to biodiversity in North America, and private landowners whose livelihood depends on livestock production make a majority of management decisions in this ecosystem (Fuhlendorf and Engle 2001). Therefore, strategies to mitigate biodiversity loss in rangelands must be compatible with livestock production.

Patch-burn grazing is an alternative rangeland management practice that has been proposed to restore historical patch dynamics and biodiversity to rangelands by simulating historical disturbance processes (Fuhlendorf and Engle 2001). Patch-burn grazing is managed with rotational fire and only a portion of a grazing unit is burned each year, instead of the entire grazing unit. Cattle are given access to the entire grazing unit without cross fencing, and stocking densities and livestock performance are comparable to traditional grazing systems such as intensive early stocking or season-long stocking (Winter et al. 2014). Previous studies have shown that patch-burn grazing can restore habitat heterogeneity to rangelands, and benefit

biodiversity of native species of grassland wildlife (Fuhlendorf et al. 2006, Coppedge et al. 2008, Fuhlendorf et al. 2010, Holcomb et al. 2014, Hovick et al. 2014, Augustine and Derner 2015). A majority of previous work has focused on birds, but other sensitive wildlife species are also of interest.

In my dissertation research, I test the hypothesis that patch-burn grazing restores habitat heterogeneity to rangelands, and that the resulting habitat heterogeneity promotes biodiversity of rangeland wildlife. I focus on mammalian responses to patch-burn grazing to gain a better understanding of wildlife responses to rangeland management, and because grassland mammals are an ecologically important group.

In Chapter 2, I compare habitat conditions and small mammal biodiversity in a *patch-burn grazing* treatment versus an annually burned and grazed *negative control*, and an ungrazed *positive control* with a four-year fire return interval. I present strong evidence for the effects of rangeland management on habitat conditions and small mammal community dynamics.

In Chapter 3, I examine population dynamics of seven species of small mammals in the three treatments to gain a more mechanistic understanding of how rangeland management affects small mammal populations. I show that habitat conditions created by rangeland management affect small mammal population dynamics, but that demographic responses differ between generalist and specialist species.

In Chapter 4, I examine coyote resource selection in response to rangeland management, and the seasonal patterns of mortality of coyotes captured at a nature reserve. I report that rangeland management influences resource selection by coyotes, and that anthropogenic mortality is important for coyotes that leave protected areas.

In Chapter 5, I summarize the implications of my research to biodiversity conservation in working landscapes and ecology, and discuss logistical and cultural barriers to implementation of new rangeland management practices on private lands in eastern Kansas.

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Chapter 2 - Patch-burn grazing increases heterogeneity and biodiversity of small mammals in managed rangelands

Abstract

Habitat heterogeneity is a key driver of biodiversity in many ecosystems. Wildlife inhabiting the native prairies of North America evolved in a heterogeneous mosaic of habitat conditions created by fire and grazing by native ungulates. Current rangeland management practices in the tallgrass prairie ecosystem evenly distribute fire and grazing across management units and promote homogeneous habitat conditions. Patch-burn grazing is a rangeland management strategy that seeks to restore heterogeneity to rangelands via fire-grazing interactions. Our 3.5-year study tested the effects of patch-burn grazing on habitat heterogeneity and small mammal community dynamics in the Flint Hills ecoregion of eastern Kansas. To study the ecological effects of patch-burn grazing, we sampled habitat conditions and the small mammal community. We assessed habitat conditions once each growing season in a *negative control* that was annually burned and grazed, a *positive control* that was burned every four years and ungrazed, and within each of three units of a *patch-burn grazing* experiment managed with rotational fire. Habitat conditions were significantly different among treatments, and a principal components analysis showed that the patch-burn grazing treatment had higher canopy cover of forbs and habitat heterogeneity than our two control units. To sample the small mammal community, we conducted monthly live trapping of small mammals on two randomly located trap grids in each of our two controls and three units of our patch-burn grazing experiment. Small mammal diversity was significantly higher in the patch-burn grazing treatment and in the positive control, versus the negative control. Moreover, a canonical correspondence analysis showed that a fire-grazing interaction was the major driver structuring small mammal communities. Patch-burn

grazing is an effective strategy for restoring heterogeneity to vegetative structure and composition, and can increase biodiversity of small mammals in managed rangelands in the tallgrass prairie ecosystem.

Introduction

Habitat heterogeneity is a key driver of biodiversity (MacArthur and MacArthur 1961, Lack 1969, Ostfeld et al. 1997, Fuhlendorf et al. 2010). In native ecosystems, habitat heterogeneity can arise from multiple drivers including nutrients, topoedaphic conditions, and disturbance (Fuhlendorf and Smiens 1999). The native prairies of North America evolved under pyric herbivory - a fire-grazing interaction where large ungulates preferentially graze areas that have recently burned (Fuhlendorf et al. 2009). Patches recovering from fire or grazing disturbance accumulate residual plant litter over multiple growing seasons, which reduces grazing intensity but increases fuel load and the probability that a patch will burn again and restart the cycle (Fuhlendorf and Engle 2001, 2004). Patches in different states of recovery from fire and grazing across the landscape differ in vegetative composition and structure, and the resulting mosaic can provide habitat heterogeneity and promote biodiversity among native species of wildlife (Fuhlendorf and Engle 2004, Sandercock et al. 2015).

The tallgrass prairie ecosystem once covered ~67 million ha in the United States, but now has been reduced by more than 96 percent (Samson and Knopf 1994, Deluca and Zabinski 2011). The Flint Hills ecoregion of Kansas and Oklahoma contains the largest remaining area of native tallgrass prairie in North America (Knapp and Seastedt 1998). The ecoregion supports an economically important grazing industry, and >95% of the area is privately owned (Hickman et al. 2004, With et al. 2008). Therefore, current rangeland management practices determine the

quality of prairie habitat available to the native fauna (Fuhlendorf and Engle 2001, 2004, Churchwell et al. 2008). Common rangeland management practices in the Flint Hills include prescribed burning in the spring, followed by intensive early stocking with steers, or season-long stocking with cow/calf pairs (Wilds and Nellis 1988, With et al. 2008). Prescribed fire is widely used and up to 48% of the area of the Flint Hills may be burned in a given year, causing air quality issues for nearby urban centers (KDHE 2010, Mohler and Goodin 2012). Spring burns are typically applied to an entire pasture, which evenly distributes livestock and grazing intensity across the vegetation in a grazing unit (Fuhlendorf and Engle 2001). Annual burning coupled with intensive grazing prevents accumulation of residual plant material, so that vegetative cover is limited to the plant biomass that exceeds grazer utilization. Current rangeland management practices lead to homogeneity of structure in grassland ecosystems, with a limited number of functional niches for native species, leading to negative impacts on plant and animal biodiversity (Coppedge et al. 1998, 2008, Fuhlendorf et al. 2012).

Patch-burn grazing is an alternative rangeland management practice that has been proposed to employ pyric herbivory to mimic historical disturbance patterns that increase landscape heterogeneity (Fuhlendorf and Engle 2001). Patch-burn grazing is managed with rotational fire and only a portion of a grazing unit is burned each year, instead of the entire grazing unit. Cattle are given access to the entire grazing unit without cross fencing, and stocking densities are comparable to traditional grazing systems such as intensive early stocking or season-long stocking. Patch-burn grazing creates diverse microhabitats needed to fulfill the life cycles of grassland animals, such as the dense litter layer preferred by some small mammal species and vegetative cover needed for concealment by ground-nesting birds (Clark and Kaufman 1991,

McNew et al. 2015, Sandercock et al. 2015). Patch-burn grazing is not widely used on private

lands, but has the potential to improve biodiversity of grassland invertebrates (Engle et al. 2008),

herpetofauna (Wilgers and Horne 2006), birds (Fuhlendorf et al. 2006, Coppedge et al. 2008,

Holcomb et al. 2014, Hovick et al. 2014, Augustine and Derner 2015), and small mammals

(Fuhlendorf et al. 2010).

Small mammals are an ecologically important group that impact ecosystems in various ways.

Rodents and shrews are facilitators of ecosystem processes through their burrowing activity and

nitrogen deposition (Laundre 1993, Ross et al. 2007), important prey items for mesocarnivores

(Sperry 1941, Fitcher 1955, Brillhart and Kaufman 1994, Brillhart and Kaufman 1995), raptors

(Fitch et al. 1946, Huebschman et al. 2000), and snakes (Trauth and McAllister 1995, Colston et

al. 2010), and can influence plant diversity through granivory or herbivory (Howe and Brown

2000, Reed et al. 2004, Ross et al. 2007, Bricker et al. 2010, Maron et al. 2012). Moreover,

small mammals are short-lived species with high fecundity and short generation times that are

likely to respond quickly to changes in environmental conditions (Reed et al. 2007). Therefore,

small mammals are likely to be a useful indicator for the effects of rangeland management

strategies on biodiversity.

Our goals for this field study were two-fold. First, we tested the effects of patch-burn grazing on

habitat conditions in the tallgrass prairie of the northern Flint Hills. Second, we tested the

potential effects of patch-burning on richness, diversity and community structure of small

mammals in the northern Flint Hills. We predicted that patch-burn grazing would increase

heterogeneity in vegetative composition and structure in tallgrass prairie, and that greater habitat heterogeneity should increase species richness and diversity of the small mammal community.

Methods

Study Site

Our research project was conducted at the Konza Prairie Biological Station (hereafter, Konza Prairie), a 3,487 hectare prairie preserve in the Flint Hills ecoregion of northeast Kansas. Konza Prairie is a core Long-Term Ecological Research (LTER) site funded by the National Science Foundation. The biological station is a landscape-level fire and grazing experiment that is divided into >60 experimental units, with replicated units that receive different combinations of prescribed fire and grazing treatments (Fig. 2.1). Native warm season grasses such as big bluestem (*Andropogon gerardii*), indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), and switchgrass (*Panicum virgatum*) dominate the plant community at Konza Prairie. Forbs are diverse, but dominant species include goldenrod (*Solidago* spp.), Baldwin's ironweed (*Vernonia baldwinii*), leadplant (*Amorpha canescens*), and round-head bush clover (*Lespedeza capitata*). Common woody shrubs include: rough-leaf dogwood (*Cornus drummondii*), wild plum (*Prunus americana*), smooth sumac (*Rhus glabra*), fragrant sumac (*R. aromatica*), inland ceanothus (*Ceanothus herbaceus*), and buckbrush (*Symphoricarpos orbiculatus*, Towne 2002).

A large-scale *patch-burn grazing* experiment (PBG) was initiated in 2010, and includes roughly the eastern third of the biological station (Fig. 2.1). The PBG replicates were sub-divided into three patches, with one patch being burned each year on a rotational basis. Cattle had access to

the entire management unit without cross fencing. We included an annually burned and grazed treatment as a *negative control* (ABG), and an ungrazed treatment that was burned every four years as a *positive control* (4BN). The ABG treatment was selected as a negative control, because it is a management strategy that seeks to uniformly distribute grazing disturbance across management units through the application of prescribed fire across the entire management unit. Moreover, we expected the ABG treatment to contain a reduced small mammal community dominated by disturbance positive species (Clark et al. 1989). We selected the 4BN treatment as a positive control, because previous research at Konza Prairie indicated that ungrazed sites not recently burned would likely contain more disturbance negative species (Clark et al. 1989, Rehmeier et al. 2005). Moreover, the 4BN treatment was ungrazed but the 4-year fire-return interval was comparable to the 3-year fire-return interval in our PBG. PBG and ABG sites were stocked with cow-calf pairs at a density of one pair per 3.24 ha for a 5-month grazing season from early May to early October each year. Patch size of units within the PBG treatment was 48.7 to 102.4 ha, and ABG and 4BN treatments were 93.8 and 54.5 ha, respectively.

Habitat Composition and Structure

We conducted habitat sampling in June and July of 2011 to 2014, including two drought years (2011-12). We sampled habitat conditions during the mid-growing season, after cattle had reduced standing biomass in the grazed treatments. Habitat measurements were recorded at five points along eight 300-m transects in the grazed and ungrazed controls, as well as in each of patch of the PBG treatment. We quantified percent canopy cover of three major plant functional groups (grasses and sedges combined, broad-leaf forbs, and woody shrubs), as well as percent cover of bare ground and dead plant litter with a 25 x 50 cm Daubenmire frame (Daubenmire

1959). We measured litter depth to the nearest 0.5 cm in the lower left corner of the Daubenmire

frame. Visual obstruction readings (VOR) were measured using a standard Robel pole with

thirteen 1-dm increments (Robel et al. 1970). At each sample point along each transect, we

recorded visual obstruction at a distance of 4 m from the Robel pole and at a height of 1 m in

each cardinal direction from the pole, for a total of four visual obstruction readings per point.

We measured percent canopy cover of habitat variables at three distances (0, 2, and 4 m) in each

cardinal direction from the Robel pole, for a total of 12 measurements of percent cover at each

point along each transect. We averaged the 12 values to obtain a single overall measurement of

each habitat variable per point. Our total sample size of points for each treatment and sub-

treatment was 160 points. A few points were censored due to observer errors, and our total

sample sizes for habitat measurements over the four growing seasons ranged from 140-150

points per treatment.

Small Mammal Diversity

We established two trap grids for sampling small mammal communities in each of the three PBG

patches and two controls, for a total of ten grids (Fig. 2.1). Grid locations were selected at

random, but subject to two constraints. To maintain independence among trap grids, grids were

separated by at least 200 m, which corresponds to twice the length of the longest published home

range axis for deer mice (*Peromyscus maniculatus*), the most abundant species of small mammal

encountered in native prairie (Douglass et al. 2006, Yarnell et al. 2007). Trap grids were also

located at least 100 m from unit boundaries to avoid potential boundary effects, and >50 m from

permanent or regularly flowing water to avoid flooding of traps during runoff from

thunderstorms (Konza LTER datasets: GIS210 and GIS211).

Each trap grid was a five-by-five square design with 25 stations and 20 m spacing between adjacent trap stations for a total area of 0.64 ha. Two extra-large Sherman live traps were set at each trap station for a total of 50 traps per grid (Model LNG 12, H.B. Sherman Trap Company, Tallahassee, FL, USA). Traps were baited with a mixture of peanut butter and rolled oats, and each trap was provisioned with polyester fiberfill to keep animals warm during October to May (Kaufman et al. 1988). To reduce heat stress to diurnal mammals, wooden A-frame structures (hereafter, trap shelters) were placed over traps for shading (Kaufman and Kaufman 1989). Trap shelters were left in place all year for weathering and to minimize potential neophobic responses of small mammals to trap stations. Our trap and bait combination effectively sampled a wide suite of the small mammal community at our site, and we captured animals ranging in mass from least shrews (*Cryptotis parva*; 3 g) up to subadult eastern cottontail rabbits (*Sylvilagus floridanus*; 400+ g).

During our 3.5-year study from June 2011 to December 2014, small mammals were trapped for three consecutive nights each month at ten trapping grids in the PBG treatment, and ABG and 4BN controls. We marked small mammals with passive integrated transponders (PIT tags hereafter; Model AB10320, FDX-B 7 x 1.35 mm, Loligo Systems, Tjele, Denmark; or "Skinny" FDX-B 8 x 1.4 mm, Oregon RFID, Portland, Oregon USA), and read tags with a handheld reader (Model APR 350 FDX/HDX Reader, Agrident, Manassas, VA, USA; or DataTracer FDX/HDX Reader, Oregon RFID, Portland, Oregon, USA). PIT tags were injected subcutaneously under loose skin at the nape, and massaged away from the insertion site to ensure tag retention. To obtain an estimate of PIT tag retention, 28% of the rodents were tagged with numbered monel

ear tags (model 1005-1, National Band and Tag Company, Newport, Kentucky, USA). PIT tag

losses were rare (<1%) and no corrections for tag loss were needed (A.M. Ricketts, *unpublished*

data). All procedures were approved by the Kansas State University Institutional Animal Care

and Use Committee (protocols 3034 and 3443), and conducted under state wildlife permits from

Kansas Department of Wildlife, Parks, and Tourism. Trap grids were sampled in 9 of 12 months

per year with some trapping sessions missing due to inclement winter weather, or unpredictable

winds during prescribed burns in March.

Statistical Analyses

Habitat, Species Richness, and Diversity

All statistical analyses were conducted in R (version 3.2.2, R Core Team 2015). We used

functions in the base packages to test for differences among fire and grazing treatments using

ANOVA or MANOVA. If a test statistic was significant, we made pairwise comparisons among

treatments and years using post hoc Tukey tests. Additionally, we conducted a principal

components analysis (PCA) on our scaled habitat data to examine relationships in habitat

structure and composition among treatments. We opted to exclude percent cover of litter and

shrubs from our PCA. Canopy cover of litter underestimates the amount of litter present,

because standing vegetation obscures litter from above. We retained litter depth as a structural

habitat component needed by some small mammals. Shrub cover was removed from the habitat

dataset for the PCA, because we were primarily interested in the effects of PBG on grassland

habitat, and shrubs were a minor habitat component in all treatments (<8%), except 4BN

(~19%).

Species Richness and Diversity

We tested for differences in the number of species of small mammals (hereafter, species richness) encountered in each treatment during each biological year. Biological years were defined as the first trapping session after a spring burn until the last trapping session prior to a burn the following spring. Treatment watersheds were usually burned during March, so the biological year of our study period ran from April to the following March. We used biological years instead of calendar years because spring fires drastically alter habitat conditions in tallgrass prairie, and effectively reset the community dynamics of small mammals at the start of the growing season (Clark and Kaufman 1990). We calculated the Shannon diversity index (hereafter, species diversity) for each grid per biological year. Here, we used the total number of captures of each species per 100 trap-nights and used the "diversityresult" function in the BiodiversityR package of R (Kindt and Coe 2005). We then used model selection based on Akaike Information Criterion corrected for small sample size (AIC_c) to identify the ANOVA models that best fit our data for species richness and diversity. Candidate model sets for species richness and diversity included the effects of state, treatment, biological year, a constant model, and models with the additive (+) or interactive (×) effects. *State* models compared five treatments: ABG, PB0, PB1, PB2, and 4BN, where numbers following PB indicate time-since fire for a given patch. *Treatment* models pooled the three PBG patches and compared three treatments: ABG, PBG, and 4BN. In preliminary analyses, we tested for but found no evidence for grid effects within treatments and we treated replicate grids as independent samples for further analyses (A. M. Ricketts, *unpublished data*).

To investigate the relationship between community dynamics of small mammals and our three treatments, we conducted a canonical correspondence analysis (CCA) on the number of captures per 100 trap-nights (CPUE) data for each species using the vegan package of R (Oksanen et al. 2015). The small mammal data were constrained by four explanatory variables: treatment, year of study, time-since fire (years), and grazing treatment (grazed or ungrazed). We did not test for the effects of state in the CCA, because state and time-since fire were confounded in our PBG treatment. Prior to conducting the CCA, we standardized our CPUE data for trapping grids so that row totals in the community matrix were equal to 1 with the "total" standardization in the function "decostand" in R package vegan, and then further standardized the data by dividing values for each species by the highest value in the community matrix for that species with the "max" standardization of function "decostand" in R package vegan. Dominant species can drive ordination analyses, especially in small communities with few species (ter Braak 1994). Our scaling procedure was a reverse Wisconsin double standardization, and effectively reduced the influence of dominant species on the ordination (Holland and Patzkowsky 2004). Variance inflation factors for all explanatory variables were less than two, so there was no need to exclude any variables from our CCA during model selection. We identified the CCA model that best fit our data using stepwise AIC_c model selection. Last, we used variance partitioning to determine the amount of variation in the small mammal community that was explained by each explanatory variable retained in the top CCA model (function "varpart", R package vegan).

Results

Habitat Responses

Across the four years of our study, habitat conditions differed significantly among the negative

control (ABG), patch-burn grazing treatments (PBG), and positive control (4BN) in June and

July (Wilk's Lambda = 0.27, $F_{4, 710}$ = 39.2, $p < 0.001$). Canopy cover of grass was significantly

lower in the year-of-fire patch than the other treatments and increased with time-since fire within

the PBG treatment. The 4BN treatment had significantly lower grass cover than the ABG

treatment ($F_{4, 710}$ = 25.1, $p < 0.001$; Fig. 2.2A). Forb cover was highest in the 1-year-since-fire

patch of the PBG treatment, and lowest in the 4BN treatment ($F_{4, 710}$ = 38.5, $p < 0.001$; Fig.

2.2B). Shrub cover was low overall and less than 20% of all treatment areas, but was highest in

the 4BN treatment ($F_{4, 710}$ = 36.2, $p < 0.001$; Fig. 2.2C). Our 4BN treatment was established in

1980, and shrub cover in this unit was relatively high at the beginning of our study in 2011

(>16%). Bare ground decreased with time-since-fire, and was significantly different among each

treatment and subtreatment ($F_{4, 710}$ = 133.2, $p < 0.001$; Fig. 2.2D). Both litter depth and VOR

increased with time-since-fire within PBG, and were highest in the 4BN treatment ($F_{4, 710}$ =

129.9, $p < 0.001$, Fig. 2.2E; and $F_{4, 710}$ = 36.6, $p < 0.001$, Fig. 2.2F).

Our PCA revealed substantial heterogeneity in habitat structure and composition among patches

within PBG, and each treatment had a distinct habitat structure and composition (Fig. 2.3). PCA

axes 1 and 2 had eigenvalues of 1.95 and 1.25, and explained 39% and 25% of the variation in

our habitat data, respectively. Loadings of variables on PCA axis 1 were ranked: percent cover

of bare ground (+0.62), litter depth (-0.56), and visual obstruction reading (-0.50). For PCA axis

2, the most important variables were percent cover of forbs (+0.74) and grass (-0.54). PCA axis

1 was associated with differences in habitat structure, whereas PCA axis 2 was associated with differences in habitat composition.

Small Mammal Responses

From June 2011 to December 2014, we captured 1,903 unique individuals of 11 species of small mammals, for a total of 6,830 handling events during 52,500 trap-nights of sampling effort (Table 2.1). Our top ANOVA for species richness was a main effects model with the effects of treatment ($F_{2, 34} = 3.7$, $p = 0.04$) and year ($F_{3, 34} = 9.7$, $p < 0.001$, Table 2.2). Treatment 4BN had significantly higher species richness at 7.5 species per grid per year than treatment ABG at ~5.5 species per grid per year (Fig. 2.4A), and 2013 and 2014 had significantly higher richness across all treatments than 2011 and 2012. Our top ANOVA for Shannon Diversity Index was a main effects model with the effects of state ($F_{4, 32} = 19.2$, $p < 0.001$) and year ($F_{3, 32} = 9.6$, $p < 0.001$, Table 2.3). Averaged across four years and two grids per treatment, species diversity was lowest in the ABG treatment at 0.5, and increased from 0.8 in PB0 to 1.3 in PB2, and to 1.2 in treatment 4BN (Fig. 2.4D). Diversity was significantly lower in the drought year of 2012 (0.7) than the other three years of our study (0.9-1.2).

Stepwise AIC_c model selection indicated that our top CCA model for describing our small mammal communities included the effects of time-since fire, grazing treatment, and year. Collectively, these three factors explained 47.6% of the variation in our small mammal community data. Our top CCA model produced five axes, and permutation tests indicated that the first four CCA axes explained significant variation (Table 2.4). CCA axes 1 and 2 had eigenvalues of 0.31 and 0.21, and explained 18.4% and 12.8% of the variation in small mammal

communities, respectively (Fig. 2.5). CCA axes 3 and 4 each explained less than 10% of the variation in the small mammal communities, and we did not consider these axes further (Table 2.4). Factor loadings indicated that CCA axis 1 was strongly associated with time-since fire and grazing treatment, but axis 2 was primarily associated with year effects (Fig. 2.5). Species with low scores for CCA axis 1 were associated with high disturbance (e.g., deer mice [pema] and thirteen-lined ground squirrels [ictr]), whereas species with high axis 1 scores were associated with longer time-since fire and low grazing pressure (e.g., hispid cotton rats [sihi]), or woody vegetation (e.g., eastern woodrats [nefl] and white-footed mice [pele]). Variance partitioning indicated that year effects, grazing activity, and time-since fire accounted for 17%, 15%, and 9% of the variation in the composition of our small mammal communities, respectively.

Discussion

Our 3.5-year field project is one of the first field studies to examine the effects of patch-burn grazing on the community structure of small mammals, and our work resulted in three major findings. First, patch-burn grazing created greater heterogeneity in vegetative structure and composition of plant functional groups, that was absent from the more homogeneous conditions in a negative control that was annually burned and grazed, and a positive control that was ungrazed with a 4-year fire return interval. Second, habitat heterogeneity created by the interaction of fire and grazing had positive effects on both biodiversity and community structure of small mammals. Species richness and diversity were high in the patch-burn grazed treatment and comparable to our positive control. Last, our canonical correspondence analysis showed that a large ecological niche was created by the patch-burn grazed treatment, and the niche

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encompassed the annually burned and grazed treatment, but was separate from an ungrazed treatment with a four-year fire return interval.

Our finding that patch-burn grazing increased habitat heterogeneity compared to the positive and negative controls was consistent with our predictions for tallgrass prairie and with previous work in Oklahoma (Fuhlendorf and Engle 2004). However, it is remarkable that patterns of heterogeneity created by patch-burn grazing were consistent among years, even when 2 of 4 growing seasons during our study experienced drought conditions (2011 and 2012). The consistency of habitat responses in a 2-year drought demonstrates that PBG can be an effective management strategy for creating habitat heterogeneity in the tallgrass prairie, even under adverse climatic conditions. Rangeland management strategies that restore heterogeneity to rangelands can also help to stabilize cattle performance during drought years (Allred et al. 2014).

The results of our gradient analysis showed that fire-grazing interactions were a key driver structuring small mammal communities in the tallgrass prairie of the northern Flint Hills. Annually burned and grazed prairie contained a small mammal community with fewer species that was dominated by generalist species such as the deer mouse. In contrast, tallgrass prairie managed with pyric herbivory contained a small mammal community that encompassed the community in the ABG treatment and a larger niche based on CCA site scores in multivariate space. In the tallgrass prairie of Oklahoma, habitats in intermediate stages of recovery from disturbance were important for herbivores such as hispid cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*, Grant et al. 1982), and habitat heterogeneity increased small mammal diversity (Fuhlendorf et al. 2010).

Higher species diversity in our patch-burn grazing treatment and positive control was due to increased abundance of less common species rather than species additions. Deer mice respond positively to fire and grazing disturbance in tallgrass prairie (Grant et al. 1982, Kaufman et al. 1988, Matlack et al. 2001), and dominated the small mammal communities in our grazed treatments. However, as time-since fire for a patch increased within the PBG and 4BN treatments, relative abundance of deer mice decreased whereas numbers of more specialist species, such as western harvest mice (*Reithrodontomys megalotis*) and hispid cotton rats, increased. Thus, the 2-years since fire patch contained the highest diversity of small mammals among patches (Fig. 2.4D). Similar patterns have been reported elsewhere for grassland bird communities. Generalist species of birds were common across all patch types within patch-burn grazed and traditional management treatments in tallgrass, shortgrass steppe, and sand sagebrush prairies, but specialist species selected different patch types and were absent from traditionally managed treatments (Fuhlendorf et al. 2006, Powell 2006, Holcomb et al. 2014, Hovick et al. 2014, Augustine and Derner 2015).

Separation of the small mammal community in our positive control without grazing and longer fire-return intervals was largely due to reduced relative abundance of deer mice, and higher abundance of a suite of species known to select habitats with heavy cover or woody vegetation, including hispid cotton rats, white-footed mice (*Peromyscus leucopus*), and eastern woodrats (*Neotoma floridana*; Kaufman et al. 2000, Rehmeier et al. 2005, Matlack et al. 2008). Our positive control included encroachment by woody plants, and had more shrub cover than our other treatment areas (~20% cover). Moreover, our results show that the lack of grazing

disturbance affected the process of vegetative cover and litter accumulation; creating suitable habitat faster for disturbance negative species after a fire than grazed areas. However, our 4BN treatment is unlikely to be adopted as a management strategy by private landowners, because restricting grazing or prescribed fire is not compatible with cattle production, and promotes conversion of grassland to shrubland (Briggs et al. 2005, Ratajczak et al. 2014).

We captured the same set of species in the annually burned and grazed treatment that were captured in the patch-burn grazing and 4BN treatments except, least shrews (*Cryptotis parva*). However, several relatively common species in the PBG treatment were rarely encountered in the ABG treatment. For instance, we captured at least twice as many hispid cotton rats, western harvest mice, and plains harvest mice in each unit of the PBG treatment than in the ABG treatment. The pattern of higher abundance for some species in the heavily disturbed state (PB0) of the PBG treatment than in ABG suggests that the temporal heterogeneity within patches created by PBG may allow persistence of these species in less suitable habitat.

An expanded ecological niche and greater diversity of small mammals in rangelands managed with patch-burn grazing is promising for other trophic levels. Deer mice are a highly nocturnal species, and are available as prey items for owls (Rehmeier et al. 2006). On the other hand, hispid cotton rats, prairie voles, and western harvest mice are often active during the daytime, and are likely more accessible prey for diurnal raptors (Swihart and Slade 1985, Danielson and Swihart 1987; A. M. Ricketts, *personal observation*). Deer mice can influence species composition of plant communities by selectively depredating large seeds, so reduced abundance of deer mice in PB1 and PB2 could have positive feedbacks on the plant community (Bricker et

al. 2010, Maron et al. 2012). Last, patch-burn grazing could affect disease dynamics.

Prevalence and transmission of zoonoses such as Hantaviruses and Lyme disease are often

reduced in mammalian communities with higher species diversity (Keesing et al. 2010, Dearing

et al. 2015).

Our field results provide strong evidence that patch-burn grazing promotes diversity of small

mammals in the tallgrass prairie in Kansas. Our study joins emerging results from a suite of field

studies that show that restoring pyric herbivory to create spatial and temporal heterogeneity in

rangelands is a useful conservation practice for maintaining biodiversity in grassland ecosystems.

In the future, focal population studies are needed to quantify the effects of habitat conditions on

demographic rates of key species of small mammals. Moreover, the effects of habitat

heterogeneity created by patch-burn grazing on predator behavior, including movements,

foraging efficiency, and energetic costs associated with moving through different habitats have

not yet been studied. Nevertheless, our results show that patch-burn grazing is an effective

management strategy to restore heterogeneity and increase biodiversity on rangelands managed

for cattle production.

Management decisions of stakeholders in working landscapes are complex, and can be

influenced by diverse factors including culture and economics. One important consideration for

introducing management practices to private lands are the financial and time costs that can be

barriers for livestock producers willing to implement new practices. Landowners in the Flint

Hills of Kansas regularly burn tallgrass prairie to control woody vegetation and increase cattle

gains, but prescribed fires are often applied using county roads or other natural firebreaks to

minimize the effort required for safe application of a controlled burn. Introducing patch-burn grazing on private lands may require establishment and maintenance of firebreaks, and could increase the amount of time and effort required to complete a burn safely. Cost sharing programs, such as Partners for Fish and Wildlife of the US Fish and Wildlife Service and the Environmental Quality Incentives Program of the Natural Resources Conservation Service, provide financial and technical assistance to landowners and are promising for implementation of conservation strategies such as patch-burn grazing on private lands (USFWS 2012; NRCS Kansas 2015).

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Table 2.1 Total number of unique individuals for the 11 species of small mammals captured at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014. Totals are given for the annually burned and grazed pasture (ABG), each patch of the patch-burn grazed pasture (PBG0-2), the patch-burn grazed pasture with all patches combined (PBG), the ungrazed treatment with a 4-year fire return interval (4BN), and all treatments combined. Abbreviated scientific names used in Figure 5 are given in parentheses following common names.

Species	Negative Control		Patch-burn Grazing			Positive Control	
	ABG	PB0	PB1	PB2	PBG	4BN	Total
Deer mouse (pema) *Peromyscus maniculatus*	217	216	160	100	476	58	751
White-footed mouse (pele) *Peromyscus leucopus*	14	85	67	86	238	168	420
Western harvest mouse (reme) *Reithrodontomys megalotis*	7	16	34	60	110	52	169
Prairie vole (mioc) *Microtus ochrogaster*	40	17	31	51	99	9	148
Hispid cotton rat (sihi) *Sigmodon hispidus*	1	6	12	41	59	47	107
Eastern woodrat (nefl) *Neotoma floridana*	3	10	12	4	26	51	80
Thirteen-lined ground squirrel (ictr) *Ictidomys tridecemlineatus*	16	23	23	14	60	2	78
Elliot's short-tailed shrew (blhy) *Blarina hylophaga*	8	8	11	27	46	11	65
Hispid pocket mouse (chhi) *Chaetodypus hispidus*	9	15	12	5	32	12	53
Plains harvest mouse (remo) *Reithrodontomys montanus*	3	6	8	6	20	2	25
Least Shrew (crpa) *Cryptotis parva*	0	1	0	4	5	1	7
Grand Totals	318	403	370	398	1171	413	1903

Table 2.2 Candidate models and model statistics for species richness for the small mammal community at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Model Structure‡	K	Dev	AIC$_c$	Δ AIC$_c$	$w_i \leq$
			Model Statistics†		
Treatment + Year	7	134.1	151.6	0	0.672
Year	5	141.9	153.7	2.2	0.229
State + Year	9	131.5	155.5	4.0	0.092
Treatment x Year	13	120.8	160.8	9.3	0.007
Constant	2	163.2	167.5	15.9	0
Treatment	4	158.7	167.9	16.3	0
State	6	157.4	171.9	20.4	0
State x Year	21	85.8	179.1	27.6	0

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion corrected for small sample size (AIC$_c$), differences in AIC$_c$ from the minimum AIC$_c$ model (Δ AIC$_c$), and AIC$_c$ weights (w_i).

‡ State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014.

Table 2.3 Candidate models and model statistics for Shannon Diversity Index for the small mammal community at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Model Structure‡	Model Statistics†				
	K	**Dev**	**AIC_c**	**ΔAIC_c**	**$w_i \leq$**
State + Year	9	-22.5	1.5	0	0.998
Treatment + Year	7	-2.8	14.7	13.2	0.001
State	6	3.2	17.8	16.2	0
Treatment	4	14.8	23.9	22.4	0
Treatment x Year	13	-5.0	35.1	33.6	0
Year	5	26.4	38.2	36.6	0
Constant	2	35.8	40.2	38.6	0
State x Year	21	-34.7	58.7	57.1	0

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c from the minimum AIC_c model (ΔAIC_c), and AIC_c weights (w_i).

‡ State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014.

Table 2.4 Results of a canonical correspondence analysis (CCA) for the small mammal community at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014. F-statistics and p-values are from permutation tests of the full CCA model or axes.

	Eigenvalue (λ)	% Variance	F	df	$p \leq$
Total Inertia	1.71	—	—	—	—
Constrained (CCA)	0.814	47.6	6.2	5	0.001
Unconstrained	0.897	52.4	—	—	—
CCA Axis 1	0.314	18.4	11.9	1	0.001
CCA Axis 2	0.218	12.8	8.3	1	0.001
CCA Axis 3	0.164	9.6	6.2	1	0.001
CCA Axis 4	0.103	6.0	3.9	1	0.003
CCA Axis 5	0.015	0.9	0.6	1	0.878

Figure 2.1 Map of study site showing locations of treatments and trapping grids at Konza Prairie Biological Station, Kansas, USA. Treatments included a negative control that was annually burned and grazed (ABG), three units of the patch-burn grazed treatment (PBG), and a positive control that was ungrazed with a 4-year fire return interval (4BN). Squares outline our 10 randomly located trap grids.
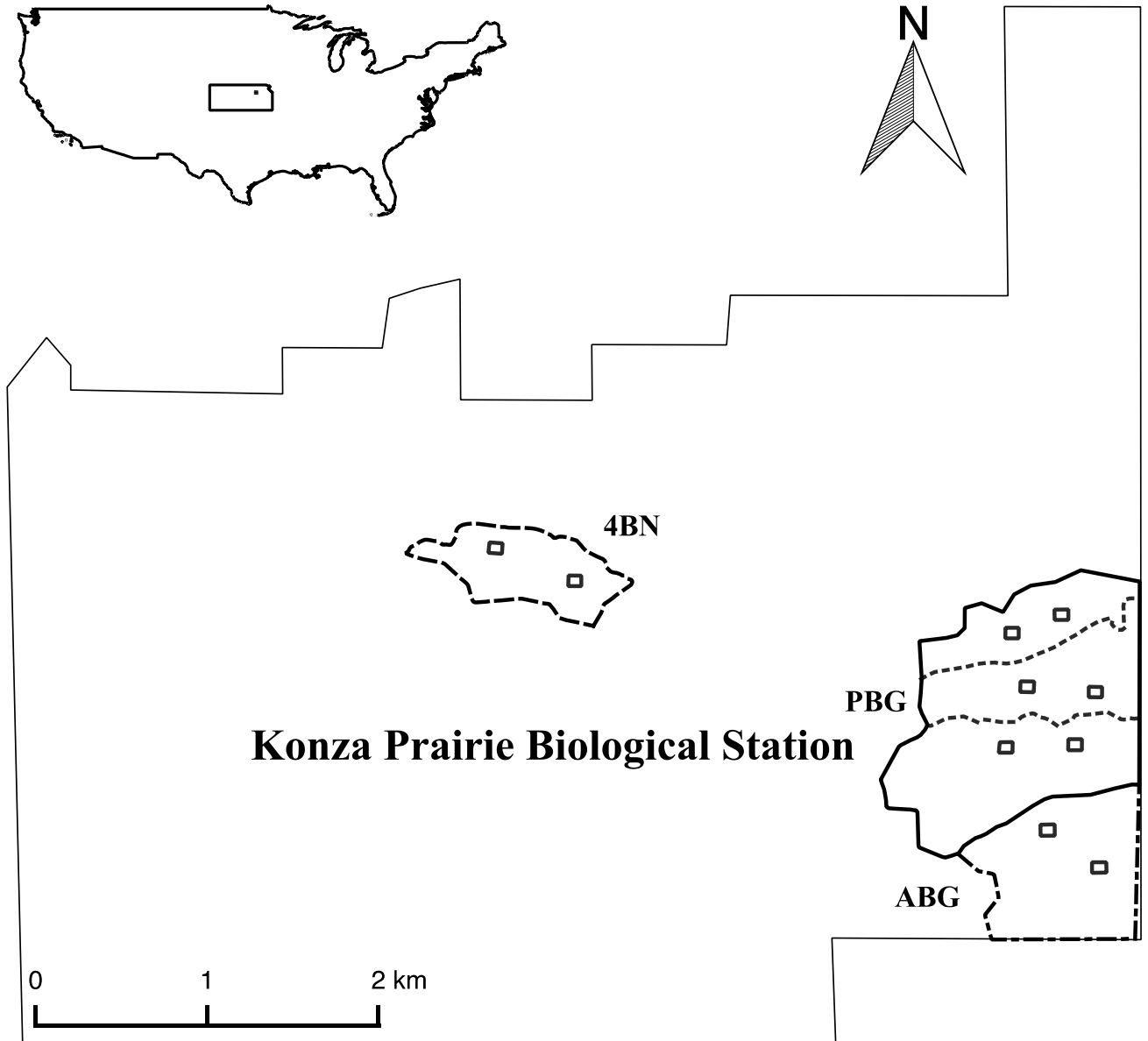
Figure 2.2 Percent cover of grasses and sedges (A), forbs (B), shrubs (C), and bare ground (D), litter depth (E), and vegetation structure as visual obstruction reading (F) in annually burned and grazed (ABG), patch-burn grazed (PB0-2), and an ungrazed treatment with a 4-year fire return interval (4BN) at Konza Prairie Biological Station, Kansas, USA from 2011-2014. Bars sharing letters above confidence intervals indicate non-significance. Sample sizes for each treatment were 140-150 points.
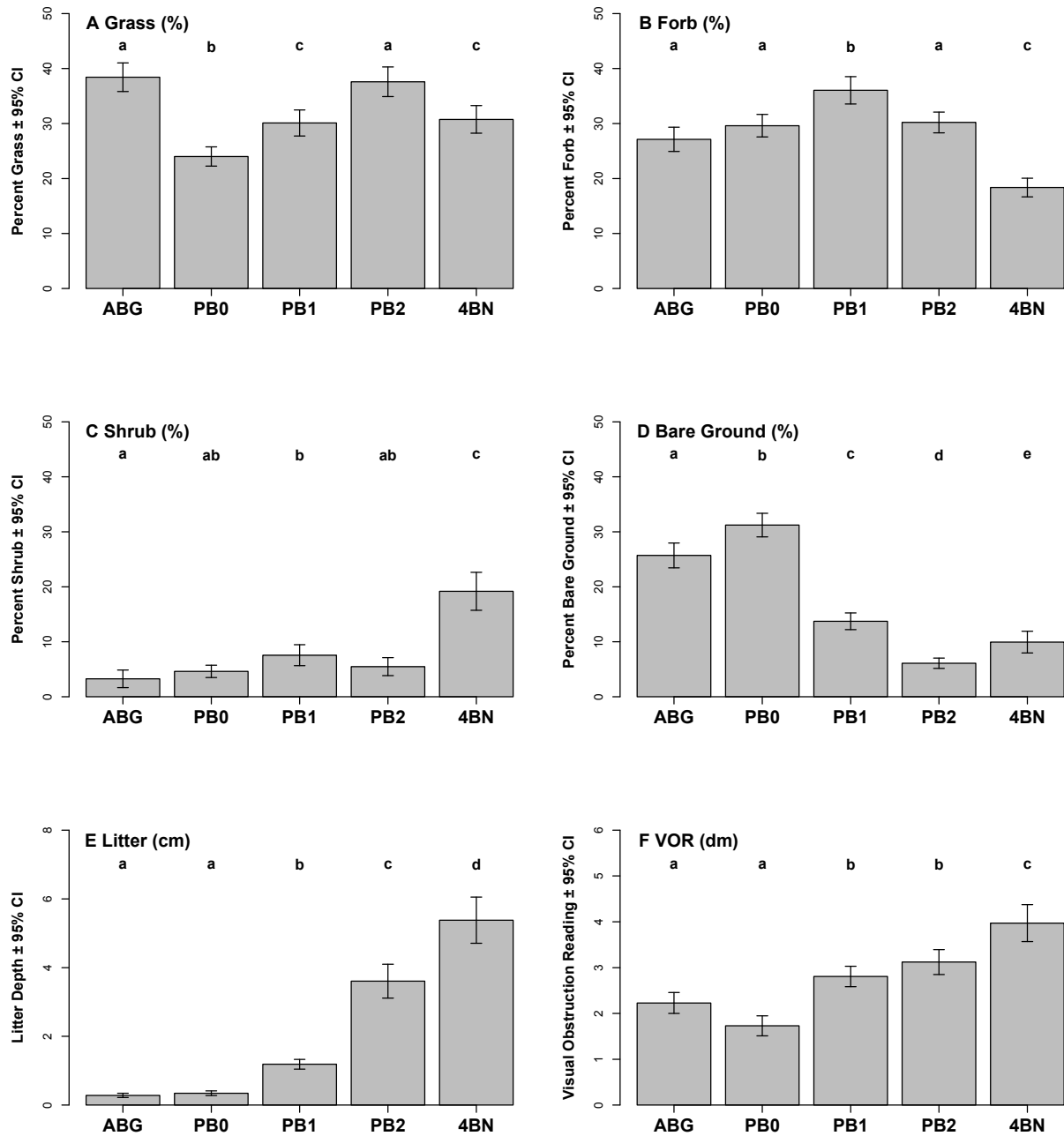
Figure 2.3 Mean scores (± 95% CI) from the first two axes of a principal components analysis (PCA) of habitat measurements in a negative control that was annually burned and grazed (ABG), each patch of the patch-burn grazed treatment (PB0-2), and a positive control that was ungrazed with a 4-year fire return interval (4BN) from June 2011 to December 2014 at Konza Prairie Biological Station, Kansas, USA. Red arrows represent loadings of percent canopy cover of grasses and sedges, forbs, and bare ground, as well as litter depth and visual obstruction reading (VOR). Numbers following PB indicate time-since fire within the PBG treatment (0-2 years).
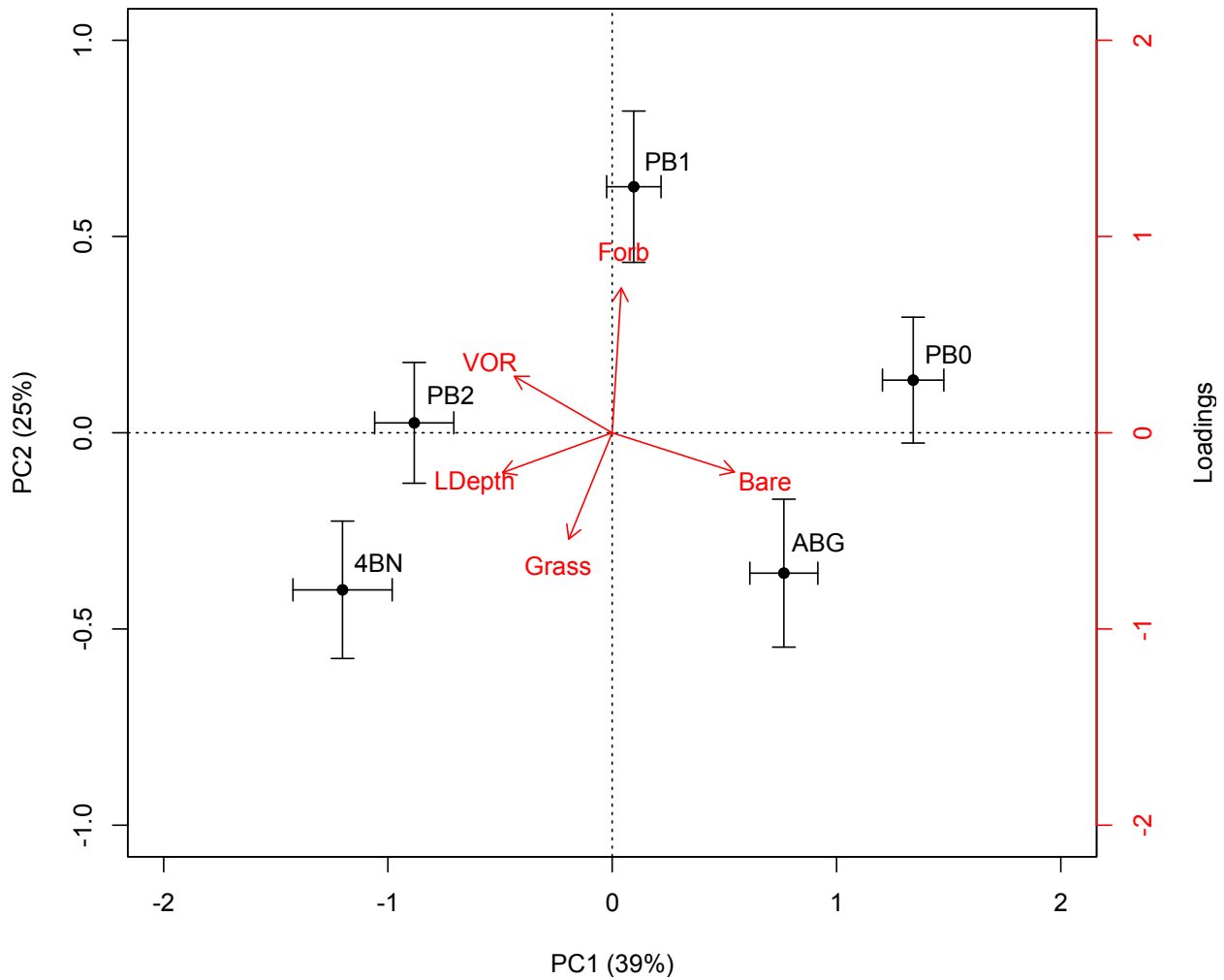
Figure 2.4 Small mammal species richness (A,B) and Shannon Diversity Index (C,D) in annually burned and grazed (ABG), all patch-burn grazed treatments combined (PBG), each patch of the patch-burn grazed pasture (PB0-2), and the ungrazed treatment with a 4-year fire return interval (4BN) at Konza Prairie Biological Station, Kansas, USA, from June 2011 to December 2014. Numbers following PB in the right panel correspond to time-since fire for a patch (0-2 years).
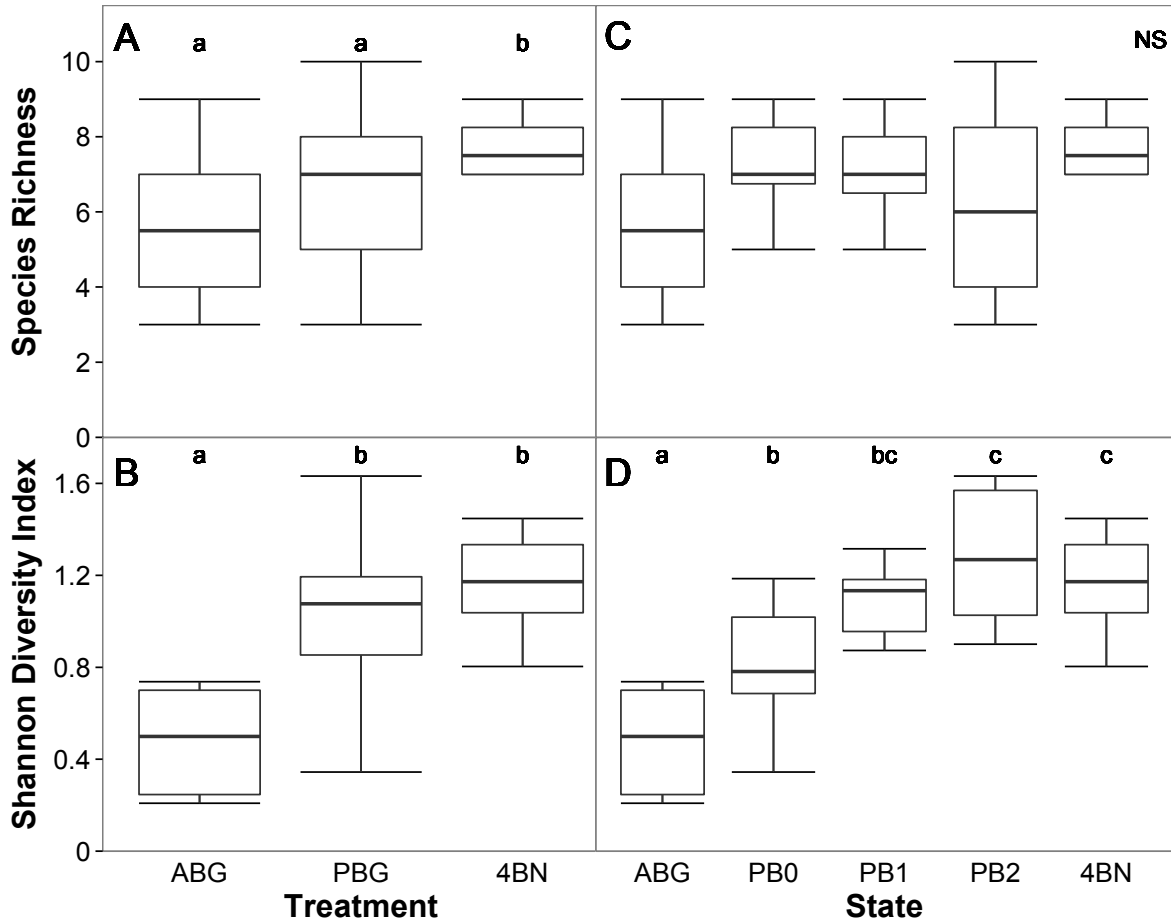
Figure 2.5 Ordination of the first two axes from a canonical correspondence analysis (CCA) showing the relationships among the small mammal community, three treatments, four biological years, and the interaction of fire and grazing from June 2011 to December 2014 at Konza Prairie Biological Station, Kansas, USA. Treatments include annually burned and grazed (ABG), patch-burn grazed (PBG), and ungrazed with a 4-year fire return interval (4BN). Eleven species of small mammals were encountered and species codes are given in table 1.
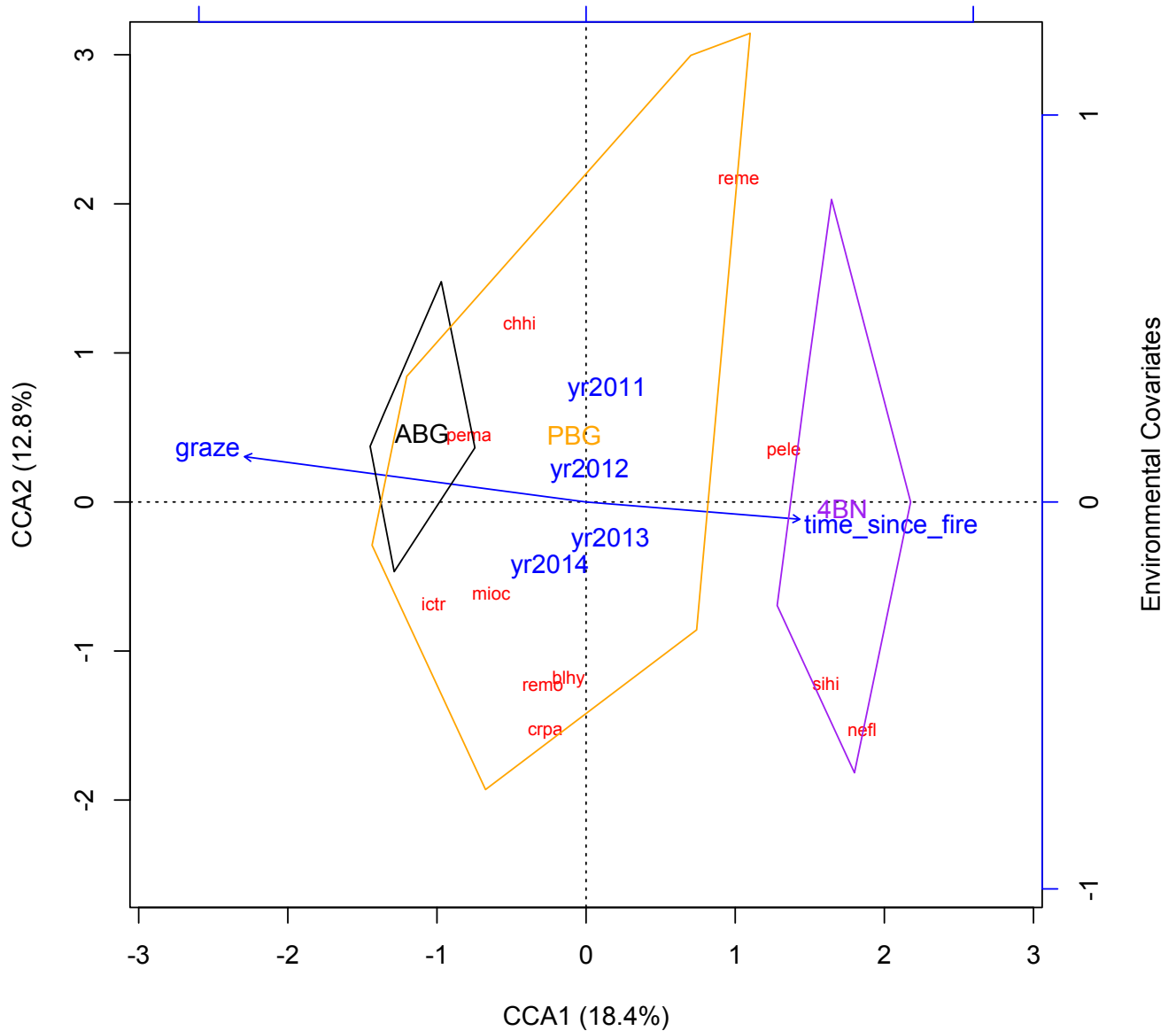
Chapter 3 - Disturbance-induced habitat heterogeneity drives small mammal population dynamics in managed rangelands

Abstract

Disturbance from fire, grazing and other ecological processes is often a driver of biodiversity. In the absence of periodic disturbance, ecosystems progress towards climax communities that tend to be homogeneous in space and time. Most grazing systems have sought to minimize the effects of grazing on the landscape by evenly distributing the effects of livestock grazing across management units. Managing rangelands for even grazing distributions leads to relatively homogeneous habitat conditions. Patch-burn grazing is a relatively new rangeland management practice that seeks to restore habitat heterogeneity and biodiversity to rangelands that are managed for livestock production. Previous studies have shown that patch-burn grazing can restore habitat heterogeneity, and increase diversity and abundance of grassland organisms. However, few studies have assessed the effects of patch-burn grazing on population dynamics of grassland animals. Our objective for this study was to evaluate the effects of habitat heterogeneity created by patch-burn grazing on demographic performance of seven common species of small mammals. We conducted monthly live-trapping at Konza Prairie biological station over 3.5 years, and used the Dail-Madsen dynamic N-mixture model to model recruitment and apparent survival from counts of small mammals as a function of three treatments: a *negative control* that was annually burned and grazed, a *positive control* that was burned every four years and not grazed, and a *patch-burn grazing* treatment that was managed with rotational fire and grazed. Rangeland management was an important factor for demographic performance of all seven species of small mammals. Different species of small mammals responded differently to the interaction of fire and grazing on the landscape, indicating that

management practices that promote heterogeneity in rangeland ecosystems will benefit a suite of species with different ecological requirements. Disturbance positive species such as deer mice generally had higher recruitment and apparent survival in areas that were recently burned and grazed, whereas disturbance negative species such as western harvest mice had higher recruitment in areas that had not recently burned and were not intensively grazed. Restoring the drivers of historical patch dynamics to managed rangelands and publicly held grasslands that are not currently grazed could have profound effects on biodiversity conservation in North America, while continuing to provide ecosystem services to society.

Introduction

Habitat heterogeneity is a driver of biodiversity in many ecosystems (Ostfeld et al. 1997; Fuhlendorf et al. 2010). For many species to coexist sympatrically, each species may be adapted to take advantage of different niche spaces available in each ecosystem (Hutchinson 1959). For the full complement of native species to persist in an ecosystem, all habitat types that existed historically in that ecosystem must be present. In the absence of periodic disturbance, ecosystems tend toward a climax community that will eventually be homogeneous in space and time. Therefore, effects of disturbance from fire, grazing and other ecological processes on habitat structure and composition are often drivers of biodiversity.

Natural resource managers have been using disturbance processes to manage wildlife in North American ecosystems for nearly a century. Leopold (1933) identified the ax, cow, match, and plow as key tools for managing succession to create habitat heterogeneity and benefit native wildlife. Managers have used tree removal from prairies, timber stand improvement, disking, and controlled burning as management tools for improving habitat conditions. Few natural

resource agencies have used cattle grazing as a tool for managing wildlife habitat. Instead, livestock grazing has been viewed as a land-use practice for private and some public lands to provide agricultural products for society and economic gain for private landowners. Accordingly, the focus of the majority of grazing systems has been to minimize the effects of grazing on the landscape through evenly distributing the effects of livestock grazing across management units (Fuhlendorf et al. 2012). Even distribution of grazing pressure across management units can be accomplished through rotational grazing systems where livestock are moved among cross-fenced areas within a pasture throughout the growing season, or through even application of fire to an entire pasture. An even grazing distribution alters ecosystem processes and has resulted in a homogenization of habitat conditions on managed rangelands in North America (Fuhlendorf et al. 2012).

Patch-burn grazing is a relatively new rangeland management practice that seeks to restore habitat heterogeneity and biodiversity to rangelands that have been managed for livestock production (Fuhlendorf and Engle 2001). Rangeland management using patch-burn grazing takes advantage of pyric herbivory, or grazing influenced by fire, to create a mosaic of different habitat conditions within a management unit (Fuhlendorf et al. 2009). Habitat heterogeneity is a key driver that increases diversity of invertebrates, grassland birds, and small mammals in native grasslands (Fuhlendorf et al. 2006; Coppedge et al. 2008; Fuhlendorf et al. 2010; Holcomb et al. 2014, Hovick et al. 2014, Augustine and Derner 2015; Chapter 2). Most studies of the effects of patch-burn grazing on wildlife have focused on species diversity and relative abundance of grassland organisms (but see Churchwell et al. 2008; Hovick et al. 2011; 2012; McNew et al. 2015; Sandercock et al. 2015). To understand the effects of patch-burn grazing on grassland

ecosystems, a better mechanistic understanding of demographic responses of animal populations within those ecosystems is an important research need.

Most studies of wildlife responses to management actions or environmental conditions are based on unadjusted counts or probability of occupancy by animals. However, relative abundance or occupancy may not detect source-sink dynamics, because these population metrics fail to consider immigration or emmigration. Thus, an area with high abundance and low apparent survival might be considered high quality habitat for a species, when the habitat is actually a population sink for a species of interest (Pulliam 1988). Abundance is often the target of management actions, but demographic mechanisms of fecundity, recruitment, and apparent survival are ultimately responsible for changes in population size among management units.

A fundamental challenge to studies of population dynamics of inconspicuous species is the problem of imperfect detection (Pollock et al. 1990). Statistical methods that provide estimates of demographic parameters corrected for imperfect detection often require large datasets for marked individuals. Uncommon species pose a problem for capture-mark-recapture methods (hereafter CMR), because sample sizes needed for these methods are often not attainable if a rare species is captured and recaptured infrequently. Recently, binomial mixture models (hereafter N-mixture models) have been developed to allow the estimation of abundance, corrected for imperfect detection, from count data for unmarked individuals (Royle 2004). The first N-mixture models were limited to closed populations without gains or losses due to births, deaths, immigration, and emigration. Dail and Madsen (2011; DM model) recently extended the single season N-mixture models for count data to dynamic N-mixture models that allow for open

population dynamics in a robust design sampling framework. Moreover, because the model structure includes transitions among open and closed periods for a population, DM models can be used to estimate recruitment (γ) and apparent survival (ω) (Hostetler and Chandler 2015). A recent study comparing results of the DM model to CMR estimates concluded that the accuracy of point estimates for abundance and vital rates were high using DM models for unmarked individuals, but estimates had less precision than estimates from CMR methods for marked individuals (Priol et al. 2014).

Small mammals are an ecologically important group that impact ecosystems in various ways. Rodents and shrews are facilitators of ecosystem processes through their burrowing activity and nitrogen deposition (Laundre 1993; Ross et al. 2007), can influence plant diversity through granivory or herbivory (Howe and Brown 2000; Reed et al. 2004; Ross et al. 2007; Bricker et al. 2010; Maron et al. 2012), and important prey items for higher trophic levels (Sperry 1941; Fitch et al. 1946; Fitcher 1955; Brillhart and Kaufman 1994; 1995; Trauth and McAllister 1995; Huebschman et al. 2000; Colston et al. 2010). Moreover, small mammals are short-lived species with high fecundity and short generation times that are likely to respond quickly to changes in environmental conditions (Reed et al. 2007).

Our main goal for this study was to test the effects of habitat heterogeneity created by patch-burn grazing on population dynamics of common species in the small mammal community of the tallgrass prairie of the northern Flint Hills. We used the Dail-Madsen (2011) model for open populations to obtain estimates of probability of detection, initial abundance, recruitment, and apparent survival for seven species of small mammals. We predicted that recruitment of non-

hibernating small mammals would show bimodal peaks in spring and fall, and that apparent survival would be lowest during winter. For the effects of rangeland management, we predicted species that are disturbance positive should have higher recruitment and apparent survival in recently burned areas that are grazed. Conversely, recruitment and apparent survival of disturbance negative species was expected to increase with time-since fire, and be higher in areas without grazing pressure.

Methods

Study Site

Our study was conducted over a 3.5 year period from June 2011 – December 2014 at Konza Prairie Biological Station (hereafter, Konza Prairie). Konza Prairie is a 3,487 ha research station in the Flint Hills ecoregion of northeast Kansas, USA (39°06′ N, 96°34′ W), and is a core Long-Term Ecological Research site funded by the National Science Foundation. The research station is a landscape-level fire and grazing experiment with >60 watershed-level experimental units that receive replicated fire and grazing treatments. The vegetative community at Konza Prairie is dominated by native warm season grasses, such as big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), indiangrass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparium*, Towne 2002). Forbs comprise much of the plant species diversity, and common species included goldenrod (*Solidago* spp.), Baldwin's ironweed (*Vernonia baldwinii*), leadplant (*Amorpha canescens*), and round-head bush clover (*Lespedeza capitata*). Common shrubs included rough-leaf dogwood (*Cornus drummondii*), wild plum (*Prunus americana*), smooth sumac (*Rhus glabra*), fragrant sumac (*Rhus aromatica*), inland ceanothus (*Ceanothus herbaceus*), and buckbrush (*Symphoricarpos orbiculatus*).

A large-scale *patch-burn grazing* experiment (PBG) was initiated in 2010, and includes roughly the eastern third of the research station (Fig. 2.1). The PBG replicates were sub-divided into three patches, with one patch burned per year in spring on a rotational basis. Cattle had access to the entire management unit without cross fencing. We included an annually burned and grazed treatment as a *negative control* (ABG), and an ungrazed treatment that was burned every four years for a *positive control* (4BN). PBG and ABG sites were stocked with cow-calf pairs at a density of one pair per 3.24 ha for a 5-month grazing season from early May to early October each year. Patch size of the three units in the PBG treatment was ranged from 48.7 to 102.4 ha, and ABG and 4BN treatments were 93.7 and 53.1 ha, respectively.

Small Mammal Sampling

Fourteen species of small mammals have been captured in rangeland habitats at Konza Prairie (McMillan et al. 1990; Chapter 2), but the seven most common species included in our analyses were: deer mice (*Peromyscus maniculatus*, pema), white-footed mice (*P. leucopus*, pele), western harvest mice (*Reithrodontomys megalotis*, reme), prairie voles (*Microtus ochrogaster*, mioc), hispid pocket mice (*Chaetodipus hispidus*, chhi), thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*, ictr), and eastern woodrats (*Neotoma floridana*, nefl). We established two replicate trap grids for sampling small mammal communities in each of the three PBG patches and two controls, for a total of ten grids (Fig. 2.1). Grid locations were selected at random, but subject to two constraints. To maintain independence among trap grids, grids were separated by at least 200 m, which corresponds to twice the length of the longest published home range axis for deer mice, the most common species of small mammal encountered in burned and

grazed prairie (Douglass et al. 2006, Yarnell et al. 2007). Trap grids were also located at least 100 m from unit boundaries to avoid potential boundary effects, and >50 m from permanent or regularly flowing water to avoid flooding of traps during runoff from thunderstorms (Konza LTER datasets GIS210 and GIS211).

Each trap grid was a five-by-five design with 25 stations and 20 m between adjacent trap stations for a total area of 0.64 ha. Two extra-large Sherman live traps (Model LNG 12, H.B. Sherman Trap Company, Tallahassee, FL, USA) were set at each trap station for a total of 50 traps per grid. Traps were baited with a mixture of peanut butter and rolled oats, and provisioned with polyester fiberfill to keep animals warm during October to May (Kaufman et al. 1988). To reduce heat stress on small mammals, wooden A-frame structures (hereafter, trap shelters) were placed over traps for shading (Kaufman and Kaufman 1989). Trap shelters were left in place year round for weathering and to minimize potential neophobic responses of small mammals to trap stations.

Small mammals were trapped for three consecutive nights each month at the ten trapping grids in the three patches of the PBG treatment, and each of the ABG and 4BN controls. Trap grids were sampled in 9 of 12 months per year with some trapping sessions missing due to inclement winter weather, or to unpredictable winds during prescribed burns in March. At capture, animals were identified to species by body size, pelage color, and other morphological traits. Handling included standard morphometric measurements and marking with PIT tags and ear tags, but we used counts of all individuals for our demographic analysis. All procedures were approved by the Institutional Animal Care and Use Committee at Kansas State University (protocols 3034 and

3443), and conducted under state wildlife permits from the Kansas Department of Wildlife, Parks, and Tourism.

Statistical Analyses

To obtain demographic estimates for small mammal populations, we employed the Dail-Madsen model (hereafter DM model, Chandler and King 2011; Dail and Madsen 2011; Hostetler and Chandler 2015). With default settings in the R package "unmarked", the DM model estimates four demographic parameters: initial abundance (λ), recruitment (γ), apparent survival (ω), and the probability of detection (p, Fiske and Chandler 2011). We chose to model population dynamics using the dynamic N-mixture approach rather than traditional CMR statistics because we encountered too few individuals for many of our study species to meet the sample size requirements needed for Cormack-Jolly-Seber or Robust Design models for estimation of demographic parameters for marked individuals. DM models are an improvement over indices such as catch per unit effort or return rates because the models account for imperfect detection. As with CMR models for marked individuals, the DM model allows demographic parameters to be modeled as a function of environmental covariates. Analyses were conducted with the "pcountOpen" function within package "unmarked" of R (R Core Team 2016; Fiske and Chandler 2011).

We started our modeling process by using AIC model selection to determine which mixture distribution for initial abundance best fit our count data for each species of small mammal. Three types of mixtures available for count data included *Poisson*, *Negative Binomial*, and *Zero Inflated Poisson*. Once we had selected the appropriate mixture for a species, we found the

model for probability of detection that minimized the AIC value. We then constructed candidate models for each species using covariates that tested the effects of rangeland management on demographic responses of small mammals, and controlled for annual and seasonal variation in population dynamics. We used a hierarchical selection process to select the candidate model(s) that minimized the model AIC values for initial abundance, recruitment, and apparent survival. The minimum AIC model was retained for initial abundance when testing models on recruitment, and the top models for abundance and recruitment were retained when testing models on apparent survival unless we encountered model convergence issues or inestimable parameters. When we encountered issues with model convergence, we only tested models where we varied the parameter of interest and set other parameters to intercept-only models. Model selection tables reflect the order of our modeling process (Tables 3.1-3.7), and are not ordered with the minimum AIC model first. Models with ΔAIC ≤ 2 of the top model were considered equally parsimonious to the minimum AIC model. We made predictions from unconstrained models for the covariate of interest, because the effects of multiple variables often made it difficult to interpret the effects when multiple covariates were present for the same parameter. Predictions of initial abundance for Zero Inflated Poisson models were made using the "predictSE" function of the R package "AICcmodavg" (Mazerolle 2016), and all other predictions were made using the "predict" function in package "unmarked".

We tested four explanatory factors in our models: years-since-fire (timesince), grazing treatment (graze), state (ABG, PB0, PB1, PB2, 4BN), treatment (ABG, PBG, or 4BN), and year coded as a categorical variable (year). *State* models considered each value of time-since fire within the patch-burn grazing treatment, and included ABG, PB0, PB1, PB2, and 4BN, where numbers

following PB indicate years since fire. *Treatment* models considered each treatment as a whole, and included ABG, PBG, and 4BN. *Graze* models considered only whether a treatment area was grazed (G) or ungrazed (U). Prescribed fires at our treatment areas were conducted in March of each year of the study. We used biological years that began in April rather than calendar years, because fires completely aboveground remove vegetation from prairie habitat, and immediately impact small mammal populations (Clark and Kaufman 1990). Season (four 3-month periods) was included as a session-specific covariate (*yearlySitecovs* in unmarked) on detection probability, recruitment, and apparent survival.

Initial abundance can only be modeled as a function of site-specific covariates versus dynamic covariates in the DM model. Abundance was a parameter of interest in our analyses and our goal was to model abundance as a function of time-since fire and grazing treatment as a surrogate for the effects of patch-burn grazing, or directly as a function of our treatments (e.g. ABG, PB0, PB1, PB2, and 4BN). Time-since fire changed for each treatment or patch each year, except for the ABG treatment, and state changed each year for the PBG patches. Therefore, we "stacked" sites by year such that one encounter history included counts for a species at one grid for one year, and each grid was represented by four encounter histories that corresponded to our four biological years.

Results

From June 2011 to December 2014, we captured 1,903 unique individuals of 11 species of small mammals, with a total of 6,830 handling events during 52,500 trap-nights of sampling effort (Table 2.2). We had a sufficient number of captures of seven species of rodents to estimate

initial abundance and population dynamics with the Dail-Madsen model. Two years of our study period experienced drought conditions (2011 and 2012).

Seasonal Variation in Detection

Probability of detection varied seasonally for five of the seven species of small mammals in our study (Tables 3.1-3.7), but the patterns differed among species. Among species where season was the best predictor for detection probability, deer mice (pema) showed the least variability with a high of 0.55 in summer and a low of 0.47 in fall (Fig. 3.1). Detection probability of thirteen-lined ground squirrels (ictr) was highest in spring (0.27), lowest in fall (0.08), and this species was unavailable for capture in winter due to hibernation (Fig. 3.1). Eastern woodrats (nefl) were most likely to be detected in fall (0.43), and least likely to be detected in spring (0.07; Fig. 3.1). White-footed mice (pele) had relatively constant detection probability in spring through fall (0.35-0.38), but significantly higher probability of detection in winter (0.58; Fig. 3.1). Detection probability of western harvest mice (reme) declined from 0.46 in spring to 0.16 in summer before rising to 0.40 in winter (Fig. 3.1). The best model for detection of hispid pocket mice (chhi) and prairie voles (mioc) was a constant model, with detection probabilities of 0.31 and 0.26, respectively (Fig. 3.1). Hispid pocket mice hibernate, and were unavailable for capture during winter.

Seasonal Variation in Recruitment and Survival

Season was included in the top model or ΔAIC <2 model set for recruitment of six of the seven small mammal species in our study (Tables 3.1-3.7). Recruitment was highest in fall or winter

for three species. Recruitment of deer mice was lowest in spring (0.39 recruits/grid/month) and highest in winter (1.40 recruits/grid/month; Fig. 3.2A). Recruitment of white-footed mice was lowest in summer (0.38 recruits/grid/month) and highest in fall (1.16 recruits/grid/month; Fig. 3.2A). Similarly, recruitment of western harvest mice was highest in fall (0.88 recruits/grid/month) and lowest in spring and summer (0.20-0.21 recruits/grid/month; Fig. 3.2A). On the other hand two species had little variation in recruitment among seasons. Recruitment of eastern woodrats and prairie voles generally low (<0.1) and showed little variability among seasons (Fig. 3.2A). Season was not included in the ΔAIC <2 model set for recruitment of thirteen-lined ground squirrels (Table 7; Fig. 3.2A). Hispid pocket mouse recruitment was relatively low when averaged across treatments and years, but was highest in summer (0.37 recruits/grid/month), and lowest in spring (0.08 recruits/grid/month; Fig. 3.2A).

The ΔAIC <2 model set for apparent survival included effects of season for deer mice, eastern woodrats, and hispid pocket mice (Tables 3.1, 3.5, and 3.6). Monthly apparent survival of deer mice averaged across all treatments was highest in fall (0.64), and lowest in spring (0.42; Fig 3.2B). In contrast, eastern woodrats had higher monthly apparent survival in spring and summer (0.96, 0.90) than in fall and winter (0.65; Fig. 3.2B). Monthly apparent survival of hispid pocket mice was highest in summer (0.63) and lowest in spring (0.19; Fig. 3.2B). Season was not included in the parsimonious model set for monthly apparent survival of white-footed mice, but this species had lower apparent survival in summer than the other three seasons (Fig. 3.2B).

Effects of Time-Since-Fire

Rangeland management affected demographic performance of small mammals in native grasslands. Time-since-fire was included in the parsimonious model set for at least one demographic parameter for all species of small mammals in our study (Tables 3.1-3.7). Recruitment decreased with time-since-fire in three species: deer mice, thirteen-lined ground squirrels, and hispid pocket mice (Fig. 3.3A). In the last two species, eastern woodrats and prairie voles, recruitment varied little with time-since-fire (Fig. 3.3A). In contrast, recruitment of white-footed mice and western harvest mice increased with time-since-fire. Patterns of apparent survival were similar to recruitment. Monthly apparent survival of deer mice and hispid pocket mice decreased as time-since-fire increased, whereas apparent survival of western harvest mice and eastern woodrats covaried positively with increasing time-since-fire (Fig. 3.3B). Last, time-since-fire was not included in the parsimonious model set for white-footed mice or prairie voles (Tables 3.2 and 3.4), but apparent survival declined with increasing time-since fire for both of these species (Fig. 3.3B). Time-since-fire was an important covariate for initial abundance for all small mammal species in our study except white-footed mice (Tables 3.1-3.7). Initial abundance of deer mice was highest in areas that had burned the previous month (Fig. 3.3C). Initial abundance of all other species tended to increase with time-since-fire, but the trend was weak for thirteen-lined ground squirrels, hispid pocket mice, and prairie voles, and with considerable uncertainty in some of the estimates (Fig. 3.3).

Effects of Rangeland Management

We tested three categorical covariates with differing numbers of levels to test the effects of our fire and grazing treatments on monthly recruitment, apparent survival, and initial abundance of

small mammals. We report results for the covariate with the greatest number of levels that our sample size would support for each species (Fig. 3.4A-C).

Three species of small mammals had higher monthly recruitment in grazed treatments than ungrazed treatments (Fig. 3.4A). Monthly recruitment of deer mice was highest in the year of fire patch of the PBG treatment (4.75 recruits/grid/month), declined with time-since fire in the PBG treatment, and was lowest in 4BN (0.69 recruits/grid/month). Similarly, thirteen-lined ground squirrels had higher recruitment in grazed treatments (0.59 recruits/grid/month) than the ungrazed treatment (0.07 recruits/grid/month). Overall, recruitment of prairie voles was low, but ABG (0.21 recruits/grid/month) and PBG (0.24 recruits/grid/month) had higher recruitment than 4BN (0.08 recruits/grid/month). Recruitment of hispid pocket mice was similar in grazed and ungrazed treatments. On the other hand, monthly recruitment was highest in 4BN for three species of small mammals. Monthly recruitment of white-footed mice was lowest in the ABG treatment (0.17 recruits/grid/month), higher and showed no pattern relative to time-since fire in the PBG treatment (0.49-1.18 recruits/grid/month), and highest in treatment 4BN (2.38 recruits/month/grid). Recruitment of eastern woodrats was highest in 4BN, and western harvest mouse recruitment was higher in PBG (0.41 recruits/grid/month) and 4BN (0.60 recruits/grid/month) than ABG (0.11 recruits/grid/month).

Monthly apparent survival of deer mice was similar among all grazed treatments (0.52-0.60), and lowest in the 4BN treatment (0.37; Fig. 3.4B). Thirteen-lined ground squirrels had constant apparent survival with regard to grazed or ungrazed areas (0.92), whereas western harvest mice had constant apparent survival relative to the three treatments (0.70). Two species of small

mammals had higher apparent survival in grazed units. Hispid pocket mice had higher apparent

survival in grazed (0.45) than ungrazed areas (0.06), but with high model uncertainty. Similarly,

monthly apparent survival of prairie voles was highest in the ABG treatment (0.95), intermediate

in the PBG treatment (0.85), and lowest in the 4BN treatment (0.23). Apparent survival of

eastern woodrats showed the opposite pattern, with the lowest apparent survival in the ABG

treatment (0.18), intermediate values in the PBG treatment (0.56), and higher apparent survival

in the 4BN treatment (0.82). Last, apparent survival of white-footed mice was highest in the

year of fire patch of the PBG treatment (0.87), and lowest in the ABG (0.23) and 4BN treatments

(0.41).

Initial abundance estimates for deer mice were similar in ABG (7.74 individuals per grid) and

PB1 (7.14 individuals per grid), lower in PB0 (4.88 individuals per grid) and PB2 (3.89

individuals per grid), and lowest in 4BN (1.68 individuals per grid; Fig. 3.4C). Initial abundance

of thirteen-lined ground squirrels and eastern woodrats was constant among treatments at 0.11

individuals per grid and 1.67 individuals per grid, respectively (Fig. 3.4C). Similarly, initial

abundance varied little among grazed and ungrazed areas for hispid pocket mice (0.14-0.35

individuals per grid). Initial abundance of prairie voles was low in all treatments, but was

highest in PBG (0.96 individuals per grid), lowest in ABG (0.00 individuals per grid, and

intermediate in 4BN (0.43). On the other hand, initial abundance was highest in 4BN for two

species. Initial abundance of white-footed mice was highest in the 4BN treatment (11.52

individuals per grid), lowest in the ABG treatment (0.13 individuals per grid), and higher in PB1

(3.14 individuals per grid) than PB0 (2.68 individuals per grid) or PB2 (1.21 individuals per

grid). Treatment 4BN had the highest initial abundance of western harvest mice (1.22

individuals per grid), followed by PBG (0.31 individuals per grid).

Annual Variation

Annual variation in population dynamics occurred to some degree with each species in our study,

and four species showed evidence of depressed recruitment during the drought years of 2011 and

2012. Averaged across all treatments, monthly recruitment of deer mice increased from 1.33

recruits per grid in the drought year of 2011 to 1.97 in 2012, and 3.10 recruits per grid in 2013,

before falling to 2.46 recruits per grid in 2014 (Fig. 3.5A). Similarly, thirteen-lined ground

squirrel monthly recruitment was low in 2011 and 2012 (0.21-0.20 recruits/grid), but increased to

0.91 recruits/grid in 2014. Recruitment of hispid pocket mice was relatively low in all years of

the study, and was depressed in the drought year of 2012. Prairie vole recruitment increased

from a low of 0.04 recruits per grid per month in 2012 to a high of 0.66 recruits per grid per

month in 2014. Monthly recruitment of eastern woodrats was low overall, and varied little

among years. By contrast, monthly recruitment of white-footed mice was similar across the four

biological years of our study, but was highest in 2012 (0.93 recruits/grid/month). Unexpectedly,

recruitment of western harvest mice was highest in the drought year of 2011 (0.99

recruits/grid/month), but low in the other three years of our study (0.20-0.30

recruits/grid/month).

Annual patterns in apparent survival of deer mice were similar to those observed for recruitment,

but with greater model uncertainty (Fig. 3.5B). Apparent survival of thirteen-lined ground

squirrels was constant among years, while apparent survival of hispid pocket mice declined from

2011-2014, and was inestimable in 2012. Apparent survival of prairie voles was moderate in 2011 and 2013 (0.80 and 0.82), was low in the drought year of 2012 (0.24), and high in 2014 (0.96). Apparent survival of eastern woodrats was low in 2011 (0.39), and increased in 2012 (0.84) before falling and remaining similar in 2013 and 2014 (0.74-0.75). Apparent survival of white-footed mice was similar among the first three biological years of our study (0.66-0.71), but was slightly higher in 2014 (0.76). Apparent survival of western harvest mice was highest in 2011 (0.86), low but with considerable model uncertainty in 2014 (0.09), and intermediate in 2012 and 2013 (0.55-0.58).

Initial abundance of all species of small mammals was low in 2011, and increased in each subsequent biological year of our field study for three species. Initial abundance of deer mice was low in 2011 (1.04), and increased in each of the remaining three years of the study (5.13-7.93; Fig. 3.5C). Initial abundance of prairie voles increased from 2011 (0.32) to 2014 (1.70). A similar pattern occurred with eastern woodrats, but with greater model uncertainty (0.16-4.39). Initial abundance of hispid pocket mice and thirteen-lined ground squirrels was low, and constant among years. On the other hand, white-footed mouse initial abundance increased from 2011 (2.15) to 2013 (6.90), before declining in 2014 (1.88). Initial abundance of western harvest mice was low in 2011 (0.00), and increased in 2012 (1.21) before falling back to 2011 levels in 2014.

Discussion

Our 3.5-year project is one of the first field studies to examine the effects of patch-burn grazing on the population demography of small mammals, and we provide the first estimates of recruitment and apparent survival a subset of study species. Moreover, our project is unique because we used the same standardized field methods, replicated trapping grids, time period, and

statistical methods to study the effects of rangeland management on population dynamics of seven common species of prairie rodents. The major finding of our work is that different species of small mammals in the tallgrass prairie respond differently to the interaction of fire and grazing on the landscape, indicating that management practices that promote heterogeneity in rangeland ecosystems will benefit a suite of species with different ecological requirements.

Seasonality

We found seasonal patterns in detection probability for five of seven species but patterns of variation in detection were not consistent among species, underscoring the importance of accounting for imperfect detection (Fig. 3.1). White-footed mice were more likely to be encountered in the winter than any other season (Fig. 3.1). Winter corresponds with a period of high recruitment for white-footed mice (Fig. 3.2), and young mice may be more susceptible to live trapping efforts than adults. Winter is also a time of year when food resources are likely scarce which could result in increased attraction of mice to baited traps. Western harvest mice were least likely to be encountered in the summer and fall (Fig. 3.1). During summer, western harvest mice are scansorial in the canopy of herbaceous cover and are less likely to be on the ground where they would have encountered our live traps (Cummins and Slade 2007). Increased detection of eastern woodrats in fall may have been due to greater activity while animals were provisioning winter food caches (Horne et al. 1998). Lower detection probability of thirteen-lined ground squirrels in fall than spring and summer was expected due to onset of hibernation (McCarley 1966).

Seasonal patterns of recruitment and apparent survival were generally similar within a species (Fig. 3.2A and B). Monthly recruitment and apparent survival of deer mice tended to be lowest in spring. We expected deer mouse recruitment to have bimodal peaks in spring and fall because the species has two breeding seasons in tallgrass prairie (Reed et al. 2007). Previous studies have shown that male dispersal and female mortality of deer mice increase during the spring breeding season (Fairbairn 1977). Our finding of low apparent survival of deer mice in spring supports increased emigration and mortality, and it is possible that our analyses did not detect the spring breeding pulse because new individuals entered the population at the same time as high losses were occurring.

Effects of Rangeland Management

Time-since-fire had the greatest effect on population dynamics of rodents in our study, but each species responded differently (Fig 3.3). Species-specific responses to time-since-fire generally followed previously described habitat associations (Grant et al. 1982; Kaufman et al. 1988; Clark et al. 1989; Matlack et al. 2001; Rehmeier et al. 2005; Fuhlendorf et al. 2010; Chapter 2), and responses were grouped according to species that show disturbance positive or negative responses in tallgrass prairie. Deer mice, thirteen-lined ground squirrels, and hispid pocket mice responded positively to fire and grazing disturbance, whereas recruitment of white-footed and western harvest mice was highest in areas with a longer period of time-since-fire.

Patterns of apparent survival generally followed variation in recruitment with the exception of white-footed mice and prairie voles. White-footed mice are associated with woody vegetation in tallgrass prairie (Clark et al. 1987), and were most abundant in our 4BN treatment. The majority

of the shrub cover on our trap grids was near the grid perimeter, and apparent survival could have been low if individuals with home ranges on the periphery of the grid were less likely to be encountered. The mixture of shrubs and native tallgrass prairie in the 4BN treatment is high quality habitat for white-footed mice (Clark et al. 1987), and it is possible that available home ranges in this area were mostly occupied and young animals were more likely to emigrate via dispersal.

We expected demographic performance of prairie voles to be highest in our ungrazed treatment, and at periods of longer time-since-fire (Grant et al. 1982; Clark et al. 1989). Unexpectedly, apparent survival of prairie voles in our study was highest in grazed treatments, and declined with time-since-fire (Figs. 3.3B and 3.4B). Recruitment and survival of prairie voles is higher in areas with greater abundance of forbs (Cole and Batzli 1979), and grazing by cattle or bison increases forb abundance and diversity in tallgrass prairie (Towne et al. 2005). Therefore, a higher abundance and diversity of forbs in our grazed treatments may have resulted in increased abundance and demographic performance of prairie voles in those treatments.

Deer mice are known to be a disturbance positive species that occur at high densities in recently burned and grazed prairie, and at lower densities in less disturbed tallgrass prairie (Grant et al. 1982; Clark et al. 1989; Fuhlendorf et al. 2010; Chapter 2). We expected apparent survival of deer mice to decline as time-since fire increased. However, apparent survival remained relatively constant from 0-3 years after controlled burns, but recruitment of deer mice declined from 0-3 years post-fire (Fig. 3.3B). Thus, lower recruitment rates and not losses to death or

permanent emigration appear to be the demographic mechanism driving lower densities of deer mice in tallgrass prairie that is not grazed or recently burned.

Grazing treatment was an important factor for demographic performance of all of our study species. The greater heterogeneity in the patch-burn grazed treatment, due to cattle selectively grazing recently burned patches increased demographic performance of some species of rodents. Recruitment of deer mice was higher in the heavily grazed year of fire patch of the patch-burn grazed treatment than in the annually burned and grazed treatment with the same time-since-fire. Similarly, recruitment of white-footed mice and western harvest mice was higher in the patch-burn grazed treatment than the annually burned and grazed treatment, and apparent survival of white-footed mice was highest in the recently burned patch of the patch-burn grazed treatment.

Annual Variation

We detected annual variation in population dynamics (Fig. 3.5), which underscores the importance of multi-year studies when making inference on wildlife responses to management actions. Our 3.5-year study period was a relatively short time series to make reliable inferences about endogenous or exogenous factors driving annual differences in small mammal population dynamics. However, recruitment and apparent survival of prairie voles and hispid pocket mice was depressed in the drought year of 2012 (Fig. 3.5A), a year that likely corresponded with a low point in the periodic cycle of vole populations at Konza Prairie (A. M. Ricketts, *pers. obs.*).

Seasonal Variation

Our estimates of monthly apparent survival from the Dail-Madsen model were similar to the range of published estimates from capture-mark-recapture (CMR) models in the literature. Analyses using multistate models on long-term data for marked individuals yielded monthly apparent survival estimates of 0.35-1 for deer mice, 0-0.85 for white-footed mice, and 0.70-0.80 for western harvest mice (Reed and Slade 2007). We did not discriminate between juvenile and adult individuals in our analyses, so our estimates of apparent survival might be biased low relative to estimates of apparent survival restricted to the adult age-class.

Conclusions

The Dail-Madsen model provided a valuable statistical framework for making inference on the population dynamics of small mammals in our study. We conducted monthly live trapping year-round for 3.5 years and logged >52,000 trap-nights of effort, but we captured less than 100 individuals for 6 of 11 study species (Table 2.1). Of the five species that included more than 100 individuals, only deer mice and white-footed mice were captured and re-captured enough to meet sample size requirements of CMR models. By using the Dail-Madsen model, we were able to study the effects of rangeland management practices on population dynamics of five additional species. The Dail-Madsen shows great promise as an analytical tool for studying demographic performance of wildlife species that are not encountered frequently enough to meet the sample needs of capture-mark-recapture methods, or when marking individuals is not practical.

Our results are consistent with previous community-level analyses of small mammal responses to rangeland management, and show that patch-burn grazing can be an effective tool for promoting

small mammal diversity in the tallgrass prairie (Fuhlendorf et al. 2010; Chapter 2). Patterns of demographic performance followed variation in abundance previously reported by Fuhlendorf et al. (2010) and in Chapter 2. Survival and recruitment covaried for each species-treatment combination except white-footed mice in the 4BN treatment, therefore, it is likely that high abundance for the seven species of small mammals included in these analyses indicates high quality habitat and not a sink habitat. Unsurprisingly, small mammals have evolved species-specific habitat relationships to take advantage of the suite of conditions created by the interaction of fire and grazing, processes that historically maintained the tallgrass prairie. Bueno et al. (2012) studied small mammal responses to grazing and concluded that rodents are poor indicators of grassland ecosystem health, because deer mice increased in response to grazing and meadow voles declined in response to grazing. Our field results support the opposite conclusion: small mammals as a group are good indicators of ecosystem health because a complete small mammal community in the tallgrass prairie reflects habitat heterogeneity and a functional ecosystem.

Our results demonstrate that re-establishing the interacting disturbances of fire and grazing promotes biodiversity in rangelands, and that patterns of small mammal diversity in rangelands managed with pyric herbivory reflect habitat quality rather than source-sink dynamics. Rangelands occupy >60% of the land surface in the United States, and constitute most of the habitat available to wildlife in native grasslands (Fuhlendorf and Engle 2001). Restoring the drivers of historical patch dynamics to managed rangelands and publicly held grasslands that are not currently grazed could have profound effects on biodiversity conservation in North America, while continuing to provide ecosystem services to society. Future research is needed to

determine if the pattern of increasing biodiversity is scale-dependent, and at what point

increasing habitat heterogeneity in managed rangelands results in habitat fragmentation.

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Table 3.1 Candidate models and model statistics for initial abundance (λ), recruitment (γ), apparent survival (ω), detection probability (p) of deer mice (*Peromyscus maniculatus*; pema) at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Mixture = *Negative Binomial*			Model Statistics†		
Model Structure‡	**K**	**Dev**	**AIC**	**Δ AIC**	**$w_i \leq$**
Detection					
λ = constant, γ = constant, ω = constant, p = season	8	4154.18	4170.19	0.00	1.00
Abundance					
λ = timesince+graze+year, γ = constant, ω = constant, p = season	13	4111.52	4137.52	0.00	0.58
λ = state+year, γ = constant, ω = constant, p = season	15	4108.72	4138.73	1.21	0.32
Recruitment					
λ = timesince+graze+year, γ = timesince+graze+year+season, ω = constant, p = season	21	3782.71	3824.71	0.00	1.00
Apparent Survival					
λ = timesince+graze+year, γ = timesince+graze+year+season, ω = yr, p = season	22	3764.56	3808.56	0.00	0.34
λ = timesince+graze+year, γ = timesince+graze+year+season, ω = timesince+yr+season, p = season	28	3753.85	3809.85	1.29	0.18

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion (AIC), differences in AIC from the minimum AIC model (Δ AIC), and AIC weights (w_i).

‡ Covariates tested for initial abundance were years since fire (timesince), grazing treatment (graze), year, state, and treatment (trt). Covariates tested for recruitment and apparent survival were those tested for abundance plus season. State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Graze models compared two treatments: grazed and ungrazed. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014, and the year ran from April (1) to March (12).

Table 3.2 Candidate models and model statistics for initial abundance (λ), recruitment (γ), apparent survival (ω), detection probability (p) of white-footed mice (*Peromyscus leucopus*; pele) at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Mixture = *Negative Binomial*	Model Statistics†				
Model Structure‡	**K**	**Dev**	**AIC**	**Δ AIC**	$w_i \leq$
Detection					
λ = constant, γ = constant, ω = constant, p = season	8	2695.08	2711.08	0.00	0.98
Abundance					
λ = trt+yr, γ = constant, ω = constant, p = season	13	2668.03	2694.03	0.00	0.36
λ = trt, γ = constant, ω = constant, p = season	10	2674.29	2694.29	0.26	0.32
λ = state+year, γ = constant, ω = constant, p = season	15	2665.48	2695.48	1.45	0.18
Recruitment					
λ = trt+yr, γ = timesince+graze+year+season, ω = constant, p = season	21	2538.62	2580.62	0.00	1.00
Apparent Survival					
λ = trt+yr, γ = timesince+graze+year+season, ω = state+year+season, p = season	31	2484.12	2546.11	0.00	0.64
λ = trt+yr, γ = timesince+graze+year+season, ω = state+year, p = season	28	2491.58	2547.58	1.47	0.31

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion (AIC), differences in AIC from the minimum AIC model (Δ AIC), and AIC weights (w_i).

‡ Covariates tested for initial abundance were years since fire (timesince), grazing treatment (graze), year, state, and treatment (trt). Covariates tested for recruitment and apparent survival were those tested for abundance plus season. State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Graze models compared two treatments: grazed and ungrazed. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014, and the year ran from April (1) to March (12).

Table 3.3 Candidate models and model statistics for initial abundance (λ), recruitment (γ), apparent survival (ω), detection probability (p) of western harvest mice (*Reithrodontomys megalotis*; reme) at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Mixture = *Zero Inflated Poisson*	Model Statistics†				
Model Structure‡	**K**	**Dev**	**AIC**	**Δ AIC**	$w_i \leq$
Detection					
λ = constant, γ = constant, ω = constant, p = season	8	1141.82	1157.82	0.00	0.99
Abundance					
λ = graze, γ = constant, ω = constant, p = season	9	1130.66	1148.66	0.00	0.49
λ = graze+timesince, γ = constant, ω = constant, p = season	10	1129.12	1149.12	0.45	0.39
Recruitment					
λ = graze, γ = timesince+graze+year+season, ω = constant, p = season	17	1002.74	1036.75	0.00	0.99
Apparent Survival					
λ = constant, γ = constant, ω = timesince+yr, p = season	12	1078.29	1102.29	0.00	1.00

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion (AIC), differences in AIC from the minimum AIC model (Δ AIC), and AIC weights (w_i).

‡ Covariates tested for initial abundance were years since fire (timesince), grazing treatment (graze), year, state, and treatment (trt). Covariates tested for recruitment and apparent survival were those tested for abundance plus season. State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Graze models compared two treatments: grazed and ungrazed. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014, and the year ran from April (1) to March (12).

Table 3.4 Candidate models and model statistics for initial abundance (λ), recruitment (γ), apparent survival (ω), detection probability (p) of prairie voles (*Microtus ochrogaster*; mioc) at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Mixture = *Zero Inflated Poisson*			Model Statistics†		
Model Structure‡	**K**	**Dev**	**AIC**	**Δ AIC**	***w_i* ≤**
Detection					
λ = constant, γ = constant, ω = constant, p = constant	4	948.30	958.30	0.00	0.88
Abundance					
λ = graze+timesince, γ = constant, ω = constant, p = constant	7	939.08	953.08	0.00	0.77
Recruitment					
λ = constant, γ = graze+year, ω = constant, p = constant	9	905.21	923.21	0.00	0.32
λ = constant, γ = graze+year+timesince, ω = constant, p = constant	10	903.69	923.69	0.48	0.25
λ = constant, γ = graze+year+season, ω = constant, p = constant	12	900.80	924.80	1.59	0.14
λ = constant, γ = treatment+year, ω = constant, p = constant	10	905.14	925.14	1.93	0.12
λ = constant, γ = graze+timesince+year+season, ω = constant, p = constant	13	899.17	925.17	1.96	0.12
Apparent Survival					
λ = constant, γ = constant, ω = year, p = constant	8	916.04	932.04	0.00	1.00

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion (AIC), differences in AIC from the minimum AIC model (Δ AIC), and AIC weights (w_i).

‡ Covariates tested for initial abundance were years since fire (timesince), grazing treatment (graze), year, state, and treatment (trt). Covariates tested for recruitment and apparent survival were those tested for abundance plus season. State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Graze models compared two treatments: grazed and ungrazed. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014, and the year ran from April (1) to March (12).

Table 3.5 Candidate models and model statistics for initial abundance (λ), recruitment (γ), apparent survival (ω), detection probability (*p*) of hispid pocket mice (*Chaetodipus hispidus*; chhi) at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Mixture = *Poisson*	Model Statistics†				
Model Structure‡	**K**	**Dev**	**AIC**	**Δ AIC**	$w_i \le$
Detection					
λ = constant, γ = constant, ω = constant, p = constant	4	535.50	543.50	0	0.56
Abundance					
λ = timesince, γ = constant, ω = constant, p = constant	5	531.06	541.06	0.00	0.52
λ = timesince+graze, γ = constant, ω = constant, p = constant	6	531.04	543.03	1.97	0.19
Recruitment					
λ = constant, γ = timesince+season, ω = constant, p = constant	7	517.89	531.89	0.00	0.61
λ = constant, γ = timesince+graze+season, ω = constant, p = constant	8	517.79	533.79	1.90	0.24
Apparent Survival					
λ = constant, γ = constant, ω = season, p = constant	6	530.55	536.10	0.00	0.29
λ = constant, γ = constant, ω = constant, p = constant	4	535.50	537.78	0.95	0.18
λ = constant, γ = constant, ω = graze, p = constant	5	533.68	537.80	1.14	0.17
λ = constant, γ = constant, ω = timesince+season, p = constant	7	530.39	538.10	1.84	0.12
λ = constant, γ = constant, ω = timesince, p = constant	5	534.51	538.10	1.96	0.11

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion (AIC), differences in AIC from the minimum AIC model (Δ AIC), and AIC weights (w_i).

‡ Covariates tested for initial abundance were years since fire (timesince), grazing treatment (graze), year, state, and treatment (trt). Covariates tested for recruitment and apparent survival were those tested for abundance plus season. State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Graze models compared two treatments: grazed and ungrazed. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014, and the year ran from April (1) to March (12).

Table 3.6 Candidate models and model statistics for initial abundance (λ), recruitment (γ), apparent survival (ω), detection probability (*p*) of eastern woodrats (*Neotoma floridana*; nefl) at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Mixture = *Negative Binomial*	Model Statistics†				
Model Structure‡	**K**	**Dev**	**AIC**	**Δ AIC**	**$w_i \leq$**
Detection					
λ = constant, γ = constant, ω = constant, p = season	9	793.54	811.55	0.00	1
Abundance					
λ = graze+year, γ = constant, ω = constant, p = season	12	761.20	785.19	0.00	0.53
λ = timesince+graze+year, γ = constant, ω = constant, p = season	13	531.04	785.44	0.25	0.47
Recruitment					
λ = constant, γ = treatment+year, ω = constant, p = season	13	731.63	757.63	0.00	0.39
λ = constant, γ = treatment+year+season, ω = constant, p = season	16	726.87	758.87	1.24	0.21
λ = constant, γ = graze+year, ω = constant, p = season	12	735.13	759.13	1.49	0.18
Apparent Survival					
λ = constant, γ = constant, ω = timesince+graze, p = season	10	783.52	803.52	0.00	0.19
λ = constant, γ = constant, ω = timesince+graze+season, p = season	13	777.65	803.65	0.13	0.18
λ = constant, γ = constant, ω = graze, p = season	9	786.34	804.34	0.81	0.13
λ = constant, γ = constant, ω = timesince+graze+year, p = season	13	778.49	804.49	0.97	0.12
λ = constant, γ = constant, ω = treatment, p = season	10	784.73	804.73	1.21	0.10
λ = constant, γ = constant, ω = graze+season, p = season	12	780.78	804.78	1.25	0.10

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion (AIC), differences in AIC from the minimum AIC model (Δ AIC), and AIC weights (*w_i*).

‡ Covariates tested for initial abundance were years since fire (timesince), grazing treatment (graze), year, state, and treatment (trt). Covariates tested for recruitment and apparent survival were those tested for abundance plus season. State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Graze models

compared two treatments: grazed and ungrazed. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014, and the year ran from April (1) to March (12).

Table 3.7 Candidate models and model statistics for initial abundance (λ), recruitment (γ), apparent survival (ω), detection probability (*p*) of thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*; ictr) at Konza Prairie Biological Station, Kansas, USA from June 2011 to December 2014.

Mixture = *Poisson*			Model Statistics†		
Model Structure‡	**K**	**Dev**	**AIC**	**Δ AIC**	$w_i \leq$
Detection					
λ = constant, γ = constant, ω = constant, p = season	6	660.96	672.97	0.00	1.00
Abundance					
λ = constant, γ = constant, ω = constant, p = season	6	660.96	672.97	0.00	0.55
λ = timesince, γ = constant, ω = constant, p = season	7	659.37	673.37	0.41	0.45
Recruitment					
λ = constant, γ = timesince+graze+yr, ω = constant, p = season	11	619.42	641.42	0.00	0.79
Apparent Survival					
λ = constant, γ = constant, ω = constant, p = season	6	660.96	672.97	0.00	1.00

† Model fit is described by the number of parameters (K), Deviance or -2 log likelihood (Dev), Akaike's Information Criterion (AIC), differences in AIC from the minimum AIC model (Δ AIC), and AIC weights (w_i).

‡ Covariates tested for initial abundance were years since fire (timesince), grazing treatment (graze), year, state, and treatment (trt). Covariates tested for recruitment and apparent survival were those tested for abundance plus season. State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time-since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Graze models compared two treatments: grazed and ungrazed. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Biological years of the study were 2011-12, 2012-13, 2013-14, and 2014, and the year ran from April (1) to March (12).
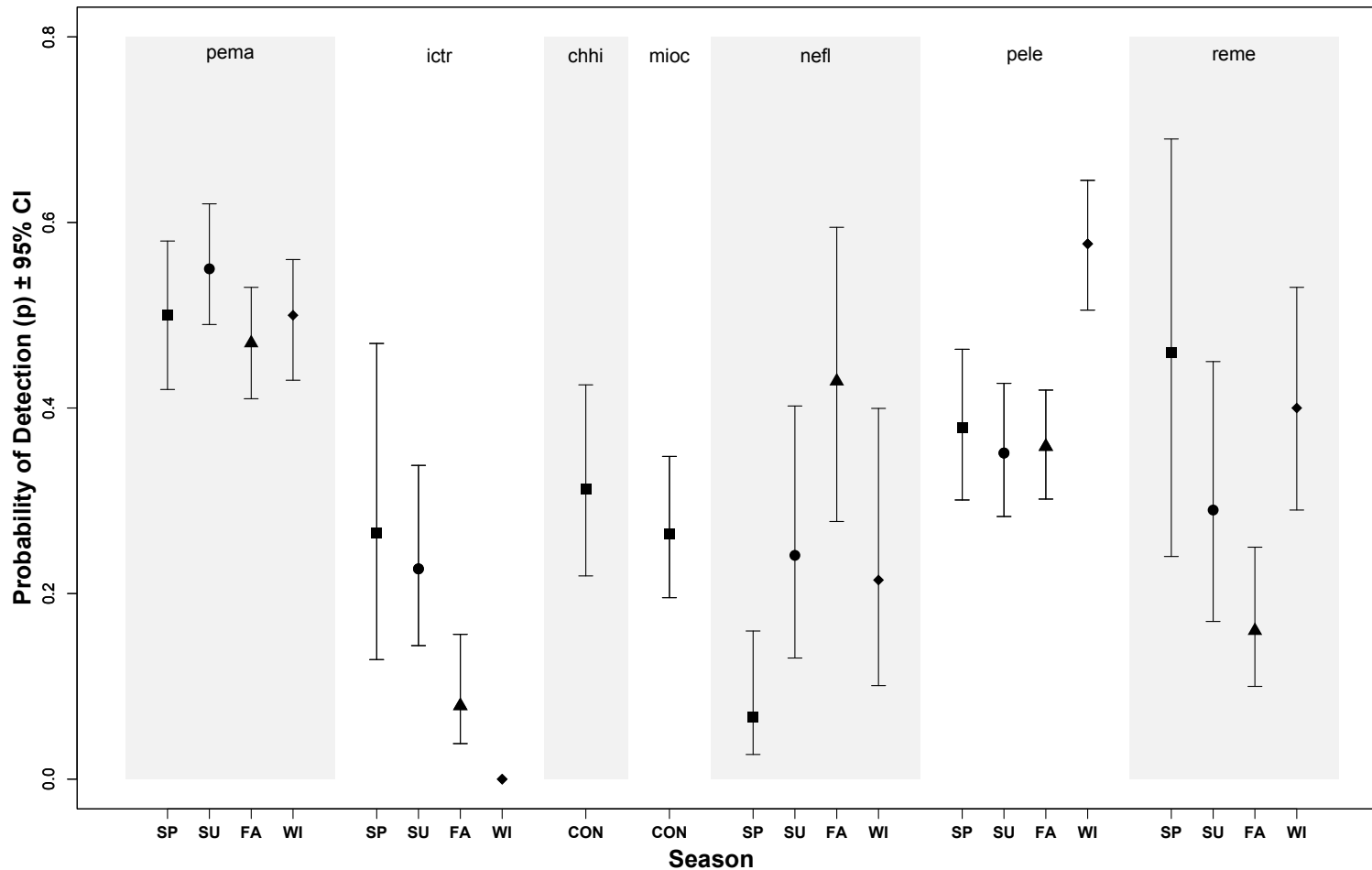
Figure 3.1 Monthly probability of detection (*p*) for seven species of small mammals captured at Konza Prairie Biological Station, Kansas, USA during four biological years from June 2011 – December 2014. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). The top model for detection probability for prairie voles and hispid pocket mice included the intercept-only model with no additional covariates (CON). Small mammal species included: deer mice (*Peromyscus maniculatus*, pema), thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*, ictr), hispid pocket mice (*Chaetodipus hispidus*, chhi), prairie voles (*Microtus ochrogaster*, mioc), eastern woodrats (*Neotoma floridana,* nefl), white-footed mice (*P. leucopus*, pele), and western harvest mice (*Reithrodontomys megalotis*, reme).

Figure 3.2 Monthly estimates of recruitment (γ; A) and apparent survival (ω; B) for seven species of small mammals captured at Konza Prairie Biological Station, Kansas, USA during four biological years from June 2011 – December 2014. Seasons for the study included spring (March – May; SP), summer (June – August; SU), fall (September – October; FA), and winter (December – February; WI). Single estimates for a species were taken from an intercept-only model. NA indicates that a species was not available during a season due to hibernation. Refer to Fig. 3.1 for species names and corresponding codes.
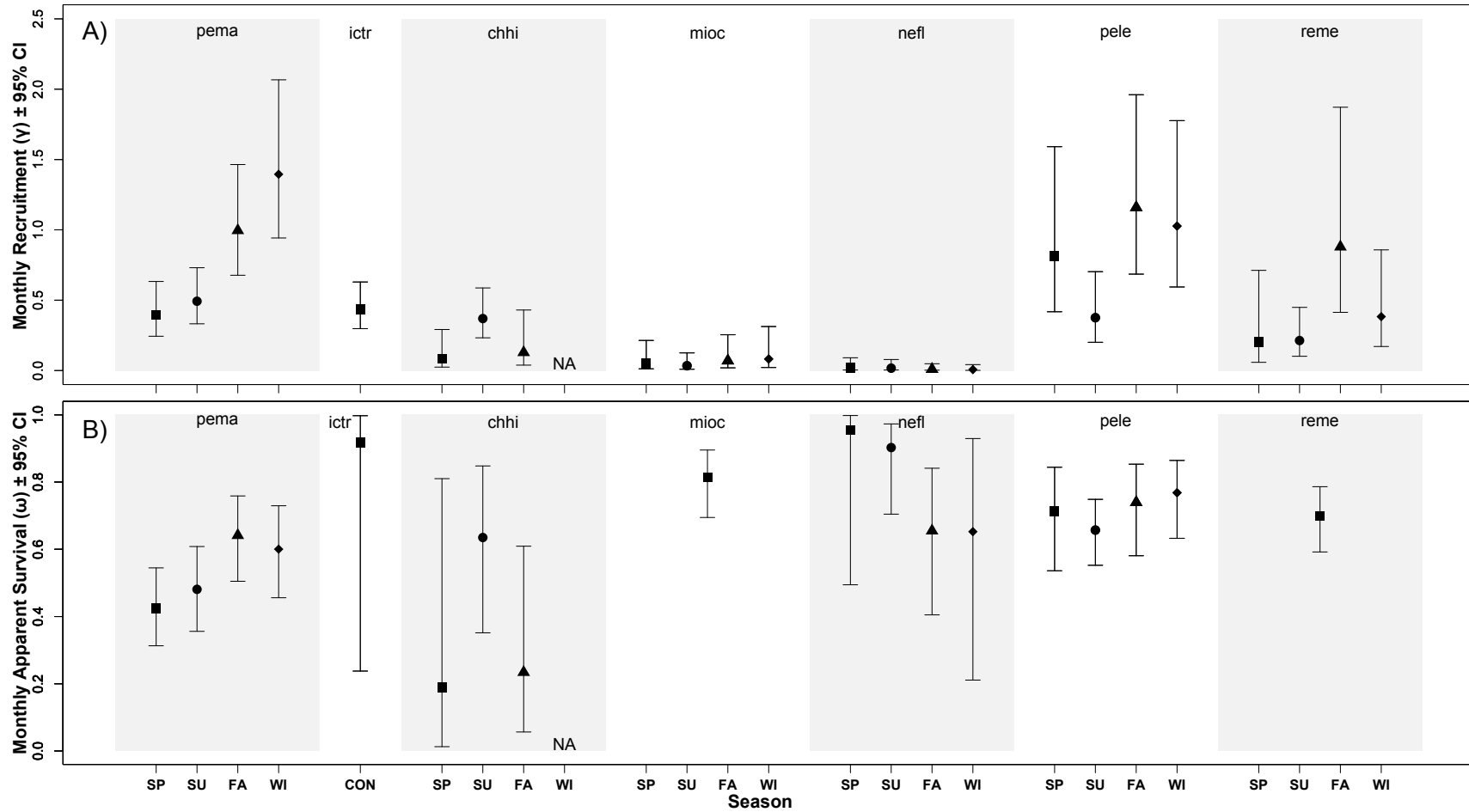
Figure 3.3 Monthly estimates of recruitment (γ; A), apparent survival (ω; B), and initial abundance (λ; C) for seven species of small mammals at zero, one, two, and three years since controlled burns at Konza Prairie Biological Station, Kansas, USA during four biological years from June 2011-December 2014. The maximum value for time-since-fire within grazed treatments was two years. Single estimates for a species were taken from an intercept-only model. Refer to Fig. 3.1 for species names and corresponding codes.
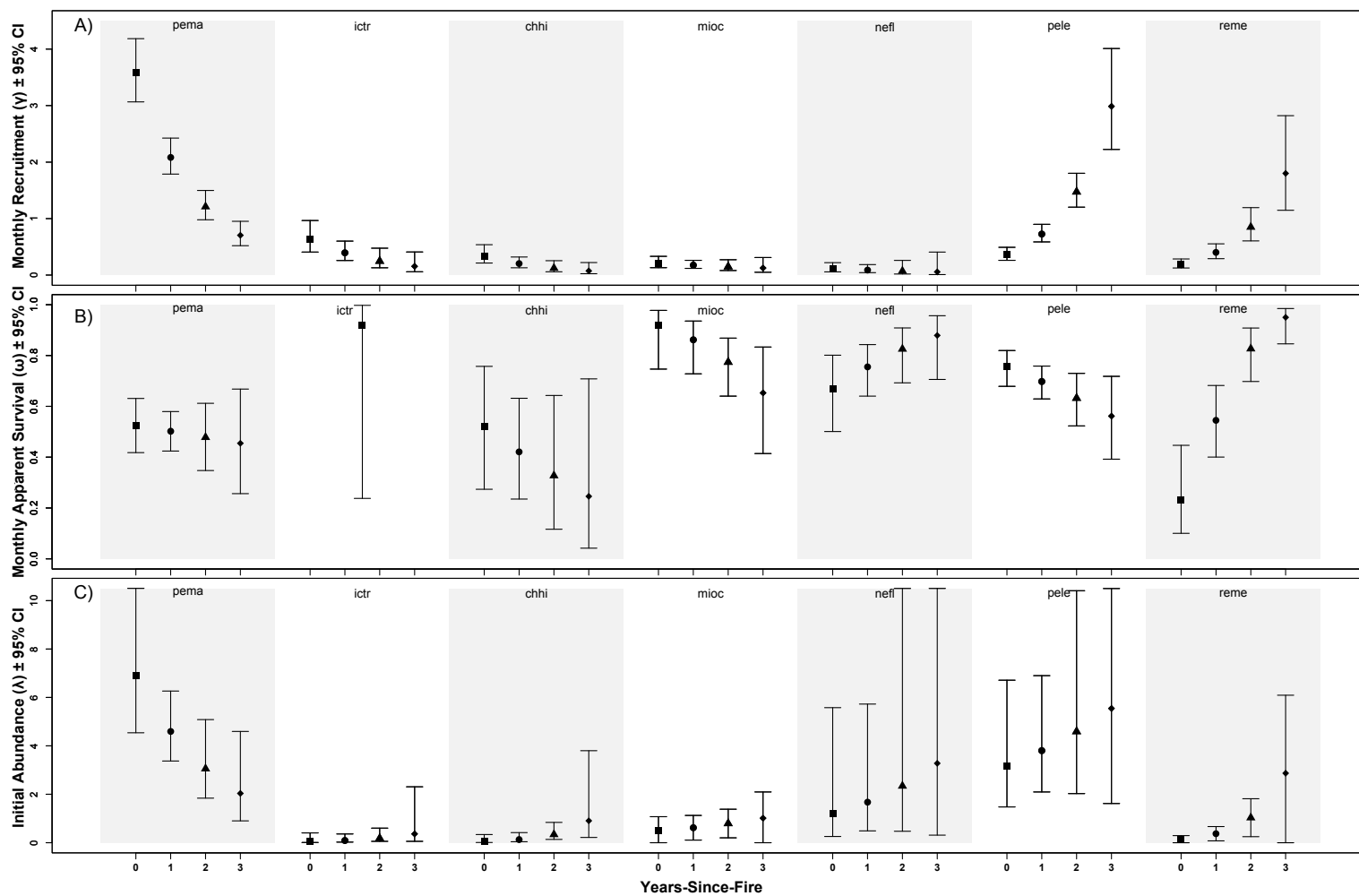
Figure 3.4 Monthly estimates of recruitment (γ; A), apparent survival (ω; B), and initial abundance (λ; C) for seven species of small mammals in annually burned and grazed (ABG), all patch-burn grazed treatments combined (PBG), each patch of the patch-burn grazed pasture (PB0-2), the ungrazed treatment with a 4-year fire return interval (4BN), grazed (G), and ungrazed (U) treatments at Konza Prairie Biological Station, Kansas, USA, from June 2011 to December 2014. Numbers following PB in the right panel correspond to time-since fire for a patch (0-2 years). Results are shown for the greatest number of factor levels our data would support for each species. Single estimates for a species were taken from an intercept-only model. Refer to Fig. 3.1 for species names and corresponding codes.
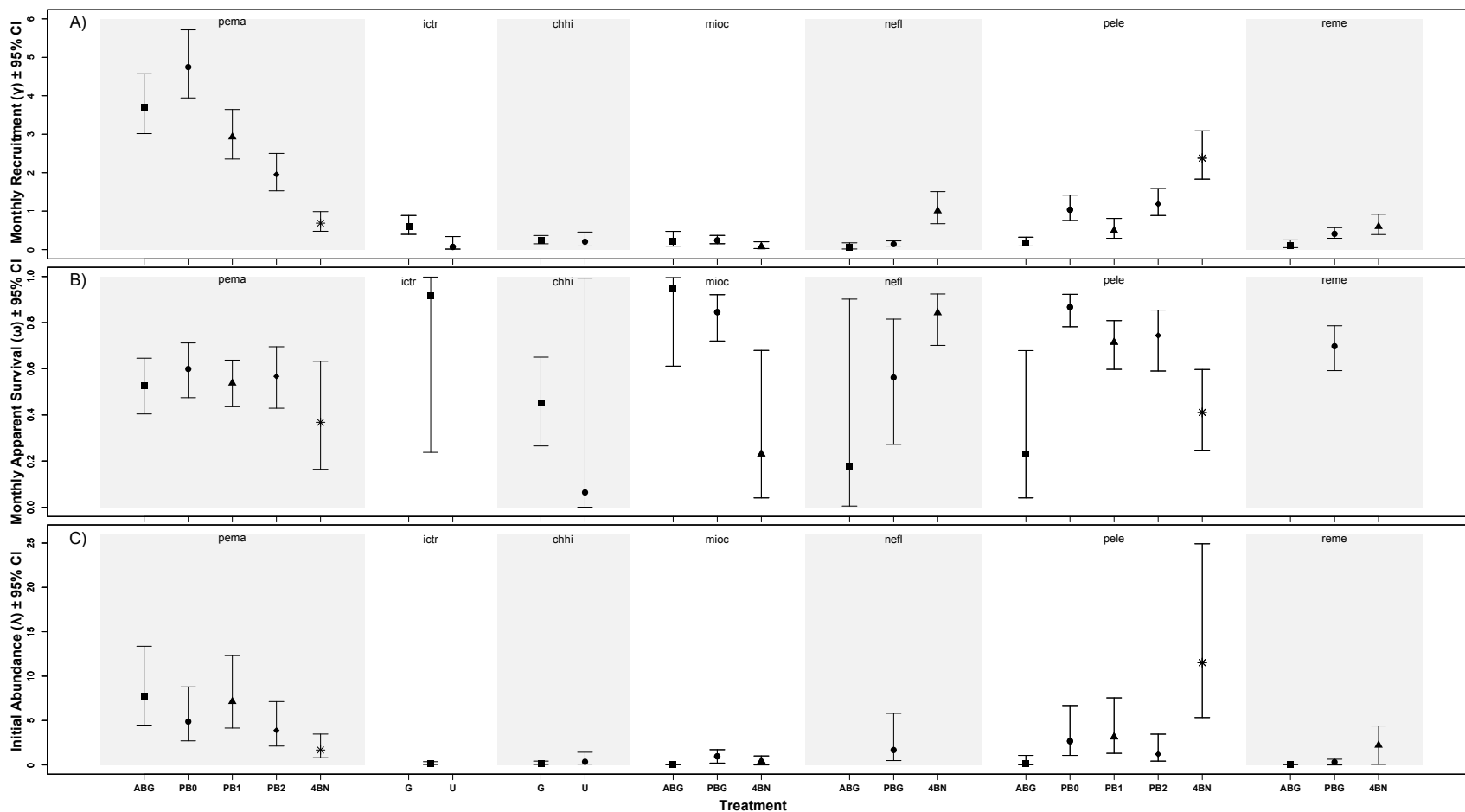
Figure 3.5 Monthly estimates of recruitment (γ; A), apparent survival (ω; B), and initial abundance (λ; C) for seven species of small mammals at Konza Prairie Biological Station, Kansas, USA during four biological years from June 2011 – December 2014. Biological years of the study ran from April to the following March in 2011 – 2012, 2012 – 2013, 2013 – 2014, and April through December in 2014. Single estimates for a species are estimates from an intercept-only model. Refer to Fig. 3.1 for species names and corresponding codes.
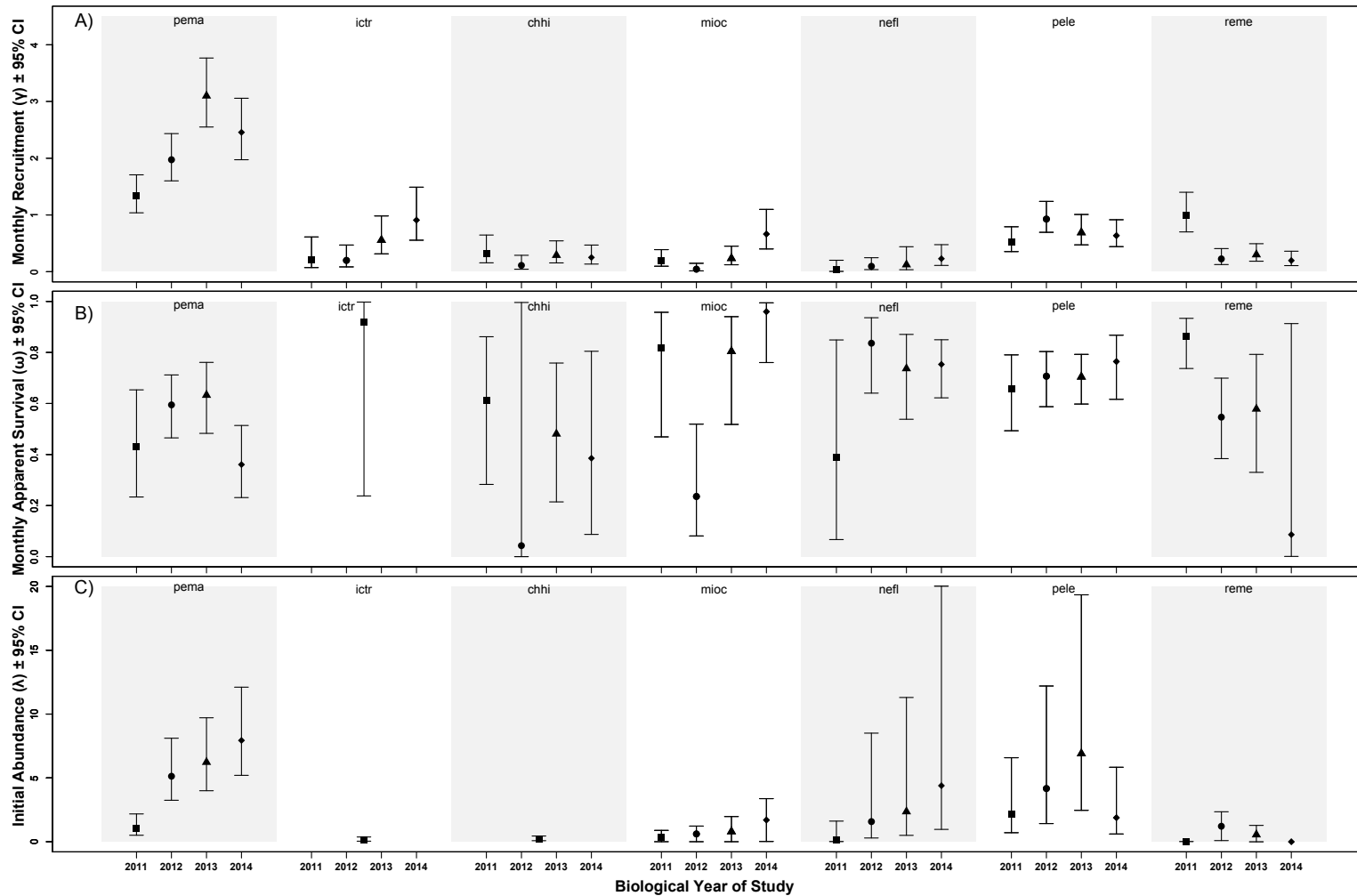
Chapter 4 - Resource selection and survival of coyotes in managed rangelands in tallgrass prairie

Abstract

Coyotes play an important ecological role in North America as predators of small mammals, ground-nesting birds, ungulates, and other mesopredators. Moreover, coyotes are an economically important species in North America because of negative impacts on livestock production and positive value as a harvested furbearer. The positive and negative economic values placed on coyotes by society subject them to high levels of mortality from anthropogenic sources. In rangelands, the interaction of fire and grazing on the landscape plays a large role in shaping habitat conditions and small mammal communities. Therefore, differences in habitat conditions and prey abundance driven by the interaction of fire and grazing are likely to play a role in how coyotes use the landscape. Our goals for this field study were twofold. First, using resource utilization functions and GPS telemetry, we tested the effects of time-since-fire and grazing treatment as components of rangeland management that may affect resource selection by coyotes. Second, we estimated annual survival and weekly mortality risk of coyotes in a population of coyotes captured at a protected reserve. From April 2013 to March 2016, we used GPS-collars to monitor 15 coyotes for resource selection, and 17 coyotes for weekly and annual survival in northeast Kansas. Coyotes in our field study showed no selection for grazed versus ungrazed areas, but selected areas with shorter time-since-fire during three seasons: prebreeding, breeding, and gestation (November through March). Surprisingly, coyotes selected habitats in which their primary small mammal prey tend to be least abundant during the seasons in which diet studies indicate they depend most heavily on small mammals as prey items. Our estimate of annual survival was intermediate (0.48) compared to other studies of coyote survival, and the

instantaneous risk of mortality peaked in the fall and remained high throughout winter. Overall, our results suggest that coyotes are selecting habitats where their preferred prey are least abundant, and are most vulnerable to mortality during dispersal. If coyotes are limiting their preferred prey species in rangelands managed with frequent fire, they may be causing a trophic cascade by reducing small mammal diversity, which could reduce plant species diversity.

Introduction

Coyotes (*Canis latrans*) play an important ecological role in North America as predators of small mammals (Brillhart and Kaufman 1994; Brillhart and Kaufman 1995; Kamler et al. 2002), ground-nesting birds (Winder et al. 2016), ungulates (Crête and Desrosiers 1995; Berger and Conner 2008; Boisjoly et al. 2010; Kilgo et al. 2012), and other mesopredators (Fedriani et al. 2000; Kamler et al. 2003; Kamler and Gipson 2004). Experimental removal of coyotes in Texas resulted in a trophic cascade in which rodent richness was significantly reduced because Ord's kangaroo rats (*Dipodomys ordii*), a competitive dominant, were released from predation pressure (Henke and Bryant 1999). Similarly, Mezqueda et al. (2006) hypothesized that coyotes might indirectly benefit Greater Sage-Grouse (*Centrocercus urophasianus*) by controlling other mesopredators, such as red fox and badgers (*Taxidea taxus*). However, coyotes accounted for more than 40% of nest predation events in a nest camera study of Greater Prairie-Chicken (*Tympanuchus cupido*) near the Flint Hills of Kansas, and low nest success due to predation is a limiting factor for this species and other ground-nesting birds (McNew et al. 2013, Winder et al. 2016). Predation by coyotes has been identified as the greatest source of mortality for red foxes (*Vulpes vulpes*) and swift foxes (*V. velox*) in Kansas and Colorado (Sovada et al. 1998; Kitchen et al. 1999), and foxes persist in habitats with low numbers of coyotes.

In addition to their ecological importance, coyotes are an economically important species in North American rangelands, and were responsible for losses of more than $18 million in sheep and lambs in 2014, and $48 million in cattle and calves in 2010 as reported by livestock producers in the United States (NASS 2011; APHIS 2015). From 2004 to 2014, USDA APHIS Wildlife Services culled an average of >75,000 coyotes per year in response to wildlife damage complaints (USDA 2004-2014). In addition to organized predator control efforts, coyotes are often subject to opportunistic shooting or poisoning by ranchers and rural residents (Gese et al. 1989). Moreover, there is growing interest in harvesting coyotes among recreational hunters via predator calling. Coyotes are also an economically important furbearer in North America. In February and April of 2016, North American Fur Auctions sold ~94,000 coyote pelts for more than $5.5 million, and 99% of coyote pelts are used to trim parkas (B. MacMillan, *pers. comm.*). Thus, the positive and negative economic values placed on coyotes by society subject them to high levels of mortality from anthropogenic sources (Heisey and Patterson 2006). Nevertheless, coyote populations in North America continue to expand in numbers and range (Levy 2012).

Coyotes are often classified by status within a social hierarchy. Residents include breeding pairs with established territories, and associated pack members that are the previous years' offspring of the breeding pair that remain in the territory and assist with pup rearing before dispersal. Transients are non-territorial individuals with large home ranges in the interstitial areas between the territories of residents. Studies of habitat selection of coyotes in rangelands have shown mixed results for patterns of habitat selection. In northeast Kansas, resident coyotes selected native prairie, whereas transients selected agricultural fields and heavier cover in areas with

introduced grasses or wooded areas (Kamler and Gipson 2000; Kamler et al. 2005). Kamler et al. (2005) hypothesized that resident coyotes selected native prairie because it contained a greater abundance of prey, and that solitary transients selected heavier cover for concealment. In eastern Colorado, coyotes selected pinyon-juniper cover and shrub-grasslands, but used open grasslands in lower proportions than expected based on availability (Gese et al. 1988).

Food availability is one factor that plays a role in habitat selection by coyotes (Gese et al. 1988; Kamler et al. 2005; Moorcroft et al. 2006). Analyses of coyote scats and stomach contents from harvested individuals have shown that coyotes prey upon small mammals year round, but that rodents are a main prey item during winter and spring (Gier 1968; Brillhart and Kaufman 1994; Kamler 2002). Moreover, coyotes selectively prey upon some small mammal species more than others. In particular, coyotes select arvicoline rodents such as voles (*Microtus* spp.) and southern bog lemmings (*Synaptomys cooperi*), and cotton rats (*Sigmodon hispidus*; Brillhart and Kaufman 1994). Insects, wild fruits, and ungulate fawns comprise the majority of coyote diets during summer and early fall (Brillhart and Kaufman 1994). Thus, coyotes are omnivorous, and capitalize on seasonally available food sources, so habitat selection is likely to covary with abundance of different food sources that coyotes use throughout the year (Gier 1968).

Previous research on space use and resource selection by coyotes has focused on use of different landcover types, such as grassland, forest, shrubland, and cropland (Gese et al. 1988; Kamler and Gipson 2000; Kamler et al. 2005), but coyote responses to habitat management in working landscapes are poorly understood. In rangelands of the Great Plains, the interaction of fire and grazing on the landscape plays a large role in shaping habitat conditions and small mammal

communities (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2010; Chapter 2). Therefore, differences in habitat conditions and prey abundance driven by the interaction of fire and grazing are likely to play a role in how coyotes use the landscape. Our goals for this field study were twofold. First, using resource utilization functions and GPS telemetry, we tested the effects of time-since-fire and grazing treatment as components of rangeland management that may affect resource selection by coyotes. Second, we estimated annual survival and weekly mortality risk of coyotes in a population captured on a protected rangeland. We predicted that coyotes would select grassland habitats with longer time-since-fire, because of increased abundance of their primary prey species in areas that have not recently burned. Additionally, we predicted that annual survival of coyotes in our study would be higher than in past studies of populations exposed to shooting by ranchers or fur trapping. Last, we predicted that coyote mortality would be highest in fall and winter, due to increased movements associated with dispersal in fall and lower food availability in winter.

Methods

Capture and Handling

Starting in April 2013, we live-captured coyotes at Konza Prairie Biological Station in northeast Kansas using padded-jaw foothold traps (#3 Soft Catch®, Oneida Victor® Limited Inc., Euclid, OH, USA) and cable restraints (KBS 1, Kaatz Bros Lures, Savanna, IL, USA; or SNARE503, The Snare Shop, Lidderdale, IA, USA). Traps were buried in shallow soil in areas with fresh tracks or scat, and baited using commercial lures or carcasses of road-killed deer. To minimize the time required for trap checks and to ensure that captured animals were processed quickly, we focused our capture effort at areas near roads and firebreaks. We physically restrained captured

coyotes with a catch-pole (ACP-5, Tomahawk Live Traps, Hazelhurst,WI, USA), and then administered 30 mg Telazol® intramuscularly. The purpose of chemical immobilization was to reduce handling stress to animals and for safe handling, rather than for anesthesia. Some coyotes were not rendered completely unconscious by the 30 mg dose of Telazol®, but this was desirable because partial immobilization led to faster recovery times. When coyotes showed signs of anesthesia induction such as side-to-side head bobbing and laying the head down, we approached the coyotes from behind, and grasped the loose skin at the nape. We closed the mouth of the coyote from below with a gloved hand and applied a muzzle by firmly wrapping electrical tape around the snout of the animal with the adhesive side of the tape away from the fur. Last, coyotes were blindfolded for the duration of handling and monitored for signs of stress. Our field procedures resulted in no handling mortality during the study. Coyotes were weighed to the nearest 0.1 kg using a digital scale (Berkley BTDFS50-1, Pure Fishing Inc., Columbia, SC, USA), sex was determined by external genitalia, and coyotes ≥10.6 kg were fitted with a GPS collar (475 g, Model 2110L, Advanced Telemetry Systems, Isanti, MN, USA). All procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocol 3252), and conducted under state wildlife permits from Kansas Department of Wildlife, Parks, and Tourism.

For the first six coyotes collared, GPS collars were programmed to obtain a GPS fix every two hours from 17:00 – 09:00, with an additional fix at 13:00 for a mid-day location for a total of 11 locations per day. Collars were equipped with programmable drop-off devices that were set to release the collar in December, so that collars could be refurbished and redeployed in February. Collars were recovered after planned e-release or from mortalities, refurbished if necessary, and

redeployed in a staggered entry design. On subsequent deployments of GPS collars on all coyotes, collars were programmed to obtain a GPS fix every hour from 17:00 – 09:00, with a mid-day location at 13:00 for a total of 18 locations per day. Drop-offs were programed to release ~350 days from the deployment date. We increased the GPS fix schedule because collar battery life was sufficient to allow for recording of additional locations.

Covariates

All data processing for spatial covariates was conducted using QGIS 2.12 and R (QGIS Development Team 2016; R Core Team 2016). Rangeland management covariates used in our spatial analyses included time-since fire (years), and whether an area was grazed or not. We had detailed information about grazing treatments for Konza Prairie, but not for surrounding privately owned land. The main uses for privately owned tallgrass prairie in the northern Flint Hills are grazing for cattle production, and some haying (With et al. 2008). Therefore, we inspected National Agriculture Inventory Program satellite imagery (NAIP) with 1 m resolution for evidence of cattle grazing (trailing, bare areas where mineral is provided, or cattle present in the image) or hay cutting (obvious mowing patterns, hay bales present in the image), or visited field sites to determine if grassland habitat was grazed or not. We did not differentiate between species of livestock or grazing systems, but most were domestic cattle with some bison or horses. We then created a categorical raster dataset of our study area with 30 m × 30 m resolution that indicated if an area was grazed (1) or ungrazed (0).

We generated time-since fire rasters for each year of our study from annual burned area rasters created from spectral analysis of MODIS imagery for 2000-2010 (Mohler and Goodin 2012), and

rasters created by Kansas Department of Health and Environment using the methodology of Mohler and Goodin (2012) for 2011-2015. Time-since-fire values were retained only for grassland or woody vegetation as classified by the 2015 US Department of Agriculture National Agricultural Statistics Service Cropland Data Layer dataset (CDL) dataset. Three other cover types included in coyote utilization distributions (UD) were urban development, cropland, or water and were given a value of 0 years-since fire. Gravel and paved roads large enough to be classified in the CDL dataset were included in the developed category. We chose 0 years-since fire for non-grassland cover because developed areas and tilled crop fields are disturbed areas, and habitat conditions in these areas would be more similar to burned than unburned prairie. Arbitrary categories for rare cover types allowed us to include all GPS locations in the analysis, but the average seasonal UD for a coyote in our study included only 8.7% non-grassland habitat.

Space Use

Movements and space use of organisms are often structured according to the annual cycle of the species. Therefore, it is important to analyze animal locations during biologically meaningful time periods for the species of interest. We modeled space use of coyotes following the six seasons proposed by Andelt and Gipson (1979) for coyotes in Nebraska: breeding, February; gestation, March and April; nursing, May and June; pup training, July through 15 September; dispersal (*sensu* "adolescence" in Andelt and Gipson 1976), 16 September through 15 November; and prebreeding, 16 November through January. Thus, if coyotes were monitored for an entire year, we generated six utilization distributions that corresponded to the six seasons for each for each coyote. Recommendations for a minimum number of animal relocations required for estimating the utilization distribution of an animal range from 30 to 200, depending

on the statistical method used to generate the UD (Aebischer et al. 1993; Millspaugh et al. 2006).

A more biologically relevant criteria is that an animal should have time to traverse its entire

home range during the period that a UD is generated, and relocations should occur at sufficiently

short intervals during the period in question to provide an accurate representation of the space

use of the individual (Laver and Kelly 2008). Our GPS fix schedule collected 10 to 17 locations

per day per coyote during the peak periods of activity, unless there were missed fixes due to

cover interfering with the collar's ability to communicate with satellites or other collar issues.

Thus, we collected a large sample of GPS locations for each animal more quickly than an

individual might be able to traverse its entire home range. Therefore, to be included in analyses

for a given season, we required that a coyote be monitored for >14 days, which resulted in more

than 140 locations for analysis. We subsampled location data for coyotes with an hourly GPS fix

schedule to match the bi-hourly schedule for coyotes in the initial deployment for all spatial

analyses.

We created utilization distributions for each coyote-season using the method of biased random

bridges (BRB), which use serial autocorrelation in location data to improve the utilization

distribution, rather than requiring temporally independent locations and ignoring finer scale

movements (Benhamou and Cornelis 2010; Benhamou 2011). Generating utilization

distributions using BRBs rather than traditional kernel methods allowed us to make full use of

our high-resolution location data for individual coyotes, rather than discarding thousands of data

points to achieve temporal independence among successive locations. Moreover, thinning

animal relocation data to achieve independence between consecutive pairs of locations ignores

biologically relevant movements, and can underestimate space use (Reynolds and Laundre

1990). We created UDs using package "adehabitatHR" in R. We set the minimum smoothing parameter for the BRB formula to one-half of the mean distance moved between locations by all coyotes in a given season (Benhamou and Cornelis 2010). Tmax, or the maximum time between successive animal locations in a movement bout was set to 12 hours. Given the crepuscular activity pattern of coyotes, we assumed that a coyote would complete each movement bout within a 12 hour period.

Resource Utilization Functions

All statistical analyses were conducted in R (R Core Team 2016). To study the effects of rangeland management on resource selection by coyotes, we used resource utilization functions (hereafter, RUFs). RUFs use a multiple linear regression framework to relate a probabilistic measure of differential space use within the utilization distribution of an animal to resources on the landscape (Marzluff et al. 2004). Furthermore, RUFs account for spatial autocorrelation in predictor and response variables using a Matern autocorrelation function (Marzluff et al. 2004). We allowed the RUF algorithm to determine the appropriate spatial range for the Matern autocorrelation function via Maximum Likelihood methods, but set the smoothness parameter to 1.5 after Marzluff et al. (2004). For some utilization distributions, the range parameter was not estimable with a smoothness of 1.5, so we reduced the value by increments of 0.5 until the range was estimable. In a few instances, the range parameter was not estimable at a smoothness of 0.5, so we reduced the value by increments of 0.1 until the range could be estimated.

Seasonal and Annual Survival

We estimated weekly survival rates for coyotes using staggered entry Kaplan-Meier models in the "survival" package of R (Therneau 2015; R Core Team 2016). No coyote mortalities occurred during handling or within one week of capture, so no individuals were excluded from the analysis due to possible effects of handling mortality. Only mortality events that occurred while GPS collars were properly functioning were included in survival analyses. Encounter histories were created for individual coyotes based on weekly time steps for a biological year that ran from 1 April to 31 March. Our data were left-censored to account for staggered entry into the population of GPS monitored coyotes, and right-censored when collars failed. Six coyotes were monitored in more than one year, or were captured and collared a second time after the first collar failed or was lost. We accounted for lack of independence in multiple samples from the same coyote using the cluster function on individual identity. We tested for differences in weekly survival among years and sexes and tested the assumption of proportional hazards using Cox proportional hazard models and the "cox.zph" function in the "survival" package.

To examine seasonal mortality risk of coyotes, we estimated hazard functions based on weekly encounter histories using smoothing spline functions in package "gss" of R (Chong 2014). To determine the appropriate value of the smoothing parameter, we reduced the smoothing parameter from the default value of 1.2 until the fitted hazard rate curve appeared over-fit with peaks and valleys. We then increased the value of the smoothing parameter by increments of 0.1 until the curve no longer contained peaks and valleys.

Results

From April 2013 to March 2016, we captured a total of 26 coyotes (17 F, 9 M). Six females and one male did not meet the minimum body mass requirement for GPS tagging (>10.6 kg), so we tagged a total of 19 coyotes (11 F, 8 M). Additionally, two coyotes (1 F, 1 M) were GPS tagged but the collars either never sent data via the Iridium satellite link or functioned for less than one week. Therefore, we GPS tagged 17 coyotes with functioning collars (10 F, 7 M) and collected movement data for 64 coyote-seasons. One female coyote was killed in a vehicle collision 14 days after GPS tagging and one male coyote was in poor health at capture, and died of an unknown disease about a month later. We excluded these two individuals from home range analyses because of limited movement data. Overall, a total of 62 coyote-seasons were included in our resource utilization function analysis. The average coyote in our study was monitored for 24.2 weeks with some coyotes leaving the monitored population due to mortality and others right-censored due to collar failure. Total sample size of individuals for movement analyses was 15 coyotes (9 F, 6 M). We encountered substantial issues with GPS collars failing prior to the anticipated battery life provided by the manufacturer, so most coyotes were not monitored for one year as we expected. Some collar failures were due to a software bug identified by the manufacturer, and others to damage to antennas and other collar hardware by coyotes.

Space Use

We found no difference in the area of 95% UD between female (24.6 km^2, n = 10) and male coyotes (21.2 km^2, n = 6), pooled across seasons ($F_{1,60}$ = 1.53, P > 0.28). Median UD size for all coyotes pooled across season was 21.7 km^2 (range = 6.6-128.9 km^2). Seven individuals were transients during at least one season with 95% UDs >60 km^2. When pooled between sexes, 95%

UD size did not differ among seasons ($F_{5,56} = 1.85$, $P > 0.11$). Male coyotes (58.8 km^2) had

larger 95% UDs than females (18.7 km^2) during the nursing season ($F_{1,9,} = 13.71$, $P < 0.01$), but

seasonal 95% UDs were similar among sexes for gestation (median female = 27.6 km^2 vs. male

= 18.8 km^2, $F_{1,10} = 0.93$, $P > 0.35$), pup training (median female = 11.5 km^2 vs. male = 21.0 km^2,

$F_{1,10} = 0.21$, $P > 0.65$), dispersal (median female = 21.4 km^2 vs. male = 20.2 km^2 M, $F_{1,10} = 1.25$,

$P > 0.28$), prebreeding (median female = 46.4 km^2 vs. male = 21.1 km^2, $F_{1,6} = 1.23$, $P = 0.31$),

and breeding (median female = 86.7 km^2 vs. male = 18.9 km^2, 19 $F_{1,5} = 2.33$, $p > 0.18$). While

there were no significant differences in home range size among seasons, some coyotes greatly

their increased movements during the dispersal and prebreeding seasons (Fig. 4.3), whereas

others did not (Fig. 4.4).

Resource Selection

Rangeland management significantly influenced resource selection by coyotes in some seasons

of the year (Fig. 4.6A-F). During the gestation period, coyotes tended to select areas within the

99% UD that had burned more recently, but the trend was not significant (Fig. 4.6A). However,

of 10 individuals included in the gestation season, seven had significant selection for more

recently burned areas, two had significant selection for longer time-since-fire, and one coyote did

not have a significant selection coefficient (Table 4.1). Coyotes did not select areas relative to

time-since-fire during the nursing season through dispersal, and population-level selection

coefficients were near zero (Fig. 4.6B-D). We found no selection for time-since-fire at the

population-level for the nursing season through the dispersal season, but a majority of GPS

monitored coyotes had significant selection for more recently burned areas within the 99% UD

during each of these three seasons (Table 4.1). During the prebreeding and breeding seasons,

coyotes selected areas within the home range that had burned more recently (Fig. 4.6E-F).

We found individual heterogeneity with regard to selection of grazed versus ungrazed areas among GPS monitored coyotes (Table 4.1), and selection of grazing treatment was not significant at the population-level for any season (Fig. 4.6A-F). During dispersal, nine of 13 coyotes selected ungrazed areas within the 99% UD, but strong selection of grazed areas by two individuals resulted in a non-significant coefficient during this time period.

Survival

We GPS monitored 17 coyotes during our three-year study period for survival. We recorded six mortality events during our study: two died by vehicle collisions, two coyotes were shot by a rancher, and two died of disease. A seventh coyote died in a vehicle collision but this mortality event was not included in our survival analyses because the GPS collar had failed several months prior to the mortality event, and the carcass and collar were recovered by a KDWPT Conservation Officer. For the two natural mortalities, we conducted initial necropsies of the coyotes and then sent samples to the Southeastern Cooperative Wildlife Disease Study (SCWDS) at the University of Georgia for diagnosis. The first coyote tested positive for Canine Distemper Virus (CDV), and morbidity associated with CDV likely was the cause of death for this individual. A second coyote mortality associated with natural causes died in mid-July, and was infested with maggots and carrion beetles by the time we found the carcass ~36 hours after the last movement detected with GPS telemetry. The head was sent to SCWDS for diagnosis, but tested negative for CDV or rabies virus. No further testing could be conducted, and we assumed that the animal died of disease because of poor condition but good teeth at capture.

Annual Survival

The assumption of proportional hazards was met by our global Kaplan-Meier model with the main effects of year and sex ($P > 0.27$). We found no differences in annual survival rate among the three years of our study ($P > 0.36$) or between male and female coyotes ($P > 0.93$), so we pooled years and sexes and proceeded to estimate annual survival rate of coyotes. Annual survival of coyotes was relatively low for coyotes in our study, but our estimate had low precision (0.48, 95% CI = 0.270 to 0.872; Fig. 4.7A).

Mortality Risk

We estimated hazard functions to investigate the instantaneous risk of mortality for coyotes throughout the different seasons of the annual cycle. The instantaneous risk of mortality of coyotes was low during the spring and summer when reproductive female coyotes are gestating and nursing, and male coyotes are provisioning females and pups (Fig. 4.7B). A peak in mortality risk occurred during dispersal and prebreeding, and instantaneous risk of mortality remained high through the end of March (Fig. 4.7B).

Discussion

Our 3-year project is one of the first field studies to examine patterns of resource selection and mortality of coyotes in relation to rangeland management using GPS technology, and resulted in three major findings. Coyotes selected areas that had burned more recently from November through March, but did not select habitat in response to rangeland management during the summer or early fall. Anthropogenic sources of mortality were the most common cause of mortality for coyotes captured at a natural area. Last, coyote mortality peaked during fall and

early winter in the absence of mortality due to harvest, and most losses occurred when animals dispersed outside the boundaries of the protected area.

We found no differences in space use among seasons, and space use differed between males and females only during the nursing season. However, we observed increased movements by some individuals in the fall during dispersal and prebreeding. The dispersal and prebreeding seasons coincide with dispersal of yearling coyotes and pack associates (Gese et al. 1989; Kamler and Gipson 2000). We did not age coyotes, but our sample of coyotes during dispersal and prebreeding did not include young of the year individuals, as their body mass was too low to meet minimum size requirements for tagging with GPS collars (>10.6 kg, Gier 1968). It is possible that the coyotes that exhibited large increases in movement during the fall and winter were pack associates, and were dispersing from natal home ranges during fall.

Greater movements in the fall and winter were associated with increased mortality risk of coyotes. The instantaneous risk of mortality in our study peaked during dispersal and prebreeding. Konza Prairie is a protected area, and no hunting or trapping of furbearers is allowed on the preserve. However, two major four-lane highways with high traffic volumes and posted speed limits of 70-75 mph border Konza Prairie to the south and east. Moreover, coyotes are regularly harvested by fur trappers and culled by ranchers at neighboring ranches. Greater movements during prebreeding and dispersal increased exposure of coyotes to sources of anthropogenic mortality, and also increased the amount of time coyotes spent in unfamiliar areas. Female coyotes may be more likely to travel long distances during fall dispersal (Knowlton 1972). Of seven mortalities in our study, two females were shot by ranchers ~12 km from the

territories they occupied during gestation, nursing, and pup training seasons. Another female that was lactating at capture in late May made an excursion in late September and was killed in a vehicle collision after not leaving Konza Prairie during the previous three months. Surprisingly, no coyotes in our study were harvested by fur trappers or hunters, despite exposure to hunting and trapping pressure at neighboring ranches (J. Mieke, *pers. comm.*). Other studies at protected areas have also reported a majority of carnivore mortalities were caused by humans when predators left the protection of the preserve (Gese et al. 1989; Woodroffe and Ginsberg 1998; Kamler and Gipson 2000). Last, a majority of coyote harvest by hunters and fur trappers occurs from November to February during the Kansas furharvesting season (Kamler and Gipson 2000). Our finding that seasonal mortality of coyotes peaks in November at the beginning of furharvesting season suggests that mortality occurring from December through February could be additive to non-furharvesting mortality.

Our annual survival estimate was intermediate (0.48) compared to published estimates of survival for coyotes from studies using telemetry and modern statistical methods (0.33-0.72; Gese et al. 1989; Kamler and Gipson 2000; Heisey and Patterson 2006; Turner et al. 2011), and was lower than estimates from other coyote populations at protected areas (~0.70; Gese et al. 1989; Kamler and Gipson 2000). Most studies of cause-specific mortality of coyotes report human caused mortality to be the primary cause of mortality, but a greater proportion of mortalities in our study were due to vehicle collisions than in previous studies on protected areas. The close proximity of Konza Prairie to two large highways likely increased the risk of coyotes to vehicle collisions relative to other studies.

Coyotes in our study showed no selection for grazed versus ungrazed areas, but instead selected areas with shorter time-since-fire during prebreeding, breeding, and gestation (not significant). Coyotes are omnivores that capitalize on seasonally available sources of food, but rely heavily on small mammal prey during the prebreeding through gestation seasons (Gier 1968; Brillhart and Kaufman 1994; Kamler and Gipson 2002). We had predicted that coyotes would select grassland habitats with longer time-since-fire, because hispid cotton rats and arvicoline rodents, the preferred small mammal prey of coyotes, typically are most abundant in areas that have not recently burned (Chapter 2).

Deer mice are the most abundant species of rodent in recently burned tallgrass prairie (Grant et al. 1982; Clark et al. 1989; Matlack et al. 2001; Chapter 2), but rarely occur in coyote scats or stomach contents (Gier 1968; Brillhart and Kaufman 1994; Kamler and Gipson 2002). Deer mice should be detectable, because harvest mice are found in coyote scats and stomachs and are smaller than deer mice (Gier 1968; Brillhart and Kaufman 1994; Kamler and Gipson 2002). Kaufman et al. (1988) attributed high densities of deer mice in recently burned areas to "disturbance-positive" responses of this species. Other authors have attributed their habitat associations to competitive exclusion from less frequently burned prairie, by competitors including prairie voles (*Microtus ochrogaster*) and hispid cotton rats (*Sigmodon hispidus*, Grant 1971; Redfield et al. 1977; Swihart and Slade 1990). Hispid cotton rats and prairie voles are most abundant in areas with greater diversity and abundance of forbs, and greater habitat structure (Chapter 2). The latter two species of rodents differ in sociality from deer mice. Both live in colonies, and maintain runways that they use when traveling or foraging. In contrast, deer mice are solitary, use many burrows within their territories, and do not maintain runways. In

areas of low cover, deer mice likely have lower predation risk than prairie voles or cotton rats, due to differences in social and travel behavior, which mammalian predators likely use as cues during foraging. By selectively preying on hispid cotton rats and prairie voles (Sperry 1941; Fitcher 1955; Gier 1968; Brillhart and Kaufman 1994; Brillhart and Kaufman 1995), coyotes may limit abundance of these species in areas of low cover such as recently burned prairie. The interaction between sociality and predation risk could give deer mice a competitive advantage in areas of higher predation risk, and seed predation by deer mice may be partially responsible for low forb diversity and abundance in annually burned prairie. Thus, coyotes might be causing a trophic cascade by limiting populations of herbivorous small mammals in recently burned areas, which could benefit deer mice, and indirectly influence vegetative composition.

Conclusions

Coyotes are heavily affected by anthropogenic influences, both in terms of mortality and resources available to them on the landscape. Our results indicate that non-harvest mortality to coyotes peaks prior to most furharvesting activities, and that annual survival of coyotes is about 50%. Timing of harvest or population control can play a critical role in the impacts of mortality on wildlife populations (Sandercock et al. 2011). Hunting and trapping seasons are generally timed to correspond to a period prior to the peak in natural or non-harvest related mortality, so that harvest mortality is negated through a density dependent compensation (Clark 1987). On the other hand, if timing of harvest coincides with periods of high natural mortality, harvest mortality is likely to be additive to natural mortality (Pollock et al. 1989). Our results suggest that harvest related mortality of coyotes is likely to be additive to non-hunting related causes.

Population control efforts targeted at reducing coyote populations could be conducted during winter to be most efficient.

As with all wildlife in working landscapes, management decisions for agricultural production affect habitat available to coyotes, but coyotes may also be indirectly affecting the habitat conditions on rangelands managed with frequent fire. Our results suggest that coyotes are selecting habitats where their preferred prey are least abundant. If coyotes are limiting those species in rangelands managed with frequent fire, they may be affecting a trophic cascade by reducing small mammal diversity, which could reduce plant species diversity. Studies of ground nesting birds such as Greater Prairie-Chickens indicate that the birds select areas with greater habitat structure for nesting (McNew et al. 2013). Coyotes in our study did not select areas relative to time-since-fire during the Prairie-Chicken nesting season (nursing and pup training seasons), indicating that nest habitat selection by ground nesting birds is not driven by habitat selection of coyotes. Future studies are needed to exclude coyotes from frequently burned tallgrass prairie to determine if coyotes are indirectly affecting the plant community through predation on small mammals.

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Table 4.1 Number of individual coyotes with significant positive selection, significant negative selection or no selection for time-since-fire or grazing treatment in Northeast Kansas from April 2013 to March 2016. Negative selection for time-since-fire indicates selection for more recently burned areas, whereas negative selection for grazing treatment indicates selection for ungrazed areas.

|	Time-since Fire			Grazing		
	Positive	**Negative**	**No Selection**	**Positive**	**Negative**	**No Selection**
Gestation	2	7	1	4	2	4
Nursing	2	5	4	3	3	5
Pup training	3	7	1	5	2	4
Dispersal	2	8	2	2	9	1
Prebreeding	0	4	4	2	4	2
Breeding	0	4	3	2	2	3

Figure 4.1 Map of study area for the effects of rangeland management on resource selection of coyotes in northeast Kansas, April 2013-March 2016. Crop includes all cropland classified by the National Agriculture Statistics Service (NASS) Cropland Data Layer (CDL), Water includes open water as classified by the NASS CDL, Developed includes all developed categories of urban habitat classified by the NASS CDL including roads, Forest/shrubland includes all forested categories and the shrub category classified by the NASS CDL, Grassland includes the grass/pasture classification in the NASS CDL and includes native prairie as well as introduced cool season pasture or hayland. Universal Transverse Mercator (UTM) coordinates, Zone 14 N, were projected in World Geodetic System 1984.
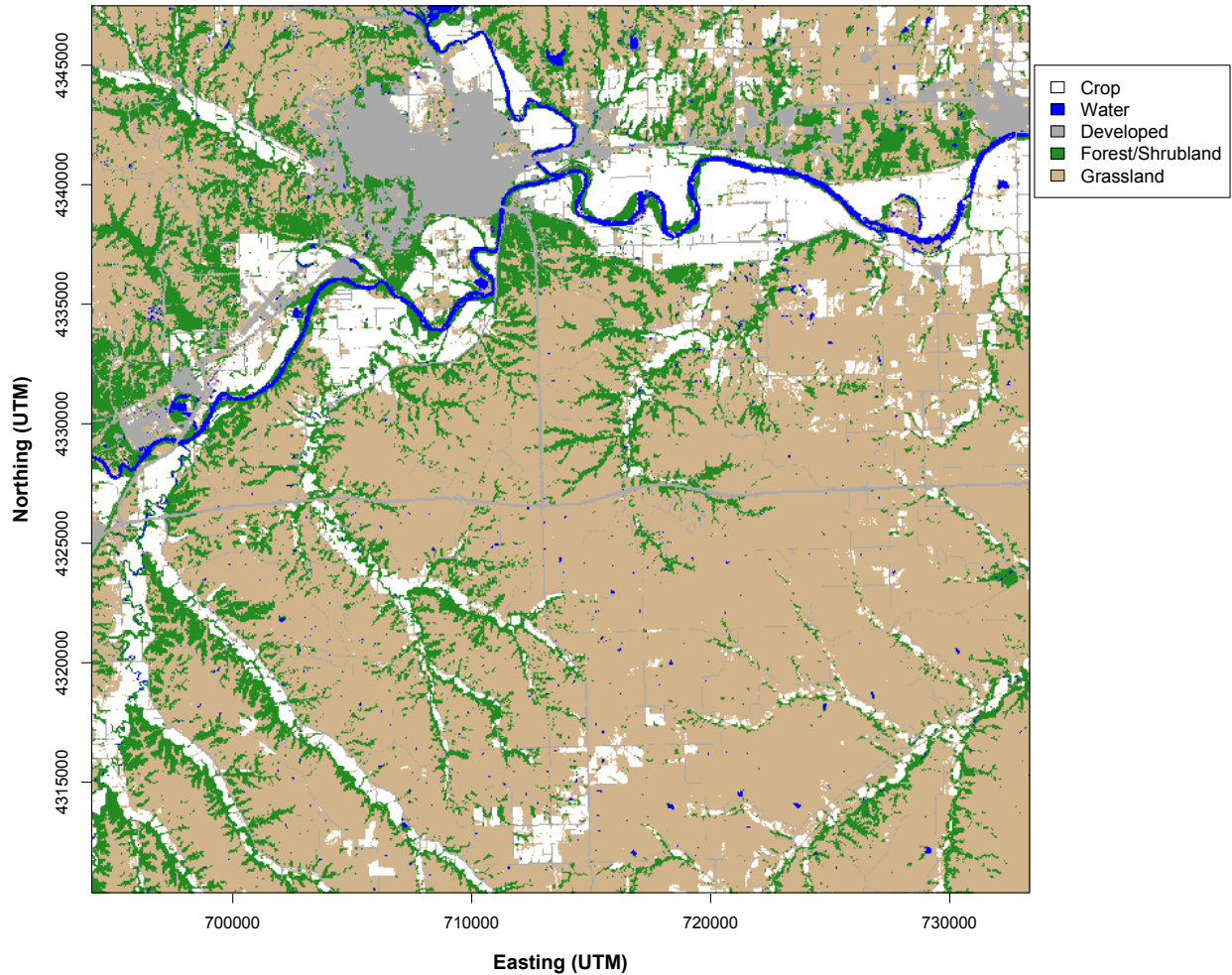
Figure 4.2 Graphical representation of raster layers for grazing treatment and time-since-fire from 2013-2015 included in resource utilization function analysis for the effects of rangeland management on coyotes in northeast Kansas from April 2013-March 2016. The grazing plot is clipped to the boundaries of coyote 99% utilization distributions.
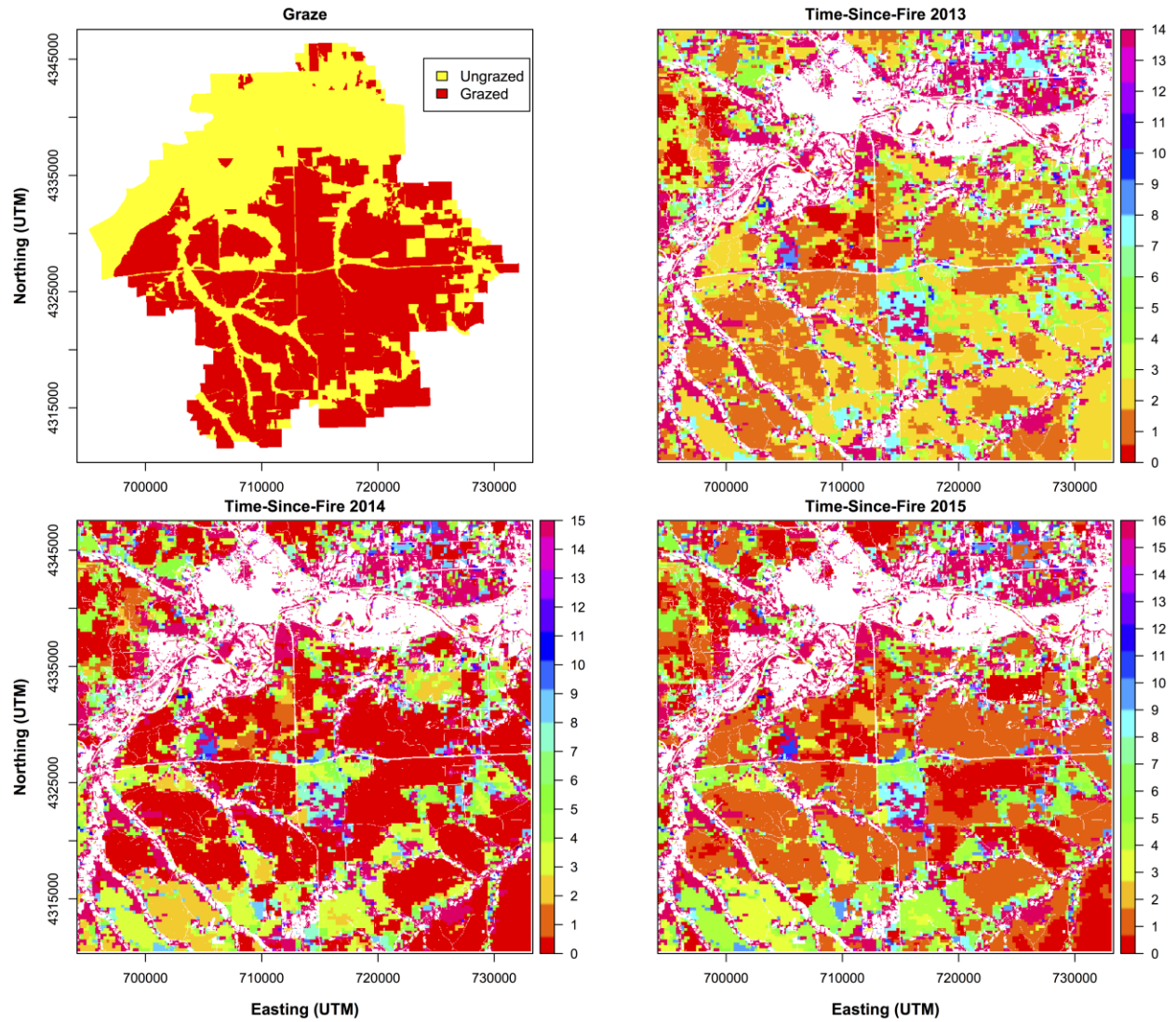
Figure 4.3 Example of 99% utilization distributions of female coyote c8336 during gestation (March-April), nursing (May-June), pup training (July-15 September) and dispersal seasons (16 September-15 November), showing use of a carcass pile on a nearby ranch during the gestation season and increased movements during the dispersal season in northeast Kansas in 2013. A rancher shot this coyote in the extreme southwest portion of the utilization distribution for the dispersal season.
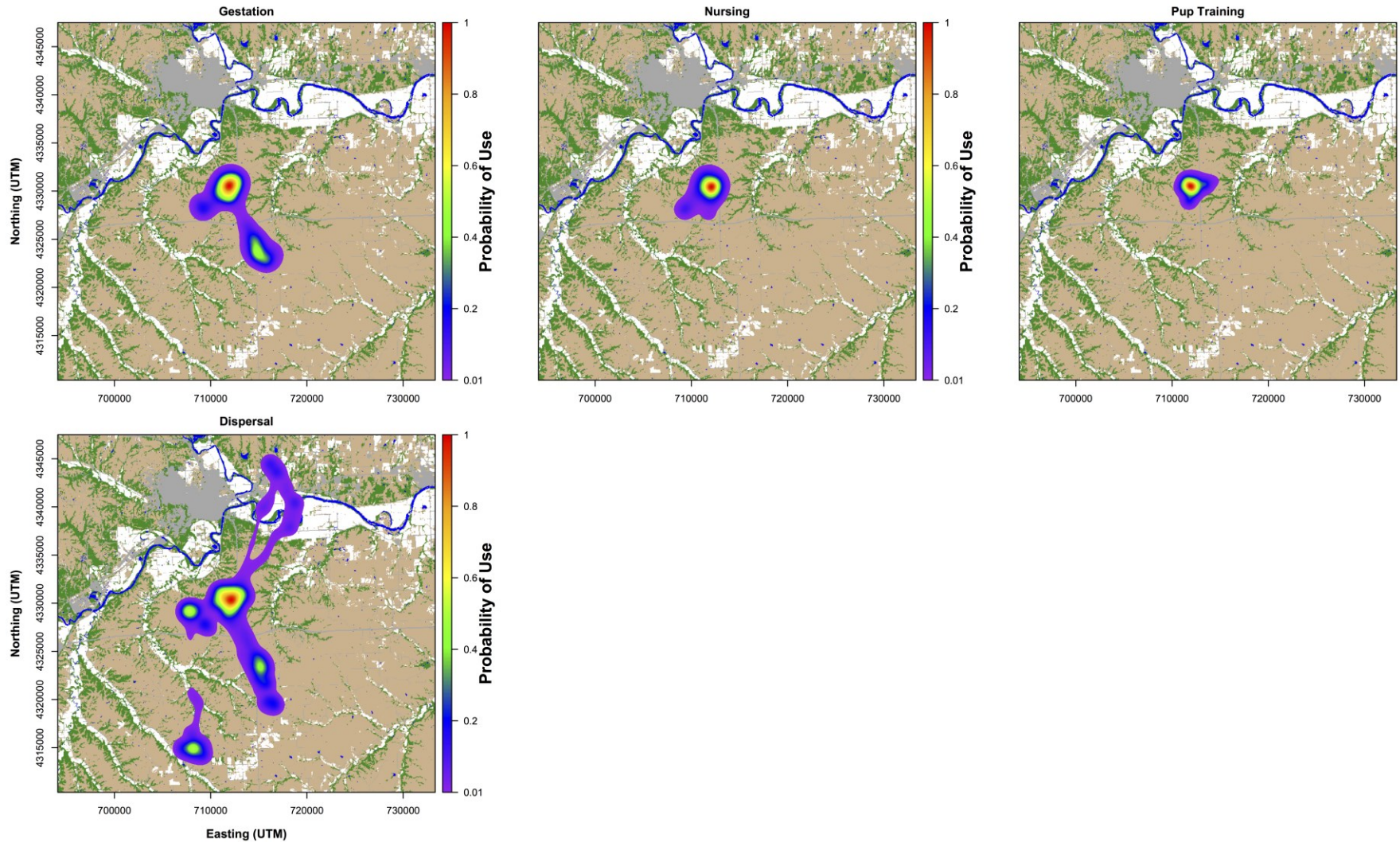
Figure 4.4 Example of 99% utilization distributions of male coyote c51970 during gestation (March-April), nursing (May-June), pup training (July-15 September), dispersal (16 September-15 November), prebreeding (16 November-January), and breeding seasons (February), showing relatively constant space use throughout the year in northeast Kansas in 2015-2016.
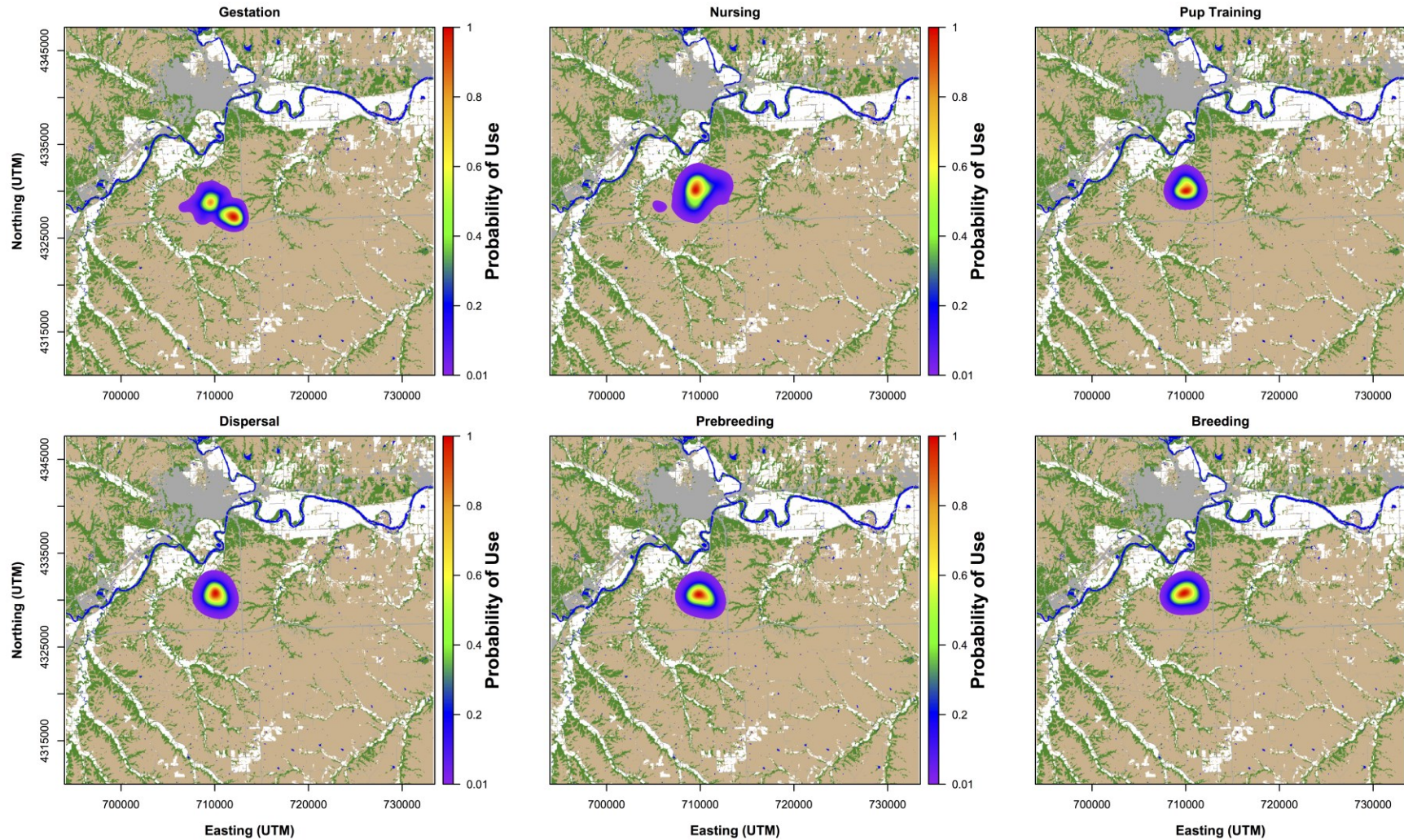
Figure 4.5 Example of 99% utilization distributions of transient female coyote c8358 during gestation (March-April), nursing (May-June), pup training (July-15 September), dispersal (16 September-15 November), prebreeding (16 November-January), and breeding seasons (February), showing relatively constant space use throughout the year in northeast Kansas in 2013-2014.
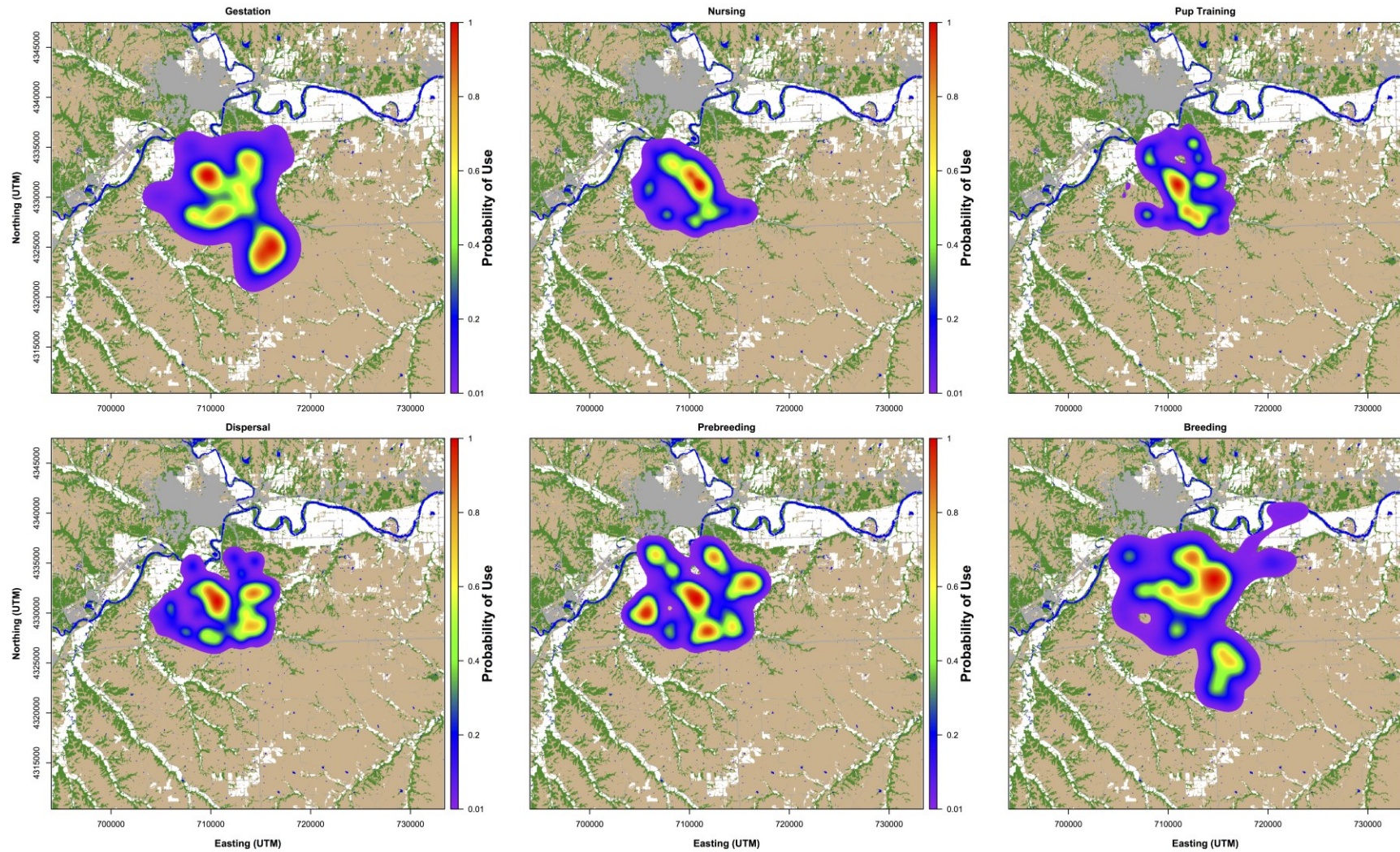
Figure 4.6 Selection coefficients for time-since-fire and grazing treatment of GPS monitored coyotes during six seasons in northeastern Kansas from April 2013 to March 2016. Six seasons of the annual cycle for coyotes were defined as: Gestation (March-April), Nursing (May-June), Pup training (July-15 September), Dispersal (16 September-15 November), Prebreeding (16 November-January), and Breeding (February). Inclusion of 0 in the 95% confidence interval indicates non-significance.
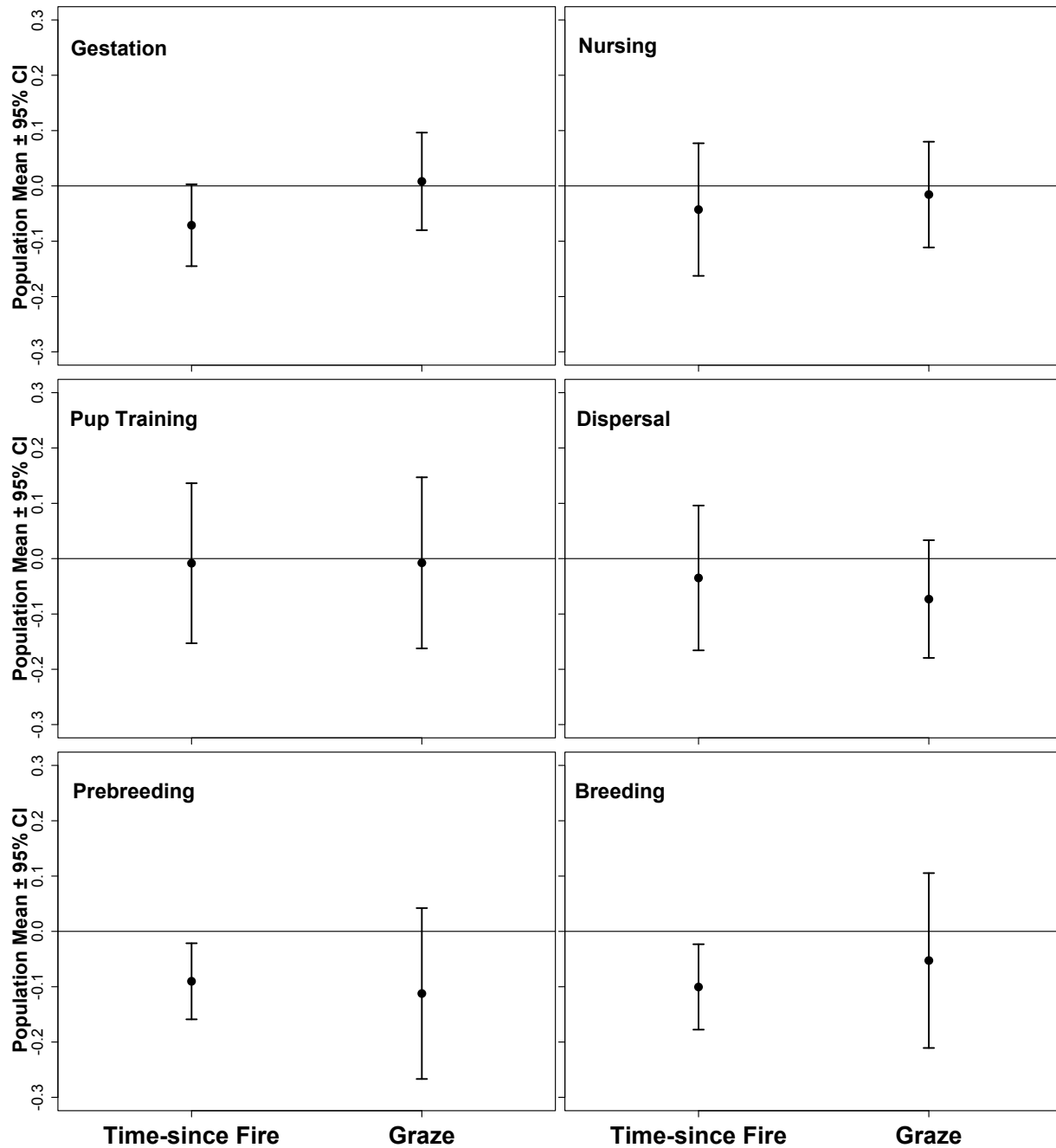
Figure 4.7 Kaplan-Meier estimates for cumulative weekly survival (A), and weekly hazard rates of mortality (B) for coyotes in northeast Kansas from April 2013-March 2016. Week 1 was set as April 1-7.
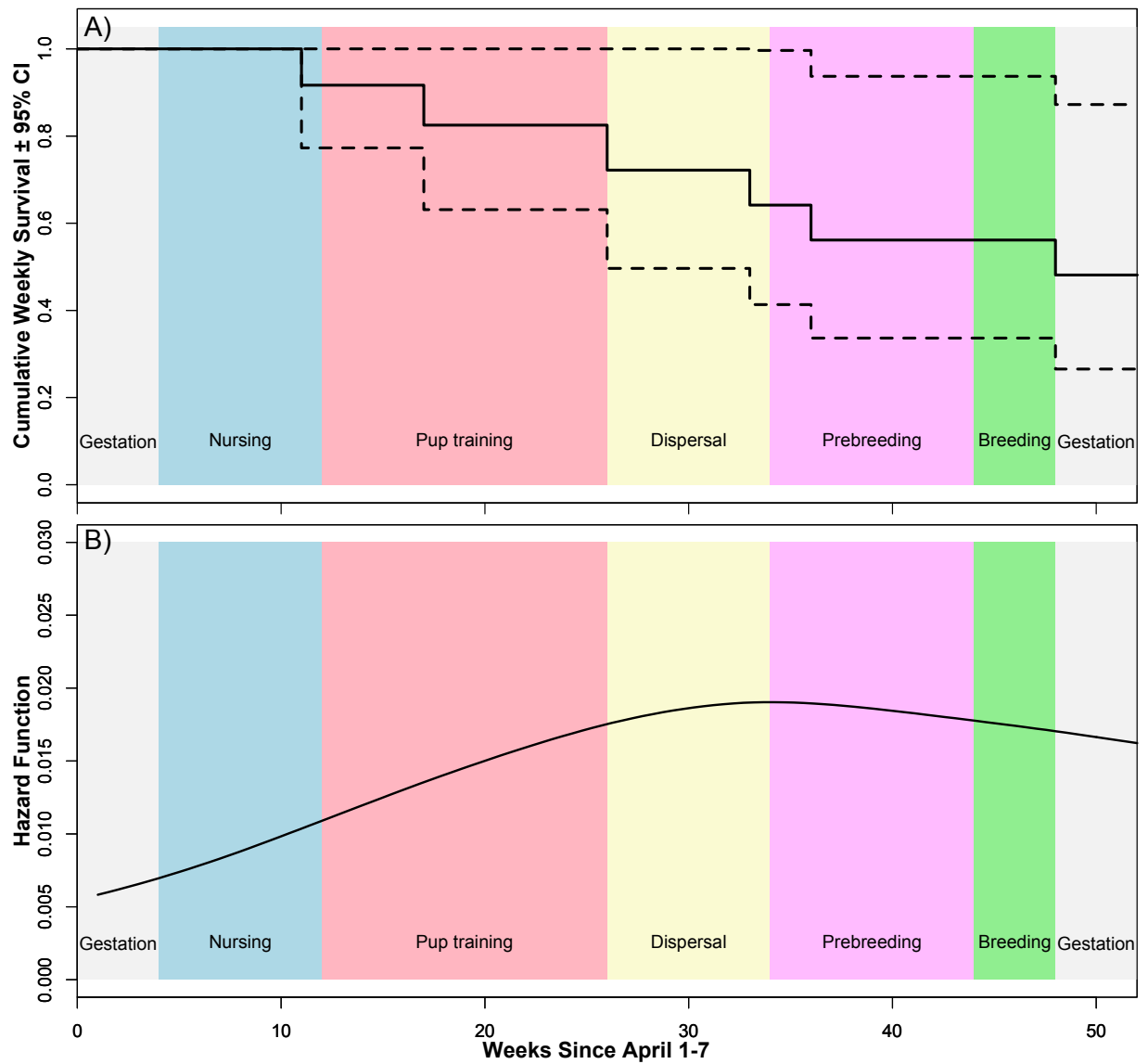
Chapter 5 - Conclusion

The tallgrass prairie of North America is a critically endangered ecosystem, home to many imperiled plants and animals, held almost entirely in private ownership, and supports a major cattle industry (Fuhlendorf and Engle 2001; Hickman et al. 2004; Hoekstra et al. 2005; With et al. 2008). Private landowners whose livelihoods depend on income from cattle production make most of the management decisions affecting remaining areas of tallgrass prairie, so conservation efforts will fail if they do not meet the needs of landowners. Moreover, grazing by large ungulates plays a large role in maintaining tallgrass prairie, so rangeland management is an important component of this ecosystem (Fuhlendorf et al. 2009). Therefore, it is vital for the conservation of native wildlife to develop rangeland management strategies for the tallgrass prairie that mimic historical processes to shape wildlife habitat on private lands, while maintaining livestock production as a primary land use.

The overall goal of my dissertation project was to determine if an alternative rangeland management strategy based on patch-burn grazing could restore habitat heterogeneity and benefit native wildlife in the tallgrass prairie using small mammals and coyotes as the study organisms of interest. Major results of my study indicate: 1) patch-burn grazing created greater heterogeneity in vegetative structure and composition of plant functional groups than in positive and negative controls; 2) habitat heterogeneity created by the interaction of fire and grazing increased small mammal richness and diversity compared to a negative control managed for uniform grazing distributions; 3) the interaction of fire and grazing structured small mammal communities in tallgrass prairie; 4) population dynamic responses of small mammals to fire and grazing disturbance are species-specific; 5) rangeland management influences resource selection

by coyotes in seasons when they depend on small mammal prey, but not during other seasons; and 6) anthropogenic sources of coyote mortality are important for coyotes on a protected area, even in the absence of harvest.

Conservation biologists sometimes view livestock production as a land use that is not compatible with biodiversity conservation (Brown and McDonald 1995). However, increased habitat heterogeneity in tallgrass prairie managed with patch-burn grazing shows that cattle production and biodiversity conservation are not mutually exclusive goals (Chapter 2). Moreover, patch-burning can provide benefits to livestock producers by providing a buffer against production losses during drought, and reducing abundances of parasitic flies that can lower weight gains among domestic cattle (Allred et al. 2014; Scasta et al. 2015).

I found that patch-burn grazing promoted biodiversity of small mammals in tallgrass prairie managed for livestock production (Chapter 2). The annually burned and grazed negative control contained a reduced small mammal community that was dominated by deer mice. On the other hand, the small mammal community in the patch-burn grazed treatment was much more even, and included species such as hispid cotton rats, western harvest mice, and plains harvest mice that were rare in the annually burned and grazed treatment. Higher diversity of small mammals has obvious benefits for each species that is more abundant in patch-burned versus traditionally managed tallgrass prairie, but benefits of increased small mammal diversity likely extend beyond the small mammal community. Deer mice dominate the small mammal community in annually burned and grazed tallgrass prairie (Chapter 2). Deer mice are a highly nocturnal species, and are available as prey items for owls (Rehmeier et al. 2006). On the other hand, hispid cotton rats,

prairie voles, and western harvest mice are often active during the daytime, and are likely more accessible prey for diurnal raptors (Swihart and Slade 1985, Danielson and Swihart 1987; A. M. Ricketts, *personal observation*). Moreover, deer mice can influence species composition of plant communities by selectively depredating large seeds, so reduced abundance of deer mice in two patches of the patch-burn grazing treatment could have positive feedbacks on the plant community (Bricker et al. 2010, Maron et al. 2012). Last, patch-burn grazing could affect disease dynamics. Prevalence and transmission of zoonoses such as Hantaviruses and Lyme disease are often reduced in mammalian communities with higher species diversity (Keesing et al. 2010, Dearing et al. 2015).

Studies of community dynamics and wildlife-habitat relationships often rely on patterns of relative abundance or counts of individuals that are not corrected for imperfect detection. However, relationships between abundance and habitat can be misleading, so it is important to measure demographic performance of organisms in response to underlying drivers of habitat conditions (Morrison 2001). In a unique analysis of recruitment and apparent survival of seven species of small mammals, I found that different species of small mammals in the tallgrass prairie respond differently to the interaction of fire and grazing on the landscape (Chapter 3). Moreover, patterns of demographic performance generally followed patterns of abundance reported in Chapter 2 and by other researchers (Fuhlendorf et al. 2010). My field results indicate that management practices that promote heterogeneity in rangeland ecosystems will benefit a suite of species with different ecological requirements.

Coyotes are important predators in rangeland ecosystems. Previous studies have shown that abundance of small mammals can be a good predictor of coyote use of the landscape (Moorcroft et al. 2006). I found that coyotes selected more recently burned areas within their utilization distribution during the prebreeding, breeding, and gestation seasons (Chapter 4). The three seasons in which coyotes selected more recently burned areas are during periods when coyotes in Kansas rely most heavily on small mammals as prey. Surprisingly, coyotes selected more recently burned areas, whereas the prey species they select, hispid cotton rats and prairie voles, tend to select areas with longer time-since-fire. My field results provide circumstantial evidence that coyotes could be limiting hispid cotton rats and prairie voles in recently burned areas, but could promote abundance of deer mice as a species rarely preyed upon by coyotes. If coyotes favor high abundances of deer mice in recently burned areas, trophic cascades could be indirectly influencing plant species composition because deer mice affect plant species composition by selectively preying on large forb seeds.

In addition to being ecologically important, coyotes are also an economically important species in North America because of negative impacts on livestock production and their value as a furbearer. Coyotes are managed as pest species in all plains states, with no regulations on method of take, year-round seasons, and no bag limits. Despite a lack of protection and heavy persecution from humans, coyotes continue to thrive and have expanded their range from being exclusively a plains species to include most of North America (Levy 2012). I found that anthropogenic sources of mortality were the main source of death for coyotes captured and marked on a protected area, and coyote mortality peaks in fall corresponding with increased movements associated with dispersal (Chapter 4). Timing of losses suggests that harvest related

mortality of coyotes in Kansas is likely additive because it coincides with a peak in annual mortality of coyotes. Furthermore, managers interested in controlling coyote populations should time control efforts to occur in fall and winter to achieve additive mortality for population reduction.

Patch-burn grazing is an effective management strategy for promoting small mammal biodiversity in the tallgrass prairie ecosystem. The results of this study, taken with previous work in Oklahoma and elsewhere, provide strong evidence that restoring the drivers of historical patch dynamics to grassland ecosystems could have important effects on biodiversity conservation in North America, while continuing to provide ecosystem services to society.

Management decisions of stakeholders in working landscapes are complex, and can be influenced by diverse factors including culture and economics. One important consideration for introducing management practices to private lands are the financial and time costs that can be barriers for livestock producers willing to implement new practices. Landowners in the Flint Hills of Kansas regularly burn tallgrass prairie to control woody vegetation and increase cattle gains, but prescribed fires are often applied using county roads or other natural firebreaks to minimize the effort required for safe application of a controlled burn. Introducing patch-burn grazing on private lands may require establishment and maintenance of firebreaks, and could increase the amount of time and effort required to complete a burn safely. Cost sharing programs, such as Partners for Fish and Wildlife of the US Fish and Wildlife Service and the Environmental Quality Incentives Program of the Natural Resources Conservation Service, provide financial and technical assistance to landowners and are promising for implementation of

patch-burn grazing and other conservation practices on private lands (USFWS 2012; NRCS

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