

Demographic responses of grassland songbirds to rangeland management in the tallgrass prairie

by

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B.S., University of Groningen, 2007

M.S., University of Groningen, 2010

AN ABSTRACT OF A DISSERTATION

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DOCTOR OF PHILOSOPHY

Division of Biology  
College of Arts and Sciences

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## Abstract

Grasslands are among the most rapidly declining ecosystems in the world. The Flint Hills ecoregion contains one of the largest remaining tracts of tallgrass prairie, but most of the area is managed with high densities of grazing animals and frequent prescribed burns, thereby reducing variation in vegetative structure. A homogeneous landscape leads to lower diversity and abundance of wildlife species, including grassland songbirds. Patch-burn grazing management has been proposed to more closely match the historical interaction between fire and selective grazing by native ungulates. Pastures managed with patch-burn grazing have a greater variety of vegetative structure and plant species composition, and as a result, higher species diversity, abundance, and reproductive success of grassland birds. However, past work has not considered potential effects of regional variation in predation risk and rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), or annual variation in climatic conditions on the effects of patch-burn grazing management on the reproductive success of grassland songbirds.

Over a six year period and at two tallgrass prairie sites, I tested the effects of patch-burn grazing on the reproductive success of three native grassland songbird species, Dickcissels (*Spiza americana*), Eastern Meadowlarks (*Sturnella magna*), and Grasshopper Sparrows (*Ammodramus savannarum*), as well as subsequent effects on the space use, movements, and survival of fledgling Dickcissels. I found only minor effects of patch-burn grazing on the reproductive success of grassland songbirds, supporting previous studies that show that patch-burn grazing does not have negative effects on demographic rates of grassland songbirds. Management regime did not affect densities or territory size of male Dickcissels, but bird densities tended to be higher and territories tended to be smaller on patches within the patch-burn

grazing treatment that were burned in the previous year. Thus, patch-burn grazing management might benefit Dickcissel populations by providing higher quality breeding habitat in unburned patches. Last, I found evidence for a potential tradeoff between habitat selection for nests vs. fledglings of Dickcissels in some rangeland management strategies. Parents that realized high reproductive success by nesting in pastures with lower cowbird densities, produced fledglings that faced high rates of depredation by snakes and showed greater movements away from those pastures. Survival rates and movements of Dickcissel fledglings were low, especially during the first week after leaving the nest, which stresses the importance of local habitat conditions. At a larger spatial scale, I tested whether regional differences in habitat structure could drive variation in apparent survival of grassland songbirds. I found that grassland- and shrubland-breeding species had higher estimates of apparent survival than forest-breeding species, contrary to the prevailing viewpoint that birds breeding in dynamic landscapes, such as frequently burned grasslands, should show lower apparent survival than species that breed in woody habitats.

The results of my field study show that restoring the historical interaction between fire and grazing on the landscape via patch-burn grazing management could benefit grassland songbirds. Moreover, my dissertation is the first study that tests the effects of patch-burn grazing management on the survival and movements of fledgling Dickcissels, and shows that high cowbird densities can cause a tradeoff between different life-stages. Future conservation efforts should take into account regional variation in species abundance, predator community composition and abundance of Brown-headed Cowbirds when assessing the effects of rangeland management on the demography of grassland songbirds.

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The results of my field study show that restoring the historical interaction between fire and grazing on the landscape via patch-burn grazing management could benefit grassland songbirds. Moreover, my dissertation is the first study that tests the effects of patch-burn grazing management on the survival and movements of fledgling Dickcissels, and shows that high cowbird densities can cause a tradeoff between different life-stages. Future conservation efforts should take into account regional variation in species abundance, predator community composition and abundance of Brown-headed Cowbirds when assessing the effects of rangeland management on the demography of grassland songbirds.

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such hard working, dedicated, and curious people. Despite the hot weather and early mornings, you stayed positive and motivated, which made my time at Konza so much more enjoyable. Although you were all different people, I thoroughly enjoyed working with all of you during the one of the hardest parts of my PhD work, and I am sure you will all make it far. During my field seasons, I have had a lot of help from a long list of people, but I want to especially thank Mary Kate Wilcox and Lia Welti for volunteering a large amount of their time to help with vegetation surveys, nest searching, and banding birds. Last, I would like to thank my field technician Kyle Wait. Kyle, you were an incredible help in the field, were always positive, and there was not a single thing I could throw at you that you were not awesome at. I still do not like country music though.

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When I moved to the United States, I left some really great friends behind. It is hard to be gone from The Netherlands for so long, but I am happy our friendship is stronger than the distance between us. I met Carol van Kershaver, Elizabeth Keijzer, Jan Erik van der Heide, and Marlies Lukkien when I started my undergraduate degree in Biology in 2004. Many things have changed since then, but I am incredibly grateful to still call you my friends. Through volleyball, I became great friends with Edwin Agema, Elske Woudstra, and Ingrid van der Heide, and I am looking forward to seeing you guys again and playing some more Barricade. Vanda de Haan, by know I have been able to call you a friend for more than half my life, and I hope we can keep that up for a lot longer.

By far the hardest part of my PhD was being so far removed from my family. My parents, Rieks and Ineke, have always been incredibly supportive, even when I moved to the other side of the world. I like to think that every positive quality that I have, is because of what you both taught me. You are the most caring parents I could have ever wished for, and I could not have completed my PhD without you. I also thank Marjolein, Annemark, and Elsemiek, who are truly the best brother and sisters anybody could hope for. There is not a day in my life that I do not miss you guys tremendously, and it is incredibly frustrating to miss the important and the little things that are going on in your lives. It means a ton that you guys are so supportive, and know that I care about you more than I can ever describe.



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## **Dedication**

To my Opa en Oma Ter Stege. Thank you so much for always being there for my mom, my brother and sisters, and me. Opa, I cannot believe my PhD has cost me the chance to say goodbye before you passed away, there is not a day where I do not think of you. Oma, I know that I do not say this enough, but you are truly one of the most important people in my life, and I love you very much.

## Chapter 1 - Introduction

Grasslands in North America have experienced major losses in the past century, with more than 90% of the historical grasslands being converted into other land-use types, including agricultural fields, forests, or urban areas (Samson and Knopf 1994, DeLuca and Zabinski 2011). In recent decades, private landowners in the Flint Hills of Kansas have started managing the majority of the remaining tracts of tallgrass prairie with high stocking rates of domestic cattle and frequent prescribed burns to maximize cattle mass gains. Unfortunately, intensive grazing and burning leads to homogeneous landscapes by reducing the variation in vegetative structure, and reduces species diversity of plants, arthropods, mammals, and grassland birds (Knapp et al. 1999, Joern 2005, Fuhlendorf et al. 2006, Powell 2006, Ricketts and Sandercock 2016). As a result, agricultural intensification has been identified as one of the main drivers for the widespread declines in grassland bird populations in North America (Samson and Knopf 1994, Herkert et al. 2003, Sauer and Link 2011, North American Bird Conservation Initiative 2016).

Historically, the tallgrass prairie was a heterogeneous landscape that was maintained by pyric-herbivory, an interaction between periodic fire and selective grazing by bison (*Bos bison*) and other native ungulates (Fuhlendorf and Engle 2001). Patch-burn grazing, a relatively new way to manage rangelands, creates higher levels of heterogeneity in vegetative structure by more closely matching the effects of the historical interaction between fire and selective grazing by native ungulates (Stebbins 1981, Knapp et al. 1999, Fuhlendorf and Engle 2001). Under patch-burn grazing management, only a section of the pasture is burned each year in a two- to four-year rotational scheme. Pasture sections are not separated by cross-fencing and cattle are free to

preferentially graze recently burned patches, which leads to higher levels of heterogeneity in vegetative structure and plant species composition (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006; 2009, Churchwell et al. 2008, Ricketts and Sandercock 2016). By increasing habitat heterogeneity, patch-burn grazing management can benefit species diversity and abundance of birds, and improve the reproductive success of grassland songbirds by reducing rates of nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Fuhlendorf et al. 2006, Powell 2006, Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016).

Nest predation is the main source of reproductive losses in songbirds, and nest survival in grassland-breeding songbirds is especially low (Martin 1992; 1995). Rangeland management has large effects on nest survival by driving vegetative structure and the amount of nest cover that is available to breeding birds (Hughes et al. 1999, Rohrbaug 1999, Winter 1999, Dechant et al. 2002, Temple 2002, Churchwell et al. 2008, Rahmig et al. 2009, Hovick et al. 2012). However, tallgrass prairie sites often have diverse predator communities, and show regional variation in which predator species is most abundant at each site (Lyons et al. 2015). Since the responses of predators to vegetative structure are predator-specific, the effects of rangeland management on nest survival of grassland songbirds are likely to show large regional variation.

Brood parasitism by Brown-headed Cowbirds is widespread among grassland songbirds (Zimmerman and Finck 1989, Jensen and Cully 2005a, Martin 2014), and leads to demographic losses via the removal of host eggs (Zimmerman and Finck 1989), higher predation risk (Jensen and Cully 2005a), and by competition between host and parasitic young (Jensen and Cully 2005a, Rivers et al. 2010), which can lead to reproductive failure in small-bodied host species (Kosciuch

and Sandercock 2008). Cowbirds often forage in association with grazing animals, but the potential relationship between rangeland management and rates of brood parasitism remains unknown. Rates of brood parasitism are influenced by the abundance of female cowbirds, but cowbird abundance can show large regional variation (Jensen and Cully 2005a; 2005b).

Last, I was interested in annual variation of the effects of rangeland management on the productivity of grassland songbirds. Climatic conditions are a major driver of primary production and vegetation height in grasslands, and could interact with fire and grazing to shape species composition and vegetative structure of managed grasslands (Briggs and Knapp 1995, O'Connor et al. 2001, Swemmer et al. 2007, Sherry et al. 2008). By altering vegetation height and nest cover by driving new vegetation growth, annual variation in weather could lead to wide variation in reproductive success of grassland birds. In addition, extreme weather event, such as extreme heat and spring storms, could lead to direct nest losses of grassland songbirds. With global climate change, it becomes increasingly important to understand how annual weather conditions can affect rates of nest survival and brood parasitism (Dawson et al. 2011, IPCC 2013, Hovick et al. 2015).

Past research on the effects of patch-burn grazing on grassland songbird demography has often been limited to a single site or species, and has not considered regional variation in predation risk or rates of brood parasitism, or annual variation in climatic conditions. As a result, the potential links between heterogeneity in vegetative structure and the reproductive success of grassland songbirds remain poorly known. In my dissertation, I assess the effects of patch-burn

grazing management on the demography of grassland songbirds in the northern Flint Hills ecoregion over a six year period at two tallgrass prairie sites.

In **Chapter 2**, I tested how heterogeneity in vegetative structure affects the settlement and space use of Dickcissels (*Spiza americana*) by comparing densities and territory sizes across experimental pastures that were managed with patch-burn grazing, or annual burns with or without grazing. I found that management regime did not affect densities or territory sizes of male Dickcissels, but densities tended to be higher and territories tended to be smaller on the patch-burn grazing patch that was burned in the previous year. Patch-burn grazing management might therefore benefit Dickcissel populations by providing higher quality breeding habitat in some patches. Combining management-specific estimates of territory size with estimates of reproductive success of grassland songbirds is essential in conservation of declining populations, since territory size could limit the number of breeding birds that benefit from high quality breeding habitat.

In **Chapter 3**, I tested how heterogeneity in vegetative structure affects the reproductive output of Dickcissels, Eastern Meadowlarks (*Sturnella magna*), and Grasshopper Sparrows (*Ammodramus savannarum*). During a 6-year field study at two tallgrass prairie sites, I estimated rates of brood parasitism, clutch size, nest survival, and fledging rates for three songbird species, and calculated the average number of fledglings produced per nest with bootstrapping. I further assessed whether variation in temperature and precipitation drives variation in the amount of available nest cover or levels of predator activity. I found that rangeland management led to minor differences in the average number of fledglings per nesting attempt in Dickcissels and

Eastern Meadowlarks. Variation in climatic conditions had a large effect on vegetative structure, but I did not find much evidence of annual variation in reproductive success of our three study species. My results support previous studies that show that patch-burn grazing does not have negative effects on demographic rates of grassland songbirds, and could provide suitable breeding habitat for species that require amounts of litter for cover that is not found in annually burned pastures.

In **Chapter 4**, I tested the effects of patch-burn grazing management on the survival and movements of Dickcissel fledglings. I equipped fledglings with small VHF radio-transmitters, and found that rangeland management had an effect on fledgling movements, but only a minor effect on fledgling survival. Fledglings moved only short distances ( $< 100$  m) during the first week after leaving the nest, which stresses the importance of local habitat conditions. I further found evidence for a potential tradeoff between habitat selection for nests and fledglings of Dickcissels in annually burned and ungrazed pastures. Parents that had high nest success by nesting in pastures with low cowbird densities, produced fledglings that faced high rates of depredation by snakes and showed greater movements away from the pasture.

Estimates of adult survival are lacking for many bird species and ecoregions, including the Great Plains. In **Chapter 5**, I used Cormack-Jolly-Seber mark-recapture models to estimate apparent survival of 17 species of birds captured with a 13-year systematic mistnetting effort in the northern Flint Hills ecoregion. I present the first estimates of apparent survival for six species of songbirds, and the first estimates from the Great Plains for thirteen species. Furthermore I found that grassland- and shrubland-breeding species had higher estimates of apparent survival

than forest-breeding species, contradicting the prevailing viewpoint that birds breeding in dynamic landscapes, such as frequently burned grasslands, should show lower apparent survival than species that breed in woody habitats. Regional differences in habitat structure could therefore drive variation in demography.

In **Chapter 6**, I conclude my dissertation with a discussion of major results, and their implications for conservation of grassland songbirds. I further summarize the novel results of my dissertation research and identify useful areas for future research.



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## **Chapter 2 - Effects of patch-burn grazing on density and space use of Dickcissels**

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## Abstract

In North America, tallgrass prairie was historically maintained as a mosaic of different habitats by the interaction between fire and selective grazing by large herbivores. In recent decades, agricultural intensification has led to more homogeneous landscapes in managed rangelands, which has been linked to widespread declines in grassland songbird populations. Patch-burn grazing management aims to restore heterogeneity in vegetative structure on the landscape by rotationally burning pasture-sections, combined with foraging preferences of cattle to graze in recently burned areas. Patch-burn grazing can increase the diversity, abundance, and reproductive success of grassland songbirds, but its effects on space use of grassland songbirds remain unknown. During a two-year field study at a nature preserve in northeast Kansas, we tested how spatial heterogeneity in vegetative structure affects the space use of Dickcissels (*Spiza americana*) by comparing densities and territory sizes across experimental pastures that were managed with patch-burn grazing, or annually burned with or without grazing. We mapped territories of individual Dickcissel males, and calculated 95% minimum convex polygons and kernel density estimators. We found that management regime did not affect densities or territory size of male Dickcissels, but densities tended to be higher and territories tended to be smaller on the patch-burn grazing patch that was burned in the previous year. Patch-burn grazing management might therefore benefit Dickcissel populations by providing higher quality breeding habitat in some patches. Unexpectedly, territory sizes decreased over the breeding season, while densities of Dickcissels did not vary, potentially indicating improving habitat conditions over the summer. With our study, we provide new estimates of Dickcissel territory size, and the first to test the effects of rangeland management on space use by males. Combining management-

specific estimates of territory size with estimates of reproductive success of grassland songbirds is essential in conservation of declining populations, since territory size could limit the number of breeding birds that benefit from high quality breeding habitat.

## Introduction

Over the past decades, songbird populations have been declining across most of North America, with grassland-obligate species showing some of the greatest losses (Samson and Knopf 1994, Sauer and Link 2011, North American Bird Conservation Initiative 2016). Grassland ecosystems are among the most rapidly declining ecosystems in the world, especially in North America, where only 10% of the historical grasslands are left (Samson and Knopf 1994, Deluca and Zabinski 2011). The majority of remaining grasslands in North America are now used for cattle production, and are often managed with higher densities of grazing livestock and more frequent burning than was historically common (Knapp et al. 1999, Fuhlendorf et al. 2006). Intensive and homogeneous use of managed rangelands leads to higher mass gains for domestic cattle, but reduces spatial variation in vegetative structure and cover in prairie habitats (Knapp et al. 1999, Fuhlendorf et al. 2006). A homogeneous landscape is associated with lower species diversity and abundance of wildlife, including arthropods (Joern 2005), mammals (Ricketts and Sandercock 2016), and grassland songbirds (Fuhlendorf et al. 2006, Powell 2006, Coppedge et al. 2008). Moreover, intensive rangeland management has been linked to increased rates of nest predation and brood parasitism of grassland songbirds (Churchwell et al. 2008, Davis et al. 2016). Thus, agricultural intensification may be one of the main drivers for widespread population declines of grassland birds in North America (Samson and Knopf 1994, Herkert et al. 2003, Sauer and Link 2011, North American Bird Conservation Initiative 2016).

Before European settlement, the tallgrass prairie was a heterogeneous landscape that was maintained by pyric-herbivory, the interaction between fire and selective grazing by large native ungulates (Stebbins 1981, Knapp et al. 1999, Fuhlendorf and Engle 2001). Since the 1980s,

rangeland management of tallgrass prairie in Kansas has included the use of annual burning and intensive early stocking with steers (IESB), or less common, season-long stocking with cow/calf pairs (SLSB; Owensby et al. 2008), resulting in a more homogeneous use of the landscape. Patch-burn grazing is a relatively new rangeland management strategy that seeks to restore heterogeneity in grasslands by more closely matching the historical interaction between fire and grazing (Fuhlendorf and Engle 2001). Under patch-burn grazing management, only one section of a pasture is burned each year in a two- to four-year rotational scheme. Pasture units are not separated by cross-fencing and cattle are free to preferentially graze recently burned patches (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, 2009, Churchwell 2008). The interaction of periodic fire and selective grazing by cattle results in a greater variety of vegetative structure and plant species composition among different pastures (Ricketts and Sandercock 2016).

As a result of higher levels of habitat heterogeneity, patch-burn grazing management can benefit species diversity and abundance of grassland birds by improving habitat quality for specialists that require undisturbed grasslands (Fuhlendorf et al. 2006, Powell 2006). Moreover, patch-burn grazing may improve the reproductive success of grassland songbirds by decreasing rates of nest predation and brood parasitism (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016). To date, the effects of patch-burn grazing management on local population density and space-use of territorial grassland birds have not been investigated.

During the breeding season, most species of grassland songbirds defend small Type A territories, in which most aspects of reproduction take place, such as courtship, mating, and the rearing of young until fledging from the nest (Nice 1941, Finck 1984, Rodewald 2017). According to the ideal free distribution, territory size declines with habitat quality and local population density, potentially due to increased costs of territorial defense when competition with

other males is high (Fretwell and Lucas 1969, Schartz and Zimmerman 1971, Harmeson 1974, Rodenhouse et al. 2003, Haché et al. 2013, Hartmann et al. 2017). However, a minimum territory size seems necessary for successful reproduction, which could restrict the number of breeding pairs that a given area can support, even if habitat quality is high (Fretwell and Lucas 1969, Krebs 1971). Alternatively, according to the ideal despotic distribution, males retain equally sized territories regardless of local density. However, high local population densities might result in spill-over of subordinate males to less suitable habitat, which could lower the average reproductive success of the population (Fretwell and Lucas 1969, Schartz and Zimmerman 1971, Holmes et al. 1996, Haché et al. 2013). Understanding the effects of rangeland management on the spatial ecology of grassland songbirds could help guide conservation efforts.

With our 2-year field study, we tested the effects of patch-burn grazing management on local population density and territory size of Dickcissels (*Spiza americana*). We conducted line-transects to estimate densities of male Dickcissels, and marked and observed male Dickcissels to compare territory areas based on 95% minimum convex polygons and kernel density estimators across rangeland management strategies. Dickcissels are strongly territorial migratory songbirds and are considered a grassland-obligatory species. Although still commonly found in the tallgrass prairie, Dickcissels have undergone large-scale population declines in recent decades (Knopf 1994, With et al. 2008, Sauer and Link 2011). Dickcissels occur in a variety of habitats, but densities are often highest in grasslands with high forb cover and tall dense vegetation that function as nest cover (Dechant et al. 2002, Temple 2002, Rahmig et al. 2009). Dickcissels have a mating system based on resource-defense polygyny, and the reproductive success of males is strongly dependent on local habitat quality. Individuals in poor habitat often fail to acquire a mate, whereas males in high quality patches are facultative polygynous with two or more

females, and have higher rates of within-pair paternity and nest success (Schartz and Zimmerman 1971, Temple 2002, Sousa and Westneat 2013). Unburned pastures in a patch-burn grazing management system could improve the quality of breeding habitat of Dickcissels by increasing forb cover, vegetation height and litter depth (Fuhlendorf et al. 2006, Ricketts and Sandercock 2016). We therefore predicted higher densities and smaller territory sizes on unburned patches within patch-burn grazing managed pastures versus recently burned patches within patch-burn grazing managed pastures, or annually burned pastures with or without grazing.

## Methods

### Study Site

We conducted our field project at the Konza Prairie Biological Station (hereafter Konza Prairie) in 2013 and 2014. Konza Prairie is located in the northern Flint Hills eco-region, one of the largest remaining tracts of native tallgrass prairie (Samson and Knopf 1994, With et al. 2008). The Konza Prairie is a 3,487-hectare tallgrass prairie preserve in Geary and Riley County, Kansas, USA, is part of the NSF-funded Long-term Ecological Research (LTER) Site Program. The Konza Prairie includes a landscape-scale fire and grazing experiment, and consists of >60 experimental pastures that receive different combinations of grazing and prescribed fire.

The tallgrass prairie at Konza Prairie is dominated by native warm-season grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiagrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). Forbs comprise much of the plant species diversity of the tallgrass prairie, but some common forbs in our study area include Baldwin's ironweed (*Vernonia baldwinii*), common yarrow (*Achillea millefolium*), goldenrod (*Solidago* spp.), leadplant (*Amorpha canescens*), milkweeds (*Asclepias* spp.), and

round-head bush clover (*Lespedeza capitata*). Woody plants are more common in unburned tallgrass prairie, and local shrub species include buckbrush (*Symphoricarpos orbiculatos*), inland ceanothus (*Ceanothus herbaceus*), rough-leaved dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and wild plum (*Prunus americana*; Towne 2002).

## Climate

The climate at Konza Prairie is relatively hot and humid during the growing season, but shows considerable annual variation. Over the past century, the average annual temperature was 12.6°C for Konza Prairie, but monthly average temperatures got as high as 25-26°C in July and August. Annual precipitation averaged 799 mm/year (SD = 175 mm/year) at Konza Prairie. About 75% of precipitation falls within the 6-month growing season (March – August), but late summer droughts in July and August are not uncommon (NOAA 2017, see methods below).

To assess annual variation in density and territory size, we obtained precipitation and temperature data for Konza Prairie from the long-term climate database of the National Oceanic and Atmospheric Administration (NOAA 2017). We obtained monthly average temperature and precipitation for the 100-year period from September 1916 to August 2016 from the closest weather station to Konza Prairie (Station ID: USC00144972). We then calculated z-scores for climatic conditions and for each growing season (6 months; March to August). To calculate z-scores, we took the average temperature or precipitation for each growing season based on monthly averages of that year to obtain a distribution of 100 averages for the past century of 1916 to 2016. We then calculated year-specific z-scores with the following equation:

$$z_i = \frac{x_i - \mu}{\sigma}$$

where  $x_i$  is the year-specific estimate of temperature or precipitation,  $\mu$  is the mean over a 100-year period, and  $\sigma$  is the standard deviation of the mean. During preliminary analyses, we did not find any temporal trends in temperature or precipitation that could have biased z-scores.

## **Experimental Treatments**

We investigated the spatial ecology of Dickcissels in three pastures with experimental treatments for rangeland management. Three pastures (49.4 – 102.4 ha) were combined to form one large pasture (219.3 ha) that was managed with rotational fire in a patch-burn grazing management regime with a 3-year rotation (PBG). One pasture was annually burned and grazed (ABG; 93.5 ha), and served as a negative control, while a third pasture was annually burned and ungrazed (ABN; 41.6 ha), and served as a positive control. Grazed pastures were stocked with cow/calf pairs at a density of 3.24 hectares per pair from early May to early October (J. Briggs and K. C. Olsen, personal communication). All pastures were treated with prescribed burns in early spring between mid-March to mid-April, and had been managed with the specified management regime for three or more years before we started our field study.

## **Density of Male Dickcissels**

To estimate densities of breeding Dickcissels, we deployed eight 300-meter line transects within each of our five experimental pastures. We randomly selected starting points for each transect within each pasture, but points were resampled if they were located within 50 meters of another starting point or within 100 meters of the edge of a pasture (Figure 2.1). The two transects closest to the center of the pasture were selected as core-transects, and were sampled three times during



late May, mid-June, and early July during both years. The other six transects were sampled only once per year, where only two transects were surveyed during each of the three sampling rounds, and parallel transects were not sampled during the same round. During each survey, we identified all birds that were seen or heard to species, determined the sex of the bird when possible, and recorded cluster size and the perpendicular distance from the bird to the transect. Since our field study focuses on territoriality of Dickcissels, we used detection records of male Dickcissels only. We also recorded the temperature, wind speed, and sky cover for each survey. All transect surveys started at sunrise and were completed before 11:00 hr. We postponed surveys during rainy or foggy conditions, or strong winds ( $> 35$  km/h) for one or two days.

To obtain a robust estimate of density for male Dickcissels, we used distance sampling techniques for line transects available in the *unmarked* package in R (Fiske and Chandler 2011; R Core Team 2017). Distance sampling allowed us to estimate bird densities, which is an improvement over using raw counts to estimate abundance per transect. Moreover, distance sampling corrects for the incomplete detection of birds along the line transect by estimating a detection probability curve. The detection probability is assumed to be perfect on the line transect, but gradually declines with perpendicular distance. Correcting observations of birds in the field for imperfect detection improves the accuracy of estimates of bird density. The general shape of the detection probability curve can be varied by using several alternate key-functions. Here, we considered three alternative functions: a half-normal, hazard rate, and a uniform key-function. With a half-normal key-function, the detection probability declines with perpendicular distance following the declining half of a normal distribution. When using a hazard-rate function, detection is assumed to be perfect for a specific perpendicular distance, and declines after that

threshold is reached. Last, a uniform key-function models a detection curve that does not vary with the perpendicular distance from each transect.

For detection probability, we considered alternative models with effects of temperature, wind speed, sky cover, year, treatment, patch-within treatment, and observer, as well as an intercept-only model. The detection probability of grassland birds was expected to be lower during inclement weather conditions, to decrease with vegetation height and structure, and may differ among observers, especially at long distances. We tested the effects of patch-burn grazing management on Dickcissel density at two separate scales. A treatment model included both control pastures and the patch-burn grazing managed pasture as a whole, while a patch-within-treatment model included both controls and all three patches of the patch-burn grazing pasture separately. We further considered models with fixed effects of year, as well as an intercept-only model. We then ran a model-set containing models with all possible combinations of explanatory variables for both the detection probability and density, as well as an intercept-only model, and ran all models with a half-normal, hazard-rate, or uniform key-function. To determine which combination of variables and key-function best explained the detection probability and density of Dickcissels, we compared AICc-values, tested the goodness-of-fit of the top-ranked model with a  $\chi^2$  test for binned data, and visually inspected the model for overdispersion (Burnham and Anderson 2002, Fiske and Chandler 2011).

### **Territory Size**

During June and July of 2013 and 2014, we mapped territory sizes of breeding male Dickcissels in each experimental pasture. In addition, we mapped the territories of a subset of individuals in both June and July 2014 to assess seasonal variation in territory size. To identify individuals, we

live-trapped Dickcissels with mist nets and playbacks, and marked each male with a unique combination of colored leg bands. To increase our sample size, we also surveyed unmarked males that could be individually identified by distinctive song or plumage (Schook et al. 2008). We determined territory size by using a mixture of flush- and spot-mapping. Flush-mapping is a technique regularly used to determine the territory size of songbirds (Wiens 1969, Fletcher and Koford 2003, Jones 2011), where an observer flushes a target-bird from a location and records GPS points for the flush location, the flightpath, and the landing location. We combined short bouts of flush-mapping with spot mapping, where we observed birds from a short distance (>50 m) to avoid disturbing the behavior of the bird. We recorded locations of all singing perches and boundaries of territorial disputes with other male Dickcissels in UTM coordinates to the nearest meter with a handheld GPS unit. We started territory mapping at sunrise, and concluded our observations before 14:00 hr to avoid inactivity by males during the hottest part of the day.

For each male Dickcissel where we obtained at least 20 unique territorial locations, we calculated 95% and 100% Minimum Convex Polygons (MCPs; Mohr 1947) and 95% Kernel Density Estimates (KDEs) with the *adehabitatHR* package in R (Calenge 2006, R Core Team 2017). Previous studies have shown that 95% surface areas and 20 unique locations provide an unbiased estimate of territory size for both techniques, while excluding outlying locations that are rarely used (MCP: Wiens 1969, Fletcher and Koford 2003; KDE: Worton 1989, Seaman and Powell 1996, Seaman et al. 1999, Leonard et al. 2008, Perkins and Wood 2014).

When using kernel density methods, selecting an appropriate smoothing parameter,  $h$ , is especially important, because smoothing restricts the distance at which individual locations influence the surface grid (Silverman 1986, Fieberg 2007, Leonard et al. 2008). Several techniques for specifying  $h$  are available in package *adehabitatHR*, including least squares cross-

validation (LSCV), an individual-specific reference smoother, and options to manually determine a set smoothing parameter for all individuals. LSCV techniques are widely used when determining space use of many animals, including songbirds (Seaman et al. 1999, Horne and Garton 2006, Leonard et al. 2008, Holt et al. 2012, Perkins and Wood 2014, Everitts et al. 2015). However, some studies found that LSCV techniques are sensitive to the number of duplicate locations, and often fail to converge when locations are close together (Silverman 1986, Hemson et al. 2005). LSCV techniques might therefore not be suitable when estimating home ranges of small-bodied songbirds. During preliminary analyses, we determined LSCV techniques were too conservative as interior areas between observations of an individual were often excluded, whereas set smoothing parameters were inappropriate due to the large variation in Dickcissel territory size. An individual-specific reference smoother that takes into account variation in point density among individuals, provided a better fit for each Dickcissel territory, with a mean  $h$  of 10.2 (range = 4.9 – 16.8,  $n = 72$  males; Figure 2.2).

We used analysis of variance to test whether territory size of male Dickcissels was affected by year, treatment, patch-within-treatment, time since fire, or the number of observations, and tested for possible interactions among our explanatory variables. To determine which combination of variables best explained territory size of Dickcissels, we compared AICc-values of all models (Burnham and Anderson 2002), and used a paired t-test to compare territory size between months. All analyses were conducted with functions of the base package of R (R Core Team 2017).

## Results

## **Climate**

Temperature and precipitation conditions at Konza Prairie differed between the growing seasons of 2013 and 2014. Both years were relatively cold, with temperatures during the growing season being especially low in 2013 ( $17.2^{\circ}\text{C}$ ,  $z = -1.62$ ), but more moderate in 2014 ( $18.2^{\circ}\text{C}$ ,  $z = -0.67$ ). Precipitation was higher during the growing season of 2013 (528.2 mm,  $z = -0.15$ ) than 2014 (455.3 mm,  $z = -0.64$ ). However, we did observe lower standing vegetation from the previous year in 2013, likely due to high temperatures ( $21.5^{\circ}\text{C}$ ,  $z = +2.31$ ) and low amounts of precipitation (407.8 mm,  $z = -0.96$ ) during the growing season of 2012 (see Chapter 3 for vegetation response).

## **Density of Male Dickcissels**

We conducted a total of 120 line transect surveys in 2013 and 2014, and recorded a total of 744 observations of male Dickcissels. We divided our observations into 10 meter bins, and truncated the data at a perpendicular distance of 125 meters from each transect because observations beyond that distance were sparse ( $n = 23$ ). In preliminary analyses, models with a hazard rate key-function had consistently lower AICc-values than models with a half-normal or a uniform key-function as the detection function. We report model selection results of models with a hazard rate key-function only.

We found high levels of support for effects of year (Relative Importance;  $\text{RI} = 1$ ) and patch-within-treatment ( $\text{RI} = 0.997$ ) on density of male Dickcissels (Table 2.1). When pooled across years, Dickcissel densities were lowest on the patch-burn grazing patch that was most recently burned ( $77.2 \pm 8.1\text{SE}$  male Dickcissels/ $\text{km}^2$ ), and tended to be lower on the annually burned and grazed pasture ( $88.9 \pm 8.8$ ) when compared to other patches, with densities being

especially high at the patch that was burned the previous year ( $117.9 \pm 10.5$ ). In general, Dickcissel density was lower in 2013 ( $81.1 \pm 5.0$ ), than 2014 ( $114.6 \pm 6.0$ ), but the magnitude of differences in density varied across treatments and patches-within-treatment (Figure 2.3). We found minor support for an observer effect on the detection probability of Dickcissels in our study (RI = 0.549), but did not find any effects of temperature, wind speed, sky cover, year, treatment, and patch-within-treatment, presumably because we avoided surveying during unfavorable weather conditions (Table 2.1).

### **Territory Size**

Between 2013 and 2014, we mapped at least 20 unique locations for 72 male Dickcissels across all three experimental treatments (2013: N = 11, 2014: N = 61). Four male Dickcissels returned to our study area and were mapped in both 2013 and 2014. The territory size of all four males was highly variable (95% MCP range = 0.08 – 0.52 ha), with two males defending a larger territory in 2014, and two males defending a smaller territory. Moreover, variation in territory size within individuals was not related to management regime, since all four males returned to the same treatment where they were originally banded at in 2013. We accepted some pseudoreplication and included both estimates of territory size for these four birds in our analyses.

Overall, the average territory size based on 95% MCPs was 0.36 ha (95% CI = 0.32 - 0.39 ha), and based on 95% KDEs was 0.87 ha (0.79 - 0.95 ha; Supplemental Figure 2.1). Variation in territory size based on 95% MCPs was best explained by the total number of unique locations (RI = 0.79, Supplemental Figure 2.2), and to a lesser extent by the number of years since the last burn (RI = 0.48; Table 2.2). Variation in territory size based on 95% KDEs was not well explained by any of our variables, although models containing time-since-fire as a factor had lower AICc

values than the intercept-only model ( $RI = 0.56$ ; Table 2.3). However, none of our models was able to explain much of the variation in territory size while using either technique (max Adj.  $R^2$ , MCP = 0.096, and KDE = 0.100). Rangeland management did not explain variation in territory size, but 95% MCPs and KDEs tended to be smaller at the patch-burn grazing patch that was burned during the previous year compared to other patches and treatments (Figure 2.4).

In 2014, we mapped the territories of 26 male Dickcissels both at the start (early-June) and end (late-July) of the breeding season. Territory size based on 95% MCPs was 0.36 ha (95% CI = 0.30 - 0.41 ha) in June, and 0.29 ha (0.24 - 0.34 ha) in July, and decreased significantly over the season (paired two-sample t-test:  $t = 2.645$ ,  $df = 25$ ,  $P = 0.014$ ; Figure 2.5A). Similarly, territory size based on 95% KDEs was 0.87 ha (0.73 - 1.01 ha) in June, and 0.66 ha (0.53 - 0.78 ha) in July, and decreased significantly over the season ( $t = 3.503$ ,  $df = 25$ ,  $P < 0.005$ ; Figure 2.5B).

## Discussion

With our 2-year field study, we provide some of the first estimates of density and territory size for Dickcissels in managed rangelands. We found that densities of male Dickcissels were similar across experimental treatments, but did differ among patches within the patch-burn grazing treatment, with densities being highest at the patch that was burned in the previous year. We found that management-specific patterns in the density of male Dickcissels might vary across years. Despite variation in Dickcissel density, we found only minor effects of rangeland management on the territory size of Dickcissels. However, we found the smallest territory sizes in the patch where Dickcissel density was highest. We also found that Dickcissels had smaller

territories in July when compared to June, although Dickcissel density was steady or slightly decreasing over the season. Seasonal declines in territory size were not related to Dickcissel density, but could potentially be explained by changes in vegetative structure and food availability throughout the breeding season.

### **Density of Male Dickcissels**

We found that densities of male Dickcissels did not differ across our rangeland management treatments, but showed considerable variation between years and among patches within the patch-burn grazing treatment. We found the highest densities of male Dickcissels in 2014 at patches that had been rested from fire for a growing season (PBG1 2014:  $143.0 \pm 15.6$ SE male Dickcissels/km<sup>2</sup>), while densities were lowest in 2013 at sites that were burned during the current year when compared to unburned patches (PBG0 2013:  $47.7 \pm 8.5$ ). Weather conditions were relatively similar between 2013 and 2014. However, standing vegetation of new growth was shorter and the amount of dead vegetation from previous years was lower in 2013, potentially due to the drought conditions at our site in 2011 and 2012. As a generalist species, Dickcissels are often found to be most abundant on pastures with a moderate burning frequency due to their preference of grasslands with high forb cover and tall dense vegetation (Deschant et al. 1999, Temple 2002, Powell 2006, Rahmig et al. 2009). Pastures that are managed with patch-burn grazing could therefore provide suitable breeding habitat for Dickcissels, since forb cover and standing vegetation is higher in unburned patches, especially following drought conditions in previous years (Fuhlendorf et al. 2006, Ricketts and Sandercock 2016, Verheijen 2017).

There could be several explanations for why we did not observe large differences in Dickcissel density among our experimental treatments. Dickcissels are an abundant species of



grassland songbird at our study site, and it could be that pastures with high quality breeding habitat have reached peak numbers of Dickcissels. As a result, the number of males that settle in suboptimal habitat might be high, thereby obscuring true differences in habitat quality among management regimes (Zimmerman 1993, Herkert 1994, Swengel and Swengel 2001).

Alternatively, the quality of individual males might differ between treatments, which would not be reflected in bird density. In Kansas, Dickcissels do not peak in numbers until late June or early July, and early arriving males may settle in high quality habitats displacing late males to sub-optimal breeding sites (Finck 1984, Temple 2002, Powell 2006, Sousa and Westneat 2013). In our study, we focused our observation efforts on males only, and it is possible that some males in sub-optimal habitat remained unmated.

We found that the effects of rangeland management on densities of male Dickcissels differed between 2013 and 2014, which might be related to annual variation in weather conditions. Densities of male Dickcissels in pastures that were burned and grazed were lower in 2013 than 2014, whereas bird densities on other treatments were only slightly depressed. On burned pastures, the standing vegetation that is available as breeding habitat is solely dependent on new vegetation growth, while grazed pastures will naturally have less standing biomass than ungrazed pastures (Ricketts and Sandercock 2016, Chapter 3). The dry spring conditions in 2013 led to below average growth rates of new vegetation that could function as nest cover. Managing pastures with fire and grazing during drought conditions might therefore lead to unsuitable habitat conditions for Dickcissels.

Previous studies have also found that local population densities of Dickcissels can show considerable annual variation, suggesting that local conditions may affect settlement decisions of a vagile, long-distance migrant (Temple 2002, Powell 2006, Rahmig et al. 2009). However, it is

still unclear which factors drive annual variation in local abundance of Dickcissels. Large-scale droughts have been found to displace Dickcissels out of their core breeding range (Temple 2002). Conversely, Rahmig et al. (2009) unexpectedly found higher densities during dry conditions, and suggested that annual variation in the local abundance of nest-predators or brood parasites could also influence habitat suitability. How climatic conditions drive Dickcissel density could therefore vary among regions. We found that in some regions, patch-burn grazing could aid in maintaining consistent densities of Dickcissels, because unburned patches within the treatment provide suitable breeding habitat.

### **Territory Size**

Dickcissel territory size in our study averaged 0.36 ha (range = 0.08 - 0.69 ha) based on 95% minimum convex polygons, and 0.46 ha (0.10 - 1.30 ha) based on 100% minimum convex polygons. Our estimates of territory size are comparable to previous studies of Dickcissels in Illinois and Kansas, which have reported average territory sizes between 0.3-1.1 ha based on 100% minimum convex polygons (Zimmerman 1966, 1971, Harneson 1974, Finck 1984). As expected, Dickcissel territories were larger and less variable when based on 95% kernel density estimators (mean = 0.87; range = 0.79 – 0.95 ha) compared to 95% minimum convex polygons. Territory sizes based on minimum convex polygons are often assumed to underestimate true territory size. However, Dickcissels are likely to maintain relatively fixed territorial boundaries, and the true territory size may lay in between estimates based on minimum convex polygons and kernel density estimators.

The average territory size of Dickcissels at Konza Prairie did not differ greatly across treatments, but tended to be smaller in the patch-burn grazing patch that was burned in the

previous year. Smaller territory sizes at the PBG1 treatment coincided with greater densities of male Dickcissels. Previous studies found that territory size declined with an increase in local Dickcissel density, likely a result of variation in habitat quality (Schartz and Zimmerman 1971, Harneson 1974). Male Dickcissels defending territories in high quality habitat are often able to secure multiple mates, maintain high levels of within-pair paternity, and apparent nest success (Sousa and Westneat 2013). Thus, higher densities and smaller territory sizes of male Dickcissels on one-year since burn patches within pasture managed with patch-burn grazing could lead to higher reproductive success.

Unexpectedly, territory size declined over the breeding season, while densities of Dickcissels at Konza Prairie did not change between June and July (B. H. F. Verheijen, pers. obs.). Zimmerman (1966) found that Dickcissel territory size increased throughout the breeding season, which coincided with lower densities of territorial males at the end of the breeding season. Males of successful nests show less territorial behavior when guiding fledglings, whereas males with failed nesting attempts might start fall-migration early (Zimmerman 1966, Temple 2002, personal observations). The unexpectedly smaller territories that we found in July may indicate a potential increase in habitat suitability, which would allow males to defend smaller territories. Previous work at Konza Prairie showed seasonal declines of both brood parasitism and nest survival of Dickcissels (Sandercock et al. 2008). In regions with high cowbird abundance, the benefits of reduced rates of parasitism might outweigh the costs of higher rates of nest predation, potentially resulting in higher perceived habitat quality and reproductive success of Dickcissels later in the breeding season (Jensen and Cully 2005b, Sandercock et al. 2008). Indeed, none of the males that were mapped twice defended a completely new territory in July, but instead stopped defending areas of the territory that were mapped in June.

## **Management Implications**

With our field study, we provide some of the first estimates of territory size for Dickcissels, and are the first to examine the effects of rangeland management on space use. We found higher densities and smaller territories of Dickcissels on the PBGI treatment, indicating that habitat in those patches might be of higher quality for breeding Dickcissels. Knowledge of how territory size interacts with population density or habitat quality could aid conservation strategies for declining populations of grassland songbirds, as territory size could limit the number of individuals that could benefit from rangeland management strategies. However, rangeland management can also have large effects on the reproductive success of grassland songbirds as habitat quality drives the number of mates, clutch size, and rates of nest predation and brood parasitism (Temple 2002, Jensen and Cully 2005a, Churchwell et al. 2008, Rahmig et al. 2009, Verheijen et al. 2017). Reproductive success is not always higher in areas that show the greatest densities and smallest territories, and including demographic parameters is essential in properly assessing habitat quality (Vickery et al. 1992). Furthermore, the effects of rangeland management on the survival and movements of fledgling Dickcissels remain largely unknown. Unfortunately for land managers, the effects of grassland management on the reproductive success of grassland songbirds are likely to be region-specific, due to geographical variation in nest predator communities and abundance of Brown-headed Cowbirds (Jensen and Cully 2005b, Lyons et al. 2015). A regional understanding of spatial and breeding biology of declining populations is therefore essential for conservation.

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**Table 2.1.** Distance sampling model selection results for Dickcissels at Konza Prairie, Riley County, Kansas, for 2013 and 2014. Model selection was based on the number of parameters ( $K$ ), Deviance, AIC and  $\Delta\text{AICc}$  values, and Akaike weights ( $w_i$ ). Possible model structures for the detection probability included an intercept-only model, and models an observer effect. When modeling Dickcissel density, we considered an intercept-only model, or models with year, treatment, and/or patch within each treatment effects. We only show models where  $w_i > 0.001$ .

Model Structure		Model Statistics				
Detection	Density	$K$	Deviance	AICc	$\Delta\text{AICc}$	$w_i$
Observer	Year $\times$ Patch	13	2719.16	2745.16	0	0.510
Constant	Year $\times$ Patch	12	2721.47	2745.47	0.32	0.430
Observer	Year + Patch	9	2732.37	2750.37	5.21	0.037
Constant	Year + Patch	8	2735.62	2751.62	6.46	0.020



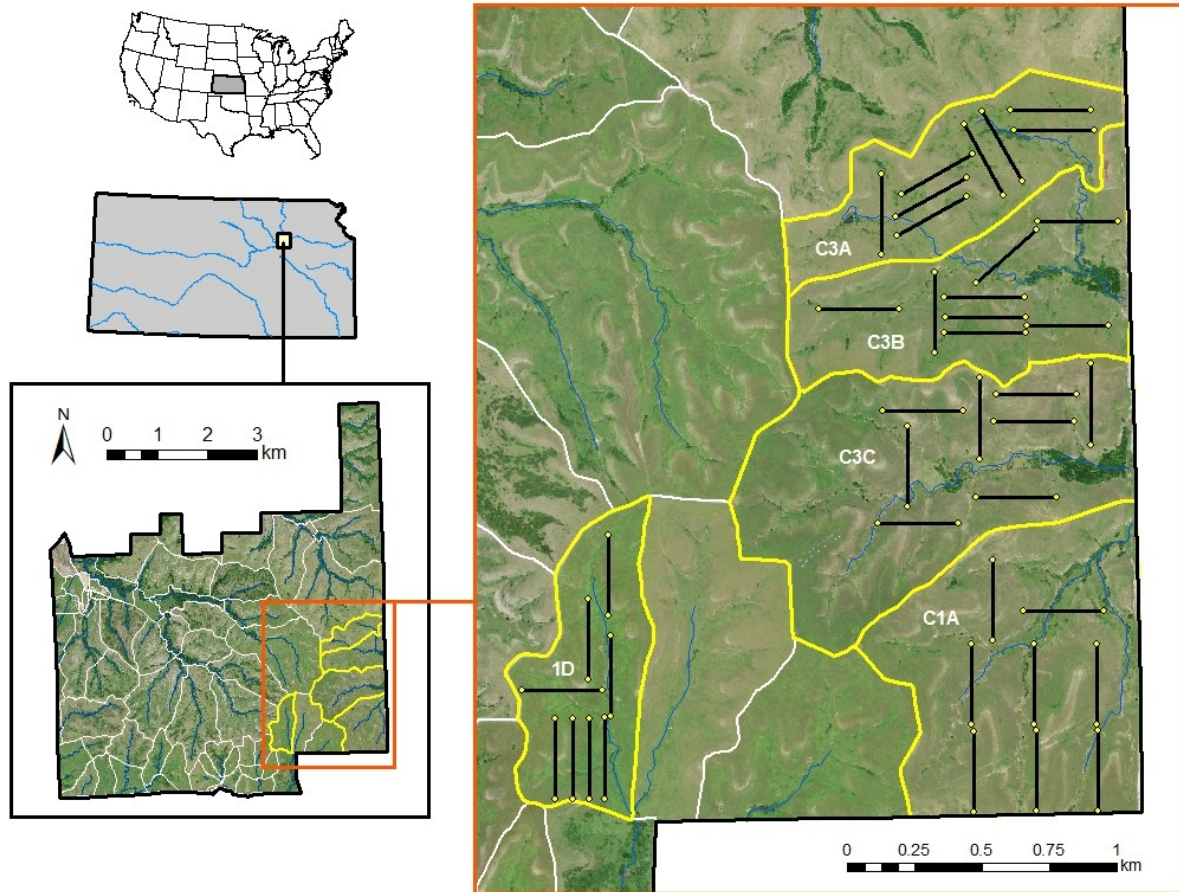
**Table 2.2.** Model selection results of Dickcissel territory size based on 95% minimum convex polygons for Konza Prairie, Riley County, Kansas (2013-2014). We considered an intercept-only model, and models with possible effects treatment, patch-within-treatment, time since last fire, the number of unique points collected for each bird (points), and a set of two-way models with effects of the number of unique points and any other variable. Model selection was based on the number of parameters ( $K$ ), Deviance, AICc and  $\Delta$ AICc values, and Akaike weights ( $w_i$ ).

<b>Model</b>	<b><math>K</math></b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>w_i</math></b>
Points	3	-90.01	-83.66	0.00	0.356
Time Since Fire + Points	5	-93.96	-83.06	0.61	0.263
Time Since Fire	4	-90.17	-81.58	2.09	0.125
Time Since Fire $\times$ Points	7	-96.69	-80.94	2.72	0.091
Constant	2	-84.17	-80.00	3.66	0.057
Treatment + Points	5	-90.34	-79.43	4.23	0.043
Patch + Points	7	-94.33	-78.58	5.08	0.028
Patch	6	-91.05	-77.76	5.90	0.019
Treatment $\times$ Points	7	-92.12	-76.37	7.29	0.009
Treatment	4	-84.60	-76.01	7.65	0.008
Patch $\times$ Points	11	-98.31	-71.91	11.75	0.001

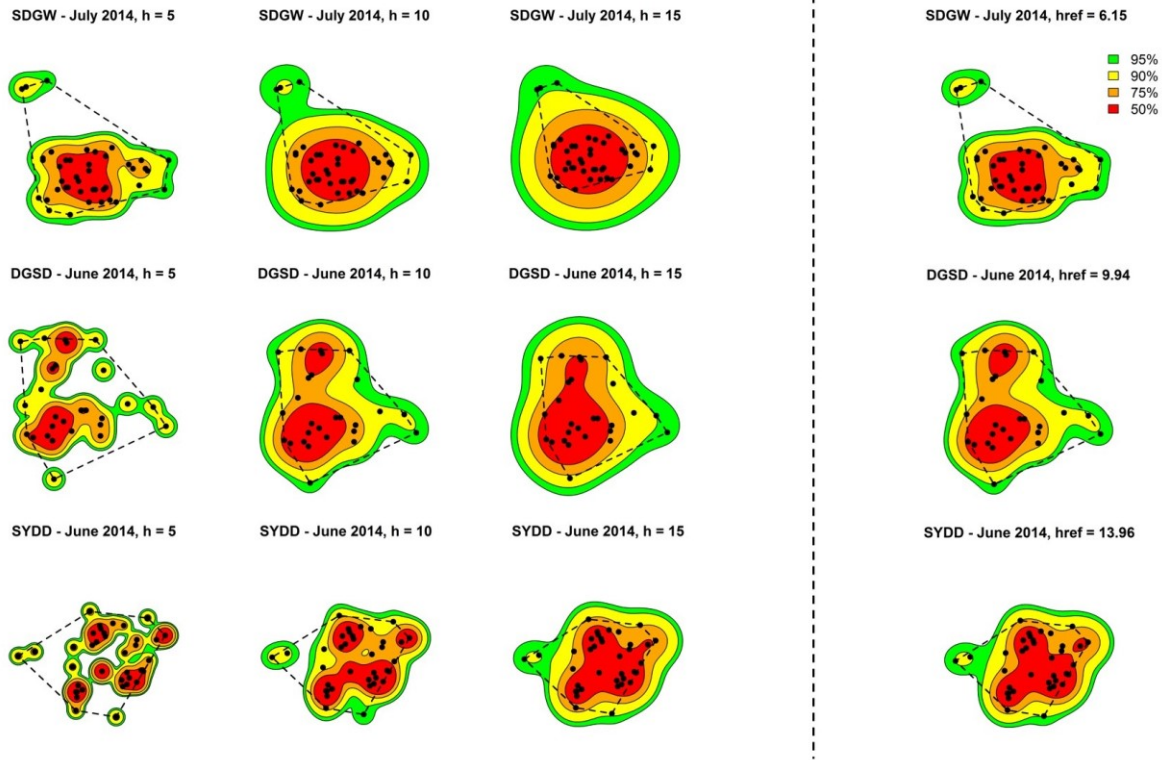
**Table 2.3.** Model selection results of Dickcissel territory size based on 95% Kernel Density Estimation for Konza Prairie, Riley County, Kansas (2013-2014). We considered an intercept-only model, and models with possible effects treatment, patch-within-treatment, time since last fire, the number of unique points collected for each bird (points), and a set of two-way models with effects of the number of unique points and any other variable. Model selection was based on the number of parameters ( $K$ ), Deviance, AICc and  $\Delta$ AICc values, and Akaike weights ( $w_i$ ).

<b>Model</b>	<b><math>K</math></b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>w_i</math></b>
Time Since Fire $\times$ Points	7	33.52	49.30	0.00	0.241
Time Since Fire	4	41.25	49.86	0.56	0.182
Time Since Fire + Points	5	39.46	50.38	1.08	0.140
Constant	2	46.29	50.46	1.17	0.134
Treatment	4	42.65	51.25	1.96	0.090
Patch	6	38.74	52.06	2.76	0.061
Points	3	45.78	52.13	2.84	0.058
Patch + Points	7	37.29	53.07	3.77	0.037
Treatment + Points	5	42.35	53.28	3.98	0.033
Patch $\times$ Points	11	27.64	54.12	4.82	0.022
Treatment $\times$ Points	7	42.09	57.87	8.57	0.003

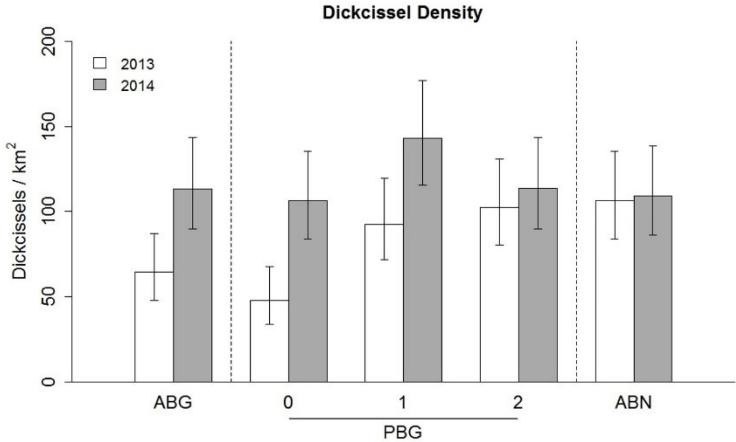
**Figure 2.1.** A map of our five experimental pastures and line transects within each pasture (right), at the Konza Prairie Biological Station, northeast Kansas (left). Experimental pastures are delineated in yellow, while 300-m transects are shown as black lines.



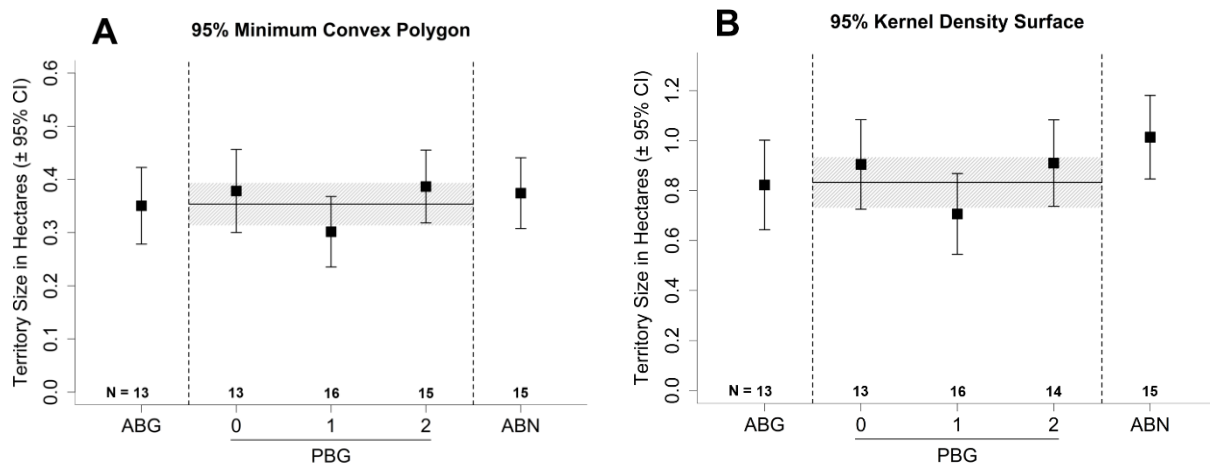
**Figure 2.2.** Three representative examples of male Dickcissels that illustrate how a variable smoothing parameter selected by the  $h_{ref}$  function might be better than one overall smoothing parameter for all birds, as the individual-specific  $h_{ref}$  successfully avoids under- and over-smoothing by taking the location density of each individual into account. Shown are kernel densities of three birds with a smoothing parameter of  $h = 5$ ,  $h = 10$ , and  $h = 15$  as well as the selected smoothing parameter by the  $h_{ref}$  function. Black dots indicate observation locations and dashed lines show a 100% minimum convex polygon overlaid on each kernel density surface.



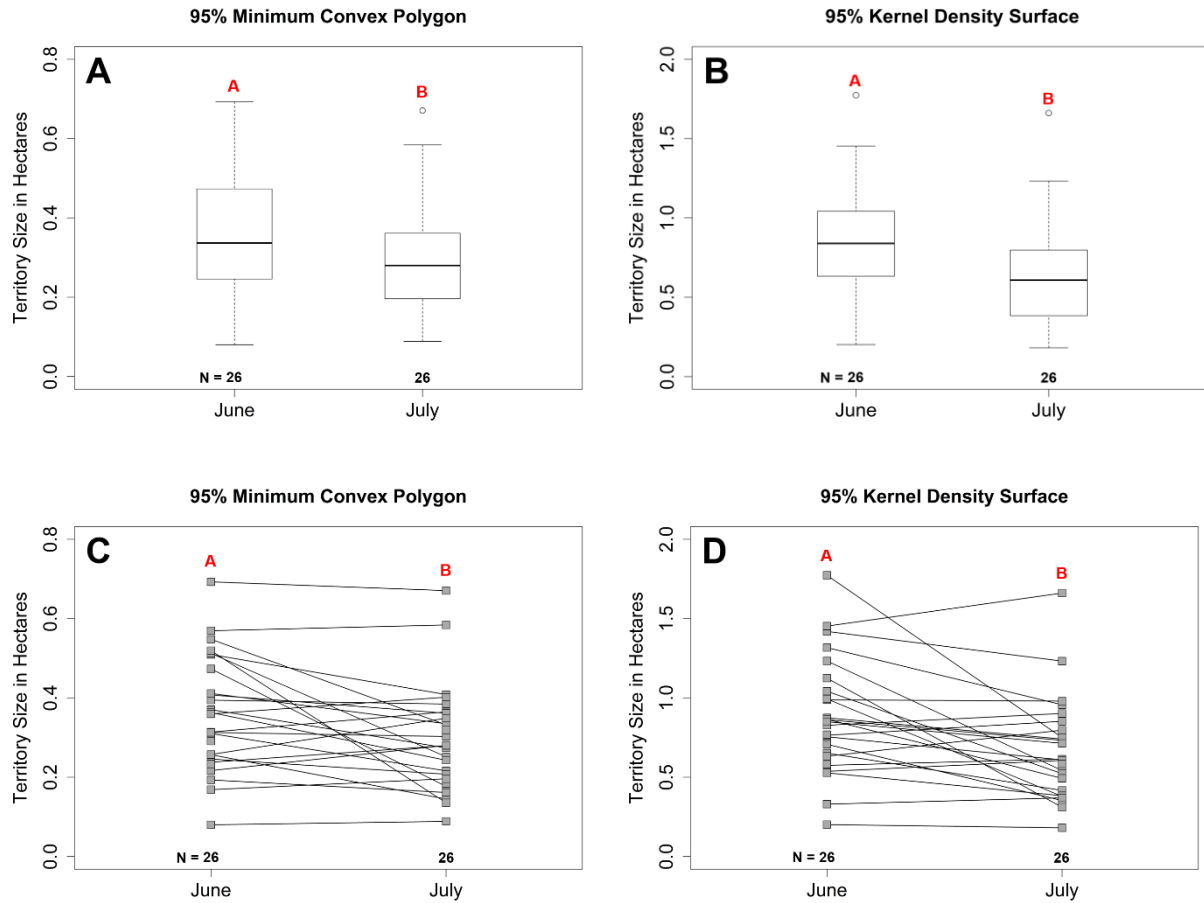
**Figure 2.3.** Density of male Dickcissels ( $\pm$  95% confidence intervals) at Konza Prairie, Kansas, 2013-2014. Estimates were calculated separately by year for five rangeland management treatments: Annual burning and grazing (ABG; negative control), patch-burn grazing (PBG, 0-2 years since fire), and annual burning without grazing (ABN; positive control).



**Figure 2.4.** Estimates of territory size for breeding male Dickcissels ( $\pm$  95% confidence intervals) based on 95% Minimum Convex Polygons (A), and 95% Kernel Density Surface (B) for Konza Prairie, Kansas, for 2013 and 2014, estimated separately for each treatment and each patch within the patch-burn grazing treatment. Treatments and patches are labeled as following: ABG = annually burned and grazed, PBG = patch-burned and grazed, 0-2 depict the years since the last burn of each patch-burn grazing patch, and ABN = annually burned and not grazed. The mean territory size and confidence interval for the patch-burn grazing treatment as a whole is depicted by the line and shaded area.

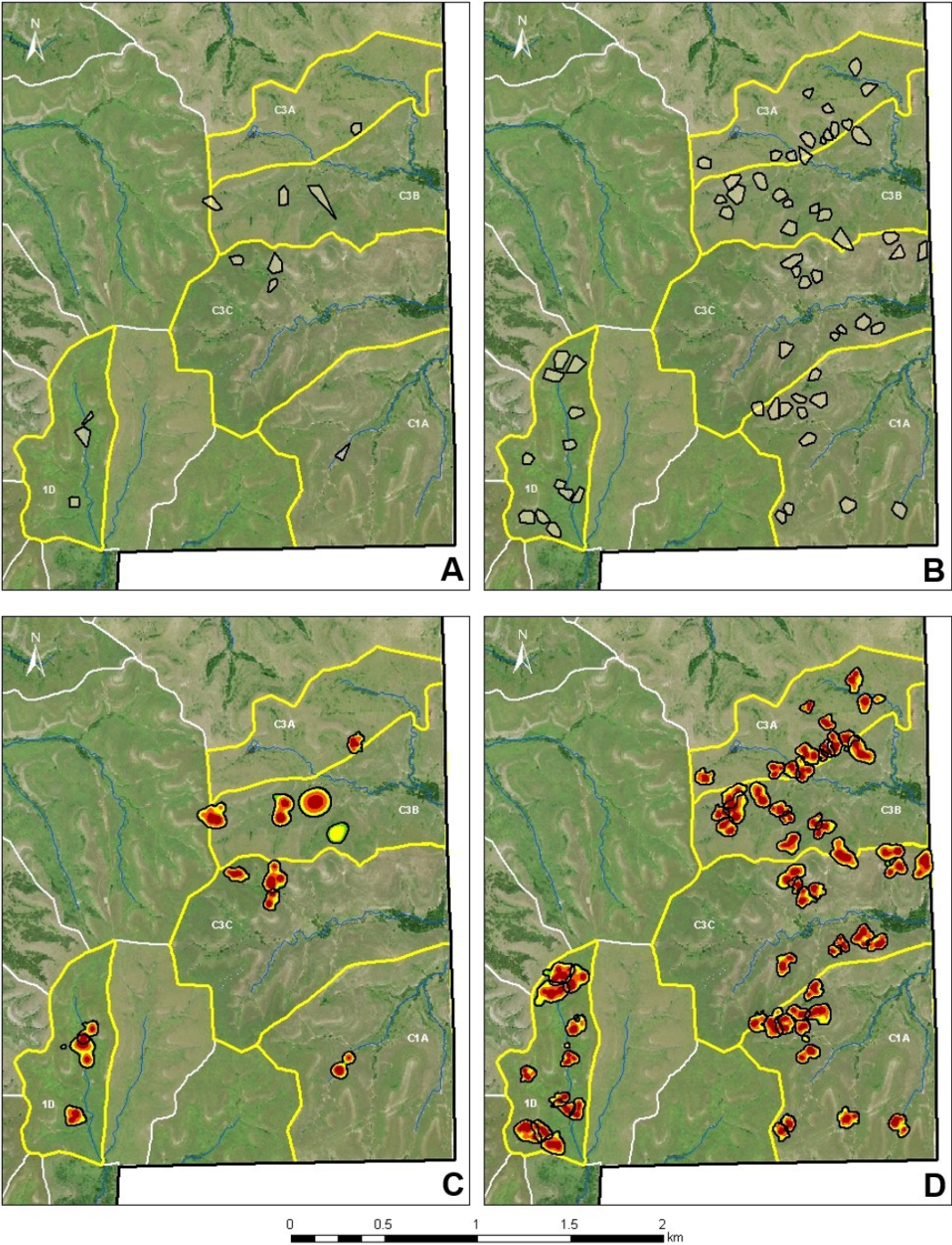


**Figure 2.5.** Estimates of territory size for breeding male Dickcissels ( $\pm$  95% confidence intervals) based on 95% Minimum Convex Polygons (A,C), and 95% Kernel Density Surface (B,D) for Konza Prairie, Kansas, estimated separately for June and July 2014. Connected gray boxes in figures C and D represent the paired nature of territory size estimates of individual male Dickcissels in June and July. Significant differences between months are shown with different lettering.



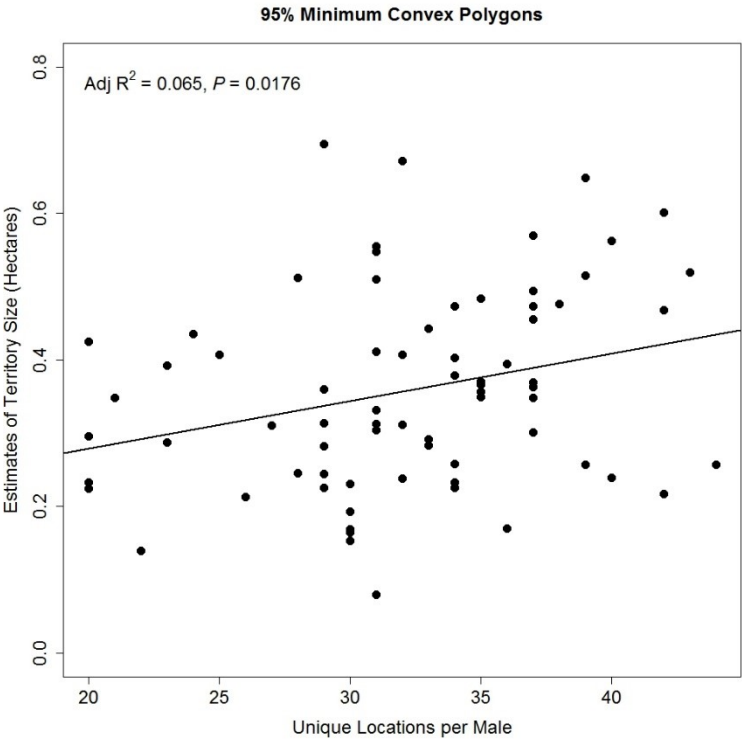


**Supplemental Figure 2.1.** Maps of territories of marked male Dickcissels at Konza Prairie, Kansas, during June 2013-2014. Territories are based on 95% Minimum Convex Polygons (A: 2013, B: 2014) and 95% Kernel Density Estimators (C: 2013, D: 2014).





**Supplemental Figure 2.2.** The relationship between the number of unique locations and territory size of male Dickcissels at Konza Prairie, Kansas, June 2013-2014. Territory size is based on 95% Minimum Convex Polygons.



## **Chapter 3 - Effects of heterogeneity in vegetative structure on reproductive success of grassland songbirds**

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*--- In preparation for The Auk ---*

## Abstract

In North America, tallgrass prairie was historically maintained as a mosaic of different habitats by the interaction between fire and selective grazing by large herbivores. In recent decades, agricultural intensification has reduced heterogeneity in vegetative structure in managed grasslands, which has been linked to widespread declines in songbird populations. Patch-burn grazing management aims to restore heterogeneity in vegetative structure on the landscape by rotationally burning pasture-sections, combined with foraging preferences of cattle to graze in recently burned areas. Patch-burn grazing can increase the diversity, abundance, and reproductive success of grassland songbirds, but potential effects of regional differences in predator community and abundance of Brown-headed Cowbirds (*Molothrus ater*), and annual variation in weather conditions, still remain largely unknown.

During a 6-year field study, we tested how heterogeneity in vegetative structure affects the reproductive output of Dickcissels (*Spiza americana*), Eastern Meadowlarks (*Sturnella magna*), and Grasshopper Sparrows (*Ammodramus savannarum*). We compared two tallgrass prairie sites that included experimental pastures that were managed with patch-burn grazing, versus control pastures that were annually burned with or without grazing. Here, we estimated rates of brood parasitism, clutch size, nest survival, and fledging rates of each songbird species, and calculated the average number of fledglings produced per nest with bootstrapping. We further tested whether variation in temperature and precipitation drives variation in the amount of available nest cover or levels of predator activity.

We found that rangeland management affected rates of brood parasitism, the average number of cowbird eggs, nest survival, and fledging rates of Dickcissels, and nest survival of

Eastern Meadowlarks. However, effects of rangeland management on variation in demographic parameters only resulted in minor differences in the average number of fledglings per nesting attempt in Dickcissels and Eastern Meadowlarks. Variation in climatic conditions had a large effect on vegetative structure, but we did not find much evidence for annual variation in reproductive success of any of our three species. Our results support previous studies that show that patch-burn grazing does not have negative effects on demographic rates of grassland songbirds, and could provide suitable breeding habitat for species that require amounts of litter for cover that is not found in annually burned pastures. Furthermore, patch-burn grazing management could benefit cattle-ranchers in a changing climate, since unburned patches could provide standing vegetation for cattle during drought conditions.

## Introduction

Grasslands are among the most rapidly declining ecosystems in the world, especially in North America, where only 10% of the historical grasslands are left (Samson and Knopf 1994, DeLuca and Zabinski 2011). A majority of the remaining grasslands in North America are now used for cattle production, and are often managed with high densities of grazing animals and frequent prescribed burns. Intensive grazing can lead to high cattle gains, but reduces the variation in vegetative structure and cover on the landscape (Knapp et al. 1999, Fuhlendorf et al. 2006). A homogeneous landscape is associated with lower species diversity and abundance of wildlife, including arthropods (Joern 2005), mammals (Ricketts and Sandercock 2016), and grassland songbirds (Fuhlendorf et al. 2006, Powell 2006). Thus, agricultural intensification may be one of the main drivers for widespread population declines of grassland birds in North America (Samson and Knopf 1994, Herkert et al. 2003, Sauer and Link 2011, North American Bird Conservation Initiative 2016).

Historically, the tallgrass prairie was a heterogeneous landscape that was maintained by pyric-herbivory, an interaction between periodic fire and selective grazing by bison (*Bos bison*) and other native ungulates (Fuhlendorf and Engle 2001). A relatively new rangeland management strategy, patch-burn grazing, has been proposed to more closely match the effects of the historical interaction between fire and selective grazing by ungulates (Stebbins 1981, Knapp et al. 1999, Fuhlendorf and Engle 2001). Under patch-burn grazing management, only a section of the pasture is burned each year in a two- to four-year rotational scheme. Pasture sections are not separated by cross-fencing and cattle are free to preferentially graze recently burned patches. A more heterogeneous use of the landscape results in a greater variety of vegetative structure and

plant species composition in the pasture (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006; 2009, Churchwell 2008, Ricketts and Sandercock 2016).

As a result of higher levels of habitat heterogeneity, patch-burn grazing management can benefit species diversity and abundance of grassland birds (Fuhlendorf et al. 2006, Powell 2006). Moreover, patch-burn grazing can improve the reproductive success of grassland songbirds by decreasing rates of nest predation and brood parasitism (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016). Unfortunately, past studies have often been limited to a single site or species, and have not considered regional variation in predation risk and rates of brood parasitism, which are known to have large effects on reproductive success (Martin 1995, Jensen and Cully 2005a). As a result, the potential links between heterogeneity in vegetative structure as a result of patch-burn grazing management and reproductive output of grassland songbirds remain poorly known.

Vegetative structure can directly affect the reproductive output of grassland songbirds by mediating rates of nest predation and brood parasitism by Brown-headed Cowbirds. Nest predation is the main source of reproductive losses in songbirds (Martin 1992; 1995), and nest survival in grassland-breeding songbirds is especially low (Martin 1992). Nest survival rates often increase with greater amounts of litter and taller vegetation heights, which improves nesting cover (Hughes et al. 1999, Winter 1999, Temple 2002, Churchwell et al. 2008, Hovick et al. 2012). Grazing and burning reduce the amount of plant litter, vegetation height, and amount of cover available throughout the breeding season (Fuhlendorf and Engle 2001; 2004, Churchwell 2008), thereby negatively influencing nest survival of grassland songbirds (Zimmerman 1997, Rohrbaug 1999, Dechant et al. 2002, Churchwell 2008, Rahmig et al. 2009). Brood parasitism by Brown-headed Cowbirds is also widespread among grassland songbirds (Zimmerman and Finck

1989, Jensen and Cully 2005a, Martin 2014), and leads to demographic losses via the removal of host eggs (Zimmerman and Finck 1989), higher predation risk (Jensen and Cully 2005a), and by competition between host and parasitic young (Jensen and Cully 2005a, Rivers et al. 2010a), which can lead to reproductive failure in small-bodied host species (Kosciuch and Sandercock 2008). Cowbirds often forage in association with grazing animals, but the potential relationship between rangeland management and rates of brood parasitism remains relatively unknown. Rates of brood parasitism are influenced by the abundance of female cowbirds (Jensen and Cully 2005a; 2005b), which has been linked to shorter grassland vegetation (Morris and Thompson 1998; Goguen and Mathews 1999; 2000; Patten et al. 2006). However, female cowbirds have large home ranges and may parasitize songbird nests outside of their preferred foraging habitat (Dijak and Thompson 2000).

In addition to spatial variation, annual variation in growing season temperature and precipitation can have large effects on the vegetative structure of grasslands. Climatic conditions are a major driver of primary production and vegetation height in grasslands, and could interact with fire and grazing to shape species composition and vegetative structure of managed grasslands (Briggs and Knapp 1995, O'Connor et al. 2001, Swemmer et al. 2007, Sherry et al. 2008). By altering vegetation height and nest cover by driving new vegetation growth, annual variation in weather could lead to wide variation in reproductive success of grassland birds. With global climate change, it becomes increasingly important to understand how annual weather conditions affect rates of nest survival and brood parasitism (Dawson et al. 2011, IPCC 2013, Hovick et al. 2015). In drought years, growth of new vegetation may be limited, which makes birds that rely on tall vegetation for nest cover more reliant on vegetation from previous years (Sherry et al. 2008). Prescribed fire removes the majority of standing vegetation from a pasture,

which could lead to high levels of nest predation and brood parasitism on recently burned pastures. Patch-burn grazing management might be more resilient to annual variation in climatic conditions if unburned areas provide a refuge, and could lead to more stable reproductive success of grassland songbirds across years (Hovick et al. 2016).

With our field study, we tested how heterogeneity in vegetative structure affects the reproductive output of three species of declining grassland songbirds by comparing experimental pastures that were managed with patch-burn grazing, versus control pastures that were annually burned with or without grazing. Our study took place at two tallgrass prairie sites to account for spatial variation in predator community composition and the local abundance of Brown-headed Cowbirds. We tested two hypotheses: the “*predation risk hypothesis*” posits that variation in vegetative structure drives reproductive success of grassland songbirds by altering nest predation rates. We predicted that predation rates would be lowest in patch-burn grazing managed pastures and highest in annually burned and grazed pastures. The “*parasitism risk hypothesis*” argues that variation in vegetative structure drives reproductive success by altering brood parasitism rates. We predicted that rates of brood parasitism by Brown-headed Cowbirds and rates of multiple brood parasitism would increase with more recent fire and the presence of grazers on the landscape.

As a second objective, we assessed the interactive effects of the annual variation in temperature and precipitation on the relationship between grassland management and reproductive output of grassland songbirds during a three- to six-year period. Here, we tested two additional hypotheses: the “*environmental variation hypothesis*” states that annual variation in temperature and precipitation drives the amount of cover and nest concealment on the landscape. We predicted that rates of nest predation and brood parasitism are higher in dry and hot years



when new growth of vegetation is low. The “*predator activity hypothesis*” suggests that annual variation in temperature could drive predator activity directly. Snakes are one of the main nest predators for grassland songbirds (Klug et al. 2010), and are more active during warmer conditions. We therefore predicted higher nest predation rates in warmer years regardless of management regime.

## **Methods**

### **Study Sites**

Our field study was conducted at two tallgrass prairie sites in Kansas. Between 2011 and 2013, we collected data at a privately-owned ranch in Chase and Greenwood County (hereafter Chase County). Between 2011 and 2016, we collected data at the Konza Prairie Biological Station (hereafter Konza Prairie), a tallgrass prairie preserve that is part of the NSF-funded Long-term Ecological Research (LTER) Site Program, and located in the Flint Hills ecoregion of Geary and Riley County, Kansas, USA.

The climate of Chase County and Konza Prairie is relatively humid during the growing season. Over the past century, the average annual temperatures were 13.3°C for Chase County and 12.6°C for Konza Prairie, but monthly average temperatures got as high as 25-26°C in July and August. Annual precipitation averaged 839 mm per year in Chase County and 799 mm per year at Konza Prairie. Generally, 75% of precipitation falls within the growing season (March – August), but late summer droughts in July and August are fairly common. Moreover, the total amount and the seasonal patterns in precipitation show considerable annual variation (NOAA 2017).

The tallgrass prairie in Chase County and Konza Prairie is dominated by native warm-season grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiagrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). Forbs comprise much of the plant species diversity of the tallgrass prairie, and common forbs in our study areas included Baldwin's ironweed (*Vernonia baldwinii*), common yarrow (*Achillea millefolium*), goldenrod (*Solidago* spp.), leadplant (*Amorpha canescens*), several milkweed species (*Asclepias* spp.), and round-head bush clover (*Lespedeza capitata*). Woody plants are relatively uncommon in frequently burned tallgrass prairie, but shrub species that were present included buckbrush (*Symphoricarpos orbiculatos*), inland ceanothus (*Ceanothus herbaceus*), rough-leaved dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and wild plum (*Prunus americana*; Towne et al. 2002). The privately owned field site at Chase County has experienced a higher fire frequency than Konza Prairie in recent decades, and therefore has a lower amount of shrub cover.

### **Study Species**

Our study focuses on three common species of grassland songbird, the Dickcissel (*Spiza americana*), Eastern Meadowlark (*Sturnella magna*), and Grasshopper Sparrow (*Ammodramus savaanarum*), which differ in nesting habitat requirements and nest architecture. The Dickcissel is a small-bodied songbird, with an average body mass of 28.5 g for males and 25.2 g for females. Within tallgrass prairie, Dickcissels select breeding habitats with dense cover, moderate to tall (25-150 cm) vegetation, moderate amounts of litter (5-15cm), and a high amount of song perches, where they build an open cup nest slightly raised from the ground (Dechant et al. 1999, Temple 2002). Eastern Meadowlarks are larger-bodied songbirds, with an average body mass of 123.2 g

for males and 100.1 for females. Eastern Meadowlarks select breeding habitats with high grass and litter cover, and high vertical vegetation density, where they build a well concealed, domed nest on the ground (Jaster et al. 2012). Our last focal species, the Grasshopper Sparrow, is a small-bodied songbird, where both sexes have an average body mass of 17.3 g. Breeding habitats of Grasshopper Sparrows at tallgrass prairie sites contain moderately open prairie, and include some bare ground and litter, where they build a well-hidden, domed nest (Vickery 1996).

### **Experimental Treatments**

At our Chase County field site, we monitored vegetation and breeding birds at two privately owned pastures. One pasture consisted of three smaller units, or patches (142 to 155 ha), and was managed with patch-burn grazing (PBG). A second pasture was annually burned and grazed, and served as a negative control (ABG, 419 ha). During the study, all pastures were early stocked with steers from mid-April to mid-July. The annually burned and grazed pasture had a stocking rate of 0.85-1.05 hectares per head, whereas the patch-burn grazing pasture was stocked at a rate of 1.05-2.09 hectares per head. Burning was conducted between late-March and early-April, except for the ABG pasture, which was not burned during 2012 and 2013 due to drought conditions and a lack of standing vegetation to carry the fire.

At Konza Prairie, our field site included three experimental pastures. Three pastures (49.4 – 102.4 ha) were combined to form one large pasture (219.3 ha) that was managed with rotational fire in a patch-burn grazing management regime with a 3-year rotation (PBG). A second pasture was annually burned and grazed and served as a negative control (ABG; 93.5 ha), and a third pasture that was annually burned and ungrazed served as a positive control (ABN; 41.6 ha). Pastures were season-long stocked by cow/calf pairs at a rate of 3.24 hectares per pair from early

May to early October (J. Briggs and K.C. Olsen, pers. comm.). Pastures at Konza Prairie were burned in the early spring between mid-March to mid-April. All experimental pastures at the Chase County and Konza Prairie sites were managed with the specified management regime for at least three years before we started our field study on grassland birds.

## **Climate**

To assess annual variation in how each management regime affects vegetation structure, we obtained precipitation and temperature data for our study sites from the long-term climate database of National Oceanic and Atmospheric Administration (NOAA). We obtained monthly average temperature and precipitation for the 100-year period from September 1916 to August 2016 from the closest weather station to each study site (Station ID, Chase: USC00141858, Konza: USC00144972). For each site, we then calculated z-scores for climatic conditions for each 6-month growing season (March to August). To calculate z-scores, we took the average temperature or precipitation for each growing season based on monthly averages of that year to obtain a distribution of 100 averages for the past century from 1916 to 2016. We then calculated site specific z-scores for each year with the following equation:

$$z_{ij} = \frac{x_{ij} - \mu_j}{\sigma_j}$$

where  $x_{ij}$  is the year and site-specific estimate of temperature or precipitation,  $\mu_j$  is the site-specific mean over a 100-year period, and  $\sigma_j$  is the site-specific standard deviation. We used year-specific z-scores of growing season temperature and precipitation as categorical variables to

explain annual variation in the vegetation characteristics of each management regime with R (R Core Team 2017).

## **Vegetation Surveys**

We sampled vegetation at each pasture during the mid-growing season of each year (June – July). We recorded vegetation measurements at five points along eight 300-meter transects in each patch within the PBG treatment, as well as in our control pastures. Transects were randomly placed within each patch or pasture, and were at least 100 meters apart. At each point, we used a Robel pole to measure the visual obstruction at a distance of 4 meter and at a height of 1 meter in each cardinal direction from the pole (Robel et al. 1970). Visual obstruction readings are a good index of aboveground biomass for prairie plants. In addition, we used a 25 x 50 cm Daubenmire frame to estimate the percent cover of grasses and sedges, broad-leaved forbs, shrubs, bare ground, and plant litter (Daubenmire 1959). We also measured the litter depth at 0, 2, and 4 meters in each cardinal direction from the Robel pole, for a total of 12 measurements at each point. We then averaged the four visual obstruction and twelve vegetation cover measurements at each point to obtain 40 measurements for each variable per pasture or patch per year.

## **Nest Monitoring**

To estimate the demographic responses of grassland songbirds to rangeland management regimes, we monitored nests of Dickcissels (*Spiza americana*), Eastern Meadowlarks (*Sturnella magna*) and Grasshopper Sparrows (*Ammodramus savannarum*) in each pasture or patch at our two study sites. We located nests by watching behavior of the attending parents and by opportunistically flushing birds. At discovery, we marked the nest at ~5 m with a small rock or

flagging tape in a random direction, and recorded the distance and compass bearing to the nest site. We monitored nests every 2-3 days until we determined the nest fate as successful or failed. During each visit, we counted all eggs and young to determine hatching and fledging success, as well as rates and intensity of brood parasitism by Brown-headed Cowbirds. We considered a nest to be parasitized if at any point during the nesting attempt a cowbird egg or nestling was encountered in the nest, and we estimated the intensity of parasitism by counting the number of cowbird offspring present. Parasitic eggs of cowbirds are easily differentiated from host eggs of Dickcissels by coloration of the eggshell, and from eggs of Grasshopper Sparrows and Eastern Meadowlarks by egg size. Moreover, cowbird nestlings lack the yellow flanges that are characteristic of Dickcissel and Grasshopper Sparrow nestlings, and lack the white down and white palate spots of Eastern Meadowlark nestlings (Rodewald 2017). We considered a nest to be *successful* if any host or cowbird chick survived until fledging, and if parents were observed defending or feeding dependent young at the nest or within the vicinity of the nest after fledging. A nest was considered to have *failed* if its contents disappeared before the expected fledging date, or if broken eggs, torn nest, a predator, or other sign at the nest site indicated that the nest contents had been destroyed by a predator, rainfall, or other causes.

### **Calculating Reproductive Success**

First, we compared parasitism rates, clutch size, nest survival, and fledging rates of each songbird species between our two sites. For site comparisons, we limited our analysis to the three-year period when we had nest data for both sites (2011-2013), and dropped data from the annually burned but ungrazed treatment, which was only monitored at Konza Prairie. If we found

significant differences between sites for all four parameters, we continued our analyses separately for Chase County and Konza Prairie.

To model rates of brood parasitism, we fit a species-specific set of logistic regression models in R (R Core Team 2017). For all our analyses, we tested the effects of patch-burn grazing management on demographic parameters at two separate scales. A treatment model included both control pastures and the patch-burn grazing managed pasture as a whole, while a patch-within-treatment model included both controls and all three patches of the patch-burn grazing pasture separately. Our final model set included an intercept-only model, and all possible combinations of the fixed effects of treatment or patch-within-treatment, year of study, and the interaction between treatment and year. We then determined which combination of variables best explained parasitism rate by comparing differences in AICc-values (Burnham and Anderson 2002). We tested the goodness-of-fit of the top-ranked model for each species with a Pearson  $\chi^2$  test, and determined potential differences among treatments and years with Wald-tests for pairwise comparisons.

To estimate clutch size for each songbird species, we excluded nests that were found in the building or laying stage and did not survive until the start of incubation, since those nests might have failed before the final clutch size was reached. We also excluded nests that were found during the brood-rearing stage, since those nests might have partial egg and/or brood loss due to predation or other causes, and might therefore underestimate the initial clutch size. We modeled clutch size of each species separately with multinomial regression models with the *nnet* package in R (Venables and Ripley 2002; R Core Team 2017). We related variation in clutch size to management regime or patch within each regime, year, and whether a nest was parasitized by cowbirds. We determined which combination of variables best explained clutch size by

comparing AIC values (Burnham and Anderson 2002), and tested the goodness-of-fit of the top-ranked model for each species with a Pearson  $\chi^2$  test. We further determined potential differences among treatments and years with Wald-tests for pairwise comparisons.

To estimate daily nest survival for each species, we discarded nests where nest fate was unknown. We then tested whether daily nest survival differed among management regimes or patches within each regime, across years, and between parasitized and unparasitized nests with nest survival models in the *RMark* package in R as an interface to Program Mark (White and Burnham 1999, Laake et al. 2016, R Core Team 2017). If multiple models were equally parsimonious ( $\Delta AIC \leq 2$ ), we used model averaging based on AIC-weights to calculate final parameter estimates and standard errors that accounted for both sampling and model-selection uncertainty. We calculated survival estimates for the entire nesting cycle (egg-laying, incubation, and brood rearing) by raising the daily nest survival to a species-specific exposure period of 24 days for Dickcissels and Grasshopper Sparrows, and 28 days for Eastern Meadowlarks (Vickery 1996, Temple 2002, Sandercock et al. 2008, Jaster et al. 2012). We used the delta-method to calculate the variance of our projected estimates of daily survival for the different exposure periods (Powell 2007).

To estimate the fledging rate per egg for each species, we limited our analyses to nests that successfully fledged at least one host nestling. We further excluded nests that were found during the brooding stage, since those nests might have had partial losses due to predation or other causes before we found the nest, and might therefore overestimate fledging rates. We used logistic regression models in R to model whether the chance of an individual egg successfully fledging from the nest varied with regime or patch within regime, year, whether the nest was parasitized or not, or the total clutch size of both host and cowbird eggs (R Core Team 2017). We



determined which combination of variables best explained fledging rate by comparing AIC values, and tested the goodness-of-fit of the top-ranked model for each species with a Pearson  $\chi^2$  test. We further determined potential differences among treatments and years with Wald-tests for pairwise comparisons.

Last, for each species we calculated the expected number of host fledglings produced per nest. To calculate the number of fledglings per nest, we included our empirical estimates of parasitism rate ( $p$ ), clutch size ( $C$ ), period nest survival ( $S$ ), and fledging rate per egg ( $F$ ), estimated separately for parasitized ( $p$ ) and unparasitized nests ( $1-p$ ), in the following equation:

$$\text{Fledglings per nest} = [ p \times C_p \times S_p \times F_p ] + [ (1-p) \times C_{(1-p)} \times S_{(1-p)} \times F_{(1-p)} ]$$

We used parametric bootstrapping to calculate the number of fledglings per nest by taking a random draw for each parameter from their parameter-specific sampling distribution. For the probabilities of brood parasitism, nest survival, and fledging rate, we used a beta distribution where the mean and standard deviation were directly taken from the top model of each parameter-specific analysis. For clutch size, we used a multinomial sampling distribution with the probabilities of each possible clutch size taken from the treatment or patch-specific multinomial regression models. We repeated random draws for 100,000 iterations to create a bootstrap distribution of the number of fledglings per nest, and calculated means and standard errors for each management regime. We compared distributions for each treatment and calculated p-values based on the distribution of the difference between two management-specific distributions in R (R Core Team 2017).

## Results

### Climate

Temperature and precipitation conditions showed considerable variation during our six-year field study (see Table 3.1). Temperatures in the growing season were relatively warm at Konza Prairie in 2011 ( $z = +1.04$ ) and at both sites in 2012 (Chase:  $z = +2.65$ ; Konza:  $z = +2.31$ ), whereas 2013 was relatively cold at both sites (Chase:  $z = -1.60$ ; Konza:  $z = -1.62$ ). Precipitation during the growing season was below average in the drought years of 2011 (Chase:  $z = -1.44$ ; Konza:  $z = -0.40$ ) and 2012 (Chase:  $z = -1.26$ ; Konza:  $z = -0.96$ ). On the other hand, 2013 was a relatively wet year for Chase ( $z = +1.38$ ), but not for Konza ( $z = -0.15$ ), and 2016 showed above average amounts of precipitation during the growing season as well (Konza:  $z = +0.95$ ; Table 3.1).

### Vegetation Surveys

First, we tested for differences in vegetation characteristics between the Chase County and Konza Prairie sites for three concurrent years in 2011-2013 in the PBG and ABG units. We found a strong site effect for most vegetation characteristics and opted to analyze the two sites separately.

At both Chase and Konza, variation in vegetation characteristics were best explained by models that included management treatment and year effects (see Supplemental Table 3.1).

Visual obstruction readings (VOR) did not differ between the patch-burn grazing and annually burned and grazed treatments at either site, but were slightly higher at the annually burned and ungrazed treatment (ABN), and tended to be lowest in the burned patch within the patch-burn grazing pasture (PBG0; Figure 3.1A-B, Supplemental Tables 3.2 and 3.3). Grass cover was higher in the annually burned and ungrazed treatment (ABN) than the patch-burn grazing or

annually burned and grazed treatments (PBG and ABG; Figure 3.1C-D, Supplemental Tables 3.2 and 3.3), while forb cover showed the opposite trend (Figure 3.1E-F, Supplemental Tables 3.2 and 3.3). At both sites, litter depth was higher in the patch-burn grazing treatment than in the annually burned and grazed and annually burned and not-grazed treatments. Within the patch-burn grazing treatment, the highest litter depths were found in the unburned patches (PBG1 and PBG2; Figure 3.1G-H, Supplemental Tables 3.2 and 3.3).

We found large annual variation in VOR, percent grass cover, and litter depth at both sites. During the drought conditions of 2012, VOR, percent grass cover, and litter depth were all lower than average, and litter depth remained low in the next year (Supplemental Figure 3.1, Supplemental Tables 3.2 and 3.3). Although our sites experienced drought conditions in 2011 as well, we did not find a vegetative response, indicating potential lag effects. At Konza Prairie, VOR was higher than average during 2014, 2015 and 2016, grass cover was higher than average in 2015 and 2016, and litter depth was higher in 2011 and 2016 following favorable growing conditions in the previous year (Supplemental Figure 3.1 and Supplemental Tables 3.2 and 3.3).

### **Nest Monitoring**

During 2011 to 2016, we monitored a total of 885 nests of three species of grassland songbirds. Our sample included 554 nests of Dickcissels (189 at Chase, 365 at Konza), 147 nests of Eastern Meadowlarks (51 at Chase, 96 at Konza), and 184 nests of Grasshopper Sparrows (82 at Chase, 102 at Konza) across all experimental pastures. When subdivided among treatments, we found relatively low numbers of Eastern Meadowlark and Grasshopper Sparrow nests at recently burned pastures (ABG, ABN, and PBG0; see Table 3.2).

## **Parasitism Rates**

Rates of brood parasitism were ~1.5 times higher at Konza Prairie (0.457 – 0.847) than Chase County (0.255 – 0.582) for all three species of grassland songbirds (Figure 3.2). We found that Dickcissel were most regularly parasitized by cowbirds (Chase:  $0.582 \pm 0.036\text{SE}$ ,  $N = 189$ ; Konza:  $0.847 \pm 0.019$ ;  $N = 365$ ), followed by Grasshopper Sparrows (Chase:  $0.390 \pm 0.054$ ,  $N = 82$ ; Konza:  $0.613 \pm 0.051$ ;  $N = 101$ ), and then Eastern Meadowlarks (Chase:  $0.255 \pm 0.061$ ,  $N = 51$ ; Konza:  $0.457 \pm 0.051$ ;  $N = 96$ ). Variation in parasitism rates of Dickcissel nests was best explained by management regime at both sites, but management regime affected parasitism rates of Eastern Meadowlarks and Grasshopper Sparrows only at the Chase County site (Table 3.3). At Konza Prairie, parasitism rates tended to be lower at the annually burned and ungrazed pasture (ABN), and tended to decline with time since fire within the patch-burn grazing pasture for all species (Figure 3.2). In contrast, we found that parasitism rates in Chase County were lower in the annually burned and grazed pasture compared to the patch-burn grazing pasture for Dickcissels, while Eastern Meadowlarks and Grasshopper Sparrows followed similar trends (Figure 3.2). Rates of brood parasitism for Dickcissels were consistently high ( $> 0.5$ ) in all treatments, and we did not find any support for a year effect on parasitism rates for Dickcissel nests at any site. Due to sparse numbers of nests for some year and treatment combinations, we were unable to test models with year by treatment or year by patch-within-treatment interactions.

## **Clutch Size**

We found that songbird nests parasitized by cowbirds had a lower number of host eggs than unparasitized nests (Figure 3.3). Multiple parasitism was uncommon for any species at Chase County, but Dickcissel and Grasshopper Sparrow nests regularly received more than one cowbird

egg if parasitized at Konza Prairie (Figure 3.3). Management regime was not important in explaining the average number of host eggs of any of our three species (RI, Dickcissel: 0.00 - 0.45, Eastern Meadowlark: 0.00, Grasshopper Sparrow: 0.00; Table 3.4), but did have a small effect on the average number of cowbird eggs of parasitized Dickcissel nests (RI = 0.46; Table 3.5). Dickcissel nests within the annually burned and ungrazed and patch-burn grazing treatments received fewer cowbird eggs if parasitized than nests in the annually burned and grazed treatment at Konza Prairie. However, Dickcissel nests received fewer cowbird eggs in the annually burned and grazed treatment than the patch-burn grazing treatment at Chase County (Figure 3.3).

### **Nest Survival**

Nest survival was generally low for all species of grassland songbirds at our two study sites. The probability of nest survival for Dickcissels was  $0.142 \pm 0.014\text{SE}$  (N = 548) and for Grasshopper Sparrows was  $0.099 \pm 0.021$  (N = 147) over a 24-day exposure period, whereas the probability of nest survival of Eastern Meadowlarks was  $0.169 \pm 0.032$  for a 28-day exposure period.

Management regime was the most important factor in explaining variation in nest survival for Eastern Meadowlarks and Grasshopper Sparrows, but not for Dickcissels. The probability of nest survival did not differ between sites for any species. The probability of daily nest survival for Eastern Meadowlarks was higher on annually burned and ungrazed pastures compared to other treatments, and was lowest in recently burned and grazed pastures (Figure 3.4). Nest survival of Grasshopper Sparrows was dependent on whether the nest was parasitized by cowbirds, and was highest for parasitized nests on the annually burned and grazed treatment (ABG; Tables 3.6 and Supplemental Table 3.4). Management regime was not a significant factor, but nest survival of

Dickcissels tended to be lowest for unburned pastures, and highest for the most recently burned patch-burn grazing patch (PBG0; Figure 3.4).

### **Fledging Rates**

Fledging rates per host egg were roughly 1.75 times higher for unparasitized Dickcissel nests at Konza Prairie (0.750, 95% CI = 0.595 - 0.860, N = 40) than parasitized nests (0.431, 95% CI = 0.362 - 0.503, N = 188), while eggs in unparasitized nests of Dickcissels at Chase, Eastern Meadowlarks at Konza, and Grasshopper Sparrows at either site followed a similar trend, and tended to have higher fledging rates compared to nests that were parasitized (Table 3.7 and Figure 3.5). Site was an important factor in explaining variation in fledging rates of Dickcissels and Eastern Meadowlarks. Fledging rates of Eastern Meadowlarks were lower at Konza Prairie than Chase County, and the difference in fledging rates between parasitized and unparasitized nests of Dickcissels and Eastern Meadowlarks was greater at Konza Prairie than Chase County (Figure 3.5). Management regime was only an important factor in explaining variation in fledging rates of Dickcissels at Konza Prairie. While fledging rates in parasitized Dickcissel nests were comparable between our patch-burn grazing (0.313, 95% CI = 0.206 - 0.444) and annually burned and grazed treatments (0.337, 95% CI = 0.145 - 0.604), fledging rates were higher on the annually burned and ungrazed treatment (0.649, 95% CI = 0.456 - 0.803). Within the patch-burn grazing treatment, fledging rates tended to decrease with time since fire (Figure 3.5).

### **Fledglings Per Nest**

The average number of fledglings per nesting attempt differed between sites in two of three species. On average, Eastern Meadowlarks produced  $0.543 \pm 0.197\text{SD}$  fledglings per nesting

attempt in Chase County, but only  $0.350 \pm 0.125$  fledglings per nest at Konza Prairie. Dickcissels produced  $0.326 \pm 0.089$  fledglings per attempt in Chase County, but only  $0.183 \pm 0.070$  fledglings per attempt at Konza Prairie. Last, Grasshopper Sparrows produced  $0.199 \pm 0.078$  fledglings per attempt in Chase County, and  $0.182 \pm 0.081$  at Konza Prairie. We did not find any differences in reproductive success among management regimes at our Chase County site for any species. At Konza Prairie, the number of fledglings per nesting attempt was dependent on management regime for both Dickcissels and Eastern Meadowlarks, but not for Grasshopper Sparrows. For Dickcissels, reproductive success was similar in the annually burned and grazed and patch-burn grazing treatments, but tended to be higher in the annually burned and ungrazed treatment. Within the patch-burn grazing treatment, the number of fledglings per nesting attempt declined with time since fire (Figure 3.6). For Eastern Meadowlarks, the number of fledglings per nesting attempt showed considerable variation on the annually burned and ungrazed treatment, but was still higher than the patch-burn grazing treatment (Figure 3.6). Although not significant, the number of Grasshopper Sparrow fledglings per nesting attempt tended to be higher at the annually burned and grazed pastures when compared to the patch-burn grazing managed pastures.

## **Discussion**

In our three to six-year field study, we found that management of tallgrass prairie with patch burn-grazing leads to higher levels of heterogeneity in vegetative structure compared to annually burned and grazed treatments. Unburned patches within the patch-burn grazing treatment have taller standing vegetation and a deeper litter layer than recently burned pastures. Despite large inter-annual variation in vegetative structure on all treatments, the reproductive

success of all of our three songbird species was similar across years. We found that rangeland management affected rates of brood parasitism, the average number of cowbird eggs, nest survival, and fledging rates of Dickcissels, and nest survival of Eastern Meadowlarks. However, potential effects of rangeland management on variation in demographic parameters were offset by large effects of brood parasitism by Brown-headed Cowbirds and only resulted in minor differences in the average number of fledglings per nesting attempt in Dickcissels and Eastern Meadowlarks, and only at Konza Prairie.

### **Effects of Management on Brood Parasitism**

Effects of management on rates of brood parasitism by Brown-headed Cowbirds differed between sites. At Konza Prairie, parasitism rates did not differ between the annually burned and grazed and patch-burn grazed treatments, but within the patch-burn grazing pasture parasitism rates tended to decline with time since fire for all three species. At Chase County, parasitism rates of Dickcissel nests were unexpectedly lower in the annually burned and grazed pasture compared to the patch-burn grazing pasture. However, the lack of burning on the annually burned and grazed pastures in Chase County due to drought conditions in 2012 and 2013 might have lowered parasitism rates.

The lack of difference in rates of brood parasitism between pastures managed with patch-burn grazing or annual burning and grazing at our study sites contrast with previous studies that found that patch-burn grazing management could decrease parasitism rates of nests of grassland songbirds compared to control treatments (Churchwell et al. 2008, Hovick et al. 2012, Hovick and Miller 2016). Two explanations may account for a lack of differences in parasitism rates among treatments in our field study. For all three songbird species, overall rates of brood



parasitism were much higher at our Chase County and Konza Prairie sites ( $p > 0.5$ ) compared to past studies that have focused on patch-burn grazing ( $p = 0.0 - 0.2$ ; Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016, Hovick and Miller 2016). Parasitism rates have often been linked to geographical variation in female cowbird abundance (Jensen and Cully 2005b), and high parasitism rates have been previously reported for songbirds at Konza Prairie (Jensen and Cully 2005a, Sandercock et al. 2008, Rivers et al. 2010b). Second, breeding cowbirds often make movements of several kilometers between foraging sites to search for host nests, and space use may occur at a larger spatial scale than our experimental pastures (42 to 419 ha.; Dijak and Thompson 2000, Jensen and Cully 2005b, B.H.F. Verheijen pers. obs.). High densities of Brown-headed Cowbirds and close proximity of experimental pastures at our study sites could have led to high and comparable parasitism rates across our treatments.

### **Effects of Parasitism on Clutch Size and Fledging Rates**

The negative effects of brood parasitism by Brown-headed Cowbirds on the reproductive success of songbird hosts have been well documented (Rothstein 1990, Lorenzana and Sealy 1999, Rivers et al. 2010b). We found further evidence that parasitized nests of all three species contained fewer host eggs, and the presence of parasitic young led to large reductions in the fledging rates of host young.

Dickcissels and Grasshopper Sparrows had higher rates of multiple parasitism at Konza Prairie than Chase County. Our findings support previous studies that found that rates of multiple parasitism events are directly related to local cowbird abundance (Jensen and Cully 2005a, Patten et al. 2006, Sandercock et al. 2008). The effects of rangeland management on the number of cowbird eggs in parasitized nests was only minimal. At Konza Prairie, parasitized nests of

Dickcissels within the annually burned and ungrazed and patch-burn grazing treatments received fewer cowbird eggs than nests in the annually burned and grazed treatment. We saw the opposite pattern in Chase County, which aligns with the unexpected higher rates of brood parasitism in the patch-burn grazing pasture compared to the annually burned and grazed pasture at that site.

Fledging rates of grassland songbirds at our sites were strongly dependent on whether a nest was parasitized by cowbirds and the number of cowbird eggs in the nest. On average, the chance of a Grasshopper Sparrow egg successfully fledging when cowbirds were present was almost half when compared to eggs from nests with only host young (47.0% vs. 83.0%), whereas negative effects of parasitism rates were minor for the young of the larger-bodied Eastern Meadowlark. Previous studies show that the negative effects of parasitism are most severe in smaller-bodied host species (Kosciuch and Sandercock 2008, Sandercock et al. 2008, Rivers et al. 2010a). The difference in fledging rates of Dickcissel and Eastern Meadowlark eggs between parasitized and unparasitized nests was lower in Chase County than at Konza Prairie, potentially due to increased competition between host and cowbird young as a result of higher rates of multiple parasitism at Konza Prairie. Our results therefore suggest that high parasitism rates could have large consequences for the reproductive success of grassland songbirds by decreasing the number of host eggs and lowering the fledging rates of the host eggs that remain in the nest.

### **Effects of Rangeland Management on Nest Survival**

Unexpectedly, nest survival was not higher on pastures managed with patch-burn grazing compared to annually burned and grazed pastures for any of our three study species. Moreover, in contrast with previous studies, nest survival of Dickcissels tended to be lower, not higher, on unburned patches within the patch-burn grazing treatment compared to other patches and

treatments (Churchwell et al. 2008, Davis et al. 2016). Low nest survival in unburned patches at our sites could potentially be caused by high activity of snakes in these areas. Snakes, such as yellowbelly racer (*Coluber constrictor flaviventris*), and Great Plains ratsnake (*Pantherophis emoryi*), are dominant nest predators in the Flint Hills ecoregion, and are often more abundant in unburned areas with higher amounts of litter and shrub cover than burned pastures (Klug et al. 2010, Lyons et al. 2015). Alternatively, nests in unburned patches could experience high losses due to depredation by Brown-headed Cowbirds. Rates of brood parasitism at our field sites were consistently higher than previous studies, regardless of burning regime, and cowbirds are known to depredate or destroy songbird nests (Arcese et al. 1996, Hoover and Robinson 2007).

Unfortunately, it is difficult to determine which predator is responsible for the partial or complete loss of a nest. In regions with high cowbird densities, nests in unburned patches within the patch-burn grazing might not be able to avoid brood parasitism by Brown-headed Cowbirds, while they might still face high levels of nest predation, potentially resulting in lower nest survival on those patches. Nest predator communities in grasslands can be diverse, and grassland systems show considerable geographical variation in the dominant nest predators and the abundance of Brown-headed Cowbirds (Pietz and Granfors 2000, Renfrew and Ribic 2003, Jensen and Cully 2005a, Lyons et al. 2015). The effects of rangeland management on reproductive success of grassland songbirds might therefore be region-specific.

### **Consequences for Reproductive Success**

Our estimates of the average number of fledglings per nesting attempt were lower at Konza Prairie than Chase County for both Dickcissels and Eastern Meadowlarks, which was driven by site differences in local cowbird abundance and higher rates of brood parasitism at Konza Prairie.

Our estimates of productivity for Dickcissels ranged between 0.183 (Konza) and 0.350 fledglings per nest (Chase), whereas previous studies in areas with low parasitism rates report a higher number of fledglings per nesting attempt (0.77–1.06, Walk et al. 2004; 1.70, Winter 1999). Earlier work on Dickcissels at Konza Prairie, reported even lower reproductive success of 0.04–0.32 fledglings per nest (Sandercock et al. 2008). Furthermore, Sousa (2012) reported exceptionally low return rates of juvenile Dickcissels at Konza Prairie, with only 2 out of 325 nestlings returning to the study area in subsequent years. Our results confirm the suggestion that areas with high levels of brood parasitism might not result in viable populations of grassland songbirds without considerable immigration from other “source” populations (Sandercock et al. 2008, With et al. 2008, Davis et al. 2016).

Although we did not find large differences in demographic rates for any species, patch-burn grazing management could regulate populations of grassland songbirds by providing nesting opportunities for species that require higher amounts of cover and litter for breeding. In our study, we consistently found higher numbers of Eastern Meadowlark and Grasshopper Sparrows nests at the unburned patches within the patch-burn grazing treatment, while numbers were low at recently burned treatments. We did find high numbers of Grasshopper Sparrow nests at the annually burned and grazed treatment in Chase County in 2012 and 2013, however this treatment was not burned in either year due to drought conditions, which led to higher amounts of litter available to nesting birds. Densities of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows are usually higher in unburned grasslands (Walk and Warner 2000, Swengel and Swengel 2001, Powell 2006, Chapter 2), and are therefore likely to be higher in unburned patches within patch-burn grazing managed pastures. Rangeland management aimed at creating patches

with litter and vegetative structure could therefore benefit certain species of grassland songbirds by providing suitable breeding habitat.

Another way that patch-burn grazing could benefit populations of grassland songbirds is by potentially improving the survival of fledglings after they leave the nest. Habitat requirements of songbird fledglings have been found to differ from preferred nesting habitats, but fledglings of grassland songbirds are not able to disperse large distances during the first weeks after leaving the nest (Kershner et al. 2004, Berkeley et al. 2007, Streby and Andersen 2011; 2013). Close proximity of suitable nesting and foraging habitat for fledglings within patch-burn grazing managed pastures could potentially improve reproductive success (see Chapter 4).

### **Management Implications**

Our results join a growing body of literature that indicate that patch-burn grazing does not negatively influence demographic rates for at least three common species of grassland songbirds in North America, and could provide suitable breeding habitat for species requiring substantial standing vegetation and litter cover that is not found in annually burned pastures. Implementing patch-burn grazing management will require landowners to maintain more firebreaks and more coordination during burns, but previous research has found that revenues from cattle grazing with patch-burn grazing practices may be comparable to those with IESB in tallgrass prairie systems (Fuhlendorf and Engle 2004, Rensink 2009, Limb et al. 2011). Furthermore, since part of the pasture is not burned when using patch-burn grazing management, pastures are likely to have higher levels of standing vegetation for cattle during drought conditions.

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**Table 3.1.** Mean growing season temperatures in Celsius ( $\pm$  SD) and precipitation in millimeters ( $\pm$  SD) for Chase County and Konza Prairie based on local weather data for a 100-year period from 1917 to 2016 (NOAA.gov). Also shown are year-specific temperature means and precipitation totals for the years that vegetation and nest data was collected on each site, and z-scores (in SD units) based on long-term weather data from 1917 and 2016.

Temperature ( $^{\circ}$ C)		Growing Season (Mar - Aug)	
Site	Year	Mean	z-score
Chase	Mean $\pm$ SD	19.1 $\pm$ 1.1	
	2011	20.0	+0.976
	2012	21.9	+2.647
	2013	17.2	-1.599
Konza	Mean $\pm$ SD	18.7 $\pm$ 1.1	
	2011	20.1	+1.042
	2012	21.5	+2.305
	2013	17.2	-1.622
	2014	18.2	-0.668
	2015	18.8	-0.104
2016	19.8	+0.820	

Precipitation(mm)		Growing Season (Mar - Aug)	
Site	Year	Total	z-score
Chase	Mean $\pm$ SD	554.7 $\pm$ 149.1	
	2011	337.6	-1.435
	2012	364.1	-1.256
	2013	757.0	1.384
Konza	Mean $\pm$ SD	547.3 $\pm$ 149.1	
	2011	491.6	-0.400
	2012	407.8	-0.963
	2013	528.2	-0.153
	2014	455.3	-0.643
	2015	625.0	+0.497
2016	691.5	+0.945	

**Table 3.2.** Number of nests of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows monitored at our Chase County and Konza Prairie sites between 2011 and 2016. Rangeland management treatments included: ABG for annually burned and grazed pastures, ABN for annually burned but not grazed pastures, and PBG for patch-burn grazing pastures, with the sub-treatments (PBG0-2) indicating the number of years since a particular sub-treatment was burned.

<b>Dickcissel</b>	<b>Chase County</b>				<b>Konza Prairie</b>						
	<b>Treatment</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>Total</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>2014</b>	<b>2015</b>	<b>2016</b>
ABG	37	51	45	133	10	2	4	8	17	22	63
ABN	-	-	-	-	0	8	19	13	28	24	92
PBG	18	15	23	56	25	5	13	68	63	36	210
- PBG0	0	1	4	5	8	1	0	17	14	5	45
- PBG1	8	4	16	28	6	2	8	37	35	21	109
- PBG2	10	10	3	23	11	2	5	14	14	10	56
<b>Total</b>	<b>55</b>	<b>66</b>	<b>68</b>	<b>189</b>	<b>35</b>	<b>15</b>	<b>36</b>	<b>89</b>	<b>108</b>	<b>82</b>	<b>365</b>

<b>Eastern Meadowlark</b>	<b>Chase County</b>				<b>Konza Prairie</b>						
	<b>Treatment</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>Total</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>2014</b>	<b>2015</b>	<b>2016</b>
ABG	2	6	10	18	1	0	0	0	0	1	2
ABN	-	-	-	-	0	1	3	2	2	1	9
PBG	10	7	16	33	7	4	6	29	20	19	85
- PBG0	1	1	0	2	1	0	0	5	1	2	9
- PBG1	8	1	4	13	1	1	1	12	7	10	32
- PBG2	1	5	12	18	5	3	5	12	12	7	44
<b>Total</b>	<b>12</b>	<b>13</b>	<b>26</b>	<b>51</b>	<b>8</b>	<b>5</b>	<b>9</b>	<b>31</b>	<b>22</b>	<b>21</b>	<b>96</b>

<b>Grasshopper Sparrow</b>	<b>Chase County</b>				<b>Konza Prairie</b>						
	<b>Treatment</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>Total</b>	<b>2011</b>	<b>2012</b>	<b>2013</b>	<b>2014</b>	<b>2015</b>	<b>2016</b>
ABG	8	21	35	64	1	0	0	4	0	1	6
ABN	-	-	-	-	0	0	0	1	1	0	2
PBG	10	5	3	18	0	0	18	39	19	18	94
- PBG0	0	0	1	1	0	0	1	4	1	1	7
- PBG1	8	1	0	9	0	0	11	19	13	4	47
- PBG2	2	4	2	8	0	0	6	16	5	13	40
<b>Total</b>	<b>18</b>	<b>26</b>	<b>38</b>	<b>82</b>	<b>1</b>	<b>0</b>	<b>18</b>	<b>44</b>	<b>20</b>	<b>19</b>	<b>102</b>

**Table 3.3.** Model selection for logistic regression models of parasitism rates of Dickcissel, Eastern Meadowlark and Grasshopper Sparrow nests in Chase County (2011 – 2013) and at Konza Prairie, Kansas (2011 – 2016). Model selection was based on the number of parameters ( $K$ ), Deviance,  $\Delta\text{AICc}$  values, and Akaike weights ( $w_i$ ). Treatment models contained patch-burn grazing (PBG) and annually burning and grazing (ABG) for both Chase County and Konza Prairie, and annually burning but no grazing (ABN) for Konza Prairie only. Patch models included all three levels of the patch-burn grazing treatment (PBG0 – PBG2) and the ABG and ABN treatments. Due to low sample sizes of Grasshopper Sparrow nests on some treatments at Konza Prairie, we were unable to model treatment or patch-within-treatment effects for this species.

Species	Site	Model	$K$	Deviance	AICc	$\Delta\text{AICc}$	$w_i$
Dickcissel	Chase	Treatment	2	242.56	246.63	0.00	0.578
		Patch	4	239.13	247.34	0.72	0.404
		Year	3	247.56	253.69	7.06	0.017
		Constant	1	256.90	258.92	12.30	0.001
	Konza	Treatment	3	300.71	306.78	0.00	0.807
		Patch	5	299.75	309.92	3.14	0.168
		Constant	1	312.88	314.89	8.11	0.014
		Year	6	303.20	315.44	8.66	0.011
Eastern Meadowlark	Chase	Treatment	2	54.57	58.82	0.00	0.546
		Constant	1	57.90	59.98	1.16	0.305
		Year	3	56.28	62.79	3.97	0.075
		Patch	4	53.92	62.79	3.98	0.075
	Konza	Constant	1	129.63	131.67	0.00	0.514
		Treatment	2	129.00	133.13	1.46	0.248
		Year	6	120.55	133.52	1.84	0.204
		Patch	4	128.69	137.14	5.47	0.033
Grasshopper Sparrow	Chase	Treatment	2	103.87	108.02	0.00	0.716
		Year	3	104.55	110.86	2.84	0.173
		Constant	1	109.69	111.74	3.72	0.111
	Konza	Constant	1	124.14	126.19	0.00	0.945
		Year	4	123.42	131.88	5.69	0.055

**Table 3.4.** Model selection for multinomial regression models for the number of host eggs for nests of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows in Chase County (2011 – 2013) and at Konza Prairie, Kansas (2011 – 2016). For Dickcissels, we modeled the number of host eggs separately for each site and for unparasitized and parasitized nests. See caption of Table 3.3 for definitions of treatments.

Species	Site	Parasitized	Model	<i>K</i>	Deviance	AICc	$\Delta$ AICc	$w_i$
Dickcissel	Chase	No	Constant	2	117.48	121.70	0.00	0.892
			Treatment	4	117.18	125.93	4.23	0.108
		Yes	Constant	3	248.06	254.32	0.00	0.548
			Treatment	6	241.74	254.70	0.39	0.452
	Konza	No	Constant	3	99.50	106.17	0.00	0.998
			Treatment	9	94.52	118.52	12.35	0.002
Yes		Constant	3	721.14	727.23	0.00	0.930	
		Treatment	9	713.69	732.40	5.17	0.070	
Eastern Meadowlark	Pooled	Pooled	Parasitism	6	298.13	310.85	0.00	1.000
			Constant	3	335.70	341.90	31.05	0.000
Grasshopper Sparrow	Pooled	Pooled	Parasitism	6	328.87	341.51	0.00	1.000
			Treatment	6	372.40	385.04	43.53	0.000
			Constant	3	380.33	386.51	45.00	0.000

**Table 3.5.** Model selection for the number of cowbird eggs among parasitized nests of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows in Chase County (2011 – 2013) and at Konza Prairie, Kansas (2011 – 2016). For Dickcissels, we modeled the number of cowbird eggs separately for each site. See caption of Table 3.3 for definitions of treatments and patches.

<b>Species</b>	<b>Site</b>	<b>Model</b>	<b><i>K</i></b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>w_i</math></b>
Dickcissel	Chase	Treatment	2	126.62	130.75	0.00	0.325
		Year	3	124.76	131.03	0.28	0.283
		Constant	1	129.32	131.36	0.61	0.239
		Patch	4	123.82	132.26	1.51	0.153
	Konza	Treatment	12	817.84	843.08	0.00	0.463
		Constant	4	835.30	843.46	0.37	0.384
		Year	24	793.47	846.51	3.43	0.083
		Patch	20	803.39	846.86	3.78	0.070
Eastern Meadowlark	Pooled	Constant	1	69.10	71.19	0.00	0.640
		Site	2	68.08	72.33	1.15	0.360
Grasshopper Sparrow	Pooled	Site	2	97.60	101.77	0.00	0.789
		Constant	1	102.35	104.41	2.64	0.211



**Table 3.6.** Model selection for nest survival models estimating daily survival rates for nests of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows monitored in Chase County (2011-2013) and Konza Prairie, Kansas (2011-2016), pooled by site. See caption of Table 3.3 for definitions of treatments and patches. Shown are models with a model weight of 0.05 or higher; for the full model selection results see Supplemental Table 3.3.

<b>Species</b>	<b>Model</b>	<b><i>K</i></b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b><math>w_i</math></b>
Dickcissel	Constant	1	1915.95	1917.95	0.00	0.316
	Patch	5	1908.59	1918.61	0.66	0.227
	Parasitism	2	1915.57	1919.57	1.62	0.140
	Patch + Parasitism	6	1908.47	1920.49	2.54	0.088
Eastern Meadowlark	Treatment	3	498.47	504.49	0.00	0.338
	Treatment + Parasitism	4	497.63	505.66	1.17	0.188
	Patch	5	497.22	507.26	2.78	0.084
	Treatment $\times$ Parasitism	6	495.23	507.29	2.80	0.083
	Watershed	13	481.23	507.49	3.01	0.075
Grasshopper Sparrow	Treatment $\times$ Parasitism	4	597.05	605.09	0.00	0.323
	Treatment + Parasitism	3	599.94	605.96	0.87	0.209
	Parasitism	2	602.27	606.28	1.20	0.177
	Constant	1	605.01	607.01	1.93	0.123
	Treatment	2	603.35	607.36	2.28	0.103

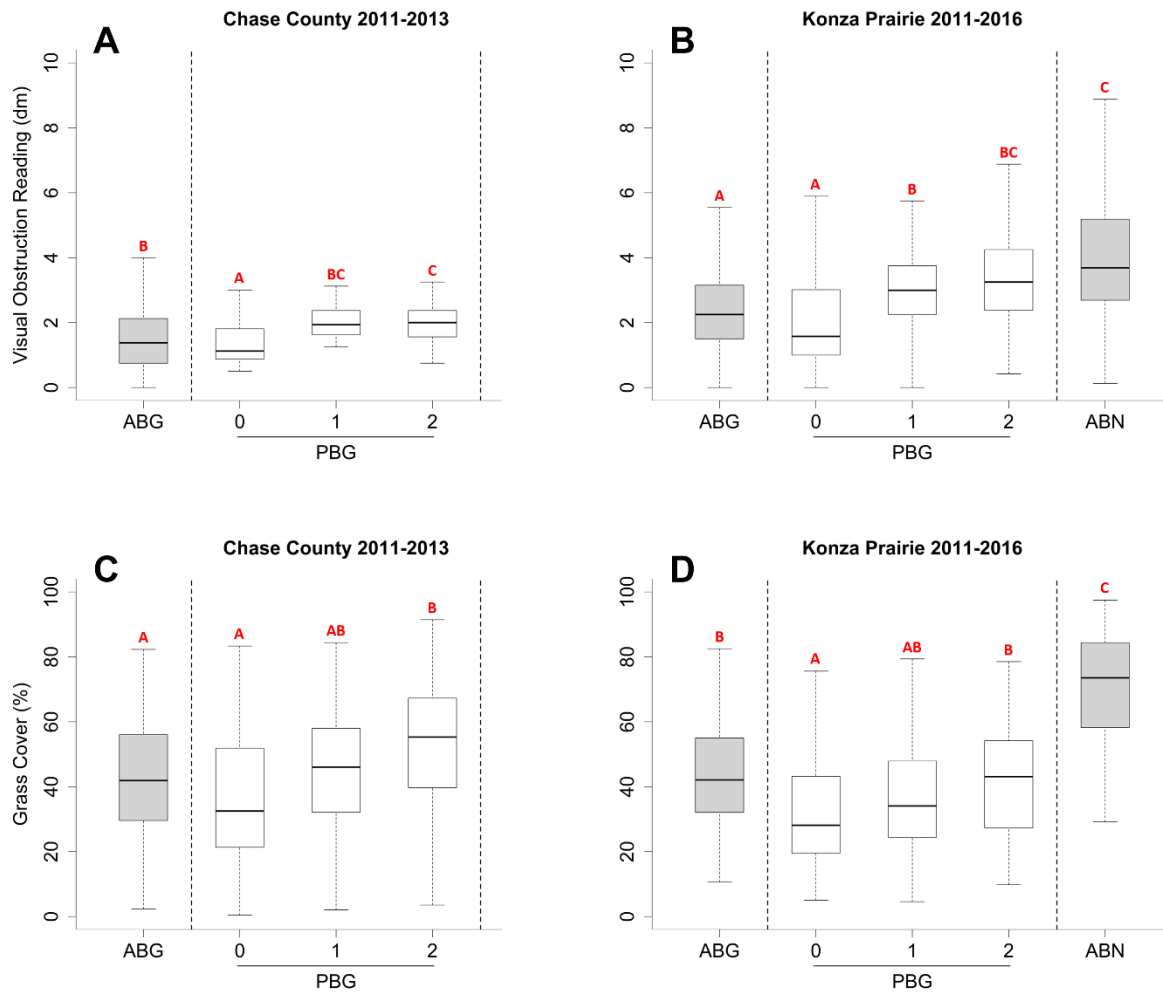
**Table 3.7.** Model selection for logistic regression models of fledging rates per host egg for Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows in Chase County (2011 – 2013) and Konza Prairie, Kansas (2011 – 2016). Nest ID was included as a random factor to control for lack of independence among eggs from the same clutch. See caption of Table 3.3 for definitions of treatments and patches, and see Supplemental Table 3.5 for the full model selection results.

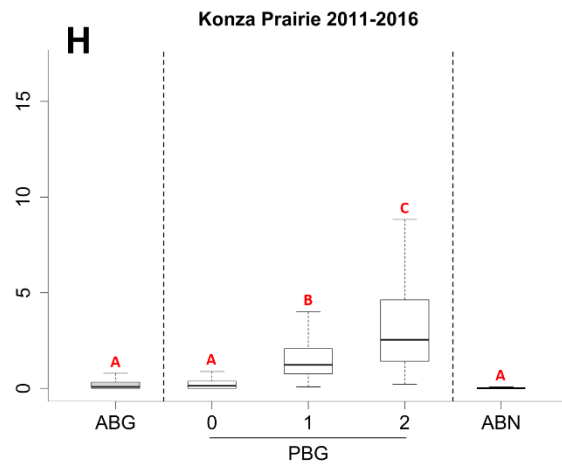
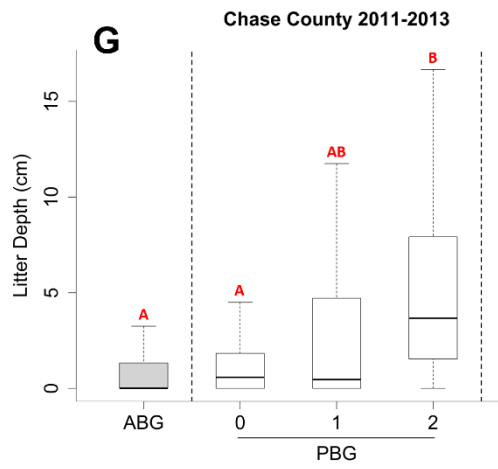
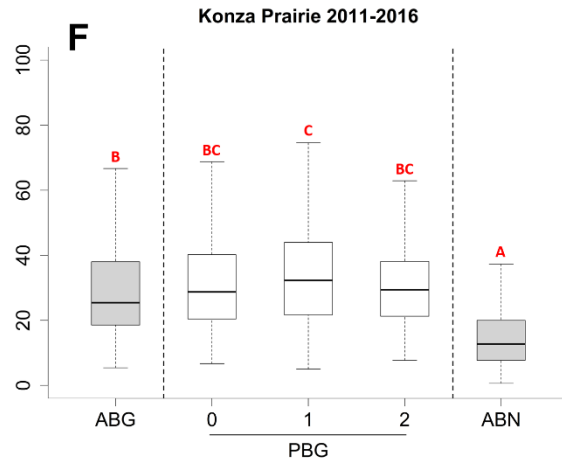
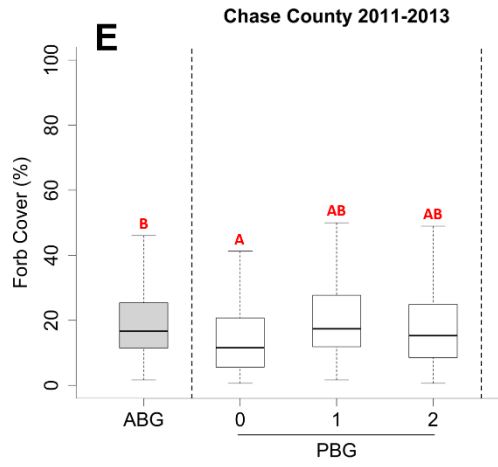
Species	Site	Parasitized	Model	<i>K</i>	Deviance	AICc	delta	weight
Dickcissel	Chase	Both	Nest ID + Clutch Size	3	201.16	207.32	0.00	0.252
			Nest ID + Clutch Size + Parasitism	4	199.92	208.17	0.86	0.164
			Nest ID	2	204.20	208.28	0.97	0.155
			Nest ID + Clutch Size + Treatment	4	200.84	209.09	1.77	0.104
			Nest ID + Parasitism	3	203.28	209.43	2.11	0.088
			Nest ID + Treatment	3	203.84	209.99	2.68	0.066
			Nest ID + Clutch Size × Parasitism	5	199.92	210.30	2.98	0.057
	Konza	No	Clutch Size	2	41.01	45.34	0.00	0.536
			Constant	1	44.99	47.09	1.75	0.223
			Nest ID + Clutch Size	3	41.01	47.68	2.34	0.166
			Nest ID	2	44.95	49.28	3.94	0.075
	Konza	Yes	Nest ID + Clutch Size + Patch	7	226.06	240.67	0.00	0.276
			Nest ID + Clutch Size + Treatment	5	230.66	241.00	0.32	0.235
			Clutch Size + Patch	6	228.92	241.38	0.71	0.194
			Nest ID + Clutch Size × Treatment	7	228.38	243.01	2.33	0.086
			Clutch Size + Treatment	4	234.86	243.08	2.41	0.083
Eastern Meadowlark	Chase	Both	Constant	1	33.15	35.26	0.00	0.267
			Nest ID	2	32.24	36.59	1.33	0.138
			Clutch Size	2	32.90	37.25	1.99	0.099
			Treatment	2	32.94	37.28	2.02	0.097
			Parasitism	2	33.13	37.48	2.22	0.088

Konza	Both	Constant	1	137.60	139.65	0.00	0.150	
		Parasitism	2	135.72	139.85	0.20	0.136	
		Nest ID + Clutch Size × Parasitism	5	130.26	140.87	1.22	0.082	
		Treatment	2	136.88	140.99	1.34	0.077	
		Treatment + Parasitism	3	134.86	141.09	1.45	0.073	
		Clutch Size	2	137.08	141.20	1.55	0.069	
		Nest ID	2	137.50	141.62	1.97	0.056	
		Nest ID + Parasitism	3	135.60	141.85	2.20	0.050	
		Grasshopper Sparrow	Both	Both	Nest ID + Parasitism	3	119.18	125.43
Nest ID + Treatment + Parasitism	4				119.07	127.48	2.05	0.129
Nest ID + Clutch Size + Parasitism	4				119.10	127.51	2.08	0.128
Nest ID	2				124.36	128.48	3.06	0.078
Parasitism	2				124.78	128.90	3.47	0.064

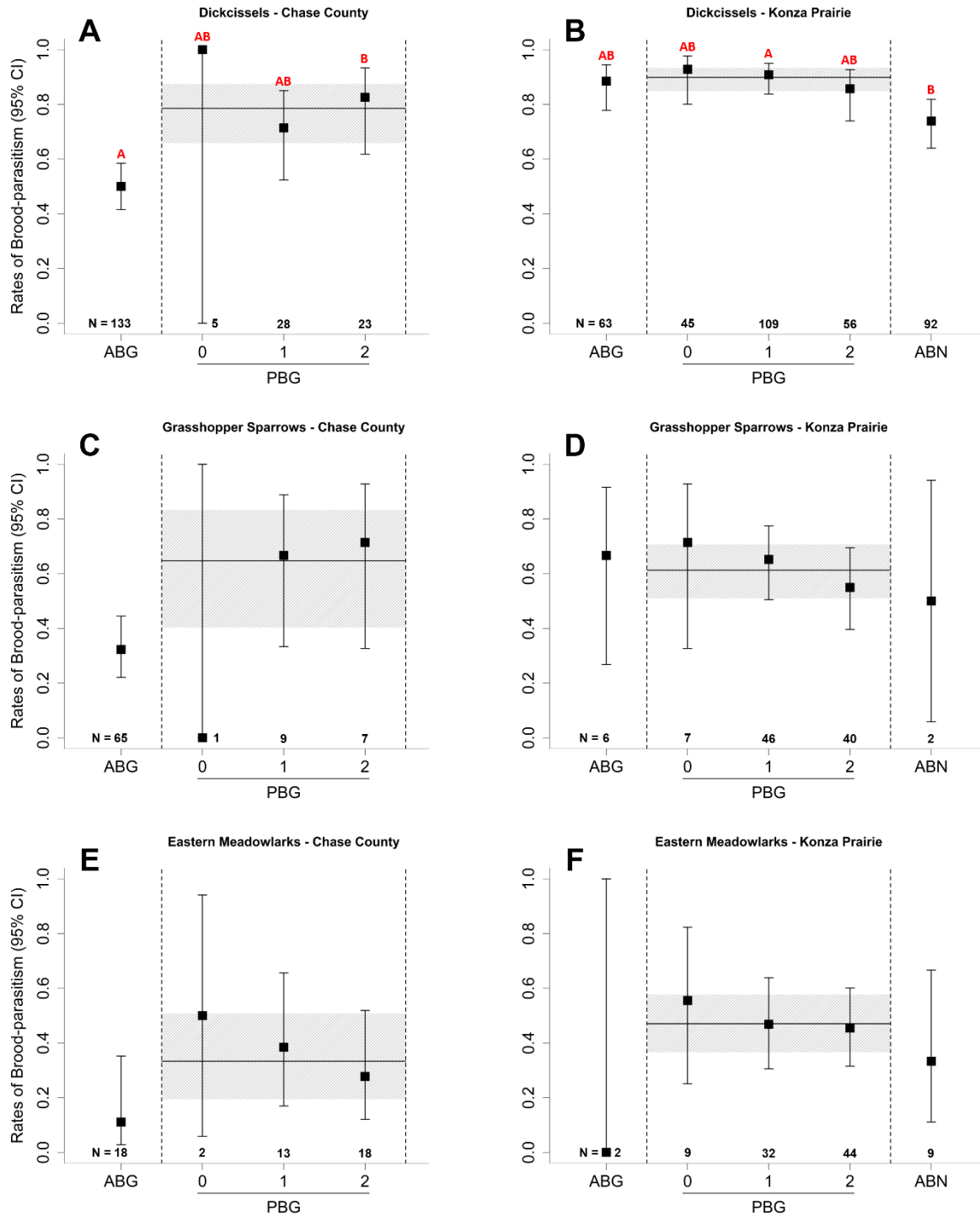
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**Figure 3.1.** Box plots of the Visual obstruction readings (VOR; A-B), grass cover (C-D), forb cover (E-F), and litter depth (G-H) for Chase County and Konza Prairie, shown separately for each management regime and patch within management. Boxes show the median and interquartile range, and whiskers show either the full range or 1.5 times the interquartile range, whichever value is closer to the median. Management regimes are labeled as follows: ABG = annually burned and grazed, PBG = patch-burn grazing, 0-2 = the number of years since a patch was last burned, and ABN = annually burned but not grazed. Significant differences ( $P < 0.05$ ) between estimates are depicted with different letters.

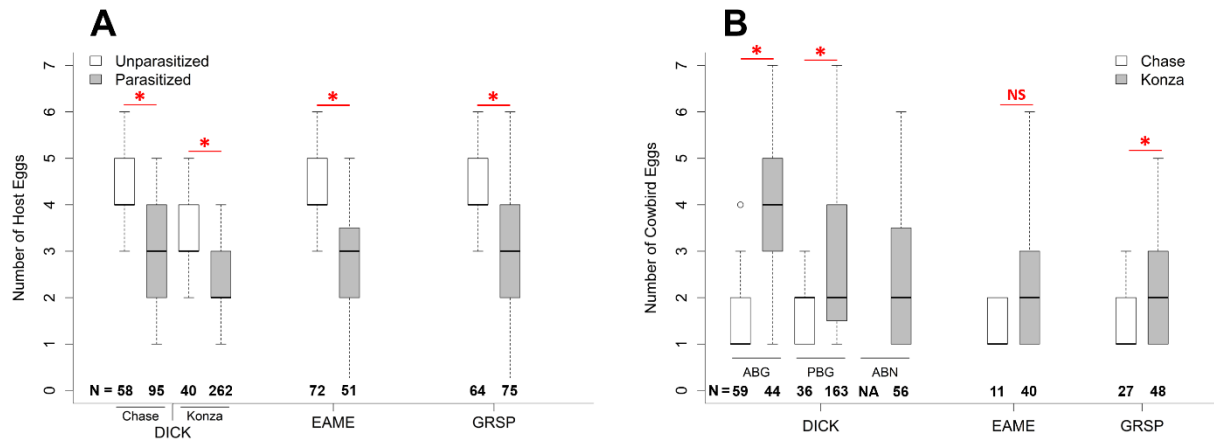




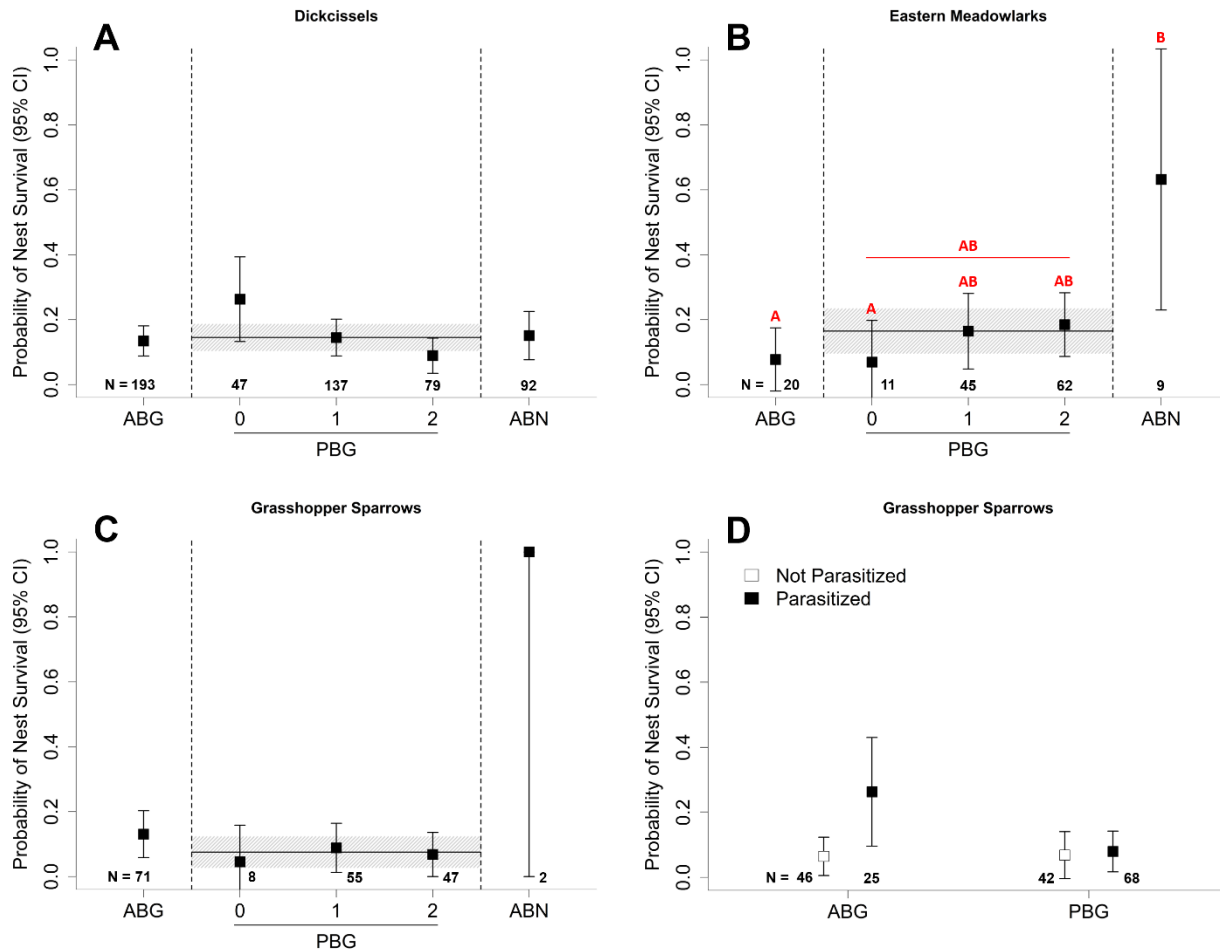
**Figure 3.2.** Rates of brood parasitism by Brown-headed Cowbirds for nests of Dickcissels (A-B), Grasshopper Sparrows (C-D), and Eastern Meadowlarks (E-F) at Chase County (2011-2013) and Konza Prairie, Kansas (2011-2016). Significant differences ( $P < 0.05$ ) between estimates are depicted by different letters. See caption of Figure 3.1 for definitions of management regimes.



**Figure 3.3.** The number of host eggs (A) and cowbird eggs (B) for unparasitized and parasitized nests of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows at Chase County (2011-2013) and Konza Prairie, Kansas (2011-2016). The number of host eggs were estimated separately for Chase and Konza for Dickcissels, and for whether a nest was parasitized or not for all three species. The number of cowbird eggs in parasitized nests was estimated separately for each site. For Dickcissels, estimates were further split by management regime. See caption of Figure 3.1 for definitions of management regimes. Stars above estimates indicate a significant difference ( $P < 0.05$ ).

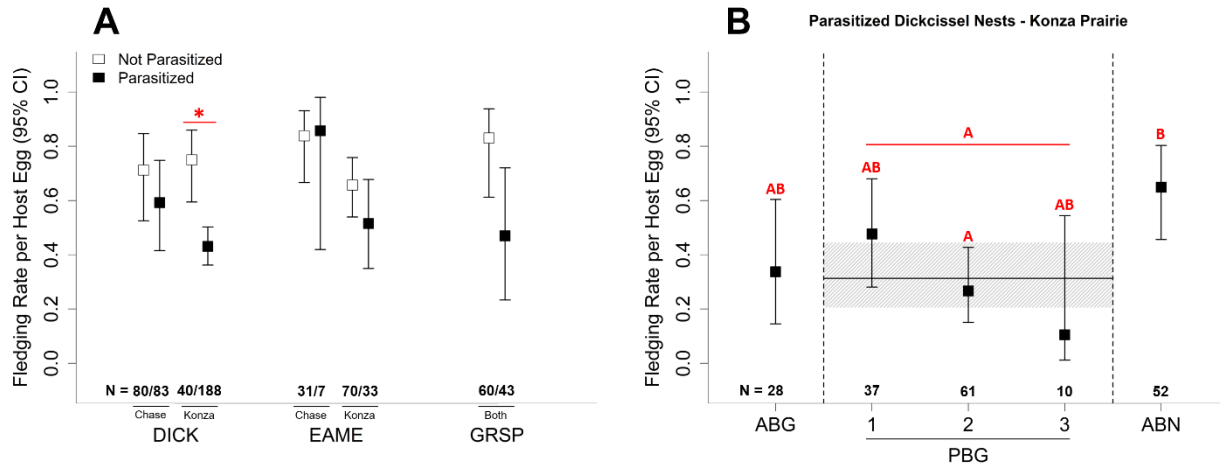


**Figure 3.4.** Estimates of nest survival for Dickcissels (A), Eastern Meadowlarks (B), and Grasshopper Sparrows (C-D) nest survival pooled across sites. Shown are estimates of nest survival for a 24 or 28-day exposure period with 95% confidence intervals, estimated separately for each management regime and patch within management regime (A-C). For Grasshopper Sparrows, we also show estimates of nest survival and whether a nest was parasitized by Brown-headed Cowbirds or not (D). Significant differences ( $P < 0.05$ ) between estimates are depicted by different letters. See caption of Figure 3.1 for definitions of management regimes.

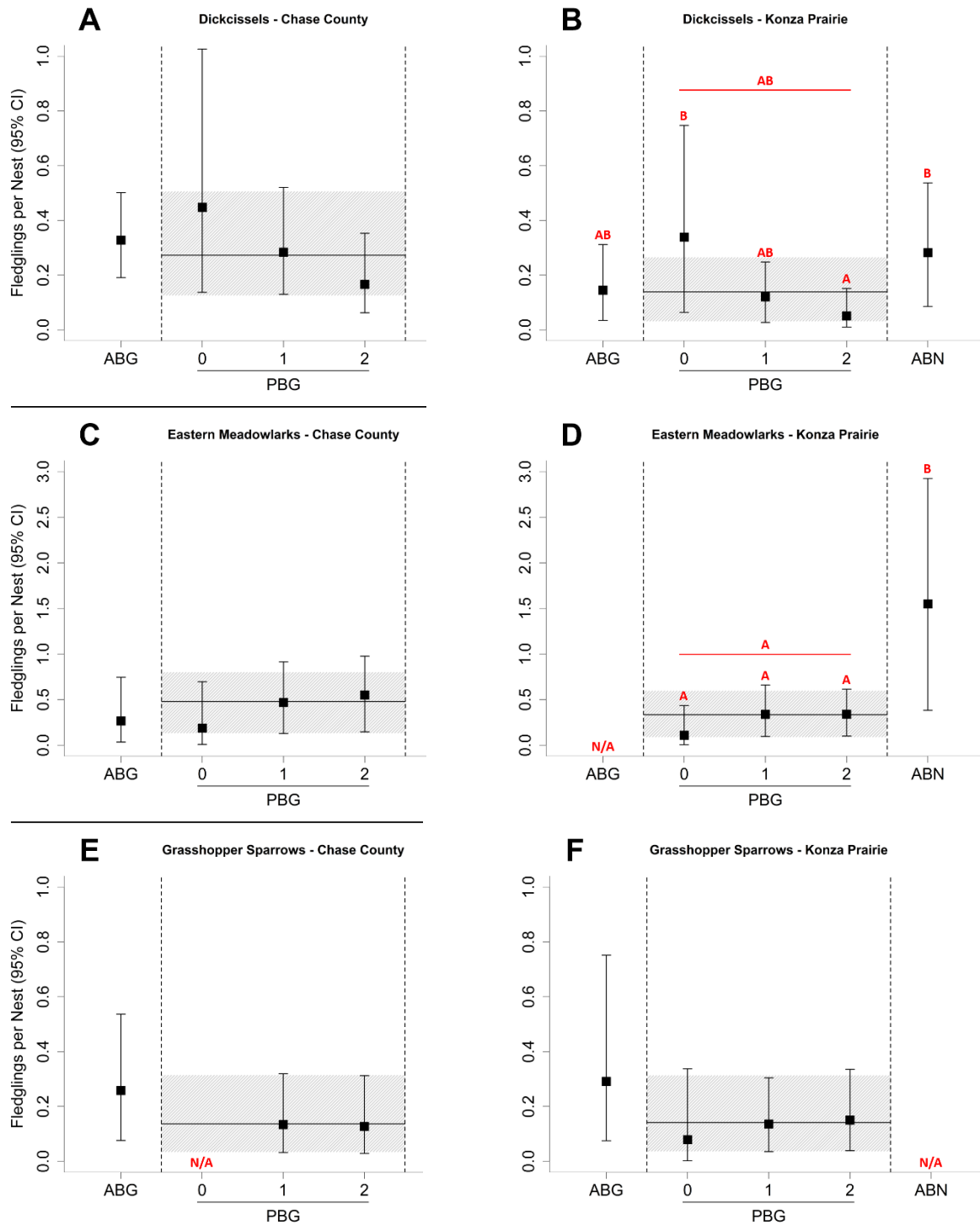




**Figure 3.5.** Estimates of fledging rates per host egg ( $\pm$  95% CI) for unparasitized and parasitized nests of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows (A) at Chase County (2011-2013) and Konza Prairie, Kansas (2011-2016). Parasitized Dickcissel nests were further separated by treatment (B). Significant differences ( $P < 0.05$ ) between estimates are depicted by different letters. See caption of Figure 3.1 for definitions of management regimes.



**Figure 3.6.** Bootstrapped estimates of the average number of fledglings per nest for Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows at Chase County (2011-2013) and Konza Prairie, Kansas (2011-2016). Significant differences ( $P < 0.05$ ) between estimates are depicted by different letters. See caption of Figure 3.1 for definitions of management regimes.



**Supplemental Table 3.1.** Model selection for linear regression of visual obstruction readings (VOR), grass cover, forb cover, and litter depth for Chase County (2011-2013) and Konza Prairie, Kansas (2011-2016). Model selection was based on the number of parameters ( $K$ ), Deviance,  $\Delta\text{AICc}$  values, and Akaike weights ( $w_i$ ). Treatment models contained patch-burn grazing (PBG) and annually burning and grazing (ABG) for both Chase County and Konza Prairie, and annually burning but no grazing (ABN) for Konza Prairie only. Patch models include each of the three patches of the patch-burn grazing treatment separately instead of the patch-burn grazing treatment as a whole.

Trait	Site	Model	$K$	Deviance	AICc	$\Delta\text{AICc}$	$w_i$	
VOR	Chase	Patch + Year	8	-920.46	1857.10	0.00	0.506	
		Patch $\times$ Year	14	-914.30	1857.15	0.05	0.494	
		Patch	6	-1038.04	2088.18	231.08	0.000	
		Year	5	-1056.41	2122.91	265.81	0.000	
		Treatment + Year	6	-1056.86	2125.82	268.72	0.000	
		Treatment $\times$ Year	8	-1056.39	2128.96	271.86	0.000	
		Constant	3	-1108.31	2222.64	365.54	0.000	
		Treatment	4	-1108.74	2225.54	368.44	0.000	
	Konza	Patch $\times$ Year	31	-2074.84	4213.53	0.00	0.997	
		Patch + Year	11	-2101.59	4225.42	11.89	0.003	
		Treatment $\times$ Year	19	-2134.80	4308.31	94.77	0.000	
		Treatment + Year	9	-2146.42	4311.00	97.47	0.000	
		Year	7	-2202.57	4419.25	205.72	0.000	
		Patch	6	-2215.57	4443.22	229.69	0.000	
		Treatment	4	-2252.24	4512.51	298.98	0.000	
		Constant	2	-2299.02	4602.05	388.52	0.000	
	Grass Cover	Chase	Patch $\times$ Year	14	-3290.01	6608.58	0.00	1.000
			Patch + Year	8	-3310.71	6637.60	29.02	0.000
			Patch	6	-3357.99	6728.08	119.51	0.000
Treatment $\times$ Year			8	-3379.62	6775.43	166.85	0.000	
Treatment + Year			6	-3384.87	6781.85	173.28	0.000	
Treatment			5	-3387.57	6785.22	176.64	0.000	
Year			4	-3394.25	6796.54	187.97	0.000	
Constant			3	-3396.94	6799.92	191.34	0.000	
Konza		Patch $\times$ Year	31	-4412.39	8888.62	0.00	1.000	
		Patch + Year	11	-4479.33	8980.90	92.28	0.000	
		Treatment $\times$ Year	19	-4498.25	9035.20	146.57	0.000	
		Treatment + Year	9	-4508.77	9035.71	147.09	0.000	
		Patch	6	-4675.96	9363.99	475.37	0.000	

		Treatment	4	-4696.83	9401.69	513.06	0.000		
		Year	7	-4832.74	9679.58	790.96	0.000		
		Constant	2	-4945.05	9894.11	1005.49	0.000		
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Forb Cover	Chase	Patch × Year	14	-2889.92	5808.38	0.00	1.000		
		Patch + Year	8	-2906.74	5829.66	21.28	0.000		
		Treatment × Year	8	-2939.35	5894.89	86.51	0.000		
		Treatment + Year	6	-2944.95	5902.01	93.62	0.000		
		Year	5	-2947.23	5904.53	96.15	0.000		
		Patch	6	-2990.82	5993.75	185.36	0.000		
		Treatment	4	-3009.03	6026.11	217.73	0.000		
		Constant	3	-3011.31	6028.64	220.26	0.000		
		Konza	Patch × Year	31	-4343.55	8750.94	0.00	0.998	
			Patch + Year	11	-4370.53	8763.29	12.35	0.002	
			Treatment + Year	9	-4376.15	8770.47	19.53	0.000	
			Treatment × Year	19	-4367.32	8773.34	22.40	0.000	
			Patch	6	-4414.58	8841.24	90.30	0.000	
			Treatment	4	-4419.90	8847.84	96.90	0.000	
		Year	7	-4500.96	9016.03	265.09	0.000		
		Constant	2	-4535.87	9075.76	324.82	0.000		
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Shrub Cover	Chase	Patch × Year	14	-2109.15	4246.85	0.00	0.978		
		Patch + Year	8	-2119.13	4254.45	7.60	0.022		
		Patch	6	-2126.48	4265.08	18.22	0.000		
		Treatment	4	-2130.37	4268.78	21.93	0.000		
		Constant	3	-2131.43	4268.90	22.04	0.000		
		Treatment + Year	6	-2128.55	4269.21	22.36	0.000		
		Year	5	-2129.62	4269.31	22.46	0.000		
		Treatment × Year	8	-2127.29	4270.77	23.91	0.000		
		Konza	Patch	6	-4108.27	8228.61	0.00	0.517	
			Treatment	4	-4110.51	8229.06	0.45	0.414	
			Patch + Year	11	-4105.80	8233.83	5.22	0.038	
			Treatment + Year	9	-4108.05	8234.27	5.65	0.031	
			Treatment × Year	19	-4103.60	8245.90	17.28	0.000	
			Patch × Year	31	-4093.14	8250.14	21.52	0.000	
			Constant	2	-4141.38	8286.78	58.16	0.000	
				Year	7	-4139.11	8292.33	63.71	0.000
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Bare Ground	Chase	Patch × Year	14	-3120.10	6268.75	0.00	1.000		

Cover		Patch + Year	8	-3143.14	6302.46	33.72	0.000
		Patch	6	-3189.60	6391.30	122.55	0.000
		Treatment × Year	8	-3244.76	6505.71	236.96	0.000
		Treatment + Year	6	-3268.20	6548.51	279.76	0.000
		Treatment	4	-3271.02	6550.10	281.35	0.000
		Year	5	-3273.22	6556.52	287.78	0.000
		Constant	3	-3276.05	6558.13	289.38	0.000
	Konza	Patch × Year	31	-4087.84	8239.53	0.00	1.000
		Patch + Year	11	-4158.55	8339.34	99.80	0.000
		Patch	6	-4294.61	8601.29	361.76	0.000
		Treatment × Year	19	-4322.59	8683.89	444.36	0.000
		Treatment + Year	9	-4338.86	8695.89	456.36	0.000
		Treatment	7	-4365.92	8745.94	506.41	0.000
Year		4	-4439.56	8887.15	647.62	0.000	
Constant	2	-4462.07	8928.16	688.63	0.000		
Litter Cover	Chase	Patch × Year	14	-2432.07	4892.70	0.00	1.000
		Patch + Year	8	-2451.07	4918.33	25.63	0.000
		Treatment × Year	8	-2533.67	5083.52	190.82	0.000
		Treatment + Year	6	-2563.77	5139.64	246.94	0.000
		Year	5	-2567.04	5144.15	251.46	0.000
		Patch	6	-2611.32	5234.76	342.06	0.000
		Treatment	4	-2620.47	5248.99	356.30	0.000
	Constant	3	-2623.76	5253.54	360.84	0.000	
	Konza	Patch × Year	31	-3305.73	6675.31	0.00	1.000
		Patch + Year	11	-3465.65	6953.55	278.24	0.000
		Treatment × Year	19	-3576.20	7191.10	515.79	0.000
		Treatment + Year	9	-3610.15	7238.47	563.17	0.000
		Patch	6	-3635.28	7282.64	607.33	0.000
Treatment		4	-3746.29	7500.62	825.31	0.000	
Year	7	-3760.09	7534.28	858.98	0.000		
Constant	2	-3867.35	7738.72	1063.41	0.000		
Litter Depth	Chase	Patch × Year	14	-2070.42	4169.40	0.00	1.000
		Patch + Year	8	-2094.73	4205.64	36.25	0.000
		Treatment × Year	8	-2216.35	4448.89	279.50	0.000
		Treatment + Year	6	-2259.20	4530.50	361.11	0.000
		Year	5	-2261.35	4532.78	363.38	0.000
		Patch	6	-2278.80	4569.72	400.32	0.000

	Treatment	4	-2333.07	4674.19	504.79	0.000
	Constant	3	-2335.23	4676.49	507.09	0.000
Konza	Patch × Year	31	-1567.63	3199.11	0.00	1.000
	Patch + Year	11	-1800.82	3623.88	424.77	0.000
	Patch	6	-1875.86	3763.79	564.68	0.000
	Treatment × Year	19	-2041.40	4121.49	922.38	0.000
	Treatment + Year	9	-2070.37	4158.91	959.80	0.000
	Treatment	4	-2121.18	4250.40	1051.29	0.000
	Year	7	-2188.56	4391.22	1192.11	0.000
	Constant	2	-2231.13	4466.26	1267.15	0.000

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**Supplemental Table 3.2.** Mean estimates ( $\pm$  SE) of visual obstruction readings (VOR), grass cover, forb cover, shrub cover, bare ground cover, litter cover, litter depth, and sample sizes for Chase County and Konza Prairie estimated for each year.

Site	Year	VOR (dm)	Grass (%)	Forb (%)	Shrub (%)	Bare (%)	Litter (%)	Litter (cm)	N
		Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	
Chase	2011	1.93 $\pm$ 0.07	45.2 $\pm$ 1.2	13.2 $\pm$ 0.6	1.3 $\pm$ 0.2	17.3 $\pm$ 1.2	7.3 $\pm$ 0.6	5.52 $\pm$ 0.44	260
	2012	1.15 $\pm$ 0.05	41.3 $\pm$ 1.1	17.3 $\pm$ 0.6	0.6 $\pm$ 0.2	16.3 $\pm$ 1.0	1.2 $\pm$ 0.2	0.77 $\pm$ 0.10	260
	2013	1.88 $\pm$ 0.06	47.1 $\pm$ 1.2	23.8 $\pm$ 0.8	0.7 $\pm$ 0.3	17.6 $\pm$ 1.0	4.3 $\pm$ 0.4	2.39 $\pm$ 0.23	260
	<b>Total</b>	<b>1.65 <math>\pm</math> 0.04</b>	<b>44.5 <math>\pm</math> 0.7</b>	<b>18.1 <math>\pm</math> 0.4</b>	<b>0.9 <math>\pm</math> 0.1</b>	<b>17.1 <math>\pm</math> 0.6</b>	<b>4.3 <math>\pm</math> 0.3</b>	<b>2.89 <math>\pm</math> 0.18</b>	<b>780</b>
Konza	2011	3.02 $\pm$ 0.18	45.3 $\pm$ 2.1	25.0 $\pm$ 1.3	4.2 $\pm$ 1.0	18.0 $\pm$ 1.6	10.1 $\pm$ 0.9	2.38 $\pm$ 0.29	105
	2012	1.83 $\pm$ 0.09	29.7 $\pm$ 1.3	22.8 $\pm$ 0.8	3.7 $\pm$ 0.6	22.1 $\pm$ 1.1	13.5 $\pm$ 0.8	1.04 $\pm$ 0.10	200
	2013	2.50 $\pm$ 0.11	38.9 $\pm$ 1.5	30.1 $\pm$ 1.1	4.7 $\pm$ 0.8	19.6 $\pm$ 0.9	7.6 $\pm$ 0.4	0.48 $\pm$ 0.05	200
	2014	3.59 $\pm$ 0.12	44.8 $\pm$ 1.3	31.7 $\pm$ 1.0	4.8 $\pm$ 0.6	15.9 $\pm$ 1.0	6.3 $\pm$ 0.4	1.25 $\pm$ 0.16	200
	2015	3.61 $\pm$ 0.12	53.0 $\pm$ 1.3	31.5 $\pm$ 1.1	5.6 $\pm$ 0.8	7.8 $\pm$ 0.5	4.2 $\pm$ 0.2	0.86 $\pm$ 0.09	200
	2016	4.03 $\pm$ 0.18	56.2 $\pm$ 1.4	24.8 $\pm$ 1.0	5.5 $\pm$ 0.8	8.8 $\pm$ 0.7	4.3 $\pm$ 0.4	1.29 $\pm$ 0.13	200
	<b>Total</b>	<b>3.10 <math>\pm</math> 0.06</b>	<b>44.6 <math>\pm</math> 0.6</b>	<b>27.9 <math>\pm</math> 0.4</b>	<b>4.8 <math>\pm</math> 0.3</b>	<b>15.1 <math>\pm</math> 0.4</b>	<b>7.5 <math>\pm</math> 0.2</b>	<b>1.12 <math>\pm</math> 0.05</b>	<b>1105</b>

**Supplemental Table 3.3.** Mean estimates ( $\pm$  SE) of visual obstruction readings (VOR), grass cover, forb cover, shrub cover, bare ground cover, litter cover, litter depth, and sample sizes for Chase County and Konza Prairie estimated for each treatment and patch within each treatment. Management regimes are labeled as follows: ABG = annually burned and grazed, ABN = annually burned but not grazed, PBG = patch-burn grazing, PBG0-2 = patch within patch-burn grazing and the number of years since last burned.

Site	Treatment	VOR (dm)	Grass (%)	Forb (%)	Shrub (%)	Bare (%)	Litter (%)	Litter (cm)	N	
		Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE		
Chase	ABG	1.53 $\pm$ 0.06	42.1 $\pm$ 1.2	19.7 $\pm$ 0.8	0.3 $\pm$ 0.1	23.7 $\pm$ 1.2	2.0 $\pm$ 0.3	1.63 $\pm$ 0.25	240	
	PBG	1.71 $\pm$ 0.05	45.6 $\pm$ 0.8	17.4 $\pm$ 0.5	1.1 $\pm$ 0.2	14.1 $\pm$ 0.7	5.3 $\pm$ 0.3	3.46 $\pm$ 0.23	540	
	<i>PBG0</i>	1.04 $\pm$ 0.06	37.7 $\pm$ 1.5	14.1 $\pm$ 0.8	0.5 $\pm$ 0.1	25.2 $\pm$ 1.3	4.4 $\pm$ 0.4	1.47 $\pm$ 0.16	180	
	<i>PBG1</i>	1.87 $\pm$ 0.07	45.7 $\pm$ 1.3	20.9 $\pm$ 1.0	1.4 $\pm$ 0.4	11.0 $\pm$ 0.8	6.9 $\pm$ 0.8	2.63 $\pm$ 0.29	180	
	<i>PBG2</i>	2.21 $\pm$ 0.07	53.4 $\pm$ 1.4	17.3 $\pm$ 0.8	1.5 $\pm$ 0.4	6.0 $\pm$ 0.8	4.5 $\pm$ 0.4	6.28 $\pm$ 0.56	180	
	<b>Total</b>		<b>1.65 <math>\pm</math> 0.04</b>	<b>44.5 <math>\pm</math> 0.7</b>	<b>18.1 <math>\pm</math> 0.4</b>	<b>0.9 <math>\pm</math> 0.1</b>	<b>17.1 <math>\pm</math> 0.6</b>	<b>4.3 <math>\pm</math> 0.3</b>	<b>2.89 <math>\pm</math> 0.18</b>	<b>780</b>
	Konza	ABG	2.46 $\pm$ 0.10	43.2 $\pm$ 1.1	28.8 $\pm$ 1.0	3.5 $\pm$ 0.6	20.6 $\pm$ 0.9	3.8 $\pm$ 0.3	0.21 $\pm$ 0.02	220
ABN		4.14 $\pm$ 0.14	69.8 $\pm$ 1.2	15.3 $\pm$ 0.7	0.6 $\pm$ 0.4	14.5 $\pm$ 0.9	2.5 $\pm$ 0.2	0.13 $\pm$ 0.02	220	
PBG		2.97 $\pm$ 0.07	36.8 $\pm$ 0.6	31.7 $\pm$ 0.5	6.6 $\pm$ 0.4	13.5 $\pm$ 0.5	10.3 $\pm$ 0.3	1.75 $\pm$ 0.08	665	
<i>PBG0</i>		2.14 $\pm$ 0.11	31.4 $\pm$ 1.1	30.8 $\pm$ 0.9	5.5 $\pm$ 0.7	24.9 $\pm$ 1.0	5.9 $\pm$ 0.5	0.25 $\pm$ 0.02	220	
<i>PBG1</i>		3.19 $\pm$ 0.11	37.0 $\pm$ 1.1	34.1 $\pm$ 1.0	7.5 $\pm$ 0.8	10.7 $\pm$ 0.6	9.5 $\pm$ 0.4	1.60 $\pm$ 0.08	220	
<i>PBG2</i>		3.58 $\pm$ 0.13	41.7 $\pm$ 1.1	30.3 $\pm$ 0.8	6.7 $\pm$ 0.8	5.1 $\pm$ 0.4	15.5 $\pm$ 0.7	3.36 $\pm$ 0.17	225	
<b>Total</b>			<b>3.10 <math>\pm</math> 0.06</b>	<b>44.6 <math>\pm</math> 0.6</b>	<b>27.9 <math>\pm</math> 0.4</b>	<b>4.8 <math>\pm</math> 0.3</b>	<b>15.1 <math>\pm</math> 0.4</b>	<b>7.5 <math>\pm</math> 0.2</b>	<b>1.12 <math>\pm</math> 0.05</b>	<b>1105</b>



**Supplemental Table 3.4.** Model selection for logistic regression models of parasitism rates of Dickcissel nests in Chase County (2011 – 2013) and at Konza Prairie, Kansas (2011 – 2016). Model selection was based on the number of parameters ( $K$ ), Deviance,  $\Delta\text{AICc}$  values, and Akaike weights ( $w_i$ ). Treatment models contained patch-burn grazing (PBG) and annually burning and grazing (ABG) for both Chase County and Konza Prairie, and annually burning but no grazing (ABN) for Konza Prairie only. Patch models include each of the three patches of the patch-burn grazing treatment separately instead of the patch-burn grazing treatment as a whole.

Species	Model	$K$	Deviance	AICc	$\Delta\text{AICc}$	$w_i$
Dickcissel	Constant	1	1915.95	1917.95	0.00	0.316
	Patch	5	1908.59	1918.61	0.66	0.227
	Parasitism	2	1915.57	1919.57	1.62	0.140
	Patch + Parasitism	6	1908.47	1920.49	2.54	0.088
	Year	6	1909.74	1921.76	3.82	0.047
	Treatment	3	1915.76	1921.77	3.82	0.047
	Patch $\times$ Parasitism	10	1902.67	1922.72	4.78	0.029
	Year + Patch	10	1903.41	1923.46	5.51	0.020
	Treatment + Parasitism	4	1915.46	1923.47	5.52	0.020
	Year + Parasitism	7	1909.61	1923.63	5.69	0.018
	Watershed	12	1899.97	1924.04	6.09	0.015
	Treatment $\times$ Parasitism	6	1913.20	1925.22	7.27	0.008
	Year + Patch + Parasitism	11	1903.32	1925.38	7.44	0.008
	Year + Treatment	8	1909.46	1925.49	7.54	0.007
	Year + Treatment + Parasitism	9	1909.22	1927.26	9.31	0.003
	Year + Patch $\times$ Parasitism	15	1897.62	1927.73	9.78	0.002
	Year + Treatment $\times$ Parasitism	11	1906.61	1928.67	10.72	0.001
	Year $\times$ Parasitism	12	1904.97	1929.04	11.10	0.001
	Year + Watershed	17	1895.64	1929.78	11.83	0.001
	Year $\times$ Parasitism + Patch	16	1898.80	1930.92	12.98	0.000
	Year $\times$ Parasitism + Treatment	14	1904.65	1932.75	14.80	0.000
	Year $\times$ Watershed	44	1847.51	1936.41	18.46	0.000
	Year $\times$ Treatment	18	1901.58	1937.74	19.79	0.000
	Year $\times$ Treatment + Parasitism	19	1901.07	1939.24	21.29	0.000
	Year $\times$ Patch	30	1880.56	1940.99	23.04	0.000
	Year $\times$ Patch + Parasitism	31	1880.34	1942.79	24.84	0.000
	Year $\times$ Treatment $\times$ Parasitism	36	1884.85	1957.45	39.51	0.000
	Year $\times$ Patch $\times$ Parasitism	60	1851.47	1973.14	55.20	0.000
Eastern Meadowlarks	Treatment	3	498.47	504.49	0.00	0.338
	Treatment + Parasitism	4	497.63	505.66	1.17	0.188
	Patch	5	497.22	507.26	2.78	0.084
	Treatment $\times$ Parasitism	6	495.23	507.29	2.80	0.083

Watershed	13	481.23	507.49	3.01	0.075	
Year + Treatment	8	492.26	508.37	3.88	0.049	
Constant	1	506.43	508.43	3.95	0.047	
Patch + Parasitism	6	496.54	508.60	4.12	0.043	
Year + Treatment + Parasitism	9	491.38	509.51	5.02	0.027	
Parasitism	2	506.09	510.10	5.61	0.020	
Year + Patch	10	491.07	511.23	6.74	0.012	
Year + Treatment × Parasitism	11	489.17	511.36	6.87	0.011	
Year + Patch + Parasitism	11	490.41	512.61	8.12	0.006	
Year	6	500.56	512.62	8.14	0.006	
Year + Watershed	18	477.31	513.81	9.32	0.003	
Patch × Parasitism	10	493.71	513.87	9.38	0.003	
Year + Parasitism	7	500.07	514.16	9.67	0.003	
Year × Parasitism + Treatment	14	489.15	517.45	12.96	0.001	
Year + Patch × Parasitism	15	487.80	518.15	13.67	0.000	
Year × Treatment	18	483.66	520.16	15.67	0.000	
Year × Parasitism + Patch	16	488.51	520.90	16.42	0.000	
Year × Treatment + Parasitism	19	483.09	521.64	17.15	0.000	
Year × Parasitism	12	497.81	522.04	17.55	0.000	
Year × Patch	29	476.26	535.55	31.06	0.000	
Year × Patch + Parasitism	30	475.46	536.84	32.35	0.000	
Year × Watershed	39	459.39	539.71	35.22	0.000	
Year × Treatment × Parasitism	34	477.93	547.69	43.21	0.000	
Year × Patch × Parasitism	54	462.02	574.49	70.00	0.000	
<hr/>						
Grasshopper Sparrow	Treatment × Parasitism	4	597.05	605.09	0.00	0.323
	Treatment + Parasitism	3	599.94	605.96	0.87	0.209
	Parasitism	2	602.27	606.28	1.20	0.177
	Constant	1	605.01	607.01	1.93	0.123
	Treatment	2	603.35	607.36	2.28	0.103
	Patch + Parasitism	5	599.66	609.71	4.62	0.032
	Patch	4	603.00	611.04	5.95	0.016
	Patch × Parasitism	8	595.42	611.54	6.45	0.013
	Year	6	601.82	613.89	8.80	0.004

**Supplemental Table 3.5.** Model selection for logistic regression models of fledging rates per host egg for Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows in Chase County (2011 – 2013) and Konza Prairie, Kansas (2011 – 2016). Model selection was based on the number of parameters ( $K$ ), Deviance,  $\Delta$ AICc values, and Akaike weights ( $w_i$ ). Clutch size models included both host and cowbird eggs in parasitized nests. Treatment models contained patch-burn grazing (PBG) and annually burning and grazing (ABG) for both Chase County and Konza Prairie, and annually burning but no grazing (ABN) for Konza Prairie only. Patch models include each of the three patches of the patch-burn grazing treatment separately instead of the patch-burn grazing treatment as a whole.

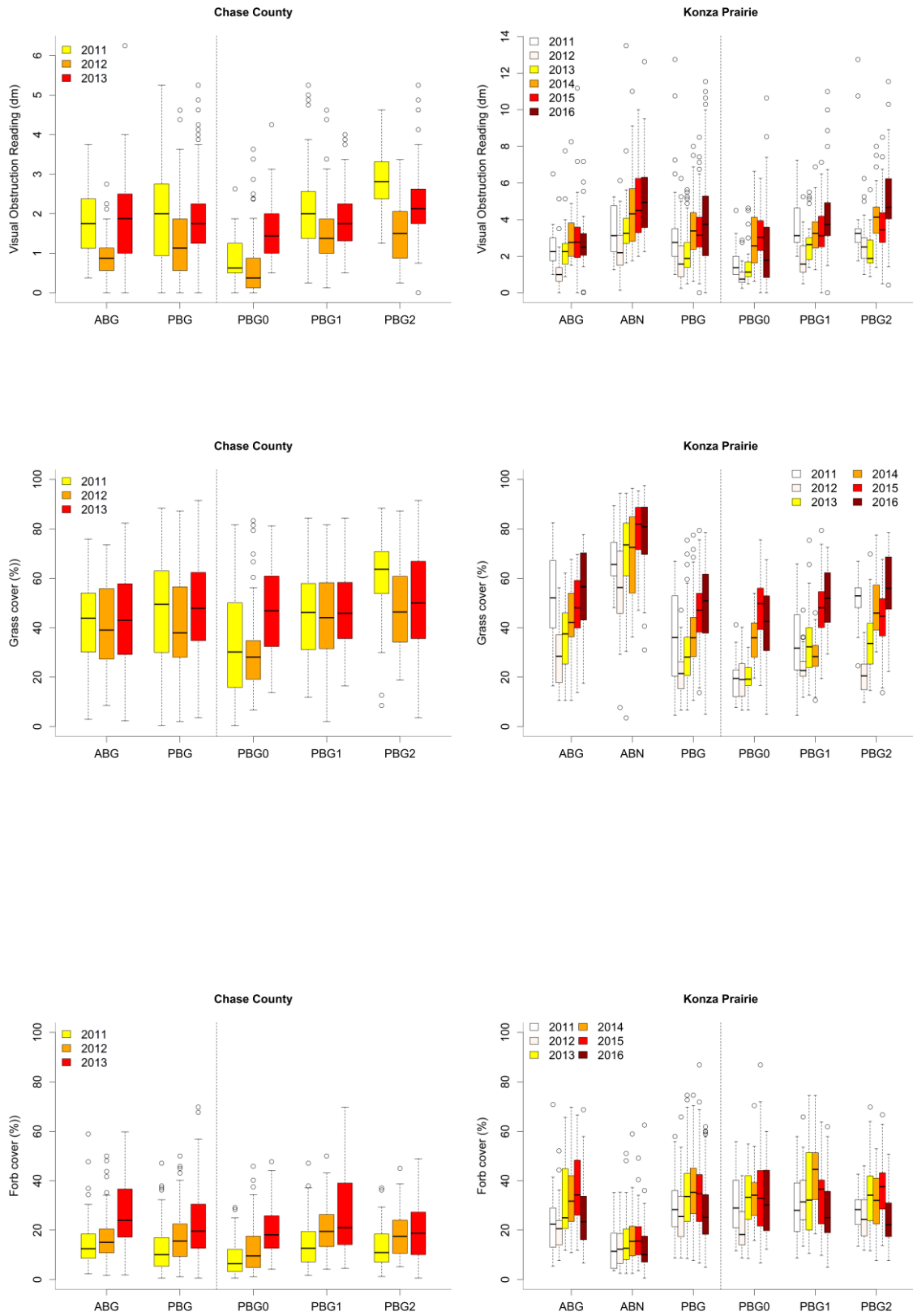
Species	Site	Parasitized	Model	$K$	Deviance	AICc	delta	weight
Dickcissel	Chase	Both	Nest ID + Clutch Size	3	201.16	207.32	0.00	0.252
			Nest ID + Clutch Size + Parasitism	4	199.92	208.17	0.86	0.164
			Nest ID	2	204.20	208.28	0.97	0.155
			Nest ID + Clutch Size + Treatment	4	200.84	209.09	1.77	0.104
			Nest ID + Parasitism	3	203.28	209.43	2.11	0.088
			Nest ID + Treatment	3	203.84	209.99	2.68	0.066
			Nest ID + Clutch Size $\times$ Parasitism	5	199.92	210.30	2.98	0.057
			Nest ID + Clutch Size $\times$ Treatment	5	200.40	210.79	3.48	0.044
			Nest ID + Treatment + Parasitism	4	203.16	211.40	4.09	0.033
			Nest ID + Treatment $\times$ Parasitism	5	202.94	213.33	6.01	0.012
			Clutch Size + Parasitism	3	208.34	214.48	7.17	0.007
			Clutch Size	2	210.48	214.56	7.25	0.007
			Clutch Size + Treatment	3	210.16	216.31	8.99	0.003
			Clutch Size $\times$ Parasitism	4	208.32	216.57	9.26	0.002
			Constant	1	215.54	217.57	10.25	0.001
			Clutch Size $\times$ Treatment	4	209.32	217.57	10.25	0.001
			Parasitism	2	213.92	217.99	10.67	0.001
			Treatment	2	215.24	219.31	11.99	0.001
			Treatment + Parasitism	3	213.88	220.02	12.71	0.000
			Treatment $\times$ Parasitism	4	213.34	221.59	14.28	0.000
Dickcissel	Konza	No	Clutch Size	2	41.01	45.34	0.00	0.536

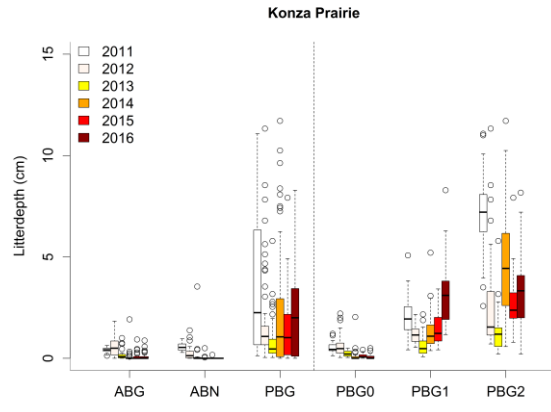
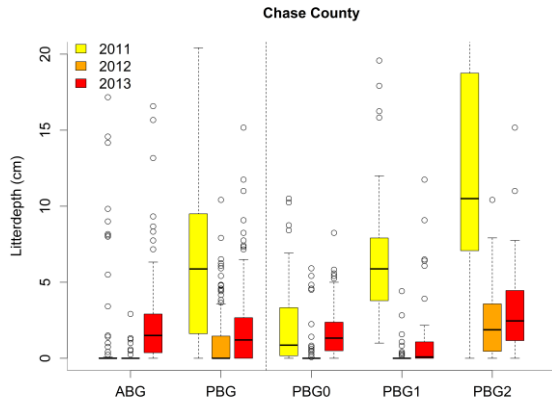
			Constant	1	44.99	47.09	1.75	0.223
			Nest ID + Clutch Size	3	41.01	47.68	2.34	0.166
			Nest ID	2	44.95	49.28	3.94	0.075
Dickcissel	Konza	Yes	Nest ID + Clutch Size + Patch	7	226.06	240.67	0.00	0.276
			Nest ID + Clutch Size + Treatment	5	230.66	241.00	0.32	0.235
			Clutch Size + Patch	6	228.92	241.38	0.71	0.194
			Nest ID + Clutch Size × Treatment	7	228.38	243.01	2.33	0.086
			Clutch Size + Treatment	4	234.86	243.08	2.41	0.083
			Clutch Size × Patch	10	223.04	244.29	3.61	0.045
			Clutch Size × Treatment	6	232.48	244.95	4.28	0.033
			Nest ID + Clutch Size	3	239.38	245.50	4.83	0.025
			Nest ID + Patch	6	234.40	246.87	6.19	0.012
			Nest ID + Treatment	4	240.34	248.56	7.88	0.005
			Patch	5	239.40	249.74	9.07	0.003
			Clutch Size	2	246.24	250.30	9.63	0.002
			Nest ID	2	247.68	251.75	11.08	0.001
			Treatment	3	246.84	252.97	12.29	0.001
			Constant	1	257.02	259.04	18.36	0.000
Eastern Meadowlark	Chase	Both	Constant	1	33.15	35.26	0.00	0.267
			Nest ID	2	32.24	36.59	1.33	0.138
			Clutch Size	2	32.90	37.25	1.99	0.099
			Treatment	2	32.94	37.28	2.02	0.097
			Parasitism	2	33.13	37.48	2.22	0.088
			Nest ID + Clutch Size	3	32.09	38.80	3.54	0.046
			Nest ID + Treatment	3	32.13	38.83	3.57	0.045
			Nest ID + Parasitism	3	32.24	38.95	3.69	0.042
			Clutch Size + Treatment	3	32.70	39.41	4.15	0.034

			Treatment + Parasitism (3)	3	32.88	39.59	4.33	0.031
			Treatment + Parasitism (4)	3	32.88	39.59	4.33	0.031
			Clutch Size + Parasitism	3	32.89	39.60	4.34	0.031
			Nest ID + Clutch Size + Treatment	4	31.95	41.16	5.90	0.014
			Nest ID + Clutch Size + Parasitism	4	32.09	41.30	6.04	0.013
			Nest ID + Treatment + Parasitism (3)	4	32.11	41.32	6.06	0.013
			Nest ID + Treatment + Parasitism (4)	4	32.11	41.32	6.06	0.013
Eastern Meadowlark	Konza	Both	Constant	1	137.60	139.65	0.00	0.150
			Parasitism	2	135.72	139.85	0.20	0.136
			Nest ID + Clutch Size × Parasitism	5	130.26	140.87	1.22	0.082
			Treatment	2	136.88	140.99	1.34	0.077
			Treatment + Parasitism	3	134.86	141.09	1.45	0.073
			Clutch Size	2	137.08	141.20	1.55	0.069
			Nest ID	2	137.50	141.62	1.97	0.056
			Nest ID + Parasitism	3	135.60	141.85	2.20	0.050
			Clutch Size + Parasitism	3	135.66	141.90	2.25	0.049
			Patch	3	136.50	142.75	3.10	0.032
			Patch × Parasitism	6	129.92	142.80	3.15	0.031
			Nest ID + Treatment	3	136.80	143.04	3.39	0.028
			Patch + Parasitism	4	134.70	143.12	3.47	0.027
			Nest ID + Treatment + Parasitism	4	134.76	143.17	3.52	0.026
			Nest ID + Clutch Size	3	137.00	143.25	3.60	0.025
			Treatment × Parasitism	4	134.84	143.25	3.60	0.025
			Nest ID + Clutch Size + Treatment	4	136.12	144.52	4.87	0.013
			Nest ID + Patch	4	136.48	144.88	5.23	0.011
			Nest ID + Patch × Parasitism	7	129.92	145.10	5.45	0.010
			Nest ID + Patch + Parasitism	5	134.64	145.27	5.62	0.009
Nest ID + Treatment × Parasitism	5	134.74	145.36	5.71	0.009			

			Nest ID + Clutch Size × Treatment	5	135.88	146.49	6.84	0.005
			Nest ID + Clutch Size + Patch	5	135.92	146.55	6.90	0.005
			Nest ID + Clutch Size × Patch	7	131.42	146.60	6.95	0.005
Grasshopper	Both	Both	Nest ID + Parasitism	3	119.18	125.43	0.00	0.361
Sparrow			Nest ID + Treatment + Parasitism	4	119.07	127.48	2.05	0.129
			Nest ID + Clutch Size + Parasitism	4	119.10	127.51	2.08	0.128
			Nest ID	2	124.36	128.48	3.06	0.078
			Parasitism	2	124.78	128.90	3.47	0.064
			Nest ID + Clutch Size × Parasitism	5	118.87	129.49	4.06	0.047
			Nest ID + Treatment × Parasitism	5	119.06	129.68	4.26	0.043
			Nest ID + Clutch Size	3	124.17	130.42	4.99	0.030
			Nest ID + Treatment	3	124.22	130.47	5.04	0.029
			Clutch Size + Parasitism	3	124.61	130.85	5.42	0.024
			Treatment + Parasitism	3	124.78	131.02	5.60	0.022
			Nest ID + Clutch Size + Treatment	4	123.99	132.39	6.97	0.011
			Clutch Size × Parasitism	4	124.35	132.76	7.34	0.009
			Treatment × Parasitism	4	124.73	133.14	7.71	0.008
			Nest ID + Clutch Size × Treatment	5	122.68	133.30	7.87	0.007
			Constant	1	132.03	134.07	8.64	0.005
			Clutch Size	2	131.81	135.93	10.51	0.002
			Treatment	2	132.01	136.13	10.71	0.002
			Clutch Size + Treatment	3	131.78	138.03	12.60	0.001
			Clutch Size × Treatment	4	130.35	138.76	13.33	0.000

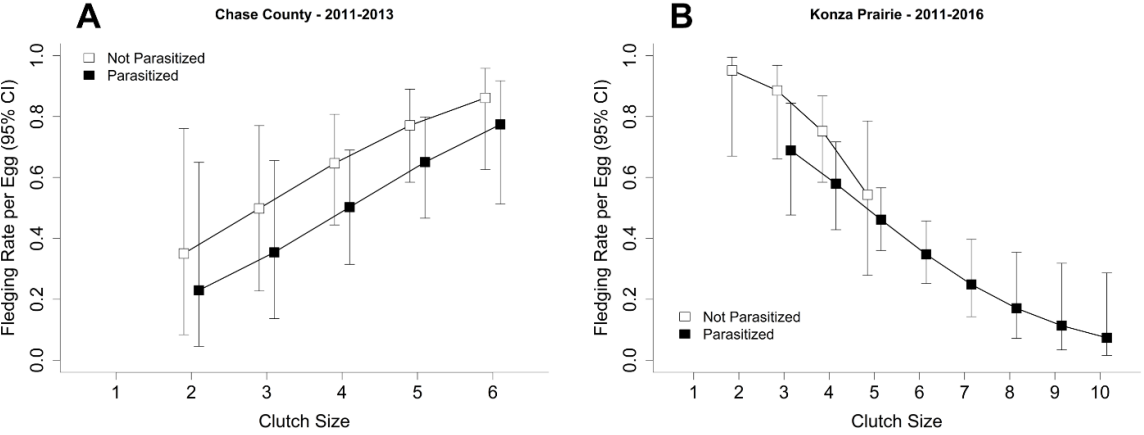
**Supplemental Figure 3.1.** Annual variation in visual obstruction readings (VOR), grass cover, forb cover, and litter depth at our Chase County (left) and Konza Prairie (right) sites.







**Supplemental Figure 3.2.** Fledging rates per egg for successful Dickcissel nests in Chase County (A) and Konza Prairie (B) estimated separately for total clutch size and whether a nest was parasitized or not.



**Chapter 4 - Fledgling survival and movements of Dickcissels in  
response to rangeland management of tallgrass prairie**

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*--- In preparation for Condor ---*

## Abstract

The reproductive success of birds is dependent on clutch size, nest survival, and how well fledglings survive after they leave the nest. However, when assessing the effects of rangeland management on the reproductive success of grassland songbirds, fledgling survival is difficult to investigate because broods are mobile. Habitat requirements might differ between the nesting and fledgling stage of grassland songbirds, and fledglings might therefore respond differently to patterns of food availability and predation risk in the landscape. Competition among young in the nest could limit wing growth and body mass gains of nestlings from larger clutches. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) increases the clutch size of host nests, and could therefore negatively affect body condition of host young due to increased competition among nestlings. With our 2-year field study, we tested the effects of rangeland management on the survival and movements of fledgling Dickcissels (*Spiza americana*), and examined whether body condition of nestlings upon leaving the nest affected fledgling survival. We attached small VHF radio transmitters to 34 Dickcissel fledglings from nests located in three rangeland management treatments that differed in fire frequency and whether grazing by cattle occurred. Rangeland management affected fledgling movements, but only had a minor effect on fledgling survival. Fledglings moved only short distances (<100 m) during the first week after leaving the nest, which stresses the importance of nesting habitat conditions. We further found evidence for a potential tradeoff between habitat selection for nests versus fledglings of Dickcissels for nests in annually burned and ungrazed pastures. Parents that had high rates of nest success by nesting in pastures with low cowbird densities, produced fledglings that faced higher rates of depredation by snakes, and showed greater movements away from the pasture. Fledgling survival is an important component of the reproductive success of grassland songbirds, and

understanding the effects of rangeland management on the ecology of fledglings is essential for conservation of declining species.

## Introduction

The reproductive success of grassland songbirds can be defined by several key stages including clutch size, nest survival, and the survival of juveniles after they leave the nest. Survival of dependent young until independence and subsequent juvenile survival are influential parameters in growth of vertebrate populations (Gaillard et al. 1998, Amundson 2010, Streby and Peterson 2011), especially in short-lived vertebrates, such as grassland songbirds (Saether and Bakke 2000, Clark and Martin, 2007, Wilson and Martin 2012). However, the majority of studies that assess the population dynamics of grassland songbirds have been limited to events in the nest, while the survival, movements, and behavior of fledglings has not received much attention.

After leaving the nest, recently fledged young of grassland songbirds are dependent on parental care in defense, feeding, and brooding for at least three weeks, a period in which they are vulnerable to predation and exposure (Anders et al. 1997; 1998, Martin 2014). Fledglings cannot readily fly after leaving the nests, and movements are often of short distances, especially during the first week (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Hovick et al. 2011). Fledglings are therefore an easy targets for predators, resulting in high rates of mortality (Anders et al. 1998, Lang et al. 2002, Kershner et al. 2004, Berkeley et al. 2007, Suedkamp Wells et al. 2007, Hovick et al. 2011, Jones et al. 2017). Due to the low mobility of fledglings, local nesting habitat might be critical for fledgling survival, especially since habitat requirements might differ between the nesting and fledgling stage of songbirds (Pagen et al. 2000, Marshall et al. 2003, Powell 2006, Streby and Peterson 2011; 2013). Unfortunately, few studies have examined the space use and habitat requirements of the fledglings of grassland songbirds, and the effects of rangeland management on fledglings

remain largely unknown (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Hovick et al. 2011).

Rangeland management-induced spatial variation in food availability and predator abundance likely plays an important role in the survival and movements of songbird fledglings. Species diversity and abundance of herbivorous insects has been linked to changes in vegetation quality and structure, but also directly to fire and grazing (Swengel 2001, Maron and Crone 2006, Lopes and Vasconcelos 2011). Arthropod abundance is often higher in burned and grazed pastures, due to the high net primary productivity and nitrogen content of plants in those pastures (Knapp et al. 1999, Joern 2005, Williams 2016). However, fledglings have to balance acquiring food with avoiding predation, and pastures with high food availability might not always lead to high survival rates of grassland fledglings. Due to low mobility in the first week, fledglings of grassland songbirds may be susceptible to depredation by snakes (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Jones et al. 2017). Snakes, such as yellowbelly racers (*Coluber constrictor flaviventris*), Great Plains ratsnakes (*Pantherophis emoryi*), and bullsnakes (*Pituophis catenifer*), are common nest predators in the tallgrass prairie of Kansas, and are more abundant in unburned pastures with dense vegetation and high shrub cover (Klug et al. 2010). However, predator communities in grasslands can be quite diverse, and the species-specific abundance of predators shows considerable regional variation (Thompson et al. 1999, Pietz and Granfors 2000, Renfrew et al. 2003, Lyons et al. 2015). How rangeland management will influence depredation rates of fledglings is therefore likely dependent on the region-specific predator community.

A second factor that can influence fledgling survival of songbirds is brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Brood parasitism is widespread among grassland birds, and the negative consequences of brood parasitism on nesting success of host species are well documented (Zimmerman and Finck 1989, Jensen and Cully 2005a, Kosciuch

and Sandercock 2008, Ortega and Ortega 2009, Rivers et al. 2010a; 2010b, Martin 2014). However, brood parasitism might have negative effects that carry over to the fledgling stage of songbirds, since increased competition with parasitic young might depress the development of host young in the nest environment (Hovick et al. 2011, Peterson et al. 2012). Proper development of wing length and body mass is important, as increased mobility allows fledglings to more easily escape predators and survive inclement weather conditions (Martin 2014, Jones et al. 2017). Rangeland management has large effects on the local abundance of Brown-headed Cowbirds (Morris and Thompson 1998, Goguen and Mathews 1999; 2000, Jensen and Cully 2005a; 2005b, Patten et al. 2006). In pastures with high rates of brood parasitism, fledgling survival rates might be impacted by competition with parasitic young in the nest, and avoiding brood parasitism might be an important driver of nest site selection by adults.

With our two-year field study, we tested the effects of habitat heterogeneity and brood parasitism on the survival, movements and development of Dickcissel fledglings (*Spiza americana*), a species of conservation concern. We compared experimental pastures that were managed with patch-burn grazing, versus control pastures that were annually burned with or without grazing. We tested the following two hypotheses: (1) Management-induced variation in vegetative structure, and associated variation in food availability and predation risk, drives survival and movements of fledgling Dickcissels. We predicted that fledgling survival would be highest and movements would be shortest on recently burned pastures, due to the positive effects of fire and grazing on arthropod abundance, while the abundance of snakes might be depressed. (2) Nestling development drives the survival and movements of fledgling Dickcissels, independent of the direct effects of management-induced variation in food availability and predation risk. Here, we predicted that fledglings with shorter wings and lower body mass upon leaving the nest would have lower survival and move shorter distances.

We also predicted that fledglings from nests that were parasitized by Brown-headed Cowbirds would have lower survival because the larger clutch size of parasitized nests leads to increased competition between nestlings, which may slow wing growth or gains in body mass.

## **Methods**

### **Study Site**

Our 2-year field study was conducted at the Konza Prairie Biological Station (hereafter Konza Prairie) located in the Flint Hills region near Manhattan, Kansas, and is part of the NSF-funded Long-term Ecological Research (LTER) Site Program. The tallgrass prairie at Konza Prairie spans 3,487 hectares in Riley and Geary County, Kansas, and consists of >60 experimental pastures that receive different combinations of grazing and prescribed fire. The climate at Konza Prairie is relatively warm and humid during the growing season, but shows considerable annual variation. About 75% of precipitation falls within the 6-month growing season (March – August), but late summer droughts in July and August are not uncommon. Over the past century, the annual temperature averaged 12.6°C for, but monthly average temperatures got as high as 25-26°C in July and August. Annual precipitation averaged 799 mm/year (SD = 175 mm/year) at Konza Prairie (See Chapter 3 for Methods).

### **Management Regimes**

We investigated survival and movements of Dickcissel fledglings in three experimental pastures. Three pastures (49.4 – 102.4 ha) were combined to form one large pasture (219.3 ha) that was managed with rotational fire in a patch-burn grazing management regime with a 3-year rotation (PBG). One pasture was annually burned and grazed (ABG; 93.5 ha), and served as a negative control, while a third pasture was annually burned and ungrazed (ABN; 41.6



ha), and served as a positive control. Pastures were grazed by cow/calf pairs at a rate of 3.24 hectares per pair from early May to early October (J. Briggs and K. C. Olsen, personal communication). All pastures were treated with prescribed burns in early spring between mid-March to mid-April, and had been managed with the same management regime for three or more years before we started our field study.

### **Fledgling Survival and Movements**

To estimate fledgling survival and movements in response to rangeland management, we monitored nests of Dickcissels in each pasture or patch at our study site. Dickcissels are small-bodied grassland songbirds (25-30 g), and a common breeding bird throughout the Great Plains (Rodewald 2017). Within grassland habitats, Dickcissels are found at sites with a range of vegetative structures, ranging from recently burned to areas that have not been burned for multiple years, and areas that grazed or ungrazed (Temple 2002). Dickcissels are a preferred host of Brown-headed Cowbirds, and Dickcissels face high rates of brood parasitism at our study site due to the high abundance of cowbirds (0.66 to 1.00 of nests; Jensen and Cully 2005b, Sandercock et al. 2008, Rivers et al. 2010a, Chapter 3).

We located Dickcissel nests by watching behavior of the attending parents and by opportunistically flushing birds. At discovery, we marked the nest at ~5 m with a small rock or flagging tape in a random direction, and recorded the GPS location, and distance and compass bearing to the nest site. We monitored nests every 2-3 days until we determined the nest fate as successful or failed. At each successful nest, we randomly selected one or two Dickcissel nestlings at 7 days old to be equipped with a transmitter as well as an USGS metal leg band.

We used small radio-transmitters (A1015, ATS, Isanti, Montana, USA), with an expected battery life of 29 days and a maximum weight of 0.5 grams. We attached

transmitters to fledglings with a figure-eight leg harness with elastic cord, a widely used technique with small-bodied songbirds (Dougill et al. 2000, Kershner et al. 2004, Berkeley et al. 2007, Suedkamp Wells et al. 2007). Transmitter packages did not exceed 3% of the body mass of Dickcissel nestlings at fledging (Rodewald 2017), and have minimal impacts on fledglings (Suedkamp Wells et al. 2003). All nestlings that were equipped with a radio-transmitter successfully fledged from the nest. After we applied transmitters, we relocated fledglings every two days during the first 30 days after leaving the nest using three element Yagi antennas and portable receivers.

For each location, we determined the fate of the bird as being alive, if we were able to detect the bird. We then recorded UTM-coordinates with a handheld GPS device, and recorded the wing chord length and body mass of fledglings we were able to catch by hand. If not encountered alive, we determined whether a fledgling died, successfully left the study area, or whether its fate was unknown. A fledgling was classified as being dead if we found carcass remains, recovered its transmitter with teeth marks or with other evidence that the fledgling was depredated, or we lost signal when fledglings were still too young to independently leave the area ( $< 7$  days). We classified fledglings as successfully left the area if we lost the signal when birds were developed enough to fly longer distances, but before batteries were expected to expire. If we could not detect a bird's signal, we searched a circular area with a radius of two miles around the last location a bird was detected, to confirm whether a fledgling left our study area. We classified fledglings as survived and stayed in the area if we lost signal of the bird around the expected expiring data of the transmitter, which we were often able to confirm by visual observation of the fledgling in the immediate area of the last location it was observed. Last, we classified the fate of a fledgling to be unknown if fledglings lost their transmitter before it expired due to a technical malfunction ( $N = 2$ ). For survival analyses, we right-censored encounter data from fledglings that successfully left the

study area, survived till the battery of the transmitter expired, and fledglings that lost their transmitter before it expired.

### **Statistical Analyses**

To estimate fledgling survival, we constructed encounter histories for each fledgling with a daily time step where entry and exit dates allowed for left- and right-censoring. Events where a bird was alive at the last encounter were coded with a zero, while a mortality event was coded with a one. We estimated fledgling survival with time-to-event models, and tested the effects of burning, grazing, and rangeland management regime on fledgling survival with Cox proportional hazards regression models with the *survival* package in R (Therneau 2015, R Core Team 2017). We tested the effects of patch-burn grazing management on fledgling survival at two separate scales. A treatment model included both control pastures and the patch-burn grazing managed pasture as a whole, while a patch-within-treatment model included both controls and all three patches of the patch-burn grazing pasture separately. To estimate fledgling movements, we calculated the distance between each observation and the original nest location for each individual, and compared total displacement from the nest among treatments with Analysis of Variance in R (R Core Team 2017).

## **Results**

During our field study, we tracked a total of 28 Dickcissel fledglings in 2015 for an average of  $12 \pm 5.4\text{SD}$  days, and six fledglings in 2016 for an average of only  $4 \pm 1.4$  days due to reduced battery life of transmitters during that year. We tracked a total of 12 fledglings in patch-burn grazing managed pastures (PBG: five in PBG0, six in PBG1, and one in PBG2),

eight fledglings in the annually burned and grazed pasture (ABG), and 14 fledglings in the annually burned and ungrazed pasture (ABN).

### **Fledgling Survival**

We confirmed depredation of seven Dickcissel fledglings, and identified predators included four snakes, including one eastern yellowbelly racer (*Coluber constrictor flaviventris*) and three unidentified snakes, one striped skunk (*Mephitis mephitis*), one unidentified mesocarnivore, and one unknown predator. Kaplan-Meier survivorship curves showed a survival probability of 0.767 (95% CI = 0.629 – 0.936) over 17 days after leaving the nest, with most mortalities occurring during the first week (Figure 4.1 and 4.2). We did not find any effects of management, grazing, or burning of immediate nesting habitat on the survival of Dickcissel fledglings (Table 4.1), but survival tended to be higher on burned pastures than unburned pastures (Figure 4.1). Furthermore, fledglings tended to be depredated within the first two days after fledging in grazed pastures, whereas fledglings in ungrazed pastures tended to be depredated at least three days after leaving the nest (Figure 4.1).

### **Fledgling Movements**

Dickcissel fledglings showed only limited movements away from their nesting sites during the first week, but displacement distances increased steadily with age (Table 4.2). Overall, displacement distance was highly variable among fledglings. We found large displacement movements (> 100 m) immediately after fledging in some individuals, while others stayed close to the nest location up to two weeks after leaving the nest (Table 4.2). Variation in the displacement distance of fledglings at seven days after fledging differed among rangeland treatments. Dickcissel fledglings in annually burned and ungrazed pastures tended to move greater distances away from the nest than in patch-burn grazing pastures (ABN = 223 ±

165SD m, PBG =  $75 \pm 25$  m; Mann-Whitney U Test:  $W = 43$ ,  $P = 0.066$ ), but not annually burned and grazed (ABG =  $87 \pm 61$  m;  $W = 32$ ,  $P = 0.240$ ; Table 4.3). Furthermore, five out of eight fledglings, from seven nests, left the annually burned and ungrazed pasture at seven days after fledging, while no fledglings left our other treatments (Table 4.3).

### **Fledgling Development**

Body condition of 7-day old Dickcissel nestlings in the nest was highly variable. Wing chord length averaged  $42.6 \pm 3.3$ SD mm ( $N = 22$ ), and ranged from 36.0 to 47.0 millimeters, while body mass averaged  $16.2 \pm 1.6$  grams ( $N = 27$ ), and ranged from 12.6 – 20.2 grams. Wing chord length and body mass tended to decrease with the number of host and cowbird nestlings in the nest (Wing RI = 0.729, Mass RI = 0.782), but did not differ between young originating from parasitized and unparasitized nests (Wing RI = 0.283, Mass RI = 0.252; Table 4.4 and Figure 4.3). We found no evidence that the survival and movements of fledglings was affected by their wing chord length or body mass at 7-days after hatching.

## **Discussion**

With our 2-year field study, we provide some of the first estimates of fledgling survival for Dickcissels. Furthermore, we are the first study to examine effects of rangeland management on the survival and movements of Dickcissel fledglings, and compare patch-burn grazing versus grazed and ungrazed pastures with annual burning. We found that depredation risk was highest for fledglings during the first couple of days after leaving the nest, and that snakes might be an important predator of fledglings at our study site in northeast Kansas. We found that fledgling survival did not differ across management regimes, but tended to be lower for unburned pastures. Dickcissel fledglings showed only short movements

(<100 m) away from the nest during the first week after leaving the nest, but total displacement from the nest was highly variable among older fledglings. Fledglings in annually burned and ungrazed pastures tended to move to surrounding pastures, and tended to show greater movements compared to other treatments. We found that both wing chord length and body mass were related to the total number of nestlings in the nest environment, but not to whether a nest was parasitized by Brown-headed Cowbirds. However, we did not find an effect of wing chord length or body mass on survival or movement distance of Dickcissel fledglings during the first three weeks after fledging.

### **Effects of Management**

We did not find clear evidence that fledgling survival was affected by the management regime of nesting habitat. However, fledgling survival tended to be lower for fledglings from nests at unburned pastures. A lack of burning could lead to higher shrub cover, denser vegetation and greater litter depth, which could increase snake abundance or activity (Klug et al. 2010). Snakes are a common predator of Dickcissel fledglings (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Jones et al. 2017), and previous work by Klug et al. (2010) shows that snakes are an abundant predator at our study site.

At a smaller spatial scale, we encountered many of our fledglings in shrubby vegetation during relocation, especially after the first week (B.H.F. Verheijen, pers. obs.). Past work on the movements of fledgling Dickcissels and Wood Thrushes (*Hylocichla mustelina*) showed that fledglings select more shrubby sites when shrubs are available close by, potentially to avoid predators (Anders et al. 1998, Fink 2003, Suedkamp Wells et al. 2007). Shrubs may therefore aid in the concealment of Dickcissel fledglings, even when average shrub cover is low, but fledglings actively move away from sites with more shrub cover on a larger spatial scale. Furthermore, which predators are responsible for fledgling

mortalities might shift when the mobility of fledglings increases, potentially reducing the depredation risk in shrubs for older fledglings.

Fledglings also actively moved away from annually burned and ungrazed pastures, despite high food availability at annually burned pastures due to the availability of high quality forage (Joern 2005, Williams 2016). The lack of grazing on annually burned pastures created dense grass cover, which might restrict the movements of fledglings. Dense vegetative structure may make it harder for fledglings to escape from predators, and may increase the activity of snakes.

### **Comparison and Population Viability**

Dickcissel fledglings at Konza Prairie had high rates of fledgling survival. We found a Kaplan-Meier survival rate of 0.78 for the first two weeks after leaving the nest, with most mortalities occurring during the first week. Other studies have reported survival rates of 0.29 over 36 days, 0.33 over 28 days, and 0.56 over 56 days (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Jones et al. 2017). However, since all other studies report significant leveling off of mortality rates after the first week, estimates of survival are likely comparable despite different periods of exposure.

Grassland songbirds generally have low nest survival, and population viability analyses of Dickcissels must assume high juvenile survival for populations to remain stable (Martin 1995; 2014, Sandercock et al. 2008, With et al. 2008, Chapter 3). Many population models assume that first-year survival of songbirds is roughly half of adult survival (Ricklefs 1973, Temple and Cary 1998). However, a population modeling effort by Fletcher et al. (2006) concluded that Dickcissel populations were not stable unless juvenile first-year survival was at least 0.5 and adult survival was 0.8. Moreover, in their analyses of population viability for Dickcissels in the Flint Hills, Kansas, With et al. (2008) concluded that

populations kept declining when juvenile first-year survival was 0.3, which is half of adult survival. For Dickcissel populations to remain stable, juvenile survival likely has to be larger than 0.5, but existing estimates of survival for fledgling Dickcissels are close to or lower than that, while they estimate survival over a much shorter time period (Berkeley et al. 2007, Suedkamp Wells et al. 2007, Jones et al. 2017). We found high fledgling survival (0.78) over the first two weeks after leaving the nest at our study site in the Flint Hills, which would at least allow a juvenile first-year survival of 0.5, assuming that juveniles have high survival during migration and on the wintering grounds.

Regional variation in fledgling survival might indicate different selection pressures on nesting Dickcissels. Earlier work showed that nest survival of Dickcissels is particularly low at Konza Prairie, mainly due to high rates of nest depredation by snakes and brood parasitism by Brown-headed Cowbirds (Jensen and Cully 2005, Sandercock et al. 2008, Klug et al. 2010, Chapter 3). Regional variation in predator community could lead to variation in predation risk of nests and fledglings, and relatively high survival of fledglings at Konza Prairie could increase selection for earlier fledging.

### **Tradeoff Between Life Stages**

Our findings seem to indicate a potential tradeoff between the nest and fledgling stages of Dickcissels, and adds to existing work that indicate that habitat requirements for nest sites might differ substantially from habitat requirements from fledglings (Streby and Anderson 2011; 2013). Related work at Konza Prairie shows that the number of fledglings per nest are high on annually burned and ungrazed pastures, mainly because nesting birds faced lower parasitism rates. As a consequence, Dickcissel nests contained more host eggs, and nestlings faced less competition with parasitic young on those pastures, leading to higher apparent reproductive success (See Chapter 3). For fledglings, the presence of predators is an



immediate risk, while the effects of brood parasitism on body condition might be less apparent. Dickcissel females that try to avoid brood parasitism by nesting in ungrazed or unburned pastures with higher vegetation densities, might reduce the survival of their fledglings, or force fledglings to disperse large distances to more suitable habitat. In contrast, the number of Dickcissel fledglings per nest was also high in patch-burn grazing patches burned in the past year due to low rates of nest depredation, and young continued to benefit from low levels of predation after fledging. In pastures managed with patch-burn grazing, burned and unburned patches are close together, and could potentially provide suitable habitat for Dickcissel fledglings in close proximity to quality breeding habitat.

### **Effects of Brood Parasitism**

We found that the total number of nestlings had a negative effect on both wing chord length and body mass of 7-day old nestlings before fledging. Whether fellow nestlings were conspecifics or parasitic young did not affect either biometric, but parasitized nests often have a higher total number of young, thereby increasing competition among nestlings (Sandercock et al. 2008, Chapter 3). Thus, brood parasitism might indirectly influence the early development of Dickcissel fledglings by increasing competition for food between host and parasitic young in the nest. The survival probability of songbird fledglings is directly related to how well developed young are upon leaving the nest (Martin 2014). Well-developed wings might allow fledglings to better escape predators, whereas higher body mass could lead to lower mortalities related to exposure to harsh weather conditions, such as extreme heat or rainstorms (Martin 2014, Jones et al. 2017). However, we found no evidence that wing chord length and body mass of nestlings at day 7 affected the survival or displacement distance of Dickcissel fledglings at our study site. The relatively low rates of depredation of fledglings at Konza Prairie might give less developed young a better chance to avoid depredation.

Alternatively, variation in rangeland management might lead to large differences in predator abundance or community composition, obscuring the relationship between the development, and the survival and movements of fledglings.

Our field study is one of the first attempts to estimate the effects of rangeland management on the survival and movements of the fledglings of grassland songbirds. Our findings join a growing body of research that stresses the importance of assessing the effects of management on fledglings, since effects on fledglings might be conflicting with the effects on nest survival and bird abundance. Furthermore, the effects of rangeland management on fledgling survival and movements might be region-dependent due to regional variation in predator community composition and the abundance of Brown-headed Cowbirds.

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**Table 4.1.** Model selection of Cox proportional hazard regression functions for fledgling Dickcissels at Konza Prairie, Kansas (2015-2016). Model selection was based on the number of parameters ( $K$ ), Deviance,  $\Delta\text{AICc}$  values, and Akaike weights ( $w_i$ ). The treatment model included three management regimes: patch-burn grazing (PBG), and annual burning with (ABG) or without cattle grazing (ABN).

<b>Model Structure</b>	<b><math>K</math></b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w_i</math></b>
Constant	1	46.24	46.24	0.00	0.506
Burning	2	45.47	47.60	1.36	0.257
Grazing	2	46.22	48.34	2.10	0.177
Treatment	3	46.12	50.51	4.27	0.060

**Table 4.2.** Displacement distance of different age classes of Dickcissel fledglings from their natal nest at Konza Prairie, Kansas (2015-2016). We report the absolute displacement from nest locations ( $\pm$  SD) in meters, the range of displacement and the number of surviving fledglings that were located at each age class. Dickcissel nestlings usually fledge at 8-9 days after hatching.

<b>Age Class (Days)</b>	<b>Mean Distance (m) <math>\pm</math> SD</b>	<b>Range (m)</b>	<b>N</b>
6-7	0 $\pm$ 0	0 - 0	30
8-9	17 $\pm$ 24	0 - 110	23
10-11	52 $\pm$ 46	0 - 232	25
12-13	93 $\pm$ 79	1 - 347	19
14-15	136 $\pm$ 129	9 - 581	20
16-17	203 $\pm$ 149	9 - 510	15
18-19	229 $\pm$ 157	49 - 534	19
20-21	303 $\pm$ 177	44 - 572	13
22-23	273 $\pm$ 195	46 - 620	15
24-25	435 $\pm$ 390	66 - 928	5
26-27	319 $\pm$ 93	236 - 420	3

**Table 4.3.** Dispersal of surviving Dickcissel fledglings from their nest site at 14-15 days after hatching at Konza Prairie, Kansas (2015-2016). Shown are the number of fledglings that stayed or left the pasture in which they were born, the average displacement distance in meters ( $\pm$  SD) and the range of displacement distance. Fledgling occurs at 8-9 days of age.

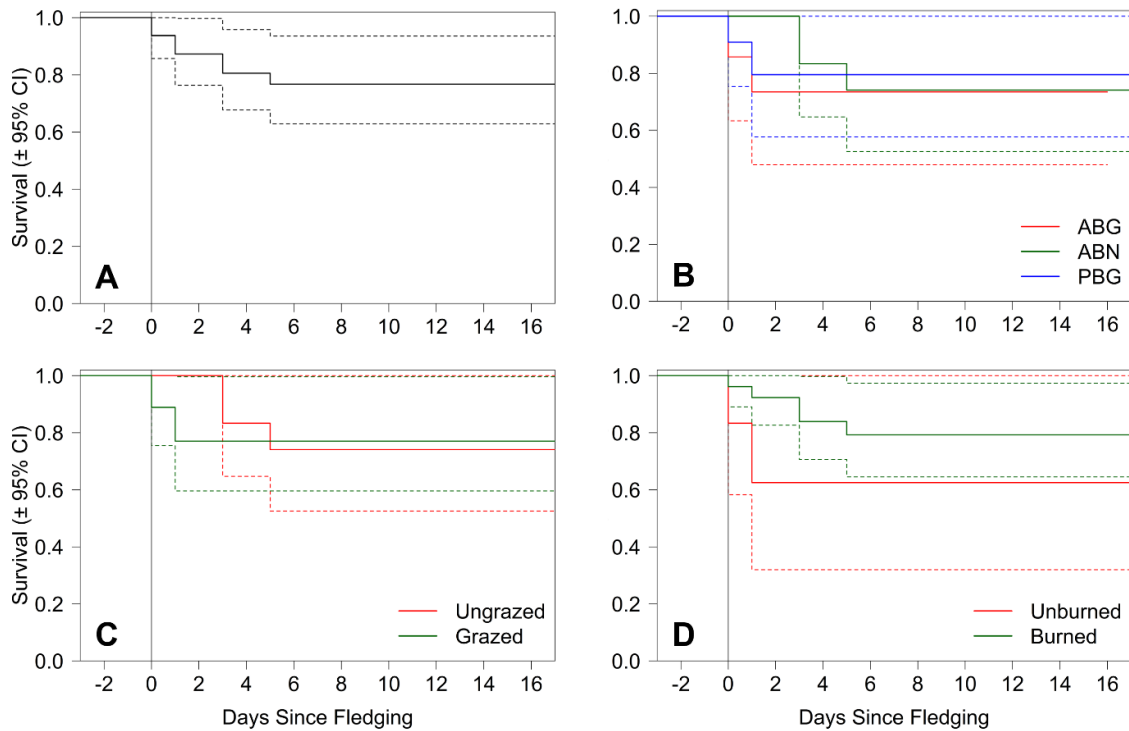
<b>Treatment</b>	<b>No. Stayed at 14-15 Days</b>	<b>No. Moved at 14-15 Days</b>	<b>Mean Distance (m) <math>\pm</math> SD</b>	<b>Range (m)</b>
ABG	5	0	87 $\pm$ 61	9 - 156
ABN	3	5	223 $\pm$ 165	89 - 581
PBG	7	0	75 $\pm$ 25	43 - 116
<i>PBG0</i>	4	0	63 $\pm$ 16	43 - 77
<i>PBG1</i>	3	0	91 $\pm$ 29	60 - 116
<i>PBG2</i>	-	-	-	-

**Table 4.4.** Model selection of linear models for wing chord length (mm) and body mass (g) of 7-day old Dickcissel fledglings at Konza Prairie, Kansas (2015-2016). Model selection was based on the number of parameters ( $K$ ), Deviance,  $\Delta\text{AICc}$  values, and Akaike weights ( $w_i$ ). We considered models with fixed effects of the maximum number of host and cowbird nestlings combined, whether a nest was parasitized, or a combination of both effects, as well as an intercept-only model.

<b>Wing Chord - Model Structure</b>	<b><math>K</math></b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w_i</math></b>
Total Nestlings	3	108.41	115.74	0.00	0.536
Constant	2	113.27	117.90	2.16	0.182
Total Nestlings + Parasitism	4	108.01	118.37	2.62	0.144
Parasitism	3	111.99	119.32	3.58	0.090
Total Nestlings $\times$ Parasitism	5	106.79	120.54	4.80	0.049

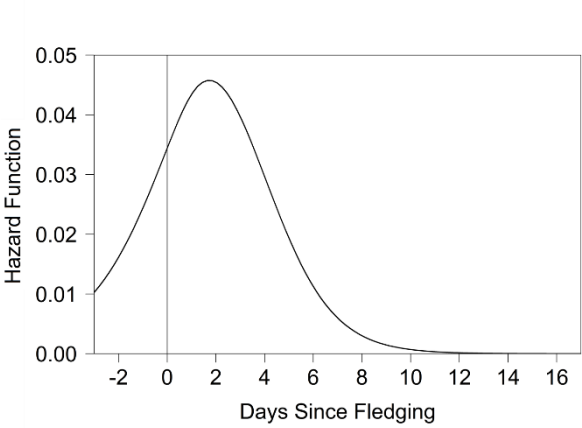
<b>Body Mass - Model Structure</b>	<b><math>K</math></b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta\text{AICc}</math></b>	<b><math>w_i</math></b>
Total Nestlings	3	97.25	104.29	0.00	0.579
Constant	2	102.25	106.75	2.46	0.169
Total Nestlings + Parasitism	4	96.97	106.79	2.50	0.166
Parasitism	3	102.17	109.21	4.92	0.049
Total Nestlings $\times$ Parasitism	5	96.95	109.80	5.51	0.037

**Figure 4.1.** Kaplan-Meier survival curves for Dickcissels fledglings at Konza Prairie, Kansas (2015-2016). We show survival curves for all fledglings (A), by management regime (B), grazing regime (C), or burning regime (D). Management regimes are labeled as follows: ABG = annually burned and grazed, ABN = annually burned and ungrazed, and PBG = patch-burn grazing.

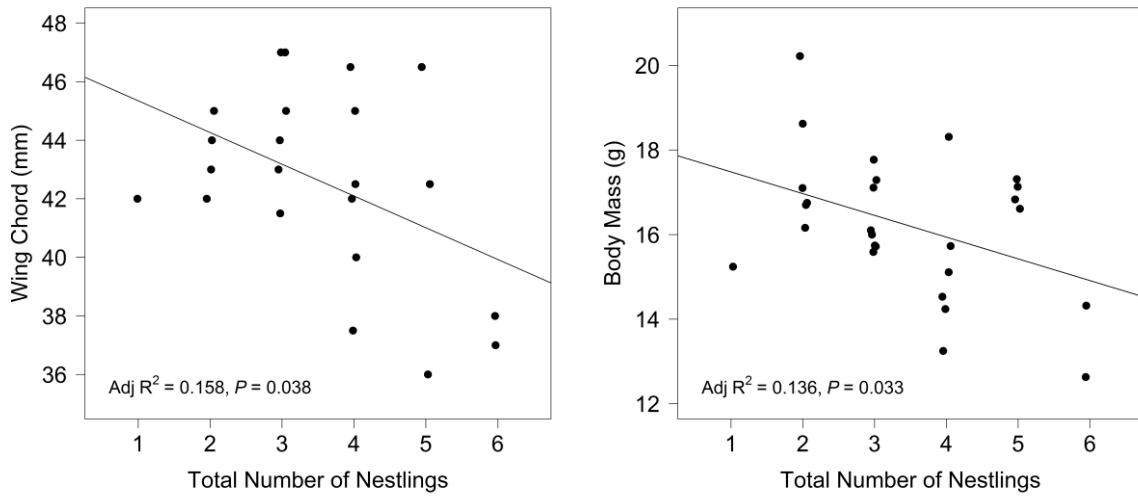




**Figure 4.2.** Hazard rate function for Dickcissel fledglings at Konza Prairie, Kansas (2015-2016).



**Figure 4.3.** Wing chord length (A) and body mass (B) of 7-day old Dickcissel nestlings at Konza Prairie, Kansas (2015-2016), in relation to the combined number of host and parasitic young in the brood. Fledgling occurs at 8-9 days of age.



## **Chapter 5 - Habitat guild drives variation in apparent survival of landbirds in the Great Plains**

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## Abstract

Many species of songbirds in the United States have shown widespread declines in population numbers during the last five decades. To understand ongoing declines and plan for conservation, researchers need reliable estimates of adult survival and site fidelity. However, variation in adult survival and site fidelity within and among species is substantial and could have consequences for management. Estimates of adult survival are lacking for many bird species and ecoregions, including the Great Plains. In this field study, we used Cormack-Jolly-Seber mark-recapture models to analyze encounter histories of 17 species of birds captured with a 13-year systematic mistnetting effort in northeast Kansas. We estimated annual rates of apparent adult survival ( $\phi$ ) corrected for the probability of capture ( $p$ ), and tested for effects of sex and breeding habitat guild. We present the first estimates of apparent survival for six species of songbirds, and the first estimates from the Great Plains for thirteen species. Apparent survival tended to be higher for males than for females, and we found a sex effect on the probability of capture for one species. Unexpectedly, grassland- and shrubland-breeding species had higher estimates of apparent survival than forest-breeding species. Our results did not support the prevailing viewpoint that birds breeding in dynamic landscapes, such as frequently burned grasslands, should show lower apparent survival than species that breed in woody habitats. We demonstrate that habitat plays an important role in the survival and site fidelity of songbirds, and that regional differences in habitat structure could drive variation in demography. Understanding the drivers of true survival and site fidelity of songbirds will allow region-specific management for species of conservation concern.

KEYWORDS: Cormack-Jolly-Seber models, habitat guilds, site fidelity, songbird, tallgrass prairie, woodpecker

## Introduction

Many bird species in North America are experiencing population declines in a wide variety of ecosystems including grasslands, shrublands and forests (Sauer and Link 2011, North American Bird Conservation Initiative 2016). Ongoing declines have been linked to habitat loss caused by land-use change and deforestation, agricultural intensification, and habitat fragmentation (Sampson and Knopf 1994, Robinson et al. 1995, Herkert et al. 2003). To address population declines and optimize conservation efforts, land managers need complete information on a species' annual cycle. Adult survival is one of the key demographic parameters in regulating population dynamics, and is especially important in declining populations of long-lived vertebrates, including many landbirds (Sæther and Bakke 2000, Crone et al. 2001, Clark and Martin 2007). Unfortunately, reliable estimates of adult survival are not available for many bird populations of conservation concern (Rodewald 2015). Return rates have been estimated for many bird species, but underestimate true survival, because they are also affected by variation in site fidelity, site propensity and probability of detection (Sandercock 2006). Apparent survival probabilities estimated by Cormack-Jolly-Seber (CJS) models for mark-recapture data are an improvement over return rates, but are still the product of true survival and site fidelity, and are best viewed as a minimum estimate of survival.

Return rates and estimates of apparent survival can be highly variable within and among bird species (Martin 1995, Rodewald 2015). For example, Grasshopper Sparrows (*Ammodramus savannarum*) have return rates that vary between 0% in the Sandhills of Nebraska (Kaspari and O'Leary 1988), and up to 50% in Connecticut (Vickery 1996), with intermediate values reported for populations in Maine, California and Kansas (Vickery 1996, Jones et al. 2007). Among- and within-species variation in return rates and estimates of

apparent survival has important consequences for conservation. Survival estimates from other species or even other populations of the same species may not be relevant for specific populations of conservation concern.

Variation in apparent survival might reflect differences in true survival among species or populations, but apparent survival rates are likely also affected by variation in site fidelity. Permanent emigration from a study site is often seen as a nuisance parameter that prevents estimation of true survival rates, but site fidelity is an important parameter when assessing population trends and planning management strategies. Among-species variation in apparent survival might be explained by ecological differences in diet or stability of breeding habitat, if site fidelity is lower among species that use ephemeral food resources or breed in annually dynamic habitats like grasslands, when compared to shrubland and forest habitats (Owens and Myers 1973, Andersson 1980, Jones et al. 2007, Schlossberg et al. 2009). Species or populations with high levels of site fidelity could be vulnerable to habitat destruction, and require different conservation strategies than vagile species with low site fidelity (Schlossberg et al. 2009).

Native grasslands in North America are dynamic ecosystems comprised of a mosaic of habitats. Habitat heterogeneity was historically maintained by annual variation in precipitation and pyric herbivory – the interaction between fire and selective grazing by native ungulates (Stebbins 1981, Knapp et al. 1998, Ahlering 2005). Since European settlement, grasslands are mostly maintained by prescribed fires and grazing by domestic cattle. Nevertheless, the quality of available habitat for grassland birds can still be variable among years, and is determined by the burning and grazing history of managed rangelands (Winter et al. 2005, Ahlering and Merkord 2016). Accordingly, birds breeding in grassland habitats generally have low return rates (2-30%; Balent and Norment 2003, Jones et al. 2007, Small et al. 2012).

In contrast to grasslands, shrubland and forest habitats are usually less dynamic. Succession of shrub habitat or early successional forests occurs at longer time-scales of decades, which exceeds the average lifespan of most small-bodied birds, and the slow growth of trees leads to long-term dynamics in forest ecosystems (Schlossberg et al. 2009). With the exception of large-scale masting events and other resources with a similar unpredictable availability, habitat structure and availability of food may be more predictable from year to year in shrubland and forest habitats, which favors a life history strategy with high site fidelity (Andersson 1980). Compared with grassland birds, higher return rates are common among bird species breeding in shrublands (mean = 35.3%, range = 20 – 52%) and forests (mean = 36.4%, range = 6 – 59%; Schlossberg et al. 2009).

The relationship between habitat stability and site fidelity may be more complex than has been previously appreciated. A majority of published return rates for shrubland- and forest-breeding birds have been estimated from field sites in temperate forest habitats of the east coast of the United States (Schlossberg et al. 2009), and may not be applicable to other ecoregions. Estimates of apparent survival of songbirds are not widely available for sites in the Great Plains, a stronghold for many grassland-breeding birds (Rodewald 2015).

Sexual differences are another source of variation in apparent survival, with males often having higher apparent survival than females. In birds, males might have higher true survival if reproductive costs are higher for females (Breitwisch 1989), or if females are relegated to lower quality habitats on wintering grounds (Ornat and Greenberg 1990, Marra 2000, Marra and Holmes 2001). However, males could also show higher apparent survival due to increased site fidelity, especially in species with male-territorial social systems (Schlossberg 2009). Males of migratory species often arrive earlier on the breeding grounds than females, and males of migratory and resident species compete for and actively defend territories on the breeding grounds (Ketterson and Nolan 1982, Francis and Cooke 1986,

Rodewald 2015). Female-biased breeding dispersal rates, where females show lower site fidelity than males, are common among territorial landbirds (Greenwood 1980, Payne and Payne 1993, Clarke et al. 1997, Cilimburg et al. 2002, Sillett and Holmes 2002). Despite sex-biases in apparent survival, field studies often focus solely on estimation of apparent survival males because of the difficulties in monitoring females (Fletcher et al. 2006, Sousa and Westneat 2013, Rodewald 2015). However, if males show higher site fidelity than females, movement patterns might differ substantially between sexes.

Here, we examine among- and within-species patterns in apparent survival for 17 species of small-bodied landbirds, using mark-recapture data from a 13-year study based on constant-effort systematic mistnetting at six banding stations in northeast Kansas that were part of the Monitoring Avian Productivity and Survivorship (MAPS) Program (DeSante et al. 2015). We compared estimates of apparent survival among species breeding in grassland, shrubland, and forest habitats based on standardized methods of the MAPS program, which facilitated direct comparison of estimates among habitat guilds. Temperate grasslands are thought to be more dynamic ecosystems than shrubland or forest habitats, and we predicted that apparent survival would be lower in grasslands if site fidelity was lower than in other habitats. We also assessed effects of sex on apparent survival and capture probability, and predicted that apparent survival would be higher for males than females, because most of our study species have male-territorial social systems.

## **Methods**

We conducted systematic mistnetting of small-bodied landbirds for 8 to 13 years per station at six MAPS banding stations at Fort Riley Military Reservation (hereafter Fort Riley) in northeast Kansas, USA (39° 15' N, 96° 50' W; see Table S1). Fort Riley is among the



largest remaining tracts of tallgrass prairie in the Flint Hills ecoregion, and is dominated by native grasslands (81%), interspersed by forest (16%) and shrubland habitats (3%, Hutchinson et al. 2015). The grassland plant community predominantly consists of warm-season grasses such as big bluestem (*Andropogon gerardii*), indiagrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*). Forests occur along low-lying streams and creeks, and are dominated by hackberry (*Celtis occidentalis*), green ash (*Fraxinus pennsylvanica*), black walnut (*Juglans nigra*), chinquapin oak (*Quercus muehlenbergii*), bur oak (*Q. macrocarpa*), and American elm (*Ulmus americana*). Shrubland communities are found along woodland edges and throughout the grassland landscape, and dominant species include rough-leafed dogwood (*Cornus drummondii*), wild plum (*Prunus americana*), smooth sumac (*Rhus glabra*), and buckbrush (*Symphoricarpos orbiculatas*; Althoff et al. 2006). Habitat management at Fort Riley includes mowing and haying, limited browsing by elk (*Cervus canadensis*), local timber harvest, and prescribed burning at two to three year intervals (Cully and Michaels 2000, Althoff et al. 2006).

Data at all six banding stations were collected following standardized MAPS protocols (DeSante et al. 2015). Each banding station consisted of ten mistnets, and stations were equally divided among grassland, shrubland and forest habitats. Stations were assumed to be independent, as the distance between adjacent stations was  $\geq 4$  km, which is substantially larger than the average territory size of many male songbirds ( $\sim 0.5$  ha; Jones 2011, Rodewald 2015). The total area of each mistnet grid averaged 4.7 hectares (range: 2.8 - 6.8 ha). Mistnets were operated once per week for two to three consecutive days during a seven to eight week period from early June till mid-August between 1993 and 2006 for a total of 8 to 13 years depending on the banding station (Table S1). Newly captured birds received a metal band with a unique number, and were identified to species, aged, and sexed by plumage or behavior (Pyle 1997). We assigned all species to one of three habitat guilds (grassland,

shrubland and forest habitat) based on species accounts in the Birds of North America series (Rodewald 2015). If a bird was recaptured, we recorded the metal band's unique number and released the bird at the capture site. Encounter histories for mark-recapture analyses for the 8 to 13-year study periods were coded as 1 for physical captures and 0 for not detected.

## **Statistical Analysis**

We analyzed encounter histories separately for each species with Cormack-Jolly-Seber models for live encounter data available in Program MARK (version 8.0, White and Burnham 1999), and tested for differences between males and females in apparent survival ( $\phi$ ) and capture probability ( $p$ ). Transient individuals can be common during systematic mistnetting of songbirds (Johnston et al. 1997, Sandercock and Jaramillo 2002), and we tested for a time-since-marking effect in our populations by classifying records as the first interval after the initial capture ( $\phi_1$ ) versus all subsequent intervals ( $\phi_{2+}$ ; Pradel et al. 1997). Lower estimates of apparent survival in the first interval after initial capture would indicate the possible presence of transients, and when time-since-marking effects are large it is best to use estimates of apparent survival from subsequent intervals for inference ( $\phi_{2+}$ , Sandercock 2006). In preliminary analyses, we found little support for time-since-marking effects on apparent survival of our study species ( $RI < 0.7$  for each species). Therefore, we reran a subset of models, and only considered possible sex effects on apparent survival and capture probability. We did not test for year effects because the capture data for a majority of species were too sparse, and we fixed the capture probability to zero for the last five years at four sites that were discontinued after 2002 (Table S1).

Our global model for all bird species contained sex dependence for apparent survival and capture probability ( $\phi_{sex}, p_{sex}$ ). We tested the fit of the global model for overdispersion in the data by estimating the variance-inflation factor ( $\hat{c}$ ) using the median c-hat procedure in

Program MARK. Candidate models were adjusted for  $\hat{c}$  and model selection criteria were based on adjusted QAIC<sub>c</sub> values. We fit all models with design matrices and a logit-link function. In the case of multiple parsimonious models ( $\Delta\text{QAIC}_c \leq 2$ ), we used model averaging based on QAIC<sub>c</sub> weights to calculate final parameter estimates and standard errors that accounted for both sampling and model-selection uncertainty. Species-specific apparent survival estimates were calculated for each sex.

We compared differences in mean apparent survival between sexes and among habitat guilds with Program Contrast (Hines and Sauer 1989). Program Contrast uses a  $\chi^2$  distribution, which is more appropriate than a z-distribution when comparing more than two groups of means (Sauer and Williams 1989). Moreover, Program Contrast uses the delta method to take the standard error of each apparent survival estimate into account when calculating the variance of groups of estimates. We conducted all  $\chi^2$  tests with a significance level of 0.05 and report mean estimates and standard errors.

## Results

Between 1993 and 2006, we captured a total of 5150 individuals of 73 different bird species. For this study, we examined the 17 most common species at our field site with more than 80 captures during our 13-year study period (Table 1). All other 56 species were infrequently trapped (<30 captures), and were not considered further. One Bell's Vireo was captured as an after-hatch-year (AHY) male in June 1994, and was caught again in June 2002, thereby setting a longevity record for this species of a minimum age of nine years and zero months (Sauer et al. 2014). The three habitat guilds of our study species included three grassland species, six shrubland species, and eight forest species (Table 1).

## Model Selection

In 12 of 17 species, a sex effect on apparent survival was supported by the top model set of equally parsimonious models ( $\Delta\text{QAIC}_c < 2$ ). A sex effect on the capture probability was found in the top model set of 13 species, and a sex effect on both apparent survival and capture probability was found in 10 out of 17 species (Table 2). The median estimate of apparent survival for all 17 species was  $\phi = 0.397$  for males (range = 0.066 – 0.697) and  $\phi = 0.335$  for females (range = 0.073 – 0.580; Figs. 1A-2A, and Table S2). In general, apparent survival estimates tended to be higher for males than females (14 of 17 species), with a median difference in apparent survival of +0.053 between males and females (range = -0.060 – 0.357). However, the relative importance (RI) of sex-dependence in apparent survival did not exceed 0.80 for any species. Likewise, when comparing sex differences in apparent survival across all 17 species, apparent survival was not significantly higher for males than females ( $\chi^2 = 1.377$ ,  $df = 1$ ,  $P = 0.24$ ).

## Habitat Guild

When apparent survival estimates were pooled across sexes for each species, apparent survival differed significantly among habitat guilds ( $\chi^2 = 6.372$ ,  $df = 2$ ,  $P = 0.041$ ).

Unexpectedly, apparent survival was lower among bird species associated with forest habitats ( $\phi = 0.292 \pm 0.019\text{SE}$ ), than species associated with shrublands ( $0.453 \pm 0.022$ ;  $\chi^2 = 4.447$ ,  $df = 1$ ,  $P = 0.035$ ) or grasslands ( $0.468 \pm 0.040$ ;  $\chi^2 = 3.976$ ,  $df = 1$ ,  $P = 0.046$ ; see Fig. 2B).

## Probability of Capture

Annual capture probabilities were generally low and variable among species for males (median  $p = 0.292$ , range = 0.049 – 0.574) and females (median  $p = 0.256$ , range = 0.120 – 0.582; Fig. 1B, and Table S2). Sex was an important factor influencing the capture probability

of Grasshopper Sparrows (RI = 1.00), where males were captured at roughly four times higher rates than females ( $p_{\text{males}} = 0.464 \pm 0.091$ , and  $p_{\text{females}} = 0.120 \pm 0.082$ ). There were no sex differences in capture probability for the other sixteen species of birds (RI < 0.80).

## Discussion

Here, we present annual estimates of apparent survival for 17 small-bodied bird species, including the first estimates of apparent survival for six species, and the first estimates for 13 species from a site in the Great Plains. We followed the standardized protocols for systematic mistnetting of the MAPS program, which facilitated direct comparison of estimates of demographic parameters among bird species. Among species variation in apparent survival was best explained by avian guilds based on breeding habitat, where we unexpectedly found higher apparent survival among shrubland and grassland birds than in forest species. Apparent survival estimates of our species showed considerable spatial variation in apparent survival compared to other published studies (Fig. 3 and Table S3), which could be attributed to differences in true survival or site fidelity. We conclude that features of breeding habitat can explain patterns of apparent survival among species but are region-specific, and that regional conservation efforts require an improved understanding of survival and site fidelity of birds.

### Sex differences

In our sample of 17 species of terrestrial birds, we found no evidence that apparent survival was higher for males than females. A potential sex-bias in apparent survival could have important implications for conservation, because it could indicate lower site fidelity among females, which could have large consequences when studying dispersal movements of a

species. On the other hand, a sex-bias in apparent survival that is caused by variation in true survival could result in overly optimistic population models if based on the apparent survival of males instead of females (Fletcher et al. 2006). The lack of evidence for a sex-bias in apparent survival in our study suggests that the use of male apparent survival might still be appropriate for models of dispersal movements or population viability.

### **Habitat Guilds**

Apparent survival of species differed among breeding habitat guilds. Apparent survival was unexpectedly higher for grassland and shrubland species than for forest species, despite an expectation for higher inter-annual stability of vegetative structure in forest habitats (Owens and Myers 1973, Andersson 1980, Jones et al. 2007, Schlossberg 2009).

Estimates of apparent survival for grassland songbirds in our study (median = 0.434, range = 0.427 – 0.542) were higher than many of the low return rates and apparent survival rates previously reported in the literature (Jones et al. 2007), but were comparable to survival estimates of small-bodied birds in general (0.40 – 0.60; Martin 1995). Estimates of apparent survival for forest species in our study (median = 0.311, range = 0.069 – 0.381) were generally lower than published estimates of return rates or apparent survival (mean = 0.364; Schlossberg 2009).

Differences between our estimates of apparent survival from CJS models and previously published estimates might be explained by geographic location and landscape configuration of our field site (Fig. 3 and Table S3). Forest habitats in the Great Plains are more naturally fragmented, and potentially of lower quality, than the contiguous tracts of forest found in the eastern United States, where many survival estimates for forest birds have been taken (Schlossberg 2009). The opposite is true for grasslands, as our study was conducted in the Flint Hills, one of the largest remaining tracts of tallgrass prairie (Knapp and

Seastedt 1998, With et al. 2008). The remaining grasslands in the eastern United States are often small and isolated (Stauffer et al. 2011). Contiguous grasslands in the Flint Hills may be relatively stable habitat, as the prevailing viewpoint that grasslands are dynamic landscapes is based on annual changes of grasslands at small spatial scales.

Small and fragmented habitat patches negatively influence breeding birds in many ways. When compared to continuous stretches of habitat, birds breeding in small and fragmented patches may have lower pairing success (Bayne and Hobson 2001, Lee et al. 2002), higher parasitism rates by Brown-headed Cowbirds (Donovan et al. 1997, Chalfoun et al. 2002, Chase et al. 2005), higher nest predation rates and predator activity (Donovan et al. 1997, Dijak and Thompson 2000, Chalfoun et al. 2002, Herkert et al. 2003), and in some cases, lower abundance of arthropods and other food resources (Van Wilgenburg et al. 2001, Zquette et al. 2002, but see Nour et al. 1998). Higher nest parasitism and predation rates, or lower food availability may decrease nest success, and many bird species are less likely to return to their breeding site after a failed nest attempt (Roth and Johnson 1993, Haas 1998, Bayne and Hobson 2002). Thus, low true survival and breeding site fidelity will result in lower apparent survival in small fragmented forest patches, which may explain the higher apparent survival of grassland birds and lower apparent survival of forest birds in our study compared to previous studies.

A second difference between our estimates of apparent survival for landbirds in the Great Plains and published estimates is that our field site was in the core of the distribution of grassland species but at the edge of the distribution of forest species. The relative location of a population within the entire range of a species could affect both true survival and site fidelity. Population abundance may be lower at the edge than the core of a species range, and dispersing individuals at the margin of a species range might be of lower quality than resident individuals from the core (Channell and Lomolino 2000, Yackulic et al. 2011). Both bird

density and individual quality could impact true survival and site fidelity, but effects might differ between the core and the periphery of a species range. Future research should therefore aim to disentangle the relationship between habitat quality and absolute spatial location within a species distribution, and possible effects on survival and site fidelity.

### **Probability of Capture**

Capture probabilities varied considerably among species and we were only able to recapture roughly one third of the birds available for capture in a given year with systematic mistnetting. Capture probabilities in this study were relatively low ( $p = 0.26 - 0.29$ ) compared to focal field studies that use target mistnetting of songbirds during the breeding season ( $p = 0.30 - 0.53$ ; Mazzerolle et al. 2005, Saracco et al. 2012).

Capture probabilities from the MAPS protocol for systematic mistnetting may be low for several reasons. First, our mistnetting grids were relatively limited in area and therefore in the number of bird territories that were covered. The territories of some birds only partly overlapped, or merely bordered our grids, which could lead to heterogeneity in the probability of capture. Second, we did not use play-backs in this study, but use of song recordings can increase capture probability, especially among territorial males (Sillett and Holmes 2002). The use of mistnets without playbacks might explain why we did not find sex effects on capture probability for any study species. In one exception, we found a sex-bias in capture probability in Grasshopper Sparrows, where the capture probability of males was roughly four times higher than that of females, which may be due to unusual levels of within-season breeding dispersal in this species (W.A. Boyle, pers. comm.). Last, our encounter histories were based on physical captures only. Even with 8 to 13-years of systematic mistnetting, the limited number of captures and recaptures prevented us from estimating survival estimates for more than 17 species of birds. We therefore recommend the use of play-backs and color



bands, and active resighting or recapturing of birds to increase the number of captures and subsequent detections.

## **Conclusion**

Here, we show that the relationship between apparent survival of birds and the stability of breeding habitat is more complex than was previously appreciated. Contrary to the prevailing viewpoint, grassland birds had relatively high apparent survival and therefore likely showed considerable site fidelity at our study site. Moreover, forest breeding species had lower survival or site fidelity, even though woodlands are a relatively stable breeding habitat. The differences between our new estimates and published estimates from other regions indicate that landscape-scale habitat stability and fragmentation may drive local apparent survival, which has not been previously recognized. Regional variation in apparent survival provides an interesting challenge for conservationists, and understanding the drivers of true survival and site fidelity of birds will be necessary for effective region-specific management.

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**Table 5.1.** Common names, scientific names, species codes, and number of captures and recaptures for 17 species of landbirds monitored at six MAPS stations at Fort Riley Military Reservation, northeast Kansas, between 1993 and 2006.

Common Name	Scientific Name	AOU-Code	Male		Female	
			Captures	Recaptures	Captures	Recaptures
<i>Forest Habitat</i>						
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	33	2	72	3
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	28	8	74	1
House Wren	<i>Troglodytes aedon</i>	HOWR	64	9	215	4
Orchard Oriole	<i>Icterus spurius</i>	OROR	42	1	55	1
Baltimore Oriole	<i>Icterus galbula</i>	BAOR	41	2	64	2
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	58	10	134	7
Indigo Bunting	<i>Passerina cyanea</i>	INBU	101	10	155	14
American Goldfinch	<i>Spinus tristis</i>	AMGO	98	6	83	6
<i>Shrubland Habitat</i>						
Bell's Vireo	<i>Vireo bellii</i>	BEVI	98	9	83	5
Gray Catbird	<i>Dumetella carolinensis</i>	GRCA	239	50	625	36
Brown Thrasher	<i>Toxostoma rufum</i>	BRTH	53	8	67	0
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE	155	20	85	5
Yellow Warbler	<i>Setophaga petechia</i>	YEWA	60	12	70	8
Field Sparrow	<i>Spizella pusilla</i>	FISP	89	14	105	1
<i>Grassland Habitat</i>						
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	44	2	127	12
Grasshopper Sparrow	<i>Ammodramus savannarum</i>	GRSP	130	34	316	8
Dickcissel	<i>Spiza americana</i>	DICK	197	16	146	1

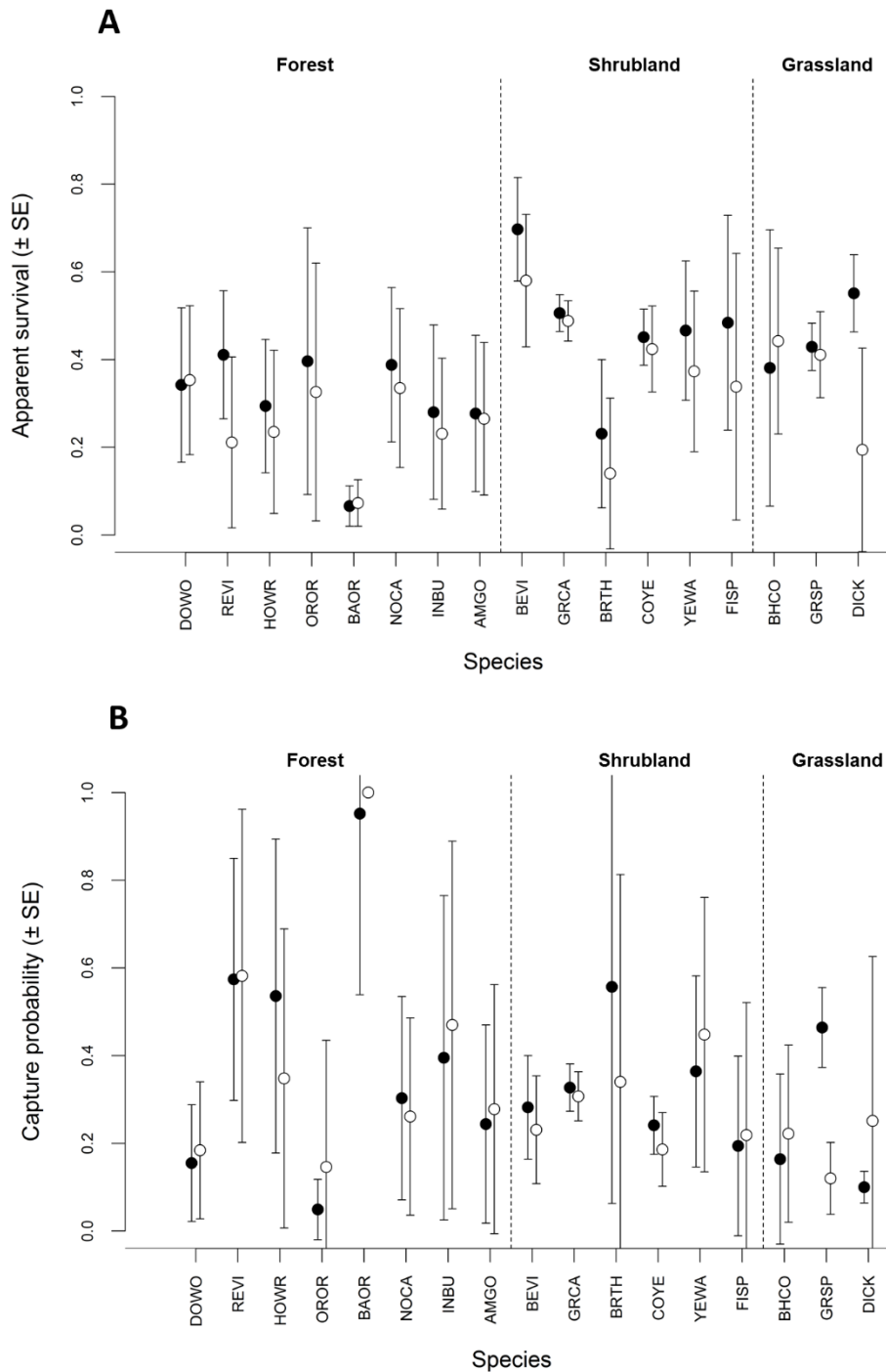
**Table 5.2.** Cormack-Jolly-Seber (CJS) model selection results for 17 bird species captured at six MAPS stations in Fort Riley Military Reservation, northeast Kansas, between 1993 and 2006. CJS models estimate apparent survival ( $\phi$ ) and probability of capture ( $p$ ). Model selection was based on the number of parameters (K), Deviance,  $\Delta\text{QAIC}_c$  values, and Akaike weights ( $w_i$ ). Parameters were modeled as sex-dependent (sex) or constant (con). Only models with  $\Delta\text{QAIC}_c < 2$  are shown. Estimates of  $\hat{c}$  were  $< 4.5$  for all species, except Yellow Warbler (5.6), Brown-headed Cowbird (6.2), Field Sparrow (8.0), and Indigo Bunting (8.6).

Common Name	Model Structure		Model Statistics			
	$\phi$	$p$	K	Deviance	$\Delta\text{QAIC}_c$	$w_i$
<i>Forest Habitat</i>						
Downy Woodpecker	con	con	2	24.76	0.000	0.530
	con	sex	3	24.39	1.841	0.211
Red-eyed Vireo	sex	con	3	21.40	0.000	0.342
	con	con	2	24.06	0.365	0.285
	con	sex	3	21.89	0.486	0.268
House Wren	con	con	2	18.38	0.000	0.341
	con	sex	3	16.54	0.247	0.301
	sex	con	3	16.89	0.603	0.252
Orchard Oriole	con	con	2	17.30	0.000	0.533
Baltimore Oriole	con	con	2	10.13	0.000	0.559
Northern Cardinal	con	con	2	16.86	0.000	0.472
	sex	con	3	16.18	1.403	0.234
	con	sex	3	16.37	1.594	0.213
Indigo Bunting	con	con	2	7.58	0.000	0.511
	sex	con	3	7.35	1.818	0.206
American Goldfinch	con	con	2	17.15	0.000	0.535
	con	sex	3	17.08	1.992	0.198
<i>Shrubland Habitat</i>						
Bell's Vireo	sex	con	3	48.87	0.000	0.351
	con	con	2	51.34	0.306	0.301
	con	sex	3	49.74	0.869	0.227
Gray Catbird	con	con	2	219.90	0.000	0.419
	sex	con	3	218.93	1.058	0.247
	con	sex	3	219.01	1.137	0.237
Brown Thrasher	con	con	2	6.67	0.000	0.347
	con	sex	3	4.92	0.422	0.281
	sex	con	3	4.92	0.422	0.281
Common Yellowthroat	con	con	2	101.02	0.000	0.334
	con	sex	3	99.01	0.047	0.326
	sex	con	3	99.77	0.802	0.224
Yellow Warbler	con	con	2	17.84	0.000	0.468
	sex	con	3	17.11	1.366	0.236
Field Sparrow	con	con	2	8.74	0.000	0.423
	sex	con	3	7.68	1.030	0.253
	con	sex	3	7.82	1.167	0.236
<i>Grassland Habitat</i>						
Brown-headed Cowbird	con	con	2	12.38	0.000	0.462
	con	sex	3	11.64	1.346	0.235

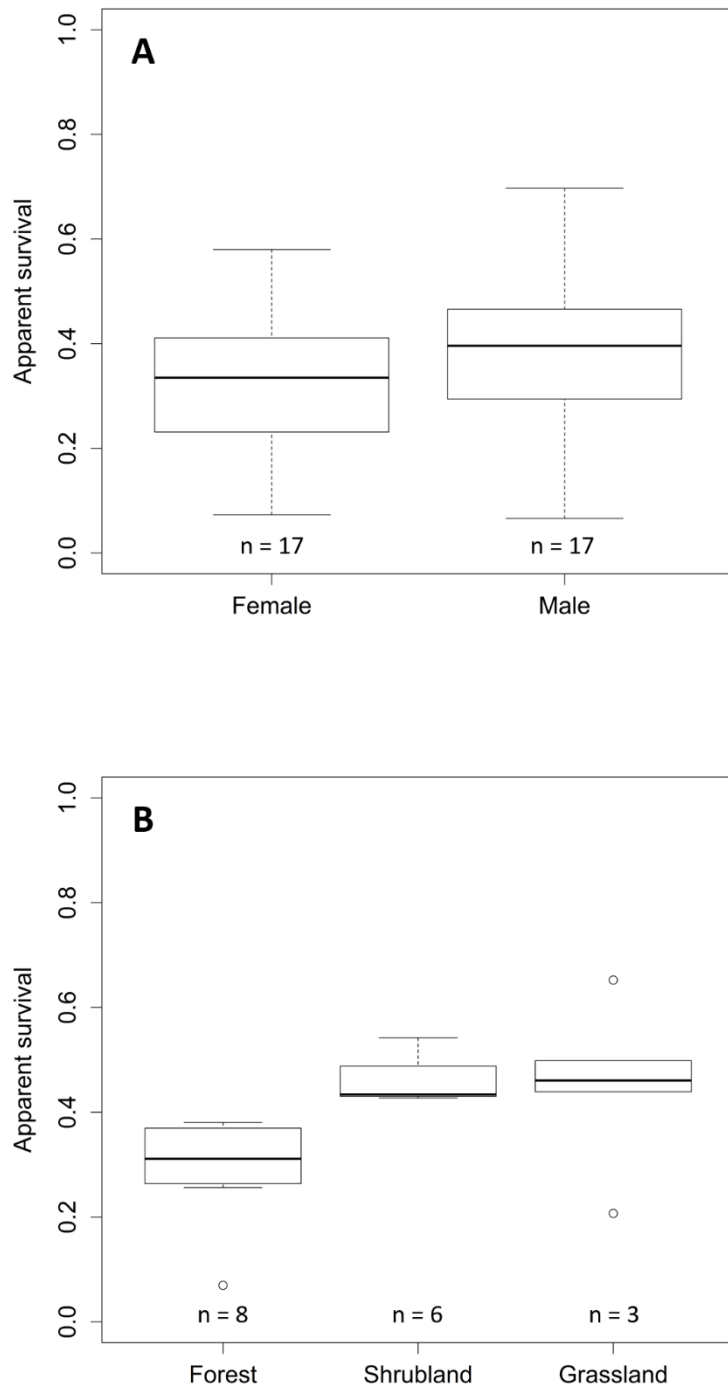
	sex	con	3	11.77	1.473	0.221
Grasshopper Sparrow	con	sex	3	91.22	0.000	0.697
Dickcissel	sex	con	3	65.94	0.000	0.517
	con	sex	3	67.14	1.200	0.284
	sex	sex	4	65.81	1.922	0.198



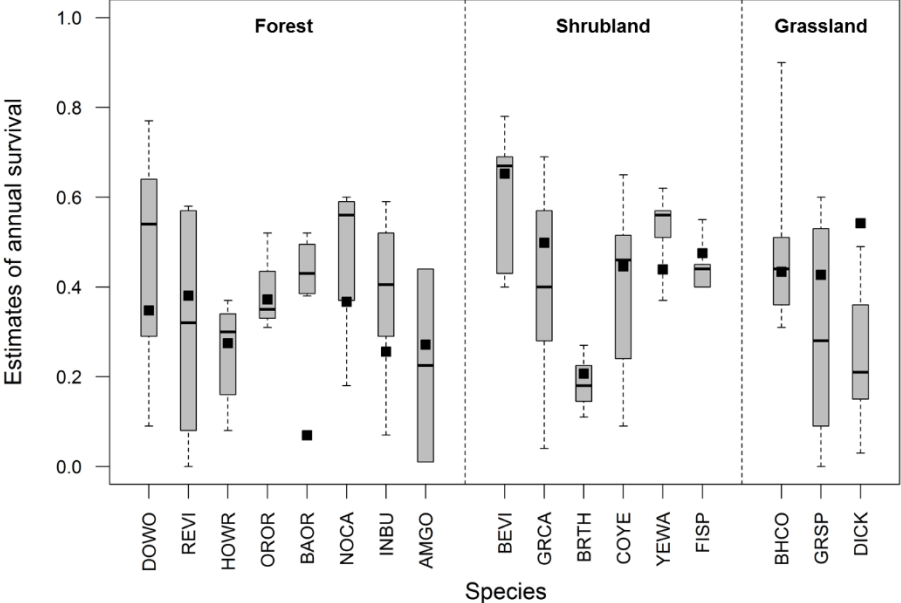
**Figure 5.1.** Estimates of A) apparent survival ( $\phi$ ), and B) probability of capture ( $p$ ) for 17 bird species captured at six MAPS banding stations in Fort Riley Military Reservation, northeast Kansas, between 1993 and 2006. Estimates are shown separately for males (black circles) and females (open circles), with  $\pm 1$  standard error. Sample sizes of marked birds are reported in Table 5.1.



**Figure 5.2.** Range of annual estimates of apparent survival by (A) sex, and (B) habitat guild for 17 bird species that were captured at six MAPS banding stations in Fort Riley Military Reservation, northeast Kansas, between 1993 and 2006.



**Figure 5.3.** Published estimates of return rates and apparent survival for the 17 bird species considered in this study (Table S3). Black squares denote new estimates of apparent survival for 17 bird species that were captured at six MAPS banding stations in Fort Riley Military Reservation, northeast Kansas, between 1993 and 2006 (this study).



**Supplemental Table 5.1.** Site names, geographic coordinates, years of banding activity, and habitat descriptions for six MAPS banding stations at Fort Riley Military Reservation in northeast Kansas, USA.

<b>Site</b>	<b>Latitude</b>	<b>Longitude</b>	<b>Years Active</b>	<b>No. of Years</b>	<b>Habitat</b>
Estes Draw	39.11139	-96.82861	1994 - 2002	9	Riparian Forest / Grassland
Kansas River	39.05583	-96.79083	1993 - 2002	10	Deciduous Forest
Myersdale Prairie	39.22611	-96.94000	1994 - 2006	13	Grassland
Richardson's Posts	39.16278	-96.81000	1994 - 2006	13	Grassland
Timber Creek	39.29111	-96.95917	1993 - 2002	10	Deciduous Forest / Old Field
Three Mile Creek	39.09500	-96.74611	1995 - 2002	8	Deciduous Forest

**Supplemental Table 5.2.** Estimates of apparent survival ( $\phi \pm 1$  SE) and probability of capture ( $p \pm 1$  SE) based on model averaging of all potential models for 17 bird species captured at six MAPS stations in Fort Riley Military Reservation, northeast Kansas, between 1993 and 2006. Parameter estimates are presented separately for females (F) and males (M). Scientific names of bird species are given in Table 5.1.

<b>Species</b>	<b>Sex</b>	<b><math>\phi \pm</math> SE</b>	<b><math>p \pm</math> SE</b>
<i>Forest Habitat</i>			
Downy Woodpecker	F	0.353 $\pm$ 0.170	0.184 $\pm$ 0.156
	M	0.342 $\pm$ 0.176	0.155 $\pm$ 0.133
Red-eyed Vireo	F	0.211 $\pm$ 0.195	0.582 $\pm$ 0.380
	M	0.411 $\pm$ 0.146	0.574 $\pm$ 0.276
House Wren	F	0.235 $\pm$ 0.186	0.348 $\pm$ 0.341
	M	0.294 $\pm$ 0.152	0.536 $\pm$ 0.358
Orchard Oriole	F	0.326 $\pm$ 0.294	0.146 $\pm$ 0.289
	M	0.396 $\pm$ 0.304	0.049 $\pm$ 0.069
Baltimore Oriole	F	0.073 $\pm$ 0.053	1.000 $\pm$ 0.000
	M	0.066 $\pm$ 0.046	0.952 $\pm$ 0.413
Northern Cardinal	F	0.335 $\pm$ 0.181	0.261 $\pm$ 0.225
	M	0.388 $\pm$ 0.176	0.303 $\pm$ 0.232
Indigo Bunting	F	0.231 $\pm$ 0.172	0.470 $\pm$ 0.419
	M	0.280 $\pm$ 0.199	0.395 $\pm$ 0.370
American Goldfinch	F	0.265 $\pm$ 0.174	0.278 $\pm$ 0.284
	M	0.277 $\pm$ 0.178	0.244 $\pm$ 0.226
<i>Shrubland Habitat</i>			
Bell's Vireo	F	0.580 $\pm$ 0.151	0.231 $\pm$ 0.123
	M	0.697 $\pm$ 0.118	0.282 $\pm$ 0.118
Gray Catbird	F	0.488 $\pm$ 0.046	0.307 $\pm$ 0.056
	M	0.506 $\pm$ 0.042	0.327 $\pm$ 0.054
Brown Thrasher	F	0.140 $\pm$ 0.172	0.340 $\pm$ 0.473
	M	0.231 $\pm$ 0.169	0.557 $\pm$ 0.494
Common Yellowthroat	F	0.424 $\pm$ 0.098	0.186 $\pm$ 0.084
	M	0.451 $\pm$ 0.064	0.241 $\pm$ 0.066
Yellow Warbler	F	0.373 $\pm$ 0.183	0.448 $\pm$ 0.313
	M	0.466 $\pm$ 0.159	0.364 $\pm$ 0.218
Field Sparrow	F	0.338 $\pm$ 0.304	0.219 $\pm$ 0.302
	M	0.484 $\pm$ 0.245	0.194 $\pm$ 0.205
<i>Grassland Habitat</i>			
Brown-headed Cowbird	F	0.442 $\pm$ 0.212	0.222 $\pm$ 0.202
	M	0.381 $\pm$ 0.315	0.164 $\pm$ 0.194
Grasshopper Sparrow	F	0.411 $\pm$ 0.098	0.120 $\pm$ 0.082
	M	0.429 $\pm$ 0.054	0.464 $\pm$ 0.091
Dickcissel	F	0.194 $\pm$ 0.232	0.251 $\pm$ 0.375
	M	0.551 $\pm$ 0.088	0.100 $\pm$ 0.036

**Supplemental Table 5.3.** Published estimates of annual survival based on return rates (R.R.), modified return rates (R.R.<sup>+</sup>), and apparent survival ( $\phi$ ) for 17 species of landbirds, associated with forest, shrubland, and grassland habitats. Data include the location of estimates, standard errors (SE), sex (M = male, F = female, MF = both sexes pooled), the number of birds captured during the study, duration of the banding effort, and published source for each field study. Modified return rates were based on multiple years of returns or controlled for age structure in the population, and were an improvement over standard return rates. Apparent survival estimates were calculated with Cormack-Jolly-Seber models.

Species	Location	Estimate	SE	Type	Sex	No. Birds	No. Years	Years	Source
<i>Forest Habitat</i>									
Downy	Kansas	0.54	N/A	R.R.	MF	136	10	1972 - 1981	Forde and Sloan 1984
Woodpecker	Pennsylvania	0.09	N/A	R.R.	MF	75	10	1978 - 1987	Rollfinke et al. 1990
	Maryland	0.64	0.07	$\phi$	MF	27	8	1980 - 1987	Karr et al. 1990
	Northeast USA	0.77	0.14	$\phi$	MF	201	5	1992 - 1996	DeSante et al. 1998
	South-Central USA	0.71	0.24	$\phi$	MF	87	5	1992 - 1996	DeSante et al. 1998
	Northwest USA	0.20	0.12	$\phi$	MF	141	5	1992 - 1996	DeSante et al. 1998
	Ohio	0.26	0.11	$\phi$	MF	404	6	1994 - 1999	Doherty and Grubb 2002
	Arizona	0.58	0.09	$\phi$	F	N/A	6	1994 - 1999	Clark and Martin 2007
	Wisconsin	0.51	0.09	$\phi$	MF	12	8	2006 - 2013	Cava et al. 2014
	Red-eyed Vireo	Pennsylvania	0.08	N/A	R.R.	MF	108	10	1978 - 1987
Vireo	Illinois	0.00	N/A	R.R.	M	2	2	1985 - 1986	Robinson 1992
	Ontario	0.11	N/A	R.R.	MF	109	2	2007 - 2008	Walters and Nol 2011
	Pennsylvania	0.53	N/A	R.R. <sup>+</sup>	MF	44	6	1962 - 1967	Savidge and Davis 1974
	New Hampshire	0.57	N/A	$\phi$	MF	201	10	1969 - 1978	Nichols et al. 1981
	Maryland	0.58	N/A	$\phi$	MF	896	12	1959 - 1970	Nichols et al. 1981
House Wren	USA	0.30	N/A	R.R.	MF	N/A	N/A	N/A	Martin 1995
	Illinois	0.21	N/A	R.R.	F	1219	7	1980 - 1986	Drilling and Thompson 1988

	Illinois	0.37	N/A	R.R.	M	547	7	1980 - 1986	Drilling and Thompson 1988 Czapka and Johnson 2000
	Wyoming	0.31	N/A	R.R.	F	185	2	1996 - 1997	
	Washington DC	0.08	0.04	R.R.	F	191	11	2000 - 2010	Evans et al. 2015
	Washington DC	0.11	0.02	R.R.	M	432	11	2000 - 2010	Evans et al. 2015
	Arizona	0.37	0.09	ϕ	F	N/A	6	1994 - 1999	Clark and Martin 2007
Orchard Oriole	USA	0.52	N/A	R.R. <sup>a</sup>	M	23	16	1960 - 1975	Searcy and Yasukawa 1981 Dowling and Omland 2009
	Maryland	0.35	N/A	R.R.	MF	78	4	2002 - 2005	
	Nebraska	0.31	N/A	R.R.	MF	989	4	1992 - 1995	Rodewald 2015
Baltimore Oriole	USA	0.47	N/A	R.R. <sup>a</sup>	F	87	16	1960 - 1975	Searcy and Yasukawa 1981
	USA	0.39	N/A	R.R. <sup>a</sup>	M	170	16	1960 - 1975	Searcy and Yasukawa 1981
	USA	0.52	N/A	R.R. <sup>b</sup>	M	27	16	1960 - 1975	Searcy and Yasukawa 1981
	Maryland	0.38	N/A	R.R.	MF	53	4	2002 - 2005	Dowling and Omland 2009
Northern Cardinal	Pennsylvania	0.18	N/A	R.R.	MF	95	10	1978 - 1987	Rollfinke et al. 1990
	Maryland	0.60	0.06	ϕ	MF	258	8	1980 - 1987	Karr et al. 1990
	Louisiana	0.37	0.02	ϕ	MF	183	2	2010 - 2011	Wolfe et al. 2013
	Washington DC	0.56	0.04	ϕ	F	402	11	2000 - 2010	Evans et al. 2015
	Washington DC	0.59	0.02	ϕ	M	603	11	2000 - 2010	Evans et al. 2015
Indigo Bunting	Pennsylvania	0.07	N/A	R.R.	MF	179	10	1978 - 1987	Rollfinke et al. 1990
	Ohio	0.29	N/A	R.R.	MF	280	5	2002 - 2006	Lehnen 2008
	Michigan	0.34	0.04	R.R. <sup>+</sup>	F	226	12	1979 - 1990	Payne and Payne 1990

	Michigan	0.47	0.02	R.R. <sup>+</sup>	F	243	12	1979 - 1990	Payne and Payne 1990
	Michigan	0.52	0.02	R.R. <sup>+</sup>	M	260	12	1979 - 1990	Payne and Payne 1990
	Michigan	0.59	0.02	R.R. <sup>+</sup>	M	215	12	1979 - 1990	Payne and Payne 1990
American Goldfinch	Pennsylvania	0.01	N/A	R.R.	MF	77	10	1978 – 1987	Rollfinke et al. 1990
	Maryland	0.44	0.04	φ	MF	2253	8	1980 – 1987	Karr et al. 1990
<i>Shrubland Habitat</i>									
Bell's Vireo	California <sup>e</sup>	0.66	N/A	R.R.	MF	49	2	2006 - 2007	Kus et al. 2010
	California <sup>e</sup>	0.69	N/A	R.R.	MF	61	2	2006 - 2007	Kus et al. 2010
	California <sup>e</sup>	0.40	N/A	R.R.	MF	77	2	2007 - 2008	Kus et al. 2010
	California <sup>e</sup>	0.78	N/A	R.R.	MF	58	2	2007 - 2008	Kus et al. 2010
	Missouri	0.43	0.07	φ	F	31	3	1996 – 1998	Budnik et al. 2000
	Missouri	0.68	0.05	φ	M	71	3	1996 - 1998	Budnik et al. 2000
Gray Catbird	Ontario	0.40	N/A	R.R.	F	67	4	1963 - 1966	Darley et al. 1977
	Ontario	0.54	N/A	R.R.	M	59	4	1963 - 1966	Darley et al. 1977
	Pennsylvania	0.09	N/A	R.R.	MF	697	10	1978 - 1987	Rollfinke et al. 1990
	Ohio	0.04	N/A	R.R.	MF	189	5	2002 - 2006	Lehnen 2008
	Pennsylvania	0.69	N/A	R.R. <sup>+</sup>	MF	27	6	1962 - 1967	Savidge and Davis 1974
	Western Midwest, USA	0.63	0.05	φ	MF	564	6	1994 - 1999	DeSante et al. 2001
	Eastern Midwest, USA	0.28	0.04	φ	MF	527	6	1994 - 1999	DeSante et al. 2001
	Washington DC	0.32	0.06	φ	F	329	11	2000 - 2010	Evans et al. 2015
	Washington DC	0.57	0.03	φ	M	646	11	2000 - 2010	Evans et al. 2015
Brown Thrasher	North Dakota	0.18	N/A	R.R.	F	154	6	1984 - 1989	Haas 1998
	North Dakota	0.27	N/A	R.R.	M	149	6	1984 - 1989	Haas 1998
	Louisiana	0.11	0.09	φ	MF	29	2	2010 - 2011	Wolfe et al. 2013



Common										Anderson and
Yellowthroat	Massachusetts	0.16	N/A	R.R.	MF	179	6	1960 - 1965		Maxfield 1967
	Pennsylvania	0.09	N/A	R.R.	MF	140	10	1978 - 1987		Rollfinke et al. 1990
	Ohio	0.32	N/A	R.R.	MF	128	5	2002 - 2006		Lehnen 2008
	Wisconsin	0.65	N/A	R.R.	M	43	4	2002 - 2005		Dunn et al. 2012
	Massachusetts	0.54	N/A	R.R. <sup>+</sup>	MF	179	6	1960 - 1965		Roberts 1971
	USA	0.46	0.30 - 0.57 <sup>h</sup>	φ	F	12110 <sup>g</sup>	12	1992 - 2003		Sarraco et al. 2012
	USA	0.49	0.41 - 0.63 <sup>h</sup>	φ	M	12110 <sup>g</sup>	12	1992 - 2003		Sarraco et al. 2012
Yellow	Ontario	0.53	0.02	R.R. <sup>+</sup>	MF	208	7	1958 - 1964		Roberts 1971
Warbler	Ontario	0.62	N/A	φ	MF	208	7	1958 - 1964		Nichols et al. 1981
	Montana	0.51	0.06	φ	F	149	5	1995 - 1999		Cilimburg et al. 2002
	Montana	0.59	0.07	φ	M	287	5	1995 - 1999		Cilimburg et al. 2002
	Manitoba	0.41 - 0.62	0.07 - 0.08	φ	F	166	9	1993 - 2001		Mazerolle et al. 2005
	Manitoba	0.48 - 0.60	0.05 - 0.06	φ	M	215	9	1993 - 2001		Mazerolle et al. 2005
	Southern New England	0.56	0.07	φ	MF	139	12	1992 - 2003		Saracco et al. 2008
	Great Lakes Plain	0.48	0.02	φ	MF	1301	12	1992 - 2003		Saracco et al. 2008
	St. Lawrence River Plain	0.57	0.03	φ	MF	350	12	1992 - 2003		Saracco et al. 2008
	Allegheny Plateau	0.37	0.10	φ	MF	243	12	1992 - 2003		Saracco et al. 2008
	Northern Spruce-Hardwoods	0.38	0.06	φ	MF	181	12	1992 - 2003		Saracco et al. 2008
	Aspen Parklands	0.19	0.04	φ	MF	205	12	1992 - 2003		Saracco et al. 2008
	Southern Rockies	0.59	0.02	φ	MF	1513	12	1992 - 2003		Saracco et al. 2008
	Central Rockies	0.56	0.03	φ	MF	468	12	1992 - 2003		Saracco et al. 2008

	Dissected Rockies	0.60	0.03	φ	MF	578	12	1992 - 2003	Saracco et al. 2008
	Sierra Nevada	0.55	0.03	φ	MF	636	12	1992 - 2003	Saracco et al. 2008
	Cascade Mountains	0.57	0.04	φ	MF	211	12	1992 - 2003	Saracco et al. 2008
	Pitt-Klamath Plateau	0.57	0.04	φ	MF	368	12	1992 - 2003	Saracco et al. 2008
	Wyoming Basin	0.59	0.02	φ	MF	918	12	1992 - 2003	Saracco et al. 2008
	Basin and Range	0.52	0.03	φ	MF	1005	12	1992 - 2003	Saracco et al. 2008
	Southern Pacific Rainforests	0.56	0.03	φ	MF	758	12	1992 - 2003	Saracco et al. 2008
Field Sparrow	Illinois	0.44	N/A	R.R.	M	25	2	1971 - 1972	Best 1977
	Pennsylvania	0.17	N/A	R.R.	MF	95	10	1978 - 1987	Rollfinke et al. 1990
	New York	0.55	N/A	R.R.	M	61	5	1985 - 1989	Nelson 1992
	Ohio	0.40	N/A	R.R.	MF	97	5	2002 - 2006	Lehnen 2008
	Midwest, USA	0.45	0.06	φ	MF	532	6	1994 - 1999	DeSante et al. 2001
<i>Grassland Habitat</i>									
Brown-headed Cowbird	USA	0.31	N/A	R.R. <sup>a</sup>	F	2290 <sup>g</sup>	> 8	NA - 1965	Fankhauser 1971
	USA	0.36	N/A	R.R. <sup>a</sup>	M	2290 <sup>g</sup>	> 8	NA - 1965	Fankhauser 1971
	USA	0.40	N/A	R.R. <sup>b</sup>	F	85	> 8	NA - 1965	Fankhauser 1971
	USA	0.49	N/A	R.R. <sup>b</sup>	M	195	> 8	NA - 1965	Fankhauser 1971
	Ontario	0.51	N/A	R.R.	F	20	2	1966 - 1967	Darley 1971
	Ontario	0.37	N/A	R.R.	M	33	2	1966 - 1967	Darley 1971
	USA	0.31	N/A	R.R. <sup>a</sup>	F	1195	16	1960 - 1975	Searcy and Yasukawa 1981
	USA	0.37	N/A	R.R. <sup>a</sup>	M	2421	16	1960 - 1975	Searcy and Yasukawa 1981

	USA	0.42	N/A	R.R. <sup>b</sup>	F	269	16	1960 - 1975	Searcy and Yasukawa 1981
	USA	0.46	N/A	R.R. <sup>b</sup>	M	1038	16	1960 - 1975	Searcy and Yasukawa 1981
	Manitoba	0.70	0.08	φ	F	290	6	1993 - 1998	Woolfenden et al. 2001
	Manitoba	0.90	0.04	φ	M	469	6	1993 - 1998	Woolfenden et al. 2001
	Colorado	0.36	0.08	φ	F	386	8	1992 - 1999	Ortega and Ortega 2009
	Colorado	0.48 <sup>c</sup>	0.05	φ	M	669	8	1992 - 1999	Ortega and Ortega 2009
	Colorado	0.46 <sup>d</sup>	0.04	φ	M	365	8	1992 - 1999	Ortega and Ortega 2009
	California	0.56	N/A	φ	F	410	7	1982 - 1988	Anderson et al. 2012
	California	0.63 <sup>c</sup>	N/A	φ	M	324	7	1982 - 1988	Anderson et al. 2012
	California	0.33 <sup>d</sup>	N/A	φ	M	260	7	1982 - 1988	Anderson et al. 2012
Grasshopper Sparrow	Nebraska	0.00	N/A	R.R.	M	85	4	1982 - 1985	Kaspari and O'Leary 1988
	New York	0.27	N/A	R.R.	F	9	5	1996 - 2000	Balent and Norment 2003
	New York	0.29	N/A	R.R.	M	35	5	1996 - 2000	Balent and Norment 2003
	Montana	0.09	N/A	R.R.	M	45	7	1998 - 2004	Jones et al. 2007
	Florida <sup>f</sup>	0.60	0.07	φ	M	48	4	1989 - 1992	Delaney et al. 1993
	Florida <sup>f</sup>	0.53	0.09	φ	M	94	3	1995 - 1997	Perkins and Vickery 2001
Dickcissel	Kansas	0.49	N/A	R.R.	M	82	5	1965 - 1969	Zimmerman and Finck 1989
	Illinois	0.20	N/A	R.R.	F	25	2	1999 - 2000	Walk et al. 2004

Iowa	0.03	N/A	R.R.	F	38	4	1999 – 2002	Fletcher et al. 2006
Iowa	0.10	N/A	R.R.	M	64	4	1999 - 2002	Fletcher et al. 2006
Maryland	0.30	N/A	R.R.	F	20	11	2000 - 2010	Small et al. 2012
Maryland	0.21	N/A	R.R.	M	38	11	2000 - 2010	Small et al. 2012
								Sousa and Westneat
Kansas	0.42	N/A	R.R.	M	38	2	2006 – 2007	2013

<sup>a</sup> based on recaptures only.

<sup>b</sup> based on recoveries only.

<sup>c</sup> for second year birds only.

<sup>d</sup> for bird past their second year only.

<sup>e</sup> Least Bell's Vireo subspecies.

<sup>f</sup> Florida Grasshopper Sparrow subspecies.

<sup>g</sup> number of birds pooled across both sexes.

<sup>h</sup> 95% confidence interval given instead of standard error.

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## Chapter 6 - Conclusions and Implications

In my dissertation, I assessed the effects of patch-burn grazing management on grassland songbird demography, and highlighted the role of regional differences in predator community composition and Brown-headed Cowbird abundance on the reproductive success of grassland songbirds. At a larger scale, I tested whether the distribution of preferred breeding habitat affected the apparent survival of songbirds across North America. My dissertation work has several key results. First of all, I found that patch-burn grazing management led to greater vegetative structure and litter depths than control treatments, and that annual variation in climatic conditions has large effects on vegetative structure. Second, Dickcissels that breed in unburned patches within patch-burn grazing managed pastures tend to have higher densities and smaller territories. Third, annual variation in vegetative structure did not lead to large differences in reproductive success of Dickcissels, Eastern Meadowlarks, or Grasshopper Sparrows. I also found that rangeland management had species-specific effects on rates of brood parasitism, clutch size, nest survival, and fledging rates of grassland songbirds, but variation in the different components of reproduction did not result in large differences in the average number of fledglings per nesting attempt. Fourth, I found that mortality rates of Dickcissel fledglings were high during the first week after leaving the nest, and survival of fledglings was not affected by rangeland management. However, Dickcissels nesting at sites with high cowbird densities might have to balance fledgling survival with avoiding the high costs of brood parasitism during the nesting stage. Last, I unexpectedly found higher apparent survival in grassland- and shrubland-breeding species than forest-breeding species of songbirds, which could indicate that site fidelity

of songbirds might be dependent on regional patterns in the distribution of preferred breeding habitat.

I found that Dickcissel densities tended to be higher and territories tended to be smaller on the patch-burn grazing patch that was burned in the previous year. Patch-burn grazing management might therefore benefit Dickcissel populations by providing higher quality breeding habitat in some patches. Territory size could limit the number of breeding birds in high quality breeding habitat, and birds that are forced to lower quality habitats often have lower reproductive success (Fretwell and Lucas 1969, Krebs 1971, Schartz and Zimmerman 1971). Patch-burn grazing management might therefore aid in the conservation of Dickcissels, and other grassland songbirds, by providing breeding birds with high quality nesting habitat in unburned patches within the pasture.

Rangeland management affected rates of brood parasitism, the average number of cowbird eggs, nest survival, and fledging rates of Dickcissels, and nest survival of Eastern Meadowlarks. However, the effects of rangeland management on demographic parameters resulted in only minor differences in the average number of fledglings per nesting attempt. I found evidence for a potential tradeoff between habitat selection during the nest and fledgling stage of Dickcissels at Konza Prairie. The northern Flint Hills ecoregion has some of the highest cowbird densities, and brood parasitism can be costly for the host species (Jensen and Cully 2005a; 2005b). Dickcissels that avoid brood parasitism by nesting in pastures with low local cowbird densities produce more fledglings per nesting attempt. However, fledglings might face higher rates of snake depredation in return, especially when snakes are locally abundant (Klug et

al. 2010). The reproductive success of grassland songbirds is therefore likely dependent on the local cowbird abundance and predator community, and the selection pressure of both factors on grassland songbirds likely differs between life-stages.

My results support previous studies that show that patch-burn grazing does not have negative effects on demographic rates of grassland songbirds, and could provide suitable breeding habitat for species that require plant litter for nesting cover that is not found in annually burned pastures (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016, Hovick and Miller 2016). However, I stress the importance of fledgling ecology in the conservation of grassland songbirds, and that the effects of rangeland management on reproductive success of grassland songbirds are likely region-specific.

I present the first estimates of apparent survival for six species of songbirds, and the first estimates from the Great Plains for thirteen species. Furthermore, I found evidence that site fidelity of grassland birds in the Midwest might not be as low as previously expected. I found higher apparent survival in grassland- and shrubland-breeding bird compared to forest-breeding species, which is counter to the prevailing viewpoint that birds breeding in dynamic landscapes, such as frequently burned grasslands, have low apparent survival (Owens and Myers 1973, Andersson 1980, Jones et al. 2007, Schlossberg et al. 2009). My findings indicate the distribution of preferred breeding habitat might be a strong driver of apparent survival of songbirds, which stresses the importance of region-specific estimates of survival for population models and conservation efforts.

Based on my findings as well as previous work, I conclude that patch-burn grazing management increases species diversity of plants, arthropods, mammals, and grassland birds (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006; 2009, Churchwell et al. 2008, Ricketts and Sandercock 2016). My work shows that patch-burn grazing does not negatively impact the reproductive success of grassland songbirds, even when rates of brood parasitism are high. Furthermore, patch-burn grazing might benefit private ranchers, since unburned patches could provide standing vegetation for cattle during drought conditions, which are likely to become more common due to climate change. Previous research has found that cattle mass gains and revenues are similar between tallgrass prairie managed with patch-burn grazing and pastures managed with annually burning and intensive early stocking (Rensink 2009, Limb et al. 2011). Patch-burn grazing might therefore be a viable option for the conservation of grassland songbirds, while still being a useful management option for cattle ranchers on private lands.



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