Ornithological Applications

AmericanOrnithology.org

Volume 124, 2022, pp. 1–22
https://doi.org/10.1093/ornithapp/duab066

RESEARCH ARTICLE

Predation, parasitism, and drought counteract the benefits of patch-burn grazing for the reproductive success of grassland songbirds

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Submission Date: July 19, 2021; Editorial Acceptance Date: December 16, 2021; Published January 13, 2022

ABSTRACT

Intensification of livestock production has reduced heterogeneity in vegetative structure in managed grasslands, which has been linked to widespread declines in grassland songbird populations throughout North America. Patch-burn grazing management aims to restore some of that heterogeneity in vegetative structure by burning discrete pasture sections, so that cattle preferentially graze in recently burned areas. Although patch-burn grazing can increase reproductive success of grassland songbirds, we know little about possible interactions with regional variation in predator communities or brood parasite abundance, or annual variation in weather conditions. Using six years of data from two tallgrass prairie sites in eastern Kansas, USA, we tested effects of patch-burn grazing on the rates of brood parasitism, clutch size, nest survival, and fledging success of three common grassland songbirds, Dickcissels (*Spiza americana*), Eastern Meadowlarks (*Sturnella magna*), and Grasshopper Sparrows (*Ammodramus savannarum*), among pastures managed with patch-burn grazing versus pastures that were annually burned and either grazed or ungrazed. Dickcissel nests experienced lower parasitism (72.8 ± 4.6% SE vs. 89.1 ± 2.2%) and Eastern Meadowlarks had higher nest survival (63.2 ± 20.5% vs. 16.5 ± 3.5%) in annually burned and ungrazed pastures than pastures managed with patch-burn grazing. However, average number of host fledglings per nesting attempt did not differ among management treatments for any species. Annual variation in weather conditions had a large effect on vegetation structure, but not on reproductive success. Probability of brood parasitism was consistently high (25.5–84.7%) and nest survival was consistently low (9.9–16.9%) for all species pooled across treatments, sites, and years, indicating that combined effects of predation, parasitism and drought can offset potential benefits of patch-burn grazing management previously found in tallgrass prairies. Although differences in reproductive success among management treatments were minimal, patch-burn grazing management could still benefit population dynamics of grassland songbirds in areas where nest predators and brood parasites are locally abundant by providing suitable nesting habitat for bird species that require greater amounts of vegetation cover and litter, generally not present in burned pastures.

Keywords: brood parasitism, demography, Flint Hills, Kansas, nest survival, population dynamics, pyric-herbivory, rangeland management, songbird, tallgrass prairie

LAY SUMMARY

- Only 3–14% of the North American grasslands that existed at the time of European settlement still remain, and most of these grasslands are now managed for intensive cattle production.
- Populations of grassland birds have shown steep declines over the past 50 years.
- Patch-burn grazing is a rangeland management strategy that uses rotational fire and grazing to reestablish historical patterns of disturbance in prairie ecosystems.
- We tested whether patch-burn grazing could improve reproductive success of three species of grassland songbirds in a six-year study at two sites in Kansas, USA.
- Overall, nest survival was low, brood parasitism was high, and we did not find the previously described benefits of patch-burn grazing management over annual burning and grazing.
- Changing how we manage our grasslands alone might therefore not be enough to combat ongoing population declines of grassland songbirds in some areas.

La depredación, el parasitismo y la sequía contrarrestan los beneficios del pastoreo en parches quemados para el éxito reproductivo de las aves canoras de pastizal

RESUMEN

La intensificación de la producción ganadera ha reducido la heterogeneidad de la estructura de la vegetación de los pastizales manejados, lo que se ha vinculado con la disminución generalizada de las poblaciones de aves canoras de pastizal en toda América del Norte. El manejo del pastoreo mediante la quema de parches tiene como objetivo restaurar parte de esa heterogeneidad en la estructura de la vegetación, quemando sectores discretos de pastizal, de modo que el ganado pastoree preferentemente en las áreas recientemente quemadas. Aunque el pastoreo en parches quemados puede aumentar el éxito reproductivo de las aves canoras de pastizal, sabemos poco sobre las posibles interacciones con la variación regional en las comunidades de depredadores o en la abundancia de parásitos de nidada, o con la variación anual en las condiciones climáticas. Utilizando seis años de datos de dos sitios de praderas de pastos altos en el este de Kansas, EEUU, evaluamos los efectos del pastoreo en parches quemados en las tasas de parasitismo de nidada, en el tamaño de las nidadas, en la supervivencia de los nidos y en el éxito de emplumamiento de tres aves canoras de pastizal comunes, *Spiza americana*, *Sturnella magna* y *Ammodramus savannarum*, considerando pastizales manejados con pastoreo en parches quemados versus pastizales que fueron quemados anualmente, ya sea pastoreados o no. Los nidos de *S. americana* experimentaron un menor parasitismo (72,8 ± 4,6% EE vs.89,1 ± 2,2%) y *S. magna* tuvo una mayor supervivencia de nidos (63,2 ± 20,5% vs 16,5 ± 3,5%) en los pastizales quemados anualmente y no pastoreados que en los pastizales manejados con pastoreo en parches quemados. Sin embargo, el número promedio de volantones hospederos por intento de anidación no difirió entre los tratamientos de manejo para ninguna especie. La variación anual de las condiciones climáticas tuvo un gran efecto en la estructura de la vegetación, pero no en el éxito reproductivo. La probabilidad de parasitismo de nidada fue consistentemente alta (25,5–84,7%) y la supervivencia de los nidos fue consistentemente baja (9,9–16,9%) para todas las especies agrupadas en tratamientos, sitios y años, indicando que los efectos combinados de la depredación, el parasitismo y la sequía pueden contrarrestar los beneficios potenciales previamente encontrados en praderas de pastos altos del manejo del pastoreo en parches quemados. Aunque las diferencias en el éxito reproductivo entre los tratamientos de manejo fueron mínimas, el manejo del pastoreo en parches quemados aún podría beneficiar la dinámica poblacional de las aves canoras de pastizal en las áreas donde los depredadores de nidos y los parásitos de nidada son abundantes localmente, al proporcionar un hábitat de anidación adecuado para las especies de aves que requieren mayores cantidades de cobertura vegetal y de hojarasca, generalmente no presentes en los pastizales quemados.

Palabras clave: ave canora, demografía, dinámica poblacional, Flint Hills, herbivoría pírica, Kansas, manejo de pastizales, parasitismo de nidada, pradera de pastos altos, supervivencia del nido

INTRODUCTION

Native grasslands are among the most rapidly declining ecosystems worldwide, with extensive habitat conversion and only limited protection (Hoekstra et al. 2005). In North America, only 3–14% of the pre-European extent of tallgrass prairie remains (Samson and Knopf 1994, DeLuca and Zabinski 2011, Augustine et al. 2019). The Flint Hills ecoregion of eastern Nebraska, Kansas, and Oklahoma contains some of the largest remaining tracts of tallgrass prairie and is a stronghold for conservation of grassland birds (With et al. 2008). Yet, much of the land is privately owned and managed with higher densities of grazing livestock and more frequent burning than was historically common (Knapp et al. 1999, Fuhlendorf et al. 2006, Mohler and Goodin 2012). These management practices often reduce spatial variation in vegetation composition and structure in prairie habitats (Knapp et al. 1999, Fuhlendorf et al. 2006) and can lower species diversity and abundance of arthropods (Joern 2005), mammals (Ricketts and Sandercock 2016), and grassland songbirds (Fuhlendorf et al. 2006, Powell 2006, Coppedge et al. 2008). Moreover, intensive grazing and frequent fires have been linked to increased rates of nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) of grassland songbirds (Churchwell et al. 2008, Davis et al. 2016). Conservation efforts should therefore not only focus on halting ongoing habitat loss, but also require a better understanding of the effects and possible benefits of different rangeland management practices to offset the ongoing population declines of grassland birds in North America (Herkert et al. 2003, North American Bird Conservation Initiative [NABCI] 2016, Rosenberg et al. 2019).

Historically, tallgrass prairies were heterogeneous landscapes maintained by periodic fire and selective grazing by bison (*Bos bison*) and other native ungulates (i.e. pyric-herbivory; Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Patch-burn grazing is a rangeland management strategy that more closely resembles the effects of pyric-herbivory compared to other grazing regimes currently in use (Stebbins 1981, Knapp et al. 1999, Fuhlendorf and Engle 2001). Under patch-burn grazing management, a section (or "patch") of a pasture is burned each year in a rotational scheme. Fire-return intervals are typically 2–4 years in productive systems like tallgrass prairie but can be longer in prairie ecosystems with lower primary production. Patches within the pasture are not separated by cross-fencing, allowing cattle to roam free and preferentially graze in recently burned patches where new vegetative growth is rich in protein (Allred et al. 2011). The resulting patterns of uneven grazing can create greater variation in vegetation structure and plant species composition (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Ricketts and Sandercock 2016). Patch-burn grazing can therefore increase species diversity and abundance by providing suitable habitat for a greater range of grassland birds at different stages of the annual cycle (Fuhlendorf et al. 2006, Powell 2006, Hovick et al. 2014a), and can improve their reproductive success by decreasing rates of nest predation and brood parasitism (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016, Hovick and Miller 2016).

Patch-burn grazing is further suggested as an attractive rangeland management technique benefitting wildlife because it can potentially buffer against spatial and temporal variation in predation, brood parasitism, and climatic conditions (Hovick et al. 2015). Nest predator community composition and the local abundance of Brown-headed Cowbirds can show considerable spatial variation in tallgrass prairie (Pietz and Granfors 2000, Renfrew and Ribic 2003, Jensen and Cully 2005a, Lyons et al. 2015). Although nest survival of grassland songbirds often increases with greater nest cover (Hughes et al. 1999, Temple 2020, Churchwell et al. 2008, Hovick et al. 2012), this relationship is likely dependent on the search behavior of different nest predators (Ringelman 2014, Lyons et al. 2015). Greater vegetative cover might increase concealment from visual predators but may be less effective against predators that search for nests using olfactory or auditory cues (Conover et al. 2010; but see Fogarty et al. 2018).

Additionally, the probability of brood parasitism is directly driven by the local abundance of female cowbirds. The Flint Hills ecoregion has a strong gradient in abundance of Brown-headed Cowbirds, where counts of cowbirds on Breeding Bird Survey routes are highest at northern sites (52–85 birds per route), intermediate at central sites (26–40 birds per route), and lowest at southern sites (13–16 birds per route; Jensen and Cully 2005a, 2005b). Locally, female cowbirds are most common in sites with shorter vegetation that are grazed by ungulates but can commute long distances to parasitize host nests (Goguen and Mathews 1999, 2000, Patten et al. 2006). Thus, the potential relationship between rangeland management and rates of brood parasitism remains unclear. Previous studies that related reproductive success of grassland songbirds to patch-burn grazing have focused on sites where Brown-headed Cowbirds were less abundant than in the northern Flint Hills (Churchwell et al. 2008, Hovick et al. 2012, Holcomb et al. 2014, Davis et al. 2016, Hovick and Miller 2016, Skagen et al. 2018). We, therefore, understand little of the potential costs and benefits of patch-burn grazing in relation to local predator community composition and cowbird abundance.

Temporal variation in growing season precipitation and temperature can also interact with rangeland management practices to affect reproductive success of grassland songbirds in several ways. Growing season rainfall is a major driver of primary production in the tallgrass prairie ecosystem and interacts with fire and grazing to shape plant species composition and vegetative structure (Briggs and Knapp 1995, Swemmer et al. 2007, Sherry et al. 2008). By altering vegetation height and concealment of nests, annual variation in growing season precipitation could directly affect the reproductive success. Furthermore, growth of new vegetation is limited in drought years, which makes ground-nesting birds that rely on vegetation cover for concealment even more dependent on accumulated plant litter from previous growing seasons (Sherry et al. 2008). Reproductive success in patch-burned and grazed pastures could therefore be more resilient to annual variation in rainfall, because unburned patches could provide refuges for breeding birds in years when new vegetation growth is limited (Hovick and Miller 2016).

Annual variation in temperature may also affect rates of nest predation through direct effects on predator activity. Snakes are one of the main nest predators of grassland songbird nests (Klug et al. 2010, DeGregario et al. 2014) and are less active during cold and hot conditions (Cox et al. 2013). Nest survival could therefore be affected by annual variation in temperature regardless of management regime or habitat structure if snakes are a locally dominant nest predator. Last, extreme weather events—both severe storms and excessive heat—can lead to higher rates of nest failure because of abandonment of nests or direct mortality of young (Hovick et al. 2014b, Ross et al. 2015, Elmore et al. 2017). Previous studies relating patch-burn grazing management to reproductive success of grassland songbirds have been relatively short (≤2 years; Churchwell et al. 2008, Hovick et al. 2012, Holcomb et al. 2014, Davis et al. 2016, Hovick and Miller 2016, Skagen et al. 2018), and with regional predictions for the Midwest ecoregion that include increased temperatures and greater intra-annual variability in precipitation (Knapp et al. 2008, IPCC 2013), it is increasingly important to understand how annual weather conditions and extreme weather events affect the relationship between rangeland management and the reproductive success of grassland songbirds.

We estimated the effects of patch-burn grazing on rates of brood parasitism, clutch size, nest survival, and fledging success (hereafter collectively referred to as reproductive success) for three species of grassland songbirds: Dickcissels (*Spiza americana*), Eastern Meadowlarks (*Sturnella magna*), and Grasshopper Sparrows (*Ammodramus savannarum*). Using data collected at two field sites in the Flint Hills Ecoregion for 1–2 rotations of a 3-year patch-burn grazing system (3–6 years), we compared estimates from patch-burned and grazed pastures to those from pastures that were annually burned with or without grazing. We predicted that the greater vegetative structure in patch-burned and grazed pastures would lead to lower rates of brood parasitism by cowbirds and higher reproductive success for our focal species compared to birds nesting in annually burned and grazed pastures. Dickcissels tend to have higher predation and parasitism rates because they are open-cup nesters with blue eggs, whereas Eastern Meadowlarks and Grasshopper Sparrows build dome-shaped nests with brown-speckled eggs (Rivers et al. 2010). Effects of rangeland management on the components of reproductive success might therefore be greater for Dickcissels compared to the other two species.

As a second objective, we examined temporal variation in the effects of rangeland management on reproductive success of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows. We predicted that rates of nest predation and brood parasitism would be higher in dry and hot years when new growth of vegetation is low, especially on recently burned pastures. However, if weather conditions affect predator activity directly, we predicted that nest survival might be lower in warmer years, with expected greater predator activity, and higher in colder years regardless of management regime.

METHODS

Study Sites

We conducted our study at two managed tallgrass prairie sites, Chase County and Konza Prairie (~120 km apart), in the Flint Hills of eastern Kansas, USA. From 2011 to 2013, we collected data at two private ranches in Chase and Greenwood counties (hereafter Chase County; 38°09'N, 96°25'W). From 2011 to 2016, we collected data at the Konza Prairie Biological Station (hereafter Konza Prairie; 39º05'N, 96º33'W), a tallgrass prairie preserve located in Geary and Riley counties that is part of the NSF-funded Long-term Ecological Research (LTER) Program.

Climatic conditions during the growing season are relatively hot and humid, with average monthly temperatures of 25–26°C in July and August (50-year average; NOAA 2017). Annual precipitation averaged 839 mm yr^{-1} in Chase County and 799 mm yr^{-1} at Konza Prairie but shows considerable annual variation (50-year averages; NOAA 2017). Generally, 75% of annual precipitation falls within the 6-month growing season (March–August), but late summer droughts are fairly common (NOAA 2017).

The tallgrass prairie habitats in Chase County and Konza Prairie are dominated by native warm-season grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). Forbs comprise much of the plant species diversity of the tallgrass prairie, and species common at both sites 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 uncommon in frequently burned tallgrass prairie, but shrub species that were present included buckbrush (*Symphoricarpos orbiculatos*), rough-leaved dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and wild plum (*Prunus americana*; Towne et al. 2002). Historically, pastures at the Chase County site have been managed with a higher fire frequency than at Konza Prairie (Mohler and Goodin 2012) and therefore had less shrub cover.

Study Species, Brood Parasites, and Nest Predators

Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows are common breeding songbirds in tallgrass prairie and frequent hosts for Brown-headed Cowbirds (Rivers et al. 2010) but species differ in nesting habitat requirements (Powell 2006). Dickcissels select nesting sites with dense cover, moderate to tall (25−150 cm) vegetation, moderate amounts of litter (5−15 cm), and a high number of song perches (Dechant et al. 2002, Temple 2020), Eastern Meadowlarks select nesting sites with tall grass, greater litter cover, and high vertical vegetation density (Jaster et al. 2020), and Grasshopper Sparrows nest in relatively open prairie with patches of bare ground and litter (Vickery 2020).

Common nest predators at our study site included several snake species (e.g., yellow-bellied racer (*Coluber constrictor flaviventris*), prairie kingsnake (*Lampropeltis calligaster*), speckled kingsnake (*Lampropeltis holbrooki*), and Great Plains ratsnake (*Pantherophis emoryi*; Klug et al. 2010)), American Crows (*Corvus brachyrhynchos*), and several species of mesocarnivores, including coyotes (*Canis latrans*). In addition, activity of Brown-headed Cowbirds can be difficult to distinguish from nest predation because females will regularly remove nest contents to induce relaying (Arcese et al. 1996, Hoover and Robinson 2007).

Experimental Treatments

At the Chase County site, we monitored vegetation and breeding birds on two privately owned pastures. One pasture consisted of three smaller patches (142–155 ha) and was managed with rotational fire in a patch-burn grazing (PBG) management regime with a 3-year fire-return interval (Figure 1). Therefore, each year the patch-burn grazing pasture consisted of a patch that was burned that spring (PBG0), a patch that was burned the previous year (PBG1), and a patch that was burned two years before

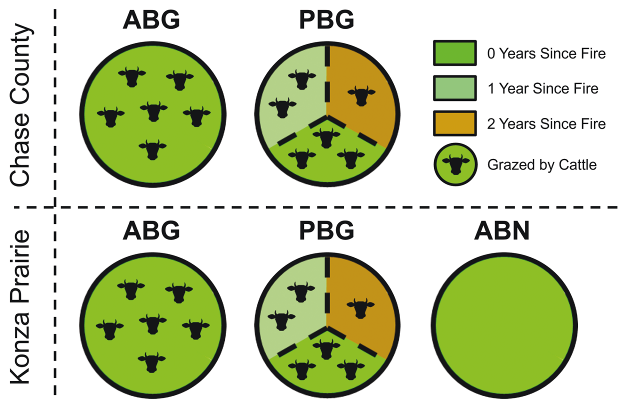

FIGURE 1. Schematic of experimental design at Chase County (2011–2013) and Konza Prairie (2011–2016), Kansas. Experimental pastures had the following management treatments: annually burned and grazed by cattle (ABG), patch-burned and grazed by cattle (PBG, 0–2 years since spring fire), and annually burned and not grazed (ABN; at Konza Prairie only).

(PBG2). A second pasture was annually burned and grazed (ABG) which reflects the dominant management strategy in the Flint Hills region (419 ha; Figure 1; With et al. 2008). All pastures were stocked with steers from mid-April to mid-July (3-month period) under an intensive early-stocking regime (IES). Stocking rates were set according to typical levels on private lands managed for cattle production with 0.85–1.05 ha per head (1.16–1.43 animal unit months [AUM]/acre) in the annually burned and grazed pasture, and 1.05–2.09 ha per head (0.58–1.16 AUM/acre) in the pasture managed with patch-burn grazing (Owensby et al. 2008).

The Konza Prairie site consisted of 3 experimental pastures (Figure 1). Three contiguous patches (49.4–102.4 ha) formed a larger pasture (219.3 ha) that was patch-burned and grazed, a second pasture (93.5 ha) was annually burned and grazed, and a third pasture (41.6 ha) was annually burned and not grazed (ABN). Konza Prairie is managed as a field experiment and stocking rates in grazed pastures were set at 3.24 ha per cow-calf pair (0.63 AUM/acre) from early May to early October (5-month period; J. Briggs and K. C. Olsen, personal communication). This type of season-long stocking (SLS) with cow-calf pairs is an alternative grazing regime in the Flint Hills but is less common than grazing with steers (With et al. 2008). Forage utilization rates were comparable between sites because cow-calf pairs consume larger quantities of dry matter than steers and grazed pastures for a longer period (Forero et al. 1989).

Spring burns in Chase County and Konza Prairie were conducted between mid-March and mid-April. However, the annually burned and grazed pasture in Chase County was not burned during 2012 and 2013 due to drought conditions and a lack of standing vegetation to carry a fire. Cattle were removed from the pasture early (mid-June) during both years. All experimental pastures were managed with the specified management regime for at least 3 yrs prior to the start of the study, and 1–2 complete rotations during the project.

Climate

To assess interactions of climate with rangeland management, we obtained precipitation and temperature data from the long-term climate database of National Oceanic and Atmospheric Administration (NOAA). We used monthly average temperature and total precipitation for the 100-year period from September 1916 to August 2016 from the nearest weather station to each study site (Station ID, Chase: USC00141858, Konza: USC00144972). We then determined the long-term averages of growing season (March–August) temperature and precipitation for each site (mean ± SD: Chase: 19.1 ± 1.1°C and 554.7 ± 149.1 mm; Konza: 18.7 ± 1.1°C and 547.3 ± 149.1 mm). For each site, we used a *z*-transformation to scale the growing season temperature and precipitation and used year-specific z-scores to explain annual variation in the vegetation characteristics of each management regime. We calculated z-scores by subtracting the average from each value and dividing the result by the standard deviation of the distribution.

Vegetation Surveys

We sampled vegetative structure and composition at each pasture in the middle of the growing season of each year (June–July). We recorded vegetation measurements at 5 equally spaced points along eight 300-m transects in the annually burned and grazed pasture, in the annually burned and ungrazed pasture, and in each patch within the patch-burn grazing treatment. Transects were randomly placed within each patch or pasture and were at least 100 m apart. As an index of aboveground biomass for prairie plants, we used a Robel pole at each point to measure the visual obstruction at a distance of 4 m and at a height of 1 m in each cardinal direction from the pole (Robel et al. 1970). At each point, we estimated percent cover of grasses and sedges, broad-leaved forbs, shrubs, bare ground, and plant litter using a 25 × 50 cm Daubenmire frame (Daubenmire 1959). We also measured litter depth at 0, 2, and 4 m in each cardinal direction from the Robel pole, for a total of 12 measurements at each point. We then averaged the 4 visual obstruction and 12 vegetation cover measurements at each point to obtain 40 measurements for each variable per pasture or patch per year.

Nest Monitoring

In each pasture, we located nests of Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows by rope dragging, watching the foraging movements of parents attending young, or opportunistically flushing birds. At discovery, we marked nest locations by placing a small painted rock or flagging tape at ~5 m 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, and the probability and intensity of brood parasitism by Brown-headed Cowbirds. We considered a nest to be unparasitized if it only contained host eggs and parasitized if we observed at least one cowbird egg or nestling in the nest during any nest visit. If a nest was parasitized, we estimated parasitism intensity as the maximum number of cowbird eggs or nestlings observed over all repeated visits. The speckled parasitic eggs of cowbirds were easily differentiated from blue host eggs of Dickcissels by coloration of the eggshell, and from host eggs of Grasshopper Sparrows and Eastern Meadowlarks by egg size. Cowbird nestlings were identified by white flanges and no palate spots versus the yellow flanges of Dickcissel and Grasshopper Sparrow nestlings and white down and white palate spots of Eastern Meadowlark nestlings (Jaster et al. 2020). We considered a nest to be successful if any host or cowbird nestling 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. In contrast, we considered a nest to have failed if the nest was either abandoned, depredated, or was not successful because of other reasons such as extreme weather events.

Statistical Analysis

To evaluate the demographic responses of the 3 focal species to management treatments, we considered 4 demographic parameters: probability of brood parasitism, clutch size, nest survival, and fledging rate per egg from successful nest. Because time periods and treatments differed between sites, we tested for site-year interactions by limiting analyses to the first three-year period and by excluding data from the annually burned and ungrazed treatment that was only monitored at Konza Prairie. If we found significant site-year interactions for any of the 4 demographic parameters, we conducted separate analyses for the Chase County and Konza Prairie sites. We analyzed each species separately and tested the effects of patch-burn grazing management on demographic parameters at 2 spatial scales. A treatment model included the annually burned and grazed pasture, the annually burned and ungrazed pasture, and the patch-burned and grazed pasture as a block (number of parameters [k] = 3), while a patch-within-treatment model included both annually burned pastures and all three patches of the patch-burned and grazed pasture separately (k = 5). Low breeding densities affected nest numbers in some year and treatment combinations, and we were unable to test full factorial models with year by treatment or year by patch-within-treatment interactions. For all analyses, we selected the most parsimonious models based on Akaike's Information Criterion values corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). If multiple models were equally parsimonious ($\Delta AIC \leq 2$), we used model averaging based on AIC_c-weights to calculate final parameter estimates and standard errors that accounted for both sampling and model-selection uncertainty. We tested the goodness-of-fit of the top-ranked models with Pearson χ^2 tests, and further determined pairwise differences by comparing 95% confidence intervals (CI) of our estimates. We conducted all analyses in R (R Core Team 2017).

Brood parasitism. We modeled the probability of brood parasitism as a binomial response (Y/N) and fit a set of species-specific logistic regression models. Our final model set included an intercept-only model and models including all possible combinations of the fixed effects of treatment or patch-within-treatment (reference category: ABG), year of study (reference category: 2013), and the interaction between treatment and year or patch-within-treatment and year.

Clutch size. To estimate effects of management regimes on clutch size, we censored nests found in the building or laying stage that did not survive until the start of incubation, since those nests might have failed before the final clutch size was reached. We also censored nests that were found during the brood-rearing stage, since those nests might have experienced partial egg or brood losses and therefore reductions in clutch size. We then modeled clutch size with multinomial regression models using the *nnet* package in R (Venables and Ripley 2002). Our final model set included an intercept-only model and models including all possible combinations of the fixed effects of treatment or patch-within-treatment, whether a nest was parasitized or not (reference category: not parasitized), year, and interactions among these fixed effects. We did not include date of clutch initiation as a covariate because preliminary analyses showed no difference in timing of clutch initiation among management treatments for any species. For Dickcissels, we modeled the number of host eggs separately for parasitized and unparasitized nests to avoid problems with model fitting caused by limited overlap in the ranges of number of host eggs between parasitized and unparasitized nests.

Daily nest survival. To estimate daily nest survival, we created encounter histories for each nest with the date of discovery, date the nest was last active, date the nest fate was determined, and the fate of the nest (0 = successful, 1 = failed). We then used nest survival models in the *RMark* package in R as an interface to program MARK to fit candidate models to test whether daily nest survival was affected by treatment, patch-within-treatment, year, or by whether a nest was parasitized or not, and tested all possible interactions among these fixed effects (White and Burnham 1999, Laake 2013). We calculated survival estimates for the entire nesting cycle (egg-laying, incubation, and brood-rearing) by raising daily nest survival to species-specific exposure periods of 24 days for Dickcissels and Grasshopper Sparrows, and 28 days for Eastern Meadowlarks (Vickery 2020, Temple 2020, Sandercock et al. 2008, Jaster et al. 2020). Last, we calculated the variance of projected estimates of daily survival for the different exposure periods using the delta method (Powell 2007).

Fledging rates per egg from successful nest. To estimate the fledging rate per egg from successful nests, we limited our analyses to nests that successfully fledged at least 1 host nestling. We further excluded nests found during the brooding stage, since partial losses due to predation or other causes before we found the nest could have led to overestimating fledging rates. We used mixed-effects logistic regression models with the *lme4* package to test whether the chance of an individual egg successfully fledging from a successful nest varied with treatment or patch-within-treatment, year, whether the nest was parasitized or not, or total clutch size of both host and cowbird eggs, and tested all possible interactions among these fixed effects (Bates et al. 2015). Nest ID was treated as a random effect to control for lack of independence among eggs within the same clutch.

Calculating Host Fledglings per Nesting Attempt

We combined our parameter estimates to calculate the expected number of host fledglings produced per nesting attempt for each species as a derived parameter. The empirical estimates of probability of brood parasitism (p), clutch size (C), period nest survival (S), and fledging rate per egg from successful nests (F)—estimated separately for parasitized (p) and unparasitized nests ($1-p$)—were combined in the following equation:

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

We used parametric bootstrapping to calculate the number of host 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 per egg, we used a beta distribution where the mean and standard errors 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. Last, we compared bootstrap distributions for each treatment and calculated p-values based on the distribution of the differences among management treatments. All values reported in the results section represent means ± standard errors (SE) unless otherwise specified.

RESULTS

Climate

Growing season temperatures were relatively warm in 2011 (Chase: 20.0°C, $z = +0.976$; Konza: 20.1°C, $z = +1.042$) and 2012 (Chase: 21.9°C, $z = +2.647$; Konza: 21.5°C, $z = +2.305$), whereas 2013 was relatively cool at both sites (Chase: 17.2°C, $z = -1.599$; Konza: 17.2°C, $z = -1.622$). Temperatures at Konza Prairie during 2014–2016 were closer to the long-term average (2014: 18.2°C, $z = -0.668$; 2015: 18.8°C, $z = -0.104$; 2016: 19.8°C, $z = +0.820$). Growing season precipitation was well below average in 2011 (Chase: 337.6 mm, $z = -1.435$; Konza: 491.6 mm, $z = -0.400$) and 2012 (Chase: 364.1 mm, $z = -1.256$; Konza: 407.8 mm, $z = -0.963$). Conversely, 2013 was a relatively wet growing season for Chase (757.0 mm, $z = +1.384$), but not for Konza (528.2 mm, $z = -0.152$). At Konza Prairie, growing season precipitation was close to the long-term average in 2014 (455.3 mm, $z = -0.643$) and 2015 (625.0 mm, $z = +0.497$), and above average in 2016 (691.5 mm, $z = +0.945$).

Vegetation Surveys

We found significant site-year interactions between Chase County and Konza Prairie for visual obstruction readings (VOR; $F_{2,1179} = 7.51$, $P < 0.001$), grass cover ($F_{2,1179} = 11.79$, $P < 0.001$), forb cover ($F_{2,1179} = 7.08$, $P < 0.001$), and litter depth ($F_{2,1179} = 14.88$, $P < 0.001$), and therefore analyzed effects of management treatments on vegetation characteristics separately for each site. Overall, visual obstruction readings were ~1.9x greater and forb cover was ~1.5x greater at Konza Prairie, litter depth was ~2.6x greater at Chase County, and grass cover was similar among sites (Figure 2). At both sites, variation in vegetation characteristics was best explained by models that included management treatment and year effects (see Supplementary Material Table S1). Visual obstruction readings did not differ between the patch-burned and grazed and annually burned and grazed treatments at either site but were slightly higher at the annually burned and ungrazed treatment, and tended to be lowest in the burned patch within the patch-burned and grazed treatment (PBG0; Figure 2A and B, Supplementary Material Tables S2 and S3). Grass cover was higher in the annually burned and ungrazed treatment than the patch-burned and grazed or annually burned and grazed treatments (Figure 2C and D, Supplementary Material Tables S2 and S3), whereas forb cover showed the opposite trend (Figure 2E and F, Supplementary Material Tables S2 and S3). At both sites, litter depth was higher in the patch-burned and grazed treatment than in the annually burned

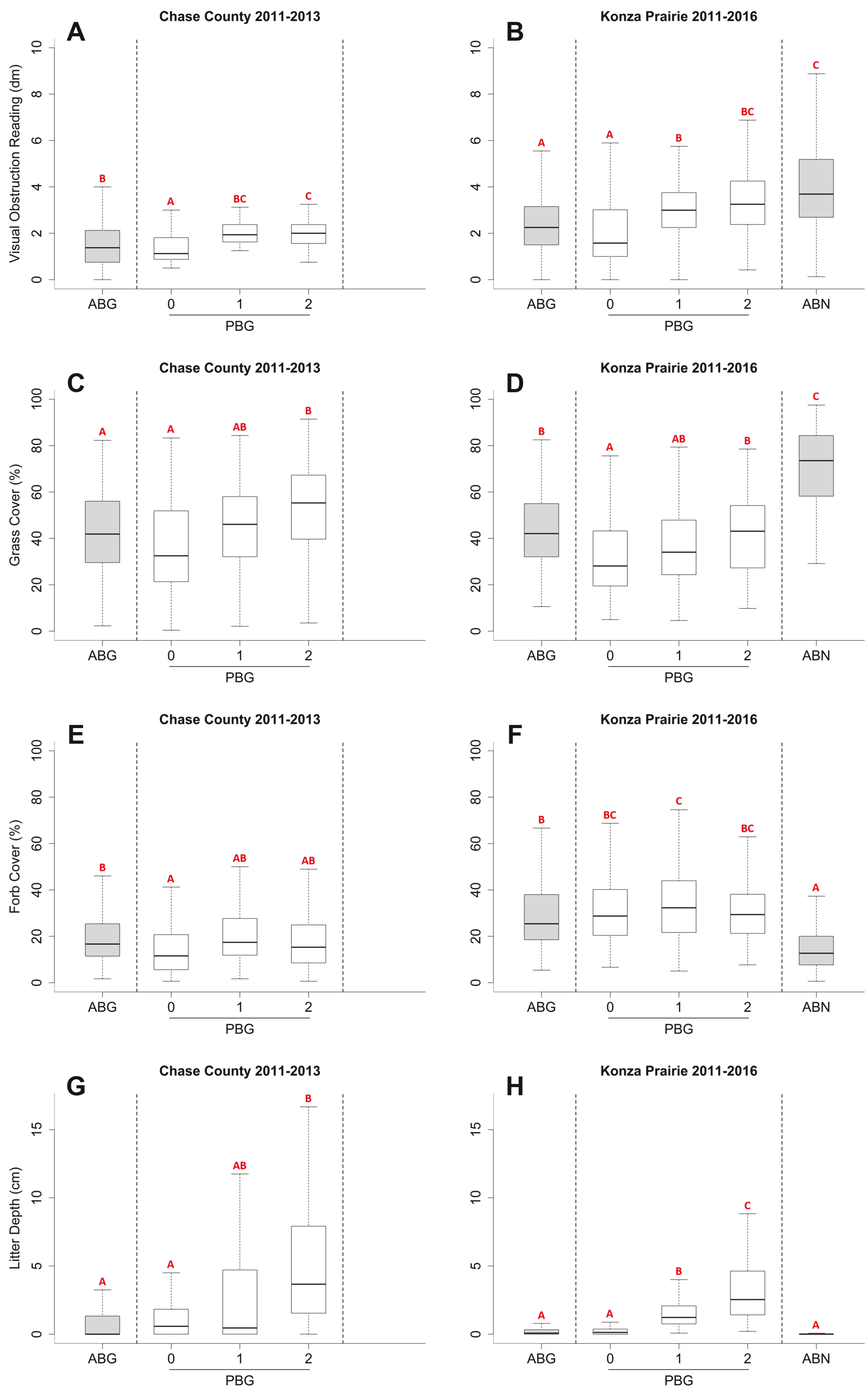

FIGURE 2. Differences in grazing and burning regime among rangeland management treatments created the desired and expected variation in visual obstruction readings (VOR; A–B), grass cover (C–D), forb cover (E–F), and litter depth (G–H) at Chase County (2011–2013) and Konza Prairie (2011–2016). Estimates were calculated separately for each rangeland management treatment: annually burned and grazed (ABG), patch-burned and grazed (PBG, 0–2 years since spring fire), and annually burned and not grazed (ABN). 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. Significant differences ($P < 0.05$) between estimates are depicted with different letters.

TABLE 1. Number of Dickcissel, Eastern Meadowlark, and Grasshopper Sparrow nests monitored in Chase County (2011–2013) and at Konza Prairie (2011–2016) for annually burned and grazed (ABG), annually burned and not grazed (ABN), and patch-burned and grazed (PBG) pastures. Nests within patch-burned and grazed pastures were further separated by the number of years since the patch the nest was found in was last burned (0–2 years since fire; PBG0–2; in italics).

Dickcissel	Chase County				Konza Prairie						
Treatment	2011	2012	2013	Total	2011	2012	2013	2014	2015	2016	Total
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*
Total	55	66	68	189	35	15	36	89	108	82	365

Eastern Meadowlark	Chase County				Konza Prairie						
Treatment	2011	2012	2013	Total	2011	2012	2013	2014	2015	2016	Total
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*
Total	12	13	26	51	8	5	9	31	22	21	96

Grasshopper Sparrow	Chase County				Konza Prairie						
Treatment	2011	2012	2013	Total	2011	2012	2013	2014	2015	2016	Total
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*
Total	18	26	38	82	1	0	18	44	20	19	102

and grazed and annually burned and ungrazed treatments. Within the patch-burned and grazed treatment, the highest litter depths were found in unburned patches (PBG1 and PBG2; Figure 2G and H, Supplementary Material Tables S2 and S3).

VOR, percent grass cover, and litter depth showed large annual variation at both sites. During the drought conditions of 2012, VOR, percent grass cover, and litter depth were all lower than the 2011–2016 average, and litter depth remained low in the next year (Supplementary Material Figure S1 and Supplementary Material Tables S2 and S3). Although both sites also experienced drought conditions in 2011, we did not find a vegetative response, indicating potential lag effects. At Konza Prairie, VOR was higher than average in 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 (Supplementary Material Figure S1 and Supplementary Material Tables S2 and S3). Although, the annually burned and grazed pasture in Chase County was not burned and duration of grazing was reduced in 2012 and 2013 due to drought conditions, we did not find any resulting differences in any measured vegetation characteristics compared to 2011 (Supplementary Material Figure S1).

Effects of Rangeland Management on Demographic Rates

From 2011 to 2016, we located and monitored a total of 885 nests, including 554 Dickcissel nests (189 at Chase, 365 at Konza), 147 Eastern Meadowlark nests (51 at Chase, 96 at Konza), and 184 Grasshopper Sparrow nests (82 at Chase, 102 at Konza), across all experimental pastures. When split by treatment, we found relatively few Eastern Meadowlark and Grasshopper Sparrow nests in recently burned pastures (PBG0, ABN, and ABG at Konza Prairie only; Table 1).

Probability of brood parasitism. Probabilities of brood parasitism by Brown-headed Cowbirds were generally high and were ~1.5× higher at Konza Prairie (0.457–0.847) than Chase County (0.255–0.582) for all 3 host species (Figure 3). Dickcissels had the highest probability of cowbird parasitism (Chase: 0.582 ± 0.036, Konza: 0.847 ± 0.019), followed by Grasshopper Sparrows (Chase: 0.390 ± 0.054, Konza: 0.613 ± 0.051), and Eastern Meadowlarks (Chase: 0.255 ± 0.061, Konza: 0.457 ± 0.051). Management regime

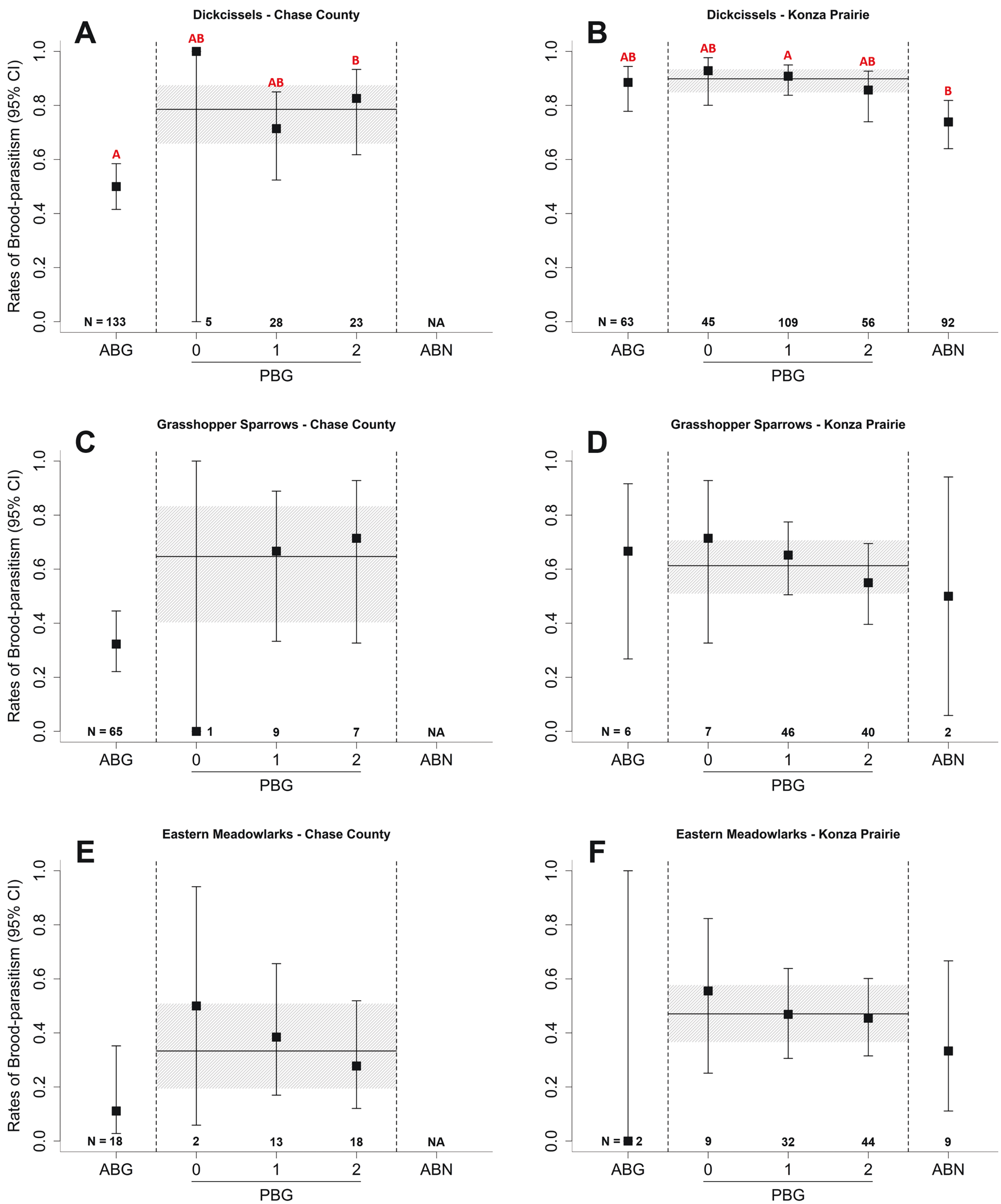

FIGURE 3. Rates of brood parasitism by Brown-headed Cowbirds for Dickcissel nests (A–B) varied among rangeland management treatments in different ways between Chase County (2011–2013) and Konza Prairie (2011–2016), with Eastern Meadowlarks (C–D) and Grasshopper Sparrow (E–F) following similar trends. Estimates were calculated separately for each rangeland management treatment: annually burned and grazed (ABG), patch-burned and grazed (PBG, 0–2 years since spring fire), and annually burned and not grazed (ABN). Horizontal black bar and gray shading represent an estimate and 95% confidence interval for all 3 patch-burn grazing patches combined. Significant differences ($P < 0.05$) between estimates are depicted by different letters. Numbers above treatment labels represent sample sizes.

TABLE 2. Model selection for logistic regression models of probability of brood parasitism 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, ΔAIC_c values, and Akaike weights (w_i). Treatment models estimated probability of brood parasitism for annually burned and grazed (ABG) pastures, annually burned and not grazed (ABN) pastures, and the patch-burned grazed pastures (PBG) as a whole (three estimates), whereas patch models also provided separate estimates for each of the three patch-burn grazing patches (PBG0–2; five estimates). Due to low sample sizes of Grasshopper Sparrow nests on some experimental treatments at Konza Prairie, we did not fit treatment or patch models at that site.

Species	Site	Model	k	Deviance	AIC_c	ΔAIC_c	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

affected probability of brood parasitism for Dickcissels at both sites, and for Eastern Meadowlarks and Grasshopper Sparrows at the Chase County site (Table 2). At Konza Prairie, the probability of brood parasitism tended to be lower at the annually burned and ungrazed pasture compared to other treatments and tended to decline with year since fire within the patch-burned and grazed pasture for all species (Figure 3). Unexpectedly, the probability of brood parasitism in Chase County was lower in the annually burned and grazed pasture compared to the patch-burned and grazed pasture for Dickcissels, with Eastern Meadowlarks and Grasshopper Sparrows following similar trends (Figure 3).

Clutch size. Songbird nests parasitized by cowbirds contained fewer host eggs than nests that were unparasitized at discovery (Dickcissel: 2.67 ± 0.06 vs. 3.92 ± 0.10, Eastern Meadowlarks: 2.76 ± 0.17 vs. 4.15 ± 0.13, Grasshopper Sparrow: 2.59 ± 0.16 vs. 4.22 ± 0.12; Figure 4). Cases of multiple cowbird eggs were relatively infrequent for any songbird species at Chase County (40.7–45.5% of parasitized nests), whereas at Konza Prairie, Dickcissel, and Grasshopper Sparrow nests regularly contained more than one cowbird egg when parasitized (76.8% and 66.7% of parasitized nests, respectively; Figure 4). Management regime did not affect host clutch size in any of the three species (Table 3), but we did detect a weak effect on the average number of cowbird eggs in parasitized Dickcissel nests (Table 4). At Konza Prairie, parasitized Dickcissel nests in the annually burned and grazed treatment contained ~1.3× more cowbird eggs on average than parasitized nests in other treatments (ABG: 3.46 ± 0.21; ABN: 2.66 ± 0.21; PBG: 2.63 ± 0.11). In contrast, Dickcissel nests received fewer cowbird eggs in the annually burned and grazed treatment (1.41 ± 0.08) than the patch-burned and grazed treatment at Chase County (1.70 ± 0.11; Figure 4).

Daily nest survival. During preliminary analyses, we found no evidence of a site-year interaction in the analyses of daily nest survival for any of the three songbird species (AIC_c Site + Year vs. Site * Year models; Dickcissel: 891.5 vs. 894.0; Eastern Meadowlark: 275.6 vs. 279.3; Grasshopper Sparrow: 378.7 vs. 378.7). We, therefore, analyzed data for Chase County and Konza Prairie together. Nest survival was generally low and did not differ between sites for any species. Overall nest survival for the entire nesting cycle was 0.142 ± 0.014 for Dickcissels, 0.099 ± 0.021 for Grasshopper Sparrows, and 0.169 ± 0.032 for Eastern Meadowlarks. Management regime explained the most variation in nest survival for Eastern Meadowlarks (Table 5). Nest survival for Eastern Meadowlarks was higher on annually burned and ungrazed pastures (0.632 ± 0.205) compared to other treatments (ABG: 0.077 ± 0.050; PBG: 0.165 ± 0.035) and tended to be lowest in recently burned and grazed patches (ABG and PBG0: 0.069 ± 0.066; Figure 5). Nest survival of Grasshopper Sparrows was best

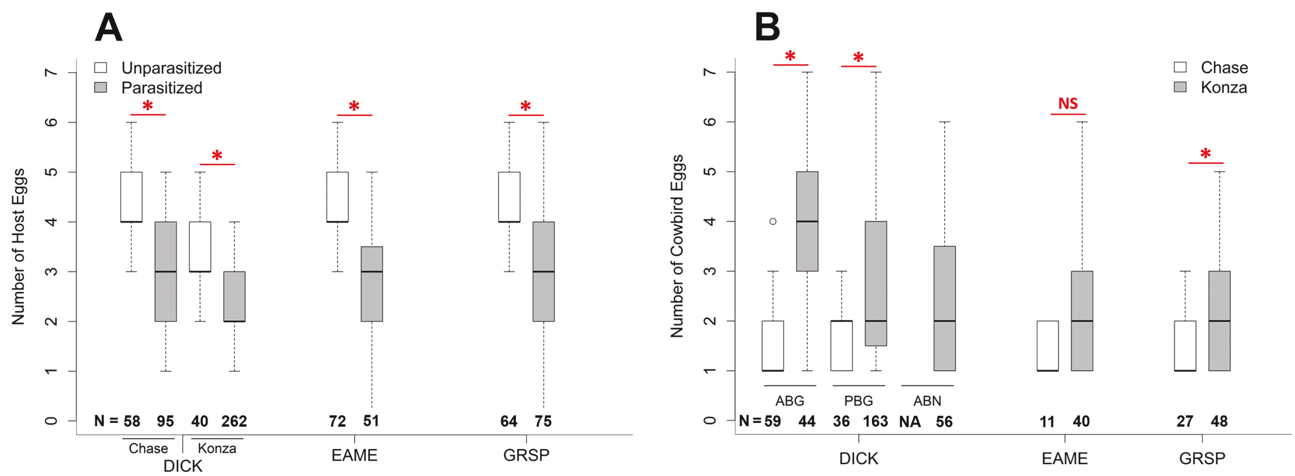

FIGURE 4. (A) Number of host eggs was lower for parasitized nest for Dickcissels, Eastern Meadowlarks, and Grasshopper Sparrows at both sites. (B) Parasitized Dickcissel and Grasshopper Sparrow nests received more cowbird eggs at Konza Prairie (2011–2016) vs. Chase County (2011–2013). Number of cowbird eggs in Dickcissel nests showed weak variation among rangeland management treatments: annually burned and grazed (ABG), patch-burned and grazed (PBG, 0–2 years since spring fire), and annually burned and not grazed (ABN). Stars above estimates indicate a significant difference ($P < 0.05$). Numbers above treatment labels represent sample sizes.

TABLE 3. 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). Model selection was based on the number of parameters (k), Deviance, ΔAIC_c values, and Akaike weights (w_i). Treatment models estimated the number of host eggs for annually burned and grazed (ABG) pastures, annually burned and not grazed (ABN) pastures, and the patch-burned and grazed pastures (PBG) as a whole, while patch models provided separate estimates for all three patch-burn grazing patches (PBG0–2) instead. For Dickcissels, we modeled the number of host eggs separately for each site and for unparasitized and parasitized nests.

Species	Site	Parasitized	Model	k	Deviance	AIC_c	ΔAIC_c	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

explained by whether the nest was parasitized by cowbirds but unexpectedly tended to be higher for parasitized nests on the annually burned and grazed treatment (Tables 5, Figure 5, and Supplementary Material Table S4). Nest survival of Dickcissels was lowest for unburned pastures, and highest for the most recently burned patch-burn grazing patch, but these differences were not statistically significant (Figure 5).

Fledging rates per egg from successful nests. Fledging rates per host egg were ~1.8× higher for unparasitized Dickcissel nests at Konza Prairie (0.750 ± 0.068, n = 40) than for parasitized nests (0.431 ± 0.036, n = 188), and patterns were similar for Dickcissels at Chase, Eastern Meadowlarks at Konza, and Grasshopper Sparrows at both sites (Table 6, Figure 6, and Supplementary Material Table S5). At Konza Prairie, fledging rates per egg of Eastern Meadowlarks were lower (0.612 ± 0.047) than at Chase County (0.842 ± 0.071) but did not differ between sites for Dickcissels and Grasshopper Sparrows. However, a significant interaction between site and brood parasitism showed that the difference in fledging rates between parasitized and unparasitized nests of Dickcissels and Eastern Meadowlarks was greater at Konza Prairie than Chase County (Figure 6). Management regime explained variation in fledging rates of Dickcissel eggs only at Konza Prairie. While fledging rates in parasitized Dickcissel

TABLE 4. Model selection for multinomial regression models 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). Model selection was based on the number of parameters (*k*), Deviance, ΔAIC_c values, and Akaike weights (w_i). Treatment models estimated the number of cowbird eggs for annually burned and grazed (ABG) pastures, annually burned and not grazed (ABN) pastures, and the patch-burned and grazed pastures (PBG) as a whole, while patch models provided separate estimates for all three patch-burn grazing patches (PBG0–2) instead. For Dickcissels, we modeled the number of cowbird eggs separately for each site.

Species	Site	Model	*k*	Deviance	AIC_c	ΔAIC_c	w_i
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 5. 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 across sites. Model selection was based on the number of parameters (*k*), Deviance, ΔAIC_c values, and Akaike weights (w_i). Treatment models estimated daily nest survival for annually burned and grazed (ABG) pastures, annually burned and not grazed (ABN) pastures, and the patch-burned and grazed pastures (PBG) as a whole, while patch models provided separate for all three patch-burn grazing patches (PBG0–2) instead. Shown are models with a model weight of 0.05 or higher; for the full model selection results see Supplementary Material Table S4.

Species	Model	*k*	Deviance	AIC_c	ΔAIC_c	w_i
Dickcissel	Patch	5	1940.28	1950.29	0.00	0.276
	Constant	1	1948.55	1950.55	0.26	0.243
	Parasitism	2	1948.11	1952.12	1.82	0.111
	Patch + Parasitism	6	1940.18	1952.19	1.90	0.107
	Year	6	1941.53	1953.55	3.25	0.054
	Patch * Parasitism	10	1933.64	1953.69	3.40	0.051
Eastern Meadowlark	Treatment	3	504.84	510.86	0.00	0.376
	Treatment + Parasitism	4	503.93	511.96	1.10	0.217
	Treatment * Parasitism	6	501.51	513.57	2.71	0.097
	Patch	5	503.58	513.63	2.77	0.094
	Patch + Parasitism	6	502.83	514.89	4.04	0.050
Grasshopper Sparrow	Parasitism	2	609.26	613.27	0.00	0.307
	Treatment + Parasitism	4	605.88	613.91	0.64	0.223
	Constant	1	612.21	614.21	0.94	0.192
	Treatment * Parasitism	6	602.78	614.85	1.58	0.139
	Treatment	3	609.18	615.20	1.92	0.117

nests were comparable between patch-burn grazed (0.313 ± 0.061) and annually burned and grazed treatments (0.337 ± 0.117), they were higher in the annually burned and ungrazed treatment (0.649 ± 0.089). Moreover, fledging rates tended to decrease with year since fire within the patch-burn grazing treatment (Figure 6).

Host Fledglings Per Nesting Attempt

On average, Dickcissels produced 0.320 ± 0.079 host fledglings per attempt in Chase County, but only 0.185 ± 0.070 fledglings per attempt at Konza Prairie. Eastern Meadowlarks produced 0.543 ± 0.196 host fledglings per nesting attempt in Chase County, but only 0.350 ± 0.125 fledglings per nest at Konza Prairie. Last, Grasshopper Sparrows had similar rates of productivity with 0.199 ± 0.078 host fledglings per attempt in Chase County, and 0.183 ± 0.081 at Konza Prairie. We did not find any differences in host fledglings per nesting attempt among management regimes at the Chase County site for any species. Dickcissels at Konza Prairie produced relatively similar numbers of host fledglings per nesting attempt in the annually burned and grazed and patch-burned and grazed treatments (ABG: 0.145 ± 0.071, PBG: 0.139 ± 0.058) but tended to produce more host fledglings in the annually burned and ungrazed treatment (0.282 ± 0.115). Within the patch-burned and grazed treatment, the number of Dickcissel fledglings per

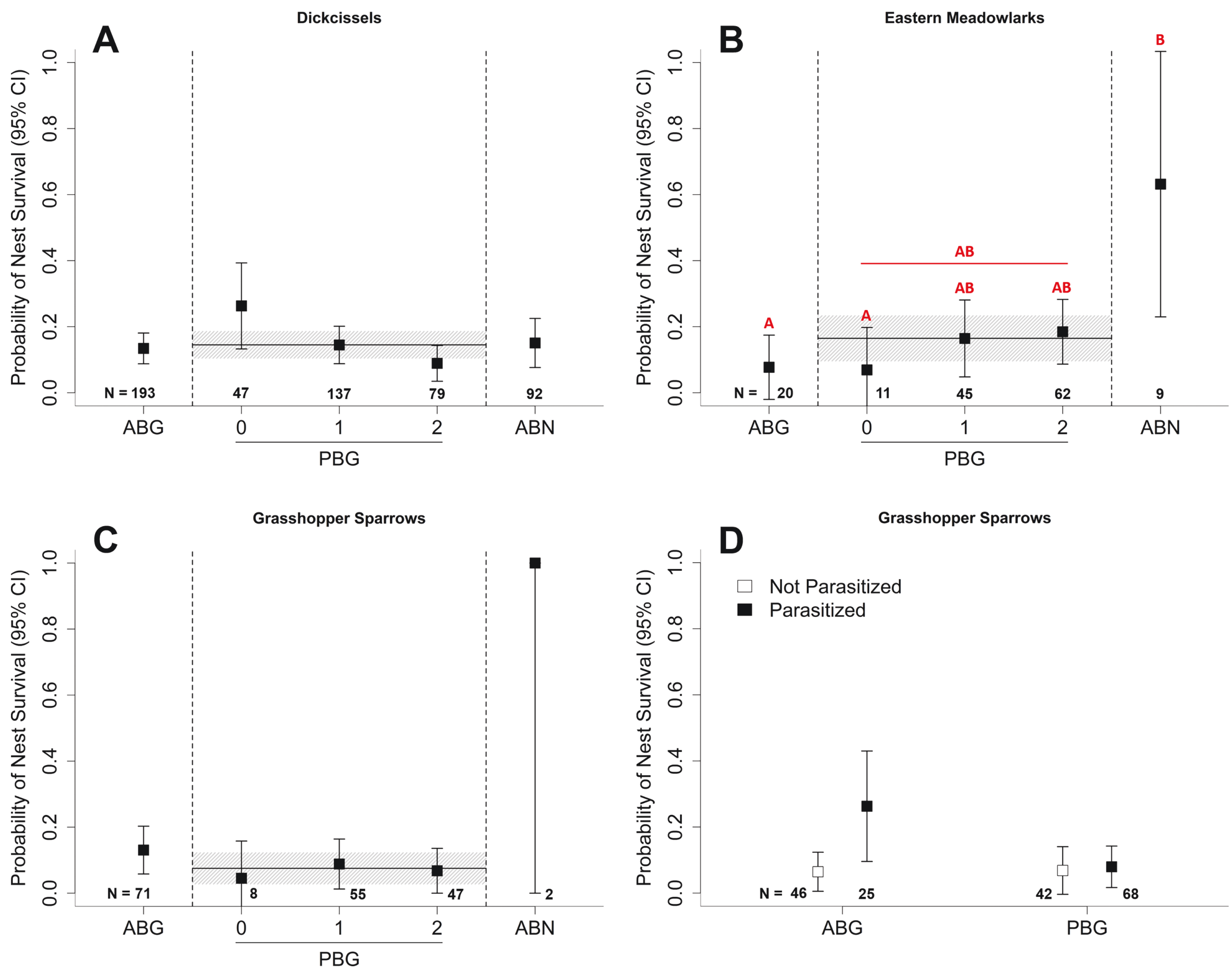

FIGURE 5. Estimates of extrapolated nest survival for Dickcissels (A), Eastern Meadowlarks (B), and Grasshopper Sparrows (C–D) were low and did not vary across sites (Chase County: 2011–2013, Konza Prairie: 2011–2016). Nest survival for Eastern Meadowlarks was higher on annually burned and ungrazed (ABN) pastures compared to patch-burned and grazed (PBG, 0–2 years since spring fire) or annually burned and grazed (ABG) pastures. Nest survival of Grasshopper Sparrows tended to be highest for parasitized nests on the annually burned and grazed treatment (D). Shown are estimates of daily nest survival extrapolated to a species-specific 24- or 28-day exposure period with 95% confidence intervals. Significant differences ($P < 0.05$) between estimates are depicted by different letters. Horizontal black bar and gray shading represent an estimate and 95% confidence interval for all 3 patch-burn grazing patches combined. Numbers above treatment labels represent sample sizes.

nesting attempt declined with years since fire (Figure 7). For Eastern Meadowlarks, the number of host fledglings per nesting attempt showed considerable variation on the annually burned and ungrazed treatment but was still higher than the patch-burned and grazed treatment (Figure 7). Although not significant, the number of Grasshopper Sparrow fledglings per nesting attempt tended to be higher at the annually burned and grazed pastures vs. the patch-burned and grazed pastures (Figure 7).

DISCUSSION

During our 3- to 6-year study at two tallgrass prairie sites in the Flint Hills of eastern Kansas, we found that rangeland management based on patch burn-grazing successfully led to greater levels of heterogeneity in vegetation structure compared to annually burned and grazed treatments. Interactions between rangeland management and vegetative structure affected the probability of brood parasitism, intensity of brood parasitism, nest survival, and fledging rates of Dickcissels, as well as nest survival of Eastern Meadowlarks. However, effects of rangeland management on the components of reproduction resulted in only small, nonsignificant, differences in average number of host fledglings per nesting attempt. Reproductive success of all three songbird species was relatively low and similar across years despite large inter-annual variation in weather conditions and vegetative

TABLE 6. 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, ΔAIC_c values, and Akaike weights (w_i). Treatment models estimated fledging rates for annually burned and grazed (ABG) pastures, annually burned and not grazed (ABN) pastures, and the patch-burned and grazed pastures (PBG) as a whole, while patch models provided separate estimates for all three patch-burn grazing patches (PBG0–2) instead. Nest ID was included as a random factor to control for lack of independence among eggs from the same clutch. Shown are models with model weights ≥0.05; for the full model selection results, see Supplementary Material Table S5.

Species	Site	Parasitized	Model	k	Deviance	AIC_c	ΔAIC_c	w_i
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	0.00	0.361
			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

structure within our experimental treatments. Our findings of limited benefits of patch-burn grazing for grassland birds in the Flint Hills ecoregion are contrary to the generally positive effects reported for reproductive success of grassland songbirds at other sites (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016, Hovick and Miller 2016). We, therefore, conclude that rangeland management practices alone might not be able to improve reproductive success of grassland songbirds at sites where nest predators and brood-parasites are abundant, or during drought. Our study joins a growing body of work suggesting that in some cases, the effects of predation, climatic variation, and topoedaphic conditions can be more important than rangeland management practices as drivers of population dynamics for grassland birds (Lipsey and Naugle 2017, Sliwinski et al. 2019, Vold et al. 2019).

Effects of Rangeland Management on Vegetative Structure and Reproductive Success

Grassland songbirds nesting in patch-burned and grazed pastures did not experience lower probabilities of brood parasitism or higher nest survival compared to annually burned and grazed pastures at our field sites in eastern Kansas, in contrast to previous work at other tallgrass prairie sites (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016, Hovick and Miller 2016). We found relatively few nests of Eastern Meadowlarks and Grasshopper Sparrows in the annually burned and grazed pasture at Konza Prairie (but not Chase County) resulting in large uncertainty in parameter estimates, which complicated comparisons of reproductive metrics among treatments for those species. However, these low sample sizes likely reflect avoidance of recently burned areas by our focal species and not a lack of sampling effort.

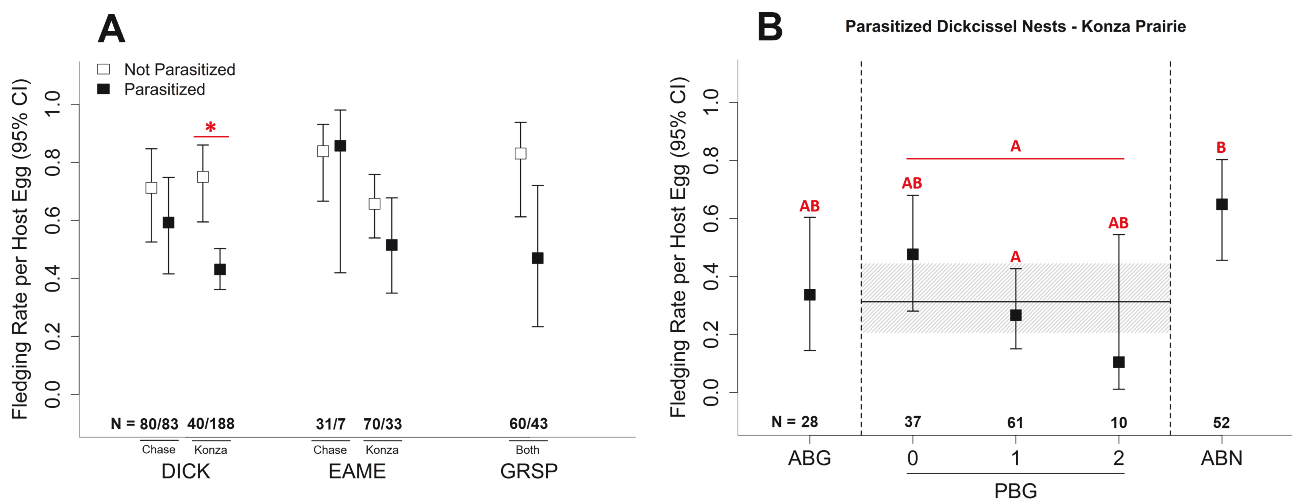

FIGURE 6. Fledging rates per host egg were higher for unparasitized vs. parasitized nests for Dickcissels at Konza Prairie (2011–2016), while patterns were similar for Dickcissels at Chase (2011–2013), Eastern Meadowlarks at Konza, and Grasshopper Sparrows at both sites (A). Fledging rates for parasitized Dickcissel nests at Konza Prairie were higher in the annually burned and ungrazed (ABN) pasture compared to patch-burned and grazed (PBG, 0–2 years since spring fire) but not to annually burned and grazed (ABG) pastures (B). Significant differences ($P < 0.05$) between estimates are depicted by different letters. Horizontal black bar and gray shading represent an estimate and 95% confidence interval for all 3 patch-burn grazing patches combined. Numbers above treatment labels represent sample sizes.

Two additional explanations may account for why probabilities of brood parasitism were similar or higher (Dickcissels in Chase County) in patch-burned and grazed compared to annually burned and grazed pastures. For all 3 songbird species, overall probabilities of brood parasitism were much higher at our field sites in Chase County (25.5–58.2%) and Konza Prairie (45.7–84.7%) compared to previous studies of patch-burn grazing (0–20%; Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016, Hovick and Miller 2016). In our study system, competition among female cowbirds to secure suitable host nests might be so high that management-related differences in habitat structure had little effect on the cumulative probability of a female cowbird detecting and parasitizing nests (Jensen and Cully 2005b). Alternatively, space use of female cowbirds may occur at a larger spatial scale than our experimental pastures (42–419 ha), because breeding cowbirds often make movements of several kilometers between foraging sites to search for host nests (Dijak and Thompson 2000, Jensen and Cully 2005b, B.H.F. Verheijen personal observation). The effectiveness of patch-burn grazing management in decreasing the probability of brood parasitism could therefore depend on pasture size and the management regimes of surrounding rangelands.

Relatively low nest survival in unburned patches in patch-burned and grazed pastures compared to previous studies could potentially be caused by both high activity of Brown-headed Cowbirds or other nest predators at our sites (Churchwell et al. 2008, Davis et al. 2016). Activity of cowbirds can be difficult to distinguish from nest predation because nest contents can be completely removed in both cases (Arcese et al. 1996, Hoover and Robinson 2007). At the same time, snakes are common 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). Nest camera studies have also shown that mesopredators, deer, and raptors destroy nest contents and that nest type and habitat structure can affect vulnerability to both diurnal and nocturnal predators (Pietz and Granfors 2000, Renfrew and Ribic 2003). In our study, it was difficult to use signs remaining at the nest to determine which predator was responsible for the partial or complete loss of a nest. Nevertheless, we conclude that reproductive losses to parasitism and predation were particularly high at our field sites in the Flint Hills which fits with geographical and temporal variation in the abundance of Brown-headed Cowbirds and regional differences in the composition of predator communities (Jensen and Cully 2005a, Lyons et al. 2015). Potential benefits of patch-burn grazing management to reproductive success of grassland songbirds may therefore be lower or nonexistent if nest predators and brood parasites are locally or regionally more abundant.

Site Differences in Demographic Parameters

Although general patterns in demographic parameters in response to our management treatments were relatively similar between sites, brood parasitism by Brown-headed Cowbirds was lower in Chase County than Konza Prairie, especially for Dickcissels and Grasshopper Sparrows in the annually burned and grazed pasture. Furthermore, we found a surprisingly large number of Eastern Meadowlark

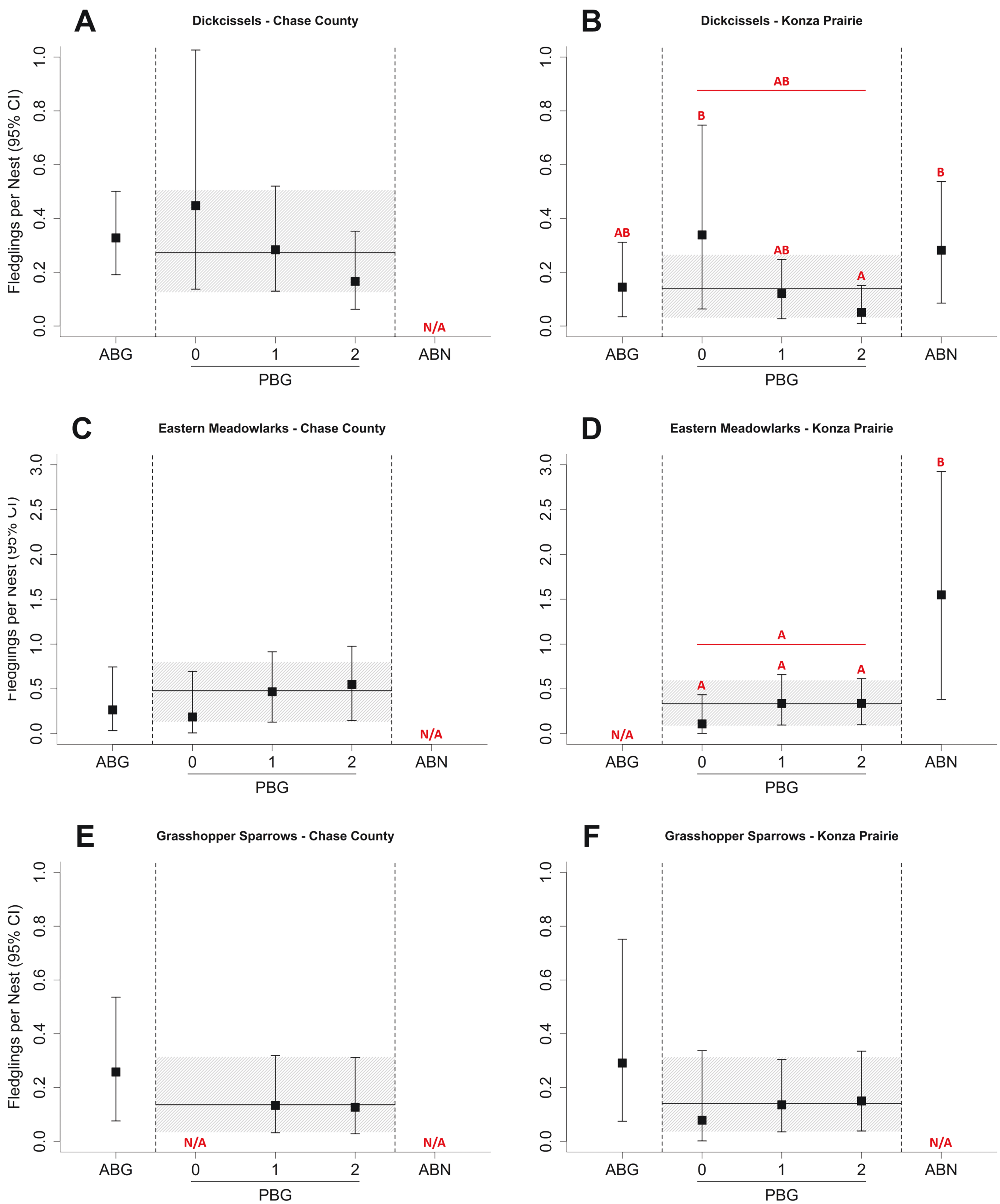

FIGURE 7. Bootstrapped estimates show that both Dickcissels (A–B) and Eastern Meadowlarks (C–D) produced more host fledglings per nesting attempt at Chase County (2011–2013) than at Konza Prairie (2011–2016), while productivity of Grasshopper Sparrows (E–F) was similar between sites. Dickcissels at Konza Prairie produced similar numbers of host fledglings across rangeland management treatments (annually burned and grazed (ABG), patch-burned and grazed (PBG, 0–2 years since spring fire), and annually burned and not grazed (ABN)), but productivity declined with years since fire (B). Eastern Meadowlarks at Konza Prairie produced more host fledglings in the annual burned and ungrazed vs. the patch-burned and grazed pasture (D). Significant differences ($P < 0.05$) between estimates are depicted by different letters. Horizontal black bar and gray shading represent an estimate and 95% confidence interval for all 3 patch-burn grazing patches combined.

and Grasshopper Sparrow nests in the annually burned and grazed pasture vs. the patch-burn grazed pasture at Chase County compared to Konza Prairie and previous studies (Davis et al. 2016). Three important ecological differences between the sites could help to explain these patterns.

First, shrub and forest cover were substantially lower at the Chase County site than at Konza Prairie due to legacy effects of more frequent fire during recent decades (Mohler and Goodin 2012). Female cowbirds use perches to search for host nests, but the linkages between shrub and forest cover and brood parasitism remain unclear (Jensen and Cully 2005b). Nevertheless, observed site differences in brood parasitism match the previously described north-south gradient in local cowbird abundance and resulting parasitism rates in the Flint Hills (Jensen and Cully 2005a).

Second, sites differed in grazing regime, with Chase County being managed with intensive early stocking with steers and Konza Prairie with season-long stocking with cow-calf pairs. However, overall forage utilization rates were comparable between sites because cow-calf pairs consume larger quantities of dry matter than steers and grazed pastures for a longer period (Forero et al. 1989). Moreover, despite differences in grazing regimes and early spring forage utilization, management treatments had similar effects on vegetation structure at both sites (Figure 2, Supplementary Material Table S2, and Supplementary Material Figure S1)

Last, the annually burned and grazed pasture at the Chase County site was not burned in 2012 and 2013 and cattle were removed earlier during the growing season due to drought conditions. An absence of prescribed fire did not affect the composition and structure of vegetation during the summer sampling period (June–July), but effects of drought and lack of fire on vegetation conditions earlier in the spring could have affected settling decisions of breeding Eastern Meadowlarks and Grasshopper Sparrows (Vickery 2020, Jaster et al. 2020). Moreover, cowbirds often forage in association with cattle and early removal of livestock may have led to lower probabilities of brood parasitism for Dickcissels and Grasshopper Sparrows on the annually burned and grazed pasture in Chase County. Local variation in legacy effects and management-specific response of ranchers to drought conditions could therefore affect how reproductive success of grassland songbirds respond to rangeland management regimes. Moreover, lack of prescribed fire and early removal of cattle during drought conditions is commonly required and leads to economic losses for ranchers who manage their pastures with annual burning and intensive early-stocking (A. Erickson, personal observation). Given regionally predicted climate change (IPCC 2013), managers might not be able to use prescribed fire as frequently when considering management strategies for the conservation of grassland birds in the future.

Annual Variation in Reproductive Success

Although annual variation in temperature and precipitation led to substantial differences in vegetation structure, we found little evidence for differences in the effects of rangeland management on specific demographic rates or annual variation in the overall reproductive success of grassland songbirds. Our results contrast with previous studies that have reported that grassland songbirds generally have lower success during drought conditions (Bolger et al. 2005, With et al. 2008, Rahmig et al. 2009). Two explanations may account for our results.

First, nest survival at our sites was overall quite low (range of means: 0.099–0.169 for all 3 species of grassland songbirds) and rates of brood parasitism consistently high, especially at Konza Prairie (0.457–0.847). When rates of nest predation and brood parasitism are already high during years with favorable weather, there is little room for variation in either metric in response to drought conditions. Songbird populations in regions with consistently high rates of nest predation and brood parasitism, like the northern Flint Hills, might therefore not be viable without considerable immigration from other "source" populations regardless of rangeland management strategy (Pulliam 1988, Sandercock et al. 2008, With et al. 2008, Davis et al. 2016).

Alternatively, annual variation in local habitat quality could result in variation in local breeding densities by driving settlement decisions of grassland songbirds at larger spatial scales (Temple 2020, Powell 2006, Rahmig et al. 2009, Verheijen et al. 2019), but greater local breeding densities do not have to result in higher reproductive success for several reasons. First, reproductive success of grassland songbirds may be subject to density-dependent processes such as territoriality that could negate positive effects of improved habitat conditions during good years (Both and Visser 2000, Sillett et al. 2004), but evidence for grassland songbirds is mixed (Winnicki et al. 2020). Second, high nest densities could attract large numbers of nest predators, and opportunistic predators might allocate more effort to searching for songbird nests. Densities of breeding Dickcissels in burned patches in pastures managed with patch-burn grazing were relatively low, especially during drought conditions (Verheijen et al. 2019), while nest survival tended to be higher on such patches compared to other treatments. If locally abundant nest predators focus their efforts on high-quality habitat with higher densities of breeding songbirds, reproductive success in those habitats might be suppressed. Nevertheless, whether brood parasites or predators are abundant at our sites, or nest predators respond to increased densities of grassland songbirds in good years, patch-burn grazing management did not substantially increase the reproductive success of grassland songbirds in any year, at least at the spatial scale of our experimental patches.

Alternative Benefits of Patch-Burn Grazing Management

Although we did not find large differences in reproductive success among management treatments, patch-burn grazing might still benefit grassland songbirds if habitats support greater fledgling survival or local breeding densities. Habitat requirements of songbird fledglings often differ from nesting habitat, while fledglings are largely unable to disperse large distances during the first weeks after leaving the nest (Kershner et al. 2004, Berkeley et al. 2007, Streby and Andersen 2011, Anthony et al. 2013). By providing a larger variety of habitats than annual burning and grazing management, patch-burn grazing could potentially improve fledgling survival by allowing fledglings to move more easily towards higher quality habitat patches (Verheijen 2017).

In addition, we found more nests of Eastern Meadowlarks and Grasshopper Sparrows in unburned patches within patch-burned and grazed pastures compared to recently burned patches or pastures (Table 1), which is consistent with previous findings that breeding densities of Eastern Meadowlarks and Grasshopper Sparrows are usually higher in unburned grasslands (Walk and Warner 2000, Swengel and Swengel 2001, Powell 2006). Patch-burn grazing management could therefore benefit populations of grassland songbirds by providing habitat for species that require higher amounts of cover and litter for breeding, habitats that are generally not present in annually burned and grazed pastures (Hovick and Miller 2016). Grasslands in the United States continue to be converted at rapid rates, with ~2.5 million acres lost per year during 2015–2019 (WWF 2021). And although regions with high rates of nest predation and brood parasitism might function as population sinks regardless of management strategy, any reproduction in unburned pastures might buy managers time to improve other local drivers of grassland songbird productivity.

CONCLUSIONS

Management strategies that aim to restore the historical interaction between periodic fire and selective grazing by large ungulates could be a useful tool for improving habitat conditions and counteracting ongoing declines in grassland bird populations (Herkert et al. 2003, North American Bird Conservation Initiative 2016, Rosenberg et al. 2019). Rangeland management regimes, such as patch-burn grazing, could be especially attractive to improve reproductive success of grassland birds on private lands used for livestock production that make up a large proportion of remaining grasslands (Fuhlendorf et al. 2006, Churchwell et al. 2008, Hovick et al. 2012, Augustine et al. 2019). However, described benefits for reproductive success might be minimal in areas where nest predators and brood parasites are locally abundant. In these areas, not grazing annual burned pastures could lead to higher productivity of Eastern Meadowlarks and could therefore be an interesting option for conservation areas not part of a private ranching operation, but overall benefits for population dynamics are likely limited by the low breeding densities of Eastern Meadowlarks. At the same time, the removal of predators or parasites from areas where they are locally abundant is unlikely to be successful because benefits are low and only short-term (Sandercock et al. 2008). Instead, managers could attempt to increase reproductive success of grassland songbirds by directly targeting local drivers of nest predator and brood parasite abundance or activity. Future assessments of the effects of grassland management strategies on grassland songbirds, therefore, require a better understanding of the composition of local predator communities and the numerical and functional response of nest predators and Brown-headed Cowbirds to rangeland management. Nevertheless, patch-burn grazing management could potentially still benefit population dynamics of grassland songbirds in areas where nest predators and brood parasites are locally abundant by providing suitable nesting habitat for bird species that require greater amounts of vegetation cover and litter, generally not present in burned pastures.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

ACKNOWLEDGMENTS

We thank the staff at Konza Prairie and private landowners in Chase and Greenwood County for allowing access to their property. We also thank C. C. Then and the many field technicians who helped collect our field data, L. B. McNew and V. L. Winder for contributing to supervision of field work at the Chase County site, and A. Joern, J. S. Lamb, L. E. Martin, K. K. McLauchlan, B. E. Ross, E. L. Weiser, and four anonymous reviewers for their helpful suggestions and feedback on previous versions of the manuscript.

Funding statement: The project was supported by the Konza Prairie LTER Program, funded by the National Science Foundation (NSF) (NSF DEB-0823341 and NSF DEB-1440484), an NSF Doctoral Dissertation Improvement Grant to B.H.F.V. (DDIG; NSF DEB-1501903), and the Kansas Department of Wildlife, Parks and Tourism. K.S.L., L.A.S., and S.K.W. were supported by the Division of Biology's

Research Experience for Undergraduates Program at Kansas State University (NSF DBI-1156571 and NSF DBI-1460802); and B.H.F.V. was supported by the Konza Prairie LTER (NSF DEB-1440484).

Ethics statement: Research was conducted under Kansas State University IACUC protocols #3265 and #3720.

Author contributions: B.H.F.V, A.N.E., and B.K.S. conceived the ideas, research questions, and experiments; B.H.F.V., A.N.E., W.A.B., K.S.L., L.A.S., E.J.W., and S.K.W. collected the field data; B.H.F.V. analyzed the data and wrote the manuscript, while A.N.E., W.A.B., E.J.W., S.K.W., and B.K.S. provided substantial editorial input into the project; B.K.S. contributed substantial field resources and funding.

Data depository: All data used in our analysis are publicly available on the EDI/LTER Data Portal: Jensen, W., Verheijen, B. 2019. PBG05 Response of bird abundance to the Patch-Burn Grazing experiment at Konza Prairie. Environmental Data Initiative. http://dx.doi.org/0.6073/pasta/e1906e4a5b59ae1d136a0c4a1dd7f4b7

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