

Impacts of a Recent Bison Reintroduction on Grassland Bird Nests and Potential Mechanisms for These Effects

Heather Herakovich,^{1,6} Christopher J. Whelan,^{2,3} Nicholas A. Barber,⁴ and Holly P. Jones^{1,5}

¹Department of Biological Sciences, Northern Illinois University, 155 Castle Drive, DeKalb, IL 60115

²Department of Cancer Physiology, Moffitt Cancer Center, 12902 USF Magnolia Drive, Tampa, FL 33612

³Biological Sciences, 845 West Taylor Street, University of Illinois at Chicago, Chicago, IL 60607

⁴Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182

⁵Institute for the Study of the Environment, Sustainability, and Energy, Northern Illinois University, 155 Castle Drive, DeKalb, IL 60115

⁶Corresponding author: Heather.Herakovich@valpo.edu; 219-448-2103

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ABSTRACT

The majority of tallgrass prairie has been converted to agriculture over the past two centuries. Restoration projects have sought to increase the quality and size of prairie fragments, with the potential to increase grassland breeding bird habitat. American bison (*Bison bison*) are being reintroduced to prairie restoration sites and the immediate impacts of these reintroductions are unclear. Our goal was to understand how bison reintroduction influences grassland bird nests and the potential mechanisms behind any change. We measured nest density, nest success, and brood parasitism with a before-after-control-impact (BACI) design to determine if bison influenced pooled nesting success of breeding passerines and field sparrows (*Spizella pusilla*), the most common nester. In addition, we measured visual obstruction and avian species composition to determine if they changed after the reintroduction. Bison did not influence nest density, brood parasitism, or visual obstruction. Pooled nest success was higher during the first 2 y in bison sites after the reintroduction but decreased the following 2 y. Bird species composition differed slightly between areas with and without bison, but this was not due to the reintroduction and was likely due to other site characteristics. Field sparrow nest success was higher before and after reintroduction in bison sites and drove the pooled nest success results in bison sites. Caution should be taken when interpreting pooled nest data, but these results suggest that bison did not negatively impact nest success of grassland nesting birds immediately following their reintroduction (<5 y).

Index terms: grassland birds; grazing; management; prairie; restoration

INTRODUCTION

Grassland ecosystems are threatened worldwide, and less than half are protected from further exploitation (Carbutt et al. 2017). North American tallgrass prairie is one of the world's most endangered ecosystems, with 96% converted for agriculture or urbanized and <1% remaining in most of the midwestern USA as fragments intermixed in an agricultural and urban matrix (Samson and Knopf 1994, 1996). The loss of prairie habitat can be attributed to both land-use changes and the loss of indigenous Native American control of the land in these areas. Indigenous communities set more frequent fires than were caused by lightning, which kept tallgrass prairie from becoming predominantly forested (Higgins 1984). The loss of prairie to forest was especially evident in the prairie peninsula region, which includes Indiana, Illinois, western Iowa, and Wisconsin, due to higher precipitation in this region than in western prairie.

Restoration efforts have focused on converting farmland and fallow fields back to prairie by establishing native plant communities and reinstating historical disturbance regimes (fire and grazing) that once occurred. Until recently, mowing and domestic cattle (*Bos taurus*) grazing have been the only management tools implemented to decrease warm season grass dominance and therefore increase forb abundance and plant diversity in prairie restorations (Fuhlendorf and Engle 2004;

McLachlan and Knispel 2005; Hamilton 2007). In lieu of cattle grazing, reintroductions of American bison (*Bison bison*) have occurred throughout the tallgrass prairie region, including restoration sites in Prairie Peninsula region states of Illinois and Indiana (McMillan 2006).

Populations of grassland bird species have declined over several decades due to the loss of grassland habitat (Brennan and Kuvlesky 2005; Askins et al. 2007; Rosenberg et al. 2019). Increases in grassland area from prairie restoration in the prairie peninsula may help these species rebound (Askins et al. 2007). Thus, current management strategies should include the preservation of grassland habitat, restoration of former grassland habitat, and the reinstatement of disturbance to these areas to help increase grassland bird survival and reproduction.

Studies on the effects that fire and grazing have on grassland bird nest success have predominantly focused on managed cattle grazing and occurred in shortgrass and mixed-grass prairie (Lusk et al. 2003; Lusk and Koper 2016; Skagen et al. 2018) or within large remnant tallgrass prairie (Zimmerman 1997; Churchwell et al. 2008; Rahmig et al. 2009; Sandercock et al. 2014; Davis et al. 2016). Very few studies have examined how nest success of grassland birds is affected by grazing in eastern restored tallgrass prairie. To our knowledge, no studies have compared nest success in areas with and without grazing or in areas with recently established grazing in this region. Compar-

isons of different cattle grazing regimes (patch-burned sites vs. completely burned and grazed sites) on grassland bird nest success and post-fledgling survival do exist for the eastern tallgrass prairie region, but they only focus on one grassland bird species, the grasshopper sparrow (*Ammodramus savannarum*; Hovick et al. 2011a, 2011b). These studies are very useful for informing eastern restored tallgrass prairie research; however, they do not detail the response of the avian community to grazing when it is newly established or from bison.

Nest success of grassland birds may differ in grazed and ungrazed areas for a variety of reasons. The predominant reasons for nest failure in grazed sites are trampling by the grazers and nest depredation. Nest failure from trampling of both simulated and natural nests increases with grazer stocking density and in areas where breeding by birds co-occurs with concentrated use by cattle (Bleho et al. 2014; Rolek et al. 2016; Sabatier et al. 2016; Sharps et al. 2017). Grazing and burning may increase nest depredation by both mammals (Matlack et al. 2001; Fuhlendorf et al. 2010; Ricketts and Sandercock 2016) and snakes (Lyons et al. 2015). In addition, grazers occasionally consume nest contents (Nack and Ribic 2005).

Grazing and fire can alter vegetation heterogeneity (providing habitat for a different nesting community), increase food availability, and increase brood parasitism, which are other possible drivers of grassland bird nest success. Grazer-modified vegetation provides a more diverse vegetation structure in some cases (Derner et al. 2009) and can increase insect abundance (Joern 2004, 2005; Moran 2014), which in turn can increase nesting habitat and food availability for a variety of bird species (Fuhlendorf et al. 2009). The vegetation structural differences in grazed and burned areas provide optimal nesting habitat for species that prefer shorter nesting vegetation (e.g., lark sparrows [*Chondestes grammacus*]; Lusk et al. 2003). However, if the avian community is dominated by species that do not prefer this type of vegetation (e.g., Henslow's sparrows [*Ammodramus henslowii*]), overall nest success of the community will be lower in this suboptimal habitat. In addition, grazing and burning can potentially increase brood parasitism by brown-headed cowbirds (*Molothrus ater*), which can decrease grassland bird nest success (Patten et al. 2006), depending on the host species and landscape context (near forest and forest host species; Peer et al. 2000, 2018; Hovick and Miller 2013).

The impacts of bison reintroduction on grassland bird nest success are unknown, so our objective was to determine how a recent reintroduction of bison influenced nest density, nest success, and brood parasitism of passerines in the first conservation-focused bison reintroduction site east of the Mississippi River. We also assessed two indirect impacts of bison presence (change in the avian nesting community and change in vegetation density) as potential mechanisms of any changes in nest success after the reintroduction. Given the small sample size per species for most species, we opted to analyze the collective impacts and those of the most common nester, the field sparrow (*Spizella pusilla*), to include a species-specific response in addition to our community-level analysis. We predicted reduced nest density and nest success initially after the reintroduction for pooled passerine species and field sparrows in areas with bison due to trampling, dislodgement, increased brood parasitism, and

nest predation. We also expected that <5 y post-reintroduction would not be enough time for a change in vegetation density or avian community composition that favored species that prefer grazing in tallgrass prairie (Pillsbury et al. 2011; Thompson et al. 2016). Thus, we expected a decline in pooled community-wide nest success in areas grazed by bison during the first few years following their reintroduction. In addition, we expected community composition and vegetation density would be related to site variables other than bison.

Methods

Study Site

Our research was conducted at Nachusa Grasslands (hereafter Nachusa) in northern Illinois, USA, from 2014 to 2018 (Figure 1). Since 1987, The Nature Conservancy (TNC) has been restoring previously cultivated land to tallgrass prairie yearly at Nachusa through revegetation, invasive species removal, and prescribed fire. Currently, Nachusa has over 1200 ha of restored prairie intermixed with prairie remnants. In October 2014, TNC reintroduced 30 American bison to 200 ha of restored and remnant prairie at Nachusa (0.15 head ha⁻¹). This is the first reintroduction of wild bison east of the Mississippi River as part of an ecological restoration of tallgrass prairie. As of 2018, there were about 133 bison inhabiting 607 ha (0.22 head ha⁻¹).

Sampling Design

We used a before-after-control-impact (BACI) design to test our predictions. We chose three *impact* sites (hereafter, bison sites) and three *control* sites (hereafter, non-bison sites) based on our ability to pair them by size and time since restoration in 2014 (Figure 1). These sites were monitored *before* bison reintroduction (2014) and *after* bison reintroduction (2015–2018). We categorized the age classes of the sites at the time the study began into young (<8 y old) restorations, old (>8 y old) restorations, and remnants (never plowed) for ease of comparison. Prescribed fire varied by site and by year depending on TNC's land management goals for those sites (average fire return interval <12 mo). Nachusa land management precluded equal numbers of prescribed fire treatments in bison and non-bison sites (Table 1), so sites were considered either burned (<12-mo fire return interval) or unburned (>12-mo fire return interval) in each study year. Bison regularly visited all three sites within the bison unit, as evidenced by grazing, bedding sites, and copious dung.

Nest Surveys

At each site, we found nests through a combination of systematic walking, haphazard walking, and behavioral cues as outlined by Winter et al. (2003). Nest searches were conducted in the morning (6:00 AM–12:00 PM, UTC –5) from early May to late July 2014–2018, excluding days with inclement weather (rain, wind >20 km hr⁻¹, and temperatures <10 °C or >30 °C). To ensure a consistent sampling effort, all sites were surveyed 1 or 2 times per week, and paired sites were surveyed equally. Once a nest was found, care was taken not to disturb the nest in any way that might influence nest success, including handling surrounding vegetation with bare hands. For each nest, we

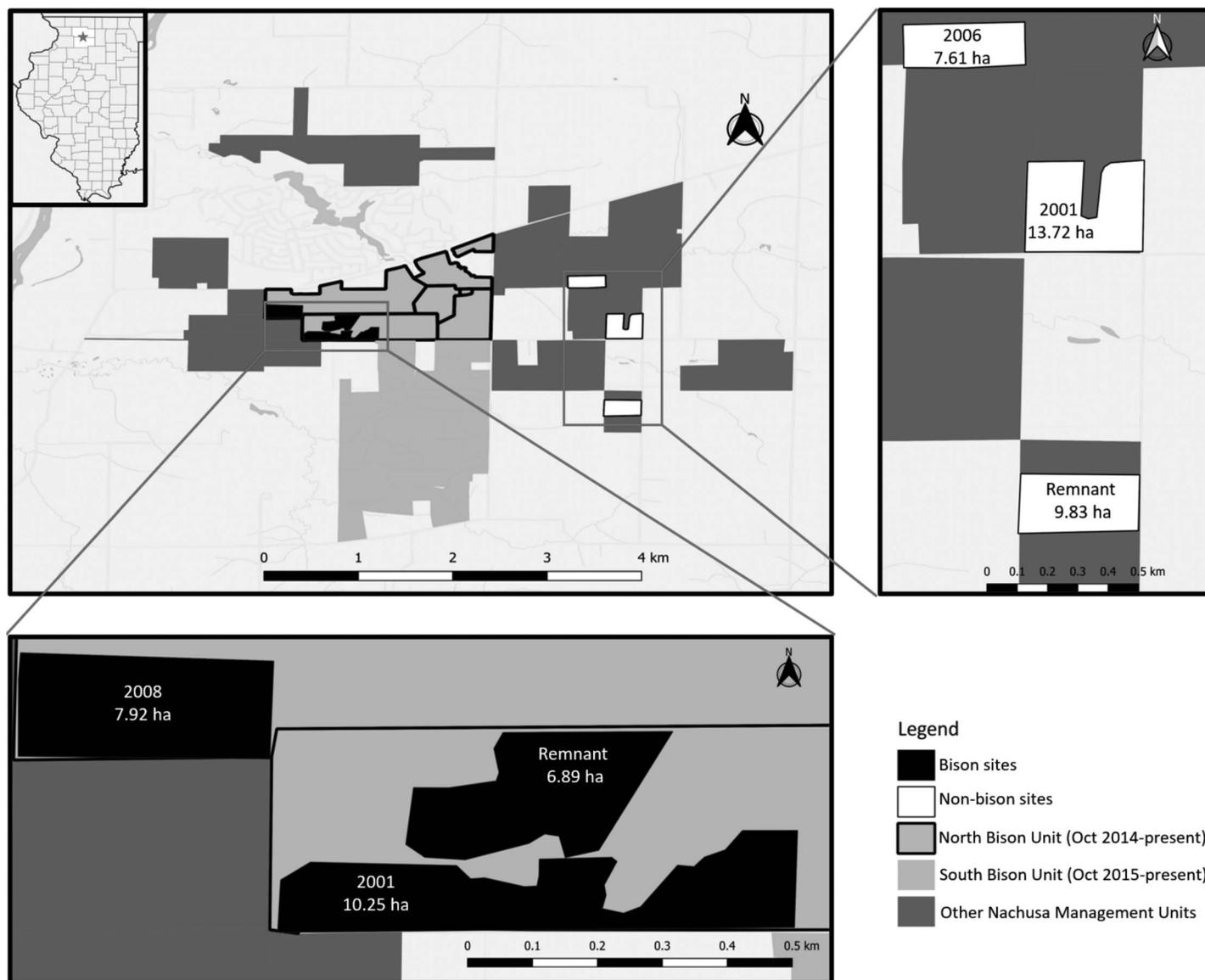


Figure 1.—Map of study sites at Nachusa Grasslands, Franklin Grove, Illinois. Areas filled with black are the sites we used that had bison present since October 2014. Areas filled with white are non-bison sites. Numbers in each area denote the year of planting and the size of the site. Areas filled with light gray are areas bison were allowed to roam (North Bison Unit—black outline, South Bison Unit—no outline). Black lines around the North Bison Unit do not denote fence line. Dark gray areas are other units at Nachusa that do not have bison.

Table 1.—Fire-return interval in months since last fire at the start of nest searching (May) for each site, each year, and overall site average at Nachusa Grasslands. The prescribed burn status at each site and if it had bison are in parentheses: burned (B), unburned (UB), bison site (G), and non-bison site (UG).

Site	2014	2015	2016	2017	2018	Avg ± SE
2008 (7.92 ha)	8 (B/UG)	3 (B/G)	15 (UB/G)	27 (UB/G)	3 (B/G)	11.2 ± 4.5
2001 (10.25 ha)	8 (B/UG)	20 (UB/G)	3 (B/G)	15 (UB/G)	3 (B/G)	9.8 ± 3.4
Remnant (6.89 ha)	8 (B/UG)	20 (UB/G)	3 (B/G)	3 (B/G)	3 (B/G)	7.4 ± 3.4
2006 (7.61 ha)	8 (B/UG)	3 (B/UG)	3 (B/UG)	3 (B/UG)	15 (UB/UG)	6.4 ± 2.4
2001 (13.72 ha)	3 (B/UG)	3 (B/UG)	3 (B/UG)	3 (B/UG)	15 (UB/UG)	5.4 ± 2.4
Remnant (9.83 ha)	3 (B/UG)	15 (UB/UG)	8 (B/UG)	20 (UB/UG)	3 (B/UG)	9.8 ± 3.4

recorded species, GPS coordinates, the number of eggs/chicks, parasitism by brown-headed cowbirds, and nest cup placement (Ralph et al. 1993; Winter et al. 2003). We checked each nest every 3 or 4 days depending on the ability to access nests (e.g., bison blocking access and weather outside of monitoring range) until the chicks fledged, the nest was depredated, or the nest was abandoned (which we defined as no parent present for a week or no hatching when expected). We excluded nonpasserine species as well as red-winged blackbirds (*Agelaius phoeniceus*), which tend to nest in close aggregations and thus may experience either (1) safety in numbers (group defense) or (2) increased predation owing to higher density. Hereafter we refer to the included passerines as the “target species.” We excluded nests that were no longer active when found and nests that could not be refound for a complete vegetation analysis ($n = 40$) for the survival and parasitism analyses. For nests with no obvious signs of success or failure ($n = 12$), we considered nests successful if they were within 3 d of expected fledge at last check and unsuccessful if chicks were not close to fledging at the last check (Jones et al. 2010).

Vegetation, Weather, and Spatial Data

After the nest was empty or failed to hatch, we quantified surrounding vegetation characteristics that may influence success. We measured percent cover of each plant type (forb, grass, and woody species) and bare ground in the immediate nest area using a 0.5 m² quadrat centered on the nest. In addition, we used a Robel pole to determine visual obstruction by vegetation at heights of 0.5, 0.8, and 1 m at distances of 2, 3, and 4 m from the nest in all cardinal directions (Robel et al. 1970). Vegetation may be denser at successful nests than unsuccessful nests because the increased amount of time the nest is active allows time for vegetation to grow (McConnell et al. 2017). To address this, we added a correction factor to our visual obstruction measurements based on the slope of visual obstruction over time multiplied by the difference in days from when the measurement was taken to the expected fledge date (Gibson et al. 2016). This corrected for any vegetation growth that may have happened between the time the nest was vacated and the day the visual obstruction measurement was taken. Bison grazing could have altered the vegetation immediately surrounding the nest if grazed between the time the nest was vacated and vegetation was measured; however, we did not see this occur at any of the monitored nests.

Vegetation measurements were also taken once per month at each vegetation control location in July 2014, June 2015, and May, June, and July 2016–2018. Vegetation control locations were at the center of both the bison and non-bison sites at least 25 m away from known nests at the time the measurement was taken to determine if vegetation was less dense overall in bison sites than non-bison sites. Visual obstruction measurements from nests and controls were averaged for each cardinal direction for the points taken at 4 m distance and 1 m height, as these measurements are less skewed and are most highly correlated with vegetation density (Robel et al. 1970). Because vegetation was not measured in the same months each year, we chose to use the data collected in July for 2014 and 2016–2018 and omit 2015 from the analysis.

We used publicly accessible precipitation and growing degree day (GDD) data from the nearest weather stations, Dixon 3.0 NNW IL (ILLE0010) and Rochelle, IL (USC00117349), to calculate the total precipitation during March and April (spring), total precipitation during the breeding season (May–July), and average GDD during the breeding season (May–July). Distance from nearest site hard-edge (stark change in habitat type), including agriculture fields, forests, or shrub/wetlands, was calculated in QGIS 3.0 to determine if edge effects played a role in nest success and bird community composition. Roads (asphalt, gravel, or dirt) were not considered a different habitat type (Walk et al. 2010).

Statistical Analyses

Pooled Nest Density, Nest Success, and Brood Parasitism: Nest density (nests ha⁻¹) was calculated for pooled nests of the target nesters for all sites each year ($n = 30$). We evaluated whether bison reintroduction influenced nest density by testing for an interaction effect between sites monitored before and after reintroduction and in bison and non-bison sites was tested using a generalized linear model (GLM) with a Gaussian family and identity link function. A significant result ($P \leq 0.05$) would indicate that bison reintroduction influenced nest density.

Nest success for the pooled nests was calculated using the logistic-exposure method (Shaffer 2004) to determine if overall nest success changed for our target species ($n = 130$ nests). This method uses a GLM with a binomial family and logistic-exposure link function to avoid biases associated with variation in exposure periods among nests. We evaluated whether bison reintroduction influenced pooled nest success by testing for an interaction among sites monitored before and after reintroduction and in bison and non-bison sites. A significant result ($P \leq 0.05$) would indicate the reintroduction of bison influenced pooled nest success.

The proportion of nests that were brood parasitized was analyzed using a GLM with a binomial family and logit link function to test the interaction described above. For each model (density, success, parasitism), if the interaction among sites monitored before and after reintroduction and in bison and non-bison sites was not significant, backward elimination was used until all variables were statistically significant ($P \leq 0.05$). We have reported the variables that were left following backward elimination, unless otherwise noted.

Field Sparrow Nest Success Analysis: Because field sparrows were the most common nester at out sites, we analyzed data from this species separately to see if bison and other variables impacted their nest success. We could not correct the visual obstruction measurement for all nests because not all of them had known laying, hatching, or fledging dates. For this analysis, we used only those nests whose fledging date was known or could be extrapolated using a typical incubation time of 10 d and nestling time of 7 d ($n = 39$ nests) (Baicich and Harrison 1997). Due to small sample size, only single term models (i.e., no interactions or additive models were assessed) were included and were analyzed using a logistic-exposure GLM (Shaffer 2004). To be included in the global model, categorical variables had to have at least 10 nests per level and continuous variables had to be uncorrelated ($r < |0.4|$). After these criteria were applied, bison,

Table 2.—Summary of nests used in the pooled analysis found in bison and non-bison sites at Nachusa Grasslands. Alpha codes, number of nests found, and total number of nests from 2014 to 2018 in order from most to least abundant. Bison sites indicate areas where bison were present. Non-bison sites include all sites in 2014 and non-bison sites 2015–2018.

Species	No. in bison sites	No. in non-bison sites	Total
Field sparrow (<i>Spizella pusilla</i> , FISP)	26	26	52
Dickcissel (<i>Spiza americana</i> , DICK)	2	26	28
Lark sparrow (<i>Chondestes grammacus</i> , LASP)	12	12	24
Song sparrow (<i>Melospiza melodia</i> , SOSP)	0	7	7
American goldfinch (<i>Spinus tristis</i> , AMGO)	1	4	5
Grasshopper sparrow (<i>Ammodramus savannarum</i> , GRSP)	1	3	4
Common yellowthroat (<i>Geothlypis trichas</i> , COYE)	1	2	3
Brown thrasher (<i>Toxostoma rufum</i> , BRTH)	0	3	3
Eastern meadowlark (<i>Sturnella magna</i> , EAME)	0	2	2
Indigo bunting (<i>Passerina cyanea</i> , INBU)	2	0	2
Total	45	85	130

fire, distance from the nearest hard edge, total spring precipitation, corrected visual obstruction, proportion of grass around the nest, total summer precipitation, and the day the nest was last active (linear and quadratic) were included in the model. Backward elimination was used until all remaining variables were statistically significant ($P \leq 0.05$) and we reported the remaining variables.

Mechanism 1: Community Composition: We used nonmetric multidimensional scaling (NMDS) with a Bray–Curtis dissimilarity index to determine if the species composition of the known nesters overlapped in bison and non-bison sites and if this composition changed from 2014 to 2018 for each site ($n = 30$). We used the function *envfit* in the package *vegan* (Oksanen et al. 2018) to determine which variables were correlated to the ordination. Because variables other than the presence of bison may have influenced species composition, we also included year, site area, site age, and whether the site was burned in the previous non-growing season (bison + year + site area + site age + burn). Correlation was assessed with 999 permutations and we reported the significant variables ($P \leq 0.05$).

If bison influenced species composition, we performed an additional analysis to determine if the differences were due to bison or to preexisting differences in the communities at these sites. First the NMDS was recomputed using only species nesting in the bison sites with year as the only variable in the model ($n = 15$). A significant effect of year indicated species composition in the bison sites changed over time. The above analysis was repeated using sites without bison to determine if year also influenced species composition at those sites. If a significant effect of year was not found in the non-bison sites, the change by year in bison sites would likely be due to bison presence. If year was not significant in the bison sites, a difference in species composition was likely due to preexisting differences in community composition (e.g., landscape composition) and not a consequence of bison reintroduction. Therefore, a separate analysis of the non-bison sites would be unwarranted. We used indicator species analysis with the function *multiplatt* from the package *indicspecies* (De Caceres and Legendre 2009) to determine which species were driving compositional differences among the significant variables found in all NMDS analyses.

Mechanism 2: Visual Obstruction: Visual obstruction measurements from vegetation control locations within the

bison and non-bison sites were compared in the BACI framework to test if vegetation density was lower in areas grazed by bison. We used measurements taken only in July (2014, 2016–2018; $n = 48$) and omitted 2015 ($n = 12$) from the analysis because they were taken in June. We compared the average visual obstruction using a GLM with a gamma family and inverse link function (Zuur et al. 2009). A significant interaction between sites monitored before and after reintroduction and with and without bison indicated that the reintroduction of bison influenced vegetation density. If the interaction was not significant, backward elimination was used until all variables were statistically significant ($P \leq 0.05$) and we reported the variables that were left, unless otherwise noted. To make sure the significance of the interaction was not being impacted by the removal of 2015 obstruction data, we modeled visual obstruction again including the June 2015 measurements.

All analyses were performed using R 3.5.1 (R Core Team 2018).

RESULTS

We found 170 nests of at least 10 species from 2014 to 2018. The most common species overall were field sparrows ($n = 64$) and dickcissels (*Spiza americana*; $n = 34$) (Table 2).

Pooled Nest Density, Nest Success, and Brood Parasitism

Bison reintroduction did not influence nest density (interaction, $t = 1.67$, $df = 29$, $P = 0.11$; Table 3, Figure 2). After backward selection, density was similar in bison sites and non-bison sites ($t = 0.701$, $df = 29$, $P = 0.49$) and before and after bison reintroduction ($t = 1.60$, $df = 29$, $P = 0.12$).

Pooled nest success of our target species increased in the bison sites after the reintroduction, while pooled nest success in non-bison sites decreased (interaction, $z = -1.97$, $df = 117$, $P = 0.05$; Table 3). Pooled nest success remained greater in bison sites during the first 2 y (2015 and 2016) after the reintroduction than non-bison sites. However, nest success did not differ between bison and non-bison sites during 2017 and 2018 (Figure 3).

Brood parasitism did not differ following bison reintroduction (interaction, $z = -0.58$, $df = 129$, $P = 0.56$; Table 3, Figure 4). However, brood parasitism varied considerably among years in non-bison sites. After backward elimination, brood parasitism

Table 3.—GLM output for the before-after-control-impact (BACI) analysis at Nachusa Grasslands on nest density (binomial), pooled nest success (logistic-exposure), and brood parasitism (binomial) before backward elimination. Models with corresponding estimates, standard error, test statistic (t for density, z for pooled nest success and parasitism), and P values are reported. If the interaction between sites before-after reintroduction (before-after) and bison sites and non-bison sites (control-impact) (BA*CI) is significant ($P \leq 0.05$), the reintroduction of bison had an impact on that variable. Significant interactions are denoted in bold.

Model	Estimate	Standard error	Test statistic	P
Nest density			t - value	
Before-After (BA)	−0.005	0.196	−0.03	0.98
Control-Impact (CI)	−0.012	0.124	−0.1	0.92
BA*CI	0.464	0.277	1.67	0.11
Nest success			z - value	
Before-After (BA)	0.873	0.218	1.84	0.07
Control-Impact (CI)	0.539	0.474	1.69	0.09
BA*CI	−1.40	0.624	−2.24	0.03
Brood parasitism			z - value	
Before-After (BA)	1.52	0.627	2.43	0.02
Control-Impact (CI)	−1.253	0.694	−1.80	0.07
BA*CI	−0.615	1.069	−0.58	0.56

differed significantly among all sites before and after bison reintroduction ($z = 2.58$, $df = 129$, $P = 0.01$) and between bison sites and non-bison sites ($z = -2.84$, $df = 129$, $P = 0.004$) with greater parasitism in non-bison sites.

Field Sparrow Nest Success

Overall nest success was greater for field sparrows in sites with bison than in sites without bison ($n = 39$, estimate = 1.18, $z = 2.31$, $df = 38$, $P = 0.02$). We found that fire in the previous nongrowing season, distance from the nearest hard edge, total spring precipitation, corrected visual obstruction, proportion of grass around the nest, total summer precipitation, and the day the nest was last active (linear and quadratic) did not influence field sparrow nest success. Since the BACI interaction could not be assessed, it is unclear if the bison reintroduction increased nest success, because field sparrow nest success increased after 2014 regardless of bison presence. Therefore, the greater nest success in bison sites cannot be attributed to bison reintroduction (Figure 5).

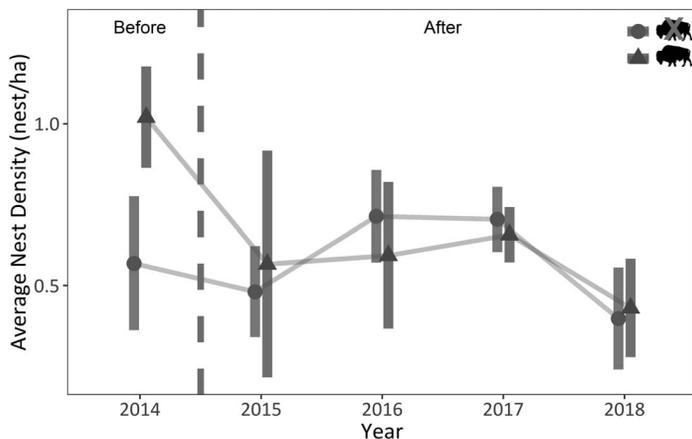


Figure 2.—Average nest density of our target species (passerines excluding red-winged blackbirds) in sites before (2014) and after (2015–2018) reintroduction and in non-bison sites (circles) and bison sites (triangles) ± 1 SE.

Mechanism 1: Community Composition

Nesting bird community composition differed between bison and non-bison sites (stress = 0.09; $R^2 = 0.156$, $P = 0.01$; Figure 6A), largely because nests of dickcissels were encountered more often in non-bison sites (IndVal = 0.77, $P = 0.01$). In contrast, nests of all other species were encountered in similar proportions in bison and non-bison sites. The relationship between community composition and site age was not significant ($R^2 = 0.159$, $P = 0.07$; Figure 6B). However, we encountered significantly more field sparrow nests in remnants and older restorations than in younger restorations (IndVal = 0.89, $P = 0.01$). In contrast, we encountered lark sparrow (*Chondestes grammacus*) nests more frequently in restorations, regardless of site age, than in remnants (IndVal = 0.67, $P = 0.04$). Nonetheless, the overall bird community within bison sites did not change during the study (stress = 0.03, $R^2 = 0.197$, $P = 0.27$).

Mechanism 2: Visual Obstruction

We found no difference in average visual obstruction due to bison reintroduction (interaction, $t = 1.11$, $df = 47$, $P = 0.27$;

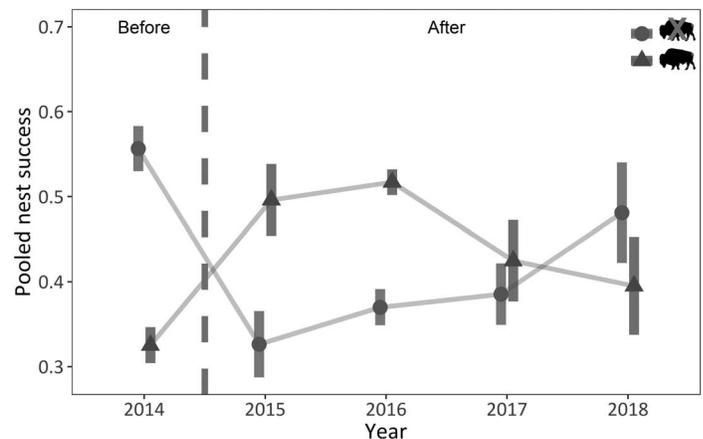


Figure 3.—Pooled nest success of our target species (passerines excluding red-winged blackbirds) in sites before (2014) and after (2015–2018) reintroduction and in non-bison sites (circles) and bison sites (triangles) ± 1 SE.

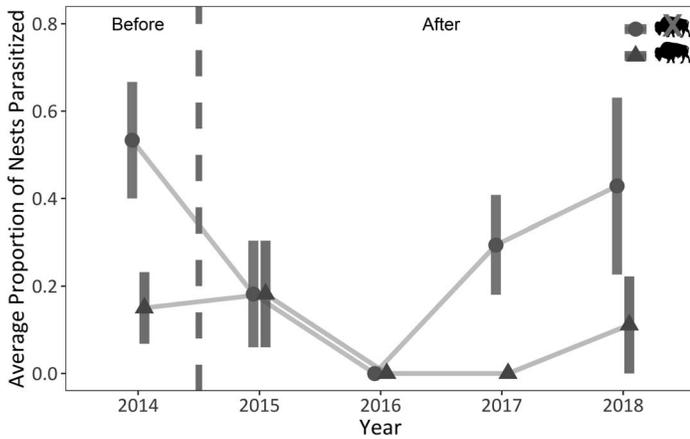


Figure 4.—Average proportion of nests that were brood parasitized by brown-headed cowbirds for target species (passerines excluding red-winged blackbirds) in sites before (2014) and after (2015–2018) reintroduction and in non-bison sites (circles) and bison sites (triangles) ± 1 SE.

Table 4, Figure 7), although variation in visual obstruction among sites was greater in 2014 than in later years, regardless of bison presence ($t = 2.24$, $df = 47$, $P = 0.03$). These conclusions were not changed by including 2015 obstruction data ($t = 0.99$, $df = 59$, $P = 0.33$).

DISCUSSION

Our results indicate that bison reintroduction appears to have increased nest success of our target passerine birds. However, the increased nest success in bison sites occurred for only the first 2 y (2015 and 2016) after the reintroduction. Nest success in bison and non-bison sites did not differ in years three and four (2017 and 2018). The greater nest success in years one and two may have been products of increased food availability (Orthopterans) and bison hair incorporated in nests, which can decrease predation risk (Joern 2004, 2005; Coppedge 2009, 2010). However, it is unclear why those benefits may have ceased in

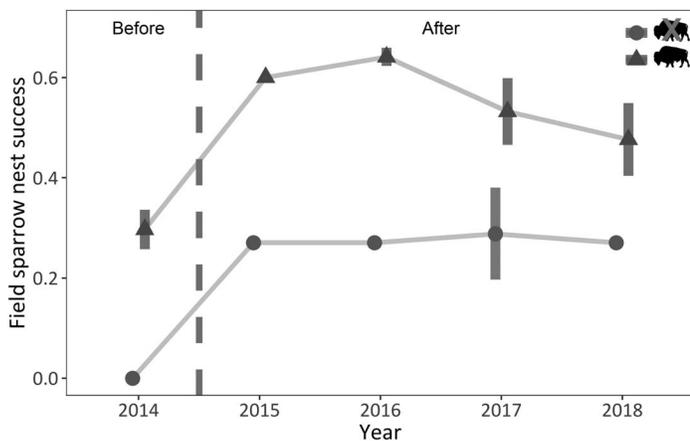


Figure 5.—Field sparrow nest success in sites before (2014) and after (2015–2018) reintroduction and in non-bison sites (circles) and bison sites (triangles) ± 1 SE.

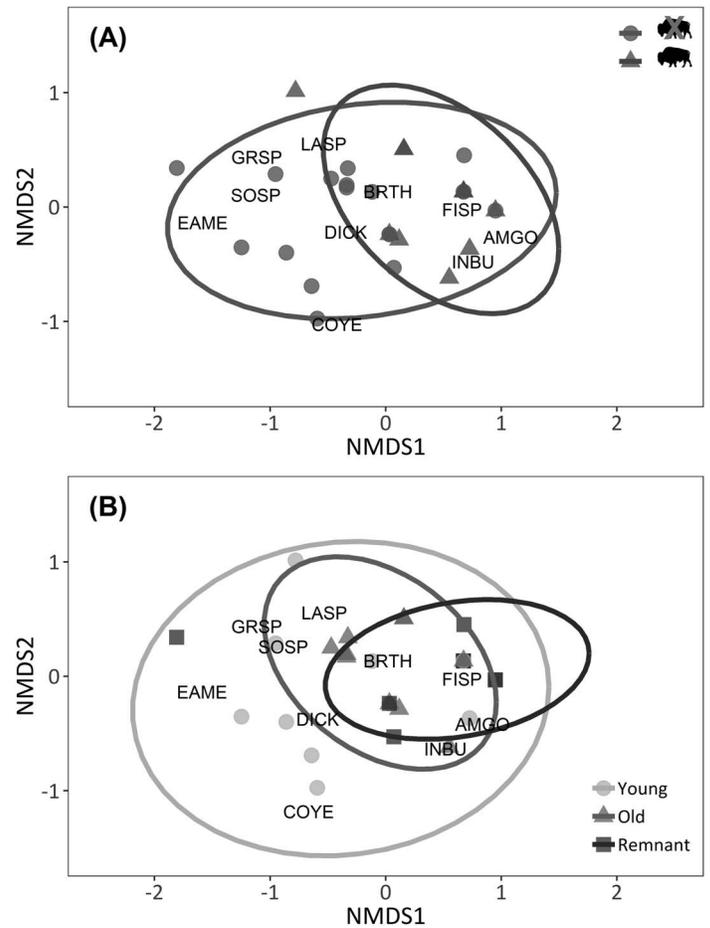


Figure 6.—Nonmetric multidimensional scaling (NMDS) plots showing the nesting species four-letter Alpha code (Table 1) for nests (stress = 0.09) (A) found in bison sites (triangles) and in non-bison sites (circles) and (B) found within different site ages (Young—circles; Old—triangles; Remnant—squares). Ellipses are 95% CI.

subsequent years. This lack of a continued strong signal in nest success beginning 3 y after the reintroduction may be due to changes in the species found at these sites.

Nests of field sparrows were the most abundant of any species in both bison sites (58%) and non-bison sites (31%). Field sparrows are predominantly associated with a shrubby forest–grassland ecotone and typically do not respond to grazing or

Table 4.—GLM output before backward elimination for the before-after-control-impact (BACI) analysis of visual obstruction (γ) at control locations within the bison and non-bison sites at Nachusa Grasslands, with corresponding estimates, standard error, t -statistic, and P values. If the interaction between sites before-after reintroduction (before-after) and bison sites and non-bison sites (control-impact) (BA*CI) is significant ($P \leq 0.05$), the reintroduction of bison had an impact on that variable. Significant interactions are denoted in bold.

Model	Estimate	Standard error	t	P
Before-After (BA)	0.003	0.003	0.32	0.31
Control-Impact (CI)	0.001	0.002	1.03	0.75
BA*CI	0.006	0.005	1.11	0.27

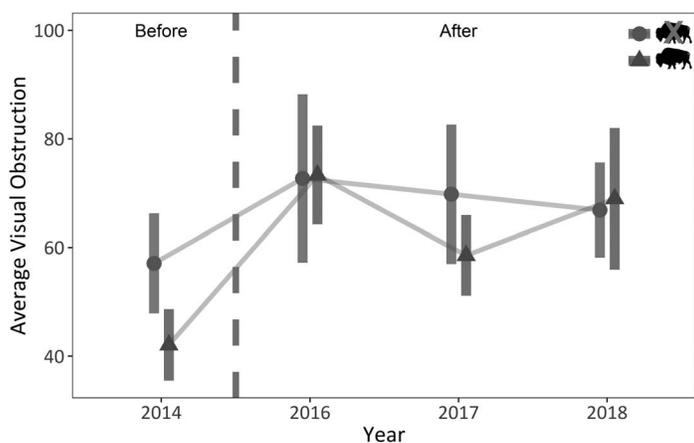


Figure 7.—Average visual obstruction (cm) at vegetation control locations before (2014) and after (2016–2018) reintroduction and in non-bison sites (circles) and bison sites (triangles) ± 1 SE.

prescribed burning if this habitat is maintained (Best 1977; Dechant et al. 2002). Although we could not assess whether the reintroduction influenced nest success of field sparrows (BACI interaction), the similar trends in nest success of field sparrows in bison and non-bison sites suggest that it did not (Figure 5). Also, the higher nest success found in bison sites was likely due to the greater amount of forested edge surrounding bison grassland sites, which is the preferred habitat of field sparrows (Best 1977). Prescribed fire and the other variables did not appear to influence nest success of field sparrows. Although the sites were burned at different frequencies, the consistent and frequent burning and the maintenance of surrounding forest and shrub cover likely contributed to the lack of a detectable impact. However, nest success remained fairly consistent in bison sites after the reintroduction, which suggests there was no negative impact of the reintroduction.

Field sparrow nests ($n = 26$) were the most abundant in bison sites followed by lark sparrow nests ($n = 12$). In the non-bison sites, lark sparrows were the third most abundant ($n = 12$). Because nest success of lark sparrows is typically greater in grazed areas (Lusk et al. 2003), their abundance in bison sites may have contributed to the overall higher pooled nest success in these sites and the lower pooled nest success in non-bison sites. This effect may have been especially important in 2015, when their nests were particularly abundant. However, field sparrows are likely driving pooled nest success in the bison sites more than lark sparrows because their nests were found more often (58%) and they share a similar nest success pattern over time with pooled nests in those sites. In non-bison sites, field sparrows ($n = 26$) and dickcissels ($n = 26$) were the most abundant nests. In contrast to bison sites, it is unlikely that field sparrows alone had as strong an effect on the pooled nest success estimates, given the opposite trends in nest success seen in non-bison sites for pooled nests and field sparrow nests. Dickcissel nests were found very infrequently in bison sites ($n = 2$). Success of dickcissel nests decreases in recently burned areas (Robel et al. 1998) and this may have contributed to the lower pooled nest success in non-bison sites from 2015 to 2017. However, this does not explain why pooled nest success was much higher in non-bison sites

before the reintroduction in 2014 because all sites were burned that year.

We are unable to explain why there was a difference in pooled nest success after bison reintroduction in the first 2 y. As predicted, the community composition of known nesting birds differed with bison treatment, but our findings suggest bison may not have driven this difference. Unlike other studies from grazed tallgrass prairies, our results did not show a shift in species composition over time in the bison sites. This could have been due to different stocking density of bison (0.1–0.2 head ha^{-1}) and forage availability at Nachusa compared to grazing studies done elsewhere (Oklahoma: 0.8 head ha^{-1} ; Fuhlendorf et al. 2006; Coppedge et al. 2008), the length of time the bison have been on the landscape (4 y vs. 10 y; Powell 2006), methodological and analytical differences, or the very frequent and consistent burn interval at Nachusa that does not resemble patch-burn grazing. Dickcissel nests were encountered more often in the non-bison sites and were the leading cause of the differences seen. This was likely because bison sites had a higher edge-to-area ratio, which dickcissels tend to avoid when nesting (Hughes et al. 1999; Jensen and Finck 2004). The community difference we detected may be a relic of landscape context differences that we could not account for in the study design (e.g., land cover of surrounding sites, restoration connectivity) between areas in which bison could be reintroduced and areas in which they could not be reintroduced.

In addition, vegetation density did not change in our study sites due to the bison reintroduction and was similar in bison and non-bison sites in 2016 and 2018. However, it is possible that our study, which was done in only a portion of the bison and non-bison restored prairie available to nesting birds, missed landscape scale changes in vegetation (e.g., increased heterogeneity across the landscape due to more frequent and larger grazed patches of shorter grass, or greater frequency of bare patches due to wallowing) due to bison that may be important to bird nest-site selection (Griebel et al. 1998). Although it is unknown when or if these shifts may occur across the entire landscape, our results suggest that they may take more than 4 y at our site under the current management.

We found no evidence that the bison reintroduction impacted nest density or brood parasitism in our study sites. Although we cannot rule out any direct impacts of bison (trampling, dislodgement, and possible depredation) on nests we did not encounter (Nack and Ribic 2005; Perlut and Strong 2011; Rolek et al. 2016; Sabatier et al. 2016), we think it highly unlikely, as we did not witness any destruction of the nests we encountered related to bison presence. The proportion of nests that were brood parasitized did not change because of the reintroduction, contrary to our expectations and other studies (Patten et al. 2006). However, the proportion of nests that were parasitized differed significantly between bison and non-bison sites.

Species composition and landscape context differences between bison and non-bison sites probably played a role in the proportion of parasitized nests. Nests of two species that sometimes reject cowbird eggs, dickcissels and eastern meadowlarks (*Sturnella magna*; Peer et al. 2000), were rarely found in bison sites so their behavior did not contribute to the overall lower parasitism found in these sites compared to non-bison

sites. However, this behavior could have contributed to the lack of parasitism seen in 2016 in the non-bison sites because most (53%) of the nests encountered were dickcissel and eastern meadowlark nests. Field sparrows typically accept cowbird eggs (Peer et al. 2000), and their nests made up 33% of those that were parasitized, but we could not determine if parasitism decreased nest success, because so few nests were parasitized ($n = 8$). Likewise, landscape context may have contributed to the overall low parasitism found in the bison sites. Cowbirds also parasitize nests of species located within forest edges at a higher rate than species nesting in grasslands (Hovick and Miller 2013). Forest edges were more abundant around bison sites and, coupled with species composition, likely influenced the differences seen between bison and non-bison sites. Long-term cowbird and bison spatial data and data on parasitism are needed to determine if bison influence the susceptibility of breeding birds to brood parasitism at Nachusa Grasslands.

We took advantage of an opportunity to examine the effects of a bison reintroduction on grassland bird nests and community composition at Nachusa. This necessarily imposed restrictions on the number of sites available for study, and, consequently, the potential sample sizes of bird species nesting within the sites. Given the small sample sizes and our pooled species analysis, we acknowledge the limitations on inferences we can draw. The brief increase in pooled nesting success immediately after the reintroduction and higher nest success of field sparrows in bison sites provided evidence that bison did not negatively impact nesting birds at Nachusa Grasslands, which was opposite of our expectations. However, caution should be taken when analyzing pooled impacts on bird species because measurements of density, success, and parasitism may disproportionately reflect the most abundant species in each treatment. However, this type of analysis may be especially useful to land managers who are concerned about how their restoration is affecting the nesting bird community and not just a single species.

Conservation and Management Implications

This is the first study to provide evidence of an immediate impact of bison reintroduction on grassland nesting birds. We found that bison reintroduction increased nest success of our target passerine species, but this impact was short-lived and influenced by the most abundant species. This short-lived increase suggests that the impacts from bison on bird nest success may need longer studies to determine overall impact on birds before it should be considered for management of tallgrass prairie restorations. Overall, the nesting bird community at the study site did not change with bison presence, and it is unknown when or if this will occur. Long-term monitoring is essential to understand how and if bison grazing may influence these birds in the future as their impacts on nesting success may be species- and site-specific. When or if a stronger effect on nest density, success, brood parasitism, or community composition will occur is unclear. Monitoring of grassland nesting birds should be implemented before, during, and after reintroduction of bison where possible to better understand impacts, especially in restorations. Our research suggests that reintroducing bison over entire landscapes will have minimal impact on nesting birds in the short term at low grazing densities. We urge caution

generalizing our results, however, when species of conservation concern inhabit a site. Such species were rare or absent from our study area, and our findings may not apply to these sensitive species.

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Heather Herakovich earned her BSc at Valparaiso University in Biology and her MSc and PhD degrees in biological sciences at Northern Illinois University in DeKalb, Illinois.

Christopher J. Whelan received a BS in Wildlife Ecology from the University of Wisconsin, Madison, and a PhD in Biological Sciences from Dartmouth College. He is an adjunct research associate professor and an applied biologist in cancer physiology conducting research focused on the evolutionary ecology of birds and cancer.

Nicholas A. Barber received a BSc in Biology from St. Louis University and a PhD in ecology from the University of Missouri-St. Louis. He is an assistant professor whose research focuses on the community ecology of natural, managed, and restored ecosystems.

Holly Jones earned degrees from UC Santa Cruz (BSc, Marine Biology and Ecology and Evolution) and Yale School of Forestry and Environmental Studies (PhD, Ecology). She is an associate professor studying restoration ecology and conservation biology.

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