

Grassland Bird Productivity in Warm Season Grass Fields in Southwest Wisconsin

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ABSTRACT.—Surrogate grasslands established through federal set-aside programs, such as U.S. Department of Agriculture’s Conservation Reserve Program (CRP), provide important habitat for grassland birds. Warm season grass CRP fields as a group have the potential for providing a continuum of habitat structure for breeding birds, depending on how the fields are managed and their floristic composition. We studied the nesting activity of four obligate grassland bird species, Bobolink (*Dolichonyx oryzivorus*), Eastern Meadowlark (*Sturnella magna*), Grasshopper Sparrow (*Ammodramus saviannarum*), and Henslow’s Sparrow (*A. henslowii*), in relation to vegetative composition and fire management in warm season CRP fields in southwest Wisconsin during 2009–2011. Intraspecific variation in apparent nest density was related to the number of years since the field was burned. Apparent Grasshopper Sparrow nest density was highest in the breeding season immediately following spring burns, apparent Henslow’s Sparrow nest density was highest 1 y post burn, and apparent Bobolink and Eastern Meadowlark nest densities were higher in post fire years one to three. Grasshopper Sparrow nest density was highest on sites with more diverse vegetation, specifically prairie forbs, and on sites with shorter less dense vegetation. Bobolink, Eastern Meadowlark, and Henslow’s Sparrow apparent nest densities were higher on sites with deeper litter; litter was the vegetative component that was most affected by spring burns. Overall nest success was 0.487 for Bobolink (22 d nesting period), 0.478 for Eastern Meadowlark (25 d nesting period), 0.507 for Grasshopper Sparrow (22 d nesting period), and 0.151 for Henslow’s Sparrow (21 d nesting period). The major nest predators were grassland-associated species: thirteen-lined ground squirrel (*Itidomys tridecemlineatus*), striped skunk (*Mephitis mephitis*), milk snake (*Lampropeltis triangulum*), American badger (*Taxidea taxus*), and western fox snake (*Elaphe vulpina*). Overall depredation rate was not affected by the number of years since the site had been burned. The diversity of vegetation on warm season CRP fields created by management using fire provides a continuum of structure for obligate grassland birds to use for breeding and habitat for a diversity of nest predators.

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INTRODUCTION

Many grassland bird species are now of conservation concern nationally and internationally because of widespread and steep population declines (North American Bird Conservation Initiative, 2009; COSEWIC, 2010). Alteration and loss of habitat (including fragmentation) are considered among the most important factors in these population declines (Brennan and Kuvlesky, 2005; Askins *et al.*, 2007). Grassland birds have faced extensive changes in habitat since settlement of North America by Europeans. For example native tallgrass prairie has been reduced to a small fraction of its historical area in the U.S. (Samson *et al.*, 1998). In the Midwest the recent population declines of grassland birds are related to rapid conversion since the 1950s of predominantly grass-based agriculture (*e.g.*, grass hay, pasture, small grains) to row-crop agriculture which is less suitable to birds as habitat (Murphy, 2003; Sample *et al.*, 2003).

Because of conversion of the prairie and oak savanna landscape to an agricultural landscape in parts of the Midwest (Drum *et al.*, 2015), conservation of grassland birds in that region is dependent on 'surrogate grasslands' (Sample *et al.*, 2003), primarily grasslands established through programs such as the U.S. Department of Agriculture's Conservation Reserve Program (CRP; *e.g.*, Johnson and Igl, 1995; Koford, 1999; Gill *et al.*, 2006; Jones-Farrand *et al.*, 2007; Niemuth *et al.*, 2007). When the CRP debuted with the 1985 Farm Bill, seed mixes for warm season grass contracts in Wisconsin were either monotypes of switchgrass (*Panicum virgatum*), simple mixes of big bluestem (*Andropogon gerardii*), switchgrass, and Indiangrass (*Sorghastrum nutans*), or a three grass mix with several forb species (Natural Resources Conservation Service, 2013). Cool season grass contracts were typically various mixes of smooth brome (*Bromus inermis*), timothy (*Phleum pratense*), Orchardgrass (*Dactylis glomerata*), and alfalfa (*Medicago sativa*). With successive Farm Bills, seed mixes for warm season grass fields became more diverse due to changing re-enrollment criteria and habitat initiatives (Farm Service Agency Online, 2016). Currently, warm season grass CRP fields as a group are diverse, ranging from the simple three grass seed mixes to diverse fields with a large variety of forbs (*e.g.*, restored prairies, Jaster *et al.*, 2014). In addition warm season grass fields are managed by disturbances such as fire (Askins *et al.*, 2007; Jones-Farrand *et al.*, 2007), which affect the field vegetation (*e.g.*, Grant *et al.*, 2011) and bird use of the managed fields (*e.g.*, Herkert, 1998 (revised 2002)).

To put warm season grass fields in context with other grassland habitats for grassland bird conservation, it would be helpful to understand how variation in vegetation types and management affects grassland bird use of fields. Much work has been done on understanding how grassland bird density patterns are influenced by vegetation structure (*see review by Askins et al.*, 2007). However, compared to density information, there is less information about grassland bird productivity across or within different habitat types (Jones-Farrand *et al.*, 2007). While nesting success of grassland birds in habitats such as cool season CRP fields, pastures, and remnant prairies has been relatively well-studied (*e.g.*, Herkert *et al.*, 2003; Renfrew *et al.*, 2005; Gill *et al.*, 2006; Walk *et al.*, 2010; Ribic *et al.*, 2012; Vos and Ribic, 2013), there has been comparatively less work on nesting success in warm season CRP fields (*e.g.*, Murray and Best, 2003; Henningsen and Best, 2005; Fletcher *et al.*, 2006; Jaster *et al.*, 2014). The objectives of this study were to determine the nesting activity of obligate grassland bird species in relation to field vegetation and fire management in warm season CRP fields. In addition we were interested in the causes of nest failure and how that might be affected by fire management. We focused on obligate grassland birds (species that require grasslands for breeding (Sample and Mossman, 1997)); the majority of which are designated

as Species of Greatest Conservation Need in Wisconsin (Wisconsin Department of Natural Resources, 2015a).

METHODS

STUDY AREA

We conducted our study May–August 2009–2011, on sites in southwest Dane, southern Iowa, and Lafayette counties in southern Wisconsin. The study sites are located within the Wisconsin Department of Natural Resources Southwest Wisconsin Grassland and Stream Conservation Area (42°38′18″N, 90°25′33″W and 43°0′45″N, 89°36′7″W; 191,862 ha) (Wisconsin Department of Natural Resources, 2015b). This conservation area is embedded within the Driftless Area, which remained unglaciated during the last glacial period. The topography consists of ridges and valleys that run south from the Military Ridge, an east-west ridge that begins west of Madison, WI and extends west to where the Wisconsin and Mississippi Rivers meet. The Driftless Area historically consisted of dry and dry-mesic prairie ridge tops and slopes with draws and valleys of oak savanna and mesic to wet prairie (Curtis, 1959; Cochrane and Iltis, 2000).

SITE SELECTION

We studied CRP fields planted with warm season grass/forb mixtures. Eleven fields were selected to span a continuum from low to high plant diversity (*i.e.*, sites dominated by warm season grasses to prairie restorations). Eight fields were used all 3 y, one field was used 2 y, and two fields were used 1 y. Fields had been enrolled in the CRP program an average of 13.7 y (SD = 1.8, range = 9 to 23 y) at the beginning of the study. Prescribed spring (April–early May) burning was used during the study by landowners to manage their fields (*i.e.*, required mid-contract management), though late season spot mowing was sometimes used to control noxious weeds. Field size averaged 26.9 ha (SD = 33.6, range = 8 – 124.8 ha). Property lines or fences were not considered field boundaries, while vegetation changes were considered (*e.g.*, a cool season CRP field composed of tall dense brome adjacent to the warm season grass field would be considered a boundary).

LANDSCAPE CHARACTERISTICS

Each year we cover-mapped an 800 m buffer around each study site using a combination of digitized orthophotos with ArcGIS (Environmental Systems Research Institute, 2011) and mapping in the field. Land uses in the 800 m buffers that did not change across the 3 y were woods (mean = 27.0%, SD = 15.0), developed (land predominantly covered by human-made structures and surfaces) (mean = 2.6%, SD = 0.8%), and wetlands (mean = 1.1%, SD = 1.1%). Change across the years occurred in two categories: pasture-idle grass-hay and row crops. Pasture-idle grass-hay in the buffer was highest in 2009 (mean = 43.4%, SD = 14.2%), declined in 2010 (mean = 39.3%, SD = 14.0%), and stayed low in 2011 (mean = 40.7%, SD = 13.3%). Row crops in the buffer were the lowest in 2009 (mean = 22.5%, SD = 8.6%), then increased in 2010 (mean = 27.5%, SD = 15.7%), and declined slightly in 2011 (mean = 24.6%, SD = 9.8%).

DATA COLLECTION

To standardize nest searching effort among the fields, all data were collected on an 8 ha study plot within each field. The study plots were placed in the center of the fields and were as rectangular in shape as possible within the size and shape limits of the fields. At least one

edge of the study plot was near a field edge (average = 9.8 m from an edge, SD = 23.6 m, n = 11).

Vegetation composition and structure.—We measured vegetation composition and structure at 16 random points per study plot between 15 June and 7 July of each year. Plant species richness, proportion cover of all forbs, prairie forbs, all grass, cool season grass, warm season grass, and litter were measured at each point using a 0.5 m x 1.0 m vegetation frame (larger size compared to the 0.2 m x 0.5 m frame used by Daubenmire, 1959). Litter depth (cm) was measured at three places (the center of the frame and 30 cm to the north and south of center) and averaged for each point. Vegetation height-density (dm) was measured using a modified Robel pole (Robel *et al.*, 1970); the pole was placed in the center of the vegetation frame and the height at which the vegetation obscured the pole was read from a height of 1.5 m at a distance of 4 m (Ribic *et al.*, 2012). Measurements were recorded in each of the four cardinal directions and averaged for each point.

Nest searching.—Study plots were searched once a week for nests from 15 May–31 July each year. Nests were primarily found using rope dragging, where three evenly spaced people dragged a 50 m sisal rope systematically through the plot. Two additional observers walked behind the rope and noted the location of flushed birds. When grass became too dense for rope searching to be effective, we used systematic walking to locate nests. For this method six to ten people spaced 2 m apart walked in a line through the study plot. Behavioral observations (*e.g.*, adults carrying nesting material or food, aggressive defense of an area) were also used to locate nests, especially during nest building and nestling stages. A few nests were found opportunistically 15 May–15 Aug. while we engaged in other activities within the study plot.

When a bird was flushed, searchers noted the location of the flush, and searched the surrounding vegetation for the nest. After finding a nest, the location was recorded using a Global Positioning System (GPS) unit, and a wire flag was placed four m to the North or South of the nest (direction was randomized). Nest contents were monitored every 2 to 3 d. At each visit to the nest, we recorded the number of eggs and chicks, the age of chicks, the presence of adults near the nest, and any Brown-headed Cowbird (*Molothrus ater*) parasitism. To avoid exposing chicks to the elements, nests were not disturbed during rain. While monitoring nests, care was taken not to alter the surrounding vegetation or create paths to the nest. Nests were considered a success if at least one chick fledged (not considering Brown-headed Cowbird chicks); nests that failed were noted as being depredated, failed due to parasitism or weather, abandoned (human caused or natural), other (*e.g.*, suspected ant infestation), or unknown. Signs of fledging included fledglings or agitated adults nearby and fecal matter or feather sheaths in the nest (Ribic *et al.*, 2012).

Nest vegetation measurements were collected within 1 wk after the final fate of the nest was recorded. Variables measured were vegetation height-density, proportion litter cover, and average litter depth (Ribic *et al.*, 2012). Nest locations were entered into a GIS and distances of nests to the nearest field edge were measured using ArcGIS (Environmental Systems Research Institute, 2011).

Video surveillance systems.—A subset of nests was monitored using miniature remote infrared video cameras (Ribic *et al.*, 2012). Cameras were placed on randomly selected obligate grassland bird nests and were evenly distributed among sites. We followed the recommendations of Richardson *et al.* (2009) when deploying cameras.

DATA ANALYSIS

We focused nest density and nest success analyses on Bobolink (*Dolichonyx oryzivorus*), Eastern Meadowlark (*Sturnella magna*), Grasshopper Sparrow (*Ammodramus savannarum*),

and Henslow's Sparrow (*A. henslowii*), the obligate grassland bird species with 15 or more nests.

Effect of fire on site vegetation.—We modeled the relationship between site-level vegetation composition, structure variables, and year since burn. Year since burn was the number of years that elapsed since a spring burn occurred. We used four burn categories: zero (breeding season immediately following the spring burn), one (1 y after the spring burn), two (2 y after the spring burn), or three plus (3 to 5 y after the spring burn). We used a linear mixed-effects model (Pinheiro and Bates, 2000) with site as a random factor. The error structure was assumed to be Gaussian. All cover variables were transformed with the arcsin square root transformation and plant species richness with the square root transformation to meet the distributional assumption. Because fields were surveyed over multiple years and observations could not be assumed to be independent, we fit different correlation structures (independence, symmetry, compound symmetry, autoregressive structure of order one). For model selection, we used an information-theoretic approach, ranking models using Akaike's Information Criterion adjusted for small sample size (AIC_c) (Burnham and Anderson, 2002). We used the model with the minimum AIC_c value to determine the structure that best fit the data. For the vegetation variables, this was compound symmetry.

Apparent nest density.—We calculated apparent nest density (nests/ha) for the four obligate grassland bird species for each site and year. We made the adjustments for nest density following Grant *et al.* (2011). As observed by Grant *et al.* (2011), adjusted nest densities were highly correlated with apparent nest densities ($r > 0.95$, all four species) and nest density results did not change. In terms of the relationship between breeding bird densities and apparent nest densities (also considered by Grant *et al.*, 2011), breeding bird density estimates based on spot mapping on the study plots (Byers, 2013) mirrored the patterns we found in apparent nest densities. Therefore, following Grant *et al.* (2011), we report apparent nest densities.

We first modeled the relationship between apparent nest density and year since burn for each species. We then investigated the relationship of apparent nest density, site vegetation variables, and log transformed field size. We developed a set of *a priori* vegetation models to avoid including vegetation variables that were highly correlated ($r > 0.70$) in the same model. We only used one- and two-variable models to avoid overfitting, given the number of observations (28 site-year combinations). The vegetation variables that were highly correlated were grass and forb cover ($r = -0.978$), cool season grass and forb cover ($r = -0.80$), plant species richness and prairie forb cover ($r = 0.77$), and litter depth and litter cover ($r = 0.93$).

We used a generalized linear mixed model with site as a random effect to model apparent nest density. Like the vegetation models, we fit different correlation structures and alternative response distributions, and then used AIC_c to determine the structure that best fit the data. For apparent nest density, the best response structure was a gamma distribution with a log link. Model selection is addressed below.

Nest success.—We used the logistic exposure method (Shaffer, 2004) for analyzing daily survival rate. We estimated species-specific nest success (the probability of fledging at least one young) by raising the daily survival rate to a species-specific nesting period. Because we had limited information on the laying period, we used the incubation and nestling periods as the nesting period. The nesting period was the average nesting period based on data collected in Wisconsin from 1998–2011, which was 22 d for Bobolink, 25 d for Eastern Meadowlark, 22 d for Grasshopper Sparrow, and 21 d for Henslow's Sparrow.

We first modeled nest success as a function of year since burn. We then modeled nest success as a function of nest vegetation, log (field size), distance to field edge, and type of field edge. Field edge type was grassy (cool season grass fields, pasture, wet meadow), agriculture (row crops, strip crops), or woody (woodlots, woody hedgerows). We used generalized linear models in R version 2.14.1 (R Development Core Team, 2012) to implement the logistic exposure method.

Model selection for apparent nest density and nest success.—As with the vegetation analysis, we used AIC_c to rank the models. For these analyses, we report the results of the models with the lowest AIC_c score and any models within 2 AIC_c units of those models. Models within 2 AIC_c units are considered competitive models (Burnham and Anderson, 2002). We also used evidence ratios based on AIC_c weights (Burnham and Anderson, 2002) to compare how much better the model with the lowest AIC_c score was in explaining the data compared to the competitive models. When an interaction was present, we plotted nest success predicted for the range of observed values to visualize the effect (Shaffer and Thompson, 2007); the other explanatory variables were fixed at the sample means.

Nest failure.—We identified the causes of nest failure for all obligate grassland bird nests that had video recordings; causes of failure were: abandoned, weather, other (*e.g.*, chicks died in the nest for unknown reasons), and predation. We included partial predation events, forced fledging, visits that did not result in predation, successful nest defense events, and scavenging events in the predation event tabulation. For nests with multiple visits by the same species of mammalian predator on the same day, each visit was considered a separate event if the visits were separated by at least 1 h; predator species were not marked and therefore individuals could not be identified. We identified individuals to species with the help of researchers from the Wisconsin Department of Natural Resources. For larger mammalian species (*i.e.*, those which were not captured on film in their entirety), we used pelage color and patterning, color and length of nails, and morphology of the forefoot to identify the species. Species were grouped according to habitat association using Ribic *et al.* (2012). Species not in Ribic *et al.* (2012) were classified based on Murphy *et al.* (1985), Allen (1986), Trani *et al.* (2007), and Kapfer *et al.* (in press).

We tabulated predation events by year since burn, predator species, taxonomic group, and habitat association. We used contingency table analyses to test whether nest predation was uniform across year since burn for all predation events, taxonomic groups, and nest predator species that depredated five or more nests. Due to low sample sizes in some of the categories, we used a Monte Carlo simulation approach to calculate P values using Tablesim (Rugg, 2003) and identified differences using residual analysis (Lloyd, 1999). We also tested for differences between distance to edge for nests depredated by the predator groups and successful nests and among nests depredated by the top five predator species. We used linear models with a Gaussian error structure. Unless otherwise specified, all analyses were performed using R version 3.2.3 (R Development Core Team, 2012) and significance was assessed at a P of 0.05.

RESULTS

We found 52 Bobolink nests, 36 Eastern Meadowlark nests, 32 Grasshopper Sparrow nests, and 20 Henslow's Sparrow nests over the three field seasons. Only six (4%) of the nests were parasitized by Brown-headed Cowbird (three Bobolink, two Eastern Meadowlark, and one Grasshopper Sparrow); none fledged a Brown-headed Cowbird chick.

Effects of spring fires on site vegetation.—At the site-level, litter cover and litter depth were affected by spring fires (litter cover: $F = 35.4$, $df = 3, 24$, $P < 0.001$; litter depth: $F = 21.1$, $df =$

TABLE 1.—Mean (standard error) of apparent nest density in relation to year since the site was burned for Bobolink, Eastern Meadowlark, Grasshopper Sparrow, and Henslow's Sparrow. Nests were found on warm season grass Conservation Reserve Program fields in southwest Wisconsin, May–August 2009–2011

Year since spring burn	Number of sites	Nests/ha			
		Bobolink	Eastern Meadowlark	Grasshopper Sparrow	Henslow's Sparrow
0	9	0.07 (0.05)	0.03 (0.02)	0.25 (0.13)	0
1	7	0.32 (0.15)	0.19 (0.06)	0.16 (0.06)	0.27 (0.12)
2	8	0.40 (0.22)	0.25 (0.12)	0.05 (0.03)	0.05 (0.02)
3	4	0.19 (0.08)	0.22 (0.08)	0.06 (0.06)	0.06 (0.06)

3, 24, $P < 0.001$) while average vegetation height-density ($F = 0.82$, $df = 3, 24$, $P = 0.50$), plant species richness ($F = 1.27$, $df = 3, 23$, $P = 0.31$), and the grass and forb cover metrics (grass cover, warm season grass cover, cool season grass cover, forb cover, prairie forb cover; $P > 0.10$) were not. Specifically, litter cover was lowest the year of the burn (year 0) (average = 0.17, $SE = 0.03$, $n = 9$) compared to post-burn years one to three (average = 0.84, $SE = 0.03$, $n = 19$) with no differences among post-burn years one to three. Litter depth was shallowest the year of the burn (year 0) (average = 0.24 cm, $SE = 0.05$, $n = 9$) compared to year one to three post burn (average = 5.32 cm, $SE = 0.41$, $n = 19$) with no differences among post-burn years one to three.

Apparent nest density.—Apparent Grasshopper Sparrow nest density was highest in the breeding season immediately following the spring burn (coefficient = 0.14, $SE = 0.01$) followed by nest densities in year one post-burn fields (coefficient = -0.04, $SE = 0.01$) (Table 1). Eighty-four percent of Grasshopper Sparrow nests were found in year zero post-burn fields (56%) and year one post-burn fields (28%). Nest densities were lowest in year two and year three post-burn fields (year two: coefficient = -0.09, $SE = 0.01$; year three: coefficient = -0.05, $SE = 0.09$) (Table 1). Apparent Grasshopper Sparrow nest density was best explained by site-level plant species richness (coefficient = 0.01, $SE = 0.005$) (Table 2), with more nests found on sites with more diverse vegetation. Plant species richness was primarily driven by prairie forb species richness ($r = 0.96$). Apparent Grasshopper Sparrow nest density was also higher on sites with shorter, less dense vegetation (coefficient = -0.006, $SE = 0.003$) (Table 2).

Henslow's Sparrow were not found nesting at any sites in the breeding season immediately following a spring burn (year zero). Apparent Henslow's Sparrow nest density was highest year one post-burn (year one: coefficient = 0.23, $SE = 0.06$; year two: coefficient = 0.08, $SE = 0.06$; year three: coefficient = 0.12, $SE = 0.08$) (Table 1). Seventy-five percent of all Henslow's Sparrow nests were found in year one post-burn fields. Year since burn was better than any vegetation metric for explaining apparent nest density for Henslow's Sparrow (Table 2). The closest vegetation model in the ranked AIC_c list was litter cover (coefficient = 0.20, $SE = 0.08$) (Table 2), with more Henslow's Sparrow nests found on sites with more litter cover. Year since burn was three times better at explaining nest density than litter cover (Table 2).

Bobolink and Eastern Meadowlark nests were found in fields in all post-burn years. Apparent Bobolink nest densities were significantly higher in year one to three post-burn compared to nest densities in year zero (year one: coefficient = 0.190, $SE = 0.074$; year two: coefficient = 0.277, $SE = 0.078$; year three: coefficient = 0.232, $SE = 0.109$) (Table 1). Apparent Eastern Meadowlark nest densities were also significantly higher in year one to three post-

TABLE 2.—Models for apparent nest density in relation to site-level vegetation for Bobolink, Eastern Meadowlark, Grasshopper Sparrow, and Henslow's Sparrow nests found on warm season grass Conservation Reserve Program fields in southwest Wisconsin, May–August 2009–2011. We report models within 2 AIC_c units of the minimum AIC_c model, the year since burn model, and the constant model. Brackets indicate a negative relationship of the variable to apparent nest density. N = number of site-year observations, K = number of parameters, and w_i = AIC_c model weight

Species	Model	N	K	ΔAIC_c	w_i	Evidence ratio
Bobolink	Litter cover	28	4	0	0.342	
	Litter depth	28	4	1.71	0.178	2.35
	Year since burn	28	5	3.19	0.085	4.92
	Constant	28	3	4.94	0.035	11.84
Eastern Meadowlark	Litter cover	28	4	0	0.482	
	Year since burn	28	5	1.69	0.207	2.33
	Constant	28	3	7.70	0.010	47.09
Grasshopper Sparrow	Plant species richness + [average vegetation height-density]	28	5	0	0.376	
	Plant species richness	28	4	0.342	0.317	1.19
	Constant	28	3	4.46	0.040	9.29
	[Year since burn]	28	5	12.05	0.001	413.2
Henslow's Sparrow	Year since burn	28	5	0	0.515	
	Litter cover	28	4	2.31	0.163	3.17
	Constant	28	3	4.66	0.050	10.30

burn compared to apparent nest densities in year zero (year one: coefficient = 0.18, $SE = 0.06$; year two: coefficient = 0.25, $SE = 0.06$; year three: coefficient = 0.28, $SE = 0.08$) (Table 1). Only 9% and 5% of Bobolink and Eastern Meadowlark nests, respectively, were found year zero post-burn fields. Peak nest densities for both species occurred 2 y after the burn (Table 1).

Apparent Bobolink nest density was best explained by litter cover (coefficient = 0.29, $SE = 0.10$) and litter depth (coefficient = 0.03, $SE = 0.01$) (Table 2). Higher apparent Bobolink nest densities were found on sites with more litter cover or deeper litter. The litter cover model was almost five times better than year since burn in explaining apparent Bobolink nest density (Table 2). Apparent Eastern Meadowlark nest density was also explained best by litter cover (coefficient = 0.27, $SE = 0.08$) (Table 2); higher apparent nest densities were found on sites with more litter cover. The year since burn model was competitive with the litter cover model (Table 2).

Nest success.—Daily survival rate (DSR) did not differ between incubation and nestling periods for any species nor did year since burn affect DSR (Table 3). Nest success was 0.487 (95% CI: 0.309 – 0.644) for Bobolink, 0.478 (95% CI: 0.289 – 0.646) for Eastern Meadowlark, 0.507 (95% CI: 0.285 – 0.695) for Grasshopper Sparrow, and 0.151 (95% CI: 0.036 – 0.346) for Henslow's Sparrow.

Bobolink daily survival rate was affected by average vegetation height-density and distance to edge (Table 3). Daily survival rate for Bobolink was higher when nests were placed in sparser, less dense cover (*i.e.*, lower vegetation-height density) (coefficient = -0.69 , $SE = 0.22$). Daily survival rate for Bobolink varied depending on the type of edge the nest was closest to (interaction coefficient = 0.04, $SE = 0.02$). Specifically, nest survival was lower when

TABLE 3.—Minimum AIC_c nest survival models and all models within 2 AIC_c units of the minimum, the constant model, the nest stage model, and year since burn model for Bobolink, Eastern Meadowlark, Grasshopper Sparrow, and Henslow's Sparrow nests on warm season grass Conservation Reserve Program fields in southwest Wisconsin, May–August 2009–2011. Brackets indicate a negative relationship of the variable to daily survival rate. N_{eff} = effective sample size, K = number of parameters, and w_i = AIC_c model weight

Species	Model	N _{eff}	K	ΔAIC _c	w _i	Evidence ratio
Bobolink	[Vegetation height-density] + Interaction of distance to field edge and type of field edge	492	5	0	0.632	
	[Vegetation height-density] + Distance to field edge	492	3	1.91	0.243	2.60
	Constant	492	1	10.24	0.004	167.49
	Nest stage	492	2	10.53	0.003	193.44
	Year since burn	492	4	11.86	0.002	376.61
Eastern Meadowlark	[Distance to field edge] + Litter depth	412	3	0	0.289	
	[Distance to field edge]	412	2	1.33	0.149	1.94
	Constant	412	1	2.91	0.068	4.28
	Year since burn	412	4	3.49	0.050	5.73
	Nest Stage	412	2	4.51	0.030	9.54
Grasshopper Sparrow	Constant	282	1	0	0.188	
	Distance to field edge	282	2	1.20	0.103	1.82
	Year since burn	282	4	1.98	0.070	2.69
	Nest stage	282	2	2.05	0.067	2.79
Henslow's Sparrow	Constant	113	1	0	0.182	
	Litter depth	113	2	1.04	0.109	1.68
	Year since burn	113	4	1.39	0.091	2.00
	Litter cover	113	2	1.59	0.082	2.22
	Log(field size)	113	2	1.98	0.068	2.69
	Nest stage	113	2	2.08	0.064	2.83

nests were placed closer to a woody/agriculture edge (distance to woody/agricultural edge coefficient = 0.04, SE = 0.01), but was unchanged when a nest was placed near a grassy edge (distance to grassy edge coefficient = -0.01, SE = 0.02) (Fig. 1).

Eastern Meadowlark daily survival rate was affected by distance of the nest to the field edge (Table 3) but, in this case, nests closer to the field edge, regardless of edge type, had a higher survival rate (coefficient = -0.017, SE = 0.007). In addition daily survival rate tended to be higher in sites with deeper litter (coefficient = 0.30, SE = 0.16).

Daily survival rates of Grasshopper Sparrow and Henslow's Sparrow nests were not affected by nest vegetation, log (field size), or distance to the field edge (Table 3).

Nest failure.—We monitored 133 nests of obligate grassland birds using a video surveillance system (122 were Bobolink, Eastern Meadowlark, Grasshopper Sparrow, and Henslow's Sparrow nests). There were 76 predator visits to 73 video-monitored nests; the predator species on 14 of the visits were not identifiable due to video system failure or poor views of the nest. Of the 62 predator visits where the individual was identified to species, the majority were depredation events (57 visits) (Table 4).

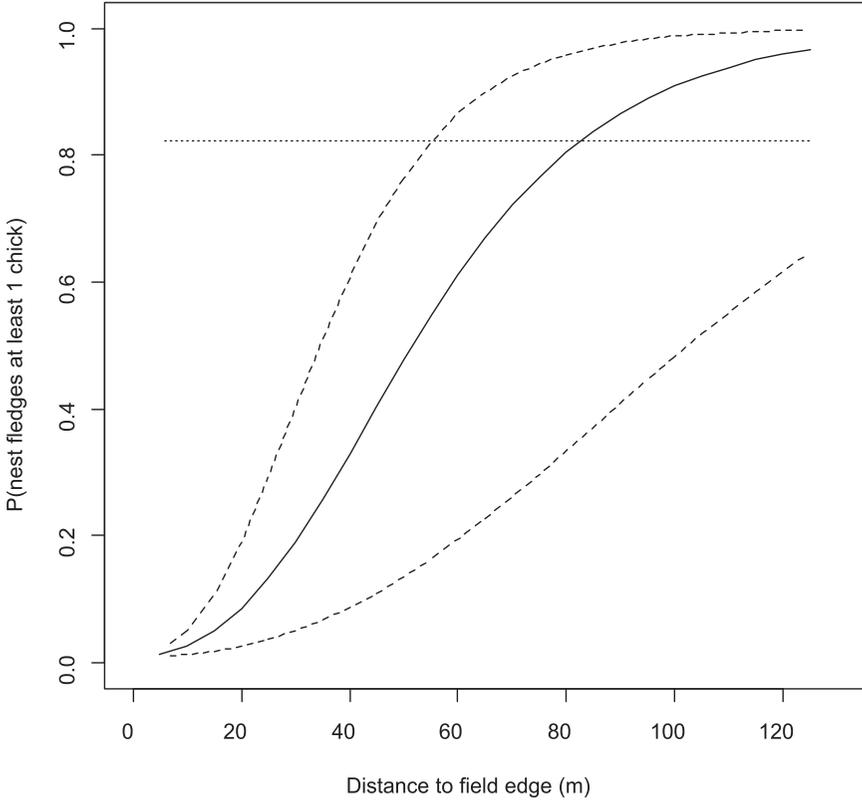


FIG. 1.—Predicted nest success by distance to a woody/agricultural edge (solid line) and grassy edge (dotted line) for Bobolink. Dashed lines are plus and minus 1 se for the woody/agricultural edge. The dotted line is the average nest success for Bobolink nests near a grassy edge; nest success did not differ for nests placed nearest to a grassy edge

Mammals accounted for almost 75% of known predator visits and 10 species were identified (Table 4). The major predator was thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*) (42.2% of mammalian visits); followed by striped skunk (*Mephitis mephitis*) (13.3%) and American badger (*Taxidea taxus*) (11.1%). All of these predators are associated with grasslands. Snakes accounted for almost a quarter of the predator visits (Table 4) and all visits by snakes were depredation events. The snake species that depredated the most nests were milk snake (*Lampropeltis triangulum*) (60% of all snake depredations) and western fox snake (*Elaphe vulpina*) (33%); both of which are associated with grasslands. The remaining predation events (2) were caused by a bird and an insect.

Overall nest depredations did not vary from a uniform distribution for year since burn ($\chi^2 = 2.64$, $P = 0.49$) and the same was true for nest depredations by mammals and snakes ($\chi^2 = 6.30$, $P = 0.41$) (Table 4). In contrast the visits of individual nest predator species varied from a uniform distribution for year since burn ($\chi^2 = 26.5$, $P = 0.02$) (Table 4). Specifically, thirteen-lined ground squirrels depredated more nests in 2 y post-burn fields (47.4% of the ground squirrel visits occurred 2 y post-burn) and more American badger depredations occurred in 3 y post-burn fields (80% of American badger visits occurred 3 y post-burn).

TABLE 4.—Species that visited obligate grassland bird nests on warm season grass Conservation Reserve Program fields in southwest Wisconsin May–August 2009–2011. Except where noted, all species visits were depredation events. Percentages in the table are in relation to total identified events

Species	Habitat association	Year since burn				Total events
		0	1	2	3	
Mammalia		9	12	13	11	45 (72.6%)
Thirteen-lined ground squirrel (<i>Ichthyomys tridecemlineatus</i>) ¹	Grassland	7	1	9	2	19
Striped skunk (<i>Mephitis mephitis</i>)	Grassland, Wetland	0	3	1	2	6
American badger (<i>Taxidea taxus</i>)	Grassland	1	0	0	4	5
Unknown mammal ²		1	3	0	1	5
Raccoon (<i>Procyon lotor</i>)	Woodland	0	1	1	1	3
Virginia opossum (<i>Didelphis virginiana</i>)	Woodland	0	2	0	0	2
Mouse (<i>Peromyscus</i> spp.)	Grassland	1	0	0	0	1
Vole (<i>Microtus</i> spp.) ³	Grassland	0	1	0	0	1
Eastern cottontail (<i>Sylvilagus floridanus</i>) ⁴	Woodland-grass edge	0	0	0	1	1
American mink (<i>Neovison vison</i>)	Woodland, Wetland	0	0	1	0	1
White-tailed deer (<i>Odocoileus virginianus</i>)	Woodland	0	0	1	0	1
Aves						
Brown-headed cowbird (<i>Molothrus ater</i>) ⁵	Woodland, Edge	0	0	1	0	1
Reptilia		4	5	6	0	15 (24.2%)
Milk snake (<i>Lampropeltis triangulum</i>)	Grassland, Wetland	3	3	3	0	9
Western fox snake (<i>Elaphe vulpina</i>)	Grassland, Wetland	1	2	2	0	5
Common garter snake (<i>Thamnophis sirtalis</i>)	Woodland, Wetland	0	0	1	0	1
Insects						
Ants (unknown spp.) ⁶	Grassland	1	0	0	0	1
Total		14	17	20	11	62

¹ Includes one successful nest defense

² Could not be identified to species due to mammal knocking camera askew or vegetation being moved in front of lens

³ Successful nest defense: vole chased from vicinity of nest by adult bird

⁴ Visit to nest; rabbit sniffed nest entrance, did not put head in nest

⁵ Egg destruction after fledge

⁶ The adult was on and off nest constantly picking at nest as chicks moved around fluffing themselves as if to shake something off; chicks die in nest; most likely insect is an ant as camera is close enough for spiders to be identifiable

Overall nest depredation (full or partial) was not affected by distance to field edge ($F = 0.003$, $df = 1$, 124 , $P = 0.95$) nor was there a difference by field edge type ($F = 1.37$, $df = 5$, 120 , $P = 0.24$). However, nests that were depredated by the top five predator species varied by distance to edge of field ($F = 3.52$, $df = 4$, 39 , $P = 0.01$). Specifically milk snakes depredated nests that were placed more in the center of the fields (mean distance from edge = 90.4 m, $SE = 16.4$, $n = 9$ visits) compared to the other major predators (mean distance from edge = 45.8 m, $SE = 5.5$, $n = 35$ visits).

DISCUSSION

We found Bobolink, Eastern Meadowlark, and Henslow's Sparrow nesting activity in warm season CRP fields was affected more by fire management while Grasshopper Sparrow nesting

activity was affected more by components of field vegetation that were not directly affected by fire.

In our study Bobolink and Eastern Meadowlark nested in fields along the full spectrum of years since burn with nest densities peaking 2 y after the burn. A similar response of apparent Bobolink nest density to fire was found by Grant *et al.* (2011) with nest densities highest during the second post-burn growing season. Powell (2008) found meadowlark densities to be higher 1 to 3 y after a burn than in the breeding season immediately following a burn. In our study increased Bobolink and Eastern Meadowlark nest densities were associated with deeper litter. Grant *et al.* (2011) also found litter to be important in determining nest densities in the mixed grass prairies of the Dakotas and eastern Montana. While Henslow's Sparrows may nest in fields the year of the burn (Winter, 1999; Crimmins *et al.*, 2016), nest densities are highest at least one year after the burn (Reinking *et al.*, 2000; Crimmins *et al.*, 2016) as we found in this study. Henslow's Sparrow require a well-developed litter layer for nesting (Herkert *et al.*, 2002) and low litter conditions immediately after a spring burn would not be conducive to Henslow's Sparrow nesting. Differences among the studies in grassland bird species' use of fields after a burn likely reflect interactions among regional species population levels, site vegetation composition and structure, fire severity, and regional differences in vegetation growing conditions.

Grasshopper Sparrow was the only species in our study to show a preference for nesting in diverse fields of mixed grasses and forbs with lower vegetation height-density, which likely reflects the species preference for open and sparse vegetation conditions (Vickery, 1996; Hovick *et al.*, 2012; Ribic *et al.*, 2012; Vos and Ribic, 2013). Grasshopper Sparrow may be indirectly affected by fire management via fire reducing the litter layer (*i.e.*, increasing bare ground) but this effect may only be evident on sites with a high forb component. In southwest Wisconsin apparent nest densities in warm season CRP fields (0 and 1 y post-burn) (this study) are higher than on cool season CRP fields (0.04 nests/ha, SE = 0.02, n = 8; calculated from data used in Ribic *et al.*, 2012; same study area as this study) but lower than on small remnant prairies (0.61 nests/ha, SE = 0.16, n = 6; calculated from data used in Ribic *et al.*, 2012).

We did a literature search for all grassland bird productivity studies up to 2015 to compare with our study; we focus here on studies that included fields with a warm season grass component. To compare across studies, we adjusted all nest success estimates (the probability of fledging at least one chick) to be on a common nesting period using information from Ehrlich *et al.* (1988). Bobolink nest success in our study (0.479; 23.5 d nesting period) was just below the upper range of values found in other warm season grass studies [range: 0.115 (tallgrass prairie; Winter *et al.*, 2006) to 0.634 (tallgrass prairie; Johnson and Temple, 1990)]. Eastern Meadowlark nest success in our study (0.441; 25.5 d nesting period) was among the higher values found in other warm season grass studies [range: 0.029 (reclaimed surface mine with mix of cool and warm season grasses and native and nonnative forbs; Graves *et al.*, 2010) to 0.564 (native prairie patches; Herkert *et al.*, 2003)]. Nesting success of Grasshopper Sparrows in our study (0.516; 20.5 d nesting period) was among the higher values found in other warm season grass studies [0.004 (reclaimed surface mine with mix of cool and warm season grasses and native and nonnative forbs; Graves *et al.*, 2010) to 0.571 (prairie barrens; Giocomo *et al.*, 2008)]. In our study Henslow's Sparrow nesting success (0.158; 20.5 d nesting period) was in the lower end of the values for other warm season grass studies [range: 0.133 (warm season grass restorations; Crimmins *et al.*, 2016) to 0.621 (cool season and warm season grass restorations; Jaster *et al.*, 2014)].

While a few studies (Hovick *et al.*, 2012; Jaster *et al.*, 2015) have found an effect of fire management on Grasshopper Sparrow nest success, we did not find such an effect for any of the species in our study. This is consistent with our finding that nest predation activity (as measured by predator visits to the nest) did not vary by year since burn. Instead, the most important factor affecting nest survival for Bobolink and Eastern Meadowlark in our study was distance to field edge. However, the effect differed for the two species. For Eastern Meadowlark, nest survival was higher closer to a field edge (regardless of edge type), while for Bobolink, nest success was lower closer to a woody/agriculture edge. Both patterns have been found for other grassland birds and both patterns have been explained by predation. Nest success higher near edges has been found by Grant *et al.* (2006), Ribic *et al.* (2012), and Ellison *et al.* (2013). These three studies all implicated thirteen-lined ground squirrel as the predator producing this pattern, a grassland species demonstrated to avoid woody edges (Ribic *et al.*, 2012). The other pattern of nest success lower closer to a woody edge is commonly assumed to be due to predators associated with woody habitat (*e.g.*, Heske *et al.*, 1999; Winter *et al.*, 2000). However, in our study, predators associated with woody habitat were minor nest predators and rarely move into CRP fields (Ribic *et al.*, 2012; Ellison *et al.*, 2013). These differing patterns may be a result of the interplay between the spatial locations of the different species' nests and the varying within-field densities of predators, a topic beyond the scope of this study.

We found grassland-associated mammals and snakes were the most important nest predators in warm season grass CRP fields. Studies using video surveillance systems in northern grasslands have found the majority of nest predations to be caused by mammals, particularly thirteen-lined ground squirrel, a grassland-associated species (Renfrew and Ribic, 2003; Davis *et al.*, 2012; Pietz *et al.*, 2012; Ribic *et al.*, 2012). Snakes have not been found to be major predators of grassland bird nests in northern grasslands (Renfrew and Ribic, 2003; Davis *et al.*, 2012; Pietz *et al.*, 2012; Ribic *et al.*, 2012), which might be due to the geographic location of the studies which coincide with or are above the latitudinal limits of most ectotherms (Thompson and Ribic, 2012). The higher proportion of snake predations in the warm season grass CRP fields of our study compared to what has been found in cool season CRP fields and pastures in our study area (Renfrew and Ribic, 2003; Ribic *et al.*, 2012; Ellison *et al.*, 2013) may be due to a difference in habitat quality. Warm season grass CRP fields may be better habitat for snakes than other grassy habitats (*e.g.*, contain more rodents as alternate prey for snakes, Ellison *et al.*, 2013; have denser cover, Lyons *et al.*, 2015) or some of the sites we used may have been closer to snake hibernacula (*e.g.*, as was found for one site in Ellison *et al.*, 2013).

We now have information on productivity of obligate grassland birds in all the major grassy habitats used for conservation in Wisconsin (Renfrew *et al.*, 2005; Ribic *et al.*, 2012; Vos and Ribic, 2013). How grassland birds use different grassy habitats for nesting depends on a range of factors, some of which humans can manipulate through vegetation management (Sample and Mossman, 1997). It has become clear multiple grassy habitats will be needed for effective grassland bird conservation in Wisconsin (Guttery *et al.*, 2017). However, information specifically on warm season grass fields is of interest for another reason, renewable energy (Energy Independence and Security Act; H.R. 6—110th Congress 2007). Warm season grass fields have a potential use as biomass feedstock which would affect their use for conservation (Paine *et al.*, 1996; Robertson *et al.*, 2012). Harvesting warm season grasses for biofuel feedstock may mimic the natural burn patterns that some prairie bird species have adapted to, as average vegetation height density and litter depth are reduced following a fall harvest (Roth *et al.*, 2005). Ultimately, whether warm season grass fields used

for biofuel feedstock can be usable for grassland bird conservation will depend on management and harvest practices (Swengel, 1996; Murray *et al.*, 2003; Robertson *et al.*, 2012; Ventura *et al.*, 2012; Uden *et al.*, 2015).

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