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Effects of Fire and Grazing on Grasshopper Sparrow Nest Survival

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ABSTRACT Patch-burn grazing is a management framework designed to promote heterogeneity in grasslands, creating more diverse grassland structure to accommodate the habitat requirements of many grassland species, particularly grassland birds. Published studies on the effects of patch-burn grazing on passerines have been conducted on relatively large (430–980 ha pastures), contiguous grasslands, and only 1 of these studies has investigated the reproductive success of grassland birds. We assessed the effects of the patch-burn grazing and a more traditional treatment on the nesting ecology of grasshopper sparrows (*Ammodramus savannarum*) in small (<37 ha pastures) grasslands located in southern Iowa from May to August of 2008 and 2009. The study pastures were grazed from May to September and prescribed burns were conducted in the spring. We investigated the effects of treatments on clutch size and modeled grasshopper sparrow nest survival as a function of multiple biological and ecological factors. We found no difference in clutch size between treatments; however, we did find a reduction in clutch size for nests that were parasitized by brown-headed cowbirds (*Molothrus ater*). Constant daily survival rates were greater in patch-burn grazed pastures than in grazed-and-burned pastures (patch-burn grazed rate $\bar{x} = 0.930$ and grazed-and-burned rate $\bar{x} = 0.907$). Competitive survival models included year, stage of nest, nest age, and cool-season grass (csg) abundance within 5 m of the nest. Overall, csg abundance had the greatest effect on survival and had a negative influence. Although survival rates were highest in patch-burn grazed pastures, multiple factors influenced grasshopper sparrow survival. Nest survival rates for both treatments were relatively low, and variables other than treatment were more instrumental in predicting grasshopper sparrow survival. We recommend decreasing overall vegetation cover if increasing nesting habitat for grasshopper sparrows is a management goal. In addition, we recommend further investigation of heterogeneity management in fragmented landscapes to better understand how it affects biodiversity in relatively small management units that typify grassland habitats in the Midwest. © 2011 The Wildlife Society.

KEY WORDS *Ammodramus savannarum*, daily survival rate, grasshopper sparrow, Iowa, nest success, patch-burn grazing, prescribed fire, tallgrass prairie.

Native grasslands in the central United States have experienced widespread conversion to cropland and many native grasslands that have not been converted have experienced a decoupling from historic disturbances, resulting in encroachment by woody vegetation (Samson and Knopf 1994, Fuhlendorf and Engle 2001). Fire suppression and the removal of large herbivores can make grasslands unsuitable for grassland-bird habitat specialists (Fuhlendorf et al. 2006). In addition, agricultural practices aimed at increasing livestock production have also been identified as negatively affecting grassland bird populations (Fuhlendorf et al. 2006, With et al. 2008). These include cross-fencing pastures, annual burning, intensive early grazing and over-stocking, and the elimination of forbs—all of which have a homogenizing effect on grassland habitats (Churchwell et al. 2008). Collectively, these practices result in decreased habitat heterogeneity in small parcels as well as at landscape scales (Fuhlendorf et al. 2006).

The use of fire and grazing in tandem is recommended to promote heterogeneity sufficient to accommodate a broader

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spectrum of habitat requirements for grassland-dependent birds (Fuhlendorf et al. 2006), and it is contended that grazing and fire do not operate independently and in many cases the interaction of these processes is more important than the sum of their independent effects (Fuhlendorf et al. 2009). Patch-burn grazing is a management framework that relies on the application of discrete fires to grasslands and allows grazing animals to freely select from burned and unburned portions of the landscape (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Free-ranging grazers focus on recently burned areas, decreasing the probability of future fires and allowing fuel to accumulate in areas with more elapsed time since fire. This process creates a shifting mosaic of grassland patches with varying structure (Fuhlendorf et al. 2009).

To date, most published studies on the effects of patch-burn grazing on grassland birds have been conducted on The Nature Conservancy's Tallgrass Prairie Preserve, a relatively large (approx. 14,000 ha), contiguous grassland in the southern Flint Hills (Osage Hills) of Oklahoma. There, researchers have reported an increase in the diversity of grassland-bird species in pastures treated with patch-burn grazing compared with those under traditional management (Fuhlendorf et al. 2006, Coppedge et al. 2008). Diversity increases under patch-burn grazing due to the increased availability of habitat extremes that result from the fire–grazing interaction (Fuhlendorf et al. 2009). In the only study to investigate nest success under patch-burn grazing, Churchwell et al. (2008) reported greater nest success for dickcissels (*Spiza americana*), a habitat generalist, in 1-yr and 2-yr post-burn patches in patch-burn grazed pastures compared to traditionally managed pastures.

In contrast to the Flint Hills, most of the remaining grassland in the Midwestern United States occurs in the form of small, privately held pastures and hayfields (Herkert et al. 1996). Extrapolating results from studies conducted on relatively large and contiguous prairie to more fragmented landscapes may result in inappropriate management strategies. Although patch-burn grazing may result in vegetation structure that is typically not available for habitat specialists on traditionally managed pastures, it is also possible that this framework may result in deleterious effects for nesting birds when applied to smaller pastures by essentially increasing fragmentation.

We examined the effects of patch-burn grazing on nest survival and clutch size in small experimental pastures representative of many grassland parcels in the Midwest. Our focal species was the grasshopper sparrow (*Ammodramus savannarum*), a grassland-obligate of widespread concern because it has declined by >70% across its range (Herkert 1994, Panjabi et al. 2005). This species is a grassland generalist and was abundant on all of our research sites. The main objective of this study was to evaluate the effect of patch-burn grazing and a more traditional treatment on grasshopper sparrow nest survival. In addition to treatment effects, we were interested in the influence of a variety of ecological parameters on nest success of this species.

STUDY AREA

Our study was conducted on 9 pastures in Ringgold County, Iowa, ranging from 22.5 ha to 37 ha and distributed within an area encompassing approximately 50 km^2. Pastures were part of a larger region called the Grand River Grasslands (approx. 40,000 ha), which was designated as a conservation opportunity area by The Nature Conservancy and the Missouri Department of Conservation (MDC) for the potential conservation value this area has for migrating and breeding grassland birds (MDC 2005). Pastures were under the jurisdiction of either the Iowa Department of Natural Resources, The Nature Conservancy, or privately owned. The study area lay within the Dissected Till Plains physiographic region, originally shaped by the Pre-Illinoin glacial advances roughly 500,000 years ago (Prior 1991). Mean annual precipitation for the area is 90–100 cm (National Climatic Data Center 2009). About 80% of the region remained in native and non-native grasslands, although woodlands and row-crop fields are common in drainages and river bottoms. On average, the landscape (within 1 km) surrounding research pastures was 12% row-crops, 62% grassland, and 24% woody vegetation (F. Pillsbury, Iowa State University, unpublished data). Dominant native herbaceous species included rough dropseed (*Sporobolus clandestinus*), sedges (*Carex* spp.), and Baldwin's ironweed (*Veronica baldwinii*; McGranahan 2008). Tall fescue (*Lolium arundinaceum*), an exotic forage species, was present on all pastures and was the dominant grass species on most (McGranahan 2008). Other common exotics included black medick (*Medicago lupulina*) and Kentucky bluegrass (*Poa pratensis*).

In 2007, research pastures were randomly assigned to either the patch-burn grazed treatment ($n = 5$) or a grazed-and-burned treatment ($n = 4$). All pastures were fenced on the perimeter and stocked with cattle for a 5-month grazing season (May–Sep) at the rate of 3.5–5.9 animal units per month per hectare (AUM/ha). In the patch-burn grazed treatment, a third of each pasture was burned sequentially so the entire pasture was burned over the course of 3 yr (2007–2009). Grazed-and-burned pastures were burned completely in the third year of the study to prevent encroachment of woody-plants. All prescribed fires were conducted between late March and late April, depending on weather conditions.

METHODS

Data Collection

We searched for nests from 0600 to 1200 (CST) from 14 June 2008 to 15 July 2008 and from 15 May 2009 to 25 July 2009. We did not conduct searches during rain events (Martin and Geupel 1993). We located most nests by systematic rope-dragging (Higgins et al. 1969) and placed a flag at 1 end of a 30-m rope every 50 m to ensure complete and systematic coverage of research pastures. In the event of a flush, we searched the immediate area extensively. If a nest was not found and the flushed bird showed signs of nesting (i.e., insistent chipping, flailing wing display, and short-circular flights), the location was marked as a probable nest site and searched again within 3 days by walking and using flushing sticks (Winter et al. 2003). We located a few nests by observing parental behavior and through incidental flushes.

When we located nests, we recorded the Universal Transverse Mercator (UTM) coordinates, candled eggs to determine age (Lokemoen and Koford 1996), and placed flagging 5 m north and 5 m south of the nest to aid in relocation. We placed nest-site flagging low in the vegetation to reduce visual cues to aerial predators. We subsequently visited nests every 3 days, with more frequent visits near stage transitions to determine ages and outcome more accurately. During each nest visit, we recorded the date, time, and number and stage of all nest contents (Ralph et al. 1993). We considered a nest to be successful if ≥ 1 conspecific young fledged. We confirmed fledging by parental behavior (i.e., alarm calls and feeding).

We measured vegetation features at each nest to quantify differences in structure and composition between the 2 treatments and to relate vegetation characteristics to daily survival rates. We standardized vegetation measurements 25 days after the calculated nest initiation dates, which is the typical nesting period for grasshopper sparrows (Vickery 1996), to reduce biases stemming from failed nests. We quantified abundance of warm-season grasses, cool-season grasses, tall fescue, forbs, bare ground, litter, and woody vegetation using a 0.5-m^2 quadrat that was centered over nests and placed at locations 5 m from nests in each cardinal direction (Dieni and Jones 2003). We estimated cover using the midpoints of the following categories: 0–5%, 6–25%, 26–50%, 51–75%, 76–95%, and 96–100% (Daubenmire 1959). We measured vegetation structure in each quadrat by recording the height at which a Robel pole was 50% obscured while standing at a distance of 4 m and viewing at 1 m above ground (Robel et al. 1970). We measured tall fescue separately from other cool-season grasses because of its dominance in research pastures (McGranahan 2008) and because it is an invasive species that has been associated with poor feeding, nesting, and roosting habitat for grassland birds (Barnes et al. 1995).

We quantified distance to woody edges, fencelines, and permanent water bodies from each nest because these edges have been identified as possible corridors for mesopredators, making nests in closer proximity more susceptible to predation (Kuehl and Clarke 2002). We quantified edge distances using ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California) and overlaying the UTM coordinates of each nest on 2-m resolution true-color digital orthophotos.

Data Analysis

We used SAS 9.2 (SAS Institute Inc., Cary, North Carolina) to compare clutch size across treatments (i.e., grazed-and-burned pastures, patch-burn grazed current-year burn, patch-burn grazed 1-yr post-burn, and patch-burn grazed 2-yr post-burn). We employed a 2-way analysis of variance (ANOVA) with a split-plot design to incorporate the potential non-independence of patches within pastures. In addition, we compared clutch size reductions of parasitized and non-parasitized nests across treatments in both years of the study using the same method. We considered patches within patch-burn pastures to be the experimental unit because each patch had a unique treatment imposed by the fire–grazing interaction (Churchwell et al. 2008). We report comparisons of parasitized and non-parasitized clutch sizes as means and standard errors.

We estimated daily nest survival using the nest survival model in program MARK (White and Burnham 1999). Program MARK uses a maximum-likelihood estimator and the use of a logit function to derive daily survival probabilities (Dinsmore et al. 2002). We also report constant (Mayfield) daily survival rates to facilitate comparisons with previous grassland bird research that used this method (Mayfield 1961), but our primary focus was identifying variables affecting nest survival.

We used a hierarchical modeling scheme to assess the effects of multiple variables on nest survival (Winter et al. 2006, Dinsmore and Dinsmore 2007). This multi-step approach was somewhat exploratory and included more models than a strictly a priori approach, but allowed us to reduce the overall model set. At each step, we ranked all models using Akaike's Information Criterion, adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We used the model with the lowest AIC_c score from each step as a base model in the next. If adding variables in a given step did not increase the parsimony of the model, then we used the base model from the previous step in the next step. After we completed all modeling we used the general approach of Burnham and Anderson (2002) for making inferences from the model set.

We included biological and ecological parameters in MARK models on the basis of expected changes in vegetation structure and composition observed in previous patch-burn studies (Fuhlendorf et al. 2006, Coppedge et al. 2008), and based on grasshopper sparrow life-history traits (Vickery 1996). We divided nesting data into 20 groups generated from combinations of year, nesting stage, and treatment. Nests found during the laying or incubation stages and surviving multiple stages could be included in multiple groups. In such cases, we censored the nest on the last day of observation for the first stage and initiated the exposure days on that same day for the second stage (Dinsmore and Dinsmore 2007). To standardize nesting seasons across both years, we set 14 May as day 1 and sequentially numbered days through 15 August.

We determined modeling steps partially on the basis of scale, or how we think a bird may have assessed the landscape. For example, we examined broad-scale effects such as whole pasture treatments first and the final set of models included measurements at the scale of the nest site. We grouped variables that were not associated with spatial scale with other related variables and incorporated them into the hierarchy in chronological order as they related to the nesting cycle.

In the first modeling step, we tested for an effect of treatment. We coded the treatments with a combination of 0 and 1 to represent the 4 different experimental units. The null model was constant survival across all treatments and across the breeding season.

In the second modeling step, we incorporated temporal patterns within and between years. Within year variation in survival may result from the timing of nest initiation for birds with nesting experience compared to those without, seasonal weather patterns, shifts in food resources, and changes in the predator community (Wiebe and Martin 1998, Dinsmore et al. 2002). Similarly, annual variation in survival may be due to weather events, cyclical increases in predator or prey abundance, resource availability, and changes in landscape composition (Rotenberry and Wiens 1989, Grant et al. 2005).

In the third step, we explored the effect of nest placement relative to 3 edge types: woody vegetation, fence-lines, and permanent water bodies. These edges have been associated with mesopredator abundance and may act as corridors, making nests in close proximity to them more vulnerable to opportunistic predation events (Renfrew and Ribic 2003).

Step 4 included parasitism by brown-headed cowbirds (*Molothrus ater*) and stage of nesting, incubation, and nestling stages for each year, plus the egg-laying stage in 2009. We examined the effects of parasitism on survival because parasitized nests have been recorded as having lower survival rates for host species (Green, 1999). Similarly, we examined nest-stage effects because survival may decrease during the nestling stage due to increases in parental activity around the nest site (Conway and Martin 2000).

In the fifth step, we investigated the effect of nest age within each nesting stage and regular nest visits by researchers. We examined age within stage because increased exposure during nest stages increases the probability of predation (Johnson and Temple 1990, Dinsmore and Dinsmore 2007), and we included nest visits to determine the effectiveness of precautions taken during data collection to prevent negative effects on nesting survival.

We added fine-scale habitat variables in the final 2 modeling steps. The sixth step included vegetation variables recorded in quadrats 5 m from the nest in each cardinal direction. The seventh and final step incorporated vegetation variables collected in a quadrat centered on the nest (see Data Collection Section).

RESULTS

In 2008 and 2009, we monitored 327 grasshopper sparrow nests (77 in 2008 and 250 in 2009). Clutch sizes differed between parasitized and non-parasitized nests across all research patches (i.e., experimental units; $F_{1,310} = 105.09$, $P < 0.001$); average clutch size for parasitized nests was 2.42 (SE = 0.12) and non-parasitized nests was 3.92 (SE = 0.07). Rates of parasitism were not different across research patches ($F_{3,310} = 0.78$, $P = 0.50$; Table 1), and the clutch sizes of non-parasitized nests were not significantly different across research patches ($F_{3,178} = 1.09$, $P = 0.35$; Table 1).

We included 323 nests with known fates in a maximum-likelihood analysis in the nest survival model of program MARK. Our results indicated that treatment had little effect on survival of grasshopper sparrow nests. Survival of grasshopper sparrow nests was influenced most by year, nest stage, age of nest, and cool-season grass (csg) abundance within 5 m of the nest (Table 2). Evidence of a year effect on survival was strong in the best model. Compared with 2009, survival in 2008 was substantially greater ($\beta_{2008} = -0.59$ on a logit scale, SE = 0.18, 95% CI was −0.96 and −0.22). Similarly, nest stage had a strong effect on survival ($\beta_{\text{stage}} = 2.16$ on a logit scale, SE = 0.38, 95% CI was 0.38 and 1.42). Nest survival was greater during the nestling stage than during incubation and decreased as nest age increased during each stage ($\beta_{\text{age}} = -0.12$ on a logit scale, SE = 0.02, 95% CI was −0.17 and −0.08). Similar to the age effect, csg abundance within 5 m of the nest had a negative effect on daily nest survival ($\beta_{\text{cool\_season\_5}} = -0.01$ 0.01 on a logit scale, SE = 0.004, 95% CI was −0.02 and −0.002). All habitat variables measured at the nest bowl were statistically non-significant with confidence intervals overlapping zero, although abundance of warm-season grass and abundance of tall fescue were included in the most competitive models (Table 2).

Mean daily nest survival rates were greater in all patch-burn grazed patches compared to grazed-and-burned pastures (Table 3). The highest average nest survival rate was in the 1-year post-burn patches (0.9305) and the current-year burn patches (0.9300; Table 3). Overall, the probability of a nest surviving the 20-day nesting period (incubation and nestling stages) was 23.1% in patch-burn grazed pastures and 14% in grazed-and-burned pastures.

Nests failed as a result of predation, abandonment, and trampling. Most cases of abandonment followed repeated losses of an individual egg from a nest, presumably by small predators or brown-headed cowbirds and not large snakes or mesopredators, which tend to consume the entire clutch (Maxon and Oring 1978, Davison and Bollinger 2000, Benson et al. 2010). Cattle trampling was responsible for the failure of 5 nests (<1.6%). Few failures were thought to be due to weather.

Table 1. Clutch size means (SE) for parasitized and non-parasitized nests of grasshopper sparrows in grazed-and-burned and patch-burn grazed (current-year burn patch, 1-yr postburn patch, and 2-yr postburn patch) pastures in Ringgold County, Iowa, 2008–2009.

		Patch-burn grazed		
Clutch type	**Grazed-and-burned**	**Current-year burn**	**1-yr postburn**	**2-yr postburn**
Parasitized	2.55 (0.21)	2.24 (0.19)	2.36 (0.36)	2.54 (0.18)
Non-parasitized	4.05 (0.07)	3.86 (0.16)	4.08 (0.16)	3.71 (0.13)
Overall	3.30 (0.10)	3.05 (0.12)	3.22 (0.20)	3.12 (0.10)

Table 2. Models explaining effects of year, temporal trends, management treatments (trt), nest age (age effect), nest stage (stage), observer effects, distance to the nearest edge (water, woody, or fenceline edges), distance to woody edges, distance to fencelines, cool-season grass canopy cover within 5 m of the nest (csg_5), all vegetation within 5 m of the nest (all_veg_5), warm-season grass canopy cover at the nest bowl (warm_season), and tall fescue canopy cover at the nest bowl of grasshopper sparrow nests in Ringgold County, Iowa, 2008–2009. Steps represent the order at which factors were added to models. The best (i.e., lowest $\Delta \mathrm{AIC}_c$[a]) 2 models from each step are shown.

Model	$\Delta \mathrm{AIC}_c$[a]	K[b]	w_i[c]	Deviance
Step 1				
S (null)	0.00	1	0.67	1069.54
S (trt)	1.39	4	0.33	1064.91
Step 2				
S (year)	0.00	2	0.99	1057.32
S (linear trend)	12.13	2	0.00	1069.45
Step 3				
S (year + distance to woody vegetation)	0.00	3	0.35	1056.25
S (year + distance to nearest edge)	0.83	3	0.23	1057.10
Step 4				
S (year + stage)	0.00	4	0.99	1043.29
S (year + parasitism)	12.01	3	0.00	1057.31
Step 5				
S (year + stage + age effect)	0.00	5	0.99	1014.91
S (year + stage + parasitism)	14.09	5	0.00	1029.01
Step 6				
S (year + stage + age effect + csg_5)	0.00	6	0.23	1011.45
S (year + stage + age effect + all_veg_5)	0.03	6	0.22	1011.49
Step 7				
S (year + stage + age effect + csg_5 + warm_season)[d]	0.00	7	0.25	1008.03
S (year + stage + age effect + csg_5 + fescue)	0.21	7	0.22	1008.26

[a] Akaike's information criterion adjusted for small sample sizes. Numbers are based on differences from the best model within each stage.

[b] The number of parameters used in each model.

[c] Model weight.

[d] Best model has an AIC_c score of 1022.0890.

We used our best model to create predictive graphs based on year (2008 and 2009), nest stage (incubation and nestling), nest age (ages 1–11 days for incubation and 1–9 days for nestling), 3 levels of csg abundance in the microhabitat (minimum, mean, and maximum of observed values), and the average recorded warm-season grass abundance at the nest site (Figs. 1 and 2). Increases in cool season grass abundance resulted in a concomitant decrease in daily survival rates. Additionally, increases in exposure (age) over the incubation and nestling stages also resulted in a decrease in daily survival rates.

DISCUSSION

Published studies on the effects of patch-burn grazing on birds have been conducted on large, contiguous tracts of grassland (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Churchwell et al. 2008, Coppedge et al. 2008), but this is the first study to investigate patch-burn grazing effects on nest survival on relatively small parcels that are characteristic of grasslands in the Midwest. Our data suggest that grasshopper sparrows tend to have higher nest survival in patch-burn grazed pastures than in pastures with a more traditional treatment, although treatment effects were not statistically significant in our survival analyses. Moderate to heavy stocking rates in this study resulted in short overall stature in the patch-burn grazed treatment, which could explain why grasshopper sparrows had slightly higher survival in that treatment. Previous studies have reported that grasshopper sparrows have an affinity for moderately disturbed grassland habitats (Whitmore 1981, Patterson and Best 1996). Further, previous work related a decrease in grasshopper sparrow nest survival to increased vertical cover

Table 3. Constant daily survival estimates (DSR; the probability that a nest survives a 1-day interval) and standard errors for grasshopper sparrow nests in graze-and-burn and patch-burn grazed (current-year burn patch, 1-yr postburn patch, and 2-yr postburn patch) pastures in Ringgold County, Iowa, USA. We also present means for each treatment.

	Grazed-and-burned		Patch-burn grazed					
			Current-year burn		1-yr postburn		2-yr postburn	
Stage and year	DSR	SE	DSR	SE	DSR	SE	DSR	SE
Incubation 2008	0.917	0.03	0.945	0.02	0.923	0.04	0.943	0.02
Nestling 2008	0.925	0.03	0.963	0.03	0.986	0.01	0.942	0.02
Laying 2009[a]	0.641	0.12	0.788	0.11	0.630	0.30	0.737	0.12
Incubation 2009	0.888	0.02	0.920	0.02	0.899	0.03	0.908	0.02
Nestling 2009	0.896	0.02	0.892	0.02	0.914	0.03	0.917	0.02
Means	0.9065		0.9300		0.9305		0.9275	

[a] Due to small sample sizes, laying stage rates were eliminated from mean computations.

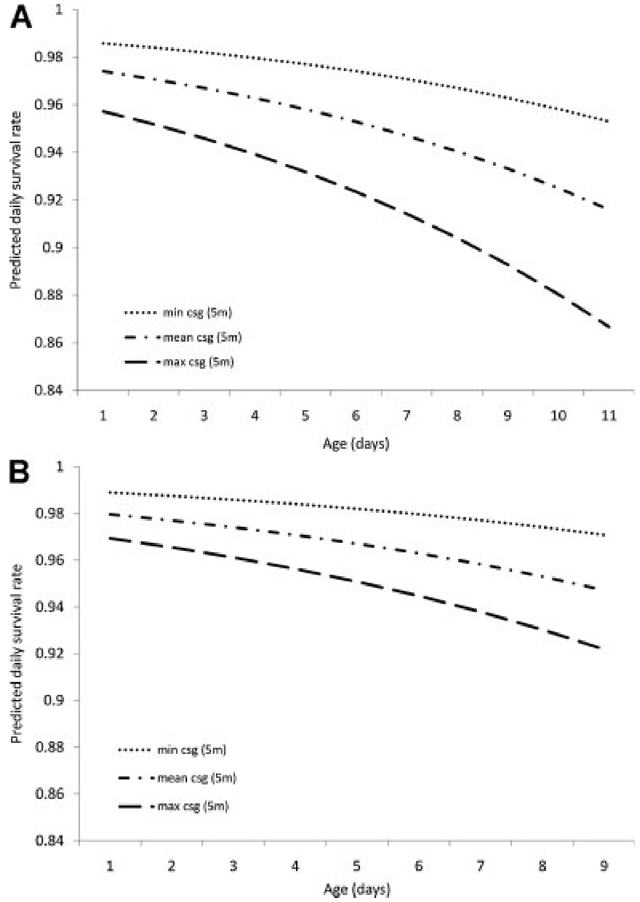

Figure 1. Daily survival rate of grasshopper sparrow nests in 2008 as a function of nest age and cool-season grass (csg) abundance in the microhabitat from the best model. Incubation (A) and nestling (B) stages for grasshopper sparrow nests in pastures treated with fire and grazing. Lines represent the minimum, mean, and maximum amount of csg abundance measured within 5 m of nest sites in Ringgold County, Iowa, USA.

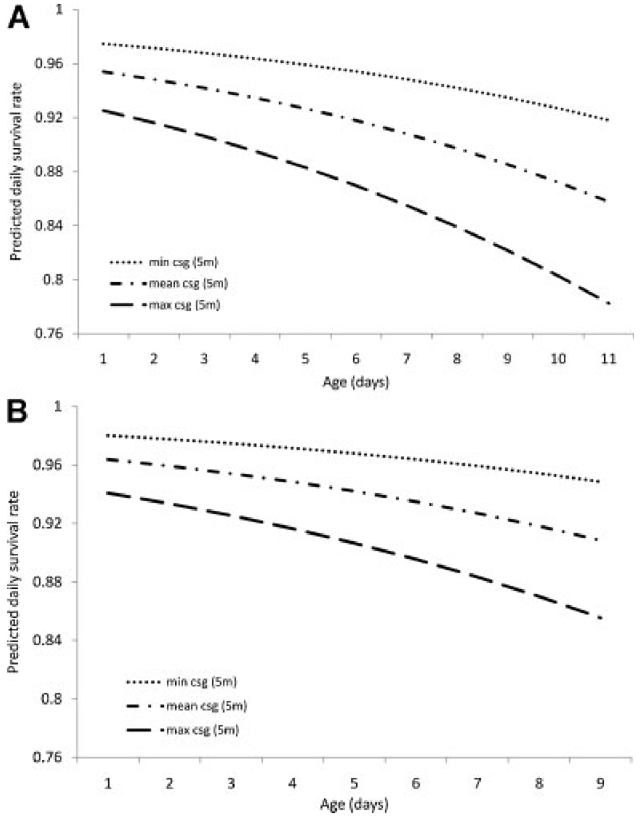

Figure 2. Daily survival rate of grasshopper sparrow nests in 2009 as a function of nest age and cool-season grass (csg) canopy cover (%) in the microhabitat from the best model. Incubation (A) and nestling (B) stages for grasshopper sparrow nests in pastures treated with fire and grazing. Lines represent the minimum, mean, and maximum amount of csg abundance measured within 5 m of nest sites in Ringgold County, Iowa, USA.

and found that grasshopper sparrows were most abundant in fields with moderate vegetation height (Patterson and Best 1996).

Fragmentation stemming from grassland conversion to row-crop agriculture, woody encroachment, high road density, and urbanization has played a role for major declines in grassland bird populations (Askins 2000, Perkins et al. 2003, Brennan and Kuvlesky 2005). Fragmentation creates edges that others have found to be associated with elevated abundances of mesopredators, resulting in increased nest predation rates near edges (Fritzel 1978, Winter and Faaborg 1999). Yet our results did not provide support for an effect of proximity to any edge on daily survival rates. We attribute this finding to 2 main factors. First, the area surrounding our study pastures was highly fragmented by roads, fence-lines, woody draws, and small woodland areas, which resulted in most nests being relatively close to edges and thus accessible to edge-associated predators. On average, the distance from nests to the nearest edge was 58.25 m, and the greatest distance from a nest to any edge was 133 m. This is much less than the 190-m distance Renfrew and Ribic (2003) recorded for predators traveling from woody edges to grassland bird nests in southern Wisconsin. Perkins et al. (2003) documented grassland nest predators known to prefer edge habitats occurring as far as 400 m from woody edges. Second, grassland predator communities may be highly complex with multiple species responsible for nest predation events (Pietz and Granfors 2000, Skagen et al. 2005). If predation events are associated with small mammals or snakes that do not favor edge habitat, distances of nests from edges would have little relationship with survival rates.

We observed a shift from typical stage-related survival of altricial species in our study. Greater survival during the nestling stage than in the incubation stage was likely a function of the abundance of egg-predators commonly found in grasslands (Pietz and Granfors 2000). Weatherhead and Blouin-Demers (2004) report that 6 out of 8 studies that identified nest predators with cameras found snakes to be the most numerous. Predation by snakes and small mammals could explain higher mortality during the incubation stage compared to the nestling stage, and the size of grasshopper sparrow eggs makes them susceptible to egg predators with smaller gape sizes (Davison and Bollinger 2000). In addition, brown-headed cowbirds have been described as egg predators (Benson et al. 2010) and were abundant in our research pastures.

Cowbirds commonly parasitized nests in our study area (24% of all nests in 2008 and 28% in 2009) and these nests had significantly lower clutch sizes than non-parasitized nests. Parasitism rates have been attributed to multiple factors that include proximity to woody edges, vegetation structure, host vulnerability, and proximity to livestock (Fondell and Ball 2004). Patten et al. (2006) examined different combinations of grazing and burning treatments in tallgrass prairie in the southern Flint Hills and found no difference in parasitism rates, likely due to the broad scale of the research pastures and relatively few perching sites for cowbirds across all treatments. Elsewhere in the Flint Hills, parasitism rates were similar in conservation reserve program (CRP) fields and grazed pastures, and were 2–5 times greater in the northern Flint Hills compared to further south (Rahmig et al. 2008). This seems to indicate drivers operating at regional scales rather than a response to grassland structure. Cowbird density in our research pastures was greater in traditionally managed pastures compared to patch-burn grazed pastures (F. Pillsbury, unpublished data), yet parasitism rates did not differ across treatments. Without further investigation it is hard to speculate why we did not see a treatment effect on parasitism rates, but it may be a result of cowbirds switching to hosts other than grassland-nesting birds in areas where woodland hosts are available (Pietz et al. 2009).

Nest survival rate decreased with increased age (Figs. 1 and 2). A similar pattern has been reported in numerous studies (Winter and Faaborg 1999, Conway and Martin 2000, Shochat et al. 2005). The older a nest is, the more time it is exposed to predators, weather, or other factors that increase the risk of failure (Grant et al. 2005). Furthermore, during the nestling stage, chicks have greater resource demands as they mature and parents are forced to make more visits to the nest on a daily basis (Martin et al. 2000). The increased activity around nest sites cues predators and can result in increased rates of predation (Skutch 1949).

Nest survival models also revealed a decrease in daily survival rates with greater csg cover and with more total vegetation canopy cover within 5 m of the nest site. We offer 2 explanations for this result. First, an increase in grass cover necessarily reduces the amount of bare ground, the primary foraging substrate for grasshopper sparrows (Vickery 1996). We do not believe that an increase in vegetation resulted in fewer food resources (e.g., invertebrates; D. Debinski, Iowa State University, unpublished data), but rather that access to invertebrates is hindered because vegetation cover limits suitable foraging areas. In Oregon, Kennedy et al. (2009) found that as bare ground decreased, the diets of nesting grassland birds shifted from ground-dwelling invertebrates to canopy-dwelling species; the diet shift was not a function of decreased invertebrate abundance, but of reduced access to ground-dwelling invertebrates (Kennedy et al. 2009). Second, more vegetation cover around nest sites may create refugia for predators such as snakes and small mammals, resulting in opportunistic predation and lower survival rates.

MANAGEMENT IMPLICATIONS

We found little difference in nest survival rates between the 2 methods of grazing and suggest that either method could be of use to create habitat for nesting grasshopper sparrows. Overall, vegetation abundance influenced nest survival and was a direct consequence of stocking rates set by land managers. We recommend stocking at a level that reduces overall biomass to the point that obvious grazing lawns are created but areas suitable for nesting remain (i.e., not a uniformly short grazing lawn). Finally, a caveat: moderate to heavy stocking rates are capable of creating nesting habitat suitable for generalists such as the grasshopper sparrow, but if managers are interested in providing habitat for specialist species, such as the Henslow's sparrow (*Ammodramus henslowii*), a more diverse management approach that includes longer periods of recovery from disturbance may be necessary.

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