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Original Article

Sparrow Nest Survival in Relation to Prescribed Fire and Woody Plant Invasion in a Northern Mixed-Grass Prairie

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ABSTRACT Prescribed fire is used to reverse invasion by woody vegetation on grasslands, but managers often are uncertain whether influences of shrub and tree reduction outweigh potential effects of fire on nest survival of grassland birds. During the 2001–2003 breeding seasons, we examined relationships of prescribed fire and woody vegetation to nest survival of clay-colored sparrow (*Spizella pallida*) and Savannah sparrow (*Passerculus sandwichensis*) in mixed-grass prairie at Des Lacs National Wildlife Refuge in northwestern North Dakota, USA. We assessed relationships of nest survival to 1) recent fire history, in terms of number of breeding seasons (2, 3, or 4–5) since the last prescribed fire, and 2) prevalence of trees and tall ($>$1.5 m) shrubs in the landscape and of low ($\leq$1.5 m) shrubs within 5 m of nests. Nest survival of both species exhibited distinct patterns related to age of the nest and day of year, but bore no relationship to fire history. Survival of clay-colored sparrow nests declined as the amount of trees and tall shrubs within 100 m increased, but we found no relationship to suggest nest parasitism by brown-headed cowbirds (*Molothrus ater*) as an underlying mechanism. We found little evidence linking nest survival of Savannah sparrow to woody vegetation. Our results suggest that fire can be used to restore northern mixed-grass prairies without adversely affecting nest survival of $\geq$2 widespread passerine species. Survival of nests of clay-colored sparrow may increase when tall woody cover is reduced by fire. Our data lend support to the use of fire for reducing scattered patches of tall woody cover to enhance survival of nests of $\geq$1 grassland bird species in northern mixed-grass prairies, but further study is needed that incorporates experimental approaches and assessments of shorter term effects of fire on survival of nests of grassland passerines. © 2017 This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS clay-colored sparrow, habitat management, nest survival, North Dakota, northern mixed-grass prairie, prescribed fire, Savannah sparrow, woody vegetation.

North American grassland birds are a high-risk ecological group; their conservation is hampered in part by an incomplete understanding of vital rates (e.g., nest survival, postfledging survival, adult survival) as drivers of long-term population change (Askins et al. 2007). Land managers are particularly interested in understanding ecological factors that influence nest loss, including habitat fragmentation and effects of management actions such as grazing and fire. Fragmentation of formerly contiguous and widespread grassland habitat generally is presumed to negatively influence avian nest survival via increased rates of predation or brood parasitism (Benson et al. 2013). Woody plant encroachment facilitated by climate change, disruption of important ecological processes (i.e., fire and herbivory), and direct tree plantings have had significant negative ecological consequences in grasslands and savannas worldwide (e.g., Ratajczak et al. 2012). In the Great Plains Region, encroachment by woody vegetation is among the primary factors that continue to fragment grasslands (Samson et al. 2004, Brennan and Kuvlesky 2005, Askins et al. 2007). In many remnant northern mixed-grass prairies (i.e., those with no cropping history), trees and shrubs have increased, in large

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part because of long-term fire suppression (Grant and Murphy 2005). Many species of grassland birds either avoid or have lower density or occurrence in prairies where low (<1.5 m) shrubs are common (Madden et al. 2000) or where woodlands and tall (≥ 1.5 m) shrubs have encroached (Murphy and Sondreal 2003, Grant et al. 2004*a*). Only Grant et al. (2006) documented the relationship between nest survival and proximity to woodland vegetation for passerines in northern mixed-grass prairies; nests relatively close to woodland edge experienced greater survival. Nest survival also can vary in relation to edges created by woody vegetation in other grassland systems of the Great Plains (e.g., Johnson and Temple 1990, With 1994, Renfrew et al. 2005, Klug et al. 2010).

On U.S. Fish and Wildlife Service National Wildlife Refuges (NWRs) and other conservation lands in the northern mixed-grass prairie region, recurrent prescribed fire is used to maintain grasslands free of significant woody plant encroachment, primarily to benefit grassland-dependent wildlife (Madden et al. 2000; Grant et al. 2010, 2011). Fire generally reduces relative abundance or nest density of grassland passerines in northern mixed-grass prairie, especially during the first postfire breeding season (Johnson 1997, Madden et al. 1999, Grant et al. 2011). Grant et al. (2017) found lower passerine nest survival in the first breeding season following late-summer fires; comparable data sets are not available elsewhere in the northern mixed-grass prairie region. In reality, general effects of fire and woody plant encroachment on breeding passerines are inadequately studied across the entire northern Great Plains, much less the relative influence of either factor specifically on passerine nest survival. To restore or maintain northern mixed-grass prairies as breeding habitat for grassland birds, land managers must better understand and be able to weigh potential ecological consequences of their use of prescribed fire to reverse invasion by woody plants.

Our objectives were to assess nest survival of clay-colored sparrow (*Spizella pallida*) and Savannah sparrow (*Passerculus sandwichensis*) in remnant northern mixed-grass prairies in relation to 1) number of breeding seasons since the last prescribed fire; 2) prevalence of tall woody cover within a mostly grassland matrix; and 3) areal cover of low shrub within 5 m of the nest. We expected that nest survival might be influenced by recent fire based on changes in vegetation, especially nest concealment (Davis 2005, Winter et al. 2005, Grant et al. 2006) or in response to fire-induced changes in potential nest predators such as deer mice (*Peromyscus maniculatus*; Pietz and Granfors 2000). We also expected that an inverse relationship between nest survival and woody cover would be related to increased parasitism by brown-headed cowbirds (*Molothrus ater;* Johnson and Temple 1990, Romig and Crawford 1995, Davis and Sealy 1998, Shaffer et al. 2003; but see Pietz et al. 2009) or changes in distribution and activity of principal nest predators associated with woody vegetation (Pietz and Granfors 2000, Renfrew and Ribic 2003, Grant et al. 2006).

STUDY AREA

Des Lacs NWR was a 1–3-km-wide, 42-km-long riverine tract that encompassed 7,913 ha of the Des Lacs River valley in Ward and Burke counties in northwestern North Dakota, USA ($\sim$48°48′N, 102°07′W). The refuge encompassed approximately 2,250 ha of native prairie that was imbedded in an agricultural landscape characterized by dryland farming for cereal and oilseed crops. In recent decades, these native prairies have become dominated by 2 native species of low shrub—western snowberry (*Symphoricarpos occidentalis*) and silverberry (*Elaeagnus commutata*)—and 2 introduced grass species—smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis;* Murphy and Grant 2005). Climate of the region was subhumid continental, with average monthly temperatures ranging from $-15°$ C in January to 20° C in July and annual precipitation averaging 43 cm (R. K. Murphy, U.S. Fish and Wildlife Service, unpublished data).

Our study occurred within 11 prairie management units (4–8 units studied/yr; Supporting Information, available online) on the northern one-half of Des Lacs NWR during the 2001–2003 breeding seasons. Units covered 28–150 ha and were 0.2–1.8 km wide. Tall woody vegetation, mostly chokecherry (*Prunus virginiana*) shrub and 3–6-m-high green ash (*Fraxinus pennsylvanica*) trees, ranged from scarce on some units to widely dispersed on others, occurring as single small patches (min. area = 0.001 ha) to 5–25-m-wide patches up to 1 km long. Our study approach was opportunistic rather than experimental mainly because habitat manipulation via prescribed fire could not be reliably scheduled by NWR staff for multiple units and years. The staff sought to optimally time prescribed fires to achieve vegetation management objectives (i.e., reduce woody vegetation and increase the structural diversity and native species composition of herbaceous vegetation). Within a relatively short season of prescribed fire opportunity, the decision to burn a given unit on a given day ultimately was driven by constraints posed especially by wind conditions, ambient temperature, relative humidity, fuel load, and fuel moisture. Prescribed fires were conducted by NWR staff during late April through mid-May or mid-August through September. At these times, dry, residual vegetation tended to dominate the prairies, sustaining relatively hot fires that effectively reduced above-ground growth of trees and tall shrubs. Areal coverage of this tall woody vegetation had been drastically reduced within many units following 2–3 prescribed fires conducted during 5–10-year periods (Fig. 1). During 1935 through the early 1990s, management units on Des Lacs NWR typically were undisturbed or grazed lightly and infrequently by livestock (Murphy and Grant 2005).

We studied clay-colored sparrow and Savannah sparrow because they dominated the breeding bird community in prairies at Des Lacs NWR (Murphy and Sondreal 2003, Ludwick and Murphy 2006); thus, we expected to find an adequate sample of nests. These 2 species differ in breeding habitat and nest site selection (Madden et al. 2000, Nenneman 2003, Davis 2005, Grant et al. 2006, Grant and Knapton 2012), offering a potentially insightful contrast in nest survival relative to fire and woody vegetation. Clay-colored sparrow is

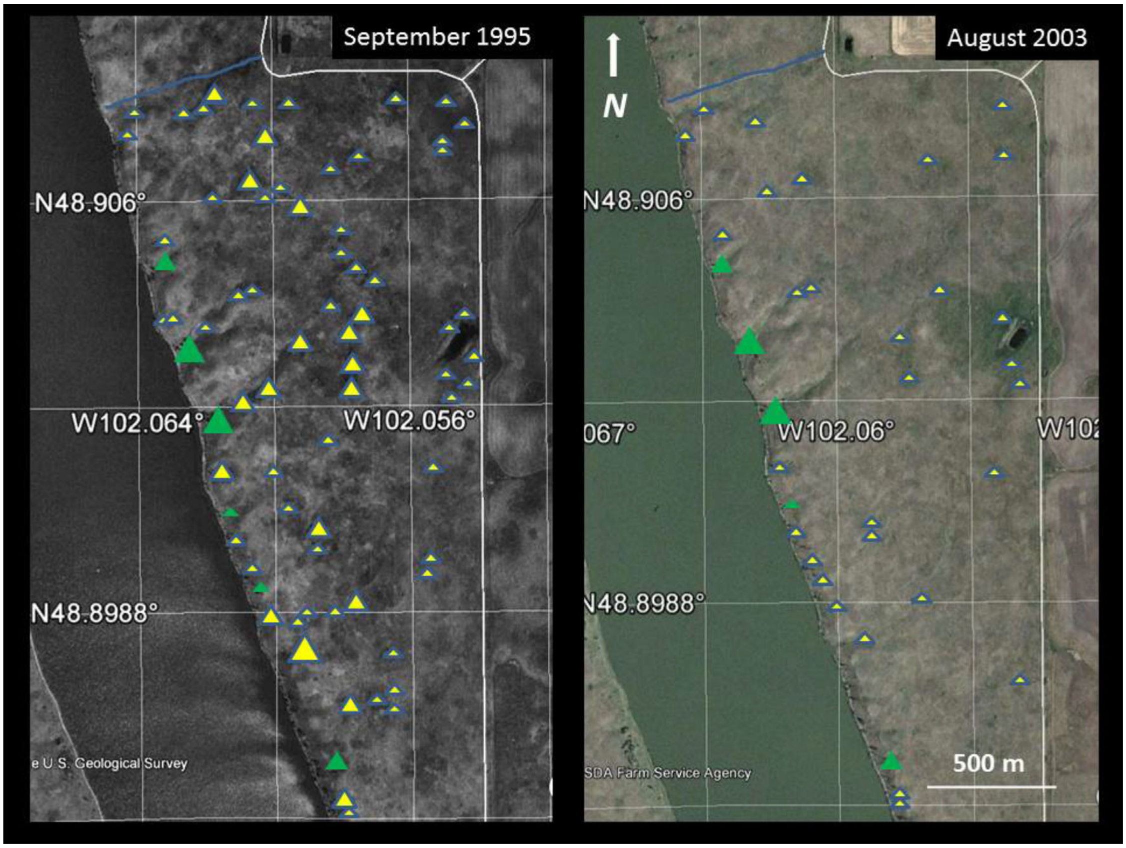

Figure 1. Example of woody vegetation change associated with prescribed burning of a prairie management unit used in a study of clay-colored sparrow and Savannah sparrow nests at Des Lacs National Wildlife Refuge in North Dakota, USA, during 2001–2003 (unit 36). The number and total areal cover of tall (>1.5 m) patches of woody vegetation decreased by approximately 56% and 88% after the unit was prescribe-burned in April 1998 and again in May 2001. Small, medium, and large triangle symbols represent patches covering 4–10 m^2, 11–30 m^2, and 31–150 m^2. Yellow triangles are tall shrub, mainly chokecherry, and green triangles are green ash trees. Tree patches and one-third of tall shrub patches with above-ground growth that survived fires were on steep hillsides or scarps near the river. Woody vegetation rooted at or below the river's high water line was not considered.

distinctly shrub-associated. During breeding season in the northern mixed-grass prairie, its occurrence increases in association with woody cover including low shrub, tall shrub, and woodland edge; the sparrow generally constructs nests 0.1–0.3 m high in low shrub and in lower branches of tall shrub. In contrast, Savannah sparrow typically breeds in areas with sparse to moderate low shrub cover and constructs its nests on the ground in moderately dense, midheight grasses with little low shrub cover; it generally avoids areas with tall shrub and woodland edge. Nests of both sparrows are readily parasitized by brown-headed cowbirds (Shaffer et al. 2003, Igl and Johnson 2007, Pietz et al. 2009). Bobolink (*Dolichonyx oryzivorus*) also is an abundant breeding species in prairie at Des Lacs NWR, but during this study only 2% of nests survived to fledge ≥1 host young, a sample insufficient to evaluate fire and woody vegetation effects on nest survival (R. K. Murphy, United States Fish and Wildlife Service, unpublished data).

METHODS

Nest Monitoring and Habitat Measurements

Methods for locating and monitoring nests were identical to those of Grant et al. (2006). We followed available protocols to both minimize disturbances to nesting birds and avoid potential biases in affecting nest fates (e.g., Martin and Geupel 1993, Winter et al. 2003). We systematically searched for nests in each unit every 3–4 days from mid-May through mid-July, using 20-m long, weighted rope drags pulled between 2 persons to flush birds from nests. Nests also were found incidentally during nest-monitoring visits. Nest locations were recorded using Global Positioning System (GPS) receivers.

A given management unit was prescribed burned 1–6 years before we examined it, with all units experiencing ≥1 full plant growing season and bird breeding season prior to being studied (Supporting Information). We did not study the first postfire breeding season because we expected to find too few nests to reliably estimate survival. Thus, we classified fire history for each unit in a given year as either 2, 3, or 4–5 breeding seasons since the last fire (NESTFIRE); all nest sites in a given unit and year were classified accordingly. Fire histories 2, 3, and 4–5 were represented by totals of 5, 7, and 6 unit-breeding seasons, respectively (Supporting Information). NESTFIRE was treated as a categorical rather than continuous variable because we anticipated that any effect would be nonlinear, with the most pronounced influence occurring most recently after fire (e.g., Grant et al. 2011, 2017). At a proximate landscape-level scale (see below), we assessed relationships between nest survival and 2 habitat variables. Patches of tall woody vegetation $\geq$1 ha were digitized from 1:7,920 aerial photographs into the Geographic Information System (GIS) ArcInfo (Environmental Systems Research Institute, Redlands, CA, USA), with boundaries verified in the field. Boundaries of patches <1 ha were recorded in the field using GPS receivers and incorporated into the GIS. We used ArcInfo to calculate the number of 3- × 3-m grid squares (i.e., ~0.001 ha, our minimum mapping unit) within 100 m of each nest (M100) that included tall woody vegetation. Although we were uncertain about spatial scales at which biotic threats to nest survival might operate, other studies of passerine nest survival in the northern Great Plains found increased predation and brood parasitism effects within 100 m of the nest (Johnson and Temple 1990, Lowther 1993, Shaffer et al. 2003, Renfrew et al. 2005). We also measured distance (m) from each nest to the nearest patch of tall woody cover (NEARWOOD).

During late July each year, we used belt transects (Grant et al. 2004*b*) to measure cover of low shrubs within 5 m of the nest (LOWSHRUB). Canopy coverage of low shrubs was recorded on successive, 1- × 5-dm belts along 4 5-m transects that radiated from the nest on random compass bearings, 90° apart. We distinguished low shrub from tall woody vegetation because at least some species of grassland passerines avoid tall woody cover while often nesting in vegetation that includes low shrub (Davis 2005).

Nest Survival

We used logistic-exposure to estimate nest survival, with model coefficients generated via the GENMOD procedure (SAS Institute 2004, Shaffer 2004). We defined period survival as the probability that a nest survived from the onset of incubation (age = 4 days) to produce $\geq$1 host fledgling and computed it as the product of estimated daily survival probabilities for each day in the incubation period (11 days) and brood-rearing period (7 days for clay-colored sparrow and 9 days for Savannah sparrow). We excluded the laying period because too few nests were found during laying to support reasonably precise estimates of survival. We used an information-theoretic approach to evaluate candidate models where competing models were ranked using Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 2002). We computed AIC_c using the effective sample size, where n was the total number of days that nests were known to survive + total number of intervals in which a failure occurred (Rotella et al. 2004). Where appropriate, we used model averaging to account for the effects of model-selection uncertainty. In such cases, we examined averaged model predictions graphically by plotting nest survival as a function of the individual explanatory variable of interest while holding other variables at their median values (Grant et al. 2005, Shaffer and Thompson 2007).

Candidate Models

We used a multistep approach to investigate whether nest survival varied with fire history, amount and proximity of woody vegetation, or nest parasitism. Nest age- and date-related variability in nest survival has been observed in both clay-colored sparrow and Savannah sparrow (Grant et al. 2005, Davis et al. 2006, Kerns et al. 2010, Grant and Shaffer 2012). Although not the primary focus of this paper, it was necessary to first account for influences of those variables before proceeding with an analysis of fire history and woody vegetation effects on nest survival. In the first step, we considered a set of 18 models in which daily survival could vary by age, nest initiation date, or both in addition to a constant-survival model. Following Grant and Shaffer (2012), we considered a suite of models that had linear, quadratic, or cubic age effects; linear or quadratic date effects; or both. In addition, we considered models that allowed stage-specific constant survival effects (i.e., survival constant within stages of incubation and brood-rearing) or stage-specific linear age effects (i.e., survival varies linearly within each stage; fig. 1 in Grant and Shaffer 2012). All models initially included terms for year, management unit, and year × unit interaction, but we evaluated whether $\geq$1 of those effects could be eliminated. We used the top model (based on minimum AIC_c) from step 1 as our "baseline survival model" to next evaluate effects of fire and woody vegetation on nest survival.

In step 2, we evaluated the relation between nest survival and fire history by adding NESTFIRE to the baseline survival model but eliminating the year × unit interaction. By replacing year × unit with year × NESTFIRE, we sought to assess whether variation in NESTFIRE among year–unit combinations was responsible for the observed interaction between year and unit in our baseline model, thereby providing support for an effect of fire.

In Step 3, we examined the potential influence of nesting near woody vegetation (M100, NEARWOODY, and LOWSHRUB). Based on *a priori* decisions, we used the natural log of M100 and NEARWOOD and arc-sine square-root transformed values of LOWSHRUB in our analyses (Grant et al. 2006). We anticipated, for example, that the influence on nest survival of an increase in M100 from 0 to 10 probably would be greater than that of an increase from 40 to 50. We evaluated 7 models in which various combinations of woody vegetation variables were added to our baseline model. More specifically, 1-variable models included either an effect for M100, NEARWOOD, or LOWSHRUB; 2-variable models included all possible 2-variable combinations; and a final model included all 3 variables.

In step 4, we looked for a direct effect of nest parasitism on survival by adding PARASIT, a time-varying covariate, to our baseline model. If at the beginning of an observation interval a nest showed no evidence of being parasitized or had no prior history of being parasitized, then PARASIT was coded as 0; otherwise PARASIT was coded as 1. We also added a model that allowed parasitism to interact with age of the nest if an age effect was evident in the best baseline model. We hypothesized that tall woody cover in the landscape might be a proximate cause of decreased nest survival, with cowbird parasitism as an underlying mechanism. We investigated this hypothesis in 2 ways. First, we used logistic regression to determine whether incidence of nest parasitism increased with our measures of woody cover M100, NEARWOOD, or LOWSHRUB. For this analysis, nests were classified as parasitized or not, regardless of when parasitism was first observed. Second, we substituted PARASIT for measures of tall woody vegetation (M100, NEARWOOD) in models used in step 3, if such models had support. If models that included PARASIT as a substitute for tall woody cover were not as well-supported as models without PARASIT, we concluded that cowbird parasitism probably was unimportant to any observed relation between nest survival and our measures of woody vegetation cover.

RESULTS

We monitored fates of 434 clay-colored sparrow nests and 141 Savannah sparrow nests, resulting in effective sample sizes of 4,225 and 1,320, respectively. Clay-colored sparrows nested in areas with more tall woody cover and used nest sites with more low shrub cover than did Savannah sparrows (Table 1). Parasitism by brown-headed cowbirds was detected at 9% and 26% of the species' nests, respectively. The baseline survival model for clay-colored sparrow nests, which included a cubic age effect, linear date effect, and interactive effects of year and management unit, accounted for 64% of model weight (Table 2). The constant-survival model accounted for <0.01% of model weight, providing strong evidence survival was not constant from the onset of incubation to fledging. Daily nest survival was greatest through midincubation (Fig. 2) and for nests initiated early in the breeding season (Fig. 3).

Survival of clay-colored sparrow nests was not related to fire history of study units (Table 2). However, there was evidence that clay-colored sparrow nest survival declined with increasing prevalence of tall woody cover in the landscape (Table 2; Fig. 4; $\hat{\beta}_{\text{M100}} = -0.151$, SE = 0.045), but not with proximity of nests to the nearest patch of tall woody cover or with low shrub cover near the nest. We found little support for more complex models that included various combinations of woody cover variables (Table 2). The relationship between nest survival and M100 could not be explained by parasitism by brown-headed cowbirds because substitution of PARASIT for M100 in logistic-exposure models increased AIC_c values by >8 units (Table 2). Furthermore, using logistic regression, we found no relationship between the probability of a nest being parasitized and M100 ($\hat{\beta} = 0.058$, SE = 0.084), LOWSHRUB ($\hat{\beta} = -0.127$, SE = 0.535), or NEARWOOD ($\hat{\beta} = -0.008$, SE = 0.151).

The top survival models for Savannah sparrow nests contained stage-specific linear age effects and either a linear or quadratic effect of date, but survival was not related to management unit or year (Table 2). The top 2 models accounted for 59% of model weight, but we chose the simpler model (i.e., linear effect of date) as our baseline model for subsequent analyses. The constant-survival model received negligible weight (<0.01%), providing strong evidence of nonconstant survival from the onset of incubation to fledging. Daily nest survival increased during incubation, declined sharply during hatching, and increased again during brood-rearing (Fig. 2). Survival was greater for nests initiated early in the breeding season (Fig. 3).

Like clay-colored sparrow, Savannah sparrow nest survival was not influenced by fire history of study units (Table 2). We found little support for any effect of nesting near woody vegetation. Although best models included M100 and NEARWOOD, there was substantial model-selection uncertainty because AIC_c values for these models were ≤0.74 units less than the AIC_c value for the baseline model (Table 2). Based on model-averaged estimates, predicted nest survival decreased with increasing values of M100 ($\hat{\beta} = -0.240$, SE = 0.132) and NEARWOOD ($\hat{\beta} = -0.458$, SE = 0.240), and increased with increasing values of LOWSHRUB ($\hat{\beta} = 0.440$, SE = 0.387). However, 95% confidence intervals included 0, supporting the notion that woody vegetation had little influence on nest survival. Evidence for an effect of parasitism by brown-headed cowbirds on survival of Savannah sparrow nests was also lacking (Table 2); model performance did not improve with substitution of PARASIT for M100 and NEARWOOD as derived from the best woody vegetation model. Furthermore, using logistic regression, we found no relationship between the probability of a nest being parasitized and M100

Table 1. Summary statistics for woody vegetation variables recorded at 434 clay-colored sparrow nests and 141 Savannah sparrow nests on Des Lacs National Wildlife Refuge in North Dakota, USA, during 2001–2003. The second row of values for each variable is from transformed data[a] used in the analyses.

	Clay-colored sparrow				Savannah sparrow			
Variable	$\bar{x}$	**SD**	**Median**	**Range**	$\bar{x}$	**SD**	**Median**	**Range**
LOWSHRUB[b]	38.3	26.7	35.0	0.0–100.0	19.0	22.2	13.0	0.0–100.0
	0.64	0.02	0.63	0.00–1.57	0.40	0.03	0.37	0.00–1.57
NEARWOOD[c]	146.6	145.8	86.5	0.7–796.0	207.5	149.1	159.7	12.7–812.5
	4.42	0.06	4.47	0.53–6.68	5.04	0.07	5.08	2.61–6.70
M100[d]	48.3	121.8	1.0	0.0–1,139.0	9.9	39.7	0.0	0.0–340.0
	1.76	0.10	0.69	0.00–7.04	0.72	0.11	0.00	0.00–5.83

[a] Arc-sine-square-root for LOWSHRUB, natural log for NEARWOOD and M100.
[b] LOWSHRUB = frequency of occurrence of low (≤1.5 m) shrub within 5 m.
[c] NEARWOOD = distance (m) to nearest patch of tall (>1.5 m) woody vegetation.
[d] M100 = no. of 3 × 3-m grid squares within 100 m that include tall woody vegetation.

Table 2. Top models of daily survival rate for 434 clay-colored sparrow nests and 141 Savannah sparrow nests at Des Lacs National Wildlife Refuge in North Dakota, USA, during 2001–2003. Models are ranked based on Akaike's Information Criterion for small samples (AIC_c), ΔAIC_c, and Akaike weights (w_i); AIC_c is based on numbers of model parameters (K), effective sample size (4,225 for clay-colored sparrow and 1,320 for Savannah sparrow), and $Log_e(L)$, the value of the maximized log-likelihood function.

Model[a]	K	$Log_e(L)$	AIC_c	ΔAIC_c	w_i
Clay-colored sparrow					
Time specific effects					
AGE^3 DATE YEAR × UNIT (Baseline model)	22	−728.78	1,501.80	0	0.64
AGE^3 DATE^2 YEAR × UNIT[b]	23	−728.76	1,503.78	1.98	0.24
AGE^2 DATE YEAR × UNIT	21	−732.72	1,507.66	5.86	0.03
Fire effects					
Baseline model	22	−728.78	1,501.80	0	0.78
AGE^3 DATE YEAR × NESTFIRE	12	−740.47	1,505.01	3.21	0.16
Woody vegetation effects					
Baseline M100	23	−723.37	1,493.01	0	0.39
Baseline M100 LOWSHRUB[b]	24	−722.72	1,493.72	0.71	0.27
Baseline M100 NEARWOOD[b]	24	−723.07	1,494.43	1.42	0.19
Baseline M100 LOWSHRUB NEARWOOD[b]	25	−722.40	1,495.11	2.10	0.14
Baseline NEARWOOD	23	−727.60	1,501.47	8.46	<0.01
Baseline model	22	−728.78	1,501.80	8.79	<0.01
Nest parasitism effects					
Baseline PARASIT	23	−727.55	1,501.37	0	0.41
Baseline model	22	−728.78	1,5014.8	0.43	0.33
Baseline PARASIT × AGE^3	26	−724.96	1,502.25	0.88	0.26
Parasitism to explain woody vegetation effects					
Baseline M100	23	−723.37	1,493.44	0	0.39
Baseline PARASIT (replace M100)	23	−727.55	1,501.10	8.36	<0.01
Baseline model	22	−728.78	1,501.80	8.79	<0.01
Savannah sparrow					
Time specific effects					
STAGE × AGE DATE (Baseline model)	7	−240.51	495.11	0	0.32
STAGE × AGE DATE^2	8	−239.64	495.40	0.28	0.27
STAGE DATE	4	−244.32	496.66	1.55	0.15
STAGE DATE^2	5	−243.54	497.13	2.02	0.12
Fire effects					
Baseline model	7	−240.51	495.11	0	0.84
Baseline NESTFIRE	9	−240.17	498.48	3.37	0.16
Woody vegetation effects					
Baseline M100 NEARWOOD	9	−238.12	494.37	0	0.22
Baseline LOWSHRUB	8	−239.37	494.85	0.48	0.17
Baseline M100 NEARWOOD LOWSHRUB	10	−237.44	495.05	0.68	0.16
Baseline	7	−240.51	495.11	0.74	0.15
Nest parasitism effects					
Baseline model	7	−240.51	495.11	0	0.28
Baseline PARASIT	9	−238.66	495.46	0.35	0.23
Baseline PARASIT × STAGE × AGE	11	−239.65	501.50	6.38	0.01
Parasitism to explain woody vegetation effects					
Baseline M100 NEARWOOD	9	−238.12	494.37	0	0.20
Baseline model	7	−240.51	495.11	0.74	0.14
Baseline PARASIT (replace M100 and NEARWOOD)	8	−239.73	495.58	1.21	0.11

[a] AGE^3 = cubic polynomial effect of nest age (days). STAGE × AGE = linear, nesting stage-specific effect of age (days). STAGE = constant survival within egg and nestling stages. DATE = linear effect of day of year. UNIT and YEAR = management unit and year effects. NESTFIRE = no. of breeding seasons since prescribed fire was applied (2, 3, or 4–5). M100 = natural log of the no. of 3×3-m grid squares that held tall (>1.5 m) woody vegetation within 100 m. NEARWOOD = natural log of distance (m) to the nearest patch of tall shrubs or trees. LOWSHRUB = arcsine-square-root–transformed frequency of occurrence of low (≤ 1.5 m) shrub within 5 m. PARASIT = binary effect of parasitism by brown-headed cowbirds.

[b] Model has minimal support (Burnham and Anderson 2002:131).

($\hat{\beta} = -0.061$, SE = 0.150), LOWSHRUB ($\hat{\beta} = 0.429$, SE = 0.615), or NEARWOOD ($\hat{\beta} = 0.254$, SE = 0.240).

DISCUSSION

Our study provides new insight into the influence of fire disturbance and woody cover on survival of grassland passerine nests in northern mixed-grass prairie, helping reveal trade-offs in decisions regarding use of prescribed fire to manage this habitat. We found that fire has little effect on nest survival of either clay-colored sparrow or Savannah sparrow when compared among postfire breeding seasons 2, 3, or 4–5, despite known differences in each species' associations with woody vegetation. We predicted that nest survival was most likely to be affected during the most recent postfire breeding season on account of potential fire-related changes in the density of nests (Grant et al. 2011, 2017), concealment of nests (Grant et al. 2006), abundances of potential nest predators (Kaufman et al. 1990, Clark et al. 1992), or nest parasitism

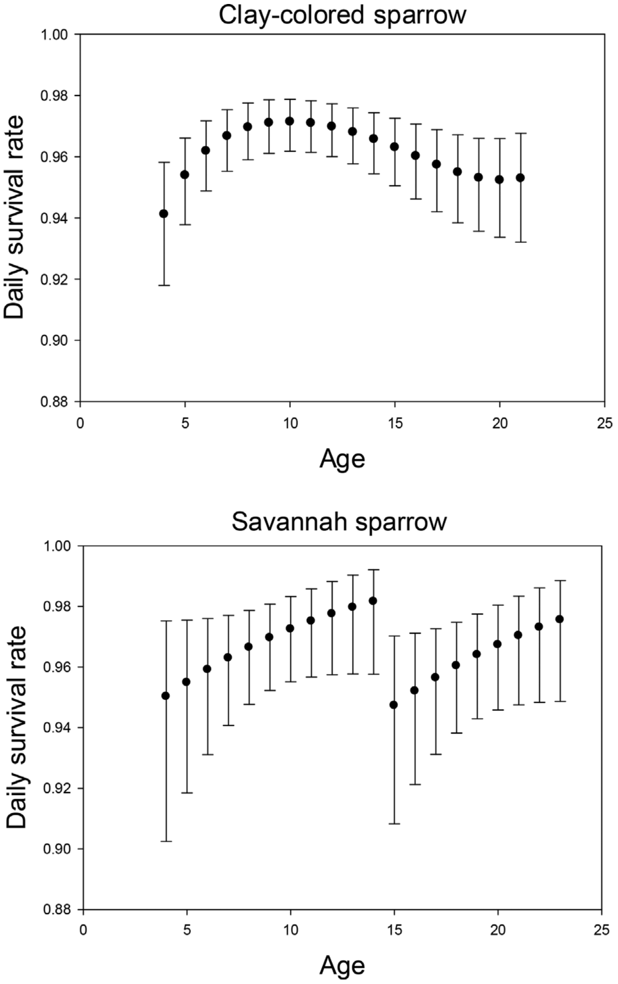

Figure 2. Daily survival rates during incubation and brood-rearing for clay-colored sparrow nests ($n = 434$) and Savannah sparrow nests ($n = 141$) in relation to nest age (days since first egg laid) at Des Lacs National Wildlife Refuge in North Dakota, USA, during 2001–2003. Incubation begins at day 5 for a typical 4-egg clutch and hatching is estimated at day 15. Error bars indicate 95% confidence intervals. Survival rates for clay-colored sparrow are from a baseline survival model that included a cubic age effect; linear date effect; and effects of year, management unit, and their interaction. Survival rates for Savannah sparrow are from a baseline survival model that contained stage-specific, linear age effects and a linear effect of date.

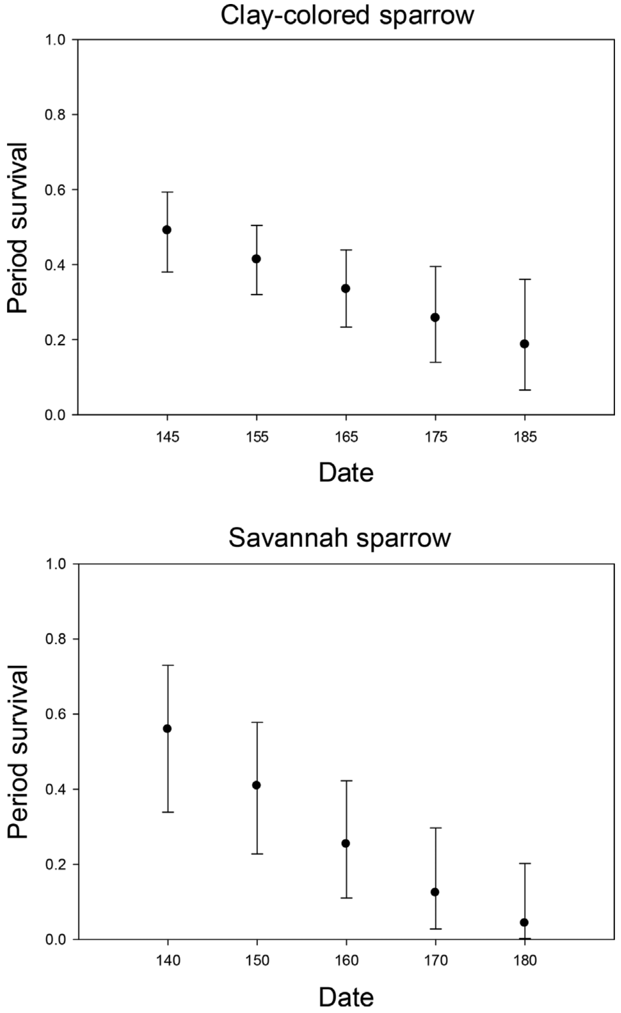

Figure 3. Period survival of nests of clay-colored sparrow ($n = 434$) and Savannah sparrow ($n = 141$) in relation to date at Des Lacs National Wildlife Refuge in North Dakota, USA, during 2001–2003. Period survival was calculated as the product of daily survival rates during the 18-day (clay-colored sparrow) or 20-day (Savannah sparrow) period that includes incubation and brood rearing. Date refers to the number of calendar days since 31 December; for example, day 155 equals 3 June. Error bars indicate 95% confidence intervals. Survival rates for clay-colored sparrow are from a baseline survival model that included a cubic age effect; linear date effect; and effects of year, management unit, and their interaction. Survival rates for Savannah sparrow are from a baseline survival model that contained stage-specific, linear age effects and a linear effect of date.

(Patten et al. 2006). During a concurrent study at J. Clark Salyer NWR 100 km from our area, nest density and nest survival for clay-colored sparrow, Savannah sparrow, and bobolink were influenced primarily during the first postfire breeding season (a period we did not evaluate), where both metrics were lower when compared with subsequent breeding seasons (Grant et al. 2011, 2017). Our results corroborate those of Grant et al. (2017), in that nest survival does not appear to be greatly influenced by fire during the second and subsequent postfire breeding seasons. No other data are published for northern mixed-grass prairie with which to compare our results, and effects reported from other grassland systems are inconsistent. For example, in northern tallgrass prairie in Minnesota, USA, predation rates for nests of grassland passerines were lower in areas burned ≤3 years previously than in areas burned less recently (Johnson and Temple 1990). In tallgrass prairies in Kansas, USA, eastern meadowlark (*Sturnella magna*) nest success was unaffected by fire, dickcissel (*Spiza americana*) nest success was greater in unburned fields, and grasshopper sparrow (*Ammodramus savannarum*) nest success was greater in recently burned fields (Rahmig et al. 2009). In tallgrass prairie in Oklahoma, USA, nest survival of all bird species combined was lowest on plots that were burned and grazed compared with plots that were either grazed or undisturbed (Shochat et al. 2005). However, we are cautious about comparing results from other grassland systems due to differences in climate, vegetation, avian species, and nest predator species (e.g., between mixed-grass and tallgrass prairie; Higgins et al. 1989; Grant et al. 2011, 2017).

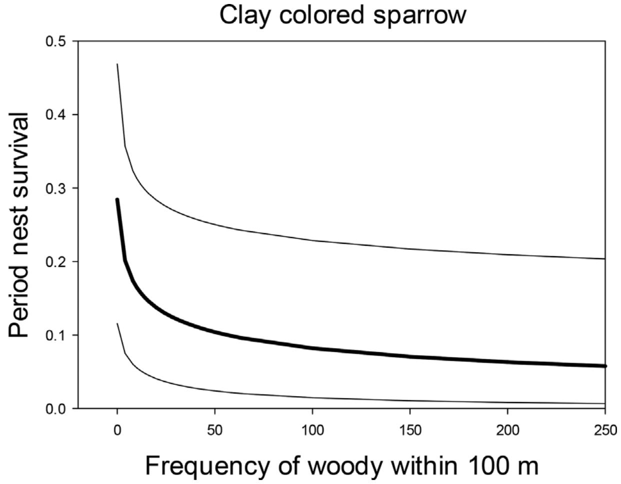

Figure 4. Period survival (and 95% confidence limits) of nests of clay-colored sparrows at Des Lacs National Wildlife Refuge in North Dakota, USA, during 2001–2003 in relation to the number of 3- × 3-m grid squares that held tall (>1.5 m) woody vegetation within 100 m. Period survival was calculated as the product of daily survival rates during the 18-day (clay-colored sparrow) or 20-day (Savannah sparrow) period that includes incubation and brood rearing. Depicted survival rates are from a model that included a cubic age effect; linear date effect; effects of year, management unit, and their interaction; and M100.

The second key finding of our study was that nest survival was not necessarily adaptive in terms of habitat selection, at least with regards to woody vegetation in our study area. We suspected sparrow nest survival might be adversely affected as cover of woody vegetation increased because certain predators may associate with woody patches or edges (Johnson and Temple 1990, With 1994, Pietz and Granfors 2000, Renfrew and Ribic 2003, Klug et al. 2010). Although clay-colored sparrow is a grassland species typically associated with woody cover (Grant and Knapton 2012), its nest survival in our study declined as patches of tall woody cover increased in the landscape. Grant et al. (2006) describe a more adaptive pattern for nesting at a site 100 km east of our study area; clay-colored sparrow and vesper sparrow (*Pooecetes gramineus*) nest survival was greater near edges provided by tall woody vegetation, sites that the species also selected for nesting. Savannah sparrow typically avoids woody cover when nesting (Wheelwright and Rising 2008), but we found at best equivocal evidence that its nest survival was related to any woody vegetation variables we examined. Habitat selection differs among grassland bird species and in theory should reflect increased fitness (nest survival in our case) associated with those features selected during nesting. In our study, clay-colored sparrows nested in areas with more tall woody cover and used nest sites with more low shrub cover than did Savannah sparrows. We suspect that Savannah sparrows may reduce potential negative influences of tall woody vegetation on nest survival simply by avoiding such cover when selecting breeding territories and nest sites (Bakker et al. 2002, Grant et al. 2004*a*, Winter et al. 2006, Keyel et al. 2013).

In a study that overlapped ours in time and space, Kerns et al. (2010) found no relationship between survival of nests of Savannah sparrow, clay-colored sparrow, or bobolink and total areal extent (m^2) of potential cover within 100 m of the nest that might harbor predators. Patches of tall woody vegetation comprised most such cover, but rock piles and surface water also were included as potential predator habitat, possibly obscuring any relationship between nest survival and woody vegetation, especially for clay-colored sparrow. The contrast with our findings for clay-colored sparrow may also be attributed in part to differences in how the 2 studies quantified woody cover. By counting 3- × 3-m grids with tall woody cover, we better characterized the scattered distribution of small (to 0.001 ha) patches of such cover within 100 m of sparrow nests; methods used by Kerns et al. (2010) likely did not account for these small patches. An understanding of nest predation is required to comprehend patterns of nest survival because most grassland passerine nests fail as a result of predation (e.g., Davis 2003, Kerns et al. 2010, Davis et al. 2016). In prairie-parkland 100 km east of our study area, survival of vesper sparrow and clay-colored sparrow nests increased with proximity to woodland edge, mainly because principal nest predators, especially thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) were less common near woodland edges than in prairie interiors (Grant et al. 2006). We found no other comparable data on effects of woody vegetation on passerine nest survival in northern mixed-grass prairie, but studies elsewhere may shed light on our results. In tallgrass prairie in eastern North Dakota and western Minnesota, clay-colored sparrow and Savannah sparrow nest survival was not influenced by tree or shrub cover in the landscape (Winter et al. 2006), supporting our findings for Savannah sparrow. In grasslands of Wisconsin, USA, nest survival for several passerine species did not increase following mechanical removal of trees from the landscape, despite a 2–4-fold increase in bird nest density during years following removals (Ellison et al. 2013). Those researchers concluded that although edge predators such as raccoon (*Procyon lotor*) decreased markedly after tree removals, this decrease was offset by an increase in grassland-associated predators, especially thirteen-lined ground squirrels; these results were strikingly similar to findings of Grant et al. (2006). We did not document occurrence of potential nest predators during our study. However, thirteen-lined ground squirrel abundances appear uninfluenced by scattered, small patches of tall shrubs and trees at Des Lacs NWR (Eddingsaas et al. 2007), which may explain why our results differ from those of Grant et al. (2006) in which prairie tracts were bordered by a distinct woodland–grassland ecotone.

Survival of clay-colored sparrow and Savannah sparrow nests appeared mostly unrelated to low shrub cover near the nest, contrary to data from several other studies. In shortgrass prairie in Colorado, USA, for example, McCown's longspur (*Calcarius mccownii*) nests next to shrubs were 2–3 times more likely to be depredated, mainly by thirteen-lined ground squirrels, than nests elsewhere (With 1994). In Kansas tallgrass prairies, passerine nest survival decreased with increasing shrub cover, in part because snakes and other nest predators were more common near shrubs (Klug et al. 2010). Similar to our results, survival of clay-colored sparrow and vesper sparrow nests in mixed-grass prairie in north central North Dakota was uninfluenced by low shrub cover near nests; however, vesper sparrow nest survival was greater near tall shrubs (Grant et al. 2006).

The effect of parasitism by brown-headed cowbirds on nest survival was at best equivocal (although predicted values suggest a weak negative effect of parasitism). We had expected that patches of trees and tall shrubs might provide ideal perch sites from which brown-headed cowbirds would locate hosts' nests (Davis and Sealy 2000, Shaffer et al. 2003, Benson et al. 2013), but found no evidence implicating brood parasitism as a factor in the declining survival of clay-colored sparrow nests associated with increased tall woody cover (M100). In an adjacent, concurrent study of effects of cattle grazing on passerine nest survival, Kerns et al. (2010) found a positive relationship between cowbird parasitism and survival of clay-colored sparrow nests. The authors reasoned that cowbirds may perceive which host nests are most likely to survive; cowbirds are not likely to depredate such nests, and many parasitized nests produce both cowbird and clay-colored sparrow fledglings. We found no evidence to support this finding by Kerns et al. (2010), although the rate of parasitism for clay-colored sparrow in our study was lower (9%) than that reported by Kerns et al. (2010; 17%). Pietz et al. (2009) suggested incidence of cowbird parasitism on nests in northern tallgrass prairie declines with increased woodland cover in the landscape; parasitism could be focused more on woodland birds because their nests may be more abundant or more readily found than nests in open grassland. Within our study area, overall abundance of passerine species is far greater in woodland edge habitat where cowbirds also are more abundant (Murphy and Sondreal 2003), yet Savannah sparrows we studied incurred nearly 3 times the rate of cowbird parasitism than did clay-colored sparrows despite nesting in more open areas.

Although not the focus of our study, we documented time-specific effects on nest survival, as have others in recent studies. Specifically, nest survival varied with age of the nest for both clay-colored sparrow and Savannah sparrow. Similar age-specific patterns of nest survival have been described for passerines breeding elsewhere in the northern mixed-grass prairie region (Grant et al. 2005, Grant and Shaffer 2012, Davis et al. 2006, 2016, Kerns et al. 2010). Nest survival declined with the date a nest was initiated, suggesting a survival advantage associated with nesting early (reviewed in Grant and Shaffer 2012).

MANAGEMENT IMPLICATIONS

Fire is a necessary and cost-effective tool for restoring northern mixed-grass prairies invaded by woody vegetation and other nonnative plants (Madden et al. 2000, Grant et al. 2010, 2011). Our results suggest that when fire is used to restore native plant composition and structure in northern mixed-grass prairies, nest survival of ≥ 2 widespread passerine species is not adversely affected. Survival of nests of clay-colored sparrow at Des Lacs NWR may be reduced where patches of tall shrubs and trees are widespread; conversely, their survival might increase when such woody cover is reduced by fire. We could not find a similar relationship for Savannah sparrow probably because this sparrow appeared to avoid nesting near woody vegetation, at least when compared to clay-colored sparrow; as such, nest predators and risk of predation among nests of the 2 species likely differ (Davis et al. 2016). Research is needed that incorporates experimental approaches and assessments of shorter term effects of fire on nest survival of grassland passerines (i.e., during the first postfire breeding season) and considers other species of grassland birds, given that ours was a local study from which limited inferences can be drawn. Meanwhile, managers should remain cautious about drawing conclusions from the limited data available on effects of fire on passerine birds in northern mixed-grass prairies, and instead focus on use of fire as a process inherent in the ecosystem's evolution (Bragg 1995, Bragg and Steuter 1995, Grant and Murphy 2005, Grant et al. 2010).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site. History of prescribed fire use on prairie management units at Des Lacs National Wildlife Refuge in North Dakota, USA.