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RESEARCH ARTICLE

# Contrasting impacts of invasive plants and human-altered landscape context on nest survival and brood parasitism of a grassland bird

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**Abstract**

*Context* Humans have altered grasslands in recent decades through crop conversion, woody encroachment, and plant invasions. Concurrently, grassland birds have experienced range-wide declines. Studies have reported effects of plant invasions and land conversion on nest ecology, but few have assessed relative impacts of these changes.

*Objectives* We compared impacts of invasive plants and landscape context on nest survival of a grassland songbird, the dickcissel (*Spiza americana*). We also compared effects on parasitism by brown-headed cowbirds (*Molothrus ater*) and tested whether parasitism affects survival.

*Methods* From 2013–2016, we monitored 477 dickcissel nests. We measured nest-site vegetation (including woody plants, tall fescue *Schedonorus arundinaceous*, and other invasive grasses) and measured landscape context at broad scales.

*Results* Nest survival declined with increasing tall fescue cover at nest sites, and parasitism was more common at nests with greater fescue and woody cover. Some evidence suggested a negative effect of row-crop cover within 1000 m on nest survival, but no landscape patterns unambiguously affected survival. Woodland cover and wooded-edge prevalence were associated with reduced parasitism risk. Parasitized nests had smaller clutches, failed more frequently, and produced fewer fledglings than non-parasitized nests.

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*Conclusions* Determining the impacts of invasive plants and other anthropogenic changes on grassland birds will aid in prioritizing management to improve habitat quality. Our results indicate that optimizing landscape context around habitats may not affect dickcissel nest survival strongly, except perhaps through effects on parasitism. In contrast, controlling tall fescue and shrubs within grasslands could benefit birds by increasing nest success and reducing parasitism.

**Keywords** Brown-headed cowbird · Dickcissel · Grassland birds · *Spiza americana* · Tall fescue · Woody encroachment

## Introduction

North American grasslands have undergone far-reaching changes in land use and land cover in the last century, with profound consequences for native wildlife. In the Central U.S., for example, grassland ecosystems have been converted to row-crop agriculture (Samson and Knopf 1994; Warner 1994), transformed by woody plant encroachment due to fire suppression and heavy grazing (Briggs et al. 2005; Engle et al. 2008), and invaded by exotic grasses that alter plant and arthropod communities (Flanders et al. 2006; McGranahan et al. 2012). In the same time frame, more than half of all grassland bird species in North America have undergone range-wide population declines (Peterjohn and Sauer 1999; Sauer et al. 2017).

Changes in land cover have diminished grassland bird populations in part through habitat loss (Coppedge et al. 2001; Murphy 2003), but avian declines are also a product of low offspring production in remaining habitats (Schmidt and Whelan 1999; Fletcher et al. 2006). Learning how changes in land use and cover affect grassland birds thus requires examining how these changes alter nest survival and brood parasitism by brown-headed cowbirds (*Molothrus ater*), which reduce host reproduction through egg removal and competition for parental care (Sealy 1992).

Multiple studies have investigated how landscape context (Herkert et al. 2003; Ribic et al. 2012; Hovick and Miller 2013) and plant invasions (Lloyd and Martin 2005; Grant et al. 2006; Nelson et al. 2017) independently influence avian nest survival and parasitism, but we know very little about the relative importance of these factors. Moreover, our understanding of the spatial scales at which invasive plants and land-use change most strongly affect avian reproduction is limited (Chiavacci et al. 2018). This uncertainty complicates conservation. Invasive plants almost inevitably emerge in grassland reserves and restorations, and controlling them requires substantial investment of time and funds (Rowe 2010). Because those resources could otherwise be put towards land-acquisition planning and additional restorations, illuminating the relative conservation value of invasive plant control, grassland expansion, and landscape optimization will improve decision-making (e.g., Pyke 2011; Rosenberg et al. 2016).

At broad spatial scales, grassland losses and proliferating wooded edges can intensify nest predation by increasing predator abundance or search efficiency (Chalfoun et al. 2002; Simonsen and Fontaine 2016), although such increases are inconsistent (Grant et al. 2006; Benson et al. 2013). In contrast, nests near wooded edges are consistently at high risk of parasitism (Benson et al. 2013), though tree cover in the landscape may mitigate this if cowbirds prefer to parasitize woodland hosts (Pietz et al. 2009; Hovick and Miller 2013). Relative to these factors, few data exist on the effects of row-crop cover. Crops can increase predator abundances (Pedlar et al. 1997; Chalfoun et al. 2002), but may not increase nest loss (Cottam et al. 2009).

At fine spatial scales, invasive grasses and shrubs can increase predation and parasitism by providing homogeneous nesting cover or creating perches for cowbirds (Lloyd and Martin 2005; Patten et al. 2006; Hovick et al. 2012). Moreover, invasive grasses often support relatively few arthropod prey (Flanders et al. 2006; George et al. 2013), and some—such as the widespread forage grass tall fescue (*Schedonorus arundinaceous*)—decrease arthropod growth rates by providing poor diets for folivores (Jokela et al. 2016). These trophic effects may increase predation by heightening demands on parental activity to provision nestlings (Martin et al. 2000).

Our goal in this study was to compare the impacts of invasive plants at fine spatial scales and landscape patterns reflecting land conversion at broad spatial scales on the survival and parasitism of dickcissel

(*Spiza americana*) nests in a U.S. grassland. We also examined whether cowbirds reduce the number of dickcissel young fledged to discern whether reducing parasitism could benefit host populations. We chose to study dickcissels, a grassland bird declining in much of its range (Sauer et al. 2017), because landscape context and invasions affect their distributions (Herkert et al. 2003; Osborne and Sparling 2013). Dickcissels also share habitat with other declining birds preyed upon by similar predators (Ribic et al. 2012), so revealing impacts on this species will lend insight into the broader avian community.

We first predicted that nests in microsites with high invasive grass cover, and tall fescue cover in particular, would experience high nest-predation rates due to poor concealment and limited food availability (Flanders et al. 2006; Hovick et al. 2012; Jokela et al. 2016). We also expected that woody plants at nest sites would increase predation and parasitism due to their use by snakes and cowbirds (Patten et al. 2006; Klug et al. 2010). We then predicted that nests in landscapes with little grassland cover but high prevalence of crops and wooded-edges would face intense predation and parasitism due to concentration into small patches with high predator and cowbird abundance (Chalfoun et al. 2002; Simonsen and Fontaine 2016). Finally, although proximity to wooded edges could increase parasitism, we predicted that woodland cover in the landscape would reduce parasitism by supporting alternative cowbird hosts (Pietz et al. 2009).

## Methods

### Study system

We investigated dickcissel nest survival and parasitism from 2013 to 2016 on 15 study pastures (14–41.1 ha in area) in Ringgold County, Iowa, USA. One pasture is privately owned and the others are managed by the Iowa Department of Natural Resources. The pastures are within the Grand River Grasslands, a region spanning the Iowa-Missouri border that represents a prime opportunity to restore tallgrass praire in a working landscape (Miller et al. 2012). The dominant land use in the Grand River Grasslands is cattle grazing, but record-high commodity prices from 2006 to 2011 recently resulted in a loss of grazed and ungrazed grasslands and an increase in row-crop acreage (Wright and Wimberly 2013). Also, though woodlands have long been present in the region, their extent is expanding as species like eastern redcedar (*Juniperus virginiana*) and Osage-orange (*Maclura pomifera*) encroach in unburned grasslands (Harr et al. 2014). Our pastures reflect a gradient of these landscape conditions, with row-crop cover within 1000 m of nests ranging from 1 to 66% and woodland cover ranging from 2 to 44% (Online Resource 1).

In addition to woody plants, the region harbors invasive herbaceous plants. Tall fescue is one of the most abundant of these species, occurring in all but one of our pastures and ranging from 0 to 63% cover within them (unpublished data). Other invasive grasses like Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), and orchard grass (*Dactylis glomerata*) are also widespread. Common native plants (e.g., Indiangrass *Sorghastrum nutans*, big bluestem *Andropogon gerardii*, goldenrods *Solidago* spp.) are mostly warm-season species.

Management varied across study pastures, including cattle grazing, spring burning, and glyphosate herbicide sprayed in November 2014 to control tall fescue (Online Resource 2). We chose this diverse mixture of pastures to identify variables influencing reproduction over a broad array of conditions. Due to logistical constraints we did not monitor all 15 pastures each year: we monitored 10 in 2013, 7 in 2014, 8 in 2015, and 6 in 2016 (dates in Online Resource 2).

### Data collection

We located dickcissel nests from May to August, 2013–2016. We searched for nests in 2013 primarily by dragging a 30-m rope over study pastures (Higgins et al. 1969). Whenever a bird flushed nearby, we searched the area for a nest. We conducted 2–4 complete drags (average = 3.6) per pasture. From 2014 to 2016, we primarily searched for nests by observing adult dickcissel behavior (Martin and Geupel 1993).We found nests through incidental flushes in all years.

We recorded nest positions with a GPS and tied flagging 2.5 m to the north and south to aid relocation. We aged eggs by candling (Lokemoen and Koford 1996) and nestlings based on development (Temple 2002). We visited nests every 1–3 days (Ralph et al.

1996), noting nest stage (laying, incubation, or nestling) and nest contents each time. Nests were considered depredated if all contents disappeared before chicks reached day 7—the earliest age of force fledging (hatch day = day 1). We confirmed fledging based on parental behavior.

To understand how invasive plants influence nest survival and parasitism at a fine spatial scale, we measured percent-cover of woody plants, tall fescue, and all cool-season grasses combined (including tall fescue) in five 0.5-$m^2$ quadrats around each nest within 21 days of nests fledging or failing. We also measured warm-season grass, forb, and litter cover within those quadrats to assess whether other plant components influenced reproduction. One quadrat was centered on the nest cup, and the other four were placed randomly 1–5 m from the cup in each cardinal direction (Hovick et al. 2012; Lyons et al. 2015). We visually estimated percent-cover and recorded estimates as the midpoints of the intervals 0%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, or 96–100% (Daubenmire 1959). At each quadrat, we estimated vegetation density, using a Robel pole to record the highest vertical decimeter interval at least 50% obstructed when viewed at 1 m off the ground and 4 m in each cardinal direction (Robel et al. 1970). We calculated average cover estimates for each vegetation variable across all five quadrats and calculated the average and standard deviation of all Robel readings (averages and ranges in Online Resource 1).

To measure landscape context altered by human activity (i.e., grassland, crop, and woodland cover; wooded-edge prevalence and proximity), we categorized land cover within 1000 m of study pastures using a 2014 orthophoto of Ringgold County (Iowa Geographic Map Server). Using ArcMap 10.4.1 (ESRI, Redlands, CA) we digitized land cover as either herbaceous (prairie, cattle pastures, and hayfields), cropland (corn and soybean fields), woodland (forests and dense shrublands), water (farm ponds and creeks), or impervious surface (roads and buildings). We used the 2014 National Cropland Data Layer to verify classifications of crops versus herbaceous cover (USDA National Agricultural Statistics Service 2017). We measured the distance from each nest to the nearest wooded edge. We then created 250 m-, 500 m-, and 1000 m-radius buffers around every nest and calculated percent-cover of herbaceous, cropland, and woodland cover—as well as the length of wooded edges—within each (averages and ranges in Online Resource 1). These distances were chosen to understand the scale at which landscape context had the strongest influence. The 250-m buffers ( ~ 19.6 ha) are similar in area to the home ranges of some small nest predators (e.g., snakes; Klug et al. 2011); the 500-m buffers ( ~ 78.5 ha) are similar to the home-ranges of some medium-sized predators (e.g., raccoons *Procyon lotor*; Beasley et al. 2007); and the 1000-m buffers ( ~ 314.1 ha) are well within the extent of cowbird home-ranges (Patten et al. 2006).

## Data analyses

We estimated daily nest survival probabilities using the logistic exposure method (Shaffer 2004). Each interval between two sequential visits to a nest was considered one replicate, and the response variable was whether the nest survived that interval. Nests were considered to have survived an interval if at least one viable dickcissel offspring remained in the nest afterwards (Hovick et al. 2012). We did not consider nests to have survived if only cowbird offspring remained; from the perspective of dickcissel fitness, these nests were effectively depredated through egg removal by cowbirds or a combination of egg removal and secondary depredation. We related nest survival to explanatory variables using PROC GLIMMIX (Littell et al. 2006) in SAS 9.4 (SAS Institute Inc., Cary, NC) to accommodate the binomial distribution of the response. We included 'PastureID' as a random variable in every model to account for potential non-independence among nests on the same pastures. We evaluated dispersion in the data based on ratios of Pearson Chi squared statistics to degrees of freedom (Littell et al. 2006). No adjustments were required.

To evaluate support for variables influencing nest survival, we compared multiple models using an information-theoretic approach (Burnham and Anderson 2002). The explanatory variables each fell into one of three groups: temporal, nest contents, and habitat variables. We therefore compared candidate models through a three-stage process that allowed for variable selection across these groups without creating an overly large model set (Benson et al. 2010a).

In the first stage, we evaluated temporal models. This stage controlled for variation in survival within and among seasons (Nest Visit Date and Year variables, respectively), potentially due to changes in predator abundance and activity (Borgmann et al. 2013). In the second stage of analysis, we compared nest-contents models. This stage controlled for differences in survival between the laying, incubation, and nestling stage (Nest Stage variable) and between nests containing different numbers of chicks (#Chicks variable). We also tested our prediction that parasitized nests have lower survival (Parasitism variable) and examined whether this effect only manifests in specific nest stages by including an interaction between Parasitism and Nest Stage.

In the final stage of analysis, we examined habitat models addressing our predictions that nest survival is negatively correlated with (a) invasive grass and woody plant cover within 5 m of nests, and (b) land cover patterns reflecting land conversion at broad spatial scales (250–1000 m). Because we directly compared the fit of all invasive plant and land cover models, this analysis allowed us to conclude which variables warrant the greatest conservation attention. We also tested whether other nest-site vegetation components—vegetation density (mean and variability of Robel height), forbs, warm-season grasses, and litter cover—influenced nest success. These variables frequently affect grassland bird reproduction (Fisher and Davis 2010).

At all three stages of the model selection process, we ranked the relative fit of candidate models using AIC adjusted for small samples (AIC$_c$) and compared them to a stage-specific base model. We considered models to be highly supported if they had Akaike weight ($\omega_i$) greater than the stage-specific base model and contributed to the cumulative top 90% of their respective stage weights (Burnham and Anderson 2002, p. 127). In the first stage, the base model was a random effects-only model. In subsequent stages, all variables from highly-supported models identified in previous stages (except uninformative variables; Arnold 2010) were included in every candidate model in the new set—including the new base model. Thus, each stage carried forward the important explanatory variables from previous stages and could then contribute additional, well-supported variables. We avoided issues associated with multicollinearity by calculating Pearson's correlation coefficients among explanatory variables and ensuring that no highly correlated variables (i.e., $|r| > 0.7$) were included in the same models (Dormann et al. 2013).

We computed parameter estimates for selected variables and predicted values of daily nest survival across each variable's observed range of values, holding other variables at their averages (Shaffer and Thompson 2007). We generated 85% confidence intervals around slopes and predicted values (85% because AIC model selection tends to select variables with slopes excluding zero at this confidence level; Arnold 2010). Finally, we computed an overall predicted fledging probability for a nest with a 4-day laying phase, 12-day incubation phase, and 9-day nestling phase (calculated as: average laying-phase daily survival probability raised to the 4th power × average incubation-phase daily survival probability raised to the 12th power × average nestling-phase daily survival probability raised to the 9th power). We calculated a 95% confidence interval for this estimate using the delta method (Powell 2007).

We next estimated the probability of nests being parasitized by cowbirds, again using PROC GLIMMIX and including 'PastureID' as a random variable. Each nest constituted one replicate, and we modelled the response variable with a binomial distribution. We excluded nests depredated before the incubation phase from this analysis; cowbirds typically parasitize nests during laying (Sealy 1992), so nests that did not survive the entire laying phase had less time in which to be parasitized and were thus incomparable to other nests. We judged the first day of each nest's incubation phase by back-calculating from our estimates of nest age, assuming 12-day incubation and 9-day nestling phases (Temple 2002). We then estimated nest initiation dates by assuming a laying phase equal in days to the maximum number of host eggs or nestlings seen in the nest (dickcissels lay one egg per day; Temple 2002) and including a correction factor to account for egg removal by cowbirds. We assumed that one host egg was removed for every 1–2 cowbird offspring in the nest (i.e., we added 1 day to the laying-phase length of a nest with 1–2 cowbirds, 2 days for nests with 3–4 cowbirds, etc.).

To evaluate support for variables influencing parasitism, we again took an information-theoretic approach. We followed a two-stage process, first controlling for temporal variation (i.e., changes in parasitism risk within and between seasons; Initiation Date and Year variables, respectively) and then comparing the effects of invasive plants and landscape context on parasitism risk. Not all habitat variables included in the nest survival analysis were used in the parasitism analysis. Specifically, we did not predict that row-crop cover in the landscape or litter cover at nest sites would influence parasitism risk, so these variables were not included in candidate models. Instead, we considered that since cowbirds follow grazing ungulates (Patten et al. 2006), presence of cattle in a pasture could increase parasitism risk. We thus included 'Cattle' in the candidate set for parasitism, assigning this categorical variable based on whether nests were built in grazed pastures (Online Resource 2). In pastures where cattle were stocked for only part of the season, we assigned this variable based on whether cattle were present during the nest's laying phase. Model selection criteria were identical to those used in the nest survival analysis. We again derived slope estimates and calculated parasitism probabilities across the range of observed values of each highly-supported explanatory variable. No highly correlated variables were included together in candidate models or in the final model.

Our final goal was to examine the effects of cowbird parasitism on reproduction. As mentioned, we tested whether parasitism reduces nest survival in our logistic exposure analysis. Furthermore, we conducted an ANOVA and Scheffé's post hoc test to examine whether dickcissel clutch sizes were greater in unparasitized nests versus nests with either one or multiple cowbird eggs. We also conducted a *t* test to determine whether more dickcissel young fledged from successful nests that had or had not been parasitized.

## Results

We found 527 dickcissel nests; 499 contained viable eggs or nestlings, and we measured vegetation at 477 of those nests. Vegetation was not measured at some nests due to mowing by managers shortly after the nest cycle. Henceforth, we only consider these 477 nests. Cowbirds parasitized 254 nests (53.3%). Parasitized nests often contained just one cowbird egg or nestling (n = 104), though some had two (n = 83), three (n = 42), four (n = 22), five (n = 2), or even six (n = 1). Non-parasitized nests that survived to incubation (n = 204) contained $\bar{x} = 3.71 \pm 0.73$ [SD] dickcissel eggs, while similar nests with one cowbird egg (n = 95) contained 3.02 ± 1.10 dickcissel eggs, and nests with multiple cowbird eggs (n = 149) contained 2.46 ± 1.07 dickcissel eggs. These means all differed from one another, indicating that cowbirds reduced host clutch size, and more so with greater parasitism intensity (ANOVA and Scheffé's post hoc test: $F_{2,\,445} = 77.43$, $p < 0.001$).

Dickcissel chicks fledged from 140 nests (29.4%). Of these, 89 produced only dickcissels (2.92 ± 1.20 per nest), while 51 produced both dickcissel (1.86 ± 0.82) and cowbird (1.47 ± 0.89) fledglings. More dickcissels fledged from successful nests without cowbirds (t-test: $t_{133} = 6.36$, $p < 0.001$). Of the 337 failed nests, 291 (86.4%) were fully depredated by predators, 25 (7.5%) were abandoned (10 perhaps due to observer-induced stress), 16 (4.8%) produced only cowbirds (1.94 ± 0.82), 3 failed during storms, cattle trampled 1, and 1 fell from its substrate.

We included 465 nests with complete habitat data in the nest survival analysis; the others contained only cowbirds at discovery. We conducted 2057 sequential visits to these nests, cumulatively representing 4866 exposure days. Only 448 nests with complete habitat data were included in the analysis of parasitism risk; the other 29 failed during the laying phase.

### Nest survival

The best temporal model included the interaction between year and nest visit date (Table 1). Nest survival decreased over the season in some years, but increased in others (Fig. 1 in Online Resource 3). Stage 2 supported an interaction between nest stage and parasitism: nest survival was lower overall in the nestling phase relative to incubation, but parasitized nests in the nestling phase had lower survival than both non-parasitized nests in the nestling phase and parasitized and non-parasitized nests in other phases (Fig. 1). Comparing the impacts of invasive plants and landscape context, an effect of tall fescue at nest sites clearly had the most support ($\omega = 0.78$); survival decreased with tall fescue cover ($\beta = -0.008$, SE = 0.003; Fig. 2a). The only other variable with support at this stage was row-crop cover within 1000 m of nests, and evidence for this effect was weak ($\omega = 0.03$). Predicted probabilities showed that cropland reduces nest survival ($\beta = -0.011$, SE = 0.006), though the confidence interval for this effect included zero (Fig. 2b).

The overall best model for daily nest survival probability therefore included Year × Nest Visit Date, Nest Stage × Parasitism, tall fescue cover at the nest site, and row-crop cover within 1000 m. The

**Table 1** Models examining the factors that influence daily nest survival probabilities of dickcissel nests in Ringgold County, IA, ranked by AIC$_c$ values. All models in all stages include 'PastureID' as a random variable. See Online Resource 1 for complete descriptions of variables

| Model | $K$[a] | Deviance | $\Delta$AIC$_c$ | Model weight ($\omega$) |
|---|---|---|---|---|
| Stage 1: temporal variables | | | | |
| Year × Nest Visit Date[b] | 9 | 1749.64 | 0.00[c] | 0.90 |
| Nest visit date | 3 | 1770.19 | 5.58 | 0.05 |
| Nest Visit Date + Nest Visit Date$^2$ | 4 | 1765.62 | 5.91 | 0.05 |
| Year + Nest Visit Date | 6 | 1769.58 | 13.89 | 0.00 |
| Intercept-only model | 2 | 1777.90 | 14.17 | 0.00 |
| Year | 5 | 1776.12 | 18.43 | 0.00 |
| Stage 2: nest-contents[d] | | | | |
| Stage × Parasitism[e] | 14 | 1706.98 | 0.00[c] | 0.93 |
| Nest stage[f] | 11 | 1718.20 | 5.15 | 0.07 |
| Parasitism | 10 | 1747.19 | 32.12 | 0.00 |
| Stage 2 base model | 9 | 1749.64 | 32.56 | 0.00 |
| #Chicks[g] | 10 | 1749.62 | 34.55 | 0.00 |
| Stage 3: nest-site and landscape variables[h] | | | | |
| Tall fescue | 15 | 1697.15 | 0.00[c] | 0.78 |
| 1000 m crop cover | 15 | 1704.05 | 6.92 | 0.03 |
| Stage 3 base model | 14 | 1706.98 | 7.80 | 0.02 |
| StDev Robel | 15 | 1705.03 | 7.87 | 0.02 |
| Avg Robel | 15 | 1702.99 | 8.06 | 0.01 |
| Cool-season grasses | 15 | 1705.20 | 8.06 | 0.01 |
| 500 m crop cover | 15 | 1735.44 | 8.09 | 0.01 |
| 1000 m herb cover | 15 | 1705.26 | 8.11 | 0.01 |
| Warm-season grasses | 15 | 1705.75 | 8.60 | 0.01 |
| 250 m crop cover | 15 | 1705.77 | 8.66 | 0.01 |
| 500 m herb cover | 15 | 1705.87 | 8.72 | 0.01 |
| 500 m woodland cover | 15 | 1706.19 | 9.05 | 0.01 |
| 250 m herb cover | 15 | 1706.22 | 9.07 | 0.01 |
| Wood (nest site) | 15 | 1706.29 | 9.17 | 0.01 |
| Forbs | 15 | 1706.49 | 9.34 | 0.01 |
| 250 m woodland cover | 15 | 1706.53 | 9.38 | 0.01 |
| 1000 m woodland cover | 15 | 1706.74 | 9.60 | 0.01 |
| Distance to woods | 15 | 1706.79 | 9.65 | 0.01 |
| 250 m wooded-edge length | 15 | 1706.86 | 9.75 | 0.01 |
| Litter cover | 15 | 1706.95 | 9.80 | 0.00 |
| 1000 m wooded-edge length | 15 | 1706.96 | 9.82 | 0.00 |
| 500 m wooded-edge length | 15 | 1706.97 | 9.83 | 0.00 |

[a] Number of parameters in the model

[b] Nest visit date: date of the end of the interval over which nest survival was recorded

[c] Minimum AIC$_c$ values: 1767.71 (Stage 1); 1735.15 (Stage 2); 1727.35 (Stage 3)

[d] The Stage 2 base model included Year × Nest Visit Date. All other models in this stage expanded upon this base model with the variables listed in the model name

[e] Parasitism: whether the nest contained any cowbirds on the visit when survival was recorded

[f] Nest stage: whether the nest was in the laying, incubation, or nestling phase at the beginning of the interval over which survival was recorded

[g] #Chicks: number of dickcissel and/or cowbird chicks in the nest at the beginning of the interval over which survival was recorded

[h] The Stage 3 base model included Year × Nest Visit Date + Stage × Parasitism. All other models in this stage expanded upon this base model with the variables listed in the model name

area under the ROC curve for this model was 0.650 (95% CI 0.618, 0.683), indicating a reasonable prediction accuracy. Averaging across all years and parasitism statuses, and holding tall fescue and row-crop cover at their average observed values, this model predicts a daily nest survival probability of 0.9364 in the laying phase, 0.9478 in the incubation phase, and 0.8952 in the nestling phase. Extrapolated over the full nest cycle, this equates to a predicted fledging probability of 0.1476 (95% CI 0.0972, 0.1980).

### Cowbird parasitism

The best temporal model for parasitism included year and initiation date (Table 2). Parasitism varied among years and declined over the season ($\beta = -0.040$, SE = 0.007; Figs. 2 and 3 in Online Resource 3). A year-by-initiation-date interaction was also supported, revealing different rates of decline among years (Fig. 4 in Online Resource 3). Annual differences were minor, however, so we only carried the main effects forward. Among the invasive plant and landscape context variables examined, woodland cover within 500 m of nests received the most support ($\omega = 0.53$). Increasing woodland was linked to reduced parasitism ($\beta = -0.071$, SE = 0.018; Fig. 3a). Below this effect, two invasive plant metrics, woody cover and tall fescue cover, were in the top 90% model set. Parasitism increased with both variables (woody: $\beta = 0.031$, SE = 0.013, Fig. 4a; tall fescue: $\beta = 0.015$, SE = 0.006, Fig. 4b). Finally, wooded edge within 500 m of nests, woodland cover within 250 m, and wooded edge within 1000 m also received support. However, these variables were correlated ($r > 0.7$), so we could not include all in the final model. To select the most important variables, we compared the $\mathrm{AIC_c}$ scores of models containing all combinations of the landscape metrics and found that woodland cover and wooded edge within 500 m (Fig. 3b) achieved the best balance of parsimony and model fit.

The overall best model for the probability of cowbirds parasitizing a nest therefore included initiation date, year, woodland cover and prevalence of wooded edges within 500 m of the nest, and woody cover and tall fescue cover at the nest site. The area under the ROC curve for this model was 0.783 (95% CI 0.741, 0.825), indicating high accuracy.

## Discussion

With many grassland birds in steep decline and their habitats primarily situated in human-dominated landscapes, it is urgent that we understand how anthropogenic changes influence avian reproduction (Fletcher et al. 2006; Sauer et al. 2017). Focusing on dickcissels, our study provides a direct comparison between the impacts of multiple invasive plants at a fine spatial scale and human-facilitated changes in land cover at broad scales. Our results clarify that these factors have unequal effects on nest survival and cowbird parasitism. For one, increasing prevalence of the invasive grass tall fescue at nest sites was associated with reduced nest survival, while evidence for an effect of landscape context on survival was limited to a tentative negative effect of row-crop cover within 1000 m of nests. In contrast, the strongest effects on parasitism occurred at a broad spatial scale, with increasing woodland cover and edge prevalence within 500 m of nests associated with low parasitism risk. Secondarily, parasitism increased with tall fescue and woody plant cover at nest sites. Together, these results suggest that row-crops and woody encroachment around dickcissel habitats at broad scales do not strongly erode habitat quality, having marginal effects on nest survival or even mitigating parasitism. In contrast, invasive plants can exacerbate predation and parasitism. Thus, management of invasions within grasslands may benefit reproduction more than optimizing landscape context around reserves.

Three caveats should be noted. First, if nest predators differ among bird species (Cox et al. 2012), habitat-mediated impacts on predation may not be identical between dickcissels and other grassland birds. Information on these issues is sparse, however, so we suggest that future studies identifying predators of multiple bird species report how many nests of each bird are depredated by each predator. As a second caveat, relationships between habitat and predation may differ between regions due to geographic variation in predator communities or interactions between landscape composition and predator densities and behaviors (DeGregorio et al. 2016; Chiavacci et al. 2018). In applying our results to other regions, it is thus important to consider how local predator communities may interact with local habitats. For example, our study region—the Grand River Grasslands—contains moderately large grassland

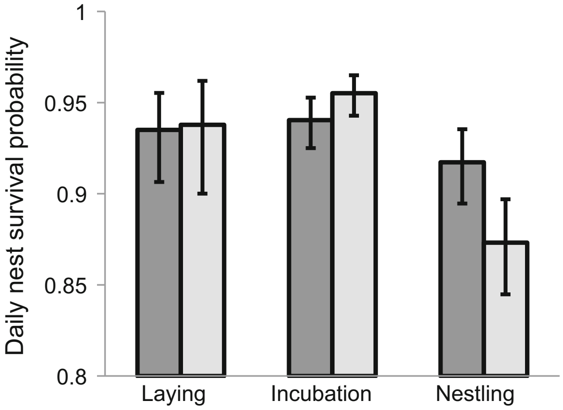

**Fig. 1** Daily survival probability for non-parasitized (dark) and parasitized (light) dickcissel nests in different stages of the nesting cycle. Bars represent 85% confidence intervals

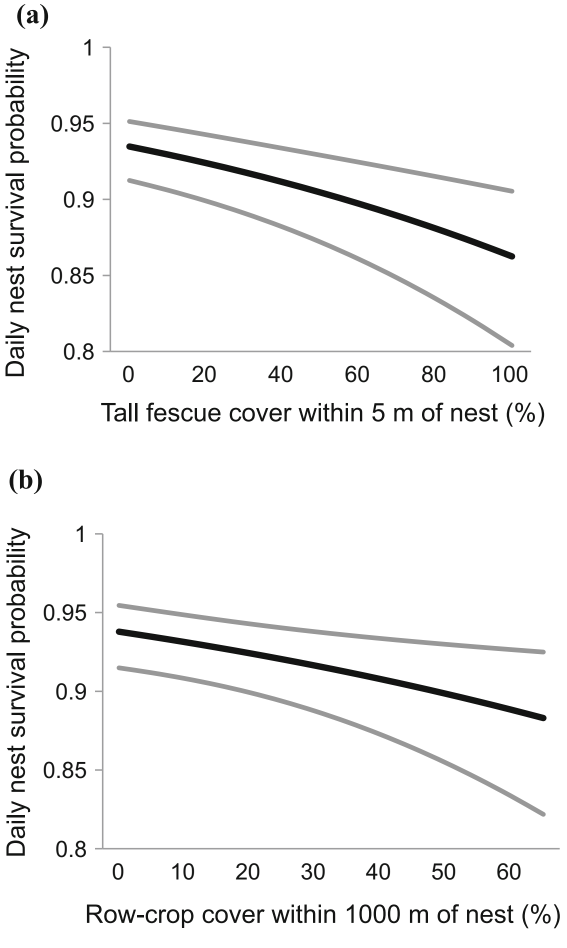

**Fig. 2** Daily nest survival probability as a function of **a** tall fescue cover within 5 m of dickcissel nests, and **b** row-crop cover within 1000 m of nests. Grey lines represent 85% confidence intervals

patches compared to many Midwestern regions (Miller et al. 2012). Stronger relationships between landscape context and nest predation may be observed in more highly fragmented grasslands (Herkert et al. 2003; but see Renfrew et al. 2005). As a final caveat, even though changes in landscape context may not reduce nest survival, they can still affect avian populations. Grassland birds often respond to land cover when selecting habitat, sometimes avoiding landscapes with limited grassland cover, so we caution not to assume that processes like woodland expansion have no conservation relevance (Coppedge et al. 2001; Grant et al. 2004; Shahan et al. 2017).

Before reflecting on individual habitat variables, it is worth noting that nest survival and parasitism varied within and among seasons. Parasitism consistently declined within seasons, potentially due to reduced cowbird activity (Benson et al. 2010a). Nest survival, in contrast, increased during some years but decreased in others. This variability is likely a product of annual differences in nest predator communities or activity patterns (Borgmann et al. 2013). Managers seeking to improve habitat quality should be cognizant of temporal variation, as it could obscure assessments of avian reproduction conducted over limited timeframes. Moreover, it is essential to account for such variation in determining the effects of individual habitat variables.

Our finding that tall fescue increases nest predation is consistent with research on grasshopper sparrows (*Ammodramus savannarum*) in the Grand River Grasslands (Lyons et al. 2015) and northern bobwhites in south-central Illinois (Osborne et al. 2012), but conflicts with a study in southwest Indiana showing that grassland bird nests built in tall fescue-dominated microsites do not have particularly low survival (Galligan et al. 2006). Our results may be more robust than those of Galligan et al. (2006), given our larger sample size (477 vs. 47–264 nests) and the fact that we used a continuous metric of tall fescue cover rather than a qualitative metric of dominance, but the effects of invasive plants on avian ecology do often depend on interplays between local predators and habitats (Nelson et al. 2017). Our results and those of Lyons et al. (2015) indicate that tall fescue increases nest predation in the Grand River Grasslands, and potentially in nearby areas of southern Iowa and northern Missouri. However, further research is needed to reveal the generalizability and mechanisms of these effects.

**Table 2** Models examining the factors that influence the probability of dickcissel nests being parasitized by brown-headed cowbirds, ranked by $AIC_c$ values

| Model | $K^a$ | Deviance | $\Delta AIC_c$ | Model weight (ω) |
|---|---|---|---|---|
| Stage 1: temporal variables | | | | |
| Year + Initiation Date | 6 | 527.02 | 0.00[b] | 0.73 |
| Year × Initiation Date | 9 | 522.79 | 1.99 | 0.27 |
| Initiation date | 3 | 548.40 | 15.25 | 0.00 |
| Year | 5 | 562.59 | 33.52 | 0.00 |
| Intercept-only model | 2 | 582.61 | 47.42 | 0.00 |
| Stage 2: nest-site and landscape variables[c] | | | | |
| 500 m woodland cover | 7 | 517.12 | 0.00[b] | 0.53 |
| Wood (nest site) | 7 | 520.06 | 2.94 | 0.12 |
| Tall fescue | 7 | 520.94 | 3.82 | 0.08 |
| 500 m wooded-edge length | 7 | 521.29 | 4.17 | 0.07 |
| 250 m woodland cover | 7 | 521.42 | 4.31 | 0.06 |
| 1000 m wooded-edge length | 7 | 522.43 | 5.31 | 0.04 |
| 1000 m woodland cover | 7 | 523.84 | 6.72 | 0.02 |
| 250 m wooded-edge length | 7 | 524.62 | 7.50 | 0.01 |
| Stage 2 base model | 6 | 527.02 | 7.84 | 0.01 |
| Cattle | 7 | 525.44 | 8.33 | 0.01 |
| StDev Robel | 7 | 525.70 | 8.58 | 0.01 |
| Distance to woods | 7 | 525.77 | 8.65 | 0.01 |
| Forbs | 7 | 526.01 | 8.89 | 0.01 |
| 500 m herb cover | 7 | 526.17 | 9.06 | 0.01 |
| Warm-season grasses | 7 | 526.39 | 9.27 | 0.01 |
| Cool-season grasses | 7 | 526.43 | 9.31 | 0.00 |
| 1000 m herb cover | 7 | 526.59 | 9.47 | 0.00 |
| 250 m herb cover | 7 | 526.82 | 9.71 | 0.00 |
| Avg Robel | 7 | 526.85 | 9.74 | 0.00 |

All models in both stages include 'PastureID' as a random variable. See Online Resource 1 for complete descriptions of variables

[a] Number of parameters in the model

[b] Minimum $AIC_c$ values: 540.04 (Stage 1); 532.20 (Stage 2)

[c] The Stage 2 base model included Year + Initiation Date. All other models in this stage expanded upon this base model with the variables listed in the model name

Tall fescue's effects on nest survival and parasitism could be driven by several factors. First, fescue provides minimal structural heterogeneity (Osborne and Sparling 2013), which may reduce effort required for predators and cowbirds to search through complex vegetation (Nelson et al. 2017). Low heterogeneity could also reduce air turbulence in plant canopies, increasing detectability of odor plumes (Conover 2007, pp. 183–187). This might explain why olfactory predators (e.g., raccoons, striped skunks *Mephitis mephitis*) frequently depredate grasshopper sparrow nests in sites with high tall fescue cover (Lyons et al. 2015). However, our results indicated no effects on nest success and parasitism of either Robel height or heterogeneity (StDev Robel), suggesting that these mechanisms may not be at work. Alternatively, tall fescue may provide a poor diet for arthropods, reducing their abundance or biomass near nests (Kirfman et al. 1986; Jokela et al. 2016). If birds compensate by increasing provisioning rates to nestlings or foraging farther from nests (Britschgi et al. 2006), increased visual cues could attract predators (Martin et al. 2000). We present no data on arthropods or provisioning, but this hypothesis is supported indirectly by the fact that dickcissel nests were depredated more frequently in the nestling phase. Moreover, in our study region, predation of grasshopper sparrow nests by garter snakes (*Thamnophis* spp.) and eastern racers (*Coluber constrictor*) increases with tall fescue cover near nests (Lyons et al. 2015). These snakes are known to depredate nests almost exclusively during the day, when visual cues are more readily available (DeGregorio et al. 2014), and garter snakes use both visual and olfactory cues to detect prey (Chiszar et al. 1981). These patterns lend

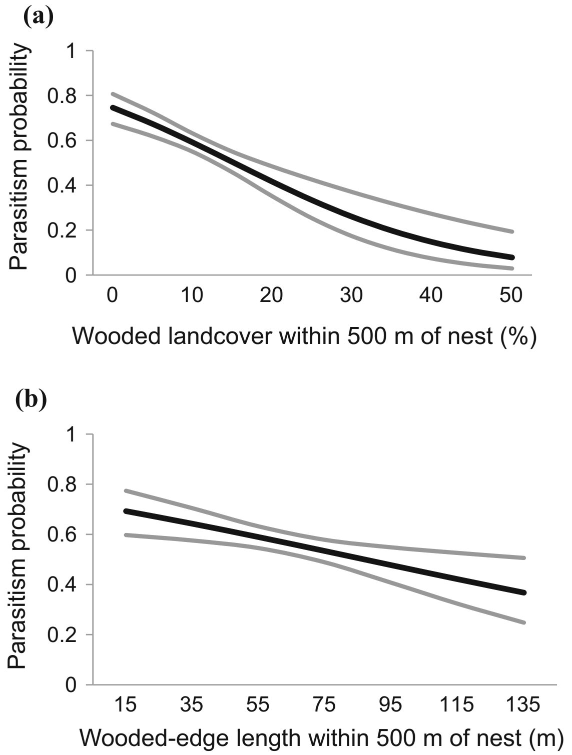

**Fig. 3** Cowbird parasitism risk as a function of **a** woodland cover and **b** wooded-edge length within 500 m of nests. Grey lines represent 85% confidence intervals

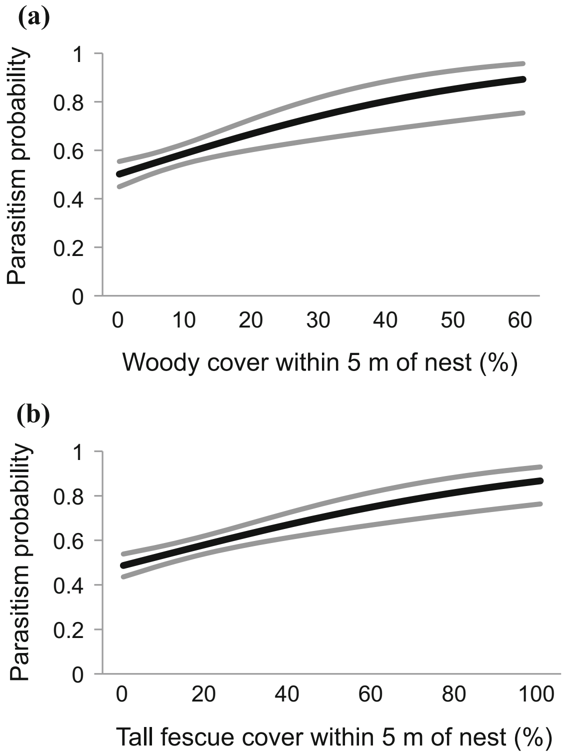

**Fig. 4** Cowbird parasitism risk as a function of **a** woody cover and **b** tall fescue cover within 5 m of nests. Grey lines represent 85% confidence intervals

plausibility to a visually-mediated effect of tall fescue on predation.

Aside from tall fescue, the only habitat variable influencing survival was corn and soybean cover within 1000 m of nests. There was high model-selection uncertainty for this effect, but the reduction in survival associated with increasing crop cover was consistent with our expectations because nest predators are often abundant along agricultural edges (Pedlar et al. 1997; Dijak and Thompson 2000; Chalfoun et al. 2002). This pattern may also arise because crop fields provide abundant forage for omnivorous predators in autumn, and may thus support abundant omnivore populations (Cottam et al. 2009). However, crops are unavailable in the summer, potentially increasing nest predation by forcing those omnivores to forage in grasslands.

Contrary to tall fescue and crops, we were surprised by the lack of relationship between woody plants and nest survival. We predicted that woody cover near nests would reduce survival due to snake predation (Klug et al. 2010) and that wooded edges in the landscape would reduce survival due to elevated predator abundance (Dijak and Thompson 2000; Chalfoun et al. 2002). It may be that predation by some predators increased near shrubs and edges, but not strongly enough to alter overall predation rates (Renfrew and Ribic 2003; Benson et al. 2010b). Alternatively, dominant dickcissel nest predators in our region may not respond to woody cover.

In contrast to effects on nest predation, we observed strong declines in parasitism with increasing tree cover and wooded-edge prevalence within 500 m of nests—a pattern consistent with previous studies of grassland bird reproduction (Pietz et al. 2009; Hovick and Miller 2013). This is unlikely a product of low cowbird abundance, since cowbirds do not avoid landscapes with high tree cover (Grant et al. 2004; Cox et al. 2012). Authors have instead suggested that when woodlands are present in the landscape, cowbirds prefer to parasitize woodland-breeding hosts rather than grassland hosts (Pietz et al. 2009; Hovick and

Miller 2013). This hypothesis is supported by studies monitoring nests across multiple habitats that have observed higher parasitism rates in forests and woodland edges versus in grasslands (Hahn and Hatfield 1995; Strausberger and Ashley 1997). However, it would be particularly notable if this mechanism also causes woodland cover to reduce parasitism of dickcissel nests, since dickcissels are highly-preferred cowbird hosts—even relative to some woodland birds (Rivers et al. 2010). If this pattern indeed resulted from cowbird host-switching, that might also explain why parasitism increased with shrub cover at nest sites: cowbirds may search for woodland hosts in shrub patches within grasslands and incidentally discover grassland bird nests nearby.

Habitat-mediated effects on parasitism have consequences for avian reproduction. As in previous studies, parasitized nests contained fewer dickcissel eggs than non-parasitized nests and fewer dickcissels fledged from parasitized nests (Benson et al. 2010a; Hovick and Miller 2013). Moreover, although survival of parasitized and non-parasitized nests was similar during laying and incubation, parasitized nests were more likely to fail in the nestling phase. This pattern has also been observed in American redstarts (*Setophaga ruticilla*; Hannon et al. 2009) and may occur because cowbird chicks beg frequently and loudly, increasing auditory cues for predators (Dearborn 1999). Extreme begging may also stimulate host parents to increase provisioning rates, intensifying visual cues (Dearborn et al. 1998). Irrespective of mechanisms, these negative effects indicate that reducing parasitism may aid grassland birds.

As North American grasslands continue to be transformed by invasive plants, plowed, and fragmented, wildlife managers face difficult choices. Conservation and restoration budgets are usually tight, and managers often need to decide whether to devote resources to invasive plant control, land purchases, or additional restorations (Rowe 2010). Moreover, when acquiring new lands, managers sometimes consider the conservation value of alternative land parcels, a choice that may be influenced by landscape context (Snyder et al. 2007). Our study provides guidance in decision-making by identifying site-level and landscape factors that should be targeted to increase habitat quality. First, because woodland cover in the landscape mitigates parasitism risk and row-crop cover appears to reduce nest survival, it would be wise for conservation managers to prioritize purchasing grasslands in landscapes with limited crop cover—or to restore nearby crop fields to grassland—rather than avoid acquiring sites near woodlands. Second, although woody cover at broad scales may not be problematic, our results suggest that controlling shrub cover within grasslands could reduce cowbird parasitism.

Finally, our finding that tall fescue exacerbates nest predation and parasitism indicates that replacing tracts of tall fescue with heterogeneous vegetation should be a priority. However, conflicting results from another region (Galligan et al. 2006) caution that fescue may not be universally harmful. We suggest that managers use adaptive management to assess the benefits of controlling tall fescue, experimentally reducing fescue in some areas (e.g., by applying herbicide in the fall, when many native grasses and forbs are dormant) while monitoring avian communities and nest survival in treated and untreated areas (Osborne et al. 2012; Osborne and Sparling 2013). If herbicide is used, this may have non-target effects (e.g., secondary invasions; Matthews et al. 2017) and impacts may vary among bird species or over time. Regardless of effects on nest success, if managers increase habitat heterogeneity at appropriate scales, this may still serve the valuable goal of increasing avian diversity (Duchardt et al. 2016).

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