

NEST PREDATION AND HABITAT SELECTION IN THE GRASSHOPPER SPARROW
(*AMMODRAMUS SAVANNARUM*)

BY

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THESIS

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ABSTRACT

Predation is the leading cause of nest failure for many birds and is an important source of natural selection that shapes avian behavior and life-history traits. However, our understanding of the relationship between habitat characteristics and nest loss and how predation affects nest-site selection is limited. Predators are not often identified, yet their behavior greatly influences nest loss patterns. Most studies of nest-site selection make unrealistic assumptions about the ability of birds to identify and access preferred habitat and few use unambiguous measures of selection. I studied how grassland management with fire and grazing influences predator-specific patterns of nest loss and whether predation influenced nest-site selection by grasshopper sparrows (*Ammodramus savannarum*). I used near-infrared video cameras to identify nest predators and followed breeding females on multiple nesting attempts within a breeding season. Burning reduced losses by snakes (*Thamnophis* and *Coluber* spp.), whereas predation by mammals and snakes increased with litter cover and fescue (*Schedonorus phoenix*) surrounding the nest. Mammals were less likely to prey upon nests with increased forb cover as well. Nest losses attributed to cowbirds (*Molothrus ater*) were unrelated to measured habitat or landscape variables and unaffected by management actions. Though nest sites did not differ from available habitat, female grasshopper sparrows did exhibit adaptive nest-site selection by selecting safer locations on subsequent breeding attempts. My results support that the use of fire can reduce nest loss, but success is contingent on predator identity. Reductions in litter and fescue and increasing forb cover can reduce predation as well. Further, grasshopper sparrows' nest-site selection is adaptive in terms of reducing nest loss, but females make more adaptive choices when re-nesting. This information can help devise effective management strategies aimed at reducing nest loss and improve our understanding of avian behavior.

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CHAPTER 1

INTRODUCTION

Predation is the leading cause of breeding failure for most passerine species and may be limiting population growth (Ricklefs 1969). Identifying the factors related to nest loss is a common goal of many research projects, yet studies that do so often find conflicting results (Lahti 2009). For example, nests in fragmented landscapes are generally thought to be associated with high rates of nest loss and parasitism (Robinson et al. 1995, Arcese et al. 1996, Herkert et al. 2003), particularly those close to habitat edges (Gates and Gysel 1978, Batary and Baldi 2004). Nevertheless, such generalizations are not well supported (e.g. Benson et al 2013).

Birds nesting in grasslands often suffer higher rates of nest loss than species in other habitats (Martin 1993). A great deal of research has attempted to identify factors influencing nest loss and practices that can reduce predation in the hope of mitigating or reversing the severe population declines experienced by grasslands birds in recent decades (Brennan and Kuvlesky 2005). Fire and grazing are commonly employed to manage grasslands (e.g. Fuhlendorf and Engle 2004, Rahmig et al. 2009, Fuhlendorf et al. 2012), yet the effects of these actions on nest loss vary considerably among regions (Johnson and Temple 1990, Kerns et al 2010, Johnson 2012, Ribic et al. 2012).

The lack of consistent predation patterns may be due to a failure to consider the underlying processes related to nest loss (Lahti 2009). Predator activity can influence nest loss patterns substantially, yet most studies group nest failures together and obscure details about the factors related to predation (Benson et al. 2010). Among grasslands, predator communities vary regionally (Pietz et al. 2012), yet evaluations of management actions often ignore such differences (Hartaway and Mills 2012). Identifying predators can help guide management actions

(Thompson and Ribic 2012). Indeed, recent studies have determined that management actions may not target the correct predators or results in changes in predator community without affecting predation rates overall (Conner et al. 2010, Ellis-Felege et al. 2012, Ribic et al. 2012, Ellison et al. 2013). Despite these important implications, examination of the effects of management on predator-specific patterns of nest loss is rare.

The importance of nest predation in avian ecology is not limited to its effects on breeding success. Predation is also a strong selective force that shapes avian behaviors such as nest-site selection (Caro 2005, Chalfoun and Martin 2007, Lima 2009). Decisions about where to nest may be influenced by innate preferences that have evolved through time, or may be learned. Birds are able to use visual or auditory cues to assess current predation risk which may influence nest placement (Zanette et al. 2011, Eicholz et al. 2012). Whether it is by natural selection, or the ability to assess risk in real time, it is generally expected that nest-site selection should maximize fitness by minimizing predation risk. Yet there are many instances where the preferred habitat characteristics of nests have no relation to nest loss, or worse, increase the likelihood a nest is preyed upon.

When nest-site selection appears to be maladaptive, some have suggested that factors other than predation are driving habitat preference. Adult and post-fledging survival, food availability, or microclimate can affect an individual's fitness as well. Trade-offs between these factors and predation may give rise to seemingly maladaptive nest-site selection patterns (Marzluff 1988, Chalfoun and Schmidt 2012). Alternatively, preferences may be shaped by long-term patterns in predation risk and birds are already minimizing their risk of predation by nesting at an "adaptive peak" (Clark and Shuttler 1999, Latif et al. 2012). In some cases, researchers suggest that maladaptive nest-site selection is an ecological trap. Anthropogenic changes to

habitats have decoupled once-reliable cues about predation risk from its current state (e.g. Gates and Gysel 1978).

However, many studies use inadequate measures of habitat preference and oversimplify the process of habitat selection. The use of bird density or nest density to infer preference is common, yet density may be an unreliable indicator of habitat quality and may not accurately reflect selection (Van Horne 1983, Robertson and Hutto 2006). Limited access to and/or information about breeding habitat quality may prevent birds from making adaptive decisions initially. Instead, adaptive decisions may only be detected when observing multiple nesting attempts (Betts et al. 2008, Kearns and Rodewald 2013).

I examined how predator-specific patterns of nest loss changed in response to management with fire and grazing and how predation influenced nest-site selection in a grassland-obligate songbird, the grasshopper sparrow (*Ammodramus savannarum*). I used near-infrared video cameras to identify nest predators and followed breeding females on multiple nesting attempts within a breeding season to help clarify how management affects nest predation patterns and whether grasshopper sparrow nest-site selection reduces nest loss. Studies of habitat selection by grasshopper sparrows use abundance of birds or nests as indicators for preference and only examine habitat selection at the territory scale or larger (Ahlering et al. 2009, Ingold et al. 2010).

THESIS ORGANIZATION

This thesis contains four chapters including two that are formatted for publication in scientific journals. Chapter 1 is a general introduction. Chapter 2 examines predator-specific patterns of nest loss and the effect of fire and grazing. Chapter 3 investigates nest-site selection patterns in

relation to predation risk. Chapter 4 summarizes results from chapters 2 and 3 and provides overall conclusions.

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CHAPTER 2

CHANGES IN PREDATOR-SPECIFIC PATTERNS OF NEST LOSS WITH FIRE AND GRAZING

ABSTRACT

1. Attempts to reduce nest predation are typically focused on habitat manipulations and predator control, but are often unsuccessful. In many cases, actions are based on incorrect or limited knowledge of nest predators. Patterns of nest loss differ among predators as a function of their ecological and life history traits. These differences suggest it is unlikely that any management approach can affect all predators. Instead, management, like predation patterns, is more likely to have species-specific outcomes.

2. We placed near-infrared video cameras at the nests of grasshopper sparrows (*Ammodramus savannarum*), a species of conservation concern, to identify nest predators and to document predator-specific changes of nest loss in response to the application of fire and cattle grazing in highly fragmented grasslands. Nest losses were expected to be related to environmental features associated with patterns in the abundance or activity of predators.

We hypothesized that nest predators would be diverse and that only a subset of species, those reliant on grasslands, would decrease in abundance or activity in recently burned areas, resulting in lower rates of predation.

3. Burning reduced losses by snakes (*Thamnophis* spp. and *Coluber constrictor*), the second most frequent nest predator, but not mammals (the most frequent) or cowbirds (*Molothrus ater*; infrequent). Mammal and snake predation was more likely at grasshopper sparrow nests with

greater amounts of tall fescue (*Schedonorus phoenix*) and litter cover. Mammals were also less likely to depredate nests with greater forb cover.

4. *Synthesis and applications.* We found that fire is not universally effective in reducing nest loss, but is contingent on predator identity. Our results indicate that burning, reducing of the cover of litter and tall fescue, and increasing forb cover can mitigate predation. Grassland management practices that include periodic fire, reduce fescue, and increase forb cover can benefit grassland birds, but success will be limited by the identity of local nest predators

INTRODUCTION

Nest predation is the leading cause of nest failure for many passerine species (Martin 1992, Thompson and Ribic 2012). Much of the literature on this topic has focused on identifying the factors that make a nest more or less likely to be depredated (Angelstam 1986, Vickery et al. 2001). For example, nests in fragmented landscapes are generally thought to be associated with high rates of nest loss and parasitism (Robinson et al. 1995, Arcese et al. 1996, Herkert et al. 2003), particularly those close to habitat edges (Gates and Gysel 1978, Batory and Baldi 2004). Nevertheless, such generalizations are not well supported (e.g. Benson et al 2013). This is because nest loss is more directly related to the identity, behavior, and activity patterns of nest predators (Lahti 2009).

When one or a few predators are responsible for nest failure, the determinants of nest loss are more easily identified and often related to the foraging behavior or activity of the dominant predator (Vickery et al. 1992, Sperry et al. 2008). Yet in many systems, predator communities are diverse (Thompson and Burhans 2003, Ribic et al. 2012) and nest loss patterns can be difficult to elucidate because the environmental factors related to predator behavior differ among species (Benson et al. 2010). Understanding how different predators respond to the environment

is important for managers trying to reduce nest loss because some management approaches may affect only a subset of species causing nest failure (Teunissen et al. 2008, Ellis-Felege et al. 2012).

Natural resource managers of North American grasslands frequently try to reduce nest mortality by modifying habitat features, often using fire. A recent meta-analysis concluded that fire was useful for increasing breeding success (Hartway and Mills 2012), yet there are many exceptions. The effect of fire on breeding success varies among regions, improving success in some areas (Johnson and Temple 1990, Rahmig et al. 2009) but decreasing it in others (Shochat 2005, Churchwell et al. 2008). In part, these differences stem from habitat preferences of species that exploit disturbed areas or avoid them (Madden et al. 1999). Nonetheless, there is a general failure in these studies to address the influence of the predator community on nest loss patterns. Predator communities can vary substantially among grasslands (Pietz et al. 2012) and there is rarely explicit consideration given to the response of predators to habitat management. Documenting the relationship between predator-specific patterns of nest loss and management actions has the greatest potential for improving conservation efforts, particularly when predator communities are complex (Teunissen et al. 2008, Thompson and Ribic 2012).

We evaluated how management of grassland habitat with fire and grazing affected predator-specific patterns of nest loss. Previous research in the area indicated the predator community may be diverse (Hovick et al. 2012). Birds nesting in fragmented grasslands, like in our study, are often exposed to predators common to grasslands including skunks (*Mephitis mephitis*) and badgers (*Taxidea taxus*), as well as generalist predators such as raccoons (*Procyon lotor*), snakes, and cowbirds (Renfrew 2003). Predation by both grassland and generalist species might be related to habitat or landscape features associated with their activity or behavioral

patterns like tree or grassland cover in the landscape, proximity to wooded edges or water, or nest concealment (Weidinger 2002, Phillips et al. 2003, Patten et al. 2011). However, we predicted that burning pastures would reduce nest loss only by those predators that forage primarily in grasslands or rely on grassland vegetation for cover and concealment (e.g. snakes, skunks; Vickery et al. 1992, Cavitt 2000), as their activity or abundance in the area may decrease following a fire. We used video cameras to identify predators and help us examine ways that management and habitat factors influenced predator-specific nest loss.

METHODS

Study Area

Our study was conducted on eight pastures in Ringgold County, Iowa, from 2010-2012. The landscapes surrounding these sites comprised 58% grasslands and pasture, 18% row crop, and 22% woodlands (unpublished data). Pastures were under the jurisdiction of the Iowa Department of Natural Resources, The Nature Conservancy, or were privately owned. Vegetation within pastures was dominated by graminoids including both native and non-native species. Other plants in pastures included forbs, sedges, and native and exotic legumes (McGranahan, 2008).

Research pastures ranged in size from 23-34 ha and were assigned to one of two treatments, patch-burn-grazed or grazed-and-burned. In patch-burn-grazed pastures (n=4), one-third of the pasture was burned sequentially every spring so the entire pasture was burned once during the three-year study. All patches within grazed-and-burned pastures (n=4) were burned in spring 2009 and again in 2012 to prevent the encroachment of woody vegetation. Pastures were stocked with cattle *Bos taurus* Bojanus from May-September ($\bar{x} = 0.8$ AUM (animal equivalent units per month) ha^{-1}). Pastures were fenced along the perimeter and cattle had free access to the patches therein.

Nest Monitoring

We focused our nest-searching efforts on the grasshopper sparrow for several reasons. Like many grassland obligate songbirds, they have experienced severe population declines in recent years (Sauer et al. 2003), are a species of conservation concern throughout much of their range, (Panjabi et al 2012), and experience high rates of nest predation (Hovick et al. 2012). We searched for nests from 05:30 to 12:00 (CST) between May 15 and July 29 in each year of the study. Each pasture was searched three times in 2011 and four times in 2010 and 2012. Most nests were located by systematic rope-dragging (Higgins et al. 1969) using a 30-m rope with aluminum cans attached every 1.5 m. Searchers placed flags at one end of the rope every 30-50 m to ensure complete coverage of pastures. Most searches included two observers who carried the rope with a third person following behind.

After locating a nest, we recorded the location with a GPS unit and placed flagging 5 m north and 5 m south to aid in relocation on subsequent visits. One host egg was candled to estimate nest age and to predict hatch date (Lokemoen and Koford 1996). If a nest contained nestlings, we aged the clutch based on feather growth characteristics, such as the emergence of pin feathers or primary feathers emerging from their sheath (Vickery 1996). We recorded clutch or brood size and the number of cowbird eggs or nestlings at each visit and documented any instance where eggs or nestlings were lost between intervals.

Video Cameras

Whereas sign at the nest has been used to determine cause-specific mortality, it is notoriously inaccurate (Thompson and Burhans 2004). Instead, we used miniature video cameras to identify predators. We placed cameras at a subset of nests, distributing them proportionately among

pastures and patches of each treatment. We constructed our camera systems *sensu* Cox et al. (2012a). Though we used several different models throughout the study, all cameras included infrared (950nm) light-emitting diodes (LEDs) that enabled us to continue recording at night. We returned to nests, with and without cameras, at 1-4d intervals to replace data cards and to avoid systematic bias. Cameras remained at nests until they produced fledglings or failed. We reviewed film to determine exact fledge dates and to identify predators if nest contents were removed between observer visits.

We placed cameras at nests in late morning and early afternoon to minimize nest abandonment. We were not able to assess whether the placement of a camera caused abandonment by observing quick returns to the nest afterward (Stake et al. 2004) because female grasshopper sparrows do not spend much time incubating or brooding during the afternoon. In 2011, it appeared that placing cameras while banding females as a part other research activities increased abandonment (n= 10), so we subsequently carried out each activity on separate visits. In 2012, we acquired digital video recorders (DVRs) which allowed us to review footage in the field. If we did not observe the female returning to incubate or brood 2-4 h after placing a camera, we removed the camera which reduced abandonment at a subset of nests. During a severe drought in mid-July 2012, we observed that some females abandoned nests after we placed a camera during the incubation stage (n=8). Therefore, we switched to placing cameras at nests only after hatching to prevent abandonment. We do not believe this biased our sample of nest predators because the change in the placement of cameras occurred late in study, affected only a small portion of nests (7 nests) and most predation occurred during the nestling stage.

Landscape and pasture measurements

For many predators, activity and abundance are influenced by landscape scale variables such as land-cover or edges. The foraging activity, movement and abundance of mesopredators such as skunks and coyotes (*Canis latrans*) have been related to tree cover or proximity to water bodies (Larivière and Messier 2000, Kuehl and Clark 2002, Phillips et al. 2003). Agricultural fields may provide food subsidies that support populations of generalist predators including raccoons or cowbirds (Chalfoun et al. 2002). Thus, we delineated woodland, grassland, open water, and agricultural fields within 1km of each pasture. We selected 1km as a threshold because variance in the proportions of land-cover classes plateaued at this distance (Pillsbury et al. 2011). Further, nest predation may be strongly related to landscape characteristics at or near this scale (Bergin et al 2000). Land cover was digitized in ArcGIS 10.0 (ESRI, Redlands, California) using 2011 National Agricultural Inventory Program 2m true color orthoimages (USDA 2011). Because predators like snakes, cowbirds or skunks tend to focus foraging or increase their activity near forest-field edges, streams, or ponds (Kuehl and Clark 2002, Weatherhead et al. 2010, Patten et al. 2011); we calculated the distance to these features for each nest. The activity and abundance of snakes and skunks are often lower in recently burned grasslands (Vickery et al. 1992, Cavitt 2000), so we quantified time-since-fire (yrs; 0, 1, 2) for every patch in our study pastures.

Nest-site measurements

Vegetation density and complexity at nest sites might decrease nest predation because of reduced visual or olfactory cues, or predator search efficiency (Martin 1993, Benson et al. 2010). Taller vegetation may increase nest concealment and breeding success in grassland birds, though the evidence is mixed (Winter et al. 2005). We returned to each nest 3-7d after nests fate was determined to quantify the vegetation composition and structure. We placed one 0.5-m² quadrat

at the nest cup and an additional quadrat in each cardinal direction within 5m of the nest (n=5 quadrats per nest). Within each quadrat, we recorded percent cover of tall fescue, C4 grasses, C3 grasses (including tall fescue), forbs, legumes, bare ground, litter cover, and shrubs. Cover was recorded as the midpoints of the following categories: 0-5%, 6-25%, 26-50%, 51-75%, 76-95%, 96-100% (Daubenmire 1959). Cover of tall fescue, C3 grasses, wooded vegetation and litter, and forbs are known to be related to nest failure or are the preferred habitat of potential nest predators (Barnes et al. 1995, Klug et al. 2010, Conover et al 2011, Duggan et al. 2011). We quantified vegetation visual obstruction (hereafter V.O.; a surrogate for vegetation height and density) at each quadrat by recording the height at which a Robel pole (Robel et al. 1970) was 50% obscured 4m from the nest and 1m above the ground in each cardinal direction (n= 4 readings per quadrat, n=20 readings per nest).

Analysis

Though cameras are critical to identifying the species responsible for nest failure, their use may bias nest predation rates (e.g. Renfrew and Ribic 2003, Pietz et al. 2012). A meta-analysis published by Richardson et al. (2009) reported that cameras reduced nest predation, but the effect was not statistically significant. To ensure that the results of any predator-specific analyses were not systematically biased by the presence of cameras, we compared survival rates at nests with and without cameras using the logistic exposure method (Shaffer 2004). Because each interval between observer nest visits is an independent Bernoulli trial, cameras were included as an interval-specific covariate.

For our predator specific analyses, our data set consisted of 1-day intervals when each nest was monitored with a camera. Our primary interest was in identifying factors related to nest loss by mammals, snakes and cowbirds as these have been identified as common nest predators

and there is much interest in reducing their impact for threatened species (Hartway and Mills 2012, Thompson and Ribic 2012). We separated fates into five categories: predation by brown-headed cowbirds, snakes, mammals (raccoons, skunks, badgers, etc.), other causes of loss (trampling, abandonment, predation by species other than the aforementioned, unknown predator due to camera failure), and survived. When camera failure prevented us from identifying a predator, we used a random number to avoid bias when estimating the number of exposure days a nest survived during the last interval (usually 2-3d) before it failed.

We used multinomial logistic regression to identify temporal and environmental variables related to predation events by the three predator groups. We included partial predation events because not all predation events result in complete nest failure (Pietz and Granfors 2000, Hovick et al. 2012) and ignoring them would underestimate the impact of some predators. Thus, the survival estimate equals the probability that a nest escaped the loss of any eggs or chicks.

We evaluated support for hypotheses explaining predator-specific nest loss using an information-theoretic approach. Our sample sizes for predators were small and complex models would thus be highly penalized and appear non-competitive (Cox et al. 2012b). Therefore, we kept our habitat models simple, including only one or two variables and restricting the combinations of variables we evaluated by constructing models in a multi-step process.

We believed that predators would be affected by habitat-related variables in a hierarchical manner and that landscape and pasture scale conditions would influence patterns of nest loss at finer scales (Thompson 2007). First, we evaluated support for the effects of tree cover, row-crop agriculture, and distance to water, and wooded edges on predator-specific patterns of nest loss. Second, the effect of management treatment, pasture size, and time since fire were assessed. Third, the effect of cover of C4 grasses, litter, tall fescue, forbs, and V.O. were evaluated. This

allowed us to evaluate support for cross-scale additive effects that, while not strictly *a priori*, were likely to have explanatory power and result in fewer overall models. Limiting the total number of models minimizes spurious results, particularly when those models include different combinations of the same variables (Burnham and Anderson 2002). At each stage, we evaluated and ranked models using Akaike's Information Criterion adjusted for small samples (AIC_c). To create additive, cross-scale models, we carried variables to the next stage only if they had a lower AIC_c than a constant survival (null) model.

To determine whether predator identification improved our understanding of how habitat conditions and management affected nest loss, we conducted an additional nest predation analysis. Here, we used logistic regression and grouped all causes of egg and chick loss together. We incorporated habitat and landscape variables in the same fashion as described above.

Predator abundance and activity may change between years, within a breeding season, or the visual and olfactory cues predators use to locate nests may increase during the nestling stage. Therefore, we evaluated support for temporal variables in our predator-specific and our combined predator analyses, using five models (including a null model). We considered effects of year, nest stage, day of year, and the additive effects of day of year and nest stage. Given the limited number of models under consideration, we evaluated these in a single step. For all analyses, we examined correlations among all variables considered for inclusion to ensure that highly correlated variables ($r > 0.7$) did not appear in the same model. Model fit was assessed with a likelihood ratio test between our global and a null model and we examined our results for evidence of overdispersion.

For all analyses, we ranked our final models by AIC_c scores. We considered models within 4 AIC_c units of the top model (lowest score) to contain substantial evidence (Burnham

and Anderson 2002). We examined 85% confidence intervals (CI's) of conditional estimates of selected variables in order to understand their relationship to nest loss by different predator groups. We used 85% CI's because AIC_c selection will support parameters at this level over a null model (Arnold 2010). We based our inference on conditional rather than model averaged estimates because the addition of a single variable results in a parameter estimate for each of the four nest failure categories (e.g. $\beta_{1 \text{ snakes}}$, $\beta_{1 \text{ mammals}}$, $\beta_{1 \text{ cowbirds}}$, and $\beta_{1 \text{ other}}$). Therefore, the penalty for the addition of one covariate is 8 AIC points (instead of two, as is more common). As a result, models which include parameters that are only informative for a single predator group may rank poorly despite the information they contain. These informative yet poorly ranked models receive low weight when model-averaging, which can reduce the estimates of ecologically meaningful variables to near zero.

RESULTS

We monitored 350 grasshopper sparrow nests from 2010-2012 (127 in 2010, 90 in 2011 and 133 in 2012) and placed cameras at 135 nests total (36 in 2010, 48 in 2011, 51 in 2012). Twenty-one nests with cameras were abandoned and omitted from analysis (3 in 2010, 10 in 2011 and 8 in 2012). Our final data set for analysis included 807 observation days at 108 nests. We monitored nests with cameras for 7.5 d on average (range 1-20 d).

We identified individual predators at 51 predation events. Mammals comprised the largest group of predators (n=21, Table 1) and included raccoons, badgers, skunks, coyotes and opossums (*Didelphis virginiana*). Snakes consumed a smaller but still substantial portion of nests (n=12, Table 1) whereas cowbirds were responsible for few predation events (n=5, Table 1). We recorded a single predation event by a white-tailed deer (*Odocoileus virginianus*), a blue jay (*Cyanocitta cristata*), a red-tailed hawk (*Buteo jaminaicensis*), a loggerhead shrike (*Lanius*

ludovicianus), and a vole (*Microtus* spp.) as well. We observed removal of dead nestlings and an egg that failed to hatch by adult grasshopper sparrows at eight nests. These events included single and multiple chick mortality and were attributed to inclement weather (n=3) or unknown natural causes (n=4). Predation by mammals resulted in complete nest failure, whereas snakes were responsible for partial and complete nest losses. Cowbird predation resulted in only partial losses. We recorded egg and chick removal by more than one species at three nests. We also observed a snake depredating the same nest on two separate occasions. Because this latter case could have been the same individual, making the two events non-independent, it was only counted once.

We found no effect of cameras on nest survival ($\beta_{camera}=-0.111$; 85% CI: -0.343, 0.121). Model selection from our predator-specific analysis revealed that the best habitat model included the effect of time-since-fire and forb cover, though there was nearly equivalent support for a model including litter cover. Models including time-since-fire and tall fescue cover received support as well (Table 2). Only predation by snakes was affected by time-since-fire. Snake predation increased in the absence of fire and was 11 times more likely in patches that had not been burned for two years than in recently burned patches (Table 3, Figs. 1 & 2). Mammals and snakes were more likely to depredate nests with more fescue and litter cover (Table 3 Figs. 1-3). Only predation by mammals declined as the cover of forbs increased at a nest. The best temporal model was the null, although effects of nest stage had some support (Table 2). Confidence intervals of conditional estimates of stage for snakes (Table 3) did not overlap zero, suggesting that snakes were more likely to prey on nests during the nestling stage. Estimated daily survival rate (conditional on the top ranked model while holding time-since-fire and forb cover at their

mean values) was 0.906, while predation rates were 0.001 for cowbirds, 0.010 for snakes, and 0.023 for mammals. These values represent the probability a single egg or chick survived a day.

In models that did not account for predator identity, selected variables were similar to those in species-specific analyses with a few exceptions (Table 4). Support for an effect of time-since-fire was greatly reduced, to the point it was only marginally supported over the null model. Forb cover received minimal support while the effect of litter cover was included in the top ranked model. C4 grass cover also received more support. The effect of stage received considerably more support and more models including temporal variables appeared to be competitive, though most of these did not reduce the deviance of the best model (e.g. > 1). Thus, many of these variables could be classified as uninformative parameters (Arnold 2010). The conditional parameter estimate for stage ($\beta = -0.40$; 85% CI: -0.755, -0.045) was much smaller than that obtained in our predator specific analysis for snakes. The relationship between temporal and habitat variables and nest loss were similar to those selected in our predator-specific analysis. Predation increased with litter and tall fescue cover and was lower during the incubation stage and nests with more C4 grass cover.

DISCUSSION

In grasslands in North America, fire generally appears to reduce nest predation (Hartway & Mills 2012). Nevertheless, there are many instances where fire is associated with increased nest loss for grassland birds (Rohrbaugh et al. 1999, Churchwell et al. 2008, Rahmig et al. 2009). Our results demonstrated that the effect of fire on predation was substantial, but only for snakes. Based on the collective evidence, we believe not all species that prey on nests change in abundance or activity in response to fire. Instead, it is important to consider how fire affects particular classes of predators. For snakes, the effectiveness of fire in reducing nest loss has a

strong biological explanation. Cavitt (2000) found that fire reduces both the abundance and activity of grassland snakes. These species may avoid recently burned areas, at least until plant growth has recovered (as few as 60d) to avoid exposure and predation (Setser and Cavitt 2003, Wilgers and Horne 2007).

The importance of vegetative cover for snakes in pastures may also explain their increased predation of nests with greater amounts of tall fescue and litter cover. Increased cover of C3 grasses like fescue has been related to nest predation elsewhere, though the underlying cause is not well understood (Giuliano and Daves 2002). We do not believe snakes preferentially use fescue per se, but benefit indirectly from its presence. Fescue is a C3 grass and becomes photosynthetically-active when most C4 grasses at our sites are still dormant. It reduces fire spread (McGranahan et al. 2013) and results in greater amounts of litter and vegetation that could serve as snake habitat, especially following spring fires.

Similar to snakes, predation by mammals increased with greater amounts of litter and tall fescue cover at the nest. The synergistic effect of fescue and litter may create preferred foraging habitat for mammalian nest predators, indirectly increasing the risk of nest loss (Vickery et al. 1992, Klug et al. 2009). However, mammalian predation decreased with increasing forb cover at nests. Increased forb cover has been related to improved nest and fledgling success elsewhere (Dion et al 2002, Berkeley et al. 2007, Conover et al. 2011) and lower levels of mammal activity (Klug et al. 2009). Forb cover may increase nest concealment and structural diversity and complexity of grasslands, thereby reducing the likelihood a nest is detected (Martin 1988, Bowman and Harris 1980). Though our results are consistent with other observed patterns of nests, we suggest caution when interpreting our results. We were required to group multiple species together, some with very different life histories (e.g. badgers and raccoons). Thus, we

may have obscured differences in patterns of grassland and generalist mammal predation (e.g. Ribic et al. 2012, Ellison et al. 2013). Thus, the relative importance of litter, tall fescue, or forb cover may vary depending on the predator community.

Predation by cowbirds seemed unaffected by habitat management or any other environmental variables that we measured. This outcome may be attributed to our small sample size, at least in part. We observed very few cowbird predation events and this limited our ability to detect patterns and make inferences. We rarely found nests during the laying stage and also avoided adding cameras until egg-laying was complete. Therefore, we likely underestimated the frequency of cowbirds preying on eggs.

Other studies have reported that snakes or cowbirds may be more likely to depredate bird nests near habitat edges (Benson et al. 2010 Cox et al. 2012), though we found no evidence of this pattern for either predator. Edges may facilitate thermoregulation for snakes and serve as perches for cowbirds (Weatherhead et al. 2010, Patten et al. 2011), increasing predator activity or abundance near edges. However, snakes may use shrubs within pastures for thermoregulation (Klug et al. 2010) and cowbirds may use other perch sites like fence lines, thereby diluting the influence of wooded edges in our study area (e.g. Benson et al. 2010). Alternatively, the pervasiveness of edges in our landscape may limit the detection of edge effects (Hovick et al. 2012).

Though we expected land cover at broad scales to influence nest loss, variability in land cover around our study pastures may have been insufficient to discern relationships with the species we observed depredating nests (Table A2). Different organisms respond to environmental variation at diverse spatial scales and highly mobile organisms, including many of the species we observed, may perceive the environment at a given scale as homogenous (Kotliar

and Wiens 1990). Cowbirds and the mammals responsible for nest failure in our landscape regularly travel ≥ 3 km in a single day (Thompson 1994, Lariviere and Messier 1997, Kamler et al. 2005), indicating they may have perceived our study area as one homogenous landscape. By comparison, the snake species we observed are less mobile, have relatively small home ranges (≤ 15 ha; (Klug et al. 2011), and may be more likely to respond to variation at finer spatial scales as a result. Predation by snakes responded only to time-since-fire and not the area burned, suggesting that burning even 33% of a 30-ha pasture may be sufficient to reduce nest loss. This could represent a minimum estimate of burned patch size necessary to diminish snake predation.

Though the species preying on nests were not affected by how cattle grazing was combined with fire, grazing still may have influenced nest predation rates. Snakes can quickly recolonize spring-burned areas in the absence of grazing (Setser and Cavitt 2003). Thus, fire in the absence of grazing may produce limited (if any) reduction in nest loss. Though Hartway and Mills (2012) suggested that livestock exclusion improves breeding success, excluding grazing may only affect the identity of nest predators without changing nest failure rates (Ribic et al. 2012).

CONCLUSIONS

Our results illustrate several approaches that may reduce nest loss in fragmented grasslands. The use of fire can mitigate predation, but by snakes only. Therefore, fire may be less useful in mitigating nest loss in regions where snakes are not a dominant predator, such as northern grasslands (Pietz et al. 2012, Thompson and Ribic 2012). Reducing litter (a by-product of burning and/or grazing; e.g. Fuhlendorf and Engle 2004) and fescue at the nest can reduce predation by snakes and mammals, while increasing forb cover can reduce losses attributed to mammals only. Tools such as predator removal may be used to further reduce mortality by

mammals and cowbirds, though such approaches can be expensive, controversial and may result in compensatory mortality (Bolton et al. 2007, Ellis-Felege et al. 2012). Managing habitats to adversely impact predators is likely to be more effective at reducing nest loss (Thompson and Ribic 2012). Though additional research is needed to better understand the relationships between predators and the habitat features at nests they consume, we recommend management that incorporates periodic burning, reductions in litter and tall fescue, and increasing forb cover as a way to improve breeding success grassland birds in fragmented landscapes with diverse predator communities. However, we stress that our recommendations are conditional for grasslands with predator communities similar to our own.

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TABLES

Table 1. Predators identified at nests with known fates in the Grand River Grasslands, Iowa 2010-2012.

Predator Classification (Species)	Number of events
Mammals	
American badger	5
Striped skunk	4
Coyote*	4
Opossum	2
Raccoon	6
Cowbirds	
Brown-headed Cowbird	5
Snakes	
Eastern Racer	2
Garter Snake	6
Snake (unknown spp.)	4
Other	
Blue Jay	1
Deer	1
Grasshopper Sparrow†	8
Red-tailed Hawk	1
Loggerhead Shrike	1
Vole	1
Total events	51

* One predator classified as a coyote may have been a domestic dog *Canis familiaris* Linnaeus.

† Egg and chick removals by parents were attributed to death by exposure or other natural causes.

Table 2. Model selection results of habitat and temporal factors related to predator-specific nest loss.

Model	K	AIC_c	ΔAIC_c	w_i	Deviance
<u>Habitat analysis</u>					
Step 1					
Null	4	724.52	0.00	0.65	716.47
Crop cover 1km	8	727.11	2.59	0.18	710.93
Tree cover 1km	8	728.89	4.37	0.07	712.71
Distance to water	8	729.73	5.22	0.05	713.55
Distance to wooded edge	8	729.74	5.23	0.05	713.56
Step 2					
Time since fire	8	722.34	0.00	0.74	706.16
Null	4	724.52	2.18	0.25	716.47
Treatment*	8	730.82	8.48	0.01	714.64
Pasture size	8	731.88	9.55	0.01	715.70
Step 3					
Time-since-fire + forb	12	719.15	0.00	0.39	694.76
Time-since-fire + litter	12	719.47	0.32	0.33	695.08
Time-since-fire + fescue	12	722.01	2.85	0.09	697.61
Time-since-fire	8	722.34	3.18	0.08	706.16
Time-since-fire + C4 grass	12	723.22	4.07	0.05	698.83
Null	4	724.52	5.36	0.03	716.47
Time-since-fire + V.O.	12	724.60	5.44	0.03	700.20
<u>Temporal analysis</u>					
Null	4	724.52	0.00	0.61	716.47
Stage	8	726.50	1.98	0.23	710.31
Stage + ordinal day	12	729.79	5.28	0.04	705.40
Ordinal day	8	728.11	3.59	0.10	711.93
Year	12	731.618	7.10	0.02	707.225

* Treatment refers to patch-burn-grazed and grazed-and-burned pasture treatments.

Table 3. Conditional parameter estimates and 85% confidence intervals from predator-specific analysis of nest predation of grasshopper sparrows. Coefficients and 85% confidence intervals in bold are considered informative because they do not overlap zero.

Parameter	Coefficient (β)	SE	85 % CI	
Time since Fire				
Snake	1.196	0.438	0.565	1.828
Cowbird	0.613	0.539	-0.163	1.390
Mammal	0.151	0.267	-0.234	0.535
Forb				
Snake	-0.010	0.021	-0.041	0.021
Cowbird	-0.047	0.035	-0.098	0.004
Mammal	-0.046	0.017	-0.071	-0.021
Litter				
Snake	0.040	0.026	0.002	0.078
Cowbird	0.071	0.050	0.000	0.143
Mammal	0.032	0.016	0.009	0.055
Tall fescue				
Snake	0.035	0.016	0.013	0.058
Cowbirds	0.024	0.023	-0.009	0.05
Mammal	0.019	0.011	0.003	0.036
Stage				
Snake	-1.290	0.778	-2.411	-0.168
Cowbird	-1.066	1.121	-2.681	0.548
Mammal	-0.596	0.489	-1.301	0.108

Table 4. Model selection results of habitat and temporal factors related to nest loss when predator identity is ignored.

Model	K	AIC_c	ΔAIC_c	w_i	Deviance
<u>Habitat analysis</u>					
Step 1					
Null	1	532.38	0.00	0.33	530.37
Crop cover 1km‡	2	533.39	1.01	0.20	529.38
Distance to wooded edge‡	2	533.45	1.07	0.20	529.44
Distance to water‡	2	534.15	1.77	0.14	530.14
Tree cover 1km‡	2	534.30	1.92	0.13	530.29
Step 2					
Time-since-fire	2	531.91	0.00	0.40	527.89
Null	1	532.38	0.47	0.31	530.37
Treatment*	2	533.64	1.73	0.17	529.63
Pasture size	2	534.36	2.46	0.12	530.35
Step 3					
Time-since-fire + litter	3	527.38	0.00	0.51	521.35
Time-since-fire + C4 grass	3	529.41	2.03	0.18	523.38
Time-since-fire + fescue	3	529.76	2.38	0.16	523.73
Time-since-fire	2	531.91	4.53	0.05	527.89
Null	1	532.38	5.00	0.04	530.37
Time-since-fire + forb	3	532.40	5.02	0.04	526.37
Time-since-fire + V.O.	3	533.71	6.33	0.02	527.68
<u>Temporal analysis</u>					
Stage	2	531.03	0.00	0.47	527.02
Null	1	532.38	1.35	0.24	530.37
Stage + ordinal day‡	3	533.04	2.01	0.17	527.01
Ordinal day	2	534.26	3.23	0.09	530.24
Year	3	536.21	5.18	0.03	530.18

* Treatment refers to patch-burn-grazed and grazed-and-burned treatments.

‡ Models may contain uninformative parameters ($\leq 2 AIC_c$ of top model without meaningful reduction of deviance).

FIGURES

Figure 1. Snake daily predation rate (DPR) of Grasshopper Sparrow nests as a function of time-since-fire and litter cover (%). Nest predation increases in the absence of fire and as litter cover and at the nest increases.

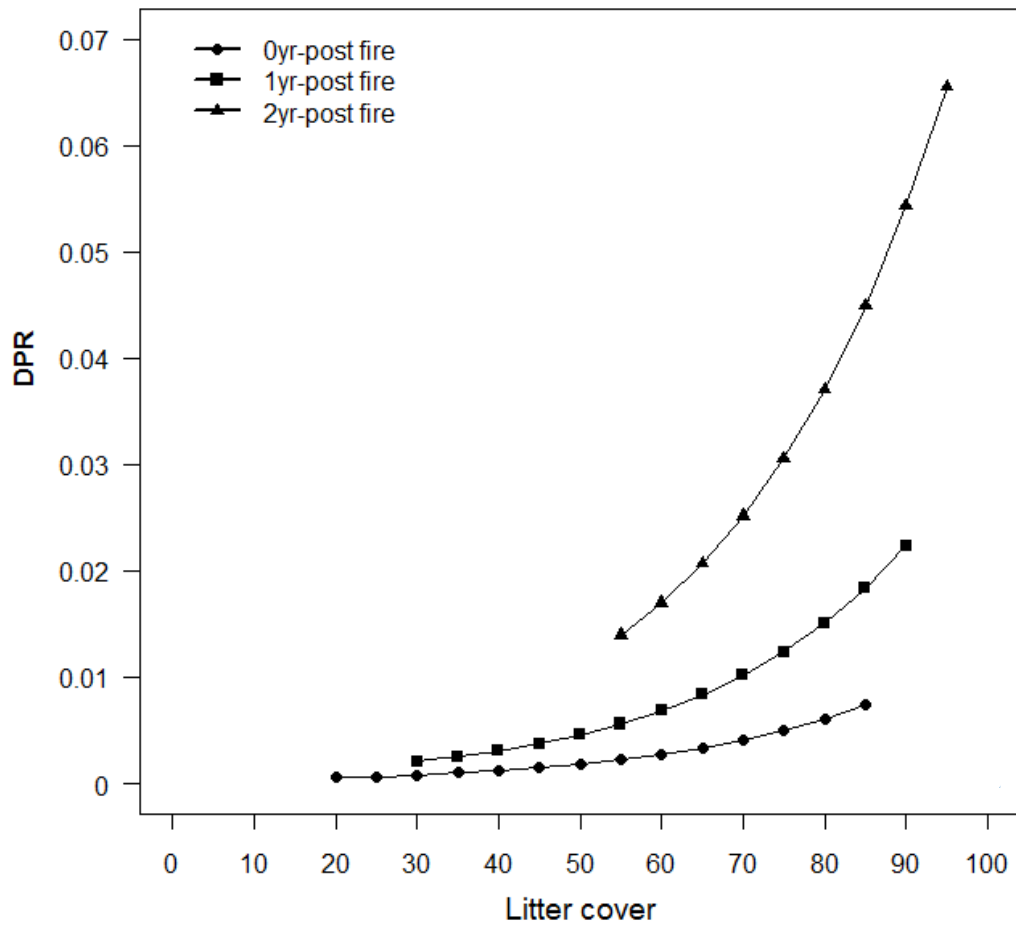


Figure 2. Snake daily predation rate (DPR) of Grasshopper Sparrow nests as a function of time-since-fire and tall fescue cover (%). Nest predation increases in the absence of fire and as tall fescue cover at the nest increases.

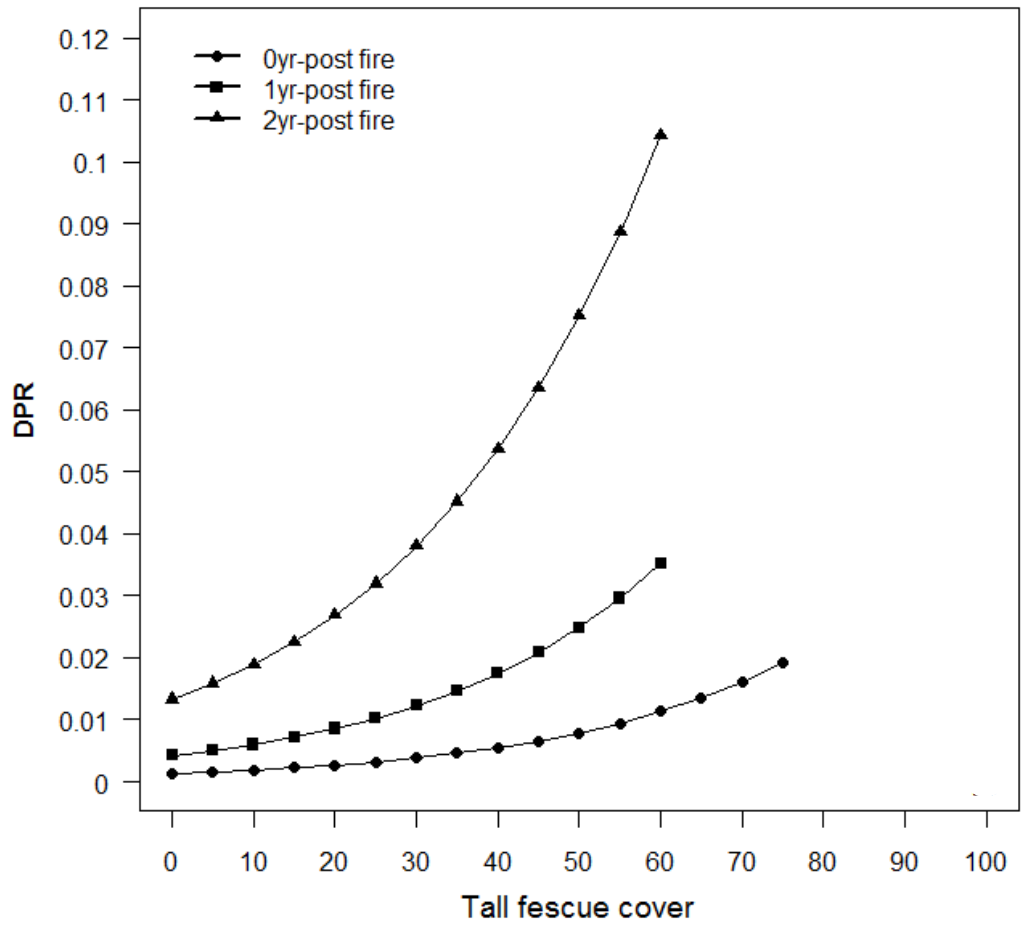
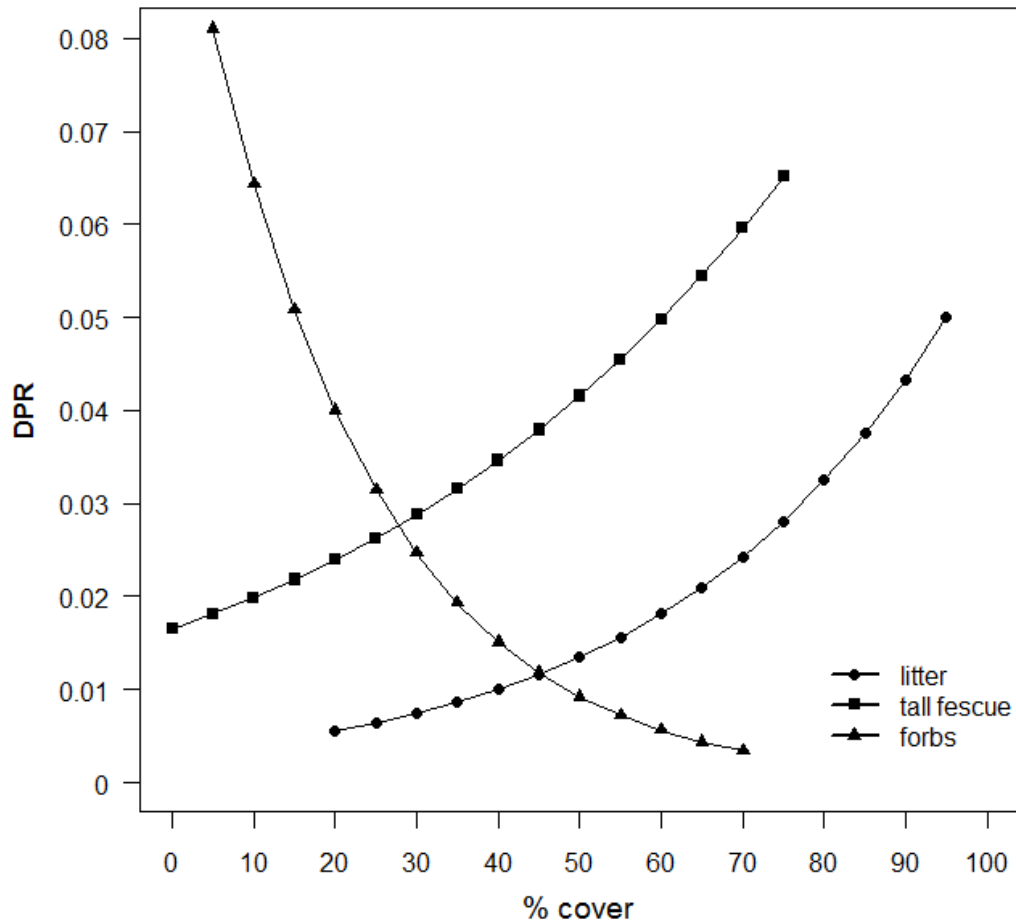


Figure 3. Mammal daily predation rate (DPR) of Grasshopper Sparrow nests as a function of vegetative cover at the nest (based on conditional model estimates). The odds a nest will be depredated by a mammal decreases with increasing forb cover, but increases with increasing cover of litter and tall fescue.



CHAPTER 3

ADAPTIVE RE-NESTING BEHAVIOR BY THE GRASSHOPPER SPARROW

(Ammodramus savannarum)

ABSTRACT

Predation is the leading cause of nest failure for many birds. Therefore, choices about where to nest should reduce the risk of nest loss, yet there are many reports of nest-site selection that appears non-adaptive in reducing nest loss. However, few studies use adequate measures of habitat preference and instead rely on metrics that oversimplify the process of habitat selection. We examined whether predation influenced subsequent selection of nest locations by grasshopper sparrows (*Ammodramus savannarum*). We quantified the habitat characteristics in pastures and at nests and asked whether birds avoided nesting in areas where there was a greater likelihood of nest failure. We also tracked individual female grasshopper sparrows through multiple nesting attempts to characterize patterns of nest-site selection and examine whether prior experience influenced subsequent choices. We could not differentiate between nests and un-occupied sites, nor did we detect an influence of previous nest fate on subsequent nest-site selection within a breeding season. However, we did observe shifts in nest-site characteristics on re-nesting attempts that were associated with lower rates of nest loss. Clarifying whether this behavior is innate or learned can improve our understanding of the habitat selection process.

INTRODUCTION

Predation is a strong evolutionary force and shapes many avian life-history traits and behaviors (Martin and Briskie 2009, Martin et al. 2011). The risk of predation can exert strong influence on selection of nest-site characteristics in particular (Orians and Wittenberger 1991, Chalfoun and Martin 2007, Zanette et al. 2011) and there is a general expectation that birds should prefer and occupy the “safest” sites. Yet studies that examine the relationship between breeding success and nest-site characteristics often report that the preferred habitat is unrelated to nest predation. Explanations for the mismatch tend to focus on alternative processes shaping nest-site selection (Chalfoun and Schmidt 2012).

Evolutionary pressure may lead to long-term optima in habitat preference that appears at odds with short-term variation in predation risk, giving the appearance that nest sites choice is unrelated to predation or even maladaptive (Clark and Shutler 1999, Chalfoun and Schmidt 2012). Evidence of selective pressure may be difficult to detect because birds are nesting at an “adaptive peak” and have already minimized their risk of predation (Clark and Shutler 1999, Latif et al. 2012). Yet in many systems, the relationship between nest-site characteristics and predation risk varies over short time spans and among geographic regions (Winter et al. 2005, Whittingham et al. 2007, Boves et al. 2013). There is growing evidence that birds are able to detect and mitigate such risk by relying on cues such as predator vocalizations or urine (Fontaine and Martin 2006, Zanette et al. 2011, Eichholz et al. 2012). Information derived from previous breeding attempts may also influence choice of nest sites (Chalfoun and Martin 2010, Kearns and Rodewald 2013). Using prior experience to inform nest-site selection can improve the odds of breeding success even when predation is persistently high (Marzluff 1988, Chalfoun and Martin 2010, Kearns and Rodewald 2013).

Many studies use metrics such as nest density or non-random habitat use as surrogates for habitat preference (Robertson and Hutto 2006). In doing so, researchers assume that birds have perfect information about their fitness in different habitats and settlement follows an ideal free distribution. Yet even if birds had perfect knowledge, nest density and non-random use may be an unreliable indicator of habitat quality if subdominant individuals are forced into lower quality habitat or habitat sinks are present (Van Horne 1983, Robertson and Hutto 2006, but see Bock and Jones 2004). Documenting territory settlement patterns, site fidelity, and changes in nest-site characteristics between breeding attempts provide a much clearer indication of habitat preferences.

We examined whether nest-site selection by the grasshopper sparrow was related to predation risk. Grasshopper sparrows are the most abundant grassland obligate songbird in our study area (Pillsbury et al. 2011) and nest in relatively high numbers on our research pastures (Hovick et al. 2012). They are described as preferring grasslands with short vegetation and bare ground, though preferences vary regionally (Vickery 1996 and citations therein). Our previous research indicated that litter cover near nests was a strong predictor of nest predation overall (see Chapter 1). Thus, we expected grasshopper sparrow nest-site selection to be adaptive and result in lower rates of nest loss. We compared nest sites with available habitat to determine if birds avoided areas where survival was likely to be lower. We also tracked nest-site selection over multiple breeding attempts by a given female to provide a clearer indication of habitat preference. Even if birds did not avoid risky nest sites initially, due to a lack of access to preferred sites, or because they were inexperienced, we expected birds to select nest sites that were safer on subsequent breeding attempts. If personal experience influences nest-site selection,

then we would expect birds' whose initial attempts failed to make more dramatic changes in nest site characteristics than individuals whose initial attempts were successful.

METHODS

We conducted our study on eight research pastures in southern Iowa from 2010-2012. Though most of the region is still in grassland (TNC, 2008), the landscape is highly fragmented by the encroachment of woody vegetation and row-crop agriculture. The landscapes surrounding these sites comprised 58% grasslands and pasture, 18% row crop, and 22% woodlands (unpublished data). Pastures were under the jurisdiction of the Iowa Department of Natural Resources, The Nature Conservancy, or were privately owned. Vegetation within pastures was dominated by both native and non-native grasses. Other plants in pastures included forbs, sedges and native and exotic legumes (McGranahan 2008). Four pastures were managed with patch-burn-grazing, whereby one third of a pasture is burned annually. The four remaining pastures were managed with a grazed-and-burned treatment and burned in their entirety in 2009 and 2012. Pastures were 23-34 ha in size and all were lightly stocked ($\bar{x} = 0.8 \text{ AUM ha}^{-1}$) with cattle (*Bos taurus*) from May through September each year.

We searched for nests between 05:30 and 12:00 (CDT) from 15 May- 29 July each year. We located nests by completely and systematically rope dragging pastures using a 30-m rope. We marked one end of our path every 30-50m to ensure complete coverage of each pasture. Each pasture was searched four times in 2010 and 2012 and three times in 2011. After locating a nest, we recorded the number of grasshopper sparrow and cowbird (*Molothrus ater*) eggs or nestlings, marked the location with a GPS unit, and placed flagging 5m north and south of the nest to aid in relocation. We candled one egg or used feather growth characteristics, such as the emergence of pin feathers, to age eggs or nestlings and estimate hatch and fledge dates (Lokemoen and Koford

1996, Vickery 1996). We checked nests at 1-4d intervals with more frequent visits when we expected clutches to hatch or nestlings to fledge. We considered a nest successful if it fledged \geq 1 host young. Nest fate was confirmed at a subset of nests by reviewing video evidence (see Chapter 1). In the absence of video data, we used parental behavior to determine nest fate.

We captured female grasshopper sparrows opportunistically in 2011 and 2012 by placing mist nets at nests. We attempted to capture females between 05:00 and 12:00 on days without rain. We did not attempt banding once the temperature exceeded 27^o Celsius or on days with winds > 11 -12 km h⁻¹ to reduce the risk of heat stress or injury to the birds. We placed mist nets in a V-shape in front of each nest and at least 3 m from the nest cup. Two observers approached the nest from behind and used 1-m bamboo sticks to flush brooding or incubating females into the net. Upon capture, we confirmed the sex of bird and recorded mass, body fat, muscle condition, and tarsus length. Females were banded with a USGS metal band and a unique combination of up to three Darvic color bands (Avinet Dryden, NY). We identified females during subsequent nesting attempts primarily by recapture, though on occasion we confirmed the identity by re-sighting color-marked birds. All procedures were approved by the University of Illinois Institutional Animal Care and Use Committee (Protocol #11073).

Whereas habitat characteristics at multiple scales can influence fitness, nest-site characteristics are often related to the risk of predation (Orians and Wittenberger 1991, Chalfoun and Martin 2007) as they influence the olfactory or visual cues used by some predators to locate nests (Martin 1992, Benson et al. 2010). Therefore, we quantified vegetation composition at the completion of nesting attempts using a 0.5m² quadrat placed at the nest cup and four additional quadrats placed within 5 m of the nest, one in each cardinal direction. Within each quadrat we visually estimated the % cover of tall fescue (*Schedonorus phoenix*), C3 grasses, C4 grasses,

forbs, bare ground, and litter. Values were recorded as the midpoint of one of the following categories: 0-5%, 6-25%, 26-50%, 51-75%, 76-95%, 96-100% (Daubenmire 1959). Fescue was reported separately because it is the most dominant C3 grass throughout our study area (McGranahan 2008) and it has been associated with reduced fitness in birds and potentially an increased abundance of nest predators (Giuliano and Daves 2002, Hovick et al. 2012). We also quantified vegetation visual obstruction (V.O.) as the highest point at which 50% of a Robel pole (Robel et al. 1970) was obscured. Measurements were recorded 4m from the nest and 1m above the ground in each cardinal direction.

To establish whether grasshopper sparrows nest sites differed from vegetation in pastures, we characterized habitat features within each pasture using methods similar to those described above. Vegetation metrics were recorded at 30 quadrats per patch, giving a total of 90 quadrats per pasture. These quadrats were placed along pre-existing bird-survey transects which traversed the research pastures (Pillsbury et al. 2011, McGranahan et al. 2012).

Analyses

Use-availability comparison

Previous analyses revealed nest predation was more likely in areas with a high proportion of litter cover (see Chapter 1). Thus, we expected that birds would avoid areas with greater litter cover in order to reduce predation risk. We used logistic regression and test if nest sites were distinguishable from available habitat based on litter cover. Because available habitat samples may include areas of potential but used nest sites, we interpreted our results as a logistic discrimination rather than an actual resource selection probability (Keating and Cherry 2004). We tested the accuracy of our discrimination using the Receiver Operating Characteristic (ROC)

because it does not rely on an arbitrary cutoff value when classifying groups (Fielding and Bell, 1997).

Tests of re-nesting patterns

We were interested in understanding how birds responded to predation within a single breeding season, so we only included re-captures of birds that occurred within that period. We excluded cases where the earlier of two nesting attempts failed due to causes other than predation. If nest-site selection was adaptive in relation to predation risk, we expected that litter cover at grasshopper sparrow nests would decrease between breeding attempts. We tested for a decrease in litter cover using a Wilcoxon sign-rank test. If birds rely more on prior experience, we predicted birds that failed on previous attempts would select sites that were more different than birds that succeeded (e.g. Chalfoun and Martin 2010). Thus, we calculated the absolute value of the difference in litter cover between nesting attempts for each female and used a Wilcoxon rank-sum test to examine whether the magnitude of change was greater following failed nests compared to successful nests. We ensured these variables met assumptions of homogeneity of variances when appropriate prior to analyses. All analyses were performed using SAS version 9.2 (SAS Institute, Cary, North Carolina).

RESULTS

We included 303 grasshopper sparrow nests monitored in our comparison of nests locations vs. available habitat. We banded 47 different females in 2011 and 87 in 2012. Our full recapture data set included 16 females on 2 nesting attempts and 2 females on 3 attempts. However, two birds banded in 2011 were not recaptured until 2012 and we censored nests where vegetation measurements were not collected ($N=1$) and where disturbance by humans or cattle led to abandonment ($N=2$). Thus, the data set used to examine nest-site selection consisted of 15

females at 29 nests; 13 females at 2 nests and 1 female at 3 nests. Six of the first-observed nest attempts were successful while eight failed.

Logistic discrimination had poor predictive ability, indicating nest sites did not differ from overall habitat conditions within pastures ($c = 0.67$). However, simple boxplots suggested that litter cover was greater at nests than at random (Fig. 4). We found evidence to support that birds made adaptive nest-site choices when re-nesting. Grasshopper sparrows reduced litter cover, thus selecting safer sites between nesting attempts ($T_{14} = -35$; $P = 0.03$; Fig. 5). We did not find any support for our prediction that birds changed nest-site characteristics more following nest failure than success ($z_{14} = -0.17$, $P = 0.86$).

DISCUSSION

Avian habitat selection studies that compare used and available locations as evidence for selection have been criticized as providing an inadequate picture of habitat “preference” (Robertson and Hutto 2006). Our results support this assertion. Our discriminant analysis suggested that among pastures managed with fire and grazing, there was no clear nest-site preference. Still, nests on average had greater litter cover than pastures (Fig 4) which would suggest that nest-site selection was maladaptive. Other selective pressures such as food, microclimate, or territory competition, etc., may be shaping nest-site selection. Grasshopper sparrows may be absent from areas that have minimal litter cover or accumulation, such as pastures that are burned annually or heavily grazed (Powell et al. 2008). Thus, if litter cover falls below some threshold, there may not be enough dead vegetation for grasshopper sparrows to construct their nests. However, following females on multiple nesting attempts revealed that they made nest-site choices that were adaptive in terms of reducing predation risk. Such patterns may only be detected when within season changes in nest sites are observed (Betts et al. 2008).

Though our analysis could not discriminate between nests and pasture on the basis of litter cover, it was surprising to find that litter cover was greater surrounding nests than within pastures. Though grasshopper sparrows exhibited an ability to select safer sites when reneating, it would appear they made poor choices on initial breeding attempts. Betts et al. (2008) attributed such a pattern to poor nest-site choices by young, inexperienced breeders. Alternatively, nest sites with low levels of litter may fall primarily within territories of dominant individuals, leading to many individuals being forced to use habitat of lesser quality (Van Horne 1983).

Nevertheless, grasshopper sparrow nest-site selection may be influenced by factors other than predation, such as food availability or microclimate conditions (e.g. Lloyd and Martin 2004, Chalfoun and Schmidt 2012). We observed several instances where grasshopper sparrow nestlings died due to weather (see Chapter 1). Further, grasshopper sparrows and other ground-foraging grassland bird species appear to favor areas with increased bare ground, due to increased access to invertebrate prey (Walk and Warner 2000, Kennedy et al. 2009, Schaub et al. 2010). Still, the avoidance of areas with accumulated litter may help grasshopper sparrows to avoid predation by predators, such as snakes and mammals (Vickery et al. 1992, Cavitt 2000, see Chapter 1) though other factors may limit their ability to do so.

We did not find evidence that changes in nest-site selection were informed by prior experience. This may have been a function of small sample size and limited power. Though the number of birds we recaptured was small, our numbers are similar to other grassland bird studies which typically report few recaptures during a breeding season (e.g. Fletcher et al. 2006, Kershner et al. 2004, Davis 2009). Recaptures for shrub and forest-nesting species are higher, though previous nest fate does not always influence reneating decisions (Chalfoun and Martin 2010, Kerns and Rodewald 2013). Using prior experience when making nest site decisions may

be an adaptation for dealing with diverse or dynamic predator communities (Chalfoun and Martin 2010, Kearns and Rodewald 2013). The predators driving nest loss patterns differ throughout the grasshopper sparrow's breeding range (Pietz et al. 2012) and there may be variation in the features that defines a safe nest location among regions (e.g. McCoy et al. 1999, Giuliano and Daves 2002, Winter et al. 2005). Thus, there may be some basis for grasshopper sparrow nest-site selection to be based on prior nest fate.

CONCLUSIONS

Many studies that report non-adaptive nest-site selection patterns relative to predation suggest the presence of ecological traps or factors other than predation risk drive habitat preference. We demonstrated that grasshopper sparrows select nest sites that reduce the risk of nest loss, though it requires tracking females on multiple nesting attempts. Like most other studies, we found that grasshopper sparrows prefer areas with less litter and more bare ground, though there is likely a minimum amount of litter required for nesting. Though this behavior reduced the risk of predation in our study area, variation in the nest predator community may limit the value of this behavior. Clarifying whether this preference is innate or results from informed decision making and how it is influenced by other habitat requirements can improve our understanding of the habitat selection process.

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FIGURES

Figure 4. Side-by-side boxplot comparison of the % litter cover at nests and within pastures.

Litter cover was greater at nest sites than in pastures on average.

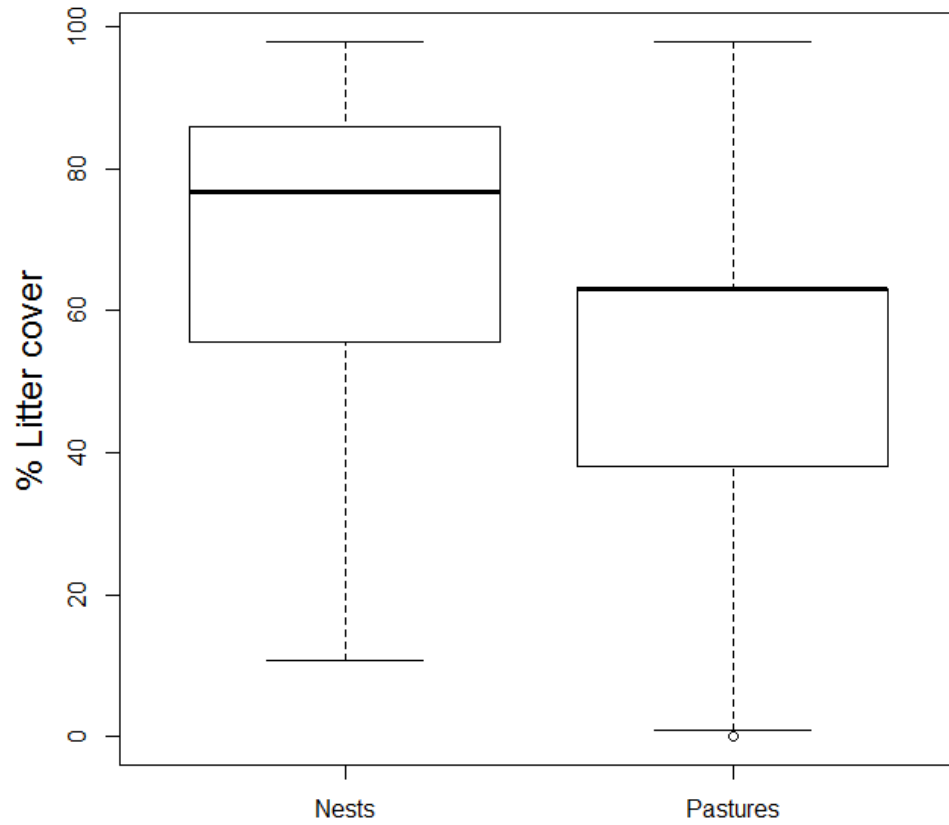
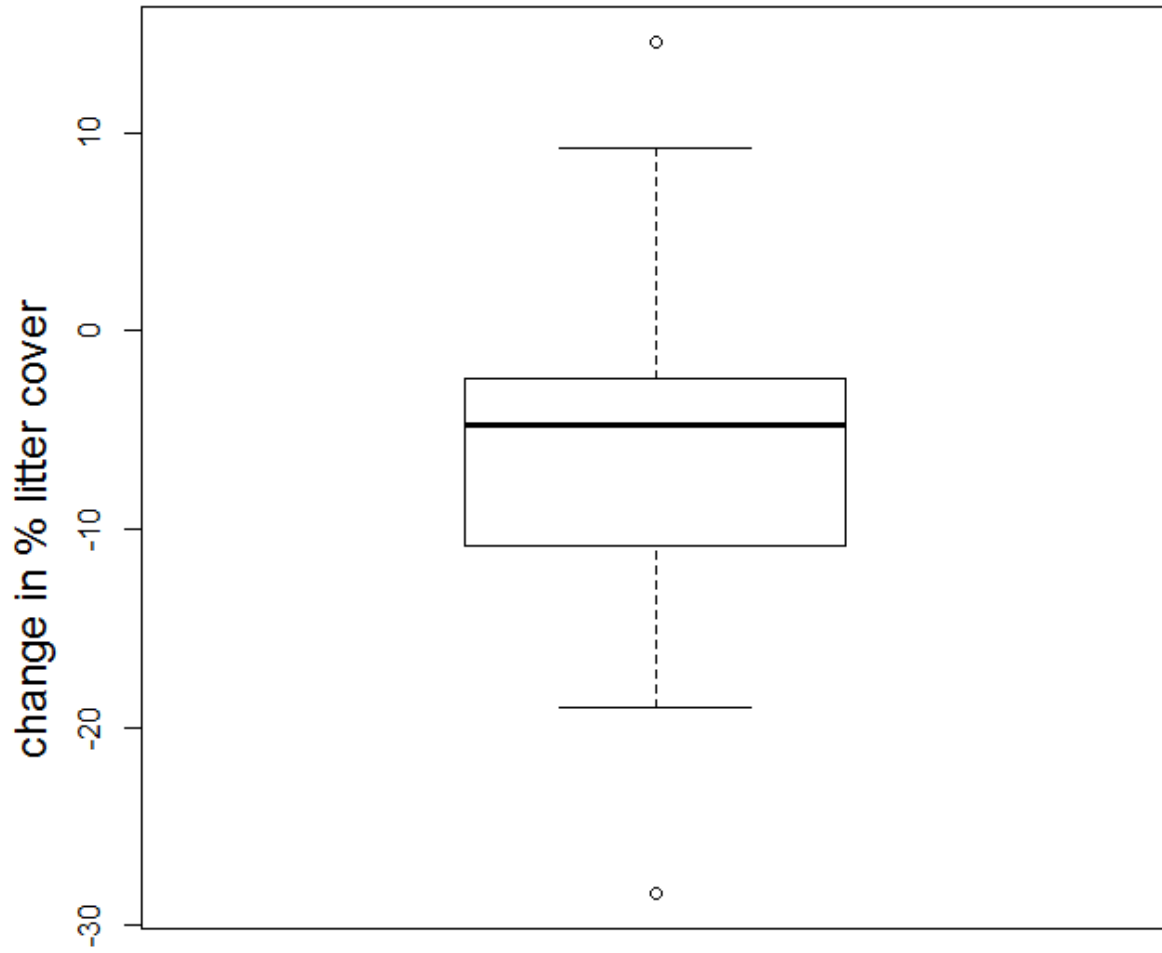


Figure 5. The change in % litter cover at nests of female grasshopper sparrows observed on multiple breeding attempts within a season. Females selected sites with lower litter cover on renesting attempts.



CHAPTER 4

SUMMARY

Though much of the remaining grassland habitat consists of small patches in fragmented landscapes, such areas can still be important to sustain grassland bird populations (Walk et al. 2010). Thus, managing these areas to improve breeding success is vital to conservation efforts. The goal of chapter 2 was to clarify the habitat characteristics related to predation by different species and how they were affected by management. I found that time-since-fire influenced the risk of predation, but only for snakes. Snakes were less likely to consume nests in recently burned area. Nests with less litter and fescue cover were less likely to be preyed upon by mammals and snakes, while increasing forb cover reduced the likelihood a nest was consumed by mammals. I was unable to identify any habitat variables related to nest loss by cowbirds. Though my results support the use of fire as a means to mitigate nest loss, success is contingent on predator identity.

I also found that grasshopper sparrows chose nest sites that reduced the risk of failure. However, comparing nest conditions to available habitat was inadequate may even suggest that nest site selection was non-adaptive at reducing predation. Instead, following breeding females on multiple nesting attempts clarified nest-site preference. However, the modest reduction in nest loss attributed to this behavior suggests that other factors may limit birds' ability to select nest sites with minimal risk of predation. Overall, my research provides strong evidence supporting restoring diversity and heterogeneity in grasslands (e.g. Fuhlendorf et. al 2012) as a way to reduce nest loss and to create preferred habitat for grasshopper sparrows.

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APPENDIX A.

Table A1. Environmental variables and related statistics selected in multinomial logistic analysis for predator-specific nest loss patterns.

	Time-since-fire (yr)			Forb cover (%)				Litter cover (%)				Tall fescue cover (%)			
	0	1	2	Mean	Std. dev.	Min	Max	Mean	Std. dev.	Min	Max	Mean	Std. dev.	Min	Max
Cowbird	1	2	2	26.2	10.4	17.8	43.0	82.2	6.2	71.0	86.0	33.1	12.8	17.2	52.6
Snake	1	3	8	33.4	10.9	16.0	48.0	81.2	17.5	29.2	95.6	36.9	18.3	13.4	63.0
Other	17	14	13	36.8	16.6	8.2	72.2	70.0	20.3	16.0	98.0	25.4	18.5	0.0	76.8
Survive	300	226	199	34.5	15.4	3.0	72.2	67.1	19.4	22.0	98.0	24.9	17.9	0.0	76.8
<u>Mammal</u>	10	4	7	25.2	13.7	3.0	48.2	74.8	13.0	52.0	88.4	31.8	23.6	0.0	63.0
<i>Skunk</i>	3	0	1	26.4	16.5	3.0	38.0	70.4	11.7	58.0	81.4	34.3	25.7	0.6	63.0
<i>Raccoon</i>	3	2	1	25.0	13.6	10.2	48.2	72.7	17.2	52.0	88.4	27.7	25.7	0.0	58.0
<i>Coyote</i>	3	0	1	25.3	13.1	7.8	39.2	71.3	13.5	57.0	86.0	45.9	27.7	5.0	63.0
<i>American Badger</i>	0	2	3	28.6	16.7	10.2	48.2	80.4	10.3	62.4	86.2	23.6	23.7	0.6	62.6
<i>Virginia Opossum</i>	1	0	1	15.2	10.7	7.6	22.8	82.6	8.2	76.8	88.4	31.7	9.8	24.8	38.6

Table A2. Land cover composition surrounding each research pasture.

Pasture	Treatment	Grass cover 1km (%)	Tree cover 1km (%)	Row-crop cover 1km (%)
Gilleland	Grazed-and-burned	55.9	18.2	22.9
Lee Trail Road	Grazed-and-burned	47.4	42.7	8.8
Pyland West	Grazed-and-burned	64.4	30.2	3.2
Sterner	Grazed-and-burned	48.1	14.5	33.5
Kellerton North	Patch-burned-grazed	68.6	6.2	21.4
Pyland North	Patch-burned-grazed	61.9	33.2	3.0
Pyland South	Patch-burned-grazed	54.2	35.8	8.1
Ringgold South	Patch-burned-grazed	54.3	29.6	13.9