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Avian Reproductive Success is Associated with Multiple Vegetation Characteristics at an Active Grassland Restoration Site in Central Georgia

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AVIAN REPRODUCTIVE SUCCESS IS ASSOCIATED WITH MULTIPLE VEGETATION CHARACTERISTICS AT AN ACTIVE GRASSLAND RESTORATION SITE IN CENTRAL GEORGIA

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Grassland bird populations are experiencing major declines due to habitat degradation, pesticide use, and fire suppression throughout North America. Large-scale grassland restoration efforts to improve and provide suitable habitat are ongoing, but there is little data on productivity of birds breeding in restored habitats, nor on the impact of specific vegetation characteristics on reproductive success. Since 2005, agriculture fields at Panola Mountain State Park in central Georgia have been undergoing restoration to warm-season grasslands; however, until now, data on nest success or productivity was lacking. The goals of this project were to: (1) quantify reproductive success and (2) determine which vegetation characteristics were associated with successful nests. From March-August 2019, we monitored all active nests, recorded nest outcome, and measured several vegetation characteristics. We used Akaike's Information Criterion (AICc) to determine which variables were most strongly associated with success. We found 52 nests of 11 species, with an overall success rate of 34.62%. Seventeen nests were cup nests, 35.29% of which were successful. The most common cause of failure for all nests was predation (91.18%). Nest type, plant height, plant height above the nest, and distance to water were most strongly associated with nest success overall; nest success was higher for nests in taller grasses with more grass above the nest, and those located further from water edges. All of these factors are linked with predation risk because they provide more concealment and/or are farther from areas where predators concentrate. We recommend that prescribed fires occur either in the winter or early enough in the spring so grasses can grow to appropriate heights and, when possible, that managers create natural buffers around abrupt water edges near nesting areas to ensure high quality, productive habitat for grassland birds.

Keywords: grassland, grassland restoration, vegetation characteristics, reproductive success, avian ecology, conservation

INTRODUCTION

Native grassland habitats across North America have been declining since European settlers began practicing agriculture and expanding westward (Samson et al. 2004). In the Southeastern U.S., 97% of grassland habitat has been lost mainly due to farming, fire suppression (Askins et al. 2007), and the introduction of nonnative, cool-season grasses (hereafter, nonnative grasses) that replaced native, warm-season grasses (hereafter, native grasses; Rothbart and Capel 2006). Grassland birds rely on grasslands during some or all of their life cycle (Askins et al. 2007) and are experiencing the steepest population decline of any avian guild in North America (Henderson and Davis 2014; Cassidy and Kleppel 2017; Rosenberg et al. 2019). Rosenberg et al. (2019) estimates that the U.S. has lost 700 million grassland birds, or 50% of the overall population, since 1970 due to habitat loss and pesticide use on agricultural landscapes and suggests that this loss will continue without large-scale efforts to restore native grassland habitat.

Restoration projects like the U.S. Department of Agriculture's Conservation Reserve Program (CRP) have resulted in increased abundance and density of grassland bird populations (Rothbart and Capel 2006). Densities of some grassland bird species are likely higher on these restored native grasslands because they provide better quality nesting habitat (Johnson and Schwartz 1993), including taller vegetation (Dechant et al. 1998; Fisher and Davis 2010; Klug et al. 2010; Murray 2014) and greater cover (Davis 2005; Fisher and Davis 2010). Taller plants provide more vertical placement options for a nest (Klug et al. 2010) and more cover provides concealment, both of which are characteristics that decrease the risk of nest predation (Davis 2005; Fisher and Davis 2010). These restoration projects also replace nonnative grasses with native grasses. This is advantageous because the growing season of native grasses coincides with the breeding season of grassland birds (they grow during or just prior to the breeding season), and they grow in clumps which makes evading predators easier and conceals movement around the nest (Rothbart and Capel 2006). Nonnative grasses, on the other hand, grow during the spring and fall and are harvested during the summer months, destroying active nests as well as the potential for future nest sites that season. They also grow in thick mats that restrict movement of wildlife (Rothbart and Capel 2006).

Habitat edges occur where grassland habitat meets forest, roads, wetlands, agriculture, and/or any form of human development (Perkins et al. 2013). Edges disrupt the continuity of a particular habitat and can decrease the presence of specialist birds along those edges (Baral 2001; Grant et al. 2004; Caplat and Fonderflick 2009). Small patches of land have a higher proportion of edges than larger patches (Sisk and Battin 2002) and while small patches of restored grassland can still attract grassland birds (Duchardt et al. 2016), there is a higher risk of predation in small patches with more edge than on large continuous restored patches (Davis 2003; Herkert et al. 2003; Keyel et al. 2013; Perkins et al. 2013). Many common nest predators in grasslands, such as squirrels, foxes, snakes, deer, crows, and hawks, are more abundant along habitat edges than within grassland interiors (Herkert et al. 2003). Conversely, large patches of land with proportionally more core habitat – at least 50 m away from the nearest habitat edge – are also associated with lower risk of predation (Herkert et al. 2003).

A critical component of grassland ecology is fire, which promotes new growth for native grasses, releases nutrients back into the soil, and prevents the growth of invasive, fire-intolerant plants (Rothbart and Capel 2006). Many of the vegetation characteristics associated with grassland bird nest-site selection, such as percent bare ground cover, vegetation density, and vegetation volume (Fisher and Davis 2010) are improved under appropriate fire regimes. Most grassland birds prefer landscapes that experience periodic burns and nest in higher densities in habitats with regular, prescribed burns compared to non-burned habitats (Rothbart and Capel 2006; Pearson and Knapp 2016; Byers et al. 2017). However, the frequency of a burn is crucial; prescribed burns should be frequent enough to prevent the return of woody vegetation, but burns that occur too often can reduce the abundance of grassland birds like Grasshopper Sparrow (*Ammodramus savannarum*) and Henslow's Sparrow (*Ammodramus henslowii*; Shaffer and DeLong 2019). Habitats that undergo rotational patch burning, when only certain portions of a habitat are burned each year, have more bare ground on the current-year burn site, which is preferred by grassland birds like Grasshopper Sparrow, Eastern Meadowlark (*Sturnella magna*), and Killdeer (*Charadrius vociferus*; Rahmig et al. 2009; Duchardt et al. 2016). In contrast, portions of the site burned in the previous year have twice as much live grass cover compared to unburned areas and are preferred by grassland birds like Savannah Sparrow (*Passerculus sandwichensis*) and Baird's Sparrow (*Ammodramus bairdii*; Davis 2005; Rahmig et al. 2009). Rotational burning creates a heterogeneous mosaic on the landscape, which is also associated with greater grassland bird diversity (Duchardt et al. 2016). Timing of prescribed burns is also a critical factor because the vegetation does not have time to regrow when burns occur too close to the start of the breeding season, resulting in delayed breeding attempts (Shaffer and DeLong 2019). When possible, prescribed fires should occur during winter months to better benefit birds in the subsequent breeding season (Shaffer and DeLong 2019).

One of the major goals of grassland habitat restoration is increasing population sizes of declining grassland birds. The presence of grassland birds has been used to infer that a habitat is productive (Keyel et al. 2013; Murray 2014; Andrews et al. 2015), however presence alone does not necessarily measure productivity (*i.e.,* successfully producing offspring) of that habitat (Horne 1983; Duchardt et al. 2016). For example, presence during migration or winter has no affect on productivity since no reproduction is occurring (Horne 1983). Providing optimal habitat for birds during each stage of their life cycle is important, but understanding the effect of restoration on measures of productivity and offspring survival provide better estimates of future population growth or decline and should be a critical measure of restoration success in managed habitats (Ludlow et al. 2014; Andrews et al. 2015; Rosenberg et al. 2016). In 2005, Georgia's Department of Natural Resources began to restore a retired agricultural habitat to native grasses in a 44.5 ha plot at Panola Mountain State Park (33°38'24.23"N 84° 9'21.50"W; PANO; Figure 1) in central Georgia through (GA DNR; Klaus 2010). Along with grassland restoration, bird populations have been monitored at the site to determine if they have taken use of the area. Although bird monitoring has occurred since 2005, there has not been any data collected on nesting success in the restored grassland. The objectives of this study were to: (1) quantify reproductive success and (2) determine habitat characteristics associated with successful nests of birds breeding in a warm-season grassland being actively managed and restored in central Georgia.

METHODS

Study Area

The restored grassland is surrounded by forest and the South River to the north, east, and south and is interspersed with small stands of 4-5 trees (Figure 1). Management currently includes rotational patch burns that alternate annually between the eastern and western halves of the field (Figure 1), revegetation with native warm-season grasses, and removal of non-grassland vegetation (*e.g.,* Johnsongrass (*Sorghum halepense*) and American Sweetgum (*Liquidambar styraciflua*)). The western half of the field was burned in mid-

April of 2019. The area is now predominantly warm-season grasses (*e.g.,* Little Bluestem (*Schizachyrium condensatum*) and Big Bluestem (*Andropogon gerardii*)). Since GA DNR began grassland restoration at this site, there has been an increase in bird abundance as well as return of migrating birds to this same site (Stumpf and Muise, 2019). Several birds breed within the restored habitat including Field Sparrow (*Spizella pusilla*), Common Yellowthroat (*Geothlypis trichas*), Red-Winged Blackbird (*Agelaius phoeniceus*), Song Sparrow (*Melospiza melodia*), Indigo Bunting (*Passerina cyanea*), and Blue Grosbeak (*Passerina caerulea*) (C.M. Muise unpubl. data). This is the first nesting study to be conducted at this site.

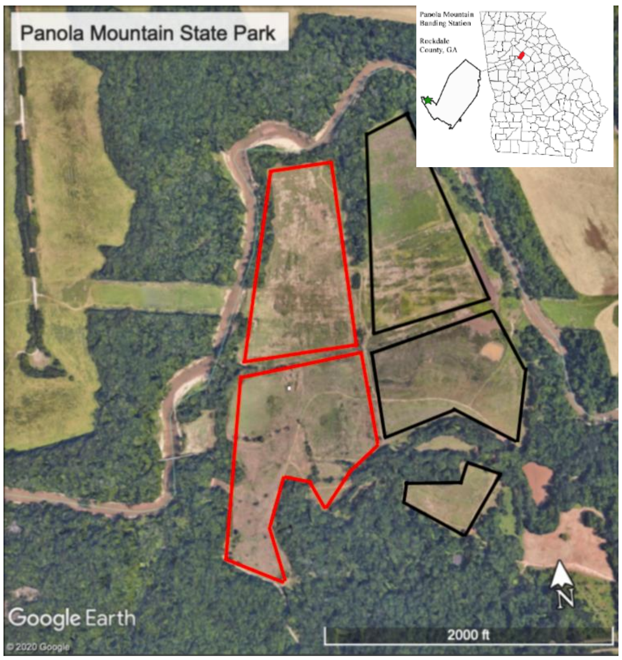

Figure 1. Resotration area of Panola Mountain State Park (PANO) in central Georgia (inset). Five nest searching polygons are outlined in black and red; the red portion was burned in mid-April 2019.

Data Collection

From March to August 2019, we searched for nests 5 days a week throughout the 44.5 ha site following Breeding Biology Research and Monitoring Database protocol (Martin et al. 1997). We divided the site into five polygons (Figure 1) and exhaustively searched each once per week to ensure complete coverage of the entire site while minimizing daily disturbance in each section. We recorded GPS coordinates and determined the stage of each active nest, and monitored nests every 2-4 days until they were complete (*e.g.,* when it was either depredated, abandoned, or fledged at least one nestling). To reduce the presence of a scent or visual trail leading to the nest, we took different routes to and from the nest each visit. We recorded nest height, nest plant height (ground to the top of the plant), plant height above the nest (top of nest to the top of the plant), plant species, concealment (average of the percent cover one meter from the nest in each cardinal direction, measured at nest height), overhead cover (percent cover of vegetation above the nest, measured looking down on the nest), and number of supporting woody branches (if applicable). To reduce disturbance during nesting, we recorded all vegetation characteristics after nests were complete. We estimated the distance from forest edge and distance from water edge using Google Earth (2019) and determined ordinal start date by either observation of the first egg in a nest or back-calculating lay date.

Data Analysis

We calculated nest success for each species as: (1) the percent of nests that produced at least one fledgling and (2) number of fledges per nest (productivity). We fit each model using the logistic-exposure method, using a binomial response (successful = 1, not successful = 0) and the logit link function (Shaffer, 2004). We used an information-theoretic approach (Akaike's Information Criterion corrected for small sample sizes [AICc]; Burnham and Anderson, 2002) to determine the effect of vegetation characteristics on nest success. Based on physical evidence (*i.e.*, scat, animal tracks, observations), we know that PANO hosts a diverse suite of nest predators, including aerial predators, mammalian ground predators, and herpetofauna predators like snakes, so we developed 27 models by combining characteristics related to predator guild and predator search method . For example, the model including overhead cover, plant height, nest type, and start date (Table 1) includes characteristics that are associated with aerial predators. Models with ΔAICc < 2.0 (hereafter, top models) were considered to have the most support (Burnham and Anderson 2002). When there were multiple top models, we performed model-averaging of all parameters and report model-averaged parameter estimates, odds ratios, and 95% confidence intervals (CI; Burman and Anderson 2002). If the null model was among the top models, we did not make any inferences from that model set. All analyses for AICc and model-averaging were performed using JMP (Version 14.1.0 2019).

We ran our initial analysis with all nests found, however, given that cavity nests (including nest boxes) differ from cup nests in abiotic conditions and structural characteristics, we removed cavity nests for a second analysis, including only the subset of data from open-cup nests. We repeated the procedure above using only open-cup nests and the same set of models. Thirty four of the 52 remaining cavity nests (65.38%) were either in no nest (Killdeer) or in nest boxes (which are not based on bird nest-site selection), so we did not perform an analysis with those. We modeled each of our most likely parameters using a binomial response (success = 0, fail = 1) and the logit link function in R (Version 3.6.2 R Core Team 2013).

Table 1. AIC model results for nest success of all birds (n=52) at Panola Mountain State Park from March-August 2019. Models with ΔAICc < 2.0 are indicated above the dashed line.

Model[1]	k[2]	AICc[3]	ΔAICc[4]	ω_i[5]
NT+PAN+PH+WD	5	58.47	0	0.48
NT+PAN+PH+WD+FD	6	60.85	2.37	0.15
NT+PAN+PH+WD+WG	7	61.15	2.67	0.13
NT+PAN+PH+WD+SD	6	61.34	2.86	0.11
PAN+NT+PH	4	63.56	5.09	0.04
NT+PH+SD	4	64.24	5.76	0.03
OC+PH+NT+SD	5	65.01	6.53	0.02
PAN+NT	3	65.48	7.00	0.01
NT+PH+SD+PAN	5	65.87	7.39	0.01
PH+PAN+NT+DC+OC	6	67.14	8.67	0.006
DC+WD	3	68.92	10.44	0.003
NT+WD	4	69.12	10.64	0.002
Null	1	69.16	10.69	0.002
PH+NT	4	69.22	10.74	0.002
PAN+WD	3	69.45	10.98	0.002
NT+FD	4	69.96	11.48	0.002
FD+WD	3	70.39	11.92	0.001
WD+PH	3	71.02	12.55	0.0009
DC+OC	3	71.02	12.55	0.0009
NT+DC	3	71.05	12.58	0.0009
DC+WD+NT	4	71.18	12.71	0.0008
WG+NT+WD	6	71.50	13.02	0.0007
OC+NT+FD	5	72.12	13.64	0.0005
PH+PAN	3	72.16	13.69	0.0005
WG+DC+NT	5	72.55	14.08	0.0004
OC+DC+CN	4	73.38	14.90	0.0002
PH+PAN+DC+OC	5	75.29	16.82	0.0001

[1] NT: Nest Type (Nest box, ground, or shrub), PAN: Plant height above nest (m), PH: Plant height (m), WD: Distance from water (m), FD: Distance from forest (m), WG: Woody or grassy bird type, SD: Start date (ordinal dates), OC: Overhead cover (%), DC: Directional cover (%), CN: Objects concealing nest (#).
[2] Number of parameters in each model
[3] Akaike information criterion corrected for small sample sizes (Burnham and Anderson 2002)
[4] Difference between AICc values of current model and most supported model
[5] Relative support for a model out of the candidate set

RESULTS

We found 52 nests of 11 species at PANO from March – August 2019 (Table 2). Thirty-five percent of all nests were successful, and 35.29% of cup nests were successful (Table 3). Overall productivity at PANO was 1.02 fledges per nest, and cup-nests fledged 0.88

fledges per nest (Table 3). Only one nest was found in the portion burned around mid-April (Killdeer; Figure 1), all others were either found in nest boxes (34 nests) or in vegetation that was burned the previous year (17 nests; Figure 1).

Table 2. Number of nests of each species and nest type (cup or cavity) at Panola Mountain State Park from March-August 2019.

Species	# of nests found	Cup or Cavity
Common Yellowthroat	7	Cup
Field Sparrow	4	Cup
Blue Grosbeak	2	Cup
Indigo Bunting	2	Cup
Red-Winged Blackbird	1	Cup
Tree Swallow	1	Cup
White-Eyed Vireo	1	Cup
Eastern Bluebird	24	Cavity
Carolina Wren	8	Cavity
Carolina Chickadee	1	Cavity
Killdeer[1]	1	-------

[1]Killdeer do not build nests

Table 3. Number of nests, number of species, reproductive success, productivity, and predation rate for nests found at Panola Mountain State Park from March-August 2019.

	All nests	Cup nests
# of nests	52	17
# of species	11	6
Reproductive success (%)	35	35.29
Productivity (fledges per nest)	1.02	0.88
Predation rate (%)	91.18	72.72

All Nests

One model was the top model (ΔAICc < 2.0) with a ω_i of 0.48 (Table 1). Nests built in taller plants (Figure 2A), with more of the plant above the nest (Figure 2B), farther from water (Figure 2C), and built in grassy vegetation are associated with a greater likelihood of success.

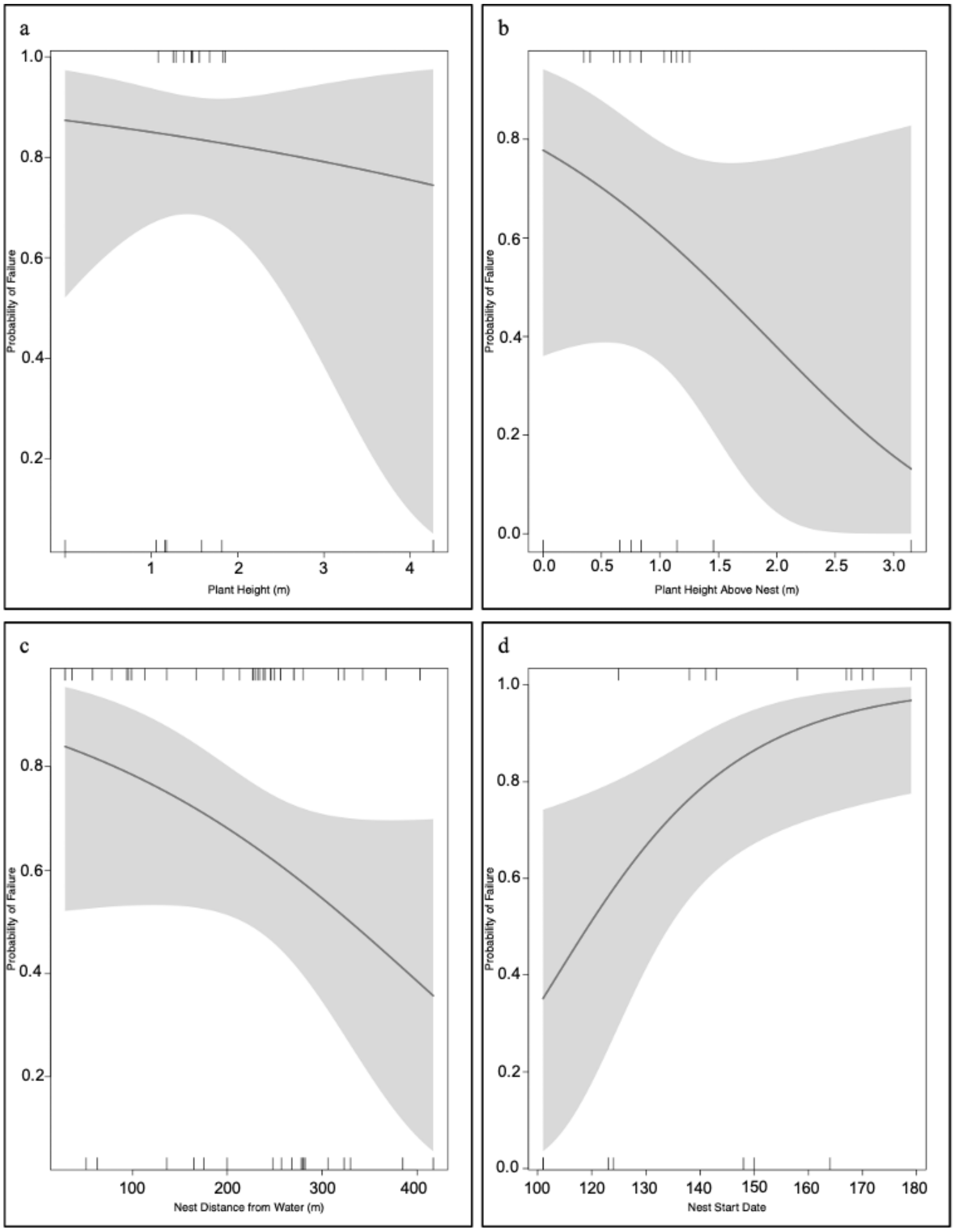

Figure 2. Estimated probability and 95% confidence interval (grey) of nest failure as a function of (a) plant height (b) plant height above the nest (c) distance from water and (d) nest start date in a restored grassland at Panola Mountain State Park from March-August 2019

Cup Nests

We found three top models (ΔAICc < 2.0) with a combined ω_i of 0.66 (Table 4). Cup nests built in taller plants, with taller vegetation above the nest, in grassy vegetation, and earlier in the season (Figure 2D) are associated with a greater likelihood of success. Model-averaging based on 740 possible models revealed that nest type, start date, and overhead cover were the three characteristics where the odds ratio confidence interval did not overlap one (Table 5).

Table 4. AIC model results on nest success of cup-nest birds (n=18) at Panola Mountain State Park from March-August 2019. Models with ΔAIC < 2.0 are indicated above the dashed line.

Model[1]	k[2]	AICc[3]	ΔAICc[4]	ω_i[5]
PAN+NT+PH	4	21.52	0	0.28
PAN+NT	3	21.54	0.019	0.27
NT+PH+SD+PAN	5	23.38	1.87	0.11
Null	1	26.31	4.79	0.025

[1] PAN: Plant height above nest (m), NT: Nest type (Nest box, ground, or shrub), PH: Plant height (m), SD: Start date (ordinal dates).
[2] Number of parameters in each model
[3]Akaike information criterion corrected for small sample sizes (Burnham and Anderson 2002)
[4]Difference between AICc values of current model and most supported model
[5]Relative support for a model out of the candidate set

Table 5. Model averaged parameter estimates ($\hat{\beta}$), standard errors (SE), and odds ratio (95% CI) for cup nests computed across all possible models (740; Burnham and Anderson 2002). Bolded characteristics have CI that do not overlap one.

Characteristic[1]	$\hat{\beta}$ (SE)	Odds ratio (CI)
NT(shrub-ground)	**-0.27 (0.10)**	**0.764 (0.624,0.937)**
SD	**-0.0079 (0.0037)**	**0.99 (0.98,0.99)**
PH	0.052 (0.10)	1.053 (0.858,1.293)
PAN	0.28 (0.15)	1.318 (0.984,1.766)
OC	**-0.0013 (0.0020)**	**0.999 (0.984,0.991)**

[1] NT: Nest type (Nest box, ground, or shrub), SD: Start date (ordinal dates), PH: Plant height (m), PAN: Plant height above nest (m), OC: Overhead(%)

DISCUSSION

Reproductive success for nests at PANO is consistent with success reported in similar studies on restored grasslands (Stauffer et al. 2011; Ingold and Dooley 2013; Davis et al. 2016). Several characteristics were associated with nest success. Overall, nest type had the strongest association with success; it was included in top models for all nests and cup nest analyses and in model-averaged parameter estimates for cup nests (Tables 1, 4, 5). Ground nests were more likely to be successful than either nest box/cavity or cup nests built in shrubby vegetation, contrary to the typical assertion that nest boxes and cavities are more likely to be successful (Martin and Li 1992; Hall et al. 2015; Martin et al. 2017). This may be because birds that use nest boxes and cavities are exposed to predation risk for a longer period of time because they have longer nesting cycles than open-cup nesters (Marin and Li 1992). Perhaps more importantly, nest boxes at PANO are often placed along trails and near forest and water edges, which are areas that predators are known to concentrate (Herkert et al. 2003) and these nests experienced high predation rates (K. Stumpf, unpubl. data). Therefore, we suggest that nest box locations factor in distance from water edges to minimize predation risk.

Other characteristics in our top models for all nest and cup-nest analyses included: plant height, plant height above the nest, and distance from the South River (Tables 1 and 4), and start date and overhead cover were important in cup-nest model-averaged parameter estimates (Table 5). Most of our nest failures were due to predation (91.18%) though a smaller number failed due to abandonment (2.94%) and inclement weather (5.88%), so it is not surprising that factors that limit predation risk had the strongest association with nest success. Snakes are the most common nest predators, especially in the Southeast (Thompson et al. 1999; Davison and Bollinger 2000; DeGreggorio et al. 2016), but aerial predators like hawks and owls and mammalian ground predators like mice and raccoons are also common at PANO (C.M. Muise pers. comm.). It is well-known that birds select nest sites that limit the risk of predation (Davis 2003; Herkert et al. 2003; Keyel et al. 2013; Perkins et al. 2013). Given that and the prevalence of depredation in our dataset; we discuss our results with respect to predation.

Many of these vegetation characteristics provide better concealment from nest predators, thereby reducing predation risk. For example, taller vegetation and more vegetation above the nest offer more nest concealment above and sometimes below the nest (Dechant et al. 1998; Fisher and Davis 2010; Klug et al. 2010; Murray 2014), which provides protection from both aerial and ground nest predators (Klug et al. 2010). Several of the characteristics that were associated with nest success also affect predator abundance or composition of predator communities. For example, predators of all types are more common near water because of the abundance of available resources (Johnson and Temple 1990; Burger et al. 1994; Sálek et al. 2010), but studies that looked at the effect of distance to water on success have shown mixed results. Nest predation has been seen in nests found closer to water (Bollinger and Peak 1995) similar to our results, but in other studies there was no association between the two (Vander Haegen and DeGraaf 1996; Saracco and Collazo 1999). In our study there is no relationship between distance to water and success when we remove nest boxes and cavity nests, indicating that the placement of those nests is driving the relationship seen in the full dataset. The nest boxes at PANO are located near the South River, and are therefore at higher risk of predation because predators are more abundant (Stumpf unpubl. data). We also found that earlier nests were more likely to be successful, likely because predator activity is lower during the late spring and early summer (Wiggens et al. 1994; Nol and Smith 1987; Verhulst et al. 1995).

Lastly, greater overhead cover was associated with lower nest success when we averaged parameter estimates across all possible combinations of models in our cup-nest analysis, though it was not in any of our top models. Overhead cover may also be linked to predator abundance indirectly, in particular for snakes, a common nest predator (DeGregorio et al. 2016). Greater overhead cover provides concealment from aerial predators not just for nesting birds but for snakes as well. In grasslands some snake nest predators disproportionately use habitats with more shrub cover and nests in those habitat experience lower nest success rates (Klug et al. 2010) Cover may also provide cooler microhabitat for ectothermic snakes to use during the hottest times of the day (Klug et al. 2010).

Management Implications

Birds serve important roles in ecosystem function (*e.g.,* pollination, pest control, seed dispersal), and both generalists and grassland birds are often used as indicators for habitat quality (McKinney and Lockwood 1999; Martinossi-Allibert 2017). In our study, grassland species and generalist species nested in the restored grassland habitat and successful nests were associated with similar factors for each, making implementation into current and future restoration projects relatively straightforward. Taller vegetation can be easily managed by restricting mowing during the months prior to breeding and with appropriate timing of annual prescribed burns. Rotational patch burning on select portions of the field can also increase vegetation height and decrease the risk of nest predation (Duchardt et al. 2016). Introducing buffer zones (areas designed to protect sensitive landscape patches from external pressures; Bentrup 2008) around the South River and the field's perimeter would be a relatively easy management strategy that may help increase reproductive success rates of nesting birds here. Finally, we suggest nest boxes be re-located to areas of the field that are further from the South River, where their probability of success may be higher. These kinds of proactive conservation efforts and restoration projects have reversed downward population trends for other guilds such as waterfowl and raptors (Rosenburg et al. 2019), and the same positive outcome is possible for grassland birds with the right land management and conservation efforts.

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