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Several Vegetation Characteristics Affect Reproductive Success of Grassland Birds at a Restored, Warm-Season Grassland in central Georgia

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Multiple Vegetation Characteristics Affect Reproductive Success

Submitted by Kayla B. Allen in partial fulfillment of the requirements for the degree of M.S. in Biology.

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PREFACE

This thesis has been written in journal format and conforms to the style appropriate to my discipline. This manuscript will be submitted for publication in Southeastern Naturalist, a peer reviewed interdisciplinary scientific journal, and therefore reflects the required formatting for this publication. Figures and tables follow the text of the manuscript as required by Southeastern Naturalist and this thesis committee.

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Chapter 1: Assessment of Vegetation Characteristics and Fire Affecting Grassland Bird Abundance on Restored Warm-Season Grasslands

Abstract: Native grassland habitats have been declining in the United States since European settlement and agriculture began, and continues today. Along with conversion of grasslands to agricultural land, settlers replaced native, warm-season grasses with non-native, cool season grasses and suppressed natural fires on the landscape. Projects like the Conservation Reserve Program have been providing incentives for farmers to convert retired agriculture fields back to native, warm-season grasses to preserve the soil and provide quality habitat for grassland-specialized wildlife which rely on the grassland ecosystem to survive. Grassland obligate bird populations have declined by 50% since 1970, which is the steepest population decline of any avian guild in North America. Because of this, restoration projects have been increasing their focus on vegetation quality and reintroducing fire on the landscape. Here, we discuss the history of fire and fire suppression on grassland ecosystems and how fire management strategies like rotational patch burning can restore habitats to natural conditions. We also discuss what specific vegetation characteristics (e.g., vegetation density and percent ground cover) have been associated with grassland bird abundance in other studies on restored grasslands. There have already been increases in grassland bird abundance on restored landscapes, but little is known about how productive these sites are for breeding birds. Also, we discuss an alternative to statistical testing and suggest an information theoretic approach that is better suited to provide recommendations for management strategies with the goal of increasing grassland bird productivity.

Grasslands in North America

Native grassland habitats have declined over 80% throughout the United States since European settlers began converting grasslands to croplands (Samson et al. 2004, Samson and Knopf 1994). In the Southeast, grassland loss is as high as 97% (Samson et al. 2004, Wall et al. 2011). During this same time, settlers also introduced non-native cool-season grasses (e.g., *Poa pratensis* (Kentucky bluegrass), *Festuca arundinacea* (tall fescue), and *Bromus inermis* (smooth brome grass); hereafter: non-native grasses) because they easily grew on the land and green up faster than the native, warm-season grasses (hereafter: native grasses; Rothbart and Capel 2006). Unfortunately, these non-native grasses are not beneficial on the landscape because they grow thick and tightly together which restricts wildlife movement, require insecticides, and grow at inopportune times of the year for certain wildlife (Rothbart and Capel 2006).

The Conservation Reserve Program (CRP), run by the United States Department of Agriculture, began the process of removing non-native grasses and replacing them with native grasses in 1985 and this practice continues today (USDA 2019). CRP pays farmers to replant fields no longer in production to encourage re-vegetation of native grasses that provide fresh food for cattle during the summer growing season (Rothbart and Capel 2006). Since native grasses do not need to be maintained with herbicides and insecticides, farmers save money while simultaneously protecting wildlife from being adversely affected by toxicity on the land (Rothbart and Capel 2006). One of the main goals of CRP is to provide suitable habitat for wildlife reliant on grasslands to survive (USDA 2019) such as voles, jumping mice, many species of sparrows, bobwhite quail, green snakes, and box turtles (Rothbart and Capel 2006). Lately, there has been a concerted effort for restoration projects to increase grassland bird populations due to their recent decline in numbers (Rosenburg et al. 2019).

Grassland structure and function is best maintained through natural forces like fire, grazing, and climate (Shaffer and DeLong 2019). Historically, fires naturally occurred across the US from processes such as lightning strikes (Askins et al. 2007, Brawn et al. 2001) which releases nutrients back into the soil and maintains the structure of the ecosystem (Askins et al. 2007). Conversely, suppressing these natural fires leads to the buildup of ground litter and encroachment of woody vegetation which inevitably outcompetes grass species (Askins et al. 2007, Samson et al. 2004). To combat this, low-intensity, frequent prescribed burns are implemented to decrease ground litter and prevent displacement of grasses by woody vegetation (Roberts et al. 2012, Stubbendieck et al. 2007). When built-up ground litter is burned, it releases nutrients back into the soil which gives grasses the resources to grow without competing for nutrients (Roberts et al. 2012, Stubbendieck et al. 2007).

A grassland obligate bird is one that is adapted and reliant on a grassland habitat for some or all of its life cycle (Askins et al. 2007). Grassland birds have declined by 50% or 700 million individuals since 1970, which is the steepest decline of any avian guild in North America (Askins et al. 2007, Cassidy and Kleppel 2017, Rosenberg et al. 2019). Fire suppression and loss of native habitat are the primary causes of their decline (Askins et al. 2007). Because grassland birds are reliant on grasslands, they serve as excellent indicators of habitat quality and health (Martinossi-Allibert 2017, McKinney and Lockwood 1999). For example, grassland birds are less abundant and may be completely absent in fragmented habitats that have proportionally more forest edges (Baral 2001, Caplat and Fonderflick 2009, Grant et al. 2004). On the other hand, grassland birds are typically the first wildlife group to return to restored lands (Ellison et al. 2013, Johnson and Igl 1995, Johnson and Schwartz 1993). In fact, grassland birds may be equally or even more abundant on restored grassland sites than on preserved, native grasslands, indicating that restoration sites may be important for increasing future population numbers (Fletcher Jr. and Koford 2002, Johnson and Schwartz 1993, Weidman and Litvaitis 2011).

Grassland birds prefer and nest in higher densities in habitats with regular, prescribed burns than non-burned habitats (Byers et al. 2017, Pearson and Knapp 2016, Rothbart and Capel 2006). However, the frequency of burning is crucial – prescribed burns must be frequent enough to prevent the return of woody vegetation, but burning too often may decrease abundance of grassland birds like *Ammodramus savannarum* (Grasshopper Sparrow) and *Ammodramus henslowii* (Henslow's Sparrow; Shaffer and DeLong 2019). In fact, rotational patch burning, where only certain portions of a habitat are burned each year, can benefit a variety of grassland bird species (Duchardt et al. 2016). Sites with rotational patch burns tend to have more bare ground on the portion burned that year which is preferred by some grassland specialists (e.g., Grasshopper Sparrow, *Sturnella magna* (Eastern Meadowlark), and *Charadrius vociferus* (Killdeer; Duchardt et al. 2016, Rahmig et al. 2009). Previous-year burned sites have twice as much live grass cover compared to unburned areas which is preferred by grassland specialists like *Passerculus sandwichensis* (Savannah Sparrow) and *Ammodramus bairdii* (Baird's Sparrow; Davis 2005, Rahmig et al. 2009). The timing of these prescribed burns is also important because birds may be forced to delay breeding if fields are burned too close to the start of the breeding season; burning during the winter should provide enough time for re-growth and not delay the return of grassland birds (Shaffer and DeLong 2019).

Grassland birds have clear vegetation preferences and many of the characteristics they prefer are dependent on regular fire practices (Fisher and Davis 2010). For example, some prefer to nest in taller vegetation (Dechant et al. 1998, Fisher and Davis 2010, Klug et al. 2010, Murray 2014) because it provides more vertical options when building their nest (Klug et al. 2010).

Some prefer denser vegetation (Fisher and Davis 2010, Murray 2014) because the increased nest concealment it provides can lower the predation risk (Klug et al. 2010, Murray 2014). Finally, some grassland birds prefer to nest in vegetation that provides greater cover, because it provides better nest concealment, and therefore, protection from both aerial and ground predators (Davis 2005, Fisher and Davis 2010).

While small patches of restored grassland may attract grassland birds back to an area (Duchardt et al. 2016), these birds are at higher risk of predation than if they were on large, continuous restored grasslands (Davis 2003, Herkert et al. 2003, Keyel et al. 2013, Perkins et al. 2013) because of edge effect. Habitat edges are abrupt changes in a particular habitat type, which, in grasslands, can include forests, roads, wetlands, agriculture, and other forms of human development (Perkins et al. 2013). Small patches of land have a higher proportion of edges than larger patches (Sisk and Battin 2002). Common predators in grasslands such as squirrels, foxes, snakes, deer, crows, and hawks (Herkert et al. 2003) are more abundant along habitat edges because edges have more cover, more food, and better microclimates (Burger et al. 1994, Johnson and Temple 1990, Sálek et al. 2010). Edges can also increase brood parasitism by *Molothrus ater* (Brown-headed Cowbirds; Herkert et al. 2003, Jensen and Finck 2004) which results in less attention given to the host birds nestlings and a decrease in reproductive fitness (Burhans 2001, Herkert et al. 2003, Hoover 2003, Ludlow et al. 2014, Rothstein 1990).

Measures of restoration success

When the goal of grassland restoration is increasing population sizes of declining grassland birds, documenting presence alone is not enough because it tells us nothing about how productive a site is (Duchardt et al. 2016, Horne 1983). For example, if birds are only present during migration or winter, productivity for that site does not increase since no reproduction is occurring (Horne 1983). Providing optimal habitat for birds during migration and over-winter is important, but understanding the effect that restoration efforts have on nest success and reproductive output is a better way to estimate future population growth trends, and it is a critical measure of restoration success in managed habitats (Andrews et al. 2015, Ludlow et al. 2014, Rosenberg et al. 2016). It is also important to determine how characteristics that birds use in nest-site selection affect productivity so these features can be included in management plans to increase reproductive output.

Information-Theoretic Approach

Scientific studies commonly analyze their results based on significance testing, where we reject the null hypothesis if our p-value is less than 0.05 (i.e., when there is less than a 5% chance that the difference between the two variables is due to random chance; Fisher 1925). However, rejecting or accepting a null hypothesis does not provide any information on the magnitude of impact of a variable and often ignores biological significance (Guthery et al. 2001). An alternative approach for determining relationships between dependent and independent variables is using a model-based information theoretic approach (Burnham and Anderson 2002). Akaike's Information Criteria (AIC) is relatively new, but is being used more and more by ecologists and wildlife biologists each year (Symonds and Moussalli 2010). Using this method, users develop a set of *a priori* models ("competing hypotheses") based on available information and determine which has the most support, based on the data collected in their study (Burnham and Anderson 2002). Using a set of models based on well-thought out biological reasons is often better than analyzing all possible factors (i.e., data dredging) which can lead to more uncertainty within the results (Burnham and Anderson 2002). Models are ranked in order of most to least support (based on a calculated AIC value; Burnham and Anderson 2002) and those within four

AIC units of the model with the most support should be considered as almost equally likely (Burnham and Anderson 2002). When we want to know the relative contribution of a single factor, we can use multimodel inference by averaging across all models in which that factor is found (Burnham and Anderson 2002). After determining which characteristics have the strongest influence, the characteristics can then be fit using generalized linear models to make predictions outside of the collected data (logistic-exposure; Shaffer 2004). These generalized linear models also provide 95% confidence intervals where smaller confidence intervals indicate more confidence that the model is accurate (Shaffer 2004). The most supported variables of influence can then be suggested to managers to provide practical changes in the future.

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Chapter 2: Multiple Vegetation Characteristics and Landscape Characteristics Affect Reproductive Success of Grassland Birds at a Restored, Warm-Season Grassland in central Georgia.

Abstract: Grassland birds are experiencing major population declines due to habitat loss and fire suppression throughout North America. Large-scale grassland restoration efforts are ongoing, but there is little data on breeding bird productivity on restored habitats, nor on the impact of specific vegetation characteristics on reproductive output. Since 2005, agriculture fields at Panola Mountain State Park, GA have been undergoing restoration to warm-season grasslands; however, up until now there has been no monitoring of nest success or productivity. The goals of this project are to 1) quantify reproductive success and 2) determine which vegetation characteristics are associated with reproductive success. From March-August 2019, we monitored all active nests and recorded nest outcome and vegetation characteristics to determine which variables were most strongly associated with success using Akaike's Information Criterion (AICc). We found 52 nests of 11 species, with an overall success rate of 34.62%. Thirty-seven of the nests were constructed by grassland obligates (5 species), 38.89% of which were successful. Nest type, plant height, plant height above the nest, and distance from habitat edges were most strongly associated with nest success of all nests. Ground nests were more likely to be successful than shrub nests or birds using nest boxes, likely because the location of nest boxes is decreasing their success. Nests built in taller vegetation, with taller vegetation above the nest, and further from edges were also more successful. All of these factors are tightly linked with predation risk because they provide more concealment and are farther from areas where predators concentrate. We recommend managers design restoration efforts that will ensure appropriate grass height and limit edges near nesting areas to ensure high quality, productive habitat for grassland birds.

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 US alone, 97% of grassland habitat has been lost mainly due to farming and fire suppression (Askins et al. 2007) and the introduction of non-native, cool-season grasses (hereafter: non-native grasses) that replace 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 (Cassidy and Kleppel 2017, Henderson and Davis 2014, Rosenberg et al. 2019). Rosenberg et al. (2019) estimates that the US has lost 700 million grassland birds, or 50% of the population overall, since 1970 due to habitat loss and pesticide use on agricultural landscapes, and this loss will continue without large-scale efforts to restore their native habitat (Rosenberg et al. 2019).

Restoration projects like the U.S. Department of Agriculture's Conservation Reserve Program (CRP; Rothbart and Capel 2006) have had positive impacts on grassland bird populations. Densities of some species of grassland birds are higher on these restored native grasslands likely because they provide better quality nesting habitat features (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 used in nest site selection that decrease the risk of predation (Davis 2005, Fisher and Davis 2010). The timing of the growing season of native grasses coincides with the demands of the breeding season of grassland birds – they grow during or just prior to, the breeding season. Non-native grasses, on the other hand, grow predominantly during the spring and fall, and are typically harvested and converted to hay during the summer months, destroying active nests as well as the potential for future nest sites that season (Rothbart and Capel 2006). Lastly, native grasses grow in clumps, which makes evading predators easier and allows cryptic movement to and from a nest (Rothbart and Capel 2006), unlike *Festuca arundinacea* (tall fescue), a common non-native grass, grows in thick, dense mats and restricts movement of wildlife (Rothbart and Capel 2006).

Habitat edges, where grassland habitat meets forest, roads, wetlands, agriculture, and/or any form of human development (Perkins et al. 2013), disrupt the continuity of a particular habitat type and can affect the presence of specialist birds along those edges (Baral 2001, Caplat and Fonderflick 2009, Grant et al. 2004). 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 to return to an area (Duchardt et al. 2016), there is a higher risk of predation in small patches with more edge than on large, continuous restored grasses (Davis 2003, Herkert et al. 2003, Keyel et al. 2013, Perkins et al. 2013). Many common 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). Similarly, large patches of land with proportionally more core habitat – at least 50 meters away from the nearest habitat edge – are also associated with lower risk of predation (Herkert et al. 2003).

A critical component of native, warm-season 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. Grassland birds prefer landscapes that experience periodic burns and nest in higher densities in habitats with regular, prescribed burns compared to non-burned habitats (Byers et al. 2017, Pearson and Knapp 2016, Rothbart and Capel 2006). 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 *Ammodramus savannarum* (Grasshopper Sparrow) and *Ammodramus henslowii* (Henslow's Sparrow; 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, *Sturnella magna* (Eastern Meadowlark), and *Charadrius vociferus* (Killdeer; Duchardt et al. 2016, Rahmig et al. 2009). 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 *Passerculus sandwichensis* (Savannah Sparrow) and *Ammodramus bairdii* (Baird's Sparrow; Davis 2005, Rahmig et al. 2009). Also, using 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 a critical factor – when burns occur too close to the start of the breeding season, the vegetation does not have time to regrow, resulting in delayed breeding attempts. When possible, prescribed fires should occur during winter months (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 (Andrews et al. 2015, Keyel et al. 2013, Murray 2014), however presence alone does not necessarily indicate how productive (i.e., successfully producing offspring) that habitat is

(Duchardt et al. 2016, Horne 1983). For example, if birds are only present during migration or winter, productivity for that site does not increase 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 provides better estimates of future population growth or decline and should be a critical measure of restoration success in managed habitats (Andrews et al. 2015, Ludlow et al. 2014, Rosenberg et al. 2016). The objectives of this study were to 1) quantify reproductive success and 2) determine habitat characteristics associated with reproductive success of birds breeding in a restored, warm season grassland habitat.

Methods

Study site

In 2005, restoration of retired agricultural habitat to native grasses began in a 110-acre plot at Panola Mountain State Park (PANO; Figure 1) in central Georgia to provide much needed habitat for declining grassland bird populations (Klaus 2010). The South River, a perennial river, borders the grassland to the north, east, and south (Figure 1). The grassland is surrounded by forest and is interspersed with small stands of 4-5 trees (Figure 1). Management currently includes rotational patch burns that alternate between the eastern and western halves of the field in different years, revegetation with native warm-season grasses, and removal of invasive vegetation (e.g., *Sorghum halepense* (johnsongrass) and *Liquidambar styraciflua* (American sweetgum)). The western half of the field was burned in mid-April of 2019. The area is now predominantly warm-season grasses (e.g., *Schizachyrium scoparium* (little bluestem), *Andropogon gerardii* (big bluestem), and *Asclepias tuberosa* (butterfly milkweed)). Several grassland birds and generalists breed at PANO including *Spizella pusilla* (Field Sparrow), *Geothlypis trichas* (Common Yellowthroat), *Agelaius phoeniceus* (Red-Winged Blackbird), *Melospiza melodia* (Song Sparrow), Indigo Bunting *Passerina cyanea* (Indigo Bunting), and *Passerina caerulea* (Blue Grosbeak); C. Muise, unpubl. data).

Field data collection

From March to August 2019, we searched for nests five days a week throughout the 110-acre site following Breeding Biology Research and Monitoring Database protocol (Martin et al. 1997). We divided the site into 5 polygons of approximately equal area (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 or abandoned or when it 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. To reduce disturbance during nesting, we recorded vegetation characteristics when nests were complete. We recorded nest height, nest plant height (ground to the top of the plant), plant height above the nest (nest height subtracted from plant height), plant species, concealment (average of the percent cover in each compass direction, measured at nest height from one meter away), overhead cover (percent cover of vegetation while looking down on the nest), and number of supporting branches after the nest was no longer active. At the end of the breeding season, we estimated the distance from forest edge and distance from water edge using nesting Google Earth (2019) and back-calculated the start date (date the first egg was laid) and converted to Julian start date.

Data analysis

We calculated nest success for each species in three ways: 1) the percent of nests that produced at least one fledgling 2) number of fledges per nest (productivity) and 3) daily nest success (Mayfield 1975). 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 several vegetation characteristics on nest success. Since our objective was to determine the effects of vegetation on grassland birds, we used only grassland nests in our initial analysis. We used a two-step modeling approach. First, we modeled the effect of each characteristic individually and retained only characteristics with ΔAICc < 4 for the second step (Milligan and Dickinson 2016). Since we do not know which nest predators are present at PANO, we constructed models for the second step under the assumption that multiple types of predators are present (e.g., aerial predators, ground predators). Each of these 27 models (Table 1) can, therefore, be thought of as a single hypothesis and the Akaike weight (ω_i) is the relative likelihood of that model being the best model in our candidate set of models (Burman and Anderson 2002). Models with ΔAICc < 4 (hereafter: top models) were considered to have the most support. If there were multiple top models, we performed model-averaging of all parameters and report model-averaged parameter estimates, odds ratio and 95% confidence intervals (CI) (Burman and Anderson 2002). If the null model, which tests the likelihood of no characteristics influencing reproductive success, 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).

After determining if any characteristics differed between grassland and generalist species (ANOVA), we combined our data and repeated the above procedure on all nests (as opposed to just grassland species) using the same candidate set of models. We then determined if there was a significant difference between characteristics of open-cup nests and birds using nest boxes (ANOVA) and again repeated the procedure above using only open-cup nests and the same set of models. We fit models of parameter effects on daily survival rate (DSR) using Shaffer's (2004) logistic exposure method which accounts for number of exposure dates for nests that were not checked daily. 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).

Results

We found 52 nests of 11 species at PANO from March-August 2019 (Table 2); 37 nests of grassland birds and 17 cup-nesting birds. Thirty-five percent of all nests were successful, 38.89% of grassland bird nests were successful, and 35.29% of cup nests were successful (Table 2). Daily nest survival was 18.62% for all nests, 21.06% for grassland birds, and 20.11% for cup nesters (Table 2). Overall productivity at PANO was 1.02 fledges per nest and grassland bird nests fledged 1.11 fledges per nest (Table 3). Only one of 52 nests was found in the portion burned around mid-April (Killdeer; Figure 1), all others were found in nest boxes (34) or in the portion of the field burned the previous year (17; Figure 1).

Grassland bird nests

Only one of 15 characteristics (plant type) was excluded from analysis (ΔAICc <4; Table 4). Eighteen models were considered top models (ΔAICc < 4.0), including the null model (Table 1). Since the null model was among the candidate set, we did not make inferences with this dataset.

All nests

There was no significant difference for any of the characteristics between grassland birds and generalist birds (Table 5), so we combined those data for the analysis of all nests. One of the

16 characteristics (plant type) had ΔAIC > 4.0 and were therefore excluded from subsequent models (Table 6). Four models were considered top models (ΔAICc <4.0) with a combined ω_i of 0.87 (Table 7). Nests built in taller plants (Figure 2), with more of the plant above the nest (Figure 3), farther from the forest edge (Figure 4), farther from water (Figure 5A), built in grassy vegetation (Figure 6), and earlier in the season (Figure 7) are associated with a greater likelihood of success. Our model-averaged parameter estimates are based on a total of 3062 possible models; nest type was the only characteristic where the confidence interval around the odds ratio didn't overlap one (CI = 0.53-0.93; Table 8).

Cup nests

Nest height, directional and overhead cover, distance from forest's edge, and number of objects concealing nests differed significantly between the birds using nest boxes and cup nesters (Table 9), so the remaining analyses used only cup nests. Five models were considered top models (ΔAICc <4.0) with a combined ω_i of 0.77 (Table 10). Nests built in taller plants (Figure 2), with more vegetation above the nest (Figure 3), farther from water (Figure 5B), in grass vegetation (Figure 6), and earlier in the season (Figure 7) 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 11).

Discussion

Reproductive success for nests at PANO is consistent with success reported in similar studies on restored grasslands (Davis et al. 2016, Ingold and Dooley 2013, Stauffer et al. 2011). Several characteristics had varying levels of association with nest success. Overall, nest type had the strongest association with success; it was included in the top models for all nests and cup nest analyses, and in model-averaged parameter estimates (Tables 7, 8, 10, 11, Figure 6). Specifically, ground nests were more likely to be successful than either nest box or cup nests built in shrubby vegetation (Figure 6), contrary to the typical finding that nest boxes are more likely to be successful (Hall et al. 2015, Martin et al. 2017, Martin and Li 1992). However, nest boxes at Panola are often placed along trails and near forest and water edges, which are areas that predators are known to concentrate (Herkert et al. 2003).

Other factors had support in some, but not all analyses; taller plants, greater plant height above the nest, greater distance from the South River, and an earlier start date were included in top models for both all nests and cup nest analyses (Tables 7 and 10), but only start date was important in cup-nest model-averaged parameter estimates (Table 8 and 11). Distance from a forest edge was only included in the top models of all nests (Table 7) and overhead cover was only important based on model-averaged parameter estimates of cup-nests (Table 11). Most of our nest failures were due to predation (91.18%), and only a handful failed for other reasons (abandonment (2.94%) and inclement weather (5.88%)), so it is not surprising that factors that limit predation risk are the factors that we found had the strongest association with nest success. Snakes are the most common nest predators, especially in the Southeast (Davison and Bollinger 2000, DeGreggorio et al. 2016, Thompson et al. 1999), but aerial predators like hawks and owls and ground predators like mice and raccoons are common at PANO (C. Muise, pers. comm.). It is well-known that birds select nest sites that limit the risk of predation, so here we discuss our results with respect to predation.

Many of the characteristics that we found to be important provide better concealment from nest predators, thereby reducing predation risk. For example, cavity nests such as the man-made nest boxes found at PANO, typically provide better concealment from predators and therefore experience less predation (Hall et al. 2015, Martin et al. 2017, Martin and Li 1992). However, our results indicate that nest boxes had a high likelihood of failure. This may be because birds that use nest boxes 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). Birds choose nest sites based on a variety of factors that reduce predation risk (Lima 2009) but given that man-made nest boxes are in fixed locations, the high failure rate in our study may be due to factors that the birds cannot select for or against. 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.

Several of the characteristics we found were associated with nest success are also those that have an effect on predator abundance or composition of the predator community at PANO. For example, predators of all types are more common near water resources because of the abundance of resources (Burger et al. 1994, Johnson and Temple 1990, Sálek et al. 2010). We found that nests that are farther from water have a higher likelihood of success, when all nests are included (Figure 5A), but there was no relationship between distance to water and nest success for open-cup nests only (Figure 5B). Studies that looked at the effect of distance to water on success have shown mixed results. Nest depredation 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 (Saracco and Collazo 1999, Vander Haegen and DeGraaf 1996). In our study, this relationship is strongest for birds nesting in nest boxes since we only see this trend when nest boxes are included in the analysis. Once again, likely because of the fixed position of the nest boxes, these nests are at higher risk of predation near water because predators are more abundant. We found that earlier nests were more likely to be successful, consistent with other studies, likely because predator activity is usually lower during the late spring and early summer (Nol and Smith 1987, Verhulst et al. 1995, Wiggens et al. 1994). Likewise, forest edges are known to harbor an abundance of all animals, including a diverse community of predators, and therefore are associated with a higher likelihood of nest predation (Keyel et al. 2013, Herkert et al. 2003). Smaller patches of habitat, like our study site, have a greater proportion of edge habitat, so grassland birds here may be at a greater risk of predation based on its relatively small size.

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, but it was not in any of our top models. We constructed several models to include overhead cover (Tables 4 and 7), but it was not in any of the most supported, top models that were biologically constructed. However, this particular characteristic is likely linked to predator concealment which indirectly affects reproductive success. Since our most-likely predators are snakes, more overhead cover is providing them with better concealment from aerial predators while seeking out nests. Therefore, it is still contributing to nest success in an important way.

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 (Martinossi-Allibert 2017, McKinney and Lockwood 1999). When the goal of a restoration project is to provide optimal habitat for nesting birds, managers should focus on features that benefit both generalists and grassland obligates. In our study, both grassland obligate and generalist species nested in the restored grassland habitat and successful nests were associated with similar factors that can be easily implemented into current and future restoration projects. 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 perimeter would be a relatively easy management strategy that may help increase reproductive success rates of nesting birds here. Finally, we suggest that nest boxes be re-located to areas of the field that are further from the South River, where their probability of failure may be lower. 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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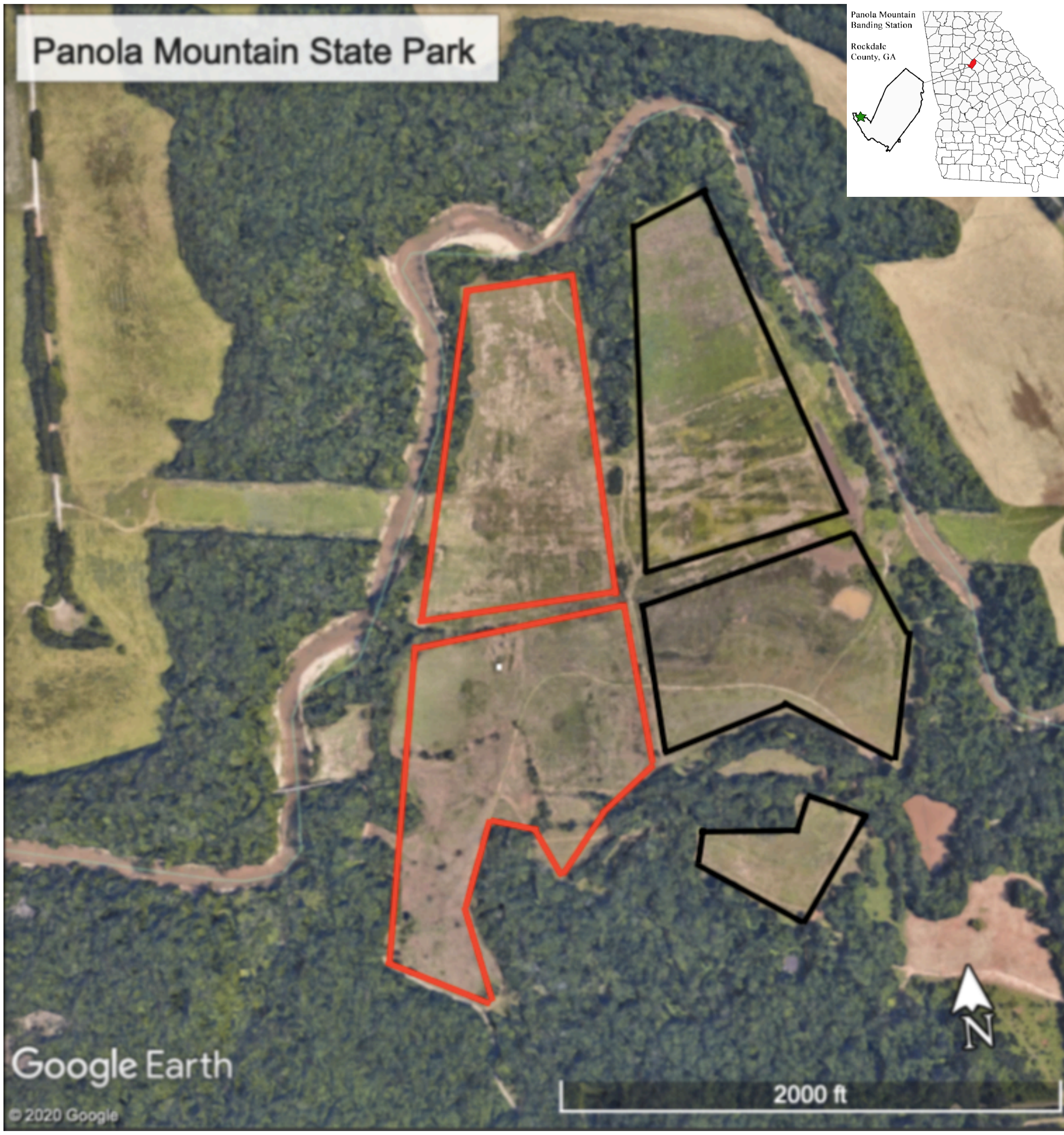

Figure 1: Restoration area of Panola Mountain State Park (PANO) in central Georgia (inset). Five nest searching polygons are outlined in black and red; red portion burned in mid-April 2019.

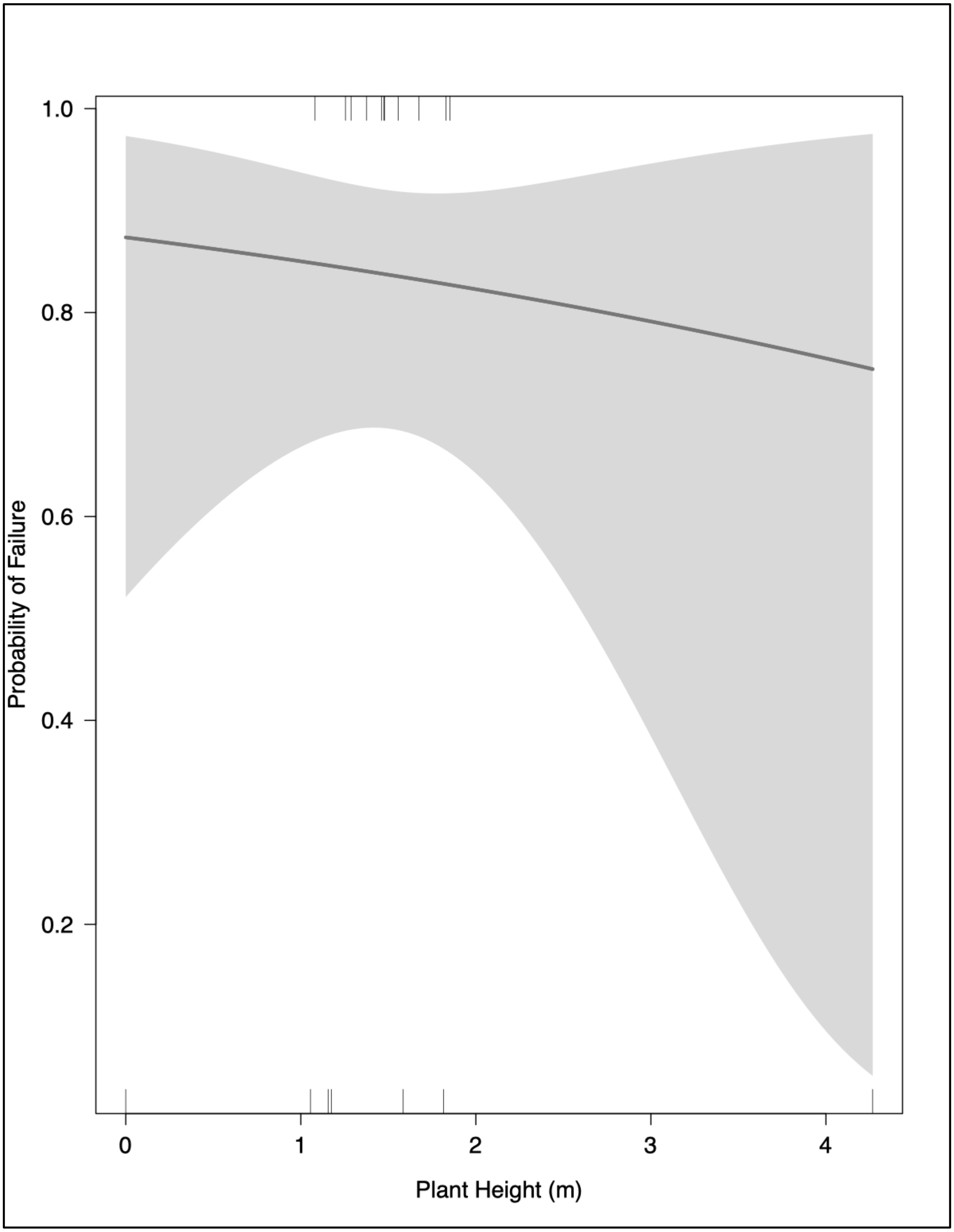

Figure 2: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of plant height of nests in a restored grassland at Panola Mountain State Park from March-August 2019.

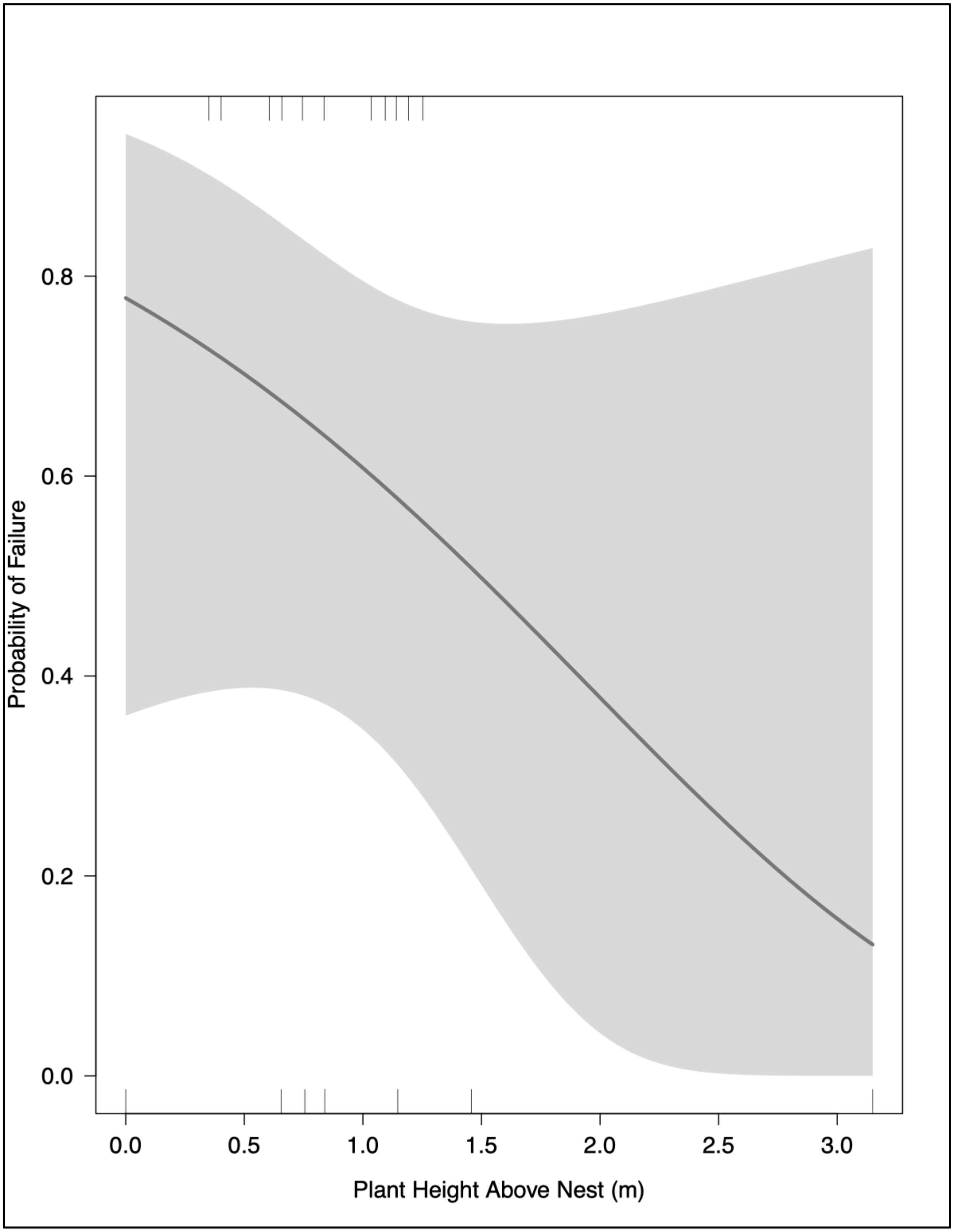

Figure 3: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of plant height above the nest of nests in a restored grassland at Panola Mountain State Park from March-August 2019.

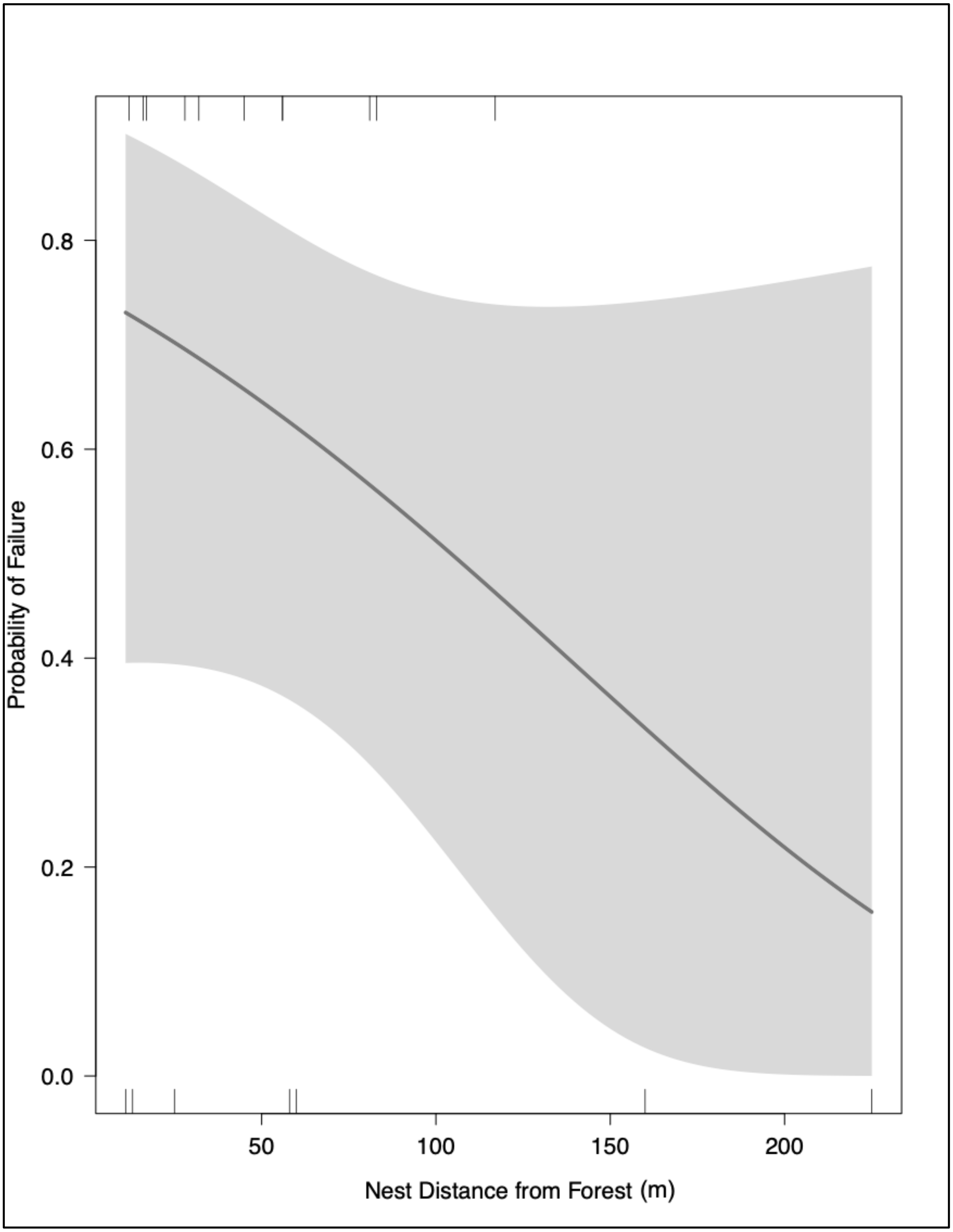

Figure 4: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of nests distance from forest in a restored grassland at Panola Mountain State Park from March-August 2019.

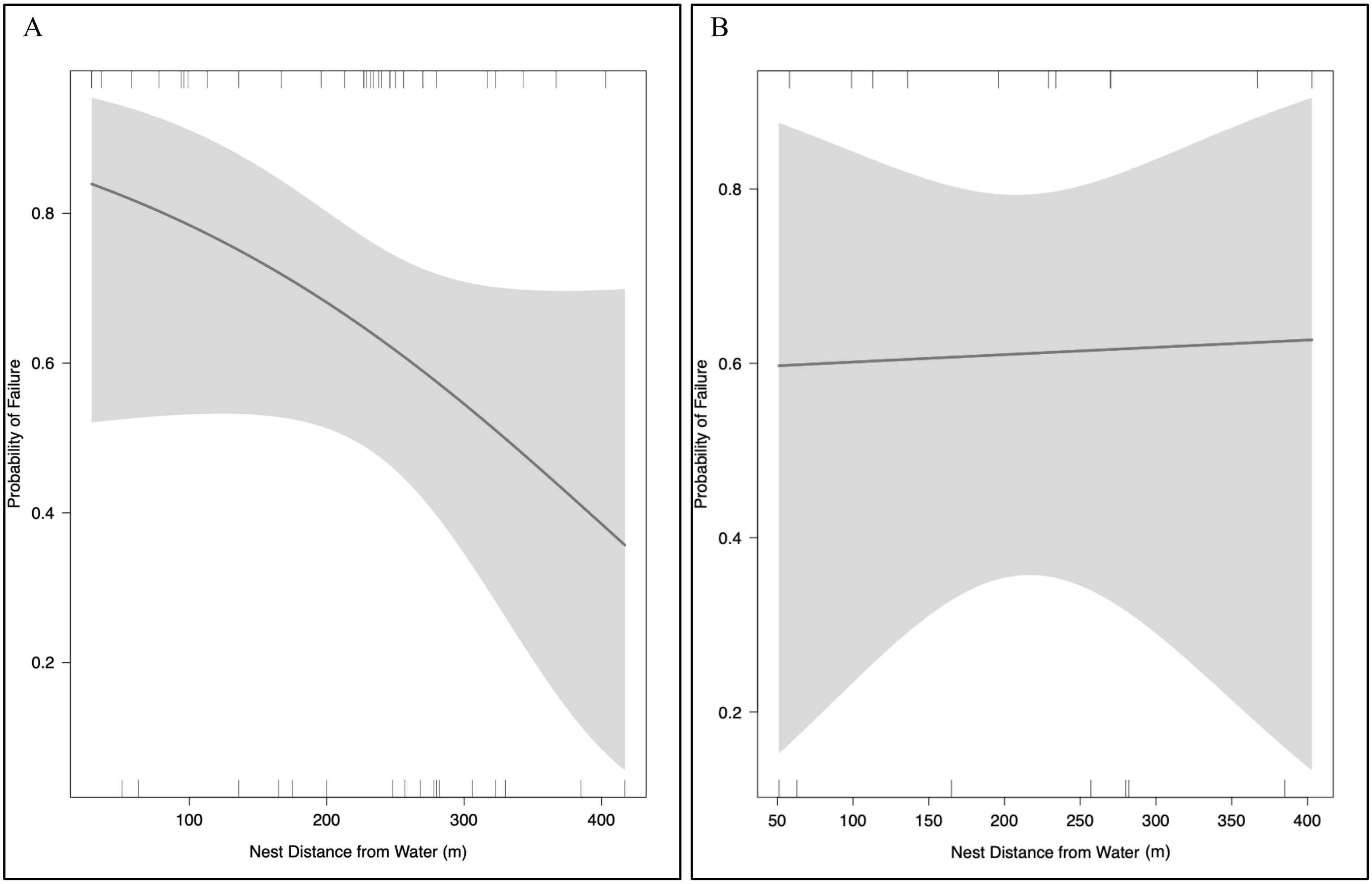

Figure 5: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of distance from water for (A) all nests and (B) open-cup nests in a restored grassland at Panola Mountain State Park from March-August 2019.

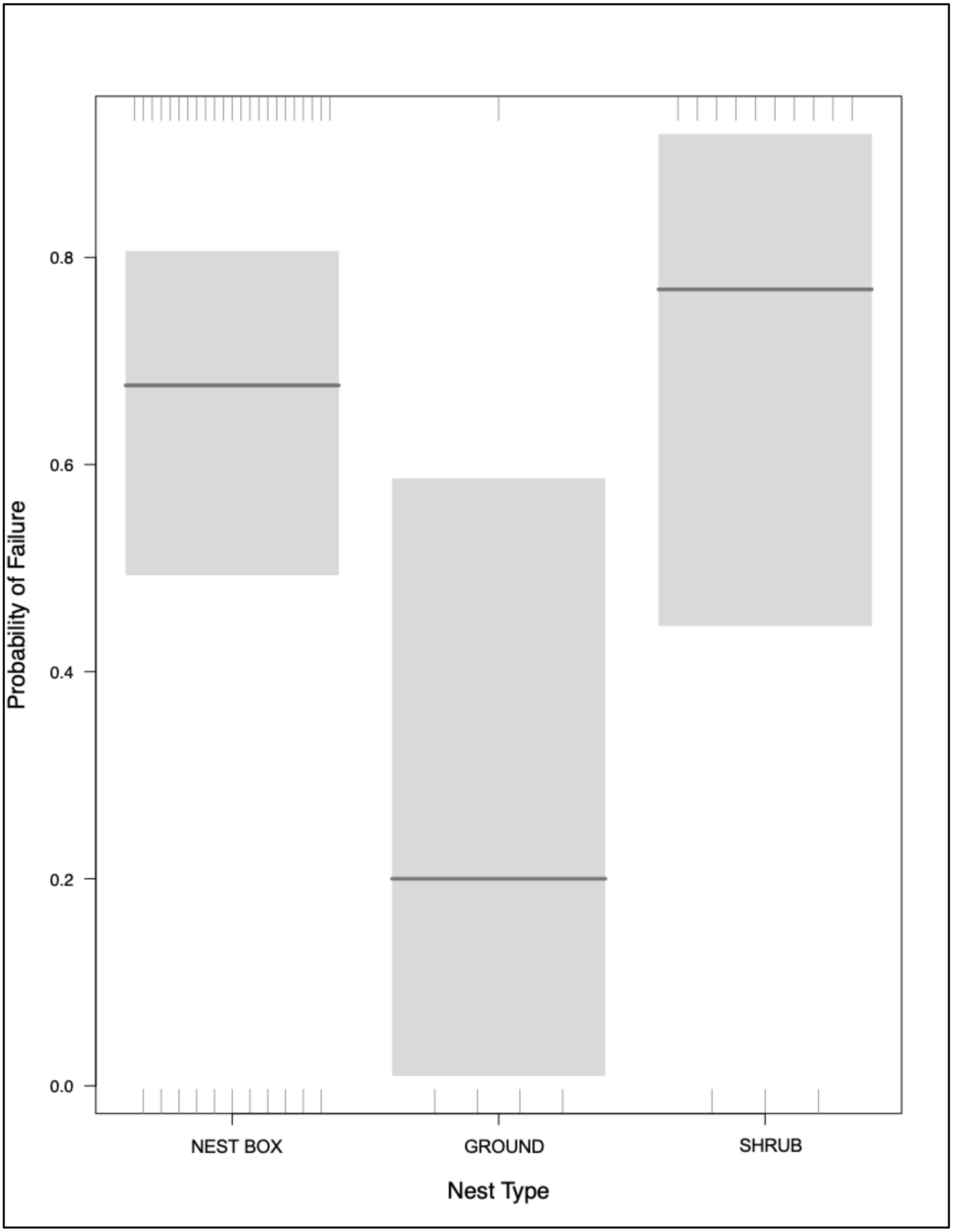

Figure 6: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of nest type of nests in a restored grassland at Panola Mountain State Park from March-August 2019.

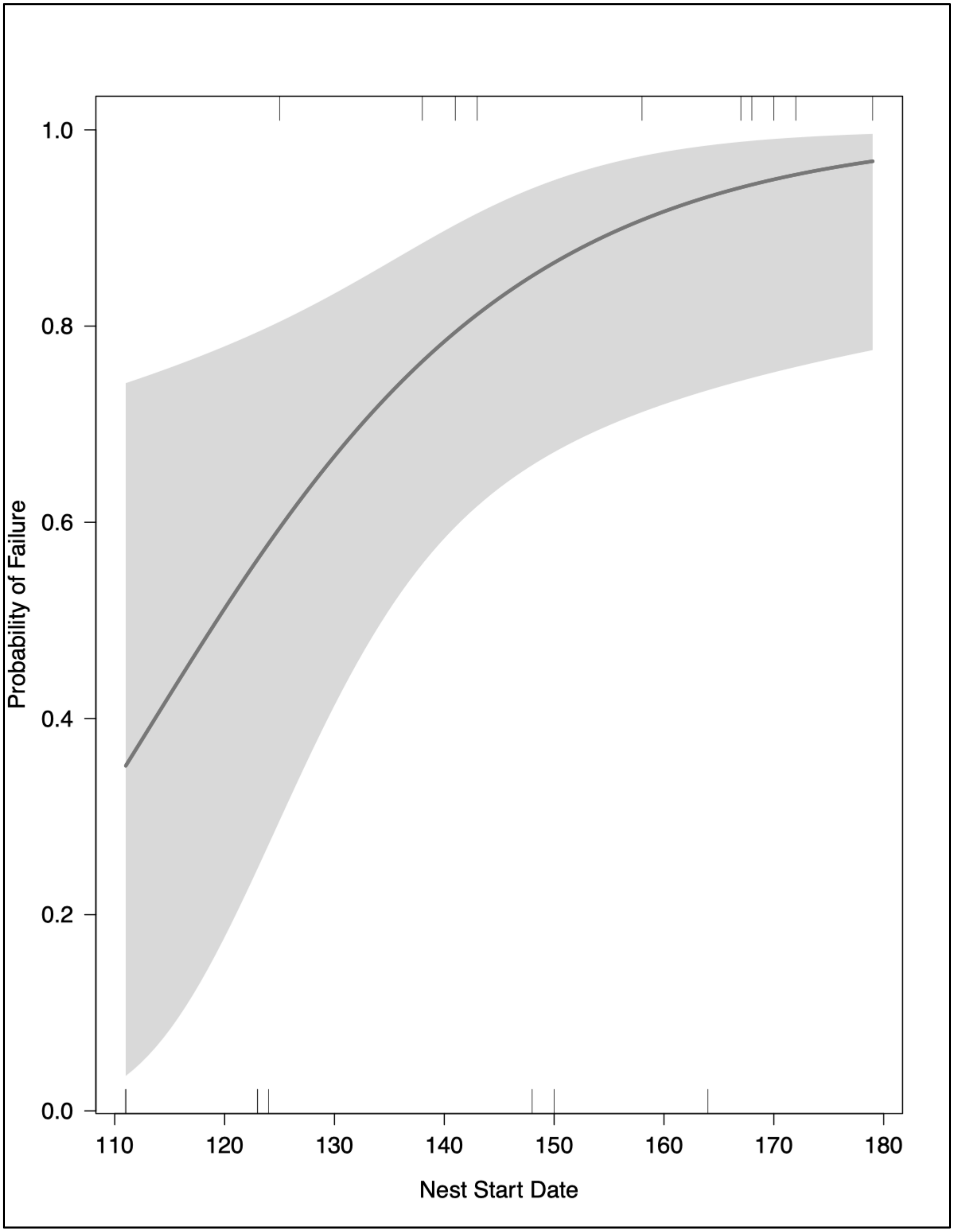

Figure 7: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of Julian start date of nests in a restored grassland at Panola Mountain State Park from March-August 2019.

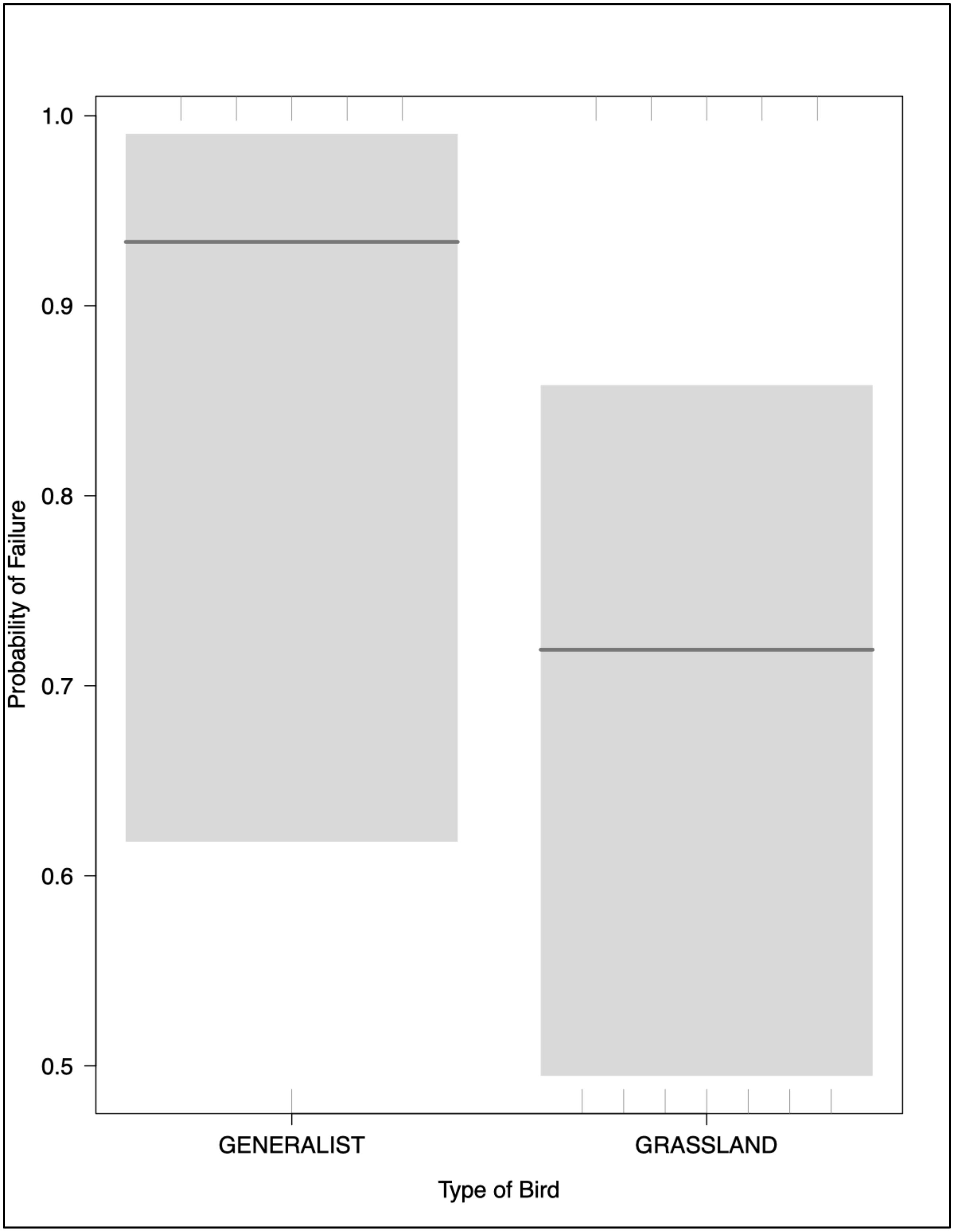

Figure 8: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of type of bird of nests in a restored grassland at Panola Mountain State Park from March-August 2019.

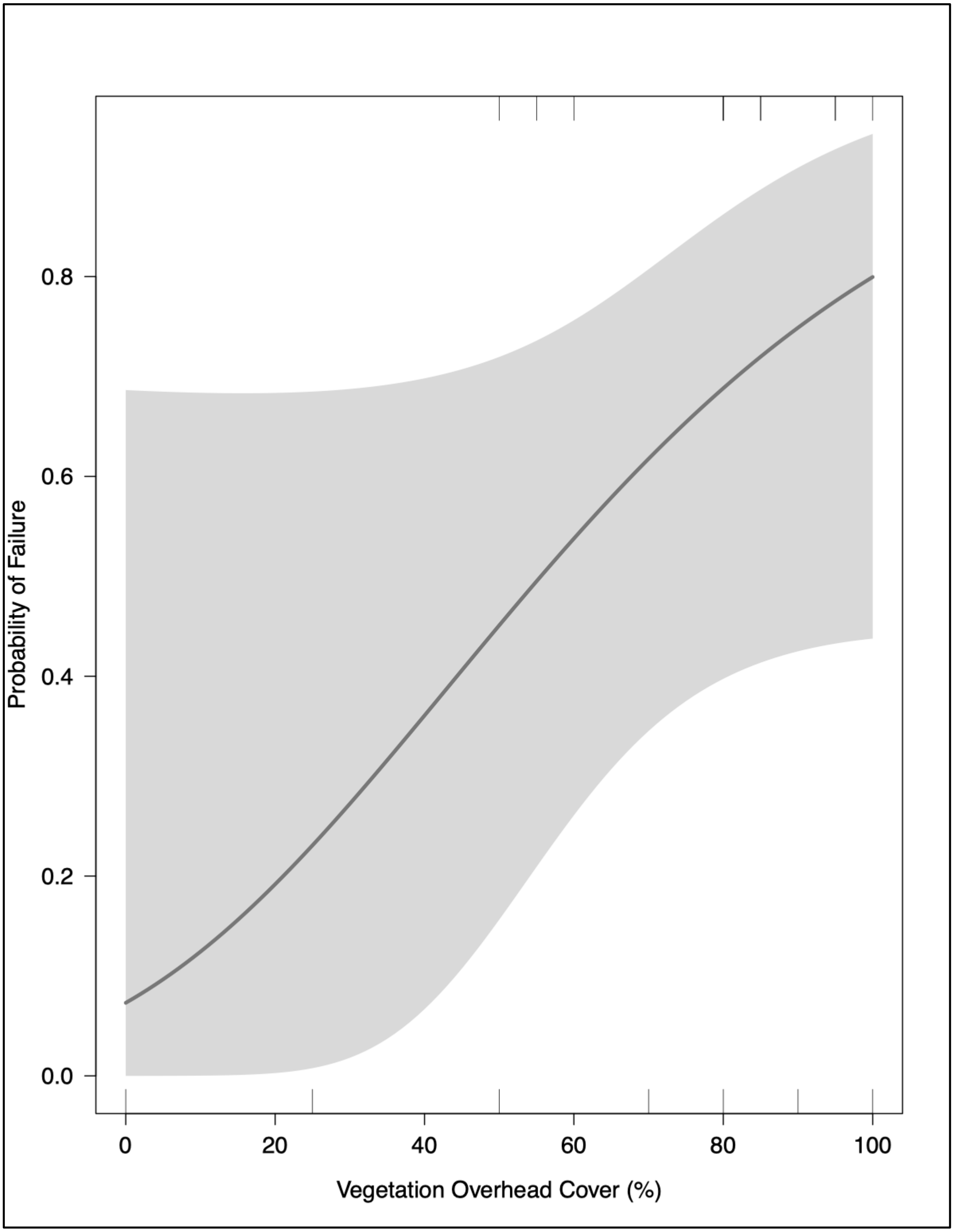

Figure 9: Estimated probability and 95% confidence interval (in grey) of nest failure as a function of overhead vegetation of nests in a restored grassland at Panola Mountain State Park from March-August 2019.

Table 1: AIC model results on nest success of grassland birds (n=13) at Panola Mountain State Park from March-August 2019. Models with ΔAICc < 4 are indicated above the dashed line.

Model[1]	k[2]	AICc[3]	ΔAICc[4]	ω_i[5]
DC+WD	2	50.25	0	0.14
WD+PH	2	50.95	0.70	0.10
Null	1	51.20	0.95	0.089
NT+WD	4	51.87	1.62	0.064
FD+WD	3	52.22	1.97	0.053
WD+PH+DC	3	52.59	2.34	0.044
WD+PH+OC	3	52.64	2.39	0.043
DC+PH	2	52.73	2.48	0.041
NH+DC	2	52.79	2.54	0.040
DC+OC	3	52.84	2.59	0.039
PAN+WD	2	52.90	2.64	0.038
PAN+NT	3	52.96	2.71	0.037
NT+FD	3	53.02	2.78	0.036
WD+FD+PH	3	53.26	3.01	0.031
PH+PAN+NT+WD	5	53.42	3.17	0.029
PH+PAN	2	53.66	3.41	0.026
NT+PH+SD	4	53.69	3.44	0.024
DC+WD+NT	4	53.74	3.49	0.023
PH+NT	3	53.79	3.53	0.022
GRGE+NT+WD	4	54.20	3.95	0.020
PAN+NT+PH	4	54.74	4.49	0.015
OC+NT+FD	4	55.10	4.82	0.013
GRGE+DC+NT	4	55.15	4.90	0.012
OC+DC+CN	3	55.35	5.10	0.011
OC+PH+NT+SD	5	55.66	5.41	0.0090
NT+PH+SD+PAN	5	56.38	6.13	0.0066
PH+PAN+DC+OC	4	57.86	7.61	0.0032
PH+PAN+NT+DC+OC	6	58.45	8.19	0.0024

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#), GRGE: Grassland or generalist bird, NT: Nest Type (Nest box, ground, or shrub).
[2] Parameter of each model
[3]Akaike information criterion corrected for small sample sizes
[4]Difference between AICc values of current model and most supported model
[5]Relative likelihood that a model is the best model

Table 2: Species, habitat type, nest type, percent success, and daily nest survival (DNS) of all nests found at Panola Mountain State Park from March-August 2019.

Species	**Habitat type**	**Nest type**	**% Successful (No. successful/total no. nests)**	**DNS (%)**
Common Yellowthroat	Grassland	Ground	28.57 (2/7)	4.53
Field Sparrow	Grassland	Ground	75.00 (3/4)	18.51
Killdeer	Grassland	Ground	100.00 (1/1)	25.88
Eastern Bluebird	Grassland	Nest Box	33.33 (8/24)	8.76
Red-Winged Blackbird	Grassland	Shrub	0 (0/1)	47.61
Carolina Wren	Generalist	Nest Box	37.50 (3/8)	12.32
Carolina Chickadee	Generalist	Nest Box	0 (0/1)	0.42
Tree Swallow	Generalist	Nest Box	0 (0/1)	36.78
Blue Grosbeak	Generalist	Shrub	0 (0/2)	6.15
Indigo Bunting	Generalist	Shrub	0 (0/2)	27.72
White Eyed Vireo	Generalist	Shrub	100.00 (1/1)	16.15
Total/Average			34.62 (18/52)	18.62

Table 3: Number of nests, fledges, and fledges per nest for each species of A) grassland bird and B) Generalist birds found at Panola Mountain State Park from March-August 2019.

A. Grassland Birds	**No. Nests**	**No. Fledges**	**Fledge/nest**
Common Yellowthroat	7	3	0.428571429
Field Sparrow	4	10	2.5
Killdeer	1	4	4
Eastern Bluebird	24	24	1
Red-Winged Blackbird	1	0	0
Total	**37**	**41**	**1.108108108**
B. Generalists			
Carolina Wren	8	10	1.25
Carolina Chickadee	1	0	0
Tree Swallow	1	0	0
Blue Grosbeak	2	0	0
Indigo Bunting	2	0	0
White-Eyed Vireo	1	2	2
Total	**52**	**53**	**1.019230769**

Table 4: AIC results of the effects of individual characteristics on nest success of grassland birds (n=13) at Panola Mountain State Park from March-August 2019. Characteristics with ΔAICc < 4 (above the dashed line) will be used in future models.

Characteristic[1]	**K**[2]	**AICc**[3]	**ΔAICc**[4]	ω_i[5]
SD	1	49.81	0	0.18
DC	1	50.46	0.66	0.13
WD	1	50.69	0.88	0.12
Null	1	51.20	1.39	0.090
OC	1	51.25	1.44	0.088
NT	3	51.28	1.47	0.086
PH	1	51.40	1.59	0.082
FD	1	52.07	2.27	0.058
NH	1	52.43	2.62	0.049
GRGE	1	52.47	2.66	0.048
PAN	1	53.32	3.52	0.031
CN	1	53.423	3.61	0.030
PT	5	56.35	6.55	0.0069

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#), GRGE: Grassland or generalist bird, PT: Plant type (#), NT: Nest type (Nest box, ground, or shrub).
[2] Parameter of each model
[3]Akaike information criterion corrected for small sample sizes
[4]Difference between AICc values of current model and most supported model
[5]Relative likelihood that a model is the best model

Table 5: Means and standard error (SE) of each characteristic of grassland species and generalist species at Panola Mountain State Park from March-August 2019. None of the variables were significantly different between the two groups (ANOVA).

Characteristic[1]	Generalist sp. mean (SE)	Grassland sp. mean (SE)	F ratio	p-value
SD	144.44 (6.79)	136.06 (4.53)	1.06	0.31
NH	1.30 (0.13)	1.12 (0.84)	1.30	0.26
PH	1.70 (0.12)	1.43 (0.078)	3.55	0.066
PAN	0.38 (0.15)	0.31 (0.10)	0.16	0.69
DC	96.95 (3.51)	93.16 (2.34)	0.81	0.37
OC	94.38 (5.21)	88.06(3.47)	1.02	0.32
FD	48.88 (15.53)	62.22 (10.35)	0.51	0.48
WD	191.44 (25.69)	228.00 (17.12)	1.40	0.24
CN	1.00 (0.073)	1.14 (0.049)	2.48	0.12

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#).

Table 6: AIC results of the effects of individual characteristics on nest success of all birds (n=52) at Panola Mountain State Park from March-August 2019. Characteristics with ΔAICc < 4 (above the dashed line) will be used in future models.

Characteristic[1]	**k**[2]	**AICc**[3]	**ΔAICc**[4]	**ω_i**[5]
SD	1	64.29	0	0.17
GRGE	1	64.42	0.13	0.16
NT	3	64.85	0.56	0.13
DC	1	64.99	0.71	0.12
OC	1	65.35	1.07	0.099
null	1	66.27	1.99	0.063
PAN	1	66.70	2.41	0.051
NH	1	66.72	2.44	0.050
WD	1	67.03	2.75	0.043
SB	6	67.22	2.93	0.039
FD	1	67.64	3.35	0.032
CN	1	68.23	3.94	0.024
PH	1	68.28	3.99	0.022
PT	6	72.03	7.75	0.0035

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#), GRGE: Grassland or generalist bird, SB: Supporting branches (#), PT: Plant type (#), NT: Nest type (Nest box, ground or shrub).

[2] Parameter of each model

[3]Akaike information criterion corrected for small sample sizes

[4]Difference between AICc values of current model and most supported model

[5]Relative likelihood that a model is the best model

Table 7: AIC model results on nest success of all birds (n=52) at Panola Mountain State Park from March-August 2019. Models with ΔAICc < 4 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	2.38	0.15
NT+PAN+PH+WD+GRGE	7	61.15	2.67	0.13
NT+PAN+PH+WD+SD	6	61.34	2.86	0.11
PH+NT+PAN	4	63.56	5.09	0.038
NT+PH+SD	4	63.56	5.09	0.027
OC+PH+NT+SD	5	65.01	13.71	0.018
PAN+NT	3	65.48	7.00	0.014
NT+PH+PAN+SD	5	65.87	7.39	0.012
PH+PAN+DC+OC+NT	6	67.14	8.67	0.0063
DC+WD	2	68.92	10.44	0.0026
NT+WD	3	69.12	10.64	0.0023
Null	1	69.16	10.69	0.0023
PH+NT	3	69.22	10.74	0.0023
PAN+WD	2	69.45	10.98	0.0020
NT+FD	3	69.96	11.48	0.0015
FD+WD	3	70.39	11.92	0.0012
WD+PH	2	71.02	12.55	0.00090
DC+OC	2	71.02	12.55	0.00090
NH+DC	2	71.05	12.58	0.00089
DC+WD+NT	4	71.18	12.71	0.00083
GRGE+NT+WD	5	71.50	13.02	0.00071
OC+NT+FD	4	72.12	13.64	0.00052
PH+PAN	2	72.16	13.69	0.00051
GRGE+DC+NT	4	72.55	14.075	0.00042
OC+DC+CN	3	73.37	14.90	0.00028
PH+PAN+DC+OC	4	75.29	16.82	0.00011

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#), GRGE: Grassland or generalist bird, NT: Nest type (Nest box, ground, or shrub).
[2] Parameter of each model
[3]Akaike information criterion corrected for small sample sizes
[4]Difference between AICc values of current model and most supported model
[5]Relative likelihood that a model is the best model

Table 8: Model averaged parameter estimates ($\hat{\beta}$), standard errors (SE), and odds ratio (95% CI) using all nests computed across all possible models (3062; Burnham and Anderson 2002).

Characteristic[1]	**$\hat{\beta}$ (SE)**	**Odds ratio (CI)**
NT (shrub & nest box - ground)	-0.066 (0.08)	0.93 (0.79, 1.10)
NT (shrub – nest box)	-0.35 (0.14)	0.70 (0.53,0.93)
DC	-0.0014 (0.0036)	0.999 (0.99,1.01)
WD	0.00066 (0.00047)	1.00 (0.99,1.00)
OC	-0.0025 (0.0030)	0.98 (0.99,1.00)
FD	0.00021 (0.00053)	1.00 (0.999,1.00)
NH	-0.14 (0.42)	0.87 (0.38,1.97)
GRGE	0.0031 (0.033)	1.00 (0.94,1.07)
PAN	0.47 (0.42)	1.59 (0.70,3.64)
SD	-0.00064 (0.0013)	1.00 (0.99,1.00)
CN	-0.0082 (0.11)	0.991 (0.80,1.23)
PH	-0.062 (0.40)	0.93 (0.43,2.07)

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#), GRGE: Grassland or generalist bird, NT: Nest type (Nest box, ground, or shrub).

Table 9: Means and standard error (SE) of each variable of nest-box species and cup-nest species at Panola Mountain State Park from March-August 2019. * indicates significant difference with $p < 0.05$ (ANOVA).

Characteristic[1]	**Nest box (SE)**	**Cup nest (SE)**	**F ratio**	**p-value**
SD	135.12 (4.63)	145.28 (6.36)	1.67	0.20
NH	1.50 (0.038)	0.56 (0.052)	212.15	0.001*
PH	1.51 (0.082)	1.52 (0.11)	0.0044	0.95
PAN	0.00 (0.066)	0.96 (0.091)	74.53	0.001*
DC	100.00 (2.01)	83.61 (2.76)	23.12	0.0001*
OC	100.00 (2.69)	71.11 (3.70)	39.84	0.0001*
FD	56.68 (10.70)	60.83 (14.71)	0.052	0.82
WD	218.03 (17.86)	214.33 (24.55)	0.015	0.90
CN	1.00 (0.046)	1.28 (0.063)	12.57	0.0009*

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#).

Table 10: AIC model results on nest success of cup-nest birds (n=18) at Panola Mountain State Park from March-August 2019. Models with ΔAICc < 4 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
PH+NT	3	24.28	2.76	0.069
PH+PAN+NT+WD	5	25.41	3.89	0.040
PH+PAN+NT+WD+FD	6	25.66	4.14	0.035
NT+WD	4	26.02	4.50	0.029
Null	1	26.31	4.79	0.025
NT+PH+SD	4	26.40	4.88	0.024
NT+FD	3	26.54	5.02	0.022
PH+PAN+NT+WD+SD	6	27.70	6.18	0.013
OC+PH+NT+SD	5	28.11	6.59	0.010
PH+PAN	2	28.28	6.76	0.0094
NH+DC	2	28.77	7.25	0.0074
DC+WD+NT	4	28.79	7.27	0.0073
DC+OC	2	28.90	7.38	0.0069
PH+PAN+NT+DC+OC	6	28.90	7.39	0.0069
DC+WD	2	28.94	7.42	0.0068
GRGE+NT+WD	4	29.48	7.96	0.0052
GRGE+DC+NT	4	29.48	7.96	0.0052
OC+NT+FD	4	29.60	8.08	0.0049
PH+PAN+NT+WD+GRGE	7	30.04	8.52	0.0039
FD+WD	3	30.52	9.00	0.0031
PAN+WD	2	30.75	9.23	0.0027
WD+PH	2	31.71	10.19	0.0017
PH+PAN+DC+OC	4	32.04	10.52	0.0014
OC+DC+CN	3	32.11	10.59	0.0014

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#), GRGE: Grassland or generalist bird, NT: Nest type (Nest box, ground, or shrub).

[2] Parameter of each model

[3]Akaike information criterion corrected for small sample sizes

[4]Difference between AICc values of current model and most supported model

[5]Relative likelihood that a model is the best model

Table 11: Model averaged parameter estimates ($\hat{\beta}$), standard errors (SE), and odds ratio (95% CI) using cup nests computed across all possible models (740; Burnham and Anderson 2002).

Characteristic[1]	**(SE)**	**Odds ratio (CI)**
NT(shrub-ground)	-0.27 (0.10)	0.764 (0.624,0.937)
GRGE	-0.0097 (0.048)	0.990 (0.901,1.09)
SD	-0.0079 (0.0037)	0.99 (0.98,0.99)
NH	-0.055 (0.14)	0.576 (0.725,1.235)
PH	0.052 (0.10)	1.053 (0.858,1.293)
PAN	0.28 (0.15)	1.318 (0.984,1.766)
CN	0.0044 (0.067)	1.004 (0.880,1.146)
DC	-0.0012 (0.0025)	0.999 (0.993,1.004)
OC	-0.0013 (0.0020)	0.999 (0.984,0.991)
FD	0.00031 (0.0074)	1.00 (0.986,1.015)
WD	-0.000025 (0.00028)	0.999 (0.999,1.000)

[1]SD: Start date (Julian dates), NH: Nest height (m), PH: Plant height (m), PAN: Plant height above nest (m), DC: Directional cover (%), OC: Overhead cover (%), FD: Distance from forest (m), WD: Distance from water (m), CN: Objects concealing nest (#), GRGE: Grassland or generalist bird, NT: Nest type (Nest box, ground, or shrub).