

CONSERVATION AND LAND MANAGEMENT PRACTICES AND THEIR IMPACT  
ON SUSTAINING BREEDING AND NON-BREEDING GRASSLAND BIRD  
POPULATIONS IN THE SOUTHEAST

by

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Conservation and Land Management Practices and Their Impact on Sustaining Breeding  
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A Dissertation submitted in partial fulfillment of the requirements for the degree of  
Philosophy at George Mason University

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## **DEDICATION**

This dissertation is dedicated to the landowners and citizen scientists of Virginia Working Landscapes.

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## LIST OF ABBREVIATIONS AND SYMBOLS

Occupancy.....	$\psi$
Detection.....	$p$
United States.....	US
Native warm-season grasses.....	WSG
Cool-season grasses.....	CSG
Breeding Bird Survey.....	BBS
Virginia Working Landscapes.....	VWL
Partners in Flight.....	PIF
Virginia Quail Recovery Initiative.....	VQRI
Normalized Difference Vegetation Index.....	NDVI

## ABSTRACT

### CONSERVATION AND LAND MANAGEMENT PRACTICES AND THEIR IMPACT ON SUSTAINING BREEDING AND NON-BREEDING GRASSLAND BIRD POPULATIONS IN THE SOUTHEAST

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Birds that depend on grass and shrubland habitats for survival are experiencing a greater decline than any other avian assemblage in North America. Habitat loss and degradation on both breeding and wintering grounds are among the leading causes of these declines, though research on wintering bird communities throughout the Americas is limited. In my dissertation I explored the response of breeding and wintering grassland bird communities to conservation and land management in the eastern US. Using point count survey data collected through a regional citizen science program, Virginia Working Landscapes, I used statistical models to predict breeding grass and shrubland bird abundance based on habitat and landscape composition. Shrubland birds exhibited increased densities in fields managed through the Virginia Quail Recovery Initiative, a targeted habitat program directed towards the conservation of Northern Bobwhites (*Colinus virginianus*). In contrast, grassland-obligate avian species exhibited higher

breeding densities in fields managed as hayfields and pastures. Results indicate that quail habitat management can be promoted as a tool to conserve habitat for early successional songbirds, but not grassland species. However, grassland fragmentation may be influencing the response of grassland birds to quail management and therefore requires further investigation. To explore how these habitats influence avian communities during the non-breeding period, I used transect data to identify differences in wintering species diversity between fields comprised of native warm-season grasses (WSG) and fields comprised of non-native cool-season grasses (CSG). WSG fields had higher species diversity than CSG fields. In addition, timing of field management influenced bird communities, with fields managed in summer or fall months exhibiting lower avian abundance than those managed in the winter or not at all. For my final chapter, I used data collected from a national citizen science program, eBird, to create an occupancy model for a declining grassland bird, the Loggerhead Shrike (*Lanius ludovicianus*). The occupancy model revealed important species-environment relationships that can be used to predict shrike occurrence throughout the southeastern portion of the US. Though open country habitats were the main driver of occupancy year-round, seasonal changes in distributions were driven by temperature and percent forest cover in the landscape, indicating a potential tradeoff of predation risk for increased cover from harsh weather in winter. The results of this work demonstrate how conservation and land management influence avian communities in eastern grasslands on multiple spatial scales during breeding and non-breeding seasons. These findings can be used to improve best

management practices of grasslands to optimize habitat quality for declining species throughout the full annual cycle.

## CHAPTER ONE : INTRODUCTION

In recent decades North America's grassland birds, which are defined as any bird species that require grassland habitat for survival (McCracken 2005), have declined in numbers and extent more than any other guild of bird species. Results from the North American Breeding Bird Survey (BBS) have shown declines in 32 of 37 North American grassland-associated species between 1966 and 2004 (Sauer et al. 2005). Research attributes these declines with the degradation and loss of grassland habitat on breeding and wintering grounds (Noss et al. 1995) and land use changes associated with intensification of agriculture (Masse et al. 2008). These factors are exacerbated by broad-scale threats such as climate change and increasing energy demands (North American Bird Conservation Initiative 2013). Although native, intact grasslands are idyllic for grassland bird conservation, most remaining grassland habitat is human-managed for economic benefits for private landowners. Given the steep declining population trends of grassland birds it is imperative that conservation research address these habitats, and their dependent species, and facilitate a more practical model of human-habitat relationships.

Private lands are important for conservation of grassland birds in North America as they comprise 85% of grasslands (including both pastures and prairie) (North American Bird Conservation Initiative 2013). In North America, 29 grassland-obligate avian species are distributed on private lands for the majority of their breeding range; 7 of

which are distributed on private lands for more than 90% of their breeding range (North American Bird Conservation Initiative 2013). Successful conservation of grassland birds depends largely on decisions made by private landowners, and conservation managers may miss important learning opportunities due to minimal access to private lands (Hilty & Merenlender 2003). As a result, several organizations are acknowledging this gap by placing more effort on private land conservation through landowner education and outreach, citizen science and habitat incentive programs (e.g. see Hilty & Merenlender 2003; Heath et al. 2008; Swallow et al. 2012). For example, Virginia Working Landscapes (VWL; [www.VAWorkingLadscapes.org](http://www.VAWorkingLadscapes.org)), a conservation initiative in Northern Virginia, works with landowners to promote biodiversity and wildlife habitat amongst working landscapes on both public and private land. To better understand how regional land management practices influence biodiversity, the program works with citizen scientists to monitor biodiversity and land management techniques on private and public properties throughout a 16-county region. Therefore, VWL offers a unique opportunity to understand the influences of private land management on bird communities in eastern U.S. grasslands.

Despite decades of research on habitat needs of breeding birds, there has been limited attention directed towards the non-breeding season (Marra et al. 2015a). For grassland birds in particular, it is speculated that the loss and degradation of habitat on wintering grounds is one of the main contributors to the observed declines (Brennan et al. 2005a), though few studies explore grassland habitats outside of the breeding season (Hovick et al. 2014). There are several challenges associated with surveying non-

breeding birds that have likely contributed to the reduced research attention. Inclement weather makes conducting surveys impractical, birds almost never vocalize during the non-breeding season, and flushing birds are hard to identify (Fletcher Jr et al. 2000). Nonetheless, multiple methods have been employed to survey winter bird communities in the south- and mid-west (e.g. see Gutzwiller 1991, 1993; McMellen & Schweitzer 2005; Twedt et al. 2008; Heath et al. 2008; Hovick et al. 2014; Saalfeld et al. 2016) with eastern grassland habitats essentially ignored. With species assemblages, land use patterns and environmental features differing by ecoregion, it is essential to fill this information gap to better understand how management of eastern grasslands impacts over-wintering species.

Species-environment relationships are important for generating best management practices and identifying conservation priority areas for declining species. Though habitat-specific relationships can reveal important information on species requirements, habitat selection is a process that occurs on multiple spatial and temporal scales (Vistnes & Nellemann 2008). For example, habitat is selected at the scale of a species' range, a home range of a particular population, a breeding territory, and even resource selection within that territory, such as a nesting site (Esely Jr & Bollinger 2001). On the other hand, temporal habitat selection is based off of differences between seasonal and daily decisions, such as changes in foraging opportunities and predation risk (Mayor et al. 2009). Ultimately, spatial and temporal scales are inextricably linked, and both require attention when exploring species distributions for conservation planning. These considerations have been explored through multi-season occupancy models (Norris et al. 2004; Norris & Marra 2007; Studds & Marra 2007; Marra et al. 2015) but have lacked



attention in grassland species. However, habitat needs should be explored at multiple spatial and temporal scales to optimize conservation opportunities for grassland birds.

The overall objective of my research was to explore how conservation and land management influenced grassland habitat structure and to determine impacts on grass and shrubland-dependent species (hereafter referred to as grassland birds). I used VWL properties to collect data on grassland bird diversity and abundance on local grasslands during two annual events - breeding (Chapter 2) and wintering (Chapter 3). In Chapter 2, I used citizen science data collected on VWL properties during the breeding season to explore how habitat management plans recommended for the conservation of Northern Bobwhite (*Colinus virginianus*) impacted non-target grassland species. This chapter aimed at identifying how conservation initiatives can influence bird communities and can be used by conservation managers to promote the implementation of such programs for a broader suite of grassland species. In Chapter 3 I utilized private lands obtained through the VWL program to compare grassland bird associations in fields comprised of native or introduced grasses during winter to explore benefits of field structure on supporting over-wintering species. This chapter identified important winter habitat needs and used the results to make inferences about optimal management practices for over-wintering species in eastern grasslands. In Chapter 4 I combined information learned in the first two chapters about essential habitat-scale features with landscape-scale features to create an occupancy model for a declining grassland bird, the Loggerhead Shrike (*Lanius ludovicianus*) in breeding and non-breeding seasons. This chapter took a landscape approach by using national-level citizen science data ([www.eBird.org](http://www.eBird.org); Sullivan et al.

2009) to identify broad-scale species-environment relationship that drive occupancy of this species throughout the southeastern United States. The output maps resulting from this chapter can be used to facilitate population-monitoring studies, identify conservation priority areas and to locate new populations while serving as a model for use in other species. Results of this dissertation demonstrate the importance of full annual cycle research for understanding habitat needs, identify impacts of private land management on breeding and non-breeding avian communities, and demonstrate the use of citizen science data in conservation research and planning.

## **CHAPTER TWO : THE UTILITY OF QUAIL MANAGEMENT PLANS FOR CONSERVING NON-TARGET SPECIES**

### **Introduction**

Grasslands are the most endangered terrestrial ecosystem in North America (Samson & Knopf 1994; Henwood 2010). Decline in grassland quantity and quality has been attributed to habitat loss and fragmentation (Herkert 1994; Cully et al. 2003) due to conversion to cropland (Rashford et al. 2011), energy and mining development (Petersen et al. 2016) urbanization (Jarzyna et al. 2016), and improper livestock management (Brockway et al. 2002). As a result, birds associated with grassland and grass-shrub habitats (hereafter referred to as grassland birds) have exhibited the most significant decline among birds in North America (Reif 2013). Though the causes of these declines vary nationwide, reforestation and habitat fragmentation intensify the declines observed in the eastern United States (Brennan, Kuvlesky & Morrison 2005). These landscape changes have created a lack of early successional and old field habitats within a landscape fragmented by roads, development, intensive agriculture, and forest (Jarzyna et al. 2016).

Due to widespread recognition of grassland habitat loss and degradation, a substantial funding base exists for the conservation, restoration and management of select grasslands in the United States. For example, U.S. Department of Agriculture (USDA) Farm Bill conservation programs have resulted in increased conservation practices on

agricultural lands, marginal cropland, and wetlands (Ciuzio et al. 2013). Conservation planning for birds in North America is more advanced than for any other vertebrate group (Ciuzio et al. 2013) and private land-use decisions to benefit birds are enhanced by the availability of financial incentive programs and conservation plans that set habitat goals for specific groups of birds. This is particularly true for conservation plans focused on game species, such as waterfowl or upland game birds (Heffelfinger et al. 2013).

The National Bobwhite Conservation Initiative (NBCI) facilitates habitat restoration for the Northern Bobwhite (*Colinus virginianus*) in 25 states by connecting landowners to information and incentive programs administered by state agencies. For example, the Virginia Quail Recovery Initiative (VQRI; [www.VAQuail.com](http://www.VAQuail.com)) has created and/or maintained 33,800 acres of quail habitat, written over 1,900 quail habitat management plans for private landowners (Puckett 2017, pers. communication), and helped distribute more than \$4.3 million in habitat management incentive funds (Puckett et al. 2015). The primary habitat management action of these initiatives is the restoration of native warm-season grasses (WSG) that provide ground-dwelling bird species with the needed bare ground and overhead cover that is missing from non-native cool-season grasses (CSG) (Moorman et al. 2017). When WSG conversion is not feasible, the VQRI recommends adding field borders to the edges of croplands or idling fields (Burger 2001). Field borders are created through the retention or re-planting of vegetation along tree lines or hedgerows and have been shown to increase avian diversity and abundance in agricultural landscapes (Heath et al. 2017). In the absence of WSG or field borders, idle

grasslands can provide suitable habitat, although field quality can vary substantially depending on the type and density of grasses (Washburn et al. 2000).

While other species-targeted conservation programs have observed benefits to species co-occurring in focal habitats (e.g., Hanser & Knick 2011; Swallow *et al.* 2012), there has not been a thorough assessment of the effects of quail habitat initiatives on non-target bird species in eastern grasslands. Although quail populations in Virginia have continued to decline over the past decade, habitat enhancement efforts may be benefitting other grassland species (Puckett et al. 2015). There is precedence for this view, as Northern Bobwhites are an umbrella species for declining grassland bird species in Oklahoma (Crosby et al. 2015a). In the Oklahoma study, bobwhite occupancy in fields was a predictor for occupancy of nine grassland bird species, five of which also occur in Virginia. However, Crosby et al. (2015a) investigated occupancy of grassland species in relation to quail occupancy, and did not directly measure habitat type or quality.

The definition of “grassland species” ranges from grassland-obligate species to those more prevalent in shrub habitat. This range of habitat preferences makes it difficult to create single management prescriptions that benefit all grassland birds. Several grassland-obligate species are sensitive to landscape contiguity whereas other species are more sensitive to proximate features, such as shrub and tree cover (Cunningham & Johnson 2006). While the VQRI has identified priority areas that promote landscape-scale contiguity, its management recommendations focus primarily on proximate habitat-scale features such as WSG establishment, shrub cover, field borders and idling land (Puckett et al. 2015). These site-specific management recommendations may limit the use

of restored fields by some grassland species. While there is growing recognition that the landscape features beyond field-specific management can affect habitat use, most research focusing on WSG restorations, and their impact on bird communities, has been conducted in the northern tallgrass prairie region (Bakker et al. 2002; Cunningham & Johnson 2006; Davis et al. 2013). Therefore, relatively little is known about the responses of grassland birds to WSG in eastern regions, where late successional fields and fragmentation are prevalent. Moorman *et al.* (2017) recently found that WSG fields in North Carolina are not a better alternative to CSG for grassland birds, but are better for shrubland birds. However, Moorman *et al.* (2017) only considered two species from each guild and did not investigate the effects of landscape composition. Also, to my knowledge, no study has quantified the potential benefits of idle land compared to WSG restorations, both recommended quail management practices.

My objective was to quantify the response of breeding grassland species to a conservation initiative (VQRI) designed for a single species - Northern Bobwhite. I evaluated how the density of 12 grassland bird species varied in response to field structure and composition, along with a suite of landscape and habitat variables. I compared grassland bird communities in WSG fields (hereafter referred to as wildlife fields), idle fields, and agricultural fields dominated by CSG (including pastures and hayfields but excluding croplands). Based on previous studies (Cunningham & Johnson 2006; Ribic et al. 2009; Moorman et al. 2017) I hypothesized that not all species would respond positively to wildlife fields, as species-specific habitat preferences will vary along with landscape and habitat effects. Specifically, I predicted that idle and wildlife

fields would support a higher density of grassland species associated with early successional and shrub-scrub habitats, while larger fields (regardless of management), would support a higher density of grassland-obligate species.

## **Methods**

### **Study Area**

This study was conducted during four breeding seasons from 2012 – 2015 on 39 public (n=6) and private (n=33) properties across a 16-county region in Virginia, US (Figure 2.1). The private field sites were acquired and surveyed through Virginia Working Landscapes (VWL), a conservation initiative convened by the Smithsonian Conservation Biology Institute (SCBI) in Front Royal, VA ([www.vaworkinglandscapes.org](http://www.vaworkinglandscapes.org)). This 16-county region is characterized by rolling hills of igneous and metamorphic bedrock with stretches of karst geology throughout the western portion (Hyland 2005). The center of the study region is intersected by Shenandoah National Park along the Blue Ridge Mountains. The land cover is dominated by eastern temperate deciduous forest with grasslands comprising approximately 30% of the study region (National Land Cover Database 2011). Most grasslands are comprised of mostly non-native cool season grasses such as tall fescue (*Schedonorus arundinaceus*), Kentucky bluegrass (*Poa pratensis*) and orchard grass (*Dactylis glomerata*). Fields converted to WSG contained a mix of grasses (e.g., big bluestem (*Andropogon gerardi*), switchgrass (*Panicum virgatum*) and Indiangrass (*Sorghastrum nutans*)) and forbs (e.g., asters (*Symphyotrichum sp.*), monarda (*Monarda sp.*), milkweeds (*Asclepias sp.*). Idle fields generally contained a variable mix of non-native CSG, with some portion of WSG,

as well as native and non-native forbs and shrubs. Average annual temperature for the entire study area ranged between 8°C and 20°C the average annual precipitation was 112.5cm (NOAA 2017).

### **Field Methods**

Field sites (n=57) were at least eight contiguous hectares of grassland and were divided into three management categories: 1) Wildlife (n=21); 2) Agriculture (n=21); or 3) Idle (n=12). Wildlife fields were managed to maintain a mix of WSG and forbs. Seventeen of the 21 wildlife fields were established and/or managed as part of the VQRI, while the remaining properties managed fields according to VQRI recommendations by burning, disking and/or selective herbicide application on a rotational basis. Agricultural fields were dominated by CSG and were managed by continuous or rotational grazing and/or by mowing (hay) at least twice annually. Idle fields were defined as any field in an early successional stage that had not been converted to WSG and was not actively managed by grazing, mowing or other means on an annual basis. Each survey field had a cluster of three sampling points, to anchor bird and vegetation surveys, which were a minimum of 100 m from field edges and 200 m from one another. If a property contained more than one survey field, adjacent survey clusters were separated by  $\geq 400$  m to reduce the probability of double-counting birds between survey fields (Davis et al. 2013).



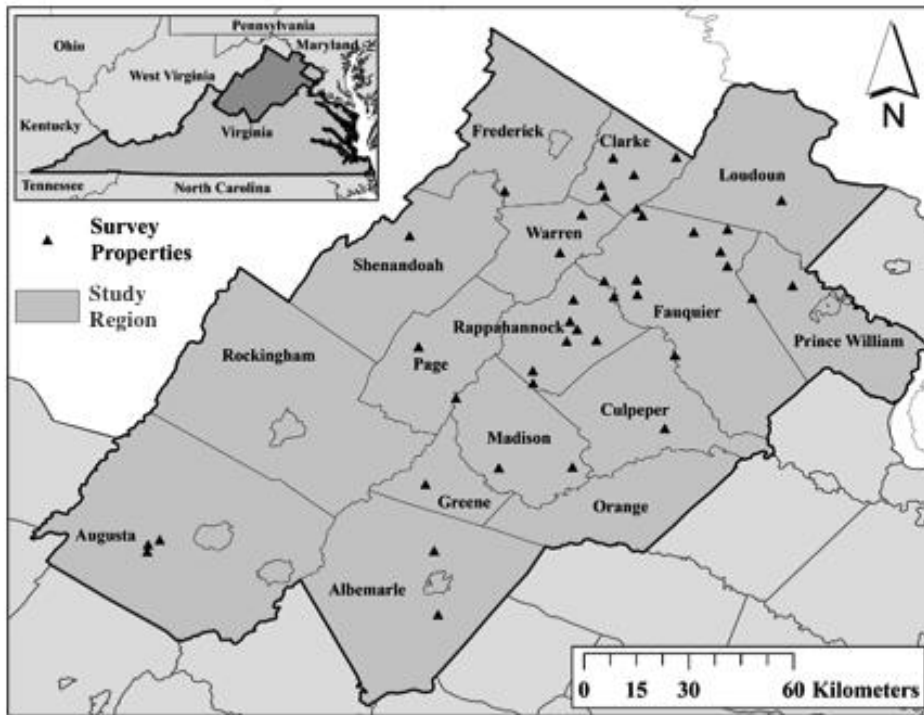


Figure 2.1. Locations of survey properties in Northern Virginia, 2012-2015. Labels are county names. Survey fields were selected opportunistically through a landowner network convened by Virginia Working Landscapes ([www.VAWorkingLandscapes.org](http://www.VAWorkingLandscapes.org)). Survey fields are a minimum of 20 contiguous acres. Each survey field contains 3 point count stations at least 200 m apart.

Approximately 50 volunteers were recruited each year to assist with bird and vegetation surveys. Volunteers were required to attend a 3 hr training session each year that explained the bird and vegetation survey protocols. Bird survey training also included field training and an annual quiz that tested surveyors on their ability to identify grassland birds by sight and sound. Volunteer birders obtaining >90 % accuracy on the annual quiz were assigned two fields per year (six point count stations) and were paired with a novice birder as a scribe.

### **Bird Surveys**

Each field was visited three times by volunteers and once by me, with each visit at least 7 days apart, between 15-May and 30-Jun of each year. Point counts were 10 minutes in length and conducted by a single observer with one scribe between 30 min before sunrise until 3 hr after sunrise (range: 0500-0900 EST) on mornings with no precipitation and wind speeds less than <20 km/hr (Gabrey et al. 1999). Surveyors used a fixed-radius method with distance bands at 0-50 m and 50-100 m. We calculated the detection probability of each species based on their distance from surveyor (Selmi & Boulinier 2004). All birds seen and heard within the survey radius were recorded and observers tracked the movement of individuals to ensure birds were not double counted within and among points. Birds observed as flyovers, beyond 100 m, and before and after the survey period were recorded as incidentals and not included in the analyses. Temperature, observer, date, time, wind speed and cloud cover were also recorded for each site visit as covariates of detection.

### **Vegetation Surveys**

Vegetation was sampled once between 1 and 30 June and again between 1 Aug and 31 August to account for the seasonal growth of both cool and warm season grasses. Seven 1 m<sup>2</sup> plots were surveyed at each of the three survey stations within a field. Plots were located at randomly chosen distances from 1 to 100 m in each cardinal direction from the bird survey point, with the heading of some lines altered to stay within the field confines. Percent cover of soil, rock, duff, and vegetation was visually estimated for each plot and recorded. All vegetation within each plot was identified to species, with unknown species collected, pressed and later identified with the assistance of botanists.

Percent shrub cover was estimated by measuring the size of all shrub patches within 100m radius of each point count station and calculating a percent total shrub cover within each point count circle. For the purpose of this study, shrubs were defined as woody vegetation < 2m height. Total number of trees present (if any) in each point count circle was also recorded as well as utility poles, fence posts and other perching features. Vegetation height was estimated by bird surveyors as short (<0.5m), medium (0.5m-1.0m) or tall (>1.0m) at the beginning of each point count survey.

### **Statistical Analysis**

I included year as a covariate in my models and each annual survey for a specific field was considered an independent survey because some sites were managed differently in different years, and because a number of the sites were not surveyed in all 4 years of the study.

Site-level covariates were calculated using the means of all variables for each field including native forb richness, proportion of native to non-native grasses, and percent shrub cover (Table 2.1). Landscape-level covariates were created by quantifying the percentage of grassland, open and forest habitats within 1 and 5-km radius buffers drawn with ArcGIS using the National Land Cover Database (NLCD, 2011). The grassland category was comprised of the NLCD categories of grassland/herbaceous, shrub/scrub and pasture/hay. Open landscape was created by combining NLCD categories of grassland/herbaceous, shrub/scrub, pasture/hay, cultivated crops and developed open space. The forest category was created by combining NLCD categories for deciduous, evergreen and mixed forest layers. For comparison among variables and

across species, I standardized covariates by centering on the mean and scaling by one standard deviation. I examined the correlation between covariates using Spearman's rank correlation coefficient. If any two variables had a correlation  $\geq 0.7$ , the most biologically relevant variable (based on our review of the literature) was kept in the model and the other discarded. Vegetation structure and landscape attributes ( $n=11$ ) were compared between field types using one-way analysis of variance (ANOVA). With significant ANOVA results ( $P < 0.01$ ), I calculated Tukey post-hoc pairwise comparisons to determine significant differences between groups. To account for multiple testing, I used the Bonferroni correction and considered significant only those covariates for which  $P < 0.05/11 = 0.004$ .

### **Modeling Density**

Bird density at each point count station was estimated using a multinomial N-mixture model (Royle 2004), which uses repeated counts to account for detectability. This model assumes a three-stage stochastic process. The first process accounts for the count data in relation to the habitat and landscape variables (Kéry et al. 2005). The second process accounts for the probability of birds being available for detection and included survey-specific variables (Table 2.1; Julian day, minutes after sunrise, wind intensity, and temperature). Year was also included as a covariate as not all sites were sampled the same years. The third process accounts for probability of detection (Royle et al. 2005) and included variables that would affect an observer's ability to detect a bird (Table 2.1; time of day, date, vegetation height, percent obstruction and wind intensity). I modeled density for all species detected on at least 10% of sites using the negative

binomial distribution to account for over-dispersion (Chandler et al. 2011). I ranked and compared all models using Akaike's Information Criterion (AIC, Akaike, 1974) and models having a difference of  $\leq 2$  AIC units were considered equally parsimonious (Burnham & Anderson 1998).

Table 2.1. List of variables included in the models for 12 grassland bird species. Sample size for categorical covariates is reported in the range column. Standard error (SE) of the mean for continuous variables is reported in parentheses.

Density submodel	Range	Mean (SE)
<i>Habitat Covariates</i>		
Site description; categorical	Agriculture: 99, Idle: 72, Wildlife: 93	
Total number of forb species per field ( surveyed in 21m <sup>2</sup> per field)	2 - 48	18.33 (0.60)
Percent of all grasses that are native per field	3.4 - 100	46.83 (1.64)
Mean percent grass cover of all surveyed plots per field	6.28 - 99.30	43.95 (1.25)
Average height of dominant vegetation	1: <0.5m, 2: 0.5-1.0m, 3: >1.0m	
Woody species cover (% of 100 m diameter circle)	1 - 45	22.23 (0.83)
<i>Landscape Covariates</i>		
Percent grassland within 1km	0 - 85	42.24 (1.21)
Percent grassland within 5km	0.7 - 72	36.39 (1.10)
Percent forest within 1km	2.2 - 88.5	44.00 (1.31)
Percent forest within 5km	15.2 - 94.5	50.10 (1.14)
Percent open space within 1km	8.5 - 96.7	51.75 (1.25)
Percent open space within 5km	5.2 - 83.8	46.02 (1.10)
<i>Availability submodel</i>		
Day of year (January 1 <sup>st</sup> = Day 1)	135 - 181	157.19 (0.14)
Time since sunrise (min)	-15 - 198	89.33 (0.55)
Wind intensity (MPH) scored according to the Beaufort Scale; categorical	0: no wind, 1: 1-3, 2: 4-7, 3: 8-12, 4: 13-18, 5: >18	
Temperature at beginning of point count (°C)	7-29	18.56 (0.04)

Year of study; categorical	2012: 60, 2013: 81, 2014: 60, 2015: 63	
<hr/>		
Detection submodel		
Day of year (January 1 <sup>st</sup> = Day 1)	135-181	157.19 (0.14)
Time since sunrise (min)	-15 - 198	89.33 (0.55)
Average dominant vegetation height at each point measured at each visit	1: <0.5m, 2: 0.5-1.0m, 3: >1.0m	
Wind intensity (MPH) scored according to the Beaufort Scale; categorical	0: no wind, 1: 1-3, 2: 4-7, 3: 8-12, 4: 13-18, 5: >18	
<hr/>		

I developed my models in 3 stages as previously described by West et al. (2016). First, I examined field type along with detection and availability covariates and compared my results to null models to determine if site-level management influenced density and to identify factors affecting availability and detection. I used the best-fit set of availability and detection covariates in all subsequent models of density. Second, I added field-level vegetation metrics to the top models from the first stage. Third, I added landscape-level metrics to the top models from the second stage. I examined the beta estimates from the highest ranked models to determine the direction and strength of the relationship between species density and model parameters. I assessed model fit using a parametric bootstrapping approach (Kéry et al. 2005) in which I compared the observed sum of the squared residuals to its expected sampling distribution based upon the top model. All analyses were conducted using R software environment version 3.1.2 (R Core Team

2015a) using function ‘gdistsamp’ in the package unmarked (Fiske & Chandler 2011) to model density.

### Modeling Bird Community Structure

I used a multivariate analytical approach to quantify the difference in grassland bird communities across years and sites. I classified 20 of the species detected as grassland, successional-scrub species, or other, according to the Breeding Bird Survey’s habitat groupings (Sauer *et al.* 2011; Table 2.2). I used this suite of species to compare species richness, Shannon diversity, and community composition between field types.

Table 2.2. List of bird species used to quantify the difference in grassland bird communities between field types across years and sites and to compare species richness. Highlighted species were observed at < 10 % of field sites and excluded from individual species models. Superscript represents level of conservation concern; 1 = Partners in Flight (PIF) Yellow Watch list; 2 = Appalachian Mountains Joint Venture (AMJV) Priority Species; 3 = >40% of breeding population in AMJV region.

Alpha Code	Common Name	Species Name	Breeding Habitat Group (BBS)
AMKE	American Kestrel	<i>Falco sparverius</i>	Other
BLGR	Blue Grosbeak	<i>Passerina caerulea</i>	Successional-scrub
BOBO	Bobolink <sup>1</sup>	<i>Dolichonyx oryzivorus</i>	Grassland
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	Successional-scrub
DICK	Dickcissel	<i>Spiza americana</i>	Grassland
EABL	Eastern Bluebird	<i>Sialia sialis</i>	Other
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	Other
EAME	Eastern Meadowlark <sup>2</sup>	<i>Sturnella magna</i>	Grassland
EATO	Eastern Towhee <sup>2</sup>	<i>Pipilo erythrophthalmus</i>	Successional-scrub
FISP	Field Sparrow <sup>2</sup>	<i>Spizella pusilla</i>	Successional-scrub
GRSP	Grasshopper Sparrow <sup>2</sup>	<i>Ammodramus savannarum</i>	Grassland
INBU	Indigo Bunting <sup>2</sup>	<i>Passerina cyanea</i>	Successional-scrub
NOBO	Northern Bobwhite <sup>2</sup>	<i>Colinus virginianus</i>	Successional-scrub
OROR	Orchard Oriole	<i>Icterus spurius</i>	Other

PRAW	Prairie Warbler <sup>1,2,3</sup>	<i>Setophaga discolor</i>	Successional-scrub
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Other
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>	Grassland
WEVI	White-eyed Vireo	<i>Vireo griseus</i>	Successional-scrub
WIFL	Willow Flycatcher	<i>Empidonax traillii</i>	Successional-scrub
YBCH	Yellow-breasted Chat <sup>2</sup>	<i>Icteria virens</i>	Successional-scrub

I created a site by species matrix of abundance and used non-metric multidimensional scaling (NMDS; Minchin 1987) based on Bray-Curtis dissimilarity (Bray & Curtis 1957; Faith et al. 1987) to explore how bird species composition varied across the sample locations. I visualized my results using a triplot of sample points, bird species, and environmental variables. I conducted all statistical analysis in R version 3.2.2 (R Core Team 2015a) and used the package vegan (Oksanen *et al.* 2013) for the NMDS.

## Results

Wildlife fields had a higher ratio of native to exotic grasses compared to Idle and Agriculture fields ( $F_{(2,261)} = 36.21, P < 0.001$ ; Table 2.3). Idle fields had highest percentage of woody cover ( $F_{(2,261)} = 33.95, P < 0.001$ ) and percent forest within 1 km ( $F_{(2,261)} = 13.5, P < 0.001$ ). Agriculture fields had the highest percent grass cover ( $F_{(2,261)} = 26.29, P < 0.001$ ) and the least number of native forb species ( $F_{(2,261)} = 54.64, P < 0.001$ ) compared to Idle and Wildlife fields.

Table 2.3. Means and standard errors (SE) for vegetation and landscape covariates in 3 habitat types in Virginia 2012-2015. Agriculture = fields dominated by non-native cool season grasses and managed at least twice annually by mowing (hay) and/or by



continuous or rotational grazing; Idle = fields in an early successional stage and not actively managed by grazing, mowing or other means on an annual basis; Wildlife = fields comprise a mix of native warm-season grasses and forbs. Superscript letters indicate significant differences between habitat types after Bonferroni correction ( $P < 0.004$ )

	Agriculture	Idle	Wildlife
Total number of forb species	12.4 (0.7) <sup>a</sup>	20.8 (0.8) <sup>b</sup>	23.6 (1.1) <sup>b</sup>
Percent of point count circle area dominated by woody cover	2.7 (0.3) <sup>a</sup>	11.4 (1.4) <sup>b</sup>	4.2 (0.5) <sup>a</sup>
Total number of trees in 100 m point count circle	31.2 (3.3) <sup>a</sup>	61.9 (6.4) <sup>b</sup>	59.7 (4.9) <sup>b</sup>
Percent grass cover	43.1 (1.8) <sup>a</sup>	39.6 (1.9) <sup>b</sup>	35.8 (1.6) <sup>b</sup>
Percent of all grasses that are native	29.1 (1.9) <sup>a</sup>	32.3 (2.0) <sup>b</sup>	62.6 (1.9) <sup>c</sup>
% grassland within 1km	50.1 (2.2) <sup>a</sup>	31.6 (2.7) <sup>b</sup>	45.0 (1.5) <sup>a</sup>
% forest within 1km	34.5 (1.6) <sup>a</sup>	52.9 (3.1) <sup>b</sup>	45.0 (2.1) <sup>c</sup>
% open space within 1km	59.7 (1.9) <sup>a</sup>	42.1 (2.7) <sup>b</sup>	52.9 (2.0) <sup>a</sup>
% grassland within 5km	39.1 (1.9)	37.1 (2.4)	36.5 (1.5)
% forest within 5km	42.8 (1.4)	50.1 (2.6)	53.2 (1.8)
% open space within 5km	49.9 (1.4)	48.2 (2.5)	44.0 (1.7)

I recorded 12 species of grass and shrubland songbirds that were present at >10% of survey fields (Table 2.4). Most common were Field Sparrows (*Spizella pusilla*; 49% of fields) and Indigo Buntings (*Passerina cyanea*; 48%). Least common were Blue Grosbeaks (*Passerina caerulea*; 11%) and Northern Bobwhites (*Colinus virginianus*; 11%). Field preferences differed among individual species (Figure 2.2). The density of shrubland species, including Common Yellowthroats (*Geothlypis trichas*), Indigo Buntings, Yellow-breasted Chats (*Icteria virens*) and Northern Bobwhites, was significantly higher in wildlife fields than agriculture and idle fields. One generalist species, the Eastern Bluebird (*Sialia sialis*), was also found at higher densities in wildlife fields. Two shrubland species, Field Sparrows and Prairie Warblers (*Setophaga discolor*)

showed significantly lower densities in agriculture fields but did not differ between idle and wildlife fields. In contrast, Grasshopper Sparrows (*Ammodramus savannarum*) and Eastern Meadowlarks (*Sturnella magna*), both grassland species, were more abundant in agriculture fields, while Red-winged Blackbirds (*Agelaius phoeniceus*), Eastern Kingbirds (*Tyrannus tyrannus*) and Blue Grosbeaks did not show significant differences across field types.

Woody shrub cover and native forb richness were the most important habitat variables for predicting shrubland bird density (Table 2.4). Shrubland species strongly preferring woody shrub cover included Common Yellowthroats, Northern Bobwhites, Prairie Warblers and Yellow-breasted Chats. Eastern Kingbirds, a generalist species, also preferred woody shrub cover. Native forb richness was associated with reduced density of density of Red-winged Blackbirds and Eastern Meadowlarks, but was associated with increased density of Field Sparrows, Grasshopper Sparrows and Indigo Buntings. Of landscape variables, percent forest within 5 km had the strongest negative relationship with avian density, particularly with grassland species including Eastern Meadowlarks, Grasshopper Sparrows and Red-winged Blackbirds. Percent forest had mixed effects on shrubland species, demonstrating a positive effect on the density of Blue Grosbeaks within 1 km and Indigo Buntings within 5 km and a negative effect on the density of Common Yellowthroats and Prairie Warblers at 1 km and 5 km, respectively. The only species responding to percent open space were Field Sparrows, having a positive relationship with open country habitats within 5 km.

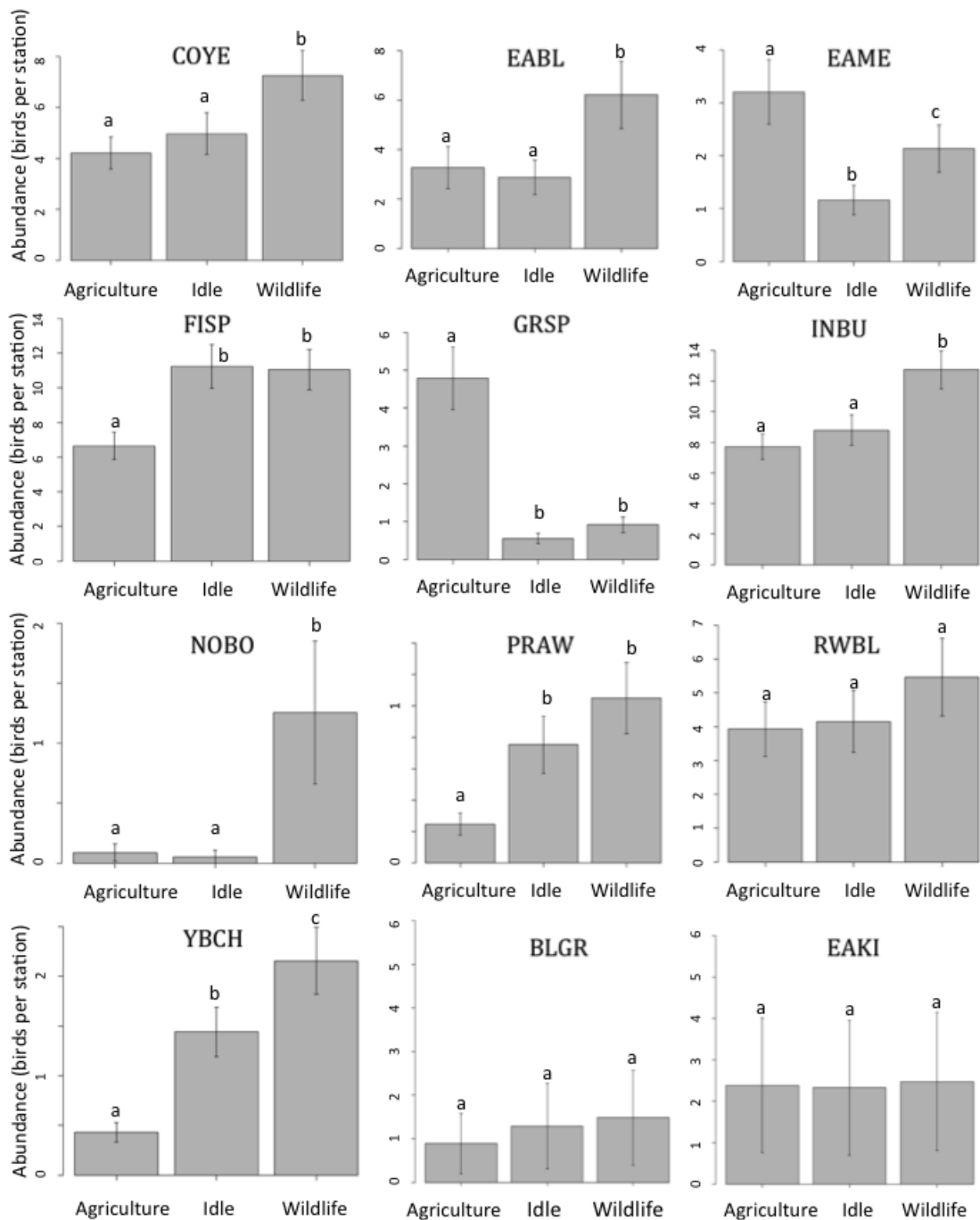


Figure 2.2 Predicted density of 12 grassland-associated bird species in agriculture, idle and wildlife fields in Virginia. Letters indicate significant differences between field types ( $P < 0.05$ ). Species codes: COYE=Common Yellowthroat; EABL=Eastern Bluebird; EAME=Eastern Meadowlark; FISP=Field Sparrow; GRSP=Grasshopper Sparrow; INBU=Indigo Bunting; NOBO=Northern Bobwhite; PRAW=Prairie Warbler; RWBL=Red-winged Blackbird; YBCH=Yellow-breasted Chat; BLGR=Blue Grosbeak; EAKI=Eastern Kingbird

Table 2.4. Beta estimates from the top models for 12 grassland-associated species in Virginia. Grouped by habitat class according to Breeding Bird Survey habitat groupings (Sauer et al. 2011).

Density	Shrubland							Grassland		Other		
	BLGR	COYE	FISP	INBU	NOBO	PRAW	YBCH	EAME	GRSP	RWBL	EABL	EAKI
Intercept	0.1699	1.601	2.4196	2.175	-2.78	0.725	0.968	0.151	-0.06	1.424	1.183	0.968
Habitat- Agriculture	-0.6685	-0.164	-0.5247	-0.132	0.642	-1.555	-1.113	1.015	1.97	-0.055	-0.129	-1.113
Habitat- Wildlife	0.0832	0.38	-0.0173	0.369	3.371	-0.115	0.214	0.607	-0.17	0.274	0.645	0.214
Forb Richness			0.3322	0.164				-0.391	0.5	-0.5		
Percent woody shrub		0.451			0.791	0.456	0.599					0.599
Percent grass cover												
Native - exotic grass ratio	-0.5732											
Grass 1km		-0.268										
Grass 5km						-0.872						
Forest 1km	0.4634											
Forest 5km				0.228				-0.84	-0.63	-0.562		
Open 1km												
Open 5km			0.1373									
<b>Availability</b>												
Date		1.27		43.8			6.37	-0.976		-5.73		6.37
Time		2.25		1.62	1.620		-41.73	-0.368				-41.73
Year	2013				3.849						4.793	
	2014				-10.00						-6.155	
	2015				-1.502						-10.46	
Wind						7.85					-0.914	
Temperature	-1.2		3.78	17.2		5.27			-1.31			
<b>Detection</b>												
Date		0.0422	0.0206		-0.133		0.0617					0.0617
Time			0.0272									
Wind				0.0206								
Height						0.101				0.0311		

Mean abundance of grassland birds per field ( $n = 5$  species), was negatively correlated with proportion of forest within 5 km (Figure 2.3A), especially in agricultural fields. Mean abundance of shrubland birds ( $n = 10$  species) was positively correlated with percent woody shrub cover (Figure 2.3B). However, woody shrub cover had a stronger relationship with shrubland birds in idle fields than in wildlife fields.

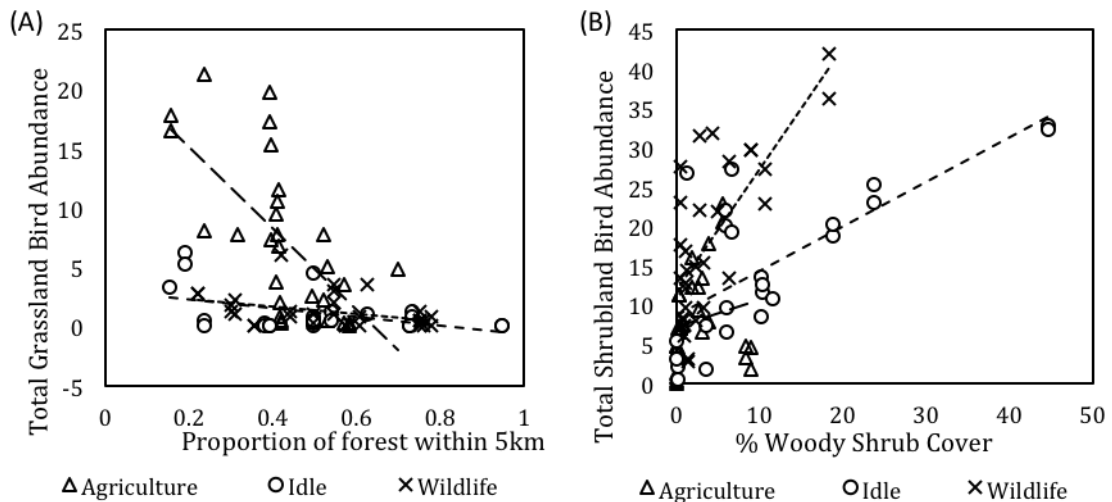


Figure 2.3. Relative abundance of (A) grassland birds and (B) shrubland birds in three habitat types. In agriculture fields, grassland birds demonstrate a 40% threshold on the proportion of forest within 5 km of a field, above which abundance drastically decreases. Abundance of shrubland birds increases with the proportion of woody shrub cover in wildlife fields but more so in idle fields.

All species were used for community analyses. An NMDS plot of all sites, species and covariates showed grassland obligate species had greater associations with grasslands and open landscapes while shrubland species showed greater associations with habitat

features, such as forb richness, proportion of native grasses and percent woody shrub cover (Figure 2.4). Shrubland species also demonstrated a higher association with the proportion of forest within 5 km.

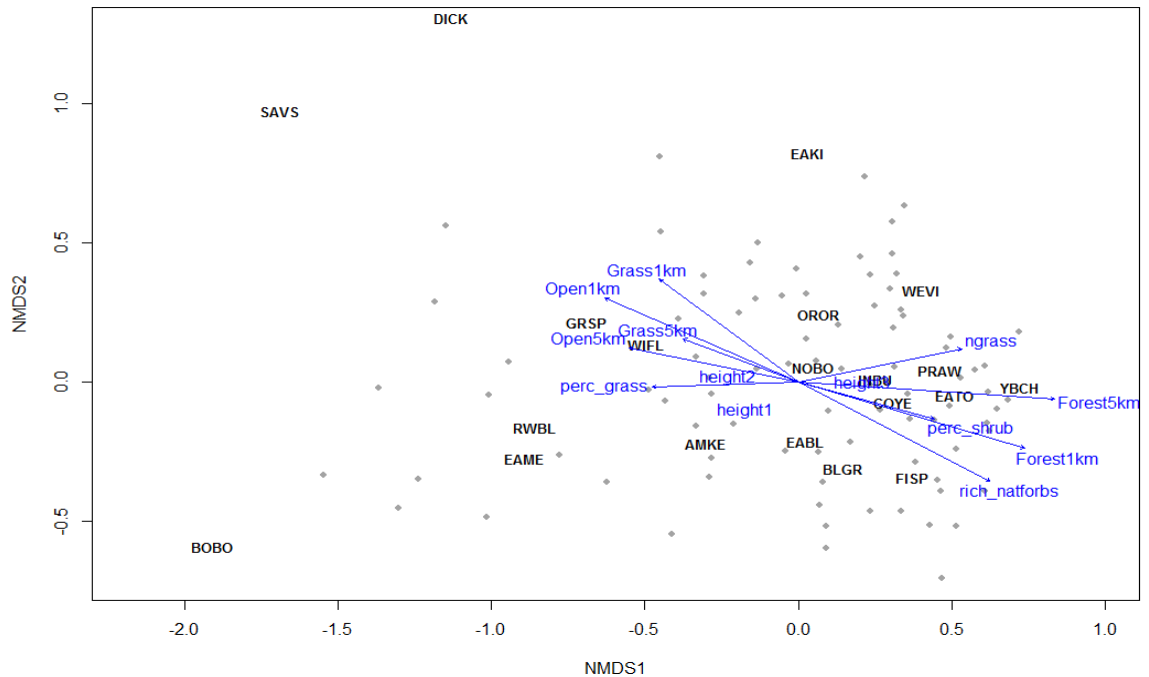


Figure 2.4. Visualization of the grassland bird community across 16 counties in Northern Virginia using nonmetric multidimensional scaling (NMDS). Gray points represent sites and 4-lettercodes represent bird species. Arrows represent continuous site covariates and point in the direction of most rapid increase and their lengths are proportional to the correlation between the covariate and site occupancy. See Table 2.2 for species codes.

## Discussion

The need to understand grass and shrubland bird associations with landscape and habitat features and the conservation practices meant to restore habitats is particularly important as population numbers decline for grassland birds, particularly in the eastern

United States. While habitat restoration projects are gaining momentum on a small scale in eastern grasslands, urban development, agricultural intensification and reforestation continue to encroach on remaining habitat (Jarzyna et al. 2016). State-level conservation initiatives that focus on grasslands, like the VQRI, play an important role in promoting management techniques that should benefit a suite of species in eastern grasslands. Here, I explored the potential benefits of this program to guilds of grass and shrubland species by quantifying the combined impacts of field management, habitat structure and landscape on species density and community structure. My results suggested that quail-specific management plans are also beneficial to several shrubland bird species in Virginia, but not to grassland obligates.

Native warm-season grasses have been promoted as a way to restore and sustain viable populations of declining early successional species (Moorman et al. 2017). In the current study, wildlife fields dominated by WSG supported a higher density of six of seven early shrubland species and one other species (Eastern Bluebird) compared to agricultural fields. Moorman et al (2017) reported territory densities of two early successional species, Indigo Buntings and Field Sparrows, to be 14.6 and 3 times greater, respectively, in WSG fields than in hayed and grazed CSG fields in North Carolina. In my study, the densities of Indigo Buntings and Field Sparrows were 1.5 and 1.7 times greater in wildlife fields than in CSG agriculture fields. However, my study considered additional species not reported in the North Carolina study. For example, I found densities of Northern Bobwhites and Prairie Warblers were, on average, 13 and 5.5 times greater in wildlife fields than in agriculture fields, respectively. The striking differences

among conspecific densities may be due to different management schedules. In my study, CSG fields were not managed during the survey season (not hayed or grazed between May 15-June 30<sup>th</sup>), which may have encouraged more shrubland birds to use these fields during that time. Information on timing of management is not reported by Moorman et al (2017).

Two species, Field Sparrows and Prairie Warblers, had comparable densities in idle fields and wildlife fields ( $P>0.05$ ), which suggests that idle and wildlife fields are comparable habitat for these species. However, when exploring the site-level habitat metrics, I found shrubland bird density increased in idle fields as woody shrub cover increased whereas wildlife fields maintained high bird density with minimal woody shrub cover (<20%). Woody cover reduces wind velocity and other impacts of weather in CSG fields, allowing vegetation to maintain an upright structure (Miller et al. 1974). Without substantial woody cover, vegetation in CSG fields is more horizontally dense while WSG maintain vertical structure with taller, denser bunch grasses and greater forb coverage than CSG (Henningsen et al. 2005). Therefore, increased woody cover is an important component for optimizing the potential for idle fields to support shrubland species whereas wildlife fields can maintain adequate habitat structure with minimal woody cover. This observation is important to consider in the context of a grazing regime, as woody cover reduces forage palatability and ease of field management (Collins & Wallace 1990). WSG, on the other hand, have been promoted for livestock forage and can be managed with moderate grazing intensity while still providing adequate cover for grassland birds (Moorman et al. 2017). Thus, creating grazing areas suitable for



shrubland birds may be more achievable through WSG establishment than idling CSG fields.

Habitat structure differed among field types and demonstrated species-specific associations in line with species habitat groupings. For example, agricultural fields had lower forb richness, woody cover and vegetation height than idle and wildlife fields. Grasshopper Sparrows and Eastern Meadowlarks, both grassland obligates, exhibited significantly higher densities in agricultural fields than in idle or wildlife fields. Both species are typically associated with fields with minimal vertical structure, sparse vegetation density and greater bare ground (Knopf 1994; West et al. 2016), features lacking in idle and wildlife fields. Additionally, Eastern Meadowlarks were negatively correlated with increased forb richness, which was higher in wildlife fields. In contrast, idle and wildlife fields contained taller vegetation, more forbs and/or woody cover. Densities of Yellow-breasted Chats, Prairie Warblers, Northern Bobwhites, Eastern Kingbirds and Common Yellowthroats were positively correlated with increased woody cover, which is characteristic of idle fields and, as previously suggested, structurally matched by native bunch grasses in wildlife fields (McCoy et al. 2001; Henningsen et al. 2005).

While habitat covariates provided information on regional site-level preferences specific to each species, it is also important to consider landscape effects in the context of grassland bird density, as many are area-sensitive (Cunningham & Johnson 2006). For example, Ribic *et al.* (2009) reported Eastern Meadowlark density increased with an greater proportion of grassland within 200 m of a field. Grasshopper Sparrows were

positively associated with the amount of grassland habitat, and negatively associated with the amount of development and forest within 5-8 km on the Delmarva Peninsula (Irvin et al. 2013). When multiple spatial extents were used to compare grassland bird densities, the largest extent (4 km) produced the strongest responses (Shahan et al. 2017). In the current study, agriculture fields had a higher proportion of grasslands and open landscapes within 1 km and 5 km than other field types, which could explain why Grasshopper Sparrows and Eastern Meadowlarks were most abundant in these fields. Although proportion of grassland was not included in top models for the grassland obligates, my results found a negative effect of forest within 5 km of the site on grassland obligates, indicating that the matrix of open and agricultural landscapes could be increasing the effect size of fields. For most grassland species, I observed a threshold of approximately 40% forest cover within 5 km of a field, below which population density declined. This threshold was also reported for Grasshopper Sparrow, Eastern Meadowlark, Northern Bobwhite and Red-Winged Blackbird, but at a much smaller scale (250 m; West *et al.* 2016). Conversely, my wildlife and idle fields had a higher proportion of forest cover within 1 km and 5 km, and were therefore likely less attractive for the grassland obligates. Interestingly, the wildlife field with the highest mean abundance of grassland species had 30% and 40% forest cover within 1km and 5 km, respectively. Though this field is only one example, it demonstrates that quail habitat can potentially be suitable for grassland obligates if forest cover is at or below the 40% threshold within the landscape. More research is required to corroborate this finding.

Quail have recently been identified as an umbrella species for grassland and shrubland bird communities (Crosby et al. 2015b). However, the results of my study demonstrated that quail habitat management practices do not significantly impact densities of grassland species in the eastern US and therefore this designation should be revised to omit grassland obligates. Also, my study indicated that there is great value in encouraging the adoption of quail management plans, regardless of their success in restoring quail populations as these plans do create suitable shrubland bird habitat. Although quail were present in only 10% of sites in the current study, quail management practices increased the density of seven of 12 species in the absence of quail, six of which are designated shrubland species. The Appalachian Mountains Joint Venture (AMJV), a partnership-based group that prioritizes and coordinates bird conservation activities within the study region, lists five of these species as in need of immediate conservation attention ([www.amjv.org](http://www.amjv.org)). Thus, quail management practices can be promoted as a tool to conserve populations of declining shrubland birds in the eastern US. For example, Prairie Warbler populations have declined by > 50% since the 1960's and are on several watch lists for the region, including Partners in Flight, Appalachian Mountain Joint Venture, Atlantic Coast Joint Venture, and the species is listed in the Virginia Wildlife Action Plan (Rosenburg et al. 2016). Prairie Warblers were as much as 7 times more abundant in wildlife fields than in agricultural fields. Therefore, the promotion of quail management practices could be an effective conservation strategy for Prairie Warblers, especially when species-specific conservation funds are limited.

## **Management Implications**

Native warm-season grasses play an important role in Northern Bobwhite conservation planning and are beneficial to the maintenance of shrubland bird populations in grasslands of the eastern U.S., where habitat fragmentation is prominent. Therefore, continued support and promotion of programs supporting habitat management for quail provides an important opportunity to manage habitat for less charismatic or directly valued species undergoing similar population declines. However, my study demonstrates that current management of quail habitat in Virginia is not suitable for grassland obligates, which are also steeply declining, due to their affiliation with open landscapes. Grassland species may benefit more from quail plans if efforts were placed on enhancing both landscape and site-specific attributes, as demonstrated by one of the wildlife sites in our study. Additionally, distinct conservation measures for grassland obligates should be ensured into the future by securing remaining large, contiguous tracts of grassland and promoting programs in these areas that provide incentives for delayed hay harvests and low-intensity grazing.

## **CHAPTER THREE : EFFECTS OF FIELD COMPOSITION AND MANAGEMENT ON GRASSLAND BIRDS OVER-WINTERING IN VIRGINIA**

### **Introduction**

The impacts of land management on grassland bird communities has been a topic of considerable attention in recent decades, as grassland birds have experienced a steeper, more consistent, decline than any other guild of birds in North America (Samson & Knopf 1994; Askins et al. 2007). Land management activities such as burning (Churchwell et al. 2008), mowing (Bollinger et al. 1990; Blank et al. 2011), use of agricultural chemicals (Martin et al. 2000; Bartuszevige et al. 2002; Newton 2004; Mineau et al. 2005) and conservation buffers (Burger et al. 2006; Berges et al. 2010) all impact breeding populations of grassland birds. For example, earlier and more frequent hay harvests result in increased nest failures for Savannah Sparrows (*Passerculus sandwichensis*), Bobolinks (*Dolichonyx oryzivorus*) and other grassland-dependent species (Perlut et al. 2006, 2011). In contrast, establishing conservation buffers increases breeding bird abundance, species richness and diversity (Berges et al. 2010) and improves nest success (Adams et al. 2013). Though we have gained much knowledge from decades of research on breeding habitats, we have limited knowledge of the habitat needs of grassland birds during the non-breeding season. However, the loss and degradation of winter habitat has been hypothesized as a major contributing factor in bird declines (Hostetler et al. 2015; Marra et al. 2015a). Therefore, there is an urgent need to

fill this information gap on non-breeding season requirements, especially for imperiled populations of grassland birds.

The quality of winter habitat affects the survival and reproduction of several long distance migrants and these factors influence population dynamics in subsequent breeding seasons (Marra et al. 1998; Studds et al. 2008; Robb et al. 2008; Costantini et al. 2010; Harrison et al. 2011; Marra et al. 2015b). Specifically, productive winter and staging habitats result in earlier departure dates and improved survival during migration in long-distance migratory species. This has been documented in American Redstarts (*Setophaga ruticilla*) wintering in the Caribbean (Marra et al. 1998; Studds et al. 2008; Marra et al. 2015b) and in Snow Geese (*Chen caerulescens atlantica*) staging in southeastern Canada (Bêty et al. 2003). In short-distance migrants and resident birds, increased food availability in winter can increase survival (Jansson et al. 1981), advance breeding dates (Salton et al. 2015), laying dates and increase fledgling success (Robb et al. 2008; Costantini et al. 2010). Of 56 species that breed in grasslands and early successional-scrub habitats in eastern North America (Eastern BBS Region; Sauer *et al.* 2011), nearly half also winter in the United States. However, many current land management recommendations for grassland birds only pertain to breeding bird habitats, leaving a deficit of information available on best management practices for lands with over-wintering species.

Vegetation structure and composition are important measures of habitat quality for birds, but optimal measures vary considerably between species groups (MacArthur & MacArthur 1961; Tews et al. 2004). For breeding grassland birds, the structure and

composition of vegetation can have a significant influence on bird communities, as increased structural heterogeneity is correlated with increased bird community diversity and stability (Hovick et al. 2015). In winter, a heterogeneous vegetation structure can provide thermal protection (Ginter & Desmond 2005), improve foraging opportunities (Bechtoldt & Stouffer 2005; Ginter & Desmond 2005) and decrease predation risk (Watts 1996). However, grasslands in the eastern US are often managed so as to leave minimal structure during winter months. For example, hay fields in eastern grasslands are harvested as late as September (Plantureux et al. 2005) and pastures are stockpiled with cattle for winter grazing (Poore et al. 2000), leading to reduced seed resources and offering limited foraging and shelter opportunities for birds during winter. Thus, timing of grassland management could have severe impacts on winter habitat suitability and associated bird survival.

While the majority of hay and pasture lands in the eastern US are comprised of non-native cool season grasses (CSG), there are also a growing number of fields being restored to native warm-season grasses (WSG), often through state conservation initiatives (Moorman et al. 2017). Warm-season grass fields increase the structural heterogeneity of fields during the growing season and are associated with higher mammal (Mengak 2004), arthropod (McIntyre & Thompson 2003), pollinator (Myers et al. 2012) and bird diversity (Flanders et al. 2006; Harper et al. 2015). Best management practices for WSG in the eastern US are designed to optimize structural heterogeneity and minimize invasions by non-native species (Washburn et al. 2000) which also benefits breeding grassland bird populations (Flanders et al. 2006). However, there is limited

research on habitat use by winter bird communities in WSG, with most of this work focused in ecoregions of the mid-west and southern US (McMellen & Schweitzer 2005; Conover et al. 2007; Plush et al. 2013; Monroe & O'Connell 2014; Hovick et al. 2015; Saalfeld et al. 2016). For example, nonnative vegetation negatively influences the density of several grassland obligate species over-wintering in the Texas coastal plains (Saalfeld et al. 2016) while birds over-wintering in the Flint Hills of Kansas and Oklahoma are positively associated with increased vegetation height (Monroe & O'Connell 2014). With variation in species assemblages, ecoregion attributes, land use and resulting habitat structure between these regions (Omernik 1987), it is imperative to understand differing responses in the bird community to optimize conservation opportunities specific to eastern grasslands.

The objective of this study was to understand how the winter bird community responds to land management and associated habitat structure in eastern US. I investigated the relative abundance of grassland birds during the winter in fields comprised of either WSG or CSG that differed in management timing. I hypothesized that the avian community would vary among management regimes, expecting that field type and management timing would strongly influence vegetation structure. I expected higher species richness and diversity in fields associated with increased structural heterogeneity. I also hypothesized that fields comprised of non-native vegetation would exhibit lower avian diversity because of increased homogeneity in the vegetation structure. Results from this study will inform best management practices for grasslands with over-wintering bird species.



## Methods

### Study Area

This study was conducted during 3 winter seasons from 2013 – 2016 on 25 properties across 11 counties in Virginia, US, that were either in public (n=4) or private (n=21) ownership (Figure 3.1). The private field sites were recruited and surveyed through Virginia Working Landscapes (VWL), a conservation initiative convened by the Smithsonian Conservation Biology Institute (SCBI) in Front Royal, VA ([www.vaworkinglandscapes.org](http://www.vaworkinglandscapes.org)). This 11-county region is characterized by rolling hills over igneous and metamorphic bedrock with stretches of karst topography throughout the western portion (Hyland 2005). The center of the study region is intersected by Shenandoah National Park along the Blue Ridge Mountains. The land cover is dominated by eastern temperate deciduous forest with grasslands comprising approximately 30% of the study region (National Land Cover Database 2011). Grasslands are mostly comprised of non-native CSG such as tall fescue (*Schedonorus arundinaceus*), Kentucky bluegrass (*Poa pratensis*) and orchard grass (*Dactylis glomerata*). Fields converted to WSG contained a mix of grasses (e.g., big bluestem (*Andropogon gerardi*), switchgrass (*Panicum virgatum*) and indiagrass (*Sorghastrum nutans*)) and forbs (e.g., asters (*Symphotrichum sp.*), monarda (*Monarda sp.*), milkweeds (*Asclepias sp.*)). Average temperature for the study months and area ranged between -10.56°C and 15.56°C (mean = 1.48°C) and the average snowfall was 13.77 cm (NOAA 2017).

### Field Methods

Field sites (n=43) were at least 8 contiguous hectares of grassland and included varying compositions of forbs and woody vegetation but were divided into two field

types: 1) WSG (n=23); or 2) CSG (n=20). Fields were also categorized by management timing: 1= Fall (Sept-Nov), 2= Summer (May-Aug); 3 = Late Winter/No management (Jan-Apr). No fields were managed during survey months. Fields managed in late winter were combined with fields with no management, as they had at least 7 months of growth prior to being surveyed. Management included burning, disking, mowing, grazing and bush-hogging. For this paper I combined all management activities and focused on vegetation attributes following management. In each field, three 200 m-long transects were established using the criteria of a minimum of 100m from field edges and 200m apart. If a property contained more than one survey field, adjacent survey clusters were separated by  $\geq 400$  m to reduce the probability of double-counting birds between survey fields (Davis et al. 2013).

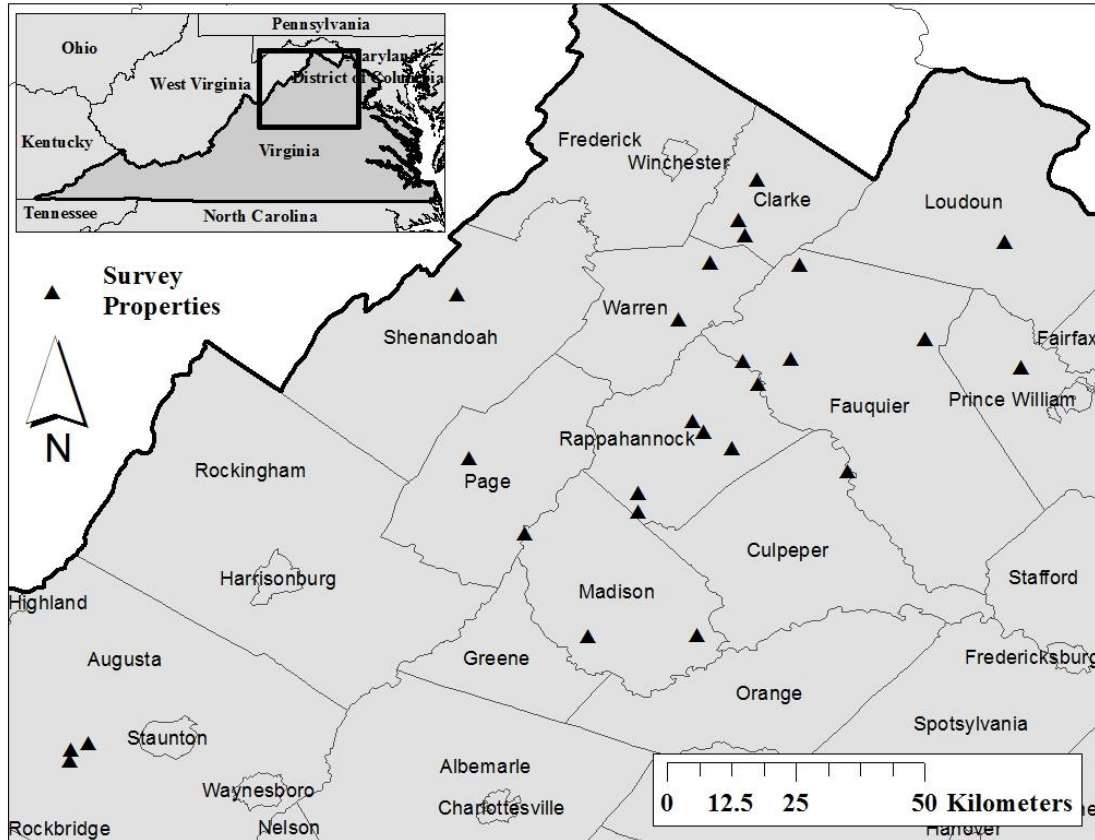


Figure 3.1. Locations of survey properties in Northern Virginia, 2013-2016. Survey fields were selected opportunistically through a landowner network convened by Virginia Working Landscapes ([www.VAWorkingLandscapes.org](http://www.VAWorkingLandscapes.org)). Survey fields were a minimum of 20 contiguous acres; thus some properties had more than one survey field >400 m apart. Each survey field contained 3 survey stations at least 200 m apart.

### Bird Surveys

Each field was visited three times during the survey period (once per month in December, January and February). Birds were surveyed using variable width transect surveys and distance sampling techniques (Buckland et al. 2001; Diefenbach et al. 2003). The line transects were surveyed for bird abundance by a single observer between 0900-1300 (EST) on days with no precipitation and wind speeds less than <20 km/h (Gabrey et

al. 1999). In contrast to breeding season, birds can be surveyed throughout the day during the non-breeding season (Fletcher et al. 2000). The observer traveled NE to SW to avoid sun glare at a rate of approximately 40m/min recording the perpendicular distance of detected birds from the centerline to the nearest 5 m over 5 minutes. A record was made of all birds regardless of detection method (e.g. flushing from ground, perched in vegetation, vocalizing). Temperature, date, time, wind speed, snow cover and cloud cover were also recorded for each site visit.

### **Vegetation Surveys**

Vegetation and structural heterogeneity of each field was measured along each line transect once a year between January and February at a time of no snow cover. Six 1 m<sup>2</sup> plots were surveyed at 40 m intervals along each transect. Percent ground cover of grasses, forbs, woody, leaf litter and bare ground was visually estimated and recorded for each plot (Daubenmire & others 1968).

Two measures were used to estimate habitat openness along multiple dimensions. For vertical visual obstruction I used a modification of the Robel method (Robel et al. 1970) using a 1-m pvc pole divided into 10 cm segments. Robel measurements were recorded in 2 opposite corners of each plot, from a distance of 2 m from the pole, resulting in 12 measures per transect. Briefly, the number of visible 10 cm segments were counted and recorded leaving those segments fully obstructed by vegetation to account for height of vertical obstruction to the nearest 5 cm. Using the same pole, the cone of vulnerability was estimated from the center point of each plot (Kopp et al. 1998) totaling 6 measures per transect. The cone of vulnerability is a 3-dimensional view of visual

obstruction and has been used as a measure of habitat structure for ground-dwelling species such as northern bobwhites (Kopp et al. 1998). The segmented pvc pole was also used to measure the height of the tallest plant in each plot to the nearest 5 cm.

### **Statistical Analyses**

Each annual survey for a field was considered an independent survey because some sites were managed differently each year, and because a number of the sites were not surveyed in all 3 years of the study.

Site-level covariates were calculated using the means of all variables for each field including percent cover of grasses, forbs, woody stems and bare ground; vegetation height; cone of vulnerability (COV) and visual obstruction (Robel). Categorical covariates included field type (WSG vs. CSG), management timing (1= Fall, 2= Summer; 3 = Late Winter/No management) and a combination of the two (management: WSG 1, WSG 2, WSG 3, CSG 1, CSG 2, CSG 3). I examined the correlation between covariates using Spearman's rank correlation coefficient and no two variables had a correlation over 0.7. Measures of habitat structure ( $n=7$ ) were compared between field types and management timing using one-way analysis of variance (ANOVA). With significant ANOVA results ( $P < 0.01$ ), I calculated Tukey post-hoc pairwise comparisons to determine significant differences between groups. To account for multiple testing, I used the Bonferroni correction and considered significant only those covariates for which  $P < 0.05/7 = 0.007$ .

I classified 16 of the species detected as grassland (n=5), successional-scrub species (n=8), or other (n=6), according to the Breeding Bird Survey’s habitat groupings (Sauer *et al.* 2011; Table 3.1). Species classified as “other” were included in the analysis due to their frequent use of my sites in winter. I calculated relative abundances by dividing the total number of detections for each species by the number of transects surveyed in each field during each year of the study.

Table 3.1. List of bird species used to quantify the difference in grassland bird communities between field types across years and sites. Superscript represents level of conservation concern; 1 = Partners in Flight (PIF) common bird in steep decline; 2 = Appalachian Mountains Joint Venture (AMJV) priority species.

Alpha Code	Common Name	Species Name	Habitat Group (BBS)
AMGO	American Goldfinch	<i>Carduelis tristis</i>	Successional-scrub
ATSP	American Tree Sparrow <sup>1</sup>	<i>Spizella arborea</i>	Other
EABL	Eastern Bluebird	<i>Sialia sialis</i>	Other
EAME	Eastern Meadowlark <sup>1,2</sup>	<i>Sturnella magna</i>	Grassland
EATO	Eastern Towhee <sup>2</sup>	<i>Pipilo erythrophthalmus</i>	Successional-scrub
FISP	Field Sparrow <sup>1,2</sup>	<i>Spizella pusilla</i>	Successional-scrub
FOSP	Fox Sparrow	<i>Passerella iliaca</i>	Successional-scrub
HOLA	Horned Lark <sup>1</sup>	<i>Eremophila alpestris</i>	Grassland
KILL	Killdeer	<i>Charadrius vociferus</i>	Other
NOBO	Northern Bobwhite <sup>1,2</sup>	<i>Colinus virginianus</i>	Successional-scrub
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Other
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>	Grassland
SOSP	Song Sparrow	<i>Melospiza melodia</i>	Successional-scrub
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	Other
WCSP	White-Crowned Sparrow	<i>Zonotrichia leucophrys</i>	Successional-scrub
WTSP	White-Throated Sparrow	<i>Zonotrichia albicollis</i>	Successional-scrub

To explore potential relationships between relative abundance of target species and habitat characteristics I used non-metric multidimensional scaling (NMDS; Minchin 1987) based on Bray-Curtis dissimilarity (Bray & Curtis 1957; Faith, Minchin & Belbin 1987). Specifically, I used relative abundances and the “metaMDS” and “envfit” functions in the vegan package (Oksanen *et al.* 2013) to project a summary of habitat use for the subset of 16 species. I chose to use the Bray-Curtis distance metric in NMDS because it is sensitive to differences in the most abundant species and less sensitive to infrequently encountered species (Pillsbury *et al.* 2011). I visualized the results using a triplot of sample points, bird species, and environmental variables, to identify the most prominent habitat characteristics to include in subsequent occupancy models.

I used multispecies occupancy models (MSOMs, (Zipkin *et al.* 2010) to determine the effects of grassland management and associated structure on non-breeding bird diversity. These models are an extension of the single-species occupancy model (MacKenzie *et al.* 2002) that analyzes detections of all species encountered during replicated surveys at a set of sites. I defined occupancy as a binary variable where presence equals one for any species that occurred within 50m of transect counts and zero otherwise. Replicated surveys over multiple visits allowed for a distinction between species that are absent and species that are present but not detected (Royle, Nichols & Kéry 2005). I assumed that occurrence and detection probabilities varied by species and were influenced by habitat management, structural characteristics and survey-specific features. I modeled the occurrence probabilities for all species at each transect dependent on whether transects were in WSG fields or CSG fields. This allowed for species level

effects to differ between the two habitat types. I also incorporated effects of management timing, as this influenced vegetation structure. In addition, I included two structural characteristics: cone of vulnerability (COV) and vegetation height based off of NMDS results. For the detection model, I included vegetation height, temperature, minutes after sunrise and day of season (Dec 1 = 1, Feb 28 = 90) as possible species-specific detection covariates. Continuous covariates for both the occurrence and detection models were standardized to have a mean of zero.

Bayesian analysis of the model was carried out using data augmentation techniques described by Royle, Dorazio & Link (2007), which allow for an estimation of the number of species in the community, including those that were unobserved during sampling. Analysis by data augmentation ensures increased precision of occurrence estimation and improved analysis of community species richness. The model was analyzed using a Bayesian approach in the programs R version 3.2.2 (R Core Team 2015) and WinBUGS (Spiegelhalter *et al.* 2003). I ran two chains of length 10,000 after a burn-in of 5,000 and thinned the posterior chains by 5. Convergence was assessed using the R-hat statistic (Zipkin *et al.* 2010).

I used the MSOM results to compare species richness, including unobserved species (n=50) between the two field types as well as under different management treatments (field type + management timing) by averaging the number of species estimated by the model for each treatment group. Species richness was compared between field types and management using one-way analysis of variance (ANOVA). With significant ANOVA results ( $P < 0.01$ ), I calculated Tukey post-hoc pairwise



comparisons of species richness. I also compared transect-specific associations of richness with COV and vegetation height.

## **Results**

Warm-season grass fields, on average, had a higher percentage of bare ground ( $P < 0.001$ ), visual obstruction ( $P < 0.001$ ) and vegetation height ( $P < 0.001$ ) than CSG (Table 3.2). Cool-season grasses had higher COV ( $P < 0.001$ ) and percent grass cover ( $P < 0.001$ ). Percent woody and percent forb did not differ between field types ( $P > 0.004$ ). Cool season fields that were not managed in Fall or Summer had a significantly higher percentage of woody cover than all other field types ( $P < 0.001$ ) and relatively high percent forb cover. Warm-season grass fields had the lowest COV but when considering fields managed in the fall, previous winter or not at all, COV did not differ between CSG and WSG (Table 3.2).

Table 3.2. Summary of covariates among habitat types and management timing. Values presented are means with standard errors in parentheses. Grey numbers represent mean values of each habitat type: CSG = Cool-season grasses; WSG = Warm-season grasses. Management timing categories are: 1= Fall, 2= Summer; 3 = Late Winter/No management. Asterisks indicate significant differences between field types (CSG vs. WSG) in grey rows while superscript letters indicate significant differences between habitat-timing combinations after Bonferroni correction ( $P < 0.007$ ).

	Vegetation Height (m)	Cone of Vulnerability (m <sup>3</sup> )	Cover (%)				Visual Obstruction (%)
			Grass (%)	Forb (%)	Woody (%)	Bare Ground (%)	
CSG Mean	0.62 (0.07)	7.45 (0.93) *	73.53 (3.08) *	13.40 (2.18)	7.67 (1.64)	15.59 (1.33)	7.87 (1.11)
1	0.21 (0.08) <sup>a</sup>	13.82 (0.80) <sup>a</sup>	85.06 (2.83) <sup>a</sup>	0.81 (0.81) <sup>a</sup>	1.15 (1.15) <sup>a</sup>	10.60 (1.51) <sup>a</sup>	1.00 (1.01) <sup>a</sup>
2	0.74 (0.06) <sup>b</sup>	4.39 (0.76) <sup>b</sup>	77.38 (2.86) <sup>a,b</sup>	21.18 (3.58) <sup>b</sup>	8.39 (2.62) <sup>b</sup>	14.98 (2.03) <sup>a</sup>	10.57 (0.75) <sup>b</sup>
3	1.15 (0.11) <sup>b</sup>	1.56 (0.48) <sup>b</sup>	46.18 (5.93) <sup>b,c</sup>	21.97 (2.32) <sup>b</sup>	17.98 (3.3) <sup>c</sup>	25.54 (1.08) <sup>b</sup>	16.03 (1.36) <sup>b,c</sup>
WSG Mean	1.32 (0.09) *	2.63 (0.56)	46.63 (3.17)	12.82 (2.34)	8.24 (1.64)	26.01 (1.61) *	17.33 (1.71) *
1	0.67 (0.30) <sup>a,b</sup>	7.62 (2.27) <sup>a</sup>	66.33 (8.72) <sup>a,b</sup>	2.00 (2.00) <sup>a</sup>	0.00 (0.00) <sup>a</sup>	25.56 (5.02) <sup>b</sup>	9.32 (3.58) <sup>b</sup>
2	1.17 (0.30) <sup>b,c</sup>	3.20 (1.37) <sup>b</sup>	47.00 (9.17) <sup>b,c</sup>	14.11 (6.85) <sup>b</sup>	3.33 (2.04) <sup>a,b</sup>	23.11 (5.85) <sup>b</sup>	10.99 (3.20) <sup>b,c</sup>
3	1.47 (0.08) <sup>c</sup>	1.56 (0.38) <sup>b</sup>	42.77 (3.31) <sup>c</sup>	14.65 (2.83) <sup>b</sup>	10.76 (1.99) <sup>b</sup>	26.66 (1.77) <sup>b</sup>	20.08 (1.96) <sup>c</sup>

A total of 7,505 individuals of 41 species of birds were detected during winter transect surveys (Table A1 in the Appendix). The model estimated 47.1 species in the whole of the region (95% Posterior Interval, PI: 44-57). Sixteen species were selected for NMDS analysis either based on their BBS habitat groupings or for their frequent use of our grasslands in winter (Table 3.1). Visualization of the NMDS demonstrated correlations of grassland-obligates to higher COV and lower visual obstruction, and a higher percentage of grass cover (Figure 3.2). In contrast, early successional species were correlated with taller vegetation and increased percentages of woody stems, forb cover, and bare ground. Cone of vulnerability explained the most variation in species composition between the survey points (MRPP;  $A = 0.498$ ;  $P = 0.000$ ; Figure 3.2). Fields with higher COV values had a higher abundance of grassland-obligates, as well as Red-Winged Blackbirds and Eastern Bluebirds. Early-successional species were most abundant in fields with lower COV.

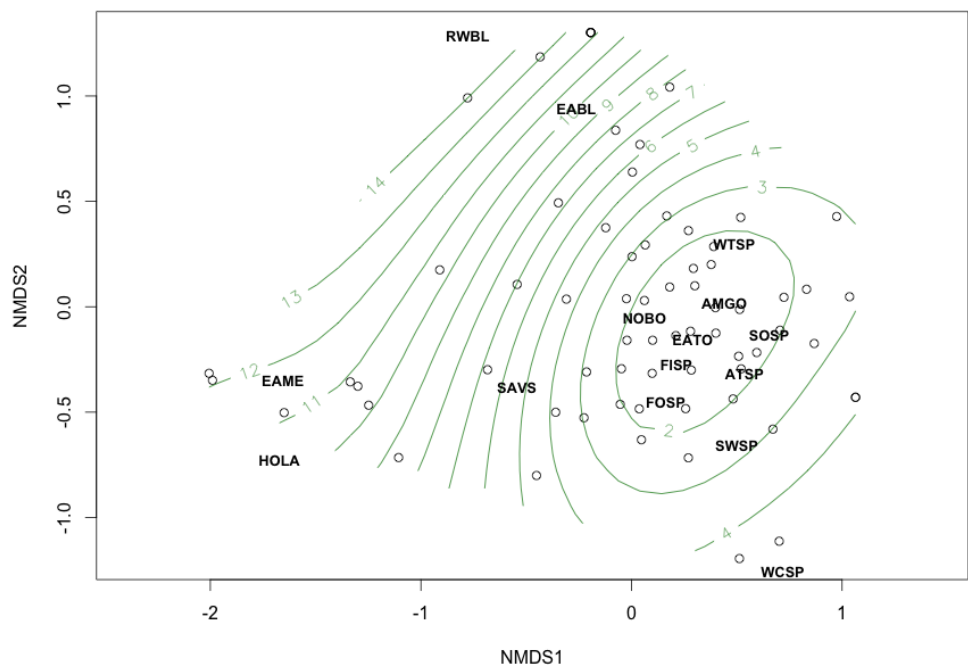
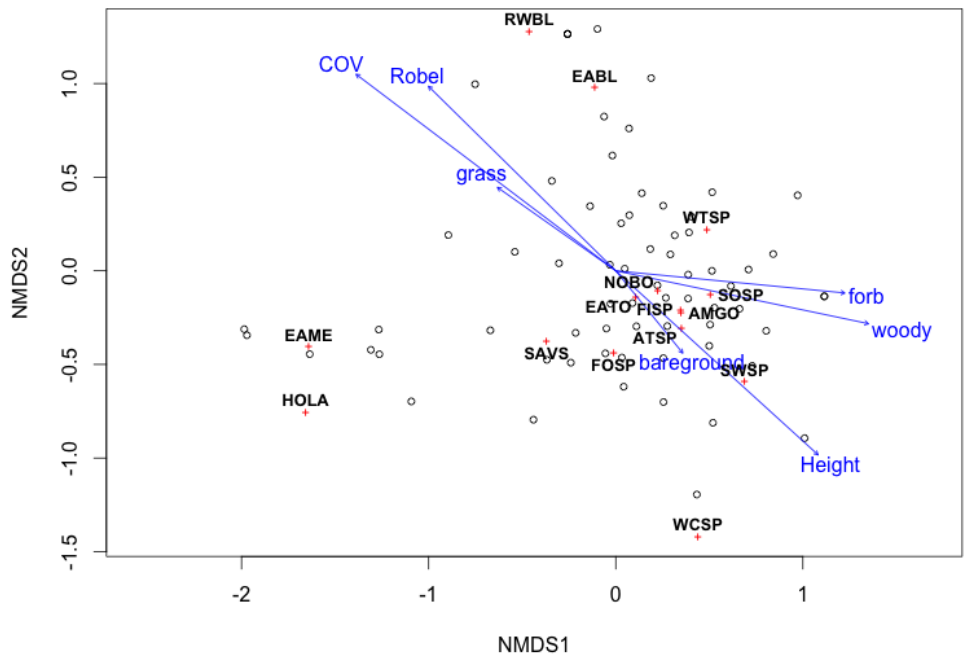


Figure 3.2. Visualization of the bird community over-wintering in Northern Virginia grasslands using nonmetric multidimensional scaling (NMDS) demonstrating (top panel) correlations of site covariates and species abundance and (bottom panel) abundance of

species based on cone of vulnerability. Circles represent sites, 4-letter codes represent bird species and arrows represent continuous site covariates and point in the direction of most rapid increase and their lengths are proportional to the correlation between the covariate and site occupancy. Fitted contours represent a continuous gradient of COV values. See Table 3.1 for species codes.

All observed species were considered for the MSOM (n=41) as were unobserved species (n=50). Transect-specific estimates of species richness were significantly higher in WSG fields than CSG ( $F_{(1,226)} = 76.21, P < 0.001$ ; Figure 3.3A) though occurrence probabilities for many species were similar in the two habitat types (Figure 3.3B). Values of species richness estimated by the model were similar to observed species richness in WSG (Observed =  $5.62 \pm 0.33$  vs. Estimated  $5.49 \pm 0.22$ ) and CSG fields (Observed =  $2.78 \pm 0.35$  vs. Estimated =  $2.86 \pm 0.19$ ).

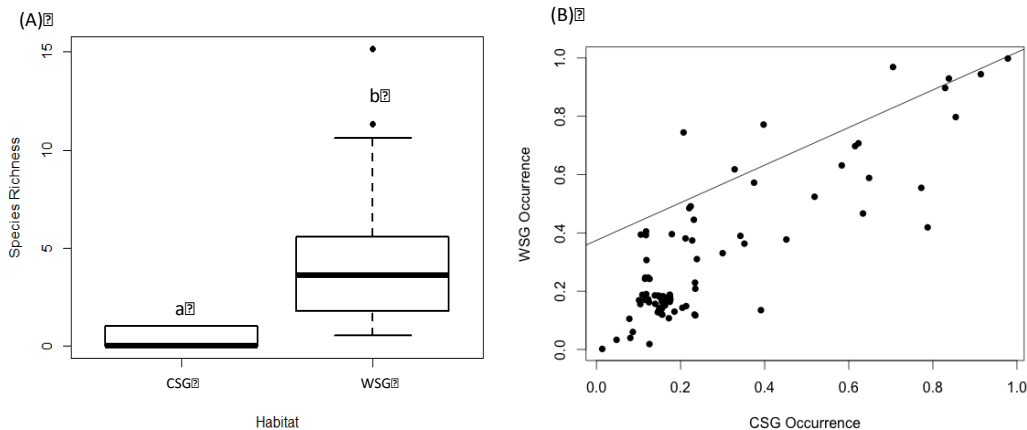


Figure 3.3. Estimated transect-specific bird species richness in fields comprised of non-native cool-season grasses (CSG) and native warm-season grasses (WSG; A) and mean estimated species-specific probabilities of occurrence in WSG vs. CSG (B).

Estimated species richness was also significantly influenced by management timing, with fields managed during the previous winter or not at all exhibiting higher estimated richness than fields managed in summer or fall ( $F_{(2,225)} = 59.36, P < 0.001$ ; Figure 3.4A). When combined with field type, WSG fields managed in the previous winter or not at all (WSG\_3) had higher estimated species richness than any other treatment group ( $F_{(5,222)} = 32.01, P < 0.001$ ; Figure 3.4B). Though CSG\_3 fields had higher estimated richness than CSG\_1 and CSG\_2 fields ( $P < 0.001$ ), they were not significantly different from WSG\_1 ( $P = 0.521$ ) and WSG\_2 ( $P = 0.999$ ) fields.

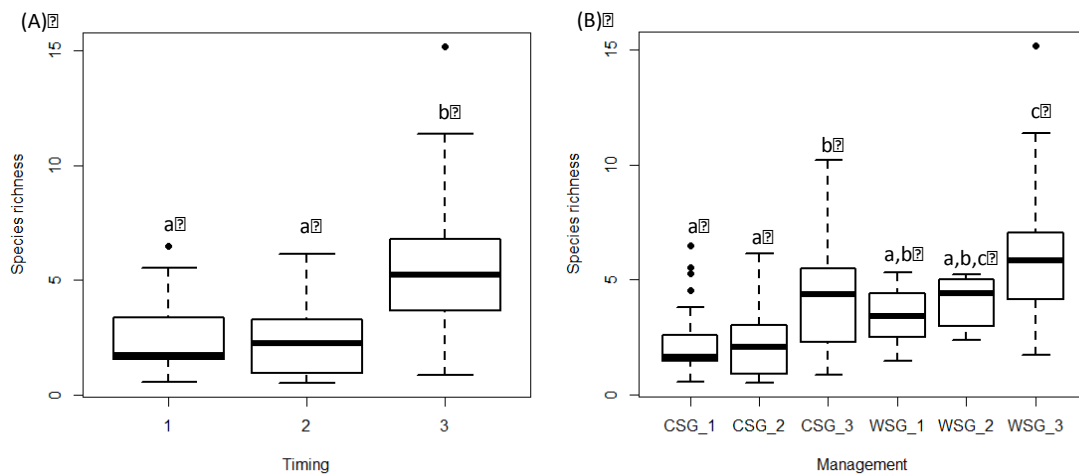


Figure 3.4. Estimated species richness in fields managed in Fall (1), Summer (2), the previous winter or not at all (3; A) and mean estimated richness in CSG vs. WSG managed in fall, summer or winter/none (B). Regardless of field type, fields managed in the previous winter or not at all had significantly higher richness than all other treatments (A). When combined with field type (B), warm season grass fields managed in the previous winter or not at all had the highest estimated species richness.

Species richness and individual species occurrence probabilities were also significantly influenced by structural characteristics. Estimated species richness was significantly higher in fields with tall vegetation ( $R^2 = 0.32$ ,  $P < 0.001$ ; Figure 3.5A) and significantly lower in fields with high cone of vulnerability measurements (COV;  $R^2 = 0.27$ ,  $P < 0.001$ ), indicating that field openness reduced species occupancy. In addition, species-specific detection probability was negatively influenced by vegetation height (Figure 3.5B).

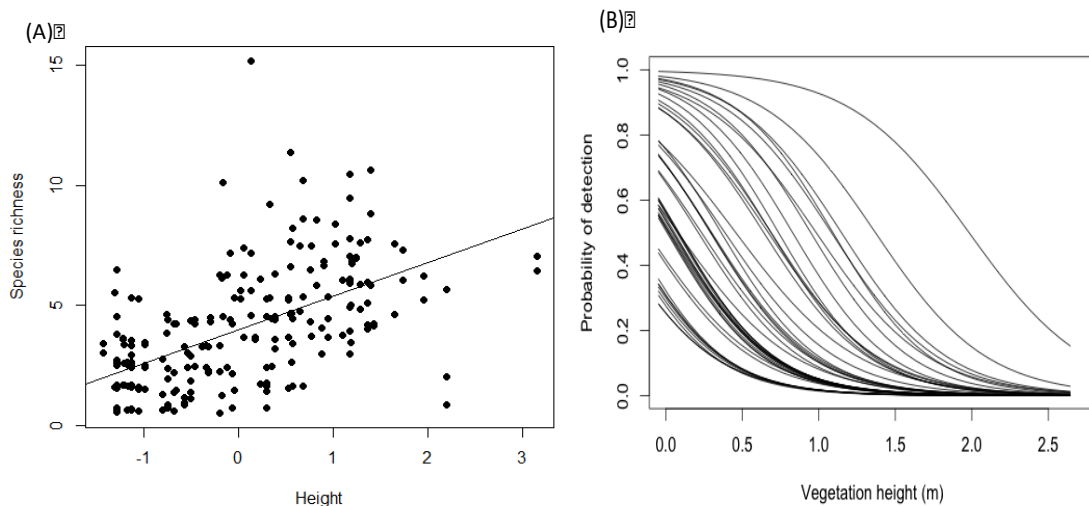


Figure 3.5. Posterior means of estimated species richness for each sampled point plotted against vegetation height (scaled; A) and species-specific sampling effects of vegetation height on detection probability (B).

## Discussion

Grass and shrubland birds have experienced greater population declines than any other guild of birds in North America, and yet we know little about habitat use and the

effects of management during their period on wintering sites. The lack of information on over-wintering grassland birds limits our ability to establish best management practices to optimize their conservation. We investigated impacts of grassland management timing on associated habitat structure for the winter bird community. Fields comprised of WSG had taller vegetation, more vertical and horizontal structure and more bare ground, resulting in significantly higher species diversity than fields comprised of non-native CSG.

Warm season grasses have been endorsed by conservation managers to improve breeding habitat for grassland and early successional species (West et al. 2016). Several recommended management practices for WSG enhance habitat quality and structural heterogeneity, resulting in increased bird diversity and reproductive success during the breeding season. For example, patch-burning and grazing, a process by which a field is burned and/or grazed in patches, creates a more heterogeneous system and increases species diversity (Fuhlendorf et al. 2006) while patch-burning also improves reproduction for nesting birds (Churchwell et al. 2008). In contrast, traditionally managed CSG, such as hayfields or pastures, are managed homogeneously with disturbances occurring frequently and uniformly across the landscape. Uniform management limits field heterogeneity and therefore only satisfies the habitat requirements of a limited suite of species (Fuhlendorf et al. 2006). This was demonstrated in the current study by a reduced suite of species occupying CSG fields in winter compared to WSG fields. In contrast, many of the WSG fields included in the study were managed using patch-burning techniques and had less frequent disturbances, resulting in increased structural heterogeneity, and thereby increased bird species diversity.



The response of bird communities to management timing can vary greatly during the breeding season (Brawn et al. 2001; Perkins et al. 2009), though few studies have explored the response of wintering bird communities. Furthermore, no studies have compared the response of winter bird communities to the timing of management in CSG vs. WSG fields. Hovick et al. (2014) explored the response of six overwintering grassland species to time since disturbance in a tallgrass prairie and found varying results, with each species demonstrating habitat-associations at different stages of regrowth. However, time since disturbance was binned into larger time windows than the current study, with shortest time since disturbance being within < 12 months and the longest being > 24 months. The current study explored the response of the winter bird community on a shorter time scale (< 12 months), as grasslands in the study region can be managed several times throughout the year. For example, traditionally managed hayfields in the eastern US are harvested earlier and more frequently than WSG, with as many as 3-4 cuttings annually (Savoie et al. 1985). In contrast, WSG fields managed for hay or biomass production are harvested later in the season to accommodate a later growing season, and only allow for one or two harvests a year (Vogel et al. 2002). Fields managed for wildlife are generally managed during winter months to coincide with optimal burning conditions (e.g., prescribed burns) or to stimulate forb growth (e.g., disking) and thus are not disturbed during the growing season (Harper 2007). My findings show that fields left undisturbed through the growing season, regardless of grass type, have significantly higher bird species diversity during the winter months than traditionally managed CSG fields. Thus, leaving CSG fields fallow throughout the growing season, or

longer, can promote similar structure to WSG, resulting in increased species diversity. However, WSG fields managed throughout the growing season did not differ significantly from CSG fields that had not been managed in fall or summer. This result suggests that WSG fields improve winter habitat quality regardless of management timing. One explanation of this result is that WSG develop later in the growing season than CSG (Newman & Moser 1988) resulting in later emergence and dispersal of seeds, potentially providing an important winter food source. Another explanation is that WSG are harvested at a taller height (20-40 cm stubble; Forwood & Magai 1992) than traditionally managed CSG fields (5 - 15 cm stubble; Gillen & Berg 2005), leaving more cover for winter birds. My vegetation surveys estimated a higher average height of fall- and summer-managed WSG fields (0.67 m and 1.17 m, respectfully), compared to the average height fall- and summer-managed CSG fields (0.21 m and 0.74 m, respectively). However, my study had few fall- (n = 5) and summer-managed (n = 3) WSG fields. Further work needs to focus on identifying optimal management timing in WSG for wintering grassland bird species.

My findings suggest that WSG fields improve winter habitat quality for a suite of early successional species, and therefore can be promoted as a conservation tool for declining species. NMDS results demonstrated that early successional species were most abundant in fields with increased structural heterogeneity, which was conducive to WSG fields. In contrast, fields with low structural heterogeneity were more conducive to grassland-obligate species with the exception of Savannah Sparrows. Similar to previous winter studies, Savannah Sparrows had less specific requirements and were observed in a

range of habitat types, vegetation heights and COV values (Hovick et al. 2014; Saalfeld et al. 2016). Previous studies have also made this observation of Eastern Meadowlarks (Hovick et al. 2014; Saalfeld et al. 2016), though my study had almost exclusive occupancy of this species in recently managed fields regardless of field composition. This could be due to differences in regional responses of vegetation to management, which differ as a function of rainfall and soil type, in addition to season of management (Baldwin et al. 2007; Twidwell et al. 2012). It is possible that increased rainfall and productive soils during the growing season in eastern regions result in denser vegetation, which deters meadowlarks during the breeding season (West et al. 2016). This result emphasizes the importance of considering regional differences in habitat structure and associated habitat-use, especially for species of concern.

Events and processes occurring during the non-breeding season can significantly influence individual performance in subsequent seasons (Harrison et al. 2011). For example, high quality wintering habitat is associated with earlier arrival dates on the breeding grounds and increased fledgling survival in American Redstarts (Norris et al. 2004). Barn Swallows (*Hirundo rustica*) demonstrate earlier arrival dates with favorable winter conditions, resulting in increased frequency of second broods and a higher number of fledged offspring (Saino et al. 2004). It is likely that short-distance migrant and resident species occupying North American grasslands in winter are similarly influenced in subsequent seasons by winter habitat quality, though these findings have not been elucidated. Therefore, timing of grassland management could have severe impacts on winter habitat suitability and associated bird survival and reproduction. Though the

results of current study do not reflect habitat-associated survival, they demonstrate patterns of habitat-use for wintering bird communities that provide a foundation for future research. For example, recent advances in the use of intrinsic markers provide opportunities to quantify winter habitat quality using habitat-specific isotopic signatures (Marra *et al.* 1998; Norris & Marra 2007; Rushing, Marra & Dudash 2016). Thus, future work should focus on comparing the quality of CSG and WSG fields as wintering habitat and the associated survival and subsequent reproduction of birds overwintering in these fields.

### **Management Implications**

My findings agree with research on grassland bird communities during the breeding season that the structural heterogeneity associated with WSG and their management support higher bird species diversity and richness in winter. This work has important conservation implications, as many researchers have speculated that North American grassland bird populations are limited by habitat during the non-breeding season (Brooks & Temple 1990a; Hostetler *et al.* 2015; Marra *et al.* 2015b). My results support the hypothesis that the composition of plant species and their management timing strongly influences vegetation structure, and these factors influence the winter grassland bird community. Without information on how land management affects survival and subsequent reproduction, these findings can lay a foundation for future research exploring the factors that influence these important responses. This work increases our understanding of avian habitat associations during winter and provides empirical support

for optimizing management practices to improve the quality of habitat for grassland birds during the non-breeding season.

## **CHAPTER FOUR : SEASONAL CHANGES IN THE DISTRIBUTION OF A PARTIAL MIGRANT**

### **Introduction**

Understanding seasonal distribution patterns of species is a fundamental part of monitoring and conserving populations. For animals that migrate, a spatial and temporal study across multiple scales is necessary to adequately identify potential focal areas for effective conservation throughout their annual cycle (Haig et al. 1998). However, migratory behavior influences seasonal variation in species-habitat associations (Sol et al. 2005; Zuckerberg et al. 2016). For example, long-distance migrants exhibit seasonal changes in habitat use (Robbins et al. 1989) while temperate short-distance migrants and residents often occupy similar habitats throughout the annual cycle (Zuckerberg et al. 2016). For species that are partial migrants, with some individuals in a population migrating and others being sedentary (Chapman et al. 2011), seasonal changes in habitat use are not well understood.

Occupancy models generate spatially explicit predictions of occurrence for species by identifying significant species-habitat associations (MacKenzie et al. 2002). Model results can guide conservation decisions by predicting a species response to important ecological events, such as climate change (Sinclair et al. 2010), biological invasions (Giljohann et al. 2011), and habitat loss (Hefley et al. 2015). Occupancy models are also used to delineate habitat for species conservation and reintroduction

programs (Pearce & Lindenmayer 1998; Monnet et al. 2015). However, they rarely incorporate annual migrations (Guisan & Thuiller 2005). Although occupancy models are well suited for studying migratory species (Jones 2011), collecting occurrence data at large scales such as in different breeding and non-breeding habitat can be logistically problematic and expensive (Haig et al. 1998). Open access databases collected by citizen scientists can provide species' occurrences across North America (Link et al. 2008; Sullivan et al. 2009; Sauer et al. 2011), and may provide the missing element to creating occupancy models for migratory species. This is especially useful for monitoring species of management concern that are listed as threatened or endangered by state or federal agencies but lack funding allocated for monitoring.

The Loggerhead Shrike (*Lanius ludovicianus*), a predatory songbird, is an example of a declining, but not yet endangered, species that is well documented by open access databases such as Breeding Bird Survey (Sauer et al. 2011) and eBird (Sullivan et al. 2009). The Loggerhead Shrike is a partial migrant, with migratory northern populations and resident southern populations (Burnside 1987; Pérez & Hobson 2007). Their total abundance in North America has declined by more than 70% since the initiation of the Breeding Bird Survey in 1966 (Rosenburg et al. 2016), but the decline has not been geographically uniform. Migratory populations in the northeastern United States and Canada are nearly extirpated, warranting a reintroduction program in Ontario (J. Steiner 2013), whereas Loggerhead Shrikes are still common in scrubland along the Gulf coast from Texas to Florida (Cade & Woods 1997). Therefore, high-density regions

in the southeast offer an opportunity to determine which environmental features are conducive to high Shrike densities throughout their annual cycle.

The causes of Loggerhead Shrike declines remain unclear and likely involve events on both the breeding and non-breeding grounds. Evidence suggests that habitat loss and degradation on the wintering grounds are the primary driver of the declines (Prescott and Collister 1993, Yosef 1994, Cade and Woods 1997, Chabot et al. 2011). However, current habitat suitability models are constructed from breeding season habitat associations alone (Yosef & Grubb 1994; Lauver et al. 2002; Etersson 2003; Jobin et al. 2005; Shen et al. 2013a) and fail to consider the non-breeding season, a period of the annual cycle that could be critically important for Shrike populations. For example, several models have identified a positive relationship with open country landscapes, such as pastures and old fields, characterized by widely-spaced shrubs and low trees (Brooks & Temple 1990b; Cade & Woods 1997; Jobin et al. 2005). More recently, satellite imagery was used to identify a negative relationship between Shrike presence and productive grassland habitats using normalized difference vegetation index (NDVI) (Shen et al. 2013a). Several of these fine-scale models suggest that Shrikes are not limited solely by habitat because of the presence of unoccupied “high quality” habitat (Lauver et al. 2002; Etersson 2003; Fornes 2004), but, these models do not incorporate climatic or landscape features. Illán *et al.* (2014) found precipitation and winter temperature to be significant predictors of bird distributions and abundance for 59% of bird species modelled in the northwestern United States. Area effects (e.g., proportion of grassland) accounted for 17% of the variation in breeding grassland bird species richness



in Wyoming (Hamer et al. 2006). Like Loggerhead Shrikes, several of these grassland species are year-round residents or partial migrants, indicating that area effects are not limited to breeding habitat use. Therefore, occupancy models incorporating climatic, landscape and site-specific features simultaneously may better identify suitable breeding and non-breeding habitat for species that exhibit partial migration.

In this chapter, I used occupancy models (MacKenzie et al. 2002) to estimate occupancy and detectability of a partial migrant, the Loggerhead Shrike, in the southeastern US during breeding and non-breeding seasons. My objectives were to: (1) estimate current Shrike occupancy across the southeastern US; (2) identify relationships between landscape-level habitat variables and Shrike occupancy during breeding and non-breeding seasons; and (3) identify differences in habitat associations between seasons. I hypothesized that site-specific habitat preferences of Shrikes would not change significantly between seasons, but that climatic and landscape-scale associations would shift occupancy patterns. In addition, I predicted that estimated occupancy would be greater in the southeast during non-breeding compared to breeding season due to the southern migration of northern populations.

## **Methods**

### **Study Area**

Environmental attributes and bird abundance data were collected from 17 physiographic areas within the mid-Atlantic and southeastern US (Figure 4.1). Though the complete range of Loggerhead Shrikes extends north into Ontario and Quebec and west of the Rockies, I limited the study area to this eastern region where Shrikes occur

year-round; an area that falls within a single terrestrial biome (temperate broadleaf and mixed forests) (Olson et al. 2001). Within this region, Shrike populations range from stable to significantly declining (Sauer et al. 2011), offering an opportunity to explore species-environmental relationships related to population decline independent of shifting biomes, as evidenced by long-distance migrants (Leisler 1990).

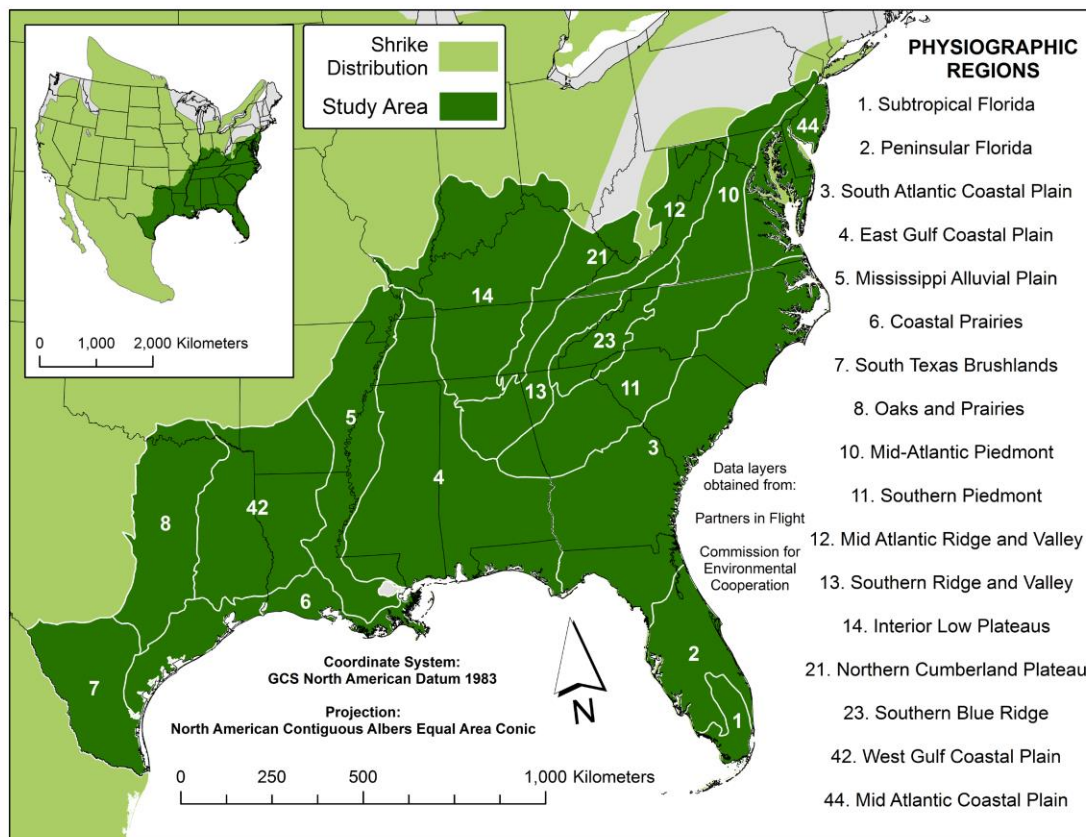


Figure 4.1. Map of study area based on 17 physiographic regions defined by Partners in Flight where Loggerhead Shrikes occur.

## **Loggerhead Shrike Detections**

Detections of Loggerhead Shrikes during both the breeding and non-breeding season were obtained from eBird (Sullivan et al. 2014), an online database of real-time bird observations populated by birders. Occurrence maps were created from a subset of eBird checklists that report observer effort, number of observers, every species detected, provided the number of Shrikes detected and used a “stationary” protocol whereby the observers remained at a single GPS location while birding. Using this protocol avoids the misidentification of observation locations that can occur when observations are submitted as one location but collected over several kilometers of birding. Breeding season records were obtained between 1 April and 30 June and for the non-breeding season between 1 November and 28 February. Eight years of data were selected (2008-2015) to coincide with the collection period for the environmental data. Years were pooled to increase the likelihood that sites were sampled multiple times and sites visited only once were eliminated from the data set. I assumed no annual change in distribution for each seasonal sampling period. I created capture histories, structured by month, for each site using Shrike detections resulting in three intervals for each sampling season. Complete checklists submitted where no Shrikes were detected were used as absence points. 41,637 locations were used to model breeding season occurrence, 3% (n=1,231) of which reported Shrike detections (Figure A.1. A in the Appendix). 47,410 locations were used to model non-breeding season occupancy, with 5% of sites (n=2,501) reporting Shrike observations (Figure A.1. B in the Appendix).

### **Detection Covariates ( $p$ )**

I used observation effort covariates to model differences in Shrike detection probability among observers and sites (Table 2 in the Appendix). These included the time spent searching for birds (in minutes; NM), the number of submitted checklists for each site (CL) and the distance of the observer to the road (in meters; RD). Distance to road was included as an observation covariate as bird watchers commonly station themselves on or near roads due to ease of traveling and concerns over property ownership (Downes et al. 2016; Lituma & Buehler 2016). ArcGIS 10.3.3 (ESRI 2015) was used to measure the Euclidean distance (shortest linear distance) from each eBird location to the nearest primary or secondary road. Month of detection (MO) was also included as an observation covariate to describe seasonal trends.

### **Occupancy Covariates ( $\psi$ )**

Environmental covariates used for breeding and non-breeding models included habitat, climate and landscape features. These covariates were selected based on perceived ecological relationships between Shrike occupancy and environmental features (Table 4.1). Karst rock formations (USGS 2004) were included in the model as a simplified binary layer of presence/absence as other species of Shrikes have been associated with this topography (Baláž 2007). The national land cover categories (USDA 2011) were collapsed to five to reflect only those land cover features relevant to Shrikes: Deciduous forest, evergreen forest and mixed forest were combined into one “forest” category; cultivated crops, open space and low-intensity development were combined into a “low development” category; pasture/hay was combined with all shrubland and herbaceous categories to form “open landscape”; all medium to high intensity

development categories were merged into “high development”; and all remaining land cover types were combined in an “other” category. Maximum normalized difference vegetation index (NDVI; Didan 2015) was calculated for breeding and non-breeding seasons respectively using the online Google Earth Engine platform (Google Earth Engine Team 2015).

Table 4.1. Data descriptions, sources and relevancy for occupancy covariates included in breeding and non-breeding models ( $\Psi$ ).

Covariate	Description	Source	Relevancy to model	Reference(s)
<i>Habitat Variables</i>				
Cover <sup>b,n</sup>	Land cover reduced to 5 general habitat classes: Open landscape, Cropland/Low Development, High development, Forest, Other	Crop Land USGS 2011	Shrikes are generally found in open landscapes with interspersed shrubs and trees such as old fields, pastures and scrublands.	Brooks and Temple 1990a, Chabot et al. 2011, Fornes 2004
karst <sup>b,n</sup>	Presence/absence of karst topography	USGS 2004	Karst landscapes provide shelterbelts of osage orange ( <i>Maclura pomifera</i> ), red cedar ( <i>Juniperus virginiana</i> ) and honey locust ( <i>Gleditsia triacanthos</i> ); all preferred nesting trees for Loggerhead Shrikes.	Pruitt and others 2000, Beckmann et al. 2001
65	max_NDVI <sup>b</sup>	MODIS 2008-2015	Loggerhead Shrikes are negatively associated with productive grassland habitats in midwestern-Canada	Shen et al. 2013a, b
	mean_NDVI <sup>n</sup>			
<i>Climatic Variables</i>				
b6 <sup>n</sup>	Minimum temperature (°C) of coldest month	BioClim	Precipitation and winter temperature are significant predictors of bird distributions and abundance in northwestern US	Illán et al. 2014
b1 <sup>n</sup>	Mean minimum temperature (°C) of coldest quarter (3 months)			
b15 <sup>b,n</sup>	Precipitation seasonality (percentage of precipitation variability)			
b16 <sup>b,n</sup>	Precipitation (mm) during the wettest quarter			
b19 <sup>n</sup>	Precipitation (mm) during the coldest quarter			
<i>Landscape Variables</i>				
perc_for <sup>b,n</sup>	% forest cover within a 2.5km radius	Crop Land USGS 2011	Area effects, such as the proportion of grassland influence grassland bird species richness	Hamer et al. 2006
perc_gras <sup>b,n</sup>	% grassland cover within a 2.5km radius	TIGER		
road_den <sup>b,n</sup>	Density of roads per square km	census 2012	Road mortality a significant thikes; Anthropogenic noise from roads drives habitat selection by birds	Blumton 1989, Kleist et al. 2016

<sup>b</sup> Covariate included in breeding models, <sup>n</sup> Covariate included in non-breeding models

The remaining climate variables were downloaded from WorldClim (Hijmans et al. 2005). The Worldclim data we used are climate rasters with a spatial resolution of 1 km<sup>2</sup>. I included monthly total precipitation of the wettest quarter (3-months), monthly total precipitation of the coldest quarter, mean minimum temperature of the coldest month, and mean temperature of the coldest quarter. These bioclimatic variables represent seasonality and extreme or limiting environmental factors (Beaumont et al. 2005). Rasters for the landscape covariates were created using the ArcGIS 10.3.3 (ESRI 2015) focal statistics tool to calculate proportions of land cover classes (% cover of grassland and forest) and line density calculations of roads (road density; U.S. Census Bureau 2012). Categorical covariates were modelled as binomial variables, and continuous covariates were standardized across the entire data set by centering to a mean value of zero (Zuckerberg et al. 2011). All rasters were resampled to a common cell size of 750 x 750 m to reflect the range of territory sizes reported for Loggerhead Shrikes (10-20 ha; (Brooks & Temple 1990c; Lauer et al. 2002; Douglas M Collister 2007) and to account for the minimum suitable habitat required surrounding a territory (50 ha; Chabot, Titman & Bird 2011; Jobin *et al.* 2005). Rasters were created and manipulated in ArcGIS 10.3.3 while R (R Core Team 2015b) was used to manipulate and organize all Shrike occurrence data. The R package “raster” (Hijmans et al. 2016) was used to extract values from habitat rasters to eBird locations.

## **Occupancy Model**

I used a single-season occupancy model (MacKenzie et al. 2002) and the package “unmarked” in R (Fiske & Chandler 2011) to analyze the habitat associations of Loggerhead Shrikes. I first tested models that included only detection covariates and used an intercept-only model for occupancy. I ranked and compared detection models using Akaike’s Information Criterion (AIC; Akaike 1974) and considered the covariates in the AIC-best detection model as useful for accounting for variation in the probability of detection. Models having a difference of  $\leq 2$  AIC units were considered equally parsimonious (Burnham & Anderson 1998). I used the best-fit set of detection covariates in all subsequent models of occupancy. I included combinations of habitat, climatic, and landscape covariates that I predicted would affect species occupancy based on the literature. Spearman’s rank correlation was used to ensure that covariates within each model were not highly correlated ( $r < 0.5$ ). I ranked and compared occupancy models using the same methods as detection models. I tested the fit of the highest-ranked occupancy models using the parboot function in unmarked. I assessed model fit using error sum of squares (SSE). Only models that fit the data ( $SSE > 0.05$ ) were used to make inferences about habitat associations. Maps of estimated breeding and non-breeding season occupancy for the entire study area were generated in ArcGIS using predicted values from the top models.

## **Results**

### **Detection Probability**

Loggerhead Shrike detection probability ( $p$ ) varied as a function of number of checklists submitted and distance to road during both breeding (Table 4.2) and non-



breeding seasons (Table 4.3). The probability of detection increased with the number of checklists submitted for each location and decreased as distance to road increased.

Detectability did not vary predictably between breeding and non-breeding locations.

Table 4.2. Parameter estimates from the top breeding season occupancy model for Loggerhead Shrikes. Variables are listed in order of contribution based on beta estimates.

Top Model <sup>†</sup> : $\Psi(\text{road\_dens}+\text{Cover}+\text{max\_NDVI}+\text{karst}+\text{perc\_for}) p(\text{CL}+\text{RD})$			
Covariate	Covariate Description	Estimate	SE
<i>Occupancy:</i>			
(Intercept)		-3.273	0.108**
Cover4	Grassland	1.011	0.109*
perc_for	% forest cover within a 2.5km radius	-0.996	0.077**
road_dens	Road Density	-0.871	0.061**
karst1	Karst present	0.673	0.078**
Cover5	High Development	-0.376	0.140*
max_NDVI	Maximum NDVI during breeding	-0.372	0.051**
Cover3	Forest	-0.150	0.157
Cover2	Other (wetlands, barren, etc.)	0.126	0.116
<i>Detection:</i>			
(Intercept)		-1.417	0.092**
CL	Number of checklists	0.921	0.083**
RD	Distance to nearest road	-0.133	0.028*

\* $P < 0.01$ ; \*\* $P < 0.001$

### Breeding Occupancy

Multimodel inference identified a single most parsimonious model for breeding season occupancy based on the lowest AIC (AIC = 10,441.07; Table 3 in the Appendix).

This model included effects of karst topography, land cover, maximum NDVI, road density and percent forest cover (Table 4.2). Model fit statistics suggested the most parsimonious model fit the data (SSE = 0.396). Probability of breeding occupancy ( $\psi$ ) was highest in dry open landscapes with a low percentage of forest cover within 2.5 km and a low road density. The presence of karst topography increased the probability of breeding occurrence while high NDVI values decreased occurrence. The most influential landscape-scale predictors of breeding occupancy were road density (Figure 2A in the Appendix) and percent forest within 2.5 km (Figure 2B in the Appendix), both demonstrating significant negative relationships with Shrike occupancy. The beta coefficients of this model were used to create a breeding season occupancy map for the southeastern US (Figure 4.2) with a range of predicted occupancy values from 0.00-0.95.

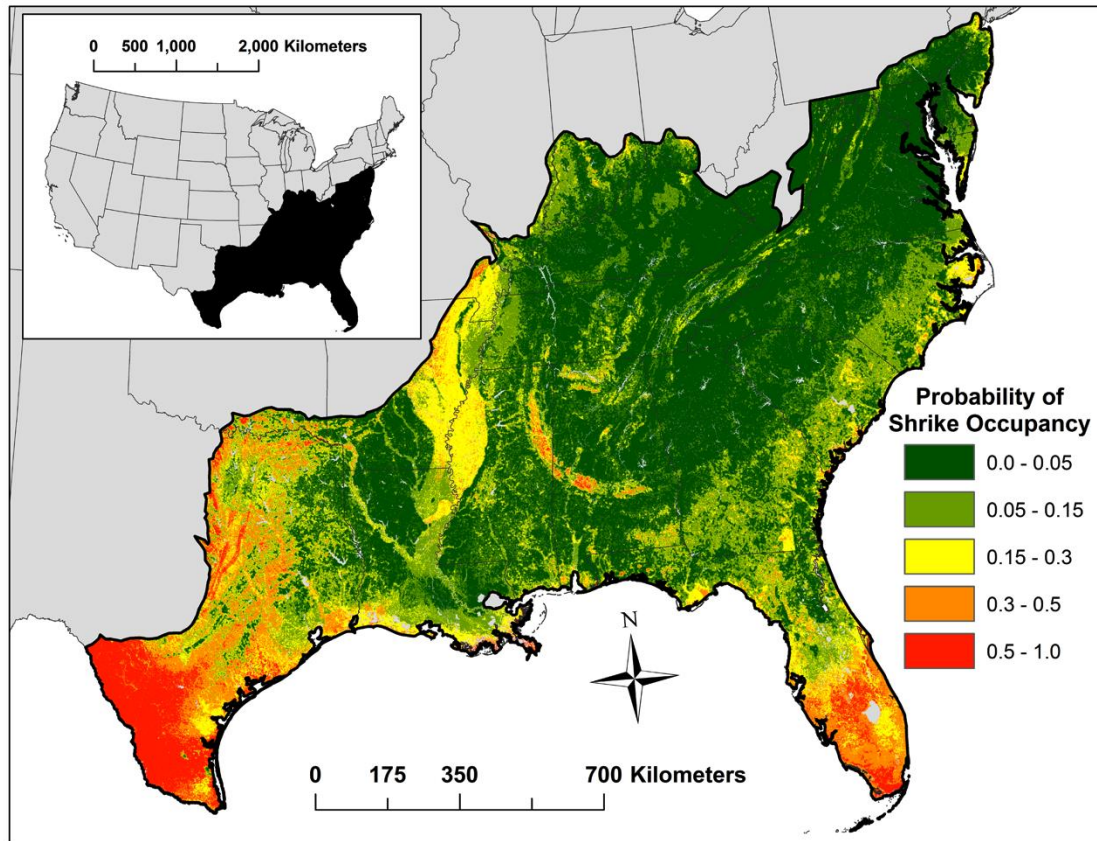


Figure 4.2. Current occupancy probability during breeding season for Loggerhead Shrikes based on predicted values from the top model. Classification breaks were derived using Jenks' Optimization (Jenks 1967) to identify natural breaks in the predicted occupancy estimates.

Table 4.3. Parameter estimates from the top winter season occupancy model for Loggerhead Shrikes. Variables are listed in order of contribution based on beta estimates.

Top Model <sup>†</sup> : $\Psi(\text{road\_dens}+\text{Cover}+\text{b11}+\text{karst}+\text{perc\_for}) p(\text{CL}+\text{RD})$			
Covariate	Covariate Description	Estimate	SE
<i>Occupancy:</i>			
(Intercept)		-2.31	0.073**
Cover4	Open landscape	1.036	0.085**
b11	Mean temperature of coldest 3 months of each year	0.998	0.057**
road_dens	Road density	-0.577	0.053**
perc_for	% forest cover within a 2.5km radius	-0.382	0.050**
Cover2	Other (wetlands, barren, etc.)	-0.222	0.086
karst1	Karst present	-0.189	0.07*
Cover5	High Development	-0.17	0.102*
Cover3	Forest	-0.075	0.116
<i>Detection:</i>			
(Intercept)		-1.157	0.059***
CL	Number of checklists	0.38	0.031***
RD	Distance to nearest road	0.016	0.017

\* $P < 0.01$ ; \*\* $P < 0.001$ ;  $P < 0.0001$

### **Non-Breeding Season Occupancy**

The top model (Table A.4. in the Appendix) for non-breeding season occupancy based on AIC included effects of land cover, percent forest, road density, temperature and karst (AIC = 19,599.55; Table 4.3). Model fit statistics suggested the most parsimonious model fit the data (SSE = 0.228). Probability of non-breeding occupancy ( $\Psi$ ) was highest in grasslands with warm winter temperatures and low road density. Percent forest within 2.5 km had a negative effect on occupancy as did the presence of karst. The most influential predictors of non-breeding occupancy were grassland land cover and mean temperature (Figure A.2. A in the Appendix), which both demonstrated positive relationships with Shrike occupancy. Similar to breeding occupancy, road density (Figure A.2. B in the Appendix) was strongly and negatively related to Shrike occupancy. The beta coefficients of this model were used to create a non-breeding season occupancy map for the study region (Figure 4.3) with a range of predicted occupancy values from 0.00-0.76.

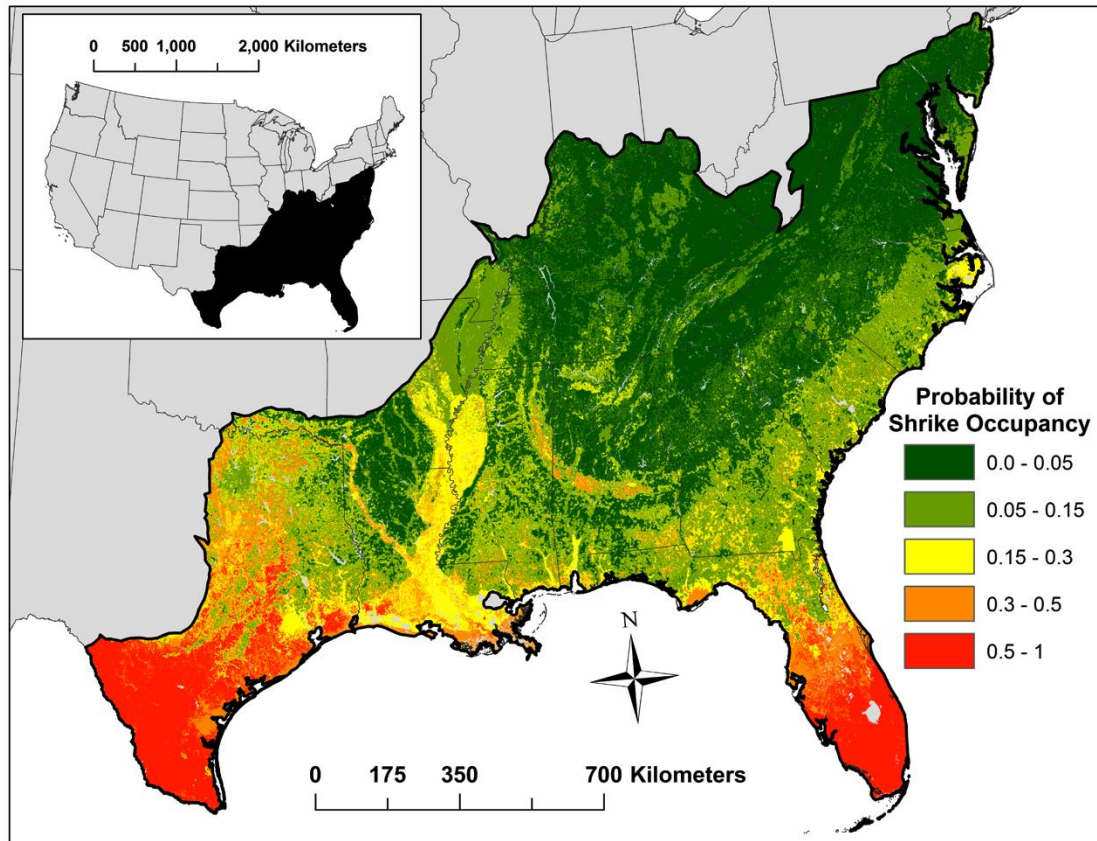


Figure 4.3. Current occupancy probability for Loggerhead Shrikes during the winter season based on predicted values from the top model. Classification breaks were derived using Jenks' Optimization (Jenks 1967) to identify natural breaks in the predicted occupancy estimates.

Maps of estimated occupancy probability show similar distribution patterns for Shrikes between the breeding and non-breeding seasons, with the breeding season model estimating slightly higher predicted occurrence patterns for areas identified as suitable by the model (mean occupancy probability for (1) breeding: 0.16 and; (2) non-breeding: 0.12). Using >5% probability of occurrence as a threshold to define potential Shrike occurrence, the non-breeding model predicted 22% more suitable area within the study

region (Figure 4.4), compared with the models created from breeding season. Covariates in both models were consistent across seasons, with the exception of NDVI being included only the breeding model and temperature being included only the non-breeding model. However, the strength of covariates used in both top models differed between seasons. Percent forest cover had a greater effect during the breeding season (beta coefficient: -0.996) than non-breeding season (beta coefficient: -0.382), having a negative effect on occupancy in both seasons. Climate-related covariates had a higher predictive ability during the non-breeding season, with warmer temperatures having a positive effect on non-breeding Shrike occupancy (beta coefficient: 0.998), while maximum NDVI had a negative influence on occupancy during the breeding season (beta coefficient: -0.372).

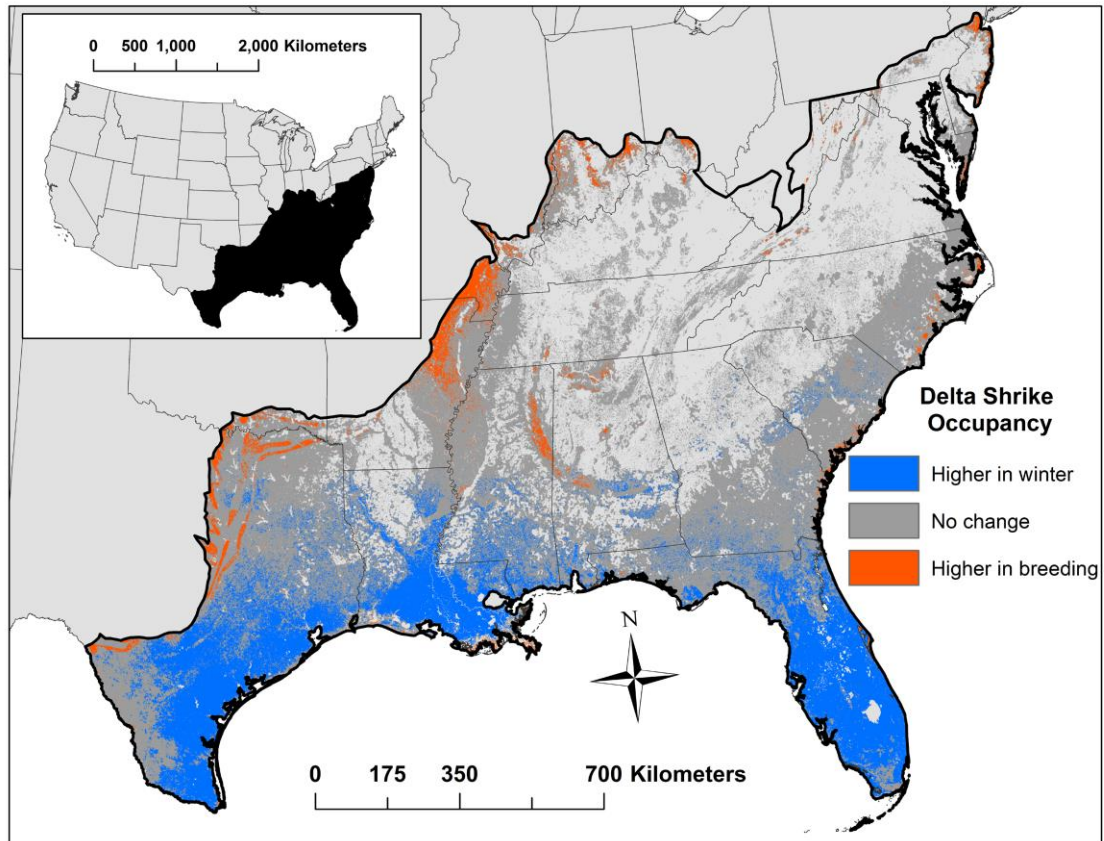


Figure 4.4. Seasonal differences in Loggerhead Shrike occupancy with a threshold of one standard deviation (0.8) from 0. Winter populations have a higher occupancy in southern regions with breeding populations having higher occupancy in northern and interior regions.

## Discussion

The conservation of a migratory species requires an understanding of habitat relationships throughout the annual cycle. Occupancy models can effectively model habitat relationships over large scales (MacKenzie et al. 2002), which is especially useful for species with large ranges or those that migrate. Recent research on non-breeding migratory songbird habitat has focused on long-distance migrants (e.g., Cooper et al.



2015, Hallworth et al. 2015, Marra et al. 2015b, Blackburn and Cresswell 2016, Rushing et al. 2016). Partial migrants have been less thoroughly studied and generally assumed to inhabit similar breeding and non-breeding habitat (Gilroy et al. 2016) like many resident species (McClure et al. 2013). This assumption could have major impacts on the conservation of partial migratory species that are in decline, as current conservation efforts are often based on data collected during the breeding season (Marra et al. 2015a). Many threatened migratory bird species appear to be declining due to changes in wintering habitats (Greenberg et al. 2005), including the Loggerhead Shrike (Brooks & Temple 1990b; Cade & Woods 1997), making the identification of non-breeding habitat requirements essential.

My occupancy models documented a seasonal shift in species-environmental relationships of Loggerhead Shrikes. During the non-breeding season, minimum temperature of the coldest 3 months was a strong predictor of occupancy. Shrikes, like other partial migrants (Chapman et al. 2011), move south in winter to seek warmer temperatures and probably increased arthropod and other prey abundance (Craig 1978). The non-breeding range shifts I documented can be used to generate predictions for how Shrikes might respond to changing environmental conditions. For example, Vélez-Espino *et al.* (2013) demonstrated that high environmental variation decreased fitness of a partial migrant, the brook trout (*Salvelinus fontinalis*), and highlighted the importance of preserving migrant and resident phenotypes throughout the eastern US to mitigate these effects. Thus, to minimize the detrimental effects of environmental change on other partial migrants, it may be important to consider the status of both migrant and resident

populations. With migrant Shrike populations currently declining more so than residents (Vallianatos et al. 2002), conservation emphasis should be placed on both the breeding and non-breeding grounds of the migrant population.

Although percent forest was included in both breeding and non-breeding models, the breeding model demonstrated a stronger, negative effect of forest cover on Shrike occupancy. Forest habitat has been linked to increased predation of Shrikes by raptors (Blumton 1989; Yosef 1994; Walk et al. 2006) particularly during the winter season. However, Shrikes also seek habitat adjacent to forests during winter for cover during inclement weather (Blumton 1989). The weaker influence of percent forest cover on non-breeding Shrike occupancy compared to breeding suggests that wintering Shrikes may prioritize cover during harsh weather over risks of predation. Meanwhile, the stronger negative relationship during breeding suggests that Shrikes may be making more of an effort to avoid predation to themselves and/or offspring during breeding by avoiding areas of dense woody vegetation.

The relationship between Shrike occupancy and forest cover also emphasizes the importance of considering landscape-scale features. Using percent forest cover within a 2.5 km radius (~2000 ha) as a surrogate measure of habitat fragmentation improved the model in both seasons (breeding season  $\Delta$ AIC: 194; non-breeding season  $\Delta$ AIC: 55), suggesting the importance of contiguous, open landscapes for Shrike conservation on a much larger scale than previously suggested. Previous studies have highlighted the importance of suitable habitat within 50 ha of occupied Shrike territories (Chabot et al. 2011, Jobin et al. 2005), which was incorporated into the cell size of the current model. I

included two additional patch sizes for incorporating percent forest – within 1.5 km (~1000 ha) and 2.5 km, with the latter consistently included in the most parsimonious models. I suggest two reasons why forest cover at this scale was negatively correlated with Shrike occupancy. First, the 2.5 km scale is likely a surrogate for habitat fragmentation (Wang et al. 2014). Second, areas with more contiguous, unfragmented open space support more Shrikes (Lagios et al. 2015), perhaps due to conspecific attraction (Etterson 2003).

Maximum NDVI was negatively related to occupancy during the breeding season. This relationship is likely the consequence of Loggerhead Shrikes selecting sparsely vegetated habitats for breeding. NDVI has been identified as important in a study of fine scale habitat use by Shrikes in Saskatoon (Shen et al. 2013a, 2013b). However, at the landscape scale considered here, scrubland habitats with karst geology likely have a relatively low NDVI compared to agricultural grasslands and forest. Shrikes, like other open-country avian predators require vegetation interspersed with bare ground (Atkinson et al. 2004; Britschgi et al. 2006). Indeed, presence of karst had a positive relationship with Shrike occupancy in the breeding model. Karst landscapes are known to exhibit relatively low productivity, as they include geologic features consistent with shallow, acidic soils with high drainage formed on limestone and dolostone (Waltham et al. 2007). In addition, karst landscapes may be associated with lower human development due to zoning regulations, and may play a role in occupancy (Dinger & Rebmann 1991). More research is needed to understand the importance of karst topography to Loggerhead Shrikes.

Both breeding and non-breeding models demonstrated that open landscapes are a strong predictor of Shrike occupancy. This result has important implications for the conservation of remaining open country habitat such as pastures, old fields and scrublands. Grassland habitats are becoming smaller and more fragmented by reforestation and development, particularly in the northeast (Cade & Woods 1997; Brennan et al. 2005a; Sleeter et al. 2013) where Shrikes are experiencing the steepest declines. Habitat loss and fragmentation has been suggested as one of the leading causes of Shrike population declines (Shen et al. 2013a). My model results suggested that conservation efforts for Loggerhead Shrikes should focus on the most contiguous, remaining areas of low-productivity shrubland, much of which is threatened by conversion to cropland, urbanization, and mining (Sleeter et al. 2013). Within these areas, managers should work to retain Shrike-specific habitat features such as scattered shrubs and trees in open country habitat (Bohall-Wood 1987; Chabot et al. 2001; Douglas M Collister 2007) and limit pesticide use (Blumton et al. 1990; Yosef 1994; Mineau & Whiteside 2013; Gibbons et al. 2015).

The decline of Loggerhead Shrikes has also been attributed to road mortality (Blumton 1989), one of the leading causes of direct anthropogenic mortality for North American birds (Loss et al. 2014). I found that road density was a significant negative predictor of Shrike occurrence in both breeding and non-breeding models. Road mortality was responsible for one third of reported winter mortalities in Virginia, with the highest mortality rates coinciding with the coldest temperatures (Blumton 1989). Noise associated with roads, which negatively affects birds during both breeding (Francis et al.

2009; Nemeth et al. 2013; Kleist et al. 2016) and non-breeding seasons (Ciach & Fröhlich 2016) could also be a factor. Further research is needed to test the relative strength of these two hypotheses.

Loggerhead Shrike occupancy in the Southeastern US is significantly greater during non-breeding than in breeding season. This has important implications for the design of future studies for Shrikes and other partial migrants. Data used to model non-breeding occupancy included non-resident and subdominant juvenile birds, in addition to residents, that may have been occupying low-quality habitat (Van Horne 1983). Quality of non-breeding habitats influences reproductive performance in the subsequent breeding season (e.g., Norris and Marra 2007, Tonra et al. 2011, Harrison et al. 2011), and as a result choices in habitat selection in winter can have important consequences on survival and reproduction (Inger et al. 2010). Thus, future studies should focus on how partial migrants use non-breeding habitats and how the quality of these habitats affect non-breeding and subsequent breeding survival and reproduction.

Occupancy models derived from citizen science data serve as a low-cost alternative to count indices and enable conservation managers to focus efforts over large areas that would otherwise be logistically impossible to monitor (Gould et al. 2012). The eBird dataset allowed me to model Loggerhead Shrike occupancy across the southeast US. However, eBird locations that are more frequently visited by birders, such as those nearby city centers or more accessible by car, reduce the number of points surveyed in the most rural and inaccessible areas, where Shrikes may be thriving. I built on the methods of Hallworth *et al.* (2015) to reduce these biases by including number of

checklists, number of minutes spent birding, and distance to road as observation covariates in the model. Number of checklists had a significantly positive relationship with detection probability in both breeding and non-breeding models, corroborating that locations more frequented by birders were more likely to have Shrikes detected if present and available for detection. Although distance to road was included in top models for both seasons, it had a much weaker effect on detectability than number of checklists, suggesting the two factors are linked. My protocol for use of citizen-science data is not species-specific and could be used as a guide for analysis of other resident or partial migrant species with large spatial extents.

In conclusion, Loggerhead Shrikes exhibit seasonal differences in occupancy across their range but only subtle shifts in habitat associations. My results provided further support that open country habitats are critical to the species, and suggested that road density and forest cover reduce Shrike occurrence. In addition, the negative influence of forest cover differed between seasons, with the breeding season exhibiting stronger negative relationships with forest. I also found that temperature was a strong predictor of occupancy during the non-breeding season. These relationships can be used to frame future research on the species' ability to withstand environmental change and to inform range-wide habitat conservation plans. While breeding season models are linked to habitat of the core breeding populations, the similarity of the important factors included in the top non-breeding model indicates that habitat limitations may not be linked to breeding activities but rather landscape features that impact adult survival. The results presented here demonstrate that occupancy models can uncover seasonally

complex species-environment relationships critical for informing conservation management of partial migrants throughout the annual cycle.

## APPENDIX

Table A.1. Total counts for all species observed in each year of surveying. Number of sites are indicated in parentheses. Three 200 m transects were surveyed at each site and each transect was visited three times within a season. Field types are CSG = cool-season grass fields and WSG = warm-season grass fields.

Alpha Code	Common Name	Species	2014			2015			2016			All years
			CSG (14)	WSG (15)	Total (29)	CSG (16)	WSG (18)	Total (34)	CSG (12)	WSG (6)	Total (18)	
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	0	0	0	6	0	6	4	0	4	10
AMGO	American Goldfinch	<i>Spinus tristis</i>	5	153	158	104	315	419	21	151	172	749
AMKE	American Kestrel	<i>Falco sparverius</i>	2	6	8	5	6	11	3	1	4	23
AMRO	American Robin	<i>Turdus migratorius</i>	48	2	50	2	4	6	11	0	11	67
ATSP	American Tree Sparrow	<i>Spizelloides arborea</i>	1	76	77	25	39	64	3	23	26	167
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	0	3	3	0	5	5	0	0	0	8
CACH	Carolina Chickadee	<i>Poecile carolinensis</i>	0	0	0	1	2	3	0	0	0	3
CAGO	Canada Goose	<i>Branta canadensis</i>	53	9	62	0	201	201	0	0	0	263
		<i>Thryothorus</i>										
CARW	Carolina Wren	<i>ludovicianus</i>	0	3	3	1	4	5	0	0	0	8
COHA	Coopers Hawk	<i>Accipiter cooperii</i>	0	0	0	0	0	0	0	1	1	1
DEJU	Dark-Eyed Junco	<i>Junco hyemalis</i>	18	36	54	65	14	79	50	17	67	200
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	0	2	2	2	6	8	0	3	3	13
EABL	Eastern Bluebird	<i>Sialia sialis</i>	49	40	89	53	128	181	15	23	38	308
EAME	Eastern Meadowlark	<i>Sturnella magna</i>	36	67	103	29	44	73	21	3	24	200
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	0	0	0	0	1	1	0	0	0	1
EATO	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	0	0	0	2	0	2	0	3	3	5
EUST	European Starling	<i>Sturnus vulgaris</i>	62	3	65	328	12	340	43	0	43	448
FISP	Field Sparrow	<i>Spizella pusilla</i>	5	79	84	83	205	288	7	65	72	444



FOSP	Fox Sparrow	<i>Passerella iliaca</i>	0	4	4	2	1	3	0	1	1	8
HOLA	Horned Lark	<i>Eremophila alpestris</i>	26	41	67	0	0	0	0	0	0	67
HOSP	House Sparrow	<i>Passer domesticus</i>	0	0	0	0	1	1	0	0	0	1
KILL	Killdeer	<i>Charadrius vociferus</i>	0	0	0	0	4	4	0	0	0	4
MODO	Mourning Dove	<i>Zenaida macroura</i>	0	0	0	0	31	31	0	0	0	31
NOBO	Northern Bobwhite	<i>Colinus virginianus</i>	0	0	0	0	4	4	0	1	1	5
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	8	11	19	11	7	18	3	5	8	45
NOFL	Northern Flicker	<i>Colaptes auratus</i>	11	18	29	0	1	1	0	0	0	30
NOHA	Northern Harrier	<i>Circus cyaneus</i>	3	12	15	2	11	13	1	2	3	31
NOMO	Northern Mockingbird	<i>Mimus polyglottos</i>	13	2	15	10	3	13	2	3	5	33
NOSH	Northern Shrike	<i>Lanius excubitor</i>	2	0	2	0	0	0	0	0	0	2
	Red-Bellied											
RBWO	Woodpecker	<i>Melanerpes carolinus</i>	0	3	3	1	1	2	0	0	0	5
RSHA	Red-Shouldered Hawk	<i>Buteo lineatus</i>	2	0	2	1	1	2	0	0	0	4
RTHA	Red-Tailed Hawk	<i>Buteo jamaicensis</i>	0	0	0	0	3	3	0	0	0	3
RWBL	Red-Winged Blackbird	<i>Agelaius phoeniceus</i>	2	2	4	9	1	10	0	0	0	14
		<i>Passerculus</i>										
SAVS	Savannah Sparrow	<i>sandwichensis</i>	15	385	400	62	345	407	5	130	135	942
SEOW	Short-Eared Owl	<i>Asio flammeus</i>	0	0	0	0	0	0	5	0	5	5
SOSP	Song Sparrow	<i>Melospiza melodia</i>	133	696	829	414	1216	1630	77	439	516	2975
SSHA	Sharp-Shinned Hawk	<i>Accipiter striatus</i>	2	0	2	0	0	0	0	0	0	2
SWSP	Swamp Sparrow	<i>Melospiza georgiana</i>	11	36	47	15	42	57	0	4	4	108
TUTI	Tufted Titmouse	<i>Baeolophus bicolor</i>	0	0	0	4	0	4	0	0	0	4
	White-Crowned											
WCSP	Sparrow	<i>Zonotrichia leucophrys</i>	0	0	0	13	1	14	0	2	2	16
	White-Throated											
WTSP	Sparrow	<i>Zonotrichia albicollis</i>	20	56	76	68	67	135	2	39	41	252
Total			527	1745	2272	1318	2726	4044	273	916	1189	7505

Table A.2. Data descriptions and sources for detection covariates included in breeding and non-breeding models ( $p$ ). Covariates were selected based on literature suggesting important detection covariates and are cited under references. All covariates were used in both breeding and winter models.

Model Covariate	Description	Data Source	Reference(s)
RD	Euclidean distance to road in meters	TIGER census 2012	Downes et al. 2016, Lituma and Buehler 2016
NM	Number of minutes spent birding	eBird	Hallworth et al. 2015
CL	Number of submitted checklists for that location	eBird	Hallworth et al. 2015
MO	Month of observation	eBird	Hallworth et al. 2015

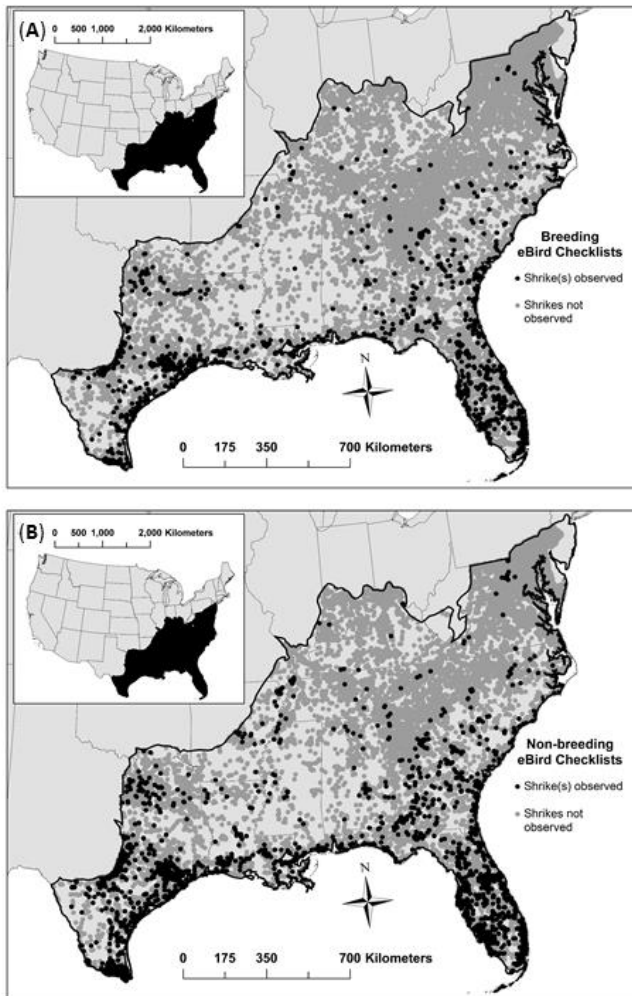


Figure A.1. Locations of birding checklists submitted to eBird during breeding (A) and non-breeding (B) seasons. Locations with Loggerhead Shrike observations show similar patterns across the seasons, with more observations submitted during winter.

Table A.3. Summary of all models considered for breeding season occupancy with the most parsimonious models listed in order from top to bottom

Model ID	Occupancy covariates ( $\psi$ )	Detection covariates ( $\rho$ )	nPars	$\Delta$ AIC
fm6	Cover+perc_for+road_dens+max_NDVI+karst	CL+RD	12	0
fm5	Cover+perc_for+road_dens+karst	CL+RD	11	62.46
fm4	Cover+perc_for+road_dens+max_NDVI	CL+RD	11	75.73
fm9	Cover+perc_for+road_dens	CL+RD	7	144.31
fm8	perc_for+road_dens+karst	CL+RD	7	162.7
fm7	perc_for+road_dens	CL+RD	6	235.02
fm2	Cover+road_dens	CL+RD	9	493.49
fm3	Cover+perc_for	CL+RD	9	508.92
fm1	perc_for	CL+RD	5	630.22
ob3	~	CL+RD	4	12065.48
ob1	~	CL	3	12161.72
ob4	~	NM+RD	4	12214.23
ob2	~	NM	3	12305.44
null	~	~	2	12324.57

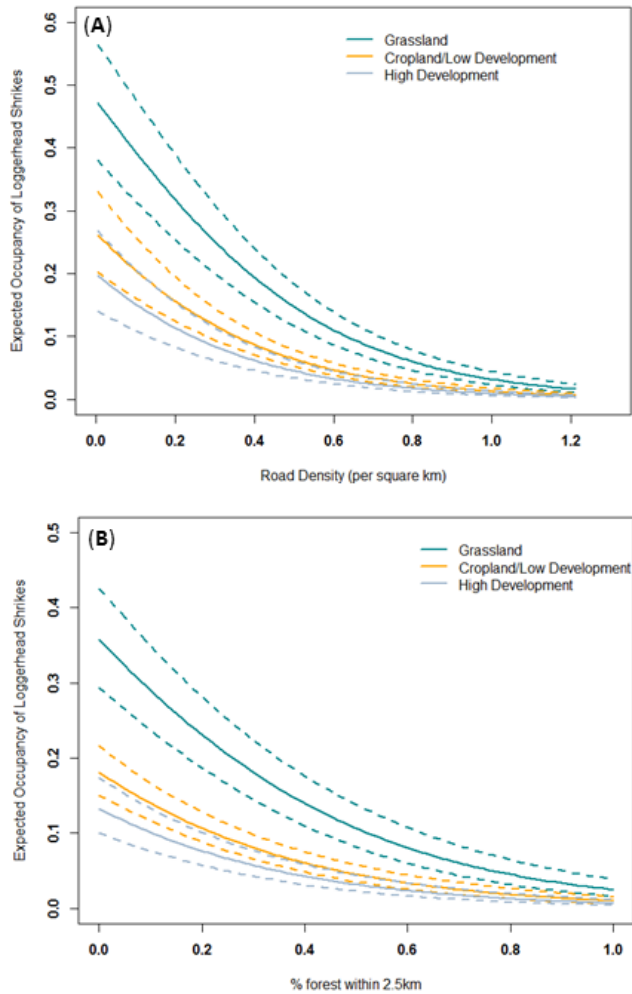


Figure A.2. Expected breeding occupancy of Loggerhead Shrikes in response to (A) road density and (B) percent forest cover within 2.5 km. Probability of breeding occupancy decreases with an increase in road density (km of road per km<sup>2</sup>) in three habitat types, indicating a negative relationship with human encroachment. Probability of breeding occupancy decreases with an increase in forest cover in three habitat types. For plotting road density, percent forest and NDVI were held constant (at their mean) while karst was set to “present”. For plotting percent forest, road density and NDVI were held constant (at their mean) while karst was set to “present”.

Table A.4. Summary of all models considered for non-breeding season occupancy with the most parsimonious models listed in order from top to bottom

Model ID	Occupancy covariates ( $\psi$ )	Detection covariates ( $p$ )	nPars	$\Delta$ AIC
fm9	Cover+b11+road_dens+perc_for+karst	CL+RD	12	0
fm8	Cover+b11+road_dens+perc_for+max_NDVI	CL+RD	12	5.01
fm6	Cover+b11+road_dens+perc_for	CL+RD	11	5.44
fm5	Cover+b11+road_dens+snow	CL+RD	11	23.43
fm4	Cover+b11+road_dens	CL+RD	10	74.54
fm1	Cover+b11	CL+RD	9	239.27
fm2	perc_for+b11	CL+RD	6	432.93
fm3	perc_for+road_dens	CL+RD	6	681.22
ob3	~	CL+RD	4	2907
ob1	~	CL	3	3003.24
ob4	~	NM+RD	4	3055.75
ob2	~	NM	3	3146.96
null	~	~	2	3166.09

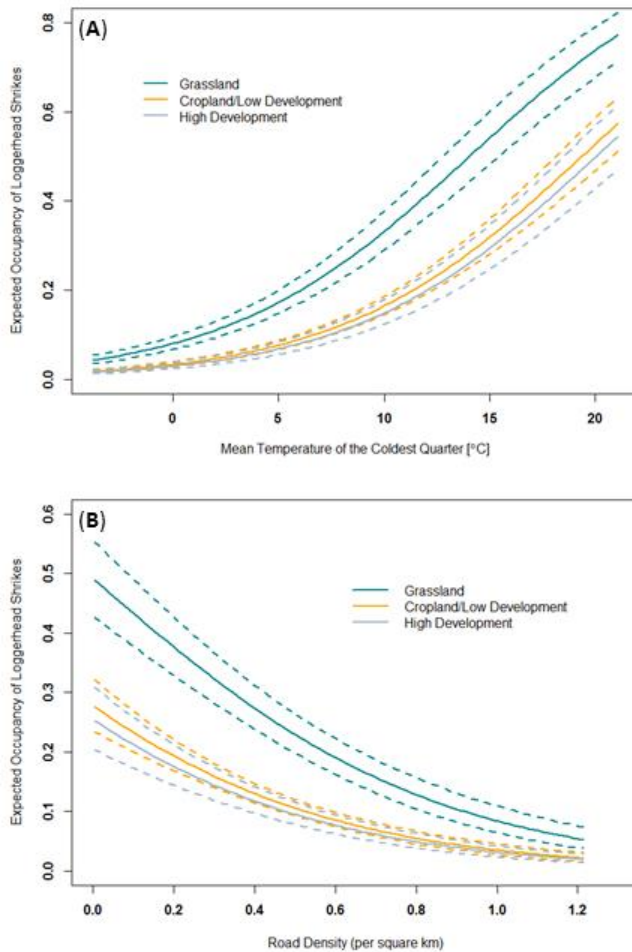


Figure A.2. Expected non-breeding occupancy of Loggerhead Shrikes in response to (A) temperature and (B) road density. Probability of occupancy during the non-breeding season increases with an increase in mean temperature in three habitat types, indicating a positive relationship with warm climate during non-breeding months. Probability of non-breeding season occupancy decreases with an increase in road density (km per square km) in three habitat types, indicating a negative relationship with human encroachment. For plotting temperature, road density was held constant (at its mean) while karst was set to present. For plotting road density, temperature was held constant (at its mean) while karst was set to present.

## REFERENCES

- Adams HL, Burger LW, Riffell S. 2013. Disturbance and landscape effects on avian nests in agricultural conservation buffers. *The Journal of Wildlife Management* **77**:1213–1220.
- Akaike H. 1974. A new look at the statistical model identification. *IEEE transactions on automatic control* **19**:716–723.
- Askins RA, Chavez-Ramirez F, Dale BC, Haas CA, Herkert JR, Knopf FL, Vickery PD. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. *Auk* **124**:1–46.
- Atkinson PW, Buckingham D, Morris AJ. 2004. What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? *Ibis* **146**:99–107.
- Bakker KK, Naugle DE, Higgins KF. 2002. Incorporating Landscape Attributes into Models for Migratory Grassland Bird Conservation. *Conservation Biology* **16**:1638–1646.
- Baláž M. 2007. On the breeding biology of the red-backed shrike (*Lanius collurio*) in the windbreaks of sw slovakia. *Acta Zoologica Universitatis Comenianae* **47**:35–39.
- Baldwin HQ, Grace JB, Barrow WC, Rohwer FC. 2007. Habitat relationships of birds overwintering in a managed coastal prairie. *Wilson Journal of Ornithology* **119**:189–197.
- Bartuszevige AM, Capparella AP, Harper RG, Frick JA, Criley B, Doty K, Erhart E. 2002. Organochlorine pesticide contamination in grassland-nesting passerines that breed in North America. *Environmental Pollution* **117**:225–232.
- Baselga A, Bonthoux S, Balent G. 2015. Temporal Beta Diversity of Bird Assemblages in Agricultural Landscapes: Land Cover Change vs. Stochastic Processes. *PLOS ONE* **10**:e0127913.
- Beaumont LJ, Hughes L, Poulsen M. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological modelling* **186**:251–270.
- Bechtoldt CL, Stouffer PC. 2005. Home-range size, response to fire, and habitat preferences of wintering Henslow's sparrows. *Wilson Bulletin* **117**:211–225.
- Beckmann JP, Kaufman GA, Kaufman DW. 2001. Influence of habitat on distribution and abundance of the eastern woodrat in Kansas. *Great Plains Research*:249–260.



- Berges SA, Moore LAS, Isenhardt TM, Schultz RC. 2010. Bird species diversity in riparian buffers, row crop fields, and grazed pastures within agriculturally dominated watersheds. *Agroforestry Systems* **79**:97–110.
- Bêty J, Gauthier G, Giroux J, Price AET. 2003. Body Condition, Migration, and Timing of Reproduction in Snow Geese: A Test of the Condition- Dependent Model of Optimal Clutch Size. *The American Naturalist* **162**:110–121.
- Blackburn E, Cresswell W. 2016. High within-winter and annual survival rates in a declining Afro-Palaeartic migratory bird suggest that wintering conditions do not limit populations. *Ibis* **158**:92–105.
- Blank PJ, Parks JR, Dively GP. 2011. Wintering Bird Response to Fall Mowing of Herbaceous Buffers. *Wilson Journal of Ornithology* **123**:59–64.
- Blumton AK. 1989. Factors affecting loggerhead shrike mortality in Virginia. Available from <http://theses.lib.vt.edu/theses/available/etd-06102012-040434/> (accessed October 14, 2016).
- Blumton AK, Fraser JD, Young RW, Goodbred S, Porter SL, Luukkonen DL. 1990. Pesticide and PCB residues for loggerhead shrikes in the Shenandoah Valley, Virginia, 1985–88. *Bulletin of environmental contamination and toxicology* **45**:697–702.
- Bohall-Wood P. 1987. Abundance, habitat use, and perch use of Loggerhead Shrikes in north-central Florida. *The Wilson Bulletin*:82–86.
- Bollinger EK, Bollinger PB, Gavin TA. 1990. Effects of hay-cropping on eastern populations of the Bobolink. *Wildlife Society Bulletin*:142–150.
- Brawn JD, Robinson SK, Thompson FR. 2001. The Role of Disturbance in the Ecology and Conservation of Birds. *Annual Review of Ecology and Systematics* **32**:251–276.
- Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs* **27**:325–349.
- Brennan LA, Kuvlesky WP, Morrison. 2005a. Invited paper: north american grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* **69**:1–13.
- Britschgi A, Spaar R, Arlettaz R. 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. *Biological Conservation* **130**:193–205.
- Brockway DG, Gatewood RG, Paris RB. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* **65**:135–152.
- Brooks BL, Temple SA. 1990a. Habitat availability and suitability for Loggerhead Shrikes in the upper Midwest. *American Midland Naturalist*:75–83.
- Brooks BL, Temple SA. 1990b. Habitat availability and suitability for Loggerhead Shrikes in the upper Midwest. *American Midland Naturalist*:75–83.
- Brooks BL, Temple SA. 1990c. Dynamics of a Loggerhead Shrike population in Minnesota. *The Wilson Bulletin*:441–450.

- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. 2001. Introduction to distance sampling estimating abundance of biological populations. Available from <http://www.citeulike.org/group/342/article/1349739> (accessed May 8, 2017).
- Burger L, McKenzie D, Thackston R, Demaso SJ. 2006. The Role of Farm Policy in Achieving Large-Scale Conservation: Bobwhite and Buffers. *Wildlife Society Bulletin* **34**:986–993.
- Burger LW. 2001. Quail management: issues, concerns, and solutions for public and private lands—a southeastern perspective. Pages 20–34 *Quail V: Proceedings of the Fifth National Quail Symposium*, Texas Parks and Wildlife Department, Austin, TX. Available from [http://www.researchgate.net/profile/L\\_Burger/publication/255606864\\_quail\\_management\\_issues\\_concerns\\_and\\_solutions\\_for\\_public\\_and\\_private\\_lands\\_a\\_southeastern\\_perspective/links/0046353a8a6b5ad5f1000000.pdf](http://www.researchgate.net/profile/L_Burger/publication/255606864_quail_management_issues_concerns_and_solutions_for_public_and_private_lands_a_southeastern_perspective/links/0046353a8a6b5ad5f1000000.pdf) (accessed December 2, 2015).
- Burnham KP, Anderson DR. 1998. Model selection and inference: a practical information-theoretic approach Springer-Verlag. New York.
- Burnside FL. 1987. Long-Distance Movements by Loggerhead Shrikes (*Movimientos distantes de Lanius ludovicianus*). *Journal of Field Ornithology*:62–65.
- Cade TJ, Woods CP. 1997. Changes in Distribution and Abundance of the Loggerhead Shrike. *Conservation Biology* **11**:21–31.
- Chabot AA, Titman RD, Bird DM. 2001. Habitat use by loggerhead shrikes in Ontario and Quebec. *Canadian Journal of Zoology* **79**:916–925.
- Chandler RB, Royle JA, King DI. 2011. Inference about density and temporary emigration in unmarked populations. *Ecology* **92**:1429–1435.
- Chapman BB, Brönmark C, Nilsson J-Å, Hansson L-A. 2011. The ecology and evolution of partial migration. *Oikos* **120**:1764–1775.
- Churchwell RT, Davis CA, Fuhlendorf SD, Engle DM. 2008. Effects of Patch-Burn Management on Dickcissel Nest Success in a Tallgrass Prairie. *The Journal of Wildlife Management* **72**:1596–1604.
- Ciach M, Fröhlich A. 2016. Habitat type, food resources, noise and light pollution explain the species composition, abundance and stability of a winter bird assemblage in an urban environment. *Urban Ecosystems*:1–13.
- Ciuzio E, Hohman WL, Martin B, Smith MD, Stephens S, Strong AM, Vercauteren T. 2013. Opportunities and challenges to implementing bird conservation on private lands. *Wildlife Society Bulletin* **37**:267–277.
- Collins SL, Wallace LL. 1990. Fire in North American Tallgrass Prairies. University of Oklahoma Press.
- Conover RR, Burger LW, Linder ET. 2007. Winter avian community and sparrow response to field border width. *Journal of Wildlife Management* **71**:1917–1923.
- Cooper NW, Sherry TW, Marra PP. 2015. Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. *Ecology* **96**:1933–1942.

- Costantini D, Carello L, Dell’Omo G. 2010. Patterns of covariation among weather conditions, winter North Atlantic Oscillation index and reproductive traits in Mediterranean kestrels. *Journal of Zoology* **280**:177–184.
- Craig RB. 1978. An Analysis of the Predatory Behavior of the Loggerhead Shrike. *The Auk* **95**:221–234.
- Crosby AD, Elmore RD, Leslie DM, Will RE. 2015a. Looking beyond rare species as umbrella species: Northern Bobwhites (*Colinus virginianus*) and conservation of grassland and shrubland birds. *Biological Conservation* **186**:233–240.
- Cully AC, Cully JF, Hiebert RD. 2003. Invasion of exotic plant species in tallgrass prairie fragments. *Conservation Biology* **17**:990–998.
- Cunningham MA, Johnson DH. 2006. Proximate And Landscape Factors Influence Grassland Bird Distributions. *Ecological Applications* **16**:1062–1075.
- Daubenmire R, others. 1968. Plant communities. A textbook of plant synecology. Plant communities. A textbook of plant synecology. Available from <http://www.cabdirect.org/abstracts/19700703090.html> (accessed November 29, 2015).
- Davis SK, Fisher RJ, Skinner SL, Shaffer TL, Brigham RM. 2013. Songbird abundance in native and planted grassland varies with type and amount of grassland in the surrounding landscape. *The Journal of Wildlife Management* **77**:908–919.
- Didan K. 2015. MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC. Available from <https://doi.org/10.5067/MODIS/MOD13Q1.006>.
- Diefenbach DR, Brauning DW, Mattice JA. 2003. Variability in grassland bird counts related to observer differences and species detection rates. *The Auk* **120**:1168–1179.
- Dinger JS, Rebmann JR. 1991. Ordinance for the control of urban development in sinkhole areas in the Blue Grass karst region, Lexington, Kentucky. Kentucky Geological Survey. Available from [http://www.uky.edu/KGS/pdf/ri11\\_29.pdf](http://www.uky.edu/KGS/pdf/ri11_29.pdf) (accessed May 8, 2017).
- Douglas M Collister SW. 2007. Territory size and foraging habitat of loggerhead shrikes (*Lanius ludovicianus*) in southeastern alberta. *Journal of Raptor Research* **41**:130.
- Downes C, Hudson M-A, Smith A, Francis C. 2016. The Breeding Bird Survey at 50: scientists and birders working together for bird conservation. *Avian Conservation and Ecology* **11**. Available from <http://www.ace-eco.org/vol11/iss1/art8/> (accessed September 13, 2016).
- Esely Jr JD, Bollinger EK. 2001. Habitat selection and reproductive success of Loggerhead Shrikes in northwest Missouri: a hierarchical approach. *The Wilson Bulletin* **113**:290–296.
- ESRI. 2015. ArcGIS Desktop: Release 10.3.3. Environmental Systems Research Institute, Redlands, CA.
- Etterson MA. 2003. Conspecific attraction in loggerhead shrikes: implications for habitat conservation and reintroduction. *Biological Conservation* **114**:199–205.
- Faith DP, Minchin PR, Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57–68.

- Fiske I, Chandler R. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software*, 43(10), 1-23. Available from <http://www.jstatsoft.org/v43/i10/>.
- Flanders AA, Kuvlesky WP, Ruthven DC, Zaiglin RE, Bingham RL, Fulbright TE, Hernández F, Brennan LA. 2006. Effects of invasive exotic grasses on south texas rangeland breeding birds. *The Auk* **123**:171–182.
- Fletcher Jr RJ, Dhundale JA, Dean TF. 2000. Estimating non-breeding season bird abundance in prairies: a comparison of two survey techniques. *Journal of Field Ornithology* **71**:321–329.
- Fletcher RJ, Dhundale JA, Dean TF. 2000. Estimating non-breeding season bird abundance in prairies: a comparison of two survey techniques. *Journal of Field Ornithology* **71**:321–329.
- Fornes GL. 2004. Habitat Use by Loggerhead Shrikes (*Lanius ludovicianus*) at Midewin National Tallgrass Prairie, Illinois: An Application of Brooks and Temple's Habitat Suitability Index. *The American Midland Naturalist* **151**:338–345.
- Forwood JR, Magai MM. 1992. Clipping frequency and intensity effects of big bluestem yield, quality, and persistence. *Rangeland Ecology & Management / Journal of Range Management Archives* **45**:554–559.
- Francis CD, Ortega CP, Cruz A. 2009. Noise Pollution Changes Avian Communities and Species Interactions. *Current Biology* **19**:1415–1419.
- Fuhlendorf SD, Harrell WC, Engle DM, Hamilton RG, Davis CA, Leslie DM. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* **16**:1706–1716.
- Gabrey SW, Afton AD, Wilson BC. 1999. Effects of winter burning and structural marsh management on vegetation and winter bird abundance in the Gulf Coast Chenier Plain, USA. *Wetlands* **19**:594–606.
- Gibbons D, Morrissey C, Mineau P. 2015. A review of the direct and indirect effects of neonicotinoids and fipronil on vertebrate wildlife. *Environmental Science and Pollution Research* **22**:103–118.
- Giljohann KM, Hauser CE, Williams NSG, Moore JL. 2011. Optimizing invasive species control across space: willow invasion management in the Australian Alps. *Journal of Applied Ecology* **48**:1286–1294.
- Gillen RL, Berg WA. 2005. Response of perennial cool-season grasses to clipping in the Southern Plains. *Agronomy Journal* **97**:125–130.
- Gilroy JJ, Gill JA, Butchart SHM, Jones VR, Franco AMA. 2016. Migratory diversity predicts population declines in birds. *Ecology Letters* **19**:308–317.
- Ginter DL, Desmond MJ. 2005. Influence of foraging and roosting behavior on home-range size and movement patterns of Savannah Sparrows wintering in south Texas. *The Wilson Bulletin* **117**:63–71.
- Google Earth Engine Team. 2015. Google Earth Engine: A planetary-scale geospatial analysis platform. Available from <https://earthengine.google.com>.
- Gould WR, Patla DA, Daley R, Corn PS, Hossack BR, Bennetts R, Peterson CR. 2012. Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the Greater Yellowstone Ecosystem. *Wetlands* **32**:379–389.

- Greenberg R, Runge MC, Marra PP. 2005. Modeling seasonal interactions in the population dynamics of migratory birds. Pages 375–389 *Birds of two worlds: the ecology and evolution of temperate-tropical migration systems*. Johns Hopkins University Press, Baltimore, MD.
- Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology letters* **8**:993–1009.
- Gutzwiller K. 1991. Estimating Winter Species Richness with Unlimited-Distance Point Counts. *Auk* **108**:853–862.
- Gutzwiller KJ. 1993. Refining the Use of Point Counts for Winter Studies of Individual Species. *The Wilson Bulletin* **105**:612–627.
- Haig SM, Mehlman DW, Oring LW. 1998. Avian Movements and Wetland Connectivity in Landscape Conservation. *Conservation Biology* **12**:749–758.
- Hallworth MT, Sillett TS, Van Wilgenburg SL, Hobson KA, Marra PP. 2015. Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. *Ecological Applications* **25**:336–347.
- Hamer TL, Flather CH, Noon BR. 2006. Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. *Landscape Ecology* **21**:569–583.
- Hanser SE, Knick ST. 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. Available from <http://pubs.er.usgs.gov/publication/70004637> (accessed January 5, 2016).
- Harper CA. 2007. Strategies for Managing Early Succession Habitat for Wildlife. *Weed Technology* **21**:932–937.
- Harper CA, Birckhead JL, Keyser PD, Waller JC, Backus MM, Bates GE, Holcomb ED, Brooke JM. 2015. Avian Habitat Following Grazing Native Warm-Season Forages in the Mid-South United States. *Rangeland Ecology & Management* **68**:166–172.
- Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* **80**:4–18.
- Heath SA, Shackelford CE, Riley CM. 2008. Project Prairie Birds: A Citizen Science Project for Wintering Grassland Birds. *Bulletin of the Texas Ornithological Society* **41**:51–59.
- Heath SK, Soykan CU, Velas KL, Kelsey R, Kross SM. 2017. A bustle in the hedgerow: Woody field margins boost on farm avian diversity and abundance in an intensive agricultural landscape. *Biological Conservation* **212, Part A**:153–161.
- Heffelfinger JR, Geist V, Wishart W. 2013. The role of hunting in North American wildlife conservation. *International Journal of Environmental Studies* **70**:399–413.
- Hefley TJ, Baasch DM, Tyre AJ, Blankenship EE. 2015. Use of opportunistic sightings and expert knowledge to predict and compare Whooping Crane stopover habitat. *Conservation Biology* **29**:1337–1346.
- Henningsen JC, Best LB, Kelly. 2005. Grassland bird use of riparian filter strips in southeast Iowa. *Journal of Wildlife Management* **69**:198–210.

- Henwood WD. 2010. Toward a strategy for the conservation and protection of the world's temperate grasslands. Available from <http://digitalcommons.unl.edu/greatplainsresearch/1074/> (accessed January 4, 2016).
- Herkert JR. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological applications* **4**:461–471.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**:1965–78.
- Hijmans RJ, Etten J van, Cheng J, Mattiuzzi M, Sumner M, Greenberg JA, Lamigueiro OP, Bevan A, Racine EB, Shortridge A. 2016. raster: Geographic Data Analysis and Modeling. Available from <https://cran.r-project.org/web/packages/raster/index.html> (accessed December 23, 2016).
- Hilty J, Merenlender AM. 2003. Studying Biodiversity on Private Lands. *Conservation Biology* **17**:132–137.
- Hostetler JA, Sillett TS, Marra PP. 2015. Full-annual-cycle population models for migratory birds. *The Auk* **132**:433–449.
- Hovick TJ, Elmore RD, Fuhlendorf SD. 2014. Structural heterogeneity increases diversity of non-breeding grassland birds. *Ecosphere* **5**:1–13.
- Hovick TJ, Elmore RD, Fuhlendorf SD, Engle DM, Hamilton RG. 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecological Applications* **25**:662–672.
- Hyland SE. 2005. Analysis of sinkhole susceptibility and karst distribution in the northern Shenandoah Valley, Virginia: implications for low impact development (LID) site suitability models. Virginia Polytechnic Institute and State University. Available from [https://www.researchgate.net/profile/Tamim\\_Younos/publication/266497445\\_analysis\\_of\\_sinkhole\\_susceptibility\\_and\\_karst\\_distribution\\_in\\_the\\_northern\\_shenandoah\\_valley\\_virginia\\_implications\\_for\\_low\\_impact\\_development\\_lid\\_site\\_suitability\\_models/links/54905ddc0cf225bf66a82c29.pdf](https://www.researchgate.net/profile/Tamim_Younos/publication/266497445_analysis_of_sinkhole_susceptibility_and_karst_distribution_in_the_northern_shenandoah_valley_virginia_implications_for_low_impact_development_lid_site_suitability_models/links/54905ddc0cf225bf66a82c29.pdf) (accessed March 28, 2017).
- Illán JG, Thomas CD, Jones JA, Wong W-K, Shirley SM, Betts MG. 2014. Precipitation and winter temperature predict long-term range-scale abundance changes in Western North American birds. *Global change biology* **20**:3351–3364.
- Inger R, Harrison XA, Ruxton GD, Newton J, Colhoun K, Gudmundsson GA, McElwaine G, Pickford M, Hodgson D, Bearhop S. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology* **79**:974–982.
- Irvin E, Duren KR, Buler JJ, Jones W, Gonzon AT, Williams CK. 2013. A multi-scale occupancy model for the grasshopper sparrow in the Mid-Atlantic. *The Journal of Wildlife Management* **77**:1564–1571.
- J. Steiner AAC. 2013. Field propagation and release of migratory Eastern Loggerhead Shrike to supplement wild populations in Ontario, Canada. *Global Re-introduction Perspectives*: 2013:80–84.

- Jansson C, Ekman J, von Brömssen A. 1981. Winter Mortality and Food Supply in Tits *Parus* spp. *Oikos* **37**:313–322.
- Jarzyna MA, Zuckerberg B, Finley AO, Porter WF. 2016. Synergistic effects of climate and land cover: grassland birds are more vulnerable to climate change. *Landscape Ecology* **31**:2275–2290.
- Jobin B, Grenier M, Laporte P. 2005. Using satellite imagery to assess breeding habitat availability of the endangered loggerhead shrike in Quebec. *Biodiversity & Conservation* **14**:81–95.
- Jones JPG. 2011. Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* **48**:9–13.
- Kéry M, Royle JA, Schmid H. 2005. Modeling avian abundance from replicated counts using binomial mixture models. *Ecological applications* **15**:1450–1461.
- Kleist NJ, Guralnick RP, Cruz A, Francis CD. 2016. Sound settlement: Noise surpasses land cover in explaining breeding habitat selection of secondary cavity nesting birds. *Ecological Applications*:n/a-n/a.
- Knopf FL. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* **15**:11.
- Kopp SD, Guthery FS, Forrester ND, Cohen WE. 1998. Habitat selection modeling for northern bobwhites on subtropical rangeland. *The Journal of wildlife management*:884–895.
- Lagios EL, Robbins KF, Lapierre JM, Steiner JC, Imlay TL. 2015. Recruitment of juvenile, captive-reared eastern loggerhead shrikes (*Lanius ludovicianus migrans*) into the wild population in Canada. *Oryx* **49**:321–328.
- Lauver CL, Busby WH, Whistler JL. 2002. Testing a GIS model of habitat suitability for a declining grassland bird. *Environmental Management* **30**:88–97.
- Leisler B. 1990. Selection and Use of Habitat of Wintering Migrants. Pages 156–174 in P. D. E. Gwinner, editor. *Bird Migration*. Springer Berlin Heidelberg. Available from [http://link.springer.com/chapter/10.1007/978-3-642-74542-3\\_11](http://link.springer.com/chapter/10.1007/978-3-642-74542-3_11) (accessed December 23, 2016).
- Link WA, Sauer JR, Niven DK. 2008. Combining breeding bird survey and Christmas Bird Count data to evaluate seasonal components of population change in northern bobwhite. *Journal of Wildlife Management* **72**:44–51.
- Lituma CM, Buehler DA. 2016. Minimal bias in surveys of grassland birds from roadsides. *The Condor*:715–727.
- Loss SR, Will T, Marra PP. 2014. Estimation of bird-vehicle collision mortality on U.S. roads. *The Journal of Wildlife Management* **78**:763–771.
- MacArthur RH, MacArthur JW. 1961. On Bird Species Diversity. *Ecology* **42**:594–598.
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**:2248–2255.
- Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM. 2015a. A call for full annual cycle research in animal ecology. *Biology Letters* **11**:20150552.
- Marra PP, Hobson KA, Holmes RT. 1998. Linking Winter and Summer Events in a Migratory Bird by Using Stable-Carbon Isotopes. *Science* **282**:1884–1886.

- Marra PP, Studds CE, Wilson S, Sillett TS, Sherry TW, Holmes RT. 2015b. Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. *Proc. R. Soc. B* **282**:20150624.
- Martin PA, Johnson DL, Forsyth DJ, Hill BD. 2000. Effects of two grasshopper control insecticides on food resources and reproductive success of two species of grassland songbirds. *Environmental Toxicology and Chemistry* **19**:2987–2996.
- Masse RJ, Strong AM, Perlut NG. 2008. The potential of uncut patches to increase the nesting success of grassland songbirds in intensively managed hayfields: a preliminary study from the Champlain Valley of Vermont. *Northeastern Naturalist* **15**:445–452.
- Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP. 2009. Habitat selection at multiple scales. *Ecoscience* **16**:238–247.
- McClure CJW, Rolek BW, Hill GE. 2013. Seasonal Use of Habitat by Shrub-Breeding Birds in a Southeastern National Forest. *Wilson Journal of Ornithology* **125**:731–743.
- McCoy TD, Ryan MR, Burger LW, Kurzejeski EW. 2001. Grassland bird conservation: CP1 vs. CP2 plantings in Conservation Reserve Program fields in Missouri. *The American Midland Naturalist* **145**:1–17.
- McCracken JD. 2005. Where the Bobolinks roam: the plight of North America's grassland birds. *Biodiversity* **6**:20–29.
- McIntyre NE, Thompson TR. 2003. A Comparison of Conservation Reserve Program Habitat Plantings with Respect to Arthropod Prey for Grassland Birds. *The American Midland Naturalist* **150**:291–301.
- McMellen AB, Schweitzer SH. 2005. A comparison of restored native grasslands and exotic grass pastures as wintering habitat for declining grassland bird species in the Southeastern United States. Page (OMara FP, Wilkins RJ, Mannelje L, Lovett DK, Rogers P a. M, Boland TM, editors).
- Mengak MT. 2004. Response of small mammal populations to fescue hayfield conversion to native warm season grasses in Bath County, Virginia. *Virginia Journal of Science* **55**:169–176.
- Miller DR, Bagley WT, Rosenberg NJ. 1974. Microclimate modification with shelterbelts. *Journal of soil and water conservation*. Available from <http://agris.fao.org/agris-search/search.do?recordID=US201303136275> (accessed May 8, 2017).
- Minchin PR. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Pages 89–107 *Theory and models in vegetation science*. Springer. Available from [http://link.springer.com/chapter/10.1007/978-94-009-4061-1\\_9](http://link.springer.com/chapter/10.1007/978-94-009-4061-1_9) (accessed March 29, 2017).
- Mineau P, Downes CM, Kirk DA, Bayne E, Csizy M. 2005. Patterns of bird species abundance in relation to granular insecticide use in the Canadian prairies. *Ecoscience* **12**:267–278.
- Mineau P, Whiteside M. 2013. Pesticide acute toxicity is a better correlate of US grassland bird declines than agricultural intensification. *PLoS One* **8**:e57457.



- Monnet A-C, Hardouin LA, Robert A, Hingrat Y, Jiguet F. 2015. Evidence of a link between demographic rates and species habitat suitability from post release movements in a reinforced bird population. *Oikos* **124**:1089–1097.
- Monroe AP, O’Connell TJ. 2014. Winter Bird Habitat Use in a Heterogeneous Tallgrass Prairie. *The American Midland Naturalist* **171**:97–115.
- Moorman CE, Klimstra RL, Harper CA, Marcus JF, Sorenson CE. 2017. Breeding songbird use of native warm-season and non-native cool-season grass forage fields. *Wildlife Society Bulletin*:n/a-n/a.
- Morelli F. 2013. Quantifying Effects of Spatial Heterogeneity of Farmlands on Bird Species Richness by Means of Similarity Index Pairwise. *International Journal of Biodiversity* **2013**:e914837.
- Myers MC, Hokschi BJ, Mason JT. 2012. Butterfly response to floral resources during early establishment at a heterogeneous prairie biomass production site in Iowa, USA. *Journal of Insect Conservation* **16**:457–472.
- Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Miranda AC, Brumm H. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proc. R. Soc. B* **280**:20122798.
- Newman PR, Moser LE. 1988. Seedling Root Development and Morphology of Cool-Season and Warm-Season Forage Grasses. *Crop Science* **28**:148–151.
- Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* **146**:579–600.
- NOAA. (n.d.). National Weather Service.
- Norris DR, Marra PP. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* **109**:535–547.
- Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences* **271**:59–64.
- North American Bird Conservation Initiative. 2013. The State of the Birds Report on Private Lands. U.S. Department of Interior: Washington, D.C. Page 48.
- Noss RF, LaRoe ET, Scott JM. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. US Department of the Interior, National Biological Service Washington, DC, USA. Available from <http://biology.usgs.gov/pubs/ecosys.htm> (accessed December 12, 2015).
- Oksanen J et al. (n.d.). Vegan: Community Ecology Package. 2013. R-package version 2.0-10. URL <http://CRAN.R-project.org/package=vegan>.
- Olson DM et al. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* **51**:933–938.
- Omernik JM. 1987. Ecoregions of the Conterminous United States. *Annals of the Association of American Geographers* **77**:118–125.
- Pearce J, Lindenmayer D. 1998. Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) in southeastern Australia. *Restoration Ecology* **6**:238–243.

- Pérez GE, Hobson KA. 2007. Feather deuterium measurements reveal origins of migratory western loggerhead shrikes (*Lanius ludovicianus excubitorides*) wintering in Mexico. *Diversity and Distributions* **13**:166–171.
- Perkins DW, Shriver WG, Vickery PD. 2009. The Effects Of Fire On The Breeding Ecology Of Florida Grasshopper Sparrows (*Ammodramus Savannarum Floridanus*) And Bachman’s Sparrows (*Aimophila aestivalis*). *Florida Field Naturalist* **37**:121–145.
- Perlut NG, Strong AM, Alexander TJ. 2011. A Model for Integrating Wildlife Science and Agri-Environmental Policy in the Conservation of Declining Species. *Journal of Wildlife Management* **75**:1657–1663.
- Perlut NG, Strong AM, Donovan TM, Buckley NJ. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. *Ecological Applications* **16**:2235–2247.
- Petersen SL, Nicholes BK, Frey SN, Heaton KM, Eggett DL. 2016. Response of greater sage-grouse to surface coal mining and habitat conservation in association with the mine. *Human–Wildlife Interactions* **10**:7.
- Pillsbury FC, Miller JR, Debinski DM, Engle DM. 2011. Another tool in the toolbox? Using fire and grazing to promote bird diversity in highly fragmented landscapes. *Ecosphere* **2**:1–14.
- Plantureux S, Peeters A, McCracken D. 2005. Biodiversity in intensive grasslands: Effect of management, improvement and challenges. *Agronomy Research* **3**:153–164.
- Plush CJ, Moorman CE, Orr DB, Reberg-Horton C. 2013. Overwintering sparrow use of field borders planted as beneficial insect habitat. *Journal of Wildlife Management* **77**:200–206.
- Poore MH, Benson GA, Scott ME, Green JT. 2000. Production and use of stockpiled fescue to reduce beef cattle production costs. *J. Anim. Sci* **79**:1–11.
- Prescott DR, Collister DM. 1993. Characteristics of occupied and unoccupied Loggerhead Shrike territories in southeastern Alberta. *The Journal of wildlife management*:346–352.
- Pruitt L, others. 2000. Loggerhead Shrike status assessment. US Fish and Wildlife Service Bloomington, Indiana.
- Puckett M, Ellis B, Brown RJ, Howell J, Whitehurst D, Moore D. 2015. A Report on the Progress by the Department of Game and Inland Fisheries to Preserve the Northern Bobwhite Quail (*Colinus virginianus*). Virginia Department of Game and Inland Fisheries, Richmond, VA. Available from [http://leg2.state.va.us/dls/h&sdocs.nsf/fc86c2b17a1cf388852570f9006f1299/125a2d6de6b88d9685257cc3006d40e5/\\$FILE/RD33.pdf](http://leg2.state.va.us/dls/h&sdocs.nsf/fc86c2b17a1cf388852570f9006f1299/125a2d6de6b88d9685257cc3006d40e5/$FILE/RD33.pdf).
- R Core Team. 2015a. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org>.
- R Core Team. 2015b. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>.

- Rashford BS, Walker JA, Bastian CT. 2011. Economics of grassland conversion to cropland in the Prairie Pothole Region. *Conservation Biology* **25**:276–284.
- Reif J. 2013. Long-term trends in bird populations: a review of patterns and potential drivers in North America and Europe. *Acta ornithologica* **48**:1–16.
- Ribic CA, Koford RR, Herkert JR, Johnson DH, Niemuth ND, Naugle DE, Bakker KK, Sample DW, Renfrew RB. 2009. Area Sensitivity in North American Grassland Birds: Patterns and Processes. *The Auk* **126**:233–244.
- Robb GN, McDonald RA, Chamberlain DE, Reynolds SJ, Harrison TJE, Bearhop S. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. *Biology Letters* **4**:220–223.
- Robbins CS, Sauer JR, Greenberg RS, Droege S. 1989. Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences* **86**:7658–7662.
- Robel RJ, Briggs JN, Dayton AD, Hulbert LC. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management*:295–297.
- Rosenburg KV, Kennedy JA, Dettmers R, Ford RP, Reynolds D, Alexander JD. 2016. Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Page 119pp. Partners in Flight Science Committee.
- Royle JA. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* **60**:108–115.
- Royle JA, Nichols JD, Kéry M. 2005. Modelling occurrence and abundance of species when detection is imperfect. *Oikos* **110**:353–359.
- Rushing CS, Marra PP, Dudash MR. 2016. Winter habitat quality but not long-distance breeding dispersal influences apparent reproductive success in a migratory bird. *Ecology*. Available from <http://onlinelibrary.wiley.com/doi/10.1890/15-1259/pdf> (accessed December 2, 2016).
- Saalfeld DT, Saalfeld ST, Conway WC, Hartke KM. 2016. Wintering grassland bird responses to vegetation structure, exotic invasive plant composition, and disturbance regime in coastal prairies of Texas. *The Wilson Journal of Ornithology* **128**:290–305.
- Saino N, Szép T, Romano M, Rubolini D, Spina F, Møller AP. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters* **7**:21–25.
- Salton M, Saraux C, Dann P, Chiaradia A. 2015. Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. *Royal Society Open Science* **2**:140390.
- Samson F, Knopf F. 1994. Prairie conservation in north america. *BioScience*:418–421.
- Sauer JR, Hines JE, Fallon J. 2005. The North American Breeding Bird Survey, results and analysis 1966-2004, version 2005.2. United States Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland. WA Laycock and RD Pieper, editors. Society for Range Management, Denver, Colorado.

- Sauer JR, Hines JE, Fallon JE, Pardieck DJ, Ziolkowski Jr. DJ, Link WA. 2011. The North American Breeding Bird Survey, Results and Analysis 1966 - 2010. Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Savoie P, Parsch LD, Rotz CA, Brook RC, Black JR. 1985. Simulation of forage harvest and conservation on dairy farms. *Agricultural Systems* **17**:117–131.
- Selmi S, Boulinier T. 2004. Distribution-abundance relationship for passerines breeding in Tunisian oases: test of the sampling hypothesis. *Oecologia* **139**:440–445.
- Shahan JL, Goodwin BJ, Rundquist BC. 2017. Grassland songbird occurrence on remnant prairie patches is primarily determined by landscape characteristics. *Landscape Ecology*:1–18.
- Shen L, He Y, Guo X. 2013a. Suitability of the normalized difference vegetation index and the adjusted transformed soil-adjusted vegetation index for spatially characterizing loggerhead shrike habitats in North American mixed prairie. *Journal of Applied Remote Sensing* **7**:073574–073574.
- Shen L, He Y, Guo X. 2013b. Exploration of Loggerhead Shrike Habitats in Grassland National Park of Canada Based on in Situ Measurements and Satellite-Derived Adjusted Transformed Soil-Adjusted Vegetation Index (ATSAVI). *Remote Sensing* **5**:432–453.
- Sinclair SJ, White MD, Newell GR, others. 2010. How useful are species distribution models for managing biodiversity under future climates. *Ecology and Society* **15**. Available from <http://dlc.dlib.indiana.edu/dlc/handle/10535/5995> (accessed November 23, 2016).
- Sleeter BM, Sohl TL, Loveland TR, Auch RF, Acevedo W, Drummond MA, Sayler KL, Stehman SV. 2013. Land-cover change in the conterminous United States from 1973 to 2000. *Global Environmental Change* **23**:733–748.
- Sol D, Lefebvre L, Rodríguez-Teijeiro JD. 2005. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings. Biological Sciences* **272**:1433–1441.
- Spellerberg IF, Fedor PJ. 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the “Shannon–Wiener” Index. *Global Ecology and Biogeography* **12**:177–179.
- Studds CE, Kyser TK, Marra PP. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of the National Academy of Sciences* **105**:2929–2933.
- Studds CE, Marra PP. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Available from <http://repository.si.edu/handle/10088/8062> (accessed May 3, 2017).
- Sullivan BL et al. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. *Biological Conservation* **169**:31–40.
- Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S. 2009. eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation* **142**:2282–2292.
- Swallow SK, Anderson CM, Uchida E. 2012. The bobolink project: Selling public goods from ecosystem services using provision point mechanisms. *Zwicky Center for*

- Food and Resource Policy, University of Connecticut, Working Paper Series. Available from <http://www.zwickcenter.uconn.edu/documents/wp16.pdf> (accessed December 2, 2015).
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**:79–92.
- Tonra CM, Marra PP, Holberton RL. 2011. Migration phenology and winter habitat quality are related to circulating androgen in a long-distance migratory bird. *Journal of avian biology* **42**:397–404.
- Twedt DJ, Hamel PB, Wodrey MS. 2008. Winter Bird Population Studies and Project Prairie Birds for surveying grassland birds. *Southeastern Naturalist* **7**:11–18.
- Twidwell D, Rogers WE, McMahon EA, Thomas BR, Kreuter UP, Blankenship TL. 2012. Prescribed extreme fire effects on richness and invasion in coastal prairie. Available from <https://www.bioone.org/doi/full/10.1614/IPSM-D-12-00017.1> (accessed May 8, 2017).
- U.S. Census Bureau. 2012. 2012 TIGER/Line Shapefiles [machine-readable data files]/prepared by the U.S. Census Bureau.
- USDA. 2011. National Agricultural Statistics Service Cropland Data Layer. USDA-NASS Washington, DC. Available from <https://nassgeodata.gmu.edu/CropScape/>.
- Vallianatos M, Loughheed SC, Boag PT. 2002. Conservation genetics of the loggerhead shrike (*Lanius ludovicianus*) in central and eastern North America. *Conservation Genetics* **3**:1–13.
- Van Horne B. 1983. Density as a Misleading Indicator of Habitat Quality. *The Journal of Wildlife Management* **47**:893–901.
- Vélez-Espino LA, McLaughlin RL, Robillard M. 2013. Ecological advantages of partial migration as a conditional strategy. *Theoretical Population Biology* **85**:1–11.
- Vistnes I, Nellemann C. 2008. The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biology* **31**:399–407.
- Vogel KP, Brejda JJ, Walters DT, Buxton DR. 2002. Switchgrass Biomass Production in the Midwest USA. *Agronomy Journal* **94**:413–420.
- Walk JW, Kershner EL, Warner RE. 2006. Low nesting success of Loggerhead Shrikes in an agricultural landscape. *The Wilson Journal of Ornithology* **118**:70–74.
- Waltham T, Bell FG, Culshaw M. 2007. Sinkholes and Subsidence: Karst and Cavernous Rocks in Engineering and Construction. Springer Science & Business Media.
- Wang X, Blanchet FG, Koper N. 2014. Measuring habitat fragmentation: An evaluation of landscape pattern metrics. *Methods in Ecology and Evolution* **5**:634–646.
- Washburn BE, Barnes TG, Sole JD. 2000. Improving Northern Bobwhite Habitat by Converting Tall Fescue Fields to Native Warm-Season Grasses. *Wildlife Society Bulletin (1973-2006)* **28**:97–104.
- Watts BD. 1996. Social Strategy and Cover in Savannah Sparrows. *The Auk* **113**:960–963.
- West AS, Keyser PD, Lituma CM, Buehler DA, Applegate RD, Morgan J. 2016. Grasslands bird occupancy of native warm-season grass. *The Journal of Wildlife Management* **80**:1081–1090.

- Yosef R. 1994. Conservation commentary: evaluation of the global decline in the True Shrikes (Family Laniidae). *The Auk*:228–233.
- Yosef R, Grubb TC. 1994. Resource dependence and territory size in Loggerhead Shrikes (*Lanius ludovicianus*). *The Auk*:465–469.
- Zuckerberg B, Bonter DN, Hochachka WM, Koenig WD, DeGaetano AT, Dickinson JL. 2011. Climatic constraints on wintering bird distributions are modified by urbanization and weather. *Journal of Animal Ecology* **80**:403–413.
- Zuckerberg B, Fink D, La Sorte FA, Hochachka WM, Kelling S. 2016. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. *Diversity and Distributions* **22**:717–730.

## **BIOGRAPHY**

Amy E.M. Johnson received her Bachelor of Science in Agriculture from the University of Guelph in Canada in 2004. After several years of working in the field of reproductive science she received her Master of Science in Environmental Science and Policy from George Mason University, focusing her research on developing assisted reproductive techniques in wolves. In 2013, Amy was awarded the Smithsonian-Mason Fellowship in Conservation Science, enabling her to pursue the research presented here.