Research Article

Effects of Grassland Management on Overwintering Bird Communities

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ABSTRACT Birds that depend on grassland and successional-scrub vegetation communities are experiencing a greater decline than any other avian assemblage in North America. Habitat loss and degradation on breeding and wintering grounds are among the leading causes of these declines. We used public and private lands in northern Virginia, USA, to explore benefits of grassland management and associated field structure on supporting overwintering bird species from 2013 to 2016. Specifically, we used non-metric multidimensional scaling and multispecies occupancy models to compare species richness and habitat associations of grassland-obligate and successional-scrub species during winter in fields comprised of native warm-season grasses (WSG) or non-native cool-season grasses (CSG) that were managed at different times of the year. Results demonstrated positive correlations of grassland-obligate species with decreased vegetation structure and a higher percentage of grass cover, whereas successional-scrub species positively correlated with increased vegetation structure and height and increased percentages of woody stems, forb cover, and bare ground. Fields of WSG supported higher estimated total and target species richness compared to fields of CSG. Estimated species richness was also influenced by management timing, with fields managed during the previous winter or left unmanaged exhibiting higher estimated richness than fields managed in summer or fall. Warm-season grass fields managed in the previous winter or left unmanaged had higher estimated species richness than any other treatment group. This study identifies important winter habitat associations (e.g., vegetation height and field openness) with species abundance and richness and can be used to make inferences about optimal management practices for overwintering avian species in eastern grasslands of North America. © 2019 The Wildlife Society.

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The effects of land management on grassland and early successional bird communities has been a topic of attention in recent decades because these species have declined more steeply than any other guild of birds in North America (Knopf and Samson 1994, Askins et al. 2007). Land management activities for grasslands such as burning (Churchwell et al. 2008), mowing (Blank et al. 2011; Bollinger et al. 1990), 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) have negative and positive effects on breeding populations of grassland and successional-scrub 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 around the edges of managed fields increases breeding bird abundance, species richness, and diversity (Berges et al. 2010) and improves nest success (Adams et al. 2013). Although knowledge has been gained from decades of research on breeding habitats, there is limited knowledge of the habitat needs of grassland and successional-scrub birds outside of the breeding season. For long-distance migrant species in general, the loss and degradation of winter habitat in central and south America has been hypothesized as a major contributing factor in bird declines (Hostetler et al.

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2015, Marra et al. 2015*a*). The majority of North American grassland and successional-scrub birds, however, are residents or short-distance migrants, in which their winter distributions are restricted within North America (Igl and Ballard 1999). Therefore, there is a need to understand non-breeding season requirements, especially for imperiled populations.

Events occurring on wintering sites can affect the survival and reproduction of several long-distance migrants, influencing population dynamics in subsequent breeding seasons (Marra et al. 1998, 2015*b*; Studds et al. 2008; Costantini et al. 2010; Harrison et al. 2011). For example, winter and staging habitats containing abundant food sources and cover result in earlier departure dates and improved survival during migration in long-distance migratory species such as American redstarts (*Setophaga ruticilla*; Marra et al. 2015*b*, 1998; Studds et al. 2008) and snow geese (*Chen caerulescens atlantica*; 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) and laying dates, and increase fledging success (Robb et al. 2008, Costantini et al. 2010). Of 56 species that breed in grassland and successional-scrub vegetation communities in eastern North America (Sauer et al. 2011), nearly half also winter in the United States, including eastern grasslands. Many current land management recommendations for eastern grassland and successional-scrub birds, however, only pertain to breeding habitats, leaving a deficit of information available on best management practices for lands with overwintering species.

Vegetation structure and composition are important environmental measures for predicting bird species richness and abundance, but optimal measures vary considerably between species groups (MacArthur and MacArthur 1961, Tews et al. 2004). For breeding grassland and successional-scrub birds, the structure and composition of vegetation can have a significant influence on bird communities; increased structural heterogeneity is correlated with increased bird community diversity and stability (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Hovick et al. 2015). In winter, heterogeneous vegetation structure can provide thermal protection (Ginter and Desmond 2005), improve foraging opportunities (Bechtoldt and Stouffer 2005, Ginter and Desmond 2005), and decrease predation risk (Watts 1996). Grasslands in the eastern United States, however, are often managed 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). This leads to reduced seed resources (Maron and Jefferies 2001) and limited forage and shelter opportunities for birds during winter. Thus, the timing of grassland management could affect winter habitat and associated bird survival.

Although the majority of hay and pasture lands in the eastern United States 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 prescriptions that recommend diverse seed mixes for optimizing wildlife (Moorman et al. 2017). When augmented with multiple forb and legume species, warm-season grass fields increase the structural heterogeneity of fields during the growing season and are associated with higher diversity in mammals (Mengak 2004), arthropods (McIntyre and Thompson 2003), pollinators (Myers et al. 2012), and birds (Flanders et al. 2006, Harper et al. 2015). Best management practices for WSG in the eastern United States are designed to increase structural heterogeneity and minimize invasions by non-native species (Washburn et al. 2000), which also benefits breeding grassland and successional-scrub bird populations (Flanders et al. 2006). There is limited research on habitat use by winter bird communities in WSG, however, with recent work (<15 studies) focused in ecoregions of the Midwest, Great Plains, and southern United States (Conover et al. 2007, Plush et al. 2013, Monroe and O'Connell 2014, Hovick et al. 2015, Saalfeld et al. 2016). Nevertheless, non-native vegetation negatively influences the density of several grassland-obligate species overwintering in the Texas, USA, coastal plains (Saalfeld et al. 2016) and overwintering bird diversity in the Flint Hills of Kansas and Oklahoma, USA, is positively associated with increased vegetation height (Monroe and O'Connell 2014).

Currently, there are no studies that address habitat use by winter bird communities in grasslands in the eastern United States. These grasslands, which include pastures, hayfields, abandoned agricultural fields, and successional scrub, comprise >20% of the landscape from Maine to Florida, USA (Sleeter et al. 2013). With variation in species assemblages, ecoregion attributes, land use, and resulting vegetation structure between eastern grasslands and other North American grasslands (Omernik 1987), it is important to understand differing responses in bird communities to optimize conservation opportunities specific to eastern grasslands.

Our objective was to understand how the winter bird community responds to grassland management and associated vegetation structure in Virginia, USA, as a proxy for eastern grasslands of the mid-Atlantic. We hypothesized that vegetation structure, which varies by field type (CSG or WSG) and management regime, would strongly influence the avian community. We expected higher species richness and abundance in fields associated with greater structural heterogeneity and that heterogeneity would be lowest in recently managed fields. We also hypothesized that fields comprised of non-native vegetation would exhibit lower avian richness and abundance because of increased homogeneity in the vegetation structure.

STUDY AREA

We conducted this study for 3 winters from 2013 to 2016 on 25 properties (property size range = 14–2,000 ha) across 11 counties in Virginia, that were either in public ($n = 4$) or private ($n = 21$) ownership (Fig. 1). We recruited and surveyed all field sites through Virginia Working Landscapes, a research-based conservation initiative convened by the Smithsonian Conservation Biology Institute (SCBI) in

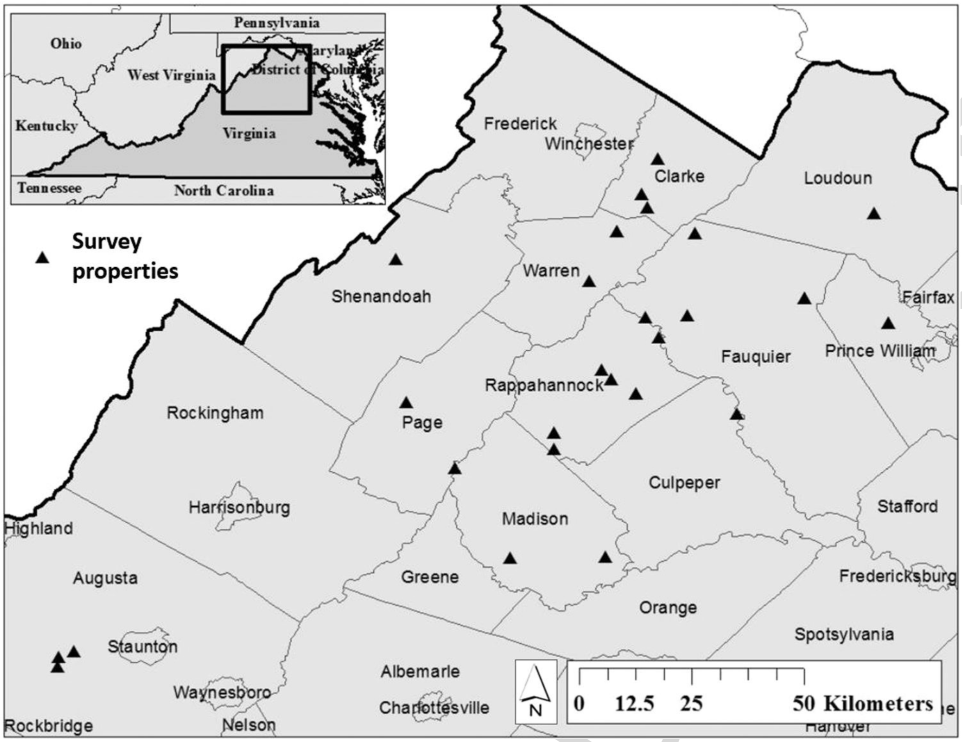

Figure 1. Locations of bird survey properties in Northern Virginia, USA, 2013–2016. Survey fields were a minimum of 8 contiguous ha; thus, some properties had >1 survey field >400 m apart. Each survey field contained 3 survey stations ≥200 m apart.

Front Royal, Virginia. (www.VAWorkingLandscapes.org; accessed 7 Oct 2018). This program works collectively with landowners, scientists and private citizens to study effects of land use and management on native biodiversity, including avian and vegetation communities, and has access to >120 properties for conducting research. Field sites were opportunistically selected based on landowner permissions, field size (>8 ha), and management (i.e., not managed during the survey season). The 11-county region used for this study was characterized by rolling hills (elevation range = 0–1,359 m) over igneous and metamorphic bedrock with stretches of karst topography throughout the western portion (Hyland 2005). The center of the study region was intersected by Shenandoah National Park along the Blue Ridge Mountains. Dominant mammal fauna in the region included white-tailed deer (*Odocoileus virginianus*), coyote (*Canis latrans*), American black bear (*Ursus americanus*), red fox (*Vulpes vulpes*), Virginia opossum (*Didelphis virginiana*), and raccoon (*Procyon lotor*; Handley 1991). The land cover was dominated by eastern temperate deciduous forest with grasslands comprising approximately 30% of the study region (National Land Cover Database 2011). Most grasslands in the region were managed for grazing livestock or growing hay and were comprised of non-native CSG such as tall fescue (*Schedonorus arundinaceus*), Kentucky bluegrass (*Poa pratensis*), and orchard grass (*Dactylis glomerata*). These fields were generally managed homogenously with grass removal (through haying or grazing) occurring frequently throughout the year. Fields converted to WSG contained a mix of native grasses (e.g., big bluestem [*Andropogon gerardi*], switchgrass [*Panicum virgatum*], indiangrass [*Sorghastrum nutans*]) and forbs (e.g., asters [*Symphyotrichum* spp.], monarda [*Monarda* spp.], milkweeds [*Asclepias* spp.]). Fields comprised of WSG in this region were generally managed once every 1–3 years by burning or bush-hogging. This region experienced 4 distinct seasons with hot, humid summers (Jun–Aug) and moderately cold winters (Dec–Feb). Average temperature for the study months (Dec–Feb; 2013–2016) and area ranged between −11 °C and 16 °C ($\bar{x}$ = 1.5 °C) and the average snowfall was 14 cm (National Oceanic and Atmospheric Administration 2017).

METHODS

Fields ($n = 41$) were ≥8 contiguous ha of grassland and included varying compositions of forbs (0–100%, $\bar{x}$ = 12.75%) and woody vegetation (0–62%, $\bar{x}$ = 8.5%) but were divided into WSG ($n = 20$) or CSG ($n = 21$). Fields were also categorized by management timing: fall (Sep–Nov), summer (May–Aug), and previous winter-unmanaged (Jan–Apr). Nine fields were managed differently in subsequent years so were surveyed multiple years as independent sites ($n = 50$). No fields were managed during survey months. We combined fields managed in the previous winter with unmanaged fields because they had ≥7 months of growth prior to being surveyed. Management included burning (annual; 10 fields), mowing (≥2 times annually; 11 fields), continuous grazing (5 fields), or bush-hogging (annual; 24 fields). In all cases, management resulted in the removal of field vegetation. Therefore, for the purpose of this study we combined all management activities and focused on vegetation attributes relative to time since last disturbance. In each field, we established 3 200-m-long transects ≥100 m from field edges and 200 m apart. If a property contained >1 survey field, we separated adjacent survey clusters by >400 m to reduce the probability of double-counting birds between survey fields (Davis et al. 2013).

Bird and Vegetation Surveys

We visited fields 3 times during the survey period (once per month in Dec, Jan, and Feb). A single observer used variable width transect surveys and distance sampling techniques to sample bird abundance (Buckland et al. 2001, Diefenbach et al. 2003) between 0900 and 1300 (EST) on days with no precipitation and wind speeds <20 km/hour (Gabrey et al. 1999). In contrast to the breeding season, birds can be surveyed throughout the day during the non-breeding season (Fletcher et al. 2000). The observer traveled southwest from the northeast to avoid sun glare at a rate of approximately 40 m/minute and recorded the estimated perpendicular distance of detected birds from the centerline to the nearest 5 m over 5 minutes. The observer recorded all birds regardless of detection method (e.g., flushing from ground, perched in vegetation, vocalizing). We also recorded temperature, date, time, wind speed, snow cover, and cloud cover for each site visit. Bird survey methods were reviewed by Smithsonian's Institutional Animal Care and Use Committee and met all requirements of the institution.

We measured vegetation and structural heterogeneity of each field along each line transect once a year between January and February at a time of no snow cover. We surveyed 6 1-m^2 plots at 40-m intervals along each transect. A single observer visually estimated and recorded percent ground cover of grasses, forbs, woody stems, leaf litter, and bare ground for each plot (Daubenmire 1968).

We estimated habitat openness along multiple dimensions in each plot using cone of vulnerability (COV) and vertical visual obstruction. The cone of vulnerability is a 3-dimensional view of visual obstruction and is used as a measure of habitat structure for ground-dwelling species (i.e., northern bobwhites [*Colinus virginianus*]; Kopp et al. 1998). Briefly, we used a 1-m polyvinyl chloride pole placed at the center of each plot to measure angles in 8 directions (N, NE, E, SE, S, SW, W, NW) from 10 cm above the ground to the top of the nearest obstructing vegetation. We used the average of the 8 measurements to estimate the angle of obstruction for each plot, and the volume of unoccupied space above each point. A higher value indicates less structural cover and therefore increased vulnerability to aerial predators. For vertical visual obstruction, we used a modification of the Robel method (Robel et al. 1970) using a 1-m polyvinyl chloride pole divided into 10-cm segments. We recorded Robel measurements in 2 opposite corners of each plot, 2 m from the pole, resulting in 12 measurements/transect. Briefly, we counted the number of visible 10-cm segments, leaving those segments fully obstructed by vegetation to account for height of vertical obstruction to the nearest 5 cm. We also used a segmented polyvinyl chloride pole to measure the height of the tallest plant in each plot to the nearest 5 cm.

Statistical Analyses

We considered each annual survey for a field to be an independent survey because some sites were managed differently each year, and because all but 7 sites were surveyed 2 out of the 3 years.

We calculated site-level covariates using the means of all variables for each field including percent cover of grasses, forbs, woody stems, and bare ground; vegetation height; COV; and visual obstruction. Categorical covariates included field type (WSG vs. CSG) and management timing (1 = fall, 2 = summer, 3 = late winter-no management). We then combined the 2 management prescriptions into a single measure (management = WSG 1, WSG 2, WSG 3, CSG 1, CSG 2, CSG 3). We examined the correlation between covariates using Spearman's rank correlation coefficient and no 2 variables had a correlation $|r_s| > 0.7$. We used a 1-way analysis of variance (ANOVA) to compare site-level covariates between field types, management timing, and combined management. With significant ANOVA results ($P < 0.01$), we calculated Tukey *post hoc* pairwise comparisons to determine significant differences between groups. To account for multiple testing, we used the Bonferroni correction and considered significant only those covariates for which $P < 0.05/7 = 0.007$ (Legendre and Legendre 1998).

We classified 16 of the detected species as target species. These species included grassland ($n = 3$), successional-scrub species ($n = 8$), or other ($n = 5$) according to the Breeding Bird Survey's groupings (Sauer et al. 2011; Table 1). We included species classified as other in the analysis because of their frequent occurrence on our study sites in winter. Although these birds do not breed in grassland and successional-scrub vegetation communities, they frequented our sites during winter, and it is likely these species are similarly affected by management activities in winter. We calculated relative abundances by dividing the number of detections for each species by the number of transects surveyed in each field during each year of the study.

To explore potential relationships between relative abundance of target species and habitat characteristics, we used non-metric multidimensional scaling (NMDS; Minchin 1987) based on Bray-Curtis dissimilarity (Bray and Curtis 1957, Faith et al. 1987). Specifically, we used relative abundances and the metaMDS and envfit functions from the vegan package (Oksanen et al. 2013) in Program R version 3.2.2 (R Core Team 2015) to project a summary of habitat use for the 16 target species. We 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). We 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.

Table 1. List of 16 target overwintering bird species used to quantify the difference in bird communities between field types across years (2013–2016) and sites (grasslands in Northern Virginia, USA). Asterisks indicate breeding occurrence, in addition to winter, in study region. Superscript represents level of conservation concern; 1 = Partners in Flight (https://www.partnersinflight.org/; accessed 14 Jun 2018) common bird in steep decline; 2 = Appalachian Mountains Joint Venture (http://amjv.org/; accessed 14 Jun 2018) priority species.

Common name	Scientific name	Vegetation association
Northern bobwhite*[1,2]	*Colinus virginianus*	Successional-scrub
Killdeer*	*Charadrius vociferus*	Other
Horned lark[1]	*Eremophila alpestris*	Grassland
Eastern bluebird*	*Sialia sialis*	Other
American goldfinch*	*Carduelis tristis*	Successional-scrub
Field sparrow*[1,2]	*Spizella pusilla*	Successional-scrub
American tree sparrow[1]	*Spizella arborea*	Other
Fox sparrow	*Passerella iliaca*	Successional-scrub
White-crowned sparrow	*Zonotrichia leucophrys*	Successional-scrub
White-throated sparrow	*Zonotrichia albicollis*	Successional-scrub
Savannah sparrow	*Passerculus sandwichensis*	Grassland
Song sparrow*	*Melospiza melodia*	Successional-scrub
Swamp sparrow	*Melospiza georgiana*	Other
Eastern towhee*[2]	*Pipilo erythrophthalmus*	Successional-scrub
Eastern meadowlark*[1,2]	*Sturnella magna*	Grassland
Red-winged blackbird*	*Agelaius phoeniceus*	Other

We 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. We defined occupancy as a binary variable where presence equals one for any species that occurred within 50 m 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 et al. 2005). We assumed that occurrence and detection probabilities varied by species and were influenced by habitat management, structural characteristics, and survey-specific features. We modeled the occurrence probabilities for all species and target 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 2 field types. We also incorporated effects of management timing because this influenced vegetation structure. In addition, we included 2 structural characteristics, COV and vegetation height, based on NMDS results. For the detection model, we included vegetation height, temperature, minutes after sunrise, and day of season (1 Dec = 1, 28 Feb = 90) as possible species-specific detection covariates. We standardized continuous covariates for the occurrence and detection models to have a mean of zero.

We conducted Bayesian analysis of the model using data augmentation techniques described by Royle et al. (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. We analyzed the model using a Bayesian approach in Program R version 3.2.2 (R Core Team 2015) and WinBUGS (Lunn et al. 2000). For each MSOM we ran 2 chains of length 10,000 after a burn-in of 5,000 and thinned the posterior chains by 5. We assessed convergence using the $\hat{R}$ statistic (Zipkin et al. 2010).

We used the MSOM results to compare species richness, including unobserved species (all species, $n = 50$; target species, $n = 25$) between the 2 field types and under different management treatments (field type + management timing) by averaging the number of species estimated by the models for each treatment group. We used 1-way analysis of variance (ANOVA) to compare species richness between field types and management. With significant ANOVA results ($P < 0.01$), we calculated Tukey *post hoc* pairwise comparisons of species richness. We also compared transect-specific associations of species richness with COV and vegetation height.

RESULTS

Warm-season grass fields, on average, had a higher percentage of bare ground ($F_{1,226} = 44.51$, $P < 0.001$), greater visual obstruction ($F_{1,226} = 47.88$, $P < 0.001$), and taller vegetation ($F_{1,226} = 75.78$, $P < 0.001$) than CSG (Table 2). Cool-season grasses had higher COV ($F_{1,226} = 50.99$, $P < 0.001$) and percent grass cover ($F_{1,226} = 81.26$, $P < 0.001$). Percent woody vegetation and percent forb cover did not differ between field types. Cool-season fields that were not managed in fall or summer had a higher percentage of woody cover than all other field types ($F_{1,226} = 42.45$, $P < 0.001$) and relatively high percent forb cover. Warm-season grass fields had the lowest mean COV, and fields managed in the summer (timing = 2), the previous winter, or unmanaged (timing = 3) had lower COV than those managed in the fall, regardless of field type (Table 2).

We detected 7,505 individuals of 41 species of birds during winter transect surveys (Table A1). The model estimated 47.1 species in the region (95% posterior interval = 44–57). We selected 16 target species for NMDS analysis based on their vegetation association groupings or for their frequent use of our grassland sites in winter (Table 1). The NMDS ordination resulted in a 2-axis solution, with a final stress of 0.143, which is within the range reliable for community data and unlikely to have been obtained by chance (Oksanen et al. 2013). The 2 axes together represented 87.6% of the variance in target bird communities, using a fit-based R^2 measure. Visualization of the NMDS demonstrated positive correlations of grassland-obligate species to higher COV, lower visual obstruction, and a higher percentage of grass cover (Fig. 2A). In contrast, successional-scrub species positively correlated

Table 2. Summary of covariates representing the vegetation community, sorted by field type and management timing, among grasslands in Northern Virginia, USA, 2013–2016. Values presented are means with standard errors in parentheses. Field types include cool-season grasses (CSG) and warm-season grasses (WSG). Management timing categories are fall (1), summer (2), and late winter or no management (3). Asterisks indicate significant differences between field types (CSG vs. WSG) in rows presenting means and superscript letters indicate significant differences between field type-timing combinations after Bonferroni correction ($P < 0.007$).

Vegetation height (m)	Cone of vulnerability (m³)	Field type and timing	Cover (%)				Visual obstruction (%)
			Grass (%)	Forb (%)	Woody (%)	Bare ground (%)	
CSG $\bar{x}$	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)^{a}	13.82 (0.80)^{a}	85.06 (2.83)^{a}	0.81 (0.81)^{a}	1.15 (1.15)^{a}	10.60 (1.51)^{a}	1.00 (1.01)^{a}
2	0.74 (0.06)^{b}	4.39 (0.76)^{b}	77.38 (2.86)^{a,b}	21.18 (3.58)^{b}	8.39 (2.62)^{b}	14.98 (2.03)^{a}	10.57 (0.75)^{b}
3	1.15 (0.11)^{b}	1.56 (0.48)^{b}	46.18 (5.93)^{b,c}	21.97 (2.32)^{b}	17.98 (3.3)^{c}	25.54 (1.08)^{b}	16.03 (1.36)^{b,c}
WSG $\bar{x}$	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)^{a,b}	7.62 (2.27)^{a}	66.33 (8.72)^{a,b}	2.00 (2.00)^{a}	0.00 (0.00)^{a}	25.56 (5.02)^{b}	9.32 (3.58)^{b}
2	1.17 (0.30)^{b,c}	3.20 (1.37)^{b}	47.00 (9.17)^{b,c}	14.11 (6.85)^{b}	3.33 (2.04)^{a,b}	23.11 (5.85)^{b}	10.99 (3.20)^{b,c}
3	1.47 (0.08)^{c}	1.56 (0.38)^{b}	42.77 (3.31)^{c}	14.65 (2.83)^{b}	10.76 (1.99)^{b}	26.66 (1.77)^{b}	20.08 (1.96)^{c}

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 (multi-response permutation procedure; $A = 0.498$; $P < 0.001$; Fig. 2B). Fields with higher COV values had a higher abundance of grassland-obligate species, red-winged blackbirds (*Agelaius phoeniceus*), and eastern bluebirds (*Sialia sialis*). Successional-scrub species were most abundant in fields with lower COV.

One MSOM considered observed ($n = 41$) and estimated ($n = 50$) species for the total bird community and another considered the observed ($n = 16$) and estimated ($n = 25$) species for only the target species. Estimates of total and target species richness were higher in WSG than CSG fields (total species: $F_{1,226} = 76.21$, $P < 0.001$; target species: $F_{1,226} = 75.21$, $P < 0.001$; Fig. 3A) though occurrence probabilities for many species were similar in the 2 field types (Fig. 3B). Values of total species richness estimated by the model were similar to observed species richness in WSG (observed $= 5.62 \pm 0.33$ vs. estimated 5.49 ± 0.22) and CSG fields (observed $= 2.78 \pm 0.35$ vs. estimated $= 2.86 \pm 0.19$).

Estimated total and target species richness was also influenced by management timing, with fields managed during the previous winter or left unmanaged exhibiting higher estimated richness than fields managed in summer or fall (total species: $F_{2,225} = 59.36$, $P < 0.001$; target species: $F_{2,225} = 81.07$, $P < 0.001$; Fig. 4A). When combining management timing and field type, WSG fields managed in the previous winter or left unmanaged (WSG 3) had higher estimated total and target species richness than any other treatment group (total species: $F_{5,222} = 32.01$, $P < 0.001$; target species: $F_{5,222} = 40.96$, $P < 0.001$; Fig. 4B). Though CSG 3 fields had higher estimated total and target richness than CSG 1 and CSG 2 fields ($P < 0.001$), they were not different from WSG 2 fields (total and target species: $P = 0.999$). Target species richness was higher in CSG 3 fields than WSG 1 ($P = 0.019$) but not different for total species ($P = 0.521$).

Structural characteristics also influenced species richness and individual species occurrence probabilities. Estimated total and target species richness was higher in fields with tall vegetation (total species: $R^2 = 0.32$, $P < 0.001$; target species: $R^2 = 0.40$, $P < 0.001$; Fig. 5A) and lower in fields with high COV measurements (total species: $R^2 = 0.27$, $P < 0.001$; target species: $R^2 = 0.35$, $P < 0.001$), indicating that field openness reduced species occupancy. However, the results of the NMDS indicated not all species respond similarly to low vegetation height. The abundance estimates of some grassland-obligate species, like horned larks (*Eremophila alpestris*) and eastern meadowlarks (*Sturnella magna*), demonstrated a negative correlation with vegetation height. In addition, vegetation height negatively influenced species-specific detection probability (Fig. 5B).

DISCUSSION

We investigated effects of grassland management timing and field type on associated habitat structure for the winter bird community using a network of public and private lands. Our results showed that fields comprised of WSG had taller vegetation, more vertical and horizontal structure, and more bare ground than fields comprised of non-native CSG, and supported our hypothesis that non-native vegetation would exhibit lower avian richness. Our results also demonstrated that, regardless of field type, fallow fields supported more species than fields managed during the summer or fall, supporting our hypothesis that species richness would be associated with greater structural heterogeneity and therefore lower in recently managed fields. We do not know how this grassland management affects survival and subsequent reproduction, but our results indicate the potential for significant effects on winter food availability and protective cover. In addition, our research demonstrates the importance of recognizing regional differences in grassland management and the resulting vegetation compositions and associated bird communities.

Warm-season grasses have been endorsed by conservation managers to improve breeding habitat for grassland and successional-scrub 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 (Fuhlendorf et al. 2006, Churchwell et al. 2008). For example, studies in tallgrass prairies have demonstrated that patch-burning and grazing, a process by which a field is burned or grazed in patches, creates a more heterogeneous landscape and increases the variety of grassland bird communities across the landscape (Fuhlendorf et al. 2006) and improves reproduction for nesting birds (Churchwell et al. 2008). Warm-season grass fields in the eastern United States are generally managed using patch-burning techniques when conditions allow, but many are also bush-hogged every 1–3 years to help slow succession. In contrast, traditionally managed CSG in the eastern United States, such as hayfields or pastures, are managed homogenously with disturbances occurring frequently and uniformly across the field. 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 our 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 richness.

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 versus WSG fields. Hovick et al. (2014) explored the response of 6 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. In their study, time since disturbance occurred over a larger time frame than in our study, however, with shortest time since disturbance being <12 months and the longest being >24 months. Our study explored the response of the winter bird community on a shorter temporal extent (<12 months) because grasslands in the study region can be managed several times throughout the year. For example, traditionally managed hayfields in the eastern United States 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 1 or 2 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). Our findings demonstrate that fields left undisturbed through the growing season, regardless of grass type, have higher bird species richness 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 heterogeneity and species richness. Warm-season grass fields managed throughout the growing season did not differ from CSG fields that had not been managed in fall or summer. This result suggests that WSG fields improve winter food availability and cover regardless of management timing. One explanation of this result is that WSG develop later in the growing season than CSG (Newman and 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 and Magai 1992) than traditionally managed CSG fields (5–15 cm stubble; Gillen and Berg 2005), leaving more cover for winter birds. Our 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 of fall- and summer-managed CSG fields (0.21 m and 0.74 m, respectively). However, our study had few fall- ($n = 5$) and summer-managed ($n = 3$) WSG fields. Therefore, further work needs to focus on identifying optimal management timing in WSG for wintering grassland and successional-scrub bird species.

The results of this study suggest that WSG fields improve winter habitat structure for a suite of successional-scrub species, and therefore can be promoted as a conservation tool for declining species in the eastern United States. The NMDS results demonstrated that successional-scrub species were most abundant in fields with increased structural heterogeneity, which was related to WSG fields. In contrast, fields with low structural heterogeneity supported more grassland-obligate species except for Savannah sparrows. Similar to previous winter studies, Savannah sparrows had less-specific requirements and were observed in a range of field and management types, vegetation heights, and

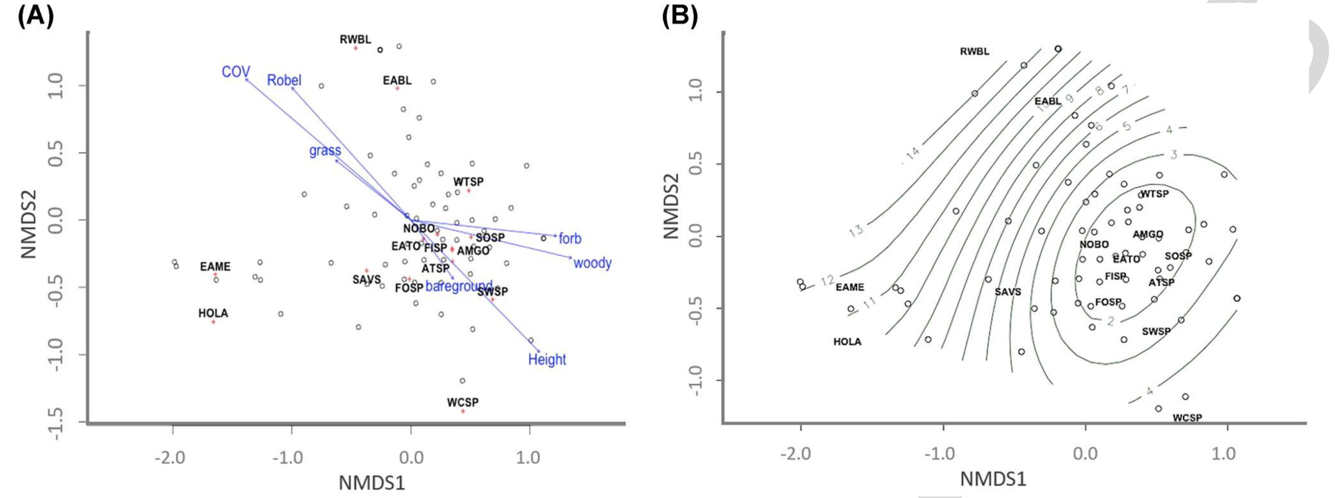

Figure 2. Visualization of the bird community overwintering in Northern Virginia, USA, 2013–2016, grasslands using nonmetric multidimensional scaling (NMDS) demonstrating A) correlations of site covariates and species abundance and B) abundance of species based on cone of vulnerability (COV). Circles represent sites, 4-letter codes represent bird species, and arrows represent continuous site covariates and point in the direction of most rapid increase; their lengths are proportional to the correlation between the covariate and site occupancy. Fitted contours represent a continuous gradient of COV values. Robel = vertical visual obstruction; grass = percent grass cover; forb = percent forb cover; woody = percent woody stem cover; bareground = percent bare ground cover; height = vegetation height in meters. AMGO = American goldfinch; ATSP = American tree sparrow; EABL = eastern bluebird; EAME = eastern meadowlark; EATO = eastern towhee; FISP = field sparrow; FOSP = fox sparrow; HOLA = horned lark; NOBO = northern bobwhite; RWBL = red-winged blackbird; SAVS = Savannah sparrow; SOSP = song sparrow; SWSP = swamp sparrow; WCSP = white-crowned sparrow; WTSP = white-throated sparrow.

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 our 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 relatively greater rainfall during the growing season and more productive soils in eastern regions result in denser vegetation, which deters meadowlarks during the breeding season (West et al. 2016). Given that meadowlarks occur in the study region year-round, this result further emphasizes the importance of considering regional differences in habitat structure and associated habitat use, especially for species of concern.

Conditions during the non-breeding season can influence individual performance in subsequent seasons (Harrison et al. 2011). For example, high-quality wintering sites (i.e., those containing abundant food sources and ample cover) are 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

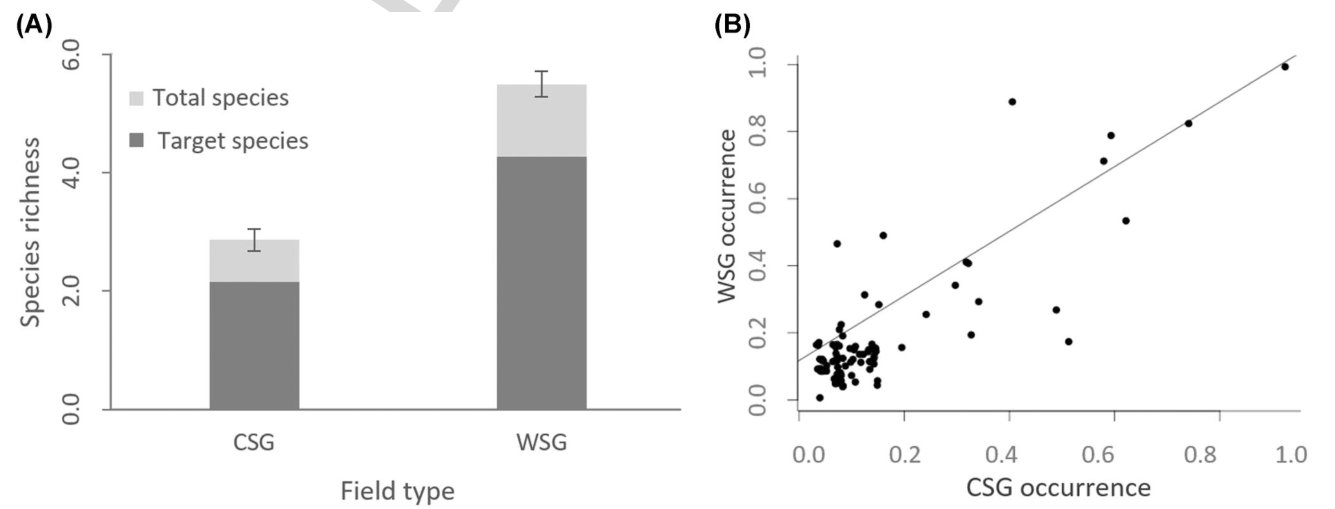

Figure 3. Estimated transect-specific total (light grey bars) and target (dark grey bars) overwintering bird species richness in Northern Virginia, USA, 2013–2016, grasslands comprised of non-native cool-season grasses (CSG) and native warm-season grasses (WSG; A) and mean estimated species-specific probabilities of occurrence in WSG versus CSG (B; the black line shows the regression line).

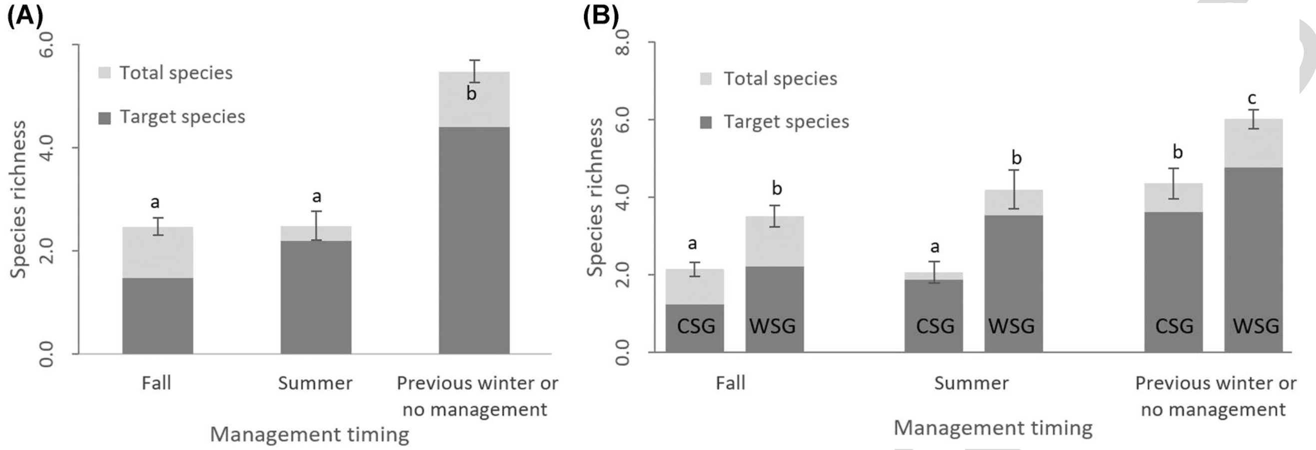

Figure 4. Estimated total (light grey bars) and target (dark grey bars) overwintering bird species richness in Northern Virginia, USA, grasslands managed in fall, summer, or the previous winter or left unmanaged, 2013–2016 (A), and mean estimated richness in fields dominated by cool-season grasses (CSG) versus native warm-season grasses (WSG) managed in fall, summer, or winter-not managed (B). Regardless of field type, fields managed in the previous winter or not managed had higher richness than all other treatments (A). When management timing was combined with field type (B), warm-season grass fields managed in the previous winter or left unmanaged had the highest estimated species richness. Letters indicate significant differences in total species richness between treatments.

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 effects on winter habitat quality and associated bird survival and reproduction in the breeding season. Though the results of our 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 and Marra 2007, Rushing et al. 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 that overwintered in these fields.

MANAGEMENT IMPLICATIONS

Our results demonstrate that the composition of plant species and the timing of their management influences vegetation structure, and therefore the bird communities overwintering in eastern grasslands. We recommend (when possible) deferring the annual mowing or bush-hogging of fields until late winter or early spring (Feb–Apr) to optimize vegetative cover for birds throughout winter. To further improve structural heterogeneity, we also recommend the conversion of fields from CSG to WSG, to support a more diverse overwintering bird community. The results of this study also demonstrate that species-specific recommendations may differ from recommendations for

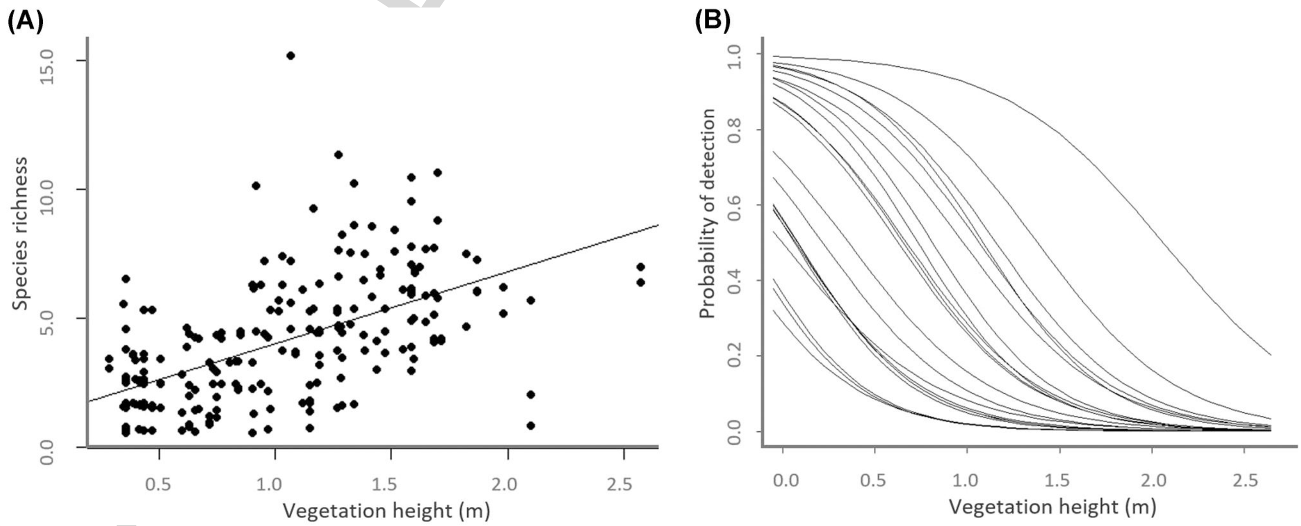

Figure 5. Posterior means of estimated overwintering bird species richness for each sampled point plotted against vegetation height (A) and species-specific sampling effects of maximum vegetation height on detection probability (B). Sampling occurred between 2013 and 2016 in Northern Virginia, USA.

whole bird communities. For example, field management for horned larks or eastern meadowlarks may differ from the rest of the bird community. Regardless, this work increases our understanding of avian habitat associations during winter and provides support for optimizing management practices to sustain birds overwintering in eastern grasslands.

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APPENDIX A. COUNTS FOR ALL SPECIES OBSERVED IN EACH YEAR OF SURVEYING

Table A1. List of all bird species documented during winter transect surveys (Dec–Feb 2013–2016) of grasslands in Northern Virginia, USA. Number of sites are indicated in parentheses. We surveyed 3 200-m transects at each site and visited each transect 3 times within a season. Asterisks indicate breeding occurrence, in addition to winter, in study region. Field types are cool-season grass fields (CSG) and warm-season grass fields (WSG).

		2014			2015			2016			
Species	**Common name**	**CSG (14)**	**WSG (15)**	**Total (29)**	**CSG (16)**	**WSG (18)**	**Total (34)**	**CSG (12)**	**WSG (6)**	**Total (18)**	**All years**
Canada goose*	*Branta canadensis*	53	9	62	0	201	201	0	0	0	263
Northern bobwhite*	*Colinus virginianus*	0	0	0	0	4	4	0	1	1	5
Mourning dove*	*Zenaida macroura*	0	0	0	0	31	31	0	0	0	31
Killdeer*	*Charadrius vociferus*	0	0	0	0	4	4	0	0	0	4
Northern harrier*	*Circus cyaneus*	3	12	15	2	11	13	1	2	3	31
Sharp-shinned hawk*	*Accipiter striatus*	2	0	2	0	0	0	0	0	0	2
Coopers hawk*	*Accipiter cooperii*	0	0	0	0	0	0	0	1	1	1
Red-shouldered hawk*	*Buteo lineatus*	2	0	2	1	1	2	0	0	0	4
Red-tailed hawk*	*Buteo jamaicensis*	0	0	0	0	3	3	0	0	0	3
Short-eared owl	*Asio flammeus*	0	0	0	0	0	0	5	0	5	5
Red-bellied woodpecker*	*Melanerpes carolinus*	0	3	3	1	1	2	0	0	0	5
Downy woodpecker*	*Picoides pubescens*	0	2	2	2	6	8	0	3	3	13
Northern flicker*	*Colaptes auratus*	11	18	29	0	1	1	0	0	0	30
American kestrel*	*Falco sparverius*	2	6	8	5	6	11	3	1	4	23
Eastern phoebe*	*Sayornis phoebe*	0	0	0	0	1	1	0	0	0	1
Northern shrike	*Lanius excubitor*	2	0	2	0	0	0	0	0	0	2
Blue jay*	*Cyanocitta cristata*	0	3	3	0	5	5	0	0	0	8
American crow*	*Corvus brachyrhynchos*	0	0	0	6	0	6	4	0	4	10
Horned lark	*Eremophila alpestris*	26	41	67	0	0	0	0	0	0	67
Carolina chickadee*	*Poecile carolinensis*	0	0	0	1	2	3	0	0	0	3
Tufted titmouse*	*Baeolophus bicolor*	0	0	0	4	0	4	0	0	0	4
Carolina wren*	*Thryothorus ludovicianus*	0	3	3	1	4	5	0	0	0	8
Eastern bluebird*	*Sialia sialis*	49	40	89	53	128	181	15	23	38	308
American robin*	*Turdus migratorius*	48	2	50	2	4	6	11	0	11	67
Northern mockingbird*	*Mimus polyglottos*	13	2	15	10	3	13	2	3	5	33
European starling*	*Sturnus vulgaris*	62	3	65	328	12	340	43	0	43	448
American goldfinch*	*Spinus tristis*	5	153	158	104	315	419	21	151	172	749
Field sparrow*	*Spizella pusilla*	5	79	84	83	205	288	7	65	72	444
American tree sparrow	*Spizelloides arborea*	1	76	77	25	39	64	3	23	26	167
Fox sparrow	*Passerella iliaca*	0	4	4	2	1	3	0	1	1	8
Dark-eyed junco	*Junco hyemalis*	18	36	54	65	14	79	50	17	67	200
White-crowned sparrow	*Zonotrichia leucophrys*	0	0	0	13	1	14	0	2	2	16
White-throated sparrow	*Zonotrichia albicollis*	20	56	76	68	67	135	2	39	41	252
Savannah sparrow*	*Passerculus sandwichensis*	15	385	400	62	345	407	5	130	135	942
Song sparrow*	*Melospiza melodia*	133	696	829	414	1,216	1,630	77	439	516	2,975
Swamp sparrow	*Melospiza georgiana*	11	36	47	15	42	57	0	4	4	108
Eastern towhee*	*Pipilo erythrophthalmus*	0	0	0	2	0	2	0	3	3	5
Eastern meadowlark*	*Sturnella magna*	36	67	103	29	44	73	21	3	24	200
Red-winged blackbird*	*Agelaius phoeniceus*	2	2	4	9	1	10	0	0	0	14
Northern cardinal*	*Cardinalis cardinalis*	8	11	19	11	7	18	3	5	8	45
House sparrow*	*Passer domesticus*	0	0	0	0	1	1	0	0	0	1
	Total	527	1,745	2,272	1,318	2,726	4,044	273	916	1,189	7,505

Summary for Online TOC: Grasslands in the eastern United States support more diverse overwintering bird communities if they remain fallow throughout the winter season and exhibit higher bird species richness when comprised of native warm-season grasses compared to non-native cool-season grasses. Best management practices for grasslands should incorporate winter management strategies to optimize protective cover for overwintering bird species.