RESEARCH ARTICLE

WINTERING GRASSLAND BIRD HABITAT SELECTION FOLLOWING SUMMER PRESCRIBED FIRE IN A TEXAS GULF COAST TALLGRASS PRAIRIE

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ABSTRACT

We examined changes in winter habitat use by four grassland passerine birds in response to summer prescribed burning within a Texas gulf coast tallgrass prairie during 2001 and 2002. We used a traditional Before-After/Control-Impact (BACI) design consisting of one treatment plot (burned during summer 2001) and one control plot (no burning during the study period, but burned in previous years) at two study areas. Examination of use versus availability suggested that savannah sparrows (*Passerculus sandwichensis*) preferred recently burned patches. In contrast, sedge wrens (*Cistothorus platensis*) and Le Conte's sparrows (*Ammodramus leconteii*) avoided recently burned patches and preferred later successional stages. Our results suggest that grassland birds partitioned the prairie mosaic along a gradient of successional ecotypes, and that post-fire succession is an important ecological process influencing wildlife habitat use. Our results also highlighted the potential to sustain grassland bird habitats by managing Texas gulf coast tallgrass prairie with 3 yr to 4 yr rotational summer burns, similar to the historic fire return interval for this habitat type. We suggest that reinstating fire on its natural return interval will produce coarse-grained (e.g., 100 ha to 300 ha) habitat mosaics within the landscape and will sustain winter habitat diversity required for the guild of wintering grassland birds.

Keywords: fire ecology, grassland birds, habitat preference, summer prescribed fire, Texas gulf coast prairie

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INTRODUCTION

Prairie habitat loss and degradation are among the most common factors influencing the decline of grassland birds (Herkert 1994, Samson and Knopf 1994, Peterjohn and Sauer 1999, Johnson and Igl 2001, Askins *et al.* 2007). Because of fragmentation and woody advancement, prairie habitats often require active management to restore and sustain their historical physiognomic and floristic distinctiveness (Collins and Wallace 1990, Davis *et al.* 2000, Briggs *et al.* 2002). Part of that ecological distinctiveness lies in the traditional openness of prairie landscapes (Johnston 1963, Axelrod 1985); restoration and or maintenance of that openness is expected to benefit grassland animal communities (Collins and Wallace 1990, Packard and Mutel 1997).

Coastal tallgrass prairie habitats evolved with the occurrence of frequent fire (e.g., every 1 yr to 3 yr; Frost 1998, Schmidt *et al.* 2002, Grace *et al.* 2005) and prescribed burns allow managers to mimic historic fire regimes and restore the traditional habitat structure and heterogeneity (Johnston 1963, Box *et al.* 1967, Scifres and Hamilton 1993, Van't Hul *et al.* 1997, Askins *et al.* 2007). Historically, most naturally occurring prairie fires took place concurrently with annual peaks in lightning incidence in late summer and early fall (Higgins 1984, Anderson 1990). Relatively high fuel loads at the end of peak growing season coupled with the typically arid south Texas summer created conditions for summer fires to be especially intense (Axelrod 1985, Steinauer and Collins 1996). While there are no definitive records of the scale of summer fires in coastal tallgrass prairies before European settlement, the early Europeans regularly observed fires ranging from tens to thousands of hectares (Frost 1998, Schmidt *et al.* 2002, Grace *et al.* 2005). The current scale and frequency of natural coastal tallgrass prairie fires is unknown due to fire suppression efforts, but the scale is likely very small given the small size of the remaining tallgrass prairie patches in the Texas gulf coast.

Prescribed fire can be used to sustain native vegetation, stem woody plant advancements, and improve forage and habitat quality for grassland wildlife species (Rohrbaugh *et al.* 1999, Main and Richardson 2002, Askins *et al.* 2007). While it is recognized that many tallgrass landscapes developed under late summer fire regimes (see Higgins 1984, Howe 1994, Umbanowar 1996), prairie managers often emphasize winter or spring application of prescribed fire. In tallgrass prairie systems, prescribed fires burning in the winter or spring are easier to control and often emphasize agricultural land uses such as promoting warm-season grass production over other herbaceous vegetation that provides nutritious forage for livestock during stressful late summer droughts (see Risser *et al.* 1981, Ansley *et al.* 1998). However, there is little agreement about which fire application strategies (e.g., season and frequency of application) are most beneficial for sustaining grassland birds (Van't Hul *et al.* 1997, Reynolds and Krausman 1998, Baldwin *et al.* 2007).

While it is more convenient for managers of tallgrass prairies to conduct prescribed fires predominantly during winter and spring, these burning schedules have the potential to remove available habitat for grassland birds during their wintering period. Traditional summer prescribed fires offer an improvement because grassland patches have 4 mo to 6 mo of growing time before the arrival of wintering grassland birds. Further, there is growing evidence that summer prescribed fires are more effective at stopping the encroachment of woody vegetation (e.g., eastern baccharis [*Baccharis halimifolia*]; Marx 2003, Grace *et al.* 2005). Briggs *et al.* (2005) suggested that woody plant encroachment is one of the greatest contemporary threats to tallgrass prairie persistence. Other threats to North America's grassland habitats include conversion to farmland, urban development, and indirect effects through modification of grazing intensity, and fire suppression (Askins *et al.* 2007).

However, research into grassland bird habitat use during the non-breeding season remains limited (Herkert and Knopf 1998, Vickery and Herkert 2001, Askins *et al*. 2007). Given the extensive loss of grasslands, investigations into management effects on winter habitat use should remain a high priority in grassland bird conservation efforts. Further, habitat loss on the wintering grounds may negatively impact recruitment (Herkert and Knopf 1998), and our knowledge of species-specific responses to prairie management activities is limited (Walk and Warner 2000, Askins *et al.* 2007).

Although grassland avifauna communities are expected to respond positively to fire-mediated improvements in habitat quality, few experiments exist that examine any changes in habitat use patterns following summer fire while also comparing them to patterns of use in surrounding unburned patches (Main and Richardson 2002). Grassland birds are often grouped within the same ecological guild; however, there is a growing body of evidence that suggests individual species do not respond similarly to prairie management practices (Bollinger 1995, Rohrbaugh *et al.* 1999, Temple *et al.* 1999, Vickery *et al.* 1999). A common pattern among habitat studies on grassland birds is, when selecting habitat, bird species discriminate uniquely among a variety of successional stages, making grassland bird habitat management problematic (Bollinger 1995, Reynolds and Krausman 1998, Madden *et al.* 1999, Baldwin *et al.* 2007). If management plans are focused on only one species or treatment, then actions may benefit some species to the detriment of others (Madden *et al.* 1999, Rohrbaugh *et al.* 1999, Baldwin *et al.* 2007). Several authors have interpreted this to suggest that prairie habitats should be managed as heterogeneous coarse-grained (e.g., 100 ha to 300 ha) mosaics in order to benefit the diversity of grassland bird habitat needs (Rohrbaugh *et al.* 1999, Temple *et al.* 1999, Walk and Warner 2000, Main and Richardson 2002).

In this study, we used a field experiment to quantify the effects of two large-scale summer prescribed fires on wintering grassland bird habitat use in a Texas gulf coast tallgrass prairie located at the Aransas National Wildlife Refuge (hereafter, Aransas). We identified changes in plant community composition and examined the response of wintering grassland bird communities to summer burning. We also examined avian species-specific habitat preferences among different intermediate stages of succession based on post-fire intervals. Finally, we explored the ecological significance of these habitat preferences by highlighting their relationship to successional changes in vegetation structure.

METHODS

Study Area

We conducted our research within Aransas' 23 895 ha Tatton Unit (hereafter Tatton), approximately 11 km east of Austwell, Texas (Figure 1). Tatton has 3065 ha of Texas gulf coast tallgrass prairie, and land managers have used rotational summer prescribed burns at 2 yr to 4 yr intervals for almost two decades. The goals of the prescribed fire program at Aransas are to maintain and restore tallgrass prairie and to provide foraging opportunities for endangered whooping cranes (*Grus americana*), other migratory grassland birds, and native wildlife. Although summer burns are used regularly at Aransas, local conditions and field logistics often result in fire treatments during other seasons besides summer. No

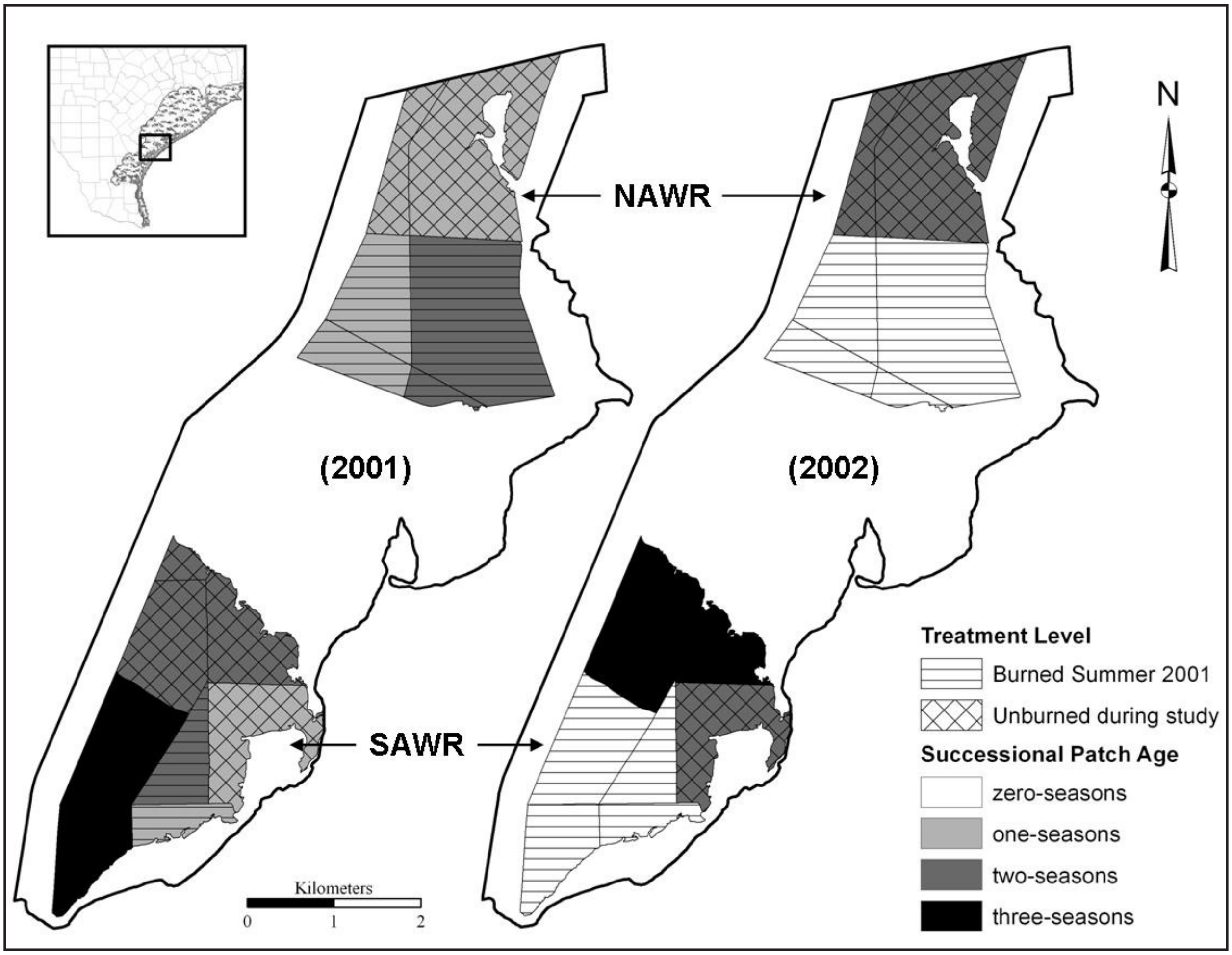

Figure 1. Distribution of study sites (control/treatment) and successional patches (seasons postburn) within the Tatton unit during winter 2001 and 2002 on the Aransas National Wildlife Refuge, Texas, USA. A prescribed burn was applied to the treatment sites of study areas North Aransas (NAWR) and South Aransas (SAWR), during the summer of 2001. Control fields were burned in previous years as part of Aransas' fire management program and appear as >0 seasons patch age prior to summer 2001 fires, and as zero-seasons patch age after summer 2001 fires. The three-seasons patch age plot in 2001 was burned during summer 2001, while the three-seasons patch age plot in 2002 remained unburned during the study.

domestic livestock have grazed Tatton since 1987.

Dominant grasses on our study site included gulf cordgrass (*Spartina spartinae*), seacoast little bluestem (*Scizachyrium scoparium* var. *littorale*), and fringed chloris (*Chloris ciliata*). Honey mesquite (*Prosposis glandulosa*) and eastern baccharis comprised the primary woody plant component within the landscape. We followed Hatch *et al.* (1999) for all vegetation nomenclature.

Field Methods

Avian Community Responses to Burning. To assess avian responses to summer prescribed burning, we used a Before-After/Control-Impact design (BACI; Green 1979, Underwood 1994, Oksanen 2001, Stewart-Oaten and Bence 2001). We sampled all study plots, unburned (control) and burned (treatment), before and after we burned, which is an appropriate design for studies intended to detect changes in resources that can be measured over short time intervals (van

Mantgem *et al.* 2001). We established two study areas within the Tatton summer prescribed burn area—one at the north end of the burn and one at the south (North Aransas and South Aransas, respectively). North and South Aransas study areas were separated by 4 km (Figure 1), and we established two plots (treatment and control) within each study area. We applied prescribed summer fire to our two treatment plots (North = 233 ha, South = 297 ha) in July 2001, and no burning occurred in control plots (North = 247 ha, South = 280 ha) during the study period. However, land managers burned the control plots in years previous to our study period.

Because of the ongoing rotational fire management program at Aransas, we did not randomly apply these summer fires. Managers apply fires repeatedly and on a rotational basis, and, as a result, the Tatton exists as a dynamic mosaic of successional conditions (Figure 1). We fit our study plots into this mosaic during winter 2001. By winter 2002, successional patches advanced another year in control plots, but our prescribed burns reset succession on the treatment plots. This mosaic offered a unique opportunity to explore avian habitat preferences among different successional stages following fire. We defined successional stage as the number of complete growing seasons that occurred since a given habitat patch was burned. For example, “zero seasons post-burn” referred to the recently burned patches we examined during the winter immediately following the 2001 summer prescribed burns. Likewise, patches with one complete growing season since burning were “one season post-burn,” and so on.

To conduct bird surveys, we established five 500 m line transects within each study plot, laid a 200 m by 200 m grid over these study plots, and randomly selected transect endpoints. We used a random bearing to establish each transect line and separated transect lines from each other, as well as from roads, firebreaks, fence lines, and drainage corridors by ≥200 m. Our winter survey period occurred from January to February and we sampled each transect four times each year during the survey period. We made consecutive visits at least two weeks apart, but did not survey on days with high winds (>20 km h^{-1}) or during precipitation events (Robbins 1981). We varied the order we surveyed the transects to minimize diurnal detection bias and surveyed all transects on the same day.

We surveyed birds using variable-distance line transects (Buckland *et al*. 1993) using two observers on each transect, with each observer responsible for detecting birds on their side of the center-line (zero-line). Observers recorded species, the number of individuals flushed, and the perpendicular distance from the zero-line. To avoid multiple counts of the same individual, observers noted the location of each alighted bird and were conservative when designating unique detections.

Fire Effects on Habitat Structure. Immediately following each avian survey, January to February 2001 and 2002, we estimated vegetation structure using five variables: (1) 100 % visual obstruction height (herbaceous density) readings, (2) large shrub (≥1.5 m) density, and (3) vegetation cover composition: (a) percent grass, (b) percent forb, and (c) percent shrub cover. We selected these habitat variables based on previous studies that examined grassland bird habitat associations in similar environments (Van’t Hul *et al.* 1997, Reynolds and Krausmann 1998, Baldwin *et al.* 2007). We sampled vegetation by randomizing the first sample point within 10 m of the bird transect origin and then sampled every 20 m thereafter. At each sample point, we made two estimates for each variable—one on each side of the transect line at a randomly selected distance between 1 m and 5 m.

We used a 200 cm by 3.5 cm Robel pole marked at 10 cm intervals to estimate 100 % visual obstruction height (VOH) (Robel *et al.* 1970). We used the 100 % VOH measurements to determine the effective cover height of herbaceous vegetation (cm). Measuring cover height in this manner offered a rapid assessment of herbaceous density (Robel *et al.* 1970). To determine large shrub density, we used a point-centered quarter method (Cottam and Curtis 1956), and then calculated estimates using the unbiased estimator as outlined in Pollard (1971). We did not attempt to estimate densities for individual species because we were primarily interested in shrub structure.

We defined vegetation cover as the percent area of ground covered by vegetation (Bonham 1989) and measured it using a 0.25 m^2 rectangular frame (Daubenmire 1959). Within each frame, we estimated the percent grass, forb, and shrub cover. To minimize observer bias, we assigned percent estimates to eight frequency classes (e.g., 0 %, >0 % to 10 %, >10 % to 25 %, >25 % to 50 %, >50 % to 75 %, >75% to 90 %, >90 % to 99 %, and 100 %; Bonham 1989).

Data Analysis

In a preliminary analysis, we determined that detectability decreased significantly beyond 25 m, while being similar below 25 m between treatments for each species. Therefore, in our analyses for this study, we constrained avian data to detections within 25 m of the transect zero-line and, subsequently, obtained estimates of density within a 2.5 ha strip. Prior to our analysis of habitat use, we calculated the mean avian density (ha^{-1}) for each transect across four visits during each winter. We analyzed habitat associations of the four most abundant grassland passerines: sedge wren (*Cistothorus platensis)*, savannah sparrow (*Passerculus sandwichensis*), Le Conte's sparrow (*Ammodramus leconteii*), and eastern meadowlark (*Sturnella magna*). Low sample sizes or absence in the first year prevented adequate statistical comparisons for other species.

We blocked transects according to year and treatment level (burned versus control) to test for changes in wintering grassland bird densities following summer prescribed fires. We used a general linear model to conduct a two-way analysis of variance (ANOVA) with full interaction to detect differences in grassland bird habitat use following summer fire. Year and treatment were the main effects, and a significant year-by-treatment interaction would indicate that changes in avian density and vegetation characteristics were related to summer prescribed fires.

To examine species-specific preferences for successional stages, we grouped transects according to the number of growing seasons post-burn across both years of study (0 years, n = 10; 1 year, n = 6; 2 years, n = 16; and 3 years, n = 8). This analysis allowed us to highlight differences in habitat use across a mosaic of seral stages as succession advanced following summer fires. Non-uniform distribution of avian densities among treatments indicated that birds were non-randomly selecting a particular habitat (Wiens 1989, Jones 2001). We conducted chi-square goodness of fit tests and compared proportional use with habitat availability for each successional stage (Neu *et al.* 1974, Byers *et al.* 1984). We defined proportional use as the proportion of birds from the total observed that were found in a given habitat type. Availability was the proportion of each habitat type within the total sampled habitat area, and greater than expected use relative to availability indicated a preference (Neu *et al.* 1974, Johnson 1980, Krebs 1999).

We conducted multiple linear regressions to identify which habitat characteristics had the greatest influence on grassland bird habitat selection. To stabilize variances, we used the natural logarithm transformation for shrub density and the arcsine-square root transformation for all proportional data (i.e., grass, forb, and shrub percent cover).

For each species, we sought the most parsimonious model that selected a subset of significant habitat variables from the total available pool. We used Mallows' C*p* criterion to select the most parsimonious model (Mallows 1973) because this criterion prevents multicollinearity among independent variables and guards against overfitting during the regression procedure (Cetin and Erar 2006). We selected the "best" models as those with small C*p* values that closely approximated the number of parameters in a given model. We also computed the standardized partial regression coefficient (β) for each model parameter to compare the relative importance of each habitat characteristic in determining grassland bird density (Zar 1996). The highest absolute values of β indicated which habitat characteristics had the largest influence on avian habitat selection. We used SPSS 10.0 for all statistical analyses (SPSS 1999) and present Bonferroni corrected 95 % confidence intervals where we made pairwise comparisons (Zar 1996).

RESULTS

Fire Effects on Habitat Structure

Summer fires had the greatest effect on herbaceous structure (Table 1). Both herbaceous density and grass cover declined following fire, but we detected no change in forb cover when measured one year after the fire. We also observed that summer prescribed fires caused declines in shrub density and shrub cover.

Herbaceous density ($R^2 = 0.72$, $P < 0.001$) and grass cover ($R^2 = 0.71$, $P < 0.001$) increased with each growing season post-burn, while forb cover decreased ($R^2 = -0.20$, $P = 0.004$). We found no significant relationship between shrub density ($R^2 = 0.01$, $P = 0.56$) or shrub cover ($R^2 = 0.05$, $P = 0.15$) with the duration of time since burning.

Avian Community Responses to Burning

Over two years of study, we detected 5779 individuals from four habitat guilds defined by Verner (1984): grassland (12 species), shrub (12 species), wetland (7 species), and aerialist (4 species) (Table 2). Wetland and aerialist guilds respectively comprised 5 % and 1 % of

Table 1. Changes in vegetation structure between winter 2001 (pre burning) and winter 2002 (post summer fires) in treatment and control plots at the Aransas National Wildlife Refuge. We reported mean parameters, Bonferroni-corrected 95 % confidence intervals (CI), and test statistics for a year × treatment interaction.

Vegetation structure	**Control sites**		**Treatment sites**			
	Unburned 2001	**Unburned 2002**	**Pre-burn 2001**	**Post-burn 2002**	$F_{3,36}$	***P***
Large shrub density ha^{-1}	0.43 (-1.74 to 2.60)	3.88 (1.71 to 6.05)	1.19 (-0.98 to 3.37)	1.01 (-1.16 to 3.18)	2.89	0.09
Herbaceous density (cm)	20.42 (17.77 to 23.06)	21.61 (18.97 to 24.26)	21.4 (18.75 to 24.26)	4.31 (1.67 to 6.96)	48.97	<0.01
% grass cover	0.71 (0.63 to 0.80)	0.78 (0.66 to 0.83)	0.75 (0.66 to 0.83)	0.38 (0.29 to 0.46)	26.79	<0.01
% forb cover	0.24 (0.15 to 0.33)	0.18 (0.09 to 0.27)	0.20 (0.12 to 0.29)	0.26 (0.17 to 0.35)	2.13	0.15
% shrub cover	0.01 (-0.01 to 0.02)	0.02 (0.01 to 0.03)	0.01 (0.01 to 0.03)	<0.01 (-0.10 to 0.02)	3.41	0.07

Table 2. List of species and total abundance at each study area for winter 2001 and 2002 combined at the North (NANWR) and South (SANWR) sites on the Aransas National Wildlife Refuge. Species designation into habitat guilds, total guild abundance, and the number of species within each guild are also reflected.

Species	NANWR	SANWR	Total
White-tailed kite (*Elanus leucurus*)	27	5	32
Northern harrier (*Circus cyaneus*)	36	32	68
White-tailed hawk (*Buteo albicaudatus*)	14	2	16
Sandhill crane (*Grus canadensis*)	236	379	615
Sedge wren (*Cistothorus platensis*)	284	205	489
Short-eared owl (*Asio flammeus*)	7	1	8
American pipit (*Anthus rubescens*)	1	0	1
Sprague's pipit (*Anthus spragueii*)	124	77	201
Savannah sparrow (*Passerculus sanwichensis*)	1471	908	2379
Grasshopper sparrow (*Ammodramus savannarum*)	29	0	29
Le Conte's sparrow (*Ammodramus leconteii*)	689	197	886
Eastern meadowlark (*Sturnella magna*)	429	165	594
Grass guild (species = 12)	3347	1971	5318
Red-tailed hawk (*Buteo jamaicensis*)	0	2	2
Cooper's hawk (*Accipiter cooperii*)	1	0	1
Crested caracara (*Caracara cheriway*)	3	3	6
American kestrel (*Falco sparverius*)	3	7	10
Merlin (*Falco columbarius*)	3	1	4
Mourning dove (*Zenaida macroura*)	6	43	49
Common ground-dove (*Columbina passerina*)	1	0	1
Eastern phoebe (*Sayornis phoebe*)	1	0	1
Loggerhead shrike (*Lanius ludovicianus*)	8	0	8
Common yellowthroat (*Geothlypis trichas*)	2	0	2
Swamp sparrow (*Melospiza georgiana*)	15	0	15
Northern cardinal (*Cardinalis cardinalis*)	1	0	1
Open shrubland guild (species = 12)	44	56	100
American bittern (*Botaurus lentiginosus*)	1	0	1
Mottled duck (*Anas fulvigula*)	0	4	4
Sora (*Porzana carolina*)	0	1	1
Long-billed curlew (*Numenius americanus*)	25	1	26
Long-billed dowitcher (*Limnodromus colopaceus*)	0	1	1
Common snipe (*Gallinago gallinago*)	1	0	1
Red-winged blackbird (*Agelaius phoeniceus*)	224	15	239
Wetland guild (species = 7)	251	22	273
Tree swallow (*Tachycineta bicolor*)	3		3
Purple martin (*Progne subis*)	5		5
Black vulture (*Coragyps atratus*)	9	13	22
Turkey vulture (*Cathartes aura*)	36	22	58
Aerial guild (species = 4)	53	35	88
Total detections (species = 35)	**3695**	**2084**	**5779**

all birds detected. Individuals in the shrub guild, which included species such as the mourning dove (*Zenaida macroura*), eastern phoebe (*Sayornis phoebe*), and northern cardinal (*Cardinalis cardinalis*), accounted for only 2 % of the avian community at Aransas.

Grassland birds accounted for 92 % of all detected individuals. Within the grassland guild, sedge wren, savannah sparrow, Le Conte's sparrow, and eastern meadowlark respectively comprised 9 %, 45 %, 17 %, and 11 % of the sampled wintering grassland bird community across years.

Grassland Bird Responses to Summer Fire and Succession

We detected no change in grassland bird density or bird species richness following application of summer prescribed fires (Table 3). Despite not detecting differences in species richness, our data suggested there was a significant turnover within the community. For instance, in 2002, we observed that sandhill cranes (*Grus canadensis*) and Sprague's pipits (*Anthus spragueii*) moved into recently burned patches, while sedge wrens and Le Conte's sparrows tended to be absent. Additionally, community evenness decreased because burned areas became dominated by large flocks of savannah sparrows.

Eastern meadowlark densities did not change with fire management, while savannah sparrow density increased within recently burned patches, and sedge wren and Le Conte's sparrow densities declined (Table 3). Grassland species also exhibited differences in patch use depending on whether patches were recently burned or whether succession had occurred over one, two, or three complete growing seasons post-burn (Figure 2). Sedge

Table 3. Grassland bird community response to summer prescribed fire. We compared guild level and species-specific responses between winter 2001 (pre burning) and winter 2002 (post summer fire) in treatment and control plots at the Aransas National Wildlife Refuge, Texas, USA. We reported mean parameters alongside Bonferroni-corrected 95 % confidence intervals (CI) and significance statistics for a year × treatment interaction.

	Control sites		**Treatment sites**			
Community characteristics	**Unburned 2001**	**Unburned 2002**	**Pre-burn 2001**	**Post-burn 2002**	$F_{3, 36}$	***P***
Avian density (ha^{-1})[a]	6.8 (3.9 to 9.6)	7.4 (4.5 to 10.2)	5.5 (2.6 to 8.4)	8.3 (5.4 to 11.1)	0.58	0.45
Species richness	6.3 (5.4 to 7.2)	5.7 (4.8 to 6.6)	6.4 (5.5 to 7.3)	5.2 (4.3 to 6.1)	0.43	0.51
Guild evenness	0.8 (2.6 to 8.4)	0.8 (2.6 to 8.4)	0.8 (2.6 to 8.4)	0.6 (2.6 to 8.4)	8.09	<0.01
Species density (ha^{-1})						
Sedge wren	0.9 (0.6 to 1.1)	1.2 (0.9 to 1.4)	0.9 (0.6 to 1.2)	0.1 (-0.2 to 0.3)	20.71	<0.01
Savannah sparrow	2.1 (0.1 to 4.1)	1.9 (-0.1 to 3.9)	1.5 (-0.5 to 3.5)	6.4 (4.3 to 8.4)	6.77	0.01
LeConte's sparrow	2.8 (1.7 to 3.8)	3.4 (2.4 to 4.5)	1.8 (0.7 to 2.8)	0.1 (-1.0 to 1.1)	5.10	0.03
Eastern meadowlark	0.4 (0.1 to 0.7)	0.7 (0.4 to 1.1)	0.4 (0.1 to 0.7)	0.5 (0.2 to 0.8)	0.47	0.49

[a] Avian densities were derived from line transect bird surveys, constrained to detections within 25 m of the transect zero-line, and were averaged for each transect across four visits during each winter extended to an estimate at the ha^{-1} scale.

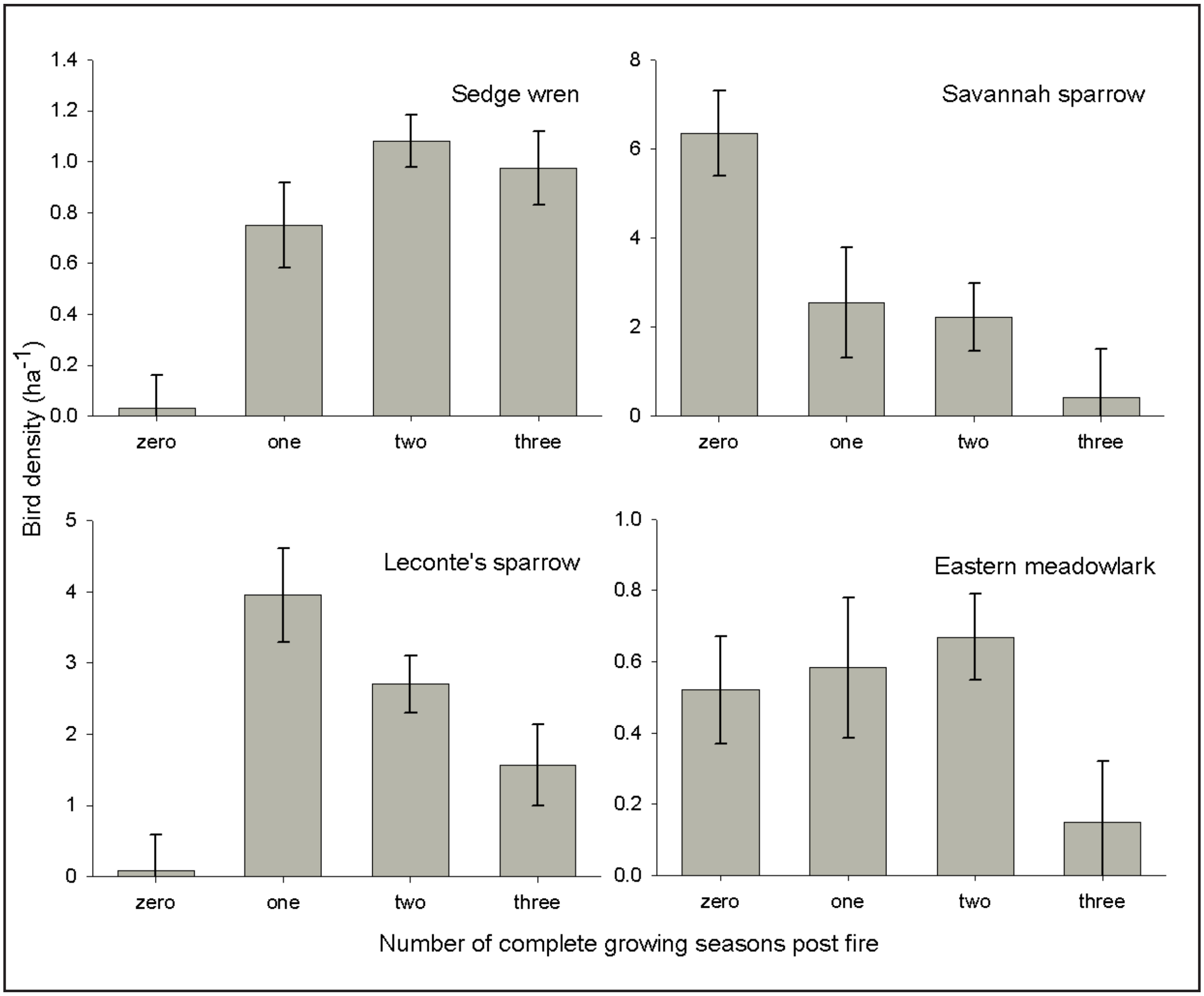

Figure 2. Differences in habitat use (± SE) among successional patches (time since burning) by four grassland passerines during winter 2001 and 2002 at the Aransas National Wildlife Refuge, Texas, USA.

wren ($F_{3, 36} = 14.75$, $P < 0.001$) and Le Conte's sparrow ($F_{3, 36} = 8.91$, $P < 0.001$) habitat use increased among patches in which at least one full growing season had occurred. Savannah sparrow habitat use tended to decline as plant succession advanced ($F_{3, 36} = 6.37$, $P = 0.001$).

Examination of use versus availability suggested that savannah sparrows preferred recently burned patches over other successional stages (Table 4). However, by the time patches experienced two complete growing seasons, savannah sparrows tended to avoid them ($\chi^2_{80} = 59.7$, $P < 0.001$). In contrast, sedge wrens ($\chi^2_{80} = 10.4$, $P = 0.015$) and Le Conte's sparrows ($\chi^2_{80} = 34.4$, $P < 0.001$) avoided recently burned patches. These results suggest that sedge wrens selected for patches with two-seasons of post-burn growth and that Le Conte's sparrow showed a preference for both one- and two-season successional patches. Eastern meadowlark habitat use did not differ between successional patches ($\chi^2_{80} = 2.9$, $P = 0.41$).

Regressions of grassland bird densities with habitat characteristics revealed that increasing herbaceous density had the greatest effect on sedge wrens and Le Conte's sparrows (Table 5). However, savannah sparrow density was negatively correlated with herbaceous density.

Table 4. Comparison of habitat use versus availability to identify grassland bird habitat preferences among successional ecotypes during winter 2001 and 2002 at Aransas National Wildlife Refuge, Texas, USA. Successional ecotypes were defined as the number of complete growing seasons that occurred prior to sampling.

		Proportional use (95 % CI)[b]			
Seral stage	**Habitat availability[a]**	**Sedge wren**	**Savannah sparrow**	**LeConte's sparrow**	**Eastern meadowlark**
Recently burned	0.25	<0.01 (<0.01 to 0.03)	0.54 (0.42 to 0.65)	0.01 (<0.01 to 0.03)	0.25 (0.15 to 0.35)
One season	0.15	0.15 (0.02 to 0.28)	0.13 (0.01 to 0.26)	0.30 (0.16 to 0.47)	0.17 (0.03 to 0.31)
Two seasons	0.40	0.58 (0.51 to 0.65)	0.30 (0.24 to 0.37)	0.54 (0.47 to 0.61)	0.52 (0.45 to 0.59)
Three seasons	0.20	0.26 (0.14 to 0.38)	0.03 (0.02 to 0.08)	0.16 (0.05 to 0.25)	0.06 (0.01 to 0.12)

[a] Availability was the proportion of each habitat type within the total sampled habitat area.
[b] Proportional use was the proportion of birds from the total observed that were found in a given habitat type and greater than expected use relative to availability indicated a preference.

Table 5. Results from multiple linear regressions (n = 40) of species density (ha^{-1}) by five habitat variables: herbaceous density ($kg\ ha^{-1}$), shrub density (ha^{-1}), and % grass, % shrub, and % forb cover at the Aransas National Wildlife Refuge, Texas, USA. We only report the most parsimonious model for each species. Standardized coefficients (β) and *P*-values reflected strength of influence on avian density. Adj-R^2 values describe the proportion of variation in avian density explained by the model.

Species	Predictor variable	β	*P*
Sedge wren	herbaceous density	0.755	<0.001
	shrub density	0.209	0.045
adj-R^2	0.651		
Savannah sparrow	herbaceous density	-0.420	0.003
	shrub density	0.535	0.001
	% shrub cover	-0.383	0.019
adj-R^2	0.369		
LeConte's sparrow	herbaceous density	0.617	>0.001
	shrub density	0.410	0.002
	% forb cover	0.302	0.014
adj-R^2	0.726		
Eastern meadowlark	% forb cover	0.470	0.002
adj-R^2	0.221		

DISCUSSION

In this study, we found that grassland birds exhibited preferences for successional patch types based on the number of full growing seasons after summer burns. These patterns were consistent with previous studies conducted in other Texas gulf coast prairies (Van't Hul *et al.* 1997, Reynolds and Krausman 1998, Baldwin *et al.* 2007). Inferences from those studies and ours suggest that grassland birds do not respond to fires, per se, but to fire-mediated changes in habitat structure. Because fire application across these studies included different seasons of application, we propose that the influence of prescribed burn seasonality may not be a determinate factor in grassland bird habitat use. Rather, the successional differences among patches following fire that reset patch succession may be a key factor determining the structure and composition of wintering grassland bird communities. Our findings were similar to those found on these birds' breeding grounds (Zimmerman 1988, Bollinger 1995, Madden *et al.* 1999).

Habitat selection is the complex behavioral decision-making process that leads to the observed patterns of partitioning among species (Jones 2001). Explanations for habitat selection can stem from species-specific food acquisition strategies (MacArthur 1958), predator avoidance (Lima and Dill 1990), or breeding constraints (Orians and Pearson 1979). However, during winter, breeding constraints on grassland bird habitat use, such as nest site selection or brood protection, are relaxed and, therefore, other considerations likely drive winter habitat selection. Winter occupation of different successional patches by various species may be driven by divergent preferences for types of habitat structure that simultaneously benefit food acquisition and predator avoidance (Lima and Dill 1990).

For instance, during the breeding season, savannah sparrows will occupy more densely vegetated habitats that provide nest protection and arthropods for developing young (Wheelwright and Rising 1993). However, during the winter, savannah sparrows become primarily ground-foraging seed-eaters that tend to feed as gregarious flocks in open areas (Grzybowski 1983a, b; Wheelwright and Rising 1993). Our results confirm this habitat use pattern where we observed higher densities of savannah sparrows in recently burned patches compared to older patches. Exploiting recently burned areas with less plant cover could facilitate food discovery but increase their exposure to predators. Savannah sparrows may mitigate this risk in winter by foraging in gregarious flocks and flushing readily to woody cover when disturbed. Balancing this risk-reward scenario could explain why we found that savannah sparrow abundance was associated with reduced plant cover and increasing shrub density.

In contrast, the sedge wren is an insectivore that is typically more solitary and secretive (Grzybowski 1983b, Herkert *et al.* 2001). Vegetation growth rates increase rapidly immediately following fires (Box *et al.* 1967, Owens *et al.* 2002), but community succession of invertebrates lags behind the recovery of above-ground vegetation (Curry 1994). The denser herbaceous vegetation typical of later successional patches may provide increased protection from predators and enhanced access to prey, which could explain sedge wren habitat preferences. In our study, sedge wrens had higher densities in older patches that had increased amounts of vegetation and subsequently greater cover. Grassland species likely partition the prairie mosaic via habitat selection and base their selection on the balance between foraging needs and predation risk (Lima and Dill 1990). However, additional research will be necessary to clarify the linkages between habitat use and the processes that influence observed patterns.

Avian selection for successional ecotypes suggests that implementing rotational burning plans that produce landscape heterogeneity at coarse scales can sustain year-round grassland bird habitat (Temple *et al.* 1999, Walk and Warner 2000). In this case, we applied 200 ha to 300 ha prescribed summer burns. Scifres and Hamilton (1993) suggested that rotational burning every 3 yr to 4 yr could help suppress woody plant succession and sustain native plants within the Texas gulf coast tallgrass prairie ecoregion. This degree of rotation allows 25 % to 33 % of management units to be burned annually such that a mosaic of successional conditions is maintained within the landscape. Further, Grace *et al.* (2005) found that summer prescribed fire increased the likelihood of mortality of the shrubby plant, eastern baccharis, by ≤55 % more than winter prescribed fire. If one of the objectives of Texas gulf coastal tallgrass prairie management is to maintain openness of the habitat, then management of eastern baccharis is critical and summer prescribed fires provide an effective control measure (Grace *et al.* 2005).

It is evident that properly managed Texas gulf coast tallgrass prairies can provide habitat for a diverse wintering avian community based on our detections of 35 species and nearly 6000 individuals over a two-year study period. Despite the tendency to emphasize concern for guild-level population declines, our results reflect a need to consider species-specific responses to prairie management activities. This study supports the idea that prairie management plans can incorporate rotational summer fires to produce a coarse-grained landscape mosaic of successional ecotypes. Implementation of summer fires should occur after the majority of grassland nesting species have completed nesting when and where possible. Rotational fire management of Texas gulf coastal prairies has the potential to meet the needs of a diversity of overwintering avian species.

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