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WINTER HABITAT ASSOCIATIONS OF FOUR GRASSLAND SPARROWS IN FLORIDA DRY PRAIRIE

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ABSTRACT.—North American grassland birds show long-term population declines that generally exceed the declines of other bird groups. Efforts to conserve grassland birds require knowledge of ecological and habitat requirements during both the breeding and nonbreeding periods of annual life cycles. Nonbreeding habitat associations may affect survival and the acquisition of resources needed for migration and breeding. We focused on the winter habitat associations of a suite of co-occurring grassland sparrows in the dry prairie of south-central Florida, an understudied region within the wintering range of Grasshopper Sparrows (*Ammodramus savannarum pratensis*) and Henslow's Sparrows (*A. henslowii*). During the nonbreeding winter months, these two migratory sparrows commingle with resident Bachman's Sparrows (*Peucaea aestivalis*) and federally endangered Florida Grasshopper Sparrows (*Ammodramus savannarum floridanus*). We investigated sparrow habitat associations within two defined plant communities of the dry prairie ecosystem, the dry-mesic and wet-mesic prairie, for four prescribed fire treatments over two consecutive winters. Grasshopper and Henslow's sparrows showed higher relative abundance in wet-mesic prairie and Bachman's Sparrows were more abundant in dry-mesic prairie across all fire treatments. Florida Grasshopper Sparrows were detected only in the first and second years post-burn; samples were too small to yield information on potential preferences between the two prairie communities evaluated. We used an information-theoretic approach to select models that best predicted abundances for each species (except Florida Grasshopper Sparrows) based on time since fire and plant community. Abundances of Grasshopper and Bachman's sparrows were best predicted by plant community association and secondly by time since fire; whereas for Henslow's Sparrows, habitat and time since fire were equally important. This is the first concurrent study of these four sparrow taxa in peninsular Florida and indicates that time since fire influences the habitat preferences exhibited by wintering sparrows, but that this role differs across co-occurring species and dry prairie plant communities. Received 31 August 2012. Accepted 3 May 2013.

Key words: Bachman's Sparrow, burn, fire, Florida Grasshopper Sparrow, Grasshopper Sparrow, Henslow's Sparrow, nonbreeding season.

Habitat loss and degradation are primary factors cited in the steady declines of grassland birds in North America, including Bachman's Sparrow (*Peucaea aestivalis*), Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*), the eastern North American subspecies of Grasshopper Sparrow (*A. s. pratensis*, hereafter, "Grasshopper Sparrow"), and Henslow's Sparrow (*A. henslowii*) (Delany et al. 1985, Sauer et al. 2011). Each of these sparrows is classified as a species of conservation concern in more than one North American region (USFWS 2008) and in several southeastern states that provide winter habitat for migratory Grasshopper and Henslow's sparrows (Sauer et al. 2011). Mitigating grassland bird declines requires better knowledge of their winter ecology, because winter habitat selection cues may differ from the cues used during the

breeding season, and managing landscapes solely for favorable breeding habitat may ignore important wintering habitat needs (Vickery and Herkert 2001, Newton 2004, Macias-Duarte et al. 2009).

The dry prairie of south-central Florida is a predominantly mesic ecosystem that provides both breeding and nonbreeding habitat for grassland sparrows. The dry prairie is a treeless, pyrogenic mosaic of plant communities comprised of more than 20 plant species per square meter ($\bar{x} = 21.6$ species/m²; range 9 to 41 species/m²) and up to 49 species per square meter in the wet calcareous community type, one of the highest plant species richness values globally at this spatial scale (Orzell and Bridges 2006a, b). Less than 10% remains of an estimated 5,000 km² of pre-settlement Florida dry prairie (Noss 2013).

Dry prairie is characterized by a predominance of saw palmetto (*Serenoa repens*), dwarf live oak (*Quercus minima*), and wiregrass (*Aristida stricta* var. *beyrichiana*). Relative abundance of these and other plants characteristic of dry prairie varies along a soil moisture gradient from graminoid-dominated wet-mesic and wet prairies to the more shrubby mesic, dry-mesic, and sub-xeric prairies. Plant communities within this heterogeneous

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mosaic can be distinguished by indicator species associated with segments of a wet to sub-xeric soil moisture gradient (Noss et al. 2008). Infrequent fire results in encroachment of woody shrubs and trees that shade out pyrogenic bunchgrasses, increased herbaceous density at ground level, and reduction or elimination of bare ground areas, which in turn impair movement, foraging efficiency, and predator detection by ground-dwelling sparrows (Vickery 1996, Bechtoldt and Stouffer 2005, Tucker et al. 2006, Cox and Jones 2009).

Lightning-ignited fires in Florida dry prairie occur approximately every two years, a rate among the highest in the world (reviewed in Noss 2013). Previous research on grassland sparrows emphasized relationships between sparrow abundance and the effects of fire frequency on vegetation structure and seed production. Fire frequency plays a key role in breeding habitat selection by Bachman's and Florida Grasshopper sparrows (Shriver et al. 1999; Shriver and Vickery 2001; Delany et al. 2002; Tucker et al. 2004, 2006), Henslow's Sparrows (Cully and Michaels 2000; Reinking et al. 2000; Powell 2006, 2008), and Grasshopper Sparrows (Powell 2006, 2008). Fire also plays an important role in wintering habitat selection for Henslow's Sparrows in Louisiana, Mississippi, Alabama, Georgia, and the western Florida panhandle (Tucker and Robinson 2003; Tucker et al. 2004, 2006; Bechtoldt and Stouffer 2005; Cox and Jones 2009; Palasz et al. 2010). Previous research suggested that winter survival of these grassland birds may be linked to fire frequency in overwintering habitat (Tucker and Robinson 2003, Thatcher et al. 2006), but other studies disputed this (Johnson et al. 2011). The effect of fire history on winter habitat selection of both the non-migratory Florida Grasshopper Sparrow (Dean 2001) and the migratory Grasshopper Sparrow (Butler et al. 2009) in Florida dry prairie has been studied, but no published information is available on winter habitat preferences of Henslow's or Bachman's sparrows in peninsular Florida. In fact, Christmas Bird Count records and published reports of Henslow's Sparrows in peninsular Florida are scarce (Robertson and Woolfenden 1992, Stevenson and Anderson 1994, Pranty and Scheuerell 1997).

We examined four co-occurring taxa of wintering grassland sparrows in Florida dry prairie over a two-year period. We hypothesized that the relative abundance of each sparrow taxon would relate to prairie plant community and to the

number of growing seasons post-fire. Knowledge of relationships between winter habitat occupancy of co-occurring sparrows and plant communities in peninsular Florida will allow better predictions of sparrow occurrence and potential viability on a landscape scale and provide a basis for habitat restoration, species recovery, and land acquisition (Noss et al. 2008).

METHODS

Study Site.—We conducted our research at Kissimmee Prairie Preserve State Park, which encompasses approximately 10,200 ha of dry prairie within the 22,500 ha Preserve (USFWS 1999). During our 2006–2008 field research, the Preserve was believed to support one of the largest extant populations of endemic, non-migratory Florida Grasshopper Sparrows (Pranty and Tucker 2006), an abundant breeding population of Bachman's Sparrows, and several species of overwintering and migratory sparrows including Henslow's, Grasshopper, Savannah (*Passerculus sandwichensis*), Swamp (*Melospiza georgiana*), Chipping (*Spizella passerina*), and small numbers of Le Conte's (*Ammodramus leconteii*), Lincoln's (*Melospiza lincolni*), and Vesper (*Pooecetes gramineus*) sparrows (P. Miller and MGK, unpubl. data).

Flush-Net Sampling.—We used flush-netting, an active sampling method in which birds are systematically driven toward a stationary line of mist nets for mark and recapture (Gordon 2000). Variations of the method involve systematic flushing of plots with individual birds flushed into a mobile mist net set up at the location of each flushed bird (Johnson et al. 2009, Palasz et al. 2010). We selected the flush-netting method to improve accuracy in identifying cryptic, closely related sparrows that might otherwise be misidentified in flight (Bechtoldt and Stouffer 2005). We assumed that all sparrows present were flushed at least once and counted or captured. We flushed sparrows using noisemakers (2 L plastic bottles containing pebbles) attached to a 30-m rope dragged over the vegetation by two observers toward a 120-m long mist net array centered within each established plot. A third observer walked behind the rope and marked sparrow flush locations with a numbered flag. The flag location was recorded with a hand-held Garmin Vista Cx GPS unit. The area sampled in each flushed plot was determined by recording WAAS-enabled GPS locations (<3 m error) at each end of the

TABLE 1. Sampling strategy for burn classes, each sampled in six plots of between 4–5 ha. Three of the six plots in each group covered predominantly wet-mesic prairie, and three plots covered predominantly dry-mesic prairie. An unscheduled burn of Five Mile Prairie occurred in the latter part of the first sampling year preventing resampling of those six plots. The total number of plots sampled (including replicate samples) in each year was 36.

	Sampling area	Burn class	# of plots	Times sampled	# of Plot samples
Year 1	Corridor Prairie	2	6	1	6
	Five Mile Prairie	2	6	1	6
	Audubon Prairie	2	6	2	12
	Duck Slough East Prairie	4	6	2	12
Year 2	5 Mile Prairie	1	6	3	18
	Audubon Prairie	3	6	3	18

mist net line and at one end of the 30-m rope at initiation of each flush transect. We calculated the relative abundance of each flushed sparrow species by burn class as the number of sparrows per 100 ha to adjust for variation in sample plot size. Although capturing flushed birds was not required for the research presented in this paper, we suggest that by doing so we were able to improve positive identification of other cryptic sparrows flushed but not captured.

Wet-Mesic Versus Dry-Mesic Prairie Habitat.—We adapted the dry prairie vegetation classification system developed by Noss et al. (2008) to two categories for this study. We defined dry-mesic prairie as populated predominantly by shrubs (e.g., *Serenoa repens*, *Quercus minima*, *Lyonia lucida*, *L. fruticosa*, *Hypericum reductum*, *Vaccinium myrsinites*, *Gaylussacia dumosa*, *Lechea torreyi*), with graminoids (e.g., *Sorghastrum secundum*, *Dichanthelium portoricense*, *Xyris caroliniana*) and non-woody forbs (e.g., *Carphephorus carnosus*, *Pityopsis graminifolia*, *Pterocaulon virgatum*). We defined wet-mesic prairie as populated predominantly by graminoids (e.g., *Ctenium aromaticum*, *Dichanthelium leucothrix*, *D. erectifolium*, *Xyris elliotii*, *X. ambigua*) and non-woody forbs (e.g., *Chaptalia tomentosa*, *Eriocaulon decangulare*, *Bigelovia nudata*, *Lachnocaulon anceps*). Wiregrass (*Aristida stricta* var. *beyrichiana*) is an abundant and characteristic grass across this habitat gradient (Orzell and Bridges 2006a, b). The same observer visually classified the vegetation within a 10-m diameter circle centered on each sparrow flush location ($n = 239$: 2006–2007; $n = 316$: 2007–2008) into one of the two habitat categories, either dry-mesic or wet-mesic, based on the presence of the selected plant indicator species (Noss et al. 2008).

Effects of Time Since Fire.—We defined burn class in this study as the number of growing seasons post-burn. Samples were taken from 27 October 2006 to 28 February 2007 (2006–2007 samples), and from 5 November 2007 to 11 March 2008 (2007–2008 samples). Migrants persisted at the study location into April or later, but flush-net sampling terminated in early March because of federal permit conditions prohibiting flush-netting in the breeding season of the endangered Florida Grasshopper Sparrow.

In the first year we sampled burn classes two and four, and in the second year burn classes one and three (Table 1); burn class sampling could not be replicated between years due to the biennial prescribed fire rotations implemented at the study site for recovery of the Florida Grasshopper Sparrow. Plots were established to ensure sampling of an approximately equal area of both dry-mesic and wet-mesic prairie within each burn class and were sized to permit systematic sampling of each plot in one work-day by a three-person field crew. Six plots, each approximately 4–5 ha, were selected in each burn class such that three plots in each group covered predominantly dry-mesic habitat and three plots covered predominantly wet-mesic habitat. Both habitat types were present to a varying extent in each plot because of the mosaic character of the dry prairie ecosystem. All plot groups were located in areas where Florida Grasshopper Sparrows were documented to be breeding in the season immediately before, after, or both before and after the winter sampling seasons.

In 2006–2007, three groups of six plots were established in burn class two prairies. One set of six plots was established in burn class four prairies. In 2007–2008, one set of six plots was

established in burn class one habitat, and one set of six plots was established in burn class three prairies. Due to biennial prescribed burn rotations in effect at the study site for the benefit of the Florida Grasshopper Sparrow, all samples from burn classes two and four were taken in 2006–2007, and burn classes one and three were sampled in 2007–2008 (Table 1).

A total of 36 plot samples were taken in each year, with 4–6 weeks between repeated samples of the same plot within a given year. Based on previous research (Carrie et al. 2002, Tucker and Robinson 2003, Butler et al. 2009, Johnson et al. 2009), we assumed that this time lapse was sufficient to consider sparrow locations in each plot as independent samples regardless of any within-season site fidelity by individual birds. Although research on wintering Henslow's Sparrows in longleaf pine habitat in southern Louisiana showed that radio-tagged birds remained within a 0.3 ha area for a period of up to three weeks (range 0.09–1.50 ha; $n = 16$ individuals using 11 locations per individual) (Bechtoldt and Stouffer 2005), we found no published literature suggesting that grassland sparrows that show fidelity to a winter home range were associated exclusively with a single plant community, so we assumed that sparrow flush locations indicated a preferred habitat association.

Statistical Analyses.—We used a 4×2 chi-square analysis to test for association between burn class and prairie habitat category (wet-mesic and dry-mesic) by species within each burn class. Florida Grasshopper Sparrows were excluded from the analyses for burn classes three and four, because the expected abundances were zero, a violation of the assumptions for chi-square tests. We used an information-theoretic approach (Burnham and Anderson 2002) to rank generalized linear models regressing predictor variables of burn class, habitat category, and interactions between these two variables against sparrow abundance by species. Because we could not replicate sampling of the same burn classes in both years, we simplified the analysis by calculating a combined relative abundance for each sparrow in each habitat category for burn classes one and two combined and for burn classes three and four combined. We obtained Akaike information criteria (AIC) scores for each candidate model using R statistical computing software (R Core Development Team 2012) and corrected these scores for small sample size (AIC_c). We calculated Akaike weights (w_i),

relative likelihood (L_i), and number of model parameters (K) for each candidate model and ranked the model weights to select the models that best predicted abundance of each species.

RESULTS

Total area sampled in each burn class was 94.4 ± 1.9 (SD) ha for burn class one, 108.5 ± 1.3 (SD) ha for burn class two, 84.2 ± 1.9 (SD) ha for burn class three, and 55.6 ± 0.6 (SD) ha for burn class four. In 2006–2007 sampling, 134 sparrows were captured; an additional 105 sparrows were identified as one of the focal sparrow taxa when flushed but were not captured. In 2007–2008 sampling, 149 sparrows were captured; an additional 167 sparrows were identified as one of the focal taxa when flushed but were not captured. During the two winters of sampling, 130 Bachman's Sparrows were captured a total of 161 times, 10 Florida Grasshopper Sparrows were captured 13 times, 78 Grasshopper Sparrows were captured 90 times, and 74 Henslow's Sparrows were captured 86 times. Recaptured birds were caught only in the plots in which they were captured initially and not in any other sampled plot. The number of unidentified birds averaged one bird per 4.1 ha; flush-net plot size ($n = 36$) averaged 4.7 ± 0.52 (SD).

Florida Grasshopper Sparrows were captured only in one set of six plots in Five Mile Prairie in both years of this study (2006–2007, burn class two [$n = 5$]; 2007–2008, burn class one [$n = 8$]). None were detected in burn class three or four prairies. The set of plots in which Florida Grasshopper Sparrows were captured was within a core breeding area for the subspecies within Kissimmee Prairie Preserve. In 2006–2007, three individuals were flushed from wet-mesic prairie and two from dry-mesic prairie. In 2007–2008, four individuals were flushed from wet-mesic prairie and four from dry-mesic prairie (Fig. 1). Although sample sizes are prohibitively small for analyses, results suggest that Florida Grasshopper Sparrows have a wintering habitat preference for burn class one and two prairie over burn classes three and four. However, potential inferences regarding habitat preferences are limited, because birds were captured only in proximity to a core breeding area, whereas none were captured in other prairies where breeding also was documented during our research period.

Bachman's, Grasshopper (*A. s. pratensis*), and Henslow's Sparrows were flushed at all sites

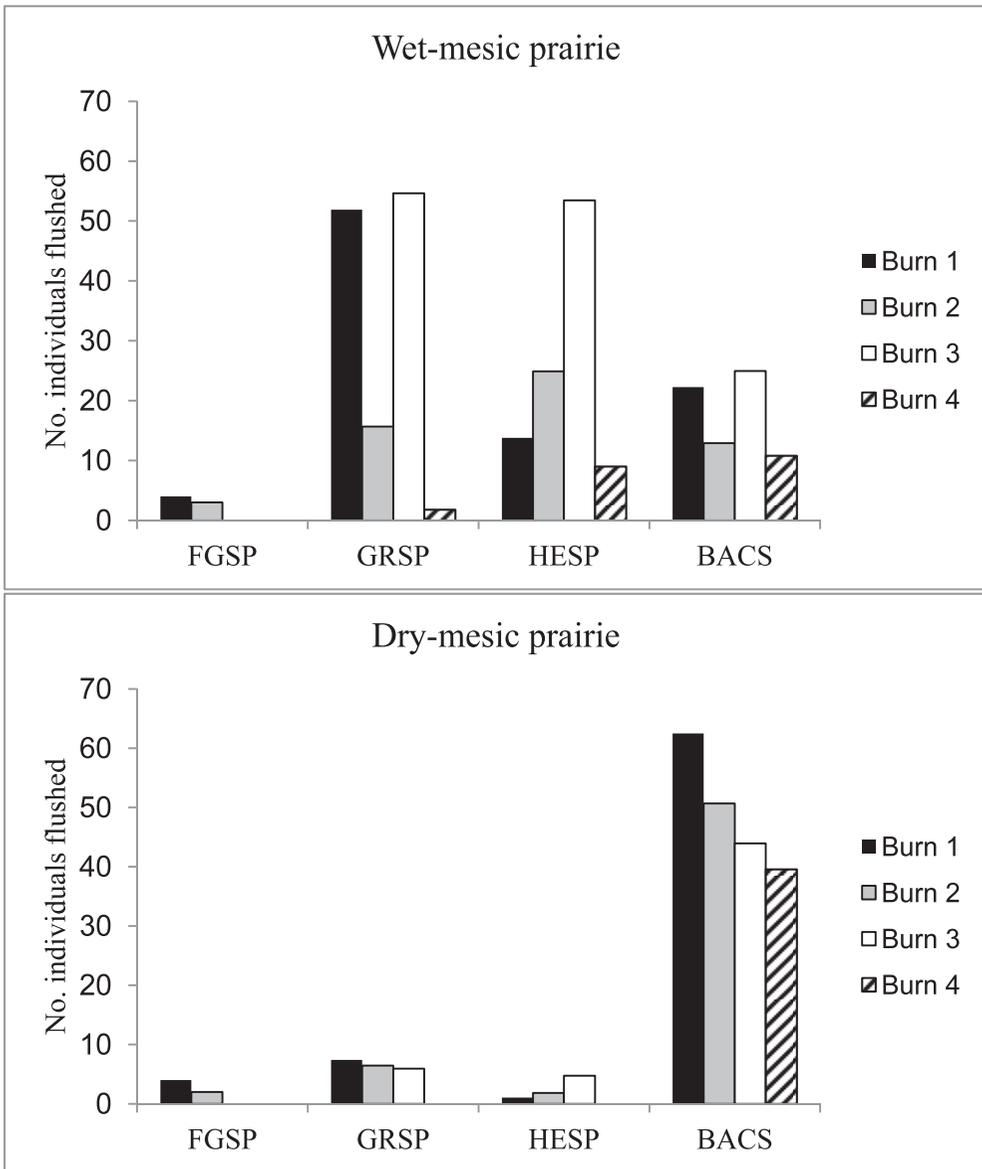


FIG. 1. Relative abundance of sparrows per 100 ha in wet-mesic and dry-mesic prairies. Burn class 2 and 4 prairies were sampled in winter 2006–2007; burn class 1 and 3 were sampled in winter 2007–2008. FGSP: Florida Grasshopper Sparrow, GRSP: Grasshopper Sparrow, HESP: Henslow's Sparrow, BACS: Bachman's Sparrow.

sampled in both winters; however, the latter two species were more abundant in wet-mesic prairie in burn classes one, two, and three than Bachman's Sparrows (Fig. 1). Bachman's Sparrows also favored burn class one and two patches, but were significantly more abundant in burn class four prairies than Grasshopper or Henslow's sparrows sampled in 2006–2007. Grasshopper

and Henslow's sparrows were more abundant in wet-mesic than in dry-mesic patches in all burn classes sampled. In contrast, Bachman's Sparrows were more abundant in dry-mesic than in wet-mesic patches in all burn classes (Fig. 1). Overall, each species showed a unique suite of responses to fire regimes that differed between wet and dry-mesic habitats.

TABLE 2. Results of 4×2 chi-square tests (all $P < 0.001$) demonstrate a lack of independence between sparrow abundance (birds/100 ha) and the two habitat categories within each burn class. FGSP: Florida Grasshopper Sparrow (*A. s. floridanus*), GRSP: Grasshopper Sparrow (*A. s. pratensis*), HESP: Henslow's Sparrow, BACS: Bachman's Sparrow.

Burn class	Sparrow	Wet mesic	Dry mesic	χ^2	df
1	FGSP	4	4	58.543	3
	GRSP	56	12		
	HESP	14	1		
	BACS	22	63		
2	FGSP	3	2	45.961	3
	GRSP	18	8		
	HESP	25	2		
	BACS	13	51		
3	FGSP	0	0	62.758	2
	GRSP	55	6		
	HESP	53	5		
	BACS	25	44		
4	FGSP	0	0	24.314	2
	GRSP	2	0		
	HESP	9	0		
	BACS	11	40		

Relative sparrow abundance was significantly associated with habitat category in all valid cases in which the expected abundance was not zero (all $P < 0.0001$; Table 2). This provides evidence that the four sparrow taxa sampled display different dry and wet-mesic habitat affinities that are also independent of burn class.

We used an information-theoretic approach to rank candidate models that predicted sparrow abundance as a function of burn class (burn classes one and two combined; burn classes three and four combined) and habitat category (dry-mesic and wet-mesic prairie; Table 3). Four models were identified as equally likely (within two AIC_c units of the best model) predictors of Henslow's Sparrow abundance (Table 3), with the best fit model including habitat and burn class without interaction effects. Two models were equally likely for Grasshopper Sparrow, with the best model including only habitat and reflecting the preference of this species for wet-mesic prairie across all burn classes (Fig. 1). The best fit model for Bachman's Sparrow also included only habitat, reflecting this species' apparent affinity for dry-mesic prairie (Fig. 1), although additional models that included burn class and interaction effects were within two AIC_c units of this model.

DISCUSSION

This study determined that the number of years since fire strongly affected grassland sparrow abundance during the winter, but that relative abundance was equally, and in some cases more strongly, related to plant community type within the wet/dry mesic prairie mosaic. Each of the four sparrow taxa showed a unique response to the combination of burn year and plant community type, indicating that management and recovery strategies should maintain the heterogeneity in plant community patterns within prairie landscapes as well as heterogeneity in vegetation structure in order to provide habitat preferred both by resident and migratory birds. The federal recovery plan for the Florida Grasshopper Sparrow (USFWS 1999) focuses exclusively on habitat management for that single species and recommends a 1–3 year burn rotation. We show that co-occurring sparrows display affinities for burn rotations that, while not identical, are largely compatible with those recommended for the Florida Grasshopper Sparrow.

Management Implications by Taxon

Florida Grasshopper Sparrow.—Despite documentation of singing male Florida Grasshopper Sparrows (*A. s. floridanus*) at all sampled sites during the breeding season between the two winters in which sites were sampled in this study, individuals of this resident, federally endangered subspecies were captured in both study years only in one set of six plots in an area that has hosted a persistent breeding subpopulation at least since 1984 (Delany and Cox 1986). We could not differentiate between the two Grasshopper Sparrow subspecies in flight; therefore, Florida Grasshopper Sparrows may have been present in burn class three or four habitat but because none were captured, they were undetected by our sampling method. Based upon the low relative abundance of Florida Grasshopper Sparrows at the single location where they were captured in both years, we predict this subspecies would be in far lower abundance, if present, in burn class three or four habitat at other sites where they were undetected by our sampling method. Although we recorded small samples of the Florida Grasshopper Sparrow ($n = 5$, 2006–2007; $n = 8$, 2007–2008), we noted that individuals were flushed almost equally from both wet-mesic and dry-mesic prairie ($n = 7$, $n = 6$, respectively).

TABLE 3. Model results of plant community habitat association and burn class regressed against relative abundances of three sparrows in Florida's dry prairie. Candidate models are ranked according to Akaike's information criteria corrected for small sample size (AIC_c) for each species. Akaike weights (w_i), relative likelihood (L_i), and number of model parameters (K) are also shown.

Model	AIC_c	ΔAIC_c	w_i	L_i	K
Henslow's Sparrow					
habitat + burn	22.80	0.00	1.00	0.36	2
habitat	23.71	0.92	0.63	0.23	1
habitat*burn + habitat	23.87	1.07	0.59	0.21	2
habitat*burn + habitat + burn	23.98	1.19	0.55	0.20	3
habitat*burn	32.79	10.00	0.01	0.00	1
habitat*burn + burn	32.87	10.07	0.01	0.00	2
burn	76.80	54.01	0.00	0.00	1
Grasshopper Sparrow					
habitat	22.37	0.00	1.00	0.56	1
habitat + burn	24.42	2.04	0.36	0.20	2
habitat*burn + habitat	26.08	3.71	0.16	0.09	2
habitat*burn + habitat + burn	26.17	3.79	0.15	0.08	3
habitat*burn	28.23	5.85	0.05	0.03	1
habitat*burn + burn	28.28	5.91	0.05	0.03	2
burn	64.57	42.20	0.00	0.00	1
Bachman's Sparrow					
habitat	27.05	0.00	1.00	0.42	1
habitat + burn	28.00	0.95	0.62	0.26	2
habitat*burn + habitat	28.96	1.91	0.38	0.16	2
habitat*burn + habitat + burn	29.01	1.96	0.38	0.16	3
habitat*burn	37.64	10.59	0.01	0.00	1
habitat*burn + burn	37.67	10.62	0.00	0.00	2
burn	55.78	28.73	0.00	0.00	1

Because this sparrow must be captured for positive subspecific identification, our sampling method proved insufficient for drawing inferences about winter habitat associations.

In 2006–2007, Florida Grasshopper Sparrows were captured in burn class two prairies and in 2007–2008, those same sample plots were in burn class one condition. These burn class associations are consistent with previous research demonstrating that this resident subspecies strongly prefers burn class one and two prairie year-round and that abundance declines steeply in areas that have gone un-burned for longer than 2 years (Shriver et al. 1999, Dean 2001, Shriver and Vickery 2001, Pranty and Tucker 2006).

Regional decline in abundance of Florida Grasshopper Sparrows, juvenile dispersal, post-breeding adult dispersal, and significantly enlarged winter home ranges compared to breeding territories (Dean 2001) may explain the low detection rates observed in this study. Based on our results, we recommend that management for Florida Grasshopper Sparrows continue to emphasize fire at a frequency of 1–3 years to

maintain a mosaic of vegetation structure along environmental gradients. Unfortunately, the recent and unexplained steep decline of Florida Grasshopper Sparrows across their known range, with predicted extinction within a few years (Florida Grasshopper Sparrow Working Group, unpubl. data) may make our recommendation purely academic.

Grasshopper Sparrow.—Migratory Grasshopper Sparrows (*A. s. pratensis*) were found in comparable abundance in burn class one and three habitat in 2007–2008 and significantly lower abundance in burn class two, sampled in 2006–2007 (Fig. 1). Grasshopper Sparrows were least abundant in burn class four, sampled in 2006–2007. Based on the comparable abundances we detected in burn classes one and three sampled in 2007–2008, we infer that in some years Grasshopper Sparrows may be at least as abundant in burn class two. The significantly lower abundance detected in 2006–2007 in burn class two prairie may have resulted from variability in breeding success within the species' breeding range, from sampling timeframe within the winter season, or

from inter-annual variation in temporal rainfall distribution at the study site with consequent prey base or vegetation density effects in the period between the 2 sample years. The Grasshopper Sparrow's preference for wet-mesic prairie habitat combined with drought conditions preceding 2006–2007 sampling may have enabled birds to occupy depression marshes and shallow sloughs, which were communities that were not sampled in this study because they normally were inundated.

Previous research on breeding Grasshopper Sparrows documented a range of relationships between breeding season abundance and time since fire. In some studies, researchers found that the sparrow was least abundant or absent in burn class one habitat and more abundant in grasslands burned two to three years prior; whereas, other studies found that Grasshopper Sparrows were most abundant in burn class one prairie with lower abundances in succeeding burn classes (Vickery 1996; USGS 2002; Powell 2006, 2008).

One previous study examined occupied breeding territory densities of Grasshopper Sparrows in relation to vegetation variables and found a strong negative relationship with woody plant cover (Ahlering 2005). Similarly, we find that overwintering Grasshopper Sparrows in Florida dry prairie have a strong affinity for graminoid and forb-dominated wet-mesic prairie devoid of woody shrubs.

In the only previous study on wintering Grasshopper Sparrows in Florida dry prairie, researchers documented that the migratory subspecies preferred burn class one prairie and recommended that dry prairie management include 2-year burn rotations. Their research also examined sparrow occupancy as a function of vegetation variables such as saw palmetto (*Serenoa repens*), forb, and litter cover but did not link the vegetation variables to dry prairie plant communities (Butler et al. 2009). In contrast, our research demonstrated that Grasshopper Sparrow abundance is linked both to fire-return interval and to plant community type. The recovery-focused fire rotations recommended for the Florida Grasshopper Sparrow (*A. s. florida-nus*) will support the migrant Grasshopper Sparrow (*A. s. pratensis*) although perhaps not at optimal levels in the case of 1-year fire return intervals.

Henslow's Sparrow.—The highest abundance of Henslow's Sparrows occurred within burn class three in 2007–2008, in contrast with most of the

previous winter research in which the species was most abundant within burn class one longleaf pine savannas in Louisiana, Mississippi, Alabama, and northwest Florida (Carrie et al. 2002, Tucker and Robinson 2003, Bechtoldt and Stouffer 2005, but see Palasz et al. 2010). In longleaf pine savannas, however, pine needle duff accumulates quickly, increasing the structural density of the herbaceous layer and interfering with free movement of ground-foraging sparrows. Relatively frequent fire rotations are needed to minimize litter depth and encourage herbaceous growth in longleaf pine savannas (Carrie et al. 2002). The affinity of wintering Henslow's Sparrows to the low litter accumulations in burn class one longleaf pine savannas throughout much of the species' winter range contrasts with the sparrow's preference for breeding habitat characterized by dense, tall grass and thick litter accumulations due to fire return intervals of 2 or more years (Cully and Michaels 2000; Reinking et al. 2000; Powell 2006, 2008).

In the treeless Florida dry prairie, litter accumulates differently in dry-mesic and wet-mesic communities. In the dry-mesic prairie, litter composed of saw palmetto fronds (*Serenoa repens*), oak leaves (*Quercus minima*), and other woody shrubs (e.g., *Lyonia lucida*, *L. fruticosa*, *Ilex glabra*, *Hypericum reductum*, *Bejaria racemosa*) accumulates more quickly than litter from the dead grasses and forbs in the wet-mesic prairie, which lacks woody shrubs. Therefore, wet-mesic prairie, with minimal litter accumulation (<0.5 cm; MGK, pers. obs.) in burn classes two and three, provides habitat structure for ground-foraging sparrows comparable to that in burn class one within longleaf pine savannas.

The winter 2007–2008 sampling period followed below-normal rainfall conditions during the spring and summer growing season of 2007 which may have inhibited regrowth and fruiting of cespitose grasses in burn class one prairie. The sparse vegetation may have provided inadequate cover or forage for Henslow's Sparrow; however, this inference conflicts with findings by previous researchers working in southern Louisiana, who found that maximum densities of wintering Henslow's Sparrows were predicted most accurately by low-density habitat structural characteristics rather than by seed composition or density (Johnson et al. 2011). In Florida dry prairie, however, prey abundances (seeds and arthropods) may be associated differently with burn class, habitat structure, and plant community type than

elsewhere in the species' winter range. Given the natural, historic fire return interval of ~2 years, on average, the 1–3 year rotations applied to benefit the Florida Grasshopper Sparrow will support overwintering Henslow's Sparrows in the wet-mesic prairie in burn classes two and three.

Bachman's Sparrow.—In contrast to the other three species of sparrows sampled in this study, Bachman's Sparrows strongly preferred dry-mesic prairie patches. Bachman's Sparrows predominantly occupy the understory of longleaf pine savannas and pine flatwoods in the southeastern United States, which have understory conditions similar to that of the dry-mesic patches within the Florida dry prairie (Abrahamson and Hartnett 1990, USFWS 1999). The species' affinity for treeless, dry mesic prairie at our study location is consistent with use of similar understory plant communities in longleaf pine savannas and pine flatwoods ecosystems elsewhere in the species' breeding range.

Bachman's Sparrow was most abundant in burn class one, but abundance declined progressively through burn class two, three, and four prairie, notwithstanding year effects between sample years. Our results are consistent with previous research on relative winter abundance and time since fire for this resident species (Tucker et al. 2004, 2006; Cox and Jones 2007), but this is the first study to establish this pattern in peninsular Florida. Management strategies for this species should emphasize frequent burn cycles (every 1–3 years) and the maintenance of dry-mesic grassland. Importantly, this strategy would equally benefit the endangered Florida Grasshopper Sparrow, which appears to utilize both wet and dry-mesic prairie habitats.

Across all four sparrow taxa sampled in this study, prairie plant community association and time since fire strongly affected relative abundance. Nevertheless, we found no linear relationship between sparrow abundance and plant community or burn class. The effect of time since fire on sparrow abundance is not consistent among species or across plant communities within the Florida dry prairie, and management strategies should account for these differences (Fig. 1). We recommend that land managers maintain a diversity of plant communities and burn rotations within grasslands, as suggested by our results and previously published studies, as opposed to managing exclusively for dry or wet-mesic communities and that managers continue to

implement regular, 1–2 year burn cycles. Managers should also generally strive for heterogeneous burns that mimic lightning fires, as opposed to the more common homogeneous or "clean" prescribed fires, because a patchy vegetation structure promotes higher overall native species richness (Keeley et al. 2009, Myers and Harms 2011, Noss 2013). Managing for a diverse prairie landscape also may allow species to shift their habitat associations in response to the increasingly variable climate in Florida (Von Holle et al. 2010). Future research on wintering sparrows in peninsular Florida should examine associations between relative abundance of sparrows, time since fire, fire seasonality, plant community type, and winter diets across multiple years to improve understanding of winter sparrow occupancy in dry prairie and other grassland communities. Longer-term studies may reveal how sparrow-plant community associations change with annual variation in climate and provide a basis for refining predictions of winter sparrow distributions given scenarios of global climate change.

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