Characteristics of Florida Grasshopper Sparrow Habitat Across a Gradient of Population Abundance and Persistence at Avon Park Air Force Range

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ABSTRACT

Population trends of Florida Grasshopper Sparrows (*Ammodramus savannarum floridanus*) at Avon Park Air Force Range (APAFR) have been monitored using standardized point counts since 1996. Data collected from 1996-2001 were used to examine the spatial distribution of Florida Grasshopper Sparrows during those years. That analysis identified areas consistently used by breeding sparrows and estimated probability contours identifying areas where 50%, 75%, and 95% of breeding sparrows were located. The population of Florida Grasshopper Sparrows at APAFR has declined drastically since 1996, and the extant sparrows are largely restricted to areas identified by the spatial analysis as containing 50% of the population. Those results suggest that the highest abundance and persistence of Florida Grasshopper Sparrows at APAFR occurs within the 50% probability contours. We measured vegetation structure across the three probability contours and a fourth zone where few to no sparrows were sighted to identify key characteristics of habitat associated with variation in abundance and persistence of Florida Grasshopper Sparrows at APAFR. Areas with the greatest probability of sparrow occurrence had greater cover of runways and tended to have more bare ground and runner oak than areas with lower probabilities of occurrence.

INTRODUCTION

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is endemic to the dry prairie habitat of central Florida and is federally listed as Endangered (U.S. Fish and Wildlife Service 1999). Presently, Florida Grasshopper Sparrows are known to exist in only four separate areas: Avon Park Air Force Range, Kissimmee Prairie Preserve State Park, Three Lakes Wildlife Management Area, and Beatty Ranch (a private ranch located in Okeechobee County; see Delany et al. 2005). Sparrows also occur on Adams Ranch, a private ranch adjacent to Three Lakes Wildlife Management Area, and are probably part of that population (Delany et al. 2005). Several studies have described habitat occupied by the Florida Grasshopper Sparrow (e.g., Delany et al. 1985, Delany and Linda 1994), but few studies have examined habitat quality and how habitat features influence the sparrows. Thus, no objective criteria (e.g., habitat models) exist to assess habitat quality. Only one study (Perkins et al. 2003) has directly addressed how habitat quality is influenced by habitat variables, and that study addressed only the influence of distance from edges (i.e., forested edges with woody vegetation >3 m tall and edges of improved pastures) on nesting success.

Delany et al. (1985) described vegetation characteristics of sites occupied by Florida Grasshopper Sparrows but did not examine how vegetation influenced distribution or demography of the birds. Delany and Linda (1994) compared vegetation structure between occupied and abandoned territories and found occupied territories had less grass cover, more bare ground and shrub cover, and higher vegetation height than abandoned territories. However, these results do not necessarily reflect selection of habitat by sparrows because abandoned territories were restricted to areas that had been converted to improved (i.e., tame) pastures (Delany and Linda 1994).

In contrast to Delany and Linda's (1994) findings, Shriver and Vickery (2001) found that territories successfully producing young had less bare ground and grass litter than unoccupied areas of native prairie; however, Shriver and Vickery (2001) did not compare successful with unsuccessful territories to ascertain what habitat features were important to reproductive success. In a study examining the influence of vegetation structure on nest placement, Delany and Linda (1998*a* and 1998*b*) found most nests (75%) were shielded by low growth of runner oak (*Quercus minima*). Small clumps of dense vegetation within more open patches appeared important for nest placement (Delany and Linda 1998*b*), but no data addressing nest success were provided. Walsh et al. (1995) noted that areas of "apparently suitable habitat" existed in close proximity to occupied habitat but remained unoccupied and suggested that behavioral inhibitions might prevent individuals from dispersing across areas of unsuitable habitat. This observation underscores the importance for objective criteria to measure habitat quality, because "apparently suitable habitat" may not reflect habitat attributes required by the sparrows. More recently Perkins et al. (2003) found that occupied habitats >400 m from edges (i.e., forest edges with vegetation >3 m tall and edges of improved pastures) were likely population sources (i.e., reproductive success exceeded mortality) and occupied habitat ≤400 m from edges were likely pop-

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ulation sinks (i.e., mortality exceeded reproduction). Although several studies (e.g., Walsh et al. 1995, Shriver et al. 1999, Shriver and Vickery 2001, Delany et al. 2002*a*) suggest that burning dry prairie habitat every two years or less is required to maintain high quality habitat, the study by Perkins et al. (2003) is the only study that directly addressed how a habitat attribute influences habitat quality, as measured by a demographic or population response, for the Florida Grasshopper Sparrow.

Population trends of Florida Grasshopper Sparrows at Avon Park Air Force Range (APAFR) have been monitored using standardized point counts (see Walsh et al. 1995, Delany et al. 1999) since 1996. The population of Florida Grasshopper Sparrows at APAFR declined from a maximum estimate of 298 individuals in 1997 (Delany et al. 2002*b*) to 17 individuals in 2003 (Tucker and Bowman 2004). Population models (Vickery and Perkins 2003) suggest a relatively high probability of extirpation within the next 50 years.

Delany (2002) used point count data collected at APAFR to examine the spatial distribution of Florida Grasshopper Sparrows between the years of 1996-2001. That analysis identified probability contours where 50%, 75%, and 95% of all sightings of Florida Grasshopper Sparrows at APAFR occurred from 1996-2001. We believe those probability contours likely represent a gradient of habitat quality. Support for this hypothesis is based on the theory of habitat selection (Fretwell 1972) and the distribution of Florida Grasshopper Sparrows during the breeding seasons of 2003 and 2004. Briefly, we would expect individuals at low population densities to select the highest quality sites and, as densities increase, to move out into lower quality sites. During 2003 and 2004 the few sparrows remaining at APAFR were located mostly within the 50% probability contours identified by Delany (2002; see Figs. 1, 2, and 3). Thus, these probability contours reflect variation in both the abundance and persistence of sparrows at APAFR. We measured vegetation characteristics across the gradient of probabilities of occurrence to examine whether differences in probabilities of occurrence of Florida Grasshopper Sparrows could be correlated with differences in vegetation structure.

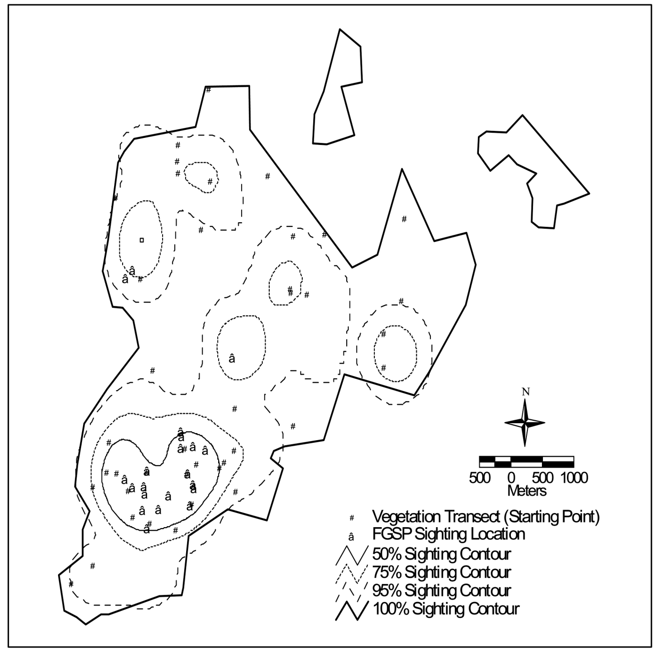

Figure 2. Location of vegetation transects, Florida Grasshopper Sparrows (FGSP) sighted during 2003 and 2004, and areas within probability contours for Florida Grasshopper Sparrows sighted 1996-2001 at Charlie/Echo Range, Avon Park Air Force Range, Florida. Vegetation transects are represented by their starting points, because the map scale is too small to display 50-m transects.

METHODS

Vegetation transects were selected using a stratified random procedure. Forty transects were equally distributed among four polygons at both Charlie/Echo Range (Fig. 2) and Delta Trail/OQ Range (Fig. 3). The four

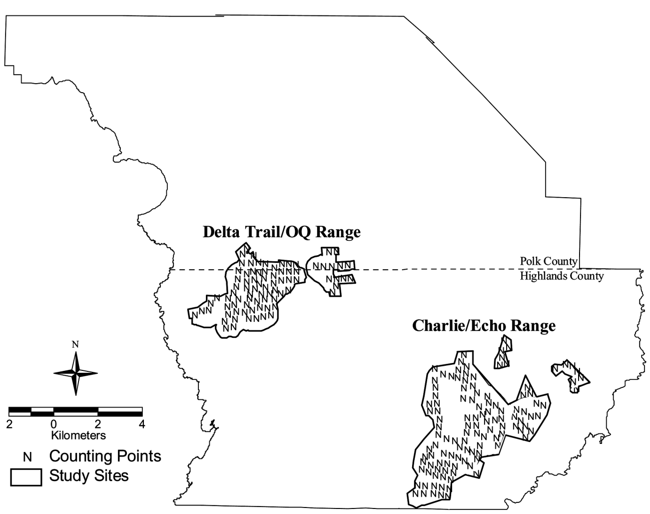

Figure 1. Location of counting points used to monitor Florida Grasshopper Sparrows at study sites included in the analysis comparing vegetation structure among zones of varying sighting probabilities at Avon Park Air Force Range, Florida.

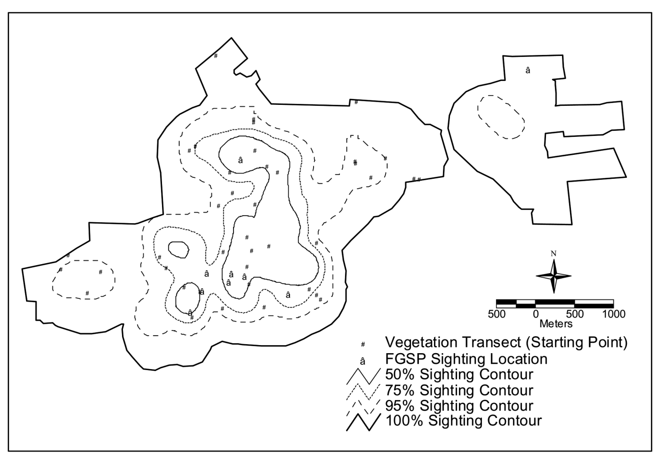

Figure 3. Location of vegetation transects, Florida Grasshopper Sparrows (FGSP) sighted during 2003 and 2004, and areas within probability contours for Florida Grasshopper Sparrows sighted 1996-2001 at Delta Trail/OQ Range, Avon Park Air Force Range, Florida. Vegetation transects are represented by their starting points, because the map scale is too small to display 50-m transects.

polygons (i.e., probability contours) represented areas containing 50%, 75%, 95%, and 100% of all sightings of Florida Grasshopper Sparrows during the years of 1996-2001. ArcView shapefiles of polygons representing the 50%, 75%, and 95% probability contours were obtained from Delany (2002). Briefly, Delany (2002) delineated these probability contours using a fixed kernel probability density estimation employing a bivariate normal density kernel and least squares cross validation to determine optimal values for the kernel smoothing parameter. The polygons representing the 100% probability contour were constructed by digitizing polygons around all areas within 100 m of the counting points (i.e., all area sampled by point counts) within each range. We used the animal movement extension of ArcView to generate ten random points within each probability contour for each of the two ranges. Random numbers between 0 and 359 were generated to dictate orientation (i.e., compass bearing) of a 50-m transect from the randomly selected points. If a compass bearing resulted in a transect extending into unsuitable habitat (e.g., depression pond or cypress dome) or into a different probability contour, an alternate random bearing was selected.

Our initial impression was that about 50% of both ranges had been burned within each of the past two years; thus, we assumed that vegetation transects were distributed equally across areas with respect to time since burning. We used ArcView GIS to examine this assumption by overlaying our vegetation transects onto maps showing burn histories of the areas and recording the dates of last burning. We summarized these burn dates as years since last burning and used 2004 as a baseline of 1 year since burning (Table 1). Because four transects at Delta Trail/OQ Range fell within a tame pasture and were managed by mowing rather than burning, we excluded those four transects from analysis. After completion of vegetation sampling we discovered errors in the GIS coverages. After correcting these errors we excluded five transects that crossed boundaries between probability zones and discovered that several other transects were contained within probability zones that differed from their original assignment. Thus, the final study design was unbalanced (Table 1).

We measured vegetation between 7 July and 27 August 2004. We recorded presence or absence of vegetation types (grass, forb, shrub, runner oak, saw palmetto, and bare ground) contacting each 10-cm height interval of a 1.5-m pole (i.e., 1.9-cm diameter PVC pipe) held vertically at each 0.5-m interval along the vegetation transects. Thus, vegetation measurements were collected at 100 sampling points along each transect. In addition we recorded presence or absence of a runway, defined as continuous open space sufficiently large (≥4.0 cm) for a sparrow to move along the ground and completely encircle the pole within a 20-cm radius, at each sampling point.

For analysis we calculated percent cover by summing the number of sampling points along each transect where vegetation types were present. In addition we calculated vertical density as the average number of 10-cm height intervals at the sampling points where vegetation types contacted the pole, and average maximum height of vegetation types across each point along the transects. Only points along transects where a vegetation type was recorded were included in calculating average maximum height to reduce colinearity between measures of height and percent coverage. We considered each vegetation transect an independent sample and, therefore treated vegetation transects as the sampling unit. Data were not normally distributed, so we used Spearman's rank correlation to examine correlations among vegetation variables.

Table 1. Number of vegetation transects sampled by years since burning (A) among probability zones for sightings of Florida Grasshopper Sparrows and (B) between ranges at Avon Park Air Force Range, Florida.

(A)	Probability zone				
Years since burning	50%	75%	95%	100%	Total
1	15	10	13	7	45
2	5	6	3	2	16
3	0	0	1	0	1
4	0	0	2	1	3
5	0	1	3	2	6
Totals	20	17	22	12	71

(B)	Range		
Years since burning	Delta/OQ	Echo	Total
1	21	24	45
2	12	4	16
3	0	1	1
4	0	3	3
5	0	6	6
Totals	33	38	71

Time since burning (TSB) varied across the vegetation transects (Table 1), so we used analysis of covariance (ANCOVA) with TSB as a covariate to compare vegetation types across the four probability contours and between ranges. Because percentages are not expected to be normally distributed, percent cover values were arcsine square root transformed prior to analysis (Zar 1984). Transformations failed to normalize most distributions, and variances were unequal among groups for most variables; however, results from parametric and nonparametric 2-factor ANOVA were equivalent, so we only report results from the ANCOVA's. When differences were found in the ANCOVA models we examined 95% confidence intervals around the marginal means to assess significant differences.

RESULTS

Within vegetation types all variables (i.e., percent cover, vertical density, and average maximum height) were highly correlated ($r_s \geq 0.336$, $P < 0.004$, N = 71) except percent cover and average maximum height of forbs ($r_s = 0.215$, $P = 0.072$, N = 71). Overall, percent cover and vertical density of individual vegetation types appeared to be equivalent measures ($r_s \geq 0.857$, $P < 0.001$, N = 71). Although correlations between average maximum height and percent cover were not as strong ($r_s < 0.518$), they were highly significant ($P \leq 0.004$) except as noted for forbs. Correlations between average maximum height and vertical density were intermediate ($r_s \geq 0.367$, $P \leq 0.002$). Percent coverage of bare ground and percent coverage of runways also were strongly correlated (r_s = 0.504, P < 0.001). Thus, we restricted our analyses to comparing percent cover of vegetation types among the four contours and between the two ranges.

Significant variation was found among the four probability contours (ANCOVA; $F_{8, 62} \geq 2.407$, $P \leq 0.025$) for four cover types: bare ground, runways, runner oak, and shrubs (Table 2). Time since burning was a significant covariate (Table 2) only for percent cover of bare ground (B = -0.057, SE = 0.020). Percent cover of all four cover types did not differ between the two ranges but did differ among the four probability contours for runways, runner oak, and shrubs. Differences in percent cover by shrubs among probability zones were inconclusive because an interaction existed between ranges and probability zones (Table 2). No interactions existed between ranges and probability zones for other vegetation types (Table 2). Percent cover of runways was greater in the 50% and 75% probability zones than the 95% probability zones and greater in the 50% than the 100% probability zones (Fig. 4). Confidence intervals for percent cover of runner oaks overlapped for each of the probability zones (Fig. 4). Percent cover of both grasses and forbs were relatively consistent between ranges and among probability zones, and percent cover of saw palmetto tended to be low in areas with the greatest probability of occurrence and relatively high in areas with low probability of occurrence, but the trend was not significant (Fig. 4).

DISCUSSION

Several studies have suggested the importance of bare ground as a habitat component for Florida Grasshopper Sparrows (Delany et al. 1985, Delany and Linda 1994, Shriver 1996). An important function of bare ground is that it provides open spaces meandering through the vegetation that allow the sparrows to forage efficiently (see Haggerty 2000 for a discussion of foraging in Bachman's Sparrows). Our measure of percent runways was an attempt to better capture this aspect of vegetation structure, because we were unsure how well percent cover of bare ground would correspond to this important attribute. For example, 20% bare ground occurring as small open spaces among individual clumps of vegetation may be an ideal configuration for runways but will not be equivalent to 20% bare ground occurring as one or a few large patches. Although percent cover of bare ground and percent cover of runways were highly correlated (r_s = 0.504, P < 0.001), percent cover of runways appeared less variable and better able to discriminate among the probability contours (Fig. 4). Furthermore, the results were consistent with the expectation that zones of higher probability of occurrence would have greater cover by runways. Also, it is noteworthy that bare ground only averaged about 6-15% across the probability zones but translated into about 43-92% occurrence of runways (Fig. 4), and that bare ground was the cover type most strongly influenced by TSB (Table 2).

We also found an apparent trend for greater percent cover by runner oak in areas with the greatest probability of occurrence; however, the trend was not significant (Fig. 4). Delany and Linda (1998a and 1998b) suggested that run-

Table 2. Results from 2-factor ANCOVA comparing percent coverage[a] among ranges and probability zones with time since burning (TSB) as a covariate for (A) bare ground, (B) runner oak, (C) runways, (D) grass, (E) forbs, (F) shrubs, and (G) saw palmetto at Avon Park Air Force Range, Florida.

Source	Sum of squares	*df*	Mean square	*F*	Probability
A. Bare ground					
Model	0.625	8	0.078	2.691	0.013
TSB	0.232	1	0.232	7.970	0.006
Range	0.011	1	0.011	0.380	0.540
Contour	0.086	3	0.029	0.988	0.404
Range * Contour	0.038	3	0.013	0.436	0.728
Error	1.801	62	0.029		
Total[b]	2.427	70			
B. Runner oak					
Model	1.530	8	0.191	3.233	0.004
TSB	0.004	1	0.004	0.059	0.808
Range	0.136	1	0.136	2.294	0.135
Contour	0.708	3	0.236	3.992	0.012
Range * Contour	0.329	3	0.110	1.856	0.146
Error	3.667	62	0.059		
Total[b]	5.196	70			
C. Runways					
Model	4.922	8	0.615	7.089	<0.001
TSB	0.152	1	0.152	1.746	0.191
Range	0.259	1	0.259	2.979	0.089
Contour	2.717	3	0.906	10.432	<0.001
Range * Contour	0.396	3	0.132	1.520	0.218
Error	5.382	62	0.087		
Total[b]	10.304	70			
D. Grass					
Model	0.496	8	0.062	1.632	0.134
TSB	0.046	1	0.046	1.216	0.274
Range	0.083	1	0.083	2.172	0.146
Contour	0.297	3	0.099	2.599	0.060
Range * Contour	0.039	3	0.013	0.341	0.796
Error	2.358	62	0.038		
Total[b]	2.854	70			
E. Forbs					
Model	0.200	8	0.025	0.719	0.674
TSB	0.005	1	0.005	0.151	0.699
Range	0.094	1	0.094	2.704	0.105
Contour	0.008	3	0.003	0.075	0.973
Range * Contour	0.022	3	0.007	0.214	0.886
Error	2.155	62	0.035		
Total[b]	2.355	70			
F. Shrubs					
Model	0.606	8	0.076	2.407	0.025
TSB	0.006	1	0.006	0.176	0.677
Range	0.018	1	0.018	0.569	0.453
Contour	0.269	3	0.090	2.853	0.044
Range * Contour	0.268	3	0.089	2.843	0.045
Error	1.950	62	0.031		
Total[b]	2.556	70			
G. Saw Palmetto					
Model	0.570	8	0.071	1.689	0.119
TSB	0.004	1	0.004	0.086	0.770
Range	0.061	1	0.061	1.438	0.235
Contour	0.372	3	0.124	2.940	0.040
Range * Contour	0.071	3	0.024	0.563	0.642
Error	2.614	62	0.042		
Total[b]	3.184	70			

[a]Percent coverage was arcsine square root transformed for analysis.
[b]Corrected total.

ner oak was an important habitat component for Florida Grasshopper Sparrows. Although percent cover by shrubs appeared to differ across the probability zones, trends differed between the two ranges. Percent cover by shrubs appeared much lower in the 50% and 75% probability zones than the 95% and 100% probability zones at Echo Range but appeared relatively consistent across the probability zones at Delta Trail/OQ Range. We suspect the greater cover of shrubs in the 95% and 100% probability zones at Echo Range may be related to the closer proximity of bombing targets in those areas. Habitat disturbances (e.g., bomb craters, plowed strips, and access trails for maintenance) from military activities around the targets appear to reduce the frequency and/or intensity of fires and may be responsible for the greater percent coverage of shrubs.

Although we did not find differences in percent cover of grasses or forbs across the probability zones (Fig. 4), the importance of these components should not be overlooked. Florida dry prairies are characterized by a diverse ground cover of herbaceous vegetation, and much of this vegetation grows in distinctive clumps (i.e., dominated by bunch grasses and other cespitose perennials). Grasshopper sparrows forage exclusively on the ground (Vickery 1996), and these clumps of vegetation provide open spaces among the individual clumps that allow room for the sparrows to maneuver and search for food. Furthermore, clumps of grasses and forbs provide an abundant substrate for arthropod prey at or near the surface of the soil and produce seeds that are especially important for overwintering sparrows. Thus, grasses and forbs are responsible for producing both critical structure (i.e., runways) and food resources for Florida Grasshopper Sparrows. We hypothesize that runways are important because they allow sparrows to maneuver among clumps of vegetation and remain relatively concealed from avian predators, and also increase availability of food resources by allowing sparrows to better access these resources.

An oversight in the initial design of this study was to assume that burning regimes were equal across probability zones. The discovery that vegetation transects were not distributed equally with respect to TSB (Table 1) forced us to include TSB as a covariate in the analyses to control for confounding effects of TSB. Furthermore, inclusion of TSB into the analyses forced us to exclude four transects located in an area managed by mowing rather than burning (i.e., a tame pasture). Exclusion of these four transects and five others that crossed boundaries of the probability zones resulted in an unbalanced study design (Table 1). The unbalanced study design likely resulted in a considerable loss of power to detect differences among groups (Zar 1984).

A major assumption of this study was that our probability of occurrence zones reflected real variation in the abundance and persistence of Florida Grasshopper Sparrows, and that by measuring variation in habitat structure across these zones we might detect variation in habitat quality. Several studies have questioned using density as an indicator of habitat quality (e.g., Van Horne 1983). We agree that more direct measures of fitness (e.g., reproductive success and survival) are better for assessing habitat quality, but most studies that have examined the relationship between density and reproductive success found that the two measures were correlated (Bock and Jones 2004). Because the zones for probability of occurrence used in our study were based not only on density but also on persistence of Florida Grasshopper Sparrows over multiple years, we believe the most parsimonious explanation for the spatial distribution across the probability zones is that those zones represent a gradient of habitat quality. Although Florida Grasshopper Sparrows exhibit high site fidelity (Delany et al. 1995, Perkins and Vickery 2001) and may use the presence of conspecifics as a cue in selecting habitat or establishing territories (i.e., conspecific attraction), site fidelity and conspecific attraction alone or in combination do not sufficiently explain the distribution of Florida Grasshopper Sparrows at Avon Park Air Force Range over the time period (1996-2001) of this study. Site fidelity and conspecific attraction might be influential factors, but sparrows in areas with the highest probabilities of occurrence, where they have persisted longest in this declining population, must have higher survival rates than sparrows in areas with lower probabilities of occurrence to consistently maintain higher densities over the number of years included in this study. We suggest that the results of our analyses provide useful insights for management and formulation of working hypotheses that should be verified using more direct measures of fitness (i.e., reproductive success and/or survival).

The only study that directly measured how a habitat feature influences habitat quality for Florida Grasshopper Sparrows is Perkins et al. (2003), and they suggested that habitat >400 m of a habitat edge was required for reproductive success to exceed mortality. Although this is extremely valuable information for conservation and management of Florida Grasshopper Sparrows, it only addresses size (i.e., area) and configuration of habitat patches. A severe shortcoming in our knowledge of Florida Grasshopper Sparrows is how vegetation structure and composition influence the birds. For example, information from Perkins et al. (2003) might be used to identify an area of dry prairie that is sufficiently large to support a population of Florida Grasshopper Sparrows, but we have no habitat models or objective criteria to evaluate the likelihood that habitat composition and structure of the area are suitable to support the species. Our study was not designed to produce such a habitat model but attempted to identify important attributes that should be considered in the development of a habitat model.

In conclusion, we found that areas with the greatest probability of occurrence of Florida Grasshopper Sparrows had a greater percent cover of runways than areas with lower probabilities of occurrence. Percent cover of bare ground and runner oak also might have been greater in areas with higher probability of occurrence, but multiple comparison tests failed to identify statistical differences. Frequent fire is required to maintain these habitat components, and percent coverage of bare ground was negatively correlated with time since burning (also see Shriver and Vickery 2001). Several studies (e.g., Walsh et al. 1995, Shriver and Vickery 2001, Delany et al. 2002a) suggest that optimal habitat conditions occur the first breeding season after fire, and that habitat conditions become very poor by the third breeding season after fire. Thus, annual or biennial burning appears to provide optimal habitat conditions for Florida Grasshopper Sparrows. A priority for future research should be to identify

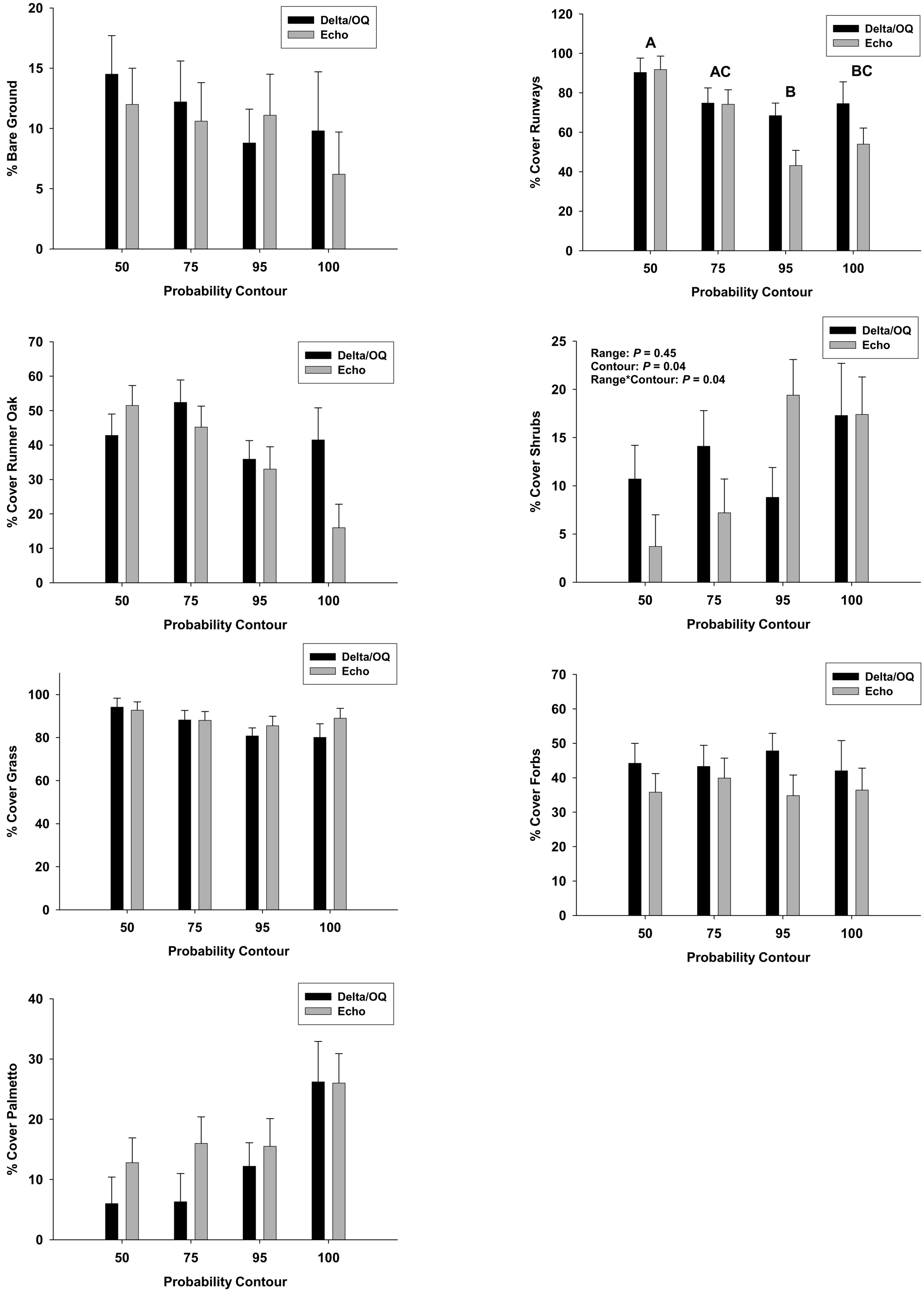

Figure 4. Graphs comparing mean percent coverages (± SE) of vegetation types among probability contours by range at Avon Park Air Force Range, Florida. Within cover types, bars not sharing common letters differed in multiple comparison tests ($P < 0.05$).

important structural and compositional components of dry prairie habitat for predicting reproductive success and survival of Florida Grasshopper Sparrows.

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