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INFLUENCE OF SEASON AND FREQUENCY OF FIRE ON HENSLOW'S SPARROWS (*AMMODRAMUS HENSLOWII*) WINTERING ON GULF COAST PITCHER PLANT BOGS

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Abstract.—Henslow's Sparrow (*Ammodramus henslowii*) is a grassland bird that has suffered drastic population declines for over 30 years. Declining populations can be largely attributed to loss of breeding habitat, but loss of wintering habitat associated with longleaf pine (*Pinus palustris*) communities, especially pitcher plant (*Sarracenia* spp.) bogs, along the Gulf Coast also may be a contributing factor. Fire is critical for restoration and conservation of remaining longleaf pine communities, but the influence of fire on wintering Henslow's Sparrows has not been evaluated. We examined the influence of season and frequency (time since burning) of fire on use of pitcher plant bogs by Henslow's Sparrows wintering in the Conecuh National Forest, Alabama, and Blackwater River State Forest, Florida, during winters of 1999–2000 and 2000–2001. Density of Henslow's Sparrows was greatest on bogs the first winter after burning. Although significant effects for season of burning were not found, bogs burned during winter typically hosted Henslow's Sparrows for only one winter, whereas bogs burned during the growing season hosted sparrows for at least three winters. Growing-season fires may be more beneficial than dormant-season fires and will prevent forced abandonment of bogs burned during winter. Frequency of seed stalks of grasses and density of forbs were the most influential vegetation parameters affecting occurrence of Henslow's Sparrows at pitcher plant bogs. Henslow's Sparrows were found on bogs as small as 0.06 ha, but were found on bogs >0.25 ha more frequently than on smaller bogs. We conclude that burning pitcher plant bogs on an annual or biennial basis during the growing season will maximize the benefits to both wintering Henslow's Sparrows and the host of other organisms associated with those unique communities. *Received 18 December 2001, accepted 12 September 2002.*

Resumen.—*Ammodramus henslowii* es una especie de ave de pastizal que ha sufrido drásticas disminuciones poblacionales a lo largo de los últimos 30 años. La disminución de las poblaciones se puede atribuir a la pérdida del hábitat reproductivo, pero la pérdida del hábitat de invernada asociado a comunidades del pino *Pinus palustris* (especialmente a las plantas del género *Sarracenia* en pantanos a lo largo de la costa del golfo) también puede ser un factor contribuyente. El fuego es crítico para la restauración y conservación de las comunidades de *P. palustris* que aún quedan, pero la influencia del fuego sobre las poblaciones invernantes de *A. henslowii* no ha sido evaluada. Examinamos la influencia de la estacionalidad y frecuencia (tiempo desde la quema) del fuego sobre el uso de pantanos de *Sarracenia* spp. por individuos de *A. henslowii* que se encontraban invernando en Conecuh National Forest, Alabama, y Blackwater River State Forest, Florida, durante los inviernos de 1999–2000 y 2000–2001. La densidad de *A. henslowii* fue mayor en los pantanos durante el primer invierno luego de la quema. A pesar de que no se encontraron efectos significativos de la estación de la quema, los pantanos quemados durante el invierno típicamente albergaron poblaciones de *A. henslowii* sólo durante un invierno, mientras que los pantanos quemados durante la época de crecimiento albergaron a estas aves por lo menos durante tres inviernos. Los fuegos durante la época de crecimiento pueden ser más beneficiosos que los fuegos durante la época de dormancia y además previenen el abandono forzado de los pantanos quemados durante el invierno. La frecuencia de tallos de pastos y la densidad de hierbas fueron los parámetros de vegetación con la influencia más importante sobre la ocurrencia de *A. henslowii* en los pantanos de *Sarracenia* spp.. Individuos de *A. henslowii* fueron encontrados en pantanos tan pequeños como de 0.06 ha, pero ocurrieron con mayor frecuencia en pantanos de más de 0.25 ha. Concluimos que la quema anual o bianual de los pantanos de *Sarracenia* spp. durante la época de crecimiento maximizará los beneficios tanto para las poblaciones de *A. henslowii* que se encuentran invernando, como para una variedad de otros organismos asociados a estas comunidades únicas.

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The longleaf pine (*Pinus palustris*) ecosystem once dominated the coastal plain of the southeastern United States and extended from Virginia to Texas (Wahlenberg 1946). Forests within that ecosystem were characterized by large, widely spaced longleaf pines with a dense ground cover of grasses and forbs (Chapman 1932). Frequent fires resulting from a high incidence of lightning strikes are the primary agent responsible for the diversity and structure of longleaf pine forests (Chapman 1932). Disruption of natural fire regimes and conversion to other land uses have resulted in the loss of 95% of that once extensive ecosystem (Outcalt and Sheffield 1996), making it one of the most heavily affected of all forested ecosystems (Noss 1989, Simberloff 1993). Concurrent with the loss of longleaf pine forests, populations of many species characteristic of those forests (e.g. Red-cockaded Woodpecker [*Picoides borealis*]) have declined and have become threatened with extinction.

Henslow's Sparrow (*Ammodramus henslowii*) is a migratory bird species that breeds in moist grasslands of the central and eastern United States (Hyde 1939) and migrates to the southeastern United States where it primarily spends the winter in open pine savannas and pitcher plant (*Sarracenia* spp.) bogs (Plentovich et al. 1998; 1999), microhabitats characteristic of the longleaf pine ecosystem. Between the years of 1966 and 1996, populations of breeding Henslow's Sparrows declined at an average rate of 8.8% per year (Peterjohn and Sauer 1999). Although loss and degradation of breeding habitat is probably the major factor contributing to decreasing populations of Henslow's Sparrows, loss of winter habitat also may be important (Askins 1993). For example, Brooks and Temple (1990) suggested that reduced overwinter survival of a migrant population of Loggerhead Shrikes (*Lanius ludovicianus*) that breeds in Minnesota and winters along the Gulf Coast probably contributed to population declines more strongly than factors occurring on the breeding grounds. Gulf Coast pitcher plant bogs, a major wintering habitat for Henslow's Sparrows (Plentovich et al. 1999), have been reduced to <3% of the area once occupied by that habitat (Folkerts 1982).

A major threat to the remaining pitcher plant bogs is alteration of natural fire regimes (Folkerts 1982, Frost et al. 1986). Traditionally, land managers have used fire primarily during the winter (dormant season), but evidence suggests that natural fires most often occurred during late spring and summer (growing season) which coincides with the season of greatest electrical storms (Robbins and Myers 1992). In addition, frequency of fire is a critically important factor. Walker and Peet (1983) found maximum species richness of plants on pitcher plant bogs burned annually, and Frost et al. (1986) stated that those habitats might require fire on a near annual basis.

Similarly, bogs not burned regularly may become unsuitable for some bird species. Plentovich et al. (1999) found that wintering Henslow's Sparrows abandoned bogs in Alabama that went without disturbance for more than four years. Furthermore, Henslow's Sparrows showed strong site fidelity during winter, suggesting that fire might have a strong negative effect on populations if burning occurred during winter (Plentovich et al. 1998). However, no studies have addressed directly the influence of season and frequency of burning on abundance of Henslow's Sparrows wintering on pitcher plant bogs. Thus, the objective of our study was to examine the influence of season and frequency (i.e. time since burning) of fire on abundance of Henslow's Sparrows.

Methods

Study sites.—During December 1999, we located 45 pitcher plant bogs in Conecuh National Forest, Alabama, and Blackwater River State Forest, Florida (Table 1). Those two forests are contiguous and separated only by the state line. Most bogs were located from maps provided by area managers, but some were found during the previous growing season during a study of Bachman's Sparrows (*Aimophila aestivalis*). Because the known habitat associations of wintering Henslow's Sparrows indicate the importance of herbaceous ground cover (Plentovich et al. 1999), we did not examine bogs that were dominated by shrub cover and only selected bogs that contained ≥50% cover by herbaceous vegetation. Although many of the bogs examined contained dense patches of shrubs, the shrubs were interspersed across the bogs and the ground cover beneath the shrubs predominately consisted of herbaceous vegetation. Because the number of bogs available for study was limited, we included all bogs that met the selection criteria regardless of location, season, and year of last burning

During summer of 2000, the area within each bog selected for study was measured using differentially corrected global positioning systems (GPS) data. We

TABLE 1. Number of pitcher plant bogs examined by year and season of last burning during study of wintering Henslow's Sparrows during winters of 1999–2000 and 2000–2001 at Conecuh National Forest, Alabama (CNF), and Blackwater River State Forest, Florida (BSF).

	Last burn[a]		Winter 1999–2000		Winter 2000–2001	
Location	Season	Year	Burn group[b]	Bogs	Burn group[b]	Bogs
CNF	Growing	1999	1	5	2	5
CNF	Growing	1998	2	13	3	13
CNF	Growing	1997	3	2	3	1
CNF	Growing	1996	3	1	3	1
CNF	Dormant	2000	–	–	1	1
BSF	Growing	1999	1	1	2	1
BSF	Growing	1998	2	4	3	1
BSF	Growing	1997	3	3	3	3
BSF	Growing	1996	3	2	3	2
BSF	Growing	1994	3	1	–	–
BSF	Dormant	2000	–	–	1	7
BSF	Dormant	1999	1	6	2	6
BSF	Dormant	1998	2	4	3	4
BSF	Dormant	1997	3	2	3	1
BSF	Dormant	1995	3	1	3	1

[a] Date stands were last burned. Growing season: 1 April–30 September; Dormant season: 1 October–31 March.

[b] Number of growing seasons since last burned. Bogs with ≥3 growing seasons were pooled into one category because of small sample size.

walked the perimeter of each bog and recorded GPS positions at 3 s intervals. PATHFINDER OFFICE (Trimble Navigation, Sunnydale, California) was used to differentially correct GPS data and to calculate area within each bog.

Bird surveys.—Because Henslow's Sparrows rarely vocalize during winter, we surveyed Henslow's Sparrows by walking bogs and counting sparrows as they flushed. Positive identification of Henslow's Sparrows was facilitated by its distinctive flushing and flight behavior and the relatively low diversity of other sparrows at the bogs. Sedge Wren (*Cistothorus platensis*) was the species most likely mistaken for Henslow's Sparrow (on the basis of flushing and flight behavior) but was easily distinguished by the wren's smaller size and distinctively rounded wings.

When a Henslow's Sparrow flushed, we marked the spot from where the bird flushed and noted where the bird flew to prevent double counting individuals. Prevention of double counting individuals was facilitated by the relatively small size of the bogs and the low number of individuals present (see Fig. 1A). We attempted to cover the entire area of the bog by systematically walking back and forth across the bog along transects spaced ~5 m apart. Thus, we walked within ~2.5 m of every point within the bogs. We conducted two surveys at 44 bogs and one survey at another bog (that bog was burned after the first survey) between 18 December 1999 and 13 February 2000. All surveys were conducted by a single observer (J.W.T.), but on 6 February 2000 a fourperson crew surveyed eight bogs that previously had been surveyed twice and found the same or fewer birds at seven of the bogs and one more bird at the other bog. Results from those confirmation surveys were not included in the analyses, but confirmed that the sampling technique was effective at detecting Henslow's Sparrows at the bogs. Although we could not measure probability of detecting individual sparrows, we were able to estimate the probability of detecting at least one sparrow if sparrows were present (see below), and that analysis suggested that our sampling technique was relatively effective for sampling Henslow's Sparrows (see below).

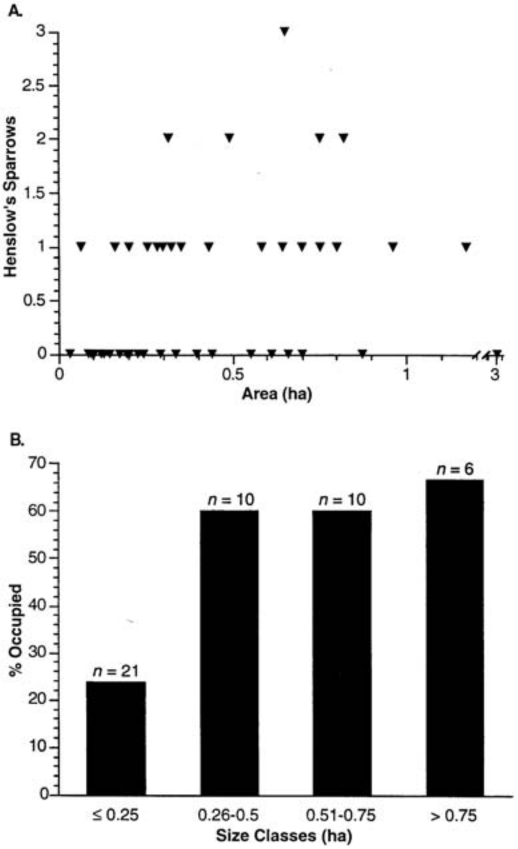

FIG. 1. (A) Maximum number of Henslow's Sparrows detected during any single count at pitcher plant bogs in the Conecuh National Forest, Alabama, and Blackwater River State Forest, Florida, during counts in winters 1999–2000 and 2000–2001 by area, and (B) percentage of bogs occupied by Henslow's Sparrows within 0.25 ha size classes.

Between 14 December 2000 and 10 February 2001, we repeated surveys (two per bog) at each of the 45 bogs examined the previous winter. In addition, we conducted two surveys at each of two additional bogs located during summer 2000. Two of the original bogs were burned after the first survey, so they were surveyed only once during winter 2000–2001.

Vegetation sampling.—We measured vegetation characteristics at 42 bogs between 5 February and 19 March 2000. We did not sample vegetation at three bogs because they were burned before vegetation could be sampled. The methods used by Plentovich et al. (1999) were followed as closely as possible to facilitate comparisons with their data from a different geographic region. Briefly, we measured vegetation characteristics at 40 points selected at random within each bog. We generated a set of random coordinates for each bog to dictate random points for sampling vegetation. At each point, we recorded the presence of vegetation within a series of 10 cm radius cylinders centered on a 200 cm pole. The series of 10 cm radius cylinders consisted of each 5 cm height interval up to 20 cm, followed by 10 cm intervals up to 200 cm. In addition to the presence of vegetation within each 10 cm radius cylinder, we recorded whether standing water was present. A spherical densiometer was used to measure canopy cover at each sampling point. Preliminary observations during the study suggested that production of grass seeds may be an important variable influencing presence of Henslow's Sparrows. Thus, we also recorded presence or absence of grass seeds (i.e. seed producing stalks) within 10 cm of each sampling point.

For analysis, we classified plant species into vegetation types and calculated vertical vegetation density for the following types: moss, litter, fern, grass (including sedges), pitcher plants and other forbs separately, shrubs (including trees), and vines. Vertical vegetation densities were calculated as the average number of 10 cm radius cylinders at the 40 sampling points where vegetation types were present. Where appropriate (e.g. percentage frequency of grass seeds), we calculated percentage frequencies for vegetation types as the percentage of sampling points where the types were present within a 10 cm radius of sampling points.

During winter 2000–2001, we sampled vegetation at eight bogs (six burned between years and two only examined in second year). Vegetation measurements during winter 2000–2001 were collected using the same protocol as used the previous winter, but we only recorded vegetation variables that were identified by analysis of data from winter 1999–2000 as important predictors for the occurrence of Henslow's Sparrows.

Statistical analysis.—For data collected during winter 1999–2000, we used a two-factor ANOVA to examine the effects of season and postburn age on the density of Henslow's Sparrows (number per count per hectare) present at pitcher plant bogs. We could not enter location as a factor in this analysis because no bogs burned during the dormant season were located at Conecuh (Table 1). Furthermore, observations suggested that bogs at the two locations were similar in vegetation composition. A univariate ANOVA was used to examine the influence of postburn age on density of Henslow's Sparrows during winter 2000–2001. Season of burning could not be included in the analysis because no bogs were burned during the previous growing season because of severe regional drought. Although data were not normally distributed, subjecting ranks of the data to ANOVA (Zar 1984) yielded equivalent results to parametric ANOVA. Thus, violations of assumptions for parametric analysis did not influence results, and only results from parametric ANOVA are presented.

Because studies of breeding Henslow's Sparrows (e.g. Herkert 1994, Winter and Faaborg 1999) have found the species to be area sensitive (i.e. require large patches of habitat for nesting), we examined the influence of area within pitcher plant bogs on Henslow's Sparrows during winter. We used Spearman's rank correlation to examine the influence of bog area on the abundance (number per count) and density of Henslow's Sparrows. We calculated the percentage of bogs occupied by Henslow's Sparrows within four size classes (≥0.25 ha, 0.26–0.50 ha, 0.51–0.75 ha, and >0.75 ha) to graphically examine the influence of area on presence of Henslow's Sparrows at pitcher plant bogs during winter. In addition, the influence of area on the presence of Henslow's Sparrows at pitcher plant bogs was examined by modeling occupancy rates (see below).

Preliminary examination of vegetation data revealed that, with few exceptions, moss and litter were restricted to ≤5.0 cm in height. Thus, those two variables were measured as percentage frequency of points where present (i.e. percentage coverage). Likewise, pitcher plants were measured as percentage coverage because measures of vertical density would give more weight to points with larger species (e.g. white-topped pitcher plant [*Sarracenia luecophylla*]) than to points with smaller species (e.g. parrot pitcher plant [*S. psittacina*]). For analysis, all measures of percentage coverage were arcsine transformed (Zar 1984), and measures of vertical vegetation density (except for grass, ferns, and vines) and area were transformed as natural logarithms. Transformations improved normality (Shapiro-Wilk test, $P > 0.05$) of all variables except vertical density of grass which was normally distributed without transformation ($P = 0.889$) and ferns, vines, and standing water which could not be successfully normalized, because they were recorded at ≤33.3% of bogs. Univariate analyses (Mann-Whitney U-tests and Spearman's rank correlation) suggested the presence of Henslow's Sparrows was not associated with vertical density or percentage coverage of ferns, vines, or standing water, so they were excluded from further analysis.

We used occupancy models (MacKenzie et al. 2002) in program MARK (White and Burnham 1999) to examine influence of vegetation variables, size (area) of bogs, season of last burning (dormant or growing season), and growing seasons since burning (nominal scale ranging from 1–3) on presence of Henslow's Sparrows at bogs. The occupancy models used maximum-likelihood methods and a logit link to estimate probability of sites being occupied and probability of detection given the site is occupied. Data used in model construction consisted of presence or absence of Henslow's Sparrows during the two sampling occasions of winter 1999–2000 (i.e. encounter histories) and individual covariates for the 42 bogs where vegetation was sampled during that winter. An assumption of occupancy models was that populations of Henslow's Sparrows were closed during the sampling period. We believe that this assumption was met reasonably because of the relatively consistent number of sparrows found between sampling occasions, and the sampling period was during a period when migration was not expected. Furthermore, Plentovich et al. (1998) found Henslow's Sparrows were site faithful within winters.

We believed that probability of detection would be influenced most strongly by density of herbaceous ground cover and was equal between sampling occasions, because vegetation growth was negligible during that period. Thus, we began our analysis by examining the influence of grass density, forb density, both grass and forb density, and total herbaceous density (i.e. sum of grass and forb densities as a composite variable) as covariates on probability of detection. Only bogs where Henslow's Sparrows were detected at least once (n= 16) were included in the analysis examining probability of detection, so probability of site occupancy was equal to unity. These analyses suggested that probability of detection was constant across bogs (see below), so we restricted the analysis examining probability of occupancy to models with a constant probability of detection; that is, probability of detection was estimated for each individual model but was constant within models and did not vary as a function of individual covariates. We used Spearman's rank correlation to test for colinearity among covariates, and examined all possible subsets of models that did not include combinations of correlated ($P < 0.05$) covariates.

We used an information-theoretic approach to direct model selection and parameter estimation (Burnham and Anderson 1998, Anderson et al. 2000). Model selection was based on using Akaike's information criterion corrected for small sample size (AIC_c), which allows selection of the most parsimonious model from a candidate set of models (Burnham and Anderson 1998). AIC_c provides an objective and repeatable method of selecting the model from a candidate set of models that best fit the data while balancing the tradeoff between bias (under-fitting) and variance (over-fitting) the model (Burnham and Anderson 1998). Furthermore, AIC_c weights were used to calculate parameter estimates and their precision across all models (i.e. model averaging and unconditional variances) which incorporated model selection uncertainty and reduced bias compared to parameter estimates from a single best model (Burnham and Anderson 1998).

Fit of the top ranked model (i.e. K-L best selected model; see Burnham and Anderson 1998) was tested by comparing the difference in model chi-squares of a null model that only included an intercept and the K-L best selected model (Menard 1995). The predictive efficiency of the K-L best selected model, using model averaged parameter estimates, was examined by calculating the proportion of all pair-wise comparisons where the predicted probability of occurrence for bogs where Henslow's Sparrows were observed was greater than at bogs where Henslow's Sparrows were not observed (Hosmer and Lemeshow 2000).

Vegetation data were collected at eight bogs during winter 2000–2001 for use in validating the model developed from data collected the previous year. The number of independent sites available for the validation analysis was limited (n = 5; i.e. three bogs burned before sampling vegetation in 1999–2000 and two bogs added in 2000–2001), so three bogs used to develop the model, but burned between years, were reexamined for the validation analysis. We estimated the optimal cutpoint for discrimination between predictions of occurrence by estimating probability of occurrence where both sensitivity and specificity of the model were maximized for data used to construct the model (Hosmer and Lemeshow 2000). We used that optimal cutpoint to classify predicted occurrences in the validation analysis, and calculated the percentage of correct classifications as a measure of predictive efficiency.

RESULTS

Henslow's Sparrows were found at 16 bogs during winter 1999–2000 and 13 bogs during winter 2000–2001. Overall, Henslow's Sparrows were found on 21 of the 47 bogs (Fig. 1A). Analysis of occupancy models (see below) found that probability of detecting at least one Henslow's Sparrow on a bog was relatively great if Henslow's Sparrows were present on the bog. This measure of detectability is not equivalent to the probability of detecting all Henslow's Sparrows on the bogs and, thus, could not be used to adjust our counts. However, our measure of detectability does suggest that most sparrows present on the bogs probably were detected, so we treated our survey results as complete counts for analysis.

The abundance of Henslow's Sparrows was correlated positively with area of bog during both winters ($r_s \geq 0.366$, $P \leq 0.013$), so we used maximum number of sparrows detected on bogs during any single count over the two winters to examine area sensitivity during winter (Fig. 1A). Although number of Henslow's Sparrows was correlated positively with area of bog ($r_s = 0.422$, $n = 47$, $P = 0.003$; Fig. 1A), density of Henslow's Sparrows was not correlated with area of bog ($r_s = 0.230$, $n = 47$, $P = 0.12$). We found Henslow's Sparrows on bogs ranging from 0.06–1.17 ha (Fig.1A). Although a plot of the data showed that Henslow's Sparrows occurred on pitcher plant bogs >0.25 ha about twice as frequently as they did on smaller bogs, 23.8% (5 of 21) of bogs ≤0.25 ha were used by Henslow's Sparrows (Fig. 1B).

Season of burning and postburn age were related to the density of Henslow's Sparrows during winter 1999–2000 ($F = 2.539$, df = 5 and 39, $P = 0.044$). Density of Henslow's Sparrows did not differ between seasons of burning ($F = 0.005$, df = 1 and 39, $P = 0.94$), but did differ among postburn ages ($F = 5.548$, df = 2 and 39, $P = 0.008$). Density of Henslow's Sparrows at bogs during the first year after burning ($\bar{x} = 2.61$, SE = 0.55) was greater ($P = 0.009$) than the density at bogs that had been burned two years ($\bar{x} = 0.51$, SE = 0.53) or ≥3 years ($\bar{x} = 0.10$, SE = 0.64). There was no interaction between season and year ($F = 0.934$, df = 2 and 39, $P = 0.40$; Fig. 2A).

Density of Henslow's Sparrows during winter 2000–2001 differed among years since burning ($F = 19.115$, df = 2 and 44, $P < 0.001$; Fig. 2B). Density of Henslow's Sparrows was greater ($q = 2.426$, $P < 0.05$) at bogs burned the previous year ($\bar{x} = 1.81$, SE = 0.24) than at bogs burned two years ($\bar{x} = 0.41$, SE = 0.20) or ≥3 years previously ($\bar{x} = 0.10$, SE = 0.13; Fig. 2B).

Occupancy models.—Many intercorrelations ($P < 0.05$) existed among covariates (Table 2). A negative correlation between canopy cover and area of bog ($r_s = -0.547$, $n = 42$, $P = 0.002$) most likely resulted from an edge effect, because few trees actually grew on the bogs. Thus, canopy cover was excluded from further analysis. Season of last burning was not correlated with any other covariate, and years since burning was not correlated with any other covariate except percentage frequency of grass seeds (Table 2). After excluding models that contained correlated covariates, the analysis of occupancy rates considered a total of 75 candidate models.

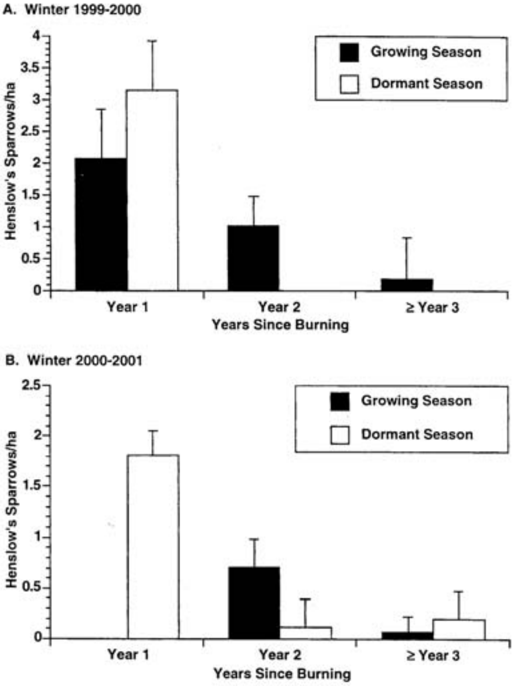

FIG. 2. Least square means (±SE) for density of Henslow's Sparrows at pitcher plant bogs by season of burning and years since burning in the Conecuh National Forest, Alabama, and Blackwater River State Forest, Florida, during (A) winter 1999–2000 and (B) winter 2000–2001. No bogs were burned during growing season 2000, so season of burning was not tested in winter 2000–2001.

Analysis examining herbaceous ground cover as a possible covariate of detection probability suggested that herbaceous ground cover had little effect on probability of detection. Although models containing total herbaceous ground cover (delta $AIC_c = 0.02$) and grass density (delta $AIC_c = 0.27$) were plausible models, the top ranked (i.e. K–L best selected model) was the model that did not contain any covariates. Detection probabilities of all five models were very similar and ranged from 0.822–0.846. Thus, probability of detection appeared constant across the bogs, so we estimated detection probability as a constant in all 75 models examining the influence of covariates on occupancy

TABLE 2. Spearman's correlation coefficients (r_s)[a] for covariates included in occupancy models examining the influence of area (hectares), season of last burning, years since burning, and vegetation structure on the occurrence of Henslow's Sparrows wintering on pitcher plant bogs in the Conecuh National Forest, Alabama, and Blackwater River State Forest, Florida, during winter 1999–2000.

	Grass seeds	Forbs	Grass	Litter	Moss	Shrubs	Pitcher plants	Years	Season
Area[b]	–0.063	0.547	0.167	–0.396	0.140	–0.529	0.403	0.094	–0.161
Grass seeds[c]		0.059	0.626	–0.479	–0.009	–0.314	–0.094	–0.654	–0.074
Forbs[b]			0.250	–0.423	0.376	–0.614	0.573	–0.084	0.039
Grass[b]				–0.614	0.144	–0.397	0.066	–0.216	–0.120
Litter[c]					–0.103	0.494	–0.055	0.057	0.138
Moss[c]						–0.308	0.489	–0.069	0.035
Shrubs[b]							–0.462	0.264	–0.109
Pitcher plants[c]								0.225	0.279
Years[d]									0.242
Season[e]									1.000

[a] Correlations significant at $\alpha = 0.05$, df = 42, r = ± 0.305.

[b] Variable measured as vertical density, except area (hectares), and transformed by natural logarithm, except for grass which was normally distributed without transformation.

[c] Variable measured as percentage coverage and transformed by arcsine square root of proportions before analysis.

[d] Years since burning (1–3).

[e] Season of burning coded as ordinal scale (dormant = 0, growing =1).

by Henslow's Sparrows. The model averaged probability of detection from the 75 models was 0.817 (95% confidence interval = 0.655–0.978).

The K–L best model for explaining the variation in occupancy of bogs by Henslow's Sparrows was clearly the model containing percentage frequency of grass seeds and density of forbs (Table 3). The relative likelihood of the model containing percentage frequency of grass seeds and density of forbs as being the K–L best selected model, based on the ratio of AIC_c weights (see Anderson et al. 2000), was over 3.5× as great as the second best model (Table 3). The K–L best model provided a much better fit to the data than a null model with no covariates included ($\chi^2 = 26.716$, df = 2, $P < 0.001$). Examination of 95% confidence intervals around the model averaged param-

TABLE 3. Covariates, number of parameters, coefficient of determination (R^2_L)[a], Akaike's information criterion adjusted for small sample size (AIC_c), delta AIC_c, and AIC_c weights for models in the 95% confidence interval around the K-L best selected model in the analysis examining the influence of vegetation structure, area (hectares), season of burning, and years since burning on occupancy of Henslow's Sparrows at pitcher plant bogs (n = 42) in the Conecuh National Forest, Alabama, and Blackwater River State Forest, Florida, during winter 1999–2000.

Covariates in model	Number of parameters[b]	R^2_L	AIC_c	Delta AIC_c	AIC_c weights
Percent frequency grass seeds + forb density	4	0.323	64.991	0	0.534
Percent frequency grass seeds + forb density + season of burn	5	0.323	67.577	2.586	0.147
Percent cover litter + percent cover pitcher plants + years since burn	5	0.302	69.36	4.369	0.060
Percent frequency grass seeds + percent cover pitcher plants + season of burn	5	0.301	69.409	4.418	0.059
Percent frequency grass seeds + percent cover pitcher plants	4	0.267	69.633	4.642	0.052
Forb density + years since burn	4	0.253	70.763	5.772	0.030
Area + percent frequency grass seeds + percent cover moss	5	0.270	72.023	7.032	0.016
Forb density + grass density + years since burn	5	0.269	72.075	7.084	0.016
Percent cover litter + percent cover pitcher plants + season of burn + years since burn	6	0.302	72.077	7.086	0.015
Forb density + season of burn + years since burn	5	0.257	73.091	8.100	0.009
Grass density + percent cover pitcher plants + years since burn	5	0.255	73.190	8.199	0.009
Percent cover pitcher plants + years since burn	4	0.223	73.250	8.259	0.009

[a] R^2_L calculated as proportional reduction in absolute value of the log-likelihood measure attributable to the covariates (Menard 1995).

[b] Number of parameters estimated in each model is one for each covariate plus two intercepts (one each for occupancy rate and detection probability).

eter estimates supported the conclusion that variation in percentage frequency of grass seeds and density of forbs were the two covariates best explaining variation in occupancy of bogs by Henslow's Sparrows (Table 4). Overall, the model containing percent frequency of grass seeds and density of forbs was "outstandingly efficient" (see Hosmer and Lemeshow 2000) at discriminating between occupied and unoccupied bogs, and predicted probabilities of occurrence were greater for occupied than unoccupied bogs in 91.6% of 416 pair-wise comparisons. The estimated occupancy rate (i.e. average species presence probability; MacKenzie et al. 2002) was estimated as 0.376, and the observed occupancy rate was 0.381.

For validation of the model, the optimal cutpoint for discriminating between predictions of presence and absence of Henslow's Sparrows was 0.34. Using this cutpoint, the model correctly classified the presence of Henslow's Sparrows at 75% of the bogs where vegetation data were collected during winter 2000–2001. The predicted probability of occurrence from the model was ≥0.784 for each of the eight bogs, but Henslow's Sparrows only were found at six of the bogs.

DISCUSSION

Although growing season fires were most common historically (Robbins and Myers 1992), we did not find a strong effect of season of burning. Our analysis for season of burning was restricted to data from winter 1999–2000, because that was the only year we were able to control for variation due to time since burning. Although we did not detect an interaction of season and time since burning during winter 1999–2000 ($P = 0.402$), plots of the data suggested a possible interaction (Fig. 2A). Densities of Henslow's Sparrows during the first winter after burning appeared ~50% greater at bogs burned in the dormant season than at bogs burned during the growing season, but densities at bogs burned ≥2 years earlier were greatest at bogs burned during the growing season (Fig. 2A). Thus, beneficial effects of burning may last two or three years longer for bogs burned during the growing season (Fig. 2A). Additional research is needed to examine that possible interaction.

Regardless of season of burning, Henslow's Sparrows were more abundant on bogs the first winter following fire than they were two or

TABLE 4. Model-averaged parameter estimates[a], 95% confidence intervals, and standardized means (±SD) for individual covariates included in the analysis examining the influence of vegetation structure, area (hectare), season of last burning, and years since burning on occupancy of Henslow's Sparrows at pitcher plant bogs in the Conecuh National Forest, Alabama, and Blackwater River State Forest, Florida, during winter 1999–2000.

	95% confidence intervals[b]			Standardize covariates	
	Estimate	Lower	Upper	Mean	SD
Intercept (detection rate)	1.494	0.417	2.571	–	–
Intercept (occupancy rate)	–0.928	–2.071	0.214	–	–
Percent frequency grass seeds[c]	1.624	0.280	2.969	0.742	0.326
Forb density[d]	1.460	0.183	2.737	0.021	0.353
Grass density[d]	0.033	–0.048	0.114	6.266	1.491
Area (hectare)[d]	0.037	–0.042	0.115	–1.213	0.910
Percent cover moss[c]	0.025	–0.031	0.080	0.650	0.190
Season of burn	–0.055	–0.418	0.308	0.714	0.457
Years since burn	–0.283	–0.805	0.240	1.929	0.712
Percent cover litter[c]	–0.110	–0.341	0.120	0.399	0.231
Percent cover pitcher plants[c]	0.376	–0.284	1.035	0.309	0.173
Shrub density[d]	–0.001	–0.003	0.001	0.367	0.573

[a] Parameter estimates are the weighted average of estimates across all 75 candidate models that included the variable (Burnham and Anderson 1998). Parameter estimates are used to calculate the logit of Y (detection rate or occupancy rate) which must be back transformed to get reconstituted estimates of Y (see Cooch and White 2001).

[b] Confidence intervals calculated from unconditional variances as ±2 SE (see Burnham and Anderson 1998, Anderson et al. 2000).

[c] Measured as percentage coverage and transformed by arcsine square root of proportions for analysis.

[d] Measured as vertical density, except for area (hectare), and transformed by natural logarithm, except for grass which was normally distributed without transformation.

more years after fire during both years of the study (Figs. 2A and B). Plentovich et al. (1998) found Henslow's Sparrows wintering on pitcher plant bogs showed a high degree of site fidelity and suggested that fire during the winter may have a negative effect on populations. Although Henslow's Sparrows can escape fire (McNair 1998), absence of herbaceous cover during the remaining season following a dormant season fire will force sparrows to seek suitable habitat elsewhere. Thus, annual dormant-season fires might be detrimental to Henslow's Sparrow unless fires occur late in the dormant season (e.g. mid March).

Several studies have found plant species richness on pitcher plant bogs is inversely related to time since burning and suggested that annual or biennial fires probably were the historic norm (Christensen 1977, Walker and Peet 1983). Our results suggest pitcher plant bogs that are burned annually during the growing season (see qualifying statements above) or biennially in either season will produce the greatest benefits for Henslow's Sparrows (Fig. 2). Furthermore, we suggest that growing season fires may be most beneficial for Henslow's Sparrows for the following reasons: (1) the beneficial effects of fire may last a few years longer when bogs are burned during the growing season (Fig. 2A), and (2) production of seeds of many grasses is enhanced by growing season fires (Biswell and Lemon 1943, Abrahamson 1984).

A surprising result of this study was that the percentage frequency of grass seeds appeared as one of the most important variables influencing the occurrence of Henslow's Sparrows on pitcher plant bogs (Tables 4). Although the winter diet of Henslow's Sparrow is poorly known (see Hyde 1939, Graber 1968), we suspect the correlation between occurrence of Henslow's Sparrow and percentage frequency of grass seeds reflects the availability of grass seeds. However, we acknowledge that the correlation could reflect other factors like productivity of arthropods as a prey resource. Likewise, the correlation between occurrence of Henslow's Sparrows and density of forbs probably reflects seed production or arthropod availability. Lack of a substantial effect of time since burning in the occupancy models (Table 4) is surprising because many species of herbaceous plants, both grasses and forbs, respond by increasing productivity during the first growing season after burning (Vogl 1973; Christensen 1977; Barker and Williamson 1988; Hartnett and Richardson 1989; Brewer 1999a, b).

In contrast to the results of Plentovich et al. (1999), we did not find an association between pitcher plants and the presence of Henslow's Sparrows at pitcher plant bogs (Table 4). However, Plentovich et al. (1999) suggested that the relationship observed between pitcher plants and presence of Henslow's Sparrows was probably an indirect result of previous burning practices that had resulted in establishment of a diverse ground cover of grasses and forbs that persisted in the absence of recent burning. Pitcher plants were abundant at most pitcher plant bogs in our study area. The strongest predictor of the presence of Henslow's Sparrows at pitcher plant bogs examined by Plentovich et al. (1999) was the density of *Panicum verrucosum*, a pioneering grass that forms dense stands following mechanical disturbances. Most pitcher plant bogs examined by Plentovich et al. (1999) had not been burned in ≥4 years, but mechanical disturbances had been more recent. Plentovich et al. (1999) suggested that the relationship between presence of Henslow's Sparrows and density of *P. verrucosum* resulted because dense patches of this grass in areas of recent mechanical disturbance provided the best available habitat and was similar in structure to the diverse ground cover of grasses and forbs resulting from regular burning. We observed little evidence of mechanical disturbance on most pitcher plant bogs in our study area, and *P. verrucosum* was rarely encountered. However, *P. verrucosum* is a prolific seed producer, and results for that grass reported by Plentovich et al. (1999) and the results for percentage frequency of grass seeds in our study probably resulted from increased seed production following recent disturbances.

CONSERVATION IMPLICATIONS

We found that Henslow's Sparrows were most abundant on pitcher plant bogs during the first winter after burning (Fig. 2). Thus, annual burning is probably most beneficial to Henslow's Sparrows, but we caution that dormant-season fire may be detrimental to Henslow's Sparrows unless bogs are burned late in the season after Henslow's Sparrows have departed for their breeding grounds.

Furthermore, most of the bogs examined had mixed burn histories and the long-term effects of annual burning need to be addressed.

Until the long-term effects of annual burning are addressed, we suggest that a biennial fire regime with ~50% of pitcher plant bogs burned each year should be employed. If pitcher plant bogs are burned each year in such a fire regime, an equal number of Henslow's Sparrows can be accommodated by either growing-season or dormant-season fires (Fig. 2A). However, we recommend that pitcher plant bogs be targeted for burning in the growing season for the following reasons: (1) the growing season is the "natural fire season" and probably will be most beneficial for bog communities as a whole, and (2) growing-season fire regimes may provide more suitable habitat than dormant-season fire regimes in years when stochastic factors (e.g. weather conditions) disrupt scheduled fires. Uncertainty in weather likely will result in alterations of any specified burning regime. Pitcher plant bogs that are burned during the dormant season may not provide suitable habitat for Henslow's Sparrows if a burning rotation is missed, whereas bogs that are burned during the growing season may provide suitable habitat for two or three years if a burning rotation is missed (Fig. 2A).

Several studies (e.g. Herkert 1994, Winter and Faaborg 1999) have concluded that Henslow's Sparrow is an area-sensitive species, requiring large habitat patches for breeding. Herkert (1994) rarely found Henslow's Sparrows breeding on grassland fragments <100 ha, and habitat area appeared to be the most important factor influencing the occurrence of Henslow's Sparrows. We found that bogs ≤0.25 ha were occupied less frequently than bogs >0.25 ha (Fig. 1B), but we think the occurrence of Henslow's Sparrows on small bogs is noteworthy and has important implications for conservation. That is, the potential importance of small bogs should not be overlooked because they provide habitat for a host of rare organisms in addition to wintering Henslow's Sparrows.

In conclusion, this study suggests that management of pitcher plant bogs to maintain habitat for Henslow's Sparrows is concordant with management to maintain the natural diversity of those habitats. Burning pitcher plant bogs on an annual or biennial basis during the growing season should provide maximum benefits to wintering Henslow's Sparrows and the host of other species associated with those unique communities. However, the long-term effects of persistent annual burning should be addressed before large-scale application.

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