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VEGETATION CHARACTERISTICS OF SWAINSON'S WARBLER HABITAT AT THE WHITE RIVER NATIONAL WILDLIFE REFUGE, ARKANSAS

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Abstract: The Swainson's warbler (*Limnothlypis swainsonii* Audubon) is a species of concern within forested wetlands across the southeastern U.S. Previous studies involving low-elevation sites may not have adequately represented the habitat affinities of this species. We examined relationships between Swainson's warbler occupancy and vegetation structure at relatively high-elevation bottomlands at White River National Wildlife Refuge (WRNWR). In 2004 and 2005, we systematically surveyed 1453 sites and collected vegetation data at 70 occupied sites ($< 5\%$ occupancy) and 106 randomly selected unoccupied sites. Occupied sites had greater canopy cover, density of cane (*Arundinaria gigantea* Walt. Chapm.) and shrub stems, litter depth, and greater and more uniform understory vegetation density than unoccupied sites. Moreover, cane and understory vegetation density were associated with more persistent habitat use. Ultimately, cane stem density was the best predictor of Swainson's warbler occupancy with an AIC_c weight of 99% over all models considered. Overall, our results suggest that cane, dense understory structure, and a well-developed leaf-litter layer are key habitat components for Swainson's warblers at WRNWR. These findings are especially relevant given the substantial decline of canebrakes throughout the Southeast. Swainson's warbler management should include enhancement of canebrakes via manipulations that mimic natural disturbances.

Key Words: *Arundinaria gigantea*, bottomland hardwood forest, canebrakes, floodplain, leaf litter, *Limnothlypis swainsonii*, understory density

INTRODUCTION

The Swainson's warbler (*Limnothlypis swainsonii* Audubon) is an inconspicuous wood-warbler that primarily inhabits bottomland hardwood (BLH) forests in the southeastern U.S. (Meanley 1971, Eddleman et al. 1980, Brown and Dickson 1994, Graves 2002, Bednarz et al. 2005). As ground-foraging litter specialists that nest in the forest understory, Swainson's warblers are dependent on a well-developed layer of leaf litter and dense understory (Meanley 1971, Brown and Dickson 1994, Bednarz et al. 2005). Swainson's warblers breed in appropriate habitats throughout the southeastern U.S. and winter on the Yucatán Peninsula and Caribbean islands (Brown and Dickson 1994).

Historically a common species in suitable habitat types (Morse 1989), the Swainson's warbler is now listed as a species of conservation concern in the southeastern U.S. because of habitat destruction on its breeding and wintering grounds, relatively low population density, and restricted range (Hunter et al. 1993, 1994; Hunter and Collazo 2001). Also, the Southeast and Midwest Working Groups for Partners in Flight ranked the Swainson's warbler as an extreme conservation concern in these respective regions of the U.S. (Hunter et al. 1993, Thompson et al. 1993).

Along with habitat loss on the wintering grounds, the loss of breeding habitat has been identified as a primary threat to the species (Thompson et al. 1993, Stotz et al. 1996, Graves 2001). Due to extensive clearing of BLH forests in the southeastern U.S., the Swainson's warbler has been restricted to seasonally inundated zones bordering rivers and swamps (Graves 2001). Moreover, this migratory species is especially vulnerable to flooding because of its ground-foraging ecology, but little is known about patterns of habitat occupancy at wetland ecotones (Graves 2001).

Within Arkansas, Bednarz et al. (2005) reported that Swainson's warbler populations have been located in both remnant canebrakes (*Arundinaria gigantea* Walt. Chapm.) and deciduous shrub thickets within floodplain habitats. Graves (2002), in a study at five localities in four states, found that canopy height, basal area, and floristics appeared to be relatively unimportant factors in habitat use, provided that a dense understory with high density of woody stems is present. On four different study areas, Bednarz et al. (2005) found that litter depth, shrub stem density, canopy closure, and shrub cover were significantly greater at occupied sites relative to random sites. In contrast, Somershoe et al. (2003) compared occupied sites with adjacent control sites and general control sites that were randomly distributed throughout his study area along the Altamaha River in Georgia and found no significant differences in vegetation structure between occupied and adjacent control sites. However, he found that control sites generally had fewer cane and shrub stems and less litter depth than occupied sites. The different conclusions reported by these studies may be confounded by the fact that extant Swainson's warbler populations seem to only occur in the higher-elevation sites within floodplains that are not frequently flooded (Bednarz et al. 2005). Studies that included sample sites at low-elevation sites in floodplains, such as Graves (2002) and Bednarz et al. (2005) may have incorporated ecological "noise" that made it difficult to elucidate key characteristics associated with occupied sites.

To determine the most effective management strategies for this species, documentation of habitat affiliations, prey availability, and population status in different habitat types is needed. Our objective was to investigate factors influencing habitat use by Swainson's warblers within the high-elevation portion (flood frequency of $>$ 2 years; Klimas et al. 2009) of BLH forest. We examined habitat use with three sets of analyses: 1) a comparison of habitat features between occupied and unoccupied sites; 2) a comparison of habitat characteristics among persistently-used, intermittently-used, and unoccupied areas; and 3) an analysis of which habitat features are most important for differentiating between occupied and unoccupied sites.

We hypothesized that sites occupied by Swainson's warblers would have greater shrub stem density, litter density, and shrub cover than unoccupied sites (Graves 2001, Bednarz et al. 2005). Also, we hypothesized that Swainson's warbler occupied sites would have a greater cane stem density and cane cover than unoccupied sites and that these variables would be associated with persistent habitat use (Brewster 1885, Meanley 1945).

METHODS

Study Area

We studied habitat use by Swainson's warblers at White River National Wildlife Refuge (WRNWR) in eastern Arkansas. The 64,750 ha refuge is located in the floodplain of the White River near its confluence with the Mississippi River, occurs in Arkansas, Desha, Monroe, and Phillips counties, and ranges from 4.8 to 16.0 km wide and is approximately 144 km long. WRNWR is one of the largest remaining contiguous tracts of BLH in the Mississippi River Valley and is listed as a Ramsar wetland of international importance (Ramsar 1971). While WRNWR primarily consists of BLH, it also contains some upland forest, agricultural fields, moist-soil impoundments, and 356 natural and man-made lakes.

Occupancy Determination

We conducted Swainson's warbler surveys at WRNWR from 1 April to 20 June in 2004 and 2005. This corresponds to the time of year that Swainson's warblers migrate into the area, establish territories, and respond most effectively to playback calling. Broadcast surveys were employed along a grid of transects at 200-m intervals at a minimum elevation of 45 m for the south unit and 48 m for the north unit. Elevation cut-offs were intended to exclude areas that typically flood on an annual basis (J. Denman, U.S. Fish and Wildlife Service pers. comm.). High elevation sites that were surveyed typically had a flood frequency of $>$ 2 years, while low elevation sites (not surveyed) had a flood frequency of $\leq$ 2 years as described by Klimas et al. (2009). Because Swainson's warblers are presumably affected by flooding, these elevation cutoffs were implemented to ensure sampling of suitable elevations for Swainson's warblers and reduce the amount of ecological "noise" that could result in confounding relationships among habitat variables and occupancy. We conducted broadcast surveys from sunrise to 1200 H daily. At each sample site, we broadcasted the Swainson's warbler's primary song for 90 sec from a dual-speaker CD player placed perpendicular to the transect line. We then recorded response vocalizations and approaching birds for 60 sec after the broadcast. The CD player was then turned to the opposite side of the transect line and the sequence was repeated (Bednarz et al. 2005). Broadcast volume was set such that observers could hear broadcasts from 50–70 m away on days with clear atmospheric conditions. In 2005, we returned to all occupied and 212 unoccupied sites from 2004. However, within a given season, we visited most sites only once, and therefore were unable to account for detectability. Because Swainson's warblers are extremely aggressive and nearly always respond to playbacks during the peak of the breeding season; there is a very high probability of detecting a Swainson's warbler by using broadcasts when one is present (Bednarz et al. 2005). Although we did not account for imperfect detection probability, we assume the misclassification probability is relatively low and similar for occupied and unoccupied sites and that comparisons of habitat characteristics between "occupied" and "unoccupied" sites should elucidate factors that are correlated with Swainson's warbler presence.

Habitat Structure

We measured vegetation characteristics from 21 June until 15 August in 2004 and 2005 on all occupied sites and we randomly selected an equal number of unoccupied sites. Unoccupied sites were selected by issuing each site a number and generating random numbers from the Microsoft Excel program. We used modified B-Bird field protocols (Martin et al. 1997, Bednarz et al. 2005) to collect data within 5-m and 11.3-m radius plots at occupied and unoccupied sites. The 5-m radius plot was divided into four quadrants and the percent cover of leaf litter, total green cover, shrubs, forbs, vines, cane, bare ground, logs, brush, grass, and water was estimated within each quadrant. Brush was defined as dead branches that were < 8 cm diameter (dbh) and were in contact with the ground. The 11.3-m radius plot was also divided into four quadrants and within each quadrant all trees were placed into size classes based on diameter at breast height (dbh) measurements (saplings ≤ 2.5 cm in diameter and $>$ 30 cm in height; poles = 2.5–7.9 cm dbh; small tree = 8.0–22.9 cm dbh; medium tree = 23.0–37.9 cm dbh; large tree ≥ 38.0 cm dbh). The mean height of overstory and midstory were estimated with a clinometer. The mean height of midstory typically included small trees and lower lateral branches from medium and large trees. Snags were counted in each quadrant and placed into two size classes (small snags ≤ 11.9 cm dbh, > 1.4 m tall; large snags $\geq$ 12.0 cm dbh, > 1.4 m tall).

We measured leaf litter depth and soil moisture at 1, 3, and 5 m from the center of the plot in each cardinal direction. A small hole was dug into the litter down to the bare soil to measure the vertical height of the leaf litter layer with a ruler. Soil moisture was measured by inserting a probe from a soil moisture meter (LIC, Lincoln, NE, USA) into the substrate approximately 5 cm.

Percent total canopy closure was measured from the center of the plot by taking four densiometer readings facing the four cardinal directions. Likewise, percent subcanopy cover was taken from the center of the plot by taking ocular estimates facing the four cardinal directions. Cane, vine, and shrub stems that are < 2.5 cm in diameter and ≥ 30 cm in height were counted in four 1-m^2 plots at a distance of 5 m from the center of the plot in each of the quadrants.

At each site, ocular estimates of the mean shrub height were made. After data collection in 2004, we recognized several additional habitat variables that we felt may reflect important components of Swainson's warbler habitat. Consequently, data for percent cover of vines, number of vine tents, and density of understory vegetation from 0–2.5 m in height were only collected in 2005 and the sample size for analysis of these variables was reduced. Vine tents were defined as conspicuous accumulations of vines created from terrestrial or hanging vines. Vegetation density was measured between 0–2.5 m in height by taking readings from a vegetation cover board (Nudds 1977). After placing the board at the center of the plot, an observer estimated the percent covered in five height intervals: 0–0.5 m, 0.5–1.0 m, 1.0–1.5 m, 1.5–2.0 m, and 2.0–2.5 m. Measurements were taken at all four cardinal directions at a distance of 5 m and 11.3 m from the center of the plot. Because heterogeneity in density may be an important factor, we also computed the coefficient of variation (CV) of density readings at a point for the five vertical readings (vertical density CV) or the four cardinal directions (horizontal density CV).

Data Analyses

To determine habitat features associated with Swainson's warbler habitat use, we used two different approaches. First, we used t-tests and Analysis of Variance (ANOVA) to examine differences in habitat variables between occupied vs. unoccupied and persistently vs. intermittently occupied sites. Further, to elucidate which habitat differences were most important for consistently predicting areas occupied by Swainson's warblers, we employed an information-theoretic approach in which we examined selected *a priori* models that we hypothesized may reflect the biology of this species. Anderson et al. (2001) and others have discouraged presenting both information-theoretic and null-hypothesis-testing results for an analysis addressing the same question with the same data; thus, we use these separate approaches to address different questions and present the results of these different analyses independently. To make all analyses more informative, we have provided estimates and standard errors for all habitat comparisons (Tables 1 and 2). While some of our null-hypothesis tests are likely to be viewed as ''significant'' due to chance, the large proportion of ''significant'' patterns strongly suggest that many of these differences are not spurious. Importantly, our use of the information-theoretic approach allowed us to assess which habitat variables were likely the best predictors of habitat use.

For analyses, we used means of the four estimates from each quadrant in the 5-m and 11.3-m radius plots. Additionally, we used means of the 12 soil moisture and litter depth measurements as an estimate for each site. Litter volume was calculated by taking the product of the mean percent litter cover, the area of the 5-m radius plot, and the mean litter depth for that site.

Habitat Structure. We used t-tests to investigate differences in habitat characteristics at sites occupied and unoccupied by Swainson's warblers (SAS PROC TTEST; SAS Institute 2004). To better meet the assumptions of the tests, we square-root or log transformed variables when necessary. For variables that did not meet the assumption of equal variances; we used the Satterthwaite approximation of degrees of freedom for analyses (SAS Institute 2004).

Additionally, we used ANOVA to investigate differences among habitat characteristics that were associated with sites that were occupied by Swainson's warblers in consecutive years, 1-year only, and non-occupied sites. Again, prior to the analyses, we square-root or log transformed variables where necessary. For variables that did not meet the assumptions of equal variances, we employed Welch's variance-weighted one-way ANOVA in SAS PROC GLM (SAS Institute 2004). For variables with significant differences, we conducted pairwise contrasts to further investigate differences among the three groups.

Habitat Predictors of Swainson's Warbler Occupancy. In an effort to determine which habitat variables are most important for influencing occupancy by Swainson's warblers, we first developed 15 *a priori* models, and then evaluated these models using logistic regression (SAS Institute 2004). Our 15 *a priori* models included habitat variables that we assumed would be good predictors of occupancy based on factors suggested to be important for Swainson's warblers from previous studies and also based on our own field observations. Prior to analyses, we performed correlation analyses (SAS PROC CORR; Cody and Smith 1997) to identify and to remove highly-correlated variables ($r > 0.6$). We evaluated models using Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 2002) and calculated an AIC_c weight for each model. We only used sites for this analysis with complete data for all variables of interest. For sites where we had 2 years of habitat data, we used the mean of the variables for the 2 years in analyses. Because we lacked understory density data for 2004, we used the 2005 data for analyses as values for this variable are highly correlated among years (unpublished data).

RESULTS

Occupancy Determination

In 2004 and 2005, we surveyed 1453 sample locations and detected Swainson's warblers at 70 (4.8%) unique sites. Of the 70 unique detection sites, 28 (40.0%) were occupied in both years, 17 (24.3%) were occupied in only 2004, and 25 (35.7%) were occupied in only 2005. We surveyed 212 sites in 2004 and 2005 that were unoccupied in both years.

Habitat Structure

Occupied and Unoccupied Site Comparisons. We collected vegetation data at 70 occupied and 106 randomly-selected unoccupied sites. Percent cover of vines, number of vine tents, density of vine and shrub stems, and density of vegetation from 0–2.5 m in height were only collected in 2005, when we sampled 53 occupied sites and 84 unoccupied sites. Overall, there were conspicuous habitat differences between occupied and unoccupied sites (Table 1). Of 70 Swainson's warbler detection sites, 57 (81.4%) had cane present within the vegetation plot compared to only 9 (8.5%) of the 106 unoccupied sites that had cane present.

Within the 5-m radius sample plot, occupied sites differed from unoccupied sites in that they had greater total canopy cover, cane cover, litter depth and volume, and soil moisture (Table 1). Additionally, differences were detected in density of cane, shrub, and total stems, with occupied sites being greater than unoccupied sites, but there were no differences in density of non-cane or vine stems (Table 1).

Within the 11.3-m radius plot, occupied sites had a greater density of snags and sub-canopy height than unoccupied sites (Table 1). Occupied sites were also associated with a lower density of large trees

Table 1. Habitat characteristics, $\bar{X} \pm$ SE, and results of t-tests between occupied (n = 70) and unoccupied (n = 106) Swainson's warbler sites on White River National Wildlife Refuge, 2004–2005.

Variable	Occupied		Unoccupied		t	P
	$\bar{X}$	SE	$\bar{X}$	SE		
5.0-m radius						
Total canopy cover (%)[a]	81.75	0.98	77.38	1.04	3.06	0.0026
Sub-canopy cover (%)	41.29	2.52	39.12	2.08	0.66	0.5087
Litter Depth (mm)	17.49	0.70	14.90	0.59	2.82	0.0054
Litter Volume (m^3)	1.24	0.06	1.03	0.05	2.47	0.0146
Soil Moisture[a]	8.19	0.14	7.68	0.14	2.62	0.0096
Shrub-layer Height (m)[b]	1.32	0.65	1.37	0.67	−0.68	0.4950
Stem Density (per ha)						
Cane Stems[a]	30,750	4,113	2,807	1,035	6.59	<0.0001
Non-cane Stems	67,411	5,000	68,774	3,766	−0.09	0.9302
Vine Stems[c]	47,929	4,537	53,134	4,603	−0.81	0.4221
Shrub Stems[ac]	23,536	3,232	9,590	952	3.05	0.0028
Total Stems	98,161	4,046	71,580	3,953	4.64	<0.0001
Percent Cover (%)						
Green Vegetation[d]	39.01	2.21	43.20	2.46	−0.37	0.7148
Grasses and Sedges[a]	3.42	0.57	3.83	0.81	−0.41	0.6846
Forbs[d]	14.96	1.37	20.63	1.99	−1.25	0.2132
Shrubs[a]	8.41	0.66	9.74	0.67	−1.41	0.1609
Vines[b]	14.54	1.31	17.43	1.54	−1.44	0.1526
Cane[a]	16.25	2.16	0.82	0.35	7.06	<0.0001
Brush[a]	4.93	0.47	6.64	0.78	−1.88	0.0621
Leaf litter[a]	87.08	1.73	81.93	2.30	1.79	0.0757
Logs[a]	1.87	0.3	2.22	0.31	−0.83	0.4052
Bare Ground	13.06	1.79	13.58	1.47	−0.22	0.8232
Water[a]	0.00	0.00	0.40	0.32	−1.25	0.2136
11.3-m radius						
Canopy Height (m)[a]	26.44	0.48	26.89	0.32	−0.79	0.4295
Sub-canopy Height (m)	12.63	0.25	11.76	0.23	2.47	0.0145
Tree Density (per ha)						
Saplings	129.88	15.46	156.55	10.22	−1.51	0.1332
Poles	123.89	12.71	148.57	9.97	−1.53	0.1275
Small Trees[a]	63.32	2.74	60.33	2.74	0.77	0.4448
Medium Trees	25.93	1.50	23.43	1.25	1.14	0.2564
Large Trees[a]	19.94	1.00	24.93	1.25	−3.00	0.0030
Small Snags	16.45	1.50	12.21	1.00	2.32	0.0215
Large Snags	17.95	1.25	13.21	1.25	2.65	0.0088
Vine Tents[c]	2.00	0.50	1.50	0.50	0.67	0.5064
Density Cover Board (%)[c]						
0–0.5 m	38.21	3.04	30.13	2.64	2.00	0.0473
0.5–1.0 m[a]	42.85	2.99	27.72	2.37	3.97	0.0001
1.0–1.5 m	45.54	2.89	26.60	2.43	4.99	<0.0001
1.5–2.0 m	49.07	3.04	24.92	2.51	6.10	<0.0001
2.0–2.5 m[a]	45.71	3.02	23.57	2.38	5.75	<0.0001
Total[abd]	44.28	2.85	26.59	2.19	4.92	<0.0001
Horizontal CV[fg]	39.97	3.84	66.01	4.62	−4.12	<0.0001
Vertical CV[agh]	23.92	1.84	39.30	4.32	−3.04	0.0029
Total CV[ai]	52.25	4.75	83.14	4.93	−4.51	<0.0001

[a] t-test for heterogeneous variances.
[b] Occupied sample size is 68 and unoccupied sample size is 103.
[c] Unoccupied sample size is 67 instead of 106 because this variable was only measured in 2005.
[d] Log transformed data.
[e] Density-board reading averaged over all height intervals.
[f] Coefficient of variation in density-board readings for north, south, east, and west measurements averaged over all height intervals.
[g] Square-root transformed data.
[h] Coefficient of variation in density-board readings for five height-interval measurements averaged over all horizontal directions.
[i] Coefficient of variation in density-board readings for north, south, east, and west measurements averaged over all height intervals and five height-interval measurements averaged over all horizontal directions.

than unoccupied sites (Table 1). We found no differences between sites for number of saplings, poles, small trees, medium trees, and vine tents (Table 1). In the 11.3-m radius sample plots, vegetation density from the ground to a height of 2.5 m was greater at occupied than unoccupied sites (Table 1). Also, occupied sites had more uniform horizontal and vertical vegetation structure than unoccupied sites (Table 1).

Sites Occupied in Consecutive Years, 1-year only, and Non-occupied Site Comparisons. We collected vegetation data from 28 sites that were occupied in consecutive years, 37 sites that were occupied in 1-year only (out of 2 years), and 38 non-occupied sites (sampled over 2 consecutive years). There were 5 sites we found occupied in 2005, but were not sampled in 2004; therefore these sites were excluded entirely from these comparisons. Overall, we found conspicuous differences in habitat characteristics between sites occupied in consecutive years, 1-year only, and non-occupied sites (Table 2, Figure 1). All 28 Swainson's warbler sites that had detections in consecutive years had cane present within the vegetation plot; 28 (75.7%) of the 37 sites that had a Swainson's warbler detection in 1-year only had cane present. However, only 5 (13.2%) of the 38 non-occupied sites had cane present.

Within the 5-m radius plot, there was a consistent trend in soil moisture, with the greatest moisture at sites occupied in consecutive years and lowest at non-occupied sites (Table 2). We observed a gradient in cane stem density (Figure 1); sites occupied in consecutive years by Swainson's warblers had the highest mean cane stem density (49,598/ha), sites occupied in only 1 year had an intermediate value (19,966/ha), and non-occupied sites had the lowest density (4,803/ha). Interestingly, shrub stem density was greater at sites occupied in only one year by Swainson's warblers than those occupied in consecutive years or non-occupied sites (Table 2). Also, Swainson's warbler sites that were occupied in consecutive years had fewer non-cane and vine stems than at sites occupied in 1-year only or non-occupied sites (Table 2).

As with cane stem density, we observed a gradient in cane cover in which sites occupied in consecutive years had the greatest mean cane cover (26.9%), sites occupied in 1-year only had an intermediate value (10.1%), and non-occupied sites had the lowest cane cover (2.1%; Table 2). Furthermore, non-occupied sites had greater vine cover than sites occupied in consecutive years or 1-year only by Swainson's warblers (Table 2).

Within the 11.3-m radius plot, the mean sub-canopy height of sites occupied in consecutive years was greater than sites that were not occupied by Swainson's warblers (Table 2). Also, sites occupied in consecutive years had fewer saplings ($P = 0.0245$) than sites not occupied by Swainson's warblers (Table 2).

Mean vegetation density of sites occupied by Swainson's warblers in consecutive years was the highest (53.4%), sites occupied 1-year only had an intermediate value (39.9%), and non-occupied sites had the lowest vegetation density (27.3%) in all height intervals except the 0–0.5 m interval (Table 2, Figure 1). Moreover, sites occupied in consecutive years by Swainson's warblers had more uniform horizontal vegetation structure and less total heterogeneity in vegetation density than sites occupied 1-year only and non-occupied sites (Table 2).

Habitat Predictors of Swainson's Warbler Occupancy

All 15 *a priori* models were better predictors of Swainson's warbler occupancy than the null (intercept only) model (Table 3). However, there were two models that performed substantially better than the other models. The best-fit model contained density of cane, vine, and shrub stems, and accounted for 83.4% of the total AIC_c weight of all models considered. The second highest-ranked model consisted of cane stems and canopy cover, this model accounted for 15.8% of the total AIC_c weight of all models considered. All other models combined accounted for $< 1.0\%$ of the total AIC_c weight of all models considered. Sums of the AIC_c weights showed cane ($\omega_i = 0.9939$), shrub ($\omega_i = 0.8336$), and vine stems ($\omega_i = 0.8336$), and canopy cover ($\omega_i = 0.1637$) to be the best predictors of Swainson's warbler occupancy (Table 3). However, cane stems seem to be the best single-variable predictor of Swainson's warbler occupancy with a combined AIC_c weight of 99.4% over all models considered.

DISCUSSION

Brewster (1885) and Meanley (1945) proposed that there was a close association of cane with the presence of Swainson's warblers. More recent studies (e.g., Graves 2001, 2002; Bednarz et al. 2005) have provided evidence that cane is not a requirement, but did not evaluate if there was a preference for cane when it was present. Graves (2001) offers evidence that Swainson's warblers may prefer non-cane over cane areas in the Great Dismal Swamp of Virginia. However, Graves (2001) also documents a positive correlation between the

Table 2. Habitat characteristics, $\bar{X} \pm$ SE, and results of Analysis of Variance for sites occupied consecutive years (n = 28), 1-year only (n = 37), and non-occupied sites (n = 38) by Swainson's warblers on White River National Wildlife Refuge, 2004–2005. Categories with matching letters indicate no significant differences.

	Occupied Consecutive Yr		Occupied 1-yr Only		Non-occupied Site			
Variable	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	F	P
5.0-m radius								
Total canopy Cover (%)	79.97	1.95	83.32	1.05	79.26	1.15	2.77	0.0677
Sub-canopy Cover (%)	37.97	3.16	41.95	3.58	40.04	3.11	0.33	0.7185
Litter Depth (mm)	17.05	0.99	18.39	1.02	15.38	0.77	2.86	0.0619
Litter Volume (m^2)	1.23	0.08	1.26	0.09	1.07	0.07	1.64	0.1986
Soil Moisture[a]	8.65 A	0.18	7.90 B	0.18	7.10 C	0.24	13.35	<0.0001
Shrub-layer Height (m)[b]	1.31	0.09	1.24	0.09	1.30	0.10	0.19	0.8278
Stem Density (per ha)								
Cane Stems[a]	49,598 A	8,283	19,966 B	2,972	4,803 C	2,219	18.92	<0.0001
Non-cane Stems	45,357 A	6,489	79,966 B	6,185	72,828 B	5,188	8.51	0.0004
Vine Stems[c]	31,964 A	4,674	54,257 B	5,906	59,667 B	5,474	6.48	0.0023
Shrub Stems[c]	13,393 AC	4,212	25,709 B	4,651	8,583 C	1,328	6.50	0.0032
Total Stems	94,955 A	5,596	99,932 A	5,346	77,632 B	5,586	4.80	0.0102
Percent Cover (%)								
Green Vegetation	39.53	3.50	39.02	3.04	45.38	3.40	1.20	0.3046
Grasses and Sedges	3.90 A	0.94	3.28 A	0.79	1.52 B	0.45	2.94	0.0572
Forbs	13.83	1.96	16.43	2.06	18.87	3.18	0.66	0.5202
Shrubs	7.42	1.18	8.61	0.80	10.07	0.86	1.97	0.1445
Vines[c]	13.27 A	2.07	15.20 A	1.80	23.04 B	2.50	5.68	0.0047
Cane[d]	26.85 A	4.11	10.05 B	1.75	2.09 C	0.95	36.19	<0.0001
Brush	6.32	0.80	4.20	0.58	5.64	0.58	2.77	0.0672
Leaf litter	90.34	1.66	84.01	2.86	85.34	2.48	1.58	0.2102
Logs	2.12	0.46	1.89	0.43	1.29	0.31	1.15	0.3195
Bare Ground	10.17	1.91	15.25	2.74	14.34	2.43	1.07	0.3481
Water	0.00	0.00	0.00	0.00	0.22	0.17	1.50	0.2289
11.3-m radius								
Canopy Height (m)	26.64	0.78	26.12	0.69	26.67	0.41	0.34	0.7094
Sub-canopy Height (m)	13.04 A	0.36	12.31 AB	0.36	11.76 B	0.31	3.24	0.0431
Tree Density (per ha)								
Saplings	91.74 A	15.95	126.89 AB	15.46	158.05 B	17.20	3.85	0.0245
Poles	107.94	17.20	134.11	19.94	157.55	17.45	1.69	0.1901
Small Trees	65.81	3.99	64.56	4.24	60.83	3.99	0.41	0.6650
Medium Trees	28.67	2.24	25.43	2.24	21.94	1.74	2.67	0.0745
Large Trees[e]	24.18 A	1.50	16.95 B	1.50	24.93 A	2.24	6.20	0.0029
Small Snags	20.19	2.24	14.21	1.74	14.46	1.99	2.59	0.0799
Large Snags	20.19 A	1.50	17.45 A	1.99	11.97 B	1.74	5.33	0.0063
Vine Tents[c]	1.25	0.50	2.49	1.00	1.99	0.75	0.77	0.4678
Density Cover Board[c] (%)								
0–0.5 m[e]	45.22	5.52	35.80	3.61	29.48	3.50	2.90	0.0600
0.5–1.0 m[e]	51.87 A	5.26	39.07 A	3.52	27.88 B	3.46	7.15	0.0013
1.0–1.5 m	57.27 A	4.77	39.50 B	3.36	27.13 C	3.50	14.23	<0.0001
1.5–2.0 m	59.29 A	5.14	44.05 B	3.67	26.63 C	3.72	14.28	<0.0001
2.0–2.5 m	53.38 A	5.18	41.03 B	3.81	25.47 C	3.57	10.31	<0.0001
Total[f]	53.41 A	4.99	39.90 B	3.37	27.32 C	3.35	10.37	<0.0001
Horizontal CV[g]	26.43 A	5.21	47.10 B	5.32	61.27 B	6.21	8.90	0.0003
Vertical CV[h]	21.34	2.78	24.45	2.42	34.20	6.56	1.83	0.1708
Total CV[i]	40.68 A	5.98	60.17 B	5.81	81.67 C	7.70	9.09	0.0002

[a] Data that Welch's variance-weighted one-way ANOVA was used on.
[b] Sample size for sites occupied in only one year is 35 instead of 37 for this variable.
[c] Sample size for non-occupied sites is 30 instead of 38 because this variable was only measured in 2005.
[d] Log transformed data.

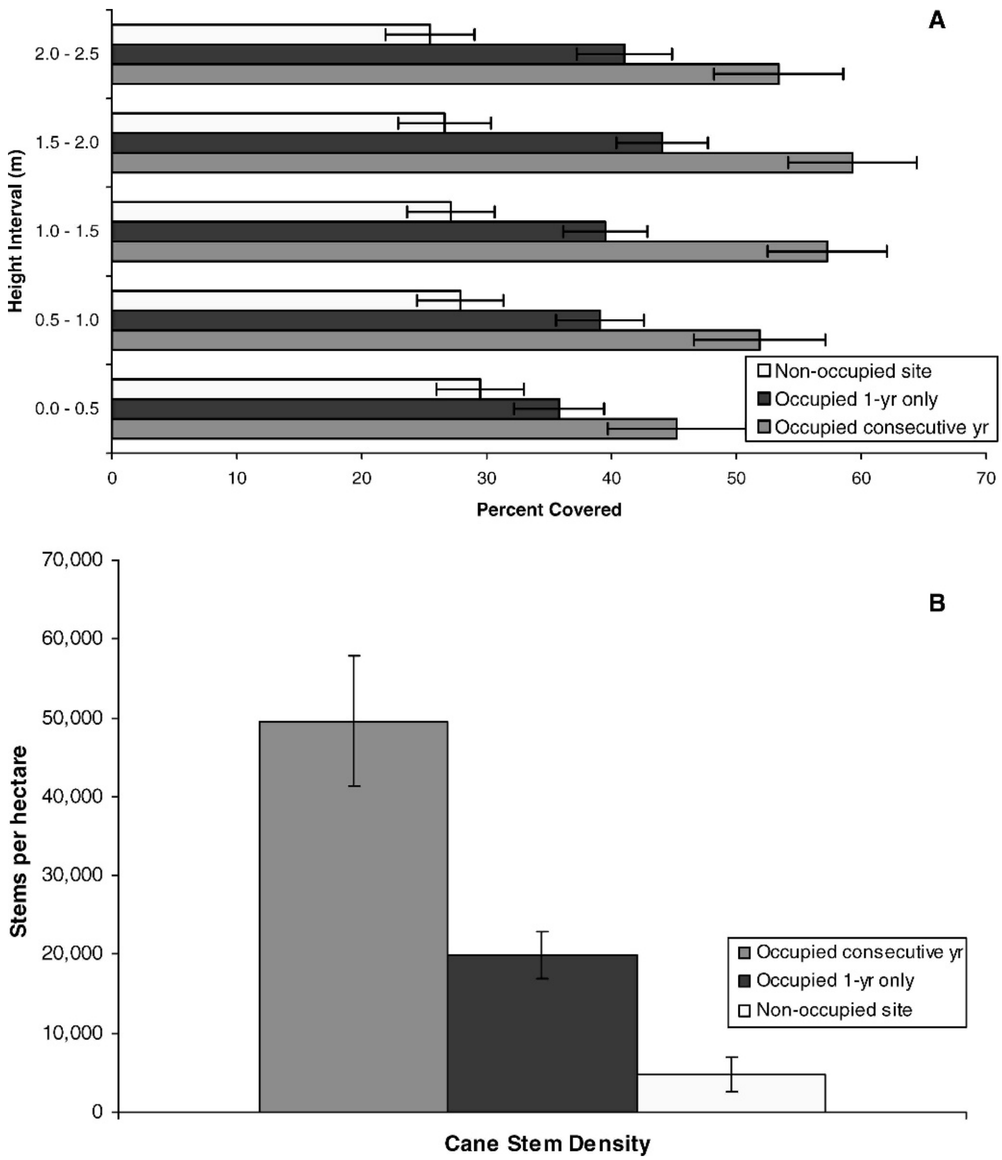

Figure 1. Percent cover at different height intervals (A) and cane stem density (B) within sites occupied in consecutive years by Swainson's warblers, 1-year only, and non-occupied sites on White River National Wildlife Refuge, 2004–2005. Error bars represent one standard error.

presence of cane and water; thus, the absence of Swainson's warblers in cane areas may be a response to the presence of water rather than the avoidance of cane. However, Graves (2002) and Bednarz et al. (2005) did not provide comparisons of occupied sites to unoccupied sites. Results from this study seem to support a cane-Swainson's warbler association, at least in the higher elevation sites of a floodplain in Arkansas. In fact, 57 (81.4%) of the 70 occupied sites contained cane. Of the 13 occupied sites that did not have cane present, four sites had cane present within 50 m.

Notably, we detected a positive relationship in percent cover of cane and density of cane stems with

←

[e] Square-root transformed data.
[f] Density-board reading averaged over all height intervals.
[g] Coefficient of variation in density-board readings for north, south, east, and west measurements averaged over all height intervals.
[h] Coefficient of variation in density-board readings for five height-interval measurements averaged over all horizontal directions.
[i] Coefficient of variation in density-board readings for north, south, east, and west measurements averaged over all height intervals and five height-interval measurements averaged over all horizontal directions.

Table 3. Habitat models and results from logistic regression models used to predict occupancy by Swainson's warblers on White River National Wildlife Refuge, 2004–2005. Models with the lowest AIC_c and largest weight (ω_i) are the best-supported models. Sign in parentheses indicates the direction of the relationship.

Model	K[a]	AIC_c	ΔAIC_c	ω_i	Concordance
Cane Stems[b] (+), Vine Stems (−), Shrub Stems (+)	4	134.08	0.00	0.834	89.90
Cane Stems (+), Canopy Cover[c] (+)	3	137.41	3.45	0.158	85.00
Canopy Cover (+), Total Stems[d] (+), Understory Density[e] (+), Litter Volume[f] (+)	5	144.55	10.31	0.004	84.30
Canopy Cover (+), Total Stems (+), Horizontal CV[g] (−), Vertical CV (−), Litter Volume (+)	6	146.50	12.08	0.002	85.20
Cane Stems (+), Litter Volume (+)	3	146.76	12.80	0.002	83.10
Cane Stems (+)	2	147.23	13.36	0.001	69.30
Understory Density (+), Litter Volume (+)	3	166.12	32.16	<0.001	76.10
Forbs[h] (+), Litter Volume (+), Understory Density (+)	4	166.93	32.85	<0.001	76.70
Understory Density (+), Horizontal CV (−), Vertical CV (−)	4	168.84	34.76	<0.001	75.90
Total Stems (+)	2	169.50	35.63	<0.001	73.60
Horizontal CV (−), Vertical CV (−)	3	170.75	36.79	<0.001	74.20
Understory Density (+)	2	171.23	37.37	<0.001	72.20
Shrub Stems (+)	2	183.44	49.57	<0.001	60.50
Shrub Stems (+), Vine Stems (−)	3	184.75	50.79	<0.001	64.20
Litter Volume (+)	2	187.75	53.88	<0.001	62.30
Null (Intercept Only)	1	191.89	58.08	<0.001	

[a] Number of model parameters.
[b] Stem density within four 1-m^2 quadrants.
[c] Total canopy cover taken from the center of the plot with a densiometer.
[d] Sum of cane, vine, and shrub stem densities.
[e] Measurement taken with a 2.5 m vegetation density coverboard.
[f] Calculated by taking the product of the mean leaf litter depth and the mean percent cover of leaf litter in the 5-m radius plot.
[g] Coefficient of variation.
[h] Percent cover of forbs with the 5-m radius plot.

the presence of Swainson's warblers (Tables 1 and 2). These results are consistent with Wright (2002), who analyzed three cane-related variables (cane stems, cane height, and cane area) and the results showed a clear relationship between cane and presence of Swainson's warblers in breeding habitat on Bond Swamp National Wildlife Refuge in Georgia. Moreover, persistent use seems to occur in canebrakes as 100% of sites occupied in consecutive years contained cane. In contrast, shrub thickets may be only receiving intermittent use by Swainson's warblers. Interestingly, the cane stem density at occupied sites our study (30,800 stems/ha) is similar to Meanley (1971; 49,421 stems/ha), Eddleman et al. (1980; 26,390 stems/ha), and Thomas et al. (1996; 56,500 stems/ha). However, other reports from five studies encompassing four localities reported less than 5,000 cane stems per ha (Peters 1999, Graves 2001, 2002, Somershoe et al. 2003, Thompson 2005). Additionally, Graves (2002) reported cane as being absent in his vegetation plots at Whiskey Bay and the Pearl River areas of Louisiana and from the Appalachicola River in Florida. Conclusions drawn from these studies are somewhat inconsistent with respect to cane. With that in mind, our results may be a function of Swainson's warblers showing a preference for cane at our study site, a function of the relatively high abundance of cane present at the study site, or a combination of these factors. Alternatively, shrub-dominated habitats may result in larger home ranges for Swainson's warblers which could make them more difficult to detect during the 2-year sample period (Anich 2008). Overall, our data clearly support that persistent use by Swainson's warblers seems to occur in cane areas, while shrub thickets seem to only get intermittent use at White River National Wildlife Refuge. Most studies (e.g., Graves 2002, Bednarz et al. 2005) reporting the use of noncane habitats by Swainson's warblers have only looked at occupancy within one year and these short-term studies may have not adequately assessed the long-term use of cane versus shrub thicket habitat.

Cane was not the only factor affecting Swainson's warbler habitat use. Our data also suggested that uniformly dense understory vegetation plays an integral part in habitat selection by Swainson's warblers (Tables 1 and 2). The importance of dense understory vegetation to Swainson's warblers is also supported by previous studies (Eddleman 1978, Bassett-Touchell and Stouffer 2006). Dense understory cover with relatively low variation may be especially important in nesting habitats, where nest concealment is important (Benson 2008). Also, a dense and uniform understory may contribute to a well-developed leaf litter layer. In fact, the amount of leaf litter may play the most crucial role in a Swainson's warbler's habitat. Past work by Graves (2001) and Bednarz et al. (2005) has recognized the importance of a well-developed layer of leaf litter and our study supports this relationship. Leaf litter is likely important because Swainson's warblers forage mainly on ground-dwelling arthropods and well established leaf litter can support an abundance of these food resources (Uetz et al. 1979, Bultman and Uetz 1984). Although the magnitude of differences in litter depth and cover seem trivial (2.6 mm and 5%, respectively), at the plot scale this translates into 20% greater litter volume at occupied relative to unoccupied sites (Table 1). Furthermore, this difference is consistent with differences in litter cover between used and random points within Swainson's warbler home ranges (Anich 2008) and the 20–25% greater litter volume observed at Swainson's warbler nests relative to random points (Benson 2008). Nonetheless, litter volume did not emerge as a consistent predictor of occupancy, suggesting that other variables may be more important for differentiating between used and unused areas.

Due to the importance of ground-dwelling arthropods and a well-developed leaf litter layer, flooding is an important phenomenon affecting Swainson's warbler occupancy. By washing out the established layer of leaf litter, flooding may change the structure of the arthropod community and restrict the amount of suitable foraging habitat. Due to the high frequency (≤ 2 years; Klimas et al. 2009) of flooding in some low-elevation areas, Swainson's warblers may be selecting habitats on higher elevations with a greater abundance of cane, a more-developed layer of leaf litter, and that provide a more consistent supply of ground-dwelling arthropods.

Additionally, occupancy seems to be influenced by stem density and, importantly, the types of stems (Table 3). The 3-variable model with cane, vine, and shrub stems as separate variables was the highest ranked model and accounted for 83.4% of the total AIC_c weight of all models considered. Whereas, the total stems model (pooled cane, vine, and shrub stems count) was a relatively ineffective predictor of Swainson's warbler occupancy, and accounted for only $< 0.1\%$ of the total AIC_c weight (Table 3). This suggests that rather than overall stem density, the types of stems is an important determinant of habitat use. Specifically, cane and shrub stems were positively associated and vine stems were negatively associated with Swainson's warbler occupancy. Moreover, cane stem density was the best predictor of Swainson's warbler occupancy with a combined AIC_c weight of 99.4% over all models considered (Table 3).

In general, Swainson's warblers used sites with relatively uniform dense vegetation cover at the shrub layer level; greater cane, shrub, and total stem density; higher values of canopy cover, subcanopy height, litter depth, soil moisture, percent cover of cane, and density of snags; and a lower density of large trees than unoccupied sites (Tables 1 and 2; Figure 1). These results are consistent with the results of other studies investigating Swainson's warbler habitat use throughout their breeding range. These studies consistently report that key components of Swainson's warbler breeding habitat include dense canopy cover often associated with disturbance gaps, dense shrub-level vegetation (cane or other species) for nesting, abundant leaf litter and sparse herbaceous vegetation, moist floodplain soils, appropriate hydrologic regimes, and substantial forest cover at the landscape scale (Meanley 1971; Eddleman 1978; Thomas et al. 1996; Graves 1998, 2001, 2002; Wright 2002, Bednarz et al. 2005).

Importantly, our findings highlight the importance of cane, which has drastically declined in the southeastern United States (Noss et al. 1995). Indeed, canebrakes have disappeared faster than any other bottomland plant community (Meanley 1971, Gagnon 2006). Less than 2% of the original population of canebrakes remains in the United States today (Noss et al. 1995). In addition to being an important understory component in BLH forests, cane is important to a wide range of game and nongame wildlife species (Platt and Brantley 1997).

Management Implications

Management of forests (in the Southeast) on public lands should focus on improving forest habitat for priority forest birds and other wildlife (e.g., Swainson's warbler; cerulean warbler, *Dendroica cerulea* Wilson; and swallow-tailed kite, *Elanoides forficatus* Linneaus; U.S. Department of Agriculture 2004). Based on the results of this study and the recommendations from the Lower Mississippi Valley Joint Venture (LMVJV Forest Resource Conservation Working Group 2007), we suggest uneven-aged group selection timber harvests should be used to mimic natural disturbances and provide canopy gaps of sufficient size to promote dense understory development, while maintaining 60–80%

canopy cover (LMVJV Forest Resource Conservation Working Group 2007). This would likely provide the dense understory structure required by Swainson's warblers while maintaining the shade and leaf litter that this species also requires.

This study, along with others (e.g., Eddleman et al. 1980, Thomas et al. 1996, Graves 2001, Wright 2002) have suggested the importance of conserving and expanding existing canebrakes. Ideally, small group-selection cuts should be implemented on areas surrounding existing canebrakes to promote rejuvenation and expansion of cane habitats. Although a mosaic of timber cuts may be beneficial, the size and intensity at which this disturbance becomes detrimental to canebrakes is unknown and we would discourage clearcuts on existing canebrakes. However, small clearcuts may be an effective management strategy for Swainson's warblers in some circumstances (Graves 2002). In addition to timber harvesting, we suggest that a rotation of small prescribed minimum-intensity fires every 10–15 years may be beneficial to Swainson's warbler habitat. However, Gagnon (2006) suggested burning canebrakes every 5 to 10 years would benefit current stands of cane. Fire disturbance can reinvigorate declining cane stands (Hughes 1957, 1966; Wright and Bailey 1982, Gagnon 2009) and the new cane stand would be more resistant to environmental stresses such as drought (Gagnon 2006). Importantly, canebrakes under complete fire exclusion will lose vigor and will be gradually replaced by woody vegetation (Hughes 1957, 1966).

Currently, management of low elevation areas has been emphasized for understory Neotropical migratory birds while higher elevation BLH forests have been overlooked (LMVJV 2007). Both cane and Swainson's warblers are generally found on the higher elevations of a BLH forest (pers. obs.) and this is where most conversion to agriculture occurs (Twedt and Loesch 1999, LMVJV 2007). Therefore, we suggest these higher elevations of a BLH forest be given priority for future management. Finally, further investigations are needed on demography, habitat use, and home range sizes in relation to management practices to ensure the development of management prescriptions that would favor the conservation of Swainson's warblers.

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