

Common Denominators of Swainson's Warbler Breeding Habitat in Bottomland Hardwood Forest in the White River Watershed in Southeastern Arkansas

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Abstract - The most intensively studied breeding population of *Limnothlypis swainsonii* (Swainson's Warbler) is in the White River watershed of southeastern Arkansas. However, because vegetation sampling protocols employed at this site have been significantly different from those used elsewhere, it has been difficult for land managers to reconcile datasets across the species' range in order to construct consensus quantitative benchmarks for optimal breeding habitat in bottomland hardwoods. We used a standardized sampling protocol to compare the physiognomic and floristic characteristics of breeding territories at 2 sites in the White River watershed with comparable data from other populations in Arkansas, Mississippi, Louisiana, Florida, and Virginia. Breeding territories in the combined dataset for this rare migratory species varied substantially in successional stage, floristic diversity, hydrology, and management history. Visual screening provided by understory thickets of saplings, vine tangles, and shrubs emerged as the most important common denominator of breeding territories in bottomland hardwood forests across the warbler's breeding range. Basal area, abundance of trees in larger-diameter classes, and floristic diversity appear to have little direct influence on habitat selection across the species' range. Although warblers are often associated with *Arundinaria* spp. (canebrakes), some of the most robust breeding populations occur in cane-free areas. Land managers tasked with generating and sustaining prime breeding habitat should strive for high counts of small woody stems (>45,000/ha or 4.5/m²) in areas that are infrequently subjected to flooding. This benchmark can be achieved through periodic canopy thinning and agroforestry clearcutting.

Introduction

A recent analysis of Breeding Bird Survey data identified *Limnothlypis swainsonii* (Audubon) (Swainson's Warbler) as the rarest migratory songbird breeding in the southeastern US, with a global population of 90,000 sparsely distributed over an estimated breeding range of 1.14 million km² (Partners in Flight Science Committee 2013). This enigmatic species attains its greatest breeding density on the coastal plain in early-successional hardwood forests characterized by an abundance of small trees and understory thickets of saplings, vine tangles, and shrubs (Graves 2002). Territories in mature forests are usually associated with disturbance gaps, but the warblers

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readily colonize anthropogenic habitats that meet its structural requirements. Structural features of the habitat appear to be more important than plant taxonomic composition in determining site occupancy. The latter point is emphatically illustrated by the recent widespread colonization of young pine plantations by Swainson's Warbler on the coastal plain from Virginia westward to Texas (Graves 2015).

Swainson's Warbler has experienced significant habitat loss and retraction of its breeding range owing to the conversion of hardwood forests to other purposes (Graves 2001, 2002) and changes in management practices on public lands (LMVJV-FRCG 2007, USFWS 2010). Concern about the warbler's conservation status has resulted in a flurry of quantitative studies of breeding habitat in hardwood bottomlands in Illinois (Eddleman et al. 1980), Missouri (Thomas et al. 1996), Virginia (Graves 2001), Florida (Graves 2002), Louisiana (Graves 2002, Henry 2004), Mississippi (Graves 2002), Georgia (Somershoe et al. 2003, Wright 2002), Arkansas (Anich et al. 2012, Bednarz et al. 2005, Benson 2008, Brown et al. 2009, Graves 2002, Reiley et al. 2013), South Carolina (Peters et al. 2005, Thompson 2005), and North Carolina (Chartier 2014). Taken together, these studies employed no fewer than 8 different vegetation sampling protocols.

The breeding biology of Swainson's Warbler has been studied most intensively in the watersheds of the White and St. Francis rivers in southeastern Arkansas (Anich et al. 2009a, b; 2012; Bednarz et al. 2005; Benson 2008; Benson et al. 2009, 2010a, b, 2011; Brown et al. 2009, 2011; Everitts et al. 2015; Pappas et al. 2010; Reiley 2012; Reiley et al. 2013, 2014). The vegetation sampling method employed in this cluster of studies was based on a modification of the Breeding Biology Research and Monitoring Database (BBIRD) protocol (Martin et al. 1997). Unfortunately, physiognomic metrics produced by the BBIRD protocol are largely incommensurate with data generated by sampling methods used at other bottomland sites in the breeding range (Eddleman et al. 1980; Graves 2001, 2002; Henry 2004; Peters et al. 2005; Somershoe et al. 2003; Thomas et al. 1996; Thompson 2005; Wright 2002). Consequently, it is difficult for land managers to develop consensus quantitative benchmarks for creating and maintaining optimal breeding habitat in bottomland hardwoods across the breeding range of this rare migratory species.

In this paper, we present new habitat data for breeding territories in the White River watershed. By employing the standardized vegetation sampling protocol introduced by Graves (2001, 2002), we were able to directly compare habitat physiognomy in the White River watershed with previously published data from Arkansas, Mississippi, Louisiana, Florida, and Virginia (Graves 2001, 2002). Here we identify the common denominators of breeding territories across all sites and offer recommendations for land managers and conservationists charged with managing breeding habitat for Swainson's Warbler.

Field-site Descriptions

Dale Bumpers White River National Wildlife Refuge (WRNWR)

WRNWR (~65,000 ha) encompasses the largest contiguous tract of hardwood bottomland forest remaining in eastern Arkansas. The refuge is a forested corridor

4–16 km wide along 87 km of the White River in Monroe, Arkansas, Phillips, and Desha counties. Lumbered intensively until the 1960s, most of the land area of the refuge is now forested with tall second-growth hardwoods. A majority of the remaining old-growth trees are hollow or broken-topped *Taxodium distichum* (L.) Rich. (Bald Cypress) found along bayous and oxbow lakes. The study area was centered on the Prairie Lakes district (34°03'N, 91°08'W), which has been permitted to regenerate and mature for 40–50 years with little human-caused disturbance other than road construction. Soils are predominately intermittently flooded Sharkey clay (NRCS 2015) at an elevation of 40–50 m asl. Higher bottoms and terraces favored by Swainson's Warbler are dominated by *Celtis laevigata* Willd. (Sugarberry) and *Acer negundo* L. (Box Elder). Understory thickets of tree saplings, *Rubus* spp. (blackberries), and *Arundinaria gigantea* (Walter) Muhl. (Giant Cane) are prevalent in canopy gaps and along roadsides. A diverse vine flora is represented in the numerous vine tangles: *Smilax* spp. (greenbriars), *Parthenocissus quinquefolia* (L.) Planch. (Virginia Creeper), *Vitis* spp. (grapes), *Berchemia scandens* (Hill) K. Koch (Alabama Supplejack), *Brunnichia ovata* (Walter) Shinners (American Buckwheat Vine), *Toxicodendron radicans* (L.) Kuntze (Eastern Poison Ivy), *Campsis radicans* (L.) Seem. ex Bureau (Common Trumpet creeper), *Bignonia capreolata* L. (Crossvine), *Ampelopsis arborea* (L.) Koehne (Peppervine), *Gelsemium sempervirens* (L.) J. St.-Hil. (Carolina Jessamine), *Cocculus carolinus* (L.) DC. (Carolina Coralbead), and *Menispermum canadense* L. (Canadian Moonseed). We noted a few occurrences of the invasive species *Pueraria montana* (Lour.) Merr. (Kudzu) in the study area. All common names and plant taxonomy follow ITIS (<http://www.itis.gov>).

Big Island

Big Island lies at the confluence of the White, Arkansas, and Mississippi rivers in Desha County, AK. Most of the island (~10,900 ha) is currently owned by the Anderson-Tully Lumber Company (Vicksburg, MS), and is intensively managed for hardwood timber production through selective cuts. Big Island supports the largest known breeding population of Swainson's Warbler in Arkansas (G.R. Graves, pers. observ.). We restricted field work to the northwestern quarter of the island (33°56'N, 91°07'W), which is less frequently flooded (43–46 m asl). Soils are montmorillonitic and components include Desha clay, Sharkey clay, and Sharkey–Commerce–Coushatta-association soils (NRCS 2015). Dominant tree species in warbler territories include Boxelder, Sugarberry, *Ulmus americana* L. (American Elm), and *Liquidambar styraciflua* L. (Sweetgum). Understory thickets of tree saplings, cane, and blackberries are abundant. The rich vine flora includes greenbriars, Virginia Creeper, Eastern Poison Ivy, Alabama Supplejack, American Buckwheat Vine, Common Trumpet creeper, Crossvine, Peppervine, Carolina Jessamine, Carolina Coralbead, *Trachelospermum difforme* (Walter) A. Gray (Climbing Dogbane), *Matelea carolinensis* (Jacq.) Woodson (Maroon Carolina Milkvine), and Canadian Moonseed. The invasive *Lonicera japonica* Thunb. (Japanese Honeysuckle) is rare in the study area.

Previously published field sites

We compared data from WRNWR ($n = 21$ territories) and Big Island ($n = 21$) with equivalent data collected following an identical field protocol at 6 other bottomland hardwood sites in the core breeding range of Swainson's Warbler: Great Dismal Swamp, VA ($n = 30$ territories); Apalachicola River, FL ($n = 12$); Pearl River, LA ($n = 7$); Whisky Bay, LA ($n = 18$); Sunflower River, MS ($n = 10$); and Crowley's Ridge, AR ($n = 6$). Site descriptions, floristics, quantitative vegetation data, and sampling dates can be found in Graves (2001, 2002).

Methods

Territory detection

We located breeding territories with the aid of song playback (Graves 1996). Playback loops were composed of a mixture of songs from 3 males. Territorial males respond to playback by approaching the sound source and delivering agitated chip notes. Songs are generally given only after playback ceases or when the sound source retreats from the responding male. We interpreted as evidence of male territorial behavior strong response to playback, the reluctance to leave a circumscribed area during "playback-and-follow" trials, mate guarding, and counter-singing with other males. Territory size in eastern Arkansas ranges from 1.1 to 38.0 ha (mean = 8.8 ± 1.2 ha; Anich et al. 2009b); thus, we conservatively considered any subsequent response within 200 m of the original discovery point to represent the same individual unless we heard 2 or more males singing simultaneously. We did not attempt to demarcate territorial boundaries with great precision. Instead, we focused on locating the central areas of territories where male responses were intense; females were often, but not always, observed during this procedure. The majority of males in eastern Arkansas arrive on breeding territories between 10 April and 15 April, and females arrive about a week later (G.R. Graves, pers. observ.). We identified territories from 26 April through 6 May: WRNWR (28 April–1 May 2003, 30 April–3 May 2004, 26–29 April 2005) and Big Island (1–3 May 2006, 5–6 May 2007).

Vegetation-sampling protocol

We designed our study to identify the common characteristics of Swainson's Warbler territories in bottomland-hardwood habitats, rather than to evaluate habitat selection through the comparison of occupied and unoccupied sites in eastern Arkansas. The Arkansas breeding population has been estimated at a scant 900 individuals in a 137,850-km² area (Rich et al. 2004); consequently, unoccupied sites are abundant even in forested landscapes in the White River watershed.

A substantial body of data indicates that males and females forage exclusively in terrestrial leaf litter, generally in small glades that are visually screened by understory thickets (Graves 1998, 2002; Meanley 1970). Foraging warblers may meander widely (>40 m from start to endpoints) across the forest floor in a single feeding bout before taking flight. Territorial males often sing from the ground while foraging. If sampling plots are randomly distributed within a large territory, some will

be located in microhabitat patches that are seldom used or avoided entirely (Anich et al. 2009b, 2012; Graves 2001). Ideally, sampling plots must be large enough to adequately capture the essence of microhabitats used by foraging and singing birds, but not so large as to include significant areas of unused habitat. In recognition of these factors, we used the vegetation-sampling protocol developed specifically for this species (Graves 2001, 2002) to characterize habitat physiognomy of the White River study sites.

We sampled a single circular plot (0.045 ha; diameter = 24 m) on each territory, centered at a site at which we observed singing by an undisturbed foraging male. Sampling at dual-purpose sites ensured that the vegetation data actually corresponded to microhabitats used by Swainson's Warbler. Pooled data from replicate plots in each territory would have provided a better measure of physiognomy but we opted for a single plot per territory because our sampling protocol was labor-intensive (~4 hours per plot).

The choice of physiognomic and floristic data to be measured was based on 2 decades of observations of breeding populations conducted before the outset of the original study (Graves 2001). We measured and identified to species all trees (diameter at breast height [DBH] > 5 cm) in the sampling plot, with the exception of *Carya* spp., which was often in bud during sampling periods. We calculated basal area (m²) per plot from raw field measurements. We did not measure canopy height in this study, but it is positively correlated with basal area (Lefsky et al. 1999). We counted and identified to species all woody vines supported by trees, with the exception of some *Vitis* ssp. specimens.

Benson and colleagues (Benson 2008, Benson et al. 2009, Brown et al. 2009) quantified understory density by counting small woody stems in four 1-m² subplots in each modified BBIRD plot. This sampling intensity is less than optimal for a structural element that is widely suspected to be of critical importance to habitat selection (Eddleman et al. 1980; Graves 2001, 2002; Meanley 1971; Thomas et al. 1996). In our study, the area sampled for small woody stems per plot was an order of magnitude larger than recommended by the BBIRD protocol. We counted small woody stems (SHRU, which includes tree saplings, shrubs, vines, *Rubus* ssp.) in the understory on 4 circular subplots (12.6 m², subplot diameter = 4 m) centered at the cardinal compass points on the perimeter of the larger plot circle (total area of 4 subplots = 50.4 m²). We identified small woody stems to species and counted cane culms on the same subplots. We obtained exact stem counts within each subplot by clipping all stems at a height of 0.5 m above the ground. We employed the coefficient of variation of stem and culm counts among the 4 subplots (CV [SHRU + CANE]) to estimate patchiness of small woody stems and cane. For comparative purposes, we present data for 15 habitat variables from the White River watershed territories (Table 1) that can be compared with comparable data in Graves (2001, 2002). We conducted vegetation surveys from 2 June through 18 July: WRNWR (26 June–19 July 2003, 25–26 May 2004, 8–10 June 2005) and Big Island (16 June–8 July 2006, 2–25 June 2007).

Table 1. Median values (ranges) of physiognomic and floristic variables measured on 0.045-ha plots on breeding territories of Swainson's Warbler on WRNWR ($n = 21$) and Big Island ($n = 21$) in the White River watershed in southeastern Arkansas.

Code	Variable	WRNWR	Big Island, AR
BAS	Total basal area of trees (dbh > 5 cm) m ² /ha	19 (2–59)	10 (4–31)
ONE	Trees (dbh = 5–14.9 cm)/ha	287 (44–640)	574 (132–2009)
TWO	Trees (dbh = 15–24.9 cm)/ha	133 (23–222)	67 (0–288)
THRE	Trees (dbh = 25–39.9 cm)/ha	67 (0–244)	23 (0–133)
FOUR	Trees (dbh = 40–59.9 cm)/ha	23 (0–89)	0 (0–45)
FIVE	Trees (dbh = 60–79.9 cm)/ha	0 (0–45)	0 (0–45)
SIX	Trees (dbh = 80 cm)/ha	0 (0–45)	0 (0)
TREE	All size classes (dbh > 5 cm)/ha	552 (287–905)	684 (265–2076)
TSPE	Tree species (dbh > 5 cm)/0.045 ha	6 (2–10)	7 (4–9)
VSPE	Vine species/0.045 ha	7 (5–9)	8 (4–11)
CANE	Cane culms/ha	13,121 (0–63,616)	0 (0–23856)
SHRU	Small woody stems (dbh < 5 cm)/ha	16,103 (2584–62,224)	72,164 (19,880–215,499)
SHRU + CANE	Small woody stems (dbh < 5 cm) + cane/ha	32,007 (15,706–79,719)	72,164 (29,820–215,499)
SSPE	Shrub species/50.3 m ² (including tree saplings)	13 (9–23)	17 (12–22)
CV [SHRU + CANE]	Coefficient of variation of small woody stems + cane among 4 shrub subplots	0.40 (0.05–0.91)	0.43 (0.18–0.65)

Statistics and hypothesis testing

We tested variables from the combined data set (White River watershed and other sites in AR, MS, LA, FL, and VA) for goodness of fit to a normal distribution with Lilliefors test. All variables exhibited significant deviations from normality even after being subjected to variance-stabilizing transformations. We therefore focused on median rather than mean values and used nonparametric Mann-Whitney *U*-tests to evaluate differences in the distributions of habitat variables observed in 2 a priori-defined study sites (Table 2). This test combines the distributions of 2 groups of values into a single sample and then assesses the range and location of the lowest group's distribution within the overall sample range against a ranked distribution that approaches normality (Hollander and Wolfe 1973). Significance values were Bonferroni-adjusted for the number of habitat variables to be tested ($P = 0.05/15 = 0.0033$). We compared vegetation variables across sites in a hierarchical fashion: (1) WRNWR vs. Big Island; (2) WRNWR vs. other sites (AR, MS, LA, FL, VA); (3) Big Island vs. other sites (AR, MS, LA, FL, VA); (4) WRNWR + Big Island vs. other sites (AR, MS, LA, FL, VA).

We evaluated the bivariate relationship between pairs of variables with Spearman rank correlation coefficients. We further evaluated the relationship of study sites with principal components analysis (PCA) of correlation matrices for key habitat variables (BAS, ONE, TREE, SHRU + CANE, CV [SHRU + CANE]). This procedure transforms a group of generally correlated habitat variables into a set of uncorrelated composite variables and is particularly useful for reducing the dimensionality of complex data sets. All analyses were performed in SYSTAT ver. 11 (SYSTAT 2004).

Results

WRNWR versus Big Island

Warbler territories surveyed on WRNWR differed significantly from those on Big Island in 6 of the 15 habitat variables (Table 2). For example, median values for basal area (BAS) were nearly twice as large on WRNWR, reflecting the removal of larger trees for lumber on Big Island. Similarly, the larger range of tree densities (TREE) on Big Island plots is due to the greater frequency of canopy gaps and regeneration patches associated with timber management. Trees in the smallest diameter class (ONE) were common at both sites, whereas trees in larger diameter classes (FOUR–SIX) were scarce. Scattered understory thickets composed of tree saplings, vine tangles, and cane were conspicuous characteristics on WRNWR and Big Island. The density of small understory woody stems and cane (SHRU + CANE) ranged from 15,706 to 79,719 stems/ha (median = 32,007 stems/ha) on WRNWR and from 29,820 to 215,499 stems/ha (median = 72,164 stems/ha) on Big Island. When we ignored the single large outlier at Big Island, the cumulative range of understory stem densities at both sites ranged from 15,706 to 105,562 stems/ha (Fig. 1). Small woody stems (SHRU) were more abundant on Big Island plots as a consequence of regeneration in canopy gaps created by selective harvest of large trees. Cane was frequently recorded on WRNWR (18 of 21 plots) but was less

common on Big Island (5 of 21 plots). Densities of cane and small woody stems (SHRU) were inversely proportional in plots on Big Island ($r_s = -0.74$, $P < 0.001$) but not significantly related on WRNWR ($r_s = -0.24$, $P > 0.05$). The coefficient of variation of small understory-stem counts (CV [SHRU + CANE]) among subplots exhibited a wide range of values, but median values were similar on WRNWR and Big Island.

The cumulative number of tree species ($n = 24$) observed on plots was identical on WRNWR and Big Island. Sugarberry (44.6% of stems), Boxelder (15.8%), hickories (5.4%), and Sweetgum (5.4%) were the most common species with DBH

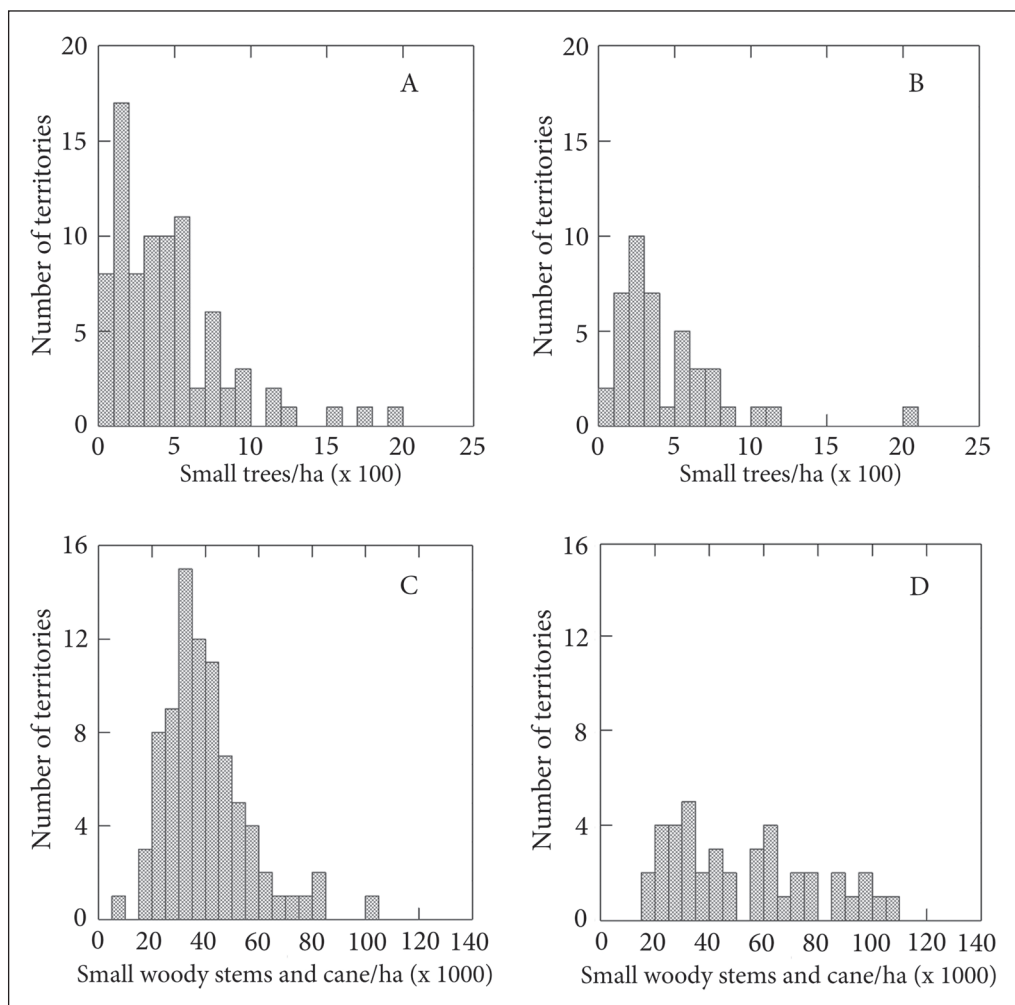


Figure 1. A: Number of trees in the smallest-diameter class (ONE) in warbler territories sampled at 6 sites from Louisiana, Mississippi, Arkansas, Florida, and Virginia (see Graves 2002). B: Comparable data (ONE) from the WRNWR and Big Island in southeastern Arkansas. C: Total number of small woody stems and cane (SHRU + CANE) on warbler territories from 6 sites in the said states. D: Comparable data (SHRU + CANE) from WRNWR and Big Island (1 large outlier was omitted). See Table 1 for habitat variables.

> 5 cm on WRNWR. Species-abundance patterns were more equitably distributed on Big Island, where 7 taxa constituted at least 5% of the stems > 5 cm DBH: Box-elder (25.7%), Sweetgum (15.0%), Sugarberry (13.0%), American Elm (12.6%), *Fraxinus pennsylvanica* Marsh. (Green Ash; 7.3%), hickories (6.6%), and *Populus deltoides* W. Bartram ex Marshall (Eastern Cottonwood; 5.1%).

Inter-watershed comparisons

We compared habitat data from WRNWR and Big Island to pooled data from 6 sites outside the White River watershed in AR, MS, LA, FL, and VA (Graves 2001, 2002). The distributions of 12 of 15 habitat variables on WRNWR were similar to those in the pooled data (Table 2). Plots on WRNWR had more cane (CANE), fewer small woody stems in the understory (SHRU), and fewer total trees (TREE). Data from Big Island were similar to those observed in the pooled sample for 7 of 15 variables. Big Island plots had lower basal area (BAS), fewer trees in intermediate diameter classes (TWO, THREE), more small woody stems in the understory (SHRU), higher vine-species richness (VSPE), and a greater number of small woody species in the understory (SSPE) (Table 2).

Based on data from the White River watershed (WRNWR + Big Island) and 6 other sites (AR, MS, LA, FL, and VA), Swainson's Warbler territories are invariably characterized by a high density of small understory stems (SHRU + CANE; mean \pm 1 SD, 45,924 \pm 25,748 stems/ha; median = 39,164 stems/ha; n = 125). Small understory-stem counts from 82% of territories fell within 1 standard deviation of the mean (20,176–71,673 stems/ha). Territories were also characterized by relatively high densities of small trees (ONE; 456 \pm 370 trees/ha). Small-tree counts

Table 2. Results of Mann-Whitney U -tests comparing median values of physiognomic and floristic variables measured on 0.045-ha plots on breeding territories of Swainson's Warbler on WRNWR (n = 21) and Big Island (n = 21) in the White River watershed in southeastern Arkansas as well as other sites representing pooled data in Graves (2001, 2002). * indicates significant P -values adjusted for the number of simultaneous tests for each set of comparisons (P = 0.05/15 = 0.0033).

Code	WRNWR vs. Big Island	WRNWR vs other sites	Big Island vs. other sites	WRNWR + Big Island vs. other sites
BAS	0.0002*	0.1200	<0.0001*	<0.0001*
ONE	0.0044	0.0640	0.0600	0.9900
TWO	0.0810	0.2500	0.0020*	0.0064
THRE	0.0310	0.1900	0.0001*	0.0008*
FOUR	0.0310	0.0150	<0.0001*	<0.0001*
FIVE	0.1000	0.0130	0.0070	0.0053
SIX	0.0190	0.8800	0.0170	0.1100
TREE	0.0290	<0.0001*	0.2000	0.0003*
TSPE	0.6100	0.6400	0.8400	0.8700
VSPE	0.0025*	0.1000	0.0003*	0.0007*
CANE	0.0003*	<0.0001*	0.9400	0.0003*
SHRU	<0.0001*	<0.0001*	0.0002*	0.4000
SHRU + CANE	0.0001*	0.3700	<0.0001*	0.0160
SSPE	0.0005*	0.4600	0.0012*	0.0100
CV [SHRU + CANE]	0.6600	0.6500	0.8500	0.6800

from 81% of territories fell within 1 standard deviation of the mean (86–826 stems/ha). Patchiness of small understory stems was relatively limited (CV [SHRU + CANE]; 0.43 ± 0.20). In contrast, habitat variables such as basal area (BAS), the abundance of trees in higher-diameter classes (TWO–SIX), and floristic diversity (VSPE, TSPE, SSPE) exhibited considerable variation across field sites and appear to have little direct influence on selection of breeding habitat (Tables 1, 2).

A principal components analysis of 5 important habitat variables yielded 3 principal components (PC) with eigenvalues >1.0 (Table 3). These collectively accounted for 84.0% of the variation recorded in Swainson's Warbler territories in the combined dataset. PC 1 (38.0% of the variance) discriminated vegetation plots with more trees (TREE), principally small trees (ONE) from plots with higher basal area (BAS), which also figured prominently in PC 2. PC 2 (25.6% of the variance) separated plots with high basal area (BAS) from plots with high densities of small woody stems and cane (SHRU + CANE). PC 3 (20.4% of the variance) exhibited positive loadings for small woody-stem density (SHRU + CANE) and negative loadings for stem patchiness (CV [SHRU + CANE]). The confidence ellipses surrounding factor scores from each of the 3 groups (WRNWR; Big Island; pooled data from other sites from AR, MS, LA, FL, and VA) exhibited considerable overlap in key habitat variables (Fig. 2).

Discussion

The breeding population of Swainson's Warbler on the WRNWR has declined precipitously since the 1970s (G.R. Graves, pers. observ.) owing to management changes that favored the restoration of forests to steady-state conditions at the expense of early-successional habitats (LMVJV-FRCG 2007, USFWS 2010). Many areas of the refuge that supported dense populations of the warbler as late as 1988 now support only a few widely scattered individuals due to the thinning of undergrowth, forest maturation, and canopy closure. In contrast, the intensively lumbered tracts on Big Island currently support a relatively dense breeding population (G.R. Graves, pers. observ.). Success in reversing local population decreases on the WRNWR and at many other sites in the breeding range may well depend on identification of the common denominators of breeding territories and application of management protocols to achieve the optimal physiognomy.

Table 3. Principal component analysis of the correlation matrix for 5 key habitat variables measured on 125 Swainson's Warbler territories in Arkansas, Mississippi, Louisiana, Florida, and Virginia. Variable codes are presented in Table 1. PC = principal component.

Variables	Component loadings		
	PC 1	PC 2	PC 3
BAS	-0.36	-0.78	0.00
ONE	0.97	0.06	0.08
TREE	0.88	-0.30	0.16
SHRU + CANE	-0.16	0.69	0.46
CV [SHRU + CANE]	0.16	0.31	-0.88

The physiognomic metrics of breeding territories of Swainson’s Warbler on WRNWR and Big Island are bracketed by those observed in bottomland hardwoods in other parts of its breeding range (Graves 2001, 2002). The addition of new data from the White River watershed geographically extends and corroborates patterns observed elsewhere (Graves 2001, 2002). The principal characteristic that links all known breeding sites, regardless of management history, is the presence of a dense understory. Patchily-distributed thickets of saplings, shrubs, vine tangles, and cane provide secure nesting sites (Benson et al. 2009, Bishop et al. 2012, Henry 2004) and an abundance of semi-concealed glades for terrestrial foraging (Graves 1998, 2002). The primary cue in habitat selection may well be something as simple as adequate visual screening of foraging and nesting sites. Other factors that likely play key roles in habitat selection are patch size, leaf-litter quality, soil type, and hydrology (Benson et al. 2011; Brown et al. 2011; Graves 1998, 2001, 2002, 2015; Meanley 1971; Reiley 2012). Our conclusions are based on associative patterns at breeding sites across the warbler’s geographic range (Graves 2002), behavioral responses to prescribed burning (Everitts et al. 2015) and natural events such as flooding (Reiley et al. 2013), and distributional responses to agroforestry management (Twedt and Somershoe 2009).

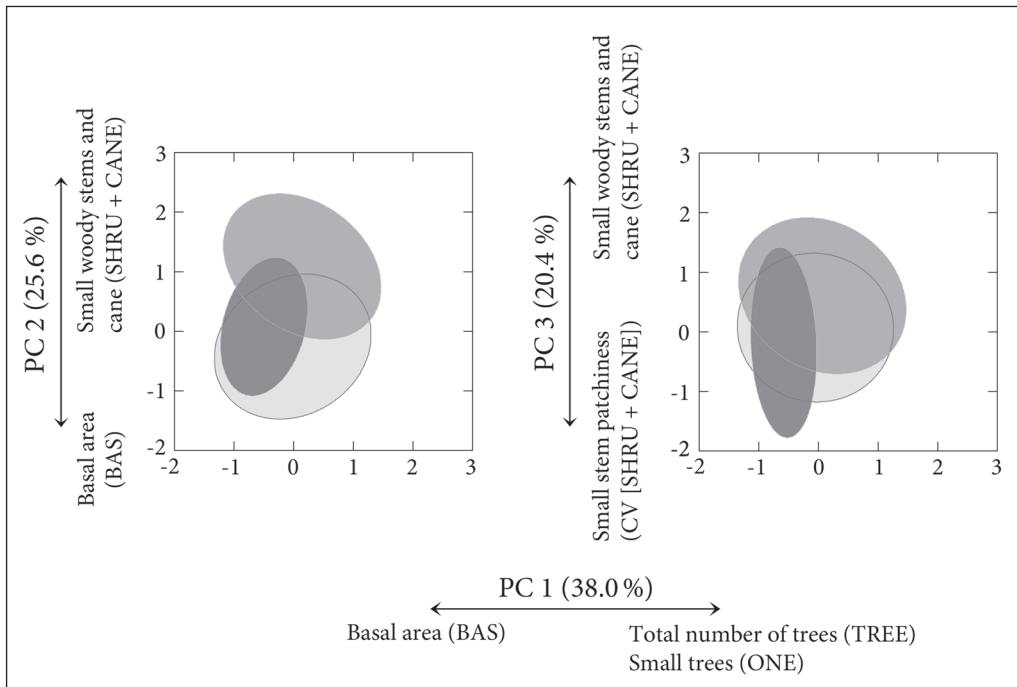


Figure. 2. Bivariate plots of 70% confidence ellipses surrounding factor scores produced by a principal components analysis (PCA) of physiognomic variables of Swainson’s Warbler breeding territories. Arrows indicate the direction of component loadings for variables that strongly influence principal components. Dark gray = WRNWR ($n = 21$ territories), medium gray = Big Island ($n = 21$ territories), and light gray = pooled data ($n = 83$ territories) from 6 sites in Arkansas, Mississippi, Louisiana, Florida, and Virginia (from Graves 2001, 2002).

Several habitat-management strategies have been proposed to stimulate the growth of thickets, vine tangles, and dense stands of young trees: (1) individual tree or small-group selection cuts to mimic tree-fall gaps (Bednarz et al. 2005, Brown et al. 2009, Chartier 2014, Pashley and Barrow 1993, Somershoe et al. 2003, Twedt and Somershoe 2009); (2) 0.25–1.2-ha patch cuts designed to simulate larger natural disturbances (Graves 2002, Twedt and Somershoe 2009); (3) small, 4–20-ha clearcuts (Eddleman et al. 1980, Graves 2002); and (4) large, up to 700-ha agroforestry clearcuts (Peters et al. 2005). Cutting schemes performed across the spectrum of plot sizes have achieved positive results (Graves 2002, Peters et al. 2005, Twedt and Somershoe 2009). Larger agroforestry clearcuts are seldom recommended as a management strategy even though they appear to be no less effective in supporting viable breeding populations of Swainson's Warbler (Graves 2002, Peters et al. 2005). Breeding populations generally respond to canopy thinning protocols a few years after cutting and may persist at densities higher than observed on control plots for a decade or more after thinning (Twedt and Somershoe 2009). Treatment intervals of 25–30 years have been recommended to maintain a regional mosaic of suitable habitat for this species (Twedt and Somershoe 2009). Regenerating clearcuts may provide suitable habitat 5–7 years post-harvest (G.R. Graves, pers. observ.) and continue to attract breeding warblers for 15–25 years after clearcutting (Peters et al. 2005).

A second management approach focuses on the establishment and restoration of canebrakes (Bednarz et al. 2005, Brown et al. 2009, Chartier 2014, Eddleman et al. 1980, Thomas et al. 1996). Naturalists have long noted the association of Swainson's Warbler and canebrakes (Brewster 1885; Howell 1911; Meanley 1945, 1971; Wayne 1886), and this correlation has influenced management recommendations for the past 35 years (Bednarz et al. 2005, Brown et al. 2009, Chartier 2014, Eddleman et al. 1980, Somershoe et al. 2003, Thomas et al. 1996, Wright 2002). Extensive cane stands may provide high-quality breeding habitat if hydrological conditions are favorable for the deposition of leaf litter necessary for ground foraging (Graves 1998; Meanley 1945, 1971; Reiley et al. 2013). Swainson's Warblers apparently cue on canebrakes because they provide dense understory screening and generate ample leaf litter. Visual understory screening also seems to be the reason the species is attracted to regenerating hardwood clearcuts and young pine plantations where cane is either a rare habitat component or absent (Graves 2002, 2015).

Declining canebrakes can be restored by canopy thinning and by small patch cuts that encourage canebrake expansion (Eddleman et al. 1980, Thomas et al. 1996). Fire management has also been prescribed as a method for invigorating decadent canebrakes (Bednarz et al. 2005, Brantley and Platt 2001, Gagnon 2009, Gagnon et al. 2013). However, a recent study showed that prescribed burning decreased vegetation density and leaf-litter depth, resulting in a significantly larger territory size for Swainson's Warbler (Everitts et al. 2015). Moreover, prescribed burning alone was insufficient to restore remnant canebrakes. Everitts et al. (2015: 292) concluded that "high-intensity fires or frequent burning could have significant negative impacts on Swainson's Warbler habitat". The *de novo* propagation of

canebrakes is horticulturally difficult, expensive, and labor intensive (Baldwin et al. 2009, Zaczek et al. 2004) and canebrake restoration and propagation is unlikely to produce enough Swainson's Warbler habitat to make a difference.

Conclusions

Land managers tasked with creating, restoring, or maintaining optimal breeding habitat in bottomland hardwoods should seek target counts of small woody stems and cane (SHRU + CANE) that exceed the mean value (~45,000/ha or 4.5/m²) observed in the combined sample of territories from Arkansas, Mississippi, Louisiana, Florida, and Virginia. Although Swainson's Warblers are often associated with canebrakes, some of the most-robust breeding populations occur in cane-free areas. Understory-density benchmarks can be attained through a range of management practices including extensive canopy thinning and agroforestry clearcutting. Rotational disturbance of bottomland hardwoods on 15–25-year cycles may be necessary to provide an adequate area of suitable habitat for Swainson's Warbler in regional landscapes.

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