

BREEDING POPULATION DENSITY AND HABITAT USE OF
SWAINSON'S WARBLERS IN A GEORGIA FLOODPLAIN FOREST

by

ELIZABETH ANN WRIGHT

(Under the direction of J. Michael Meyers and Robert J. Warren)

ABSTRACT

I examined density and habitat use of a Swainson's Warbler (*Limnothlypis swainsonii*) breeding population in Georgia. This songbird species is inadequately monitored, and may be declining due to anthropogenic alteration of floodplain forest breeding habitats. I used distance sampling methods to estimate density, finding 9.4 singing males/ha ($CV = 0.298$). Individuals were encountered too infrequently to produce a low-variance estimate, and distance sampling thus may be impracticable for monitoring this relatively rare species. I developed a set of multivariate habitat models using binary logistic regression techniques, based on measurement of 22 variables in 56 plots occupied by Swainson's Warblers and 110 unoccupied plots. Occupied areas were characterized by high stem density of cane (*Arundinaria gigantea*) and other shrub layer vegetation, and presence of abundant and accessible leaf litter. I recommend two habitat models, which correctly classified 87-89% of plots in cross-validation runs, for potential use in habitat assessment at other locations.

INDEX WORDS: Neotropical migrant, Bird, Songbird, Avian, Swainson's Warbler, *Limnothlypis swainsonii*, Bond Swamp National Wildlife Refuge, Ocmulgee River, Georgia, Bottomland forest, Floodplain, Natural disturbance, Cane, Canebrake, *Arundinaria gigantea*, Population density, Distance sampling, Bird survey methods, Habitat use, Habitat models, Logistic regression

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ELIZABETH ANN WRIGHT

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ELIZABETH ANN WRIGHT

Major Professors: J. Michael Meyers
Robert J. Warren

Committee: Robert J. Cooper
J. Whitfield Gibbons

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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DEDICATION

To my father, Dr. Malcolm R. Wright;

In remembrance of my mother and my aunt,
Mary Louise Waters Wright and Catherine Anne Waters Eschbach;

And for all those beings I've encountered along the way
who inspired me with their passion, beauty, and imagination.

Disillusionment of Ten O'Clock

The houses are haunted
By white night-gowns.
None are green,
Or purple with green rings,
Or green with yellow rings,
Or yellow with blue rings.
None of them are strange,
With socks of lace
And beaded ceintures.
People are not going
To dream of baboons and periwinkles.
Only, here and there, an old sailor,
Drunk and asleep in his boots,
Catches tigers
In red weather.

– Wallace Stevens

Emancipate yourself from mental slavery
None but ourselves can free our minds.

– Robert Nestor Marley

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Chapter I

INTRODUCTION

The canebrakes stretch along the slight rises of ground, often extending for miles, forming one of the most striking and interesting features of the country. They choke out other growths, the feathery, graceful canes standing in ranks, tall, slender, serried, each but a few inches from his brother, and springing to a height of fifteen or twenty feet. They look like bamboos; they are well-nigh impenetrable to a man on horseback; even on foot they make difficult walking unless free use is made of the heavy bush-knife. It is impossible to see through them for more than fifteen or twenty paces, and often for not half that distance. Bears make their lairs in them, and they are the refuge for hunted things.

– Excerpt from Theodore Roosevelt, “In the Louisiana Canebrakes” (1908)

Anthropogenic alteration of habitats used by Nearctic-Neotropical migratory birds during the various phases of their annual cycle has been implicated as a principal cause of population declines observed in many species (Terborgh 1989, Lovejoy 1992, Robbins et al. 1993, Peterjohn et al. 1995, Askins 2000, Pashley et al. 2000). Although ornithologists for several decades have debated the relative conservation importance of habitats used by Nearctic-Neotropical migrants for breeding, overwintering, and migration, an integrated view is emerging (Martin 1992, Terborgh 1989, Sherry and Holmes 1995, Holmes and Sherry 2001). Recent research provides evidence that events occurring during each discrete phase of the annual cycle can directly influence other phases in substantive ways (Marra 1998). Thus, an “all-season” approach to habitat conservation for Nearctic-Neotropical migrants may be warranted.

Literally dozens of studies have examined habitat selection and use by avian species, but no single theory appears to have been widely accepted. Habitat selection – i.e., the behavioral and psychological mechanisms by which birds or other animals

determine which areas to occupy and use during various parts of their annual and life cycles – may be influenced in birds by a number of interacting ecological processes and environmental factors operating at multiple scales (Lack 1933, Cody 1985). Settlement of individuals in a given habitat may not reflect a conscious decision-making process but rather a programmed response, established genetically or during the nestling/fledgling stage, involving recognition of the features of a particular habitat type in which the individual was successfully reared, the so-called “niche gestalt” (James 1971). Habitat selection may reflect processes such as intra- and interspecific competition, as evidenced by individual and social behaviors such as territoriality and density-dependent habitat use (Grinnell 1917, Fretwell and Lucas 1969, Martin 1998), along with the apparent selection of habitats to avoid predation (Martin 1998) and competition for localized resources such as food and nest sites (Grinnell 1917, Gill 1995).

Environmental features that appear to influence habitat selection at various scales include structure and species composition of vegetation (Lack 1933, MacArthur and MacArthur 1961, James 1971, Holmes and Robinson 1981, Rotenberry 1985), climate (Grinnell 1917), topography (Johnston and Odum 1956), hydrology and soils (Grinnell 1917), presence of ecological edges (Grinnell 1917, Johnston and Odum 1956), habitat heterogeneity (Cody 1985, Robbins et al. 1989), and overall area of intact (unfragmented) habitat available (Robbins et al. 1989). Individual birds may engage in a hierarchical process (Johnson 1980) in which visible features of the landscape, such as vegetation structure and topography, are used as “proximate cues” to gauge whether specific habitats – from landscape to microsite scales – can provide those factors ultimately needed for survival and reproduction, such as sufficient food, mating opportunities, secure nest sites, and protection from predators, parasites, and

meteorological conditions (Lack 1933, James 1971, Anderson and Shugart 1974, Johnson 1980, Robinson and Holmes 1984, Cody 1985, Martin 1998).

Availability and selection of suitable habitats may be especially critical for Nearctic-Neotropical migratory birds given their extreme mobility and consequent need to locate fitness-maximizing habitats several times each year (Cody 1985).

Understanding habitat selection and use thus is an essential element in conservation efforts for Nearctic-Neotropical migrants, yet adequate information is lacking for many species (Martin 1992, Finch and Stangel 1993, Askins 2000).

Loss of appropriate natural habitats as the result of human activities apparently has not affected all Nearctic-Neotropical migratory bird species and groups equally. This may be because the extent and intensity of anthropogenic disturbance has been greater in habitat types most desirable for human use, such as those best-suited for agriculture, timber harvest, or silviculture (Askins 2000, Brawn et al. 2001). Conversely, certain habitat types have been affected inordinately by human suppression of fires, floods, and other natural disturbances integral to ecosystem function (Brawn et al. 2001, Hunter et al. 2001, Reice 2001). Many Nearctic-Neotropical migrant species of high conservation concern breed in temperate zone habitats that have been subjected to long-term anthropogenic insults involving both intensive human use and suppression of natural disturbance – e.g., grasslands, pine and oak savannas, and riparian forests (Askins 2000, Brawn et al. 2001). The songbird I studied, the Swainson's Warbler (*Limnothlypis swainsonii*), is such a species.

SWAINSON'S WARBLER

The Swainson's Warbler (Fig. 1), first described by John James Audubon in 1834, is a Nearctic-Neotropical migrant songbird in the family *Parulidae*, the wood warblers (AOU 1998, Brown and Dickson 1994). It is a small (130-140 mm total length),

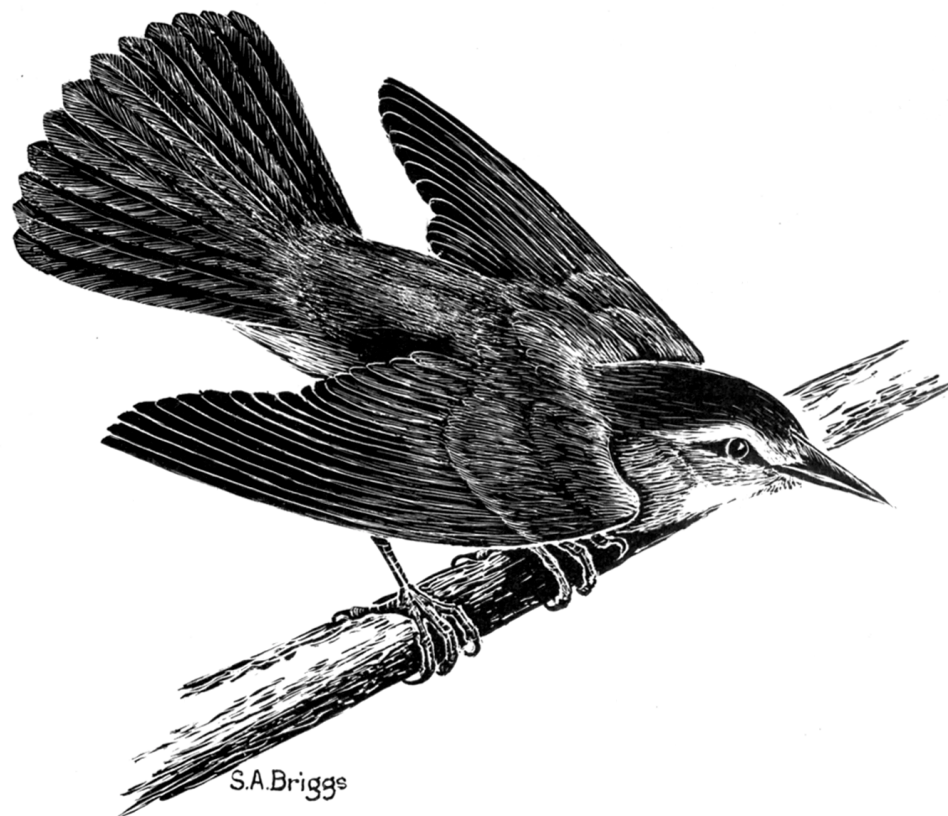


Figure 1. Swainson's Warbler male in territorial defense posture, as depicted by S. A. Briggs (in Meanley 1971).

insectivorous bird lacking the bright coloration and striking sex- and age-specific dimorphism often seen in members of this family. Dorsal plumage is mostly reddish- to grayish-brown, and ventral plumage an unstreaked white to yellowish-white. The bill is relatively large for a wood warbler, with a sharp point and thick base (Meanley 1971, Brown and Dickson 1994, Gough et al. 1998).

The species's breeding range is restricted to the southeastern United States. Most breeding populations occur in the Atlantic and Gulf Coastal Plain from southern Virginia west to Texas and Oklahoma. However, Swainson's Warblers also breed in portions of the southern Piedmont and Cumberland Plateau extending north to Illinois and Missouri, in sporadic Coastal Plain populations in Maryland and Delaware, and at low elevations in the southern Appalachian Range as far north as West Virginia. The species's wintering range comprises the Bahamas, several Caribbean islands, and portions of Mexico, Guatemala, and Belize (Meanley 1971, Brown and Dickson 1994, Rappole et al. 1995, Sauer et al. 2001).

Swainson's Warbler population status and trends are poorly known (Brown and Dickson 1994). Relative abundance of Swainson's Warblers on Breeding Bird Survey (BBS) routes within the species's breeding range (Eastern and Central BBS regions) for 1966-2000 was only 0.12-0.13 individuals per route ($N = 108$ routes). Analysis of BBS data shows no significant trend (at $\alpha = 0.05$) in Swainson's Warbler populations survey-wide during this period (trend +2.9%; $p = 0.07$; $N = 108$ routes; 95% confidence interval = -0.2-6.0%; relative abundance = 0.12 individuals/route). BBS results for Swainson's Warblers in individual states, BBS regions, and physiographic strata within the species's breeding range, as well as survey-wide, are so imprecise that a change in abundance in the range of 3-5% per year could not be detected over the long-term (Sauer et al. 2001). Thus, there is no reliable quantitative evidence as to whether Swainson's Warbler breeding populations are increasing, declining, or stable.

Anecdotal evidence, however, suggests that Swainson's Warbler breeding populations may be declining as the result of extensive human alteration of bottomland hardwood forests in alluvial floodplains of the southeastern U.S., the species's principal breeding habitat (Meanley 1971, Brown and Dickson 1994, Pashley et al. 2000). Due to threats on both the breeding and wintering grounds, the Swainson's Warbler is ranked as an extremely high priority species for conservation attention under the Partners in Flight avian species prioritization scheme (Pashley et al. 2000). In the Mid-Atlantic and lower Midwest, near the limits of its range, this species is among the top three Nearctic-Neotropical migrant species in terms of management priority; in the Gulf Coastal Plain and Mississippi Alluvial Valley, it has been listed among the top five species of concern for bottomland forest habitats (Brown and Dickson 1994). Additional information about Swainson's Warbler population status and trends, as well as reproductive success, population demography, and habitat preferences, is needed for conservation and management (Brown and Dickson 1994, Hamel et al. 1996, Pashley et al. 2000).

BIRD SURVEY METHODS

Existing broad-scale avian monitoring programs such as the BBS, which uses a road-based sampling methodology, do not sample all species, habitats, and geographic regions equally well (Bystrak 1981, Sauer et al. 2001). BBS methods may not adequately sample species, such as the Swainson's Warbler, that are uncommon or elusive, that have restricted ranges or patchy (uneven) distributions, or that breed in habitats not well represented along road networks (e.g., forest interior species, wetland species) (Bystrak 1981, Robbins et al. 1986, Keller and Scallan 1999). Riparian species may be oversampled on BBS routes in high-elevation areas in the western United States yet undersampled on routes in the eastern lowlands, due to differences in the typical orientation of roads with respect to floodplain topography (Droege 1990). To estimate

population trends reliably, special survey methods may be needed for individual species, species groups, habitat types, or geographic areas (Robbins et al. 1986, Hamel et al. 1996, Bibby et al. 2000, Sauer et al. 2001). Given the low number of BBS detections of Swainson's Warblers (Sauer et al. 2001), it appears that development of a specialized survey methodology may be useful in conservation efforts for this species.

Many different methods are available to inventory and monitor avian populations (Ralph and Scott 1981, Ralph et al. 1993, Bibby et al. 2000). The utility of a given method depends on several factors, including the life history and habitat preferences of the species in question, the specific objectives of the study, and the availability of personnel and funding (Ralph et al. 1993, Hamel et al. 1996, Bibby et al. 2000). Differences in detectability among species and habitats, as well as weather conditions and observer abilities, can influence survey results substantially by controlling the size of the area effectively sampled (Dawson 1981). As a result, absolute population density (versus relative abundance) cannot be estimated reliably using standard line transect and point count survey methods unless some adjustment is made to account for differences in detectability (Emlen 1971, Jarvinen and Vaisanen 1975, Emlen 1977, Dawson 1981, Buckland et al. 2001, Rosenstock et al. 2002).

The time-intensive method of territory mapping (e.g., spot-mapping, Breeding Bird Census), involving as many as 10-12 visits to a fixed census plot throughout the breeding season, typically has been used to estimate avian density (International Bird Census Committee 1970, Ralph et al. 1993, Bibby et al. 2000). However, a relatively new method known as distance sampling (Buckland et al. 1993, Buckland et al. 2001), which builds on previous efforts to incorporate measures of detectability in bird and other wildlife surveys (e.g., Emlen 1971, Jarvinen and Vaisanen 1975, Emlen 1977), permits estimation of density using a modified version of point count or line transect survey methods. The distances at which individuals are detected are measured and

used to calculate a “detection function” that accounts for individuals present but not detected in the study area; the density estimate then is adjusted accordingly (Buckland et al. 1993, Buckland et al. 2001). Public domain software is available to carry out these calculations (Thomas et al. 1998).

SOUTHEASTERN FLOODPLAIN FORESTS

Floodplain habitats, such as bottomland hardwood forests in the southeastern United States, are characterized by extraordinarily high ecological productivity and biological diversity resulting from periodic natural disturbance by flooding (Wharton et al. 1982, Keddy 2000, Brawn et al. 2001). Flood-borne sediments transport nutrients into the terrestrial portion of the system, making soils remarkably fertile (Wharton et al. 1982, Keddy 2000, Reice 2001). Southeastern U.S. floodplains exhibit especially high productivity as a result of climatic conditions, which provide a long growing season (Pashley and Barrow 1993). Dynamic disturbance associated with flooding also continually alters topography, resulting in heterogeneity of habitats – i.e., “patchiness” – that promotes floral and faunal diversity by accommodating species with varying life history requirements (Pashley and Barrow 1993, Brawn et al. 2001, Reice 2001).

Largely due to their high productivity, floodplain forests have been subject to intensive human use and large-scale alteration. Bottomland hardwood forests in the southeastern U.S. have been destroyed or degraded as the result of conversion to agriculture and timber production, as well as alteration of natural hydrologic disturbance regimes due to construction of flood control and water supply projects (Noss et al. 1995, Askins 2000, Pashley et al. 2000, Sallabanks et al. 2000). It is difficult to determine the exact amount of bottomland hardwood forest habitat lost to anthropogenic disturbance; one estimate indicates that the 12 million ha of bottomland forest remaining today in the

southeastern U.S. may be less than 50% of what was present at the time of European settlement (Hodges 1994). Others cite losses as great as 70% (Askins 2000).

Southeastern U.S. floodplains provide critical habitat for many species of birds, as well as other wildlife (Hunter et al. 1993, Forsythe and Roelle 1990, Pashley et al. 2000, Sallabanks et al. 2000, Reice 2001). Bird species in addition to the Swainson's Warbler that breed in bottomland hardwood forests and have been identified as conservation priorities include: Prothonotary Warbler (*Protonaria citrea*), Hooded Warbler (*Wilsonia citrina*), Acadian Flycatcher (*Empidonax virescens*), and Yellow-Billed Cuckoo (*Coccyzus americanus*). Bottomland hardwood forests also serve as important migration corridors and stopover sites for large numbers of migratory birds that breed elsewhere (Meanley 1971, Hunter et al. 1993, Pashley et al. 2000, Sallabanks et al. 2000). Because of their importance for both breeding and migration, and the extent to which they have been altered and degraded by human activities, bottomland hardwood forests are considered "habitats of special concern" for Nearctic-Neotropical migrants in the southeastern U.S. (Hunter et al. 1993). Askins (2000) notes that a disproportionate number of the North American bird species known or believed to be extinct were bottomland hardwood forest specialists during the breeding and/or wintering seasons (Carolina Parakeet, *Conuropsis carolinensis*; Ivory-billed Woodpecker, *Campephilus principalis*; Bachman's Warbler, *Vermivora bachmanii*), or used these areas intensively during migration (Passenger Pigeon, *Ectopistes migratorius*).

In Georgia, it appears that private land management activities that adversely affect bottomland forest ecosystems have increased over the past few years, following several decades of relative stability. These include conversion of bottomlands to pine plantations, and timber harvests involving the practice of "high-grading" in which only the largest and most valuable trees are removed (N. Klaus, Georgia Department of Natural Resources, personal communication). Recent drought conditions, along with human

population growth, may result in further degradation of floodplain forests in this region as new dams and reservoirs are built to meet demand for water (U.S. Geological Survey 2000).

Canebrake habitats, a once-prominent feature of floodplain forests in the southeastern U.S., may be preferred by breeding Swainson's Warblers in some portions of the species's range, although localized habitat preferences appear to vary and other shrub-level vegetation is used in areas that lack large canebrakes (Meanley 1945, Meanley 1971, Meanley 1972, Brown and Dickson 1994, Graves 2001, Graves 2002). These dense, nearly monotypic stands of *Arundinaria gigantea*, a native bamboo (family *Poaceae*) commonly known as cane, covered vast areas of the southeastern U.S. at the time of European settlement (Platt and Brantley 1997). Little is known about canebrake ecology, in part because expansive cane stands largely were eliminated prior to the 20th century, disappearing more quickly than any other bottomland habitat type (Platt and Brantley 1997, Brantley and Platt 2001). Bachman's Warbler may have been a canebrake specialist (Remsen 1986), and many other wildlife species use canebrakes extensively or exclusively, including the Hooded Warbler, Swamp Rabbit (*Sylvilagus aquaticus*), and at least six species of *Lepidoptera* – five of which are listed as species of conservation concern due to habitat alteration (Meanley 1972, Miller and Miller 1999, Brantley and Platt 2001).

Limited research indicates that intermediate levels of disturbance – e.g., dynamic effects of flooding and windstorms (scouring, treefalls), infrequent lightning-caused fires that constrained growth of competing woody vegetation, and death of overstory foliage caused by huge roosting flocks of the now-extinct Passenger Pigeon – may have contributed historically to the development and maintenance of cane stands (Platt and Brantley 1997, Brantley and Platt 2001). Native American agricultural practices such as controlled burning likely expanded canebrakes (Platt and Brantley 1997, Brantley and

Platt 2001). However, greater anthropogenic disturbance resulting from overgrazing and clearing of bottomlands for agriculture by European settlers, coupled with suppression of natural disturbances such as fire and flooding, has resulted in destruction or degradation of most canebrake communities (Platt and Brantley 1997, Brantley and Platt 2001). It is estimated that less than 2% of the canebrakes present at the time of European settlement remain; as a result, they are considered a “critically endangered ecosystem” (Noss et al. 1995).

Although the “endless wilderness of canes” described by William Bartram and others has been virtually extirpated (Platt and Brantley 1997), cane occurring as isolated plants or small thickets remains common in many areas of the southeastern U.S. (Miller and Miller 1999, Brantley and Platt 2001). Cane grows primarily in bottomland forest ecosystems which are subject to seasonal flooding, yet colonies may be killed by prolonged inundation. Large canebrakes therefore tend to occur at relatively high elevations within the floodplain, such as the natural levee (front) immediately adjacent to the river channel (Hodges 1994, Platt and Brantley 1997). In limited experimental studies, fertilization promoted growth and expansion of cane (Platt and Brantley 1997), perhaps indicating a relationship with the high soil fertility typical of floodplain forests (Wharton et al. 1982, Keddy 2000, Platt and Brantley 2001, Reice 2001).

PREVIOUS HABITAT STUDIES

Until recently, there were few detailed quantitative studies of Swainson’s Warbler breeding habitat preferences, although Meanley (1945, 1966, 1971) and others published substantial descriptive information. Due to conservation concern for this species, habitat studies since have been conducted at several sites near the edge of its breeding range in Illinois (Eddleman et al. 1980), Missouri (Thomas et al. 1996), and Virginia (Graves 2001), and in forests managed for commercial silviculture in South

Carolina (Peters 1999) and Louisiana (Bassett 2001). Results from these studies may not reflect characteristics of breeding habitat in the species's core breeding range (Graves 2002), or in areas managed primarily for conservation purposes. A new study, however, assesses habitat characteristics at five locations within the core breeding range in Arkansas, Mississippi, Louisiana, and Florida (Graves 2002).

Swainson's Warblers build nests in the understory (Meanley 1971, Brown and Dickson 1994). Virtually all recent habitat studies indicate that dense shrub-layer vegetation is critical in breeding territories, where it is typically denser than in areas unoccupied by Swainson's Warblers (Thomas et al. 1996, Peters 1999, Bassett 2001, Graves 2001, Graves 2002). Overly dense understory vegetation, however, may be a negative factor (Graves 2001). There has been conflicting evidence about the relative importance of understory structure versus species composition (Graves 2002). The presence of cane, once thought to be requisite in prime breeding habitat, appears to be associated with territories in some locations, but not in others (Meanley 1971, Eddleman et al. 1980, Thomas et al. 1996, Peters 1999, Graves 2001, Graves 2002). Specific habitat preferences may vary geographically (Graves 2002), and according to what shrub-level species are present.

Characteristics of ground-level habitat may be important in breeding territories because Swainson's Warblers forage for insects and other small arthropods almost exclusively in leaf litter (Meanley 1971, Graves 1998). Results of previous studies regarding leaf litter depth and coverage have been contradictory, showing no consistent relationship between Swainson's Warbler presence and litter layer characteristics (Thomas et al. 1996, Peters 1999, Bassett 2001). This may be because Swainson's Warblers tend to nest and forage in different areas of their territories (Graves 2001), and litter measurements thus may not have been taken in foraging areas. Graves reported that the presence of moist organic soils covered with abundant leaf litter was

characteristic of territories at the Virginia site, and that litter depth and coverage may be crucial for territories in general (Graves 1998; Graves 2001). Soil types also may influence Swainson's Warbler breeding distribution (Peters 1999; G. R. Graves, Smithsonian Institution, personal communication).

Dense herbaceous ground cover may affect Swainson's Warbler habitat use by potentially inhibiting foraging; Meanley (1971) found little herbaceous ground cover in breeding territories. In Louisiana and in one year of the Missouri study, areas occupied by Swainson's Warblers had less herbaceous ground cover than did unoccupied areas (Thomas et al. 1996, Bassett 2001). In the Illinois study area, which had overall herbaceous plant cover of 34%, there was virtually no herbaceous vegetation at locations where individuals were observed foraging (Eddleman et al. 1980).

Graves (2001) identified hydrology as the "driving force" in determining the placement of Swainson's Warbler territories at the Virginia site: standing or pooled water was recorded in 61% of unoccupied plots, but not in any territories. Inundation during the breeding season may inhibit foraging, and deep flooding may destroy nests (Meanley 1971). Hydroperiod along with flood dynamics may affect species composition and density of vegetation (Wharton et al. 1982), as well as litter depth and coverage (personal observation). Conversely, nutrient transport and dynamic effects of flooding may exert positive influences on development and maintenance of appropriate Swainson's Warbler breeding habitat, depending on flood timing and intensity (Wharton et al. 1982, Keddy 2000, Brawn et al. 2001). Peters (1999) recommended landscape-scale investigations of the role of flooding and other hydrologic factors in influencing breeding distribution of Swainson's Warblers.

The importance of canopy height and canopy cover in Swainson's Warbler breeding territories is unclear. Thomas et al. (1996) found lower canopy and sub-canopy heights in areas occupied by Swainson's Warblers versus unoccupied areas.

Peters (1999) found lower canopy and midstory height at nest sites than in unoccupied areas, but no difference in canopy height between overall territories and unoccupied areas. Graves (in press) asserted that canopy height may not be very important in determining suitable breeding habitat if understory requirements are met. Several studies have found mean canopy cover (overstory trees only) of approximately 80% to 90% in areas occupied by Swainson's Warblers, but this parameter did not differ between occupied and unoccupied areas (Eddleman et al. 1980, Thomas et al. 1996).

Swainson's Warblers once were thought to breed almost exclusively in late successional forest (Meanley 1971, Graves 2002). More recently, however, breeding populations have been discovered and studied in habitats at relatively early successional stages, such as pine plantations and managed hardwood stands <40 years old (Carrie 1996, Peters 1999, Bassett 2001). It appears that disturbance gaps in the forest canopy may be important in late successional habitats to promote the dense shrub-level vegetation used for nesting (Eddleman et al. 1980, Hunter et al. 2001, Graves 2002). There is debate over whether such gaps should be created artificially through silvicultural practices to benefit Swainson's Warblers, or will occur sufficiently through natural processes (Eddleman et al. 1980, Bushman and Therres 1988, Soule et al. 1992, Hunter et al. 2001, Graves 2002). Evidence regarding the effectiveness of artificial gap creation in stimulating understory vegetation in bottomland forests appears to be limited and inconclusive (Soule et al. 1992, Moorman and Guynn 2001). Whether artificial gaps may produce adverse effects similar to those observed in conjunction with forest fragmentation – e.g., increased nest predation or brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) – also is unclear and likely depends on the size of openings created (Brawn et al. 2001, Moorman and Guynn 2001). Potential fragmentation effects may be of special concern for Swainson's Warblers because they

are considered an area-sensitive species requiring relatively large blocks of contiguous forest habitat (Robbins et al. 1989, Kilgo et al. 1998, Graves 2002).

Two previous studies included the development of binary logistic regression models intended to identify important characteristics of Swainson's Warbler breeding habitat, and to predict the presence (or absence) of breeding territories based on these characteristics. In the Missouri study (Thomas et al. 1996), involving habitat data from canebrakes in six different river floodplains, a three-variable model derived from 1992 data correctly classified 71% of the plots in the modeling dataset ($N = 59$ plots, 29 occupied and 30 unoccupied) as occupied or unoccupied by Swainson's Warblers. This model, however, had only 35% classification accuracy in verification with a new dataset collected in 1993. The authors then created a five-variable model based on pooled data for the two years ($N = 90$ plots, 45 occupied and 45 unoccupied), which correctly classified 73% of the plots in the modeling data set. In this model, cane density, overstory % canopy cover, and overstory tree diameter at breast height (dbh) were positively correlated with Swainson's Warbler presence, while overstory tree height and plot distance to water were negatively correlated with Swainson's Warbler presence. In the Virginia study, Graves (2001) created a more successful five-variable model that correctly classified 90% of the plots in the modeling dataset ($N = 74$ plots, 30 occupied and 44 unoccupied). *Smilax* stem density was positively correlated with Swainson's Warbler presence, while cane stem density, total number of trees, number of medium-sized trees (25-39.9 cm diameter), and basal area of swamp black gum (*Nyssa sylvatica* var. *biflora*) were negatively correlated with Swainson's Warbler presence. Nine more parsimonious models created for this site, comprising two to three of the five variables listed above, had classification accuracies of 81-87% for the modeling dataset. Apparently, neither the Missouri habitat model based on the two-year pooled data nor any of the Virginia models was subjected to verification or cross-validation.

STUDY AREA

My research was conducted at Bond Swamp National Wildlife Refuge (BSNWR; 32°44' N, 83°35' W), established in 1989 and administered by the U.S. Fish and Wildlife Service (USFWS). BSNWR comprises 2,630 ha of forested floodplain wetlands and adjacent uplands in Bibb and Twiggs counties, Georgia, approximately 10 km south of Macon (Figs. 2 and 3). The refuge is managed primarily to preserve, protect, and enhance local floodplain ecosystems associated with the Ocmulgee River, a tributary of the Altamaha River. Most of BSNWR typically is inundated by seasonal floodwaters in late winter through spring, although some swamp forest areas remain inundated year-round. Specific habitat types include floodplain forest, tupelo gum (*Nyssa aquatica*) swamp, and mixed pine/hardwood ridges, along with beaver swamps, oxbow lakes, and tributary creeks (USFWS 2000).

Approximately 200 bird species are believed to use the refuge as breeding, migration, or wintering habitat, although wildlife populations have not been well documented. BSNWR provides habitat for one of Georgia's three populations of black bears (*Ursus americanus*), and several endangered fish species are found in this portion of the Ocmulgee River. Non-native feral hogs pose one of the most significant threats to the health of refuge ecosystems (USFWS 2000).

BSNWR is located in the upper portion of the Coastal Plain physiographic province, just below the Fall Line separating the Coastal Plain from the Piedmont. In the vicinity of the refuge, known as the Fall Line Hills District, older crystalline rocks characteristic of the Piedmont give way to the relatively young Cretaceous sediments of the Coastal Plain (Clark and Zisa 1976). Topography is level to rolling. The Ocmulgee River and its tributaries in this area exhibit relatively wide floodplains and frequent meanders (Clark and Zisa 1976).

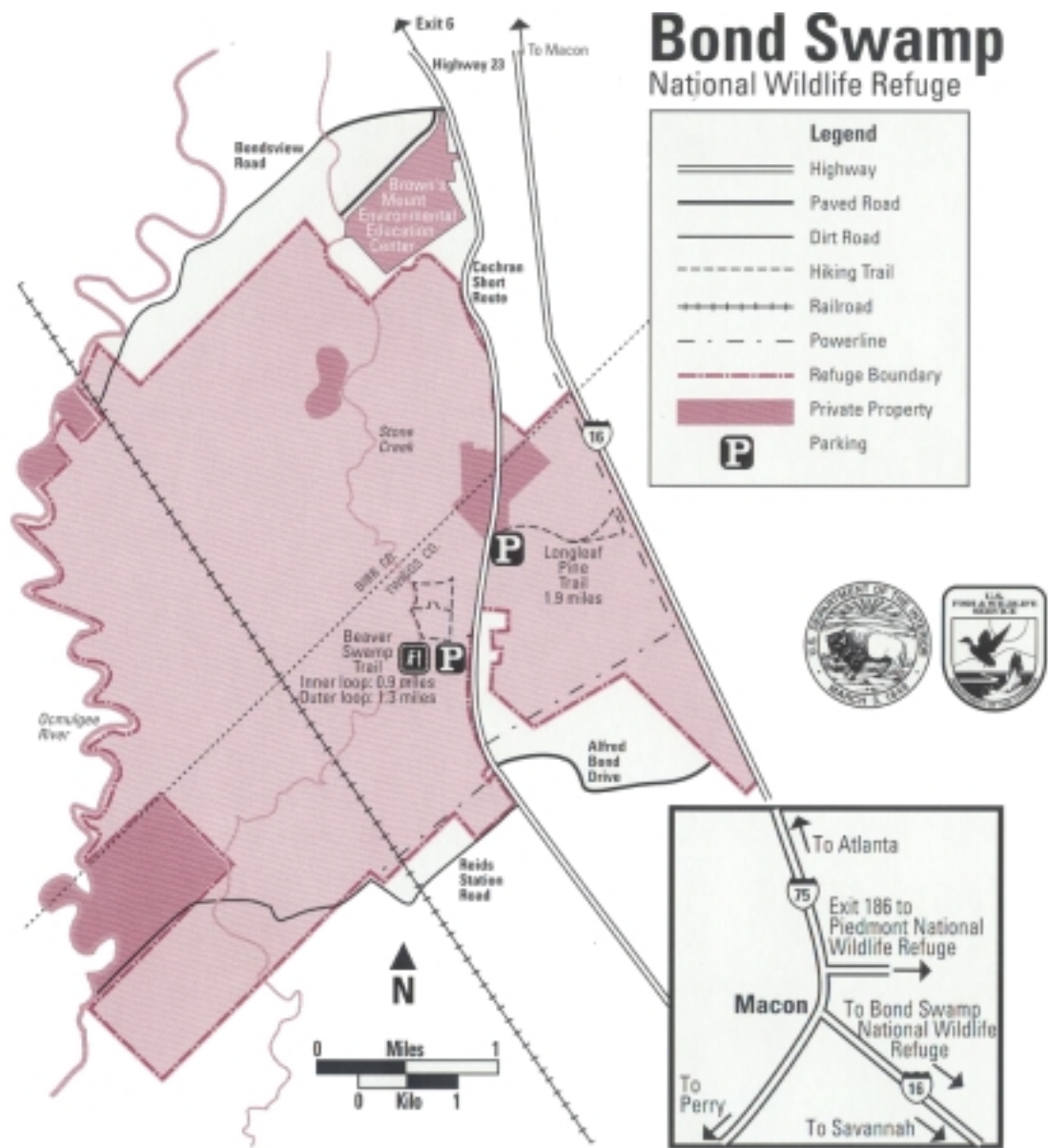


Figure 2. U.S. Fish and Wildlife Service map of Bond Swamp National Wildlife Refuge, Georgia.

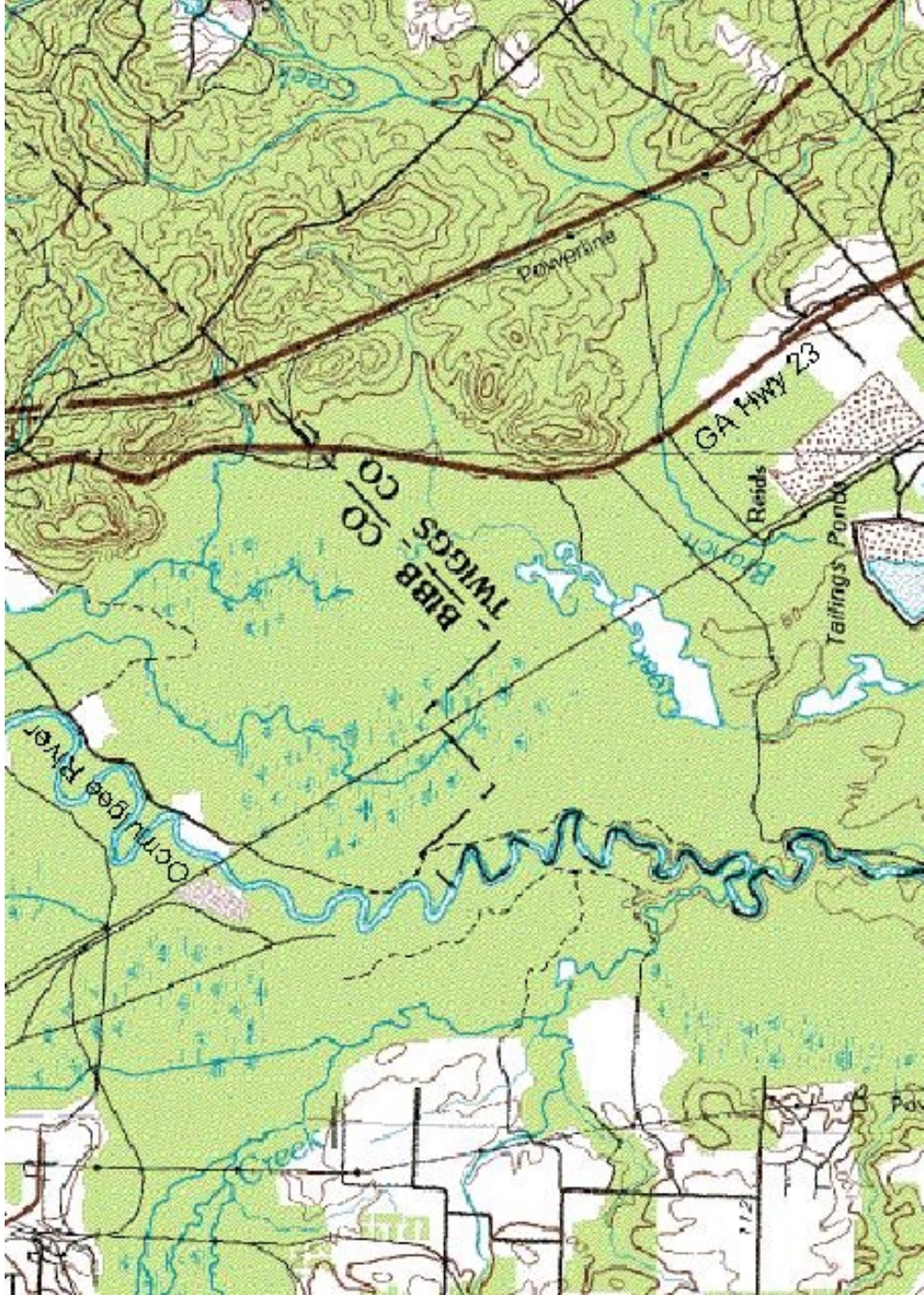


Figure 3. Topographic map of Bond Swamp National Wildlife Refuge and vicinity, Georgia, adapted from U.S. Geological Survey Macon East quadrangle 1:24,000 scale topographic map (1981).

Climate in the vicinity is warm and humid. Mean annual high temperature at Macon is 24 C, and mean midsummer high temperature is 32 C. Winters are relatively short, and the growing season is long. Relative humidity averages 88% during the morning and 54% during the afternoon. Mean annual precipitation totals 122 cm (National Climate Data Center 2001).

Most of BSNWR is located along the east bank of the Ocmulgee River, although USFWS recently acquired a small parcel west of the river. Only one paved road crosses the refuge (Georgia Highway 23, near the eastern edge of the property), but there is a network of dirt and gravel roads, as well as railroad tracks and transmission line rights-of-way. Most roads other than the state highway have little traffic or are abandoned. Two hiking trails cover small areas of the refuge, and hunting and fishing are permitted seasonally in designated areas. Public use is relatively limited, however, and a special-use permit is required for access to some areas. Few details are known about prior land-use history. There is evidence of clear-cutting or selective timber harvesting in most portions of the refuge, and high-grading practices may have been employed (N. Klaus, Georgia Department of Natural Resources, personal communication). Old-growth forest (trees >120 years old, diameter at breast height ≥ 2 m) remains in some areas (J. M. Meyers, USGS Patuxent Wildlife Research Center, personal communication).

My study area encompassed approximately 1,740 ha of floodplain forest within the main portion of BSNWR, bounded on the west by the Ocmulgee River and on the east by Georgia Highway 23. This area included all bottomland hardwood forest habitats in the main portion of the refuge, but excluded bottomlands west of the river and pine-dominated uplands east of Highway 23. Dominant tree species in the study area were water oak (*Quercus nigra*), swamp chestnut oak (*Quercus michauxii*), laurel

oak (*Quercus laurifolia*), overcup oak (*Quercus lyrata*), sweetgum (*Liquidambar styraciflua*), tupelo gum (*Nyssa aquatica*), sugarberry (*Celtis laevigata*), red maple (*Acer rubrum*), ash (*Fraxinus* sp.), American elm (*Ulmus americana*), and sycamore (*Platanus occidentalis*), along with loblolly pine (*Pinus taeda*) in some areas. Approximate forest age ranged from 30 to >120 years (J. M. Meyers, personal communication). Mean (minimum-maximum) dbh measurements for large specimens of the dominant tree species, based on the dbh of the largest diameter tree in each of 174 0.25-ha vegetation plots, were 60.4 cm (36.0-121.0 cm) for water oak ($n = 28$ trees/plots), 64.7 cm (54.4-94.0 cm) for swamp chestnut oak ($n = 10$), 70.4 cm (44.8-123.6 cm) for laurel oak ($n = 20$), 76.8 cm (46.7-171.0 cm) for overcup oak ($n = 11$), 56.2 cm (38.2-74.0 cm) for sweetgum ($n = 20$), 81.1 cm (52.0-125.0 cm) for tupelo gum ($n = 13$), 66.2 cm (46.0-89.1 cm) for sugarberry ($n = 13$), 58.2 cm (44.9-86.3 cm) for red maple ($n = 9$), 58.6 cm (40.2-93.2 cm) for ash species ($n = 11$), and 49.8 cm (40.4-60.0 cm) for loblolly pine ($n = 8$) (E. A. Wright and J. M. Meyers, unpublished data).

Cane (*Arundinaria gigantea*) was a prominent feature of the understory, particularly on the natural levee immediately adjacent to the river. Vines were relatively abundant, including poison ivy (*Toxicodendron radicans*), greenbriar (*Smilax* sp.) and grape (*Vitis* sp.). Sawtooth palmetto (*Serenoa repens*), dwarf palmetto (*Sabal minor*), and semi-aquatic and aquatic forbs (e.g., *Saururus cernuus*, *Boehmeria cylindrica*, *Peltandra virginica*, *Sagittaria* sp.) and grasses occurred in less well-drained areas, while blackberry (*Rubus* sp.) dominated large sunny openings in drier areas. Invasive exotic understory species such as Chinese privet (*Ligustrum sinense*), Japanese stilt grass (*Microstegium vimineum*), climbing fern (*Lygodium* sp.) and Chinese tallow tree (*Triadica sebifera*) were present in limited areas.

Meanley (1945, 1971) conducted some of his most extensive investigations of Swainson's Warbler natural history along the upper Ocmulgee River in the vicinity of

BSNWR, and described canebrakes in this area as “the ideal habitat for the breeding of the Swainson’s Warbler.” To my knowledge, no intensive studies of Swainson’s Warbler population status or habitat use in the Ocmulgee River floodplain have been conducted since Meanley’s work from the 1940s through early 1970s.

RESEARCH OBJECTIVES

The specific objectives of my research were to: 1) estimate breeding population density of Swainson’s Warblers at BSNWR; and 2) develop a habitat model that would be sufficiently parsimonious for practical use (i.e., comprising few variables), yet highly accurate in identifying suitable Swainson’s Warbler breeding habitat at my study site and perhaps other locations. More generally, I sought to expand knowledge of a little studied species in need of conservation attention, provide useful management information, and lay the groundwork for future research.

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Chapter 2

ESTIMATING DENSITY OF A SWAINSON'S WARBLER BREEDING POPULATION WITH DISTANCE SAMPLING¹

¹Wright, E. A. and J. M. Meyers. To be submitted to Journal of Field Ornithology.

ABSTRACT

We used distance sampling methods to estimate breeding population density of Swainson's Warblers (*Limnothlypis swainsonii*), an inadequately monitored Nearctic-Neotropical migrant songbird species of high conservation concern, in 2001 at a 1,740-ha floodplain forest site within Bond Swamp National Wildlife Refuge, Georgia. We detected 27 Swainson's Warblers along 21 random transects with total length of 18.36 km. Mean density of Swainson's Warbler breeding territories (singing males) in our study area was 9.4/km², and mean abundance was 163 singing males. Our distance sampling results had high variances (CV = 0.298) due primarily to low encounter rate, but appear reasonable based on our knowledge of the population at this site derived from mapping of Swainson's Warbler locations, tape playback surveys, and other methods we used in 2 yr of a related habitat study. Distance sampling may not be very effective for monitoring Swainson's Warbler populations in general, because we were unable to obtain density and abundance estimates with low variances even at a site with a relatively large population at apparently high density. Further research is needed to determine the best methods for assessing population status and trends in rare to uncommon species such as the Swainson's Warbler.

Key words: Swainson's Warbler, *Limnothlypis swainsonii*, distance sampling, Bond Swamp, breeding population density, Nearctic-Neotropical migrant, bird survey methods.

INTRODUCTION

Existing broad-scale avian monitoring programs such as the annual Breeding Bird Survey (BBS), which uses road-based sampling, do not sample all species, habitats, and geographic regions equally well (Bystrak 1981, Sauer et al. 2001). BBS methods may not adequately sample species that are uncommon or elusive, that have restricted breeding ranges or patchy (uneven) distributions, or that breed in habitats not well represented along roads (e.g., forest interior species, wetland species) (Bystrak 1981, Robbins et al. 1986, Keller and Scallan 1999). Riparian species may be undersampled on BBS routes in the eastern lowlands, due to the typical orientation of roads with respect to floodplain topography (Droege 1990).

The Swainson's Warbler (*Limnothlypis swainsonii*), a cryptically colored and relatively uncommon Nearctic-Neotropical migratory songbird that breeds predominantly in floodplain forests of the southeastern United States (Brown and Dickson 1994), is an example of a species inadequately monitored by BBS methods. Relative abundance of Swainson's Warblers on BBS routes within the species's breeding range (Eastern and Central BBS regions) for 1966-2000 was only 0.12-0.13 individuals per route. Analysis of BBS data shows no significant trend (at $\alpha = 0.05$) in Swainson's Warbler populations survey-wide during this period (trend +2.9%; $p = 0.07$; $N = 108$ routes; 95% confidence interval = -0.2-6.0%; relative abundance = 0.12 individuals/ route). Due to the species's low relative abundance, BBS results are so imprecise that a long-term population change of 3-5% per year would be undetectable (Sauer et al. 2001).

Anecdotal evidence suggests that Swainson's Warbler populations may be declining as the result of agricultural, forestry, and watershed management practices that have altered floodplains in the southeastern U.S. substantially (Brown and Dickson 1994, Askins 2000, Pashley et al. 2000). The Swainson's Warbler is considered an extremely high priority species for conservation attention under the Partners in Flight

species prioritization scheme (Pashley et al. 2000). Additional information about this species's population status and trends is required for conservation and management (Brown and Dickson 1994, Hamel et al. 1996, Pashley et al. 2000).

Line transect or point count surveys provide only an index to relative abundance – not an estimate of absolute density – unless variation in detectability occurring among species and habitats, or resulting from factors such as weather conditions and observer abilities, is taken into account (Emlen 1971, Jarvinen and Vaisanen 1975, Emlen 1977, Buckland et al. 1993, Bibby et al. 2000, Buckland et al. 2001). The time-intensive method of territory mapping (e.g., spot-mapping, Breeding Bird Census), which involves multiple visits to a fixed census plot throughout the breeding season, traditionally has been used to estimate avian density (International Bird Census Committee 1970, Bibby et al. 2000). However, a newer set of methods collectively known as distance sampling (Buckland et al. 1993, Buckland et al. 2001) permits estimation of density using modified point count or line transect survey techniques. The observer measures and records the distance from the point or transect to each individual bird detected. These distance data are used to derive a “detection function” that accounts for individuals present but not detected in the study area, and the density estimate is adjusted accordingly (Buckland et al. 1993, Buckland et al. 2001).

We used distance sampling methods to estimate density of Swainson's Warbler breeding territories within a floodplain forest located in central Georgia, U.S. To our knowledge, such methods have not been used previously for this species nor have they been used extensively for bird surveys in similar habitats. Other methods we used to locate and map Swainson's Warbler territories as part of a related habitat study provided information to assess the efficiency and effectiveness of our distance sampling survey.

STUDY AREA

We conducted our study within Bond Swamp National Wildlife Refuge (BSNWR; 32°44' N, 83°35' W), established in 1989 and administered by the U.S. Fish and Wildlife Service (USFWS). BSNWR comprises 2,630 ha of forested wetlands and adjacent uplands in Bibb and Twiggs counties, Georgia, approximately 10 km south of Macon. The refuge is managed primarily to preserve, protect, and enhance local floodplain ecosystems associated with the Ocmulgee River, a tributary of the Altamaha River. Most of the refuge typically is inundated by seasonal floodwaters in late winter through early spring, although some portions remain inundated year-round. Habitat types include bottomland hardwood forest, tupelo gum (*Nyssa aquatica*) swamp, and mixed pine/hardwood ridges, along with beaver swamps, oxbow lakes, and tributary creeks (USFWS 2000). Topography is level to rolling; the Ocmulgee River and its tributaries in this area exhibit relatively wide floodplains and frequent meanders (Clark and Zisa 1976). Climate is warm and humid. Mean annual high temperature at Macon is 24 C, and mean midsummer high temperature is 32 C. Relative humidity averages 88% during the morning and 54% during the afternoon, and mean annual precipitation totals 122 cm (National Climate Data Center 2001).

Our study area encompassed approximately 1,740 ha of bottomland hardwood forest bounded on the west by the Ocmulgee River and on the east by Georgia Highway 23, thus encompassing nearly all floodplain forest habitats within the refuge. Dominant tree species were water oak (*Quercus nigra*), swamp chestnut oak (*Quercus michauxii*), laurel oak (*Quercus laurifolia*), overcup oak (*Quercus lyrata*), sweetgum (*Liquidambar styraciflua*), tupelo gum (*Nyssa aquatica*), sugarberry (*Celtis laevigata*), red maple (*Acer rubrum*), ash (*Fraxinus* sp.), American elm (*Ulmus americana*), sycamore (*Platanus occidentalis*), and loblolly pine (*Pinus taeda*). Forest age ranged from approximately 30 to >120 years. Cane (*Arundinaria gigantea*) was a prominent feature of the understory,

particularly on the natural levee adjacent to the river; in other areas, sawtooth palmetto (*Serenoa repens*), dwarf palmetto (*Sabal minor*), blackberry (*Rubus* sp.), or aquatic and semi-aquatic forbs and grasses dominated the understory.

METHODS

We conducted surveys for Swainson's Warblers along 21 transects of unequal lengths, totaling 18.36 km, between 31 May and 20 June 2001 (non-continuous; surveys were suspended for approximately 1 wk due to flooding that prevented site access). Groups of transects were established systematically from random starting points in each portion of the study area, oriented to cross anticipated ecological gradients. The starting point for the first transect in each group was placed at a randomly selected distance of 175-200 m from the refuge boundary. Subsequent transects in the same area were parallel to the first transect, and were separated from adjacent transects by randomly selected distances of 350-400 m. The 21 transects thus covered most bottomland and wetland areas within the refuge to ± 200 m on each side of the transect. We marked the entire length of each transect with biodegradable cotton twine, recorded its compass bearing, and obtained Universal Transverse Mercator (UTM; NAD 83) coordinates for its start and end points using a Magellan XL2000 hand-held Global Positioning System (GPS) unit.

Each transect was surveyed by a single observer who walked its length starting at local sunrise and ending within 2 h. Upon detecting a Swainson's Warbler, we used a compass bearing relative to the transect bearing to move to a point on the transect perpendicular to the bird's location. We recorded UTM coordinates for that point, and measured the perpendicular distance (m) from the point to the bird. Laser rangefinders were used for distance measurements where possible, but understory vegetation was typically too dense. Most distances were measured by pacing to the bird's location;

paces subsequently were converted to meters based on each observer's measured pace length.

We used Distance 3.5 software (Thomas et al. 1998) to estimate density and abundance of singing (territorial) males at BSNWR from the transect survey data, following methods outlined in Buckland et al. (2001). We employed visual examination of histograms and chi-square goodness-of-fit tests as complementary techniques to determine whether our transect survey data should be grouped into distance intervals prior to modeling. Based on this exploratory analysis, we grouped our data into 30-m intervals (Fig. 4) to improve their fit to a generalized detection function curve, and to reduce the effect of minor measurement errors that may have occurred during data collection (Buckland et al. 2001). We ran six types of analytical models (varying combinations of key functions and series expansions) recommended by Buckland et al. (2001) as robust for analysis of line transect survey data: uniform + cosine, uniform + simple polynomial, half-normal + cosine, half-normal + hermite polynomial, hazard-rate + cosine, and hazard-rate + simple polynomial. Akaike's Information Criterion (AIC) scores were used to select the best model (lowest AIC) for density estimation.

We also located Swainson's Warbler territories at BSNWR by four other methods during the 2001 breeding season, as part of a related habitat study: intensive searches, opportunistic detections during site reconnaissance and transect layout, tape playback surveys, and single-visit territory mapping. For individuals located by the first two methods, we recorded UTM coordinates of the location from which the observer first detected the bird, the distance (meters) and compass bearing from that point to the bird, and the detection method (aural or visual).

Tape playback surveys were conducted along the same transects used for the distance sampling surveys, on the same morning and immediately following completion of each distance sampling survey. We played pre-recorded Swainson's Warbler songs

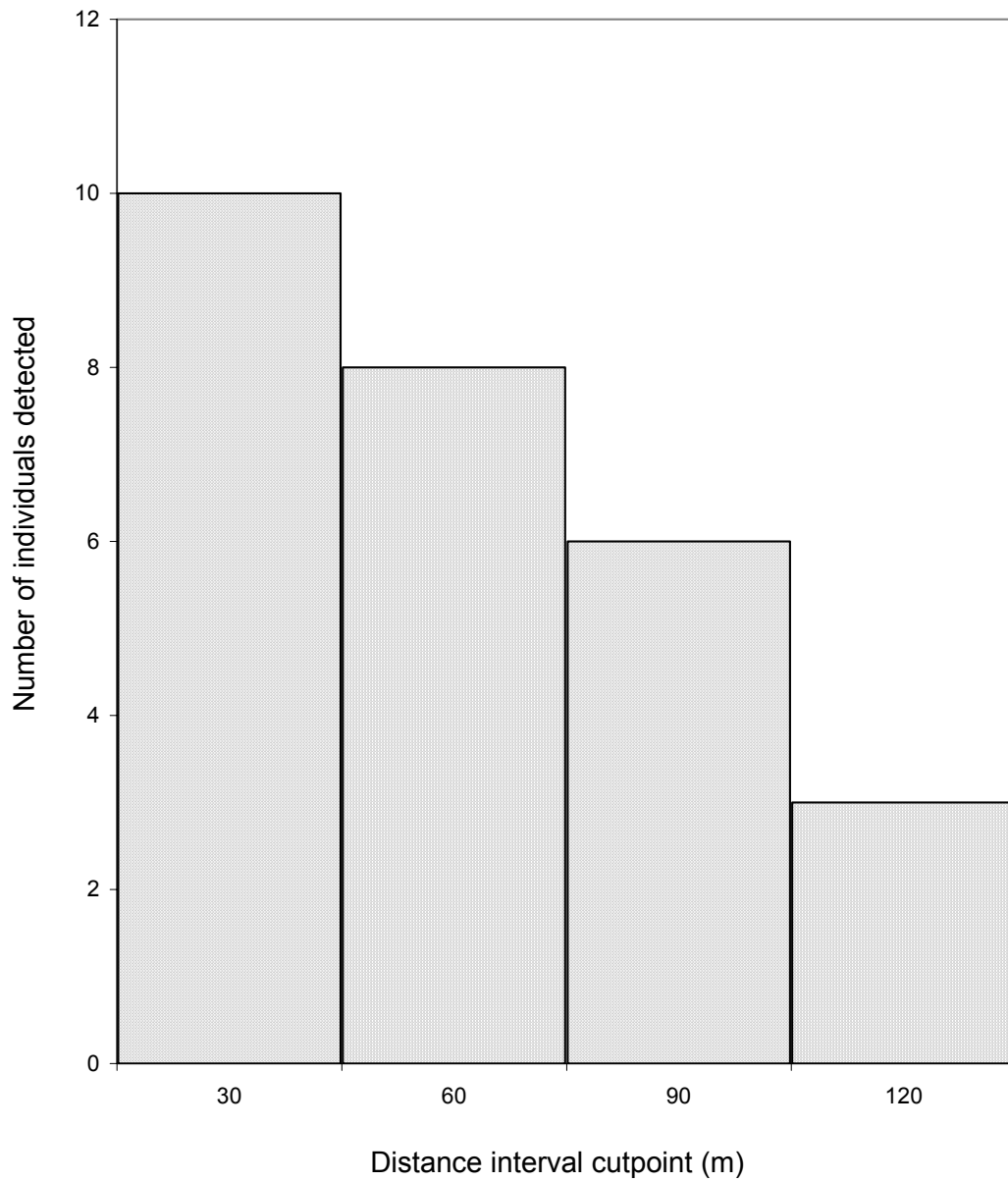


Figure 4. Swainson's Warbler detections in transect surveys at Bond Swamp National Wildlife Refuge, Georgia, 31 May-20 June 2001; detection distances grouped into 30-m intervals (cutpoint is interval upper bound).

and calls every 250-300 m while walking back from the transect's end point to its start point. At each playback location, we broadcast 2-3 song phrases followed by chip notes for 20-30 s on portable cassette recorders with amplified 5-cm speakers (Radio Shack model AMX9, output 2 w) set to a volume approximating normal vocalizations. We recorded the UTM coordinates of each playback location, the approximate distance and compass bearing from that location to each Swainson's Warbler detected within 3 min after the tape broadcast, and the detection method. We did not derive a density estimate from the playback data because exploratory modeling efforts indicated that movement toward the observer would have altered the detection function and produced an unrealistically high density estimate, as suggested by Buckland et al. (1993). However, we used Distance 3.5 to determine encounter rate and effective strip width surveyed with playback.

Territory mapping occurred from early May through mid-June. We followed singing males as they moved through their territories, maintaining a distance of at least 10 m between the observer and the bird, and used GPS units to record UTM coordinates for each location at which the individual bird was observed. Each individual was followed for at least 1-2 h, or for a longer period if necessary to obtain a minimum of 10 locations. Most territories were mapped in a single visit, but we made repeated visits over several days or weeks in a few instances to obtain a sufficient number of locations. We produced a map of each territory using Microsoft Excel 97 software (Microsoft Corporation 1996) to create a scatterplot of the UTM East and North coordinates for each location at which the individual was observed.

RESULTS

We detected 27 Swainson's Warblers, all of which were singing males, in our distance sampling transect surveys. The encounter rate (rate at which individuals were

detected per unit transect length) was 1.47 singing males/km ($CV = 0.238$; $df = 20$). The greatest distance at which an individual was detected was 120 m. Probability of detection for an individual within the area bounded by this maximum detection distance was 0.65 ($CV = 0.179$; $df = 26$), and effective strip width surveyed on each side of transects (maximum detection distance x probability of detection) was 78.5 m ($CV = 0.179$; $df = 26$). Two models had identical AIC scores that were the lowest among all our models: half-normal + cosine and half-normal + hermite polynomial (both with AIC = 72.601). These models produced identical density estimates of 9.4 singing males (territories)/km² (95% confidence interval = 5.2-16.9 singing males (territories)/km²; $CV = 0.298$; $df = 39$). Estimated number of Swainson's Warbler territories (i.e., abundance of singing males) in our study area was 163 (95% confidence interval = 90-294; $CV = 0.298$; $df = 39$).

In tape playback surveys, we detected 43 Swainson's Warblers within the study area boundaries, 10 of which responded only with chip notes; we thus could not determine whether these 10 individuals were territorial males. Overall encounter rate (singing males plus chipping birds of unknown sex) in the playback surveys was 2.3 individuals/km ($CV = 0.18$; $df = 20$). Effective strip width surveyed was 30.9 m ($CV = 0.117$; $df = 41$).

We mapped 56 individual Swainson's Warbler territories using a mean of 19.2 locations ($SE = 0.91$) per territory. The total number of individuals we detected through intensive searches and opportunistic detections (excluding detections we determined were duplicate observations of a previously detected individual) was 86, of which 84 were singing males.

DISCUSSION

The number of Swainson's Warblers detected in our transect surveys was below the minimum standards for density estimation using distance sampling methods. Buckland et al. (1993, 2001) recommend at least 60-80 observations, although as few as 40 may suffice in some cases. A study evaluating the effectiveness of distance sampling using older analysis methods (software program TRANSECT) suggested that at least 100 observations may be required to produce a reliable density estimate (Verner and Ritter 1988). Still, our mean density and abundance estimates appear reasonable given our knowledge of Swainson's Warbler populations at BSNWR derived from tape playback surveys, territory mapping, and other methods. During the 2002 breeding season, 54 singing males were detected and 36 territories mapped in portions of the study area where we had been unable to conduct intensive searches or map territories in 2001; we also re-located many of the 2001 territories, but did not re-map them, in 2002 (J. M. Meyers, unpublished data). Our combined data for 2001 and 2002 represent coverage of 100% of the study area over the 2 yr. While we cannot be certain that each 2002 detection represented an additional territory not counted in 2001, or that our counts of singing males did not include duplicate detections (since not all territories were mapped), the overall number of singing males detected during the 2 yr (138) was relatively close to our mean abundance estimate (163) from distance sampling.

Meanley (1971) reported an encounter rate of 5.9 singing males/km on a 3.2-km transect in the Bond Swamp area in 1968, but this may represent maximal (versus mean) abundance or may include migrants (no date specified). During migration (3 May 2001), Meyers encountered 6.0 males/km on a 2.5-km transect (oriented North-South) in optimal habitat along the Ocmulgee River at BSNWR (J. M. Meyers, unpublished data). Graves (in press) reported approximate densities at five sites in four states within the species's core breeding range (Arkansas, Florida, Louisiana, Mississippi) derived

from transect surveys involving at least 3 independent continuous playback runs for each transect (playback along entire transect; runs on different days) (G. R. Graves, personal communication). Extrapolating from his results, mean density for these five sites was approximately 10 males/km² (range = 3.8-20.5 males/km²) – similar to the mean density estimate for our study area derived through distance sampling. Prior estimates of Swainson's Warbler abundance and density may not be directly comparable to our results, however, due to variation in survey methods, scales, and timing, as well as the quality of habitat surveyed (Brown and Dickson 1994).

The small number of detections in our distance sampling surveys, relative to the number of territories and individuals we determined were present by other methods in 2001, may have resulted in part from survey timing. Individuals were not singing as intensively during our transect surveys as they had been 2-4 wk earlier (~30% reduction in singing rates), and the delay in our surveys due to flooding may have exacerbated this problem. Singing behavior may change as the breeding season progresses, and earlier surveys – perhaps commencing in mid-May (~15-21 May in our study area) – may be warranted for Swainson's Warblers (Wilson and Bart 1985; Meanley 1968, 1971; Brown and Dickson 1994; G. R. Graves, personal communication). However, surveys conducted too early may be problematic due to the presence of migrating individuals that may not remain to breed in the area surveyed.

Distance sampling methods may be ineffective for detecting changes in populations of relatively rare species such as the Swainson's Warbler. We were unable to achieve the recommended number of detections although we surveyed a relatively large area with a substantial population at apparently high density. Nearly two-thirds of the variance associated with our density estimate (63.8%) was attributable to encounter rate – i.e., the relatively small number of individuals we detected. Where Swainson's

Warblers are less abundant or breed at lower densities, it may be impossible to obtain density estimates with low variances through distance sampling.

Further research is needed regarding the relative effectiveness of distance sampling and alternate density estimation methods for Swainson's Warblers and other uncommon species in habitats not adequately sampled by BBS methods. To gauge population trends reliably, special survey methods may be needed for individual species, species groups, or habitat types (Robbins et al. 1986, Hamel et al. 1996, Bibby et al. 2000, Sauer et al. 2001).

Although we employed it primarily to locate habitat plots, our single-visit mapping approach appeared to be efficient in delineating territories at BSNWR. We spent ~2-3 person-hours locating and mapping the movements of each individual, and are confident that the 56 areas we mapped represent discrete territories based on counter-singing we heard and visual examination of our maps. (We eliminated from our dataset several additional territories that we believed might be duplicates.) In comparison, we expended ~4.5 person-hours for each detection obtained in our distance sampling transect surveys, about 50% to conduct the surveys and 50% for transect layout.

More than one visit (i.e., mapping on >1 day) may be needed to map Swainson's Warbler territories adequately. However, the standard breeding bird spot-mapping approach, involving as many as 10-12 visits to each territory spaced throughout the breeding season, may be infeasible both because of its labor-intensiveness and because shifts in territory occupancy may occur with re-nesting or double-brooding (J. L. Thompson, North Carolina State University, personal communication). Bibby et al. (2000) suggest that as few as five appropriately timed visits may suffice for single-species territory mapping. A mapping approach involving five or fewer visits in mid-May to mid-June (Meanley 1971, Peters 1999) may be adequate to estimate population density. It also could facilitate collection of additional habitat data and reproductive data

– e.g., through identification of nest locations for intensive monitoring and/or observation of reproductive index parameters (Vickery et al. 1992) – needed to assess demography and long-term viability of Swainson’s Warbler populations (VanHorne 1983, Pulliam 1988, Martin 1992, Brown and Dickson 1994).

Tape playback may be useful in locating individuals and mapping territories, based on our work and that of Graves (1996, in press). This approach, however, should be used with caution given the potential for movement of individuals toward the observer – as evidenced by the 61% reduction in effective strip width in our playback surveys, compared with unaided surveys – and possibly far outside their normal territory boundaries (R. J. Cooper, University of Georgia, personal communication). Potential adverse effects of investigator disturbance on breeding populations also should be considered when using tape playback (Brown and Dickson 1994).

Meyers and Odum (2000) emphasize the inherent difficulty of monitoring uncommon to rare bird species. As our study shows, it may be difficult or impossible to obtain reliable density and abundance estimates for use in determining Swainson’s Warbler population trends through distance sampling. Both distance sampling and territory mapping methods of density estimation may be too labor-intensive for widespread practical use. It may be appropriate to monitor Swainson’s Warbler breeding populations by collecting presence/absence data over a large geographic area, perhaps employing tape playback, and using a probability approach based on changes in occurrence over time to assess population trends (Nichols et al. 1998a, Nichols et al. 1998b, Meyers and Odum 2000).

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Chapter 3

MANAGEMENT MODELS FOR SWAINSON'S WARBLER BREEDING HABITAT IN A GEORGIA FLOODPLAIN FOREST¹

¹Wright, E. A. and J. M. Meyers. To be submitted to Journal of Wildlife Management.

ABSTRACT

We examined habitat use of a Swainson's Warbler (*Limnothlypis swainsonii*) breeding population with the objective of developing a multivariate habitat model sufficiently parsimonious for practical use, yet highly predictive of Swainson's Warbler presence. We measured 22 habitat variables in 56 plots occupied by singing male Swainson's Warblers, and in 110 randomly selected plots in unoccupied areas. Occupied plots were placed in the 50 m x 50 m area used most intensively by each male during 1-2 hours of observations, in which we recorded a mean of 19.2 locations/male. In univariate comparisons, 12 variables differed between occupied and unoccupied plots. We used two binary logistic regression techniques to develop a set of alternative habitat models, ranking them based on AIC_c scores. Density of cane (*Arundinaria gigantea*) and density of other shrub layer vegetation, both positively correlated with Swainson's Warbler presence, were the most important variables in distinguishing occupied from unoccupied areas. Leaf litter depth and % litter cover also showed strong positive correlations with Swainson's Warbler occupancy, while % canopy cover, % water cover, and % broad-leaved forb cover had negative correlations. We employed a split-sample cross-validation procedure to assess model predictive capability. Classification accuracy of highly-ranked three- to six-variable models in cross-validation runs was 87-89%, compared with 91% for a 13-variable model that had lowest (best) AIC_c score of all models. We recommend two specific models for Swainson's Warbler habitat assessment, and provide instructions for their use.

INTRODUCTION

Anthropogenic alteration of habitats used by Nearctic-Neotropical migratory birds during the various phases of their annual cycle has been implicated as a principal cause of population declines observed in many species (Terborgh 1989, Lovejoy 1992, Robbins et al. 1993, Peterjohn et al. 1995, Askins 2000, Pashley et al. 2000). Loss of appropriate natural habitats as the result of human activities apparently has not affected all Nearctic-Neotropical migrant species and groups equally. This may be because the extent and intensity of anthropogenic disturbance has been greater in habitat types most desirable for human use, such as those best-suited for agriculture and silviculture (Askins 2000, Brawn et al. 2001). Conversely, certain habitat types have been affected inordinately by human suppression of fires, floods, and other natural disturbances integral to ecosystem function (Brawn et al. 2001, Hunter et al. 2001, Reice 2001). Many Nearctic-Neotropical migrant species of high conservation concern breed in temperate zone habitats that have been subjected to long-term anthropogenic insults involving both intensive human use and suppression of natural disturbance – e.g., grasslands, pine and oak savannas, and riparian forests (Askins 2000, Brawn et al. 2001).

The Swainson's Warbler (*Limnothlypis swainsonii*), a Nearctic-Neotropical migrant songbird that breeds predominantly in bottomland hardwood forests within the alluvial floodplains of the southeastern United States, appears to be declining in part due to human alteration of its preferred breeding habitat (Meanley 1971, Brown and Dickson 1994, Askins 2000, Pashley et al. 2000). Bottomland hardwood forest ecosystems in the southeastern U.S. have been destroyed or degraded extensively as the result of conversion to agricultural and silvicultural use, as well as alteration of natural hydrologic disturbance regimes resulting from construction of flood control and water supply projects (Noss et al. 1995, Askins 2000, Pashley et al. 2000, Sallabanks et

al. 2000). It is difficult to determine the exact amount of bottomland forest habitat lost to anthropogenic alteration; one estimate indicates that the 12 million ha of bottomland forest remaining in the southeastern U.S. today may be less than 50% of what was present at the time of European settlement (Hodges 1994), but others cite losses as great as 70% (Askins 2000). Canebrakes within bottomland hardwood forests may be preferred breeding habitat for Swainson's Warblers in some areas (Meanley 1971). These dense, nearly monotypic stands of a native bamboo commonly known as cane (*Arundinaria gigantea*) were once widespread throughout the southeastern U.S., but essentially have been extirpated (Noss et al. 1995, Platt and Brantley 1997, Brantley and Platt 2001). Along with the factors that altered bottomland forest ecosystems in general, fire suppression may have played a role in the demise of canebrakes (Platt and Brantley 1997, Brantley and Platt 2001).

Until recently, there were few detailed quantitative studies of Swainson's Warbler breeding habitat preferences, although Meanley (1945, 1966, 1971) published thorough descriptive information. Due to conservation concern for this species, several habitat studies have been conducted in recent decades near the edge of the breeding range in Illinois (Eddleman et al. 1980), Missouri (Thomas et al. 1996), and Virginia (Graves 2001), and in forests managed for commercial silviculture in South Carolina (Peters 1999) and Louisiana (Bassett 2001). Results from these studies may not reflect characteristics of breeding habitat in the species's core breeding range (Graves 2002), or in areas managed primarily for conservation purposes. A new study, however, assesses habitat characteristics at five locations within the core breeding range in Arkansas, Mississippi, Louisiana, and Florida (Graves 2002). Based on these studies, factors important in defining Swainson's Warbler breeding habitat may include dense canopy cover interspersed with disturbance gaps, dense shrub-level vegetation (cane or other species) for nesting, abundant leaf litter and sparse herbaceous vegetation for

foraging, moist floodplain soils, appropriate hydrologic regimes, and substantial forest cover at the landscape scale (Meanley 1971, Eddleman et al. 1980, Thomas et al. 1996, Graves 1998, Kilgo et al. 1998, Peters 1999, Bassett 2001, Graves 2001, Graves 2002).

We investigated Swainson's Warbler breeding habitat characteristics at a site in the Ocmulgee River floodplain in central Georgia, with the objective of developing a habitat model sufficiently parsimonious for practical use but highly accurate in predicting the presence of breeding territories. Although Meanley (1945, 1971) described canebrakes in this vicinity as "ideal habitat for the breeding of the Swainson's Warbler" and conducted some of his most detailed investigations of the species's natural history there, no intensive habitat studies employing modern multivariate methods appear to have been published for the area.

STUDY AREA

We conducted our study within Bond Swamp National Wildlife Refuge (BSNWR; 32°44' N, 83°35' W), established in 1989 and administered by the U.S. Fish and Wildlife Service (USFWS). BSNWR comprises 2,630 ha of forested floodplain wetlands and adjacent uplands in Bibb and Twiggs counties, Georgia, approximately 10 km south of Macon, and is managed primarily to preserve, protect, and enhance local floodplain ecosystems associated with the Ocmulgee River. Most of BSNWR typically is inundated by seasonal floodwaters in late winter through early spring, and some areas remain inundated year-round. Habitat types include bottomland hardwood forest, tupelo gum (*Nyssa aquatica*) swamp, and mixed pine/hardwood ridges, along with beaver swamps, oxbow lakes, and tributary creeks (USFWS 2000). Few details are available about prior land-use history. There is evidence of clearcutting or selective timber harvesting in most portions of the refuge, but old-growth forest (trees >120 years old, diameter at breast

height ≥ 2 m) remains in some areas. Topography is level to rolling, and the Ocmulgee River and its tributaries in this area exhibit relatively wide floodplains and frequent meanders (Clark and Zisa 1976). Climate is warm and humid, with a mean annual high temperature of 24 C and mean midsummer high temperature of 32 C at Macon. Relative humidity averages 88% during the morning and 54% during the afternoon, and mean annual precipitation totals 122 cm (National Climate Data Center 2001).

Our study area encompassed approximately 1,740 ha of floodplain forest bounded on the west by the Ocmulgee River and on the east by Georgia Highway 23, including virtually all bottomland hardwood forest habitats within the refuge. Dominant tree species were water oak (*Quercus nigra*), swamp chestnut oak (*Quercus michauxii*), laurel oak (*Quercus laurifolia*), overcup oak (*Quercus lyrata*), sweetgum (*Liquidambar styraciflua*), tupelo gum (*Nyssa aquatica*), sugarberry (*Celtis laevigata*), red maple (*Acer rubrum*), ash (*Fraxinus* sp.), American elm (*Ulmus americana*), sycamore (*Platanus occidentalis*), and loblolly pine (*Pinus taeda*). Forest age ranged from approximately 30 to >120 years, and tree diameter at breast height (dbh) from 30 to 200 cm. Mean (minimum-maximum) dbh for large specimens of the dominant tree species, based on the dbh of the largest diameter tree in each of 174 0.25-ha vegetation plots, was 60.4 cm (36.0-121.0 cm) for water oak ($n = 28$ trees/plots), 64.7 cm (54.4-94.0 cm) for swamp chestnut oak ($n = 10$), 70.4 cm (44.8-123.6 cm) for laurel oak ($n = 20$), 76.8 cm (46.7-171.0 cm) for overcup oak ($n = 11$), 56.2 cm (38.2-74.0 cm) for sweetgum ($n = 20$), 81.1 cm (52.0-125.0 cm) for tupelo gum ($n = 13$), 66.2 cm (46.0-89.1 cm) for sugarberry ($n = 13$), 58.2 cm (44.9-86.3 cm) for red maple ($n = 9$), 58.6 cm (40.2-93.2 cm) for ash species ($n = 11$), and 49.8 cm (40.4-60.0 cm) for loblolly pine ($n = 8$) (E. A. Wright and J. M. Meyers, unpublished data).

Cane (*Arundinaria gigantea*) was a prominent feature of the understory, particularly on the natural levee immediately adjacent to the river. Vines were abundant, including poison ivy (*Toxicodendron radicans*), greenbriar (*Smilax* sp.) and grape (*Vitis* sp.). Sawtooth palmetto (*Serenoa repens*), dwarf palmetto (*Sabal minor*), and semi-aquatic and aquatic forbs (e.g., *Saururus cernuus*, *Boehmeria cylindrica*, *Peltandra virginica*, *Sagittaria* sp.) and grasses occurred in less well-drained areas, while blackberry (*Rubus* sp.) dominated large sunny openings in drier areas. Invasive exotic understory species such as Chinese privet (*Ligustrum sinense*), Japanese stilt grass (*Microstegium vimineum*), climbing fern (*Lygodium* sp.), and Chinese tallow tree (*Triadica sebifera*) were present in limited areas.

METHODS

Field and laboratory methods

We located and mapped Swainson's Warbler territories from late April through mid-June 2001. Initial locations of singing males were determined during distance sampling surveys we conducted along 18.36 km of randomly placed line transects (21 unequal length transects) as part of a study to estimate breeding population density, through tape playback surveys along the same transects (see below), and through opportunistic detections and intensive searches of suitable habitat. We followed singing males as they moved through their territories, maintaining a distance of at least 10 m, and used Magellan XL2000 Global Positioning System (GPS) units to record Universal Transverse Mercator (UTM; NAD 83) coordinates for each location at which the individual was observed. Each individual was followed for 1-2 h, or longer if necessary to obtain at least 10 GPS locations. Most territories were mapped in a single visit, but we made repeated visits in a few cases to obtain the minimum number of locations. We mapped 56 territories by this method, with a mean of 19.2 ($SE = 0.91$) locations/territory.

We used Microsoft Excel 97 software (Microsoft Corporation 1996) to create a scatterplot map of the UTM East and North coordinates (meters) for each location at which a given male was observed (Fig. 5). With these maps, we identified the 50 m x 50 m area used most intensively by each male during our observations (greatest number of locations), where we then located a 50 m x 50 m plot for habitat measurements. UTM coordinates obtained from the maps were used to locate the plot center in the field.

We established 50 m x 50 m random plots for habitat measurements in areas unoccupied by Swainson's Warblers along the same 21 random transects used for our distance sampling surveys. Occupied versus unoccupied areas were identified through our territory mapping work, distance sampling surveys, and tape playback surveys we conducted along the transects between 31 May and 20 June 2001. Each tape playback survey began within 2 h after local sunrise (immediately following completion of the distance sampling survey on that transect) and ended by ~10:00 h. We broadcast 2-3 pre-recorded song phrases followed by chip notes for 20-30 s every 250-300 m along the transects, using portable cassette recorders with amplified 5-cm speakers (Radio Shack model AMX9, output 2 w) set to a volume approximating normal vocalizations. We recorded UTM coordinates for each playback location, and the distance and compass bearing to each individual detected within 3 min. All three observers had prior training and field experience in identification of Swainson's Warblers.

We allocated the total number of unoccupied random plots among the 21 transects based on each transect's proportion of the total transect length. Random numbers tables generated in Excel 97, representing random distances in kilometers (to 0.01 km) from the transect start point, were used to determine plot locations. We used Excel 97 to determine the distance (nearest 0.01 km) of each Swainson's Warbler territory from the transect start point, based on UTM coordinates and the Pythagorean

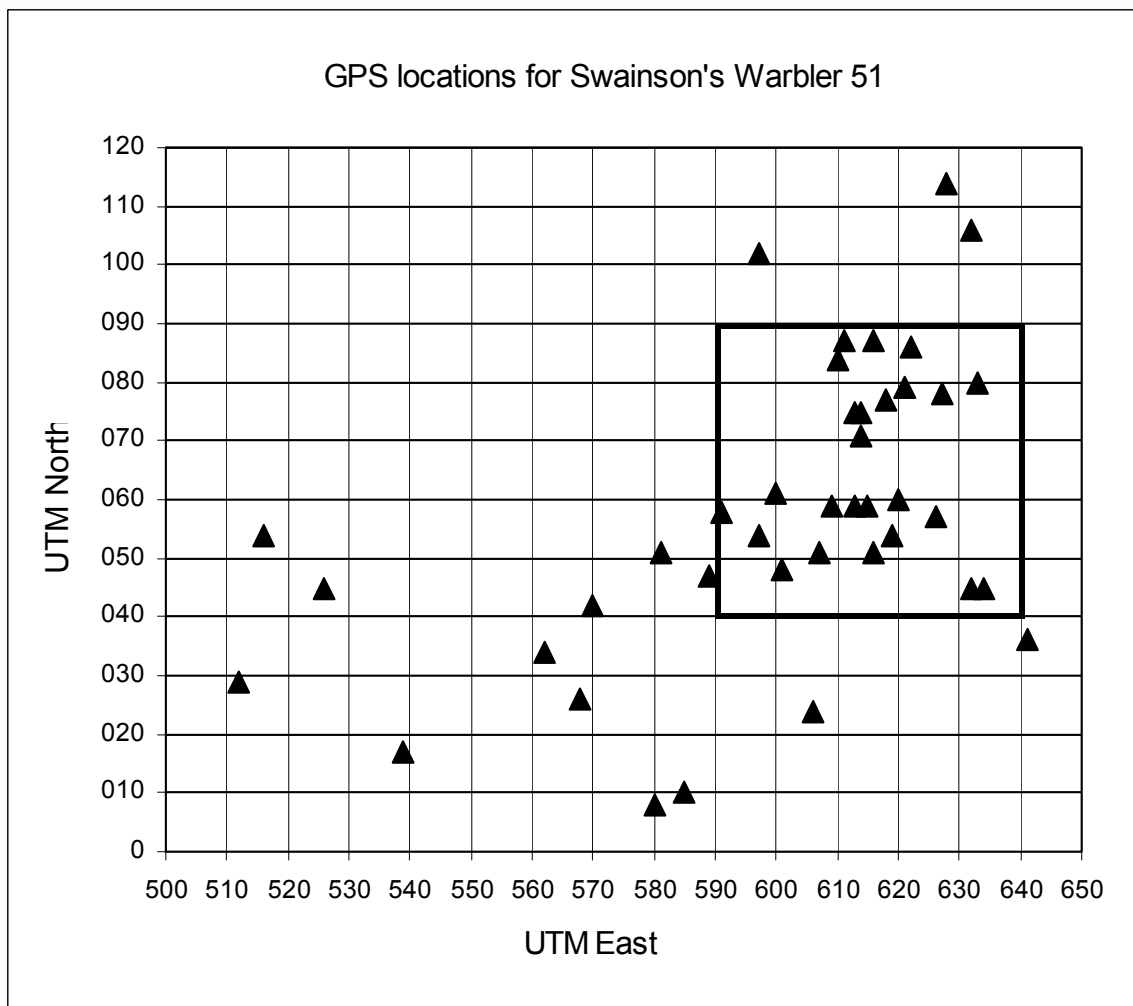


Figure 5. Sample scatterplot map of Swainson's Warbler GPS locations; outlined quare indicates 50 m x 50 m area with greatest number of detections, used as habitat plot location.

theorem, and eliminated random numbers that would have placed a plot within 100 m of the center of a Swainson's Warbler habitat plot or the location where an individual (unmapped) was detected during transect surveys. Centers of unoccupied plots were located in the field by using GPS units to measure the appropriate random distance along the transect from its start point.

We measured 22 habitat variables in occupied and unoccupied plots between 20 June and 1 August 2001. Two perpendicular 50-m transects were placed through the plot center, oriented to the cardinal compass directions. We counted the number of cane stems (CANESTEM) and the combined number of shrub, sapling, and vine stems (SHRUSTEM) (< 2.5 cm diameter, < 3 m tall) along each transect out to 1.75 m (belt transects 3.5 m wide, with total length of 96.5 m). We used ocular sighting tubes (Winkworth and Goodall 1962) to sample presence or absence of: 1) canopy cover (%CANOPY); 2) live ground cover (< 0.5 m tall) of broad-leaved forbs (%BRFORB) or grasses (%GRASS); and 3) non-live ground cover of leaf litter (%DEAD), water (%WATER), or bare soil (%NONE) at 1-m intervals along the transects, for a total of 100 point samples per plot in each of the three categories. We subsequently converted these presence/absence counts to percentages (e.g., for %CANOPY variable, % of samples with canopy cover present). We measured leaf litter depth (LITTER; to nearest mm) at 5-m intervals along the transects; the plot mean of these 20 point samples was used in data analysis. We recorded total cane area (CANEAREA; m²) and average cane height (CANEHT; to nearest 0.25 m) within the plot as the mean of visual estimates by two observers, using 3- or 5-m poles marked at 0.25-m intervals to gauge height. We measured diameter at breast height (BIGDBH; nearest 0.1 cm) and distance from the plot center (BIGCTR; nearest 0.1 m) for the largest diameter tree, and counted the number of downed trees (TREEFALL) and large canopy openings (CANOPEN). We used Jim-Gem Cruise-All tools (scale 10x) to take basal area

readings (BASAL; feet²/acre, converted to meters²/hectare) by sighting from the plot center.

We collected soil samples from the uppermost 20 cm of soil, consisting of four subsamples taken along the perpendicular transects at 12.5 m from the plot center in each cardinal direction. Samples were placed in airtight plastic bags and refrigerated to prevent decay. In January and February 2002, samples were dried, sieved (2 mm sieve), and analyzed for textural class – % sand (%SAND), silt (%SILT), and clay (%CLAY) – by hydrometer method, electrical conductivity (CONDUCT; deciSiemens/m), and pH. Two pH analyses were performed: pH in water (PHH₂O) and pH in CaCl₂ (PHSALT); the latter method, in effect, standardizes background ionic strength to improve comparability among samples from areas with differing moisture levels. Soil analyses were performed by the Phillips Laboratory, The University of Georgia, using standard methods published by the American Society of Agronomy and Soil Science Society of America (Gee and Bauder 1986, Rhoades 1996, Thomas 1996).

Statistical analysis

We used SAS Version 8 (SAS Institute 2001) for all statistical analyses, and initially examined our data using univariate methods. Of the 22 habitat variables in our dataset, 20 showed significant departures from normality. Standard transformations (e.g., arcsin, log, square root) failed to normalize most variables. Thus, we used Wilcoxon rank-sum tests to compare them between occupied and unoccupied plots. Significance was determined using a Bonferroni-adjusted $\alpha = 0.00227$ ($0.05/22$) to account for the number of simultaneous tests.

We used SAS PROC LOGISTIC to develop a multivariate habitat model using stepwise binary logistic regression, at a significance level of 0.05 for entry and retention of variables in the model. To avoid potential multicollinearity, we prepared a Pearson

correlation matrix prior to regression analysis and eliminated 4 variables (CANEHT, CANEAREA, %NONE, %SILT) that were highly correlated ($r > 0.70$) with others in our dataset. We used SAS macro APLR (Moore 2000a) for additional modeling in an optimization (versus significance testing) framework. The APLR macro calculates all possible logistic regression equations, constrained by a user-specified maximum number of variables in the resulting model. We performed multiple APLR modeling runs specifying different maximum numbers of variables (1-18) in an effort to develop the most parsimonious yet highly predictive models possible. Models were selected for further evaluation based on corrected Akaike's Information Criterion (AIC_c) scores. We used SAS macro CVLR (Moore 2000b) for cross-validation of the selected models under a split-sample approach; 50% of observations (selected randomly by the program for each iteration) were withheld from modeling and used as a validation dataset. Models also were evaluated based on their practical utility – i.e., the amount of work involved in measuring variables included in the model, and the likelihood that relevant measurements could be repeated reliably among years or locations.

RESULTS

We located 84 singing male Swainson's Warblers in the study area, and mapped enough locations to generate 50 m x 50 m habitat plots for 56 of these individuals. In univariate analyses using Wilcoxon rank-sum tests, 12 of 22 habitat variables differed (Bonferroni-adjusted $\alpha = 0.00227$) between the occupied plots ($n = 56$) and unoccupied random plots ($n = 110$) (Table 1; we present both means and medians to facilitate comparison with previous studies). Two additional variables approached significance, one of which (%WATER) was important in several of our multivariate habitat models.

Stepwise binary logistic regression analysis (significance level of 0.05 for entry and retention of variables) produced a habitat model comprising four variables: cane

Table 1. Wilcoxon rank-sum tests of habitat variables measured in plots occupied versus unoccupied by Swainson's Warblers at Bond Swamp National Wildlife Refuge, Georgia, during the 2001 breeding season.

Variable ^a	Occupied (<i>n</i> = 56)			Unoccupied (<i>n</i> = 110)			Wilcoxon test	
	Mean (SE)	Median (range)		Mean (SE)	Median (range)		Z ^b	Pr > Z ^c
CANEHT	1.58 (0.093)	1.50 (0-3.00)		0.66 (0.069)	0.25 (0-2.50)		6.8077	< 0.0001
CANEAREA	1623 (135.5)	2200 (0-2500)		518 (85.3)	0 (0-2500)		6.5786	< 0.0001
CANESTEM	424 (39.8)	421 (0-1216)		102 (16.0)	6 (0-680)		7.1123	< 0.0001
SHRUSTEM	358 (30.9)	315 (42-1328)		139 (11.1)	104 (0-522)		7.1623	< 0.0001
%DEAD	88 (1.6)	91 (44-100)		72 (2.0)	77 (2-100)		5.1234	< 0.0001
%NONE	12 (1.6)	8 (0-56)		23 (1.6)	22 (0-78)		-4.4902	< 0.0001
%WATER	0 (0.2)	0 (0-7)		5 (1.4)	0 (0-95)		-2.7369	0.0062
%BRFORB	15 (1.1)	15 (0-47)		9 (0.8)	7 (0-38)		4.8934	< 0.0001
%GRASS	6 (0.8)	3 (0-29)		6 (1.0)	3 (0-67)		1.0244	0.3056
LITTER	15 (0.8)	14 (3-32)		11 (0.9)	8 (0-53)		5.2376	< 0.0001
%CANOPY	86 (1.2)	89 (63-99)		92 (0.6)	94 (59-100)		-4.3210	< 0.0001
BIGDBH	58.1 (2.11)	56.0 (35.3-121.0)		68.0 (2.2)	63.6 (38.0-180.6)		-2.9595	0.0031
BIGCTR	12.7 (0.86)	12.9 (1.0-24.6)		12 (0.6)	10.9 (1.3-24.1)		0.9034	0.3663
TREEFALL	1 (0.2)	1 (0-4)		1 (0.1)	1 (0-6)		-0.5348	0.5928
CANOPEN	2 (0.1)	2 (0-5)		1 (0.1)	1 (0-4)		4.2682	< 0.0001
BASAL	18 (0.9)	18 (5-32)		25 (0.9)	23 (9-73)		-4.9437	< 0.0001
PHH20	5.1 (0.03)	5.1 (4.4-5.5)		5.0 (0.02)	5.1 (4.4-5.7)		0.3826	0.7020
PHSALT	4.6 (0.04)	4.6 (3.9-5.3)		4.5 (0.03)	4.5 (3.8-5.2)		1.5321	0.1255
%SAND	68 (1.8)	65 (45-92)		68 (1.3)	67 (37-97)		-0.3774	0.7059
%SILT	29 (1.7)	32 (4-52)		28 (1.1)	28 (1-55)		0.7771	0.4371
%CLAY	4 (0.3)	4 (1-10)		5 (0.3)	4 (1-17)		0.2447	0.8067

^a CANEHT = average cane height (m); CANEAREA = total cane area (m²); CANESTEM = number of cane stems in 337.75 m²; SHRUSTEM = number of shrub + vine + sapling stems (<2.5 cm diam.) in 337.75 m²; %DEAD = % leaf litter cover; %NONE = % bare soil (no litter/ water cover); %WATER = % water cover; %BRFORB = % broad-leaved forb ground cover; %GRASS = % grass ground cover; LITTER = leaf litter depth (mm); %CANOPY = % canopy cover; BIGDBH = largest tree dbh (cm); BIGCTR = BIGDBH tree distance (m) from plot center; TREEFALL = number of downed trees; CANOPEN = number of large canopy openings; BASAL = basal area (m²/ha); PHH20 = soil pH in water; PHSALT = soil pH in CaCl₂; %SAND = soil % sand; %SILT = soil % silt; %CLAY = soil % clay; CONDUCT = soil conductivity (dS/m)

^b normal approximation of Z-statistic

^c significance level is Bonferroni-adjusted $\alpha = 0.00227$ (0.05/22)

stem density (CANESTEM), shrub stem density (SHRUSTEM), leaf litter depth (LITTER), and % water cover (%WATER). The first three variables were positively correlated with Swainson's Warbler occupancy, while % water cover was negatively correlated. (This model was identical to the top-ranked four-variable model we developed using the APLR macro, discussed below; parameter estimates and other results for the stepwise regression model thus appear in Table 2 below).

The top-ranked model ($AIC_c = 64.13$) we produced using the APLR macro with the maximum number of variables set at 18 (i.e., all variables in our modeling dataset potentially could have appeared in the resulting model) contained 13 variables. This model correctly classified 95.8% of plots as occupied or unoccupied without cross-validation (testing the model against the same dataset used to create it), but its classification accuracy dropped to 90.6% in cross-validation (CVLR) runs. Variables in this model positively correlated with Swainson's Warbler presence were CANESTEM, SHRUSTEM, %DEAD, BIGCTR, BASAL, PHSALT, %SAND, %CLAY, and CONDUCT, while negatively correlated variables were %BRFORB, %CANOPY, BIGDBH, and TREEFALL.

Several more parsimonious models we developed using the APLR macro – the top- or second-ranked models, based on AIC_c scores, for runs in which we specified a maximum of three to six variables (Table 2) – had CVLR classification accuracies of 87-89%. These included a four-variable model ($AIC_c = 80.94$) identical to the model we produced using stepwise logistic regression, which correctly classified 91.6% of plots without cross-validation and 88.6% of plots in a CVLR run. Models comprising seven to 10 variables achieved only 2-3% greater CVLR classification accuracy than those with three to six variables. Models that included just one or two variables (Table 2) related to shrub-level vegetation density (CANESTEM or CANESTEM + SHRUSTEM) had CVLR classification accuracies of 76.0% and 85.9%, respectively.

Table 2. Binary logistic regression models^a of habitat characteristics predicting Swainson's Warbler occupancy (singing males) at Bond Swamp National Wildlife Refuge, Georgia, in 2001: top-ranked one- to six-variable models, plus second-ranked three-variable model, based on AIC_c scores.

Variable ^b	Coefficient ^c	Model AIC _c	% Correctly classified	Cross-validation mean (SE) % correctly classified
y-intercept	-1.9615	158.57	76.51	75.96 (0.11)
CANESTEM	0.0056			
y-intercept	-6.4761	89.61	85.54	85.92 (0.10)
CANESTEM	0.0085			
SHRUSTEM	0.0138			
y-intercept	-8.1246	86.56	87.95	87.04 (0.10)
CANESTEM	0.0096			
SHRUSTEM	0.0140			
LITTER	0.0887			
y-intercept	-6.9803	83.91	88.55	87.46 (0.10)
CANESTEM	0.0096			
SHRUSTEM	0.0154			
%WATER	-0.3965			
y-intercept	-8.8305	80.94	91.57	88.59 (0.10)
CANESTEM	0.0109			
SHRUSTEM	0.0158			
%WATER	-0.4107			
LITTER	0.0945			
y-intercept	-1.3022	78.43	92.17	89.07 (0.09)
CANESTEM	0.0107			
SHRUSTEM	0.0175			
%DEAD	0.0774			
%BRFORB	-0.1457			
%CANOPY	-0.1267			
y-intercept	-2.0727	76.93	91.57	88.66 (0.10)
CANESTEM	0.0114			
SHRUSTEM	0.0186			
%DEAD	0.0699			
%WATER	-0.2942			
%BRFORB	-0.1313			
%CANOPY	-0.1160			

^a General form of regression equation for models: $\text{logit}(y) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k$, where α is the y-intercept, β_1 is the coefficient for independent habitat variable x_1 , etc., and y is the binary dependent variable representing Swainson's Warbler occupancy (occupied = 1, unoccupied = 0).

^b CANESTEM = number of cane stems in 337.75 m²; SHRUSTEM = number of shrub + vine + sapling stems (<2.5 cm diameter) in 337.75 m²; LITTER = leaf litter depth (mm); %WATER = % water cover; %DEAD = % leaf litter cover; %BRFORB = % broad-leaved forb ground cover; %CANOPY = % canopy cover.

^c Data in this column are values (α) for the y-intercept and β -coefficients for habitat variables.

DISCUSSION

Model utility

The top-ranked habitat model, containing 13 variables, performed essentially no better in cross-validation runs than models with far fewer variables. This suggests that the additional variables in the larger model may represent “noise” in our dataset (Hosmer and Lemeshow 2000) – i.e., spurious effects that may not recur at other times or locations. Several of the variables included in the 13-variable model (e.g., %SAND, %CLAY, BIGCTR, PHSALT) did not differ between occupied and unoccupied areas in our univariate analyses, and BASAL was positively correlated with Swainson’s Warbler presence in this model even though the mean for this variable was lower in occupied than unoccupied areas. These results, however, could reflect interactions among the variables that would not be apparent in univariate analysis. The 13-variable model may provide information of scientific interest, but would be inefficient for applied use in habitat assessment and management.

Several of our more parsimonious models may have substantial practical utility, based on their high classification accuracies in cross-validation runs. (The Appendix provides instructions for managers regarding use of our habitat models.) The four-variable model that emerged from both our stepwise logistic regression and APLR analyses would permit rapid habitat assessment, and its parameters make sense biologically in terms of Swainson’s Warbler nesting and foraging behavior. However, consistent measurement of the variable %WATER (% water cover), which also appeared in the top-ranked three-variable model, may be problematic due to seasonal and year-to-year variation in precipitation and resultant flooding. This variable also may be redundant, in an inverse sense, of the LITTER (leaf litter depth) variable included in the four-variable model. We did not measure depth of leaf litter covered by standing water, since this litter was not accessible to Swainson’s Warblers for foraging. Using

our methods, therefore, mean litter depth necessarily would be reduced in areas with substantial water coverage.

The second-ranked model comprising three variables – CANESTEM (cane stem density), SHRUSTEM (shrub + vine + sapling stem density), and LITTER (leaf litter depth) – may be best-suited for practical application, even though it appears to be a somewhat less effective model than others with three to six variables based on AIC_c scores. Classification accuracy of this model was nearly as great as the four-variable model and the top-ranked three-variable model. Requisite measurements can be made quickly, and should be relatively unaffected by extraneous factors. In areas lacking substantial cane patches, overall density of shrub-level vegetation potentially could serve as an appropriate surrogate for the separate CANESTEM and SHRUSTEM variables in this model and others in our set, although this would require further testing.

The top-ranked five-variable model may be of interest, despite its relatively large number of parameters, because it is the most parsimonious model that includes the variable %CANOPY (% canopy cover). Measurement of this variable may be warranted to assess current canopy conditions and monitor successional or anthropogenic change, because there is ongoing debate about whether artificial canopy gaps should be created to promote and maintain suitable Swainson's Warbler breeding habitat (Eddleman et al. 1980, Bushman and Therres 1988, Soule et al. 1992, Hunter et al. 2001, Graves 2002). The %CANOPY variable also may assume greater importance in distinguishing Swainson's Warbler territories from unoccupied areas if the model is applied at sites that have a greater proportion of early successional habitat than our study area. The %DEAD (% leaf litter coverage) variable in this model may serve as a surrogate for the LITTER variable included in our three- to four-variable models. The two variables showed a fairly high correlation ($r = 0.677$) in our Pearson correlation analysis. Both relate to availability of foraging opportunities, and we observed that leaf litter typically

was shallow or non-existent in plots lacking substantial litter coverage. Biological significance of the %BRFORB (% live ground cover) variable is questionable at our study site, though perhaps not at other locations, because neither occupied nor unoccupied plots had large amounts of dense herbaceous vegetation, and the mean difference was small.

Habitat characteristics

Taken collectively, odds ratios derived from the regression coefficients (Table 2; odds ratio = e^{β_i} , where β_i is the regression coefficient for the i th independent variable) (Menard 1995, Motulsky 1995, Hosmer and Lemeshow 2000) for variables in our highest ranking one- to six-variable models indicate that the likelihood a singing male Swainson's Warbler was present in our study area increased by approximately 1% with each 30 stems/ha increase in cane stem density, 1-2% with each equivalent increase in shrub + vine + sapling stem density, 9-10% with each 1 mm increase in leaf litter depth, and 7-9% with each 1% increase in litter cover. Conversely, the likelihood of a territory being present decreased by 25-34% with each 1% increase in water cover, 12-14% with each 1% increase in broad-leaved forb cover, and 11-12% with each 1% increase in canopy cover. Specific probabilities associated with each variable depend on the other parameters in a given model, and the relationships between habitat variables and Swainson's Warbler presence indicated by the odds ratios are not necessarily linear. For example, Graves (2001) found that excessively dense shrub-level vegetation may be a negative factor for breeding Swainson's Warblers; this would be difficult to judge based on our data, since occupied plots at BSNWR typically had far greater cane and shrub stem density than unoccupied areas.

Cane stem density (CANESTEM) was the single most important predictor of Swainson's Warbler presence in our study area. This variable appeared in all our

habitat models, and the CANESTEM-only model had substantial classification accuracy (~76% with or without cross-validation). Only 10 of the 56 occupied plots had little or no cane, and we observed that most sizable cane patches were occupied by one or more Swainson's Warblers. Estimates from our belt transect counts indicate that cane stem density in occupied plots was equivalent to ~12,500 stems/ha (mean and median values similar), compared with a mean of 3,020 stems/ha and median of 177 stems/ha in unoccupied plots. Eddleman et al. (1980) reported mean cane density of 26,390 stems/ha in Illinois, and Meanley (1966) reported approximately 49,000 stems/ha in the vicinity of our study area, but these results may not be directly comparable to ours because of differences in methods. Graves (in press) found no cane in territories at three sites in Louisiana and Florida, and a range of from zero to ~73,000 cane culms/ha (with median values of zero) at two sites in Arkansas and Mississippi.

Although not used in our modeling work because of their high correlations with the CANESTEM variable (which we selected over other cane-related variables because the stem count measurement had greater precision and accuracy), mean values for estimated within-plot cane area (CANEAREA) and average cane height (CANEHT) also were much greater in occupied areas. The correlations we found among these three variables were intuitively reasonable based on our field observations. It appeared that both cane stem density and height were far greater in large cane patches than small ones, and that stems in larger patches also were more woody and of larger diameter. Median and mean values for CANEAREA within occupied plots represented 88.0% and 64.9%, respectively, of the total plot area, compared with a median of 0% and mean of 20.7% for unoccupied plots. Our results for the three cane-related variables clearly indicate that cane is a major component of Swainson's Warbler breeding habitat at BSNWR; this may reflect a preference for cane in our study area, its high availability there, or both.

High density of other shrub layer vegetation (SHRUSTEM) was nearly as important as cane stem density in distinguishing occupied from unoccupied areas at BSNWR. The SHRUSTEM variable appeared in all top-ranked models with 2 or more variables, and a 1-variable model containing only SHRUSTEM ($AIC_c = 159.76$) performed nearly as well as the CANESTEM-only model. Mean and median values for SHRUSTEM in occupied plots were equivalent to 10,600 and 9,326 stems/ha, respectively, compared with a mean of 4,115 stems/ha and median of 3,079 stems/ha in unoccupied plots. Overall structure of the shrub layer may be critical in determining suitable breeding habitat, since Swainson's Warblers typically nest at heights of 1-2 m and have been associated with a variety of shrub, vine, and sapling species in various geographic areas (Meanley 1971, Brown and Dickson 1994, Carrie 1996, Graves 2002). Mean and median values for combined CANESTEM and SHRUSTEM density in our occupied plots were equivalent to 23,153 and 21,791 stems/ha, respectively. Graves reported much higher median values, in the range of 30,000 to 50,000 stems/ha, for combined cane and shrub stem density at five sites in the core breeding range (Graves 2002), but his counts included cane and shrub stems <5 cm in diameter (vs. our counts of stems <2.5 cm in diameter for SHRUSTEM, and all stems regardless of diameter for CANESTEM) and excluded vines totaling ~1,000-5,000 stems/ha (site medians). Our SHRUSTEM count included vines, such as greenbriar (*Smilax* sp.) and grape (*Vitis* sp.), which appeared to be relatively abundant within occupied areas at BSNWR. At sites in South Carolina (Peters 1999) and Virginia (Graves 2001), presence and density of vines were among the most important predictors of Swainson's Warbler presence, and all nests found at the South Carolina site incorporated either vines or cane.

Both leaf litter depth (LITTER) and percent litter cover (%DEAD) were greater in occupied than unoccupied plots. These variables appeared alternately (one or the other present) in highly-ranked models containing three or more variables – suggesting that

they may serve as surrogate indicators for availability of foraging opportunities, since Swainson's Warblers forage almost exclusively in leaf litter (Meanley 1971, Graves 1998). The mean difference in litter depth between occupied and unoccupied areas at our site was small in absolute terms (4 mm) but relatively large on a percentage basis, with mean litter depth roughly 50% greater in territories. Even a small absolute difference in litter depth may be important, in terms of food availability and foraging efficiency, for a small-bodied species such as the Swainson's Warbler.

The mapping approach we used to locate habitat plots, intended to place them in areas used by Swainson's Warblers for multiple purposes, may have contributed to the clarity of our results regarding leaf litter characteristics. Individuals may nest and forage in different areas, and foraging areas do not necessarily have the dense cane or other shrub layer vegetation associated with nest sites (Meanley 1971, Graves 1998, Peters 1999, Graves 2001). In previous studies that showed no consistent correlation between Swainson's Warbler presence and leaf litter variables, litter characteristics were measured either around single detection points (e.g., point count or mist-net locations) or at systematically selected locations within occupied cane stands (Thomas et al. 1996, Peters 1999, Bassett 2001). These areas may not have been used intensively for foraging.

Our results regarding water cover also make sense in terms of Swainson's Warbler foraging behavior. Standing water was recorded in only four of 56 occupied plots. The variable %WATER (% water cover), negatively correlated with Swainson's Warbler presence, appeared in most of the top-ranked habitat models with three or more variables. Both Meanley (1971) and Graves (2001) identified inundation during the breeding season as a negative factor for Swainson's Warblers: presence of standing water may inhibit or preclude foraging by impeding access to leaf litter, and deep flooding during the breeding season may destroy nests as well. The hydrophytic

tree species tupelo gum, typically dominant in swamp forest areas at BSNWR (many of which had standing water in midsummer 2001, despite several consecutive years of drought), was not among the top three dominant or co-dominant tree species recorded in any of the 56 occupied plots.

Percent broad-leaved forb cover (%BRFORB) was higher in occupied than unoccupied plots in our study area, and appeared in habitat models with five or more variables. Previous studies in Illinois, Missouri, and Louisiana found less herbaceous ground cover in territories than unoccupied areas (Eddleman et al. 1980, Thomas et al. 1996, Bassett 2001). However, the mean for %BRFORB at our site was 15% in occupied plots, versus 9% in unoccupied plots, and a difference of this magnitude may not be biologically meaningful. In many plots, substantial leaf litter was present beneath herbaceous vegetation, which typically was sparse or patchy. Herbaceous ground cover may not be a negative factor for Swainson's Warblers unless its abundance and density are sufficient to inhibit foraging in underlying leaf litter, or to prevent litter accumulation.

Canopy cover (%CANOPY) also was important, although not one of the few most significant variables, in distinguishing between occupied and unoccupied areas. While occupied plots had less dense canopy cover than unoccupied plots, the magnitude of the difference was relatively small: 86% mean canopy cover in territories versus 92% in unoccupied areas (medians 89% and 94%, respectively). Occupied plots had twice as many large canopy openings (CANOPEN) as unoccupied areas, but the numeric magnitude of this difference was small (2 vs. 1) and counts for this variable involved observer judgments about which openings were "large." There was no difference in the number of downed trees (TREEFALL) between occupied and unoccupied areas. We observed, however, that there appeared to be a relatively large number of treefalls throughout the study area. The substantially lower mean basal area (BASAL) we recorded in occupied plots may reflect an actual difference, or may have

been an artifact of our methods. Because we visually estimated basal area with a sighting tool, rather than directly measuring it, the presence of dense shrub-level vegetation possibly biased the data toward lower values in occupied areas. Our results for these four variables provide limited evidence to support the hypothesis (Hunter et al. 2001, Graves 2002) that Swainson's Warblers are associated with canopy gaps, or early successional patches, within late successional forest.

Although none of the soil-related variables appeared in our more parsimonious habitat models, univariate analysis (Wilcoxon test) showed that soil electrical conductivity (CONDUCT) was greater in occupied than unoccupied plots. We measured this variable as an indicator of soil fertility, which limited research shows may be important in creation and maintenance of cane habitat (Platt and Brantley 1997). The mean difference in soil conductivity between occupied and unoccupied areas was small, and its biological significance is unclear. There appears to be little basis for assessing a difference of this magnitude in forest soils, because conductivity typically is used in soil science to examine large changes in salinity resulting from fertilization of agricultural lands (Rhoades 1996). We observed that many of the large, dense cane patches in our study area occurred on the natural levee adjacent to the river, which may receive substantial nutrient inputs from sediment deposition when floodwaters first contact the terrestrial zone. Nutrient cycling in forested wetlands of the southeastern U.S. is highly complex (Messina and Conner 1998), however, and relationships between nutrients and vegetation characteristics may not be readily discernible.

MANAGEMENT IMPLICATIONS

Several of the habitat models we produced – especially the three-variable model containing the variables CANESTEM, SHRUSTEM, and LITTER, and the top-ranking five-variable model – may be useful in assessing habitat for Swainson's Warblers at

sites other than BSNWR, as indicated by the high classification accuracy (~90%) of these models in cross-validation runs. We plan to verify the models using habitat data collected during the 2002 breeding season, both within portions of our study area where we were unable to map Swainson's Warbler locations in 2001 and on adjacent lands. Additional verification with data collected in other geographic areas would help determine whether these models are applicable to a range of breeding locations.

Our habitat models and other results show clear patterns of breeding habitat use in our study area, which accord with those observed in previous quantitative studies and with descriptive information about Swainson's Warbler natural history. We detected a relatively large number of Swainson's Warblers at BSNWR and dense breeding populations have occurred in this vicinity for more than 50 years (Meanley 1971), suggesting the presence of high-quality breeding habitat. Reproductive data are needed, however, to assess habitat quality and preferences more fully, and to examine population status and demography (VanHorne 1983, Cody 1985, Pulliam 1988, Martin 1992, Martin 1998). BSNWR may be an especially good location for reproductive studies because it has a large Swainson's Warbler breeding population, which may help researchers achieve reasonable sample sizes. Comparisons of reproductive parameters between our study area and other sites would be useful, especially in determining whether canebrakes offer any benefits over other breeding habitat types.

Conservation of the sizable remnant of canebrake habitat at BSNWR should be a management priority because of its intensive use by breeding Swainson's Warblers and its status as part of an "endangered ecosystem" type (Noss et al. 1995). Further research is needed with regard to cane ecology and management (Platt and Brantley 1997). Most of the few extant studies appear to have been conducted in the context of forage production for livestock (e.g., Hughes 1966) or in different forest types than those at BSNWR (e.g., peatlands dominated by pond pine, *Pinus serotina*) (Frost 1995).

Cane patches apparently may die off suddenly, and little is known about natural regeneration or potential restoration methods (Hughes 1966, Brantley and Platt 2001).

Prescribed burning and creation of artificial canopy gaps through silvicultural practices have been suggested as management techniques to promote the dense shrub-level vegetation – cane or other species – used by breeding Swainson's Warblers (Eddleman et al. 1980, Brantley and Platt 2001, Hunter et al. 2001, Graves 2002). Our results strongly support previous findings regarding the importance of understory structure in breeding habitat, and provide some additional evidence that canopy openings may be necessary habitat features. However, there appears to be little experimental evidence demonstrating the effectiveness of the proposed management techniques in floodplain forest or canebrake habitats similar to those at BSNWR (Soule et al. 1992, Thomas et al. 1996, Brantley and Platt 2001, Moorman and Guynn 2001).

Nor is it clear whether such habitat management practices are warranted in our study area. Shrub-level vegetation density may decrease in the future due to increased shading as the forest canopy closes with succession (Braun 1950, Odum 1971, Brantley and Platt 2001, Hunter et al. 2001, Graves 2002). However, it is possible that natural disturbance (e.g., treefalls resulting from flooding and windthrow) will set back succession in enough areas to maintain the spatial heterogeneity apparently required by breeding Swainson's Warblers; the number and size of natural canopy openings might even increase as the forest ages, due to the death of large trees (Wharton et al. 1982, Bushman and Therres 1988, Messina and Conner 1998, Brawn et al. 2001, Holmes and Sherry 2001, Reice 2001). The role of flooding and other hydrologic parameters in creating suitable breeding habitat merits further investigation (Askins 2000, Brantley and Platt 2001). Both flood dynamics and nutrient deposition may play significant roles at BSNWR and other breeding locations with relatively natural hydrologic regimes (Wharton et al. 1982, Platt and Brantley 1997, Messina and Conner 1998, Mitchener

and Haeuber 1998, Keddy 2000). Human demand for water withdrawals and flood protection may be a much greater threat than forest succession to Swainson's Warbler populations in these areas (Mitchener and Haeuber 1998, Nilsson and Berggren 2000, U.S. Geological Survey 2000).

Decisions regarding silvicultural and other habitat management approaches also should take into account the potential for damage to existing canebrake habitat, unintended promotion of exotic plant species that commonly invade bottomlands (e.g., Chinese privet, Chinese tallow tree), and possible adverse effects of induced edge on the forest community (Harris 1988, Nature Conservancy 2000a, 2000b; Nilsson and Berggren 2000, Sallabanks et al. 2000; Brantley and Platt 2001). If prescribed burning is employed, effects on leaf litter depth and coverage should be considered in determining the burn interval, season, and intensity, so as to avoid reducing Swainson's Warbler foraging opportunities.

We suggest that proposed habitat management techniques be tested primarily through experiments conducted in industrial forests with Swainson's Warbler breeding populations (Peters 1999, Bassett 2001, Brantley and Platt 2001) before being implemented on a broader scale. BSNWR and other areas managed for conservation purposes can serve as reference sites, and as laboratories to examine the effects of natural disturbance and successional change on creation and maintenance of appropriate breeding habitat (Finch and Stangel 1993, Brawn 2001). Habitat management measures can be applied at these sites later if found to be effective and necessary. Permanent monitoring plots for Swainson's Warblers and their breeding habitat should be established at BSNWR and other locations to assess population trends in conjunction with habitat changes resulting from natural disturbance, successional processes, or management experiments. Following verification, our five-variable habitat model may be especially useful for such monitoring because it includes

variables reflecting canopy, shrub, and ground layer vegetation density, as well as leaf litter coverage. All these parameters appear to be critical in determining habitat suitability for breeding Swainson's Warblers, and may furnish important evidence regarding the need for, and utility of, proposed management strategies.

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APPENDIX: USE OF HABITAT MODELS

The procedures for application of our habitat models, other than the field measurement methods for individual variables, are similar regardless of which specific model is employed. We recommend use of the three-variable model containing the variables CANESTEM, SHRUSTEM, and LITTER, or the five-variable model containing the variables CANESTEM, SHRUSTEM, %DEAD, %BRFORB, and %CANOPY for habitat assessment – i.e., to determine whether a given area is likely to be occupied by a Swainson's Warbler, based on measurements of the habitat variables in the selected model. An example using the three-variable model follows, including details of how to calculate either the odds or the probability of Swainson's Warbler occupancy, which are

closely related and represent different ways of expressing the same information.

(Equations and explanatory text below are based on material in Menard 1995, Motulsky 1995, and Hosmer and Lemeshow 2000.)

After making field measurements using the methods described for the variables CANESTEM, SHRUSTEM, and LITTER in the “Field and laboratory methods” section of this paper, write a logistic regression equation that: 1) follows the general form of the equation shown in the footnote to Table 2; and 2) uses the values for the intercept (α in the general equation) and the regression coefficient (e.g., β_1 in the equation) associated with each variable (e.g., x_1 for the first variable in the model), as given in the body of Table 2. The basic equation for our recommended three-variable model thus would be:

$$\text{logit}(Y) = -8.1246 + 0.0096 \text{ CANESTEM} + 0.0140 \text{ SHRUSTEM} + 0.0887 \text{ LITTER}$$

Insert the value you measured for each variable within your habitat plot in place of the corresponding variable code in the basic equation above. Thus, if CANESTEM = 400, SHRUSTEM = 300, and LITTER = 15, the equation now would read as follows:

$$\text{logit}(Y) = -8.1246 + 0.0096(400) + 0.0140(300) + 0.0887(15) = 1.2459$$

Logit(Y) is the natural logarithm of the odds that the plot in which you measured the three variables is occupied by a Swainson’s Warbler, in which case $Y = 1$ ($Y = 0$ for an unoccupied plot). The logit can be converted to the odds by exponentiation, which entails rearranging the $\text{logit}(Y) = 1.2459$ equation into the following form:

$$\text{Odds}(Y = 1) = e^{1.2459} = 3.4761$$

The solution for the above equation can be calculated with a scientific calculator, using the “e^x” key, or in Excel. To use Excel: 1) type the exponent 1.2459 into a blank worksheet cell, 2) click on the cell where you want the result to appear, and then click on the f_x button on the toolbar near the top of the screen, 3) click on “Math & Trig” in the left-hand column of the small window that opens, 4) scroll down the right-hand column in this window and double-click on “EXP”; 5) type the number of the cell where you typed the exponent 1.2459 in the space following “NUMBER” in the new window that opens (or select this cell by clicking on it); and 6) click “OK.”

Thus, the odds that the hypothetical habitat plot is occupied by a Swainson’s Warbler are 3.4761 to 1. In other words, based on the habitat measurements given, this plot is about 3.5 times more likely to be occupied by a Swainson’s Warbler than it is to be unoccupied. The calculated odds can be converted to a probability (P) using the following equation:

$$P(Y = 1) = \text{Odds}(Y = 1) / (1 + (\text{Odds}(Y = 1))) = 3.4761 / (1 + 3.4761) = 0.7766$$

This probability result indicates that the likelihood of Swainson’s Warbler occupancy in the hypothetical plot is nearly 78%.

Chapter 4

SUMMARY AND CONCLUSIONS

My research indicates that there is a relatively large breeding population of Swainson's Warblers at Bond Swamp National Wildlife Refuge (BSNWR), and one at apparently high density, even though I was unable to obtain precise estimates of abundance and density through the distance sampling methods employed in this study. Distance sampling, while perhaps generally useful in addressing issues of detectability in bird surveys, may not be practicable for surveying relatively uncommon species such as the Swainson's Warbler because encounter rates may be too low for reliable estimation of population density. These techniques should be tested at other sites, however, since my study was the first of which I am aware to have used them for surveys of this species.

Other approaches to inventory and monitoring of Swainson's Warbler populations should be considered as well. The single-visit mapping technique I used to locate plots for vegetation measurements within breeding territories was time-efficient, relative to my distance sampling transect surveys, and appeared to perform well in identifying territorial boundaries. It may be possible to develop a mapping method intermediate between the one employed in this study and the typical 10-12 visit spot-mapping protocol that could provide reliable estimates of population density. Repeated mapping visits may facilitate collection of basic reproductive index data or identification of nest locations for intensive monitoring, as well as ongoing habitat assessment. Alternative monitoring approaches that do not involve density estimation also should be examined; it simply may be impossible, or too labor-intensive, to obtain density

estimates with low variance for rare to uncommon species such as the Swainson's Warbler. Such species might be monitored more effectively using presence/absence data.

Regardless of the approach taken, reliable methods for monitoring Swainson's Warbler breeding populations are critically needed. Because this species is so poorly detected in existing broad-scale bird surveys such as the BBS, declines that potentially could lead to localized or larger-scale extinction of populations may not be discovered in a timely manner.

Results of the habitat modeling portion of my study indicate that high density of shrub layer vegetation, abundant and accessible leaf litter, absence of standing water during the breeding season, and possibly the presence of openings in the forest canopy are features strongly associated with Swainson's Warbler breeding habitat at my study site. My habitat results generally coincide with those of studies conducted previously at various locations within the breeding range. Cane patches were used more heavily by Swainson's Warblers at my site than has been reported in several other recent studies. Whether this was due to the high availability of cane at BSNWR, or indicates some special preference or benefit associated with such habitats, is a question beyond the scope of my study. Comparisons of Swainson's Warbler reproductive success in canebrakes and other habitats, including pine and hardwood forests managed primarily for silviculture, may be illuminating.

Several of the three- to six-variable habitat models I developed may have great practical utility in assessment and management of Swainson's Warbler breeding habitat. These models should be tested to determine their validity for broader application, using data collected at other locations and in other years, but their high classification accuracy (~90%) in cross-validation runs suggests that they will perform well. Other Swainson's Warbler habitat models reported in the literature either were not verified in this manner,

or had little predictive capability for the verification data set. I recommend use of either the three-variable model containing the variables CANESTEM, SHRUSTEM, and LITTER, or the five-variable model containing the variables CANESTEM, SHRUSTEM, %DEAD, %BRFORB, and %CANOPY, for habitat assessment. Use of the former model would be more time-efficient because it requires fewer measurements. The latter model may be preferable, however, because it incorporates a measure of canopy cover that could be critical in areas with a greater proportion of early successional habitat than my study area, or may provide important information about the use of canopy gaps by breeding Swainson's Warblers. For model testing and application in areas lacking substantial canebrake habitat, the CANESTEM and SHRUSTEM variables potentially could be combined into a single measure of shrub layer vegetation density – although this would require further analysis. Because Swainson's Warblers apparently select for large areas of late successional forested wetland habitat at the landscape scale, my models may not perform well in areas with a greater diversity of successional stages than my study area, in smaller habitat fragments, or in dissimilar habitat types (e.g., for populations in the southern Appalachians or in managed forests).

My study provides little direct insight into the question of whether using silvicultural techniques to create artificial canopy gaps would benefit Swainson's Warblers. Although my results for several canopy-related variables appear to support the hypothesis that canopy openings are important in breeding territories, I would not recommend implementation of silvicultural approaches for Swainson's Warbler habitat management at BSNWR in the immediate future. Too little is known about their potential effectiveness, and possible risks to the endangered canebrake community appear great unless very low-impact silvicultural techniques (which may be too costly because of their labor-intensiveness) are employed. Artificial canopy gap creation also may be unnecessary at sites like BSNWR that have relatively natural hydrologic

regimes; natural disturbance from flooding and windstorms may well be sufficient to maintain suitable breeding habitat, even with forest succession. A single management prescription for all Swainson's Warbler breeding areas thus may be inappropriate. Experimental studies should be conducted in less sensitive areas, such as industrial forests already managed for silviculture, to test proposed habitat management approaches prior to widespread use.

Ongoing monitoring of the Swainson's Warbler breeding population in my study area is warranted. The population is relatively large, and inhabits an ecosystem type that in itself deserves conservation attention. Permanent monitoring plots could be established at BSNWR not only to assess the status of the Swainson's Warbler population, but to monitor changes in its canebrake habitat – and resulting biological feedback in terms of Swainson's Warbler population parameters – with forest succession. If variables relating to hydrology and nutrient cycling are incorporated in such studies, this approach also may yield useful information about the role of natural disturbance regimes in creating and maintaining appropriate habitat for Swainson's Warblers and other members of the southeastern U.S. floodplain fauna. Ultimately, based on my field study, literature review, and discussions with other researchers, it appears that conservation of remaining “natural” bottomland hardwood forest habitats to the maximum extent practicable – which would entail greater efficiency in human use of both water and forest products – may be the single most effective management strategy for Swainson's Warbler breeding populations.