

ABSTRACT

THOMPSON, JENNIFER LAURIE. Breeding biology of Swainson's Warblers in a managed South Carolina bottomland forest. (Under the direction of Richard A. Lancia)

Conservation plans for the southeastern U.S. have identified Swainson's Warblers (*Limnothlypis swainsonii*) to be among the more vulnerable Neotropical migrants. The Swainson's Warbler (SWWA) is currently ranked as the second most endangered breeding songbird in the Southeast. However, a lack of life history information, in particular breeding, jeopardizes sound management decisions. Management plans for SWWA typically focus on cane regeneration in mature bottomland hardwood forests, although SWWA has been detected in early successional forests in the absence of cane. My study examined a population in Britton's Neck, South Carolina, located in the core of its breeding range, on timberland owned and managed by International Paper Co. From 1999-2001, I conducted a comprehensive breeding biology study that examined nesting, territory, vegetative, and landscape characteristics.

I discovered 98 SWWA nests from 1999-2001, 63 of which were active. Based on a 23-day nesting cycle, SWWA nesting success equaled 60% using the Mayfield success estimator. Contrary to the notion that SWWA require mature forests to breed, SWWA bred successfully in 20-year old regenerating clearcuts. Multiple brooding, where a pair initiates nesting attempts after their first is successful, was detected in 20% of the pairs. An individual's seasonal fecundity was doubled by multiple nesting attempts, increasing the young per female from 1.5 to 3.7. Brown-headed Cowbirds (*Molothrus ater*) parasitized

only 10% of nests. SWWA parents did not desert parasitized nests or expel Cowbird eggs or chicks. No SWWA chicks were observed fledging in the presence of Cowbirds.

The apparent population density was 17 territories/km², equaling the highest density ever recorded for SWWA. However, SWWA density varied across the site, with one-fifth the site containing 59 territories/km², compared to the remaining four-fifths with 12 territories/km². The area that contained the highest population density also had the highest nest density. I examined vegetative differences between nests built in high- versus low-density areas using a discriminant function analysis (DFA). The results of the DFA indicated understory thickets accounted for the largest difference between high- and low-density nest sites. Nests in the high-density area were more associated with thickets, which are tangles of cane, vines, blackberry, shrubs, and/or trees. Ninety-percent of nests were built less than 5 meters from a thicket, with the vast majority inside thicket edges.

Studies of Neotropical migrants have found nest site availability to drive distribution of some species, particularly Black-throated Blue Warblers (*Dendroica caerulescens*). Using digital photogrammetry, I compared the position of understory thickets and hydrologic features at nest, territory, and unused habitat. Leaf-on and leaf-off photographs were orthorectified using ERDAS Imagine Software. Understory thickets were then delineated from leaf-off and leaf-on photographs using a spectral analysis and Stereo Analyst, respectively. The Stereo Analyst classification of understory thickets proved to be the most effective. SWWA selected nest sites in closer proximity to understory thickets compared to random points in territories or unused habitat. Understory thickets at nest sites were larger than those found in the territory or surrounding habitat, and the nest understory thickets were two times larger in the high-density area than nests in the low-density area.

**BREEDING BIOLOGY OF SWAINSON'S WARBLERS IN A MANAGED
SOUTH CAROLINA BOTTOMLAND FOREST**

by
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Chair of Advisory Committee

This dissertation is dedicated to the memory of my uncle, Robert Jordan Leach, Jr.,
whose strength and humor will always inspire me.

BIOGRAPHY

I was born on April 15, 1975 in Syracuse, New York, to Sharon Ann and Ray Otis Thompson. After some moving around, my family settled in Wilkes-Barre, Pennsylvania, where they remain to this day. Summers were spent in southern Maine in a camp on Kennebunk Pond, where my Mom spent her summers as a child. No matter where I settle, Maine will always be home. I have one younger brother, Trevor, who surprised us all with an entrance my sophomore year of high school.

I graduated from Hanover Area High School in June 1993 and began college at Bloomsburg University of Pennsylvania the next fall. My area of concentration was Biology with a pre-med emphasis. Much to my parent's dismay, I changed my path after taking two field courses to fulfill my graduation requirements, Wetlands Ecology and Marine Biology. After graduating in August 1997, I landed an internship at Alligator River National Wildlife Refuge in North Carolina. I was part of a trail hacking crew that sampled Atlantic White Cedar regeneration in a pocosin.

The spring of 1998, Kimberly Peters hired me as a field technician to work on the Swainson's Warbler project in South Carolina. The subsequent season I was the field crew leader. In August 1999, I began my graduate coursework under the guidance of Richard Lancia. That semester I began teaching lab sections, which I continued for 14 subsequent courses. I spent two more field seasons in South Carolina, completing my last season the summer of 2001. The summer of 2003 I taught Conservation of Natural Resources as the primary instructor and also participated in the Preparing the Professoriate Program that year. I defended my Ph.D. in May 2005, and I am beginning my teaching career at Wake Technical Community College in the Fall 2005.

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CHAPTER 1

BREEDING BIOLOGY AND SUCCESS OF SWAINSON'S WARBLERS

***(Limnothylops swainsonii)* IN A MANAGED LANDSCAPE**



1.1 INTRODUCTION

The gently sloping Coastal Plain of the Southeast creates ideal conditions for meandering rivers with wide floodplains (Gosselink et al. 1990). Floodplain forests are generally more productive than uplands partly due to the nutrient rich sediments delivered by floodwaters (Martin et al. 1993). Increased productivity yields more leaf litter, in turn supporting more microbes and invertebrates through litter decomposition, resulting in a greater food supply for higher vertebrates (Martin et al. 1993). Accordingly, bottomlands support some of the highest bird densities in the southeastern U.S., with densities approaching two to four times higher than pine or mixed pine/hardwood forests (Dickson 1978).

Bottomland forests are thought to be one of the most rapidly diminishing wetland ecosystems (Gosselink et al. 1990). Conversion of bottomlands for agriculture, reservoirs, pine plantations, urbanization, and flood control projects threatens these areas and the species they support (Graves 2001, Askins 2000). Since European settlement, 69% of bottomland hardwood forests in the lower 48 states have been lost (Gosselink and Lee 1989), with the Southeast one of the hardest hit (80% loss, Turner et al. 1981). Between 6.6 and 13 million ha of bottomland hardwood forest remain in the Southeast (Martin et al. 1993), compared to a conservative pre-European estimate of 17.7 million ha (Klopatek et al. 1979). The remaining southern bottomlands are severely fragmented, a situation not expected to improve with exploding human population growth in the Southeast (Askins 2000).

Conservation efforts on public lands alone will not be sufficient to maintain bottomland hardwood forests. The role of private lands in bottomland conservation needs to be considered, because the largest portion is owned by individuals (8,410,000 ha; 68%),

followed by the forest industry (2,893,000 ha; 24%), and finally the public (916,000 ha, 8%; USDA Forest Service 1988, Conner and Hartsell 2002). Since many bottomland hardwood forests are converted to pine plantations, it is imperative that timber companies play a role in managing for bottomland avian species (Hunter et al. 1999). People typically view the public landscape as havens for ecological diversity to the exclusion of private lands. However, in areas such as the Southeast, where public lands comprise a small percentage of the land area, conservation efforts should focus on creating partnerships with private landowners in order to maintain species and ecological functioning.

Loss of bottomland habitat has had a substantial impact on avian species. Three of the five songbirds known to be southeastern bottomland specialists have disappeared, including the Carolina Parakeet (*Conuropsis carolinensis*), Ivory-billed Woodpecker (*Campephilus principalis*), and Bachman's Warbler (*Vermivora bachmanii*; Askins 2000). Only two specialists remain: the Prothonotary Warbler (*Protonotaria citrea*) and Swainson's Warbler (*Limnothlypis swainsonii*; Askins 2000). Although more than half the specialists have been lost, Prothonotary and Swainson's Warblers (SWWA) can be retained if the remaining floodplain forests are protected and restored (Askins 2000). Bottomland forests, along with the species residing there, appear to be particularly vulnerable and in need of special attention.

SWWA is a neotropical migrant known to breed in the Southeastern U.S. and winter in the Caribbean basin. Breeding habitat is found in bottomland hardwood forests of the Coastal Plain and high mountain riverine areas. Meanley (1971) described one of the mountain habitats to resemble a Coastal Plain bottomland on the side of a hill. SWWA has probably always been rare, considering it was lost from science for 50 years following its

discovery, and mountain populations were unknown for more than 100 years (Brown and Dickson 1994). Frequently, SWWA is compared to Bachman's Warblers because of their affinity for cane, fondness for similar habitat, and bright white eggs (Brown and Dickson 1994). Considering the disappearance of Bachman's Warbler, loss of bottomland hardwood forests, rareness, and poorly understood life history, SWWA has sparked much ornithological interest.

SWWA forages by lifting leaves and searching the ground and leaf undersides for concealed prey and is considered a dead leaf specialist (Meanley 1970). It has the longest bill of any parulid nesting in North America, which may facilitate the capture of large, fleeing prey (Strong 2000). Meanley (1945, 1971) found crickets, ground beetles, caterpillars, ants, and spiders as the primary food items, with beetles most commonly selected. SWWA in Jamaica selectively foraged for beetles, since it consumed beetles in larger number than would be expected by abundance (Strong 2000).

Nests tend to be placed in shrub/vine tangles at the margin between dense gaps and closed canopy forest (Meanley 1971, Peters 1999, Norwalk 2003). The outer nest is composed of dead leaves, resembling a clod of debris deposited by a flooding event (Graves 1996, Burt 2001). Interspersed among nests are numerous leaf drapes that may serve as decoys for predators, or at the very least for researchers. SWWA builds a nest larger than those of some birds nearly twice its size, such as the Northern Cardinal (*Cardinalis cardinalis*; Burt 2001). The closest avian associates to SWWA are the White-eyed Vireo (*Vireo gilvus*), Hooded Warbler (*Wilsonia citrina*), Kentucky Warbler (*Oporornis formosus*), Northern Cardinal, and Rufous-sided Towhee (*Pipilo erythrophthalmus*; Meanley 1971).

SWWA has been identified as a species of concern, due to destruction of breeding and wintering habitat, relatively small population size, and a small wintering range (Graves 2002). Conservation plans for Neotropical migrants the southeastern U.S. consider SWWA among the more vulnerable migrants (Hunter et al. 1993, Kirkconnell 1996), and SWWA is currently ranked as the second most endangered breeding songbird in the Southeast (Graves 2002). Within the past 30 years, several populations have disappeared along the northern periphery of their historic breeding range in Delaware, Maryland, Missouri, and Illinois (Graves 2001), although data from the Breeding Bird Survey (BBS) suggests SWWA has undergone a significant range-wide population increase from 1966-1988 (Sauer and Droege 1992). However, small sample sizes may hamper the ability of the BBS to detect population trends in SWWA (Brown and Dickson 1994). In 1977, 26 SWWA were detected on 17 of 1,832 BBS routes, a sample too small to determine trends accurately (Brown and Dickson 1994). SWWA is a species in need of management and monitoring attention, but the lack of available information jeopardizes sound management decisions (Graves 2001).

The difficulty in studying SWWA can be attributed to the dense and thorny habitats it frequents, secretive habits, monomorphic sexes, and cryptic coloration (Meanley 1971). Descriptions of its obscurity are numerous: it is one of North America's least understood avian species (Brown and Dickson 1994); the least known songbird of the southern U.S. (Meanley 1971); and its breeding and wintering biology is the most poorly understood of the migratory warblers (Brown and Dickson 1994, Graves 1996). SWWA habitat is just as noteworthy: the breeding grounds have been described as inhospitable, forbidding, and frequently impenetrable (Graves 1992). Due to these factors, basic life history information is lacking, with breeding biology particularly unknown (Brown and Dickson 1994).

According to Meanley (1969: 246), “ Observations of their breeding biology have been made by few persons,” a statement still relevant today. Nine breeding studies exist, but more than half examined two nests or less. The remaining four studies examined at least 15 nests and were conducted by Meanley (1945, 1969, 1971, 1982), Sims and DeGarmo (1948), Thomas et al. (1996), and Peters (1999). Brooke Meanley has completed the most comprehensive study of SWWA to date. According to Burt (2001), “Meanley had studied this bird for more than 30 years, and in a variety of its swampy strongholds. He has found more nests than any other person alive; about three dozen.” Although SWWA builds the largest nest of any North American warbler (Kaufmann 1996), these nests are incredibly difficult to find. According to Brown and Dickson (1994), “Finding its inconspicuous nests is a formidable task, and many researchers have spent entire field seasons searching for them with little or no success”.

The objective of my study was two-fold. First, knowledge of SWWA life history, in particular breeding, is needed to make sound management decisions. My goal was to undertake a comprehensive breeding biology study, a task limited to one population due to the time constraints involved with locating nests. Findings from this study could be used to guide management recommendations. Secondly, I planned to evaluate the productivity of SWWA in the managed landscape. Traditionally, SWWA have been associated with mature bottomland forests, but some studies indicate early successional landscapes are important (Carrie 1996, Peters 1999, Graves 2000, Graves 2001). Timberlands could provide suitable habitat for SWWA, which would partner interests of private landowners with conservation. However, very little research has examined SWWA productivity, especially in the managed

landscape (Peters 1999). I intended to close this gap in knowledge using a three-pronged approach of nest searching, territory mapping, and vegetative sampling.

In the first chapter, I describe SWWA breeding biology, including details of the nesting cycle, nesting success, multiple brooding behavior, population density, and site fidelity. Following the introduction, Chapter One is divided into three sections: site fidelity, population density, and breeding biology, each of which contains separate methods and results. The amount of material contained in these sections necessitated their division into separate parts. In Chapter Two, I document habitat use around nest sites to examine the role of floristic and physiognomic factors in site selection. Vegetative characteristics of nests located in areas with high SWWA density versus low-population density were examined, as well as vegetative differences between successful and failed nests. Finally, Chapter Three is an examination of the impact of landscape level characteristics on site selection using soft-copy photogrammetry techniques.

1.2 SITE DESCRIPTION

I studied a SWWA population located in the Atlantic Coastal Plain near Britton's Neck, South Carolina, on the Woodbury Tract (33° 52' N, 79° 22' W). The tract is located on a peninsula at the confluence of the Great and Little Pee Dee rivers (Figure 1). Included in the landscape, ranging from 0-25 m above sea level, are small isolated wetlands, sand ridges, planted loblolly (*Pinus taeda*) and longleaf pine stands (*Pinus palustris*), and large expanses of riparian bottomland hardwoods (Peters 1999, Norwalk 2003). The 8,000-ha tract is owned and managed by International Paper Company.

The study area is a 150-ha bottomland hardwood forest on the northwestern side of the peninsula (Figure 1). A 6.77-km, U-shaped road encircles a swamp located in the center of the site. The road is on higher ground and is flanked by bottomland hardwood forest where I focused my efforts. A 25 x 25-m grid originates from the road and extends 0-150 m into the forest on both sides. The grid was used to record nest and territory locations, which were referenced to grid locations in ArcView 3.2 (ESRI 1992-1999). Grid markers, nests, and mist net locations were recorded using a Trimble GeoExplorer II, Global Positioning System (Trimble Navigation Limited, 2001). Points were differentially corrected using Pathfinder Office (Trimble Navigation Limited, 1999) and exported as shapefiles into ArcView 3.2.

The site tends to experience drying in late summer to early fall, followed by wet winters, and frequent early spring flooding. Flooding typically lasts between 2 to >25% of the breeding season (Martin et al. 1993). Bottomland hardwood forests are divided into five zones based on soil moisture and hydrology, with the lower zones experiencing more flooding, resulting in higher levels of soil nutrients (Gosselink et al. 1990, Wharton et al.

1982). SWWA primarily uses Zones III through V, wetlands ranging from semi-permanently to temporarily flooded (Gosselink et al. 1990). Zone V is at the highest level of the bottomland and contains less water tolerant species, such as saw palmetto (*Sabal minor*) and American holly (*Ilex opaca*; Gosselink et al. 1990). Two soil types were found on the site, Chastain and Pee Dee (Peters 1999).

SWWA uses bottomland hardwood forests dominated by broad-leaved deciduous trees, consisting of sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), ironwood (*Carpinus caroliniana*), elm (*Ulmus* spp.), hackberry (*Celtis laevigata*), sycamore (*Platanus occidentalis*), and green ash (*Fraxinus pennsylvanica*). Common understory species include holly (*Ilex* spp), palmetto, hawthorne (*Crataegus* spp.), greenbrier (*Smilax* spp.), peppervine (*Ampelopsis arborea*), poison ivy (*Toxicodendron radicans*), grape (*Vitis* spp.), blackberry (*Rubus* spp.), and cane (*Arundinaria gigantea*).

The study site was harvested in 1983 by Georgia Pacific Corporation for pulpwood, sheared, and allowed to naturally regenerate (Peters 1999). Shearing is a site preparation technique where all saplings and stumps are removed using a KG blade mounted on a bulldozer (Peters 1999). The stand is brought down to ground level, which resulted in more even-aged regeneration. Drainages were interspersed across the site and not cut during the 1983 harvest, resulting in a mosaic of young and more mature hardwoods. Shortly following harvest, the tract was sold to International Paper Company and continues to be managed for wood fiber production. The site has not been replanted, thinned, or treated with herbicides since the last harvest.

In 1996, research began on the Woodbury Tract to assess breeding bird distribution and relative abundance (Mitchell et al. 2001). During point count and mist-netting surveys,

SWWA was detected in substantial numbers. Kimberly Peters began searching for SWWA nests in 1997, and I continued the work from 1999-2001. I narrowed the original study area down to the 150-ha site where SWWA was concentrated on initial surveys. A variety of techniques were used to study SWWA, including nest searching, nest monitoring, territory mapping, banding, vegetative sampling, and photogrammetry. Sampling began shortly after males arrived in early April and continued through the end of July.

1.3 SITE FIDELITY

1.3.1 METHODS

Prior to 1999, banding sites were positioned across the Woodbury Tract for avifauna censusing. Once the study focus shifted entirely to SWWA in 1999, I discontinued all banding sites except for those in the 150-ha stand. Four banding locations (45 nets total) were spread out over this area and run once every two weeks (Figure 2). Net arrays were positioned in a linear pattern, 150-m apart or less, and typically 25 m off of logging roads (Norwalk 2003). Nets were placed along edge habitat, such as sloughs and understory thickets, in order to maximize SWWA captures.

Twelve-meter long mist nets were used to capture birds through constant effort mist-netting or else target netting. Constant effort mist-nets were setup at one of the four banding sites, and birds were captured from first light until noon or the temperature rose above 90°F. Technicians checked nets once every forty-five minutes and brought all captures back to the banding station to collect morphological measurements. Constant effort netting was most effective at capturing SWWA males whose territories intersected banding sites. However, target nets were needed to capture females and males outside banding areas.

Playback tapes were used to attract males to target nets, and were especially effective during courtship and territory establishment (Norwalk 2003). Females were typically unresponsive to playback tapes and exceedingly difficult to capture. Meanley (1969) suggested flushing SWWA females from the nest into a nearby mist net. I had limited success with this technique, because females turned from the net at the last minute. Instead, I monitored nests to identify common exit and entrance routes used by adults, particularly the female. When the adult was away, I would set up a target net along one of these routes,

usually within 7 m of the nest. The net would be opened early the next morning and checked every 30 minutes. Every effort was made to minimize nest disturbance as much as possible, and if an adult reacted adversely, I would abandon the attempt. This technique turned out to be particularly effective for capturing females and the occasional male.

Although SWWA was the focus of my banding efforts, other species captured were sexed, aged, measured for morphology (Appendix 1, species list), and fitted with U.S. Fish and Wildlife Service (USFWS) aluminum bands. Morphological measurements included: weight, unflattened wing chord, cloacal protuberance (males rated as small, medium, or large), and brood patch (females rated as smooth, partially vascularized, or vascularized). Plumage was not useful for aging or sexing SWWA, as in many other species. Skulling, a technique examining the amount of skull pneumatization, was used to differentiate hatch-year SWWA from adults, and the presence or absence of breeding morphology was used to determine sex. Birds of unknown sex were either hatch-year birds or adults lacking apparent breeding morphology.

Five to six days after hatching, I fitted SWWA chicks with USFWS bands and took morphological measurements. SWWA adults were fitted with three additional plastic bands, one black and white split band to identify birds to my study site and two solid color bands. The black and white split was placed above the aluminum band, and a unique combination of two color bands was added to the opposite leg, each one of ten possible colors. The color bands allowed us to resight individuals without recapturing them, imperative during territory mapping and nest monitoring (Norwalk 2003).

1.3.2 RESULTS

Effort was not constant between banding sites, because Big Pig 1 and Horseshoe nets were run for 6 years, compared to 3 years at Crossroad/Dead Pig and Big Pig 2. After accounting for effort and the number of nets, Crossroads/Dead Pig had the most initial SWWA captures (0.44 birds/net/day), followed by Horseshoe (0.28 birds/net/day), Big Pig 2 (0.28 birds/net/day), and Big Pig 1 (0.13 birds/net/day). A density grid of initial captures and recaptures was created in ArcView 3.2 using a kernel estimator with a 100-m radius (Figures 3 & 4). Both grids also indicated the highest capture rate was at Crossroads/Dead Pig, even though the grids were not corrected for effort or net numbers. Despite three more years of banding at Big Pig 1, it had the lowest initial capture density (Figure 3).

Five most common species captured, in order of magnitude were: Prothonotary Warbler (*Protonotaria citrea*), Northern Cardinal, SWWA, Hooded Warbler, and Carolina Wren (*Thyrothorus ludovicianus*). Mist nets were effective trapping devices for SWWA due to their ground foraging habits (Norwalk 2003). Over six breeding seasons, we captured 292 SWWA and color banded 163. Average weight was 14.1 g (± 0.20) with an unflattened wing chord of 68.1 mm (± 0.38). I observed a skewed sex ratio, with 2.3 times more males ($n = 126$) captured than females ($n = 54$). Once nesting began, males were more mobile than females, increasing their likelihood of capture. The preponderance of males may reflect both a higher male capture probability and perhaps a greater abundance of males.

Aside from banding, more males were detected returning between years, with 45 males versus 16 females. However, taking into account the fewer number of females captured, the rates are identical. The oldest SWWA was a male known to be at least six-years old. Nearly 80% (231 of 292) were not detected in years subsequent to initial banding

(Table 1). Excluding juveniles, a cohort known to have low natal site fidelity, 30% (61 of 205) of SWWA adults returned between years. Some birds disappeared for a season or more only to reappear again the next year (Table 1; i.e. bird detected 2 seasons over 4-year period). In undetected years, birds may be residing on the Woodbury Tract but not captured, or may have moved to a new spot entirely. The average distance moved between years was 194.6 m (± 7.01), ranging from zero to 1,611 m. Eleven birds returned to the same net, with one bird captured at the same location three years running.

Hatch-year SWWA accounted for 30% of the total captures (87 of 292), with sixty-four banded in the nest and the remaining captured in constant effort mist nets. The ratio of SWWA juveniles to adults was 1: 3.3. Two males banded as juveniles returned in subsequent years, less than 3% of the juveniles captured returned (2 of 87). One was banded as a nestling and returned to a location 1.3 km away, and the other male was banded during constant effort mist-netting and resighted two years later 1.6 km away.

1.4 POPULATION DENSITY

1.4.1 METHODS

Spot mapping began in early April, because males establish territories almost immediately after their arrival (Meanley 1969). Territory locations were recorded on repeated visits, with a minimum of 8 suggested (Ralph et al. 1993). Technicians walked a road from sunrise to midday listening for males and identifying color bands. Locations were recorded by estimating distance and azimuth to the nearest grid marker. X,Y coordinates of grid markers were corrected according to distance and azimuth data (Appendix 2, formulas), and then uploaded into ArcView 3.2 for territory delineation.

I used clusters of observations, collected on a minimum of five days, to delineate a territory (Bibby et al. 2000). Oftentimes, territory locations did not include a color band observation. Countersinging data were used to aid in decision-making, especially in areas of high SWWA density (Bibby et al. 2000). I used the US Geological Survey's Animal Movement extension to calculate kernel probability contours for point clusters. The contours subdivided territories into areas where the male was detected 50% and 95% of the time.

1.4.2 RESULTS

From 1998-2001, 2,967 territorial locations were recorded with 50 males identified. Average number of points collected per territory was 35.6 (± 2.01) on 10.3 days (± 0.51), with 23, 28, 18, and 13 territories mapped from 1998-2001, respectively. The drop in territory numbers seen in 2000 and 2001 was not a biological issue, but rather logistical. Fewer territory points were collected the last two years, because the technician's time was redistributed to extended nest observations. For the most part, male occupancy did not

change over time; the only difference was insufficient visits to warrant calling a point cluster a territory. Eight males returned in subsequent years to setup territories, with six defending the identical territory. One male defended the same territory for four years, two males for three, and three males for two years running. For the two males that shifted location, one moved 40 m and the other 1,000 m.

A territory point density grid was created in ArcView 3.2 using a kernel estimator with 100-m radius (Figure 5). The highest densities were observed on Crossroads/Dead Pig, similar to the banding results, and a Big Pig site that was defended by unmated males each year. Meanley (1968) believed SWWA males sang more when unmated, which would explain the concentration of points at the Big Pig site. Technicians were able to map these males all season, whereas mated males received less attention because they quieted once nesting began. Nests were detected on 61% of 1998 territories (14 of 23), 54% of 1999 (15 of 28), 72% of 2000 (13 of 18), and 54% of 2001 territories (7 of 13). Three fledgling groups were observed with males that did not have nests discovered on their territories, proof of at least three missed nests.

Average 95% territory size was 1.56 ha (± 0.12), ranging from 0.31 to 6.21 ha. Crossroad/Dead Pig territories averaged 1.19 ha (± 0.11) compared to the rest at 1.92 ha (± 0.24), a significant difference ($t = -2.83$, $P = 0.0072$, $n = 51$). Apparent population density was less in 1998 (15.3 territories/km²) compared to 1999 (18.7 territories/km²), due to increased effort by technicians in 1999. Ten territories were delineated at Crossroad/Dead Pig in 1998 and 1999, a density of 58.8 territories/km² (Figure 6), compared to 9.8 territories/km² (1998, $n = 13$) and 13.5 territories/km² (1999, $n = 18$) on the rest of the site. Territories covered the Crossroad/Dead Pig area, many of which overlapped. Meanley

(1971) believed SWWA was semi-colonial under the right conditions, a phenomenon that may be occurring on the Crossroad/Dead Pig site.

1.5 BREEDING BIOLOGY

1.5.1 METHODS

Nest searching began the third week of April and continued through the end of July. I searched the entire grid for nests at least twice a week, systematically rotating around the site. In addition to systematic searches, I spot-searched continuously while territory mapping, banding, vegetative-sampling, etc. The key to successful nest searching was being in the right place with the appropriate nest search image in mind. Martin and Geupel (1993) suggest keying in on female behavior to locate nests, but SWWA females are typically unwilling to lead you to the nest. William Burt (2001:32) sums up my nest searching technique in his description of locating Black Rail nests (*Laterallus jamaicensis*), “I’d simply search the salt grass aimlessly and mindlessly, endlessly, until I got lucky, and my eye caught the artificial twist of grass signaling the presence of nest canopy.” Instead of the salt marsh, I positioned myself at the edge of understory thickets and viny tangles investigating every clump of leaves for three white eggs.

I followed Martin and Geupel’s (1993) suggestions for minimizing observer-induced nest mortality, by avoiding dead end trails to nests, using different paths each check, plus maintaining distance during nest building. Nests were checked at least every three days until six days after hatching, at which point they were checked daily. Daily checks were an attempt to minimize unknown nest outcomes, which typically occur the last several days of the nesting cycle. Whenever possible, I checked nest contents using binoculars or a scope instead of physical checks. This technique was not appropriate until the eggs hatched, but was particularly useful at preventing premature fledging near the end of nesting.

Nest check data were analyzed using Mayfield's nesting success estimate. Mayfield's success estimator is based on the number of days nests were observed, rather than dividing successful by total nests. The latter technique is biased high since nest mortality is a function of time; nests discovered late in the nesting cycle suffer fewer observed losses (Mayfield 1975). Nesting success is defined as the survival of any nest contents, meaning partial losses due to egg failure or disappearance are ignored (Mayfield 1975). Nests observed for less than 24 hours were excluded from the analysis (9 of 79), and the remaining observations were oriented in a chronology matrix used to estimate exposure period.

The exposure period and losses during this time were compiled and used to calculate the daily nest survival rate, s , which was estimated by,

$$s = 1 - \frac{L}{E},$$

where L is the number of losses occurring during nest observation, and E is the total number of exposure days (Manolis et al. 2000). Separate daily survival estimates were calculated for incubation and nestling periods plus each year, with the standard error the binomial standard error for a sample (Zar 1999, Hazler 1999),

$$SE(s) = \sqrt{\frac{s(1-s)}{L-1}}.$$

If daily nest survival rates do not differ between phases of the nesting cycle, the probability of nest survival from incubation through fledging would be:

$$P(\text{success}) = s^d,$$

where d is total days in the nesting cycle.

Unfortunately, some nest outcomes cannot be judged, a case Mayfield is unclear about how to treat (Manolis et al. 2000). For that reason, many researchers exclude data

from nests with unknown fates; a situation leading to negatively biased results and increased variance estimates (Manolis et al. 2000). Discarding valuable nesting information is a luxury most studies do not have, especially in Neotropical migrant research. Manolis et al. (2000) recommended a modification to Mayfield's method that allowed unknown nests to be included in the exposure period. The method, termed Last Active B, ended the exposure period on the last active observation for nests with unknown fates, and at the mid-point between last active and first inactive observation for nests of known fate (Manolis et al. 2000).

Extended nest observation periods were used to identify parents, in order to estimate the impact of renesting and multiple brooding on demographics. During the 2000-2001 breeding season, I monitored nests for 30-120 minutes with a spotting scope set up 10-15 m from the nest. When visibility was limited by understory density, I moved to a closer vantage point, but discontinued observations if the parents reacted adversely. Observation positions were chosen in order to view birds entering or exiting the nest. Once a parent began incubating or feeding, it tended to sit on top of its color bands making identification nearly impossible.

Only birds carrying food to the nest and/or incubating were considered the parents. Males singing in the area or birds captured in nearby nets did not qualify. Male identification was difficult during incubation, because he does not incubate eggs and typically does not feed the female at the nest. During incubation, the female was the only parent likely to be observed, but she remained stationary for long periods of time making identification difficult. The nestling period was the best chance to identify parents, because both adults made frequent provisioning visits to the nest.

1.5.2 RESULTS

1.5.2a Nesting summary

One hundred and fifty nests were discovered over the course of the project, with 79 active and 71 inactive. Two graduate student projects spanned this time period, and during my tenure 63 active and 35 inactive nests were discovered for a total of 98 nests (1999-2001). The majority of active nests were found during incubation. A breakdown of the discovery status was: 21 discovered before egg laying, 9 during egg laying, 38 during incubation, and 11 during the nestling phase. Regarding inactive nests, the fresh condition of most nests indicated they were built the same year discovered, but I either missed activity or the birds deserted the nest.

Forty percent of the nests (60 of 150) were concentrated in 28.2 ha, which comprised less than 20% of the 150-ha searched. The highest nest density was at Crossroads/ Dead Pig (kernel density estimator, 100-m radius; Figure 7), which is the same as the banding and territory results. Compared to the rest of the site, this area had the highest SWWA population density, productivity, and return rates. In Chapters 2 and 3, I will test for differences in vegetative and landscape characteristics of Crossroads/ Dead Pig versus the rest of the site.

1.5.2b Pairing

Males arrived during the first two weeks of April followed by females several days later, which is comparable to Meanley's (1969) observations in Georgia, Arkansas, and Louisiana. Pair bonds were formed shortly thereafter (Meanley 1969). I never observed a

male's courtship display, but I did witness one instance of copulation. A pair was foraging within 5 m of each other, when the female began fluttering her wings and chipping, resembling a fledgling begging for food. Immediately following the female's display, the male pounced on top of her for less than a second.

Of twenty-two pairs observed, I was able to assess pair fidelity of five pairs that initiated multiple nesting attempts the same year. Pair bonds were retained on subsequent attempts, except for a female that switched mates after a second nest failed. For the remaining pairs, the initial breeding attempts were all successful except for one with an unknown outcome. Between years, no individuals ($n = 6$) bred with the same mate. For example, one female was observed with a male at a 2000 nest, where she was not the breeding female. The following year the same male paired with this female, rather than the mate from the previous season.

1.5.2c Nesting cycle

First nests were built in late April or early May, two to four weeks after the first males arrived. The female is believed to be the sole nest builder, based on Meanley's (1971) observations of two females over three days of building. My only observation of nest building was a bird, of unknown sex, carrying three loads of leafy material from a beaver dam to a nest.

Nest initiation, the laying of the first egg, began one to six days after nest completion (Table 2). The earliest initiation I observed was on April 28 in year 1999, and the latest July 6 in year 2001. The earliest and latest on record were April 28 with small embryos (Wayne 1910) and July 13 (Perry 1886). When nest initiation dates were plotted over a

season, two peaks were observed. This bimodal distribution may be related to a nesting strategy, known as double brooding, that will be discussed later in the chapter. The first initiation peak occurred the first week of May, and the second peak fell the second week of June, however, there was substantial yearly variation. The bimodal distribution implies a synchronicity of brooding, otherwise nest failures would be expected to smooth out the peaks. The synchronicity could be driven by a factor such as food availability, that would encourage pairs to nest at the same time.

Of initial nesting peaks, the earliest was observed in 2001 with each prior year falling one week later (Figures 8-11). The three-week delay in nesting seen in 1998 may be due to a massive flood that spring (Figure 12). I think water levels at the onset of breeding influence the start of nest initiation, with substantial flooding causing a delay. When does flooding exert the most influence on nest initiation? Both 1999 and 2001 experienced flooding events of similar severity, but peak flooding differed by a month (early April 2001 versus early May 1999). If April flooding were significant, I would expect nest initiations with the following chronology from earliest to latest: 1999, 2001, 2000, and 1998. Instead, nest initiations followed May flooding events, with earliest to latest: 2001, 2000, 1999, and 1998.

Hydrology patterns in May appear to have significant effects on the start of nesting, which can impact the ability of birds to reneest and attempt multiple broods later in the season.

According to Meanley (1971: 60), “Eggs were laid daily until the clutches were complete, and incubation began with the laying of the last egg in each.” Mean clutch size was 3.10 eggs (± 0.10 ; $n = 76$), with as few as one and as many as seven eggs laid. The clutch of seven was unusual because it contained four more eggs than average. I documented chicks missing after each of two nest checks. Of the six eggs that hatched, only two fledged.

Incubation lasted two weeks on average (13.85 ± 0.28 days), and only nests where activity was observed from egg laying through incubation were included in this estimate ($n = 14$). All eggs in a nest typically hatched on the same day. Fifty-nine percent (143 of 236) of the eggs laid produced a chick, with a mean number of 2.60 chicks per nest (± 0.12) and 1.88 chicks per pair (± 0.16).

The nest outcome can be in doubt, unless fledging is observed or fledglings are later detected. At the end of the nesting cycle, it was difficult to differentiate between fledging and nest failure because predation events left little or no sign of nest trauma. I classified a nest as successful if: fledging was observed, fledglings were detected, or the chicks reached the potential fledging interval and their condition appeared far enough advanced (Appendix 3). Since 95% of the nests fledged eight days or later after hatching, I began the potential fledging interval at eight days. The majority of unknown outcomes arose from this period as well (85%, 16 of 19 unknown outcomes). Missed nest checks due to flooding, logistical constraints, or the end of the field season were the primary reasons for unknown nest fates.

Only nests observed from hatching through fledging were used to calculate the length of the nestling period ($n = 20$). The nestling period lasted 9.94 days (± 0.10), with 2.39 fledglings per successful nest (± 0.16). Because fledging was rarely observed, I assumed all nestlings present on the last check day fledged. Number of fledglings per pair ranged from 1.04-1.60, depending on the treatment of unknown nest fates (1998-2001). Assuming half the unknown nests failed and half fledged, the number of fledglings per pair was 1.32 (± 0.14). Forty-two percent of the eggs laid produced a fledgling (100 of 236), with 1 to 4 fledglings per successful female.

Nests observed from initiation through fledging were used to calculate the mean length of the nesting cycle at 23.3 days (± 0.61 ; $n = 7$). Figure 13 summarizes nesting cycle length divided into four categories: empty, initiation, incubation, and fledging. Boxes for all the categories, except empty, are incomplete due to small sample sizes. Days originate from zero, hatching day, with positive values representing the nestling period and negative values pre-hatching. Most nests were empty on day $-18.0 (\pm 0.25)$, egg laying began on day $-16.0 (\pm 0.25)$, incubation started on day $-13.8 (\pm 0.27)$, and fledging occurred on day $9.9 (\pm 0.10)$.

An unusual nest was observed in 2000, where a Northern Cardinal (NOCA) female adopted nine-day-old SWWA nestlings. On the ninth day, the NOCA female fed the SWWA chicks eight times over a 3-hour period. After feeding, she would swallow the fecal sacs and leave the nest, presumably to forage. Between one of the feedings, she fed a NOCA fledgling directly below the nest. When the NOCA female returned to the nest, she would defend against the SWWA parents. Once she left, the parents would return and feed the chicks. Three days later the nest was found on the ground with bird excrement nearby, but the fledglings were never resighted.

1.5.2d Nesting Success

Thirty of the active nests failed (38%) with depredation the leading cause, followed by Brown-headed Cowbird (*Molothrus ater*) parasitism, and lastly desertion. Two predator interactions were observed during the study, both involving black rat snakes (*Elaphe obsoleta*). In one case, a snake was found coiled around an eight-day-old nestling. The observer startled the snake, at which point it dropped the nestling and retreated. Afterwards, the female led the chick to cover, and the fledgling was resighted six days later with an adult.

The other instance occurred ten minutes after a nest check, when a snake swallowed three eggs in a 4-meter-high nest. Other potential nest predators use the site, including corvids, raptors, feral pigs, and small mammals; however, I never observed them involved in a depredation event.

Brown-headed Cowbirds (BHCO) reduce the likelihood of successful SWWA nesting attempts. Less than 10% of SWWA nests ($n = 8$) were parasitized by BHCO. I found no evidence of SWWA fledging in the presence of BHCO chicks, and SWWA appears to be a naïve host. Parents accepted the addition of a BHCO egg, and did not desert after SWWA eggs or chicks disappeared. BHCO chicks hatched at least a day before SWWA chicks and were 2-3 times larger, thus giving them a feeding advantage. One BHCO chick was fed on four of six food carries, whereas the SWWA was fed only twice.

Parasitized nest outcomes were as follows: one depredated during incubation; three nests reached the potential fledging interval, but fledglings were never sighted; and two fledged BHCO, but all SWWA chicks disappeared before the potential fledging interval. Only nine of nineteen SWWA eggs hatched, a 12% reduction in hatching probability from 59% to 47%. Six of nine SWWA chicks disappeared one to six days after hatching, and only three reached the potential fledging interval. I was unable to relocate these fledglings, so there is no direct evidence of SWWA chicks fledging in the presence of BHCO.

Snakes become more active as the temperature increases, so I expected to see a positive relationship between initiation date and failure rate, but there was no difference ($\chi^2 = 5.00, P = 0.287, n = 26$). However, I did detect a relationship between failure rate and stage of nesting cycle. Sixty-five percent of failures ($n = 15$) occurred during incubation, compared to 35% ($n = 8$) during the nestling phase. The day before hatching accounted for

nearly 20% ($n = 4$) of the failures, the largest percentage for any day. Although nests appeared to be more vulnerable during incubation, it is important to consider the exposure period. Since nest mortality is a function of time, the incubation period would have a higher failure probability because it lasted four more days than nestling (Mayfield 1975). Secondly, chances are my failure estimates are biased low towards the end of nesting due to unknown nest outcomes.

Seventy nests were observed for 1,088 exposure days, during which time 23 losses were observed (Table 3). Overall, the incubation period had a lower daily nest survival rate than nestling, but was not significant, so the two periods were pooled (Figure 14). The pooled daily nest survival rates did not differ significantly between years, and were also pooled (Figure 15, Table 4). Notice the improvement in precision of daily nest survival rates over time as sample size increased. The pooled daily nesting survival rate was 0.979 (± 0.004), and the overall nesting success rate was 61.0% (95% CI = 47.6 – 74.5%).

1.5.2e Multiple nesting attempts

I assessed breeding behavior of SWWA by monitoring 37 of 45 active nests for 208.5 hours in 2000-2001. Fifty-six parents were identified, but this included only 42 individuals (20 males, 22 females). The discrepancy between parents identified and the number of individuals was due to renesting and double brooding attempts, which resulted in some pairs detected at more than one nest. Renesting occurred when birds initiated a second nesting attempt after the first failed, whereas double brooding was the result of a pair initiating a second attempt after the first was successful.

I observed three occurrences of renesting, with 1 success, 1 failure, and 1 unknown outcome, plus six instances of double brooding. Two cases were detected in 2000 and 4 in 2001, accounting for 9% and 17% of the total nests each year. The difference between years was likely due to an improvement in my ability to identify adults at the nest, rather than a biological difference. In all first nesting attempts, except one, fledglings were sighted either leaving the nest or during post-fledging observations. In the remaining nest, fledglings were never resighted, but the nestlings were well within the potential fledging interval. Outcomes of the double brooding attempts were as follows: two failures, two successes, and two unknown outcomes due to the end of the field season. All parents, except one individual, were identified in the first nesting attempt, and all except three were identified in second attempts.

After accounting for renesting and multiple brooding (2000-2001), the average number of nests per female was 1.29 (± 0.099). Multiple nesting attempts can have a substantial impact on seasonal fecundity, the number of young produced per female per breeding season. When females were assumed to single brood (2000-2001), the seasonal fecundity was 1.5 (± 0.217) young per female. However, the fecundity of multiple-brooded females was 3.7 (± 0.853) young per female, with 1 to 9 young produced per season. When single and multiple brooded females were combined, the overall seasonal fecundity was 1.9 (± 0.327), which was not significantly different from estimates assuming all females were single brooded ($t = -1.13$, $P = 0.2628$, $n = 79$).

Is double brooding a rare behavior or a common strategy used by SWWA to maximize reproductive output? Of the nests monitored in 2000-2001, 16% (6 of 37) were a double brooding attempt, but parents were not identified at all the nests. I identified 56 of 74

nesting individuals, so correcting for parental identifications 21.4% (12 of 56) of nests were double brooded. Can SWWA behavior in the years prior to 2000 be inferred? Holmes et al. (1992) discovered a bimodal distribution in nest initiation dates corresponded with double brooding in Black-throated Blue Warblers (*Dendroica caerulescens*). In my study, all years followed a bimodal distribution including 1998 and 1999 (Figures 8 & 9). Although I do not have direct evidence of double brooding prior to 2000, nest initiation plots suggest double brooding may be occurring to some extent each year.

Not only can SWWA rear two broods in one season, but may attempt as many as three. Two pairs initiated three nesting attempts, one a potential example of triple brooding. A male was observed at three nests with the following outcomes: first successful; second reached the potential fledging interval, but no fledglings were sighted; and third had an unknown outcome. Nesting activity spanned at least 80 days, with the first attempt initiated on May 1st and the last nest expected to fledge on July 27th. The other individual with three nesting attempts was a double-brooded female. Her nesting activity spanned at least 82 days. The first nest fledged, but the second failed during incubation. After that failure, the female began a third nest of unknown outcome with a different male, which was the only instance of mate switching I observed.

The elapsed time between nesting attempts ranged from 6-25 days, with a mean of 11.6 days (± 2.2 ; $n = 10$). The triple-brooded pair waited only 6 days between first and second attempts, and 9 days between the second and third attempts. Average initiation date for first attempts was May 11, ranging from April 28 through June 2. Second attempts ranged from May 28 - July 6, with the average falling on June 18. Both of these estimates were approximately a week later than the overall peaks in nesting. One pair initiated the

latest first and second nesting attempts, June 2 and July 6. Considering a nesting cycle required 24 days plus a week for reneating, there was ample time for this pair to have initiated an earlier attempt.

One male was identified double brooding both years, though the occurrences were with different females. As of 2001, this male was at least five-years old. Are older individuals more likely to double brood than younger birds? Holmes et al. (1992) observed a relationship between age of adult and frequency of double brooding. The largest age difference in SWWA was between single brooded (2.4 ± 0.33 y.o.) and double-brooded males (3.2 ± 0.70 y.o.). Older males tended to double brood more often than younger males, but the difference was not significant ($t = -1.07$, $P = 0.299$, $n = 22$). Single (1.4 ± 0.19 y.o.) and double-brooded females (1.2 ± 0.20 y.o.) did not show a significant difference in age either ($t = 0.57$, $P = 0.578$, $n = 20$). However, females were significantly younger than males ($t = -3.78$, $P = 0.0007$, $n = 42$), a difference likely due to the fewer number of females captured.

Sixty percent (9 of 14) of nests initiated by multiple brooding pairs were concentrated in an area measuring 31 ha, with the remaining nests grouped 650 m away (Figure 16). The two clusters located the farthest away were initiated by the same male, but were from different years. Only 18 m separated the 2000 and 2001 nesting attempts, where on average birds placed nesting attempts 73.3 m apart between years (± 26.94 , $n = 5$). Within a season, the average distance between nesting attempts of multiple-brooded pairs ranged from 10.7 to 159.8 m, with a mean of 63.6 m (± 20.28 , $n = 7$). Pairs positioned reneating attempts further apart than multiple-brooding attempts (222.7 ± 44.72 m, $n = 3$).

1.5.2f Post fledging observations

Juvenile survival, movement, and behavior are difficult to measure; therefore, they are seldom incorporated into breeding studies. Only one observation of a SWWA juvenile has been made, where Meanley (1969) observed a group of fledglings two days out of the nest. On my site, I canvassed the area surrounding a nest once fledging had occurred. My intent was not only to confirm fledging, but also to gain insight into the post-fledging period. Detecting fledglings was difficult, but observing a family group was even harder. The main limiting factor was parental response: if an adult would not accept your presence, the rest of your time was spent chasing down the group. For that reason, I was only able to follow eight family groups for 1-29 days (13.4 ± 2.77). Typically if a group was observed once, future observations became easier.

Groups were usually resighted inside a male's territory. Fledglings tended to stay near the nest for the first several days, usually within 50 m. At this stage, juveniles were less mobile and hid in viny tangles or thick forbs on the ground. Adults brought food directly to the fledglings. As the young matured and their mobility increased, they would move short distances, but typically stay close to each other. Fledglings vocalized frequently, perhaps to indicate their position to parents and other fledglings. Between feedings, fledglings attempted to forage, sometimes poking at dead leaves or gleaning off live leaves, without catching prey. Three weeks after leaving the nest, juveniles aggressively begged for food while the male foraged. Juveniles would follow closely behind the male, chasing him down whenever he procured food. After several minutes, the male would flee to a new location leaving the young behind. Three weeks after fledging the male continued to feed the juveniles, but less frequently.

One of the family groups split their brood of fledglings. For the first five days after fledging, the male and female were observed foraging together. After capturing prey, they would separate and carry food to separate groups of fledglings located about 30 m apart. Following the fifth day, the female disappeared from the group, while the male continued to care for both groups of fledglings. The female was observed one-week later initiating a second nesting attempt. I was able to observe the male for 20 more days as he continued to care for the young, while the female incubated the new clutch. Once the chicks hatched in the second nest, the male split time between feeding the fledglings and nestlings. After repeated attempts, I could no longer resight the male or the fledglings.

In all groups, adults fed fledglings through the last observation period, with the latest observation 29 days after fledging. Only females cared for three of the groups (days 1-13), and only males cared for 3 other groups (days 1-29). Two groups were observed with both the male and female caring for the fledglings. In both cases, parents split the brood, and the female disappeared after the fifth day to leave the male with sole responsibility. In four of the family groups observed, the female initiated a second nesting attempt while the male was feeding the fledglings.

1.6 DISCUSSION

SWWA was successful on the Woodbury Tract in 1998-2001 as indicated by: 1) nesting success, 2) seasonal fecundity, 3) site fidelity, and 4) population density. My study proved SWWA could breed successfully in a managed landscape. These findings along with Graves' work (2001, 2002) challenge the prevailing notion that SWWA requires mature forests to breed (Eddleman et al. 1980, Thomas et al. 1996). Under certain conditions, managed landscapes with forests in various stages of succession may have untapped potential for SWWA conservation.

1.6.1 Nesting success

Meanley (1971) believed SWWA had lower nesting success compared to other warbler species, because only 19% of the nests he monitored fledged young. However, he used a traditional estimator that did not consider exposure period or include nests of unknown outcome. When success estimates were based on the Mayfield method, values ranged from 60 – 65% for a 23-day nesting cycle (Table 5; Peters 1999, Thomas et al. 1996). My estimate had the smallest 95% confidence interval (60, 47.6 - 74.5%) due to the greater number of nests discovered.

How does my estimate of SWWA nesting success compare to other species? Martin (1992) found a 46% success rate to be typical for shrub nesting species in the forested landscape. In South Carolina bottomland hardwood forests, Sargent et al. (1997) found Hooded Warblers to have a 29% nesting success rate and Kentucky Warblers 35%. In that framework, SWWA appears to be doing fairly well on the Woodbury Tract with a success rate of 60%.

1.6.2 Seasonal fecundity

Is nesting success an adequate measure of a site's avian productivity? Typically, Mayfield nesting success estimates are used to assess breeding productivity, a strategy appropriate for single-brooding birds. However, the mating systems of wood warblers appear to be more complex and variable than once thought (Graves 1992), making productivity a function of more than nesting success alone. Not accounting for multiple nesting attempts leads to conservative estimates of avian productivity (Nagy and Holmes 2004, Thompson et al. 2001).

Traditionally, researchers believed Neotropical migrants did not have time to rear more than one brood per season (Holmes et al. 1992). Although most temperate zone wood warblers are single brooded, studies of marked individuals have indicated double brooding to be an uncommon, but regular occurrence in several species (Miller 2003). Holmes et al. (1992) found double brooding to be the most important cause of high annual production in Black-throated Blue Warblers. Ogden and Stutchbury (1996) found double-brooded Hooded Warbler females to produce 60% more fledglings than single-brooded females, a phenomenon I observed in SWWA as well.

Multiple nesting attempts more than doubled SWWA fecundity, with multiple nesting females averaging 3.7 young, compared to 1.5 young per single-brooded female. In the population as a whole, multiple brooding increased fecundity estimates from 1.5 to 1.9 young per female, but was not a significant increase. I cannot compare SWWA fecundity on the Woodbury Tract to other areas, because no other estimates have been published. Fecundity estimates for other forest breeding passerines are as follows: Prairie Warblers (*Dendroica discolor*) fledged 1.1 fledglings per female (Nolan 1978), 3.0 young per Wilson's

Warbler female (*Wilsonia pusilla*; Stewart 1973), and 2.0 fledglings per Wood Thrush female (*Hylocichla mustelina*; Powell et al. 1999). SWWA females are replacing themselves, and fecundity estimates appear to be in line with other species.

Double brooding can have a significant impact on an individual's fecundity, but its impact on the population as a whole will be minimal if it is infrequent. Is double brooding a common breeding strategy used by SWWA? Miller (2003) published the only account of double brooding in SWWA, where he observed one instance. I documented six cases of double brooding, with 21% of pairs initiating double brooding attempts (2000-2001). Compared to other species, 48% of Black-throated Blue Warbler females initiated a second attempt after their first was successful (Holmes et al. 1992), and 26% of Hooded Warbler females double brooded (Ogden and Stutchbury 1996). Apparently, double brooding is not as rare as previously thought, but potentially a common strategy employed by older birds to maximize reproductive output.

Were 2000 and 2001 unusual years, or are SWWA regularly double brooding? Although I do not have direct evidence for years prior to 2000, plots of nest initiation dates can yield information about double brooding. Holmes et al. (1992) noticed a bimodal distribution of nest initiation dates corresponded with double brooding in Black-throated Blue Warblers. SWWA nest initiation dates followed a bimodal distribution for all years, indicating double brooding to be occurring to some extent each year. The ability of SWWA to support more than one brood on a territory and possibly as many as three, points to the habitat quality found on the Woodbury Tract.

Even though SWWA arrive later than some other warbler species (Meanley 1982), it was still successful at completing multiple brooding attempts. Despite the benefits of

increased fecundity, multiple brooding may have negative consequences for adults. Ogden and Stutchbury (1996) observed double-brooded Hooded Warblers molting three weeks later than single-brooded birds. A delayed molt can postpone an adult's arrival to the wintering grounds, in turn reducing their ability to obtain a winter territory since many migrants are territorial on their breeding grounds (Ogden and Stutchbury 1996). Poor quality winter habitat can result in the accumulation of less fat, in turn impacting spring migration and an individual's productivity.

Rearing two broods required approximately 75 days, assuming 2 days for nest building, 12 days between nesting attempts, and using the mean nesting cycle parameters (Table 2). Fledglings were not self-sufficient once they left the nest- they required at least three more weeks of parental care. While the male cared for the first brood, the female initiated the second attempt. If a pair initiated their first attempt on May 1st, they would require until August 4th to rear both broods. At which point, the parents needed to molt and prepare for fall migration; thus, multiple brooding is a compromise between energetics and reproduction.

1.6.3 Site fidelity

Almost 30% of SWWA adults returned in years subsequent to banding. Some birds demonstrated strong fidelity to previous locations, with 10 birds caught in the same net and six males observed defending identical territories between years. Little information is available regarding SWWA site fidelity, so the next best comparison is to other wood warbler species. Holmes and Sherry (1992) observed 27% of American Redstarts returned the year following banding, and 37% of Black-throated Blue Warblers. Site attachment of

breeding birds is often influenced by the nesting success of the previous season (Holmes and Sherry 1992), and is an indirect measure of habitat quality.

Natal site fidelity does not appear to be strong in SWWA, but I did detect two adults returning to locations less than 2 km from where they banded as juveniles. Holmes et al. (1992) never resighted any of the 300 Black-throated Blue Warbler nestlings they banded, and Eliason (1986) observed 8% of 173 Black Poll nestlings returning. According to Holmes et al. (1992:331), “Returns of birds to natal areas are usually very low, and often difficult to detect if study areas are small.” The fact I observed any juveniles returns is impressive considering the number banded.

1.6.4 Population density

The apparent population density of SWWA on the Woodbury Tract was 17 territories/km². Only two other studies have estimated SWWA population density: Wright and Meyers (unpublished) found 9.4 singing males/km² and Graves (1992) found the highest density ever published, 17 singing males/km². The Woodbury Tract appears to be supporting significant SWWA numbers, since SWWA density is comparable to Graves’ (1992) density estimate. Size of SWWA territories varied dramatically between studies: I found territories to average 1.92 ha; Graves (2001) found territories ranging between 3 -18 ha in the Great Dismal Swamp; and Meanley (1971) mapped territory sizes between 0.12 ha and 1.94 ha.

The Crossroads/Dead Pig site averaged 59 territories/km², compared to the rest of the site with 12 territories/km². In addition to density differences, there were also significant size differences between Crossroads/Dead Pig (1.19 ha) and the rest of the site (1.92 ha). According to Brown and Dickson (1994), “Habitat type and quality are important

determinants of territory size; birds occurring in groups indicating good quality habitat, usually have smaller territories than those in isolated territories.”

SWWA may be semi-colonial as seen in Wood Warblers (*Phylloscopus sibilatrix*) and Pied Flycatchers (*Ficedula hypoleuca*; Bibby et al. 2000). According to Meanley (1969), “During the breeding season SWWA were found in groups or “colonies” like Kirtland’s Warblers, as isolated pairs, or as unmated males”. Meanley (1969) found territory sizes where birds occurred in groups to be smaller than isolated territories, which coincides with my Crossroad/Dead Pig results. Territories in this area overlapped considerably compared to the more isolated territories found on the rest of the site. Due to territory size and overlapping boundaries, I think SWWA is semi-colonial at Crossroads/Dead Pig.

1.6.5 Conclusions

Pairs were almost replacing themselves each season (1.9 young per pair), and many appeared to maximize the number of nests attempted. At least 20% of the population was double brooding, and its impact on fecundity was substantial. Mayfield nesting success was 60% for a 23-day nesting cycle, and the largest cause of nest loss was likely due to depredation followed by BHCO parasitism. Only 10% of SWWA nests were parasitized, but increases in BHCO numbers could have significant impacts on the population. SWWA appears to be a naïve host and suffers a 30% reduction in the number of eggs producing fledglings in the presence of BHCO.

I did not locate every nest. On three occasions, I observed fledglings with males in whose territories I had searched, but did not find nests. Despite intensive nest searching efforts, nests were not discovered in 40% of the territories. A portion of the territories lacked

nests because the males were likely unmated, as evidenced by their singing frequency. However, the majority was likely due to nests missed by researchers, which speaks to the ability of SWWA to conceal nests (at least from researchers). Even if a nest was discovered on a territory, how likely is it I found all attempts? For this reason, it is probable my estimate of multiple brooding was conservative.

Information about the post-fledging period is important, but difficult to collect. Typically, studies are only able to use nesting success as an estimator of productivity, although juvenile survival is known not to be 100%. Powell et al. (1999) found productivity was overestimated when juvenile survival was ignored. Radio transmitters could be used to assess juvenile survival and also track within season dispersal movements. My post-fledging information indicated juveniles remain on the male's territory up until three weeks after fledging at which point they disappear. Nolan (1978) found Prairie Warbler juveniles to move off a male's territory after approximately three weeks. For management purposes, it would be important to know what type of habitat SWWA juveniles require in order to plan habitat needs.

Banding, nesting, and territory results all indicated the Crossroads/ Dead Pig area to contain the highest density of SWWA. Territory size was smaller in the high versus low-density area, which may indicate increased habitat quality at Crossroads/ Dead Pig (Meanley 1971, Nolan 1978). More nests were also discovered there along with higher numbers of SWWA banded and recaptured. Can I pinpoint characteristics driving SWWA density on the site? In the next two chapters, I will examine the influence of physiognomic and floristic factors at landscape and microsite levels on SWWA distribution. Understanding forces

affecting SWWA distribution at the site level would be important for guiding management decisions.

One factor exerting an influence on SWWA, whether directly or indirectly, is hydrology. In a bottomland hardwood forest, hydrology is the driving force behind vegetative distribution, soil composition, and litter fauna (Martin et al. 1993). Hydrology directly impacted nesting phenology, with May flooding events delaying nest initiation by as much as three weeks. Plus, many believe SWWA to be inextricably linked with cane (Eddleman 1980, Meanley 1971, Thomas et al. 1996), a plant that grows in the highest elevations of the bottomland (Martin et al. 1993). Another critical factor for SWWA that is affected by hydrology is the abundance of leaf litter fauna. Few investigators have examined the litter fauna of Zones II through V (Martin et al. 1993), and no studies have looked at SWWA distribution compared to invertebrate abundance. Altered hydrologic regimes, resulting from flood control and hydroelectric power generation, may be a threat to SWWA, through interruption of normal hydrologic cycles thus affecting litter fauna and vegetation.

How similar is my site to other managed southern bottomlands? The site was allowed to naturally regenerate and has not been intensively managed since the harvest. Is this a common management strategy for other managed bottomland hardwood forests? If not, it may be important to work with foresters to encourage them to manage their site in a similar fashion. Is this SWWA population representative of others? Research is needed at additional managed sites for comparison to my productivity estimates.

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Table 1. Detection history of SWWA from 1996-2001, Britton's Neck, South Carolina; numbers off the diagonal represent birds not detected every season of the observation period.

Observation Period	Number seasons detected					TOTAL
	1	2	3	4	5	
1 year	231					231
2 years		32				32
3 years		5	13			18
4 years		2	3	2		7
5 years		2	0	0	2	4
TOTAL	231	41	16	2	2	292

Table 2. Mean SWWA nest cycle parameters in Britton's Neck, South Carolina, 1998-2001.

Parameter	<i>n</i>	Number (SE)	Range
Nest empty ¹	14	2.64 (0.51)	1-6
Egg laying ²	14	3.07 (0.24)	2-5
Clutch size ³	76	3.10 (0.10)	1-7
Incubation period ⁴	14	13.85 (0.27)	11-15
Chicks ⁵	55	2.60 (0.12)	1-6
Nestling period ⁶	17	9.94 (0.10)	9-11
Fledglings ⁷	33	2.39 (0.16)	1-4
Nesting cycle ⁸	7	23.28 (0.61)	20-25

¹ Days nest empty before egg laying.

² Days of egg laying from first egg to last.

³ Eggs laid per active nest.

⁴ Length of incubation from the last egg laid until hatching.

⁵ Chicks hatched per active nest.

⁶ Length of nestling period from hatching until fledging.

⁷ Fledglings per successful nest.

⁸ Length of nesting cycle from start of incubation through fledging.

Table 3. SWWA nest outcomes in Britton's Neck, South Carolina, 1997-2001.

Nest Outcome	1997	1998	1999	2000	2001	TOTAL
Successful	0	5	5	10	10	30
Failed	1	2	7	6	6	22
BHCO parasitism	0	1	1	3	3	8
Unknown	2	5	5	3	4	19
Total Active	3	13	18	22	23	79

Table 4. Daily SWWA nest survival rates, exposure days, and losses divided by nesting period and year, Britton's Neck, South Carolina, 1997-2001.

Year	<i>n</i>	INCUBATION			NESTLING			POOLED
		Exposure Days	Losses	Daily Survival (SE)	Exposure Days	Losses	Daily Survival (SE)	Daily Survival (SE)
1997	3	34.0	1	0.970 (0.029)	13.0	0	1.0	0.979 (0.021)
1998	13	62.0	2	0.968 (0.022)	58.0	0	1.0	0.983 (0.012)
1999	18	160.5	4	0.975 (0.012)	74.0	1	0.986 (0.013)	0.979 (0.009)
2000	22	211.5	5	0.976 (0.010)	118.5	3	0.975 (0.014)	0.976 (0.008)
2001	23	232.5	5	0.978 (0.009)	124.0	2	0.984 (0.011)	0.980 (0.007)
All years	79	700.5	17	0.976 (0.006)	387.5	6	0.984 (0.006)	0.979 (0.004)

Table 5. Nest cycle parameters from SWWA breeding biology studies ($n > 2$ nests).

Researchers	<i>n</i>	BHCO Parasitism	Clutch size (SE)	Fledglings per nest (SE)	% Successful (fledged/total)	Daily Survival Rate (SE)	Mayfield Nesting Success, % (95% CI)
Meanley 1969	36	3	2.90 (0.23)	-	19	-	-
Peters 1999	16	1	2.82 (0.13)	1.20 (0.36)	31	0.982 (0.010)	65.5 (40.4- 100)
Sims & DeGarmo 1948	16	3	-	-	37	-	-
Thomas et al. 1996	17	0	3.65 (0.12)	2.12 (0.36)	70	0.980 (0.013)	62.5 (33.8- 100)
Thompson 2005	63	6	3.10 (0.10)	2.39 (0.16)	38	0.978 (0.005)	59.6 (47.6- 74.5)

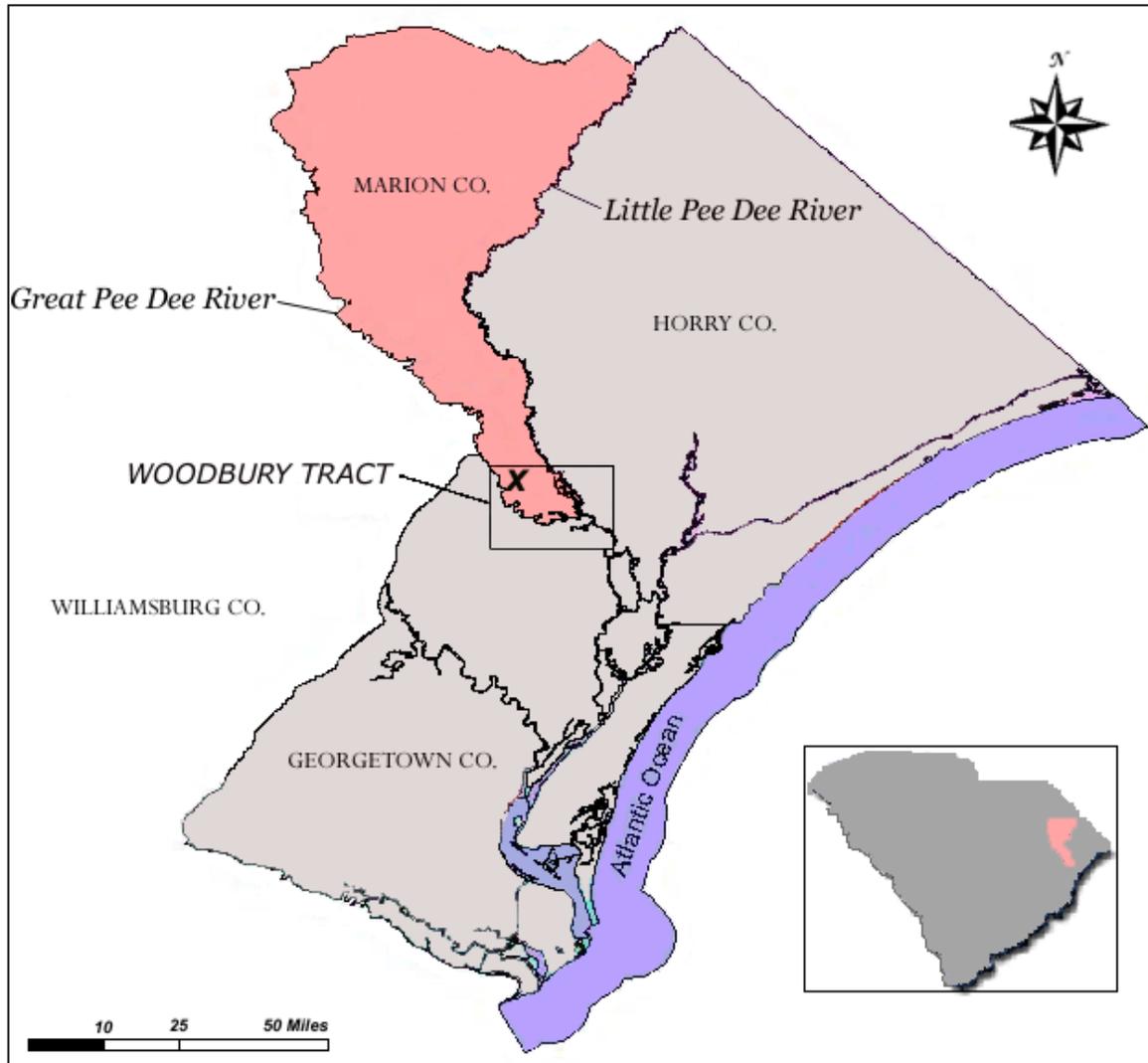


Figure 1. Location of Woodbury Tract at the confluence of the Great and Little Pee Dee rivers; research site (X) located on northwestern side of Tract in Britton's Neck, South Carolina (1996-2001), inset highlights Marion County, South Carolina.

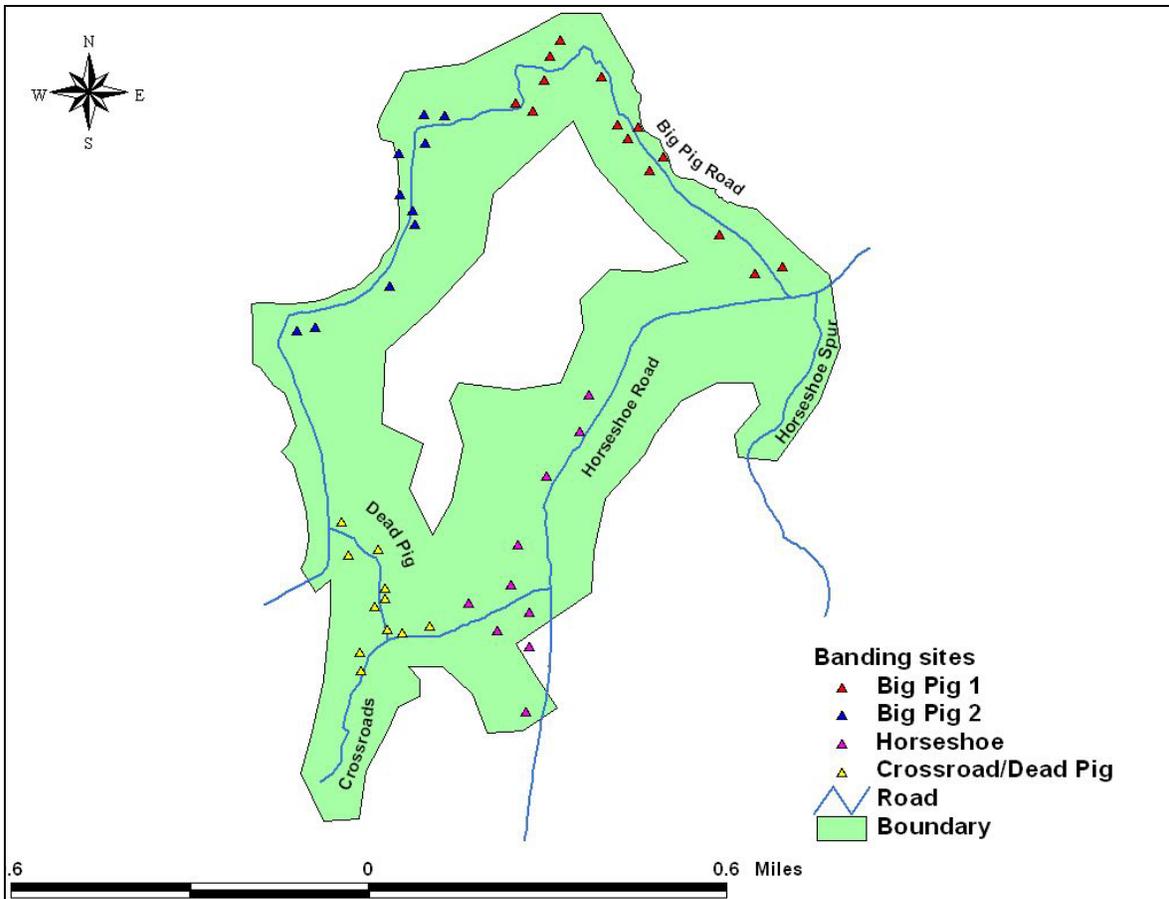


Figure 2. Banding sites and net locations ($n = 45$) in Britton's Neck, South Carolina, 1999-2001. Boundary delineates sampling area for nest searching and territory mapping.

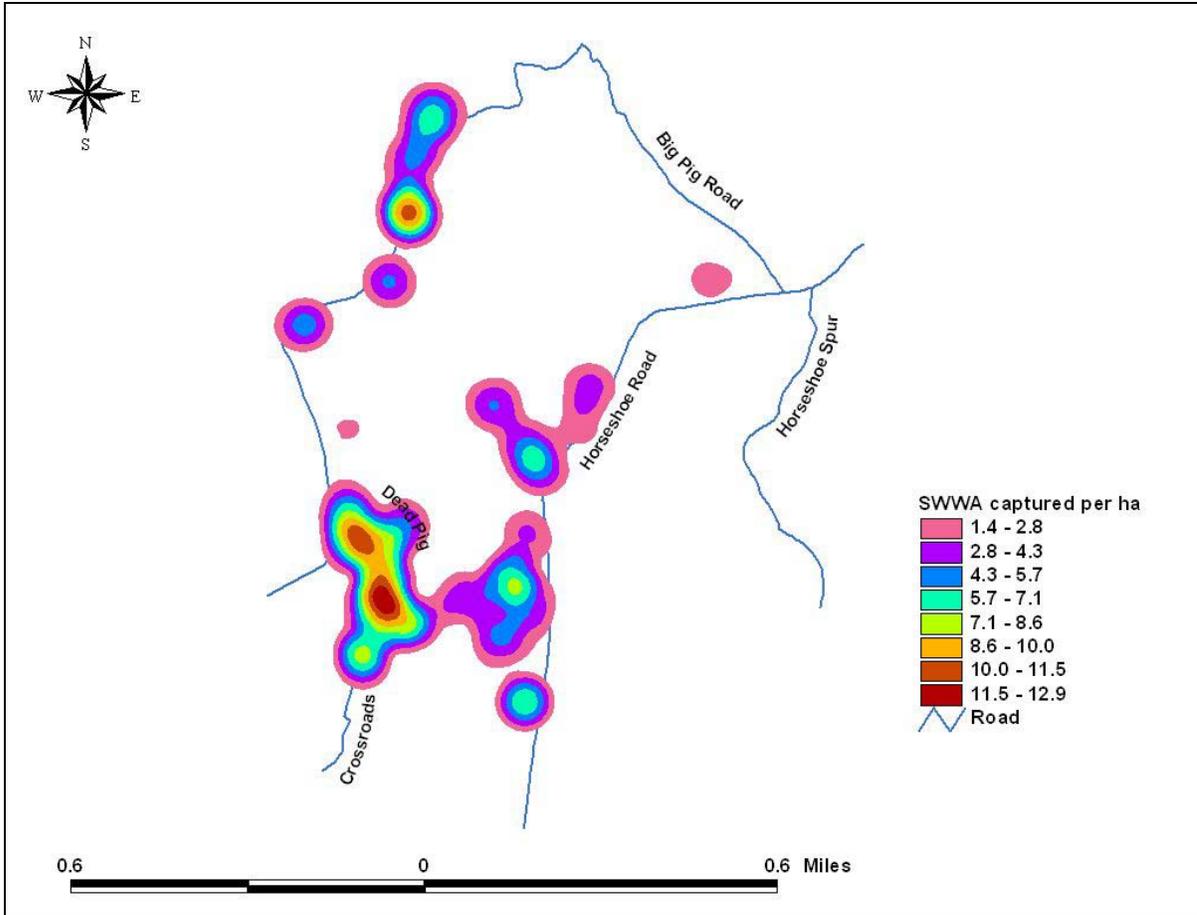


Figure 3. Initial SWWA capture density ($n = 292$) calculated using a kernel density estimator with 100-m radius, Britton's Neck, South Carolina, 1996-2001.

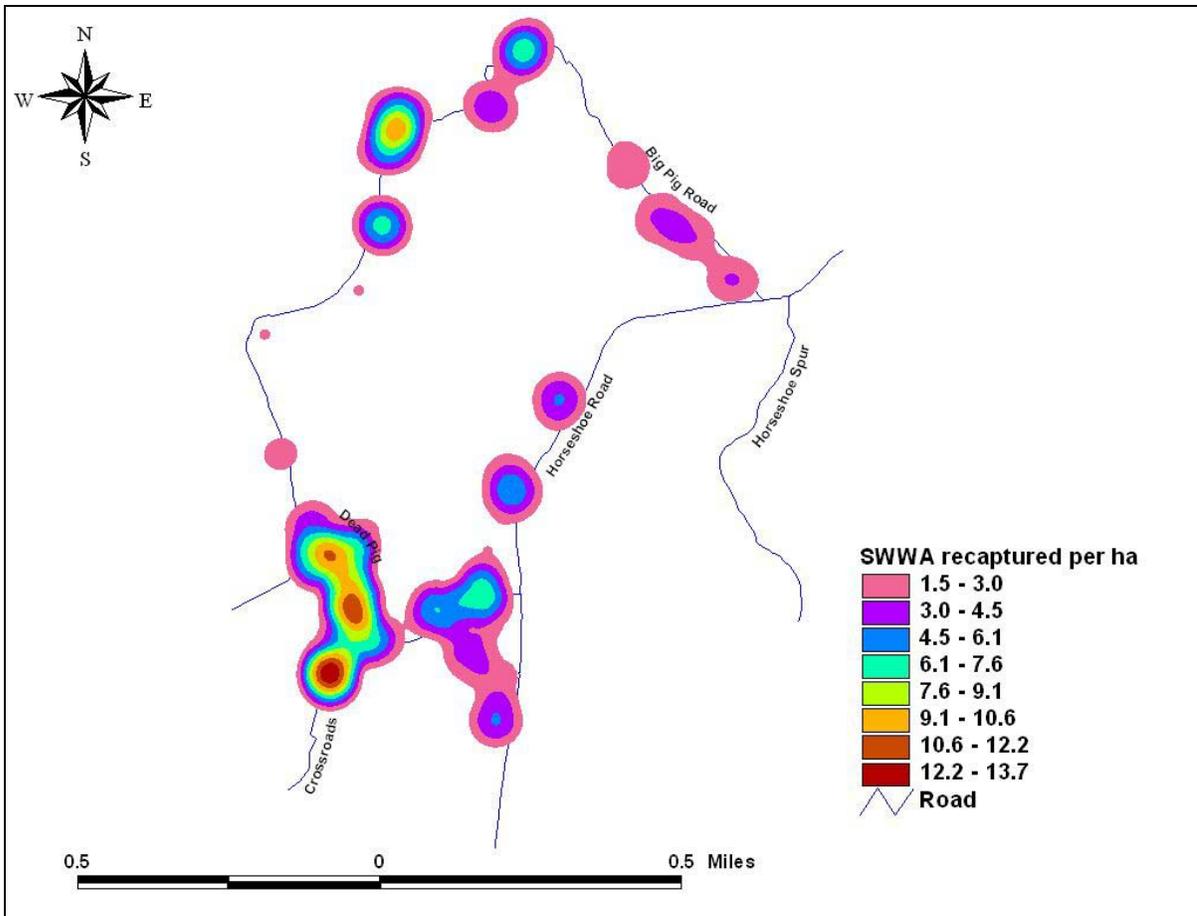


Figure 4. Recaptured SWWA density ($n = 202$), including within and between year recaptures, calculated using a kernel density estimator with 100-m radius, Britton's Neck, South Carolina, 1997-2001.

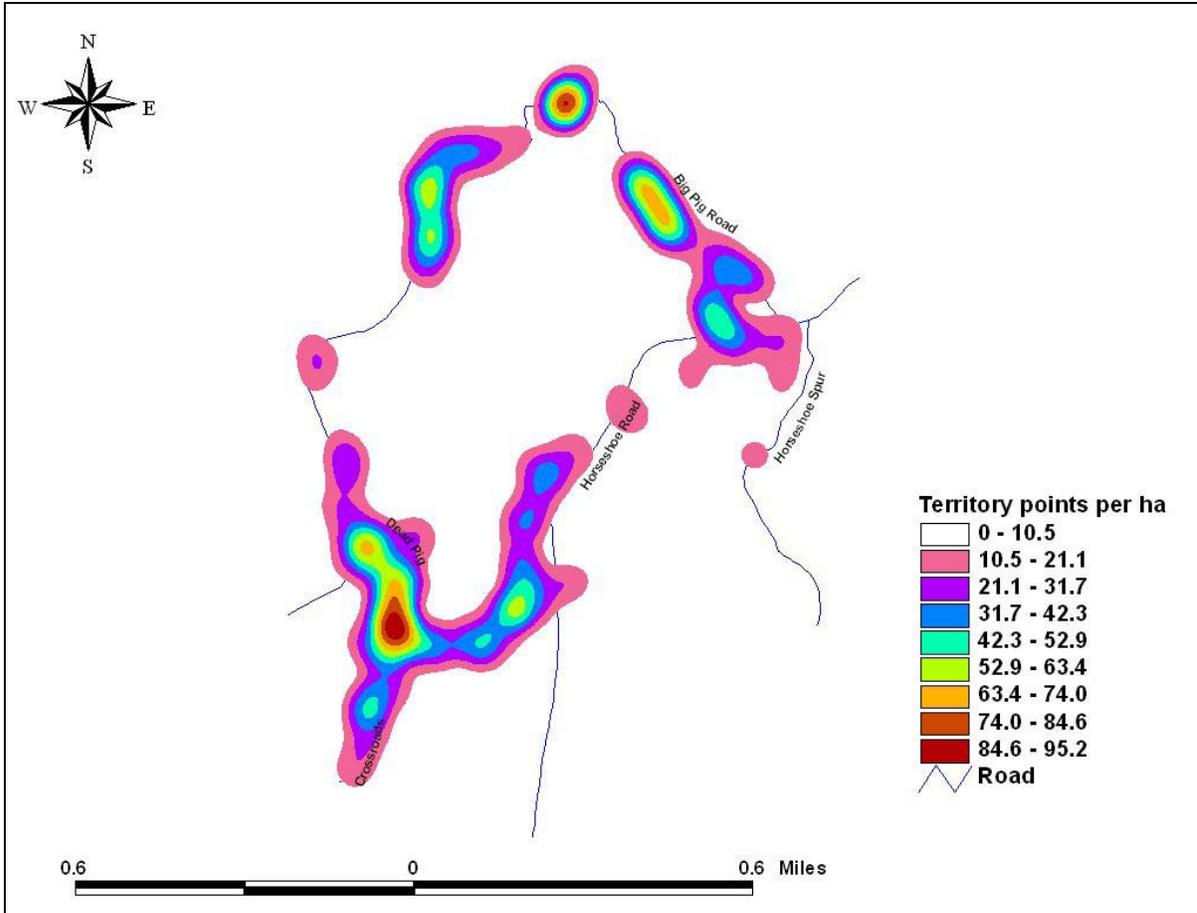


Figure 5. SWWA territory point density ($n = 2,967$) calculated using a kernel density estimator with 100-m radius, Britton's Neck, South Carolina, 1999-2001.

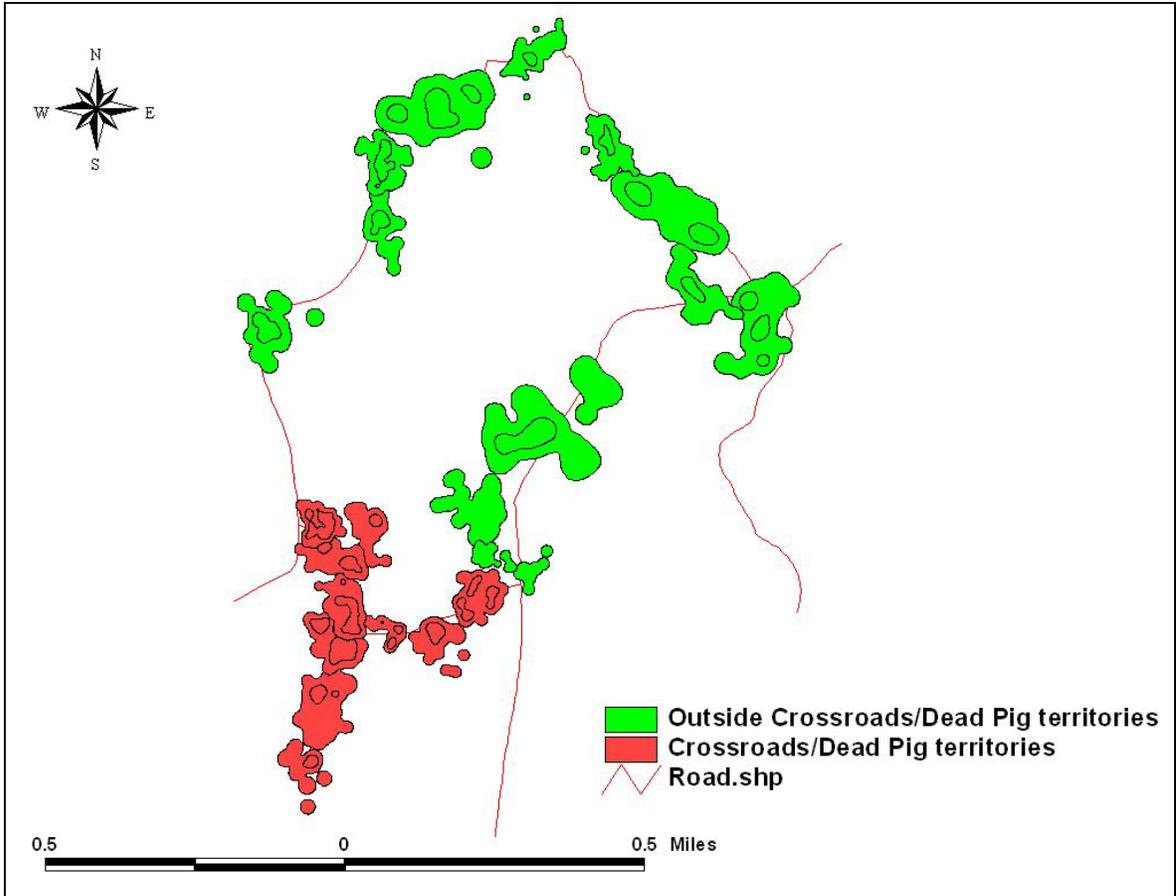


Figure 6. 1998 SWWA territories in Britton's Neck, South Carolina; ellipsoids inside territories represent male locations 50% of the time.

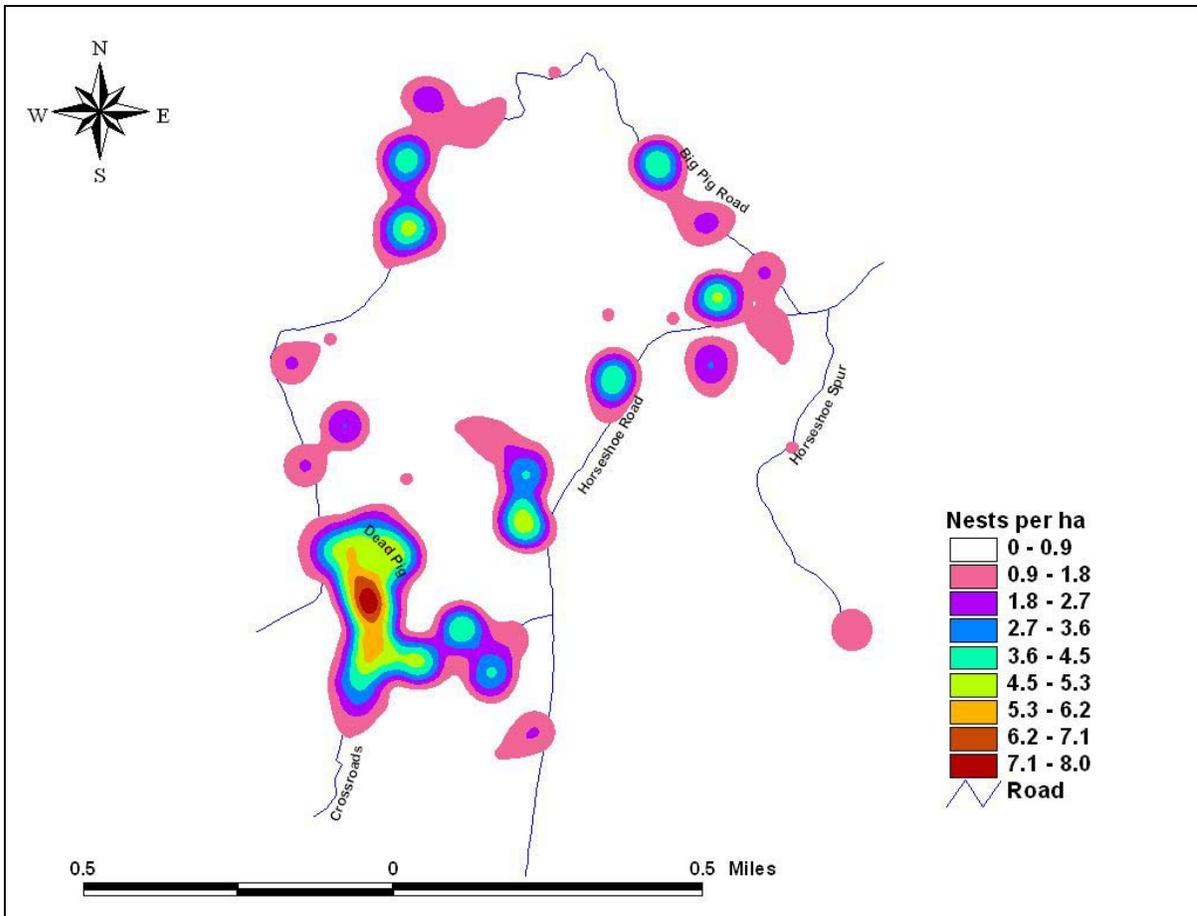


Figure 7. SWWA nest density ($n = 150$) calculated using a kernel density estimator with 100-m radius, Britton's Neck, South Carolina, 1997-2001.

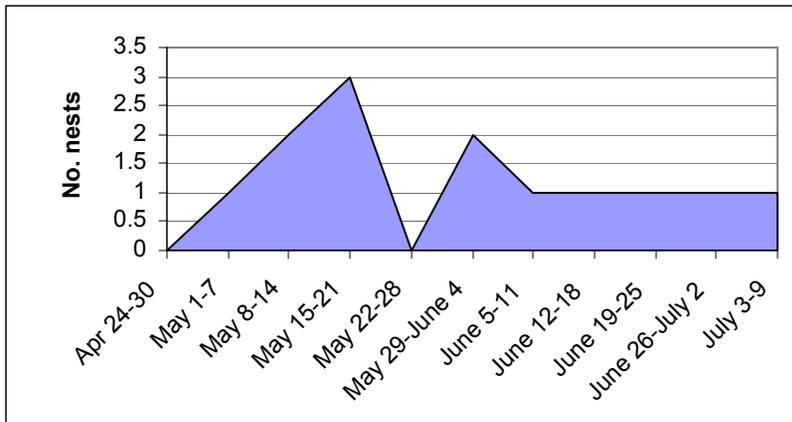


Figure 8. Initiation dates of 1998 SWWA nests in Britton's Neck, South Carolina ($n = 13$).

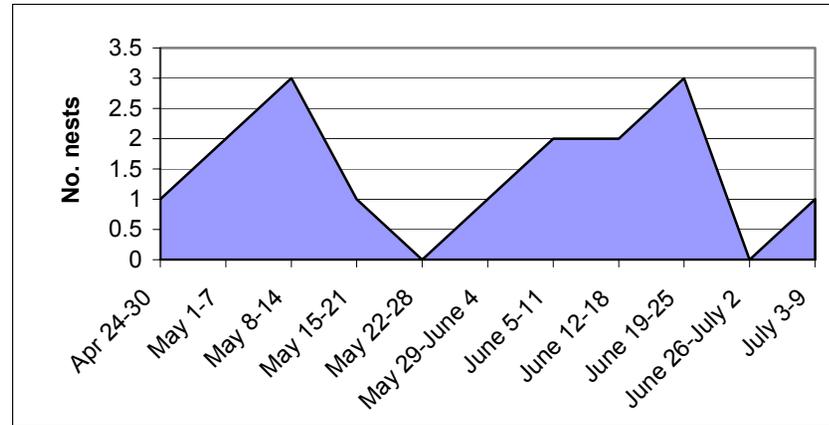


Figure 9. Initiation dates of 1999 SWWA nests in Britton's Neck, South Carolina ($n = 18$).

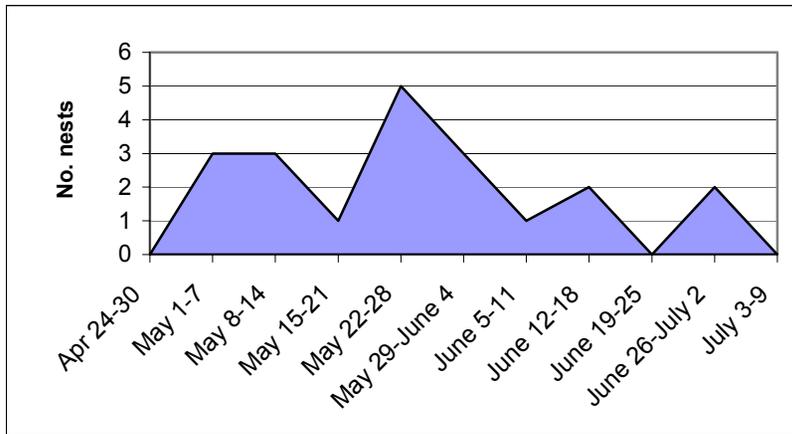


Figure 10. Initiation dates of 2000 SWWA nests in Britton's Neck, South Carolina ($n = 22$).

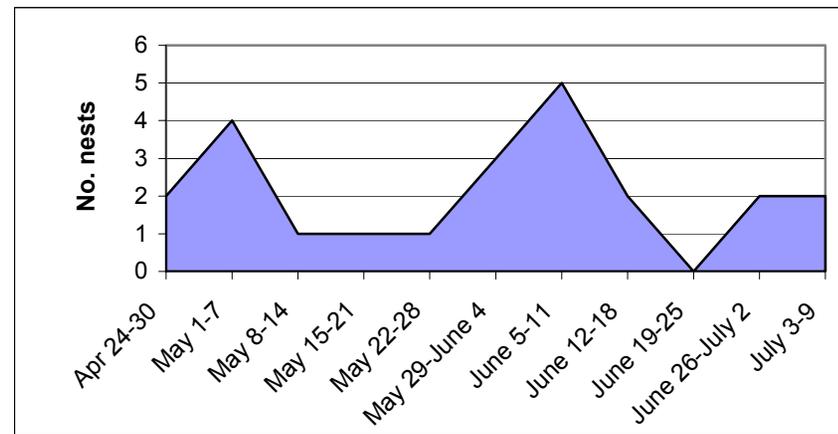


Figure 11. Initiation dates of 2001 SWWA nests in Britton's Neck, South Carolina ($n = 23$).

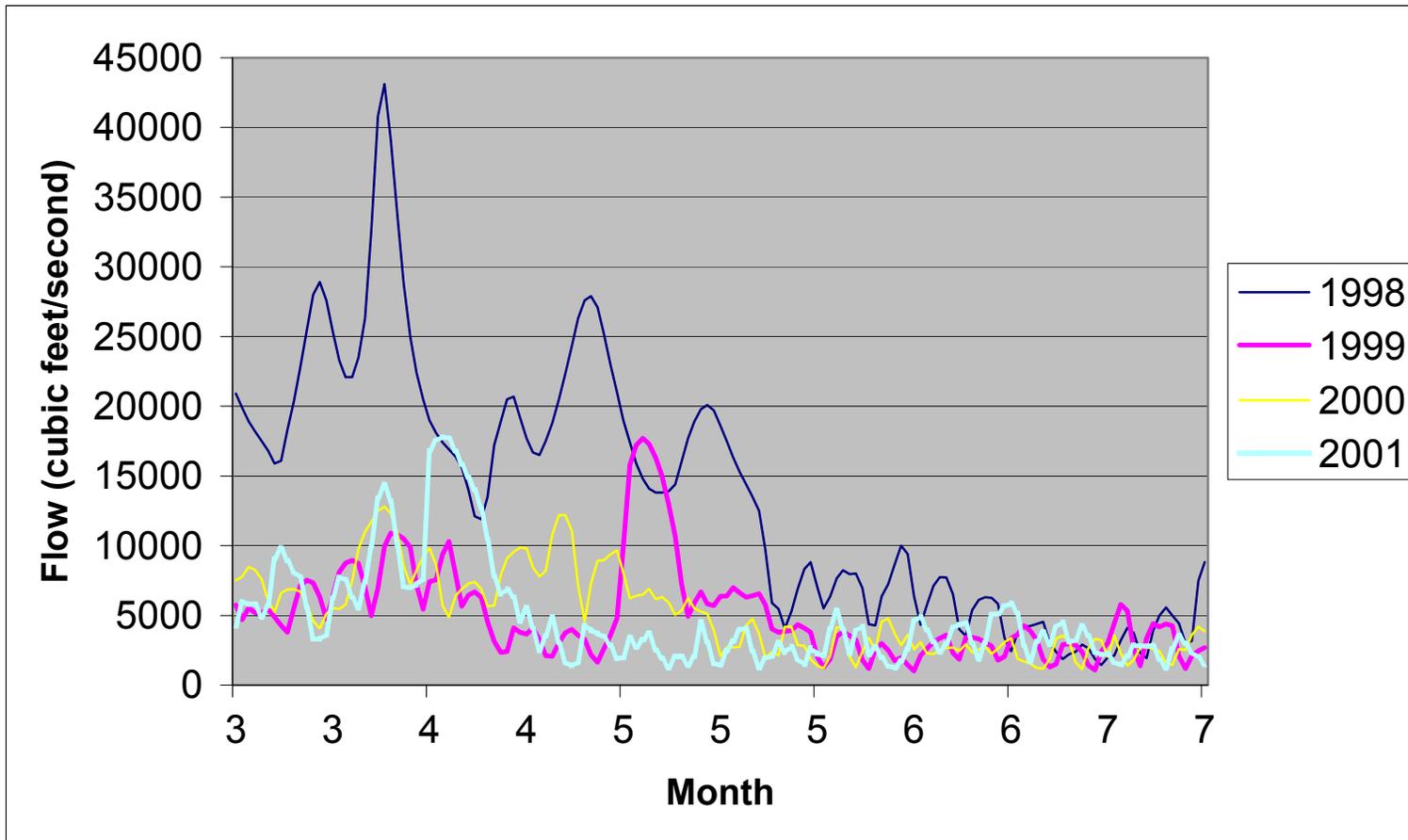


Figure 12. Hydrograph of water releases from Pee Dee dam on Great Pee Dee River from March-July 1998-2001, 30 miles upstream of Woodbury Tract.

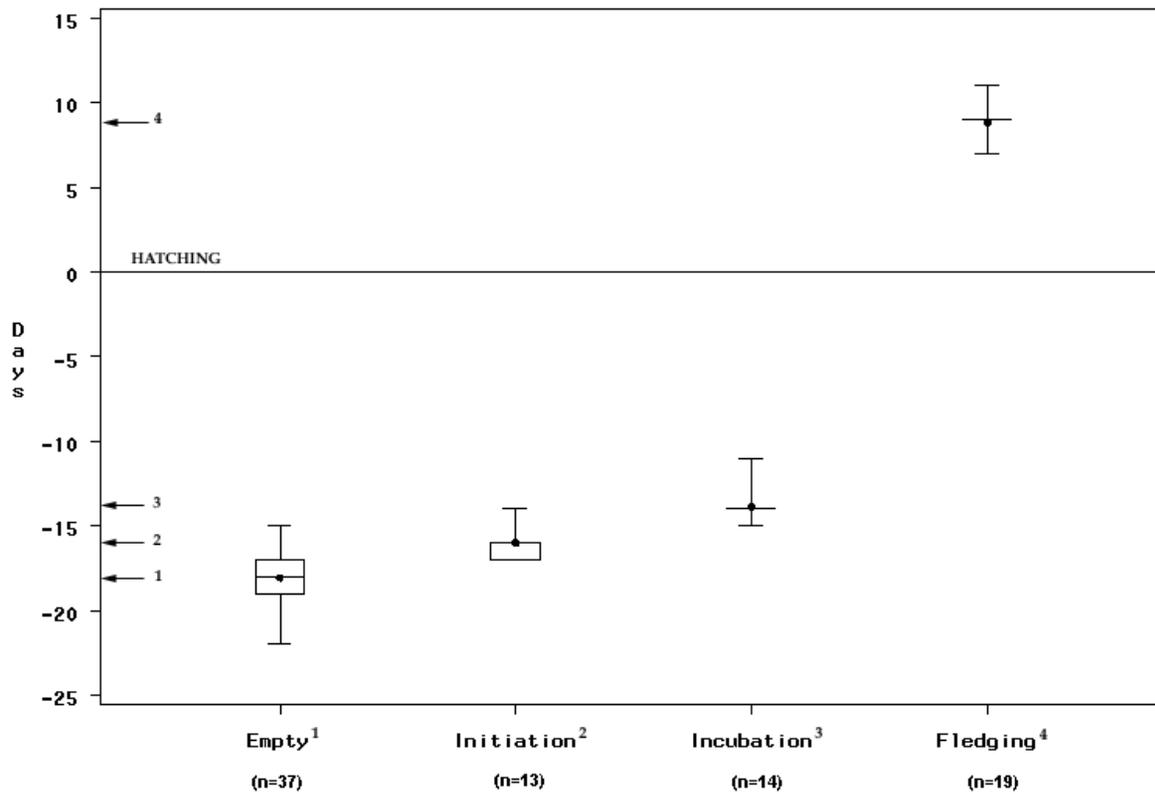


Figure 13. Mean day of activity for completion of nest building, initiation, incubation, and fledging; y-axis arrows indicate mean for each category, Britton's Neck, South Carolina, 1999-2001.

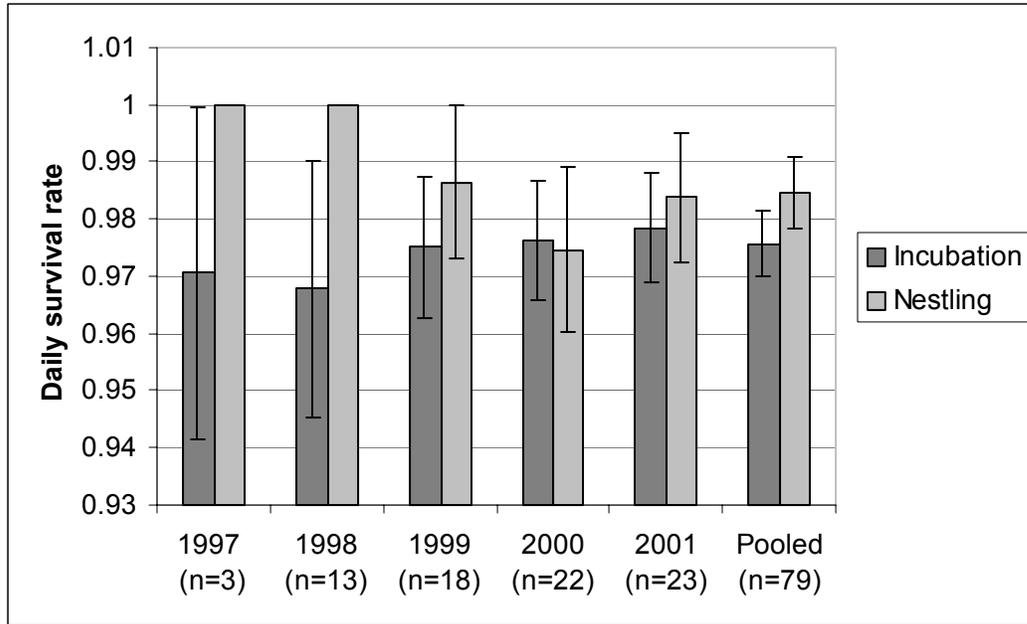


Figure 14. Daily survival rates of SWWA nests during incubation and nestling periods, 1997-2001, Britton's Neck, South Carolina.

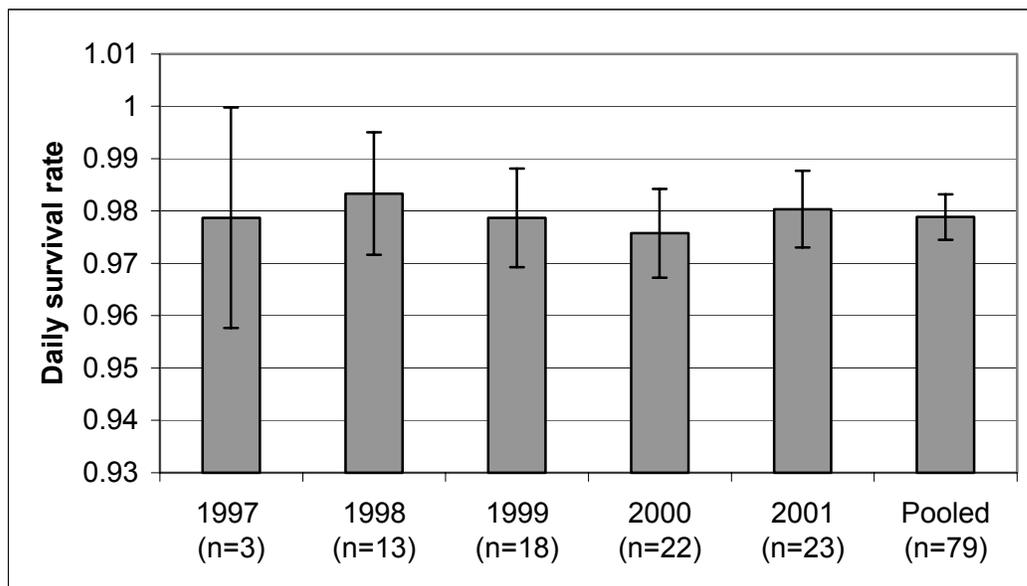


Figure 15. Daily survival rates of SWWA nests with pooled incubation and nestling periods, 1997-2001, Britton's Neck, South Carolina.

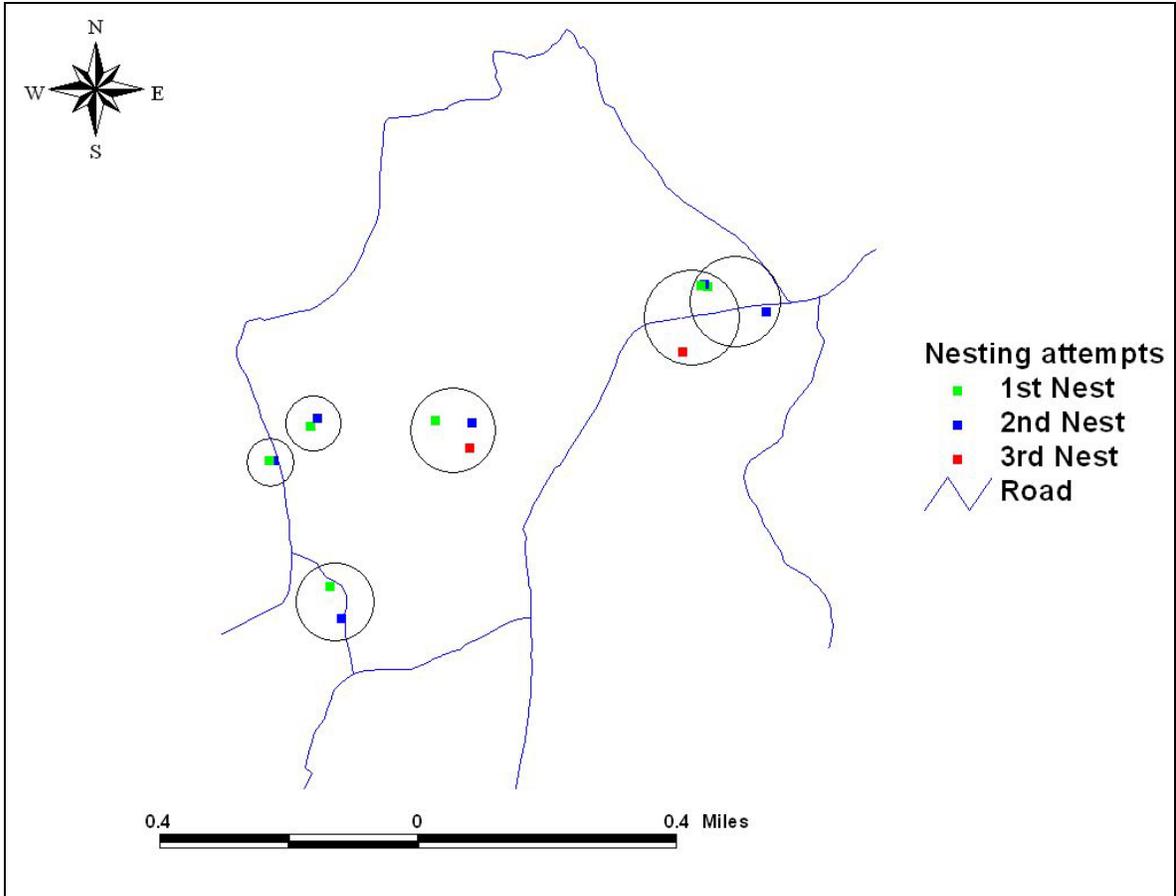


Figure 16. SWWA nesting attempts initiated by multiple-brooding pairs in Britton's Neck, South Carolina, 2000-2001; nests located in the pair of overlapping circles were initiated by the same male over two years.

CHAPTER 2

HABITAT USE BY SWAINSON'S WARBLER AT NESTS BUILT IN HIGH AND LOW-DENSITY SITES AND WITH DIFFERENT OUTCOMES

2.1 INTRODUCTION

SWWA has long been associated with giant cane (*Arundinaria gigantea*), harkening back to Brewster's early account describing cane as an essential component of prime habitat (1885). Meanley (1945:395) agreed saying, "Cane in a mature or immature form *must* be present, and I know of no occasion when I have seen or heard this warbler on its breeding grounds that a growth of cane was not in sight." However, SWWA has been identified in a diversity of habitats, some lacking cane completely (Graves 2002): young loblolly pine plantations (3-18 years old, Carrie 1996), managed bottomland hardwood forests (< 30 years old, Peters 1999), young hemlock (Lanham and Miller unpublished), rhododendron-laurel thickets (Brooks and Legg 1942), old and second growth bottomland hardwood forests (Meanley 1971), and mature cove hardwoods (Meanley 1966). Typical notions of SWWA favoring "damp bottomland hardwoods with good growth of cane" (Brown and Dickson 1994:4) may need to be rethought.

Studies of breeding populations in Missouri and Illinois, at the periphery of SWWA range, indicate cane to be a critical habitat component (Eddleman et al. 1980, Thomas et al. 1996). However, habitat requirements of core breeding populations in Georgia and South Carolina may differ. Graves (2002) found no cane at a site in Georgia with the highest SWWA population density on record, and also observed less cane in territories compared to non-use plots in the Great Dismal Swamp (Graves 2001). Other factors important to SWWA distribution have been identified as greenbrier (*Smilax* spp.) abundance (Graves 2001), the absence of standing water (Graves 2001), and the presence of vine masses (Peters 1999). At my field site in South Carolina, Peters (1999) found vine cover to be the primary characteristic associated with SWWA distribution. However, at a nearby older site

(harvested in 1970), cane was the primary characteristic (Peters 1999). Accordingly, Graves (2001, 2002) and Peters (1999) believe hydrology, floristics, and disturbance regime all interact to influence SWWA habitat preferences, rather than a single habitat attribute.

Aside from being viewed as a species dependent on cane, SWWA is typically linked with mature forests for breeding. According to Dickson et al. (1993), habitat management plans should set aside mature bottomland forests and allow young stands to mature. Suggestions for harvest are typically limited to small operations geared towards cane regeneration and maintenance in mature forests (Eddleman et al. 1980, Pashley and Barrow 1993). Typically, management plans overlook early successional habitat for SWWA conservation, even though studies on the Atlantic and Gulf Coast indicate a preference for early successional forest or disturbance gaps in primeval forest (Carrie 1996, Peters 1999, Graves 2001, Lanham and Miller unpublished). In the first chapter, I documented a SWWA population successfully breeding on industrial forest in 20-year-old regenerating clearcuts, not the typical portrayal of prime SWWA habitat.

Collectively, these studies suggest current management plans and conservation efforts for SWWA should be redefined. In particular, recommendations for core breeding populations should not be predicated on data obtained from geographically peripheral populations (Graves 2002). More research is needed on populations in the core area and those using early successional forest, to examine the role of cane and other factors. Most published information on SWWA is descriptive and lacks quantitative analysis (Brown and Dickson 1994). Only six quantitative habitat studies have been conducted, three of which were in the core region (Graves 2002, Peters 1999, Somershoe et al. 2003).

Of six habitat studies, only two have intensively examined vegetation at SWWA nests

($n > 5$; Peters 1999, Thomas et al. 1996). Other studies focused on SWWA habitat usage at: male singing perches (Eddleman et al. 1980, Somershoe et al. 2003), occupied canebrakes (Thomas et al. 1996), and territories (Peters 1999, Graves 2001, 2002). Despite its importance, vegetation at the nesting site has received little attention, due to the scarcity of nests discovered. Caughley (1994) stressed the importance of incorporating both habitat and demographic information into conservation planning. The presence of individuals is no guarantee that habitat is positively related to habitat quality (Caughley 1994).

Nest site availability has been shown to affect the distribution of some avian species, a pattern long recognized in cavity nesters but only more recently suggested in open cup nesting species (Martin 1988, Steele 1993). Steele (1993) found nest site requirements to be more important than foraging sites, in habitat selection by Black-throated Blue Warblers (*Dendroica caerulescens*). According to Martin and Roper (1988), an advantage of habitat containing many potential nest-sites is less efficient predator searches, thereby reducing nest predation. SWWA shares Black-throated Blue Warbler's preference for nesting in dense understory and is an open-cup nester as well, thus nest site availability may be a factor in SWWA distribution. An illustration of this phenomenon may be the larger SWWA territories found in mature forests compared to early successional forests (Graves 2002), resulting in far lower breeding densities in mature forests. Thinner understory results in fewer nest sites, in turn forcing males to defend larger areas in order to contain adequate nest sites.

Nest site availability may drive distribution within similar habitat. As was seen in Chapter 1, Crossroads/Dead Pig had the highest SWWA population density, capture rate, and productivity of the site (Figure 1). Considering the relatively small size of the study area and

its identical harvest history, the difference in site occupancy is surprising. Does Crossroads/Dead Pig offer more available nesting habitat than the rest of the site? Are there vegetative differences between nests located in Crossroads/Dead Pig compared to the rest of the site? I will explore these questions in Chapters 2 and 3. Besides vegetation, foraging sites and predation could play a role in SWWA distribution, areas of research beyond the scope of this project.

Scale is an important consideration when investigating habitat associations. Martin (1992) called for studies to examine habitat associations at multiple scales. Hill and Hamer (2004) report the spatial scale of sampling can have marked effects on the results obtained, and suggest future studies address this issue by examining effects at different spatial scales. I investigated SWWA habitat associations at the local and individual level. Did vegetation around nest sites differ at the local level, namely the high versus the low-density area? Evidence suggests passerines choose among gross habitat types on the basis of physiognomy, but may be sensitive to floristic cues when selecting microhabitats (Rotenberry 1985). Did nest sites differ in terms of floristic or physiognomic factors? I used discriminant analysis to investigate these questions with three main hypotheses: 1) nests built in the Crossroads/Dead Pig area were closer to understory thickets than nests found on the rest of the site, 2) successful nests were more concealed by understory thickets compared to failed nests, and 3) physiognomic factors were more important than floristic factors at driving nest distribution.

2.2 METHODS

2.2.1 Vegetative sampling

I used a modified version of the James and Shugart method (1970) to sample vegetation, with parameters similar to those used in BBIRD standard protocol (Montana Cooperative Wildlife Research Unit 1997, Peters 1999). Nest site and nest patch characteristics were measured in July, at least a week after fledging in order to minimize disturbance to juveniles. Microhabitat data, such as nest height and substrate species, were collected at the nest site, and vegetation was sampled inside three circular plots with 5, 11.3, and 50-m radii from the nest (Figure 2). The 5 and 50-m plots were further subdivided into four quadrats according to the four cardinal directions. A total of 44 habitat variables (Table 1) were measured at 83 active and inactive nests. Not all 98 nests could be included in the vegetative sampling (1999-2001), because some were still active at the end of the field season.

Nine microhabitat variables were measured describing features of the nest and substrate species. In the 5-m plot (0.0078 ha), counts were made of cane, blackberry (2001 only), and small woody stems less than 8-cm diameter at breast height (dbh). Woody stems were identified to species, and all but vine stems were counted. Instead, vine species were recorded as being present or absent. All counts were reported in stems per ha rather than stems per plot, in order to allow a comparison between variables measured in different plots. Litter depth was measured along the four cardinal directions at 2.5 and 5 m from the plot center. I visually estimated the percent of ground covered by each of twelve ground cover variables: bare ground, cane, fern, forbs, grass, leaf litter, logs, marsh, palmetto, shrub, vines, and water.

In the 11.3-m plot (0.040 ha), a count was made of woody stems greater than 8-cm dbh. Count data were recorded according to species, and divided between one of 13 size classes ranging from 8 to >68-cm dbh. Counts were used to calculate the basal area per ha, following James and Shugart's approach (1970):

$$B = \sum_{i=1}^{14} \left[\frac{7.854 \times 10^{-5} DBH^2 S_i}{A} \right],$$

where B was the basal area per ha, S_i the count of a size class, DBH the median value of each size class, and A the plot size. Dominant canopy and midstory species were recorded at each plot, along with respective heights. In addition, vertical density of the understory was measured using a 2.5-m x 10-cm cover board divided into 5 sections. At each section, the percent of the board covered by vegetation was recorded.

Many terms are used in the literature to refer to areas of dense understory, such as canopy gaps, light gaps, treefall gaps, or vine masses. The terminology is confusing because canopy, treefall, and light gaps refer to canopy structure. Although canopy openings often result in thick understory, the relationship is not infallible thereby making these terms indirect descriptors. The terms understory thicket and vine mass are more appropriate, because they refer directly to the understory structure. However, vine mass is less suitable, because it restricts composition to vine species alone, where many other plant types can be found in dense understory, such as cane, blackberry, saplings, or shrubs. Understory thicket provides the clearest description of understory structure.

In the 50-m plot (0.78 ha), the distance of understory thickets from the nest and their corresponding size were measured. To be classified as an understory thicket, the area had to be large and thick enough to require a machete to traverse. Only one understory thicket was

mapped per cardinal direction. This strategy worked well to estimate thicket density in the immediate nest vicinity, but may have underestimated numbers near plot edges. Thicket data were used to calculate: percent of 0.78-ha plot covered by thickets, thicket density within 10 m and 25 m of the nest, size of closest thicket, mean size of thickets, and distance to the closest thicket. Thicket host species were recorded along with vine species present. In addition, distance to the nearest road, slough, and swamp from the nest was measured.

2.2.2 Statistics

All analyses were performed using SAS Version 8 software (SAS Institute Inc. 1999-2001). I used a canonical discriminant analysis to identify habitat variables contributing to the largest differences between: 1) core and noncore nests, 2) successful versus failed nests, and 3) 2 x 2 matrix of area versus nest outcome. Core nests will henceforth refer to the Crossroads/Dead Pig area, and the rest of the site will be known as noncore (Figure 3). I used the Kernel density estimates from Chapter 1 to delineate boundaries between areas, with the core area encompassing 17 ha and the noncore 133 ha.

Assumptions of discriminant analysis are that the data in both groups have a multivariate normal distribution and the covariance matrices of each group are the same (Der and Everitt 2002). SAS procedures allow you to test each of these assumptions. The advantage of using multivariate over univariate approaches is that overlapping classes may be more distinct when examined from a multivariate point of view rather than viewed separately (SAS Institute Inc. 1989). The following procedure was used for each of the three tests.

I reduced the original 44 variables to 16 by removing those thought to be highly correlated or insignificant (Figure 4). Variables were tested for normality using Shapiro-Wilk goodness of fit tests and normal probability plots (PROC UNIVARIATE). If variables were non-normal, a log, square root, or $\log(X + 1)$ transformation was used to correct the distribution. Log transformations were not appropriate for variables with zero values, in which case $\log(X + 1)$ was more suitable.

Some variables were non-normal even after transformation; therefore, a nonparametric test was necessary. A Kruskal-Wallis ANOVA was used to further reduce the number of variables by throwing out those with H values less than 1, since they were most likely to be noise (Huberty 1994). All remaining variables were entered into a stepwise discriminant analysis (PROC STEPDISC) to find a subset best describing the differences between classes. Variables were chosen to enter or leave the model according to a 0.10 significance level from an F test of an analysis of covariance, where variables already chosen act as covariates and the variable under consideration is the dependent variable (SAS Institute 1989). A 0.10 significance level is more conservative than the SAS default of 0.15 (SAS Institute Inc. 1989).

Finally, variables chosen by the stepwise analysis were used in a canonical discriminant analysis (PROC DISCRIM). Despite some non-normal variables, a parametric analysis was used since discriminant analysis is known to be robust against departures from normality (Hand 1981). A Chi-square test examining the homogeneity of within covariance matrices was used to determine whether a quadratic or a linear discriminant function was needed.

Cross-validated results were used to assess the performance of each discriminant analysis. Cross-validation, also known as the leaving-out method, derived the discriminant function on the basis of $(n - 1)$ subjects and was then used to classify the observations not included (Der and Everitt 2002). The procedure was repeated n times, each time omitting a different observation, with the results summarized in a classification matrix (Der and Everitt 2002). Cohen's kappa statistic, K , was calculated for each classification matrix to test whether the model classified observations significantly better than chance alone (Titus et al. 1984, Norment 1993). Cohen's kappa statistic was calculated using the following equation:

$$K = \frac{\hat{P}_o - P_c}{1 - P_c},$$

where \hat{P}_o is the proportion of samples classified correctly, and P_c is the sum of the chance expected proportion of agreement (Titus et al. 1984).

2.3 RESULTS

2.3.1 VEGETATIVE CHARACTERISTICS

2.3.1a Nest microhabitat

Of the 98 nests discovered from 1999-2001, microhabitat data were collected for 92 nests and circular plot data were collected for 83 nests. Nests were positioned closest to sloughs (35.04 ± 5.24 m), followed by swamps (52.51 ± 5.41 m) and roads (57.34 ± 6.29 m). Nest height averaged 1.5 m (± 0.07), and ranged from 0.51 m to 3.73 m (Table 2). Host species tended to be small and short, with an average host height of 2.8 m (± 0.18) and diameter at breast height of 2.8 cm (± 0.72). The large size of SWWA nests was not due to the inner cup size (diameter = 6.02 ± 0.11 cm), but rather to a bulky outer cup (diameter = 13.67 ± 0.37 cm).

SWWA seldom used herbaceous vegetation for nesting substrate, but preferred woody species instead. Vines were the most common substrate type (33%, 43 of 129), followed by cane (38 of 129), shrubs (20 of 129), trees (16 of 129), palmetto (*Sabal minor*; 7 of 129), and blackberry (*Rubus* spp.; 5 of 129). Of 19 substrate species, the 5 most common in order of magnitude were cane, grape vine (*Vitis* spp.), greenbrier, holly (*Ilex* spp.), and palmetto. Most vegetation was alive, except for 10% that could not be identified. More than one nesting substrate could be used at a nest, explaining why substrate numbers ($n = 129$) were greater than the number of nests sampled.

2.3.1b Understory thickets

In the 0.78-ha plot, 194 understory thickets were mapped with at least 2.34 (± 0.13) thickets per plot. Nearly 90% (73 of 83) of SWWA nests were less than 5 m from a thicket,

with two-thirds (57 of 83) located inside thickets (Figure 5). On average, nests were located 1.78 m (± 0.50) from a thicket, and only two nests were further than 50 m from a thicket. Typically, SWWA does not nest in the center of thickets, but instead along the edges in vine tents and tangles. If not in a vine tangle, nests were positioned in the limbs of a small tree or shrub, between cane leaflets, or palmetto fronds.

The number of thickets did not reflect the area covered by thick understory, because almost half (95 of 194) the thickets were small in size (1-250 m²). On average, plots were 35.1% (± 3.37) covered by understory thickets, with 6% (5 of 83) of the plots 100% covered. Thicket density was highest closest to the nest (35.3 ± 1.89 thickets per ha), and decreased with distance (10.0 ± 0.58 thickets per ha).

Understory thickets were usually composed of several plant types aside from vines, such as live trees, cane, shrubs, fallen trees, snags, and palmetto. Most common thicket host was live trees (38.3%, 111 of 290), followed by shrubs (22.7%, 66 of 290). In the 0.0078-ha plots (5-m radius), vines were detected in 95% of the plots (79 of 83). Nine vine species (Table 3) were detected in the 0.0078-ha plots with grape most common (20.4%), followed closely by greenbrier (19.1%). The frequency with which species were used as nesting substrates followed plot densities, with the exception of poison ivy (*Toxicodendron radicans*). Poison ivy was not used for nesting even though it encompassed 12% of the vine detections.

2.3.1c Stem count

Cane was absent from almost one third of the 0.0078-ha plots (24 of 83). A total of 2,753 cane stems were counted, with 4,256 (± 739.74) stems per ha and a range of 0 to

39,743 stems per ha (Table 2). The average cane height ranged from 0.16 m to 7.0 m, with a mean of 2.22 m (± 0.08). Blackberry distribution was similar to cane, also absent from almost a third of the plots (10 of 34), and averaging 3,756 (± 920.51) stems per ha. In 2001, the only year blackberry stems were sampled, a total of 909 blackberry stems were counted, compared to 908 cane stems. Although the abundance of blackberry was similar to cane, it was the least common nest substrate ($n = 5$).

Small trees and shrubs (<8-cm dbh) were more common than larger size classes (>8-cm dbh), with 2,861 (± 215.38) stems per ha compared to 296 (± 16.25) stems per ha, respectively. Average basal area of all size classes >1-cm dbh was equal to 15.50 (± 0.63) m²/ha. Thirty woody species less than 8-cm dbh were recorded, with 1,853 stems counted and 5.46 (± 0.22) species per plot. The five most common species in order of magnitude were holly, American hornbeam (*Carpinus caroliniana*), red maple (*Acer rubrum*), hackberry (*Celtis laevigata*), and elm (*Ulmus* spp; Table 4). Holly accounted for 42% (776 of 1,853) of the stems counted.

Twenty-seven woody species (Table 4) ranging from 8-68-cm dbh were recorded, a total of 1,812 trees. Ninety percent (1,640 of 1,812) of the trees fell in the 8-22-cm category. The average number of species per plot was 6.45 (± 0.201), and the top five woody species were sweet gum (*Liquidambar styraciflua*), hackberry, red maple, green ash (*Fraxinus pennsylvanica*), and water hickory (*Carya aquatica*), respectively. The dominant canopy species was sweet gum at a height of 45.8 ft, and dominant midstory species was red maple at a height of 20.9 ft. Compared to the species found in the <8-cm dbh size class, red maple and hackberry were the only top five retained, whereas holly was visibly absent.

Is there a relationship between the occurrence of cane, small trees, and/or blackberry? There was a negligible relationship between the occurrence of cane and small trees (slope = -0.193, $R^2 = 0.003$) or between cane and blackberry (slope = -0.222, $R^2 = 0.054$). However, a negative relationship was observed between small trees and blackberry (slope = -2.083, $R^2 = 0.452$). Blackberry is a shade-intolerant species commonly found in the center of understory thickets, where thick tangles of blackberry and vines typically preclude trees.

2.3.1d Ground cover

On average, leaf litter (67.80 ± 1.43) and vines (21.66 ± 1.15) covered almost 90% of the ground. Marsh vegetation (0) and water (0.68 ± 0.33) were the least common ground cover components, and herbaceous vegetation covered 10% of the ground.

2.3.1e Comparison of habitat studies

Peters (1999) examined SWWA habitat selection at nesting, territory, and non-use points on the Woodbury site from 1997-1998. Comparing her study and mine, the majority of nest site variables had similar values, with the exception of a few (Table 2). Considerable differences existed between (%) bare ground, cane stems, woody stems < 8-cm dbh, woody stems 8-22-cm dbh, and size of understory thickets.

From 1998-2001, there was a significant increase in the leaf litter depth ($F = 33.22$, $P = < 0.0001$, Figure 6), mirrored by a significant decrease in the percent of bare ground ($F = 9.74$, $P = 0.0002$, Figure 7). A 1998 flood brought water levels 2.5 times higher than average spring flood heights. The scouring from the 1998 flood may have reduced the amount of leaf

litter and increased bare ground, which reverted back to its pre-flood condition over time through litter accumulation.

The differences observed in counts of small woody stems and cane, plus size of understory thickets may be due to the areas sampled. In 1997-1998, two-thirds of the nests (26 of 39) were located outside the core area, whereas I sampled evenly between core and noncore sites. The next section on discriminant analysis will describe the largest vegetative differences between core and noncore areas. These results will clarify the discrepancy between studies with regard to these variables.

2.3.2 DISCRIMINANT ANALYSIS

2.3.2a Core vs. noncore nests

Vegetation was sampled from 40 core nests (1.18 nests per ha), and 43 noncore nests (0.323 nests per ha), for a total of 83 active and inactive nests. Seventeen habitat variables were examined for significant area differences. One variable, blackberry, was excluded from the analysis, even though it showed a significant difference, because data were only collected in 2001. Blackberry stem counts equaled 20.2 (± 10.88) stems per plot in the core area versus 35.89 (± 9.21) in the noncore, a significant difference at the 0.10 level ($F = 3.75$, $P = 0.0627$).

Thirteen of the 16 variables were non-normal, with 6 normal after the transformation. H values were greater than one for 8 of 16 habitat variables (Table 5). Stepwise discriminant analysis selected 5 of the 8 variables (Table 6; CNHT, SWMP, LOGS, AREA, PALM). A Chi-square test of the homogeneity of within covariance matrices indicated the matrices were not homogenous ($\chi^2 = 54.1$, $P > \chi^2 = < 0.0001$), thus necessitating the use of a quadratic discriminant function instead of a linear. Core and noncore nests were discriminated significantly (Wilks' lambda = 0.668, $F = 7.44$, $P < 0.0001$) using these 5 variables in a canonical discriminant analysis. The eigenvalue equaled 0.496 with a squared canonical correlation (R^2) of 0.332. The equation for the canonical discriminant function was:

$$\text{DF Score} = 0.5874X_1 - 0.5247X_2 + 0.5884X_3 - 0.3743X_4 + 0.3685X_5,$$

where X_1 was CNHT, X_2 was $\sqrt{\text{SWMP}}$, X_3 was $\sqrt{\text{LOGS}}$, X_4 was $\sqrt{\text{PALM}}$, X_5 was $\sqrt{\text{AREA}}$. X_1 , X_2 , and X_3 shared similar magnitudes, whereas X_4 and X_5 exerted less influence on the canonical variable. This model correctly classified 77.1% of the nests (64 of 83, Table 7), an

efficiency 54.1% better than expected by chance (Cohen's kappa $Z = 4.93$, $P = < 0.0001$).

Nests were misclassified between core and noncore nests almost equally.

Discriminant function analysis indicated (%) ground covered by logs to be the largest discriminator between core and noncore nests, followed in magnitude by cane height, distance to swamp, (%) ground covered by palmetto, and area covered by thickets. Core nests were positively correlated with the canonical variable (Table 8), tending to have taller cane, more logs, more area covered by thickets, be further from swamps, and contain less palmetto than noncore nests. The average canonical discriminant score for core nests was $28.20 (\pm 1.90)$, Figure 8), compared to noncore nests $19.11 (\pm 1.85)$, Figure 9), a significant difference ($t = 3.42$, $P = 0.0010$). There was considerable overlap between the two classes, but a trend can be seen with noncore nests scoring lower than core nests.

Although the number of cane stems was not incorporated into the canonical variable, there was a positive relationship between cane height and the amount of cane present on nest plots (Figure 10; slope = 3.376, $R^2 = 0.626$). Forty-two percent (18 of 43) of noncore plots lacked cane, compared to only 18% (7 of 40) of core plots. There was also significantly more cane used as a nesting substrate at core nests ($\chi^2 = 23.65$, $P = < 0.0001$; 24 of 31). In contrast, saplings and palmetto were used significantly more often at noncore compared to core nests. Noncore nests constituted 81 (13 of 17) and 85 (6 of 7) percent of the occasions where trees ($\chi^2 = 6.56$, $P = 0.0104$) and palmetto ($\chi^2 = 4.70$, $P = 0.0301$) were used as nesting substrate, respectively.

2.3.2b Successful vs. failed nests

I used a discriminant analysis to examine vegetative differences between successful and failed nests. Vegetative data from 45 of 83 nests were used in the analysis, with 24 successful and 21 failed nesting attempts. Inactive nests and those with unknown outcomes were excluded from the analysis, thus explaining the reduced sample size. Nest failures were not clustered in either the core or noncore area, and successful nest outcomes were distributed almost equally across both areas (Figure 11).

Fourteen of 16 variables were non-normal, with 7 of these normal after transformation. H values were greater than one for 4 of 16 habitat variables (Table 9). Stepwise discriminant analysis selected only one of the 4 variables (GRAS; $F = 5.43$, $P = 0.0246$). A Chi-square test of the homogeneity of within covariance matrices indicated the matrices were homogenous ($\chi^2 = 1.208$, $P > \chi^2 = 0.2718$), thus necessitating the use of a linear discriminant function. Successful and failed nests were discriminated significantly (Wilks' lambda = 0.885, $F = 5.43$, $P = 0.0246$) using this variable. The eigenvalue equaled 0.1294 and the squared canonical correlation (R^2) equaled 0.114. The equation for the canonical discriminant function was:

$$\text{DF Score} = 1.0503X_I,$$

where X_I was $\sqrt{\text{GRAS}}$. This model correctly classified 67.9% of nests (30 of 44, Table 10), an efficiency 40.6% better than chance (Cohen's kappa $Z = 3.26$, $P = 0.0006$). Nests were equally misclassified between successful and failed nests.

Percent of ground covered by grass was the only discriminator between successful and failed nests. Failed nests were positively correlated with grass, whereas successful nests were negatively correlated (Table 11). The average canonical discriminant function score for

failed nests was 1.83 (± 0.34 , Figure 12) and successful nests 0.96 (± 0.24 , Figure 13); there was a significant difference even though both groups overlapped considerably ($t = 2.11$, $P = 0.0404$). There was no difference in nesting substrate used at successful versus failed nests.

2.3.2c Area x outcome

Number of failures was similar between core ($n = 11$) and noncore nests ($n = 10$), with differences in the number successful (core = 10, noncore = 14). However, when area was considered, the core area was more productive than noncore with 0.65 young fledged per ha (22 young in 34 ha) compared to 0.36 young per ha (42 young in 116 ha), respectively.

Fourteen of 16 variables were non-normal, and only one was normal after transformation. H values were greater than one for 11 of 16 habitat variables (Table 12). Stepwise discriminant analysis selected 4 of the 11 variables (Table 13; CANE, GRAS, AREA, LOGS). A Chi-square test of the homogeneity of within covariance matrices indicated the matrices were homogenous ($\chi^2 = 43.37$, $P > \chi^2 = 0.0543$), thus necessitating the use of a quadratic discriminant function. Three canonical discriminant functions were calculated using these variables, with two of the functions insignificant ($P = 0.205$, $P = 0.2789$). Successful and failed nests from the core versus noncore areas were discriminated significantly with the first function (Wilks' lambda = 0.401, $F = 3.28$, $P = 0.0005$). The eigenvalue equaled 0.9947 and the squared canonical correlation (R^2) was 0.4986. The equation for the first canonical discriminant function was:

$$\text{DF Score} = 0.7422X_1 - 0.6467X_2 + 0.5648X_3 + 0.4823X_4,$$

where X_1 was $\sqrt{\text{CANE}}$, X_2 was $\sqrt{\text{GRAS}}$, X_3 was AREA, X_4 was $\sqrt{\text{LOGS}}$. This model correctly classified 56.1% (24 of 43, Table 14), an efficiency 40.8% better than expected by chance

(Cohen's kappa $Z = 3.22$, $P = 0.0006$). Failed, core nests (5 of 9) were most often misclassified, followed in order by successful, noncore (7 of 14); failed, noncore (4 of 10); and successful, core (3 of 10). In all groups, the most common classification errors were due to incorrect outcome (68.4%, 13 of 19), not area (31.6%, 6 of 19).

Discriminant function analysis indicated cane to be the largest discriminator between the four categories, followed in magnitude by (%) ground covered by grass, area covered by thickets, and (%) ground covered by logs. The only group positively correlated with the canonical variable was successful, core nests (Table 15). Successful, core nests occurred in areas with more cane, logs, and area covered by thickets, plus less grass than the other categories. The average canonical discriminant function score for failed, core nests was $39.28 (\pm 4.08)$, Figure 14), successful, core nests was $40.15 (\pm 4.67)$, Figure 15), failed, noncore nests was $18.81 (\pm 3.89)$, Figure 16), and successful, noncore nests was $28.19 (\pm 3.57)$, Figure 17); significantly different means ($F = 5.80$, $P = 0.0021$). Nests were grouped according to area more strongly than by outcome. Within each group, failed nests scored lower than successful nests, meaning successful nests had more cane, area covered by thickets, and logs, but less grass than failed nests. The two groups with the least amount of similarity were failed, noncore nests and successful, core nests.

Two measures of the strength of the discriminant analysis are Wilks' lambda and R^2 . For the three analyses, the strongest Wilks' lambda and R^2 resulted from the analysis of outcome and area simultaneously. The weakest Wilks' lambda and R^2 occurred when only outcome was considered. Cross validation results indicated all analyses categorized nests better than chance alone, with the area analysis performing best. Surprisingly, area and outcome considered simultaneously performed only slightly better than outcome, even

though it had the highest Wilks' lambda and R^2 values. Small sample sizes for each of the nest x outcome categories appeared to be hampering the cross validation results.

2.4 DISCUSSION

Habitat selection by SWWA at nests was influenced by both physiognomic and floristic factors. Vegetation at core nests differed significantly from noncore nests, with cane one of the largest discriminators between the two. One third of nesting plots lacked cane completely, with 72% of these plots located in the noncore area. The importance of cane at core nests was a surprising result considering my cane counts were 6 to 13 times less than numbers reported by Meanley (1971; 50,000 stems per ha), Eddleman et al. (1980; 26,390 stems per ha), and Thomas et al. (1996; 56,500). Apart from the high cane counts of these 3 studies, 7 other localities had less than 5,000 cane stems per ha (Graves 2001, 2002, Peters 1999, Somershoe et al. 2003), three of which lacked cane completely (Graves 2002; Louisiana and Florida).

The discrepancy between studies cannot be attributed solely to differences between peripheral and core populations, since research was distributed across both regions. For example, Meanley (1971) and Somershoe et al. (2003) counted 50,000 and 1,746 cane stems per ha in Georgia, respectively. Studies also differed with respect to cane distribution on a site; Graves (2001; Great Dismal Swamp) found more cane on unoccupied sites (23,300 stems per ha) than within territories (4,400 stems per ha), whereas Peters (1999; South Carolina) found territories to contain more cane than non-use plots. Why the huge variability between studies with respect to cane? I think SWWA selects habitat based on the understory structure, whether created by cane, vines, shrubs, saplings, blackberry, or palmetto. The diversity of habitats occupied by SWWA, some lacking cane completely, supports my interpretation.

Although cane discriminated between high and low-density nest sites, I think it indirectly measured the presence of understory thickets. Cane was a typical component of understory thickets, along with many other plant types, and did not usually form monotypic stands on my site. Therefore, cane and understory thickets were not mutually exclusive. Two other discriminators between core and noncore nests were related to understory thickets. Logs were evidence of fallen trees, which would open up the canopy for the many shade-intolerant species of understory thickets. Lastly, area covered by understory thickets was a direct measure. Ninety percent of nests were less than 5m from a thicket, with two thirds located inside thickets. Core nest plots were 45% covered by thickets, compared to only 28% of noncore plots. According to Graves (2002), scattered understory thickets were the most conspicuous characteristics of breeding territories, and Meanley (1971) identified greenbrier as commonly associated with SWWA. Understory thickets turned out to be the biggest discriminator between core SWWA nests and noncore.

Two other features, unrelated to thickets, found to discriminate between core and noncore nests were distance to the nearest swamp and palmetto presence. Noncore nests were closer to swamps and contained more palmetto than core nests. These results appear to conflict because palmetto is found in Zone V of the bottomland (Martin et al. 1993, Miller and Miller 1999), at the highest elevation, whereas swamps are at the lowest elevation. However, nests associated with palmetto were localized in a small portion of noncore area and not representative of the entire area.

None of the variables found to discriminate between core and noncore nests were identified when examining nest outcome. Grass was the only significant discriminator, with failed nests positively related to the presence of grass. Grass is very shade-intolerant and

would be found in the most open areas. Open areas provide less cover, thus perhaps leaving a nest more vulnerable to predation. Although SWWA is associated with understory thickets, which commonly contain central open areas, it tends to use the darker, more concealed thicket edges. The association of nest failures and grass may indicate a poor choice of nest site in terms of concealment.

When outcome and area were considered simultaneously, successful, core nests were positively related to cane, area covered by thickets, and logs, with a negative relationship to grass. Two of the variables selected for area were dropped in this analysis, swamp distance and presence of palmetto. Noncore nests were negatively related to all variables except grass, and the largest difference between groups was successful, core nests and failed, noncore. The canonical variable was more successful at distinguishing between core and noncore nests than nest outcome. Failure rates were similar between core and noncore nests; however, core nests produced 0.65 young per ha compared to 0.36 young per ha in noncore nests.

Hydrology also has direct and indirect effects on SWWA distribution. Nesting areas were not subject to prolonged flooding during the breeding season, as evidenced by little to no standing water around nest sites. In the Great Dismal Swamp, water was unrecorded on territory plots, but detected on 61% of unoccupied plots (Graves 2001). Hydrophytic species, such as bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*), comprised less than 1% of the trees counted on nesting plots, similar to what Graves (2002) observed on territory plots. Hydrology can also affect available leaf litter as the scouring from the 1998 flood showed. Three years after flooding, leaf litter accumulation was approaching pre-flood conditions.

The effects of periodic or prolonged flooding are crucial selective stresses on the distribution of bottomland hardwood plants, with elevation responsible for the degree of flood exposure (Wharton et al. 1982). Areas occupied by SWWA follow a gradient from Zone II through V, with nesting concentrated in the highest zones of the bottomland. The most common nesting substrates were found in Zones IV and V, with cane, American holly, and palmetto from Zone V and woody vines and deciduous holly from Zone IV (Martin et al. 1993, Wharton et al. 1982). The top five woody species from the 0.0078-ha and 0.04-ha plot were also from Zones IV and V. According to plant species, SWWA nests are located on the highest ground of the bottomland.

Factors significant between core and noncore nests were not selected as important for distinguishing nest outcome. Grass, a potential measure of nest concealment, was most commonly found at failed nests. However, it was not identified in the discriminant analysis of area. Nests built in the highest-density area, core nests, were most often characterized by the presence of understory thickets. A simultaneous examination of nest area and outcome retained thicket variables and grass as discriminators. The two categories that differed most were successful, core nests and failed, noncore nests. Core nests did not have a different failure rate from noncore nests, indicating predation not to be a factor in SWWA distribution. The core area did produce more young than noncore, due to more nests built in a smaller area. The core area appears to offer more available nest sites than noncore, a relationship I will explore further in Chapter 3 by examining territories and unused habitat.

2.4.1 Management implications

The variability in the role of cane between studies and the importance of understory thickets on my site, suggest managing for SWWA is much more complicated than a single species approach. Management plans should reflect this complexity and not depend on cane exclusively. Somershoe et al. (2003:152) suggest, “ providing a combination of both dense canebrakes and open understory habitat,” by thinning canopy and planting cane. If nest-site availability drives SWWA distribution, as I think it does, open understory is the opposite of this species nesting requirements. Also, restoring cane is an expensive and often highly unsuccessful endeavor (Brantley and Platt 2001).

Some suggest creating small canopy openings (<4 ha) in mature forests to encourage cane growth and maintenance (Thomas et al. 1996, Dickson et al. 1993). Aside from encouraging cane, these openings could boost understory thicket growth. SWWA breeding density is considerably lower in mature forests characterized by closed canopy and sparse undergrowth (Graves 2002). Graves (2001) found SWWA territories in a 50 year-old forest to range between 3-18 ha. Peters (1999) found territories in 30 year-old forests to be larger (2.3 ha) than those in 17 year-old forests (1.8 ha). As forests mature, territories appear to grow in size and may reflect reduced habitat quality for SWWA (Brown and Dickson 1994). Territory size may depend on availability of understory thickets, with a male in mature forest forced to defend a larger territory in order to contain sufficient nesting or foraging habitat.

Although small timber cuts have the potential to increase SWWA density, I am hesitant to recommend carving up mature forest for SWWA management. Small cuts result in an increased edge-to-area ratio, which may in turn increase edge effects, i.e. BHCO parasitism (Pashley and Barrow 1993). Interior species could be impacted by increased

predation and parasitism rates, not to mention adverse effects on SWWA. In Chapter 1, SWWA was shown to be naïve BHCO hosts, and to suffer substantial losses in the presence of BHCO. Some recommend this technique for SWWA management (Eddleman et al. 1980, Thomas et al. 1996), although the effectiveness of this measure has not been proven.

The benefit of clearcutting over patch cuts is a reduced edge-to-area ratio. The scale of harvest is at least an order of magnitude larger in clearcutting than patch cuts.

Clearcutting creates a disturbance in the canopy that has been likened to large-scale gaps created by hurricanes, tornadoes, ice storms, flooding, collapse of large trees, insects, and disease (Almquist et al. 2002, Borman and Likens 1979, Graves 2001). Accordingly, frequent gap simulations should be incorporated in forest management efforts aimed at this species (Graves 2001). The density differences on my site are surprising considering the entire site was clearcut. At the nest site, differences appear to be mostly due to the presence of understory thickets. Whether or not that translates into territory and non-use sites will be investigated in the next chapter.

Logging in floodplain forests is almost completely reliant on clearcut systems with natural regeneration (Rummer et al. 1997), as was seen on my field site. Typically, no site preparation is used with natural regeneration thereby resulting in less site disturbance (Rummer et al. 1997). After a bottomland timber harvest, it is important to allow the site to naturally regenerate, and not convert to pine. Conservationists need to be active in encouraging timber companies to maintain bottomland hardwood sites, since many bottomlands are considered “developable” for pine plantations (Rummer et al. 1997). Of particular importance is the role early successional forest may play in SWWA management and the need to partner timber interests with SWWA conservation.

More research is needed at other managed sites and in mature forest, to compare with my productivity estimates, examine the role understory thickets play in distribution, and follow site occupancy as a stand matures. Although more labor intensive, breeding productivity needs to be examined in future studies. Researchers often assess SWWA habitat quality by the number of singing males and territories (Eddleman et al. 1980, Graves 2001, 2002, Somershoe et al. 2003). These measures are indices of habitat quality, but do not directly measure a site's breeding productivity. As was seen in Chapter 1, unmated males sing more frequently than mated males, increasing their likelihood of detection and potentially biasing habitat quality results. In wildlife populations, it usually suffices to study the female portion of the population because fecundity is dependent on them (Johnson 1996). From Chapter 1, females were captured 2 times less often than males, indicating a higher male capture probability and/or greater abundance of males. Studies focusing on males alone could be missing a major limiting factor of SWWA populations- females.

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Table 1. Habitat variables sampled at SWWA nest sites and three plots surrounding the nest (0.0078-ha, 0.04-ha, and 0.78-ha) in Britton's Neck, South Carolina, 1999-2001 (adapted from Peters 1999).

Microhabitat	0.0078-ha plot	0.04-ha plot	0.78-ha plot
Distance of nest from stem (m)	Cane stem count	Woody stems >8cm dbh:	No. understory thickets (1-4)
Nest height above ground (m)	Cane height (m)	Stem count	Distance of thicket from nest (m)
Nest dimensions:	Blackberry stem count (2001 only)	Species present	Area of thicket (m ²)
Inner cup diameter (cm)	Vine species present	Dominant species:	Vine species present
Outer cup diameter (cm)	Woody stems <8cm dbh:	Canopy species present	Host species of thicket
Inner depth (cm)	Stem count	Canopy height	Distance of nest to closest:
Outer depth (cm)	Species present	Midstory species present	Road
Host species	Litter depth (cm)	Midstory height	Slough
Host height (m)	Percent of ground covered by:	Low vertical density (0-1.5m)	Swamp
Host dbh (cm)	Bare ground	High vertical density (1.5-2.5m)	
	Cane		
	Fern		
	Forbaceous		
	Grass		
	Leaf litter		
	Logs		
	Marsh vegetation		
	Palmetto		
	Shrub		
	Vines		
	Water		

Table 2. Means (SE) of habitat variables sampled at SWWA nest sites and surrounding plots (0.0078-ha, 0.04-ha, and 0.78-ha) in Britton's Neck, South Carolina, 1999-2001 (Thompson) and 1997-1998 (Peters 1999).

Habitat Variables	1999-2001 Nest (n = 83)	1997-1998 Nest (n = 39)
Microhabitat		
Nest height (m)	1.46 (0.07)	1.57 (0.11)
Host height (m)	2.77 (0.18)	1.75 (0.17)
Host dbh (cm)	2.79 (0.72)	0.50 (0.10)
Distance from stem (m)	1.18 (0.80)	2.52 (1.99)
Inner cup diameter (cm)	6.02 (0.11)	5.85 (0.15)
Outer cup diameter (cm)	13.67 (0.37)	11.23 (0.38)
Inner depth (cm)	4.25 (0.82)	3.05 (0.12)
Outer depth (cm)	8.46 (0.28)	7.51 (0.26)
% Ground cover		
Leaf Litter	67.80 (1.43)	62.59 (3.39)
Vines	21.66 (1.15)	26.20 (3.39)
Forb	6.09 (0.57)	3.70 (0.88)
Cane	5.60 (0.57)	5.42 (1.57)
Shrub	5.05 (0.62)	3.53 (1.10)
Bare ground	4.06 (0.52)	24.22 (2.94)
Grass	3.32 (0.43)	4.21 (2.05)
Logs	2.32 (0.25)	3.90 (0.59)
Palmetto	1.60 (0.38)	1.10 (0.63)
Fern	0.77 (0.41)	0.35 (0.35)
Water	0.68 (0.33)	0.10 (0.10)
Marsh	0.00 (0.00)	0.00 (0.00)
Litter depth (cm)	2.66 (0.07)	0.81 (0.11)
Avg. cane height (m)	2.22 (0.08)	2.18 (0.17)
No. woody species per plot (<8cm dbh)	5.46 (0.22)	-
No. woody species per plot (>8cm dbh)	6.45 (0.20)	-
Low vertical density (0-1.5 m)	73.17 (2.58)	66.17 (3.88)
High vertical density (1.5-2.5 m)	73.48 (2.97)	74.68 (3.16)
Stem Count		
Cane count per ha	4256.4 (739.74)	2294.9 (771.79)
Blackberry count per ha	3756.4 (920.51)	-
Woody stem <8-cm dbh per ha	2861.5 (215.38)	2151.3 (270.51)
Woody stem 8-22-cm dbh per ha	260.5 (12.5)	588.5 (51.25)
Woody stem 23-37-cm dbh per ha	32.5 (3.0)	59 (13.75)
Woody stem 38-52-cm dbh per ha	2.75 (0.5)	1.25 (8.75)
Woody stem ≥53-cm dbh per ha	0.25 (0.25)	3.75 (9.75)
Understory thickets		
No. thickets	2.34 (0.13)	2.71 (0.24)
Min. distance to thicket	1.78 (0.50)	3.32 (2.39)
Size closest thicket (m ²)	2047.6 (260.41)	-
Size all thickets (m ²)	1790.4 (240.05)	3178.72 (1522.11)
Thicket density /ha within 10 m of nest	35.30 (1.89)	-
Thicket density /ha within 25 m of nest	10.00 (0.58)	-
Percent plot covered by thicket	35.06 (3.37)	-

Table 3. Vine species used as nesting substrate at SWWA nests, and detected in 0.0078-ha and 0.78-ha nest plots in Britton's Neck, South Carolina, 1999-2001.

Species	Common name	Microhabitat (n = 92)	0.0078-ha (n = 83)	0.78-ha (n = 83)
<i>Vitis spp.</i>	Grape	10.1 ^a	20.4	22.5
<i>Smilax spp.</i>	Greenbrier	8.5	19.1	19.2
Unknown vines	-	8.5	-	-
<i>Bignonia capreolata</i>	Crossvine	3.1	12.7	11.2
<i>Parthenocissus quinquefolia</i>	Virginia creeper	1.5	12.5	9.8
<i>Ampelopsis arborea</i>	Pepper vine	0.8	14.3	18.2
<i>Campsis radicans</i>	Trumpet creeper	0.8	7.4	11.0
<i>Berchemia scandens</i>	Supplejack	-	1.2	0.8
<i>Gelsemium rankinii</i>	Carolina jasmine	-	-	0.7
<i>Toxicodendron radicans</i>	Poison ivy	-	12.4	6.6
		33.3 ^b	100.0	100.0

^a Percent of total detections.

^b Microhabitat is not out of 100% because other types of nesting substrate were used.

Table 4. Woody species used as nesting substrate at SWWA nests, and top 6 species detected in 0.0078-ha and 0.04-ha nest plots in Britton's Neck, South Carolina, 1999-2001.

Species	Common Name	% Total Woody Species		
		Microhabitat (n = 92)	< 8-cm dbh (n = 83)	> 8-cm dbh (n = 83)
<i>Ilex spp.</i>	Holly spp.	7.0 ^a	19.2	
<i>Acer rubrum</i>	Red maple	3.9	11.8	11.7
<i>Carpinus caroliniana</i>	American hornbeam	3.9	14.1	
<i>Ilex deciduas</i>	Deciduous holly	3.9	13.6	
<i>Ilex opaca</i>	American holly	3.1	9.1	
Unknown trees	-	1.3		
<i>Celtis laevigata</i>	Hackberry	0.8	7.0	16.9
<i>Cornus florida</i>	Dogwood spp.	0.8	^c	-
<i>Crataegus spp.</i>	Hawthorn	0.8		
<i>Ligustrum spp.</i>	Privet spp.	0.8		
<i>Liquidamber styraciflua</i>	Sweetgum	0.8		24.4
<i>Myrica cerifera</i>	Wax Myrtle	0.8		-
<i>Acer negundo</i>	Box elder	- ^b		
<i>Betula nigra</i>	River birch	-		
<i>Carya aquatica</i>	Water hickory	-		5.1
<i>Diospyros virginiana</i>	Persimmon	-		
<i>Fraxinus pennsylvanica</i>	Green ash	-		7.0
<i>Morus rubra</i>	Red Mulberry	-		
<i>Nyssa sylvatica</i>	Gum spp	-		
<i>Pinus taeda</i>	Loblolly pine	-	-	
<i>Platanus occidentalis</i>	Sycamore	-		5.0
<i>Populus deltoids</i>	Cottonwood	-		
<i>Quercus alba</i>	White oak	-		-
<i>Quercus laurifolia</i>	Swamp laurel oak	-		
<i>Quercus lyrata</i>	Overcup oak	-		
<i>Quercus michauxii</i>	Swamp chestnut oak	-	-	
<i>Quercus nigra</i>	Water oak	-		
<i>Quercus phellos</i>	Willow oak	-		
<i>Quercus spp.</i>	Oak spp	-		
<i>Rhus spp.</i>	Sumac	-	-	
<i>Salix nigra</i>	Black willow	-		
<i>Styrax spp.</i>	Snowbell	-		-
<i>Taxodium distichum</i>	Bald cypress	-		-
<i>Ulmus alata</i>	Winged elm	-		-
<i>Ulmus Americana</i>	American elm	-		
<i>Ulmus rubra</i>	Slippery elm	-		
<i>Ulmus spp.</i>	Elm spp.	-		
<i>Vaccinium arboreum</i>	Blueberry	-		-
		27.900	74.800	70.100

^a Percentages of total counts.

^b Dash marks indicate species was not detected.

^c Empty spaces indicate species was detected, but not included in the top 6 species.

Table 5. Means (SE), transformations, normality, and Kruskal-Wallis test results for habitat variables comparing core versus noncore SWWA nest sites in Britton's Neck, South Carolina, 1999-2001.

Code	Variable	Mean (SE)		Transformation type	Normal after transformation	Kruskal-Wallis ANOVA	
		Noncore	Core			H	P
NSHT	Nest height above ground (m)	1.43 (0.10)	1.48 (0.10)	LOG	Y	< 1	
CANE	Cane stem count	21.7 (7.64)	44.7 (8.44)	SQRT	NO	13.13	0.0005
CNHT	Cane height (m)	3.37 (0.66)	7.97 (0.91)	NONE	NO	18.83	0.0001
WSL8	Woody stem count (<8cm dbh)	21.79 (1.43)	22.33 (2.06)	SQRT	Y	< 1	
WSG8	Woody stem count (>8cm dbh)	21.23 (1.34)	22.97 (1.61)	NONE	Y	< 1	
BASL	Basal area (m ² /ha)	15.52 (0.86)	15.51 (0.97)	NONE	Y	< 1	
LITR	Litter depth (cm)	2.63 (0.15)	2.76 (0.20)	NONE	Y	< 1	
	Percent of ground covered by:						
BARE	Bare ground	4.04 (1.22)	3.97 (1.08)	LOG (X + 1)	NO	< 1	
FORB	Forbaceous	5.5 (1.05)	6.69 (1.13)	LOG (X + 1)	Y	1.45	0.2325
GRAS	Grass	3.03 (0.66)	3.68 (1.06)	SQRT	NO	< 1	
LOGS	Logs	1.97 (0.46)	2.69 (0.55)	SQRT	NO	1.19	0.2793
PALM	Palmetto	2.49 (1.05)	0.61 (0.61)	LOG (X + 1)	NO	5.52	0.0212
SHRU	Shrub	6.46 (1.64)	3.44 (0.95)	LOG (X + 1)	NO	2.54	0.1166
AREA	Area covered by thicket (m ²)	2216.2 (338.99)	3503.0 (467.92)	SQRT	Y	5.2	0.0252
SLGH	Distance to slough	39.91 (8.34)	29.66 (6.23)	LOG	Y	< 1	
SWMP	Distance to swamp	70.29 (8.76)	34.78 (4.75)	SQRT	Y	14.42	0.0003

Table 6. Habitat variables selected by stepwise discriminant analysis, significant at the 0.10 level for core versus noncore SWWA nests in Britton's Neck, South Carolina, 1999-2001.

Step	Variable entered	Partial R^2	F	$P > F$	Wilks' lambda	$P < \text{Lambda}$
1	CNHT	0.1621	15.28	<0.0002	0.8379	0.0002
2	SWMP	0.0687	5.75	0.0189	0.7804	<0.0001
3	LOGS	0.0631	5.18	0.0256	0.7312	<0.0001
4	PALM	0.0495	3.96	0.0501	0.6949	<0.0001
5	AREA	0.0382	2.98	0.0885	0.6684	<0.0001

Table 7. Classification matrix of cross-validated results (classification rate) from discriminant analysis of core versus noncore SWWA nests in Britton’s Neck, South Carolina, 1999-2001.

Actual	Classified Core	Classified Noncore	TOTAL
Core	30 (75)	10 (25)	40 (100)
Noncore	9 (20.93)	34 (79.07)	43 (100)
TOTAL	39 (46.99)	44 (53.01)	83 (100)

Table 8. Class means of canonical variable describing habitat differences between core versus noncore SWWA nests in Britton’s Neck, South Carolina, 1999-2001.

Area	Class means
Core	0.7042
Noncore	-0.6870

Table 9. Means (SE), transformations, normality, and Kruskal-Wallis test results for habitat variables comparing successful versus failed SWWA nests in Britton's Neck, South Carolina, 1999-2001.

Code	Variable	Mean (SE)		Transformation type	Normal after transformation	Kruskal-Wallis ANOVA	
		Fail	Success			<i>H</i>	<i>P</i>
NSHT	Nest height above ground (m)	1.31 (0.15)	1.40 (0.10)	LOG	Y	< 1	
CANE	Cane stem count	23.55 (6.08)	31.50 (8.76)	SQRT	NO	< 1	
CNHT	Cane height (m)	4.57 (1.03)	4.91 (1.05)	SQRT	NO	< 1	
WSL8	Woody stem count (<8cm dbh)	23.35 (3.97)	22.54 (3.01)	SQRT	Y	< 1	
WSG8	Woody stem count (>8cm dbh)	20.84 (1.60)	22.25 (2.14)	NONE	Y	< 1	
BASL	Basal area (m ² /ha)	14.85 (1.38)	15.48 (1.16)	SQRT	NO	< 1	
LITR	Litter depth (cm)	2.43 (0.21)	2.94 (0.21)	NONE	Y	3.02	0.0898
	Percent of ground covered by:						
BARE	Bare ground	4.35 (1.81)	2.77 (1.22)	LOG (<i>X</i> + 1)	NO	1.49	0.2288
FORB	Forbaceous	7.09 (1.38)	4.91 (1.46)	LOG (<i>X</i> + 1)	Y	3.65	0.0628
GRAS	Grass	5.37 (1.57)	2.09 (0.79)	SQRT	NO	5.55	0.0233
LOGS	Logs	2.01 (0.54)	1.99 (0.64)	SQRT	NO	< 1	
PALM	Palmetto	0.97 (0.61)	2.99 (1.74)	LOG (<i>X</i> + 1)	NO	< 1	
SHRU	Shrub	3.51 (1.34)	5.43 (2.25)	LOG (<i>X</i> + 1)	Y	< 1	
AREA	Area covered by thicket (m ²)	3197.08 (714.64)	3390.83 (550.82)	SQRT	Y	< 1	
SLGH	Distance to slough	21.47 (3.76)	41.99 (12.28)	LOG	Y	< 1	
SWMP	Distance to swamp	42.47 (8.82)	49.62 (10.71)	SQRT	Y	< 1	

Table 10. Classification matrix of cross-validated results (classification rate) from discriminant analysis of successful versus failed SWWA nests in Britton’s Neck, South Carolina, 1999-2001.

Actual	Classified Failure	Classified Successful	TOTAL
Failure	13 (65)	7 (35)	20 (100)
Successful	7 (29.17)	17 (70.83)	24 (100)
TOTAL	20 (45.45)	24 (54.55)	44 (100)

Table 11. Class means of canonical variable describing habitat differences between successful versus failed SWWA nests in Britton’s Neck, South Carolina, 1999-2001.

Outcome	Class means
Failure	0.3849
Success	-0.3208

Table 12. Means (SE), transformations, normality, and Kruskal-Wallis test results for habitat variables comparing area versus outcome at SWWA nests in Britton's Neck, South Carolina, 1999-2001.

Variables	Mean (SE)				Transformation type	Normal after	Kruskal-Wallis	
	0C	0N	2C	2N			H	P
Nest height above ground (m)	1.30 (0.13)	1.32 (0.26)	1.43 (0.15)	1.38 (0.14)	NONE	NO	< 1	
Cane stem count	33.00 (10.59)	14.10 (4.93)	64.40 (15.62)	8.00 (3.22)	SQRT	NO	5.82	0.0022
Cane height (m)	6.71 (1.56)	2.42(1.03)	8.57 (1.66)	2.30 (0.85)	NONE	NO	5.47	0.0031
Woody stem count (<8cm dbh)	17.60 (2.75)	29.10 (7.18)	29.90 (4.84)	17.28 (3.28)	NONE	NO	2.05	0.12229
Woody stem count (>8cm dbh)	19.55 (1.68)	22.10 (2.66)	23.60 (3.97)	21.28 (2.42)	SQRT	NO	< 1	
Basal area (m ² /ha)	11.97 (1.46)	17.73 (2.00)	17.63 (2.09)	13.95 (1.20)	NONE	Y	3.25	0.0319
Litter depth (cm)	2.34 (0.26)	2.53 (0.34)	2.97 (0.35)	2.92 (0.28)	NONE	Y	1.27	0.2967
Percent of ground covered by:								
Bare ground	4.52 (2.31)	4.18 (2.91)	2.72 (1.48)	2.80 (1.85)	LOG (X + 1)	NO	< 1	
Forbaceous	9.02 (2.09)	5.16 (1.68)	3.37 (0.95)	6.00 (2.40)	LOG (X + 1)	Y	1.52	0.2249
Grass	7.09 (2.84)	3.65 (1.30)	0.65 (0.42)	3.12 (1.26)	SQRT	NO	2.3	0.0925
Logs	2.05 (0.80)	1.97 (0.75)	2.75 (0.80)	1.45 (0.95)	SQRT	NO	1.58	0.2086
Palmetto	0 (0.00)	1.95 (1.17)	0 (0.00)	5.12 (2.88)	LOG (X + 1)	NO	1.07	0.3742
Shrub	3.22 (1.44)	3.80 (2.35)	2.50 (0.71)	7.52 (3.78)	LOG (X + 1)	NO	< 1	
Area covered by thicket (m ²)	5023.80 (1058.29)	1370.35 (542.95)	4238.20 (927.86)	2785.57 (653.34)	NONE	NO	2.92	0.0458
Distance to slough	19.44 (3.59)	23.30 (6.52)	23.40 (7.97)	55.21 (19.83)	NONE	NO	1.55	0.2173
Distance to swamp	29.80 (8.72)	56.55 (15.09)	35.60 (7.47)	59.64 (17.36)	NONE	NO	< 1	

Table 13. Habitat variables selected by stepwise discriminant analysis, significant at the 0.10 level for area versus outcome SWWA nests in Britton's Neck, South Carolina, 1999-2001.

Step	Variable entered	Partial R^2	F	$P > F$	Wilks' lambda	$P < \text{Lambda}$
1	CANE	0.3521	6.7	0.001	0.6479	0.001
2	GRAS	0.1873	2.77	0.0559	0.5265	0.0006
3	AREA	0.1684	2.36	0.088	0.4379	0.0004
4	LOGS	0.1791	2.47	0.0783	0.3595	0.0002

Table 14. Classification matrix of cross-validated results (classification rate) from discriminant analysis of successful versus failed SWWA nests in Britton's Neck, South Carolina, 1999-2001.

Actual	Classified				TOTAL
	Fail, core	Fail, noncore	Success, core	Success, noncore	
Fail, core	4 (44.44)	0 (0)	3 (33.33)	2 (22.22)	9 (100)
Fail, noncore	1 (10)	6 (60)	0 (0)	3 (30)	10 (100)
Success, core	2 (20)	1 (10)	7 (70)	0 (0)	10 (100)
Success, noncore	2 (14.29)	5 (35.71)	0 (0)	7 (50)	14 (100)
TOTAL	9 (20.93)	12 (27.91)	10 (23.26)	12 (27.91)	43 (100)

Table 15. Class means of canonical variable describing habitat differences between area versus outcome of SWWA nests in Britton's Neck, South Carolina, 1999-2001.

Area x Outcome	Class means
Core, failure	-0.03048
Noncore, failure	-0.62905
Core, success	1.66167
Noncore, success	-0.0717999

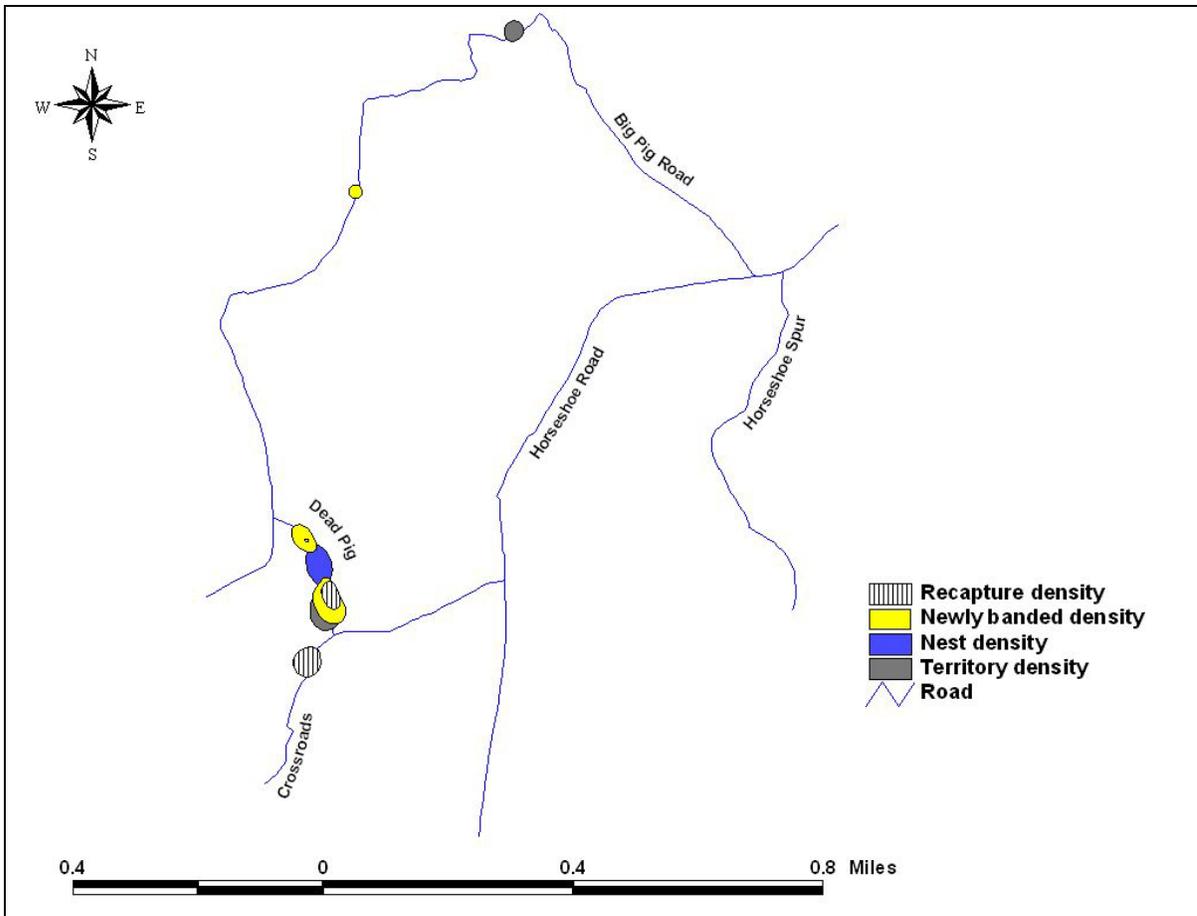


Figure 1. Adapted from kernel density estimates (100-m radius) of SWWA banding, territory, and nest data; top 2 of 8 density levels (top 25% of data) for each sampling technique; Britton's Neck, South Carolina, 1997-2001.

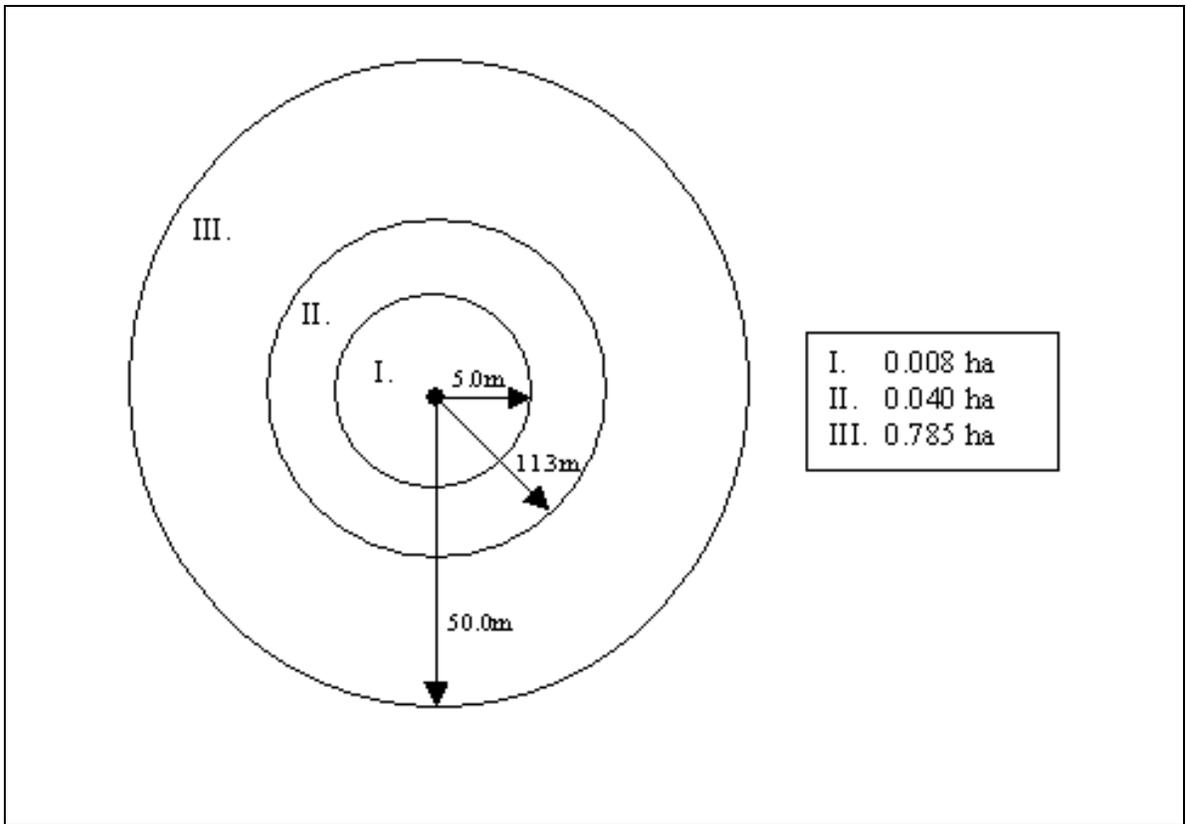


Figure 2. Circular plots centered at 5-, 11.3-, and 50-m radii from the nest used for vegetative sampling.

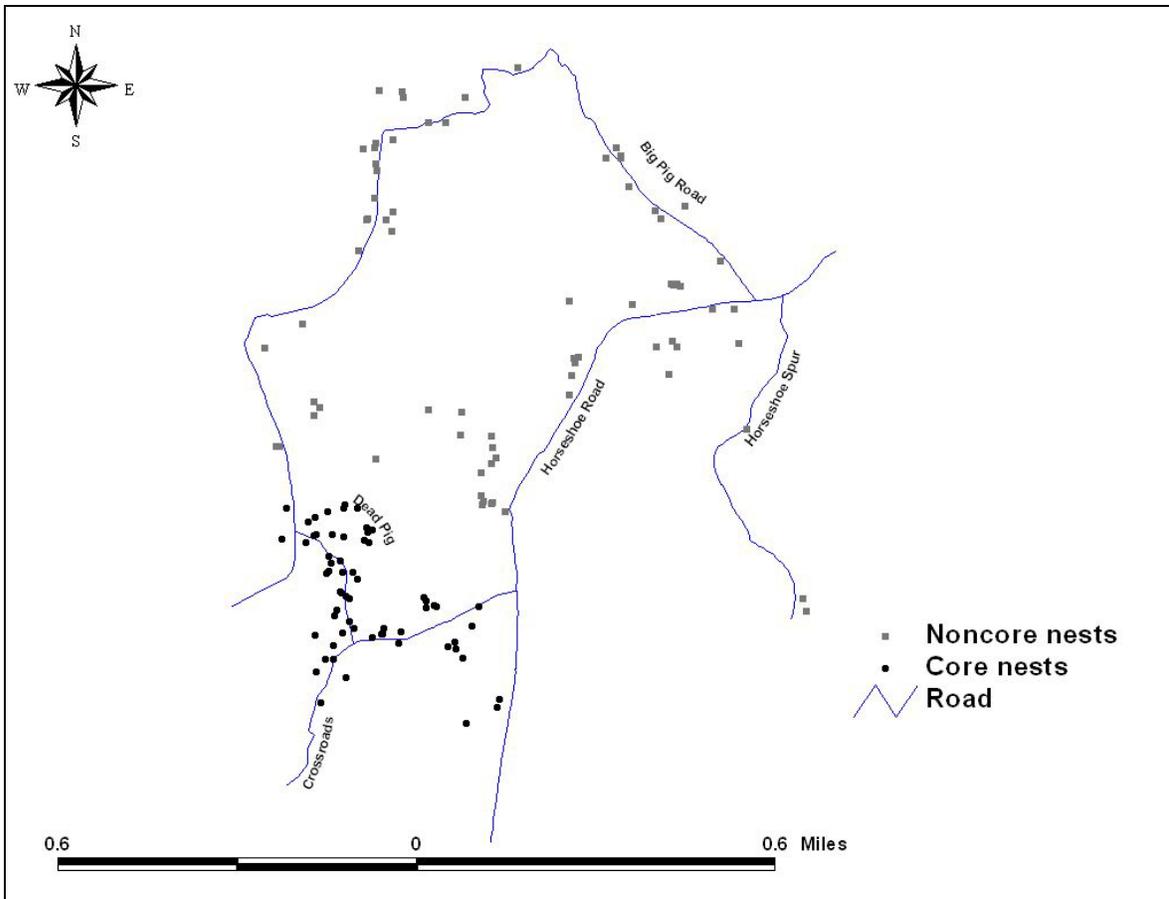


Figure 3. Distribution of core and noncore SWWA nests in Britton's Neck, South Carolina, 1997-2001.

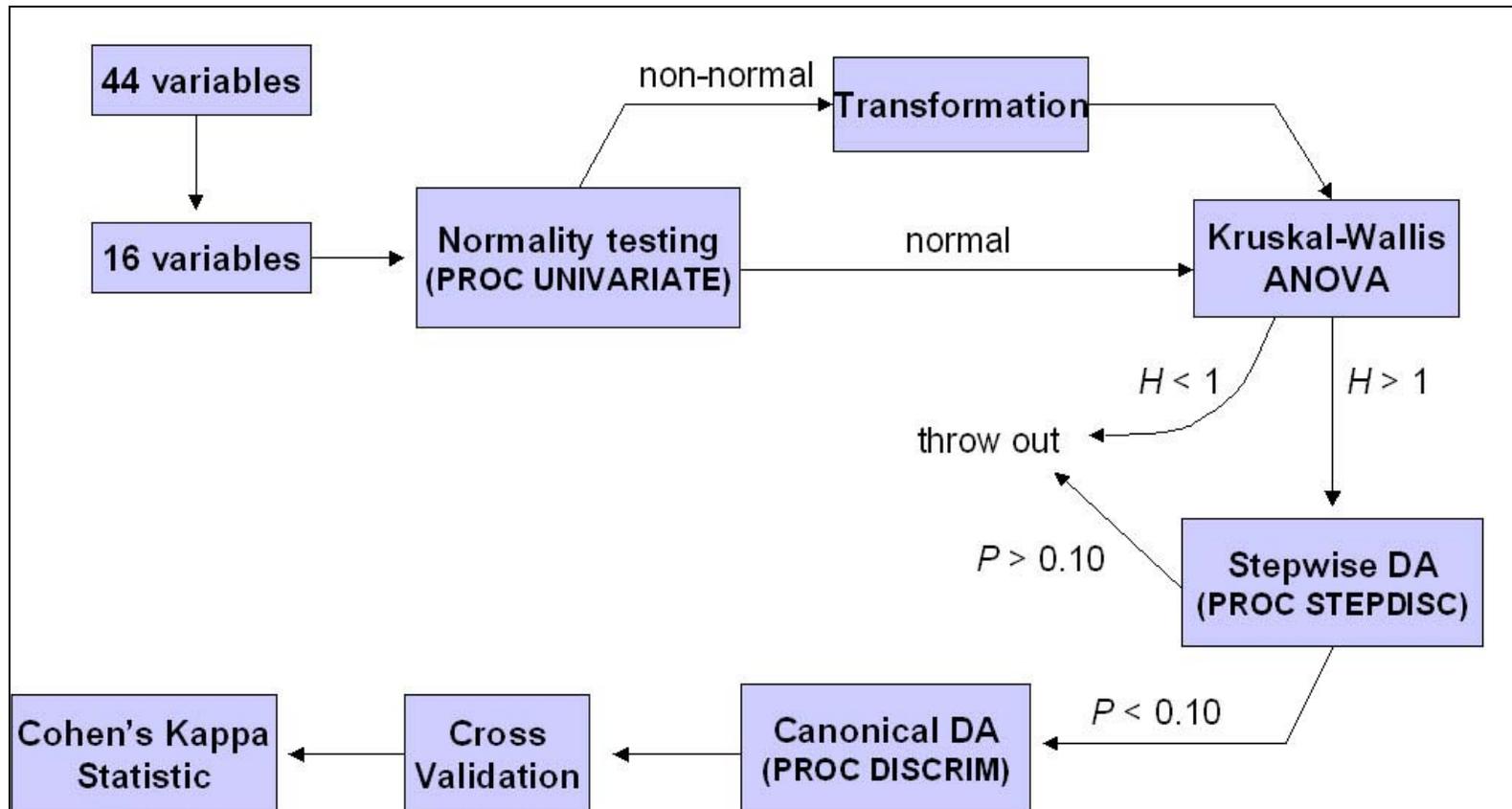


Figure 4. Flow chart highlighting the steps followed to select physiognomic and floristic variables for a canonical discriminant function analysis.

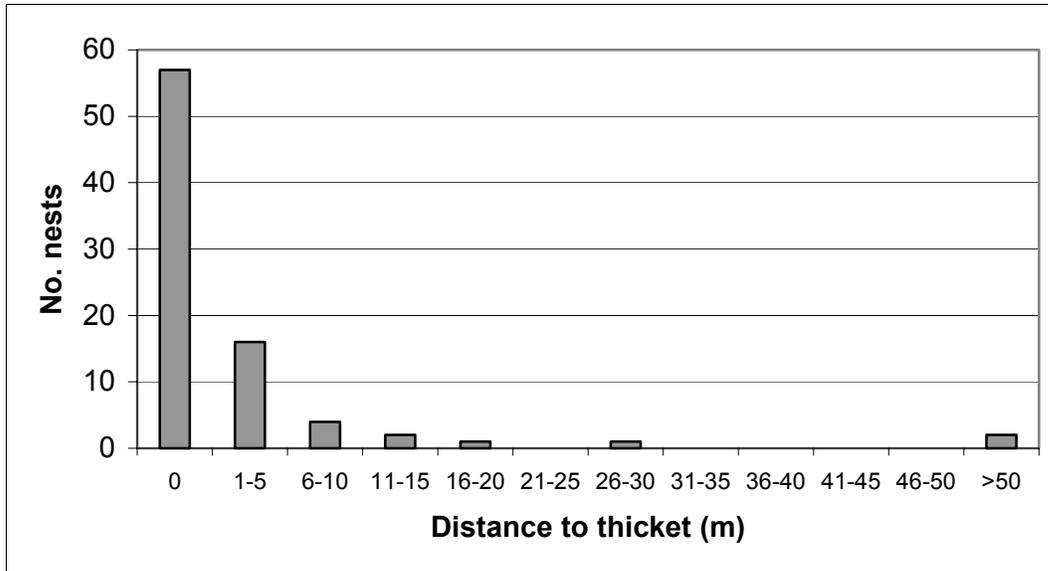


Figure 5. Distance (m) of SWWA nests ($n = 83$) to closest understory thicket in Britton's Neck, South Carolina, 1999-2001.

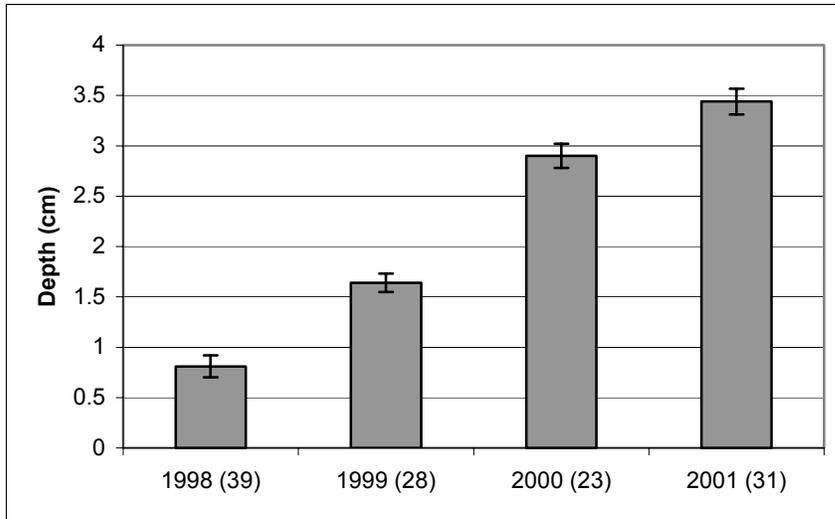


Figure 6. Mean litter depth measured on 0.0078-ha plots at SWWA nests in Britton’s Neck, South Carolina, 1998-2001 (sample size in parentheses).

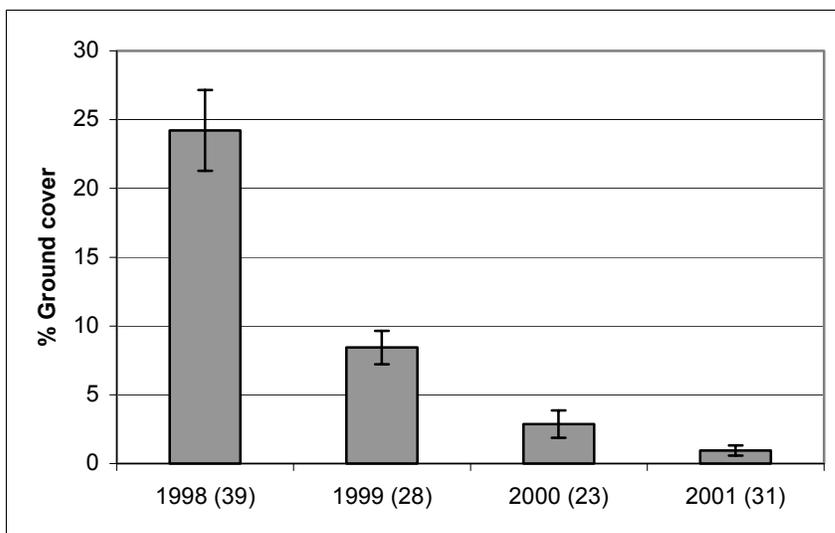


Figure 7. Mean (%) bare ground measured on 0.0078-ha plots at SWWA nests in Britton’s Neck, South Carolina, 1998-2001 (sample size in parentheses).

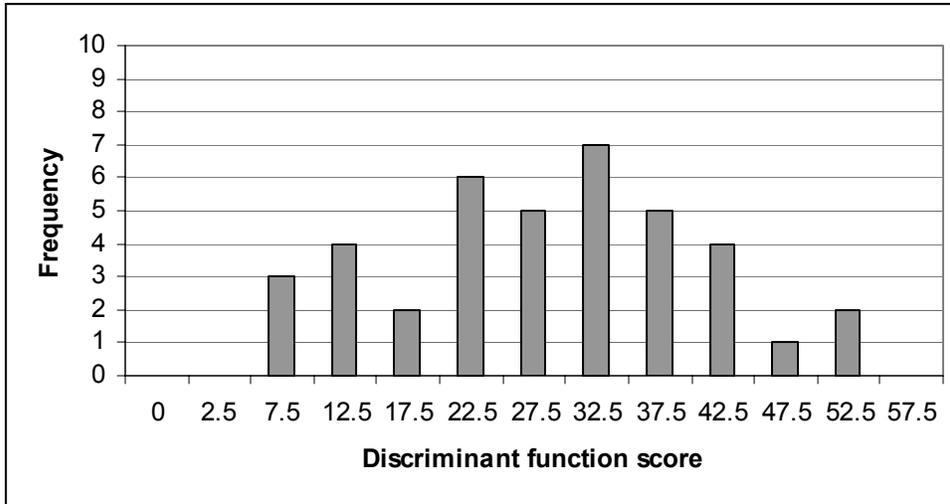


Figure 8. Frequency distribution of canonical function scores for core SWWA nests ($n = 40$) in Britton's Neck, South Carolina (1999-2001).

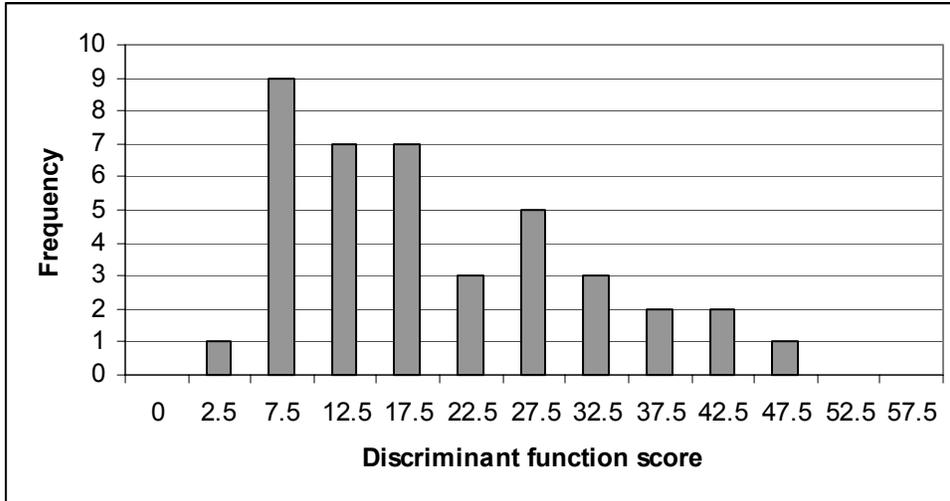


Figure 9. Frequency distribution of canonical function scores for noncore SWWA nests ($n = 43$) in Britton's Neck, South Carolina (1999-2001).

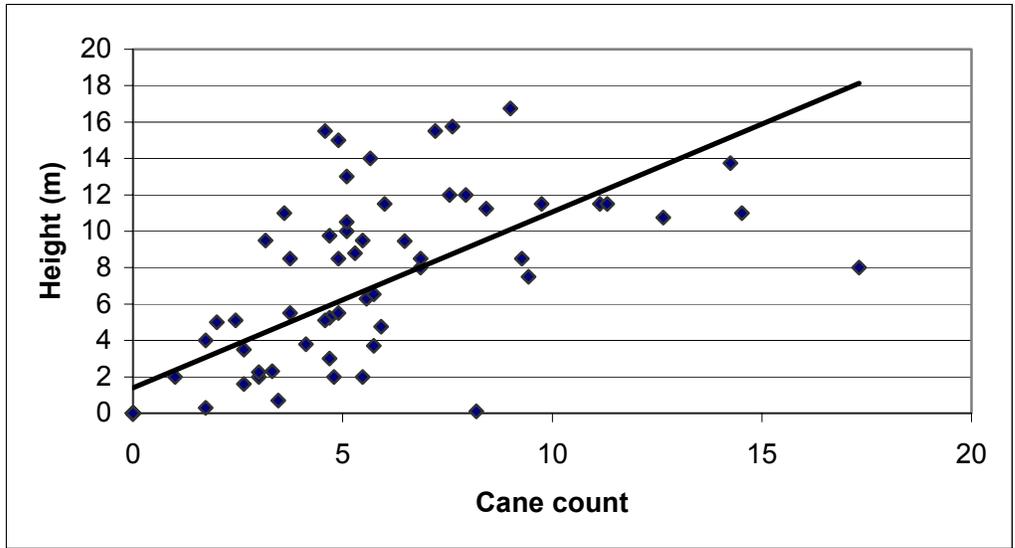


Figure 10. Cane height versus cane count (square-root transformed) for SWWA nests in Britton's Neck, South Carolina, 1999-2001.

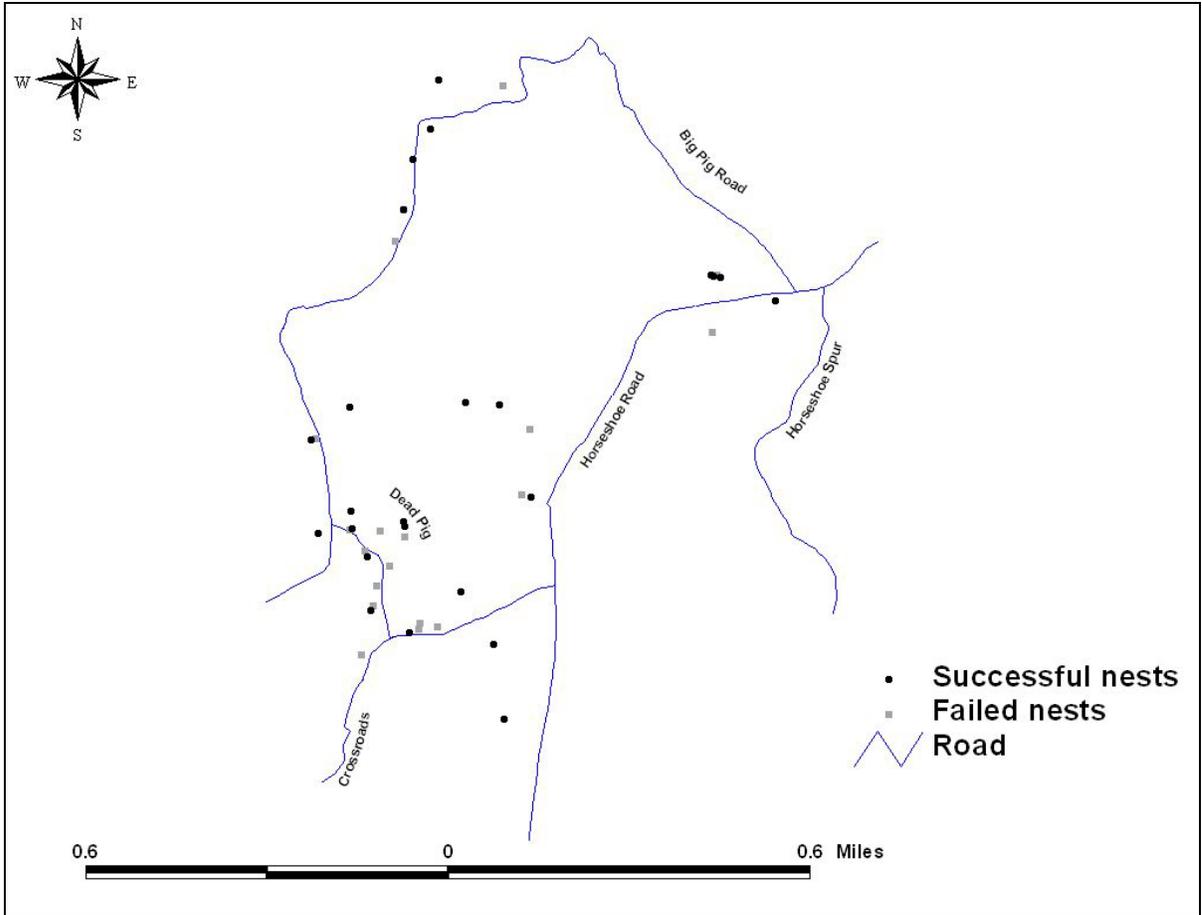


Figure 11. Distribution of successful and failed SWWA nests in Britton's Neck, South Carolina, 1999-2001.

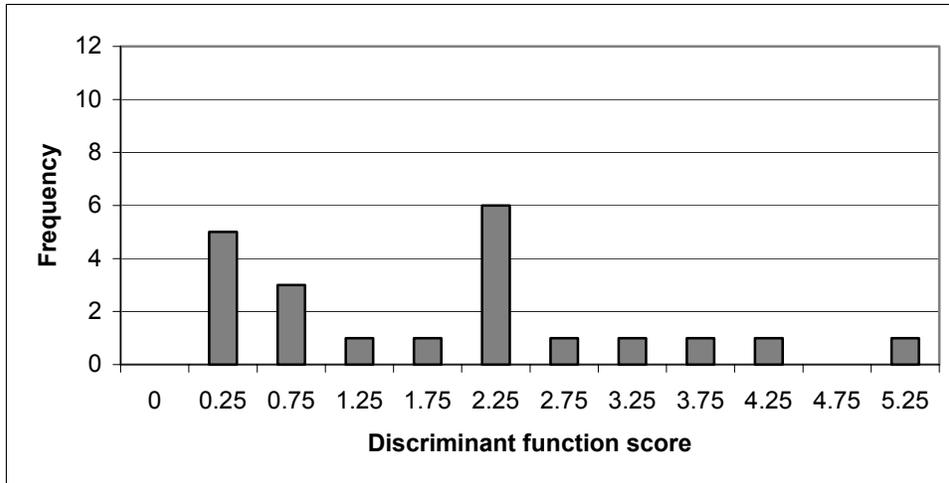


Figure 12. Frequency distribution of canonical function scores for failed SWWA nests ($n = 21$) in Britton's Neck, South Carolina (1999-2001).

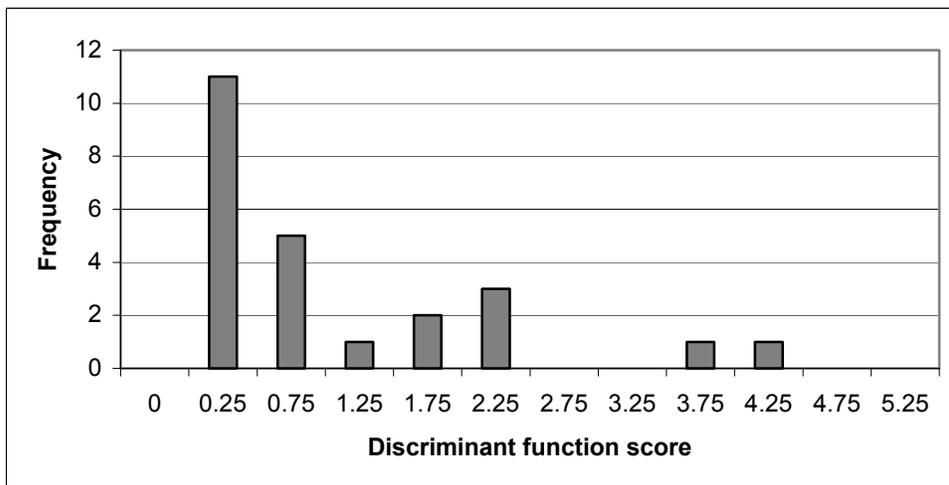


Figure 13. Frequency distribution of canonical function scores for successful SWWA nests ($n = 24$) in Britton's Neck, South Carolina (1999-2001).

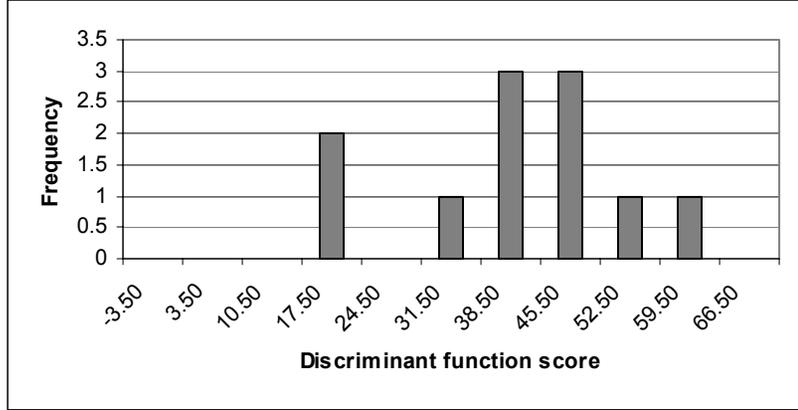


Figure 14. Frequency distribution of canonical function scores for failed, core nests ($n = 11$) in Britton's Neck, SC (1999-2001).

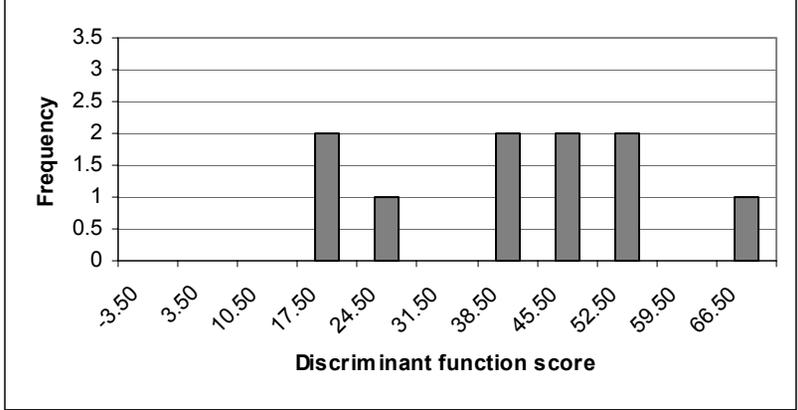


Figure 15. Frequency distribution of canonical function scores for successful, core nests ($n=10$), Britton's Neck, SC (1999-2001).

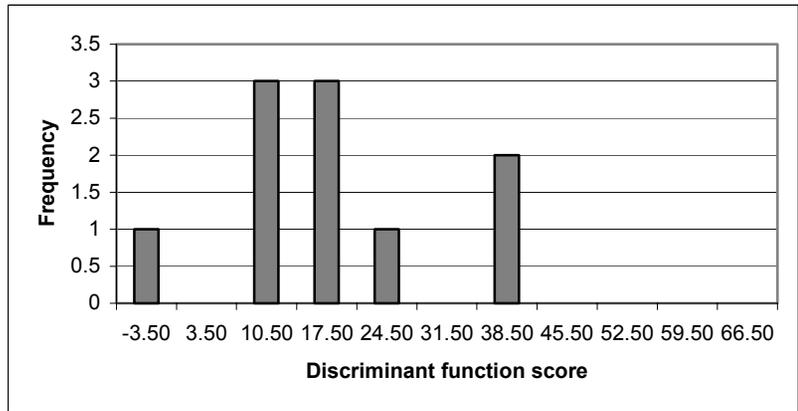


Figure 16. Frequency distribution of canonical function scores for failed, noncore nests ($n=10$) in Britton's Neck, SC (1999-2001).

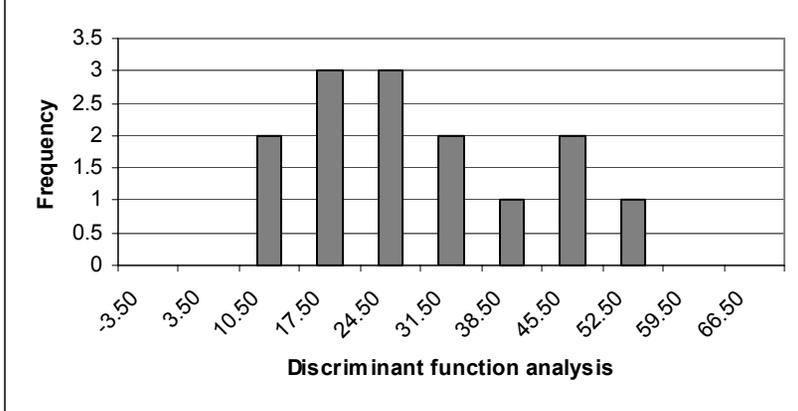


Figure 17. Frequency distribution of canonical function scores for successful, noncore nests ($n=14$) in Britton's Neck, SC (1999-2001).

CHAPTER 3

**AERIAL PHOTOGRAPHY TO EXAMINE SWAINSON'S WARBLER NEST-SITE
SELECTION IN RELATION TO HYDROLOGY AND UNDERSTORY THICKETS**

3.1 INTRODUCTION

According to Rotenberry (1985), physiognomy, or vegetative structure, is believed to be more important to avian occupancy patterns than taxonomic composition. In Chapter 2, I found both physiognomic and floristic factors to distinguish high-density SWWA nesting sites from low density. However, most of the discriminators were either direct or indirect measures of understory thickets. Nests were typically built in understory thickets or else within close proximity. Thickets appear to be one of the most important components at the nesting site, but without information on habitat at larger spatial scale, I cannot comment on nest-site selection, only habitat use (Jones 2001). Are thickets being selected disproportionately at nesting sites compared to territory and unused habitat?

Nest-site availability has been shown to play a role in habitat selection of Neotropical migrants, such as Black-throated Blue Warblers (Steele 1993, Bilke 1984). The influence of available nest sites on SWWA distribution, i.e. understory thickets, will be examined in this chapter. Few studies (Graves 2001, 2002, Peters 1999) have examined how understory thickets effect SWWA distribution, and the ones that have either counted vine stems on vegetation plots or other small-scale distribution. Configuration of understory thickets in the larger scale landscape has not been considered.

Landscape structure has been shown to influence how “ideal” and “free” animals move through a landscape (Jones 2001, Petit and Petit 1996). In a bottomland hardwood forest, hydrologic factors have a strong impact an animal’s ideal free distribution. Hydrology drives the ecology of the bottomland hardwood forest (Gosselink and Turner 1978), and SWWA is not exempt. Elevation and hydrology affect plant distributions in turn reflecting SWWA nest-site selection. In this chapter, I will examine hydrologic factors, such as

sloughs and swamps, in relation to nesting, territory, and unused habitat. Swamps refer to areas of the bottomland that are either permanently flooded or flooded during the majority of the breeding season.

In order to assess the role of understory thickets and drainages in nest-site selection, I used digital photogrammetry. Photographs provide information on landscape level characteristics, with easier data collection and potentially more accurate results than ground-based data from Global Positioning System (GPS) locations. Information is gathered using remote sensing, which is the collection of information from a remote vantage point, and is directly accessible for use in a Geographic Information System (GIS). Feature information was collected from a series of large-scale, color infrared aerial photographs taken in 1996 and 1998. The 1996 photographs were collected during leaf-off, and the 1998 photographs were captured during leaf-on, henceforth referred to as leaf-off and leaf-on photography.

Technical advances in digital photogrammetry over the last several years allow for the production of orthorectified photographs in digital format, with a resolution capable of mapping individual trees (Cameron et al. 2000). Orthorectification creates a planimetric image from a photograph and corrects for terrain and camera imprecision (Wolfe 1983). ERDAS Imagine (ERDAS, Inc. 1999a) software was used to relate coordinates from a Digital Elevation Model (DEM) and camera calibration to the aerial photographs. Once orthorectified, features can be delineated directly on the computer instead of the traditional method requiring feature transfer from hard-copy photographs to the GIS, an error prone process (Millinor 2000). Therefore, I decided to follow a digital procedure using orthorectified aerial photographs with features delineated directly on the computer (Koch 2001, Millinor 2000).

Different techniques were necessary to delineate understory thickets on leaf-off and leaf-on photographs due to the amount of living green vegetation present, which reflect bright red on color infrared photographs (Lillesand et al. 2004). Leaf-on photographs were dominated by living green vegetation; therefore, it was impossible to distinguish between hardwoods and thickets based on infra-red reflectance. Instead, changes in canopy height were used to detect canopy gaps and infer the presence of understory thickets. Canopy gaps were delineated in Stereo Analyst, a module of ERDAS Imagine (ERDAS, Inc. 2000) allowing features to be delineated directly on screen. The program allowed for computer-based 3-D viewing, where overlapping images captured from two different vantage points were viewed simultaneously (ERDAS, Inc. 2000). Stereoscopic viewing and sharp zoom-in capabilities allowed canopy gaps to be more interpretable, since tree crowns and height were visible (Koch 2001).

On the leaf-off photographs, pockets of living green vegetation were visible within a matrix of hardwood trees. At the time of photograph capture, only evergreen species or early leafing deciduous species would contain living green vegetation. Since few evergreen trees are present on the site (Table 1), the evergreen species were likely to be understory species, such as cane, vines, and American holly, all common components of understory thickets. I used these pockets of living green vegetation as a direct measure of understory thickets by grouping pixels of similar spectral values into spectral classes (Verbyla and Chang 1997).

The goal of this portion of the study was three-fold. First, I compared delineation of understory thickets using leaf-off versus leaf-on photography: 1) Visual analysis to delineate canopy gaps from leaf-on photographs using Stereo Analyst, or 2) a spectral analysis to delineate pockets of living green vegetation from leaf-off photographs. Second, I chose the

output that was the best predictor of understory thickets to examine SWWA nest-site selection in terms of physiognomic features, by comparing nest sites to territory and non-use plots. Third, I examined SWWA distribution to determine if density depends on the distribution of thickets and/or drainages.

3.2 METHODS

3.2.1 Leaf-on photography

Eight color infrared (CIR) aerial photographs at a scale of 1:6,000 were taken April 13, 1998 (Figure 1). Two flight lines were flown at 3,000 ft using a Wild RC30 camera with a 153.41-mm focal length. The photographs were scanned using an Epson 1640XL scanner at 400 dpi (dots-per-inch). Deciding on an appropriate scanning resolution is a compromise between file storage space and resolution (Koch 2001).

ERDAS Imagine Version 8.6 software (ERDAS, Inc. 1999a) was used to orthorectify photographs, with reference images from the Snow Island quadrangle. The horizontal reference image was based on United States Geological Survey (USGS) National Aerial Photography Program photographs (1:40,000, black and white), and the vertical reference was a USGS DEM with a 30-m resolution. The projection used was Universal Transverse Mercator, Zone 17, GRS 1980, North American Datum 1983.

Photographs were orthorectified in ERDAS Imagine using aerial triangulation (Figure 2), a batch process that is much faster than single image processing because fewer ground control points are needed (Koch 2001). First, a camera model had to be defined specifying the interior orientation of the camera. A camera calibration report was obtained from the USGS Optical Science Laboratory, containing information on focal length, fiducial orientation, and principal point. Fiducial points were placed on the photographs and adjusted until the root mean square error (RMSE) was less than 1 m.

Orthobase, a module of ERDAS Imagine, uses tie points to establish the overlap between photographs and creates a block based on this relationship. I manually placed a approximately two tie points in overlap areas, and then ran the automatic tie point generator

to increase the number of tie points. Once a block was established, at least six ground control points were placed on a reference source, Digital Orthophoto Quarter Quadrangle (DOQQ) in my case, and then matched on the photograph (Koch 2001). The DOQQ provided the X,Y coordinates while the DEM provided the Z coordinate (Koch 2001). Ground control points were positioned across the block of images, with at least one every third image (Koch 2001). Aerial triangulation was run converting tie points into ground control points and generating additional reference points, thus increasing ground control (ERDAS, Inc. 1999b). Once the RMSE for the entire block fell below 1 m, the image was resampled using the nearest neighbor method to create an orthophotograph.

Features were delineated using Stereo Analyst, where 3-D viewing was facilitated through use of stereo eyewear, known as Crystal Eyes (Koch 2001). Two images, representing right and left perspectives, alternated on the screen at a rate of 115 frames per second (Koch 2001). The eyewear responded to signals from an infrared emitter positioned above the computer monitor that synchronized the glasses to the refresh rate of the screen (Koch 2001). The effect allowed the viewer to see a single image in 3-D, which made changes in canopy height particularly obvious.

Features greater than a minimum mapping unit (mmu) of 0.001 ha were delineated, and saved as ArcView 2-D shapefiles. My classification scheme identified 6 features: swamp, road, slough, clearcut, river, and canopy gap (Table 2). Any remaining areas constituted bottomland hardwood forest. I used canopy height, texture, and color to distinguish between categories, with canopy height particularly useful in distinguishing small canopy gaps. Swamps were classified separately from canopy gaps, even though when viewed from above swamps appear as canopy gaps, just wetter than the areas used by

SWWA. Since the purpose of this mapping effort was to assess SWWA habitat, the two features were differentiated. Also, the edge of a swamp is a dynamic feature that can change from year to year depending on hydrology. I delineated swamp edges by comparing leaf-off and leaf-on photographs, plus my knowledge of the site.

3.2.2 Leaf-off photography

Four CIR photographs (Figure 3) were captured on March 12, 1996 at a scale of 1:15,840 with a Wild RC10 camera (152.86-mm focal length). The photographs were scanned using an Epson 1640XL scanner at 600dpi, and were orthorectified with the same horizontal and vertical reference images used for the leaf-on photographs. Stereo viewing was unnecessary for the spectral analysis and the entire site was covered in a single image; therefore, only one image was orthorectified.

Single image orthorectification followed a similar procedure to aerial triangulation, except tie points were unnecessary. Interior orientation was set with information from the camera calibration report, and six or more ground control points were placed until the RMSE fell below 1 m. The image was resampled using the nearest neighbor method and converted to an orthophotograph, which was converted into a GRID layer consisting of three bands. In ArcView 3.2 (ESRI 1992-1999), the infrared band was assessed to determine the spectral response that best represented understory thickets. A range of pixel values between 140 and 200 was assigned to the class “thicket” and converted to a new GRID for analysis.

3.2.3 *Quality assessment*

Accuracy assessment is the last critical step in map creation, with two types of accuracy assessed, positional and thematic (Congalton and Green 1999). Positional accuracy refers to how precisely map items are located relative to their position on the ground (Congalton and Green 1999). Millinor (2000) found positional accuracies to be well above the USGS National Park Vegetation Mapping Program standards when digital methods were used. I compared road positions and other features easily located on the orthorectified image to GPS data collected from my site, and found locational accuracy to be reasonable. Because absolute positions were not as crucial to my analyses as relative positions, I decided to forego a formal assessment of positional accuracy and only examined thematic accuracy.

Assessment of thematic accuracy typically uses other aerial photographs or ground truthing (Congalton and Green 1999). Congalton and Green (1999) encourage ground truthing as the most reliable method of collecting reference data. A rule of thumb is to collect 50 samples for each vegetation type; however, sample numbers can be adjusted depending on the relative importance of each category within a mapping protocol (Congalton and Green 1999). In my case, all the features were easy to view with the exception of canopy gaps. I decided to focus my thematic assessment on that category.

I assumed a 1 to 1 correlation of canopy gaps to understory thickets, an assumption which may be incorrect because understory thickets do not always form below canopy gaps. Sample locations should be representative of the map and chosen without bias (Congalton and Green 1999). For that reason, I used a stratified random sample to choose sample points. The Animal Movement extension for ArcView was used to randomly place a group of points inside canopy gaps and outside gaps. Sample points were located in the center of polygons,

and at least 25 m outside polygons to avoid edge issues. In a GIS, I buffered ground truth points with a 2-m buffer. If a canopy gap or understory thicket fell within the buffer, it was classified as an understory thicket.

In the field, I navigated to sample points with a Trimble GeoExplorer III, Global Positioning System (Trimble Navigation Limited, 2001). Once at a point, I sampled an area equal to ½ the mmu (Congalton and Green 1999), approximately a 2-m radius around the point. I recorded if an understory thicket was present or absent within 2 m, without any prior knowledge of the GIS classification. Thickets had to be large and thick enough to require a machete to traverse.

The results of ground truthing and thematic mapping were compared in an error matrix. The overall accuracy is the sum of the diagonal cells, and was compared to the 80% accuracy standard required by the USGS National Park Service Vegetation Mapping Project (Bailey et al. 1994). The calculated accuracy was compared to the standard using a student's *t* distribution (Bailey et al. 1994):

$$t = \frac{\hat{p} - p}{\sqrt{\frac{p(1-p)}{n}}},$$

where \hat{p} was the overall accuracy, p the 80% accuracy standard, and n the sample size. A confidence interval was constructed using the following equation (Bailey et al. 1994):

$$\hat{p} \pm \left\{ z_{\alpha} \sqrt{\frac{\hat{p}(1-p)}{n} + \frac{1}{(2n)}} \right\},$$

where z_{α} was from the *z*-distribution at significance level α .

The relationship of features, such as sloughs, swamps, and understory thickets, to nest, territory, and non-use plots was assessed in ArcView 3.2. The Animal Movement extension was used to place random points in territories and non-use locations. Inside the survey boundary, 150 non-use points were located outside territories and away from nests, plus 150 territory points were randomly selected inside 1998 and 1999 territories. These two years were used, because time invested in territory mapping was limited in 2000 and 2001. Distances of each plot to nearest slough, swamps, and understory thicket were measured using the Nearest Features extension v.3.8a for ArcView.

All analyses were performed using SAS Version 8 software (SAS Institute Inc. 1999-2001). Variables were tested for normality using Shapiro-Wilk goodness of fit tests and normal probability plots (PROC UNIVARIATE). If variables were non-normal, a log, square root, or $\log(X + 1)$ transformation was used. Log transformations were not appropriate for variables containing zero values, in which case $\log(X + 1)$ was more suitable. Student's *t*-test and ANOVA were used to compare means of variables.

3.3 RESULTS

3.3.1 Leaf-on photography

The set of leaf-on photographs were orthorectified using aerial triangulation, with a RMSE of 0.144 m (Table 3). A total of 142 ground control points were used in a quality assessment to examine which type of photography, leaf-on or leaf-off, would be better for identifying understory thickets. Ground control points were sampled in March 2005, with 56 found inside understory thickets and 86 outside (Figure 4). The quality assessment examined how often this relationship held true for areas identified as gaps on the photographs.

The most common error involved overestimating understory thickets on the basis of gaps (23%, 33 of 142), where a gap was identified on a photograph but a thicket was absent on the ground. Sixty-seven percent (96 of 142; Table 4) of canopy gaps contained understory thickets. Less commonly (9%, 13 of 142), thickets showed up on the ground in places that were not identified as gaps on the GIS. Errors were evenly distributed across the site. I only assessed the presence of understory thickets when ground truthing, and not the presence of canopy gaps; therefore, I cannot estimate the omission error for canopy gaps.

Large canopy gaps were more often associated with understory thickets than small gaps. Of the gaps corresponding to thickets, the average gap size measured in the GIS was $537.2 \pm 126.8 \text{ m}^2$ ($n = 43$), compared to gaps in which no thickets were found at a size of $292.3 \pm 59.2 \text{ m}^2$ ($n = 33$), a difference significant at the 0.10 level ($t = 1.75$, $P = 0.085$). In summary, larger canopy gaps appeared more likely to correspond with the presence of understory thickets. Although a gap in the canopy does not guarantee the presence of an understory thicket, the results suggest canopy gap and size were fair estimators of understory thickets.

3.3.2 Leaf-off photography

A single leaf-off photograph was orthorectified when the ground control point RMSE fell below 1 m. A site visit on March 12, 2005 coincided with the same date as photograph capture in 1996. Although I ground truthed the same date as photo collection, conditions were unlikely to be identical between 1996 and 2005, but the information should provide an idea of site conditions. As expected, cane, American holly, and some of the woody vines had living leaves. Deciduous trees that leaf early (Radford et al. 1983), such as red maple, were flowering but had not yet begun to leaf-out. In addition, the majority of blackberry plants were in full leaves. Blackberry, a deciduous species with early leafing, was a common component of understory thickets, as seen in Chapter 2. In the early spring, the amount of living green vegetation found within understory thickets compared to the forest makes CIR photographs useful for thicket delineation.

Areas of infrared reflectance correctly corresponded to understory thickets 59.1% (84 of 142; Table 5) of the time. The most common error involved overestimating understory thickets on the basis of infrared reflectance (26%, 37 of 142), where living green vegetation on a photograph was not a thicket on the ground. Understory thickets were classified as absent when they were in fact present 15% (21 of 142) of the time. Larger understory thickets ($465.1 \pm 118.2 \text{ m}^2$) were classified correctly more often than smaller thickets ($390.6 \pm 93.9 \text{ m}^2$), an insignificant difference ($t = 0.49$, $P = 0.623$). Features such as swamps and drainages were readily apparent by their lack of red color (Figure 5). The southern fourth of the map was less vivid than the rest, due to flooding in that area.

I was able to classify understory thickets better using leaf-on photography compared to leaf-off photography, but the leaf-on classification was significantly different from the

80% accuracy standard ($t = 3.75$). The 90% confidence interval for the leaf-on map of understory thickets was 61.7% to 73.5%. The reduced accuracy may be the result of temporal changes between photograph capture and ground-truthing. A nine and seven year gap occurred between the times of photograph collection and ground truthing. During this lapse, understory thickets may have disappeared or appeared due to gap succession and perturbations, thus impacting my accuracy results.

3.3.3 Site features

Leaf-on photographs were used for the remaining analysis. Since large canopy gaps were reasonable indicators of understory thickets, I will refer to understory thickets for the rest of the discussion. One hundred-fifty hectares were surveyed; of that, understory thickets comprised 23 ha (15%), swamp covered 21 ha (14%), and clearcuts 3 ha (2%). The remaining 103 ha was bottomland hardwood forest (Figure 6). A total of 771 understory thickets was delineated, with an average size of $360.2 \pm 26.69 \text{ m}^2$, and a range of 11 to $14,225 \text{ m}^2$. In GIS, thicket shapes appeared distorted compared to ground shape, which was probably due to tree crown shape. Understory thickets covered 25% (8.5 of 34 ha) of the core area, compared to 13% of the noncore area (15 of 116 ha). Core understory thickets were larger ($506.4 \pm 85.5 \text{ m}^2$, $n = 168$) than noncore thickets ($319.5 \pm 29.8 \text{ m}^2$, $n = 603$), a significant difference ($t = 2.91$, $P = 0.004$).

3.3.4 Nest, territory, and non-use plots

Nest, territory, and non-use plots were positioned across the study area (Figure 7). Nests were significantly closer to understory thickets than territory and non-use points ($F =$

14.04, $P = <0.0001$, Table 6), with territories closer than non-use. Plots in core ($F = 13.72$, $P = <0.0001$) and noncore areas ($F = 7.18$, $P = 0.0009$) also differed significantly in respect to distance from understory thickets. In both areas, nests were closest to understory thickets, followed by territory points, and lastly non-use. Although noncore nests were slightly closer to understory thickets ($t = 0.99$, $P = 0.325$), noncore territory ($t = -1.51$, $P = 0.132$) and non-use points ($t = 1.57$, $P = 0.118$) were further from thickets than core plots. In both core ($F = 6.35$, $P = 0.002$) and noncore plots ($F = 1.32$, $P = 0.269$), understory thickets near the nest were larger than those found near territory points, and lastly non-use (Table 7). However, the only significant difference was between thicket size at core and noncore nests ($t = 2.67$, $P = 0.009$), with core nests positioned closer to much larger understory thickets.

Territory points were located farthest from swamps, with nests and non-use points closer and almost equal, a difference significant at the 0.10 level ($F = 2.83$, $P = 0.06$). Nests were seldomly located inside swamps, but when present were along the edges (Figure 8). Plots within core ($F = 8.58$, $P = 0.0003$) and noncore areas ($F = 44.09$, $P = <0.0001$) differed significantly in respect to swamps (Table 8). Core nests and non-use points were closer to swamps than noncore nests and non-use ($t = -2.84$, $P = 0.005$).

Nests were closest to sloughs, followed by territory points, and finally non-use points, a nonsignificant difference ($F = 1.77$, $P = 0.172$). Oftentimes, nests were positioned along sloughs, especially in the core area where there was a concentrated network of drainages (Figure 9). Plots in the core area differed in respect to distance from sloughs ($F = 7.17$, $P = 0.001$), while noncore plots did not differ significantly ($F = 0.28$, $P = 0.757$). Core nests were closer to sloughs, with territory points positioned farther away, and non-use plots the farthest (Table 8).

3.4 DISCUSSION

3.4.1 Photographic assessment

My results indicated understory thickets can be assessed using large-scale aerial photography, and in turn be used to assess SWWA habitat. Although thematic accuracies fell below suggested map accuracy standards, I think the issue was due more to elapsed time between photograph capture and ground truthing than an inability to identify understory thickets. There was a 9 and 7-year lapse between photographs and ground truthing for leaf-off and leaf-on photographs, respectively. According to Congalton and Green (1999), accuracy assessment data should be collected soon after the collection date of remotely-sensed data to avoid changes in land cover. During the elapsed time, the site did not experience major changes such as harvest or hydrologic shifts. However, gap succession could have resulted in understory thickets shrinking and disappearing. The type of error supports this scenario, because understory thickets were most often overestimated and the older photography, which was more prone to this error. Large understory thickets were most likely to be classified correctly, which makes sense because they would be easier to detect and take the longest to change.

Spectral analysis was less accurate at predicting understory thickets than canopy gaps delineated in Stereo Analyst. Unsupervised classification assumes spectral classes are pure representations of land cover, but is not always the case (Verbyla and Chang 1997). However, the reduced leaf-off accuracy could be the result of temporal changes rather than a less effective method. Choosing the appropriate classification method requires weighing a tradeoff between processing time and accuracy, and may be site dependent. Manual interpretation with Stereo Analyst, although more accurate, is a labor-intensive technique.

For small areas, Stereo Analyst may be more appropriate than spectral analysis, but its suitability decreases with increasing size. Timing is an important consideration when using leaf-off photography, in order to miss the leafing of early trees like red maple. More research is needed to assess these techniques and their ability to predict understory thickets, and in turn SWWA occupancy.

3.4.2 Habitat selection

Nest, territory, and non-use plots differed the most in terms of their distance to understory thickets. SWWA chose nest sites in closer proximity to understory thickets than was seen at random territory or non-use points. Peters (1999) found similar results with SWWA nesting in denser habitat than found at territory points. For many Neotropical migrants, foliage density is greater at the nest site than surrounding territories (Hoover and Brittingham 1998). Recall from Chapter 2, two-thirds of nests were located inside understory thickets, and almost all were less than 5 m from a thicket. Nests were located an average of 2 m from a thicket, compared to 6 m in Chapter 3. Presumably, the farther distance is due to aerial photography unable to pick up small thickets that were sampled on the ground.

SWWA chose to nest near large understory thickets, larger than those available at territory or non-use points. Core plots were located near larger thickets than noncore, with the largest difference between nests followed in decreasing magnitude by territories and unused habitat. The distance of core and noncore plots followed the overall results, with nests closest to thickets followed by territories and lastly non-use. There was not a significant difference between core and noncore plots in respect to distance. Comparing

ground survey results in Chapter 2 to the aerial photograph classification in Chapter 3, core nests were 5 m closer to thickets and noncore nests were 2 m closer in ground surveys. Again, I overestimated distance when using my aerial photograph classification, probably due to an inability to pick up smaller thickets.

Overall, no significant difference was detected between plot types and distance to slough. However, when areas were separated core plots were highly significant. Core nests were positioned closer to sloughs than territories and lastly unused habitat. Core plots were always closer to sloughs than noncore plots, but the difference was most extreme between nests. The relationship of core plots to sloughs mirrored what was seen with understory thickets. Areas differ with respect to the number of drainages, and SWWA appears to select areas near sloughs for core nests. Ground results from Chapter 2 differ in that noncore nests were closer to sloughs than core nests. Comparing Chapter 2 and 3 results, core nests were exactly the same distance, but noncore nests were 51 m closer to sloughs on the ground. The noncore area may contain more small drainages that cannot be detected by aerial photographs.

Plot types differed significantly in respect to their distance to swamps, and the significance increased when core and noncore plots were separated. Nest and non-use plots were closer to swamps than territories, a difference retained between areas. Core plots were closer to swamps than noncore in all cases. Within each area, territories were the furthest from swamps and nests and non-use points were closer and found at a similar distance.

Oftentimes, habitat preferences are assumed to be adaptive without demonstration of increased fitness in preferred habitats (Jones 2001). SWWA selected understory thickets for nesting and chose thickets based on size, a characteristic most pronounced in the high-density

area where nest thickets were 2 times larger than at noncore nests. The core area offered more available nest sites, with 25% of core area covered by thickets and only 13% of noncore. Pairs nesting in the core area had fitness benefits, since almost 2 times more young were fledged off of smaller territories (1.19 versus 1.92 ha). Presumably, males defending a smaller territory should expend less energy on defense and food collection, and possibly have more energy to invest in reproduction.

3.4.3 Understory thicket formation

Considering the importance of understory thickets to SWWA occupancy, it is important to understand how they arose. Core thickets tended to be larger than noncore (784 m² vs. 518 m²), and the core area was more covered by thickets. Why the discrepancy between two areas harvested identically? Smaller thickets were probably the result of small disturbances like tree falls; however, I will make inferences on the causes of larger thickets. Several thickets were so large (4800 m²) it is unlikely they were caused by a tree fall, especially a 20-year old tree. A larger scale disturbance caused by a hurricane or flooding would be required to cover an area that large. Or else, the harvest technique left residual impacts to the landscape.

Large thickets were dominated by tangles of vines and blackberry, with relatively few saplings. Following harvest, thickets are quickly covered by lush vegetation (vines, briars, switchcane, herbs, and shrubs), but often within a few years saplings emerge with vine and shrub species declining (Martin et al. 1993). If the large understory thickets on my site were the result of the 1983 harvest, they would have persisted for 20 years and appear to be arrested in terms of thicket succession. Poor regeneration at thickets may result from harvest

impacts, or perhaps hydrology differences. Leaf-on photography indicated the core area to contain more drainages and swamps than noncore. The core area may be at a lower elevation and subject to more severe and prolonged flooding, which could impact vegetative regeneration.

Heavy equipment can break down stable soil aggregates, thus leading to compaction, in turn reducing plant growth (Brady 1984). Skidders were probably used on my site because 96% of timber was extracted by ground skidding in 1986 (Stokes and Schilling 1997). Skidders can impact soil through compaction, puddling and displacement, an issue exacerbated in wet areas (Hatchell et al. 1970). Wet sites can require more roads because deep ruts force loggers to abandon original trails (Hatchell et al. 1970). On South Carolina and Virginia sites, primary skid trails comprised 12.4% of timberland, secondary skid trails 19.9%, and log decks 1.5% (Hatchell et al. 1970). Loblolly pine exhibited reduced stocking and retarded height in areas, with areas containing log decks most impacted followed by areas with primary skid trails and secondary trails (Hatchell et al. 1970). If the core area is wetter, as it appears to be, logging operations may have had more of an adverse effect resulting in poor tree regeneration.

Aside from harvest impacts, microtopography of floodplain forests affects many features of the stand, including hydrology, soil properties, and species richness, even though bottomlands have only small-scale topographic variation (Almquist et al. 2002, King and Antrobus 2001, Wharton et al. 1982). Evidence suggests thicket formation is affected by topography in steep terrain, but few studies have examined thicket formation in relatively, level terrain as found in bottomland hardwood forests (Almquist et al. 2002). Almquist et al. (2002) found thicket abundance was greater on ridges than on slopes or bowls in a Texas

bottomland hardwood forest. Along sloughs banks, ridges are formed where floodwaters drop sediment as they crest the banks (Wharton et al. 1982). Following Almquist's et al. (2002) results, these areas would be expected to have more understory thickets. As was seen earlier in the results, SWWA core nests were also selected according to slough position. This selection may be due to more understory thickets along slough banks.

3.4.4 Hydrologic considerations

The whole bottomland system is dependent on hydrology, which needs to be conserved as much as possible to maintain bottomland ecology (Wharton et al. 1982). Damming may severely modify or eliminate the hydroperiod, allowing for clearing of floodplains for agriculture and pine plantations (Wharton et al. 1982). Flood control coupled with the increasing demand for hardwood pulpwood and lumber products since the 1980's, will continue to pressure bottomland hardwood resources (Stokes and Schilling 1997).

A less obvious consequence of damming is the effect of flow regulation. The Army Corp of Engineers commonly holds back floodwaters for recreational and hydroelectric purposes, and then releases large quantities of water at once (Jean Richter, U.S. Fish and Wildlife Service, Roanoke River Refuge, personal communication). Discharges held artificially high will flood bottomlands more severely, possibly destroying SWWA nesting attempts. In terms of SWWA breeding, high flood months are April and May. As was shown in Chapter 1, May flooding can push back nest initiations by as much as three weeks. Aside from the obvious consequences of destroying nests, delaying nesting may impact fecundity by not allowing enough time for multiple nesting attempts. Multiple nesting attempts were shown in the first chapter to more than double fecundity. It is important to

work with the Army Corp of Engineers to advocate for smaller water releases, especially during May.

Bottomlands support a rich bird community that swells to several times its resident size during the migratory season, and exists as an interface between aquatic and terrestrial habitats (Kellison and Young 1997). Red river bottoms are laden with nutrients from upstream, thus are highly productive for plant growth and animal diversity (Kellison and Young 1997). Damming reduces silt and its associated nutrient inputs downstream of dams, which can impact plant, invertebrate, and vertebrate communities downstream (Wharton et al. 1982). Hydrology appears to be the driving force influencing vegetation and distribution of SWWA in the Great Dismal Swamp (Graves 2001).

3.4.5 Swainson's Warbler Conservation Plan

US Fish and Wildlife Service conservation objectives in the South Atlantic Coastal Plain are to maintain and improve the habitat quality for 30 sites over 6,000 acres for SWWA (Hunter et al. 1999). How large a population would an area this size support? The average territory size on the Woodbury Tract, a 20-year old forest, was 1.6 ha. In a 50-year old forest, Graves (2001) found territories to range between 3-18 ha. The population size these sites would support depends on forest age. In an early successional forest, a 6,000-acre reserve could support approximately 1,556 pairs. According to Graves' (2001) territory estimates, mature forest would support between 135 to 809 pairs. More research is needed to confirm these territory estimates, but on a coarse scale it appears SWWA conservation would best be served by working in early successional habitat.

I do not wish to diminish the importance of mature bottomland hardwood forest; it is a critical resource for many species. First and foremost, these areas need to be conserved for their own intrinsic value. However, I do not advocate carving up mature forest for SWWA management, when early successional habitat may be just as valuable by providing more available nesting sites. Timber companies and private landowners managing bottomlands for timber should be encouraged to maintain these sites as bottomland hardwood forest. Conservation easements and tax breaks could be used to make the proposition more attractive to landowners. From my research, managed bottomland forests have the potential to provide timber and habitat for SWWA and many other Neotropical migrants, such as Prothonotary and Hooded Warblers.

To date, assessment criteria of potential SWWA habitat are not available. From my study, understory thickets and hydrology were the most important factors driving SWWA distribution. Remote sensing could be used to assess suitable SWWA habitat, and prioritize acquisition efforts accordingly. Leaf-off photography, capturing areas of living green vegetation during late winter to early spring, would provide the most cost and time efficient method of assessing understory thickets. On my site, the high-density area was 25% covered by understory thickets, compared to 13% coverage of the low-density area. As a manager, I would look for sites with at least 15% understory thicket coverage. Configuration of thickets in relation to sloughs and swamps could also be important. When choosing appropriate tracts of land, efforts should focus on larger tracts over smaller, due to impacts of BHCO parasitism and nest predation.

Research programs need to be initiated examining many aspects of SWWA biology. The impacts of altered hydrologic regimes on litter fauna and SWWA distribution should be

assessed. Breeding biology should be studied on other managed, early successional sites to determine if my results are representative. In addition, no quantitative breeding information exists for mature landscapes. Until those data are available, SWWA management should focus on both early successional and managed sites. On the Woodbury Tract, I would be interested in comparing soil characteristics from core and noncore areas and also in examining the soil fauna, both issues potentially impacting distribution.

First and foremost, conversion of bottomland forests to agriculture, pine plantations, reservoirs, and housing developments must be curbed. The ecological and biological value of bottomland hardwood forests cannot be matched by any of these land uses. In addition, the slow degradation of bottomland hardwood forests by altered flow needs to be minimized as much as possible. In terms of SWWA, bottomland sites should be prioritized according to those with the least hydrologic disturbance, located in the Coastal Plain, covering the largest areas, with substantial understory thicket coverage.

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Table 1. Deciduous and evergreen species found on Woodbury Tract, Britton's Neck, South Carolina, 1999-2001.

Species	Common Name	Leaf cycle
Trees and shrubs		
<i>Acer rubrum</i>	Red maple	Deciduous
<i>Carpinus caroliniana</i>	American hornbeam	Deciduous
<i>Ilex deciduas</i>	Deciduous holly	Deciduous
<i>Ilex opaca</i>	American holly	Evergreen
<i>Celtis laevigata</i>	Hackberry	Deciduous
<i>Cornus florida</i>	Dogwood spp.	Deciduous
<i>Crataegus spp.</i>	Hawthorn	Deciduous
<i>Ligustrum spp.</i>	Privet spp.	Semi-evergreen
<i>Liquidambar styraciflua</i>	Sweetgum	Deciduous
<i>Myrica cerifera</i>	Wax Myrtle	Semi-evergreen
<i>Acer negundo</i>	Box elder	Deciduous
<i>Betula nigra</i>	River birch	Deciduous
<i>Carya aquatica</i>	Water hickory	Deciduous
<i>Diospyros virginiana</i>	Persimmon	Deciduous
<i>Fraxinus pennsylvanica</i>	Green ash	Deciduous
<i>Morus rubra</i>	Red Mulberry	Deciduous
<i>Nyssa sylvatica</i>	Gum spp	Deciduous
<i>Pinus taeda</i>	Loblolly pine	Evergreen
<i>Platanus occidentalis</i>	Sycamore	Deciduous
<i>Populus deltoids</i>	Cottonwood	Deciduous
<i>Quercus alba</i>	White oak	Deciduous
<i>Quercus laurifolia</i>	Swamp laurel oak	Semi-evergreen
<i>Quercus lyrata</i>	Overcup oak	Deciduous
<i>Quercus michauxii</i>	Swamp chestnut oak	Deciduous
<i>Quercus nigra</i>	Water oak	Semi-evergreen
<i>Quercus phellos</i>	Willow oak	Deciduous
<i>Rhus spp.</i>	Sumac	Deciduous
<i>Salix nigra</i>	Black willow	Deciduous
<i>Styrax spp.</i>	Snowbell	Deciduous
<i>Taxodium distichum</i>	Bald cypress	Deciduous
<i>Ulmus alata</i>	Winged elm	Deciduous
<i>Ulmus Americana</i>	American elm	Deciduous
<i>Ulmus rubra</i>	Slippery elm	Deciduous
<i>Vaccinium arboreum</i>	Blueberry	Semi-evergreen
Woody vines		
<i>Ampelopsis arborea</i>	Pepper vine	Deciduous
<i>Berchemia scandens</i>	Supplejack	Deciduous
<i>Bignonia capreolata</i>	Crossvine	Evergreen
<i>Campsis radicans</i>	Trumpet creeper	Deciduous
<i>Gelsemium rankinii</i>	Carolina jasmine	Evergreen
<i>Parthenocissus quinquefolia</i>	Virginia creeper	Deciduous
<i>Smilax smallii</i>	Greenbrier	Semi-evergreen
<i>Toxicodendron radicans</i>	Poison ivy	Deciduous
<i>Vitis rotundifolia</i>	Muscadine grape	Deciduous
Miscellaneous		
<i>Arundinaria gigantea</i>	Giant cane	Evergreen
<i>Rubus spp.</i>	Blackberry	Deciduous

Table 2. Classification rules for thematic mapping of leaf-on CIR aerial photographs collected on April 13, 1998, Britton's Neck, South Carolina.

Coloration	Characteristic	Classification category
Dark (water)	Linear, width < 25 m, located in forest interior.....	1. Slough
	Linear, width > 25 m.....	2. River
	Nonlinear.....	3. Swamp
Light	Linear.....	4. Road
	Abrupt edge, smooth texture, usually larger than 1 ha.....	5. Clearcut
	Rough edge and texture, typically small (0.01 ha).....	6. Canopy Gap

Table 3. Aerial triangulation results for leaf-on CIR aerial photographs, Britton's Neck, South Carolina.

Feature	Value (m)
RMSE	0.1444
Ground X	0.1997
Ground Y	0.1187
Ground Z	0.6277
Image X	0.1609
Image Y	0.0664

Table 4. Error matrix comparing results of understory thicket mapping from leaf-on CIR aerial photographs to 2005 ground truthing data, Britton’s Neck South Carolina.

Classified	Actual		Total (% correct)
	Thicket present	Thicket absent	
Present	43	33	76 (56)
Absent	13	53	66 (90)
Total (% correct)	56 (77)	86 (61)	142

Table 5. Error matrix comparing results of understory thicket mapping from leaf-off CIR aerial photograph to 2005 ground truthing data, Britton’s Neck South Carolina.

Classified	Actual		Total (% correct)
	Thicket present	Thicket absent	
Present	35	37	72 (49)
Absent	21	49	70 (70)
Total (% correct)	56 (62)	86 (57)	142

Table 6. Mean distance (m) and standard error of SWWA nest, territory, and non-use plots to the nearest swamp, slough, and understory thicket using thematic map information created from leaf-on CIR aerial photographs, Britton's Neck, South Carolina, 1997-2001.

Feature	Mean distance, m (SE)			<i>F</i>	<i>P</i>
	Nest (<i>n</i> = 121)	Territory (<i>n</i> = 150)	Non-use (<i>n</i> = 150)		
Swamp	59.24 (4.83)	75.29 (5.46)	59.64 (5.92)	2.83	0.06
Slough	64.67 (6.14)	77.08 (6.26)	79.94 (5.18)	1.77	0.172
Understory thicket	6.32 (0.69)	13.30 (1.89)	19.39 (1.90)	14.04	<0.0001

Table 7. Mean understory thicket size (m²) and standard error of closest thicket to Swainson's Warbler nest, territory, and non-use points in core versus noncore areas using thematic map information created from leaf-on CIR aerial photographs, Britton's Neck, South Carolina, 1997-2001.

Plot type	Mean thicket size, m ² (SE)		<i>t</i> _{area}	<i>P</i> _{area}
	Core	Noncore		
Nest	1213.34 (206.38)	646.86 (102.15)	2.67	0.009
Territory	747.55 (124.15)	520.08 (82.74)	1.58	0.117
Non-use	390.92 (93.23)	386.38 (125.12)	0.02	0.9842
	<i>F</i> _{plot}	6.35	1.32	
	<i>P</i> _{plot}	0.002	0.269	

Table 8. Mean distance (m) and standard error of Swainson's Warbler nest, territory, and non-use plots in core versus noncore areas to the nearest swamp, slough, and understory thicket using thematic map information created from leaf-on CIR aerial photographs, Britton's Neck, South Carolina, 1997-2001.

Feature	Mean distance, m (SE)						
	Plot type	<i>n</i>	Core	<i>n</i>	Noncore	<i>t</i> _{area}	<i>P</i> _{area}
Swamp							
Nest		49	40.99 (4.74)	72	71.65 (7.10)	-2.84	0.005
Territory		54	62.20 (7.28)	96	82.66 (7.94)	-1.32	0.189
Non-use		36	36.74 (9.91)	114	66.88 (7.01)	-3.16	0.002
	<i>F</i> _{swamp}		8.58		44.09		
	<i>P</i> _{swamp}		0.0003		<0.0001		
Slough							
Nest		49	40.07 (5.43)	72	81.41 (9.16)	-3.47	0.0007
Territory		54	55.93 (5.24)	96	88.98 (9.13)	-1.15	0.251
Non-use		36	74.04 (7.95)	114	81.81 (6.35)	-0.19	0.849
	<i>F</i> _{slough}		7.17		0.28		
	<i>P</i> _{slough}		0.001		0.7575		
Understory thicket							
Nest		49	7.12 (1.09)	72	5.75 (0.89)	0.99	0.325
Territory		54	8.85 (1.39)	96	15.81 (2.82)	-1.51	0.132
Non-use		36	25.78 (5.17)	114	17.37 (1.87)	1.57	0.118
	<i>F</i> _{gap}		13.72		7.18		
	<i>P</i> _{gap}		<0.0001		0.0009		

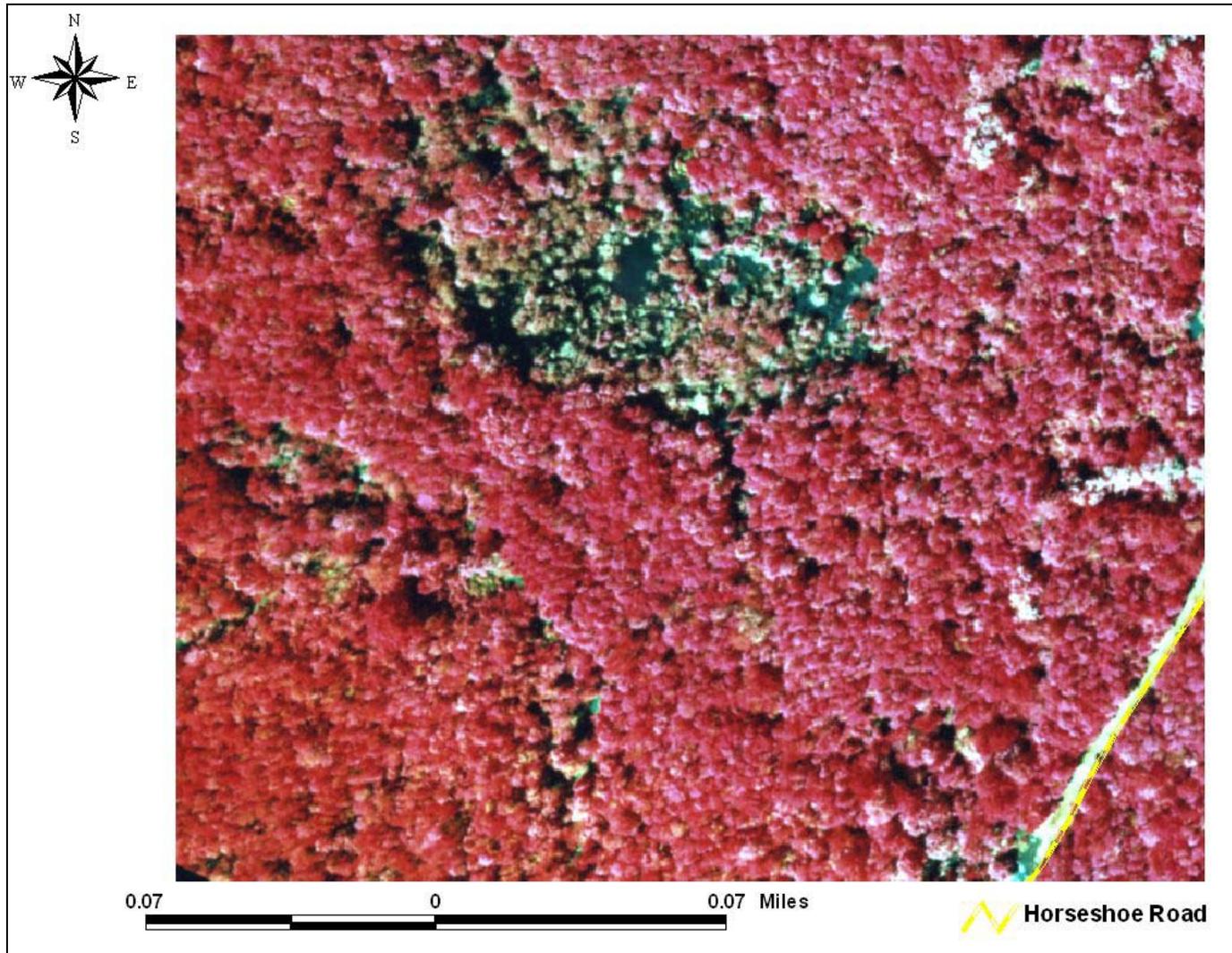


Figure 1. CIR aerial photograph captured April 13, 1998 of field site during leaf-on at a scale of 1:6,000, Woodbury Tract, Britton's Neck, South Carolina. Portion of image has been enlarged to show swamp in the center and surrounding canopy gaps.

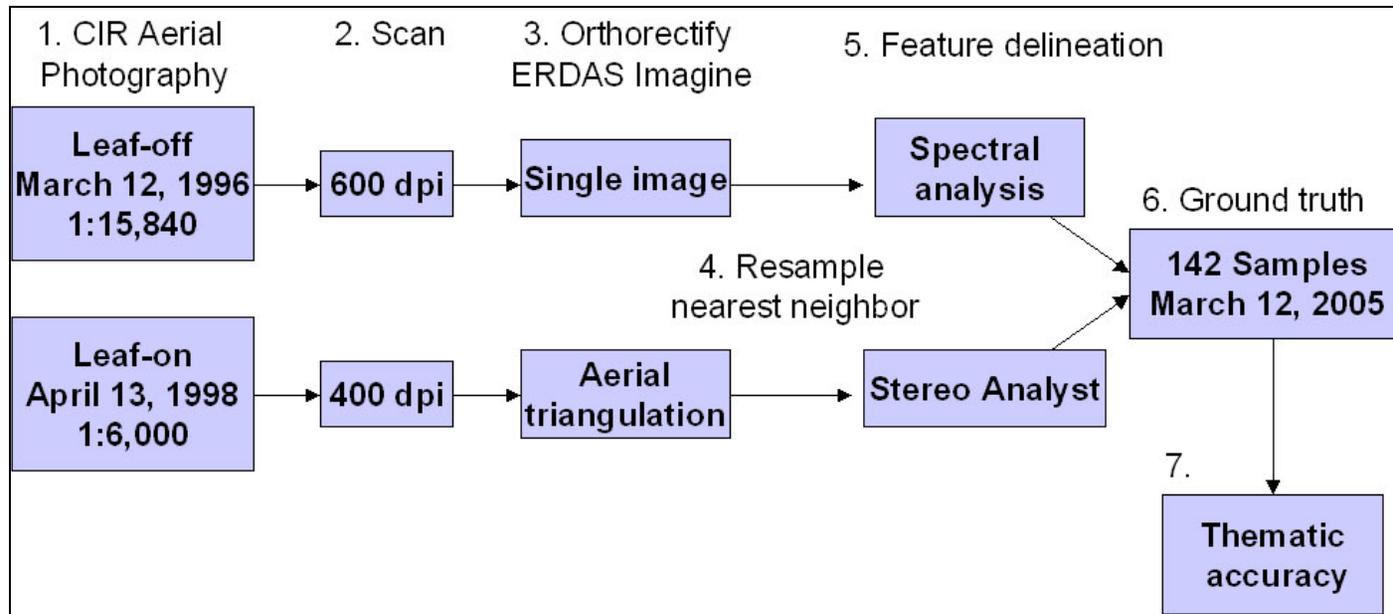


Figure 2. Flow chart highlighting the steps necessary to delineate understory thickets from leaf-on and leaf-off photographs.

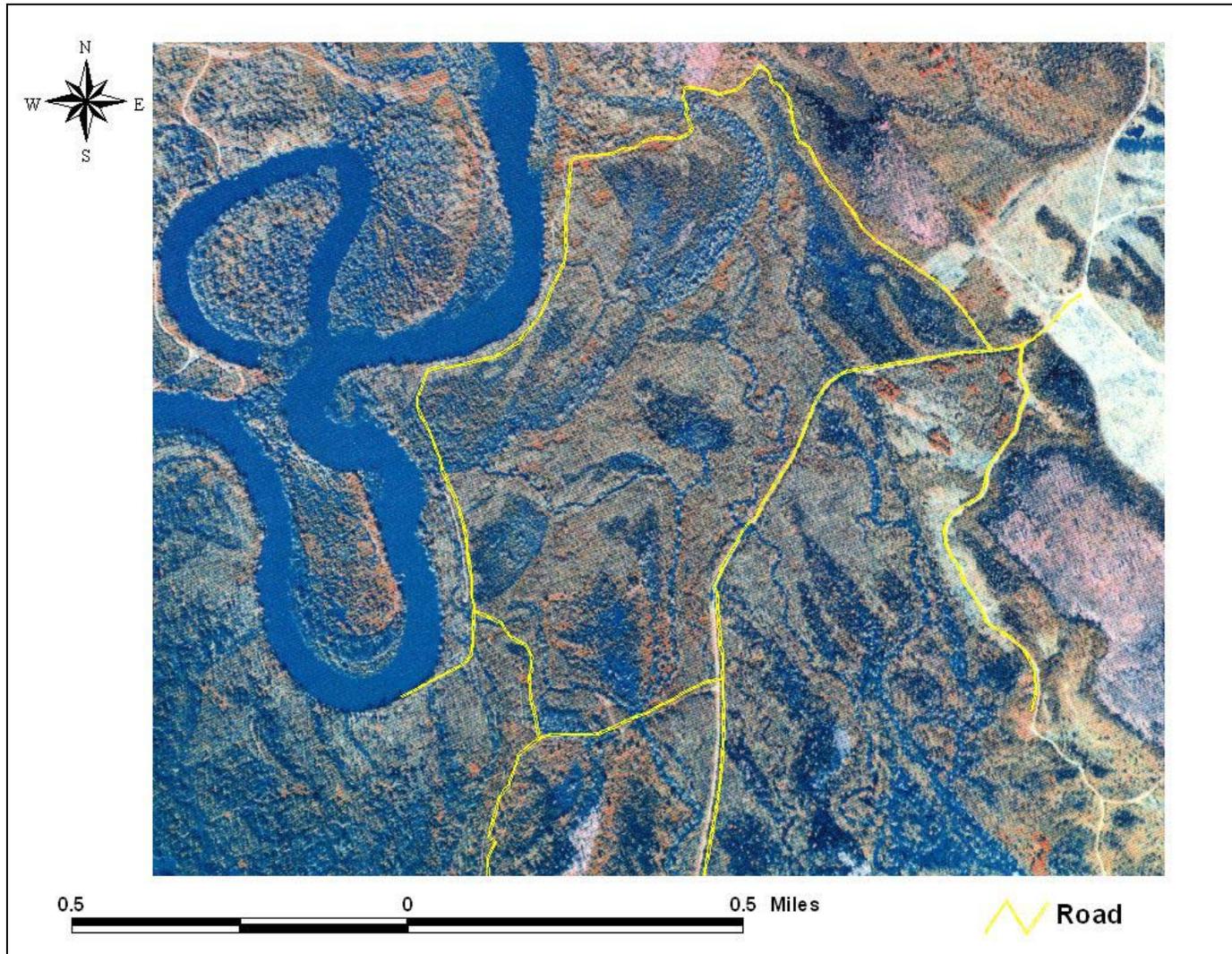


Figure 3. CIR aerial photograph captured March 12, 1996 of field site during leaf-off at a scale of 1:15,840, Woodbury Tract, Britton's Neck, South Carolina. Notice red to orange areas associated with living green vegetation of understory thickets.

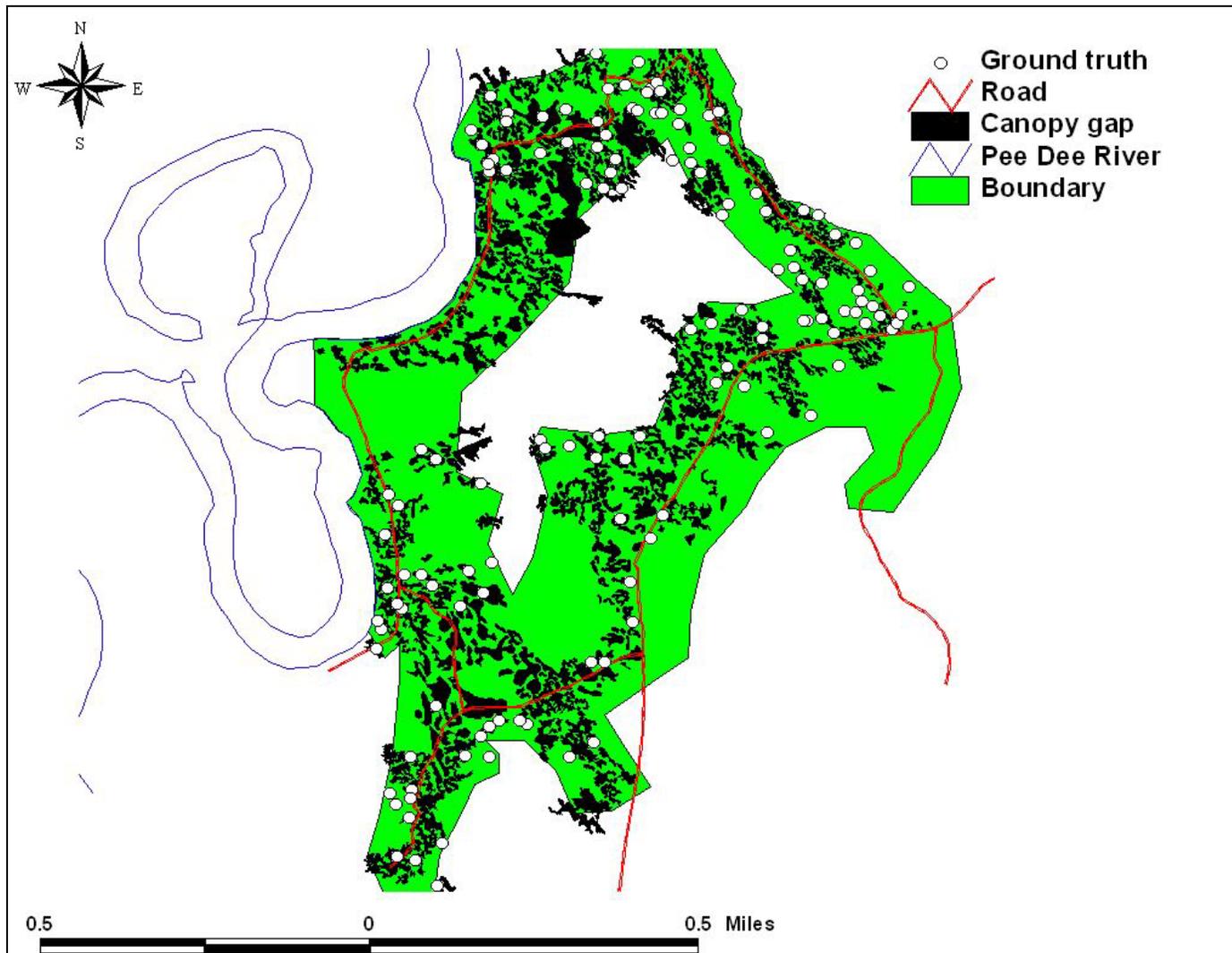


Figure 4. Distribution of 2005 ground truth samples relative to canopy gap locations for a thematic accuracy assessment of leaf-on CIR aerial photographs, Britton's Neck, South Carolina

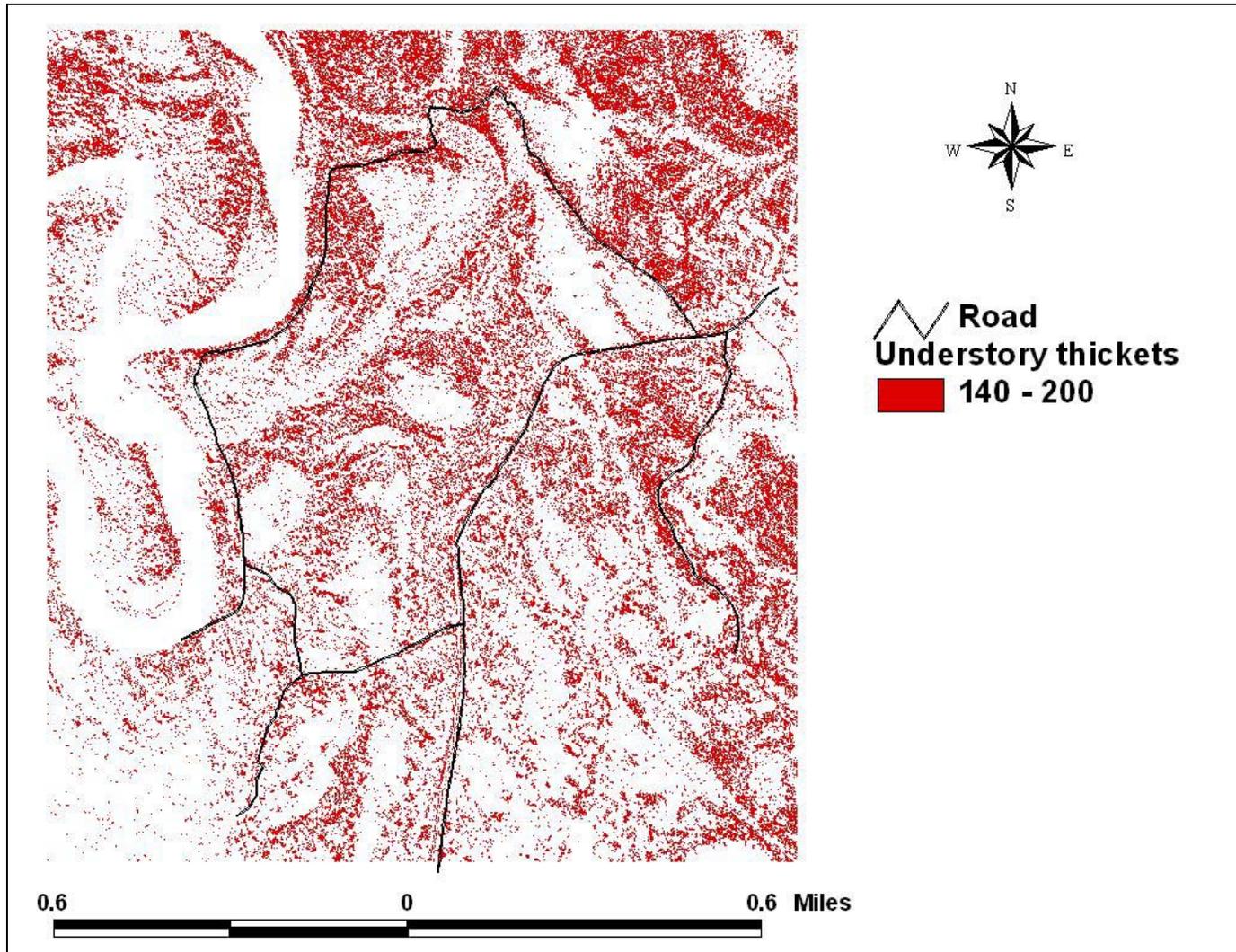


Figure 5. Understory thickets selected by spectral analysis of the red band (140-200 width) of leaf-off CIR aerial photograph, Britton's Neck, South Carolina.

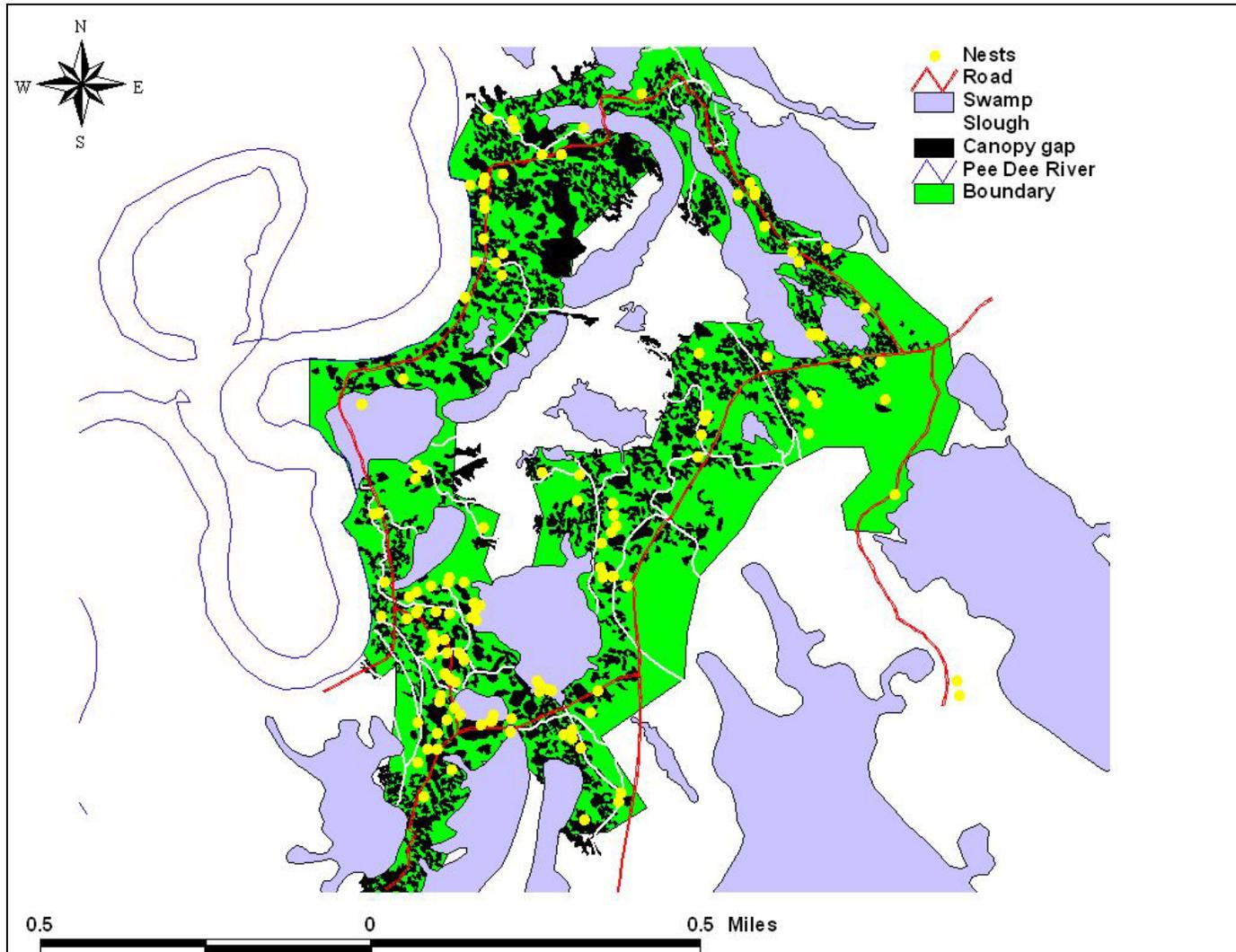


Figure 6. Thematic map comparing SWWA nest locations to swamp, slough, and understory thickets, created from leaf-on CIR aerial photographs of Britton's Neck, South Carolina.

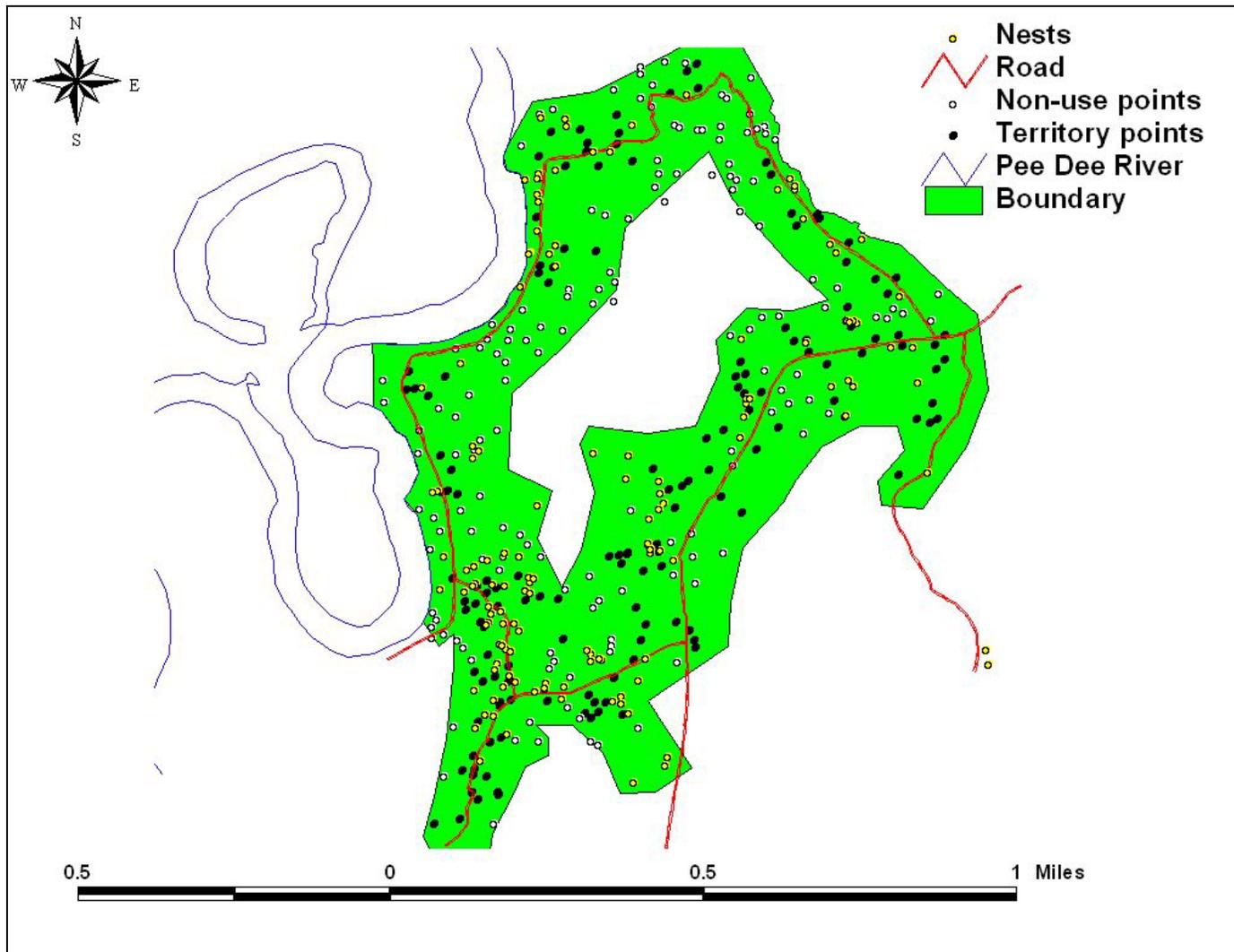


Figure 7. Plot locations used to analyze the role of swamps, sloughs, and understory thickets in SWWA nest and territory distribution in Britton's Neck, South Carolina, 1997-2001. Map was created from leaf-on CIR aerial photographs.

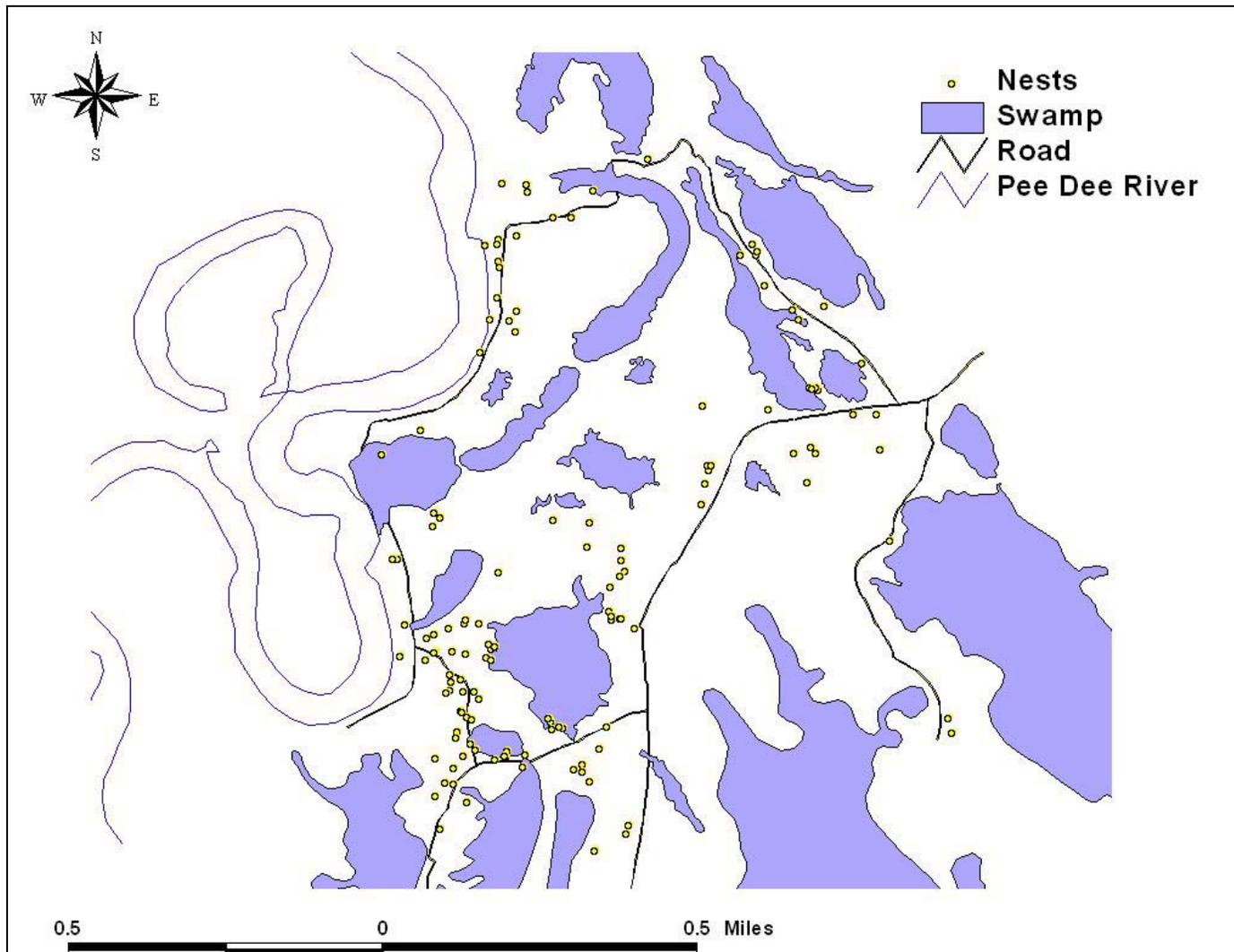


Figure 8. Thematic map comparing SWWA nesting sites to swamps in Britton's Neck, South Carolina, 1997-2001. Map was created from leaf-on CIR aerial photographs.

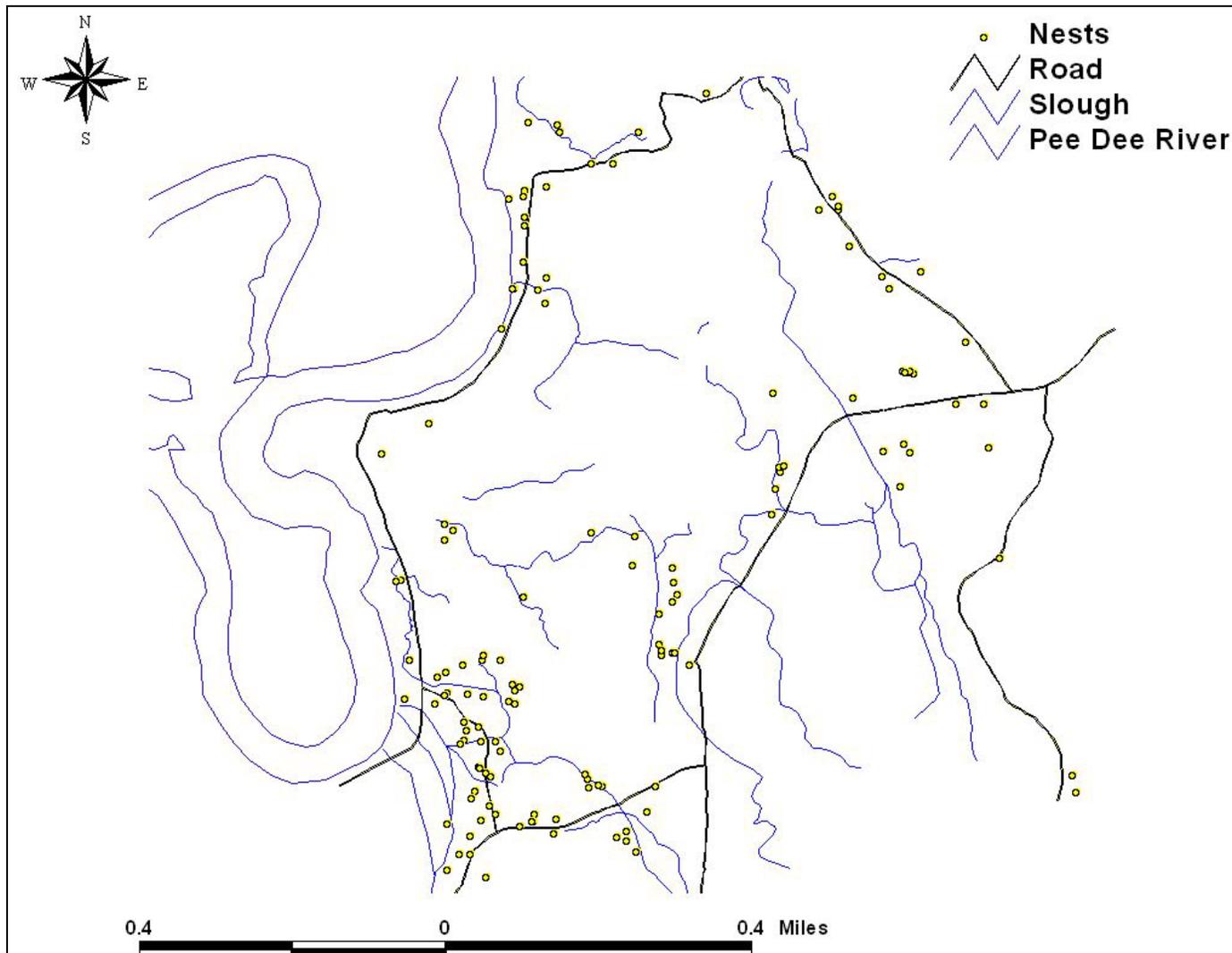


Figure 9. Thematic map comparing SWWA nesting sites to sloughs in Britton's Neck, South Carolina, 1997-2001. Map was created from leaf-on CIR aerial photographs.

APPENDIX

Appendix 1. Avian species captured during mist-netting operations in Britton's Neck, South Carolina, 1996-2001; top five species in bold print.

Common Name	Scientific Name	<i>n</i>
Acadian Flycatcher	<i>Empidonax virescens</i>	147
American Redstart	<i>Setophaga ruticilla</i>	88
Bachman's Sparrow	<i>Aimophila aestivalis</i>	1
Black-and-White Warbler	<i>Mniotilta varia</i>	8
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	1
Blue Grosbeak	<i>Guiraca caerulea</i>	4
Blue Jay	<i>Cyanocitta cristata</i>	1
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	17
Blue-winged Warbler	<i>Vermivora pinus</i>	1
Brown Thrasher	<i>Toxostoma rufum</i>	1
Brown-headed Cowbird	<i>Molothrus ater</i>	14
Brown-headed Nuthatch	<i>Sitta pusilla</i>	2
Carolina Chickadee	<i>Parus carolinensis</i>	19
Carolina Wren⁵	<i>Thyrothorus ludovicianus</i>	210
Common Grackle	<i>Quiscalus quiscula</i>	4
Common Yellowthroat	<i>Geothlypis trichas</i>	80
Downy Woodpecker	<i>Picoides pubescens</i>	24
Eastern Bluebird	<i>Sialia sialis</i>	13
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	17
Eastern Tufted Titmouse	<i>Parus bicolor</i>	52
Eastern Wood-Pewee	<i>Contopus virens</i>	10
Empidonax Flycatchers		4
Field Sparrow	<i>Spizella pusilla</i>	10
Gray Catbird	<i>Dumetella carolinensis</i>	6
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	15
Hairy Woodpecker	<i>Picoides villosus</i>	4
Hermit Thrush	<i>Catharus guttatus</i>	6
Hooded Warbler⁴	<i>Wilsonia citrina</i>	220
Indigo Bunting	<i>Passerina cyanea</i>	62
Kentucky Warbler	<i>Oporornis formosus</i>	15
Lincoln's Sparrow	<i>Melospiza lincolnii</i>	5
Louisiana Waterthrush	<i>Seiurus motacilla</i>	7
Myrtle Warbler	<i>Dendroica coronata</i>	1
Northern Cardinal²	<i>Cardinalis cardinalis</i>	311
Northern Mockingbird	<i>Mimus polyglottos</i>	1
Northern Parula	<i>Parula americana</i>	33
Northern Waterthrush	<i>Seiurus noveboracensis</i>	32
Orchard Oriole	<i>Icterus spurius</i>	6
Ovenbird	<i>Seiurus aurocapillus</i>	28
Pine Warbler	<i>Dendroica pinus</i>	12
Prairie Warbler	<i>Dendroica discolor</i>	37
Prothonotary Warbler¹	<i>Protonotaria citrea</i>	929
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	3
Red-eyed Vireo	<i>Vireo olivaceus</i>	51

Common Name	Scientific Name	<i>n</i>
Summer Tanager	<i>Piranga rubra</i>	57
Swainson's Thrush	<i>Catharus ustulatus</i>	3
Swainson's Warbler³	<i>Limnothlypis swainsonii</i>	291
Swamp Sparrow	<i>Melospiza georgiana</i>	1
Veery	<i>Catharus fuscescens</i>	10
White-eyed Vireo	<i>Vireo gilvus</i>	122
White-throated Sparrow	<i>Zonotrichia albicollis</i>	7
Wood Thrush	<i>Hylocichla mustelina</i>	18
Worm-eating Warbler	<i>Helmitheros vermivorus</i>	2
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	4
Yellow-breasted Chat	<i>Icteria virens</i>	38
Yellow-throated Warbler	<i>Dendroica dominica</i>	12
TOTAL		3,077

¹⁻⁵ Five most common species

Appendix 2. Formulas used to calculate X,Y coordinates of Swainson's Warbler territory points from known grid locations in Britton's Neck, South Carolina, 1998-2001.

$$XY \text{ Angle} = MOD (450 - \text{Bearing}, 360) \quad (1)$$

$$\text{Radius} = \text{Radians} (XY \text{ Angle}) \quad (2)$$

$$\Delta X = \text{Distance} * \text{COS} (\text{Radius}) \quad (3)$$

$$\Delta Y = \text{Distance} * \text{SIN} (\text{Radius}) \quad (4)$$

$$\text{Output } X = X \text{ Coordinates} + \Delta X \quad (5)$$

$$\text{Output } Y = Y \text{ Coordinates} + \Delta Y \quad (6)$$

Appendix 3. Developmental criteria used to judge age of Swainson's Warbler chicks in Britton's Neck, South Carolina, 1999-2001.

Day	Chick Condition
0	Dark pink mass, head down
+1	Eyes closed, small and naked, down on head and back, lacking pin feathers, wings are buds
+2	Eyes closed, mouths open, down on body, pin feathers under surface of wings, lacking pin feathers on neck and back
+3	Eyes closed; downy head and neck with a little down on back, pin feathers emerging from below wing surface; pin feathers below surface on back, sides of breast and below chin
+4	Eyes beginning to open, downy heads, pin feathers emerged on wings, beginning to emerge down midline of back and sides of breast
+5	Grey down on head, pin feathers emerged down midline of back and neck, sides of breast, chin, backs of legs, and all over wings; rest of body naked including belly
+6	Down on head either forms a crown or has degenerated into two pronounced tufts, wing feathers are either still in pins or beginning to emerge, pin feathers on head, no tail feathers
+7	1/2 out of pins on lesser and median coverts, greater coverts and other wing feathers still in pins; head a mixture of pins, down, and full feathers; feathers emerging down back of neck, middle of back, backs of legs, and sides of breast; midline of breast and sides of back bald
+8	Lesser and median coverts out of pins; greater coverts and other wing feathers still in pins.
+9	Two pronounced tufts of down on head; head fully feathered; wing feathers all or mostly out of pins; breast fully feathered, feathers out of pins on back, some skin visible on neck, tail feathers developing that are short and stubby; ready to fledge