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Recent large-scale colonisation of southern pine plantations by Swainson's Warbler *Limnothlypis swainsonii*

GARY R. GRAVES

Summary

Swainson's Warbler *Limnothlypis swainsonii* is a secretive species of high conservation concern with an estimated global breeding population of 90,000 individuals sparsely distributed across 15 states in the south-eastern United States. Its status as one of the rarest songbirds in North America has been attributed to the scarcity of breeding and wintering habitat. Although the warbler was once thought to be a habitat specialist of lowland canebrakes, it is now known to breed in a wide spectrum of broadleaf forest habitats linked by the common denominator of high stem densities and visual screening in the understorey stratum. Scattered instances of a fundamental habitat expansion into early seral stages of even-aged pine plantations were first observed in east Texas in 1992. Here I report that the colonisation of pine plantations is not only locally extensive in Texas but that it is widespread on the coastal plain eastward to south-eastern Virginia. During two decades of field surveys, breeding territories ($n = 297$) were documented in young pine plantations in 95 counties and parishes in 10 states. Occupied plantations were mostly 6–12 m tall (median = 7.5 m), corresponding to 8–15 years after planting. Soil type and the presence of interspersed broadleaf vegetation may be important co-factors in plantation occupancy. The chronology of this breeding niche expansion is poorly known but it appears to have occurred after the 1970s, most likely catalysed by the rapid growth of pine plantation silviculture after World War II. As late as 2001, it was believed that > 90% of the breeding population occurred in broadleaf floodplain forest. The recent range-wide colonisation of pine plantations changes the calculus. If the current trend continues, forest lands managed for short-rotation pine plantations will support the majority of breeding populations by the end of the 21st century.

Introduction

The explosive growth of pine plantation silviculture in the south-eastern United States during the past century has raised concerns among conservationists who have warned that short harvesting rotations geared toward maximum production of wood products will lead to a decrease in avian species diversity and abundance. This alarm was summarized by Terborgh (1989:168) "These southern pine plantations are a biological desert. One finds a few pine warblers, cardinals, and towhees, but little else....Although classified as 'forest' in land-use surveys, pine plantations are hardly better as habitat for migrants and other wildlife than... Iowa cornfields."

Until the early 20th century, southern forest lands were left to regenerate naturally after cutting and millions of hectares of cutover lands lay in waste (Wakeley 1945, Williams 1989). Less than 200 ha of pine plantations had been planted by 1920 in the vast pine belt extending from eastern Texas to Virginia (Wakeley 1954). After the first experimental pine plantations were established in Louisiana in 1922, plantation silviculture developed rapidly in the 1930s,

was slowed during World War II, and then increased swiftly in the post-war era (Wakeley 1954). The area successfully planted with pine increased to 0.30 million ha by 1945 (Wakeley 1945). By 1952, pine plantations were planted on 0.74 million ha in 12 south-eastern states (USDA Forest Service 1988). By 1985, this total had increased more than tenfold to 8.46 million ha, mostly on forest industry and private lands (Table 1). By 2010, more than 15.8 million ha were managed as pine plantations (Wear and Greis 2012).

What is not generally recognised in ecological literature is that the typical industrial pine plantation, composed of densely planted even-age stands covering 5–200 ha, represents a fundamentally new wildlife habitat in the south-eastern United States. At the time of Terborgh's essay (1989), southern pine silviculture was little more than 60 years old (Wakeley 1954, Fox *et al.* 2007) and few studies of avian communities in southern pine plantations had been published (Dickson and Segelquist 1979, Repenning and Labisky 1985). Although the deleterious effects of short-rotation plantation forestry were known for the Red-cockaded Woodpecker *Picoides borealis*, the only avian species in the south-eastern United States that requires old growth pines (Ligon 1970, Jackson *et al.* 1979), there were limited published data to indicate that plantation silviculture might have neutral or even positive effects on populations of some migratory and resident avian species. It is now known that a number of species attain high breeding populations in southern pine plantations (Dickson and Segelquist 1979, Dickson *et al.* 1993, Wilson and Watts 2000, Henry 2004, Loehle *et al.* 2005, Bassett-Touchell and Stouffer 2006, Hazler *et al.* 2006, Legrand *et al.* 2007, Hanberry *et al.* 2012).

In this paper, I report the large-scale colonisation of southern pine plantations by Swainson's Warbler *Limnothlypis swainsonii*, a rare migratory songbird which ranks near the top of state and federal species lists of conservation concern in the United States (Hunter *et al.* 1993). Low population size has been attributed to habitat limitation on the breeding grounds (Graves 2001, 2002) and a small wintering range in the Caribbean basin (Terborgh 1989). A recent analysis of North American Breeding Bird Survey (BBS) data estimated the global breeding population at 90,000 individuals, sparsely distributed across 15 states from Texas to Virginia (Partners in Flight Science Committee 2013). The endangered Kirtland's Warbler *Setophaga kirtlandii* is the only Nearctic-Neotropical migratory songbird breeding in eastern North America with a lower global population (Partners in Flight Science Committee 2013). Partners in Flight assigns a Continental Concern Score (CCS), ranging from 4 (lowest concern) to 20 (highest concern), to avian species that breed in the United States (Partners in Flight Science Committee 2012). Swainson's Warbler received

Table 1. Area (in thousands of hectares) of pine plantations in the south-eastern United States in 1952 and 1985 (extracted from USDA Forest Service 1988), the last year for which plantation statistics by state and ownership type were available before the publication of Terborgh's 1989 essay.

States	1952				1985			
	Public	Forest industry	Private	Total	Public	Forest industry	Private	Total
Alabama	16.2	12.6	38.1	66.9	15.4	555.9	386.2	957.5
Arkansas	4.0	8.5	9.7	22.2	13.4	275.7	111.7	400.8
Florida	8.1	50.6	59.1	117.8	134.8	984.6	338.1	1457.5
Georgia	2.4	92.3	49.8	144.5	40.1	1153.0	535.6	1728.7
Louisiana	25.1	4.0	12.6	41.7	34.8	363.6	198.8	597.2
Mississippi	36.0	31.6	47.4	115.0	55.9	395.5	246.6	698.0
North Carolina	4.5	8.9	25.5	38.9	44.1	419.8	189.5	653.4
Oklahoma	0.8	0.4	1.2	2.4	12.1	86.6	8.5	107.2
South Carolina	8.1	38.5	47.8	94.4	80.6	424.3	278.5	783.4
Tennessee	17.0	3.6	22.3	42.9	7.3	57.1	64.4	128.8
Texas	9.5	6.5	22.3	38.3	21.9	351.8	95.1	468.8
Virginia	0.4	9.7	8.5	18.6	10.5	257.1	206.1	473.7
Total				743.6				8455.0

a CCS of 13. Had it not been for a recent uptrend in BBS population data, which will be discussed later in this paper, it would likely have been assigned a CCS of 16–17 (high conservation concern) based on its historic rarity.

Interest in the natural history of Swainson's Warbler has been unusually intense since it was discovered in the early 1830s in South Carolina (Audubon 1834, Brewster 1885, Meanley 1971, Graves *et al.* 1996). Knowledge of its breeding habitat has grown incrementally since the 1880s when a breeding population was discovered in tangled thickets and canebrakes on the coastal plain of South Carolina (Brewster 1885). Until the 1940s, the warbler was widely considered a habitat specialist restricted to canebrakes in lowland swamps and bottomland forest. The known diversity of breeding habitats took a quantum leap when this secretive warbler was discovered in rhododendron and mountain laurel thickets in the cooler altitudes of the Appalachian Mountains (Brooks and Legg 1942). This finding challenged the prevailing wisdom on habitat stereotypy and provoked disbelief in more than a few sceptics until specimens and evidence of nesting were procured (Murray 1939, Brooks and Legg 1942). One prominent ornithologist commented: "No more amazing example of distribution could be imagined than the occurrence of this bird of the southern swamps in such places" (Murray 1939). In hindsight, the discovery of breeding warblers in habitats as varied as rhododendron thickets in the Appalachian Mountains and lowland canebrakes hinted at a latent plasticity in habitat selection. By the 1990s, breeding had been documented in a surprisingly wide spectrum of habitats including disturbance gaps in old growth bottomland forest, regenerating broadleaf clearcuts, pocosins and bays, riverside canebrakes, palmettos in bottomland forest, and Appalachian thickets (Meanley 1971, Eddleman *et al.* 1980, Graves 2001, 2002).

A second remarkable expansion in habitat selection was reported in 1992 when Swainson's Warbler was found nesting in young loblolly pine plantations in eastern Texas (Carrie 1996). Other published reports of breeding in unthinned pine plantations were forthcoming from south-eastern Louisiana (Henry 2004, Bassett-Touchell and Stouffer 2006, Legrand *et al.* 2007). As unanticipated as these reports were, they only hint at the true geographic extent of pine plantation occupancy on the coastal plain of the south-eastern United States. Here I report dozens of breeding populations of Swainson's Warbler in pine plantations in 10 states from Texas to Virginia discovered during two decades of field surveys (Figure 1). I provide information on (1) the stand height and age of occupied pine plantations, (2) co-factors such as soil type associated with occupancy, (3) decadal chronology of plantation colonisation, (4) evidence of reproduction in pine plantations, and (5) the geographic extent of colonization of pine plantations. Finally, I discuss the influence of pine silviculture on the conservation of Swainson's Warbler.

Methods

Survey of breeding populations

Geographic surveys of Swainson's Warbler breeding populations were conducted from 1988 through 2014 (Graves 1992, 1998, Winker *et al.* 1999, 2000, Graves 2001, 2002, Winker and Graves 2008). Some territories were located along established census transects (Graves 2001, 2002) but most were detected during the systematic exploration of habitat along secondary and primitive roads and less frequently on foot trails or by canoe. Most territories were located with the aid of playback of recorded songs. The majority of males in coastal plain populations arrive on breeding territories between 10 April and 15 April (Meanley 1971). Females arrive about a week later. Egg dates in Louisiana have been recorded as early as 19 April (Henry 2004). Strong response to playback, the reluctance to stray from a particular area during "playback-and-follow" trials (Graves 1996), mate guarding, and counter-singing with other males were interpreted as evidence of male territorial behaviour. Because of large territory size (Graves 2001, Anich *et al.* 2009), I conservatively considered any subsequent response within 200 m of the original discovery point to represent the same individual unless two or more males were heard singing simultaneously. Territorial determinations were made from 22 April to 30 June.

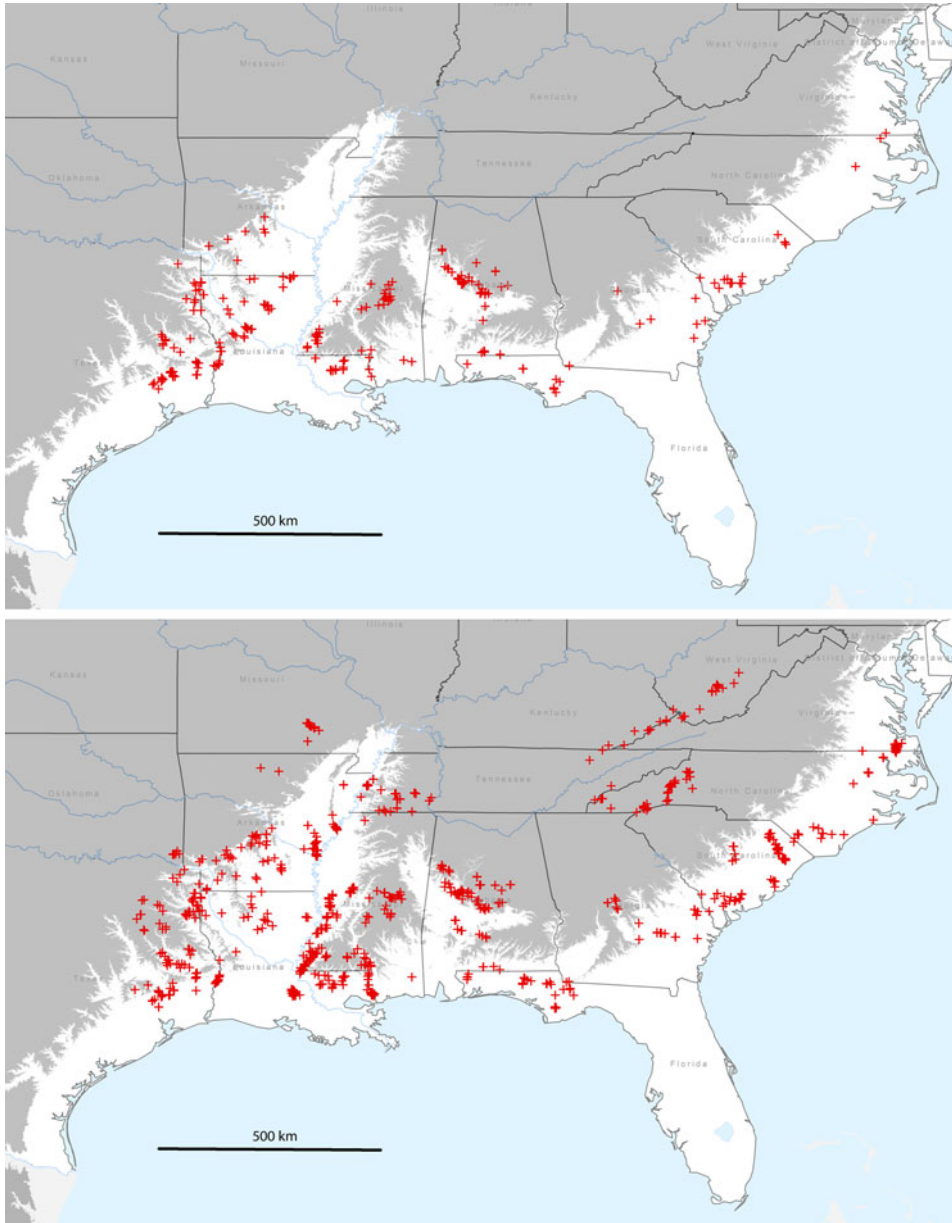


Figure 1. Geographic distribution of Swainson's Warbler breeding territories in pine plantations (top panel; $n = 297$) and in habitats other than pine plantations (lower panel; $n = 1,402$). Grey shading indicates area above 100 m (asl).

Classification of habitat and measurement of stand height

A forest stand was classified as a pine plantation if 50% or more of the stand was composed of native pines (loblolly *Pinus taeda*; slash, *P. elliotii*; shortleaf, *P. echinata*; longleaf, *P. palustris*) established by planting or direct seeding (USDA Forest Service 1988). Evidence of row spacing

was obvious in most commercial pine plantations. A few plantations contained a mixture of loblolly and slash or longleaf pines. However, most plantations surveyed in the breeding range of Swainson's Warbler were planted exclusively in loblolly pine. Many warbler territories in pine plantations also encompassed narrow buffer strips of broadleaf streamside or roadside vegetation. If most of the territory overlapped stands of planted pines, then the territory was classified as "pine plantation." In the remainder of the paper, I refer to pine plantations that held warbler territories as "occupied." However, the failure to detect a territorial male did not necessarily mean that a pine plantation was unoccupied because males may have been beyond the effective range of playback during the survey. Thus, I was unable to estimate the proportion of pine plantations that supported breeding territories. It is important to stress that this was not a study of habitat selection in which census sites were randomly chosen and then checked for territorial occupancy.

Several definitions of even-age stand height in pine plantations have been proposed for site indexing (Sharma *et al.* 2002). I defined stand height as the midpoint between the tallest tree (m) in the stand and the average height of the subdominants. Tree heights were determined with optical and laser rangefinders. Owing to time constraints, I made no attempt to quantify plantation size, habitat fragmentation, or the differences between occupied and unoccupied pine plantations. Nor did I attempt to directly age pine plantations, measure spacing or thinning, or ascertain pre-planting treatments or herbicide use in stands.

Characterisation of soils

Swainson's Warbler is a terrestrial dead-leaf specialist (Meanley 1970, Graves, 1998) that feeds on litter arthropods (Savage *et al.* 2010, Brown *et al.* 2011). The distribution of soils is believed to be an important determinant of local and regional patterns of habitat selection in Swainson's Warbler (Graves 1998, 2001, 2002), to the extent that soil type and moisture influence the accumulation and decay of leaf litter and the taxonomic diversity and abundance of litter arthropods.

I compiled soil data for Swainson's Warbler territories located in pine plantations from the online database maintained by the United States Department of Agriculture (Natural Resources Conservation Service 2013). Soil type and distance to water table, two pedological characteristics that correlate with soil moisture, were recorded for each territory. Soil types form a continuum that varies in accordance with a range of factors, including the frequency of soil particle sizes, horizon depths, depositional history, drainage, and slope. I binned soil types in five general categories ranked by the predominant particle size, from fine to coarse: (1) clays; (2) silt loams, (3) loams, (4) sandy loams, and (5) sands. The distance to water table for each soil type was generally presented as a range (in inches) in the online database. For purposes of classification, the minimum distance-to-water table (DWT) value for each soil type was binned in three distance categories: (1) < 0.5 m; (2) 0.5–2.0 m; and (3) > 2.0 m.

Results

Swainson's Warblers ($n = 297$ territories) were detected in pine plantations across a wide swath of the coastal plain from eastern Texas to south-eastern Virginia from 1995 to 2014 (Figure 1). As a measure of geographic dispersion, territories in pine plantations were located in 95 counties or parishes in 10 states. An additional 1,402 breeding territories were located in other habitats from 1988 to 2014 (Fig. 1).

Pine plantations were planted on a wide variety of soil types. Most plantations occupied by warblers were planted on sandy loams, with fewer on loams, silt loams and clays (Table 2). A majority of territories were on soils that normally have high water tables (< 0.5 m below the surface). Most territories were underlain by one soil type ($n = 187$), with fewer on two ($n = 108$), or three soils ($n = 2$). Territories overlapping two or more soil types were usually located at the ecotone between floodplains and better drained flanking slopes. The elevation of occupied pine plantations varied from 2–182 m (above sea level): 0–50 m ($n = 132$ territories); 51–100 m

Table 2. The number of Swainson's Warbler territories in pine plantations by soil type and distance to water table (DWT). For territories overlying two or more soil types, data are presented for the soil with the minimum DWT.

Soil types	Distance to water table (m)		
	< 0.5	0.5–2.0	> 2.0
Clays	17	0	0
Silt loams	71	10	8
Loams	23	3	5
Sandy loams	55	34	67
Sands	0	3	0
Totals	166	50	80

($n = 117$ territories); 101–150 m ($n = 44$ territories); >150 m ($n = 4$ territories). Highland sites (> 100 m; 16.2 % of total) occurred primarily in the loess bluffs from the Tunica hills of southern Louisiana through central Mississippi and in several locations above the fall line in Alabama.

Warbler territories in pine plantations occurred in a relatively narrow range of stand heights, mostly 6–12 m (Figure 2). No territories were observed in stands less than 4 m tall and few were located in plantations taller than 14 m. The median height of pines in occupied plantations was 7.5 m ($\bar{x} = 8.4 \pm 2.3$; range, 4–22.5 m, $n = 256$) (Figures 2 and 3). Most occupied plantations had a broad-leaf component (saplings, vines, shrubs), particularly at roadsides and along stream margins.

Discussion

Short-rotation pine plantations (25–35 year cycles) represent a fundamentally new ecosystem in the south-eastern United States that has increased in area by five orders of magnitude in the past century from less than 200 ha in 1920 to more than 15.8 million ha today (Wakeley 1945, 1954, Wear and Greis, 2012). Before the 1920s, large contiguous tracts of densely-planted, even-aged monocultures of pine were non-existent. In essence, southern pine silviculture constitutes one of

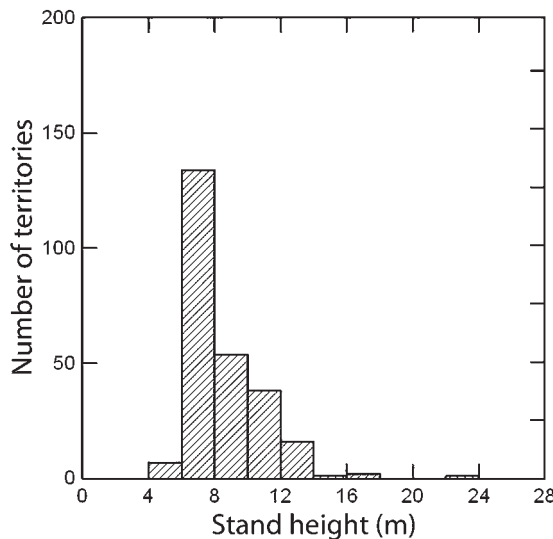


Figure 2. Stand height (m) of pine plantations occupied by breeding Swainson's Warbler ($n = 256$ territories).

the largest habitat manipulation experiments conducted in North America since the arrival of Europeans, yet our understanding of the effects of plantation silviculture on avian populations and the degree to which migratory and resident species have adapted to the novel physiognomy of early seral stages of even-aged pine plantations is rudimentary at best. This stems from the fact that there have been no comprehensive longitudinal studies of avian community composition in pine plantations from planting to harvest, with the possible exception of Dickson *et al.* (1993). To compound matters, none of the previous studies have focused on the distribution and abundance of focal species in southern pine plantations at multiple sites across the vast southern pine belt. The present survey of Swainson's Warbler breeding populations offers new insight on the nature and geographic extent of pine plantation colonisation.

Age and stand height of pine plantations occupied by Swainson's Warbler

Growth rates of southern pines depend on site characteristics, planting density, thinning, fertilization, and volume of broadleaf vegetation (Wakeley 1954). On average, the height of dominant trees in loblolly pine stands on coastal plain sites reaches 4 m about six years after planting, 8 m after 10 years, and 12 m after 15 years (Amateis and Burkhart 1985). My survey data show that > 90% of warbler territories occurred in stands 6–12 m tall (corresponding to 8–15 years after planting)(Figure 3). This suggests that unthinned even-aged pine plantations provide suitable breeding habitat for ~7–8 years during the typical 25–35 year rotation cycle, providing that other



Figure 3. Young loblolly pine plantations occupied by territorial male Swainson's Warblers in Escambia County, Alabama (top panel, stand height = 9.5 m) and in Neshoba County, Mississippi (bottom panel, stand height = 6.5 m).

requirements are met such as planting density, soil type, distance from water table, and interspersed broadleaf saplings, shrubs, and vines. If silvicultural practices shift toward wider tree spacing, earlier thinning, or a greater application of herbicides to reduce broadleaf growth, then suitability for Swainson's Warbler will commensurately decrease.

Earlier reports of Swainson's Warbler in pines gave similar ranges of plantation ages. Carrie (1996) reported that occupied loblolly pine plantations in eastern Texas ranged in age from 3 to 18 years ($\bar{x} = 14.0 \pm 4.2$ years, $n = 11$). In south-eastern Louisiana, the warbler was found breeding in unthinned loblolly pine stands that were 9–14 years old (Henry 2004) and in 7–24 year old stands (Bassett-Touchell and Stouffer 2006). A third study in the same area of Louisiana found Swainson's Warblers in unthinned pine stands that were 7–9 years old (Legrand *et al.* 2007). In contrast, occupancy of broadleaf habitats is largely uncoupled from canopy height and tree age as long as the understorey stem density is sufficient (Graves 2001, 2002).

Co-factors in the occupancy of pine plantations

The same factors that appear to influence breeding habitat selection of Swainson's Warbler in broadleaf bottomland forests (Meanley 1971, Eddleman *et al.* 1980, Graves 2001, 2002, Peters *et al.* 2005, Brown *et al.* 2009) appear to be operative in pine plantations. The common denominator linking breeding territories in pine plantations, bottomland broadleaf forests, and Appalachian forests is high stem or foliar density in the understorey (Graves 2001, 2002, Henry 2004, Bassett-Touchell and Stouffer 2006). Although the growth form of even-aged pine plantations differs from that of dense stands of broadleaf saplings and shrubs, the foliar distribution and visual screening effects are similar. Local breeding populations of Swainson's Warbler abandon both pine plantations and broadleaf habitats when the understorey thins due to stand maturation and canopy closure.

Most occupied pine plantations exhibit a significant broadleaf component along roadsides and stand borders (Carrie 1996, Henry 2004, Bassett-Touchell and Stouffer 2006). As previously mentioned, the warbler forages almost exclusively in terrestrial dead-leaf litter (Meanley 1970, Graves 1998). Although their foraging behaviour in pine plantations is unknown, published data from broadleaf habitats (Graves 1998, Brown *et al.* 2011) suggest that deciduous leaf litter is an integral component of breeding territories. It remains to be determined whether this is true for territories in pine plantations.

Occupied pine plantations were planted on a variety of soil types (Table 2). A surprisingly large number of territories occurred on sandy loams with comparatively low water tables (distances > 2 m). This observation suggests four possibilities:

- Rainfall events are frequent enough to maintain adequate moisture in the leaf litter on well drained soils.
- Soil moisture may not be as critical to the litter arthropods consumed by Swainson's Warbler as is generally believed.
- Dense shade and thermal insulation of young pine plantations facilitates the retention of residual moisture and the maintenance of elevated humidity levels in the leaf litter during rainless periods.
- Major soil types encompassed local areas of moister soil that were too small to map.

Data in hand are insufficient to determine which explanation is correct. In a broader context, pine plantation silviculture appears to facilitate the warbler's upslope colonisation of drier sandy loams.

The chronology of colonisation of pine plantations

The chronology of colonisation is poorly known because few biologists systematically searched for Swainson's Warbler in pine plantations before Carrie's report (1996) in San Jacinto County, Texas. Other studies of unthinned pine plantations in eastern Texas conducted from 1975 through 1992

found no evidence of breeding warblers. Dickson and Segelquist (1979) failed to find the species in even-aged pine stands (mean stand height, 4.4 and 13.5 m) in Nacogdoches County, Texas in 1975. In the most comprehensive study, annual censuses in a large pine plantation (~5 km²) in the same county from 1977 (two years after planting) through 1992 (17 years after planting) also failed to detect Swainson's Warbler (Dickson *et al.* 1993). A third study of breeding bird populations in Cherokee, Houston, and Nacogdoches counties in eastern Texas that focused on narrow broadleaf streamside corridors in young pine plantations in 1984–1985 reported similar negative results (Dickson *et al.* 1995). My surveys in eastern Texas did not commence until 2008, so they provide little information on the timing of colonisation. However, Swainson's Warbler now occurs in pine plantations in Cherokee, Houston, and Nacogdoches counties as well the remainder of breeding range in eastern Texas, with documented territories in 17 counties (Figure 1).

Colonisation of pine plantations in other parts of the warbler's breeding range is likely to have occurred at least one to two decades before it was actually documented. In 1974, Swainson's Warbler was reported breeding in control plots of mature mixed broadleaf-pine forest in Livingston Parish, Louisiana, but not in loblolly pine plantations, six, 20, and 46 years old (Noble and Hamilton 1975). In 1998–1999, the warbler was reported breeding in loblolly pine plantations in adjacent Tangipahoa Parish, and in 2000 from Livingston Parish and three additional parishes in south-eastern Louisiana (Bassett-Touchell and Stouffer 2006). Overall, they detected Swainson's Warblers in 23 out of 124 pine plantations (Bassett-Touchell and Stouffer 2006). Henry (2004) and Legrand *et al.* (2007) found the warbler to be a predictable breeder in pine plantations in the same area during 2002–2004. My recent surveys (2007–2011) documented breeding territories in pine plantations in 21 parishes in Louisiana distributed throughout the pine-dominated regions of the state (Figure 1).

The unfolding story is similar in the remainder of the warbler's breeding range on the coastal plain. Recent surveys (2006–2014) documented the occupancy of unthinned pine plantations in Alabama ($n = 14$ counties), Mississippi ($n = 14$ counties), Arkansas ($n = 8$ counties), Georgia ($n = 7$ counties), South Carolina ($n = 6$ counties), Florida ($n = 5$ counties), North Carolina ($n = 2$ counties), and Virginia ($n = 1$ county). Collectively, these data suggest that range-wide colonisation of pine plantations occurred after the 1970s, catalysed by the massive post-World War II increase in plantation silviculture.

Population trends from the North America Breeding Bird Survey (BBS) from eastern Texas are consistent with the hypothesis that widespread colonisation of pine plantations occurred in the early 1990s. The BBS is a cooperative census programme conducted annually since 1966, involving thousands of census routes and observers in the United States and Canada (Sauer *et al.* 2012). Each route has 50 census stops. BBS data were downloaded from the website maintained by the U.S. Geological Survey (Patuxent Wildlife Research Center 2013). Analysis was restricted to census routes in eastern Texas because the most comprehensive early studies of avian populations in young pine plantations (1975–1992) were conducted in this area (Dickson and Segelquist 1979, Dickson *et al.* 1993, Dickson *et al.* 1995) and because Texas supports 33% of the global breeding population of Swainson's Warbler (Partners in Flight Science Committee 2013). Comparison was restricted to routes ($n = 20$) on which Swainson's Warbler had been recorded at least once during the review period (1980–2012). The number of routes censused in a given year varied from six to 18 ($\bar{X} = 11.5 \pm 4.5$). BBS data show a marked non-linear increase from 1980 to 2012 in the average number of territorial males recorded per route (Figure 4). The inflection point occurred in the early 1990s, coincident with a period of rapid expansion of pine silviculture in eastern Texas where plantations increased from 0.47 million ha in 1985 (USDA Forest Service 1988), to 0.74 million ha in 1992 (Rosson 2000), and 1.09 million ha in 2011 (Cooper and Bentley 2012).

Reproduction in pine plantations

The only information on nesting productivity of Swainson's Warbler in pine plantations originates from a limited area in south-eastern Louisiana where Henry (2004) showed that breeding density, clutch size, hatching rates, and reproductive success in pines were similar to those

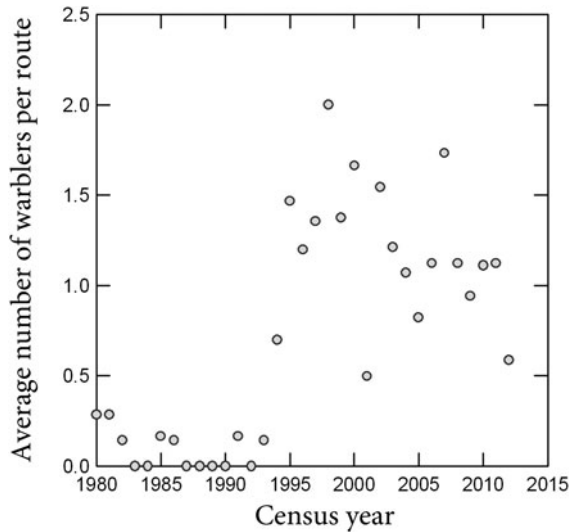


Figure 4. Average number of Swainson's Warblers recorded per route on BBS census routes in eastern Texas from 1980 to 2012.

observed on adjacent plots in bottomland broadleaf forest of the Pearl River drainage. Moreover, reproductive success in Louisiana pine plantations (Henry 2004) was roughly equivalent to estimates from broadleaf bottomland habitats in southern Missouri (Thomas *et al.* 1996), eastern Arkansas (Benson *et al.* 2010), and South Carolina (Bishop *et al.* 2012). Although there are too little data to draw broad conclusions about nesting productivity in these fundamentally different habitats, there is no evidence thus far to suggest that nesting populations in pine plantations are any less productive than in broadleaf bottomland habitats or that pine plantations act as population sinks (Pulliam 1988) or ecological traps (Battin 2004).

Geographic extent of occupancy of pine plantations

The results of the present survey indicate that Swainson's Warbler has not only extensively colonised pine plantations in eastern Texas (Carrie 1996) and south-eastern Louisiana (Henry 2004, Bassett-Touchell and Stouffer 2006, Legrand *et al.* 2007), but has apparently expanded its breeding habitat niche to include pine plantations throughout its breeding range on the coastal plain from Texas to Virginia. Perhaps not coincidentally, the two peaks of current breeding abundance (2006–2011) according to BBS data occur in south-eastern Texas and central Alabama (<http://www.mbr-pwrc.usgs.gov/bbs/ra2011/ra06380.htm>) where the colonisation of pine plantations has been extensive (Figure 1). The presence of territories in pine plantations on the loess bluffs of Mississippi and in the piedmont areas of central Alabama suggest that the phenomenon may not be restricted to the coastal plain. However, the warbler has not been detected thus far in pine plantations in the Appalachian Mountains, on the Cumberland Plateau, or in the Ouachita or Ozark mountains.

Decadal trends in population distribution

Graves (2001) suggested that > 90% of breeding populations of Swainson's Warbler occurred in broadleaf floodplain forest in the lower Mississippi Valley and on the coastal plain from eastern Texas to south-eastern Virginia. That calculation, however, was made more than a decade before the extent of the recent expansion of breeding populations into pine plantations was realised and before

management changes that favoured maturation and restoration of broadleaf forests to steady-state conditions at the expense of early successional habitats were fully implemented on public lands in the south-eastern United States (LMJVJ Forest Resource Conservation Group 2007, U.S. Fish and Wildlife Service 2010). Breeding populations of Swainson's Warbler in the broadleaf bottomland forests on public lands in the lower Mississippi Valley and on the Gulf Coastal Plain have steadily decreased since the cessation of large-scale timber sales in the 1970s (author's pers. obs.). As a prime example, several sites in White River drainage in eastern Arkansas that supported relatively dense breeding populations in the 1980s were completely devoid of breeding birds a decade later owing to the maturation of habitat and the consequent thinning of the understory.

Conclusions

Population limitation caused by the scarcity of early successional broadleaf habitat on the breeding grounds may be offset by the warbler's recent and rapid colonisation of pine plantations. Behavioural plasticity in habitat selection may explain why Swainson's Warbler has survived two centuries of intense forest clearing and habitat alteration while Bachman's Warbler *Vermivora bachmanii*, which bred in similar microhabitats in the south-eastern United States (Wayne 1907, Hamel 1986), has become extinct. Southern pine silviculture has expanded into regional patchworks of even-aged plantations that now cover more than 15.8 million ha on the coastal plain from east Texas to Virginia. Given the 25–35 year rotation cycles commonly prescribed for private and commercial plantations, and a ~7–8 year window of habitat suitability for Swainson's Warbler in a typical stand, roughly a quarter of pine plantations will be in the appropriate seral stage at any given moment. Of broader significance, southern pine plantations are projected to increase to 27.1 million ha by 2060 (Wear and Greis 2012). If current distributional trends continue, forestry lands managed for short-rotation pine plantations will soon support a majority of the global breeding population of Swainson's Warbler.

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