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Integrating Wildlife Conservation with Commercial Silviculture — Demography of the Swainson's Warbler (*Limnothlypis swainsonii*), a Migrant Bird of Conservation Concern in Southern Pine Forests, USA

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Additional information is available at the end of the chapter

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Abstract

Intensively managed pine (*Pinus* spp.) forests encompass over 15.8 million hectares in the southeastern United States and provide an important source of wood products and an economic return to landowners. Given the extent of this landscape and the diversity of management goals and stakeholders, understanding how these forests can also be managed for biological diversity is important. Swainson's warbler (*Limnothlypis swainsonii*; SWWA), a species of high conservation priority, has been documented occupying young, unthinned pine plantations (a novel habitat type), but demographic assessment is lacking. We compared breeding phenology and reproductive success of SWWA in commercial loblolly pine (*Pinus taeda*) stands versus bottomland hardwood forest (the historical habitat type). Timing of nesting, clutch size, and hatching rates were not significantly different with 59% (n = 32) of eggs hatching in pine versus 69% in bottomland hardwood (n = 52). Mayfield estimates of nesting success were similar in pine (27%) versus hardwoods (32%) within and across years. These results indicate that closed-canopy, short-rotation pine stands can provide suitable breeding habitat for SWWA. We also review the value of intensively managed pine landscapes for avian conservation in general.

Keywords: Silviculture, biodiversity, habitat conservation, biodiversity, Swainson's warbler, *Limnothlypis swainsonii*

1. Introduction

Globally, plantation forests are increasing by an estimated 13 million hectares annually [1], comprising approximately 264 million hectares, and predicted to reach 345 million hectares by 2030 [2]. These forests are critical for meeting global wood supply demands as forests dedicated to wood fiber production produce substantially more volume of wood per hectare than natural forests [2,3]. Although the primary management objective of these forests is to provide commodities, they can simultaneously contribute to conservation of biological diversity [4-7].

For perspective, the southeastern United States has produced more timber than any other country in the world since 1986, yielding more than a million jobs and \$51 billion dollars (USD) to the economy in 2009 [8,9]. Contributing largely to this productivity are intensively managed pine (*Pinus* spp.) forests, which increased in area from nearly none in 1952 to approximately 15.8 million hectares in 2010 [9]. These plantation forests currently comprise about 19% of the forested area in the region, 86% of which are privately owned [9], and are expected to stabilize in area, thus remaining an important component of forests in the southeastern United States [10,11]. Although forested area has remained relatively stable from the early 1900's to 2007, urbanization is increasing and is considered the greatest threat to this forest cover [10,11].

Intensively managed pine forests contribute to the conservation of biological diversity, including habitat conditions for diverse avian communities [12-16], albeit with limitations [13, 17,18]. Conservation value of intensively managed forests depends on the silvicultural regimes, including rotation length, stand establishment methods, stocking density, thinning regimes, and intermediate treatments (e.g., prescribed fire, herbicide application, and fertilizer use); landscape context; physiographic region; resemblance to natural forest structure; landscape scale features such as corridors and edges; and other factors. Given the extent of this silvicultural landscape, its importance to forest conservation, its economic value, and a diversity of management goals and stakeholders, it is critical to understand how commercial forests can simultaneously be managed to conserve biological diversity, particularly on private land.

Bird communities respond predictably to changes in vegetation structure in different silvicultural regimes and stand ages. Some species occupy young pine forests following clear-cuts, whereas others prefer more mature stages of succession within these broad classes [12,14,15,19,20]. For example, species of high conservation concern inhabit even-aged, thinned pine plantations in response to prescribed fire and herbicide applications [14]. Migratory bird species typically found in deciduous forests may occupy mature, even-aged pine plantations, primarily in the presence of a well-developed understory. In southeastern US pine plantations these species include Acadian flycatcher (*Empidonax virens*) [21], red-eyed vireo (*Vireo olivaceus*), wood thrush (*Hylocichla mustelina*), worm-eating warbler (*Helmitheros vermivora*) [22], ovenbird (*Seiurus aurocapillus*), and Swainson's warbler (*Limnothlypis swainsonii*) [12,23,27,37]. Thus, pine plantations are not just occupied by habitat-generalist birds.

Recently, Swainson's warblers (SWWA), a species of conservation concern [24], have been documented occupying intensively managed pine stands in the southeastern United States [25-27]. SWWA are attracted to high stem densities and thicket-like conditions within unthinned pine plantations, which are similar structurally to switch cane (*Arundinaria gigantea*)

thickets in bottomland hardwood forests [25-27], the habitat complex in which this species was first documented and remains best studied. However, understanding effects of forest management on avian species such as SWWA necessitates understanding treatment impacts on demographic parameters, and not just abundance [28,29]. To better understand use of a novel habitat condition by a conservation priority bird species, we compared breeding phenology and reproductive success of SWWA between intensively managed loblolly pine stands versus cane thickets within bottomland hardwood forests. Given abundant evidence that SWWA use pine plantations in Louisiana [25-27] we tested the hypothesis that the species experiences demographic success (based on abundance and nesting characteristics) in pine stands comparable to that in bottomland hardwoods. We discuss our results in the context of how contemporary silvicultural practices in southeastern pine plantations are likely to impact species of conservation concern such as SWWA.

2. Methods

Study areas – We conducted this study during five breeding seasons, 1999-2003, in southeastern Louisiana, United States in five of the Florida Parishes (counties) north of Lake Pontchartrain (Figure 1). In this region, lower elevations associated with river systems and drainages supported both extensively forested and highly fragmented tracts of bottomland hardwood forest. More upland areas, once dominated by longleaf pine (*Pinus palustris*) savannahs, have been converted to agriculture, towns, and suburbs, and over 80,000 ha of loblolly pine plantations. Elevation above sea level did not exceed 150 m in any of the study sites.

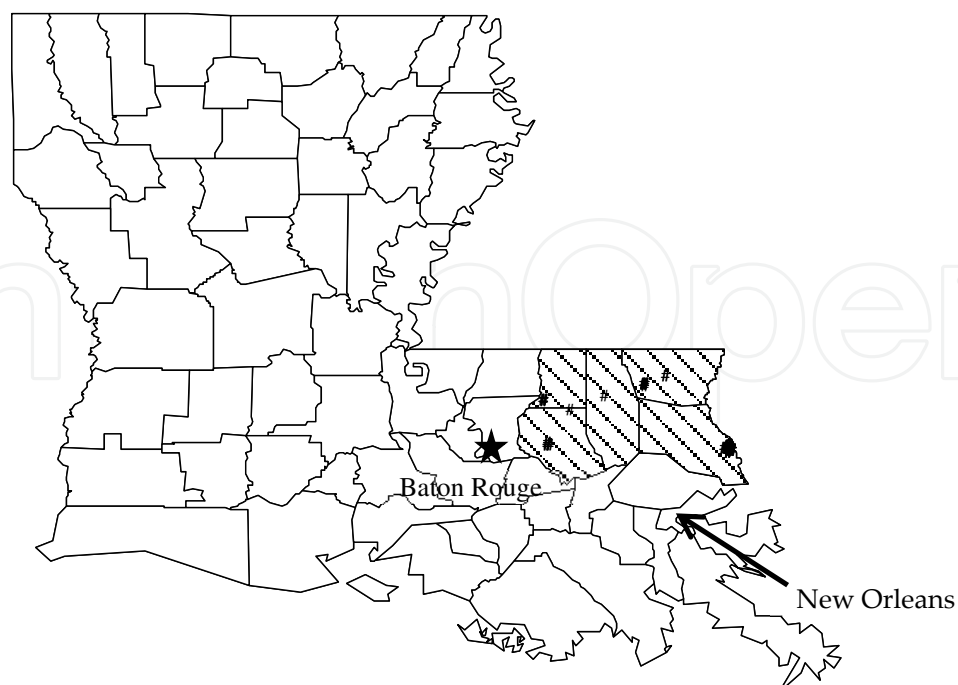


Figure 1. Map of Louisiana, USA showing Parishes (cross-hatching) where study sites were located (black circles).

Our bottomland hardwood site was located in the Honey Island Swamp unit of the Pearl River Wildlife Management Area (PRWMA) in St. Tammany Parish (30°23'N, 89°43'W; managed by the Louisiana Department of Wildlife and Fisheries; Figure 2a). Honey Island Swamp is a floodplain that was extensively logged in the 1940-1950s, and strip-type thinned in 1987-88 for a more selective harvest of specific tree species. During our study, most of this area was mature second growth with canopy trees of water oak (*Quercus nigra*), basket oak (*Q. michauxii*), laurel oak (*Q. laurifolia*), sweetgum (*Liquidambar styraciflua*), black gum (*Nyssa sylvatica*), bald cypress (*Taxodium distichum*), hickories (*Carya* spp.), and magnolias (*Magnolia* spp.). Midstory trees included red maple (*Acer rubrum*), ironwood (*Carpinus caroliniana*), swamp dogwood (*Cornus foemina*), hollies (*Ilex* spp.), buttonbush (*Cephalanthus occidentalis*), and silverbell (*Halesia diptera*). The understory was interspersed with southern switchcane, arrowwood (*Viburnum dentatum*), wax myrtle (*Myrica cerifera*), Chinese privet (*Ligustrum sinense*), dwarf palmetto (*Sabal minor*), blackberry (*Rubus* sp.) thickets, and occasionally dense stands of water oak and/or other hardwood saplings. Numerous bayous and smaller drainages (often containing cypress and gums) dissected the study area, and flooded most frequently during spring and summer. We surveyed over 25 km of roads, trails, and drainages within approximately 2,300 ha. We considered Honey Island Swamp to be high-quality breeding habitat for SWWAs due to its higher density of breeding pairs compared to other large tracts of hardwood forests that we surveyed (including Bogue Chitto National Wildlife Refuge contiguous with PRWMA and Sherburne WMA in the Atchafalaya River Basin).

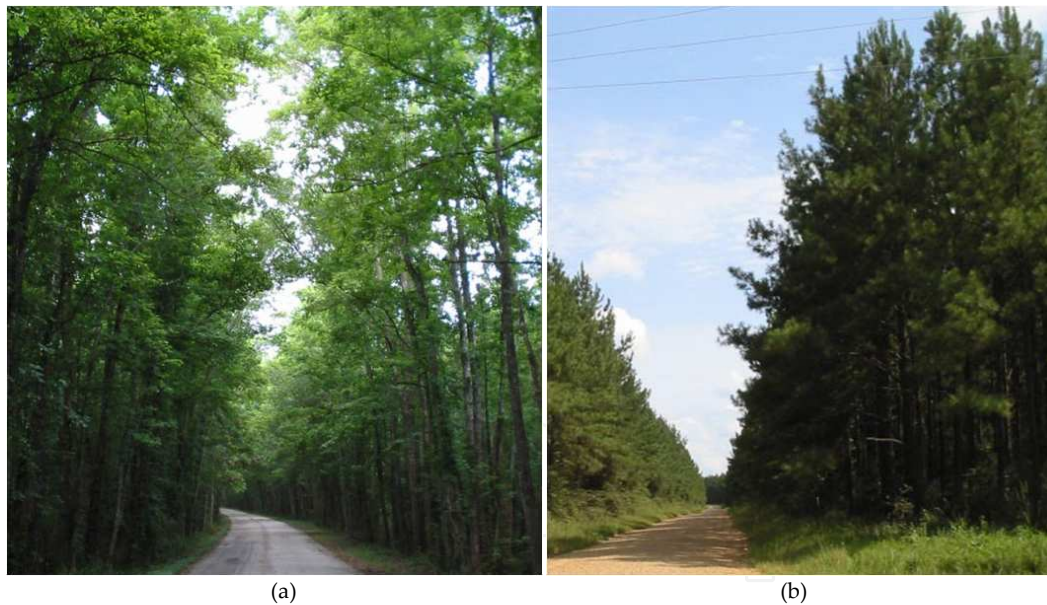


Figure 2. Bottomland hardwood (a) and commercial loblolly pine (b) forests where Swainson's warbler nests were located in St. Tammany Parish and Washington Parish, respectively, southeast Louisiana, USA. Photographs by Donata R. Henry.

We surveyed pine plantations ($n = 35$) located in Washington (30°46'N, 90°12'W), Livingston (30°24'N, 90°47'W), St. Helena (30°40'N, 90°48'W), Tangipahoa (30°42'N, 90°27' W), and St. Tammany (30°28'N 90° 02'W) Parishes of Louisiana on land owned and managed by Weyerhaeuser Company for pine sawtimber production (Figure 2b). Pine stand size ranged from 50

to 200 ha. Typical management of these stands included clear-cut harvest of existing stands followed by mechanical and chemical site preparation, planting of loblolly pine seedlings at approximately 1,700 seedlings/ha, herbicide release treatment, thinning, and then final harvest at 25-35 years of age. Pine stand canopies were composed of loblolly pine, with hardwood species in the midstory including crab apple (*Malus* spp.), red maple, and sweetgum. Typical understory shrubs included yaupon (*Ilex vomitoria*), wax myrtle (*Myrica cerifera*), and huckleberry (*Gaylussacia* spp.). Sites in Livingston Parish also contained abundant dwarf palmetto in the understory.

Study species – Due to its small wintering range and specialized habitat requirements in tropical forests, SWWA has been ranked among the Neotropical-Nearctic migratory wood warblers most vulnerable to tropical deforestation [30]. Simultaneously, its primary breeding grounds have undergone a history of habitat decline due to high agricultural demands for alluvial soils of southeastern US floodplains [31]. The breeding and wintering ranges of SWWA largely overlap those of Bachman's warbler (*Vermivora bachmanii*), a species now presumed extinct [32]. Of 19 species of bottomland hardwood breeding birds in Louisiana, SWWA was determined to have the narrowest niche breadth [32] as a patchily distributed, ground-foraging insectivore that maintains large territories (up to 2.5 ha) and builds open cup nests approximately 0.3–3 m off of the ground [33,34] (Figures 3 and 4). Long considered a species restricted to mature bottomland hardwood forests of the Gulf Coastal Plain, in the 1930s SWWA were discovered in low elevation *Rhododendron* thickets of the southern Appalachian Mountains [35]. More recently, SWWA have been reported in loblolly pine plantations in Texas [36], North Carolina [12], and Louisiana [25-27, 37].



Figure 3. Swainson's warbler nest with adult and two nestlings in a bottomland hardwood forest in the Pearl River Wildlife Management Area, St. Tammany Parish, southeast Louisiana, USA. Photograph by Walter C. Clifton.



Figure 4. Swainson's warbler nest with two nestlings in a commercial loblolly pine forest in Washington Parish, south-east Louisiana, USA. Photograph by Donata R. Henry.

SWWA distribution surveys and nest searches – Each field season, we extensively traveled in vehicles and on foot to survey and locate stands containing breeding pairs of SWWA across both study areas with playback songs and chip notes of SWWA along all accessible roads, trails, and drainages during late March-late April. Prior to our study, the highest number of detections of SWWA in pine plantations in the Florida Parishes had been in unthinned, closed canopy, pole-stage (8-14-year old) stands [26]. Thus, we extensively surveyed stands that both met these criteria and were reliably accessible for nest searching.

We determined number of breeding pairs/km² in both habitat types by mapping territory locations on area maps. Thus, estimates provided herein are based on observed pairs per area surveyed rather than extrapolated statistically from point counts (distance sampling) or transects, and our estimates did not include nonbreeding individuals. We marked territorial boundaries with flagging tape by following singing males, using song playback (minimally), observing aggressive interactions of territorial males, and observing color-banded males.

We searched for nests in all stands where evidence of breeding pairs was found based on our extensive distributional surveys. We eliminated stands with too few territories or with recent history of thinning. We revisited and surveyed stands annually, and included them in nest searching as long as evidence of breeding was found (n = 12 stands).

Nest searching extended from the last week of April to first week of August all years. We located nests primarily by searching entire territories systematically, examining all nest-like

vegetation clumps and potential nest sites within the range of potential nesting heights. Males typically did not sing near nests, although we followed them and flagged singing positions to help establish territorial boundaries and determine search areas. We also used cues such as adults carrying nesting material, food, or fecal sacs. However, due to the elusiveness of SWWA and shrub density within nesting areas, these cues tended to be uncommon or difficult to detect. Once we located a nest, we checked it every two-four days until the nesting attempt failed or young fledged. We used different paths to approach nests during nest checks to decrease predator cues, and we used binoculars at a distance (3-5 m) to confirm presence of nestlings when appropriate. In some instances, we delayed nest checks due to extreme flooding. We considered nests successful that fledged at least one chick. If we could not locate fledglings when a nest was checked on the anticipated fledge date, we considered a nest successful if it contained feather sheathing and/or castings, and fecal material on the rim of the nest cup, as these signs are characteristic of fledged nests [38]. We considered nests failed if (1) we found nests empty or destroyed before the anticipated fledge date; (2) if remains of nestlings were found in nests; or (3) if nests were found empty on the anticipated fledge date and we could find no sign of recent fledgling activity in the nest cup (described above), fledglings, or adults carrying food.

Statistical analysis – We quantified clutch size, clutch start and completion dates, duration of incubation and nestling stages, percent of eggs hatched, percent of nestlings fledged, and length of breeding season. We calculated nesting success with direct comparisons of nest fates (successfully fledged nests/total nests) and the Mayfield method [39] in both habitat types. Although other methods for estimating or modeling nesting success are available, we found little difference in these models for this species [40] particularly with short intervals (2 days) between nest checks [41]. We used 25 exposure days (14 incubation days plus 11 nestling days [33]) in calculating Mayfield estimates, and the midpoint method [39] for determining the last active date of nests when nestlings fledged or nests failed prior to the last nest check. We tested the hypothesis that habitat type and year affected mean clutch size using a two-way analysis of variance with habitat type (pine or hardwood), year, and a habitat-by-year interaction term. We used chi-squared tests to examine the hypothesis that clutch size, number of hatched versus failed eggs, fledged versus failed nestlings, and fledged versus failed nests differed within years between habitat types. We also used program MARK [42] to compare reproductive success between habitat types. We set an *a priori* alpha level of 0.05 for statistical tests.

3. Results

We detected SWWAs in 15 of 35 pine stands surveyed. In 2001-2003, we found 171 nests: 138 of known fate and 33 of undetermined fate. We found 53 nests (31%) in pine and the remaining 118 in bottomland hardwoods. Additionally, we included reproductive data from 14 bottomland hardwood nests in 1999-2000 (Table 1). Density of breeding pairs in both habitat types varied with site heterogeneity; SWWAs were consistently patchily distributed and clustered in areas of dense understory vegetation. Densities ranged from 3 to 10 breeding pairs/km² in pine compared to 4 to 12 in bottomland hardwood.

Timing of breeding was similar between habitat types, with earliest egg laying dates occurring within the same 4-day period (27-30 April) all three years, with two exceptions: in 2002, 2 nests in bottomland hardwood were exceptionally early; one clutch started (first egg laid) on ~19 April and another on ~22 April (Figure 5). We found evidence of active nests in late July in pine, while in bottomland hardwood we recorded nests fledging as late as the first week of August (Figure 6). Incubation and nestling periods were consistent with previous records [31], lasting from 13 to 15 days and 10 to 12 days, respectively.

| | 1999-2000 | 2001 | | 2002 | | 2003 | 2001-2003 | | |
|------------------------------|-----------|------|------|------|------|------|-----------|------|------|
| | HARD | PINE | HARD | PINE | HARD | PINE | HARD | PINE | HARD |
| Total number of eggs | 37 | 28 | 40 | 27 | 78 | 50 | 109 | 105 | 227 |
| Total number of nestlings | 23 | 16 | 28 | 20 | 57 | 26 | 71 | 62 | 156 |
| Hatching success (%) | 0.62 | 0.57 | 0.70 | 0.74 | 0.73 | 0.52 | 0.65 | 0.59 | 0.69 |
| Nests with known clutch size | 14 | 9 | 14 | 5 | 18 | 16 | 38 | 30 | 70 |
| Nests with known fate | 14 | 11 | 20 | 12 | 29 | 21 | 45 | 44 | 94 |
| Nests fledged | 7 | 5 | 7 | 7 | 12 | 5 | 16 | 17 | 35 |
| Fledging success (%) | 0.50 | 0.45 | 0.35 | 0.58 | 0.41 | 0.24 | 0.36 | 0.39 | 0.37 |

Hatching estimates do not include nests that were predated before egg laying was completed. No significant differences ($p<0.05$) were found.

Table 1. Hatching and fledging success of SWWA in bottomland hardwood (HARD) compared to pine (PINE) habitat types in southeast Louisiana, 1999-2003 [25].

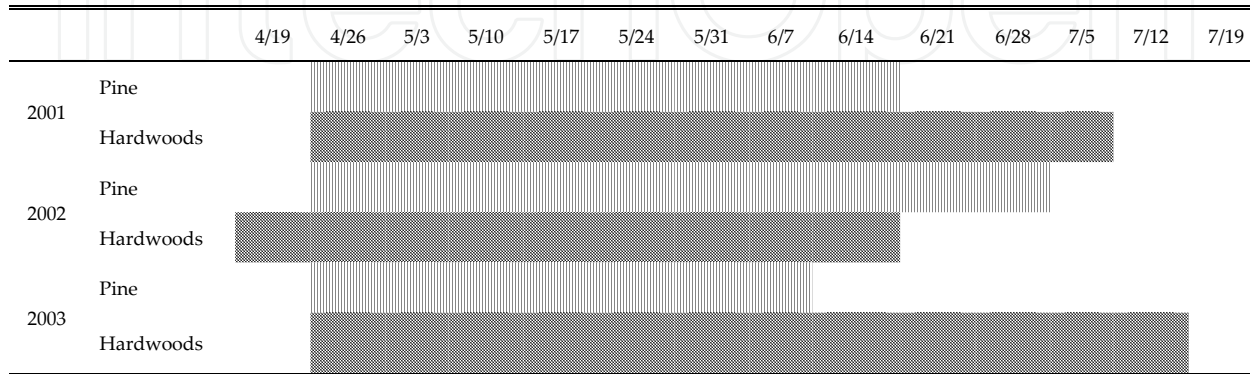


Figure 5. Comparison of the duration of the observed laying period for SWWA in pine versus hardwood habitat types [25].

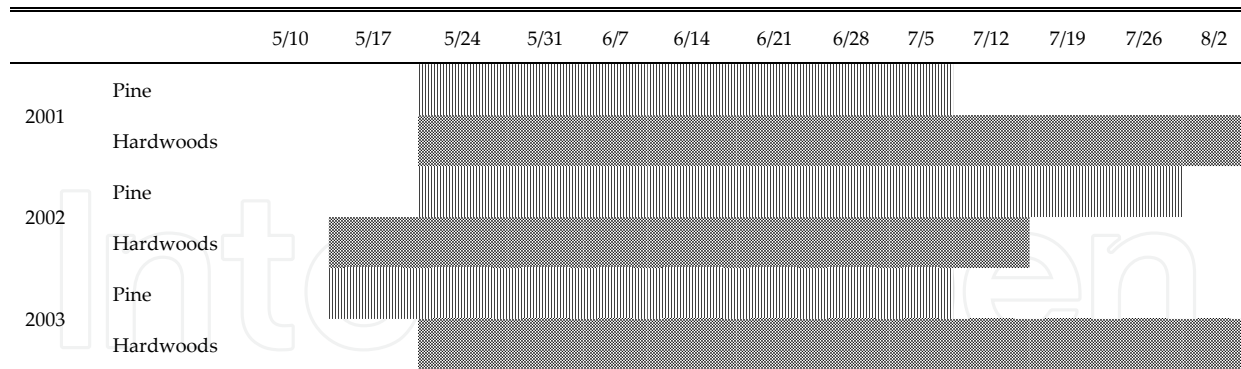


Figure 6. Comparison of the duration of the observed fledging period for SWWA in pine versus hardwood habitat types [25].

Average clutch size for all nests ($n = 84$) was 3.3 ± 0.55 (range 2-4 eggs; Table 2). Clutch size did not differ significantly between habitat types ($F_{1,76} = 1.70$, $p = 0.20$) or years ($F_{2,76} = 1.21$, $p = 0.30$). The interaction of habitat \times year was also not significant ($F_{2,76} = 2.33$, $p = 0.10$). In 2002, females in bottomland hardwood more frequently produced clutches of 4 than clutches of 2-3 eggs ($\chi^2 = 6.14$, $p = 0.01$; Table 3). We did not find any conclusive evidence of double brooding, but females were not color-banded in this study, which made it difficult to confirm double brooding.

| | HARDWOOD | | PINE | | t-value | p |
|----------------|-----------------|----|-----------------|----|---------|------|
| | Mean \pm SD | n | Mean \pm SD | n | | |
| Clutch size | 3.35 ± 0.59 | 52 | 3.23 ± 0.49 | 32 | 0.49 | 0.62 |
| Brood size | 3 ± 0.71 | 45 | 2.75 ± 0.79 | 24 | 0.77 | 0.44 |
| No. Fledglings | 3.04 ± 0.69 | 28 | 3 ± 0.65 | 15 | 0.13 | 0.89 |

Table 2. Mean \pm 1SD of clutch size, number of nestlings per nest, and number of fledglings per nest for SWWA nests found in bottomland hardwood and pine habitat types in southeast Louisiana, 2001-2003 [25].

| | 2001 | | 2002* | | 2003 | |
|--------|----------|------|----------|------|----------|------|
| | HARDWOOD | PINE | HARDWOOD | PINE | HARDWOOD | PINE |
| 2 eggs | 0 | 0 | 1 | 0 | 2 | 1 |
| 3 eggs | 7 | 8 | 4 | 7 | 17 | 8 |
| 4 eggs | 3 | 1 | 10 | 1 | 8 | 6 |

An * indicates that a chi-squared test comparing clutches of 2&3 vs. 4 eggs yielded a p-value < 0.05 .

Table 3. Clutch sizes for SWWA nests found during the building/laying/ or incubation stages in bottomland hardwood compared to pine in southeast Louisiana, 2001-2003 [25].

Hatch rate did not differ significantly between habitat types ($p \geq 0.05$). Overall average brood size ($n = 70$) was 2.9 ± 0.75 nestlings, and did not differ between pine (2.75 ± 0.79 , $n = 24$) and bottomland hardwood (3 ± 0.71 , $n = 45$; Table 1). Average number of fledglings per nest also did not differ between pine (3 ± 0.65 , $n = 15$) and bottomland hardwood (3.04 ± 0.7 , $n = 28$). Overall nesting success rate ranged from 24 to 58% (direct estimates) and 13 to 44% (Mayfield estimates; Tables 4 and 5). We found no significant difference ($p > 0.2$) in number of nestlings fledged or successful nests between sites in all years, or in years pooled (Table 6). However, a comparison of survival probability for incubation and nestling stages, and overall reproductive success, as determined by Mayfield estimates, does reveal significant trends (Table 7). In 2001, nest survival was higher in pine, while in 2003 it was higher in bottomland hardwood. In 2002, incubation and nest survival were higher in bottomland hardwood, while probability of a nestling surviving was higher in pine. Despite this annual variation, survival across all years combined did not differ between habitat types ($p > 0.1$; Table 7). Due to difficulty of finding nests in pine, sample sizes were relatively small in 2001 and 2002, and we found few nests during the incubation stage in 2002. Thus, we argue that results for years pooled probably provide the most accurate estimate of reproductive performance in pine.

| | 2001 | 2002 | 2003 | 2001-2003 |
|------------------------------|------|------|------|-----------|
| Total number of eggs | 68 | 105 | 159 | 332 |
| Total number of nestlings | 44 | 77 | 97 | 218 |
| Hatching success (%) | 0.65 | 0.73 | 0.60 | 0.66 |
| Nests with known clutch size | 23 | 23 | 54 | 100 |
| Nests with known fate | 31 | 41 | 66 | 138 |
| Nests fledged | 12 | 19 | 21 | 52 |
| Fledging success (%) | 0.39 | 0.46 | 0.32 | 0.38 |

Table 4. Summary for comparison by year of breeding data from bottomland hardwood and pine habitat types combined [25].

| | 2001 | 2002 | 2003 | 2001-2003 |
|-------------------|--------------|--------------|--------------|---------------|
| Eggs hatched | 1.192 (0.27) | 0.000 (0.99) | 2.486 (0.12) | 3.175 (0.074) |
| Nestlings fledged | 1.407 (0.23) | 1.667 (0.20) | 0.354 (0.55) | 0.726 (0.39) |
| Nest success | 0.327 (0.57) | 0.981 (0.32) | 0.911 (0.34) | 0.025 (0.87) |

Values indicate the χ^2 value with the p-value in parentheses. Df = 1. No significant differences were found between habitat types.

Table 5. Results of chi-squared tests comparing reproductive metrics for SWWA between pine and bottomland hardwood habitat types in southeastern Louisiana, 2001-2003.

| | 2001 | 2002 | 2003 | 2001-2003 |
|------------|----------------|----------------|--------------|--------------|
| Incubation | 11.69 (<.001)* | 40.54 (<.001) | 2.88 (0.09) | 2.43 (0.12) |
| Nestling | 3.48 (0.06) | 53.17 (<.001)* | 9.15 (0.003) | 0.081 (0.78) |
| Nest | 9.9 (0.002)* | 5.05(0.02) | 8.56 (0.003) | 0.60 (0.44) |

Values indicate the χ^2 value with the p-value in parentheses. Df = 1, $p < 0.05$. Results with an "*" indicate that the survival probability was higher in pine. Results with a "" indicate that the survival probability was higher in hard woods.

Table 6. Results of chi-squared tests comparing Mayfield estimates of pine and bottomland hardwood habitat types for specific reproductive variables.

| | 2001 | | | 2002 | | | 2003 | | | All years | | |
|---|-------|-------|-------|-------|-------|-------|--------|-------|-------|-----------|-------|-------|
| | PINE | HARD | Total | PINE | HARD | Total | PINE | HARD | Total | PINE | HARD | Total |
| <i>Incubation stage</i> | | | | | | | | | | | | |
| Days | 74 | 88 | 162 | 33 | 166 | 199 | 126 | 231 | 357 | 233 | 485 | 718 |
| Losses | 2 | 5 | 7 | 3 | 4 | 7 | 7 | 9 | 16 | 12 | 18 | 30 |
| Mortality | 0.027 | 0.057 | 0.043 | 0.090 | 0.024 | 0.035 | 0.056 | 0.039 | .045 | 0.052 | 0.037 | 0.042 |
| Daily survival probability | 0.973 | 0.943 | 0.957 | 0.91 | 0.976 | 0.965 | 0.944 | 0.961 | 0.955 | 0.948 | 0.963 | 0.958 |
| Probability of surviving incubation stage | 0.68* | 0.44* | 0.54 | 0.26* | 0.71* | 0.61 | 0.45 | 0.57 | 0.52 | 0.48 | 0.59 | 0.55 |
| <i>Nestling stage</i> | | | | | | | | | | | | |
| Days | 52 | 69 | 121 | 38 | 123 | 161 | 48 | 154 | 202 | 138 | 346 | 484 |
| Losses | 2 | 4 | 6 | 0 | 6 | 6 | 5 | 9 | 14 | 7 | 19 | 26 |
| Mortality | 0.038 | 0.058 | 0.049 | 0 | 0.49 | 0.037 | 0.104 | 0.058 | 0.069 | 0.051 | 0.055 | 0.054 |
| Daily survival probability | 0.962 | 0.94 | 0.951 | 1 | 0.951 | 0.963 | 0.896 | 0.942 | 0.931 | 0.949 | 0.945 | 0.946 |
| Probability of surviving nestling stage | 0.65 | 0.52 | 0.57 | 1* | 0.58* | 0.66 | 0.30* | 0.51* | 0.45 | 0.56 | 0.54 | 0.54 |
| Probability of fledging | 0.44* | 0.23* | .36 | 0.26* | 0.41* | 0.40 | 0.134* | 0.30* | 0.23 | 0.27 | 0.32 | 0.30 |

Table 7. Mayfield estimates of the reproductive success of SWWA in pine compared to bottomland hardwood habitat types in southeast Louisiana, 2001-2003. Results with an "*" indicate that there was a significant difference ($p < 0.05$) between habitats.

We used 98 nests, monitored for 1,114 exposure days during April 26–August 7 (a 104-day breeding period) to estimate nest survival probabilities. Results were similar to those obtained for egg and nestling survival probabilities with the Mayfield method, with no difference in daily survival probability in pine (0.9604), bottomland hardwood (0.9599), and both habitat types combined (0.9601).

We attributed nest failure to predators in 77% of failed nests ($n = 26$) in pine and 83% of failed nests ($n = 59$) in bottomland hardwood. We also found evidence of one adult killed on a nest in bottomland hardwood. We only observed four cases involving nest parasitism by brown-headed cowbirds (*Molothrus ater*), specifically in pine sites in St. Helena Parish in 2001 and in Livingston Parish in 2003; and in bottomland hardwood once each in 2002 and 2003. Only one cowbird egg or chick was discovered per nest. Thus, only two nests in each habitat type were parasitized by brown-headed cowbirds (8% in pine and 3% in bottomland hardwoods). In 10% of failed nests, abandonment was the cause in pine and 8% in hardwood; weather (overexposure to cold, wet conditions during a tropical storm or loss of nests to flooding) caused 8% of nest failures in pine stands and 5% in hardwood.

We suspected polygyny in one male's territory in bottomland hardwood, where two active nests were found during laying within 3.5 m of each other. Each female laid a clutch of three eggs; only one nest successfully fledged three young, while eggs in the other nest were destroyed by a bird (holes poked in the eggs) soon after laying. Although females were not banded, we suspect that it was the same female from the destroyed nest who renested within 6 m of her first nest and eventually fledged three young. We also observed four other instances in Honey Island Swamp and one in a pine site where we found active nests in close proximity to one another (within 10 m), but could not definitively determine if these were cases of polygyny or alternatively aggregated nest placement by pairs from adjacent territories.

4. Discussion

Our study is the first to monitor SWWA nesting in pine plantations, the first to compare SWWA nesting success in two different habitat types, and one of the few with sample sizes greater than 20 nests per habitat type (others include [40, 43]). Comparing density, breeding phenology, clutch size, nesting success measured multiple ways, impacts of predators and brood parasites, and comparing the two forest types for combined years did not reveal any significant differences. Thus, multiple lines of evidence support our hypothesis that SWWA reproductive success in pine plantations with suitable habitat is equal to that of bottomland hardwoods. Sample sizes were too small to confirm there were in fact no differences between habitat types (e.g., in frequencies of nest predation or brood parasitism), but based on consistency of these largely independent measures of nesting ecology, these two habitat types differ little for SWWA.

Breeding phenology did not differ by habitat with the exception of 2002, when breeding was documented one week earlier in bottomland hardwoods. In 2002, we found clutches of 4 eggs significantly more frequently in bottomland hardwoods than in pine stands, probably

correlated with earlier nesting date, as larger clutches tended to occur earlier in the breeding season. Older, more-experienced, or more-fit pairs may preferentially select bottomland hardwoods, although SWWA males arrived on breeding territories at the same time in both pine and bottomland hardwood, demonstrating that bottomland hardwoods are not necessarily being preempted by experienced males. Instances of earlier clutch initiation date and larger clutch size, in addition to somewhat higher breeding density (although this was not tested), indicate that bottomland hardwoods may have provided slightly better habitat conditions than pine plantations. However, small sample sizes, difficulty of finding nests during laying, and the fact that these trends were not observed consistently every year precludes any such generalization without more data.

Additionally, annual adult survival was not examined in this study, so we do not know if populations in the two habitat types have identical population growth rate. Morphological data [25] suggest no ecotypic variation or population segregation by breeding habitat. We also did not account for differences between stands within each habitat type, which probably vary in quality, but rather combined all nests by habitat type due to limited sample sizes. Thus, we cannot be certain of no local variation within habitat type. Finally, because very few individuals were marked in our study we were unable to identify re-nesting attempts. Fates of all nests found were included in analyses. Therefore, estimates of nest success reported here may not accurately represent success of birds that may have reared young after second or third attempts [44].

SWWA appear able to move among habitat patches in an ideal free distribution pattern [45,46]. We found unoccupied stands of seemingly suitable dense canebrakes in Honey Island Swamp and areas newly colonized by SWWA where growth in thinned or cleared tracts that had previously been unoccupied reached higher breeding density during our study. Similarly, we witnessed SWWA moving out of a 14-year-old unthinned pine stand that had been actively used for breeding for at least 3 years, into an adjacent 21-year-old pine stand that had already been thinned for 6 years. Thus, although distribution and abundance of SWWA is not well known in any part of its range, it appears to be patchily distributed throughout suitable environments, suggesting low overall population density and unsaturated breeding habitat. As in our study, viable canebrakes were not saturated with birds and did not appear to limit populations of SWWA in southern Missouri [47] or correlate with greater nesting success in eastern Arkansas [43]. SWWA could be considered colonial breeders based on these patchy distributions [31], which may be attributed to social stimulation affecting habitat selection [48]. Coloniality, or dense populations occupying smaller territories, are reported to be indicative of higher quality habitat conditions and higher resource productivity [33,49], but see [28].

Because reproductive success of SWWA was comparable in two habitat types compared here, suggesting individuals freely select suitable breeding habitat [e.g., 26], we posit that pine plantations, where appropriate habitat conditions exist, do not constitute population sinks for this species. This finding is consistent with other recent studies documenting avian nesting success in general in pine plantations [20,50,51]. Secondly, pine plantations in our study differed considerably from bottomland hardwoods, both floristically and physiognomically, suggesting that SWWA does not select breeding habitat based just on structural characteristics like broad-leaved versus needle-leaved trees [25]. Although we did not measure landscape

features that could influence presence of SWWA in pine stands, scarcity of suitable bottomland hardwoods in the study region (longleaf pine savannah historically being the primary forest type in the area) suggests that SWWA are not simply spilling over from adjacent habitat types.

4.1. Conservation implications

In addition to SWWA, other migratory species of conservation concern that are traditionally, if not exclusively, associated with hardwood forests have been frequently detected breeding in pine plantations, including (in our study) worm-eating warbler, hooded warbler (*Wilsonia citrina*), Kentucky warbler (*Oporornis formosus*), white-eyed vireo (*Vireo griseus*), wood thrush, and yellow-billed cuckoo (*Coccyzus americanus*). Use of pines by so many breeding forest interior, understory ground and shrub-nesting birds indicates that pine plantations provide suitable breeding habitat. SWWA typically experience low rates of nesting success as reported (in limited accounts, see [25,40]) across their range, and so are particularly sensitive to predators and other limiting factors on their breeding grounds. Thus, we suggest that they may serve as sensitive indicators of habitat quality. If so, then our results support the conclusion that pine plantations provide suitable breeding habitat not only for SWWA, but also for the larger community of understory breeding birds. More extensive, large-scale monitoring programs may reveal other “novel” landscapes for species of conservation concern.

A positive implication of this finding is that pine plantations in the United States is predicted to persist [9], which should help sustain abundant SWWA in Louisiana and other southeastern states [27]. However, the temporal windows of suitable habitat conditions (pole stage and mature pine) within pine forest patches is short, and forest products companies generally thin stands while closed canopy conditions still exist. Thinning can negatively affect avian reproductive success [52]. Nonetheless, it is important to recognize that short stand rotations mean that as many stands are becoming suitable for SWWA as are deteriorating throughout a landscape; this may mitigate against the short duration that particular stands are available for this species [27].

Because closed canopy pine stands with little herbaceous growth are generally considered to be of minimal biodiversity value, planting pines on wider rows and thinning as early as possible is generally recommended to improve herbaceous vegetation conditions and thus overall biodiversity within stands [18,53]. However, within the range of SWWA, consideration should be given to the value of closed canopy plantations to this species [this study, 24,25,27,37] when making management decisions. Additionally, management decisions during early rotation affect successional trajectories in intensively managed pine stands [15,53,54] and could affect habitat suitability for SWWA structurally and temporally.

Plantation forestry may become increasingly important for conserving biological diversity generally. For example, *Acer saccharum* forests in eastern Ontario managed for maple syrup provide suitable breeding habitat for cerulean warblers (*Dendroica cerulea*), another species of conservation concern [55]. Even-aged spruce plantations in Scotland support a higher density and diversity of native songbirds than the moorlands they replaced, without negatively impacting regional diversity [56]. Survival rate of wild turkey (*Meleagris gallopavo*) females in intensively managed pine landscapes in Mississippi was equivalent to traditional hardwood and mature pine habitat conditions associated with this species [57]. Young conifer plantations

provided suitable foraging sites for the rare woodlark (*Lullula arborea*) in Britain [58], where 19 threatened fungal species were also recorded in conifer plantations, and species richness did not differ from natural forests [59]. Thus, silvicultural landscapes can increase geographic-scale (Beta) diversity. Such findings should encourage better understanding when commercial management is not incompatible with wildlife conservation.

Because SWWA is poorly detected and difficult to monitor with broad-based methods such as breeding bird surveys, no data exist on long-term population trends. Data are sparse on local distributions of SWWA rangewide, making it difficult to detect shifts in habitat use (e.g., [27], present study). Thus, more and better surveys of forest interior species are needed to assess current status and future viability. The opportunity to conserve species on private lands where the economic incentive exists to maintain forest cover should not be overlooked, particularly in regions where most forest land is privately held [9].

More research is needed on the breeding ecology of SWWA in novel habitat types to identify whether results found here are general. A comparison of reproductive success within pine in response to stand characteristics and management history would provide a better guide to management practices necessary for sustaining SWWA populations. More investigations *sensu* Graves [27] into landscape features associated with pine stands occupied by SWWA may also help to identify habitat conditions relative to reproductive success. Research is also needed on the temporal window of stand ages suitable for reproduction and population growth by SWWA, and how this window might conflict with commodity-production objectives.

In summary, our research has demonstrated that SWWA has expanded its local range in southeastern Louisiana into pine plantations, and is experiencing similar levels of reproductive success in this and in bottomland hardwoods, the historically most important habitat type. Our prediction that pole stage pine plantations are not an ecological trap for SWWA is supported, but more information is needed on how silvicultural regimes across the southeast United States may affect demographic parameters of forest interior bird species of present or future conservation concern [37]. Contributions of intensively managed forest landscapes for conservation have commonly been underrated, and must be recognized to develop and encourage management practices that integrate conservation of biological diversity with silviculture across broad landscapes. These forests should not be seen as surrogates for or threats to conservation of natural forests, but rather as potential contributors to maintenance of local and regional biodiversity.

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