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# Effects of insectivorous birds on tree growth in the Maurepas Swamp

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EFFECTS OF INSECTIVOROUS BIRDS ON TREE GROWTH IN THE MAUREPAS  
SWAMP

A Thesis  
Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Master of Science

in

The School of Renewable Natural Resources

by  
David M. Fox  
B.S., University of Washington, 1993  
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## **DEDICATION**

This work is dedicated first to my parents, John and Geraldine Fox, my sister Tamara Fox, my late grandfather Ralph Miller, and my extended family with thanks for their constant support in all of my endeavors. Second, it is dedicated to Phil Stouffer with thanks for his patience. To Larry Wood, Gary Zenitsky, Bob Cooper, and the entire bird crew that worked at White River National Wildlife Refuge in 1997, thank you for making that field experience the best of my life. Finally, this work is dedicated to the people of Louisiana, with the hope that the knowledge gained during this study will be of some value in the effort to restore our coastal forested wetlands.

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## ABSTRACT

Coastal forests in Louisiana are in decline due to natural and human caused changes in the hydrology of the region. Baldcypress and water tupelo trees have been further stressed by caterpillar herbivory in recent decades. Regeneration of water tupelo is crucial for cavity creation for nesting habitat for secondary cavity nesting bird populations. Insectivorous birds have been shown to decrease insect-caused leaf damage on trees in other ecosystems. Two experiments examining effects of insectivorous birds on tree growth were conducted in degraded areas of the Maurepas Swamp in southeastern Louisiana. In the first experiment, nest boxes were added to study plots in degraded swamp in an attempt to increase densities of secondary cavity nesting birds, and to determine if increased insectivorous bird abundance resulted in improved shoot growth of baldcypress saplings. Prothonotary Warblers were the only bird species to utilize nest boxes, nest boxes did not significantly increase densities of Prothonotary Warblers, and insectivorous bird abundance was not correlated with baldcypress shoot growth. In the second experiment, bird exclosures were erected around planted baldcypress and water tupelo seedlings. Leaf damage on trees within bird exclosures and those with an insecticide treatment was not significantly different from controls. Foraging observations of Prothonotary Warblers and Northern Parulas, and video nest monitoring of Prothonotary Warbler nests during caterpillar activity, suggest that birds demonstrate a functional response to baldcypress leafroller caterpillars. Results of video nest monitoring suggested that successful Prothonotary Warbler nests active during baldcypress leafroller activity have the potential to protect 76 grams dry weight of baldcypress foliage. However, birds only foraged on baldcypress taller than 2m, and forest tent caterpillars were only observed to be consumed during the first and final caterpillar instar stages. Planted baldcypress seedlings grew faster than planted water tupelo, and water

tupelo seedlings had zero height growth, or died-back four times as frequently as baldcypress. Insectivorous birds provide baldcypress some protection from caterpillar herbivory, but birds may offer little protection to water tupelo, especially trees less than 2m tall.

## CHAPTER 1. INTRODUCTION AND LITERATURE REVIEW

### Overview

Indirect, positive effects of predators on plants are called trophic cascades. I performed two experiments in the Maurepas Swamp in southeastern Louisiana in 2003-2005 to determine whether birds positively affect tree growth via their consumption of herbivorous caterpillars. In this chapter I review and integrate literature about trophic cascade theory, experiments of birds' effects on herbivorous insects and plants, coastal forest degradation and loss in Louisiana, and then describe how the bird-herbivorous caterpillar-tree trophic cascade may be an important interaction chain for maintaining the health and stability of Louisiana's coastal forests. This thesis is formatted in the journal style, and the next two chapters describing my experiments contain abbreviated, but extensive versions of this introductory chapter.

### Trophic Cascade Theory

An emergent property of multi-species assemblages is the generation of indirect effects. Indirect effects occur when direct effects of interactions between species pairs (e.g. predation, competition, mutualisms) are transmitted indirectly to species that do not participate in the direct interaction (Wootton 1994). In a species assemblage exhibiting indirect effects, the effects of "donor" species on "transmitter" species indirectly influence "receiver" species (Morin 1999). Indirect effects may arise through a chain of interacting species, in which variation in the abundance of the donor affects the abundance of the transmitter, resulting in variation in the abundance of the receiver (e.g. apparent and exploitative competition, trophic cascades) (Wootton 1994, Morin 1999). Alternatively, variation in the abundance of the donor may cause an interaction modification (higher-order interaction) between two species that interact directly. Interaction modifications may result in changes in the per capita effect of the transmitter on the

receiver, without changing the abundance of the transmitter (Morin 1999). Although the role of indirect effects in structuring communities has recently received much attention from community ecologists, their importance is still poorly understood (Halaj and Wise 2001).

One type of indirect effect is a trophic cascade (Paine 1980, Carpenter et al. 1985). In classical predator-driven trophic cascades the direct effects of a predator (donor) are passed through an interaction chain, first reducing the abundance of an herbivore (transmitter), then indirectly increasing populations or biomass of producers (receiver) (Wootten 1994, Morin 1999). Interaction modifications may also produce trophic cascades. In these “behaviorally mediated” trophic cascades, herbivory is reduced by predators’ effects on the per capita effects of herbivores on producers, causing an increase in producer populations or biomass (Schmitz 1994).

The classical trophic cascade concept was implied in the seminal paper by Hairston et al. (1960, hereafter referred to as HSS) in which it was hypothesized that “the world is green” due to predator control of herbivore populations. First, HSS reasoned that in terrestrial three trophic level ecosystems (producer, herbivore, and predator) plants generally experience negligible amounts of herbivory. Therefore, plant populations are not controlled by herbivores and must be controlled by competition for resources (bottom-up control). Second, because herbivore populations are not resource limited, as evidenced by large standing crops of plants, they must be limited by predators (top-down control) rather than by competition. Predators limit their own resources (herbivores), and are therefore limited by competition.

Fretwell (1977) and Oksanen et al. (1981) extrapolated the HSS model to chains longer and shorter than three trophic levels. In these “exploitation ecosystem hypothesis” (EEH) models, the maximum number of “functional” trophic levels (those able to affect lower, adjacent

trophic levels) in an ecosystem is determined by primary productivity, and the relative importance of top-down and bottom-up forces on biomass of an individual trophic level varies with food chain length (Power 1992). EEH predicts that herbivores will be predator limited in food chains of three or five links, and the standing crop of plants will be high. In contrast, plant populations will be grazer limited in food chains of two or four links, and standing crops of plants will be low. Therefore, landscapes will appear alternately green (in 1, 3 and 5 trophic level systems) and then brown (in 2 and 4 trophic level systems) along a gradient of increasing primary productivity. In systems with three (or 5) functional trophic levels, the strength of trophic cascades should increase with primary productivity because predator biomass should increase as they consume “excess” herbivores (Fretwell 1977, Oksanen et al. 1981, Hunter and Price 1992, Power 1992, Strong 1992).

The HSS and EEH models predict that cascading effects of top-down forces of higher trophic levels, if present, will control standing crops of plants. However, there are three major criticisms of the HSS and EEH hypotheses. First, the HSS and EEH models assume species to be consolidated into trophic levels interacting strongly in a linear food chain. However, ecosystems generally are not composed of homogeneous groups of species with similar diets, but are complex webs, with multiple, reticulating connections between species (Strong 1992, Persson 1999, Polis et al. 2000, see Polis and Strong 1996 for a review). This heterogeneity within webs may cause direct effects of predation to be diffused via intraguild predation, omnivory, and compensation by less vulnerable species at lower levels, rather than propagating to lower non-adjacent levels in a linear fashion (Hunter and Price 1992, Strong 1992, Polis and Strong 1996). For example, many vascular plants have evolved physical or chemical defenses against herbivory and are not palatable to herbivores (Strong 1992). Therefore, food web heterogeneity may buffer

herbivore effects on plants because loss of undefended plants may result in increased biomass of defended plants (Strong 1992, Schmitz 1994, Persson 1999). Plants may also exhibit compensatory growth following herbivory (Stowe et al. 2000). Therefore, bottom-up effects of plant resources, or resource quality on herbivore populations, may mute predator effects (Sipura 1999, Persson 1999, see Price et al. 1980 for a review). Strong (1992), Polis and Strong (1996), and Polis et al. (2000) predicted that trophic cascades should be expected in low diversity systems with vulnerable plant communities. Examples of such systems include many aquatic systems and unnaturally simple agricultural systems. Many aquatic systems have a “vulnerable algal turf”, and individual plants are generally undefended and frequently eaten whole (Strong 1992). Agricultural systems generally have artificially low diversity and relatively undefended plants (Polis et al. 2000). Third, top-down forces may be weakened by factors that reduce predator efficiency, such as territoriality, competition for other resources (e.g. water, nesting habitat) (Power 1992, Polis and Strong 1996), and environmental heterogeneity in space and time that may provide refugia for herbivores (Hunter and Price 1992, Polis and Strong 1996). Any of these factors may attenuate the strength of potential trophic cascade before they reach the producer level (Pace et al. 1999).

Strong (1992), Polis and Strong (1996), and Polis et al. (2000) predicted that trophic cascades should be expected in low diversity systems that approach the structural simplicity of a food chain and have vulnerable plant communities. There is evidence that trophic cascades do operate in such systems. In freshwater aquatic systems effects of piscivorous fish populations may cascade through four trophic links, suppressing planktivorous fish, which in turn releases zooplankton to control phytoplankton (Power et al. 1985, Carpenter et al. 1985, Brett and Goldman 1996, Carpenter et al. 2001). Trophic cascades are the basis for biological control

programs in agricultural systems (Polis et al 2000), and insect enemies of herbivorous insects have been shown to reduce insect pest populations and indirectly reduce damage to crop plants in agricultural systems (e.g. Carter and Rypstra 1995, Hooks et al 2003).

Three lines of evidence suggest that trophic cascades may not be limited to simple aquatic and terrestrial systems. First, there is correlational evidence that reduction in top predator populations by humans has eliminated cascading effects in some systems (Paine 1980, Pace et al. 1999, Wootton 1994, Terborgh et al. 2001). The best-known example from North America is probably the reduction in forest regeneration, understory vegetation biomass, and plant diversity due to ungulate browsing following reduction or extirpation of gray wolf populations (*Canis lupus*) (Pace et al. 1999, McLaren and Peterson 1994, Rooney and Waller 2003, for additional examples cascading effects of top predator removal see Paine 1980, Pace et al. 1999, Wootton 1994, Terborgh et al. 2001). Second, invasive herbivores have been successfully controlled with the use of biological control organisms, albeit with numerous examples of ecological disasters (see Hoddle 2004 for a review). Third, experimental variation in abundance of predator taxa produces cascading effects in many systems (for reviews see Pace et al. 1999, Schmitz et al 2000, Halaj and Wise 2001).

### **Trophic Cascade Experiments**

Significant effects of predators on plants have been demonstrated in a variety of terrestrial predator-herbivorous insect-plant systems by varying predator abundance (for reviews see Pace et al. 1999, Schmitz et al 2000, Halaj and Wise 2001). Lizard removal increased overall insect damage caused to foliage on shrubs on small Bahaman islands (Spiller and Schoener 1990) and rainforest canopy in Puerto Rico (Dial and Roughgarden 1995). An ant predator specialist beetle was introduced onto *Piper* plants in lowland tropical rainforest that

resulted in a four level trophic cascade in which mutualistic ant populations of *Piper* plants were decreased, resulting in an increase of herbivorous arthropods and increased foliage-insect damage on study plants and neighboring *Piper* plants (Letourneau and Dyer 1998). Ant exclusion on white birch (*Betula pubescens*) in Finland increased folivorous caterpillar populations and leaf damage caused by caterpillars (Karhu 1998). Praying mantis (*Tenodera sinensis*) addition in an old-field community reduced insect herbivore populations, resulting in increased plant biomass in experimental plots (Moran and Hurd 1998).

Marquis and Whelan (1994) predicted that birds should have strong, positive indirect effects on plants on which they forage, based on three lines of evidence: 1) birds are conspicuous predators of defoliating insects and limit insect populations in many systems; 2) insect herbivory can reduce the growth of plants; and 3) bird exclosures increase insect herbivore damage on study plants relative to controls.

Birds are conspicuous predators of defoliating insects and they have the potential to consume large numbers of forest insects due to their mobility and high metabolic rates (Kirk et al. 1996). Most breeding passerine birds in temperate forests feed primarily on insects (Holmes and Schultz 1988), and caterpillars are the most important insect taxon in the diets of breeding passerine birds in temperate forests (Holmes and Schultz 1988). Many species of caterpillars are folivorous, relatively large, conspicuous on leaf surfaces and are energetically profitable food items for insectivorous birds (Holmes and Schultz 1988).

Insect defoliation of many tree species reduces the rate at which trees accumulate woody biomass, and the effect is generally proportional to the severity of defoliation (Muzika and Liebhold 1999, Goyer and Chambers 1997, Souther-Effler 2004, Tucker et al. 2004, Chambers et al. 2005, for a review see Smith 1971). Birds have been shown to have significant impacts on

low and moderate populations of forest insects (Dahlsten and Copper 1979, Holmes et al. 1979, Loyn et al. 1983, Crawford and Jennings 1989, Torgerson et al. 1990, Gunnarsson 1996, Parry et al. 1997, Sanz 2001, see Otvos 1979 and Holmes 1990 for reviews).

Birds may exhibit numerical and or functional responses to outbreaks of caterpillars (Morris et al. 1958, Buckner and Turnock 1965, Holmes and Schultz 1988, Crawford and Jennings 1989, MacCulloch 2001), and they have the potential to destroy enormous numbers of caterpillars. In a study of bird predation of spruce budworm (*Choristoneura fumiferana*) in New Hampshire and Maine, Crawford and Jennings (1989) estimated that more than 85,000 spruce budworms/ha were consumed by just five bird species within the bird community during low and transitional spruce budworm infestations. Takekawa and Garton (1984) examined stomach contents of Evening Grosbeaks (*Coccothraustes vespertinus*) and estimated that individual birds ate 12,600-26,400 western spruce budworms (*Choristoneura occidentalis*) over the course of an outbreak in Washington, and the entire bird community was estimated to consume 7-12.7 million budworms per square kilometer. Turček (1957 as cited in Bruns 1960) found that Great Tits consumed 50 Tortricid moth caterpillars (10-15% of their body weight) in 90 minutes, an estimated that Great Tits consume 300 of these caterpillars per day.

However, as caterpillar populations increase to epidemic levels the proportion of the caterpillar population eaten by birds decreases (Crawford and Jennings 1989, for reviews see Otvos 1979 and Holmes 1990) due to satiation, or territorial behavior exhibited by most breeding insectivorous birds. Territoriality results in intraspecific interference competition for food resources (Power 1992), and places a limit on the numerical response of territorial birds to epidemic caterpillar populations. Thus, cascading effects of birds on plants may be damped during insect outbreaks. Holmes (1990) suggested that although birds may not have significant

impacts on epidemic populations of caterpillars, birds may increase the time it takes for caterpillar populations to reach epidemic populations, increase the rate at which caterpillar populations decline following outbreaks, and increase the periodicity of caterpillar outbreaks.

In many studies of bird-herbivorous insect-plant systems, birds decreased insect-herbivore damage on plants by reducing local abundance of insect-herbivores (Atlegrim 1989, Bock et al. 1992, Marquis and Whelan 1994, Sipura 1999, Strong et al. 2000, Greenburg et al. 2000, Murakami and Nakano 2000, MacCulloch 2001, Sanz 2001, Van Bael et al. 2003, Van Bael and Brawn 2005, but see Forkner and Hunter 2000, Lichtenberg and Lichtenberg 2002).

The bird exclosure study by Marquis and Whelan (1994) is the most frequently cited positive evidence for the operation of trophic cascades in terrestrial systems. Marquis and Whelan (1994) caged white oak (*Quercus alba*) saplings in Missouri for two years and compared insect abundance, leaf damage and leaf, twig and total aboveground biomass production of caged saplings and controls to saplings that were sprayed with insecticide. Numbers of leaf chewing insects were consistently and frequently significantly higher on caged trees, lowest on sprayed trees, and intermediate on control trees. Reduction of leaf chewing insects by birds resulted in a similar, significant pattern of leaf damage among treatments; leaf damage was greatest on caged trees, lowest on sprayed trees, and intermediate on controls. Effects of leaf damage led to significant differences in leaf production and total aboveground biomass production between treatments; caged trees produced one-third less aboveground biomass than sprayed trees, primarily due to reduced leaf biomass production in caged trees, with controls producing intermediate values.

However, in a similar study on white oak saplings under two canopy classes in Arkansas, Lichtenburg and Lichtenburg (2002) found that excluding birds had no effect on abundances of

leaf-chewing insects relative to controls, although leaf damage was significantly higher in the cage treatment. Saplings growing under more open canopy were more productive than saplings growing under closed canopy; however variation in sapling productivity had no effect on overall herbivore density or bird predation. Contrary to predictions, height growth and above ground biomass production was greater in caged trees, possibly due to reduced damage by white-tailed deer, or a compensatory growth response to herbivory (Lichtenburg and Lichtenburg 2002).

Strong et al. (2000) performed a bird exclusion study on understory sugar maple (*Acer saccharum*) saplings in New Hampshire, similar to the study by Marquis and Whelan (1994), but included a caterpillar addition treatment in their design. Treatment effects on leaf damage were significant and similar to those observed by Marquis and Whelan (1994); leaf damage was highest on caged trees, lowest on sprayed trees, and intermediate on control trees. Caterpillar populations on trees varied among treatments, but pooled arthropod censuses showed that caterpillar populations on trees in the caterpillar addition treatment were reduced to levels similar to those on caged trees, and uncaged trees had the lowest numbers other than trees in the insecticide treatment. Leaf damage on trees in the caterpillar addition treatment was greater than that of caged trees in only one of two years. Presumably, these similarities between caterpillar addition and caged trees were due to the response of birds to the increased prey abundance on trees with the caterpillar addition treatment. Increased leaf damage did not produce a significant effect on aboveground biomass production. Strong et al. (2000) hypothesized that this may have been due to lower density of caterpillars on study trees in New Hampshire relative to the Missouri study. Eighty-five percent of the herbivorous insects on sugar maples were Homoptera, which are not a major component of insectivorous bird diets in New Hampshire, and Homopteran density was not affected by the enclosure treatment. Strong et al. (2000) also

hypothesized that differences in bird effects on biomass production may have been due to the later timing of herbivory in New Hampshire relative to Missouri, and lower primary productivity of understory sugar maples compared to white oak saplings in Missouri.

Van Bael et al. (2003) and Van Bael and Brawn (2005) studied the effects of productivity on the strength of bird-insect-tree trophic cascades in Panamanian tropical rainforest. Van Bael et al. (2003) compared effects of birds on leaf damage on branches of relatively productive overstory trees to that of relatively unproductive conspecific saplings in the understory in a seasonally dry rainforest. In the wet season, when insect abundance was highest, birds significantly decreased insect abundance and leaf damage on canopy branches accessible to birds relative to caged canopy branches. Insect abundance and leaf damage were not significantly different between caged and accessible understory saplings. Van Bael and Brawn (2005) compared the results of the previous experiment to results from a similar experiment conducted in moist, evergreen Panamanian rainforest. Van Bael and Brawn (2005) predicted that bird predation would have a greater effect on leaf damage in the seasonally dry forest where short-lived and less fibrous leaves are produced in abundance in the wet season, and that the effects of bird predation would be lower in the wetter forest where fewer, fibrous, long-lived leaves are produced continuously. They also predicted that bird exclosures would have no significant effects on less productive understory trees in the wet forest. As predicted, arthropod density and leaf damage did not differ between caged canopy branches and controls, nor was there a significant effect of bird exclosure on the response variables in understory saplings. These experiments demonstrated that cascading effects of predators may not necessarily be diffused in a species rich food chain, and that predator abundance and effects on herbivores may increase with primary productivity as predicted by EEH.

Forkner and Hunter (2000) studied the relative effects of top-down and bottom-up forces on planted red oak seedlings in Georgia with a factorial manipulation of fertilization and bird predation. Fertilization increased oak growth and generally increased herbivorous and predaceous insect abundance, but bird predation alone did not affect herbivore abundance or leaf damage. Therefore, the authors concluded that bottom-up forces of fertility dominated the interactions between birds, insects and oak saplings. It was noted that the leaf chewing insect community may have been depauperate because forest insects had to colonize seedlings in the interior of an old-field, which may have possibly damped effects of predators on leaf damage.

Sanz (2001) studied the indirect effects of birds on Pyrenean oak forest in Spain by artificially increasing the abundance of cavity nesting birds via the addition of nestboxes. Mean breeding cavity nesting bird density was 5 pairs/ha in a stand with nestbox addition versus 1.5 pairs/ha in a control stand. Mean caterpillar density was generally lower in the stand with nestbox addition, and caterpillar body mass, frequency of leaf damage, and proportion of leaf area missing were significantly lower in the stand with nestbox addition. These differences were presumably due to greater bird predation of caterpillars in the stand with nestbox addition.

Murakami and Nakano (2000) studied species-specific bird foraging effects on leaf damage by manipulating bird density and taxon. Large bird enclosures were erected around entire sections of oak forest canopy in Hokkaido, Japan and stocked with either a single Great Tit (*Parus major*) or European Nuthatch (*Sitta europea*) for two months. Great Tits fed on caterpillars and Nuthatches fed on ants, which are an arthropod predator of caterpillars. Great Tits significantly reduced caterpillar density and leaf damage, while nuthatches significantly reduced ant density, resulting in higher caterpillar density relative to controls and increased leaf

damage. This study demonstrated that cascading effects of predators may be buffered via intraguild predation, but also shows that birds differ in their species-specific functions. The authors concluded that negative feedback of decreased bird species richness, due to anthropomorphic degradation of forests, and loss of species-specific bird foraging effects may accelerate forest degradation.

A major criticism of most studies of indirect effects of predators on plants is that while predators frequently reduce herbivore damage to foliage, indirect effects of predators on plant biomass production frequently are not tested, are unreported, or have no significant effect (Polis et al. 2000, but see Marquis and Whelan 1994, Moran and Hurd 1998). Meta-analyses of trophic cascade experiments performed by Schmitz et al. (2000) and Halaj and Wise (2001) confirm that indirect effects of predators on plants have strong positive effects on leaf damage, but generally attenuate before affecting biomass production. Therefore, herbivory might not have a fitness cost to some plants.

Another criticism of many trophic cascade studies is that most report on cascading effects of predators on a single plant species, and not on the entire plant community as in a classical trophic cascade (but see Moran and Hurd 1998). In studies where predators did affect biomass production of the plant species in question, compensatory growth of neighboring plants was not investigated (but see Letourneau and Dyer 1998). Therefore, Polis et al. (2000) argued that evidence for trophic cascades, even within a subset of species, is limited. Polis et al. (2000) also suggests that these “species-cascades” do not carry the same biological significance for ecosystem processes as a community level cascade, unless the affected plant is a dominant species within the ecosystem (Polis et al. 2000).

The rarity of experimental evidence for terrestrial trophic cascades, even species-cascades, with effects strong enough to affect biomass production of plants may be due to heterogeneity within food chain levels in species rich systems as argued by Strong (1992) and Polis and Strong (1996). However, the great difference in time scale of plant dynamics between terrestrial and aquatic systems has been cited as a possible cause for the differing results between aquatic and terrestrial trophic cascade experiments (Pace et al. 1999, Chase 2000, Holt 2000, Power 2000, but see Bell et al. 2003). Plant community dynamics of aquatic systems with algae at their base may occur over weeks, while the dynamics of terrestrial systems with long-lived grasses, shrubs or trees at their base take place over years or decades (Chase 2000, Power 2000). Due to the logistical difficulty in performing long-term ecological experiments, the duration of most terrestrial trophic cascade experiments is one or two growing seasons (Schmitz et al. 2000, Halaj and Wise 2001), which is far shorter than the population dynamics of long-lived terrestrial plants.

Logistical difficulties associated with studying canopy trees has also restricted most studies of predator-herbivore-tree interactions to sapling trees, which are less productive and therefore less likely to exhibit positive effects of predators (Strong et al. 2000, Van Bael et al. 2003, Van Bael and Brawn 2005). While decreased predator abundance may not produce a statistically significant effect on biomass production of a plant in any given year, the cumulative impact of increased herbivory over several plant generations might affect plant competitive ability and community composition (Holt 2000), plant productivity (Marquis and Whelan 1994), and ecosystem resilience (Scheffer et al. 2001, Ellison et al. 2005).

Indirect effects of predators on ecosystem resilience may be especially important if the receiver plant species is a foundation species within the ecosystem (Polis et al. 2000, Scheffer et

al. 2001, Terborgh et al. 2001). A foundation species is “a single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes” (Dayton 1972, as cited in Ellison et al. 2005). Trees are foundation species within forested ecosystems (Ellison et al. 2005). Outbreaks or introductions of insect herbivores are contributing to the loss of foundation species in North American forest ecosystems (Ellison et al. 2005) and may destabilize forest ecosystems (Tilman 1996, Scheffer et al. 2001). Forest ecosystems which possess only one or two foundation species are inherently less resilient to disturbance due to their lack of functional redundancy (Ellison et al. 2005).

Gradual anthropogenic changes in abiotic conditions may decrease the resiliency of ecosystems, making them more prone to undergo catastrophic shifts to alternate stable states following perturbations (for reviews see Scheffer et al. 2001, Folke et al. 2004). Natural and anthropogenic forces have altered the hydrology of most coastal swamps in Louisiana. Louisiana’s coastal forests have only two foundation tree species (baldcypress and water tupelo), and both of these tree species have been subject to widespread, repeated defoliation by caterpillars in recent decades. The cumulative impacts of hydrological alterations, insect defoliation and the interactions of these stressors have reduced the resiliency of the coastal forest ecosystem in Louisiana, and it is now on the brink of ecological collapse (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1998, hereafter cited as Coast 2050 1998).

### **Importance of Louisiana’s Coastal Forests**

Cypress-tupelo swamp forests are an important and unique ecosystem in the southeastern United States (Conner et al. 1986, Conner and Toliver 1990). Cypress swamps are found on floodplains of rivers and streams along the Mississippi Alluvial Valley, from southern Illinois to

southern Louisiana and the Gulf of Mexico, and along the Gulf Coast and the Atlantic Coastal Plain to Delaware (Mitsch and Gosselink 2000). Highly flood-tolerant baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) dominate the overstory of much of the swamp forest in coastal Louisiana (Conner and Day 1976, Conner and Toliver 1990), due in part to their ability to produce secondary roots with the capacity to oxidize the area surrounding their roots (rhizosphere) in flooded, anaerobic soils (Pezeshki et al. 1990). Swamp red maple (*Acer rubrum* var. *drummondii*) and ash species (*Fraxinus* spp.) frequently dominate the understory (Conner and Day 1976, Höppner 2002, Shaffer et al. 2003).

Baldcypress is one of the most ecologically and economically valuable trees in southeastern wetland forests (Brown and Montz 1986). Baldcypress was the dominant tree in the Lower Mississippi Alluvial Valley (LMAV) and the Coastal Plain of Louisiana prior to European settlement (Matoon 1915). Reliable estimates of the historic area of cypress-tupelo swamps in Louisiana are unavailable, but early estimates range from 0.67-3.64 million hectares (Conner and Toliver 1990). The great disparity in these early estimates is most likely due to the use of different forest classification schemes (Chambers et al. 2005).

Coastal forests in Louisiana have great ecological and societal values for water quality improvement (Kuenzler 1989), floodwater storage, storm surge protection (Danielsen et al. 2005), timber production, commercial and recreational fish and wildlife harvest, and wildlife habitat (for a review of coastal forest functions and values see Chambers et al. 2005).

Coastal forests of Louisiana are critical stopover habitat for millions of Neotropical migratory bird species of the eastern United States (Barrow et al. (in press), as cited in Chambers et al. 2005). The Neotropical Migratory Bird Conservation Program, also known as “Partners in Flight” (hereafter referred to as PIF) has listed 14 of 19 bird species which breed in the LMAV

as being of greatest conservation concern ([www.rmbo.org/pif/scores/scores.html](http://www.rmbo.org/pif/scores/scores.html), Carter et al. 2000). Prothonotary Warblers (*Protonotaria citrea*), a Neotropical migratory warbler, is ranked second only to the Ivory-billed Woodpecker (*Campephilus principalis*) in terms of conservation concern, and 85% of Prothonotary Warblers breed within the LMAV ([www.rmbo.org/pif/scores/scores.html](http://www.rmbo.org/pif/scores/scores.html), Carter et al. 2000). Bottomland hardwood forests are used more heavily than cypress-tupelo swamp by most Neotropical migratory birds (Stouffer and Zoller, unpublished data), but widespread destruction of bottomland hardwood forests along the Gulf coast by hurricanes Katrina and Rita in 2005 may increase the relative importance of cypress-tupelo forest as stopover habitat for migrating birds.

In addition to Neotropical migratory birds, coastal forests in Louisiana are also important habitat for fish, herpetofauna, waterfowl, wading birds, threatened birds of prey such as Bald Eagles (*Haliaeetus leucocephalus*) and Swallow-tailed Kites (*Elanoides forficatus*), and threatened mammals such as the Louisiana black bear (*Ursus americanus luteolus*), the southeastern bat (*Myotis austroriparius*) and Rafinesque's big-eared Bat (*Plecotus rafinesquii*) (for a review see Chambers et al. 2005).

### **Coastal Forest Loss**

Between 1883 and 1991, as much as 77% of southern bottomland hardwood forests were lost (The Nature Conservancy, as cited in Mitsch and Gosselink 2000) primarily due to logging; flood control projects that allowed wetland forest to be converted to agricultural land; conversion to drained and “bedded” pine plantation; and/or conversion from wetland forest to other wetland types (Dahl and Johnson 1991, Dahl 2000, Mitsch and Gosselink 2000). The LMAV currently contains 2 million ha of forested wetland (Twedt and Loesch 1999), which is the largest area of forested wetland remaining in the United States (Mitsch and Gosselink 2000). However,

forested wetland remaining in the LMAV is highly fragmented, which has reduced the functional capacity of this ecosystem to provide ecological services to wildlife and human populations (Twedt and Loesch 1999).

Greater than 50% of the remaining forested wetland in the LMAV is located in Louisiana (Twedt and Loesch 1999), but much of the forested wetland in coastal Louisiana is at risk of converting from cypress-tupelo swamp forest to open marsh (Shaffer et al. 2003, Chambers et al. 2005). It is estimated that 42% of the remaining swamp in the Louisiana Deltaic Plain will be lost by 2050 (Coast 2050 1998). Loss of coastal wetland forests had not been addressed specifically until recently, most likely because the transition of swamp to open marsh results in little wetland loss *per se* (Conner and Day 1988, Chambers et al. 2005).

Between 1930 and 1990, Louisiana lost nearly 486,000 hectares of coastal wetlands (Barras et al. 2003), and it is estimated that an additional 255,000 hectares of coastal wetlands will be lost by 2050 (Coast 2050 1998). The massive, rapid loss of wetlands threatens Louisiana's entire coastal wetland ecosystem and by extension the industries, human population centers and societal infrastructure dependent on coastal wetland health (Coast 2050 1998).

The causes of wetland loss in Louisiana are complex and involve both natural and anthropogenic changes to the hydrology of the region and their interactions (Day et al. 2000, Day et al. 2001, Gosselink 2001, Chambers et al. 2005; for extensive reviews of the causes of wetland loss in coastal Louisiana see Boesch et al. 1994, Coast 2050 1998, U.S. Army Corps of Engineers 2004). The main natural cause of wetland loss in coastal Louisiana is relative sea-level rise (RSLR) due to subsidence and eustatic sea-level rise (Day and Templet 1989, Boesch et al. 1994, Coast 2050 1998). Much of the Mississippi River Delta area is experiencing RSLR of 0.3-1.2m per century (Day and Templet 1989, Gagliano 1998 as cited in Coast 2050 1998),

and this elevation loss has resulted in submergence of low-lying coastal wetlands, increased area of permanently flooded wetlands, increased flood depth and duration in seasonally flooded wetlands, and increased salinity in formerly brackish or freshwater wetlands (Day and Templet 1989, Boesch et al. 1994, Coast 2050 1998).

The main anthropogenic cause of wetland loss in coastal Louisiana is the interruption of natural deltaic building processes by the construction of flood control levees, and the construction of canals for logging, shipping and oil extraction operations (Day and Templet 1989, Boesch et al. 1994, Coast 2050 1998, Day et al. 2000, LCA 2004). The Mississippi River delivers 240 billion kg of sediment to the Gulf of Mexico annually (Goolsby 2000, as cited in Shaffer et al. 2003). Historically, a portion of the river's sediment load was distributed across the deltaic plain during spring flood events, building or maintaining the elevation of active deltas and their associated wetlands (Coast 2050 1998, Shaffer 2003, Chambers et al. 2005). However, by 1828 levees along the Mississippi River were nearly continuous from Baton Rouge to New Orleans (McPhee 1987), and many distributary channels into coastal wetlands had been dammed (McPhee 1987, Day and Templet 1989). Therefore, flood control levees have reduced or eliminated mineral sediment accretion in most coastal wetlands for almost 200 years.

Canals oriented north-south have facilitated the flow of saltwater into historically freshwater wetlands, (Day and Templet 1989, Boesch 1994, Coast 2050 1998). Canals and associated spoil banks oriented east-west have impeded sheet flow across wetlands, resulting in large areas with permanent standing water (Coast 2050 1998).

Nutria (*Myocastor coypus*), introduced from South America into Louisiana for use as fur animals (Conner and Toliver 1990), have destroyed extensive areas of marsh vegetation and baldcypress plantings (Blair and Langlinais 1960, Conner et al. 1986, Conner and Toliver 1987,

Conner and Flynn 1989, Conner and Toliver 1990, Beville 2002). Nutria are aquatic mammals and baldcypress seedlings in flooded areas are more vulnerable to nutria herbivory (Blair and Langlinais 1960, Conner and Toliver 1987). As RSLR floods more coastal forest, more baldcypress regeneration will become vulnerable to nutria herbivory. The Louisiana Department of Wildlife and Fisheries only allows recreational hunting of nutria during six months of the year, and, strangely, imposes a limit of five nutria per hunter per day (Louisiana Department of Wildlife and Fisheries Hunting Regulations 2005-2006, <http://www.wlf.state.la.us/apps/netgear/index.asp?cn=lawlf&pid=443>).

Soils of coastal wetlands typically have low bulk densities, are highly organic, and are consolidated primarily by living root networks (Nyman et al. 1990, Shaffer et al. 2003). The elevation of some coastal wetlands is maintained by organic sediment input from wetland plants (Nyman et al. 1990), which may account for up to 50% of sediment accretion (Day and Templet 1989, Coast 2050 1998). Therefore, effects of flooding, salinity, nutria herbivory, and interactions of these stressors on plant productivity produce a negative feedback loop where decreased plant productivity decreases organic sediment accretion, thereby increasing the rate of RSLR. Levee construction has produced another negative feedback loop where mineral sediment accretion deficits increase the rate of RSLR, which decrease plant productivity due to flooding, salinity stress and nutrient starvation, which in turn reduces organic sediment accretion and further increases the rate of RSLR. These stressors and negative feedback loops have been operating for as much as 200 years without significant amelioration, and they have decreased the resilience of the entire coastal wetland ecosystem.

## Logging History of Louisiana's Coastal Forests

The Swamp Lands Act of 1849 transferred ownership of more than 4 million hectares of flooded federal land in Louisiana to the state (Chambers et al. 2005). State levee boards sold much of this public property to land speculators for as little as 3 cents per acre, and large tracts of baldcypress swamp were then sold to northern timber companies (Wilt 2005).

Logging of baldcypress was limited to easily accessible trees along the edges of bayous until the invention of an efficient pullboat logging system in 1890 (Mancil 1980), and the development of swamp railroad logging systems at the turn of the last century (Conner and Toliver 1990, A. Dranguet personal communication). These new logging technologies allowed cypress forests to be harvested efficiently, and from 1890-1925 almost all of the merchantable cypress stands were harvested in southern Louisiana (Mancil 1980). Norgress (1947, as cited in Chambers et al. 2005) estimated that 647,500 ha of swamp had been harvested in Louisiana by 1934, and the Louisiana Department of Conservation (1934, as cited in Chambers et al. 2005) estimated that only slightly more than 9,000 ha of baldcypress remained standing in the state in the mid-1930s. The standing volume of baldcypress throughout its range has probably been reduced more than any American tree except the American chestnut (*Castanea dentata*) (Walker 1984).

During logging operations, dynamite was used to clear stumps from countless numbers of skid trails (Mancil 1980). Steam skidders were used to drag many loads of logs along these skid trails to the edges of bayous or rail lines, and this repeated gouging of the soft, saturated soil created ditches up to 2m deep and 1500m long (Mancil 1980). These water-filled ditches are still obvious features across the landscape (Mancil 1980, personal observation), and water that would normally flow across the surface of the wetland during flood events is now partly confined within these skid trails, creating stagnant water conditions in interior swamp

(Thompson 2000, Chambers et al. 2005), and allowing salt water to penetrate formerly freshwater wetlands deeply and unimpeded (G. Shaffer, personal communication).

### **Coastal Forest Regeneration**

Following the mass-harvest of baldcypress-tupelo swamp in Louisiana, some forests regenerated naturally due to favorable regeneration conditions in the 1920s (Chambers et al. 2005), and the standing volume of baldcypress increased from 15 million m<sup>3</sup> to 41 million m<sup>3</sup> between 1954 and 1984 (Conner and Toliver 1990). Approximately 404,000 ha of cypress-tupelo swamp currently exist in coastal Louisiana (Chambers et al. 2005), with most of the volume located in the Deltaic Plain. However, stands in many baldcypress-tupelo swamps are not fully stocked, suggesting that environmental stresses are affecting regeneration and stand growth (Chambers et al. 2005). The standing volume and basal area of baldcypress in coastal Louisiana has not increased substantially since 1984, and recent basal area estimates suggest that standing volume of water tupelo is in decline (Chambers et al. 2005).

Altered hydrological conditions in Louisiana's coastal forest have reduced or eliminated natural regeneration of baldcypress and water tupelo, and reduced these trees' productivity (for a review see Chambers et al. 2005). Neither baldcypress (Demaree 1932) nor water tupelo (Huenneke and Sharitz 1990) seeds germinate in water, and submerged cypress seedlings die within 3-6 weeks (Demaree 1932, Souther 2000). Therefore, increased flooding due to RSLR has decreased the probability of natural regeneration of many stands of baldcypress-tupelo forest (Conner et al. 1986, Conner and Toliver 1990, Chambers 2005).

Greenhouse studies have shown that flooding decreases photosynthetic rates of baldcypress (Pezeshki et al. 1987, Pezeshki et al. 1989) and water tupelo (Pezeshki et al 1989), and flooding, especially flooding with stagnant, standing water, reduces productivity of swamp

forest tree species (Hook et al. 1970 as cited in Dickson and Broyer 1972, Dickson and Broyer 1972, Harms 1973, Conner and Day 1976, Conner et al. 1981, Conner and Day 1992, Megonigal and Day 1992, Keeland and Sharitz 1995, Goyer and Chambers 1997, Souther 2000, Shaffer et al. 2003, Souther-Effler 2004). Saltwater intrusion into formerly freshwater wetlands due to RSLR and canals reduces photosynthetic rates of baldcypress (Pezeshki et al. 1987, Campo 1996) and water tupelo (Pezeshki et al 1989), and reduces productivity of swamp forest tree species (Pezeshki et al 1989, Shaffer et al. 2003, Souther-Effler 2004). Productivity of marsh plants (Gough and Grace 1998, Shaffer et al. 2003) and swamp forest trees (Pezeshki et al. 1987, Pezeshki et al. 1989, Pezeshki et al. 1990, McCarron et al. 1998, Souther-Effler 2004) may be further reduced by interactions between flooding and salinity stressors.

### **Caterpillar Herbivory in Coastal Forests**

In addition to flooding, salinity, and interactions of these stressors, baldcypress and water tupelo in coastal forests of Louisiana have been subject to repeated annual herbivory by caterpillars in recent decades. The main insect herbivore of water tupelo in coastal forests of Louisiana is the forest tent caterpillar (*Malacosoma disstria*, hereafter referred to as FTC). Early instar FTC may feed on flowers of water tupelo, reducing seed production (Batzer and Morris 1978), and Conner and Day (1976) hypothesized that FTC herbivory of water tupelo may have produced and maintained nearly pure stands of baldcypress which existed before intensive logging began. Large outbreaks of FTC have been recorded in Louisiana since 1931 (Conner and Day 1976), and regular outbreaks have occurred since 1948 (Nachod and Kucera 1971 as cited in Chambers et al. 2005). FTC defoliate 120,000-240,000 ha of swamp forest in Louisiana each spring (Goyer et al. 1990). The increased severity of outbreaks in Louisiana may be due to

cypress logging and the subsequent increase in the proportion of water tupelo in swamp forests (Conner and Day 1976).

Batzer and Morris (1978) summarized the life cycle of FTC. FTC are univoltine insects (one generation per year). Female FTC moths lay cylindrical egg masses of 100 to 350 eggs that encircle small twigs, mostly on branches in the upper portion of the crown. FTC larvae overwinter in the eggs, and then hatch in the spring in response to swelling of twigs during leaf-out. The larvae go through five instar stages in 5-6 weeks, during which they feed on buds and foliage. Most leaf damage is done during their fourth and fifth instar stages. Mature larvae spin cocoons in folded leaves or crevices and pupate for about 10 days. Adult moths then emerge, mate, lay eggs and die within about one week.

Viral diseases and starvation are the primary agents of FTC mortality in most coastal forest in Louisiana. The main parasite of FTC in Louisiana is the parasitic fly *Sarcophaga houghi*, whose maggots feed on FTC pupae (Batzer and Morris 1978, Smith and Goyer 1986). *Sarcophaga houghi* larvae begin pupation on leaves near their host, and continue pupation in the leaf litter after leaf fall (Smith and Goyer 1986). Therefore, most *S. houghi* drown in frequently flooded swamp forests and *S. houghi* is unable to respond to FTC populations in a density-dependant manner (Smith and Goyer 1986). Other insect predators and parasites of FTC may require dry soil conditions to complete their life cycle as well (R. Goyer, personal communication). Female FTC in Louisiana produce twice as many eggs compared to FTC populations in the northern United States and Canada (Parry et al. 2001). Low mortality from natural enemies coupled with high reproductive rates of FTC in flooded swamp forest in Louisiana produce starvation driven cycles of caterpillar outbreaks (Smith and Goyer 1986, Parry et al. 2001) which occur on average every five years (Rejmánek et al. 1987).

Many bird species are known to depredate tent caterpillars (Witter and Kulman 1972, as cited in Parry et al. 1997), but FTC are protected by setae, and many birds were observed to eat only the viscera of late-instar FTC (Parry et al. 1997 and citations therein). Parry et al. (1997) found that bird predation was more influential in depressing experimental populations of final-instar FTC larvae and pupae than parasitoid insects. However, Smith and Goyer (1986) found that bird predation accounted for only a small percentage of FTC pupal mortality in swamps in Louisiana.

Repeated defoliation of water tupelo in Alabama by FTC over 20 years has reduced radial growth by as much as 75% (Batzer and Morris 1978). Simulated, complete defoliation reduced height growth and biomass production of 2-year-old water tupelo seedlings; although salinity stress lowered biomass production more than defoliation (Souther-Effler 2004). Conner and Day (1992) found that mature water tupelo began diameter growth later in the spring and grew more slowly than did baldcypress, and they hypothesized that this was due to the energetic cost of re-leafing the crown following spring defoliation by FTC.

Baldcypress had been noted for its lack of serious insect pests for decades (Brown and Montz 1986), until the recent discovery of the baldcypress leafroller (*Archips goyerana*, hereafter referred to as BCLR). BCLR are an emerging pest species of baldcypress in southern Louisiana (Kruse 2000). The first outbreak of BCLR was recorded in 1983 in Iberville Parish, Louisiana (Goyer and Lenhard 1988) and by 1993 it had spread eastward to swamp forest in the Pontchartrain Basin (Goyer and Chambers 1997) and had infested 70% of the growing stock of baldcypress in Louisiana (Meeker and Goyer 1993). BCLR have been classified as a sibling species of the fruittree leafroller (*A. argyrospila*), a widespread polyphagous insect pest of orchard trees with many sibling species differentiated by food plant preference (Kruse 2000).

BCLR feed exclusively on baldcypress foliage (Meeker and Goyer 1994) and outbreaks of BCLR have occurred annually since their discovery (Goyer and Chambers 1997). There is a direct, linear relationship between percent defoliation and annual diameter growth of baldcypress (Chambers et al. 2005). BCLR have defoliated the baldcypress component of as much as 200,000 ha of swamp forest in a single year (Chambers et al. 2005), and high populations of BCLR are expected to persist in the forested wetlands of southern Louisiana, causing decreased diameter growth of mature trees, and increased dieback and mortality of small and stressed baldcypress trees (Goyer and Chambers 1997, Ward and Mistretta 2002).

Like FTC, BCLR are univoltine insects. Female BCLR moths lay flat, irregularly shaped masses of about 50 eggs on twigs <0.7 cm diameter in April-May (Goyer and Lenhard 1988). Larvae over-winter in the eggs and hatch in response to bud break in late February or early March (Goyer and Chambers 1997). Newly hatched BCLR larvae are minute (<2mm), and burrow into opening leaf buds, making infestations difficult to detect (Goyer and Chambers 1997). As baldcypress leaves expand, developing BCLR larvae produce silk and roll needles to surround themselves, and larger larvae tie adjacent branchlets together (Kruse 2000, personal observation). The larvae go through 5 instar stages and most of their leaf consumption is done during the fourth and fifth instar stages (R. Goyer, personal communication). BCLR larvae feed on leaves for 8-10 weeks and grow to about 2cm in length (Goyer and Chambers 1997). Caterpillars then pupate for 8 to 12 days inside leaves rolled and tied with silk (Braun et al. 1990). Adult moths mate, lay eggs, and die within about two weeks after emergence (Goyer and Chambers 1997).

Braun et al. (1990) listed 12 species of parasitic or predaceous insects and two bird species that depredate BCLR. Braun et al. (1990) found that a parasitoid wasp, *Itopectis*

*conquisitor*, was the most common insect predator of BCLR on his sites. Meeker and Goyer (1993) identified two viral diseases that kill BCLR. Braun et al. (1990) and Wei (1996 as cited in Goyer and Chambers 1997) found no egg parasitoids of BCLR, and predators, parasites and viruses appear to have only a damping effect on BCLR populations (Goyer and Chambers 1997), resulting in persistently high BCLR populations (Goyer and Chambers 1997). Goyer and Chambers (1997) found that defoliation ratings of trees in seasonally flooded and permanently flooded plots were greater than those of trees on drier plots. This might be due in part to the negative effects of flooding on the predator and parasite community as observed in FTC parasite populations.

Individual trees vary in their susceptibility to defoliation of baldcypress by BCLR (Meeker and Goyer 1993). Baldcypress foliage exhibits two morphologies: branchlets may be flat with leaves extending at right angles to main axis; or leaves may be appressed as in pond cypress (*T. ascendens*). Both leaf morphologies may be expressed on an individual tree, but appressed foliage is more common in the upper portion of crowns, and constitutes a greater proportion of the crowns of taller trees (Meeker and Goyer 1993). Meeker and Goyer (1993) found that defoliation on trees expressing the open leaf morphology was significantly greater than trees expressing the appressed morphology. BCLR oviposition frequency did not differ between trees of the two leaf morphologies (Meeker and Goyer 1993). Therefore, appressed leaves are either less suitable food and/or shelter (Meeker and Goyer 1993). BCLR larvae sheltered by appressed foliage are highly conspicuous (personal observation) and might be more vulnerable to predators. Goyer and Chambers (1997) found that BCLR concentrate on small understory trees (perhaps as a result of dispersal from overstory trees), defoliation is more severe on understory trees, and die-back on flooded understory trees was greater than that of seasonally

flooded trees. Because BCLR concentrate on small trees and more than 90% of the foliage of small trees is of the open morphology (Meeker and Goyer 1993), regeneration of baldcypress, especially in permanently flooded areas, may be inhibited by BCLR defoliation, and the area in which regenerating baldcypress is affected by the interaction of permanent flooding and BCLR herbivory will increase with RSLR.

### **The Maurepas Swamp**

The Pontchartrain Basin in southeastern Louisiana (Figure 1-1) historically contained more than 188,400 ha of nearly contiguous swamp forest as evidenced by the ubiquity of logging ditches across the landscape (personal observations). As of 1990, 86,282 ha of swamp forest remained in the Pontchartrain Basin (Coast 2050). Within the Pontchartrain Basin, the Maurepas Swamp (Figure 1-1) contained 57,000 ha of the remaining swamp forest in 1990 (Lane et al. 2003, as cited in Souther-Effler 2004), and it is one of the largest contiguous tracts of wetland forest remaining in the LMAV.

The Maurepas Swamp was almost completely deforested by logging operations between 1900 and 1925 (Mancil 1980, A. Dranguet personal communication). Some of the cypress-tupelo forest in the Maurepas Swamp regenerated following logging operations (G. Shaffer personal communication). However, like most coastal forests in Louisiana, regeneration and productivity of baldcypress and water tupelo in the Maurepas Swamp is inhibited by increased flooding depth and duration, salt water intrusion, nutria damage to small trees, and defoliation by caterpillars (Shaffer et al. 2003). Historically, Bayou Manchac, the only east-flowing distributary of the Mississippi River, flowed into the Maurepas Swamp. However, in 1815 Bayou Manchac was partially filled to prevent British troops from attacking New Orleans from the north during the War of 1812 (Haydel 1998), and a permanent dam was built in 1828

(McPhee 1987). Therefore, except for major floods of the Mississippi River (which occurred periodically until the 1930s when levees along the Mississippi River were heightened in response to the devastating flood of 1927 [Barry 1997]), the Maurepas Swamp has been isolated from riverine inputs of freshwater, nutrients and sediment for almost 200 years.

Höppner (2002) and Shaffer et al. (2003) described the vegetative characteristics of the Maurepas Swamp. The healthiest regenerated cypress-tupelo stands in the Maurepas Swamp have a closed canopy of dominant baldcypress and water tupelo, little herbaceous vegetation, and a sparse mid-story canopy (Höppner 2002, Shaffer et al. 2003), although historic photographs of logging operations in the Maurepas Swamp show a dense understory layer of saplings (personal observation). Swamp that has been degraded by various stressors has an open canopy with widely spaced dominant baldcypress, and intermediate and co-dominant baldcypress, water tupelo and swamp tupelo (*Nyssa sylvatica* var. *biflora*). The mid-story of degraded swamp is dominated by swamp red maple, pumpkin ash (*Fraxinus tomentosa*) and green ash (*Fraxinus pennsylvanica*). The herbaceous layer is dense, continuous, and dominated by *Peltandra virginica*. Most water tupelo in degraded swamp exhibit crown dieback to some degree, and their tops are frequently broken 3-10m above the ground (personal observations). Soil bulk density in the degraded areas of the Maurepas Swamp is similar to that of open marsh (Shaffer et al. 2003), and the integrity of the soil in the Maurepas Swamp is maintained by the living root systems of the plant community (G. Shaffer, personal communication).

Much of the degraded forest in the Maurepas Swamp is beginning to transition to open marsh (Shaffer et al. 2003). Shaffer et al. (2003) reported that overall tree mortality in degraded swamp is approximately 2% per year. Approximately two-thirds of the swamp is currently in a highly degraded state and 16% of the swamp has already converted to open marsh or open water

(J. Zoller personal communication, Chambers et al. 2005). As swamp forest health and canopy cover decline, the ecological services of coastal forests, upon which human and wildlife populations depend, will be lost.

Bird species richness is generally highly correlated with foliage height diversity (MacArthur and MacArthur 1961). Zoller (2004) confirmed this correlation in the Maurepas Swamp; species richness and abundance of forest birds in the Maurepas Swamp was highly correlated with foliage structural complexity. Species richness and abundance of forest birds in the Maurepas Swamp was lower, although not significantly so, between healthy and degraded swamp during the breeding season; and species richness, forest bird, and total bird abundances were significantly lower in marsh habitat during the breeding season.

Populations of many insectivorous bird species have declined in recent decades (Sauer et al. 2005), and declines in forest-bird populations may have implications for forest productivity and stability due to reduced bird predation on defoliating insects (Marquis and Whelan 1994, Murakami and Nakano 2000). Zoller (2004) found that forest bird species richness and abundance were not significantly different between healthy and degraded swamp, however tree mortality is high in most of the Maurepas Swamp, and it is estimated that 42,460 ha of swamp will be lost in the Pontchartrain Basin by 2050 (Coast 2050). Therefore, as trees die due to stress, and formerly forested sites transition to open marsh, populations of forest birds in the Maurepas swamp will decline over an increasing area. The loss of bird species richness may result in decreased functionality of the insectivorous bird guild and increase caterpillar herbivory on remaining trees, decreasing the stability of the swamp ecosystem even further, and accelerating the rate at which degraded swamp transitions into open marsh.

No water tupelo regeneration has been observed during 15 years of research in the Maurepas Swamp (G. Shaffer, personal communication). Baldcypress regeneration in degraded swamp is widely scattered, and appears to occur mainly on coarse woody debris (CWD) left from logging operations or on fallen trees (personal observations). CWD may provide micro-relief for the germination and establishment of baldcypress seedlings in the permanently flooded conditions in the swamp (Chambers et al. 2005), but logs are poor sites for regenerating water tupelo seedlings, either due to predation of water tupelo seeds while on these exposed features, or because logs may move during seedling establishment (Huenneke and Sharitz 1990). As CWD decomposes and RSLR increases, the probability of natural regeneration of baldcypress and water tupelo regeneration decreases. In areas where natural regeneration of baldcypress and water tupelo is doubtful, planting of seedlings may be necessary to ensure that stands are adequately stocked (Chambers et al. 2005).

### **Restoration Efforts in the Maurepas Swamp**

Diversions of freshwater from the Mississippi River into degraded swamps and marshes have been suggested as a method for ameliorating freshwater, nutrient and mineral sediment deficits caused by levee construction (Day et al. 2000, Höppner 2002, Shaffer 2003). A diversion of water from the Mississippi River into the Maurepas Swamp via Hope Canal has been planned, and is in the final stages of design (LCA 2004, G. Shaffer personal communication). Positive effects of freshwater flushing, and input of nutrients and sediment should offset negative effects of increased flooding of swamp forest caused by the diversion (G. Shaffer, personal communication). However, increased flooding will retard natural regeneration of baldcypress and water tupelo (Souther 2000). Therefore, the diversion will need to be closed

periodically to allow forest regeneration after abiotic conditions have been improved (Souther 2000, G. Shaffer personal communication).

Baldcypress and water tupelo have exacting germination and seedling establishment requirements (Demaree 1932, Souther 2000, Huenneke and Sharitz 1990). Therefore, planting baldcypress and water tupelo seedlings may accelerate forest restoration, especially at the beginning of operation of the Maurepas Swamp diversion. When adequately protected from nutria and other herbivorous mammals, artificial baldcypress regeneration success in the southeastern United States has generally been high, and planted seedlings have occasionally grown better than naturally regenerated trees (for a review see Chambers et al. 2005). However, baldcypress planting success in the Maurepas Swamp has been variable.

The east side of Lake Maurepas transitioned into open marsh in the 1950s (G. Shaffer personal communication) and is generally more saline than more forested areas on the west side of the lake (Shaffer et al. 2003) and also receives higher pulses of salinity due to its proximity to Lake Pontchartrain (G. Shaffer personal communication). Baldcypress seedlings planted on the east side of Lake Maurepas between 1991-1996 had 78% survival in 1998 when protected from nutria, but nearly 100% mortality when unprotected (Myers et al. 1995, as cited in Chambers et al. 2005). Most surviving seedlings subsequently died during a drought in 1999-2000, due to increased interstitial salinity (Shaffer et al. 2003). Thousands of baldcypress seedlings have been planted in marsh on the east side of Lake Maurepas each year since 1999, but mortality due to salinity stress and nutria herbivory is high (Chambers et al. 2005, M. Greene personal communication). Greene (1994) found that diameter growth of baldcypress seedlings planted in marsh on the east side of Lake Maurepas is reduced by 25% when climbing vines are allowed to entangle seedlings.

Survival of planted baldcypress on the west side of Lake Maurepas is better. A property owner, Glen Martin, has established a wetland mitigation bank of baldcypress plantings near Blind River. Martin plants thousands of baldcypress saplings, grown from locally collected seed sources each spring, and survival is 80-90% (Chambers et al. 2005, J. Robinson personal communication). Beville (2002) planted baldcypress seedlings on both the east and west sides of Lake Maurepas, and both groups experienced high mortality. Seedling protectors were only nominally effective on the east side where 85% were destroyed by nutria and nearly all other seedlings were killed by salinity. Seedling survival was better on the west side, but still only 26%.

Only one effort has been made to plant water tupelo in the Maurepas Swamp. “A couple of thousand” water tupelo seedlings were planted on the east side of Lake Maurepas in marsh on Jones Island in the 1999-2000 planting season (M. Greene and G. Shaffer personal communication). “A few” lived for at least two years, but none are known to survive today (M. Greene personal communication). It should be noted that 1999-2000 were drought years (Shaffer et al. 2003), and salinity levels on the Manchac land bridge were as much as 9 ppt (G. Shaffer personal communication). No water tupelo seedlings have been planted on the west side of the lake.

## **Objectives**

Part I: Manipulation of densities of breeding cavity nesting birds through the addition of nest boxes.

The objectives of this study were:

- 1) Determine if nest box addition to degraded areas of the Maurepas Swamp increase abundance of breeding cavity-nesting birds.

- 2) Determine if breeding bird density is correlated with shoot growth of naturally regenerated baldcypress saplings.

Part II: Effects of birds on growth of planted baldcypress and water tupelo.

The objectives of this study were:

- 1) Determine if planted baldcypress and water tupelo seedlings survive and grow in degraded areas of the Maurepas Swamp.

This is the first field study in the Maurepas Swamp that includes planted water tupelo seedlings, from which I hope to determine survival and growth rates in this habitat. Growth rates of baldcypress seedlings planted on the west side of the lake have not been determined for a large sample of trees (Beville 2002). Water tupelo seedlings do not survive in marsh on the east side of Lake Maurepas (M. Greene personal communication), but baldcypress seedlings survive and grow on the west side of Lake Maurepas, sometimes with high survival rates. Therefore, I expect to find that water tupelo planted on the west side of the lake have lower survival and growth rates than baldcypress, but that mortality will be lower than that observed on the east side of Lake Maurepas.

- 2) Determine if birds reduce insect-herbivore damage to planted baldcypress and water tupelo, and whether defoliation affects height and diameter growth of these trees.

Evidence for trophic cascades operating on understory trees is limited. However BCLR are known to congregate on understory saplings (Goyer and Chambers 1997), and birds may show functional responses to increased caterpillar populations (Strong et al. 2000). PROW usually

forage below 7m (Petit et al. 1990, Petit 1996), and in some areas of their range PROW forage below 3m (D. Drumtra personal communication, personal observations). Therefore I expect that birds will exhibit a functional response to these BCLR on small baldcypress and reduce leaf damage caused by BCLR.

The Maurepas Swamp offers the opportunity to test a system in which birds are probably the most important agents of caterpillar mortality as compared to terrestrial systems with diverse insect predators (Goyer et al. 1990, Goyer and Chambers 1997). Birds are a major source of caterpillar mortality in swamp forest (Braun et al. 1990) and parasites and parasitoids are less effective in reducing caterpillar populations in swamp forest than on drier sites, but it is uncertain whether bird predation of caterpillars will be beneficial to small, planted trees. I expect to find that trees accessible to birds experience less leaf damage than caged trees, and that decreased leaf damage will result in increased height and diameter growth.

I am not aware of any studies that have investigated the effects of insectivorous birds on defoliation of baldcypress and water tupelo, or in any type of flooded forest ecosystem. This is the only study of which I am aware in which abundance of insectivorous birds will be quantified for the purpose of correlating insectivorous bird abundance with defoliation and tree growth measurements. Furthermore, I am unaware of any study that examines the effect of insectivorous birds on tree growth within the context of habitat restoration.

### 3) Describe foraging of common insectivorous birds on BCLR and FTC.

I am not aware of any studies that have investigated the effects of birds on BCLR, nor am I aware of any studies of the effects of birds on FTC in cypress-tupelo forests. I expect to find that birds will eat both FTC and BCLR. FTC are protected by setae, therefore I expect to find

that birds prey upon FTC less frequently than BCLR, require longer handling times to consume FTC, and that birds consuming FTC exhibit feeding behaviors to avoid the setae.

## CHAPTER 2. EFFECTS OF NEST BOX ADDITION ON PROTHONOTARY WARBLER (*PROTONOTARIA CITREA*) POPULATIONS AND BALDCYPRESS (*TAXODIUM DISTICHUM*) SHOOT GROWTH

### Introduction

Outbreaks or introductions of defoliating insects can destabilize forest ecosystems (Ellison et al. 2005, Scheffer et al. 2001). Effects of insect outbreaks on ecosystem stability might be especially severe in ecosystems in which resilience has been reduced by gradual anthropogenic changes in abiotic conditions. Gradual anthropogenic changes in abiotic conditions may decrease the resiliency of ecosystems, making them more prone to undergo catastrophic shifts to alternate stable states following perturbations (for reviews see Scheffer et al. 2001, Folke et al. 2004). Forest ecosystems with few foundation tree species, such as cypress-tupelo swamps, are inherently less resilient to perturbations due to their lack of functional redundancy (Ellison et al. 2005).

### Coastal Forest Loss

The entire coastal wetland ecosystem in Louisiana is on the brink of ecological collapse (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1998, hereafter cited as Coast 2050 1998). Between 1930 and 1990, Louisiana lost nearly 486,000 hectares of coastal wetlands (Barras et al. 2003), and it is estimated that an additional 255,000 hectares of coastal wetlands will be lost by 2050 (Coast 2050 1998). This massive, rapid loss of wetlands threatens Louisiana's entire coastal wetland ecosystem and by extension the industries, human population centers and societal infrastructure dependent on coastal wetland health (Coast 2050 1998).

The causes of wetland loss in Louisiana are complex and involve both natural and anthropogenic changes to the hydrology of the region and their interactions (Day et al. 2000, Day et al. 2001, Gosselink 2001, Chambers et al. 2005, for extensive reviews of the causes of wetland

loss in coastal Louisiana see Boesch et al. 1994, Coast 2050 1998, Louisiana Coastal Area Comprehensive Ecosystem Restoration Study 2004, hereafter cited as LCA 2004). Relative sea-level rise (RSLR) (Day and Templet 1989, Boesch et al. 1994 Coast 2050 1998), and the interruption of natural deltaic building processes by the construction of flood control levees, and canals for logging, shipping and oil extraction operations (Day and Templet 1989, Boesch et al. 1994, Coast 2050 1998, Day et al. 2000, LCA 2004) are the main causes of coastal wetland loss in Louisiana. RSLR and levee and canal construction have resulted in increased flooding depth and duration and saltwater intrusion in formerly freshwater marsh and swamp forest ecosystems.

Although most wetland loss in Louisiana has occurred in coastal marshes, coastal forest health and regeneration have been negatively affected by changes in abiotic conditions. Natural regeneration of many stands of cypress-tupelo forest has been inhibited by increased flooding (Conner et al. 1986, Conner and Toliver 1990, Chambers 2005) because neither baldcypress (*Taxodium distichum*) (Demaree 1932) nor water tupelo (*Nyssa aquatica*) (Huenneke and Sharitz 1990) seeds germinate in water, and submerged baldcypress seedlings die within 3-6 weeks (Demaree 1932, Souther 2000). Increased flooding, salinity, and interactions of these stressors also reduce baldcypress and water tupelo productivity (for reviews see the literature review in this volume, Chambers et al. 2005).

The Pontchartrain Basin in southeastern Louisiana historically contained more than 188,400 ha of nearly contiguous swamp forest as evidenced by the ubiquity of logging ditches across the landscape (personal observations). As of 1990, 86,282 ha of swamp forest remained in the Pontchartrain Basin (Coast 2050), most of it within the Maurepas Swamp. The Maurepas Swamp was almost completely deforested by logging operations from 1900-1925 (Mancil 1980, A. Dranguet personal communication), but some of the cypress-tupelo forest in the Maurepas

Swamp has regenerated following logging operations. The Maurepas Swamp contained 57,000 ha of the swamp forest remaining in the Pontchartrain Basin in 1990 (Lane et al. 2003, as cited in Souther-Effler 2004), and it is one of the largest contiguous tracts of wetland forest remaining in the Lower Mississippi Alluvial Valley (LMAV). However, the health of most coastal forest in Louisiana, including the Maurepas Swamp, has been negatively affected by anthropogenic changes in abiotic conditions.

Approximately two-thirds of the Maurepas Swamp is currently in a highly degraded state and 16% of the swamp has already converted to open marsh or open water (J. Zoller personal communication, Chambers et al. 2005). Overall tree mortality in degraded areas of the Maurepas Swamp is approximately 2% per year (Shaffer et al. 2003), and it is estimated that 42,460 ha of swamp will be lost in the Pontchartrain Basin by 2050 (Coast 2050 1998). Baldcypress regeneration in degraded swamp is widely scattered, and appears to occur mainly on coarse woody debris (CWD) left from logging operations or on fallen trees (personal observations). No tupelo regeneration has been observed during 15 years of research in the Maurepas Swamp (G. Shaffer, personal communication). CWD may provide micro-relief for the germination and establishment of baldcypress seedlings in the permanently flooded conditions in the swamp (Chambers et al. 2005), but logs are poor sites for regenerating water tupelo seedlings (Huenneke and Sharitz 1990).

Soil bulk density in degraded areas of the Maurepas Swamp is similar to that of open marsh (Shaffer et al. 2003), and the integrity of the soil in the Maurepas Swamp is maintained by the living root systems of the plant community (G. Shaffer, personal communication). Much of the interior of the Maurepas Swamp is permanently flooded, and large areas of the understory are covered by mats of floatant marsh (G. Shaffer personal communication). As forest cover is lost in

the Maurepas Swamp, it is feared that the area will not transition to open marsh, but will instead transition directly to open water, with accelerated transition rates due to wave erosion from interior ponds (G. Shaffer personal communication).

#### Caterpillar Herbivory in Coastal Forests

In addition to flooding, salinity, and interactions of these stressors, baldcypress and water tupelo in coastal forests of Louisiana have been subject to repeated annual caterpillar herbivory in the spring in recent decades. Forest tent caterpillars (*Malacosoma disstria*, hereafter referred to as FTC) are the main insect herbivore of water tupelo in coastal forests of Louisiana. Large outbreaks of FTC have been recorded in Louisiana since 1931 (Conner and Day 1976), and regular outbreaks have occurred since 1948 (Nachod and Kucera 1971 as cited in Chambers et al. 2005). FTC defoliate 120,000-240,000 ha of swamp forest in Louisiana each spring (Goyer et al. 1990). The increased severity of outbreaks in Louisiana may be due to cypress logging and the subsequent increase in the proportion of water tupelo in swamp forests (Conner and Day 1976).

Baldcypress had been noted for its lack of serious insect pests for decades (Brown and Montz 1986), until the recent discovery of an emerging pest species, the baldcypress leafroller (*Archips goyerana*, hereafter referred to as BCLR), in 1983 in Iberville Parish, Louisiana (Goyer and Lenhard 1988). By 1993 BCLR had infested 70% of the growing stock of baldcypress in Louisiana (Meeker and Goyer 1993). BCLR have defoliated the baldcypress component of as much as 200,000 ha of swamp forest in a single year (Chambers et al. 2005).

Caterpillar outbreaks in frequently flooded forests may be persistently severe because some common insect enemies of caterpillars on drier sites are absent (Braun 1990, Wei 1996 as cited in Goyer and Chambers 1997). This may be because some insect enemies of caterpillars require unsaturated soil for pupation, and pupae drown in frequently flooded sites (Smith and

Goyer 1986, R. Goyer personal communication). Female FTC in Louisiana produce twice as many eggs compared to FTC populations in the northern United States and Canada (Parry et al. 2001). Low mortality from natural enemies coupled with high reproductive rates of FTC in flooded swamp forest in Louisiana produce cycles of caterpillar outbreaks that are starvation driven (Smith and Goyer 1986, Parry et al. 2001), and models indicate that FTC outbreaks are expected to occur about every five years (Rejmaneck et al. 1987).

Insect defoliation reduces the rate at which many trees species accumulate woody biomass, and the effect is generally proportional to the severity of defoliation (Muzika and Liebhold 1999, Goyer and Chambers 1997, Souther-Effler 2004, Tucker et al. 2004, Chambers et al. 2005, for a review see Smith and Mittler 1971). The main effect of caterpillar defoliation on baldcypress (Goyer et al. 1990, Goyer and Chambers 1997, Souther-Effler 2004) and water tupelo (Abrahamson and Harper 1973, Souther-Effler 2004) is a reduction in woody biomass production, and the interaction of flooding and caterpillar herbivory further reduces growth of baldcypress (Goyer and Chambers 1997, Souther-Effler 2004). There is a direct, linear relationship between defoliation severity and annual diameter growth of baldcypress (Chambers et al. 2005), and repeated defoliation of water tupelo in Alabama by FTC over 20 years has reduced radial growth by as much as 75% (Batzer and Morris 1978). Both FTC and BCLR are univoltine (one generation per year) and usually stop feeding in May (personal observations). Defoliated baldcypress and water tupelo usually produce a second “flush” of leaves soon after defoliation events (G. Shaffer, personal communication; Ward and Mistretta 2002). Conner and Day (1992) hypothesized that the energetic cost of refoliating the crown following spring defoliation by FTC caused reduced radial growth of water tupelo. High populations of BCLR are expected to persist in the forested wetlands of southern Louisiana, causing decreased

diameter growth of mature trees, and increased dieback and mortality of small and stressed baldcypress trees (Goyer and Chambers 1997, Ward and Mistretta 2002).

### Effects of Birds on Caterpillars

The lack of density-dependent responses of insect enemies to caterpillar outbreaks might increase the relative importance of birds as agents of caterpillar mortality in coastal forests in Louisiana. Birds are conspicuous predators of defoliating insects and they have the potential to consume large numbers of forest insects due to their mobility and high metabolic rates (Kirk et al. 1996). Most breeding passerine birds in temperate forests feed primarily on insects (Holmes and Schultz 1988), and caterpillars are the most important insect taxon in the diets of breeding passerine birds in temperate forests (Holmes and Schultz 1988). Many species of caterpillars are folivorous, relatively large, conspicuous on leaf surfaces and are energetically profitable food items for insectivorous birds (Holmes and Schultz 1988).

Birds may exhibit numerical and or functional responses to outbreaks of caterpillars (Morris et al. 1958, Buckner and Turnock 1965, Holmes and Schultz 1988, Crawford and Jennings 1989, MacCulloch 2001), and they have the potential to destroy enormous numbers of caterpillars. In a study of bird predation of spruce budworm (*Choristoneura fumiferana*) in New Hampshire and Maine, Crawford and Jennings (1989) estimated that more than 85,000 spruce budworms/ha were consumed by just five bird species within the bird community during low and transitional spruce budworm infestations. Turček (1957 as cited in Bruns 1960) found that Great Tits (*Parus major*) consumed 10-15% of their body weight in a tortricid moth caterpillar in 90 minutes, and estimated that they consume 300 of these caterpillars per day.

Birds have been shown to have significant impacts on low and moderate populations of forest insects (Dahlsten and Copper 1979, Holmes et al. 1979, Loyn et al. 1983, Crawford and

Jennings 1989, Torgerson et al. 1990, Gunnarsson 1996, Parry et al. 1997, Sanz 2001, see Bruns 1960, Otvos 1979 and Holmes 1990 for reviews). However, as insect populations increase to epidemic levels, the proportion of insects eaten by birds decreases and their effectiveness in controlling insect populations declines dramatically (Betts 1955, Bruns 1960, Morris et al. 1958, Holmes 1990). Although birds may not have significant impacts on epidemic populations of caterpillars, Holmes (1990) suggested that bird predation on defoliating insects may increase the time it takes for caterpillars to reach epidemic populations, increase the rate at which populations decline following outbreaks, and decrease the frequency of outbreaks.

Indirect, positive effects of predators that are passed to producers are called trophic cascades. In many, (Atlegrim 1989, Bock et al. 1992, Marquis and Whelan 1994, Sipura 1999, Strong et al. 2000, Greenburg et al. 2000, Murakami and Nakano 2000, MacCulloch 2001, Sanz 2001, Van Bael et al. 2003, Van Bael and Brawn 2005) but not all (Forkner and Hunter 2000, Lichtenberg and Lichtenberg 2002) trophic cascade studies in bird-herbivorous insect-plant systems, birds decreased foliage damage on plants by reducing local abundance of insect-herbivores. These indirect effects of predators may be especially important if the receiver plant species is a foundation species within an ecosystem (Polis et al. 2000, Scheffer et al. 2001, Terborgh et al. 2001). Populations of many North American insectivorous bird species have declined in recent decades (Sauer et al. 2005), and these declines may have implications for forest productivity and stability due to reduced bird predation on defoliating insects (Marquis and Whelan 1994, Murakami and Nakano 2000).

Zoller (2004) found that insectivorous bird species richness and abundance declined dramatically between forested and marsh habitats in coastal Louisiana. Zoller (2004) found that these declines are due primarily to decreased structural complexity of habitat with loss of tree

cover. As trees continue to die due to stress, populations of insectivorous forest birds will decline over an increasing area in coastal forests. Decreased bird abundance and bird species richness may result in decreased functionality of the insectivorous bird guild and increase caterpillar herbivory in stressed swamp forest. Increased caterpillar herbivory will most likely result in decreased tree growth, decreased stability of the swamp ecosystem, and accelerate the rate at which degraded swamp transitions into open marsh.

### Secondary Cavity Nesting Birds

Of the passerine bird species that breed in eastern North America, 17% nest in holes of some kind (von Haartman 1957), and breeding populations of cavity nesting birds may be limited by suitable nesting sites (von Haartman 1957). Among cavity nesting birds which breed in forests, primary cavity nesting birds (PCNB), such as woodpeckers, are able to excavate nesting cavities in trees, while secondary cavity nesting birds (SCNB) do not excavate nesting cavities and they must rely on cavities excavated by PCNB or tree cavities produced by rot. Because SCNB must rely on existing cavities, populations of SCNB are frequently nest-site limited (Newton 1994).

A large proportion of the insectivorous bird community in the Maurepas Swamp is composed of SCNB (Zoller 2004, personal observations). The lack of tupelo regeneration in the Maurepas Swamp is of concern for SCNB because naturally created cavities are more abundant in hardwood tree species than in conifers (baldcypress), due to differing physiological responses to limb death and rot. When hardwood limbs die a protective layer of gum-filled cells protects sapwood at the base of the limb, but leaves the heartwood vulnerable to rot (Waters et al. 1990, Newton 1994). In conifers, resin protects both the sapwood and heartwood from fungal infection and rot (Peace 1962 as cited in Waters et al. 1990 and Newton 1994). As tupelo die without

replacement, naturally occurring cavities will become rarer, leading to increased cavity limitation of breeding populations of SCNB in the swamp.

Newton (1994) reviewed studies in which cavity availability was experimentally altered and found that breeding densities of 24 of 26 SCNB species were limited by cavity availability. However, Waters et al. (1990) found that blocking cavities had no effect on the overall number of breeding territories or nests of SCNB relative to control plots in oak-pine woodlands in California, and concluded that populations of SCNB are not always cavity limited. Nevertheless, studies have demonstrated that breeding densities of SCNB may be increased by increasing cavity abundance via nestbox addition to forest stands (Bruns 1960 and references therein, Dahlsten and Copper 1979, Minot and Perrins 1986, East and Perrins 1988, Brawn and Balda 1988, Caine and Marion 1991, Newton 1994 and references therein, Sanz 2001, Twedt and Henne-Kerr 2001).

Brawn and Balda (1988) conducted a nestbox addition study of cavity limitation of SCNB populations by provisioning ponderosa pine (*Pinus ponderosa*) stands in Arizona with nest boxes. Nest boxes were added to a dense, un-thinned stand with many tree cavities, a heavily thinned (open) stand with few tree cavities, and a moderately thinned stand with an intermediate number of tree cavities. After boxes had been in place for four years, SCNB density on the treated dense plot was not significantly different from the control. SCNB densities were significantly higher relative to controls in the treated thinned and open stands and increased consistently with time. In the fourth year of the study SCNB densities on the treated thinned and open stands had 2.3 and 7.6 times more SCNB pairs/ha compared to control plots, respectively, and densities had not reached an asymptote. Over 90% of the SCNB nests located on the treated thinned and open stands were in boxes. However, only three of six species in the

SCNB community responded to nest boxes, most likely because the species which did not exhibit significant responses were relatively uncommon. Densities of Violet-green Swallows (*Tachycineta thalassina*) were significantly higher on treatment stands, and this may be due to the fact that they do not defend feeding territories around their nest cavities (Brawn and Balda 1988). Cavity availability may limit SCNB populations when a bird species is common and surplus or floater individuals (Brawn and Balda 1988) or subdominant individuals (Newton 1994) that would not breed in a cavity limited situation are available to take advantage of surplus nest sites.

Bruns (1960) reviewed results of “economic bird protection” forestry practices in Europe, including studies in which forest stands were provisioned with nest boxes. In stands provisioned with a surfeit of nest boxes breeding bird densities of 25 or more pairs/ha were observed and bird populations were increased 5-20 times that of stands without nest boxes (Bruns 1960 and references therein). Although Bruns (1960) implied that these density responses were solely for SCNB, it was not stated explicitly. Bruns (1960) did not list the species of SCNB that used nest boxes in studies with the most dramatic increases of breeding SCNB, nor did he report the proportion of the increased SCNB population which was due to species which do not establish feeding territories around nest sites (e.g. *Ficedula* spp.).

Although the majority of the studies described above suggest that SCNB are limited by cavity availability, long term nest box studies reveal that SCNB densities reach an asymptote regardless of nest box density. Minot and Perrins (1986) studied the effects of nest box density on Blue Tit (*Parus caeruleus*) and Great Tit density and found that they increased linearly with nest box density, but even at very high Tit density some nest boxes remained vacant. Nest boxes are frequently used by SCNB even in situations where cavities are not limited (Bruns 1960 and

references therein, Brawn and Balda 1988). For example, in the fourth year of the nestbox addition study by Brawn and Balda (1988), 30% of SCNB nests in the treatment stand with high cavity density were in nest boxes, yet SCNB densities on the treatment plot were not significantly different from the control. Therefore, nestbox use may be compensatory rather than additive (Waters et al. 1990).

Species-specific responses should be considered when interpreting results of nestbox addition studies. Differences in species responses to increased cavity availability may reflect their natural history. Species that do not defend feeding territories around the nest cavity (e.g. Collared Flycatchers, *Ficedula albicollis*, Violet-green Swallows) may reach higher densities than species which defend a feeding territory around the nest cavity. There is evidence that nestbox addition may increase breeding densities of some territorial SCNB species such as Mountain Chickadees (*Poecile gambeli*) (Dahlsten and Copper 1979), Great and Blue Tits (Minot and Perrins 1986, East and Perrins 1988), Western Bluebirds (*Sialia mexicana*) (Brawn and Balda 1988, Purcell et al. 1997), and Pygmy Nuthatches (*Sitta pygmaea*) (Brawn and Balda 1988, Purcell et al. 1997). It may be that cavity availability outside of defended territories limits SCNB populations and not cavity abundance *per se* (Newton 1994).

Cavity security is at least as important as cavity availability, for if nest cavities are vulnerable to predation or parasitism, they may become ecological traps for birds. In addition to increasing breeding densities of SCNB, nest boxes may reduce nest predation rates, thereby increasing nest success (East and Perrins 1988, Purcell et al. 1997, Mitrus 2003, Drumtra 2006). Purcell et al. (1997) compared nest success parameters of Western Bluebirds, Plain Titmice (*Parus inornatus*), House Wrens (*Troglodytes aedon*) and Ash-throated Flycatchers (*Myiarchus cinerascens*) nesting in nest boxes and tree cavities. Western Bluebirds, Plain Titmice and

House Wrens nesting in boxes had lower predation rates and fledged more young than birds nesting in tree cavities (Purcell et al. 1997). Ash-throated Flycatchers did not benefit from nesting in boxes (Purcell et al. 1997). East and Perrins (1988) reported that nest success of Great Tits nesting in boxes was nearly 50% greater than that of Great Tits nesting in tree cavities, and nest success of Blue Tits nesting in boxes was approximately one-third greater than that of Blue Tits nesting in tree cavities. Increased nest success of birds breeding in boxes may increase SCNB density if one includes nestlings and fledglings in SCNB breeding density estimates.

From the standpoint of natural control of caterpillar populations, the maximum density of SCNB should be defined as the maximum number of breeding adults plus the maximum number of nestlings a pair of birds is able to fledge during the time when caterpillars are available. Regardless of whether nestbox studies are conclusive in determining if SCNB populations are limited by cavity availability, nestbox addition and resulting increased SCNB abundance has been shown to decrease caterpillar abundance in some forests (Bruns 1960 and references therein, Dahlsten and Herman 1965 as cited in Kirk et al. 1996, Dahlsten and Copper 1979, Sanz 2001). In studies reviewed by Bruns (1960) caterpillar populations in stands provisioned with nest boxes were one-third to 100 times lower than in stands without nest boxes. Dahlsten and Herman (1965 as cited in Kirk et al. 1996) found that populations of the lodgepole pine needle miner (*Coleotechnites milleri*) were reduced by 30% in forest stands provisioned with nest boxes for Mountain Chickadees (*Poecile gambeli*). Dahlsten and Copper (1979) stocked white fir (*Abies concolor*) branches with Douglas fir tussock moth (*Orgyia pseudotsugata*) cocoons in areas with and without nest boxes. Areas with nest boxes had significantly more Mountain Chickadees relative to areas without nest boxes, and the proportion

of cocoons depredated by birds differed significantly by area, presumably due to increased bird predation within the area provisioned with nest boxes.

Addition of nest boxes to forest stands, and subsequent increased SCNB density may reduce caterpillar herbivory in forest stands (Bruns 1960 and references therein, Sanz 2001). Bruns (1960) reported qualitative results for several experiments in which forest stands provisioned with nest boxes “remained green”, or caterpillar populations “remained low” during regional outbreaks. Sanz (2001) compared SCNB density, caterpillar populations, caterpillar body mass and leaf damage between a plot provisioned with nest boxes and a control plot in Pyrenean oak (*Quercus pyrenaica*) forest in Spain. SCNB density was 5 pairs/ha in the area with nest boxes and 1.5 pairs/ha in the control area. Caterpillar density, frass production, caterpillar body size, the proportion of leaves damaged and the proportion of leaf area missing were consistently, and frequently significantly lower within the nestbox area presumably due to bird predation of caterpillars.

The Prothonotary Warbler (*Protonotaria citrea*, hereafter referred to as PROW) is a common, insectivorous SCNB in wetland forests of the Gulf Coast, the LMAV and the Atlantic Coastal Plain (Petit 1999). PROW are one of only two species of wood-warblers (Parulinae) in North America which are SCNB, the other being Lucy’s Warbler (*Vermivora luciae*), which breeds in arid areas of the southwestern U.S.

PROW are frequently the most commonly detected bird species during point counts (Sallabanks et al. 1993, Zoller 2004) in wetland forests within their breeding range. Mitchell and Lancia (1990 as cited in Sallabanks et al. 1993) detected an average of 2.7 PROW per 25m radius 10-minute point count in South Carolina. In high quality habitat defended territory sizes may be as small as 0.5 ha (Petit 1989), and territories frequently abut one another (Walkinshaw

1953, personal observations). Relative abundance of PROW is greatest in southern Louisiana and coastal areas of southeastern Virginia and northeastern North Carolina as measured by North American Breeding Bird Survey (BBS) data. The number of PROW detected along BBS routes in Louisiana declined by 3.3% between 1966 and 2004 (Sauer et al. 2005), but because BBS survey points are located along roadways, it is unlikely that populations of PROW in interior swamps in Louisiana have been adequately sampled.

PROW readily accept nest boxes (Petit and Fleming 1987, Petit 1989, Blem and Blem 1991, Petit and Petit 1996, Petit 1999, Zoller 2004). Petit (1999) cited Petit and Petit (1996) as evidence that breeding densities of PROW may be increased 5-6 times with the addition of nest boxes. However, Petit and Petit (1996) examined how equal numbers of nest boxes along a hydrological gradient affected PROW breeding density, and while they found that PROW nested at higher densities in boxes situated closer to water, they did not compare PROW density on the plot with nest boxes to a control plot without boxes.

Success (fledging at least one young from a clutch of eggs) of PROW nests in nest boxes may be higher than in natural nests. Apparent nest success of PROW nests in natural nests was 22% over a five year study in Arkansas (Drumtra 2006). Apparent nest success of PROW nests in nest boxes in forested habitat in the Maurepas Swamp was 74% in the second year of the study by Zoller (2004). Drumtra (2006) found that apparent nest success of PROW was 57% in nest boxes, that the rate of nest parasitism by Brown-headed Cowbird (*Molothrus ater*) was 16% in nest boxes versus 26% in natural cavities, and nests in natural cavities were more than twice as likely to be depredated than those in nest boxes in a bottomland hardwood forest in Arkansas. Apparent nest success of PROW nests in nest boxes in forested habitat in the Maurepas Swamp

was 74% (Zoller 2004). Apparent nest success of PROW nests in nest boxes in Tennessee ranged from 32-57% (Petit and Petit 1996).

Zoller (2004) conducted the only controlled study of the effects of nestbox addition on PROW breeding density. The timing of Zoller's (2004) study in the Maurepas Swamp overlapped with a nest box study I conducted in the same habitat type which is described later. Zoller (2004) installed nest boxes made from milk cartons at 50m spacing within three habitat types in the Maurepas Swamp. In the second year of this study, after nest boxes had been in place for one year, one of 75 boxes in marsh habitat, 60% of boxes in healthy swamp forest, and 92% of nest boxes in degraded swamp forest habitat showed some evidence of use by PROW. Zoller (2004) found that significantly more PROW were detected during point counts and line transects in plots with nest boxes than on control plots in degraded habitat. Zoller (2004) also found that territories of a subsample of PROW in degraded habitat on plots with nest boxes were centered on active nests within nest boxes, and those territories frequently abutted one another. These data suggest that PROW may be cavity limited in degraded swamp habitat.

Evidence of cavity limitation of breeding populations of PROW is supported by additional evidence. First, male PROW with territories that do not include suitable nesting cavities remain unpaired during the breeding season (personal observations). Second, PROW nest in a variety of excavated and natural cavities (Petit 1999), but PROW appear to prefer to nest in cavities excavated by DOWO in other wetland forests (Walkinshaw 1953, Wood and Cooper unpublished manuscript, personal observations). Densities of cavities excavated by DOWO in degraded areas of the Maurepas Swamp are lower than in other wetland forests (personal observation), perhaps due to lower densities of DOWO in degraded swamp relative to healthy swamp and other wetland forests. PROW frequently nest in natural cavities created by

tree rot in the Maurepas Swamp (Zoller personal communication, personal observation).

However, results of a study of PROW nesting in tree cavities in Arkansas showed that PROW nested in cavities excavated by woodpeckers far more frequently (91%) than in natural cavities produced by tree rot, and PROW nests in natural cavities were more likely to be parasitized by Brown-headed Cowbirds (*Molothrus ater*, hereafter referred to as BHCO) and contained more BHCO eggs than excavated nests (Wood and Cooper unpublished manuscript). The fact that the Maurepas Swamp has persistently high populations of palatable BCLR suggests that PROW densities are not limited by food.

Caterpillars are the most important insect taxon in the diets of breeding passerine birds in temperate forests (Holmes and Schultz 1988), and caterpillars are among the most frequently consumed prey items of common SCNB in swamp forests in Louisiana, including PROW (Petit et al. 1990, Petit and Petit 1996, Petit 1999), Carolina Chickadee (*Poecile carolinensis*, hereafter referred to as CACH) (Mostrom et al. 2002), and Eastern Tufted Titmice (*Baeolophus bicolor*, hereafter referred to as ETTI) (Grubb and Pravosudov 1994). Braun (1990) observed two SCNB, PROW and CACH, depredating BCLR in swamp forest in Louisiana.

## Objectives

This study overlapped the study of cavity limitation of PROW by Zoller (2004). At the time this study began, the nest boxes added to degraded swamp by Zoller (2004) had had only marginal success in attracting nesting PROW. Despite the abundance of dead and dead-topped trees in degraded swamp, cavities excavated by DOWO and other woodpecker species suitable for SCNB appeared to be limited. Observations of PROW nesting in open-topped cavities in 2001 (Zoller personal communication) corroborated this observation. Therefore, I attempted to

increase breeding PROW density with a different nest box design, and also added nest boxes suitable for other SCNB to increase overall SCNB density on my study plots.

In this study I hypothesized that: 1) addition of nest boxes to degraded swamp forest habitat would increase breeding densities of SCNB and the number of successful SCNB nests relative to control plots 2) increased densities of breeding SCNB would increase overall insectivorous bird abundance on plots with nest boxes and 3) increased bird abundance would result in increased growth of baldcypress saplings due to cascading effects of bird predation on BCLR.

This is the first study of cascading effects of birds on tree growth in a wetland forest, but was also part of a larger effort to characterize the biota of the Maurepas Swamp prior to construction of a structure to divert Mississippi River water into the swamp to ameliorate changes in hydrological conditions caused by construction of flood control levees along the Mississippi River. The diversion is expected to increase freshwater, sediment and nutrient inputs into the swamp, increase primary productivity of swamp and marsh plant communities, and increase the stability of the swamp (Höppner 2002, Shaffer et al. 2003). Data collected during this study and the study by Zoller (2004) will provide pre-diversion baseline data on the breeding bird community with which the effects of the diversion may be evaluated.

## **Methods**

### **Study Site**

Lake Maurepas (Figure 2-1) is a 235km<sup>2</sup> oligohaline lake located in the Pontchartrain Basin in southeast Louisiana. The area surrounding Lake Maurepas was nearly contiguously forested baldcypress-tupelo swamp until it was completely logged in the early 1900s. Some of the forest in the Maurepas Swamp regenerated following logging; however most of this

regenerated forest has been severely degraded, primarily due to regional hydrological alterations. Forest degradation and/or poor regeneration has resulted in a mosaic of wetland habitat types in the Maurepas Swamp, generally on a salinity gradient from east to west. Wetlands on the east and south sides of Lake Maurepas are more saline (Shaffer et al. 2003), and most of these wetlands adjacent to the lake have transitioned to open marsh. The west side of the lake receives some riverine input of freshwater from the Amite River Diversion Canal and storm water run-off from Hope Canal and is less saline (Shaffer et al. 2003). However, most of the swamp forest on the west side of the lake is degraded.

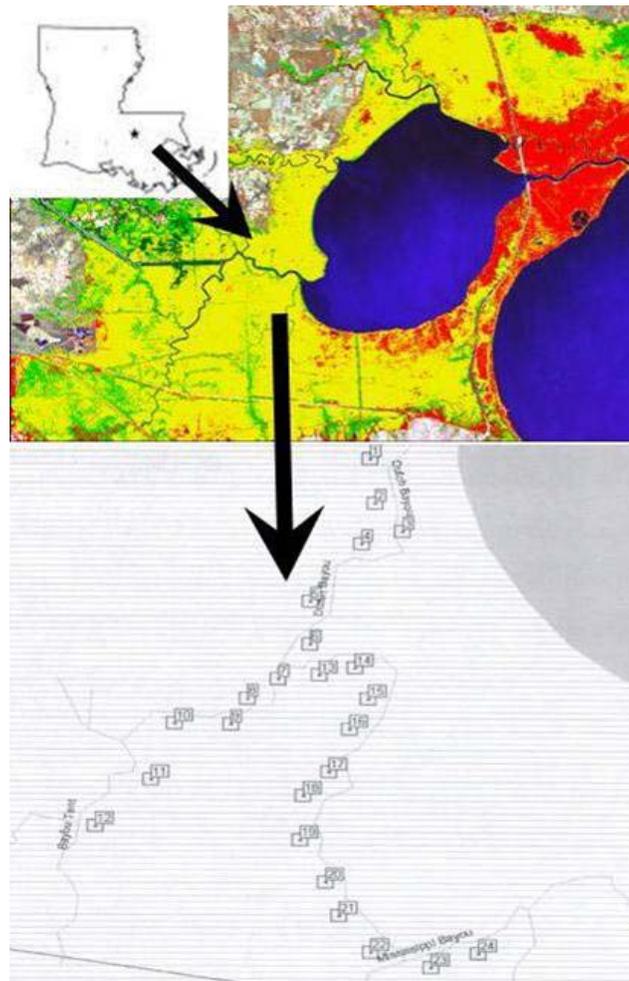


Figure 2-1. Maurepas Swamp and study sites used in 2003.

Approximately two-thirds of the Maurepas Swamp is currently in a degraded state (Figure 2-1, degraded swamp coded yellow, photograph courtesy G. Shaffer and J. Zoller, Chambers et al. 2005). Höppner (2002) and Shaffer et al. (2003) described the vegetative characteristics of the Maurepas Swamp. Degraded areas of the Maurepas Swamp have an open canopy with widely spaced dominant baldcypress, and intermediate and co-dominant baldcypress, water tupelo and swamp tupelo (*Nyssa sylvatica* var. *biflora*). The mid-story of degraded swamp is dominated by swamp red maple, pumpkin ash (*Fraxinus tomentosa*) and green ash (*Fraxinus pennsylvanica*). The herbaceous layer is dense, continuous, and dominated by *Peltandra virginica*. Most water tupelo in degraded swamp exhibit crown dieback to some degree, and their tops are frequently broken 3-10m above the ground (personal observations).

I conducted this study in degraded swamp habitat on the west side of Lake Maurepas on land owned by Blind River Properties and in the Maurepas Swamp Wildlife Management Area (Maurepas Swamp WMA). The Richard King Mellon Foundation donated two tracts of swamp forest within the Maurepas Swamp, totaling more than 25,300 hectares, to the Louisiana Department of Wildlife and Fisheries in 2001. These forest tracts were designated as the Maurepas Swamp WMA. The Maurepas Swamp WMA is located along the south shore of Lake Maurepas beginning about 40km west of New Orleans and extending west to Sorrento, Louisiana, with the two tracts straddling a private inholding owned by Blind River Properties along Hope Canal on the west side of Lake Maurepas.

### Study Plot Selection

Twenty-four 1-ha study plots were laid out with a compass and hip chain or 50m tape at the west end of Lake Maurepas in the Maurepas Wildlife Management Area and adjacent private property along Dutch Bayou, Bayou Tent, and Bayou Mississippi on 13-26 February 2003

(Figure 2-1). Study plots were established at least 100m from major bayous to avoid edge effects, and separated by at least 200m to ensure independence with respect to bird territories. Within each study plot a 3x3 grid with nine grid points spaced at 50m was marked with tree flagging. In the colored map in Figure 2-1, degraded swamp is shown in yellow, swamp which has transitioned into open marsh in red, closed canopy swamp forest in green (photo courtesy G. Shaffer and J. Zoller).

### Nest Boxes

In an attempt to increase breeding densities of SCNB on experimental plots, I randomly assigned a nest box treatment to half of the study plots. Inexpensive, lightweight “nest bottles” (hereafter referred to as nest boxes) were made from plastic beverage bottles (Drumtra 2006) which were donated by Constar Plastics (Reserve, Louisiana). Bottles were immersed in gray latex paint matching the color of water tupelo boles in the Maurepas Swamp, and several drainage holes were punched through the bottom of each bottle. Nest boxes varied in size, entrance diameter and placement to attract different species of SCNB.

I used three species-specific nest box designs. Diameters of one-liter plastic drink bottles are approximately the diameter of cavities excavated by Downy Woodpeckers (*Picoides pubescens*, hereafter referred to as DOWO), which are frequently used by SCNB such as PROW and CACH (Petit 1999, Wood and Cooper unpublished manuscript, personal observations). One-liter nest boxes with an entrance diameter of 3.2cm were hung on distal ends of branches with coat hangers at an average height of 5.3m for CACH. One-liter bottles with an entrance diameter of 3.5cm were attached to boles of small trees with strapping tape at a mean of 1.3m above the water for PROW. Nest boxes of this type have been effective in attracting nesting PROW in Arkansas and South Carolina (D. Drumtra unpublished data, L. Wood personal

communication). Two-liter bottles have approximately the cross-sectional area of some common wooden nest box designs that have attracted many species of cavity nesting birds (personal observations). Two-liter nest boxes with an entrance diameter of 6.5cm were hung from branches against the boles of trees with coat hangers at a mean height of 5.2m for ETTI and Great Crested Flycatchers (*Myiarchus crinitus*).

Between 28 February and 7 March 2003 one nest box of each type was installed within 15m of each of the nine grid points on experimental plots, for a total of 27 bottles per plot. PROW prefer to nest in shaded areas (Blem and Blem 1994), so I placed nest boxes in the most shaded area possible, but in some cases nest boxes were located in areas with almost no canopy cover. A small amount of baldcypress planer shavings was added to the bottom of the boxes at the time they were installed to naturalize the look of the cavity. At points on the perimeters of experimental plots nest boxes were installed within the plot with very few exceptions. Logistical difficulties of working in the swamp greatly reduced the number of times nest boxes could be checked during the experiment. Nest boxes were checked about every two weeks after 1 April 2003. In some cases checks were separated by as much as three weeks. Most boxes were checked frequently enough to determine occupancy rates and apparent nest success of active nests.

Because nest boxes were clustered within 15m of grid points, it was assumed that all boxes at a point were included in the territory of a single male SCNB. Male PROW add moss or other vegetation to cavities within their territories before females arrive and females ultimately select the nest cavity (Petit 1999). Therefore, the presence of these “dummy nests” in nest boxes was used as indication of occupancy by a territorial male PROW. Nest success was assessed by the condition of the nest, the presence of droppings in or near the nest, and/or fledglings detected

near the nest. Nests which were assumed to have fledged at least one young were categorized as successful nests. Wasps may exclude PROW from nest boxes (Blem and Blem 1991), so wasp nests were removed from nest boxes whenever possible.

### Breeding Bird Surveys

Relative abundance of insectivorous birds on study plots was quantified to determine if local bird abundance was positively correlated with growth of study trees. Relative abundance of insectivorous birds was estimated by performing three rounds of 10-minute variable radius point counts at the center of each plot following a slightly modified version of the Lower Mississippi Valley Joint Venture Program protocol for monitoring forest interior bird populations (Mississippi Valley Joint Venture Program 2004). Point counts began as soon as possible after sunrise and counts were completed before or soon after 10AM. All birds seen and heard during the 10-minute sampling period were recorded, and the distance to the location of the bird was estimated at the time it was first detected. Movements of birds were noted to avoid recounting an individual. Spring passage migrant birds and birds flying over plots were recorded, but not included in analyses. Detections of all bird species at all distances were recorded, but only detections of insectivorous birds estimated to be within the plots were used in analyses of effects of birds on tree growth. I conducted all point counts personally to reduce observer bias. Point counts were conducted on 16-23 April, 20-26 May and 20-23 June 2003.

### Tree Growth Measurements

Within each quadrant of each study plot I selected a baldcypress sapling less than 4.5m tall for study. I had originally planned to perform an exclosure study similar to that by Marquis and Whelan (1994), but I was unable to design and build bird exclosures before baldcypress leaf-out in the spring of 2003. I had also planned to compare leaf damage on study trees between nest

box and control plots, but baldcypress saplings began losing large numbers of leaves in summer when I began estimating leaf damage. Therefore, I examined the relationship between breeding bird abundance and mean shoot growth of baldcypress saplings. In 2004, I haphazardly selected 30 shoots distributed evenly throughout the crown on each study tree. Growth of shoots in 2003 was easily identified on most twigs from budscale scars. Twigs on which budscale scars were not obvious were discarded and another twig was selected for measurement. I measured the length of each shoot from the 2003 budscale scar to the terminal bud to the nearest millimeter.

### Statistical Analyses

All statistical analyses were performed with SAS version 9.1 (SAS Institute 2005). All data met the assumptions of parametric statistics, and significance level for all tests was set at  $\alpha=0.05$ . Means are reported with their associated standard errors.

The effects of nest box addition on SCNB are frequently measured by comparing numbers of territories of SCNB within nest box plots to control plots (e.g. Brawn and Balda 1988). However, determining the number of territories on plots was not possible due to the difficulty of traversing study plots and tracking individual birds. Therefore, SCNB detections, including detections of fledglings, over all three point counts were summed and PROC TTEST was used to compare the total number of point count detections of SCNB between nest box and control plots.

The effect of the nest box treatment on the mean shoot growth of baldcypress saplings was analyzed as an ANCOVA with a randomized block design blocked on plot, and the total number of bird detections included as a covariable in the analysis.

## Results

As the study progressed, it became evident that the hydrology of some study plots was markedly different from the others, making them very difficult, and in some cases dangerous to survey. Therefore, three plots were dropped from the shoot growth experiment before all rounds of point counts were completed. A fourth plot had almost no baldcypress saplings shorter than 4.5m or taller than 1.4m. Therefore, it was not included in the analysis of the effects of birds on shoot growth of baldcypress, but point count data collected on this plot was included in point count analyses.

### Breeding Bird Surveys

A total of 947 detections of insectivorous birds were recorded over the three rounds of point counts within study plots. The total number of insectivorous birds detected per study plot over the three counts ranged from 33-65 (mean=47.35± 1.55 SE). Detections of SCNB accounted for slightly more than 42% of the total number of insectivorous bird detections recorded during the three rounds of point counts (Table 2-1).

PROW were the most frequently detected SCNB species during point counts. An average of 3.7 PROW were detected per point count, and PROW detections accounted for nearly 26% of the total number of detections (Table 2-1). Northern Parula (*Parula americana*, hereafter referred to as NOPA) were the second most frequently detected insectivorous bird during point counts (Table 2-1). An average of 2.6 NOPA were detected per point count, and they accounted for just over 18% of the total number of detections. Carolina Wrens (*Thryothorus ludovicianus*, hereafter referred to as CARW) were the third most frequently detected bird species and accounted for about 10.6% of the total number of bird detections. The other two common SCNB in the Maurepas Swamp, CACH and ETTI, were the fourth and fifth most commonly detected

bird species during point counts, accounting for 9.5% and 6.6% of the total number of point count detections respectively. An average of 1.4 CACHs and less than one ETTI were detected per point count.

Table 2-1. Numbers of insectivorous birds detected during three rounds of point counts on study plots in 2003 and their percent of the total number of insectivorous bird detections.

Common Name	Scientific Name	Species Code	Number of Detections	Percent of total
Prothonotary Warbler	<i>Protonotaria citrea</i>	PROW	246	25.98
Northern Parula	<i>Parula americana</i>	NOPA	172	18.16
Carolina Wren	<i>Thryothorus ludovicianus</i>	CARW	100	10.56
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	90	9.50
Tufted Titmouse	<i>Baeolophus bicolor</i>	ETTI	63	6.65
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO	62	6.55
Yellow-throated Warbler	<i>Dendroica dominica</i>	YTWA	46	4.86
Great-crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL	34	3.59
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	31	3.27
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	21	2.22
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	20	2.11
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	BGGN	19	2.01
Indigo Bunting	<i>Passerina cyanea</i>	INBU	18	1.90
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	YBCU	11	1.16
White-eyed Vireo	<i>Vireo griseus</i>	WEVI	6	0.63
Yellow-throated Vireo	<i>Vireo flavifrons</i>	YTVI	6	0.63
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	2	0.21
TOTAL			947	100.00

All bird species listed in Table 2-1 except YBCU (see Table 2-1 for common names) were observed depredated BCLR at least one time after caterpillars had grown to about 1cm long. Only PROW, NOPA, YTWA, CACH, and ETTI (see Table 2-1 for common names) were consistently observed depredated BCLR while they were available. Although CARW were the third most frequently detected bird species during point counts, they were rarely observable, and

appeared to forage primarily in the herbaceous layer. Among the more common insectivorous birds, I observed GCFL, RBWO, and RWBL depredating BCLR only once each. I observed a GCFL fly to a baldcypress branch approximately 10m high where it startled a BCLR from a leaf or its shelter either while perching or by purposely beating its wings against the leaves on the branch. The GCFL then flew down to the BCLR as it dropped on a silk line from the branch. A RWBL perched and gleaned a BCLR from its shelter on a baldcypress sapling approximately 3m tall. A RBWO clung to the bole of a 3m tall baldcypress sapling at about 1m from the ground and removed a BCLR from its shelter.

PROW and NOPA were frequently observed foraging on BCLR after BCLR had grown to about 1cm long. NOPA began foraging on BCLR earlier than any other warbler species, and presumably consumed smaller BCLR than other warblers. PROW and NOPA primarily foraged on the outer edges of tree crowns. CACH and ETTI were more thorough in their foraging behavior and appeared to forage closer to tree boles than PROW and NOPA (see Chapter 3, Foraging Observations).

### Nest Boxes

PROW were the only bird species that used nest boxes, so the following results of the nest box experiment concern only PROW. Nest boxes on plots dropped from the shoot growth study were checked less frequently than nest boxes on plots included in the shoot growth study. However, most nests were checked frequently enough to determine clutch sizes and to assess apparent nest success. In cases where nests were not checked frequently enough to determine reproductive output by birds, sample sizes were reduced accordingly.

Sixty-four of the 108 grid points (59.3%) had at least one nest box that showed some sign of occupancy by the local territorial PROW male or pair (Table 2-2). The most frequently used

Table 2-2. Summary of observations of nest box use and nesting parameters of Prothonotary Warblers in the Maurepas Swamp.

\*Does not include nests for which final clutch size was unknown. † Does not include depredated or abandoned nests. ‡ Does not include flooded nests.

	Grid points occupied	Grid points with active nests	Grid points with successful nests	Active nests	Depredated nests	Eggs*	Unhatched eggs†	Successful nests‡	Number fledged
Total	64 (59.3%)	39 (36.1%)	33 (30.6%)	51	10 (19.6%)	206	21 (10.2%)	36 (70.6%)	138
Range per plot	0-9	0-7	0-6	0-11	0-4	4-47	0-9	0-6	0-27
Mean per plot (SE)	5.3 (0.81)	3.3 (0.63)	3.0 (0.52)	4.3 (0.97)	0.91 (0.39)	18.7 (3.99)	1.9 (0.80)	3.3 (0.57)	12.5 (2.25)
Mean per nest (SE)	-	-	-	-	-	4.5 (0.15)	0.51 (0.14)	-	3.9 (0.19)

plant in dummy nests of male PROW, and in the basal layer of active PROW nests in nestboxes in the Maurepas Swamp was the invasive floating aquatic plant *Salvinia molesta* (D. Fox and J. Zoller personal observations). The number of occupied grid points per plot ranged from 0-9 (mean  $5.3 \pm 0.81$ ) (Table 2-2). The earliest date of nest initiation, estimated by backdating, was approximately 10 April. The latest nest was initiated on approximately 20 June and fledged three young on 20 July. Nest boxes at 39 grid points (36.1%) had active nests (nests that contained at least one egg) (Table 2-2). The number of grid points per plot with active nests ranged from 0-7 (mean =  $3.3 \pm 0.63$ ) (Table 2-2). Six other nest boxes contained complete nests, and two nest boxes contained nest cups without linings. This indicated occupancy by a pair of birds, but none were observed with eggs and they did not appear to have been depredated. These nests were not included in calculations of apparent nest success.

A total of 51 nests with at least one egg were found in nest boxes at the 39 grid points with active nests. The number of active nests in nest boxes per plot over the course of the study ranged from 0-11 (mean =  $4.3 \pm 0.97$ ) (Table 2-2). Of the 51 active nests in nest boxes, 14 (27.5%) failed due to predation, abandonment or accident. In PROW boxes attached to tree boles, nine nests were depredated, and one nest was abandoned.

In CACH boxes hung from distal ends of branches, one nest was depredated, two nests were abandoned, and one nest with nestlings fell during a storm and was assumed to have failed. One nest in an ETTI box was abandoned. Depredated nests were usually disheveled with nest material partially pulled out of the entrance, most likely by raccoons (*Procyon loctor*). At least two nests were depredated during the nestling stage. Two of the seven depredated nests were found with incomplete clutches, and were depredated before the next check. Another two nests found with incomplete clutches were assumed to have been abandoned between checks, and two

nests with complete clutches were abandoned during the incubation stage. One nest was checked too infrequently to determine final clutch size. Nest material in the four abandoned nests was wet, and it was assumed that these nests had been flooded during heavy rains which occurred in May and June. The discovery of these flooded nests prompted me to remove all nest boxes except those with active nests in late June. Excluding the five nests for which final clutch size was unknown, the remaining 46 nests contained a total of 206 eggs, and clutch size ranged from 2-6 eggs (mean= $4.5 \pm 0.15$ ) (Table 2-2).

Thirty-nine nests (76.5%) survived to hatching. Nests that were known to survive to hatching contained 168 eggs, of which 21 (12.5%) failed to hatch (Table 2-2). Thirty-three grid points (30.6%) had a nest that fledged at least one young (successful nest) (mean per plot= $4.3 \pm 0.97$ ) (Table 2-2). Excluding 5 nests which were flooded or fell, 36 of 46 nests (78.3%) were assumed to have succeeded, as determined by the condition of the nest, the presence of droppings in or near the nest, and/or fledglings detected near the nest. Excluding one plot on which no nests were found in nest bottles, the number of successful nests per plot ranged from 1-6 (mean= $3.3 \pm 0.57$ ) (Table 2-2). Excluding one nest which was assumed to have fledged but for which the clutch size was unknown, a total of 138 young were assumed to have fledged from nest boxes (Table 2-2). Excluding one plot on which no nests were found in nest bottles, the number of young fledged from nest boxes per plot ranged from 0-27 (mean= $12.5 \pm 2.25$ ) (Table 2-2). Excluding one nest which was assumed to have fledged but for which the clutch size was unknown, the number of young fledged per successful nest attempt ranged from 1-6 (mean= $3.9 \pm 0.19$ ) (Table 2-2).

When nests in flooded or fallen boxes were excluded, apparent nest success was 24 of 33 nests (72.7%) in PROW boxes, 8 of 9 (88.9%) in CACH boxes and 4 of 4 (100%) in ETTI

boxes. The full 3x2 contingency table of nest box type and nest success was not analyzable with a chi-squared test due to small values for nest failures in ETTI and CACH boxes. Therefore, I collapsed these two hanging nest box designs into a single category and performed Fisher's exact test in PROC FREQ on the resulting 2x2 contingency table of nest success in hanging boxes vs. PROW boxes. Apparent nest success in hanging nest boxes was not significantly different from that of nests in PROW boxes ( $p=0.24$  two-sided Fisher's exact test).

Because PROW were the only SCNB species that used nest boxes and other SCNB were relatively less abundant, the analysis of the effects of nestboxes on SCNB activity was restricted to the effect on PROW activity. Total numbers of PROW detections recorded on plots with nest boxes ranged from 9-17 (mean= $13.1 \pm 0.78$ ) and on control plots total PROW detections ranged from 7-16 (mean= $11.45 \pm 0.97$ ). The number of Prothonotary Warbler detections recorded on nestbox plots was not significantly different than on control plots ( $t_{(19)} = 1.31$ ,  $p=0.2067$ , Figure 2-2).

### Baldcypress Shoot Growth

Neither the nest box treatment ( $F_{1,17}=1.03$ ,  $p=0.32$ ), nor the covariable of total insectivorous bird detections ( $F_{1,17}=0.96$ ,  $p=0.34$ ) significantly affected the mean shoot growth of baldcypress saplings. Pooling the bird covariable into the error term did not improve the significance of the test of nest box effect on mean shoot growth ( $F_{1,18}=0.63$ ,  $p=0.44$ ).

## **Discussion**

### Breeding Bird Surveys

Results from point counts were similar to those obtained by Zoller (2004) in degraded areas of the Maurepas Swamp. The combined detections of the three most abundant Neotropical migrant bird species in degraded areas of the Maurepas Swamp, PROW, NOPA and YTWA (see

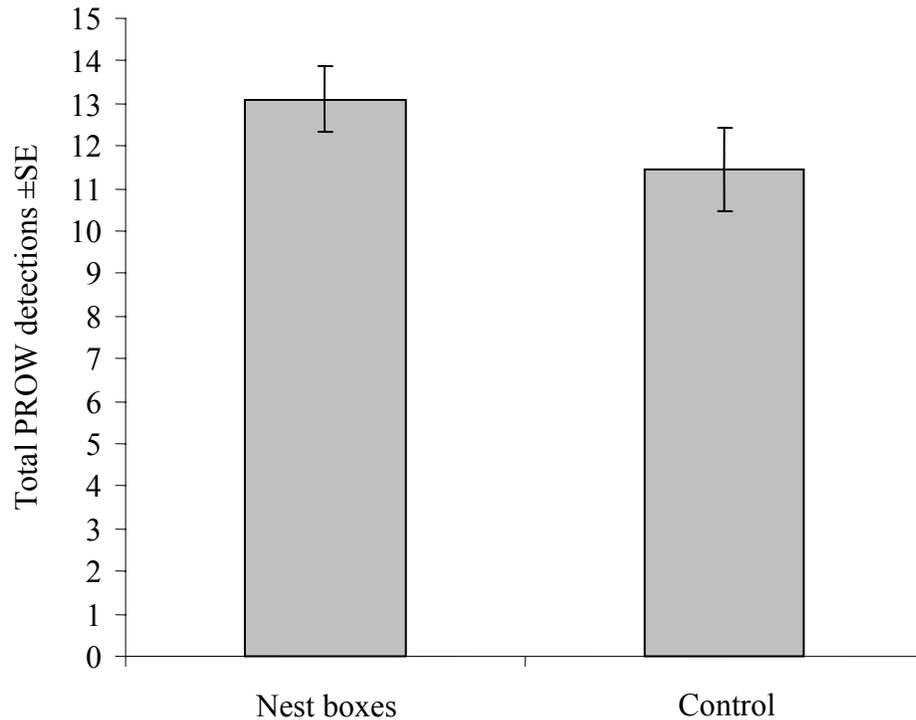


Figure 2-2. Total numbers of PROW detections on plots with nest boxes and control plots.

Table 2-1 for common names), accounted for 49.6% of the total number of detections in my study, and for 54% of the total in the study by Zoller in 2003 (2004). My point count locations were 40m further into the interior of the swamp than Zoller's (2004) point count locations in degraded swamp, and this may have accounted for some of the difference in proportions of the three warbler species detected between our studies. However, I detected an average of 7.5 breeding Neotropical migrant birds per point count, a result similar to those obtained by Zoller (2004) in degraded swamp. As a group, SCNB accounted for slightly more than 42% of the total number of point count detections. However, Zoller (2004) and I found that the resident SCNB species, CACH and ETTI, accounted for fewer than 10% of the detections.

The numerical dominance of PROW in degraded areas of the Maurepas Swamp was similar to results of studies of breeding bird community composition in other southern wetland

forests (Sallabanks et al. 1993 and references therein). My point counts included birds detected within a 1-ha study plot, and the relative abundance of PROW was probably lower than that observed by Mitchell and Lancia (1990 as cited in Sallabanks et al. 1993) who detected 2.7 PROW per 25m radius point count. Studies in which high densities of PROW are reported (Mitchell and Lancia 1990 as cited in Sallabanks et al. 1993, Petit 1996, R. Cooper unpublished data, personal observations) were conducted in high quality bottomland hardwood or cypress-tupelo swamp with intact forest structure. However, my results are notable because the high relative abundance of PROW was observed in an area with reduced forest cover, and in plots that were purposely established away from preferred PROW breeding habitat adjacent to permanently standing water (Petit and Petit 1996).

#### Nest Boxes

PROW were the only bird species to utilize nest boxes, and total PROW detections were not significantly different between plots with nest boxes and control plots, but 1.65 more PROW were detected on plots with nest boxes. This result differs from those obtained by Zoller (2004), who found that PROW were apparently cavity limited in degraded areas of the Maurepas Swamp. Although nest box addition had no effect on my study plots, the high variability of the number of active nests found in nest boxes among my plots suggests that PROW are at least locally cavity limited. The most likely explanation for the difference between the results of our experiments is that a greater proportion of Zoller's nestboxes were occupied and fledged young.

Brawn and Balda (1988) and Zoller (2004) observed that there was a time lag in SCNB response to nest box addition. In the first year of Zoller's (2004) study, only three of 100 nest boxes contained a successful nest, while in the second year 50 of 100 nest boxes contained an active nest. Therefore, my nest boxes may have been in place for too short a time, and

significant results might have been obtained had the study continued for another year.

Alternatively, my nest boxes may have been used less frequently than Zoller's because they were less suitable nesting sites due to their high temperatures, or other nest site parameters assessed by SCNB. However, many of my nest boxes were utilized in the first breeding season in which they were present. The immediate use of newly installed nest boxes has been cited as circumstantial evidence of cavity limitation of SCNB (Newton 1994).

The lack of a significant response by PROW to nest box addition in my study may also have been due to the spacing of the nest boxes and the large number of water tupelo and swamp red maple snags and live trees with natural cavities produced by tree rot. It had been assumed that PROW would choose to nest in boxes because these natural cavities are selected less frequently by PROW in Arkansas (Wood and Cooper unpublished manuscript). Because of the difficulty of working in the swamp, it was not possible to locate many SCNB nests in tree cavities. However, during this study and another study in the same area in 2004 (see Chapter 3), several PROW nests were found in tree cavities. The majority of these nests were in open-topped cavities, or cavities with large entrance holes, produced by tree rot in water tupelo or swamp red maple.

Nests found in natural cavities were frequently separated by 50m or less, and PROW detections per point count averaged 3.7 on 1-hectare plots in this study. Therefore, the natural density of PROW in degraded areas of the Maurepas Swamp may have been equal to, or greater than the density of nestboxes. If natural densities of PROW in degraded areas of the Maurepas Swamp are indeed as high as relative abundance and observational data suggest, then nest boxes spaced at 50m may have been too diffuse to increase PROW abundance.

The failure of CACH and ETTI to utilize nest boxes may have been due to the relative scarcity of these birds within the study area. An average of 1.4 CACH, and less than one ETTI were detected per point count, and were detected 2.5 and about 3.7 times less frequently than PROW. Brawn and Balda (1988) suggested that common SCNB species should be more likely to demonstrate a response to increased cavity availability because common SCNB are more likely to be cavity limited. Brawn and Balda (1988) also found that habitat structure influenced the response of some SCNB species to nest box addition. In open habitat, foliage and bark gleaner density did not increase with the addition of nest boxes, while the density of aerialist and ground foragers did increase (Brawn and Balda 1988). The lack of closed canopy forest, and not suitable nest cavities, may have limited population density of CACH and ETTI in degraded areas of the Maurepas Swamp.

The instability of hanging nest boxes may have deterred CACH and ETTI from nesting in nest boxes. CACH and ETTI may also have found nest boxes made from plastic bottles unsuitable nesting habitat. In a study utilizing the same basic nest box design in which natural cavities were blocked, Drumtra (2006) found no SCNB other than PROW and a single CARW nesting in nest boxes. CARW frequently nest in cavities, but are more plastic in their nesting behavior than obligate SCNB (personal observations), and were not grouped with other SCNB in this study. Nest boxes suitable for CARW were not added to study plots because they forage in the herbaceous layer (personal observations), and were not expected to significantly affect tree growth. CARW also typically select low cavities for nesting (personal observations), and low nest boxes would probably have been flooded on my study plots.

PROW may have found plastic nest boxes less suitable than available natural cavities. Petit and Fleming (1987) found that PROW nested in nest boxes made from milk cartons more

frequently than nest boxes made from PVC. PROW occupied plastic nest boxes at slightly more than 59% of my grid points (spaced at 50m), while in the study by Zoller (2004) in similar degraded habitat 92% of nest boxes made from milk cartons, spaced at 50m, were occupied. Furthermore, Zoller (2004) found that 62% of his boxes in degraded swamp habitat contained an active nest, while only 36% of my grid points contained an active nest. However, Blem and Blem (1991) found PROW nests in 34% of wooden nest boxes in tidal swamp in Virginia.

Mean clutch size of PROW nesting in my nest boxes in the Maurepas Swamp was 4.5 eggs, which was similar to the average observed in Tennessee (4.7eggs) (Petit 1989) and Wisconsin (4.3 eggs) (Flaspohler 1996), intermediate between mean clutch sizes for early (4.96 eggs) and late nests (3.94 eggs) in Virginia (Blem et al. 1999), and lower than the mean clutch size in Michigan (5.07 eggs) (Walkinshaw 1953) and Illinois (5.0 eggs) (Hoover 2003). Although female PROW nesting in nest boxes were not aged, there appeared to be a high proportion of females with extensive green plumage around the head and neck, which is consistent with Pyle's (1997) description of one year old females. Because birds were unmarked, the number of nests attempted by individual females was unknown. These demographic parameters may have influenced mean clutch size in my study because one year old female PROW lay fewer eggs than older female PROW in their first nest attempts (Blem et al. 1999). If my nest boxes were less desirable nesting habitat for some reason, there may have been a greater proportion of young female PROW using nest boxes.

PROW may have avoided my plastic nest boxes because they may have been hotter nesting sites than available natural cavities. Blem and Blem (1994) found that nest boxes with maximum daily temperatures of 35-39°C were only used in the early portion of the breeding season. While most of my nest boxes were shaded for the entire day, several grid points were

located in areas with little canopy cover. The temperature of a plastic nest box without nestlings in June at noon in full sunlight was 40°C, and I observed nestlings in fully shaded plastic nestboxes gular-fluttering. Nestlings in nest boxes made from milk cartons were not observed gular-fluttering (J. Zoller personal communication). Prolonged exposure to temperatures of 36-39°C may be lethal to eggs (Webb 1987).

It is uncertain whether nest box temperature had an effect on egg hatchability in this study. Successful nests in my study contained an average of 0.51 unhatched eggs, which is lower than that of most PROW clutches in nest boxes in Virginia described by Blem et al. (1999). The percentage of unhatched eggs in my study (10.2%) was higher than that observed in two studies in Tennessee; Petit (1989) found that 7.1% of PROW eggs in nests in nest boxes failed to hatch, and Petit and Petit (1996) found that 3% of eggs in nest boxes located adjacent to standing water failed to hatch, but 15% failed to hatch in nest boxes located farthest away from standing water. The effect of female age and timing of nest attempt may confound these results because one year old female PROW produce significantly more infertile eggs in their first clutch (Blem et al. 1999).

A mean of 3.9 young were assumed to have fledged from successful nests in nestboxes. This result may be high because nests were not checked as they approached the fledging date, and some nests may have been depredated without evidence of failure. Alternatively, my results may be low if nests assumed to be completely depredated were partially successful and evidence of fledging was not observed. The mean number of young assumed to have fledged in my study is similar to results obtained by Petit (1989) in Tennessee where an average of 4.43 young in early nest attempts and 3.98 young in late nests attempts fledged from successful nests in nest boxes. Fewer young were fledged per successful nest in my nest boxes than successful nests in

nest boxes adjacent to the water's edge in Tennessee where an average of 5.5 young were fledged from early, successful nests (Petit and Petit 1996). However, the mean number of young fledged from early, successful nests in nest boxes farthest from the water's edge (4.0 young) was similar to the result I obtained (Petit and Petit 1996). Again, the effect of female age and timing of nest attempt may confound my results because one year old female PROW lay fewer eggs in their first clutch (Blem et al. 1999).

Apparent nest success was similar between nests in plastic nest boxes (70.6%) and those in milk cartons (72.5%) (Zoller 2004) in the Maurepas Swamp. Apparent nest success of PROW in nest boxes in degraded habitat in the Maurepas Swamp was higher than apparent nest success rates of PROW in Arkansas in plastic nest boxes (57%) and natural cavities (22%) (Drumtra 2006), in wooden nest boxes in Tennessee (32-57%) (Petit and Petit 1996) and in natural cavities in Wisconsin (38%) (Flaspohler 1996). A fledgling survey of 24 study plots in degraded areas of the Maurepas Swamp suggested that apparent nest success of PROW in natural cavities is approximately 50% (see Chapter 2). A fortuitous situation may exist for breeding PROW in degraded areas of the Maurepas Swamp where numerous, predation-prone cavities are available, but the diversity and abundance of nest predators is relatively low. Canopy cover is not continuous, and the site is frequently saturated or flooded, and may be unsuitable habitat for some arboreal animals (e.g. rat snakes (*Elaphe spp.*), raccoons, flying squirrels (*Glaucomys volans*), eastern gray squirrels (*Sciurus carolinensis*) which are known to depredate PROW nests in bottomland forests (Petit 1999, Drumtra 2006, personal observations).

Raccoons were present in degraded areas of the Maurepas Swamp, but their abundance appeared to be low relative to drier sites (personal observations). Raccoons were assumed to have depredated most nests in my study and the study by Zoller (2004). However, very few

eastern gray squirrels, and only two Texas rat snakes (*Elaphe obsoleta lindheimerii*) have been observed in this area (personal observations, J. Zoller personal communication). In a small mammal trapping study, Menzel (2003) captured no small mammals in an area of healthy swamp included in the study by Zoller (2004). My hanging nest boxes appeared to provide the greatest protection from raccoons because they were hung from the distal ends of slender branches.

Red-bellied Woodpeckers (*Melanerpes carolinus*, hereafter referred to as RBWO) are common nest predators in the Maurepas Swamp (Zoller 2004, this study), and woodpeckers are assumed to be responsible for many PROW nest failures in other areas of the LMAV (Hazler et al. (2003). Hazler et al. (2003) described several eyewitness accounts of RBWO depredating nests of several cup nesting species, but only provided circumstantial evidence for RBWO depredation of PROW nests. I personally observed two PROW nests in natural cavities being depredated by RBWOs in degraded areas in the Maurepas Swamp. In both cases I discovered the nest by the alarm call of the female PROW as the nests were depredated. In both cases the nests were depredated in the egg stage, and I observed the RBWOs removing eggs, flying away with them, and returning to remove a second egg. In one case the nest was in an open-topped cavity, and in the second case the cavity entrance was approximately 10cm wide by 6cm high. Drumtra (2006) suggested that plastic nest boxes similar to my design provided protection from RBWO because the plastic cannot be excavated. I assume that my hanging nest boxes provided protection from woodpeckers because there were no perching sites available for a bird as large as a RBWO on the bottle, and the entrance hole (3.2cm) is probably too small for a RBWO to probe easily.

PROW are frequent BHCO hosts (Petit 1989, Petit 1999, Hoover 2003, Drumtra 2006, personal observations), and they are the only SCNB in North America that is frequently

parasitized by BHCO (Petit 1999). Reported parasitism rates of nests in nest boxes range from 0% (Petit 1989) to 50% (Hoover 2003). Parasitism rates of natural nests range from 12.3% (Goertz 1977) to 41% (Hoover 2003). BHCO parasitism reduces clutch size, hatching success, and nestling mass and survival of PROW (Hoover 2003). However, in this study and the study by Zoller (2004) no PROW nests in nest boxes or in natural cavities contained BHCO eggs. BHCO were present, but rare in degraded areas of the Maurepas Swamp. I detected eight BHCO adults during the three rounds of point counts in 2003 (0.009% of the total number of insectivorous bird detections). During three field seasons of breeding bird research in degraded areas of the Maurepas Swamp (see Chapter 3) I detected only 5 BHCO fledglings. I was able to determine the host species feeding a BHCO fledgling in three cases, and in each case the host was a NOPA.

Several concerns prompted me to discontinue this nest box study after the first year. First, concerns over access to private property which developed at the end of the first field season caused me to shift all research activities onto the Maurepas WMA in 2004 (see Chapter 3). Second, it was unethical to continue the study with plastic nest boxes after the discovery of flooded nests and nestlings gular fluttering in nest boxes. Third, traversing one hectare study plots, and travel between study plots limited the number of times nest boxes could be checked.

#### Baldcypress Shoot Growth

Nest box addition and insectivorous bird abundance did not significantly affect mean shoot growth of baldcypress saplings. The non-significant effect of the nest box treatment was to be expected given that nest boxes did not attract SCNB other than PROW, and even PROW relative abundance was not affected by nest box addition. There are several reasons why the number of insectivorous bird detections was not well correlated with shoot growth of

baldcypress saplings in this experiment. First, it was not possible to map insectivorous bird territories on my study plots to test effects of birds on individual trees. All of the insectivorous bird species which were observed on my plots are territorial, and each tree was, at most, included in the territory of only one pair of each insectivorous bird species. Therefore, the experimental design was probably too coarse to accurately reflect reality. Second, of several biotic and abiotic variables which might have influenced shoot growth and improved the fit of the model were not measured. Salinity and flood depth and duration were not measured, and these abiotic variables and their interactions have been shown to decrease productivity of baldcypress (Conner and Day 1976, Pezeshki et al. 1987, Pezeshki et al. 1989, Goyer and Chambers 1997, Souther 2000, Shaffer et al. 2003, Souther-Effler 2004). BCLR density and defoliation were not measured on study trees, so a clear interaction chain linking birds, BCLR, defoliation, and shoot growth was not documented. Third, and probably most importantly, the terminal buds of baldcypress shoots, which are responsible for primary elongation of shoots and contain leaves produced in the previous growing season, were not inspected for damage immediately following the period of BCLR activity.

The nest box treatment may not have a significant effect on shoot growth of baldcypress due to the timing of nesting of PROW utilizing nest boxes. A pair of PROW which successfully fledges the mean of 3.9 young effectively triples the number of birds being provisioned with insects in that territory. However, the timing of hatching is critical for them to have an effect on BCLR and growth of baldcypress. Birds were first observed foraging on BCLR on 17 April 2003, and the first BCLR pupae were first observed on 26 April 2003. Therefore, if PROW had higher nest success in nest boxes than in natural nests, nests must still have hatched at the latest by 8 May when most BCLR were assumed to have pupated for the effects of these additional

nestlings to positively influence baldcypress growth via consumption of BCLR. Of 15 nests in nest boxes which were initiated early enough for nestlings to hatch by 8 May, 11 (25% of all nests) survived until the fledgling stage. However, only 5 of these nests hatched before 30 April. Furthermore, effects of birds on BCLR density and defoliation on baldcypress shorter than about 5m may not be significant. Birds observed foraging on trees less than 4m tall generally made few attacks and left the tree quickly. Most foraging observations of birds on baldcypress were on trees taller than 2m, and birds were frequently observed foraging above 10m (see Chapter 2). Optimal foraging theory predicts that birds should forage on the substrate on which it may obtain the most food per unit effort. Larger mature trees have more foliage than saplings, and it is arranged on large branches which allow birds to perch and search large volumes of foliage without flying.

Despite the shortcomings of my study, several important observations concerning PROW breeding biology were made during this study and the study conducted by Zoller (2004). This study and the study by Zoller (2004) were the first studies of PROW breeding ecology in one of the most dense and least studied populations within its breeding range. The difficulties of working in swamp habitats have been cited as a reason why studies of PROW in swamps are rare (Flaspohler 1996, Sallabanks et al. 1993), and it is unlikely that our studies will be replicated in the foreseeable future due to these difficulties. During field work in the Maurepas Swamp between 2002 and 2005, the first arrival of male PROW was observed between 9 and 12 March (J. Zoller personal communication, personal observations). Zoller observed the first PROW egg as early as 1 April (J. Zoller personal communication), which is three to four weeks earlier than the timing listed in the species account by Petit (1999). Most PROW in Louisiana and Arkansas leave their territories before 10 July (personal observations), but the last PROW nest in my nest

boxes fledged three young on 20 July. During both nest box studies there were no recorded incidents of BHCO parasitism of nests in nest boxes or tree cavities. Effects of female age and timing and number of nest attempts may have confounded some of our nesting parameter estimates, so more detailed studies are required to accurately characterize this population of PROW.

Both PROW and NOPA are among the bird species of highest conservation concern in the LMAV ([www.rmbo.org/pif/scores/scores.html](http://www.rmbo.org/pif/scores/scores.html), Carter et al. 2000), and PROW are listed as being a species of continental conservation importance (Rich et al. 2004). The fact that PROW have high apparent nest success rates (see Chapter 3) and experience no BHCO parasitism suggests that the population of PROW in the Maurepas Swamp may be an important source population in the LMAV. Partners in Flight has characterized the Maurepas Swamp as being a large forested area of low restoration priority and of only moderate protection priority (Twedt et al. 1999). However, considering the high relative abundance of bird species of high conservation concern in the Maurepas Swamp, and the precariousness of the Maurepas Swamp ecosystem, it may be prudent to review this assessment. Without restoration and protection, these dense populations of Neotropical migrant warblers of high conservation concern will decline over an increasing area as trees die due to flooding, salinity and herbivory stressors. The high relative abundance of these two bird species in degraded areas of the Maurepas Swamp is further justification for efforts to restore the hydrology and productivity of these forests.

## CHAPTER 3. EFFECTS OF INSECTIVOROUS BIRDS ON GROWTH OF PLANTED BALDCYPRESS (*TAXODIUM DISTICHUM*) AND WATER TUPELO (*NYSSA AQUATICA*) SEEDLINGS IN THE MAUREPAS SWAMP

### Introduction

#### Trophic Cascade Theory

An emergent property of multi-species assemblages is the generation of indirect effects. Indirect effects occur when direct effects of interactions between species pairs (e.g. predation, competition, mutualisms) are transmitted indirectly to species that do not participate in the direct interaction (Wootton 1994). Although the role of indirect effects in structuring communities has recently received much attention from community ecologists, their importance is still poorly understood (Halaj and Wise 2001). One type of indirect effect is a trophic cascade (Paine 1980, Carpenter et al. 1985). In classical predator-driven trophic cascades the direct effects of a predator (donor) are passed through an interaction chain, first reducing the abundance of an herbivore (transmitter), then indirectly increasing populations or biomass of producers (receiver) (Wootton 1994, Morin 1999).

The classical trophic cascade concept was implied in the seminal paper by Hairston et al. (1960, hereafter referred to as HSS) in which it was hypothesized that “the world is green” due to predator control of herbivore populations. HSS reasoned that because herbivore populations are not resource limited, as evidenced by large standing crops of plants, they must be limited by predators (top-down control) rather than by competition. Predators limit their own resources (herbivores), and are therefore limited by competition.

Fretwell (1977) and Oksanen et al. (1981) extrapolated the HSS model to chains longer and shorter than three trophic levels. In these “exploitation ecosystem hypothesis” (EEH) models, the maximum number of “functional” trophic levels (those able to affect lower, adjacent

trophic levels) in an ecosystem is determined by primary productivity, and the relative importance of top-down and bottom-up forces on biomass of an individual trophic level varies with food chain length (Power 1992). EEH predicts that herbivores will be predator limited in food chains of three or five links, and the standing crop of plants will be high. In contrast, plant populations will be grazer limited in food chains of two or four links, and standing crops of plants will be low. In systems with odd numbers of trophic levels, the strength of trophic cascades should increase with primary productivity because predator biomass should increase as they consume “excess” herbivores (Fretwell 1977, Oksanen et al. 1981, Hunter and Price 1992, Power 1992, Strong 1992).

The HSS and EEH hypotheses have received three main criticisms. First, these models assume species to be consolidated into trophic levels interacting strongly in a linear food chain. However, ecosystems are typically complex webs, with multiple, reticulating connections between species (Strong 1992, Persson 1999, Polis et al. 2000, see Polis and Strong 1996 for a review). Direct effects of predation may be diffused via intraguild predation, omnivory, and compensation by less vulnerable species at lower levels, rather than propagating to lower non-adjacent levels in a linear fashion (Hunter and Price 1992, Strong 1992, Polis and Strong 1996). Second, many vascular plants have evolved physical or chemical defenses against herbivory, and plant communities as a whole are not palatable to herbivores (Strong 1992) and loss of undefended plant species or biomass may be compensated for by increased biomass of defended plants (Strong 1992, Schmitz 1994, Persson 1999). Third, top-down forces may be weakened by factors that reduce predator efficiency, such as territoriality, competition for other resources (e.g. water, nesting habitat) (Power 1992, Polis and Strong 1996), and environmental heterogeneity in

space and time that may provide refugia for herbivores (Hunter and Price 1992, Polis and Strong 1996).

Strong (1992), Polis and Strong (1996), and Polis et al. (2000) predicted that trophic cascades should be expected in low diversity systems that approach the structural simplicity of a food chain and in those which have vulnerable plant communities. Examples include simple agricultural systems and freshwater systems with algae at their bases. In freshwater aquatic systems, effects of piscivorous fish populations may cascade through four trophic links (Power et al. 1985, Carpenter et al. 1985, Brett and Goldman 1996, Carpenter et al. 2001) resulting in low biomass of algae, which supports the EEH hypothesis for four level systems. Trophic cascades are the basis for biological control programs in artificially simple agricultural systems (Polis et al 2000), in which predaceous insects have been shown to reduce insect pest populations and indirectly reduce damage to crop plants in agricultural systems (Carter and Rypstra 1995, Cerruti et al. 2003).

#### Trophic Cascade Experiments

Top predator removal by humans has produced easily observed cascading effects in some systems. The best-known example from North America is probably the extirpation of gray wolf (*Canis lupus*) populations which has reduced forest regeneration, understory vegetation biomass, and plant diversity due to ungulate over-browsing (Pace et al. 1999, McLaren and Peterson 1994, Rooney and Waller 2003, for additional examples cascading effects of top predator removal see Paine 1980, Pace et al. 1999, Wootton 1994, Terborgh et al. 2001). Varying predator abundance in designed experiments has demonstrated significant effects of predators on plants in a variety of terrestrial predator-herbivorous insect-plant systems (Spiller and Schoener 1990, Dial and

Roughgarden 1995, Karhu 1998, Letourneau and Dyer 1998, Moran and Hurd 1998, for reviews see Pace et al. 1999, Schmitz et al 2000, Halaj and Wise 2001).

Marquis and Whelan (1994) predicted that birds should have strong, positive indirect effects on plants on which they forage, based on three lines of evidence: 1) insect herbivory can reduce the growth of plants; 2) birds are conspicuous predators of defoliating insects and limit insect populations in many systems; and 3) bird exclosures increase insect herbivore damage on study plants relative to controls.

Insect defoliation of many tree species reduces the rate at which trees accumulate woody biomass, and the effect generally is proportional to the severity of defoliation (Muzika and Liebhold 1999, Goyer and Chambers 1997, Souther-Effler 2004, Tucker et al. 2004, Chambers et al. 2005, for a review see Smith and Mittler 1971). Birds are conspicuous predators of defoliating insects and they have the potential to consume large numbers of forest insects because of their mobility and high metabolic rates (Kirk et al. 1996). Most breeding passerine birds in temperate forests feed primarily on insects (Holmes and Schultz 1988), and birds have been shown to have significant impacts on low and moderate populations of forest insects (Dahlsten and Copper 1979, Holmes et al. 1979, Loyn et al. 1983, Crawford and Jennings 1989, Torgerson et al. 1990, Gunnarsson 1996, Parry et al. 1997, Sanz 2001, see Otvos 1979 and Holmes 1990 for reviews).

Caterpillars are the most important insect taxon in the diets of breeding passerine birds in temperate forests (Holmes and Schultz 1988). Many species of caterpillars are folivorous, relatively large, conspicuous on leaf surfaces and are energetically profitable food items for insectivorous birds (Holmes and Schultz 1988). Birds may exhibit numerical and or functional responses to outbreaks of caterpillars (Morris et al. 1958, Buckner and Turnock 1965, Holmes

and Schultz 1988, Crawford and Jennings 1989, MacCulloch 2001), and they have the potential to destroy enormous numbers of caterpillars. Turček (1957 as cited in Bruns 1960) found that Great Tits consumed 50 Tortricid moth caterpillars (10-15% of their body weight) in 90 minutes, an estimated that Great Tits consume 300 of these caterpillars per day. In a study of bird predation of spruce budworm (*Choristoneura fumiferana*) in New Hampshire and Maine, Crawford and Jennings (1989) estimated that more than 85,000 spruce budworms/ha were consumed by just five bird species within the bird community during low and transitional spruce budworm infestations. Takegawa and Garton (1984) examined stomach contents of Evening Grosbeaks (*Coccothraustes vespertinus*) and estimated that individual birds ate 12,600-26,400 western spruce budworms (*Choristoneura occidentalis*) over the course of a year during an outbreak in Washington, and the entire bird community was estimated to consume 7-12.7 million budworms per square kilometer.

As caterpillar populations increase to epidemic levels however, the proportion of the caterpillar population eaten by birds decreases (Bruns 1960 and references therein, Crawford and Jennings 1989, for reviews see Otvos 1979 and Holmes 1990) due to satiation, or territorial behavior exhibited by most breeding insectivorous birds. Thus, cascading effects of birds on plants may be damped during insect outbreaks. Holmes (1990) suggested that although birds may not have significant impacts on epidemic populations of caterpillars, birds may increase the time it takes for caterpillar populations to reach epidemic populations, increase the rate at which caterpillar populations decline following outbreaks, and increase the periodicity of caterpillar outbreaks.

In many, (Atlegrim 1989, Bock et al. 1992, Marquis and Whelan 1994, Sipura 1999, Strong et al. 2000, Greenburg et al. 2000, Murakami and Nakano 2000, MacCulloch 2001, Sanz

2001, Van Bael et al. 2003, Van Bael and Brawn 2005) but not all (Forkner and Hunter 2000, Lichtenberg and Lichtenberg 2002) studies of bird-herbivorous insect-plant systems, birds decreased insect-herbivore damage on plants by reducing local abundance of insect-herbivores (see the literature review this volume). In several of the aforementioned studies bird exclosures were erected around plants, and leaf damage on accessible plants was compared to controls.

The bird exclosure study by Marquis and Whelan (1994) is the most frequently cited positive evidence for the operation of trophic cascades in terrestrial systems. Marquis and Whelan (1994) caged white oak (*Quercus alba*) saplings in Missouri for two years and compared insect abundance, leaf damage and leaf, twig and total aboveground biomass production of caged saplings to saplings that were sprayed with insecticide and controls. Numbers of leaf chewing insects were consistently, and frequently significantly higher on caged trees, lowest on sprayed trees, and intermediate on control trees. Reduction of leaf chewing insects by birds resulted in a similar, significant pattern of leaf damage among treatments; leaf damage was greatest on caged trees, lowest on sprayed trees, and intermediate on controls. Effects of leaf damage led to significant differences in leaf production and total aboveground biomass production between treatments; caged trees produced one-third less aboveground biomass than sprayed trees, primarily due to reduced leaf biomass production in caged trees, with controls producing intermediate values.

A similar study on white oak saplings under two canopy classes in Arkansas found that excluding birds had no effect on abundances of leaf-chewing insects relative to controls, although leaf damage was significantly higher in the cage treatment (Lichtenburg and Lichtenburg 2002). Other bird exclosure studies have found that birds reduce leaf damage on plants, but biomass production is generally not less than that of controls (Strong et al. 2000,

Forkner and Hunter 2000). Meta-analyses of trophic cascade experiments performed by Schmitz et al. (2000) and Halaj and Wise (2001) confirm that indirect effects of predators on plants have strong positive effects on leaf damage, but generally attenuate before affecting biomass production.

Strong et al. (2000) performed a bird exclusion study on understory sugar maple (*Acer saccharum*) saplings in New Hampshire, similar to the study by Marquis and Whelan (1994), but included a caterpillar addition treatment in their design. Caterpillar populations on trees varied among treatments, but pooled arthropod censuses showed that caterpillar populations on trees in the caterpillar addition treatment were reduced to levels similar to those on caged trees, presumably due to bird predation. Leaf damage on trees in the caterpillar addition treatment was greater than that of caged trees in only one of two years. Presumably, these similarities between caterpillar addition and caged trees were due to the response of birds to the increased prey abundance on trees with the caterpillar addition treatment. Treatment effects on leaf damage were significant and similar to those observed by Marquis and Whelan (1994); leaf damage was highest on caged trees, lowest on sprayed trees, and intermediate on control trees. However, increased leaf damage did not produce a significant effect on aboveground biomass production. Strong et al. (2000) hypothesized that this may have been due to lower density of caterpillars on study trees in New Hampshire relative to the Missouri study.

A criticism of many published trophic cascade studies is that most report on cascading effects of predators on a single plant species, and not on the entire plant community as in a classical trophic cascade (but see Moran and Hurd 1998). Therefore, Polis et al. (2000) argued that evidence for trophic cascades, even within a subset of species, is limited. Polis et al. (2000) also suggested that these “species-cascades” do not carry the same biological significance for

ecosystem processes as a community level cascade, unless the affected plant is a dominant species within the ecosystem (Polis et al. 2000).

Indirect effects of predators on ecosystem resilience may be especially important if the receiver plant species is a foundation species within the ecosystem (Polis et al. 2000, Scheffer et al. 2001, Terborgh et al. 2001). A foundation species is “a single species that defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes” (Dayton 1972, as cited in Ellison et al. 2005). Outbreaks or introductions of insect herbivores are contributing to the loss of foundation tree species in North American forest ecosystems (Ellison et al. 2005) and loss of these species may destabilize forest ecosystems (Scheffer et al. 2001).

The great difference in time scale of plant dynamics between terrestrial and aquatic systems has been cited as a possible cause for the differing results between aquatic and terrestrial trophic cascade experiments (Pace et al. 1999, Chase 2000, Holt 2000, Power 2000, but see Bell et al. 2003). Most studies of predator-herbivore-tree interactions have been restricted to short-term studies on sapling trees, which are less productive and therefore less likely to exhibit positive effects of predators (Strong et al. 2000, Van Bael et al. 2003, Van Bael and Brawn 2005). While decreased predator abundance may not produce a statistically significant effect on biomass production of a plant in any given year, the cumulative impact of increased herbivory over several plant generations might affect plant competitive ability and community composition (Holt 2000), plant productivity (Marquis and Whelan 1994), and ecosystem resilience (Scheffer et al. 2001, Ellison et al. 2005).

The decline and loss of foundation tree species within forested ecosystems has caused changes in their associated bird communities (Darveau et al. 1997, Tingley et al. 2002, Zoller

2004). Darveau et al. (1997) found that breeding bird species richness and abundance, but not herbivorous insect abundance, was correlated with declining forest health. Furthermore, populations of many insectivorous bird species have declined in recent decades (Sauer et al. 2005). Declines in forest-bird populations may have implications for forest productivity and stability due to a negative feedback loop on forest health caused by reduced bird predation on defoliating insects and subsequent increased insect herbivory (Marquis and Whelan 1994, Murakami and Nakano 2000).

Forest ecosystems which possess only one or two foundation species are inherently less resilient to disturbance due to their lack of functional redundancy (Ellison et al. 2005). Gradual anthropogenic changes in abiotic conditions may decrease the resiliency of ecosystems, making them more prone to undergo catastrophic shifts to alternate stable states following perturbations (for reviews see Scheffer et al. 2001, Folke et al. 2004). Cypress-tupelo swamp forests in coastal Louisiana are an example of such a forest ecosystem.

### Coastal Forest Loss

Greater than 50% of the remaining forested wetland in the LMAV is in Louisiana (Twedt and Loesch 1999), but much of the forested wetland in coastal Louisiana is at risk of converting from cypress-tupelo swamp forest to open marsh (Shaffer et al. 2003, Chambers et al. 2005). It is estimated that 42% of the remaining swamp in the Louisiana Deltaic Plain will be lost by 2050 (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1998, hereafter cited as Coast 2050 1998). The causes of wetland loss in Louisiana are complex and involve both natural and anthropogenic changes to the hydrology of the region and their interactions (Day et al. 2000, Day et al. 2001, Gosselink 2001, Chambers et al. 2005, for extensive reviews of the causes of

wetland loss in coastal Louisiana see Boesch et al. 1994, Coast 2050 1998, Louisiana Coastal Area Comprehensive Ecosystem Restoration Study 2004, hereafter cited as LCA 2004).

The cumulative effects of natural and anthropogenic alterations to the hydrology of Louisiana's coastal forests have been acting to destabilize these ecosystems for almost 200 years. These forests have only two foundation tree species (baldcypress and water tupelo), and both of these tree species have been subject to widespread, repeated defoliation by caterpillars in recent decades. The cumulative impacts of hydrological alterations, insect defoliation and the interactions of these stressors have threatened the entire coastal ecosystem with ecological collapse (Coast 2050 1998).

Almost all of the merchantable cypress stands were harvested in southern Louisiana from 1890 to 1925 (Mancil 1980). Following the mass-harvest of baldcypress-tupelo swamp in Louisiana, some forests regenerated naturally due to favorable regeneration conditions in the 1920s (Chambers et al. 2005). However, altered hydrological conditions in many of Louisiana's coastal forests have reduced or eliminated natural regeneration of baldcypress and water tupelo, and reduced these trees productivity (for a review see Chambers et al. 2005).

The main natural cause of wetland loss in coastal Louisiana is relative sea-level rise (RSLR) due to subsidence and eustatic sea-level rise (Day and Templet 1989, Boesch et al. 1994 Coast 2050 1998). The main anthropogenic cause of wetland loss in coastal Louisiana is the interruption of natural deltaic building processes by the construction of flood control levees, and the construction of canals for logging, shipping and oil extraction operations (Day and Templet 1989, Boesch et al. 1994, Coast 2050 1998, Day et al. 2000, LCA 2004). By 1828 levees along the Mississippi River were nearly continuous from Baton Rouge to New Orleans (McPhee 1987), and many distributary channels into coastal wetlands had been dammed (McPhee 1987, Day and

Templet 1989). Therefore, flood control levees have reduced or eliminated mineral sediment accretion in most coastal wetlands for almost 200 years. Canals have facilitated the flow of saltwater into formerly freshwater ecosystems (Boesch et al. 1994, Coast 2050 1998, LCA 2004).

Flooding (Hook et al. 1970 as cited in Dickson and Broyer 1972, Dickson and Broyer 1972, Harms 1973, Conner and Day 1976, Conner et al. 1981, Conner and Day 1992, Megonigal and Day 1992, Keeland and Sharitz 1995, Goyer and Chambers 1997, Souther 2000, Shaffer et al. 2003, Souther-Effler 2004) and saltwater intrusion (Pezeshki et al 1989, Shaffer et al. 2003, Souther-Effler 2004) into formerly freshwater wetlands reduces productivity of swamp forest tree species. Interactions between flooding and salinity stressors may further reduce swamp forest tree productivity (Pezeshki et al. 1987, Pezeshki et al. 1989, Pezeshki et al. 1990, McCarron et al. 1998, Souther-Effler 2004).

The elevation of some coastal wetlands is maintained by organic sediment input from wetland plants (McCaffrey and Thomson 1980), which may account for up to 50% of sediment accretion (Day and Templet 1989, Coast 2050 1998). Therefore, effects of flooding, salinity, and interactions of these stressors on plant productivity produce a negative feedback loop in which decreased plant productivity decreases organic sediment accretion and increases the rate of RSLR (Nyman et al. 1993). Levee construction has produced another negative feedback loop where mineral sediment accretion deficits increase the rate of RSLR, which decrease plant productivity due to flooding, salinity stress and nutrient starvation. These plant stressors reduce organic sediment accretion and further increase the rate of RSLR. These stressors and negative feedback loops have been operating for as much as 200 years without significant amelioration, and have increased the precariousness of the entire coastal wetland ecosystem.

## Caterpillar Herbivory in Coastal Forests

In addition to flooding, salinity, and interactions of these stressors, baldcypress and water tupelo in coastal forests of Louisiana have been subject to repeated annual herbivory by caterpillars in recent decades. The main insect herbivore of water tupelo in coastal forests of Louisiana is the forest tent caterpillar (*Malacosoma disstria*, hereafter referred to as FTC). Large outbreaks of FTC have been recorded in Louisiana since 1931 and FTC defoliate 120,000-240,000 ha of swamp forest in Louisiana each spring (Goyer et al. 1990). Female FTC in Louisiana produce twice as many eggs compared to FTC populations in the northern United States and Canada (Parry et al. 2001) and starvation is the primary agent of FTC mortality in coastal forests in Louisiana (Rejmánek et al. 1987, R. Goyer personal communication). Low mortality from natural enemies coupled with high reproductive rates of FTC in flooded swamp forest in Louisiana produce starvation driven cycles of caterpillar outbreaks (Smith and Goyer 1986, Parry et al. 2001) which are predicted to occur on average every five years (Rejmaneck et al. 1987).

Baldcypress had been noted for its lack of serious insect pests for decades (Brown and Montz 1986), until the discovery of an emerging pest species of baldcypress in southern Louisiana, the baldcypress leafroller (*Archips goyerana*, hereafter referred to as BCLR) in 1983. By 1993 BCLR had infested 70% of the entire growing stock of baldcypress in Louisiana (Meeker and Goyer 1993). BCLR feed exclusively on baldcypress foliage (Meeker and Goyer 1994) and outbreaks of BCLR have occurred annually since their discovery (Goyer and Chambers 1997). BCLR have defoliated the baldcypress component of as much as 200,000 ha of swamp forest in a single year (Chambers et al. 2005). High populations of BCLR are expected to persist in the forested wetlands of southern Louisiana, causing decreased growth,

dieback, and mortality of stressed baldcypress trees (Goyer and Chambers 1997, Ward and Mistretta 2002).

Repeated defoliation of water tupelo in Alabama by FTC over 20 years has reduced radial growth by as much as 75% (Batzer and Morris 1978). Simulated, complete defoliation reduced height growth and biomass production of 2-year-old water tupelo seedlings; however salinity stress lowered biomass production more than defoliation (Souther-Effler 2004). Conner and Day (1992) found that mature water tupelo began diameter growth later in the spring and grew more slowly than did baldcypress, and they hypothesized that this was due to the energetic cost of refoliating the crown following spring defoliation by FTC. There was also a direct, linear relationship between percent defoliation and annual diameter growth of baldcypress (Chambers et al. 2005), perhaps due to the energetic cost of refoliating the crown, as in water tupelo.

Insect predators and parasites of FTC may require dry soil conditions to complete their life cycle (Smith and Goyer 1986, R. Goyer, personal communication), and may not respond to caterpillar outbreaks in frequently flooded forests in a density dependent fashion.

Braun et al. (1990) and Wei (1996 as cited in Goyer and Chambers 1997) found no egg parasitoids of BCLR, and predators, parasites and viruses appear to have only a damping effect on BCLR populations (Goyer and Chambers 1997), resulting in persistently high BCLR populations (Goyer and Chambers 1997). Goyer and Chambers (1997) found that defoliation ratings of trees in seasonally flooded and permanently flooded plots were greater than those of trees on drier plots. This might be due in part to negative effects of flooding on the predator and parasite community observed in FTC parasite populations (Smith and Goyer 1986).

Because insect enemies of caterpillars may be rare in frequently flooded coastal forests, the relative importance of birds as agents of caterpillar mortality may be increased. Many bird

species are known to depredate tent caterpillars (Witter and Kulman 1972, as cited in Parry et al. 1997), but FTC are protected by setae, and many birds have been observed to eat only the viscera of late-instar FTC (Parry et al. 1997 and citations therein). Parry et al. (1997) found that bird predation was more influential in depressing experimental populations of final-instar FTC larvae and pupae than parasitoid insects in Canada. However, Smith and Goyer (1986) and other studies cited in Parry et al. (1997) found that bird predation accounted for only a small percentage of FTC pupal mortality. Braun (1990) listed Prothonotary Warblers (*Protonotaria citrea*, hereafter referred to as PROW) as one of the main avian predators of BCLR in infested coastal forests. The PROW is a Neotropical migratory warbler which breeds in high densities in coastal forests in Louisiana (Carter et al. 2000, personal observations) Eighty-five percent of PROW breed within the LMAV, and the PROW is ranked second only to the recently rediscovered Ivory-billed Woodpecker (*Campephilus principalis*) in terms of conservation concern by The Neotropical Migratory Bird Conservation Program ([www.rmbo.org/pif/scores/scores.html](http://www.rmbo.org/pif/scores/scores.html), Carter et al. 2000).

Bird species richness is generally highly correlated with foliage height diversity (MacArthur and MacArthur 1961). Zoller (2004) confirmed this correlation in the Maurepas Swamp; species richness and abundance of forest birds in the Maurepas Swamp was highly correlated with foliage structural complexity. Zoller (2004) found that species richness and abundance of forest birds in the Maurepas Swamp was lower, although not significantly so, between healthy and degraded swamp during the breeding season because of increased shrub and herbaceous vegetation in degraded swamp. However, breeding bird species richness and total bird abundances were much greater than in marsh habitat (Zoller 2004).

Although Zoller (2004) found that forest bird species richness and abundance were not significantly different between healthy and degraded swamp, overall tree mortality in some degraded swamp is 2% per year (Shaffer et al. 2003). It is estimated that 42,460 ha of swamp will be lost in the Pontchartrain Basin alone by 2050 (Coast 2050). Therefore, as trees die due to stress, and formerly forested sites transition to open marsh, populations of forest birds will decline over an increasing area. The loss of bird species richness may result in decreased functionality of the insectivorous bird guild and increase caterpillar herbivory on remaining trees, decreasing the stability of the swamp ecosystem even further, and accelerating the rate at which degraded swamp transitions into open marsh.

#### The Maurepas Swamp

The Maurepas Swamp (Photograph above map in Figure 3-1) contained 57,000 ha of the remaining swamp forest in 1990 (Lane et al. 2003, as cited in Souther-Effler 2004), and it is still one of the largest, contiguous tracts of wetland forest remaining in the LMAV. The Maurepas Swamp was almost completely deforested by logging operations from 1900-1925 (Mancil 1980, A. Dranguet personal communication). Some of the cypress-tupelo forest in the Maurepas Swamp regenerated following logging operations (G. Shaffer personal communication). However, like most coastal forests in Louisiana, regeneration and productivity of baldcypress and water tupelo in the Maurepas Swamp is inhibited by increased flooding depth and duration, salt water intrusion, and defoliation by caterpillars (Shaffer et al. 2003). The Maurepas Swamp has been isolated from riverine inputs of freshwater, nutrients and sediment for almost 200 years, due to flood control levee construction and the damming of Bayou Manchac, the only east-flowing distributary of the Mississippi River in the region, during the War of 1812.

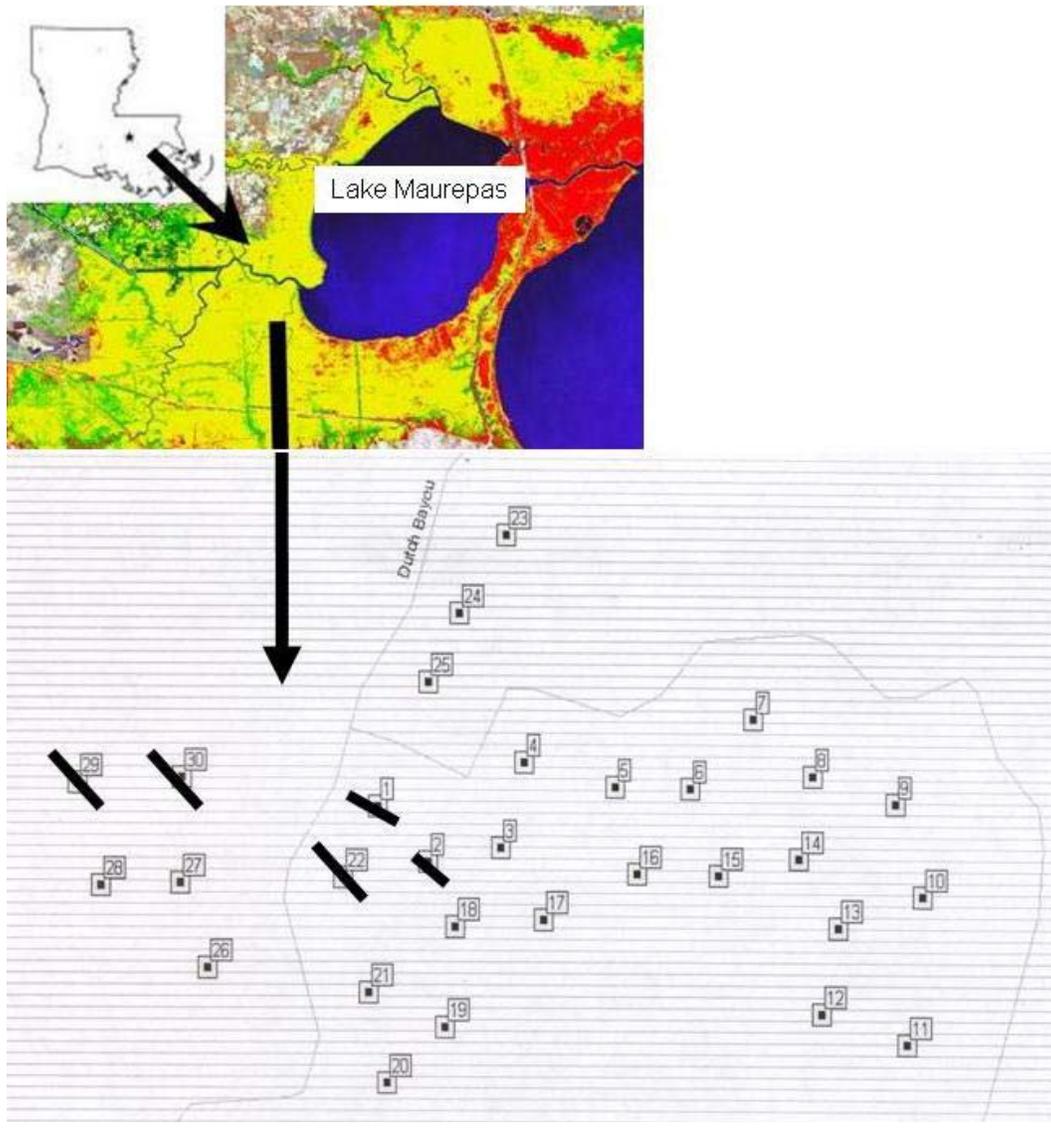


Figure 3-1. Map of study sites used in 2004-2005 in the Maurepas Swamp WMA, Louisiana. Lines through plots indicate that the plot was partially or completely destroyed by nutria, or dropped from the study. Image above map courtesy G. Shaffer and J. Zoller.

Much of the degraded forest in the Maurepas Swamp is beginning to transition to open marsh (Shaffer et al. 2003). Shaffer et al. (2003) reported that overall tree mortality in degraded swamp is approximately 2% per year. Approximately two-thirds of the swamp is currently in a highly degraded state (shown in yellow in Figure 3-1) and 16% of the swamp has already

converted to open marsh or open water ( shown in red in Figure 3-1) (J. Zoller personal communication, Chambers et al. 2005). As swamp forest health and canopy cover decline the ecological services of coastal forests that cannot be supplied by coastal marshes, and upon which human and wildlife populations depend, will be lost.

#### Restoration Efforts in the Maurepas Swamp

Diversions of freshwater from the Mississippi River into degraded swamps and marshes have been suggested as a method for ameliorating freshwater, nutrient and mineral sediment deficits caused by levee construction (Day et al. 2000, Höppner 2002, Shaffer 2003). A diversion of water from the Mississippi River into the Maurepas Swamp via Hope Canal has been planned, and is in the final stages of design (LCA 2004, G. Shaffer personal communication). Positive effects of freshwater flushing, and input of nutrients and sediment should offset negative effects of increased flooding of swamp forest caused by the diversion (G. Shaffer, personal communication). However, increased flooding, albeit with fresh water, will retard natural regeneration of baldcypress and water tupelo (Souther 2000). Therefore, the diversion will need to be closed periodically to allow forest regeneration after abiotic conditions have been improved (Souther 2000, G. Shaffer personal communication).

Baldcypress and water tupelo have exacting germination and seedling establishment requirements (Demaree 1932, Souther 2000, Huenneke and Sharitz 1990). Therefore, planting baldcypress and water tupelo seedlings may accelerate forest restoration, especially at the beginning of operation of the Maurepas Swamp diversion. When adequately protected from nutria (*Myocastor coypus*) and other herbivorous mammals, artificial baldcypress regeneration success in the southeastern United States has generally been high, and planted seedlings have

occasionally grown better than naturally regenerated trees (for a review see Chambers et al. 2005). However, baldcypress planting-success in the Maurepas Swamp has been variable.

No water tupelo regeneration has been observed during 15 years of research in the Maurepas Swamp (G. Shaffer, personal communication). Baldcypress regeneration in degraded swamp is widely scattered, and appears to occur mainly on coarse woody debris (CWD) left from logging operations or on fallen trees (personal observations). CWD may provide micro-relief for the germination and establishment of baldcypress seedlings in the permanently flooded conditions in the swamp (Chambers et al. 2005), but logs are poor sites for regenerating water tupelo seedlings (Huenneke and Sharitz 1990). As CWD decomposes and RSLR increases, the probability of natural regeneration of baldcypress and water tupelo regeneration decreases. In areas where natural regeneration of baldcypress and water tupelo is doubtful, planting of seedlings may be necessary to ensure that stands are adequately stocked (Chambers et al. 2005).

The east side of Lake Maurepas transitioned into open marsh in the 1950s (G. Shaffer personal communication) and is generally more saline than more forested areas on the west side of the lake (Shaffer et al. 2003). Baldcypress seedlings planted on the east side of Lake Maurepas between 1991 and 1996 had 78% survival in 1998 when protected from nutria, but nearly 100% mortality when unprotected (Myers et al. 1995, as cited in Chambers et al. 2005). Most surviving seedlings subsequently died during a drought in 1999-2000, because of increased interstitial salinity (Shaffer et al. 2003). Thousands of baldcypress seedlings have been planted in marsh on the east side of Lake Maurepas each year since 1999, but most have been killed by salinity stress and nutria herbivory (Chambers et al. 2005, M. Greene personal communication). Greene (1994) found that diameter growth of baldcypress seedlings planted in marsh on the east

side of Lake Maurepas is reduced by 25% when climbing vines are allowed to entangle seedlings.

Survival of planted baldcypress on the west side of Lake Maurepas is better. A property owner, Glen Martin, has established a wetland mitigation bank of baldcypress plantings near Blind River. Martin plants thousands of baldcypress saplings each spring, grown from locally collected seed sources, and survival is 80-90% (Chambers et al. 2005, J. Robinson personal communication). Beville (2002) planted baldcypress seedlings on both the east and west sides of Lake Maurepas, and both groups experienced high mortality. Seedling protectors were only nominally effective on the east side where 85% were destroyed by nutria and nearly all other seedlings were killed by salinity. Seedling survival was better on the west side, but still only 26%.

Only one effort has been made to plant water tupelo in the Maurepas Swamp. “A couple of thousand” water tupelo seedlings were planted on the east side of Lake Maurepas in marsh on Jones Island in the 1999-2000 planting season (M. Greene and G. Shaffer personal communication). “A few” lived for at least two years, but none are known to survive today (M. Greene personal communication). No water tupelo seedlings have been planted on the west side of the lake.

## **Objectives**

The objectives of this study were:

- 1) Determine if planted baldcypress and water tupelo seedlings survive and grow in degraded areas of the Maurepas Swamp.

Baldcypress seedlings survive and grow on the west side of Lake Maurepas, sometimes with high survival rates, but growth rates have not been determined for a large sample of trees

(Beville 2002). Water tupelo seedlings do not survive in marsh on the east side of Lake Maurepas (M. Greene personal communication), but no planting experiments have been conducted on the west side of the lake. I hope to determine survival and growth rates of planted baldcypress and water tupelo seedlings in degraded swamp on the west side of Lake Maurepas. I expect to find that water tupelo planted on the west side of the lake have lower survival and growth rates than baldcypress, but that survival will be higher than that on the east side of Lake Maurepas.

2) Determine if birds reduce insect-herbivore damage to planted baldcypress and water tupelo, and whether defoliation affects height and diameter growth of these trees.

Evidence for trophic cascades operating on understory trees is equivocal. However BCLR are known to congregate on understory saplings (Goyer and Chambers 1997), and birds may show functional responses to increased caterpillar populations (Strong et al. 2000). PROW generally forage below 7m (Petit 1999), and in some areas frequently forage below 3m (D. Drumtra personal communication, personal observations). Therefore I expect that birds will respond to these BCLR infestations and reduce leaf damage. The Maurepas Swamp offers the opportunity to test a system in which birds are probably the most important agents of caterpillar mortality as compared to terrestrial systems with diverse insect predators (Goyer et al. 1990, Goyer and Chambers 1997). While birds are a major source of caterpillar mortality in swamp forest (Braun et al. 1990), it is uncertain whether bird predation of caterpillars will be beneficial to small, planted trees. I expect to find that trees accessible to birds experience less leaf damage than caged trees, and that decreased leaf damage will result in increased height and diameter growth.

I am not aware of any studies that have investigated the effects of insectivorous birds on defoliation of baldcypress and water tupelo, or in any type of flooded forest ecosystem. Strong et al. (2000) suggested that a more complete bird exclosure experiment would include insectivore abundance in analyses, and this is the only study of which I am aware in which abundance of insectivorous birds, including their breeding stage, will be quantified for the purpose of correlating insectivorous bird abundance with defoliation and tree growth measurements. Furthermore, I am unaware of any study that examines the effect of insectivorous birds on tree growth within the context of habitat restoration.

3) Describe foraging behavior of common insectivorous birds on BCLR and FTC.

The main goal of this portion of the study was to determine whether birds consume BCLR and FTC, and whether PROW provision their nests with these caterpillars. I am not aware of any studies that have investigated the effects of birds on BCLR, nor am I aware of any studies of the effects of birds on FTC in cypress-tupelo forests. I expect to find that birds eat both FTC and BCLR. FTC are protected by setae, therefore I expect to find that birds prey upon FTC less frequently than BCLR, and they may exhibit feeding behaviors to avoid their setae.

## **Methods**

### **Study Area**

Lake Maurepas is a 235-km<sup>2</sup> oligohaline lake located in the Pontchartrain Basin in southeast Louisiana. The area surrounding Lake Maurepas was nearly contiguously forested baldcypress-tupelo swamp until it was completely logged in the early 1900s. Most of the forest which regenerated following logging has become severely degraded, primarily due to regional hydrological alterations. Forest degradation and/or poor regeneration has resulted in a mosaic of wetland habitat types in the Maurepas Swamp, generally on a salinity gradient from east to west.

Wetlands on the east and south sides of Lake Maurepas are more saline (Shaffer et al. 2003), and most of these wetlands adjacent to the lake have transitioned to open marsh. The west side of the lake receives some riverine input of freshwater from the Amite River Diversion Canal and storm water run-off from Hope Canal and is less saline (Shaffer et al. 2003). However, most of the swamp forest on the west side of the lake is degraded.

I conducted this study in degraded swamp habitat on the west side of Lake Maurepas in the Maurepas Swamp Wildlife Management Area (WMA). The Richard King Mellon Foundation donated two tracts of swamp forest within the Maurepas Swamp, totaling more than 25,300 hectares, to the Louisiana Department of Wildlife and Fisheries in 2001. These forest tracts became the Maurepas Swamp WMA. The Maurepas Swamp WMA is located along the south shore of Lake Maurepas beginning about 40km west of New Orleans and extending west to Sorrento, Louisiana, with the two tracts straddling a private inholding along Hope Canal on the west side of Lake Maurepas.

#### Study Plot Selection

In the winter of 2004, I established 30 study plots in degraded swamp adjacent to Dutch, Mississippi and Tent Bayous in the Maurepas Swamp WMA (Figure 3-1). The center point of each plot was >100m from neighboring points to ensure independence for territories of the most common insectivorous birds. Points were established >75m from the edge of major bayous to avoid edge effects. Center point coordinates and distances between points were obtained with a hand-held Garmin® GPS unit.

#### Tree Planting

I obtained one-year-old baldcypress and two-year-old water tupelo nursery stock from the Louisiana Department of Natural Resources Nursery in Monroe, Louisiana in February 2004.

Trees were kept in cold storage until they were taken to the field for planting. Seedlings were sorted roughly by size before planting to make an attempt to plant larger seedlings in areas with deeper flooding and increase seedling survival rates during the study. Seedlings were marked with tree marking paint 8cm above the root collar, and diameters were measured 2cm above the paint mark (10cm above the root collar). Paint marks were made below the point where diameters were measured because tree-marking paint may cause growth irregularities (J. Chambers, personal communication). Seedling height was measured from the root collar to the end of the longest shoot. Seedling diameters were measured with calipers 10cm above the root collar (2cm above the paint mark) to the nearest tenth of a millimeter. Baldcypress seedlings were 37-109cm tall ( $77.9 \pm 0.80$  SE) and 5-17mm diameter ( $9.3 \pm 0.15$  SE). Water tupelo seedlings were 48-97cm tall ( $70.7 \pm 0.61$  SE) and 4.3-18mm diameter ( $8.4 \pm 0.11$  SE).

Between 9 February and 21 March 2004, nine of each tree species were planted with a dibble or by hand, within 15m of the center point of each of the 30 study plots. Trees were planted on the highest ground available, and an attempt was made to plant trees at least 1m from conspecific crowns. Each tree was protected from nutria damage with a Vexar® mesh tree protector. Twice during the 2004 growing season, competing herbaceous vegetation within a 1m radius of each planted tree was flattened by stepping upon it, and herbaceous vegetation growing within tree protectors was removed periodically in 2004 to reduce competition with other plants and improve survival during the first year of the study. Greene (1994) found that entangling vines can reduce growth of planted baldcypress, so entangling vegetation was cleared from tree crowns periodically throughout the study. The proportion of the crown shaded by herbaceous vegetation was estimated in summer 2005 for inclusion as a covariable in statistical analyses (see

below). Three of each tree species within each plot were randomly assigned to one of the following treatments: control, *Bacillus thuringiensis* insecticide spray, or bird enclosure.

#### Insecticide Treatment

*Bacillus thuringiensis* var. *kurstaki* (hereafter referred to as Bt) is a biological control agent that is species-specific to caterpillars and larvae of some beetles and mosquitoes (Swadener 1994). The alkaline environment of insects' guts transforms protein crystals within bacterial spores into an endotoxin, which then create pores in the midgut membrane. Affected insects stop feeding and starve to death. Bt is the only type of insecticide approved for use in wetland environments in Louisiana (R. Goyer personal communication). Bt is effective in reducing caterpillar populations (Rodenhouse and Holmes 1992), including FTC (Abrahamson and Harper 1973) and BCLR (R. Goyer personal communication) caterpillar populations.

I used Thuricide® (Certis USA) formulation of Bt, which is readily available in local gardening stores. Thuricide was mixed to the manufacturer's specifications for fruit trees, and applied with a spray bottle until all leaf surfaces were wet, or covered with droplets. Bt is degraded by UV light, so trees were sprayed as late in the day as possible, generally after 3pm. Trees were sprayed before the fourth instar stage of BCLR in both years. Trees assigned to the Bt treatment were sprayed once on 19-21 April 2004, and in 2005 Bt was applied on 4-7 April and again on 23 April-1 May. In 2005, during the second Bt application, all obvious herbivorous insects were manually removed from study trees.

#### Bird Enclosures

Bird enclosures were constructed from ½" PVC pipe, ½" steel conduit and agricultural bird netting with a 1" mesh. Crosspieces were constructed by inserting two 2.5' sections of ½" PVC into a 3-way ½" PVC connector, in parallel. A 1/8" diameter hole was drilled through the

top of three-way PVC connector, then a 1" bolt was dropped into the connector, and the threaded end was pulled out through the top of the connector. One-eighth inch holes were drilled at mid-length through five-foot lengths of ½" diameter PVC pipe, and then the 5' length of PVC was bolted to the three way connector to form crosspieces with 5' diagonals. A 1/8" groove was cut into the end of each arm of the crosspieces, perpendicular to the opening of the PVC. A loop of twine was seated in these grooves around the perimeter of the PVC crosspieces, and the twine was tightened and tied to hold the arms of the cross pieces at right angles. Crosspieces were collapsed and reassembled in the field.

Nets were constructed with agricultural bird netting (supplied by J& M Industries, Ponchatoula, Louisiana) with a mesh width of approximately 2.5-cm. Thirty-foot long sections of bird netting were folded to halve their length, and then the cut ends were sealed with clear packing tape to form 15' tall cylinders. One end of each cylinder was tied closed with twine to form 15' tall "bags" of netting. These net bags were laid flat, then rolled and stored in plastic bags for transport into the field.

In the field, a 5' section of steel conduit was driven vertically into the substrate next to trees assigned to the bird exclosure treatment as deeply as possible while still allowing the netting to be arranged around the tree without touching the branches. A short (6-10-cm) sleeve of ½" PVC was fitted on the upper end of the conduit, and a ½" PVC connector was fitted on the upper end of this sleeve (however, this step was found to be unnecessary as ½" diameter PVC pipe fits snugly around ½" diameter steel conduit). A 5' section of ½" PVC was inserted into the parallel end of the three way connector on top of the conduit, forming a central pillar for the bird exclosure. Crosspieces were then fitted onto the upper end of the central pillar. Twine held the arms of the crosspieces at 90-degree angles and also supported the net material around the

perimeter of the crosspiece. Plastic bottles were fitted onto the distal ends of the arms of the crosspiece to allow netting to slide over the ends of the crosspiece without becoming snagged. Each enclosure frame was enclosed in a net bag with the closed end of the bag at the top of the crosspiece. Slack netting was taken up at the top and tied to the crosspiece, and the bottom edges of the nets were pulled taut and staked to the substrate. Plastic bottles were then removed, and any additional slack was taken up by tying knots into the netting wherever necessary. The height of each enclosure was depended on the height of the tree and the depth to which I could drive the conduit.

In 2004 bird enclosures were placed over study trees between 8 and 21 April, and removed between 3 and 5 May. In 2005 enclosures were placed over study trees between 21 March and 1 April, and removed on 10 June, prior to landfall of tropical storm Arlene.

#### Leaf Damage Estimates

Leaf damage estimation methods differed between tree species. On baldcypress, I counted the total number of leaves and the number of chewed leaves within each crown, and then calculated the proportion of chewed leaves within each crown. On water tupelo I estimated the percent leaf area removed for each leaf, and noted the causative agent (e.g. virus, insect chewing, browning). The total leaf area damaged was then calculated for each water tupelo crown.

Bundle scars from abscised leaves were counted as leaves with 100% damage.

Because tree protectors limited birds' access to foliage within tree protectors, I calculated leaf damage proportions of foliage accessible to birds outside the tree protectors, and for the entire crown. Leaf damage estimates on study trees were performed after caterpillars pupated in both years. Leaf damage estimates were performed on 1-20 June 2004, and 25 May-28 June 2005.

## Tree Growth Measurements

Tree height growth was measured from the paint mark made at 8-cm prior to planting to the end of the longest shoot produced in 2004, and in 2005 height growth was measured to the end of the longest live shoot to determine the final live height at the end of the study.

Incremental height growth of trees in each year was calculated by subtracting the final height at the end of each growing season from the initial height at the beginning of each growing season. Height growth of the 2004 growing season was measured in spring 2005, and height growth of the 2005 growing season was measured in November 2005. In some cases where trees had been clipped at the base by nutria or died from unknown causes, a height growth measurement was made by reconstructing the tree.

A limited number of diameter measurements were made after the 2004 growing-season. However, measurements of 2004 diameter growth were discontinued because it was necessary to cut tree protectors to insert calipers, and nutria had damaged many tree protectors at the same height. Therefore, total diameter growth over the two growing seasons of the study was measured in November 2005.

## Breeding Bird Surveys

Relative abundance of insectivorous birds on study plots was quantified to determine if local bird abundance was negatively correlated with leaf damage on experimental trees. Relative abundance of insectivorous birds was measured by performing 10-minute variable radius point counts at the center point of each plot following modified versions of the Lower Mississippi Valley Joint Venture Program protocol for monitoring forest interior bird populations (Mississippi Valley Joint Venture Program 2004). All birds seen and heard during the 10-minute sampling period were recorded, and the distance from the center point to the location of the bird

was estimated at the time it was first detected. Movements of birds were noted to avoid recounting an individual. Birds flying over the plot were recorded, but not included in analyses. Detections of all bird species at all distances were recorded, but only detections of insectivorous birds within a 50m radius of the center point were used in analyses. I conducted all point counts personally to reduce observer bias.

Breeding bird survey methods differed between years. Point counts are generally limited to times between 30 minutes before sunrise and 10AM (Mississippi Valley Joint Venture Program 2004). However, in 2004 I conducted point counts without regard for time of day, but followed each 10-minute point count with a 50-minute intensive bird survey to locate birds which may not have been detected during late counts and determine the reproductive status of insectivorous birds that included study plots in their territories (resident pairs). Logistical problems with this method (see results) prompted me to alter my point count method in 2005. In 2005, I conducted three rounds of traditional 10-minute point counts which ended before 10:15AM. Point counts were conducted between 24 April and 9 May 2004, and 4-8 April, 16-19 April and 14-18 May 2005.

Nestlings and fledglings of adult birds add to the total number of insectivorous birds in an area. In 2005, I determined if resident pairs of PROW, Carolina Chickadees (CACH) and Northern Parula (NOPA) (see Tables 2-1 and 3-2 for common names) were feeding nestlings or fledglings during the period of BCLR caterpillar activity using behavioral observations collected during point counts and/or observations collected during an intensive bird survey following the last of the three point counts. Intensive bird surveys in 2005 were conducted on each plot on the same day in which the last point count was conducted. Intensive surveys lasted for a maximum

of 50 minutes or until the breeding status for resident pairs of PROW, CACH and NOPA was determined.

Due to unequal sampling effort in 2004, the number of nestlings or fledglings detected was added to the total of the final count in 2005 only. In cases where PROW nests were found and the number of nestlings was known, the number of nestlings was added to the count. NOPA and CACH nests were too high to inspect. In cases where fledglings were detected, a conservative estimate of four fledglings was added to the count for that resident pair of adults.

### Foraging Observations

Foraging substrate preferences may suggest effects of bird foraging on forest succession (Marquis and Whelan 1994). Selective foraging of insectivorous birds on particular tree species may decrease leaf damage, and increase tree growth relative to trees which are foraged upon less frequently by insectivorous birds. Foraging observations of the most common insectivorous birds were collected opportunistically throughout the study in and around study plots during the breeding season in 2004-2005, and a limited number of foraging observations from 2003 collected in the same area were included in the dataset. Foraging observation data were recorded following a reduced version of the classification scheme described by Remsen and Robinson (1990). Bird species, foraging substrate, foraging maneuver height, and when possible, prey species taken were recorded.

### PROW Nest Video Monitoring

I supplemented foraging observation data with video recordings of adult PROW provisioning nestlings. Video recordings were made between 28 April and 13 May 2005, to determine whether adult PROW fed BCLR and FTC larvae and pupae to their nestlings, and the proportion of nestling diet these caterpillars comprised. PROW nests were selected for this study

because they were relatively easy to find, PROW are relatively imperturbable at the nest (personal observations), and several were low enough to place the camera directly next to the nest entrance to view adults' bill contents. Recordings were made with a Canon ZR200Mini DVC and/or a SONY Handycam CCD-TRV308 HI-8 videocassette recorder. Camera battery supply and battery life limited the numbers of recordings to a maximum of four 1-hour recordings per day. The number of recordings of individual nests depended upon the availability, proximity and developmental stage of active nests. Video cameras were mounted on tripods and placed as close to the nest entrance as possible, either by standing the tripod next to the nest, or by strapping the tripod and camera to the nest tree. Videotapes were reviewed in the lab, and the number of provisioning trips per 1-hour sampling period was recorded. Prey items were counted and identified when possible, but in the majority of cases prey were recorded as either BCLR, other caterpillar or unidentified. Recordings of nests in which adults did not visit the nest or females brooded young for extended periods of time were not included in analyses.

### Statistical Analyses

All statistical analyses were performed with SAS 9.1 unless otherwise stated. The significance level for all tests was set at  $\alpha=0.05$ . In cases where main effects were significant at  $\alpha=0.05$ , *a posteriori* Tukey-Kramer adjusted multiple comparison tests were conducted to discern means, and letter groupings were generated with Saxton's Macro (Saxton 1998). Means are reported with their associated standard errors. In post ANOVA or ANCOVA multiple comparisons, Tukey-Kramer adjusted means and their associated standard errors are reported.

Larger trees were planted in more flooded plots to improve survival of trees during the study. Abiotic conditions of plots were expected to vary, but variances due to plot condition were not of interest. Therefore, I blocked analyses *a priori* on plot to remove these sources of

variation. All block interactions were assumed to be non-significant to improve model stability and the power of tests of treatment effects.

To test if treatments affected tree survival, a simple logistic regression of treatment on mortality at the end of the study was performed in PROC LOGISTIC. Trees that did not have treatments applied to them (e.g. those killed by nutria before treatment application) were not included in this analysis.

Leaf damage was assessed differently between tree species because species differed in their physiological responses to leaf damage. In analyses of baldcypress leaf damage, the dependent variable was the proportion of leaves that had been damaged by insects. In analyses of water tupelo leaf damage the dependent variable was the proportion of leaf area that had been damaged. Analyses of leaf damage were performed on the subset of exposed foliage accessible birds outside tree protectors, and on the entire crown. Treatment effects on leaf damage were analyzed as an ANCOVA with a randomized block design in PROC MIXED. The mean number of birds detected during point counts during the time of caterpillar activity, including the conservative estimate of the number of young fledged by PROW, NOPA and CACH in the final round of counts in 2005, was the main covariable of interest in these analyses. The distance to the edge of the crown of the nearest conspecific tree (caterpillar source) and the date on which leaf damage was assessed were also included as covariables in the model. Non-significant covariables were removed from the models with a reverse step-wise selection process.

The dependent variable in height growth analyses was the percent increase in height of living portions of trees. Trees that died back to the root collar and resprouted were not included in height growth analyses. Numbers of plots included in the study changed between years (see results) and caused many missing cells. Therefore, height growth analyses were performed

separately by year. Because leaf damage was assumed to affect height growth (Souther-Effler 2004), height growth analyses were conducted separately by species to include the differing leaf damage measurements as covariables in the height growth models. Treatment effects on percent height growth of seedlings were analyzed as an ANCOVA with a randomized block design in PROC MIXED. Covariables included in analyses of percent height growth in 2004 included: the initial height of the tree at planting, and the amount of leaf damage on the entire crown in 2004 (percent leaf area damaged in the case of tupelo, and percent of leaves damaged in the case of baldcypress). The covariables in the analyses of percent height growth in 2005 included: the maximum height of the tree in 2004; the percent height growth of the tree in 2004 (a measure of vigor); the amount of leaf damage on the entire crown in 2004, and the amount of leaf damage on the entire crown in 2005 (see above). Non-significant covariables were removed from the models in a reverse step-wise selection process.

Treatment effects on the total percent diameter growth over the two growing seasons of the study were analyzed as an ANCOVA performed separately by species to allow species-specific leaf damage measures to be included in the models. Covariables in the analyses of percent diameter growth included: the initial diameter of the tree and the percent height growth of the tree in 2004. The analysis of baldcypress percent diameter growth also included the total percent of leaves chewed in 2004 and 2005, and the analysis of water tupelo percent diameter growth included the total percent leaf damage in 2004 and 2005. Non-significant covariables were removed from the models in a reverse step-wise selection process.

Continuous foraging observations were collected, but only the first foraging maneuver performed by a bird after it was detected and the first maneuver it performed after moving to a different tree were assumed to be independent for the purposes of statistical analysis. Because

BCLR are a novel food item for insectivorous birds, it was of interest to determine whether common insectivorous birds in the Maurepas Swamp exhibit a functional response to BCLR by foraging more frequently on baldcypress in the presence of BCLR. Therefore, 2x2 contingency tables of BCLR presence/absence and water tupelo and baldcypress tree species were constructed using pooled foraging observations over the duration of the study. A Fisher's exact test was conducted in PROC FREQ to determine if the tree species upon which insectivorous birds foraged were associated with BCLR presence. The nature of functional responses of the most abundant insectivorous birds to BCLR presence were examined with PROC TTEST by comparing mean foraging maneuver heights and mean heights of baldcypress foraged upon between times when BCLR were present and times when BCLR were absent.

## **Results**

There were a number of logistical difficulties that affected the implementation of the full study design in 2004. These difficulties limited the amount and quality of data collected and constrained subsequent analyses.

The number of man-hours required to install the bird exclosures on study plots was seriously underestimated. Therefore, treatments were applied to only 20 of the 30 study plots in 2004. The netting of bird exclosures was partially immersed during a flood in late April-early May 2004, and I discovered that the portions of the net exclosures in the water acted as gill nets, capturing sunfish (*Lepomis spp.*) alligator gar (*Lepisosteus spatula*), water snakes (*Nerodia spp.*) and cottonmouths (*Agkistrodon piscivorus*). Live animals were cut from the nets and released, but many snakes and fish died in the nets. Therefore, bird exclosures were removed in early May after being in place for a maximum of less than one month. However, exclosures were in

place during late instar stages of caterpillars and most leaf damage is caused by the fourth and fifth instar stages of BCLR and FTC (R. Goyer personal communication).

Nutria destroyed most seedlings on two plots within a few days of planting. A three week flood event in mid-May closed local rivers to boat traffic and interrupted research activities. At the beginning of the flood, the Bt treatment had been applied only once to trees assigned to that group. After the flood event, both baldcypress leafrollers and forest tent caterpillars had finished their pupal stage. Therefore, I discontinued bird counts and Bt applications and began assessing leaf damage on the planted saplings before they started to lose leaves from the first flush of foliage.

Study set up progressed more smoothly in 2005, partly because most exclosure frames were in the field from the previous year. Bird exclosures were modified to exclude fish and snakes during flood events by sewing an approximately 1m tall skirt of crawfish bag material (supplied by J&M Industries, Pontchatoula, Louisiana) to the bottom of the agricultural netting. Nutria had partly or completely destroyed seedlings on two additional plots, and one plot was determined to be too distant from the bayou to sample efficiently and safely (Figure 3-1). Therefore, 24 plots were included in the study in 2005. The lack of replication in years in which some plots were treated and sampled constrained some analyses.

### Tree Survival

Treatments (Bt, exclosure, control) did not significantly affect survival of trees (Wald  $\chi^2_{(2, df)} = 1.1887, p=0.5519$ ). Overall mortality of baldcypress was similar to that of water tupelo (18.6 and 15.6% respectively, Table 3-1), but the causes of mortality differed between tree species. All baldcypress mortality was due to nutria chewing through tree protectors and through

the base of the stem. In water tupelo 33.3% of the mortality was due to unknown causes, and the remainder was destroyed by nutria.

Table 3-1. Mortality and growth parameters of 270 planted baldcypress and 270 planted water tupelo seedlings in the Maurepas Swamp over two growing seasons. Unadjusted means are reported with their associated standard errors and sample sizes.

	Baldcypress		Water tupelo	
	2004	2005	2004	2005
Killed by nutria (%)	15 (5.6%)	35 (13%)	19 (7%)	9 (3.3%)
Dead, cause unknown (%)	0	0	3 (1.1%)	11 (4.1%)
Total mortality by year (%)	15 (5.6%)	35 (13%)	22 (8.1%)	20 (7.4%)
Mean total percent defoliation (SE)	-	-	29.0 (1.27) n=171	45.6 (1.22) n=199
Mean total percent of leaves chewed (SE)	15.5 (0.95) n=174	26.6 (1.16) n=203	-	-
Mean height growth (cm) (SE)	22.6 (0.71) n=211	19.5 (0.98) n=204	26.6 (0.94) n=193	8.0 (1.02) n=185
Mean percent height growth (SE)	30.3 (1.10) n=211	20.3 (1.06) n=204	38.4 (1.42) n=193	8.6 (1.14) n=185
Total percent height growth (SE)	-	56.3 (1.76) n=219	-	41.9 (2.46) n=221
Mean diameter growth (mm) (SE)	-	10.0 (0.31) n=224	-	3.6 (0.18) n=226
Mean percent diameter growth (SE)	-	123.9 (4.01) n=224	-	39.3 (2.05) n=226

### Breeding Bird Surveys

Point counts were interrupted by flooding in 2004, and only one complete round of 1-hour point counts on all study plots was completed, although on some plots I performed two or

three counts. Changing my point count methodology in 2005 to standard 10-minute point counts, with a fledging survey following the last count, permitted me to complete two rounds of point counts during the time caterpillar activity, and the final count and fledging survey soon after BCLR pupated. Because of unequal sampling effort in 2004, and for the purpose of comparison to other standardized 10-minute point count studies, only 2005 point count data are summarized in Table 3-2.

Table 3-2. Numbers of insectivorous birds detected within 50m during three rounds of 10-minute point counts in 2005, and their percent of the total number of insectivorous bird detections.

Common Name	Scientific Name	Species Code	Number of Detections	Percent of total
Prothonotary Warbler	<i>Protonotaria citrea</i>	PROW	294	33.11
Northern Parula	<i>Parula americana</i>	NOPA	227	25.56
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	114	12.84
Yellow-throated Warbler	<i>Dendroica dominica</i>	YTWA	44	4.95
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	40	4.50
Eastern Tufted-titmouse	<i>Baeolophus bicolor</i>	ETTI	34	3.83
Carolina Wren	<i>Thryothorus ludovicianus</i>	CARW	29	3.27
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	BGGN	27	3.04
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO	14	1.58
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	12	1.35
Common Grackle	<i>Quiscalus quiscula</i>	COGR	11	1.24
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	9	1.01
Indigo Bunting	<i>Passerina cyanea</i>	INBU	9	1.01
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	8	0.90
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	YBCU	6	0.68
Great-crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL	5	0.56
Eastern Bluebird	<i>Sialia sialis</i>	EABL	3	0.34
Yellow-throated Vireo	<i>Vireo flavifrons</i>	YTVI	1	0.11
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO	1	0.11
<b>TOTAL</b>			<b>888</b>	<b>100.00</b>

The results of point counts in 2004 and 2005 (Table 3-2) were similar to those obtained in 2003 (see Table 2-1) in that PROW and NOPA were the most commonly detected insectivorous

bird species, but the relative proportions of detections for more rare species differed (see Tables 2-1 and 3-2). However, part of this difference resulted from the different methodologies between studies (see Chapter 2 methods). Overall means of  $14.4 \pm 0.9$  SE and  $12.8 \pm 0.44$  SE insectivorous birds were detected per point count in 2004 and 2005 respectively (Table 3-3).

Table 3-3. Mean number of detections of insectivorous birds per point count in 2004 and 2005, and 2005 fledging survey results.

Year	Number of counts	Mean detections per count (SE)	Number of 24 plots with nestlings or fledglings in 2005		
			PROW	NOPA	CACH
2004	1-3	14.4 (0.90)	-	-	-
2005	3	12.8 (0.44)	13 (54.2%)	19 (79.2%)	17 (70.1%)

From fledgling surveys or knowledge of the reproductive status of the resident pairs of PROW, NOPA and CACH gained from point counts, it was determined that PROW had fledged young on 13 of 24 plots, NOPA had fledged young on 19 of 24 plots, and CACH had fledged young on 17 of 24 plots during BCLR activity (Table 3-3). On 12 of 24 plots, both PROW and NOPA fledged young, and on 9 of 24 plots (37.5%) PROW, NOPA and CACH fledged young during BCLR caterpillar activity.

#### Foraging Observations

First instar FTC were observed on my study plots on 30 March 2004 and FTC hatched between 21 March and 5 April in 2005. Newly hatched BCLR are minute, and they burrow into baldcypress buds after hatch, making them very difficult to detect (Goyer and Chambers 1997, personal observations). Early (probably 2nd) instar BCLR were first observed near my study plots on 23 March 2004. In 2005, BCLR were first detected when I observed NOPA foraging on BCLR about 1cm long (probably the third instar stage) in large baldcypress on 7 April.

Collecting foraging observations in the swamp was difficult. The low soil bulk density made walking through the swamp difficult, and the ubiquity of cottonmouths made it necessary to concentrate on the ground instead of visually tracking focal birds. Even with the occasional availability of field technicians and volunteers dedicated to collecting foraging observations, only about two independent foraging observations were collected per hour. Due to the difficulty of collecting foraging observations, I focused efforts on collecting foraging observations of the most common insectivorous birds, PROW and NOPA. A total of 291 PROW and NOPA foraging observations were collected in and around study plots during field work in 2003-2005. Of the 291 foraging observations, 152 and 91 independent foraging observations were collected for PROW and NOPA respectively, and only these were used in subsequent foraging analyses.

Most bird species that depredated BCLR were observed foraging on BCLR after the caterpillars had entered the third instar stage. NOPA began foraging on BCLR earlier than any other warbler species, and presumably consumed smaller BCLR than other warblers. Almost all insectivorous birds in the Maurepas Swamp were observed depredating BCLR (see the results section in Chapter 2). Only PROW, NOPA, YTWA, CACH, and ETTI (see Table 3-2 for common names) were consistently observed depredating BCLR while they were available, but few foraging observations of more rare bird species were collected. Both PROW and NOPA frequently hovered at the outer edges of tree crowns while pulling BCLR from their shelters. PROW also hopped through mid-portions crowns along main branches, reaching and pulling BCLR from nearby shelters. CACH and ETTI were more thorough in their foraging behavior and appeared to forage through a greater cross-section of the crown and closer to tree boles than PROW and NOPA. Birds continued to depredate BCLR after they had pupated. The leaf shelter within which BCLR pupates is basically the same configuration as that in which the caterpillar

shelters and they are probably more vulnerable than the caterpillar stage because they are not mobile as pupae.

In contrast to BCLR, which were depredated from about the third instar stage through the pupal stage, FTC caterpillars were observed to be depredated by birds, with the exception of Yellow-billed Cuckoos (*Coccyzus americanus*, hereafter referred to as YBCU), during two specific FTC caterpillar instar stages. PROW, NOPA, CACH and YTWA (see Table 3-2 for common names) were observed gleaning newly hatched FTC caterpillars from expanding water tupelo buds and flowers. However, birds other than YBCU continued to depredate early instar FTC caterpillars for only about one or two weeks. YBCU are able to consume hairy caterpillars with impunity, and they were the only species observed to depredate FTC caterpillars between the times when they had grown longer than about 1.5cm to the time they began a “resting” period in the late fifth instar stage before pupation. PROW were observed depredating FTC caterpillars after FTC had entered the resting period before pupation.

PROW were observed attempting to depredate FTC pupae, but they appeared to have great difficulty in penetrating the layer of silk used to roll leaves about the actual FTC cocoon. PROW were observed struggling to penetrate the exterior layer of silk by grasping it with their bills and pulling on it while hovering. In one case a PROW repeatedly hung its full weight from the silk while grasping it with its bill. This bird was ultimately successful in extracting the pupa, but only after several minutes of effort, and in two cases where PROW successfully extracted the pupa, the pupal case was crushed and the birds consumed only a portion of the viscera. Only PROW were observed depredating FTC pupae, however it is almost certain that more acrobatic birds, such as CACH and ETTI, depredated FTC pupae and probably with greater success.

The frequency with which PROW (Figure 3-2, Figure 3-4) and NOPA (Figure 3-3, Figure 3-4) foraged upon baldcypress or water tupelo shifted between times when BCLR were present and when they were absent. Both PROW and NOPA were more likely to forage on baldcypress than on water tupelo while BCLR caterpillars were present (Figure 3-4, for both species two-sided Fisher's exact tests  $p < 0.0001$ ). However, PROW frequently foraged in the herbaceous layer while BCLR were both present and absent (Figure 3-2). PROW were difficult to observe while they foraged in the herbaceous layer, but were most frequently observed depredating large, dead and dying dragonflies (order Odonata), and hawking live dragonflies while foraging in the herbaceous layer.

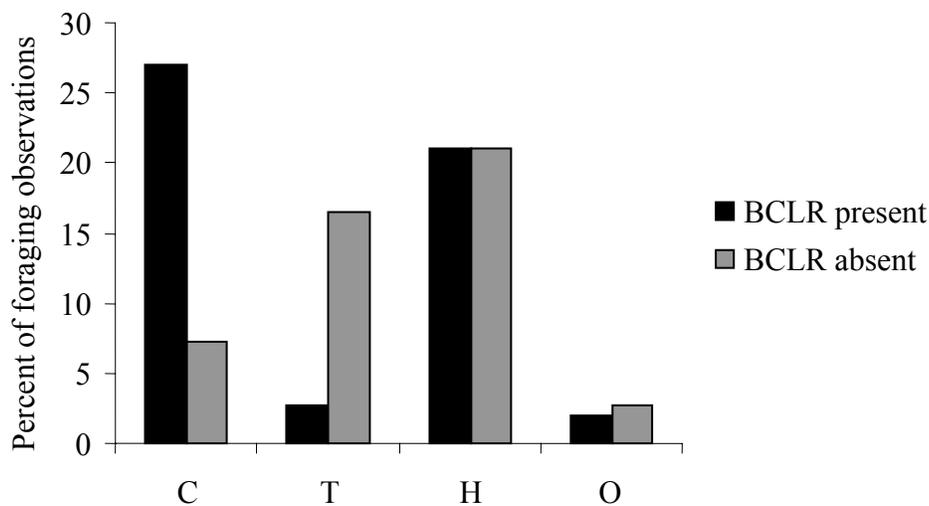


Figure 3-2. Distribution of PROW foraging substrates while BCLR caterpillars were present and absent. C=baldcypress, T=water tupelo, H=herbaceous layer, O=other tree species.

During BCLR caterpillar activity, PROW and NOPA foraged most frequently on trees taller than 5m (Figures 3-5 and 3-6 respectively), and neither species was observed foraging on baldcypress under 2m tall (Figures 3-5 and 3-6). Slightly fewer than 10% of PROW foraging observations were in canopies of rare, large (>20m tall), remnant baldcypress left behind during

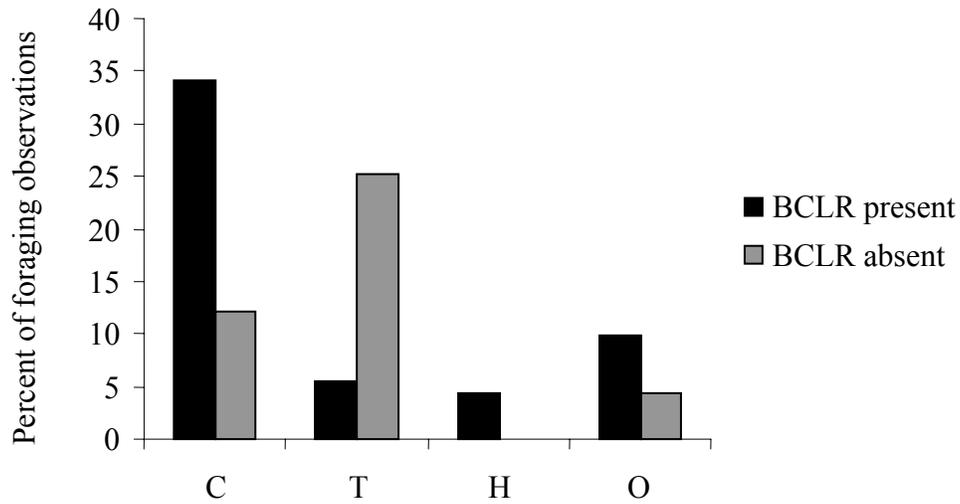


Figure 3-3 Distribution of NOPA foraging substrates while BCLR caterpillars were present and absent. C=baldcypress, T=water tupelo, H=herbaceous layer, O=other tree species.

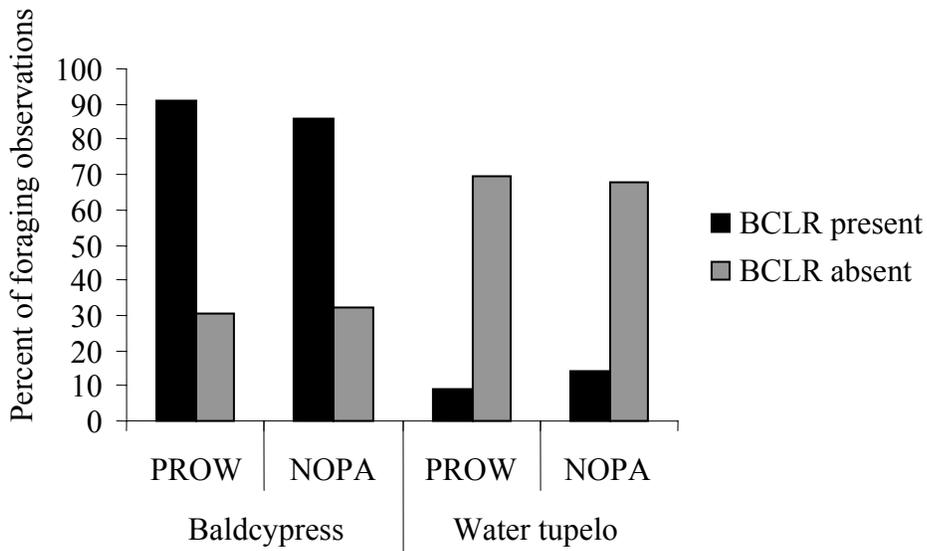


Figure 3-4. Percent of PROW and NOPA foraging observations on baldcypress and water tupelo while BCLR were present and absent.

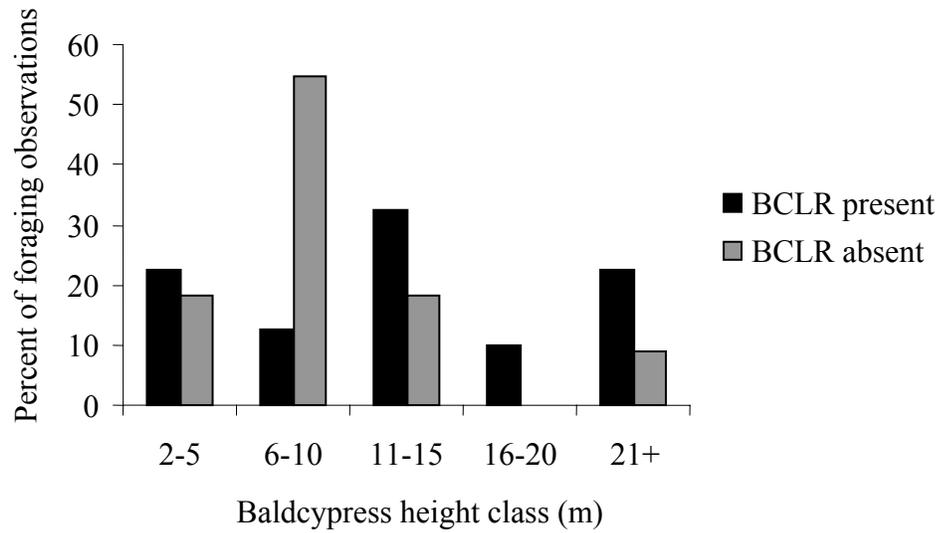


Figure 3-5. Distribution of PROW foraging observations among height classes of baldcypress while BCLR were present and absent.

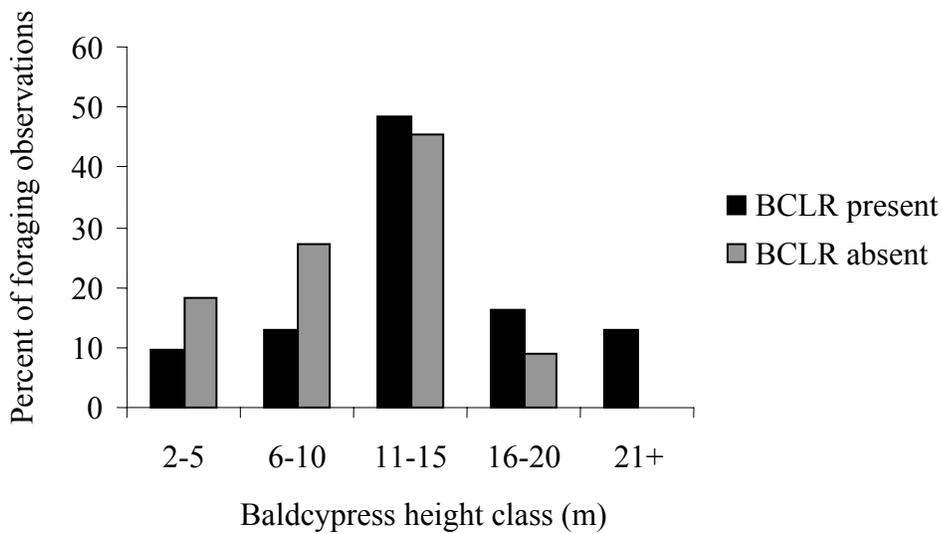


Figure 3-6. Distribution of NOPA foraging observations among height classes of baldcypress while BCLR were present and absent.

logging operations (Figure 3-5). The overall mean height of PROW foraging maneuvers was 4.1m±0.37 (n=152), and the overall mean foraging height of NOPA was 7.2m±0.49 (n=87). Mean foraging maneuver height and foraging substrate height of PROW and NOPA increased with BCLR presence (Table 3-4), but BCLR presence did not have a significant effect on mean PROW foraging maneuver height on baldcypress ( $t_{50}=0.16$ ,  $p=0.88$ , Table 3-4, Figure 3-7) or mean NOPA foraging maneuver height on baldcypress ( $t_{40}=1.20$ ,  $p=0.24$ , Table 3-4, Figure 3-8). Mean height of baldcypress trees foraged upon by PROW did not differ significantly with BCLR caterpillar presence ( $t_{50}=1.38$ ,  $p=0.17$ , Table 3-4, Figure 3-9), but the mean height of baldcypress trees foraged upon NOPA was significantly greater while BCLR were present ( $t_{40}=2.10$ ,  $p=0.0417$ , Figure 3-10).

Table 3-4. Mean foraging maneuver and substrate heights of PROW and NOPA while BCLR were present and absent.

	PROW		NOPA	
	BCLR present	BCLR absent	BCLR present	BCLR absent
Overall mean maneuver height (SE)	4.6 (0.56) n=80	3.5 (0.47) n=72	8.2 (0.84) n=44	6.2 (0.47) n=43
Overall mean foraging substrate height (SE)	7.8 (0.96) n=80	4.4 (0.59) n=71	12.2 (1.15) n=44	8.0 (0.49) n=42
Mean maneuver height on baldcypress (SE)	7.7 (0.69) n=41	8.0 (1.53) n=11	7.2 (1.53) n=31	9.4 (0.69) n=11
Mean height of baldcypress foraged upon (SE)	13.6 (1.2) n=41	10.2 (1.8) n=11	14.7 (1.27) n=31	9.9 (1.43) n=11

#### Defoliation

Few caterpillars were observed on study trees in either year and caterpillar defoliation was not severe in either year. This was expected in 2004 because both FTC and BCLR overwinter in eggs laid in the previous year, and study trees were not available as substrate in

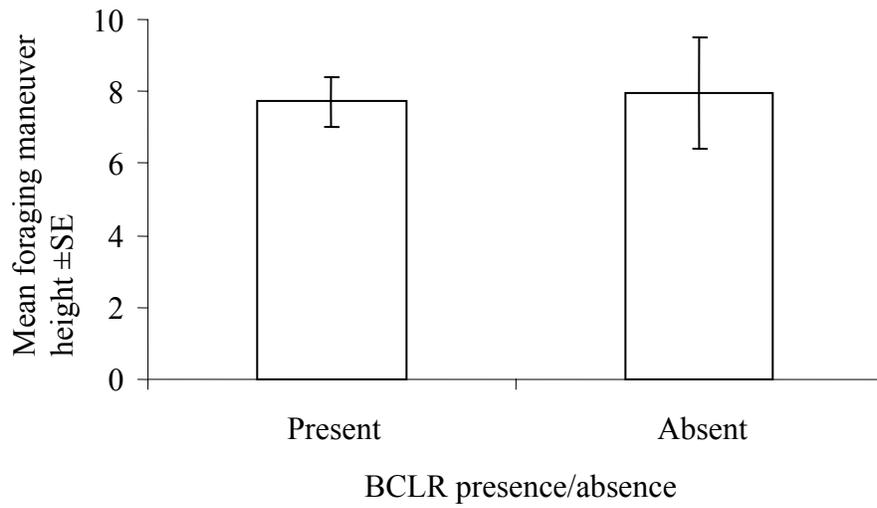


Figure 3-7. Mean foraging maneuver height of PROW on baldcypress while BCLR were present and absent.

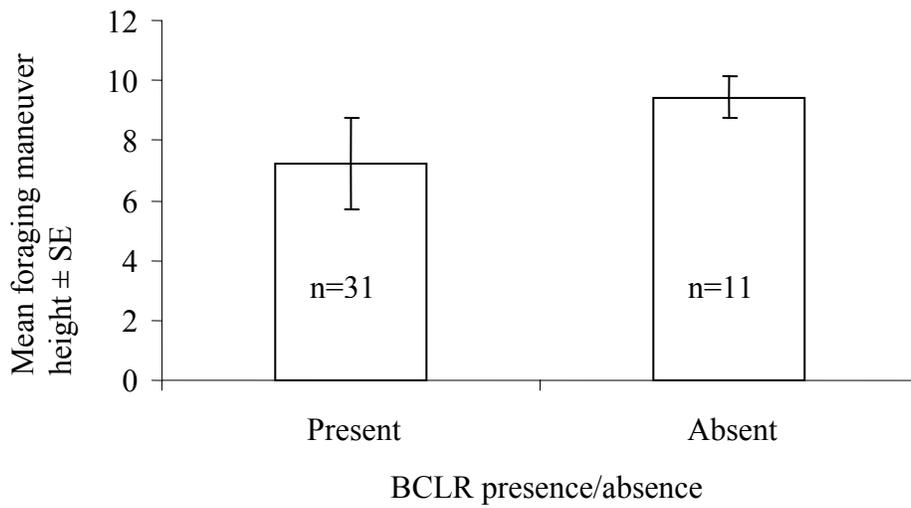


Figure 3-8. Mean foraging maneuver height of NOPA on baldcypress when BCLR were present and absent.

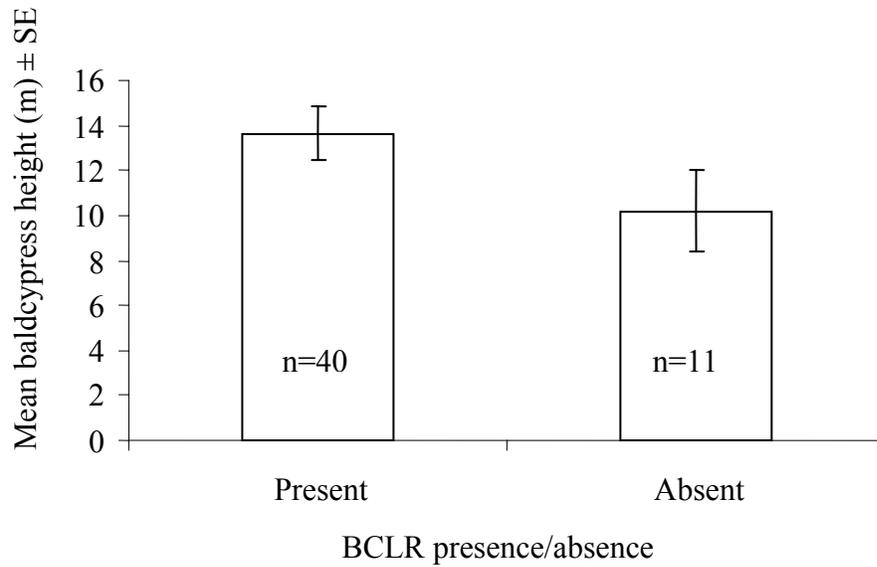


Figure 3-9. Mean height of baldcypress foraged upon by PROW when BCLR were present and absent.

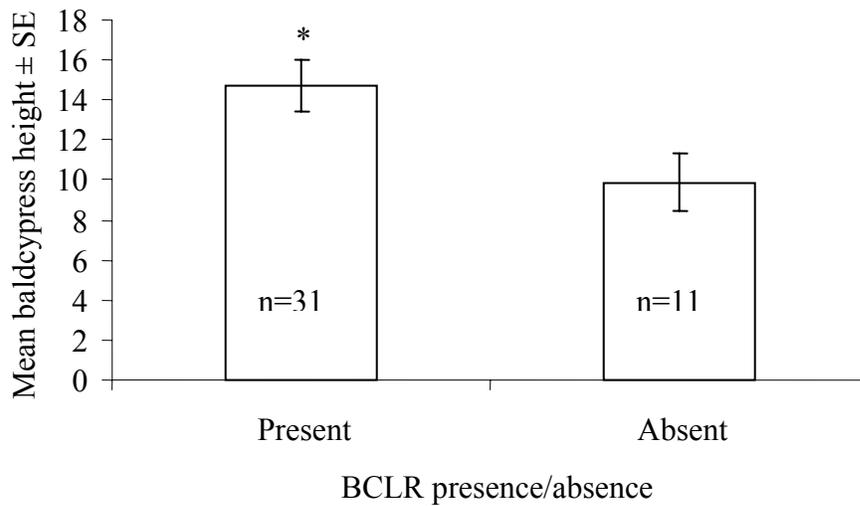


Figure 3-10. Mean height of baldcypress foraged upon by NOPA when BCLR were present and absent. Asterisk indicates a significant difference  $p < 0.0001$ .

2003. Only two FTC egg cases were observed on planted water tupelo in the summer of 2004. BCLR egg masses are difficult to observe, so it is uncertain how frequently planted baldcypress were utilized by BCLR moths. Populations of FTC and heavy defoliation of mature water tupelo in and around my study sites were patchy, but appeared to be greater in 2004 than in 2005. BCLR population levels were difficult to assess because BCLR are more cryptic in their coloration and behavior than FTC. However, BCLR were ubiquitous, and leaf damage on mature trees and study trees was frequent, although BCLR did not completely defoliate any trees in my study site.

Both planted and mature water tupelo were affected by what was most likely a fungal disease in both years (D. Ferrin personal communication). Affected leaf tissue became necrotic, and confounded estimates of leaf damage caused by insects. However, this disease was ubiquitous among planted water tupelo and for the purposes of analyses it was assumed that disease damage was equal among trees. In 2005, the skirts on bird exclosures occasionally enclosed large numbers of recently hatched grasshoppers (family Acrididae). However, defoliation of water tupelo by grasshoppers was severe in only a few cases. Some planted water tupelo foliage was consumed by caterpillars other than FTC, but these caterpillars were rare. Water tupelo were occasionally browsed by white-tailed deer (*Odocoileus virginianus*), primarily during high water events when palatable vegetation above the water line was probably rare.

Twigs of planted baldcypress were frequently galled by cypress twig gall midges (*Taxodiomyia* spp.). Baldcypress loopers (*Anacamptodes pergracilis*), were occasionally observed on planted baldcypress, but baldcypress loopers are not a serious pest of baldcypress in Louisiana (R. Goyer personal communication).

## Leaf Damage

Mean total percent defoliation of water tupelo was 29%  $\pm$ 1.27 SE in 2004 and 45.6%  $\pm$ 1.22 SE in 2005 (Table 3-1). Mean total percent of baldcypress leaves chewed was 15.5%  $\pm$ 0.95 SE in 2004 and 26.6%  $\pm$ 1.16 SE in 2005 (Table 3-1).

ANCOVAs of leaf damage measures indicated that treatments did not cause significant variation in the proportion of leaves damaged on baldcypress in the exposed portion of the crown outside the tree protectors ( $F_{2,344}=1.29$ ,  $p=0.2763$ , Table 3-5), or the entire crown ( $F_{2,346}=2.08$ ,  $p=0.127$ , Table 3-6).

Table 3-5. ANCOVA of percent of exposed baldcypress leaves damaged.

Effect	F-value	p
Treatment	$F_{2,344}=1.29$	0.2763
Year	$F_{1,372}=19.24$	<0.0001

Table 3-6. ANCOVA of percent of leaves damaged on entire baldcypress crowns.

Effect	F-value	p
Treatment	$F_{2,346}=2.08$	0.127
Year	$F_{1,371}=45.96$	<0.0001

Treatments did not have a significant effect on the percent of leaf area damaged on water tupelo in the exposed portion of the crown outside the tree protectors ( $F_{2,339}=2.09$ ,  $p=0.1257$ , Table 3-7), or the entire crown ( $F_{2,344}=0.48$ ,  $p=0.6216$ , Table 3-8). The year main effect was significant in analyses of leaf damage measures for both species in the exposed crown (baldcypress  $F_{1,372}=19.24$ ,  $p<0.0001$ , Table 3-5; water tupelo  $F_{1,343}=99.79$ ,  $p<0.0001$ , Table 3-7) and the entire crown (baldcypress  $F_{1,371}=45.96$ ,  $p<0.0001$ , Table 3-6; water tupelo  $F_{1,350}=69.52$ ,  $p<0.0001$ , Table 3-8), and leaf damage was consistently greater in 2005 on both tree species (Tables 3-5 through 3-8, Figures 3-11 through 3-14). In water tupelo, the covariable of leaf

damage sampling date was significant for the exposed crown ( $F_{1,86}=62.15$ ,  $p<0.0001$ , Table 3-7) and the entire crown ( $F_{1,94.7}=75.98$ ,  $p<0.0001$ , Table 3-8). The influence of the significant leaf damage sampling date covariable, suggests that treatments had no effect on percent leaf damage of water tupelo, or that any possible treatment effects were masked by the effect of time on defoliation.

Table 3-7. ANCOVA of percent leaf damage on exposed water tupelo leaves.

Effect	F-value	p
Treatment	$F_{2,339}=2.09$	0.1257
Year	$F_{1,343}=99.79$	<0.0001
Leaf damage sampling date	$F_{1,86}=62.15$	<0.0001

Table 3-8. ANCOVA of percent leaf damage on entire water tupelo crowns.

Effect	F-value	p
Treatment	$F_{2,344}=0.48$	0.6216
Year	$F_{1,350}=69.52$	<0.0001
Leaf damage sampling date	$F_{1,94.7}=75.98$	<0.0001

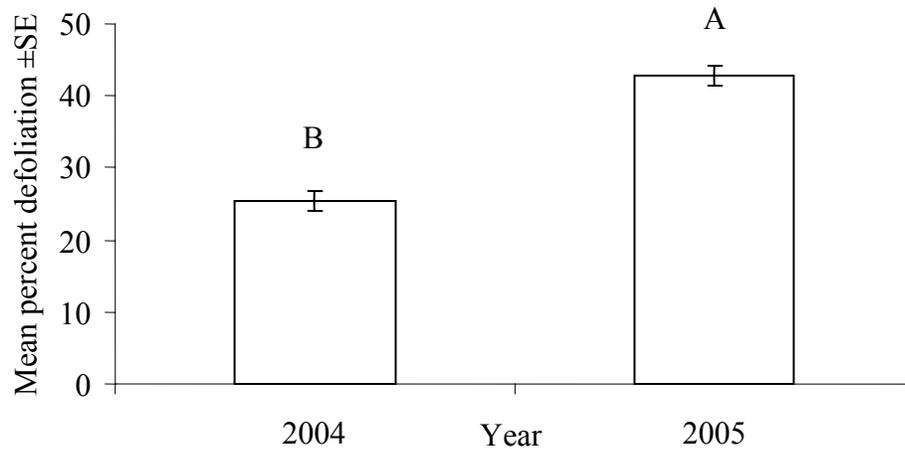


Figure 3-11. Mean percent damage on water tupelo leaves outside tree protectors by year.

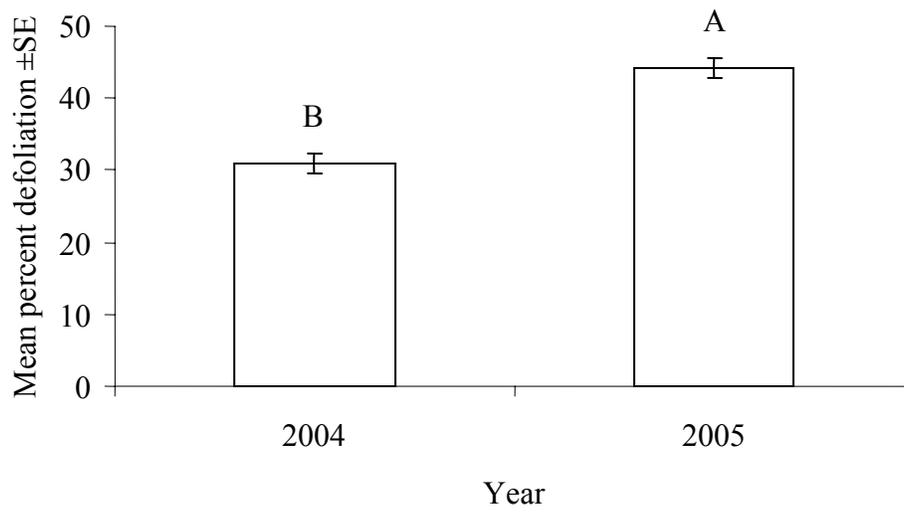


Figure 3-12. Mean percent damage on entire water tupelo crowns by year.

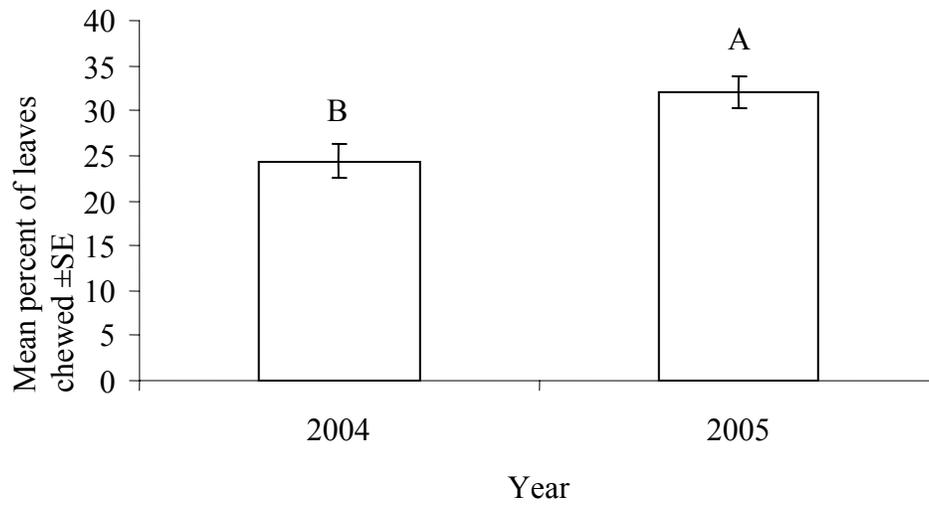


Figure 3-13. Mean percent of exposed baldcypress leaves chewed by year.

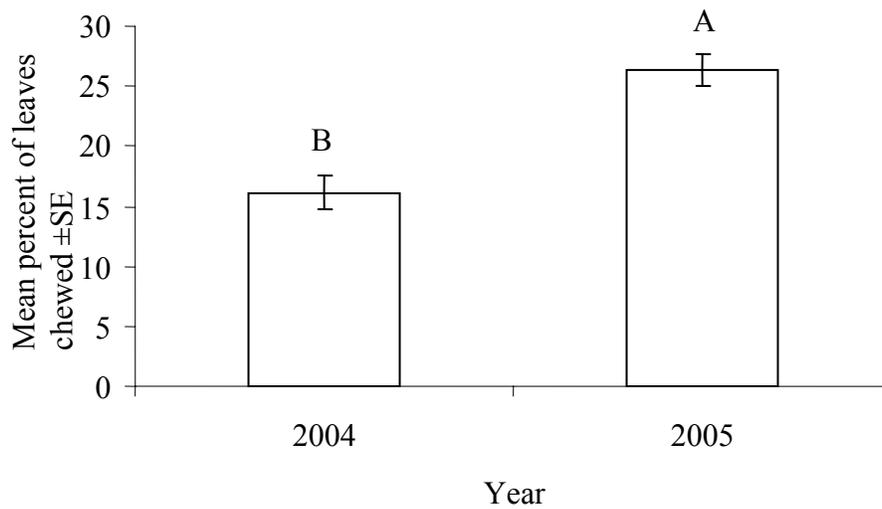


Figure 3-14. Mean percent of baldcypress leaves chewed on entire crowns by year.

### Height Growth

The mean total percent height growth of surviving planted seedlings after two growing seasons, including trees on plots which were dropped from the study due to nutria damage or safety concerns, was 56.3%±1.76 SE for baldcypress and 41.9%±2.46 SE for water tupelo.

Mean percent height growth of both species was lower in 2005 relative to 2004 (Table 3-1). Baldcypress percent height growth was approximately one-third less in 2005 than in 2004, and water tupelo percent height growth in 2005 was almost 4.5 times less than in 2004 (Table 3-1). A comparison of percent height growth between years may be inappropriate because of differences in measurement methodology, but the decline in increment height growth is reflected in the frequency with which apical shoots died back. Twelve baldcypress and 47 water tupelo included in height growth analyses had zero height growth or negative height growth at the end of the two growing seasons of the study. Many planted water tupelo exhibited partial die-back of

the leader in at least one year, but a lateral bud usually assumed apical dominance and height growth was continued. I suspect that many of the water tupelo seedlings may have exhibited this growth pattern while growing at the nursery because many seedlings had kinked stems that may have been produced by the assumption of apical dominance by lateral buds.

Baldcypress seedlings were entangled by vegetation more frequently than water tupelo, probably because baldcypress usually had more low, lateral branches within the herbaceous layer than did water tupelo seedlings.

Treatments did not have a significant effect on height growth of baldcypress in 2004 ( $F_{2,137}=1.10$ ,  $p=0.3348$ , Table 3-9, 3-15), but the initial height at planting was a significant covariable in the model ( $F_{1,137}=34.71$ ,  $p<0.0001$ , Table 3-9). Treatments did not have a significant effect on height growth of baldcypress in 2005 ( $F_{2,170}=0.66$ ,  $p=0.5205$ , Table 3-10, Figure 3-16), but the maximum height attained by seedlings in 2004 ( $F_{1,170}=13.35$ ,  $p=0.0003$ ) and the percent of leaves chewed on the entire crown in 2005 ( $F_{1,170}=5.19$ ,  $p=0.0240$ ) were significant covariables in the model (Table 3-10).

Table 3-9. ANCOVA of 2004 baldcypress height growth.

Effect	F-value	p
Treatment	$F_{2,137}=1.10$	0.3348
Initial height in 2004	$F_{1,137}=34.71$	<0.0001

Table 3-10. ANCOVA of 2005 baldcypress height growth.

Effect	F-value	p
Treatment	$F_{2,170}=0.66$	0.5205
Height in 2004	$F_{1,170}=13.35$	0.0003
Percent of leaves chewed in 2005	$F_{1,170}=5.19$	0.0240

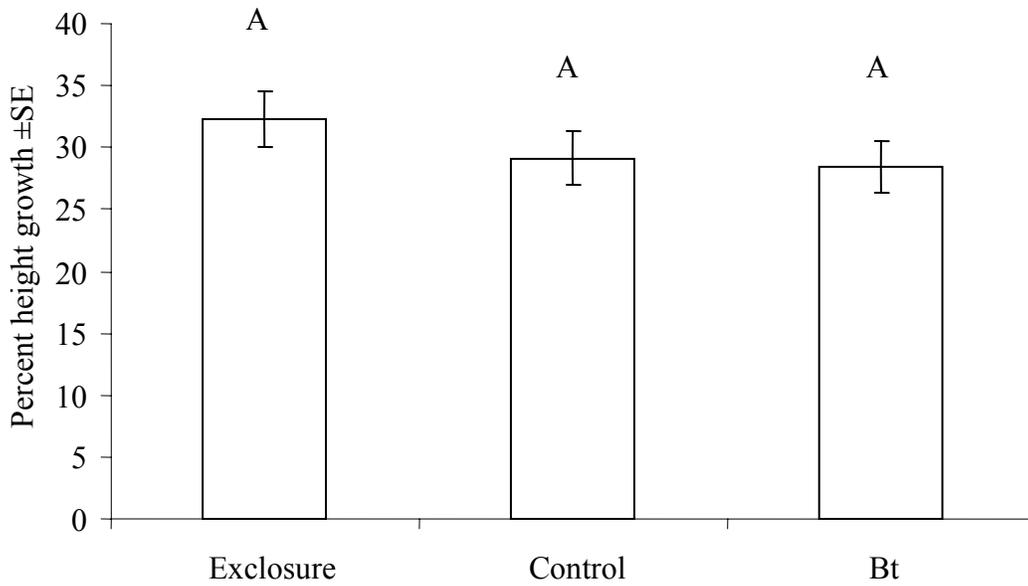


Figure 3-15. Percent height growth of baldcypress in 2004.

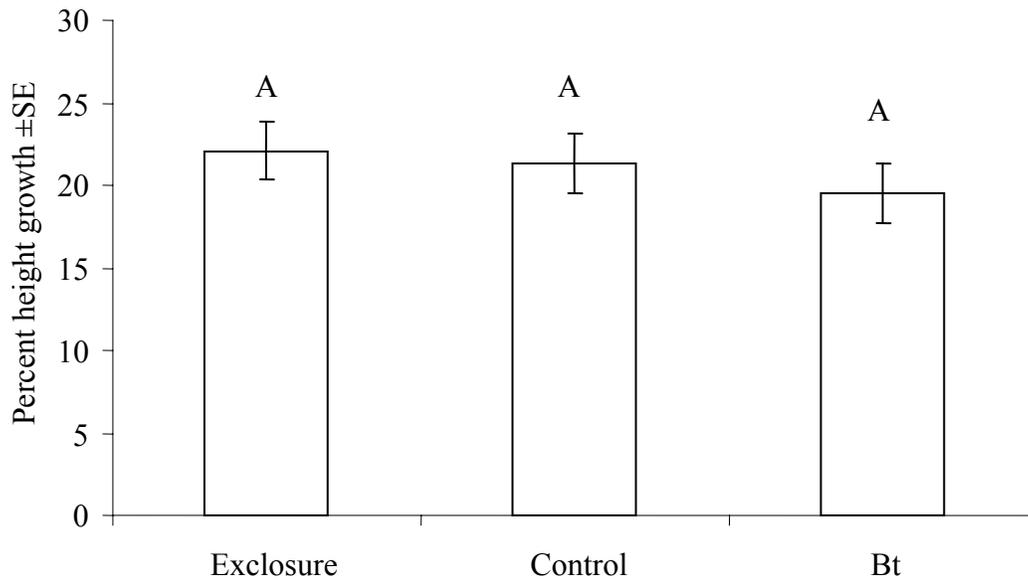


Figure 3-16. Percent height growth of baldcypress in 2005

The treatment effect on height growth of water tupelo seedlings in 2004 was significant ( $F_{2,118}=4.13$ ,  $p=0.0185$ , Table 3-11, Figure 3-17), but uninterpretable due to the interaction

Table 3-11. ANCOVA of 2004 water tupelo height growth.

Effect	F-value	p
Treatment	$F_{2,118}=4.13$	0.0185
Initial height	$F_{1,118}=5.85$	0.0171
Percent defoliation in 2004	$F_{1,118}=4.06$	0.0463
Percent defoliation 2004 * treatment	$F_{2,118}=4.33$	0.0153

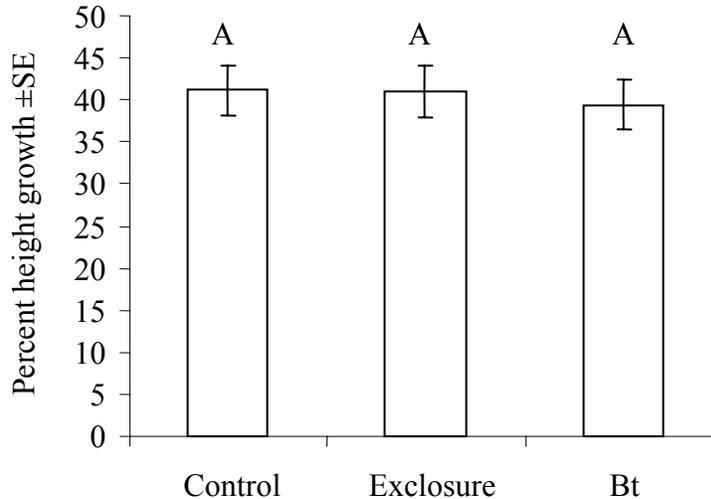


Figure 3-17. Percent height growth of water tupelo in 2004.

between the treatment main effect and the percent defoliation covariable in 2004 ( $F_{2,118}=4.33$ ,  $p=0.0153$ ). The slope of the relationship between defoliation and percent height growth in 2004 was negative for the exclosure and control treatments, but the Bt treatment had an unexpected slight positive slope. The adjusted mean percent height growth was not significantly different between treatments (Figure 3-18). The initial height at planting ( $F_{1,118}=5.85$ ,  $p=0.0171$ ) and the percent defoliation in 2004 ( $F_{1,118}=4.06$ ,  $p=0.0463$ ) were significant covariables in the model (Table 3-11). Treatments also had a significant effect on height growth of water tupelo seedlings in 2005 ( $F_{2,158}=7.66$ ,  $p=0.0007$ , Table 3-12, Figure 3-18), and the maximum height attained in 2004 ( $F_{1,158}=7.28$ ,  $p=0.0077$ ) was a significant covariable in the model.

Table 3-12. ANCOVA of 2005 water tupelo height growth.

Effect	F-value	p
Treatment	$F_{2,158}=7.66$	0.0007
Height in 2004	$F_{1,158}=7.28$	0.0077

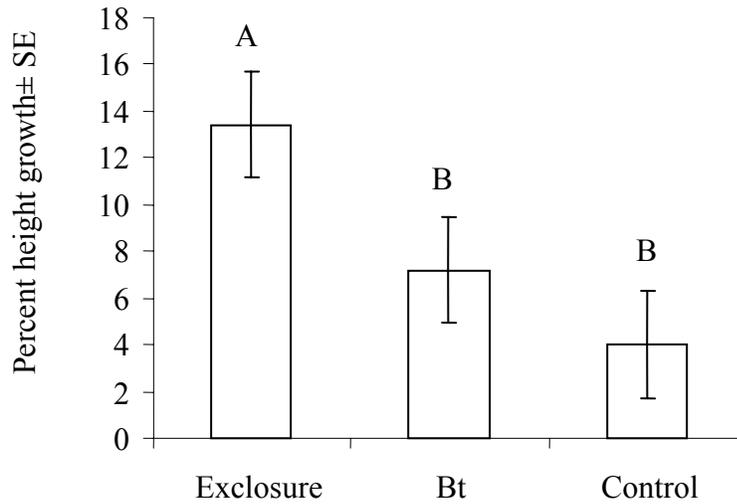


Figure 3-18. Percent height growth of water tupelo in 2005.

Treatments did not have a significant effect on height growth of baldcypress (Tables 3-9 and 3-10, Figures 3-15 and 3-16), but percent height growth of water tupelo in the exclosure treatment was unexpectedly greater relative to control trees in 2005 (Tables 3-11 and 3-12, Figure 3-18). Therefore, trees in the Bt and control groups were pooled by species and a Bonferonni protected ( $\alpha=0.025$ ) post-hoc, single factor ANOVA with a randomized block design blocked on plot, was performed with tree species as the main effect in the model to compare total percent height growth over the two year study between species. Percent height growth of baldcypress and water tupelo was significantly different ( $F_{1,290}=18.04$ ,  $p<0.0001$ ), and significantly greater in baldcypress (Figure 3-19).

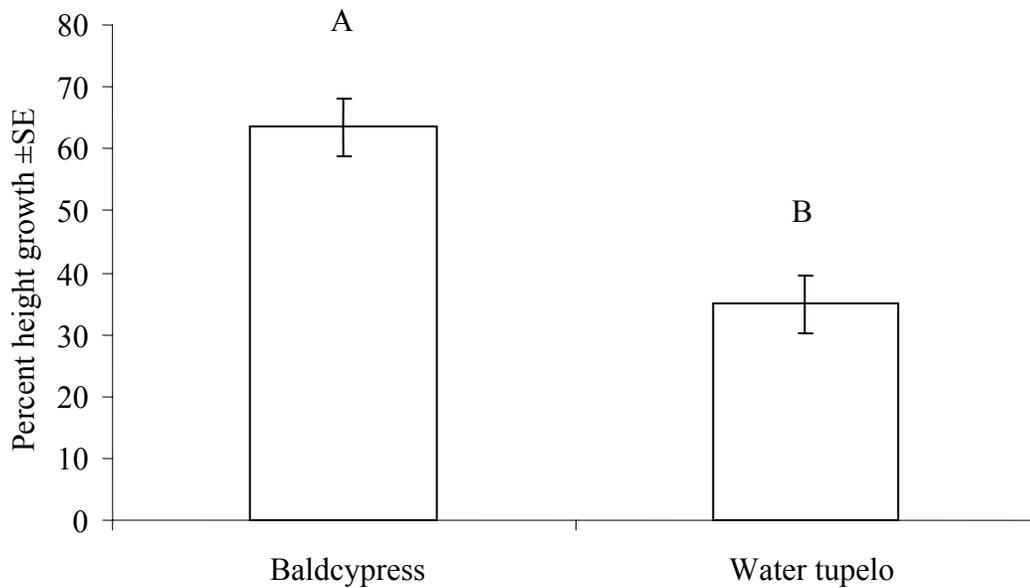


Figure 3-19. Comparison of total percent height growth for pooled Bt and control baldcypress and water tupelo over two years.

### Diameter Growth

The treatment effect on total percent diameter growth of baldcypress was non-significant ( $F_{2,178}=0.65$ ,  $p=0.5237$ , Table 3-13, Figure 3-20), but the initial diameter ( $F_{1,178}=13.19$ ,  $p=0.0004$ ) and percent height growth in 2004 ( $F_{1,178}=9.67$ ,  $p=0.0022$ ) were significant covariables in the model (Table 3-13). The treatment effect was significant for total percent diameter growth of water tupelo ( $F_{2,153}=3.91$ ,  $p=0.0221$ , Table 3-14, Figure 3-21) and significant covariables in the model included initial diameter ( $F_{1,153}=9.96$ ,  $p=0.0019$ ), percent height growth in 2004 ( $F_{1,153}=27.32$ ,  $p<0.0001$ ) and total percent defoliation in 2005 ( $F_{1,153}=10.74$ ,  $p=0.0013$ ).

Treatments did not have a significant effect on percent diameter growth of baldcypress, but percent diameter growth of water tupelo was unexpectedly greater in the exclosure treatment

Table 3-13. ANCOVA of total percent diameter growth of baldcypress.

Effect	F-value	p
Treatment	$F_{2,178}=0.65$	0.5237
Initial diameter	$F_{1,178}=13.19$	0.0004
Percent height growth in 2004	$F_{1,178}=9.67$	0.0022

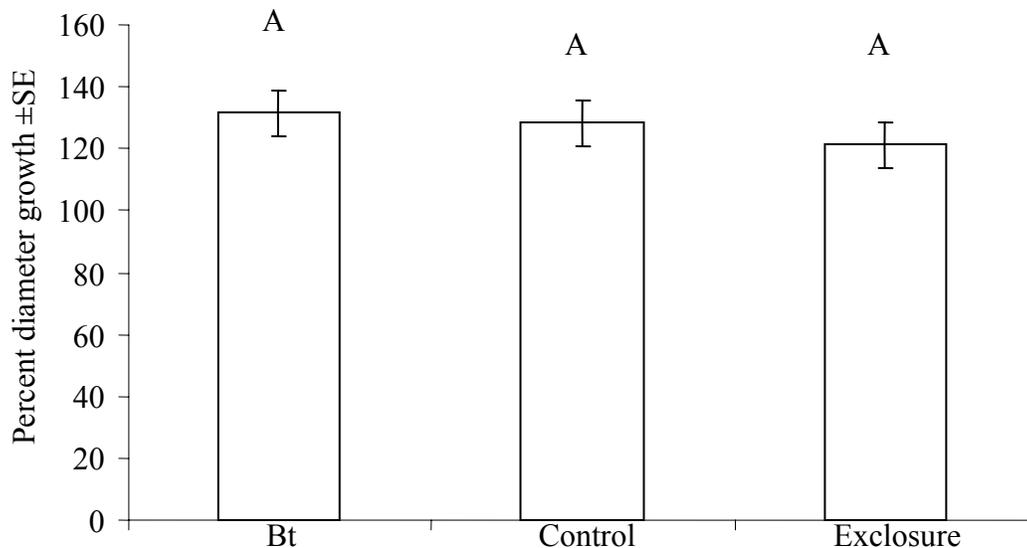


Figure 3-20. Percent diameter growth of baldcypress.

Table 3-14. ANCOVA of total percent diameter growth of water tupelo.

Effect	F-value	p
Treatment	$F_{2,153}=3.91$	0.0221
Initial diameter	$F_{1,153}=9.96$	0.0019
Percent height growth in 2004	$F_{1,153}=27.32$	<0.0001
Total percent defoliation in 2005	$F_{1,153}=10.74$	0.0013

relative to controls (Figure 3-21). Therefore, trees in the Bt and control groups were pooled by species and Bonferonni protected ( $\alpha=0.025$ ) post-hoc, single factor ANOVA with a randomized block design blocked on plot, was performed with tree species as the main effect in the model to compare percent diameter growth over the two year study between species. Total percent

diameter growth over two growing seasons was significantly different between species ( $F_{1,296}=293.16, p<0.0001$ ), and significantly greater in baldcypress (Figure 3-22).

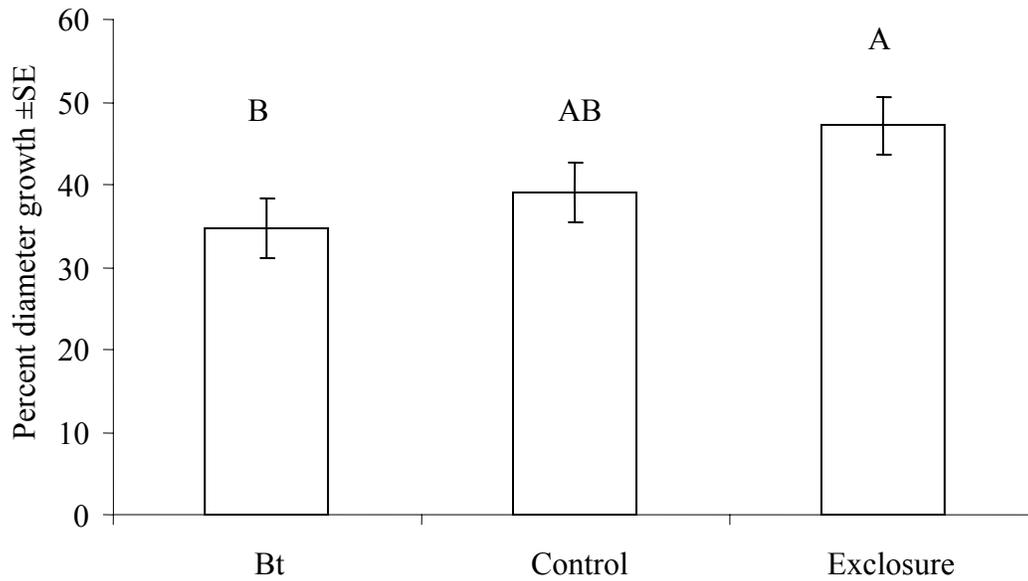


Figure 3-21. Percent diameter growth of water tupelo.

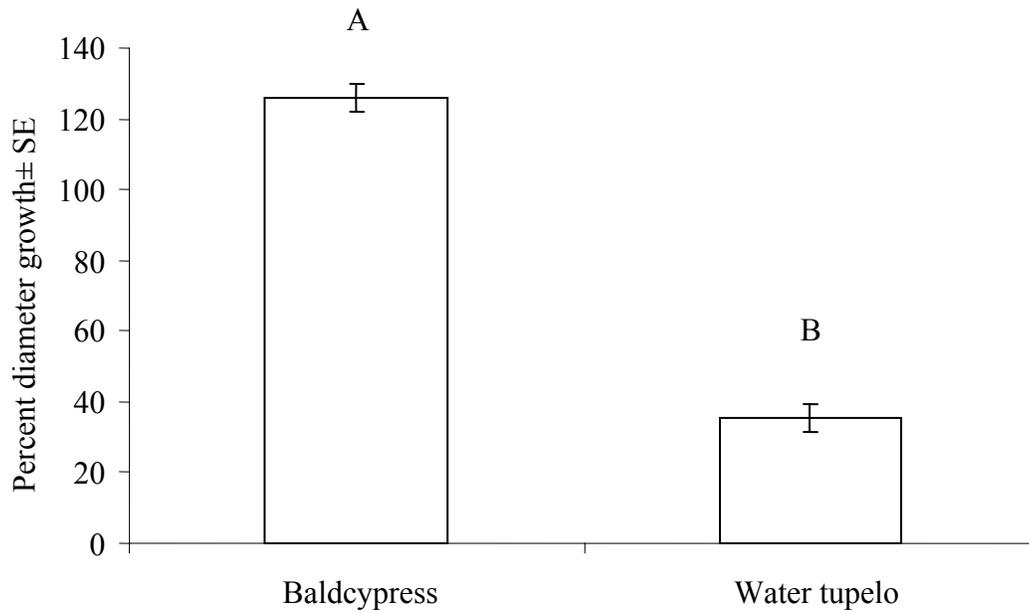


Figure 3-22. Comparison of percent diameter growth of pooled Bt and control baldcypress and water tupelo.

## PROW Video Nest Monitoring

Six PROW nests low enough to be effectively monitored with video cameras were sampled between 28 April and 13 May 2005. Recordings were made between 7:30AM and 5:30PM. Individual nests were recorded three to six times, and yielded twenty-six useable 1-hour video recordings, during which 164 nest provisioning trips in which the adult's bill was visible were recorded. Mean provisioning rate of nests by adult PROW ranged from 2-25 trips per hour (mean= $7.7 \pm 0.94$ SE visits/hour).

Many food items were not identifiable beyond simple categorization as lepidopteran larvae or not, but craneflies (family Tipulidae), spiders (order Araneae), dragonflies and dragonfly nymphs, and moths were among the food items provisioned by adult PROW. BCLR were easily identified by their bright green color and short, stout shape. Although other caterpillars of similar appearance may have been present in the study area, PROW were never observed depredating larvae of similar appearance. Baldcypress loopers were a darker green and were longer than BCLR. Nests were provisioned most frequently with lepidopteran larvae of various species including BCLR, FTC, unidentified large larvae, and what were assumed to be baldcypress loopers from their shape size and color. The most easily identified food items brought to nests were dragonflies. Ten provisioning trips (6.1%) included a dragonfly or a portion of a dragonfly. Of 164 provisioning trips where the adult's bill was visible, 126 (76.8%) contained at least one lepidopteran larva.

BCLR were fed to nestlings throughout the sampling period, but their frequency of occurrence in provisioning trips declined with time. In a conservative evaluation of the video recordings, sixty-five of 164 provisioning trips (39.6%) contained what were assumed to be BCLR. Nests were provisioned with 0 to 45 BCLR per hour (mean= $6.33 \pm 1.82$  SE). Two nests were provisioned with FTC caterpillars after 10 May. Eleven provisioning trips included FTC

caterpillars (6.7%) and two trips included FTC pupae. FTC were included in a relatively small proportion of the total number of provisioning trips, but during the two 1-hour sampling periods when FTC were recorded, these nests were provisioned repeatedly with FTC.

## **Discussion**

### Tree Growth and Survival

The first objective of this study was to determine whether planted baldcypress and water tupelo seedlings survive and grow in a degraded area of the Maurepas Swamp on the west side of Lake Maurepas. Survival of both species of planted seedlings had similar survival, but baldcypress were frequently destroyed by nutria despite being protected with Vexar® tree protectors. More effective tree protectors are available, but their cost was prohibitive in this study. In this study, nutria did not appear to consume baldcypress seedlings as reported by Blair and Langlinais (1960), rather they generally appeared to clip seedlings and leave them uneaten. The rapidity with which nutria destroyed baldcypress seedlings inside tree protectors was less than that observed by Conner and Toliver (1987), but mortality due to nutria damage increased in the second year of the study and there is no reason to believe trees will become less vulnerable with time. Black willow (*Salix nigra*) and buttonbush (*Cephalanthus occidentalis*) as large as 7cm in diameter were felled by nutria on my study plots, and many of the tree protectors showed evidence of nutria damage. In the White River National Wildlife Refuge, AR, nutria are invading bottomland hardwood forests, and I have observed widespread nutria girdling of trees greater than 30cm in diameter. Therefore, nutria may continue to threaten regenerating forests, even if trees survive past the seedling and sapling stages. One step toward reducing nutria damage may be for hunting of nutria to be encouraged by changing current Louisiana hunting regulations that limit harvest numbers to five nutria per hunter per day.

Survival of planted water tupelo seedlings was slightly higher than that of planted baldcypress seedlings, but 5% died from unknown causes and nearly four times as many water tupelo had zero or negative height growth over the two years of the study. This result was unexpected because planted water tupelo seedlings were two years old and baldcypress seedlings were one year old, and I expected that the performance of these older water tupelo seedlings would equal that of one year old baldcypress.

Total percent height and diameter growth of baldcypress were significantly greater than that of water tupelo, and was probably due in part to the frequency with which tupelo seedlings died-back. Die-back of leaders of planted water tupelo seedlings may result from the same factors that cause crown die-back and death of mature water tupelo in degraded swamp, but abiotic factors which negatively affect water tupelo growth, such as salinity and flood depth and duration, were not measured in this experiment. Kennedy (1970 as cited in Dickson and Broyer 1972) found that flooding 15-25cm above the soil decreased growth of water tupelo, and complete inundation caused tops to die back. No natural regeneration of water tupelo has been observed in the Maurepas Swamp for at least fourteen years (G. Shaffer personal communication).

Even with freshwater diversion into the swamp, planting water tupelo may be a costly, but necessary step for swamp restoration (Stanturf et al. 2001). The slower growth of water tupelo seedlings relative to baldcypress seedlings suggests that abiotic conditions in the swamp probably will need to be ameliorated prior to any water tupelo planting. The positive effects of throughput of water and elevation are apparent along the edges of bayous and ditches created during logging operations. Long, linear strips of relatively healthy forest survive along the edges of these channels, and the edges of channels are a few centimeters higher than the surrounding

land, and are adjacent to flowing water. Salinity levels are lower in wetlands on the west side of Lake Maurepas than on the east side of the lake, but stagnant water (e.g. Hook et al. 1970) and salinity levels as low as 3ppt negatively affect productivity of water tupelo (e.g. Pezeshki et al 1989, Dicke and Toliver 1990, Souther-Effler 2004), so implementation of the planned diversion of freshwater into this area may be a necessary first step before even planted water tupelo could survive and grow well.

Ensuring that standing mature water tupelo and future water tupelo regeneration persist is crucial for PROW populations, because water tupelo provides most of the nesting cavities for PROW in the Maurepas Swamp (personal observations, see Chapter 1).

#### Effects of Birds on Tree Growth

The second objective of this study was to determine whether birds reduce insect herbivore damage on baldcypress and water tupelo foliage via their consumption of leaf-chewing insects, and whether these effects cascade to increase tree growth. Leaf damage measures of trees assigned to the bird enclosure and Bt treatments were not significantly different from controls for either the exposed portions of tree crowns outside tree protectors or the entire crown.

Mean percent damage on water tupelo leaves, and mean percent of baldcypress leaves chewed, outside tree protectors and on entire crowns, was significantly greater in 2005 than in 2004. This result was expected because FTC and BCLR overwinter as eggs, and study trees were not available egg-laying substrates in the summer of 2003 for female moths. I did not survey trees for BCLR egg masses, but I assume that BCLR laid eggs on planted baldcypress in summer of 2004, which resulted in more BCLR herbivory on planted baldcypress in 2005. However, FTC egg masses are much more obvious than BCLR egg masses, and few FTC egg masses were observed on planted water tupelo in summer of 2004 and spring of 2005. One

might assume that FTC populations could have been higher in 2005 than in 2004, but FTC were not observed on planted water tupelo with great frequency. Herbivorous insects other than FTC may have produced damage observed on water tupelo in 2005 (e.g. grasshoppers), or abiotic conditions may have increased the frequency with which leaves were lost which may have inflated damage estimates.

There are several possible reasons why the treatments failed to produce a significant effect on leaf damage. The most likely reason for the failure of the bird exclusion treatment to produce a significant effect on leaf damage is that while PROW were frequently observed foraging in the herbaceous layer, neither they, nor any other bird species, was observed foraging on planted seedlings. PROW that were carefully observed foraging in the herbaceous layer appeared to focus their searches at the water surface, or on the lower surfaces of the herbaceous vegetation. Because the herbaceous layer in degraded swamp is dense and more or less continuous, the leaf blades form a nearly continuous canopy that obscured the upper portions of the crowns of planted seedlings from the view of PROW foraging in the herbaceous layer. Even if birds were able to view entire crowns of planted seedlings, it is uncertain that the structure of the seedlings would permit a bird to perch on the small, flimsy branches of these trees. Furthermore, no foraging observations of PROW and NOPA were recorded on baldcypress shorter than 1.5m tall.

The most likely reason for the failure of the Bt treatment to produce an effect on leaf damage is that Bt is degraded by UV light. Nearly all planted seedlings were underplanted in areas with little canopy cover, and although I applied the Bt treatment as late in the day as possible, UV indices in Louisiana in spring were consistently high and Bt droplets were exposed to several hours of daylight during each application. Baldcypress which were assigned to the Bt

treatment were found to have been recolonized by BCLR and/or baldcypress loopers between applications of Bt. Without repeated spraying at shorter intervals, it is doubtful that this treatment would be effective in reducing caterpillar abundance on study trees without controlling the source populations in larger conspecifics. Alternatively, droplets of Bt spray may have been too large for caterpillars to ingest. Water tupelo leaves wet evenly when sprayed with Bt, but droplets on baldcypress often coalesced into larger drops, perhaps due to increased surface tension created between the closely spaced leaves on twigs.

Aerial application of Bt to entire stands has been effective in controlling FTC (Abrahamson and Harper 1973) and BCLR (R. Goyer personal communication), but protecting coastal forests with aerial spraying might disrupt the ecology of the swamp because Bt is lethal to mosquito larvae. However, limited aerial application of Bt to small study plots within the swamp could be used to determine effects of caterpillar herbivory on growth parameters of mature trees, and effects of BCLR on the foraging ecology of insectivorous birds.

In addition to reasons why specific treatments may have failed, there are several general reasons why treatment effects on leaf damage were non-significant. First, leaf damage sampling periods were prolonged, and effects of early season herbivory on water tupelo may have been masked by the spread of the fungal disease over time, which probably accounts for the significance of the leaf damage assessment date covariable in analyses of water tupelo damage. Water tupelo also appeared to abscis damaged leaves more rapidly than baldcypress, which probably inflated damage estimates on water tupelo and may explain why the damage assessment date covariable was significant for water tupelo damage but not baldcypress leaf damage. Furthermore, both baldcypress and water tupelo produce multiple flushes of leaves during a growing season, and new, undamaged leaves expanded before I was able to sample. In

most studies of bird-herbivorous insect-tree trophic cascades, the basal tree species in the interaction chain has been a species that produces a single flush of leaves (but see Van Bael and Brawn 2005). In experiments utilizing trees which produce one flush of leaves, estimates of damage caused by herbivorous insects was relatively simple to obtain and could be assessed toward the end of the growing season. In contrast, rapid leaf replacement and the scale at which this study was executed made obtaining good point-estimates of leaf damage difficult to obtain. Defoliation measures differed between species in this study, making direct comparisons of defoliation severity between species impossible. However, it is difficult to imagine a common leaf damage estimation method for the two species, given that leaves on baldcypress twigs are so small relative to water tupelo leaves.

Strong et al. (2000) suggested that early season caterpillar herbivory in the study by Marquis and Whelan (1994) was responsible for the differences in herbivory effects on tree biomass production between their studies because early season herbivory may have greater effects on cumulative photosynthate accumulation. This was a study of early season defoliation by BCLR and FTC, and I expected that early season herbivory would affect growth of trees. However, other insect herbivores were present on my study sites after the spring treatment application, and it is unknown what effect these herbivores had on trees. Grasshoppers were observed consuming water tupelo foliage during the study, and Bt does not affect orthopterans. Baldcypress loopers were present on baldcypress seedlings, but not numerous. However, baldcypress loopers are present on baldcypress in low numbers throughout the growing season in Louisiana, and they may have as many as eight generations per year (R. Goyer personal communication). Baldcypress loopers are also larger than BCLR, and usually consumed entire baldcypress twigs, as opposed to BCLR that frequently consumed about half of the leaves on a

twig. Because of the difficulty of working in the swamp, and the need to remove bird exclosures before tropical storms caused floods in this study area, the study was restricted to times when the dominant insect herbivores were present.

Leaf damage has been shown to decrease baldcypress (Goyer and Chambers 1997, Souther-Effler 2004) and water tupelo growth (Conner and Day 1992, Souther-Effler 2004). Treatments had no effect on leaf damage measures in either species, and it was assumed that if treatments had no effect on leaf damage, then there should be no reason for treatments to have significant effects on height and diameter growth of planted seedlings. However, treatment effects on seedling height and diameter growth were significant for water tupelo, and the greater height and diameter growth of water tupelo in the exclosure treatment was opposite from my prediction that tree growth would be lowest in the bird exclosure treatment. This result is also surprising because there was more foot traffic around trees in the exclosure treatment, which frequently resulted in trenching around the perimeter of exclosures. Defoliation had a negative effect on height growth of water tupelo in 2004 in the exclosure and control treatments, but I am at a loss for an explanation for the slight positive relationship between percent height growth and percent defoliation in water tupelo in 2004. The greater growth of water tupelo in the bird exclosure treatment in 2005 highlights a major weakness of the study; there was no control for the bird exclosure structures. I have no knowledge of the soil chemistry in my study area, however if tree growth is affected by sulfides in my study area, then sulfides may have reacted with the iron in the steel conduit used to support the bird exclosures to form insoluble ferrous sulfide, and tree growth may have been improved. A simple solution for this problem could have been to drive a small section of conduit next to all trees in the experiment

Leaf damage in one year may be correlated with tree growth in the following year (Marquis and Whelan 1994). Ideally, a common defoliation measure would have been used between the tree species, and a more efficient repeated measures design, with defoliation in the previous year included as a covariable to determine if early season defoliation affects height and diameter growth in the following year, would have been used to test treatment effects on tree growth. An examination of the apical buds of planted seedlings for damage immediately following the period of caterpillar activity might be a more informative (and certainly far less time consuming) variable for inclusion in height growth analyses than estimating the proportion of leaves or the percent of the crown that was damaged. This is because the apical buds contain leaves produced in the previous growing season and are responsible for primary elongation of the leader. However, damage to baldcypress buds caused by newly hatched BCLR may be difficult to discern because early first instar BCLR burrow into opening buds soon after hatching and the minute caterpillars may not cause damage obvious to the naked eye.

No insect censuses were conducted on study trees. To demonstrate a clear interaction chain between birds, herbivorous insects and trees, it must first be shown that birds decrease the number of herbivorous insects on trees that are available for them to forage upon relative to those trees from which they are excluded.

Given the shortcomings of this experiment, the results obtained in this study might have been expected when viewed from the standpoint of the Exploitation Ecosystem Hypothesis (EEH). Recall that Fretwell (1977) and Oksanen et al. (1981) predicted that the strength of trophic cascades should increase with primary productivity because predator biomass should increase as they consume “excess” herbivores. In this study, very small and therefore relatively low-productivity trees were studied. Insects should not be abundant on low-productivity trees,

and birds should not be expected to forage on these unproductive substrates. Foraging observations of PROW and NOPA confirm that their foraging efforts are generally on larger, more productive trees with presumably greater densities of caterpillars. Viewed in this light, results of this study are more tenuous than, but similar, to those obtained in other studies of trophic cascades on low productivity saplings and seedlings (Forkner and Hunter 2000, Van Bael et al. 2003, Van Bael and Brawn 2005).

#### Effects of Birds on Caterpillars

The third objective of this study was to describe the foraging behavior of common insectivorous birds on BCLR and FTC. In both years of the study, FTC hatched within one week of the time that BCLR had grown to about 1cm long, at which point NOPA began foraging on BCLR. Insectivorous birds almost certainly exhibited functional responses to recently hatched FTC. However, few foraging observations were collected before FTC hatch to compare to foraging observations collected during the first instar stage of FTC. Common insectivorous birds such as PROW, NOPA and CACH were frequently observed gleaning small FTC caterpillars from water tupelo foliage, but birds did not continue to forage on FTC for more than about ten days.

Foraging on early life-stages of FTC was noted in Bay-breasted Warblers (Sealy 1979), and Bay-breasted warblers stopped foraging on FTC after they had grown to about 20mm long. No birds other than Yellow-billed Cuckoo were observed depredating FTC after they had grown to about 15mm long. No foraging observations of PROW depredating late instar FTC were collected, but on 10 and 13 May 2005, two PROW nests that were monitored with video cameras were provisioned with late instar FTC repeatedly during the 1-hour sampling periods. In other video recordings, at least two nests were provisioned once each with what were assumed to have

been FTC pupae. FTC pupae appeared to be relatively well protected from birds by the outer layer of silk around their cocoons. In a FTC pupal stocking experiment in the Maurepas Swamp, 80 of 320 (25%) stocked FTC were assumed to be depredated by birds (D. Fox unpublished data), but the predation rate may have been artificially high because stocked pupae did not have an outer layer of silk protecting the cocoons.

FTC are among the most widespread caterpillar species in North America, but reasons for birds' avoidance of FTC from the late first instar stage until the late fifth instar stage of the caterpillars when they are once again depredated by birds are unknown. FTC are protected by setae, and birds may be able to consume small FTC with small setae. However, observations of PROW depredating late fifth instar FTC still remain to be explained. Parry (1997 and references therein) noted that some birds that depredate large FTC may consume only the viscera of caterpillars to avoid their setae. However, PROW were not observed exhibiting this behavior.

One hypothesis to explain the renewed predation of FTC by PROW is that caterpillars go through several physiological changes in preparation for pupation which may make these large caterpillars palatable at this stage. First, some species of caterpillars which are protected by setae shed their setae prior to spinning their cocoons (I. Rodden personal communication, personal observations). In the Maurepas Swamp, an unidentified species of caterpillar that is heavily defended by setae incorporates shed setae in the construction of its cocoon. However, it is unknown whether FTC shed their setae prior to pupation, but it should be a simple matter to observe late fifth instar FTC to determine whether setae are shed before pupation. Second, the food bolus in a caterpillar's gut can comprise a significant proportion of the weight of a caterpillar. Should the food bolus be distasteful to birds, as the food bolus of aspen (*Populus* spp.) in gypsy moths (*Lymantra dispar*) is distasteful to chickadees in some areas (R. Lindroth

personal communication), then as caterpillars approach pupation and purge their gut, they may once again become palatable to birds (R. Lindroth and L. Dyer personal communication). This would also explain why birds consume early instar FTC, because small caterpillars would have smaller food boluses. Third, many caterpillar species sequester distasteful foliar chemical compounds within their bodies as a deterrent to predators. In some caterpillar species, these sequestered chemical defenses are also purged prior to pupation (L. Dyer personal communication). If FTC sequester distasteful chemical compounds from water tupelo, and then purge them prior to pupation, then this would explain the bimodal predation of FTC by PROW because young caterpillars would need to feed for a time before becoming unpalatable.

Regardless of the cause of birds' avoidance of FTC, the fact remains that most insectivorous birds in the Maurepas Swamp do not depredate FTC while they feed and defoliate water tupelo, and therefore provide little protection to the trees. The apparent ineffectiveness of PROW, the numerically dominant insectivorous bird in the Maurepas Swamp, in depredating FTC pupae also suggests that they exert little control over FTC populations. Smith and Goyer (1986) found that FTC survival of  $\geq 0.7\%$  resulted in population increase in the following year. Therefore, the lack of density dependent responses of pupal parasites because of drowning of parasite puparia in flooded forests (Smith and Goyer 1986), and the ineffectiveness of birds as FTC predators suggests that unless flooding is reduced via sediment accretion, allowing parasite populations to increase, population cycles of FTC in the swamp will not be regulated by predation and caterpillar herbivory will continue to cause die-back of water tupelo.

In contrast to the case of FTC, BCLR, a novel, emerging insect pest of baldcypress, were depredated by most insectivorous birds in the Maurepas Swamp both during the time when they were feeding on baldcypress and when they were pupating. NOPA began foraging on BCLR

after they had grown to about 1cm long and PROW began foraging on BCLR within a few days after that. Analyses of PROW and NOPA foraging observations suggest that both species, and probably most other insectivorous bird species for which foraging data were not collected, exhibited a functional response to BCLR presence. There was a dramatic shift in the proportion of foraging observations which were observed on baldcypress at about the time that FTC either became unpalatable or BCLR became a profitable food item upon which to forage. Results of video monitoring of PROW nests confirm that BCLR are a main food item in the diet of PROW nestlings. Anecdotally speaking, most insectivorous birds foraged heavily on BCLR while they were present.

Mean foraging maneuver height and foraging substrate height of PROW and NOPA increased while BCLR were present. These responses may not be due strictly to BCLR presence; however PROW and NOPA foraged on taller baldcypress while BCLR were present, and in the case of NOPA the mean height of baldcypress trees foraged upon was significantly taller than when BCLR were absent. This result is predicted by EEH, because larger, more productive trees should support a greater biomass of herbivores, and therefore should support a greater biomass of predators. Optimal foraging theory would also predict this result because birds foraging on larger trees may obtain more food per unit energy expended than when foraging on smaller trees. Birds foraging on large baldcypress may perch on large branches, search larger volumes of foliage for prey from a single vantage point than when perched on branches of smaller baldcypress, and access prey more easily from branches with large volumes of foliage arranged laterally around perches.

Because PROW, NOPA, and most other insectivorous birds in the study area (personal observations) foraged primarily on baldcypress taller than 5m, the implication is that baldcypress

less than 5m tall obtain little protection against BCLR herbivory from birds. These small regenerating trees must be encouraged to grow quickly to obtain benefits provided by insectivorous birds. Experiments simulating effects of the proposed diversion into the Maurepas Swamp have shown that freshwater flushing increases baldcypress and water tupelo productivity (Souther-Effler 2004), and sediment deposition increases productivity of plants in the herbaceous layer (Shaffer et al. 2003). The most aggressive and most logical step to take to improve the health of the Maurepas Swamp and increase productivity of trees remaining in the swamp is to restore flows of freshwater into the swamp via a diversion of Mississippi River water.

Due to the low sample sizes of observations and the pooling of foraging observations collected in different years (Petit et al. 1990), caution should be used when drawing conclusions from analyses of foraging observations in this study. However, anecdotal information gathered during three years of field work in the study area, plus data collected during video monitoring of PROW nests strongly suggests that insectivorous birds probably reduce defoliation of mature baldcypress by BCLR to some degree.

A rough estimate of the protection value of a pair of nesting PROW to baldcypress may be calculated by using results from video monitoring of nests in combination with data on baldcypress foliage consumption by BCLR. Meeker and Goyer (1994) found that fourth and fifth instar BCLR consume an average of 0.15g dry weight of baldcypress foliage before they pupate. The rate at which PROW provisioned their nests with BCLR averaged 6.33 BCLR per hour. PROW nestlings fledge after ten days, and using a conservative estimate of eight foraging hours per nest-day yields the following formula:  $6.33 \text{ BCLR/hr} * 8\text{hr/day} * 10 \text{ days} * 0.15\text{g dry weight baldcypress foliage/BCLR} = 76\text{g dry weight of baldcypress foliage protected per successful PROW nest active during BCLR activity}$ . This estimate is probably low because

PROW probably provision their nests for more than eight hours per day, and the formula does not account for any BCLR consumed by adults. This calculation of the protective value of a nesting pair of PROW to baldcypress is one of, if not the first, calculation of its kind (R. Cooper personal communication), but it is a simple estimate that could easily be replicated in other systems where nest provisioning rates and leaf biomass consumed by caterpillars are known. Takegawa and Garton (1984) calculated the value of birds as natural control agents of defoliating caterpillars in terms of the cost that would otherwise be incurred for spraying to produce the same caterpillar mortality rate as that caused by birds.

The protective value of PROW to baldcypress may be less than that of the second most abundant insectivorous bird, NOPA. This is because PROW exhibit a bimodal foraging height pattern even during BCLR activity. Nearly 49% of all PROW foraging observations were observed in the herbaceous layer or on trees other than baldcypress, but only 29.5% of NOPA foraging observations were observed on trees other than baldcypress, and less than 5% of NOPA foraging maneuvers were in the herbaceous layer. Relative abundance of NOPA is slightly less than that of PROW, but NOPA begin foraging on BCLR earlier than any other observed bird species, and results from the fledging survey performed on study plots in 2005 suggest that NOPA are 25% more likely to fledge a clutch of young during the time of BCLR activity than PROW. Therefore, in terms of retaining the functionality of the insectivorous bird guild in the Maurepas Swamp, conservation of NOPA may be equally as important as conservation of PROW.

The emergence of BCLR as a pest of baldcypress in stressed swamp forests is certainly an additional stressor and a danger to the resiliency of the swamp ecosystem, but because they are palatable to birds, the situation is not as dire as one which could arise if an unpalatable

herbivore were to outbreak. PROW and NOPA breed at very high densities in the Maurepas Swamp (personal observations), they arrive in the Maurepas Swamp in early March (personal observations, J. Zoller personal communication), before BCLR activity begins, and adult PROW and NOPA consume and feed many BCLR to their nestlings (this volume).

Zoller (2004) reported that as a whole, breeding migrant birds are rare in habitats which have transitioned to open marsh. However, Zoller's( 2004) habitat types were categorical, and no studies of changes in the bird community have been conducted along a continuum of canopy cover. PROW nest in cavities in dead trees, whereas NOPA require Spanish moss (*Tillandsia usneoides*) for nesting. PROW also appear to have a broader foraging niche than NOPA, because PROW frequently forage in the herbaceous layer. As canopy cover is lost in the swamp, snags might continue to provide nesting habitat for PROW until cavities are no longer nestable, and PROW might be able to obtain enough food in the herbaceous layer, but NOPA nesting and foraging habitat will be lost with canopy cover. Therefore, PROW might persist at higher densities than NOPA as trees die and canopy cover decreases due to abiotic stressors and caterpillar herbivory in the Maurepas Swamp.

In addition to the direct effects of bird predation on BCLR, higher-order interactions may occur as a result of reduced herbivory due to bird predation of BCLR. First, BCLR are much more obvious to humans, and almost certainly to birds, when they attempt to construct shelters of baldcypress leaves with appressed morphology. BCLR moths do not differentiate between trees with flat or appressed foliage when selecting trees on which they lay their eggs (Meeker and Goyer 1993). Therefore, baldcypress with greater proportions of appressed leaves may have a selective advantage over baldcypress with more leaves of flat morphology due to increased bird foraging efficiency and reduced BCLR herbivory. Second, herbivory may reduce the frequency

with which plants are colonized by mycorrhizal fungi (Gehring and Whitham 2002). Symbiotic mycorrhizal fungi increases nutrient absorption by tree roots and the indirect effect of birds on mycorrhizal fungi colonization may be especially important in highly reduced, nutrient starved wetlands. Therefore, direct effects of birds on BCLR may affect baldcypress productivity via multiple indirect pathways.

Although significant effects of birds on insect herbivore leaf damage and growth of planted baldcypress and water tupelo seedlings were not demonstrated in this experiment, foraging observations, video nest monitoring and the estimate of the protective value of a single species of nesting insectivorous bird to baldcypress foliage against BCLR herbivory strongly suggest that birds may be integral to maintaining the resiliency of the Maurepas Swamp ecosystem. However, Darveau et al. (1997) found that sugar maple (*Acer saccharum*) forest decline in Quebec was positively correlated with declines in insectivorous bird species richness and abundance, much like the results obtained by Zoller (2004) in the Maurepas Swamp, but leaf chewing caterpillars on saplings were positively correlated with forest decline. Therefore, if abiotic conditions in the swamp continue to deteriorate it is feared that insectivorous bird species richness and abundance will decline over an increasing area, increasing negative effects of caterpillars on tree productivity as predicted by Marquis and Whelan (1994), Strong et al. 2000, and Murakami and Nakano (2000).

## CHAPTER 4. SUMMARY AND CONCLUSIONS

Results from the nest box addition experiment and the bird exclosure experiment suggest that birds did not affect growth of naturally regenerated baldcypress saplings or planted baldcypress and water tupelo seedlings. However, both studies were flawed in their execution, and care should be taken when drawing conclusions from these results. First, baldcypress and water tupelo have indeterminate growth, and a timelier and more rapid estimate of leaf damage and growth should have been made to provide an accurate comparison of treatments. Second, the results obtained in this study might have been expected when viewed from the standpoint of the Exploitation Ecosystem Hypothesis (EEH). In this study, very small and therefore relatively low-productivity trees were studied. Foraging observations of PROW and NOPA confirm that their foraging efforts are generally concentrated on larger, more productive trees with presumably higher densities of caterpillars.

Birds may protect baldcypress taller than 2m from some baldcypress leafroller herbivory, but probably do not protect water tupelo foliage from forest tent caterpillar herbivory. This is of concern because both mature and planted water tupelo, and water tupelo regeneration, appear to be more severely impacted by abiotic growing conditions than baldcypress in the Maurepas Swamp. Should the water tupelo component of the forest within the Maurepas Swamp continue to be lost, then it is likely that populations of secondary cavity nesting birds, including an extremely dense and productive population of Prothonotary Warblers, will decline as cavity trees die and decay without replacement.

The cypress-tupelo swamp on the west side of the Maurepas Swamp is in decline, but a diversion of fresh water from the Mississippi River has been planned and designed. If the

diversion is constructed and fresh water input, with its associated load of sediment and nutrients, is restored to the swamp, then it is expected that plant productivity and organic sediment accretion will increase (Shaffer et al. 2003). While the freshwater diversion into the Maurepas Swamp may not completely ameliorate changes to the hydrology of the area caused by the construction of flood control levees and the damming of Bayou Manchac, it will most likely decrease the rate at which forest within the Maurepas Swamp transitions into open marsh and decrease the rate at which populations of Prothonotary Warblers and Northern Parulas decline in the swamp.

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## VITA

David M. Fox was born at The Presidio in San Francisco, California on 16 May 1968 to Geraldine and John Fox. He attended Corcoran High School in Syracuse, New York during his freshman year, then City Honors High School in Buffalo, New York from which he graduated in 1986. David attended Erie Community College in Buffalo, New York and The State University of New York at Geneseo in Geneseo, New York during his freshman year, and then attended The University of Washington in Seattle, Washington from which he graduated with a Bachelor of Science degree in Forestry with a concentration in wildlife science in 1993. David spent several of the next nine years traveling and working as a field technician for various wildlife field projects. David's favorite field experience was during three summers of field work in the White River National Wildlife Refuge for graduate students under Dr. Robert J. Cooper. David began his Master's Degree at Southeastern Louisiana University under Dr. Philip C. Stouffer in the fall of 2002, and then followed Dr. Stouffer to the Louisiana State University School of Renewable Natural Resources in Baton Rouge, Louisiana when Dr. Stouffer took a position there in 2003.

During the time in which David worked as a field technician, he learned to dislike measuring vegetation, and vowed that research for his Master's Degree would not involve vegetation measurements. However, he designed the projects described in this volume, and much of his time was spent measuring leaf damage and tree growth. Had David remembered Shakespeare's Hamlet, and Polonius's advise to his son, "This above all, to thine own self be true, and it must follow, as the night the day, thou canst not then be false to any man.", then David might have enjoyed earning his Master's Degree.