COMMUNITY DYNAMICS OF CAVITY-NESTING BIRDS IN OLD-GROWTH LONGLEAF PINE FORESTS

by

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(Under the Direction of Robert J. Cooper)

ABSTRACT

Old-growth longleaf pine (*Pinus palustris*) forests of the Southeastern Coastal Plain have declined to merely 0.00014% of their original extent. The Red-cockaded Woodpecker (*Dryobates borealis*) is an endemic keystone species of these forests, excavating cavities in living pines that are used by many other species. Few studies have investigated the community of cavity-nesting birds inhabiting old-growth longleaf. In this thesis, the community was studied by (1) assessing species richness and densities across a range of sites in old-field and old-growth pine forests, (2) quantifying nest site partitioning in old-growth forests and identifying potential for competition, and (3) investigating hypotheses to explain Red-cockaded Woodpecker cavity kleptoparasitism. Results suggest that old-growth longleaf pine forests constitute high-quality habitats for the community because of the abundance of Red-cockaded Woodpecker cavities and snags. Conserving remnant patches and striving for old-growth conditions on younger stands will continue to provide habitat for a diversity of cavity-nesting birds.

INDEX WORDS: Cavity-nesting Birds, Old-growth Longleaf Pine, Red-cockaded Woodpecker, Nest Site Selection, Cavity Kleptoparasitism, Snag Management

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LONGLEAF PINE FORESTS

by

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B.S., Florida State University, 2018

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment

of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2020

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December 2020

ACKNOWLEDGEMENTS

This work would have not been possible without the help of many individuals that I feel grateful to have worked alongside. First, I would like to my co-advisers, Bob Cooper and Jim Cox for providing me the opportunity to pursue this project and for guiding me for the past two and a half years. Bob Cooper introduced me to the world of wildlife management and experimental design, fielded my never-ending questions, and gave me the opportunity to become a teaching assistant for ornithology (one of my favorite parts of my time at Warnell). His door was always open, and he always gave meaningful and thoughtful advice. Jim Cox, who has been a mentor to me since undergrad, first introduced me to the world of avian biology and encouraged me to undertake this project. He has always been extremely supportive and patient throughout the years, and I am grateful that he was part of my graduate experience. He, too, fielded my never-ending questions, always with a smile on his face. Working with Bob and Jim has been truly been a rewarding experience, and their kindness and sense of humor made the tougher times smoother. During my time at Warnell, they have helped me in my quest to become a better scientist, and for that I am forever grateful.

My committee members, Richard Chandler and James Martin, provided insightful guidance during experimental design planning and quantitative analyses, and were patient while I fielded questions and had to change graduation dates. Richard provided me with the opportunity to be a teaching assistant for applied population dynamics, which helped me gain more experience teaching and the chance to learn even more about the subject. Both James and Richard were always supportive and encouraging. I also want to extend a thank you to my lab and office mates, including those in the Warnell Avian Research Group, who always entertained my stats questions and provided comic relief in the office.

I am thankful to have had the help of Zach Vickers, my field technician, who trekked countless miles through the blistering heat of Florida in June and July. I also want to thank all the wonderful friends I have made both within and outside of Warnell. Several folks have supported me immensely during my time here, forming friendships I know will last a lifetime. I will forever be grateful for their encouragement. Thank you to my partner, Peter, who was very kind, patient, and supportive during both highs and lows that is grad school. And finally, thank you to my parents, Renee and Jonathan, who always encouraged me to pursue my dreams, and only looked at me a little funny when I told them I wanted to study birds for the rest of my life.

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CHAPTER 1

INTRODUCTION

Background

Cavity-nesting Bird Communities, Nest Site Limitations, and Nest Site Partitioning

Community-wide studies investigating relationships among members are vital to provide informed decision making in conservation of natural resources and can aid in forest management by improving knowledge of species' requirements (Martin and Eadie 1999, van der Hoek et al. 2017). Because tree cavities serve as nest and roost sites for many taxa, the process of cavity creation serves as a critical mechanism that influences cavity communities worldwide (Blanc and Walters 2008b). These communities show a keystone species-driven pattern of organization, making them well suited for community investigation and analysis (Martin and Eadie 1999). Cavity-nesting birds are also prolific in their spread across avian families and comprise at least 18.1% of avian species worldwide, of which 49% are obligate cavity-nesters (van der Hoek et al. 2017). Species within these communities interact through a complex web based on the creation of and competition for cavities that serve as roost and nest sites (Lawler and Edwards Jr 2002). Guilds within the community consist of primary excavators, typically woodpeckers (*Picidae*), which excavate cavities; weak primary excavators, which can excavate their own cavities in softer wood; and secondary cavity nesters, which rely entirely on existing cavities. Additionally, both primary and weak primary excavators may use existing cavities, but this is species-specific (Martin and Eadie 1999).

Primary excavators provide up to 77% of the cavities used by secondary cavity-nesting species in North American habitats (Cockle et al. 2011). As a result, these communities exist in a tiered structure with individual members connected via ecological interdependencies (Martin and Eadie 1999). Generally, secondary cavity-nesting birds tend to be more limited by nest sites than excavators are; some secondary cavity-nesting species' abundances and distributions are affected by cavity availability due to their dependence on existing cavities (Short 1979, Newton 1994). However, primary excavators can also be nest site limited based on availability of dead and dying trees suitable for excavation (Li and Martin 1991). Snags may be limited in forests where management includes the removal of dead and dying trees, which are common practices in the southeastern United States (McComb et al. 1986).

Because cavities are an important resource that have the potential to limit populations, interspecific competition for cavities can be severe. Species using similar or common resources may avoid competition either by narrowing their niche or by utilizing a portion of their niche that decreases overlap with other species' niches (Colwell and Fuentes 1975). Nest site selection implies that individual species prefer certain sites for nesting and avoid others (Kosinski and Winiecki 2004). Individual characteristics of nest sites can limit use by some cavity-nesting species (Lorenz et al. 2015), creating ecological niches within the community. Species may differ in preferred sizes of cavity and entrance hole, cavity height and location, degree of seclusion, and distance to preferred foraging sites (Van Balen et al. 1982, Nilsson 1984). Primary excavators can tolerate excavating in harder wood than weak excavators, such as nuthatches (*Sittidae*), which require more decayed wood for excavation (Raphael and White 1984). Cavities as nest sites vary in quality, and the availability of high-quality cavities may be limited by high degrees of competition (Nilsson 1984), especially for species with greater niche overlap. Patterns of nest site selection and use are critical to understanding population ecology and evolution of cavity-nesters, including how nest sites affect interspecific interactions (Lindell 1996, Martin et al. 2004). Cavity-nesting communities seem particularly well suited to study nest partitioning based on the high degree of nest reuse and interdependencies between species.

Remnant Old-growth Longleaf Pine Forests

In his southeastern travels, Bartram (1791) described the Southeastern Coastal Plain as covered by a "vast forest of the most stately pine trees that can be imagined…" Longleaf pine (*Pinus palustris*) forests once blanketed the southeast, covering up to 97 million ha pre-European settlement, stretching from southeastern Virginia to central Florida and west into eastern Texas (Wahlenberg 1946a, Frost 1993, Stout and Marion 1993). Across the range, there are 3 broad categories of longleaf pine forests based on soil and hydrologic characteristics - flatwoods, sandhills, and clayhills (Abrahamson and Hartnett 1990). Longleaf pine forests are one of the most biologically diverse ecosystems in the United States, with 90 species of migratory and residential bird species documented, including up to 19 cavity-nesting species (Engstrom 1993, Means 2007). However, native longleaf currently inhabits less than 3% of its original range. A long history of land conversion, fire suppression, intense logging, and urbanization has ultimately decimated the habitat (Ligon et al. 1986, Van Lear et al. 2005), leaving very few undisturbed remnant patches (Wahlenberg 1946a). Second- and third-growth forests now constitute much of the remaining longleaf range. Old-growth longleaf stands occupy even less area than younger forests, an estimated 0.00014% of their original pre-settlement extent (Varner and Kush 2004). Old-growth longleaf pinelands contain many large trees (>50 cm diameter at breast height; DBH), long-lived and large snags, down woody debris, and many mixed-aged patches within the forest. Stands will typically develop old-growth characteristics around 120 years of age, but mature old forests have age classes upwards of 200 years old (Platt et al. 1988). Old-growth longleaf stands are especially important because they provide benchmarks for natural area management, reconstructed climatic data, are among some of the highest quality habitats for native biodiversity, and are valued cultural resources (Varner and Kush 2004). Additionally, old-growth pine snags, which persist up to 20 years on the landscape, have strong influences on cavity-nesting bird richness and abundance (Miller and Marion 1995, Conner and Saenz 2005).

The Red-cockaded Woodpecker: A Keystone Species in Southern Pine Forests

Fire-maintained pine forests are typically characterized as relatively cavity-depauperate environments due to a lack of snags, low tree density, and low hardwood component (Conner et al. 2001). Many oaks (*Quercus* sp.) are more susceptible to fungal decay and develop natural cavities while they are living, but pines are more resistant and often are not excavated for cavities until they are dead (Bull et al. 1997). In this system, the endemic and threatened Red-cockaded Woodpecker (*Dryobates borealis*) acts as a keystone species, excavating cavities exclusively in living pines, the dominant substrate of fire-maintained pine forests (Ligon 1970). A suite of other taxa, including herpetofauna, insects, mammals, and birds commonly usurp Red-cockaded Woodpecker cavities for nest and roost sites (Jackson 1978, Neal et al. 1992, Kappes Jr and Harris 1995, Kappes Jr 1997, Loeb and Hooper 1997).

Red-cockaded Woodpeckers are cooperative breeders, and this life history trait is often linked to cavity excavation time in live pine trees (Jackson 1978, Walters 1990, Conner et al. 2001), which can take an average of 3.7-6.3 years in longleaf pines (Conner and Rudolph 1995). Red-cockaded Woodpeckers live in family groups containing one pair and 1-3 helpers, typically male offspring of the dominant breeding male (Lennartz et al. 1987). Each member of a family requires its own roosting cavity, and the dominant male's roost cavity becomes the nest cavity during the breeding season (Conner et al. 2001). Individuals without cavities are forced to roost in the open, making them vulnerable to predation and weather (Carter et al. 1989). Because these competitive interactions are negative for Red-cockaded Woodpeckers and beneficial for the cavity usurpers, Kappes Jr (1997) has described these usurpers as cavity kleptoparasites, rather than cavity competitors. To prevent kleptoparasitism, Red-cockaded Woodpecker management has focused on the use of metal cavity-hole restrictors as described in Carter et al. (1989). Some studies have also suggested snag retention and the addition of artificial nest boxes can alleviate cavity competition (Wood 1983, Loeb and Hooper 1997), but findings have remained contradictory, with others suggesting that Red-cockaded cavities are usurped regardless of snag densities (Harlow and Lennartz 1983, Everhart et al. 1993). More information on community-level interactions is required for effective Red-cockaded Woodpecker management (Blanc and Walters 2008a).

Study Area: The Red Hills Physiographic Region of Northwest Florida and Southwest Georgia

The pineland dominated Red Hills physiographic ecoregion (ca. 100,000 ha) roughly extends from Tallahassee, Florida to Thomasville, Georgia and is one of the largest contiguous tracts of privately owned land under multiple ownerships, about half of which are under conservancy easements that balance consumptive use with sustainable management. Many plantations are managed for Northern Bobwhites (*Colinus virginianus*) or sustainable timber operations, including timber salvaging and selective harvesting. Over 100 breeding bird species have been documented in the Red Hills during the Florida Breeding Bird Atlas Project, making the Red Hills one of the most diverse bird breeding grounds in Florida and earning recognition as an important bird area (National Audubon Society 2013). The Red Hills also supports the largest population of Red-cockaded Woodpeckers on private lands and the sixth largest population across its range (Cox et al. 2001, National Audubon Society 2013). Because Red-cockaded Woodpecker habitat management consists of prescribed burns, selective timber harvest, and hardwood reduction (Engstrom and Palmer 2005), the Red Hills contain some of the best remaining examples of old-growth longleaf pine forests due to an extended history of proper habitat management, especially frequent prescribed burns that maintain open canopies and prevent encroachment of hardwood species (Means 1996). The cavity-nesting bird community associated with these forests is outlined in Table 1.1, though this is not a comprehensive list of every species found across all 19 longleaf pine natural communities.

The Red Hills are representative of clayhill longleaf pine forests, which feature fine-textured sediments, high pH, denser canopy vegetation, and very high floral diversity (Carr et al. 2010). The main sites for this research were conducted across four privately owned longleaf pine plantations in Thomas County, Georgia (Figure 1.1). All plantations were managed using 1-2-year fire return intervals and are ≥ 800 ha, but timber age and snag densities varied. Arcadia, Greenwood, Melrose, and Sinkola contained patches of old-growth longleaf pine forests with many old trees. Arcadia encompasses the Wade Tract, an old-growth research site under easement by Tall Timbers Research Station. Each property contains patches (30-200 ha) of old-growth longleaf pine forests with many old (>200 years) large trees and ground cover dominated by wiregrass (*Astrida stricta*) and other fire-adapted grasses.

Study Significance

The influence of snag densities on cavity-nesting bird richness and abundances has been well documented in southeastern pine plantations (McComb et al. 1986, Land et al. 1989, Caine and

Marion 1991, Miller 2010). Management suggestions for cavity-nesting birds in these systems include increasing rotation age, limiting sizes of single-aged forests, avoiding large gaps, and retaining snags (Land et al. 1989). However, there have been very few studies of cavity-nesting bird communities in old-growth pinelands where Red-cockaded Woodpeckers act as ecosystem engineers. Little is known about the influence Red-cockaded Woodpecker cavity availability has on community structure, interactions, and nest site selection (Kappes 2004, Blanc and Walters 2008a). Additionally, the degree to which competition for Red-cockaded Woodpecker cavities is influenced by local snag densities remains contradictory in the literature, warranting additional studies (Harlow and Lennartz 1983). Some suggest that snag retention or the addition of artificial cavities alleviates competition for Red-cockaded Woodpecker cavities (Loeb and Hooper 1997, Blanc and Walters 2008a), but Everhart et al. (1993) found no relationship, suggesting a potential preference for Red-cockaded Woodpecker cavities

Management intended to promote diversity needs to consider quantitative assessments of the complex web of interactions within the community (Bednarz et al. 2004), which serves as the fundamental impetus of this study. The overarching goal of this thesis is to describe dynamics of the cavity-nesting bird community in old-growth longleaf pine forests, especially in relation to the Red-cockaded Woodpecker. More specifically, the aim of this research is to investigate the influence and diversity of nest site availability on cavity-nesting community dynamics and nest site niche partitioning, as well as to quantify competition for Red-cockaded Woodpecker cavities. The results of this thesis will provide ecological data to support more effective management for the cavity-nesting community of fire-maintained pinelands by highlighting the important role of resources in old-growth forests for community dynamics.

Thesis Structure

This chapter provides a general overview and background information on cavity-nesting bird communities and the importance of longleaf pine forests for biodiversity. Studying cavity-nesting communities in remnant old-growth longleaf pine stands can provide context as to how these communities historically functioned and coexisted. The importance of the endemic Red-cockaded Woodpecker, a keystone excavator in old-growth southern pine forests, is highlighted. Finally, the study significance and potential implications are outlined.

Chapter two assesses cavity-nesting bird species richness and densities along a gradient of managed pine forests, from managed old-field forests to unmanaged old-growth longleaf pine forests, which differ in abundances of snags and Red-cockaded Woodpecker cavities. Additional important forest characteristics for cavity-nesting birds are also discussed regarding similar future assessments.

Chapter three examines nest site niche partitioning among the cavity-nesting bird community by quantifying characteristics of species-specific nest sites in old-growth longleaf pine forests. Based on amount of nest site niche overlap, species are identified that may be subject to interspecific competition.

Chapter four examines Red-cockaded Woodpecker cavity kleptoparasitism in old-growth longleaf pine forests. Two hypotheses are presented that may explain kleptoparasitism; (1) limited local snag availability influences the frequency of kleptoparasitism, or (2) nesting in Red-cockaded Woodpecker cavities promotes higher nesting success than other types of cavities available. Nest success of two common kleptoparasites that are also primary excavators (Red-headed Woodpeckers [*Melanerpes erythrocephalus*] and Red-bellied Woodpeckers [*M. carolinus*]) are compared in Red-cockaded Woodpeckers cavities and cavities in snags.

The fifth chapter summarizes major findings and conclusions, as well as highlights areas for future work based on results from each study and the overall system. The results from this research will help inform managers conserve and promote a rich diversity of cavity-nesting bird species by providing more information on the resources and interactions of the historical landscape of the region.

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Tables

Table 1.1. List of breeding cavity-nesting bird species (n = 17) inhabiting the Red Hills region of the Southeastern Coastal Plain and their ecological guild within the cavity-nesting community.

Guild	Common Name	Scientific Name
Primary excavator	Downy Woodpecker	*Dryobates pubescens*
	Hairy Woodpecker	*Dryobates villosus*
	Northern Flicker	*Colaptes auratus*
	Pileated Woodpecker	*Dryocopus pileatus*
	Red-bellied Woodpecker	*Melanerpes carolinus*
	Red-cockaded Woodpecker	*Dryobates borealis*
	Red-headed Woodpecker	*Melanerpes erythrocephalus*
Weak primary excavator	Brown-headed Nuthatch	*Sitta pusilla*
	Carolina Chickadee	*Poecile carolinensis*
Secondary cavity nester	Chimney Swift	*Chaetura pelagica*
	Eastern Bluebird	*Sialia sialis*
	European Starling	*Sturnus vulgaris*
	Great Crested Flycatcher	*Myiarchus crinitus*
	Purple Martin	*Progne subis*
	Tufted Titmouse	*Baeolophus bicolor*
	White-breasted Nuthatch	*Sitta carolinensis*
	Wood Duck	*Aix sponsa*

Figures

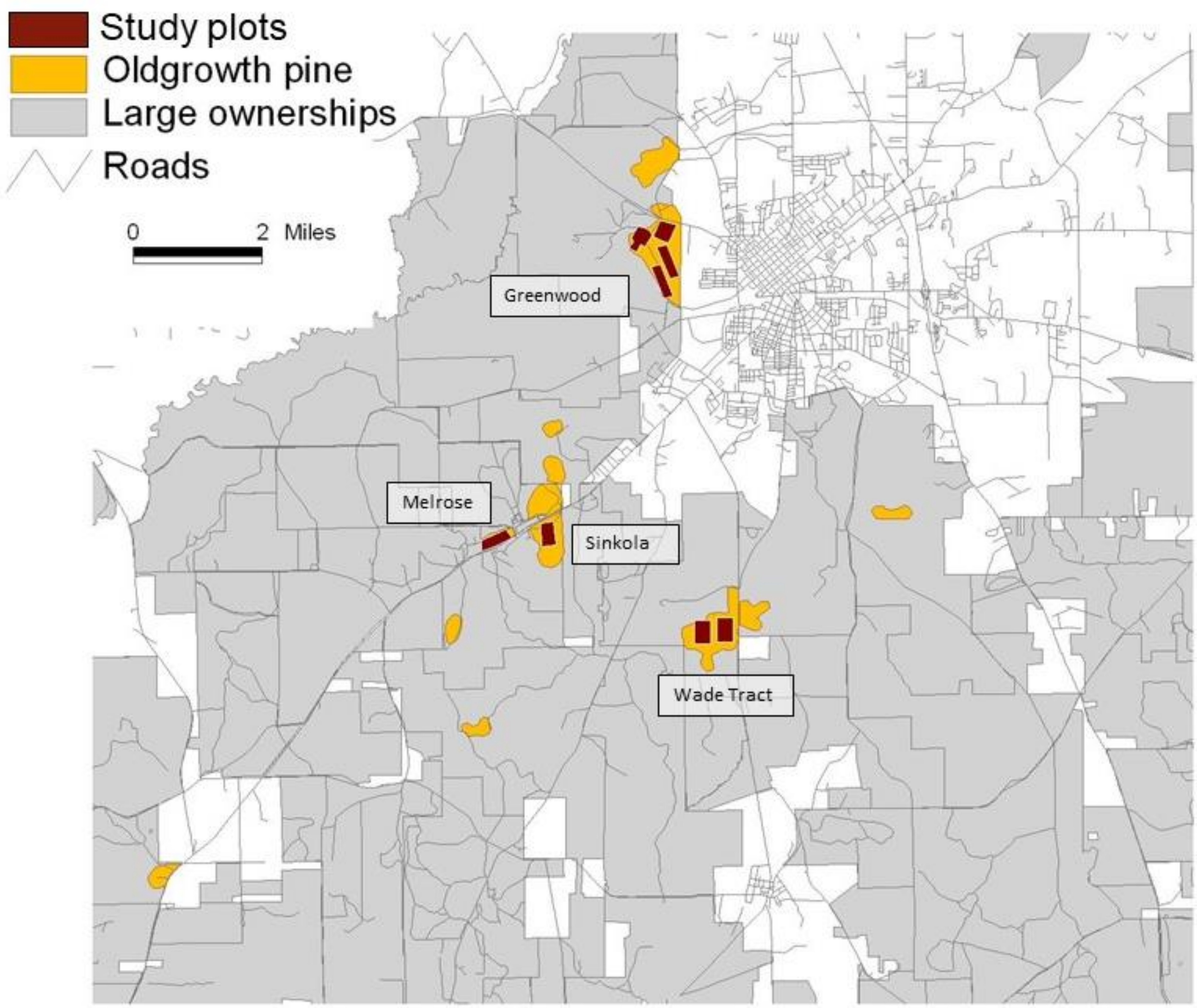

Figure 1.1. Study plots (*n* = 8) within four privately owned longleaf pine plantations (Greenwood, Melrose, Sinkola, and the Wade Tract) located in the Red Hills region in Thomas County, Georgia. Each plot (20 ha) was strategically placed to encompass only old-growth longleaf pine stands.

CHAPTER 2

CAVITY-NESTING BIRD DENSITIES IN MATURE SOUTHEASTERN PINE FORESTS: EFFECTS OF SNAG MANAGEMENT AND AN ECOSYSTEM ENGINEER[1]

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Abstract

The relationship between cavity-nesting birds and snags is one of the better-studied ecological examples of the effects a limiting resource may have on species with similar resource needs. Snags are used for roosting, nesting, displaying, and foraging, and it is generally assumed that snags influence cavity-nesting bird densities and richness. In the southeast, most old-growth longleaf pine forests have been replaced by younger old-field and managed pine forests. Cavity-nesting birds in managed pine forests have been well studied and led to the conclusion that these forests are lower quality due to a lack of snags. However, old-growth forests contain many remnant cavities that may supplement snags. The Red Hills region of northwest Florida and southwest Georgia hosts some of the last remaining old-growth longleaf pine (*Pinus palustris*) forests and the largest Red-cockaded Woodpecker (*Dryobates borealis*) population on private lands. Red-cockaded Woodpeckers are keystone excavators, creating cavities in living pines that are used by over 24 other species. In this study, we assessed cavity-nesting bird densities and species richness in old-growth longleaf pine forests and mature old-field pine forests that varied in their management and therefore availability of nest sites. We conducted point counts and collected data on vegetation characteristics that we believed would influence cavity-nesting birds on 10 privately-owned properties in the southwest Georgia. We estimated densities of 11 cavity-nesting birds. Only two species were correlated with snags and six species were correlated with Red-cockaded Woodpecker cavities. Densities of those same 6 species were greater in old-growth sites than old-field pineland sites, and old-growth sites had greater species richness. Our results suggest that old-growth longleaf pine forests, specifically those that that have Red-cockaded Woodpecker cavities, provide high quality habitat for several cavity-nesting bird

species. Finally, we provide suggestions of applicable environmental covariates that would be useful in similar assessments of cavity-nesting birds in southern pine forests.

Introduction

Cavity-nesting birds represent about one-third of the breeding birds associated with forest communities (Martin and Eadie 1999). Primary excavators, such as woodpeckers (*Picidae*), are important drivers of avian richness and forest health and often act as keystone species in their respective ecosystems (Mikusiński et al. 2001, Drever et al. 2008). There has been growing conservation concern for cavity-nesting species because of specific requirements they have for dead and dying trees used for displaying, foraging, nesting, and roosting (Martin and Eadie 1999). Cavity-nesting bird communities have been relatively well studied in intensively managed and younger pine forests. Under these conditions, strong competition for limited cavities or suitable substrates for excavation was regularly observed and led to recommendations for snag retention and creation or the addition of artificial cavities (Scott 1979, Dickson et al. 1983, Raphael and White 1984, Caine and Marion 1991, Schreiber 1992, Homyack et al. 2011). However, second-growth forests with artificially enhanced cavity resources still may not capture the natural diversity once found in different forest types. In the Southeastern Coastal Plain, longleaf pine (*Pinus palustris*) forests were once one of the most expansive ecosystems, dominating over 60 million acres and co-dominating over another 30 million. Longleaf pine forests are dependent on fire for regeneration and preventing encroachment by hardwood species (Wahlenberg 1946, Platt et al. 1988). In the eastern half of the Coastal Plain, wiregrass (*Astrida stricta*) is closely associated with longleaf pine; two long-lived keystone species that are resistant to, but facilitate fire (Platt et al. 1988, Landers et al. 1995). Animals and plants of these forests have evolved in response to frequent, low-intensity fires (Stout and Marion 1993). A long history of suppressing natural fires, land conversion to agriculture and short-rotation plantations, exploitative harvest, and urbanization resulted in near complete extirpation of old-growth conditions (Wahlenberg 1946, Landers et al. 1995, Wear and Greis 2002, Van Lear et al. 2005). Less than 3% of longleaf pine forests are extant, and much of what remains are second- or third-growth forests. Old-growth stands occupy an estimated 0.00014% of their original range (Means 1996, Varner and Kush 2004). Old-field succession of abandoned farmlands has shifted landscapes towards shortleaf (*P. echinata*) and loblolly (*P. taeda*) pine-hardwood mixed habitats in areas that were once longleaf forests (Nowacki and Abrams 2008).

Longleaf pine forests are some of the most biologically diverse ecosystems in North America (Landers et al. 1995) and host a rich assemblage of cavity-nesting birds (Engstrom 1993). The most emblematic cavity-nesting bird of mature longleaf pine is the threatened Red-cockaded Woodpecker (*Dryobates borealis*), which excavates cavities exclusively in living pine trees, the dominant substrate of fire-maintained pine forests (Ligon 1970). These cavities provide a long-term resource on the landscape (Conner and Rudolph 1995). At least 24 species of birds, reptiles, mammals, and insects have been documented using Red-cockaded Woodpecker cavities as nest and roost sites, including up to 10 species of cavity-nesting birds (Jackson 1978, Harlow and Lennartz 1983, Carter et al. 1989, Conner et al. 1997, Walters 2004). Because of their ability to excavate in the dominant resource of the historic landscape, Red-cockaded Woodpeckers act as ecosystem engineers and are a keystone species of mature southeastern pine forests (Conner et al. 2001). Despite being one of the most heavily studied and managed endangered species (Walters 1991), little is understood about the influences of Red-cockaded Woodpecker cavity availability on cavity-nesting bird abundances (Blanc and Walters 2008a). The younger forests that now dominate the region lack important characteristics of old-growth, including mature trees, vertical and horizontal heterogeneity, and persistent snags (Nowacki and Abrams 2008). Studying the behavior of organisms in old-growth forests may be instructive; for example, studying woodpecker behavior in old-growth forests can provide insight as to which old-growth characteristics are important and should be maintained or mimicked in forests for woodpecker management (Lennartz and Lancia 1989).

Although fire-maintained pine forests are typically characterized as cavity-deficient habitats (Conner and Rudolph 1995), old-growth longleaf pine forests may have densities of up to 15 snags/ ha (Schwarz 1907). In fact, it may be inappropriate to consider only snag densities when characterizing old-growth longleaf pine forests because of the cavity resource provided by remnant Red-cockaded Woodpecker cavities. The number of nests sites in old, unmanaged forests is generally not limiting for breeding densities of cavity-nesting birds (Wiebe 2011). For example, in an experimental manipulation of sand pine scrub stands, Greenberg et al. (1995) found mature forests contained richer assemblages and higher abundances of cavity-nesting birds than did disturbed (i.e., salvaged and clear cut) treatment plots. McComb et al. (1986) suggested that snag resources in Florida were probably deficient for primary cavity-nesting species in young (0-30-year-old) pine stands, especially in logged forests. Snags may be especially limiting in forests where management includes the removal of dead or dying trees, a common practice in southeastern pine forests (McComb et al. 1986). Yet, few studies have assessed cavity-nesting birds in old-growth longleaf pine forests.

The goal of this study was to assess cavity-nesting bird densities and richness across a gradient of sites from managed old-field pine forest to unmanaged old-growth longleaf pine forests where individual sites manage snags differently and subsequently differ in nest site availability. We predicted that, in general, old-growth forests, even those that are managed for timber, would support higher diversity and abundances of cavity nesting birds than would old-field pinelands because of the cavity resources that Red-cockaded Woodpeckers provide in old-growth sites, and potentially because of higher snag density in these sites. Thus, we expected strong relationships between cavity-nesting birds and the two cavity resources – snags and Red-cockaded Woodpecker cavities. We also provide suggestions for future assessments of cavity-nesting birds in southern pine forests regarding appropriate environmental variables to consider.

Methods

Study Sites

We studied cavity-nesting birds in the Red Hills region of southwest Georgia and northwest Florida. The Red Hills consists of several privately owned tracts containing stands in various states of conservation and management, and represents a large, relatively contiguous, high quality pine landscape where conservation is prioritized (Varner and Kush 2004). Old-growth longleaf pine stands occupy an estimated 400 ha in the Red Hills, with most sites frequently burned for Northern Bobwhites (*Colinus virginianus*) and managed for timber (Neel 1971). Pristine areas are dominated by longleaf pine in the overstory, various oak species in the midstory, and wiregrass covering much of the forest ground, although herbaceous plant diversity is among the highest recorded for any ecosystem (Outcalt 2000). Mature pinelands occur on former agricultural lands abandoned in the early 1900s and are now dominated by loblolly or shortleaf pine and old-field grasses. Many quail hunting properties in the Red Hills have been managed for over 70 years by the Stoddard-Neel system, which focuses on maintaining mature timber and multi-aged forest with an open mid-story and low tree densities through single-tree selection (Moser et al. 2002). Because of habitat requirements for frequent fire, managing for quail often benefits other pine and grassland species (Block et al. 1995). Many properties in the Red Hills also practice salvage harvesting, in which dead or dying trees are removed. Other harvest regimes include individual tree selection, in which trees are harvested at the current growth rate over a certain time interval.

This study took place from 2016-2019 across 10 private pineland plantations in the Red Hills region of northwest Florida and southwest Georgia (Table 2.1). All plantations were ≥ 800 ha and managed using 1-2-year fire return intervals, but timber age and snag densities varied. Four properties (Arcadia, Greenwood, Melrose, and Sinkola) contained patches (30-200 ha) of old-growth longleaf pine forests with many old (>200 years) large trees and ground cover dominated by wiregrass and other fire-adapted grasses. Arcadia also encompassed the Wade Tract, a special old-growth research site created through a conservation easement held by Tall Timbers Research Station. Timber management within the old-growth stands found on the other 3 properties consisted of salvaging lightning-killed trees for high-value heartwood (≥ $5 per cm). Sunnyhill contained mature longleaf pine (> 80 years old) where trees struck by lightning also were quickly salvaged. Foshalee, Avalon, Osceola, and Tall Timbers represented examples of old-field pine forests, dominated by mature loblolly and shortleaf pine and lower densities of mature longleaf pine intermixed. Avalon, Foshalee, Osceola, and Sunnyhill also perform periodic pine thinning harvests. Thinning operations performed every 8-10 years cull a mix of different size classes while retaining pine basal area ca. 4-8 m^2 ha^{-1} (Moser et al. 2002). Ground cover conditions range from undisturbed patches with many native forbs and grasses to areas of former agricultural lands that now contain mature pines, but support fewer forbs and grasses. All sites were maintained as open pinelands with frequent prescribed fire (1-2 year).

Field Methods

Point count stations (n = 10-20) were systematically distributed across each property and separated by ≥ 300 m, in which the first point was placed randomly. Point counts are conducted on a recurring basis at each of these properties as part of a long-term monitoring project by Tall Timbers Research Station. Because we related vegetation measurements from data collected in 2019, we used the most recent point count data available for each property. Most counts were conducted in 2018 and 2019, with two properties having most recent data from 2016. Point counts were conducted for five minutes each and all occurred between sunrise and 10:00 AM. We recorded the presence and location of all cavity-nesting birds that were seen or heard. We used three distance bands to record bird locations: 0-50 m, 51-100 m, and 101-200 m. Flyovers were counted in a separate category and were not used in analyses because those individuals may not have been utilizing the habitat.

We used distance sampling or the point-centered quarter method (Cottam et al. 1953) to estimate the density of snags surrounding each count station. Sites where snags were recorded with distance sampling involved the observer standing at the point count station and using a range finder to measure the distances to all visible snags. Snags recorded using the point-centered quarter method involved the observer standing at the point count location and recording the distance to the nearest snag in four quadrants determined by the cardinal directions. We classified each snag into two categories based on decay, early-stage and late-stage snags. Early-stage snags were $\geq$ 4 meters tall, had an intact bole, and retained most primary and tertiary branches and limbs. Late-stage snags were < 4 meters and showed signs of advanced decay through charring and loss of bark. Often, the boles of late-stage snags were not entirely intact and contained few or no limbs. Cavity resources associated with the Red-cockaded Woodpecker were based on a recurring survey of cavity trees conducted every 8-10 years (Cox et al. 2001). The most recent inventory was completed in 2018. Red-cockaded Woodpecker cavities in old-growth sites consisted of natural excavations, but the woodpecker cavities on other sites included both natural and a few (≤ 4) artificial cavities (all inserts) excavated to help expand the Red-cockaded Woodpecker population. Because artificial inserts are also used by several other cavity-nesting species, we did not differentiate between artificial and natural cavities.

Quantitative Analyses

In ArcGIS (ESRI. 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) we utilized the National Land Cover Database (NLCD) 2016 to measure the percentage of surrounding land cover at each count station using a radial buffer of 200 meters to determine the percentage of surrounding forest cover. This included land cover classes of dense pine, open pine, hardwood, mixed-pine, and forested (but not herbaceous) wetlands. We used the same 200-meter buffer to determine the number of Red-cockaded Woodpecker cavities surrounding each count station using inventory data. We used RStudio (RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA), a wrapper for program R (R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/) to conduct all other analyses. We used package 'Rdistance' to estimate snag densities on sites where standard distance sampling was used by fitting detection functions using Akaike's Information Criterion (AIC) and selecting the models with the lowest AIC values (Burnham and Anderson 2002). For sites sampled with the point-centered quarter method, we used the equation described by Warde and Petranka (1981) that included a correction factor to correct densities for sites in which snags were missing from one or more quadrants within count stations. Due to the nature of the correction factor equations, we could not calculate associated confidence intervals. Because we believed densities of early-stage and late-stage snags might be related, we used a Pearson's product-moment correlation test to assess the relationship between the two snag classes.

Linear regression models were used to compare both the number of individual cavity-nesting birds detected per point and the number of species of cavity-nesting birds detected per point to snag densities and number of Red-cockaded Woodpecker cavities. We then used package 'unmarked' to fit detection functions for each species at each site and ranked models to estimate densities within each site using AIC (Burnham and Anderson 2002). We used linear models to compare these species-specific density estimates from unmarked to each measured covariate: snag density, average Red-cockaded Woodpecker cavity density, and average percent forest cover for each site. A one-way analysis of variance (ANOVA) was used to compare overall density estimates among sites and to compare species richness among sites. Significant main effects were followed by a Tukey's Honest Significant Difference test. For all hypothesis tests we used statistical significance of $P < 0.05$.

Results

Densities of early-stage snags varied from 0 to 1.8 snags/ha and late-stage snags varied from 0.14 to 6.3 snags/ha (Table 2.2). The Wade Tract had the highest density of both early-stage (1.8 snags/ha) and late-stage snags (6.3 snags/ha). Densities of the two snag types were strongly correlated ($R = 0.93$, $P < 0.001$; Figure 2.1) suggesting timber salvaging precludes development of both snag types. Because early-stage snags and late-stage snags were highly correlated, we combined densities of the two snag types and treated them as a single variable for a measure of overall snag densities used in subsequent analyses. Red-cockaded Woodpecker cavities (both natural and artificial) varied from 0-23 cavities within 200 m of count locations ($\bar{x}$

± SD; x̄ = 5.01 ± 5.51) and percent of surrounding forest cover varied from 0.32 to 0.99 within the 200 m buffer (x̄ = 0.85 ± 0.12; Table 2.2).

We recorded a total of 16 cavity-nesting bird species across 10 properties consisting of 8 primary excavators and 8 secondary cavity-nesters (Table 2.3). The number of cavity-nesting bird species detected per point count was highest on the Wade Tract (x̄ = 7.13 ± 3.44), and was typically higher on old-growth sites (Figure 2.2), which also generally correlated with higher snag densities and Red-cockaded Woodpecker cavity densities. The Wade Tract had the highest total species richness (*n* = 13) and Foshalee had the lowest (*n* = 5). Old-growth sites had significantly higher species richness (x̄ = 11.6 ± 0.89) than old-field sites (x̄ = 9.0 ± 3.1) at the site-level ($F_{9,133}$ = 13.2, $P < 0.001$; Table 2.4). The number of individual cavity-nesting birds and the number of species of cavity-nesting birds detected per point count were not related to Red-cockaded Woodpecker cavities ($F_{1,8}$ = 0.88, R^2 = 0.10, P = 0.38; $F_{1,8}$ = 1.05, R^2 = 0.06, P = 0.34; Figure 2.3). The number of individual cavity-nesting birds and the number of species of cavity-nesting birds detected per point count were also not significantly related to snag densities ($F_{1,8}$ = 0.12, R^2 = 0.02, P = 0.74; $F_{1,8}$ = 0.09, R^2 = 0.01, P = 0.78; Figure 2.3). Five cavity-nesting birds (Carolina Chickadee, Downy Woodpecker, Chimney Swift, Hairy Woodpecker, and Purple Martin; scientific names provided in Table 2.3) were rarely detected during counts and were not included in subsequent analyses due to low detection probabilities.

We estimated densities of 11 cavity-nesting bird species on the 10 sites. Densities of individual species ranged from 0.01 to 0.37 (x̄ = 0.19 ± 0.13 birds/ha). Density estimates of all cavity-nesting birds combined differed significantly among sites ($F_{9, 100}$ = 2.60, P = 0.01; Figure 2.4), but only between the Wade Tract and Avalon and the Wade Tract and Foshalee. Species-specific density estimates indicated large variation between both species and sites (Figures 2.5

and 2.6). Red-headed Woodpeckers had the highest densities (0.37 individuals/ha) and Wood Ducks the lowest densities (0.01 individuals/ha) overall. Great Crested Flycatchers, Red-bellied Woodpeckers, White-breasted Nuthatches, and Red-headed Woodpeckers occurred most consistently (present in all ten study sites). Brown-headed Nuthatches, Tufted Titmice, Northern Flickers, and Pileated Woodpeckers were present at 90% of the sites. Eastern Bluebirds were present at 80% of sites. Red-cockaded Woodpecker occurrences were restricted to 60% of sites, and Wood Ducks were the least detected species, present in 40% of sites. Several species were significantly denser in old-growth than in old-field pine forests, including Eastern Bluebirds ($Z = 3.43$, $P < .001$), Great Crested Flycatchers ($Z = 3.61$, $P < 0.01$), Northern Flickers ($Z = 4.68$ $P < 0.001$), Red-cockaded Woodpeckers ($Z = 4.08$, $P < 0.001$), Tufted Titmice ($Z = 3.76$, $P < 0.001$), and White-breasted Nuthatches ($Z = 2.80$ $P < 0.012$; Figure 2.8). Additionally, although Brown-headed Nuthatches and Pileated Woodpeckers were nearly twice as abundant in old-growth longleaf sites as in old-field pineland sites, those differences did not achieve significance (Figure 2.7).

Only densities of Pileated Woodpeckers ($P = 0.036$) and Eastern Bluebirds ($P = 0.009$) were significantly related to snag densities (Table 2.5). Eastern Bluebirds ($P = 0.024$), Tufted Titmice (P = 0.016), Great Crested Flycatchers ($P = 0.059$), Northern Flickers ($P = 0.012$), Red-cockaded Woodpeckers ($P = 0.003$), and White-breasted Nuthatches ($P = 0.023$) were significantly influenced by Red-cockaded Woodpecker cavities (Table 2.5). Forest cover was significantly related to densities of Eastern Bluebirds ($P = 0.002$), Northern Flickers ($P = 0.017$), and Red-cockaded Woodpeckers ($P = 0.013$; Table 2.5).

Discussion

Density estimates of Northern Flickers, Red-cockaded Woodpeckers, Eastern Bluebirds, Tufted Titmice, Great Crested Flycatchers, and White-breasted Nuthatches were significantly related to Red-cockaded Woodpecker cavities, a resource more abundant in old-growth sites. Those same six species also had significantly greater densities in old-growth longleaf pine forests. Further, old-growth sites had higher species richness and number of cavity-nesting birds detected even on sites where lightning-struck trees were salvaged (e.g., Melrose and Sinkola) than did old-field sites that were subject to less intensive means of timber management. Surprisingly, densities of only two species, Eastern Bluebirds and Pileated Woodpeckers, were correlated with snag resources, which is discussed in more detail later.

In coniferous forests where naturally occurring cavities are uncommon, woodpeckers play a critical role in excavating cavities for secondary cavity-nesters (Bull et al. 1997). Our findings reflect the value of the long-lived cavities provided by Red-cockaded Woodpeckers, emphasizing the essential role they play as excavators. Unsurprisingly, Red-cockaded Woodpeckers were more abundant in old-growth forests and were strongly related to cavity densities. As keystone species, it can be expected that the presence and abundances of other species will co-vary with Red-cockaded Woodpecker densities. Cox and Meyer found that four of six woodpecker species increased since Red-cockaded Woodpeckers were reintroduced to an old-field pine plantation in North Florida (J. Cox, Tall Timbers Research Station, unpublished data.). In our study, Red-cockaded Woodpecker cavities influenced several species, including White-breasted Nuthatches, which commonly use Red-cockaded Woodpecker cavities. In fact, population declines of White-breasted Nuthatches have been linked to declines in Red-cockaded Woodpecker populations (Leonard Jr 2005). Tufted Titmice were also strongly related to Red-cockaded Woodpecker cavities, and have been documented use these cavities as nest sites in the spring (Rudolph et al. 1990, Loeb and Hooper 1997), and roost sites in the fall and winter (Conner et al. 1997). Great Crested Flycatchers are generalists, and in coniferous forests they rely heavily on cavities excavated by other birds, including Red-bellied Woodpeckers, Northern Flickers, Pileated Woodpeckers, and Red-cockaded Woodpeckers (Miller 2010). In our study, Great Crested Flycatchers were also more abundant in old-growth sites, and this too may be an indicator of close links associated with higher abundances of primary excavators on those sites. Northern Flickers, a primary excavator, were significantly related to the density Red-cockaded Woodpecker cavities, suggesting these cavities are important not only for secondary cavity nesters, but for all cavity users.

In addition to the cavity resources that Red-cockaded Woodpeckers provide for other cavity-nesting birds, habitat conditions required for Red-cockaded Woodpeckers, including frequent fires and open mid- and under-stories also promote diversity of other species (Conner et al. 2002). Structural components of old-growth longleaf forests, such as mature trees, broken limbs, mixed age-class distributions, and complex crown structure are less common in younger forests (Engstrom 1993). Old-growth longleaf pine forests provide high-quality habitat for Brown-headed Nuthatches, who favor well-decayed snags for nesting and roosting and live pine trees for foraging. These vegetation characteristics are typical of mature, fire-maintained pine forests where frequent fire sustains an open understory and creates snags (Bent et al. 1948). Brown-headed Nuthatches, which also use similar snags, provide cavity resources for other small secondary cavity-nesting birds, such as Eastern Bluebirds (Stanback et al. 2019). Our density estimates indicate these short, well-decayed snags are common on sites like the Wade Tract.

Several species were not as dense in old-growth sites. Red-bellied Woodpeckers occupy a wide-range of hardwood-dominated forests across their range in addition to mature pinelands. They usually select relatively large snags or dead limbs on live trees for nest sites (Shackelford et al. 2000), but also commonly use Red-cockaded Woodpecker cavities in pinelands. In fact, Red-bellied Woodpeckers are the most common cavity kleptoparasite of Red-cockaded Woodpecker cavities (Harlow and Lennartz 1983, Conner et al. 1997, Loeb and Hooper 1997). They are considered kleptoparasites because these interactions are often positive for the usurper and negative for Red-cockaded Woodpeckers (Kappes Jr 1997) and could contribute to declines of Red-cockaded Woodpeckers. Pileated Woodpeckers were generally more abundant in old-growth sites, but not significantly. Like Red-bellied Woodpeckers, Pileated Woodpeckers use Red-cockaded Woodpecker cavities but must enlarge the entrance hole (Conner et al. 1991, Saenz et al. 1998). Pileated Woodpeckers numbers were higher on sites that contained higher abundances of large snags (e.g., the Wade Tract, Greenwood, and Arcadia). Similarly, Northern Flickers enlarge Red-cockaded Woodpecker cavities, making them suitable for other larger secondary cavity-nesters (Dennis 1971, Blanc and Walters 2008b). Another common woodpecker of these forests, the Red-headed Woodpecker, also requires open areas maintained with frequent fires or sites with decreased midstory hardwood and canopy cover (Provencher et al. 2002). In these sites, they nest in large pine snags, especially those with little bark (Blanc and Walters 2008a). Red-headed Woodpeckers also use both active and abandoned Red-cockaded Woodpecker cavities (Carter et al. 1989, Conner et al. 1997). Although these three excavating species can be common in other forest types, populations occurring in pine forests may be more dependent on Red-cockaded Woodpecker cavities, especially in sites where snags of appropriate size and decay are limiting.

Surprisingly, neither the density estimates of most species, nor site-level species richness, was related to snag densities. These results should be interpreted with the caveat that it is possible that we did not classify snags into suitable enough classes used for selection by different species, and that factors such as height and degree of decay based on a ranked scale are more important than overall snag densities. For similar future assessments of cavity-nesting birds in southern pine forests, we recommend quantifying densities of snags using these more detailed parameters. Late-stage snag resources are especially important for species like Brown-headed Nuthatches, which need well-decayed wood for excavation, and for Eastern Bluebirds, which also use these snags. The point-centered quarter method and standard distance sampling used in this study may have biased estimates because late-stage snags are short and can be difficult to detect from far distances. This may have resulted in lower observed densities than what was there. Clustering of snags may have affected detection probabilities as well. Recording individual snags within subplots and measuring factors such as snag height, decay, and diameter at breast height may provide a fuller picture of what specific resources cavity-nesting birds are utilizing. It may be more appropriate to quantify cavity densities in addition to snag densities in old-growth forests, as cavity densities tend to be higher in older forests (Wiebe 2011).

Another metric that may be important is to further categorize Red-cockaded Woodpecker cavities into active and enlarged/abandoned densities and to consider artificial cavities in a separate category. Our study indicated that Red-cockaded Woodpecker cavity numbers were important influences on Red-cockaded Woodpecker densities. While species like Red-headed Woodpeckers, Red-bellied Woodpeckers, Great Crested Flycatchers, and Tufted Titmice can use un-enlarged cavities, Pileated Woodpeckers, Wood Ducks, and other species across the longleaf pine range, such as American Kestrels (*Falco sparverius*) and Eastern Screech Owls (*Megascops* *asio*), use enlarged and abandoned cavities as nest and roost sites that often have been enlarged by Northern Flickers (Blanc and Walters 2008a). Clayhill longleaf forests, like the ones in this study, contain different species composition than other longleaf eco-types and do not provide suitable breeding habitat for American Kestrels, which prefer more open ground cover attributed to sandhill longleaf pine forests (Hoffman and Collopy 1987).

Additionally, forest structural characteristics such as basal area, which we did not quantify, can be an important factor for some species of cavity-nesting birds. Red-cockaded Woodpeckers and Eastern Bluebirds prefer open, savanna-like conditions where pine basal area ranges from 2.5-10 m^2/ha (Hamel 1992). Frequent burning and tree thinning create high quality Red-cockaded Woodpecker habitat, including more open canopies, more large trees, and more herbaceous ground cover (James et al. 2001). Conversely, Pileated Woodpeckers prefer areas with higher basal area (Conner and Adkisson 1976). In addition to basal area, snag basal area can be a more important indicator of cavity use than factors such as diameter at breast height (Swallow et al. 1986). Assessing these and other environmental factors may help elucidate important forest characteristics for cavity-nesting birds and lead to better management guidelines.

Old-growth longleaf pine forests have become exceedingly scarce with only an estimated 3900 ha remaining. Habitat quality within some tracts may be compromised by urban surroundings, invasive species, uncertain management futures, fragmentation, and groundcover degradation (Varner and Kush 2004). Despite the challenges facing the historic landscape of the south, we recommend conserving and restoring old-growth patches within a landscape to increase biodiversity across the gradient of longleaf forest types (Smith et al. 2017). Old-growth forests that support Red-cockaded Woodpecker populations support a diverse number of other species. Remnant and abandoned Red-cockaded Woodpecker cavities may be especially important in areas with intensive timber salvaging (Blanc and Walters 2008a). Scattered remnant old-growth patches and trees can provide breeding sites for Red-cockaded Woodpeckers and other woodpeckers that also make use of adjacent second-growth forests for activities such as foraging (Engstrom and Sanders 1997). In areas that are salvaged, we recommend retaining densities of ≥ 3 snags/ha (combined early and late-stage snags). McComb et al. (1986) recommended ≥ 6 snags/ha in Florida pine forests for cavity-nesting birds, but did not quantify Red-cockaded Woodpecker cavities. Maintaining a diversity of snag resources will promote a greater diversity of cavity nesting species. For younger forests that may lack abundant cavity resources, we recommend snag retention/creation or the addition of artificial cavities. Old-growth forests with higher cavity densities may allow for lower snag densities that will still support a high diversity and abundance of cavity-nesting species.

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Tables

Table 2.1. Site descriptions of study sites ($n = 10$) located within the Red Hills physiographic region of northwest Florida and southwest Georgia. All properties are under conservancy easements managed by Tall Timbers Research Station. Salvaging describes removal of lightning-killed trees for heartwood. Thinning operations consist of periodic mixed-age pine thinning taking place every 7-10 years, while retaining a basal area of 4-8 m^2 per ha^{-1}.

Site	Acronym	Location	Habitat	Timber management
Arcadia	ARCA	Thomas CO, FL	Old-growth longleaf	Thinning
Avalon	AVAL	Leon CO, FL	Old-field pinelands	Salvaging
Foshalee	FOSH	Leon CO, FL	Second-growth with some mature trees*	Thinning
Greenwood	GREN	Thomas CO, GA	Old-growth longleaf	Salvaging
Melrose	MELR	Thomas CO, GA	Old-growth longleaf	Harvesting
Osceola	OSCE	Thomas CO, GA		Thinning
Sinkola	SINK	Thomas CO, GA	Old-growth longleaf	Thinning
Sunnyhill	SUNN	Leon CO, FL	Old-field pinelands	Salvaging
Tall Timbers Research Station	TTRS	Leon CO, FL	Old-field pinelands	Thinning
Wade Tract	WADE	Thomas CO, GA	Old-growth longleaf	None

*For analyses, we considered Foshalee an old-field pine forest because it is a second-growth forest and does not contain many old-growth trees

Table 2.2 Site-specific vegetation characteristics. PCQ refers to the point-centered quarter method and DIST refers to standard distance sampling. Red-cockaded Woodpecker (RCWO) cavities and percent forest cover are presented as mean ± standard deviation.

Site	Snag measurement method	Early-stage snags (per ha)	Late-stage snags (per ha)	Total snag density (per ha)	RCWO cavities (per 200 m^2)	Percent forest cover (per 200 m^2)
ARCA	PCQ	0.44	0.86	1.30	3.3 ± 5.4	0.87 ± 0.07
AVAL	PCQ	0.21	0.30	0.52	0.80 ± 2.1	0.86 ± 0.09
FOSH	PCQ	0.26	0.85	1.10	0.20 ± 0.75	0.80 ± 0.11
GREN	PCQ	0.76	2.30	3.00	6.1 ± 8.5	0.83 ± 0.09
MELR	DIST	0.29	0.54	0.83	5.6 ± 3.9	0.87 ± 0.08
OSCE	PCQ	0.56	0.14	0.70	2.5 ± 2.1	0.83 ± 0.18
SINK	DIST	0.00	0.86	0.86	7.5 ± 3.6	0.94 ± 0.18
SUNN	PCQ	0.36	0.41	0.77	1.1 ± 2.3	0.74 ± 0.13
TTRS	DIST	1.50	3.40	4.80	1.7 ± 3.2	0.80 ± 0.13
WADE	DIST	1.80	6.30	8.10	8.2 ± 5.5	0.98 ± 0.02

Table 2.3. Cavity-nesting bird species (n = 16) detected during point count surveys between 2016 and 2019 in old-growth longleaf and old-field southeastern pine forests and their ecological guild within the cavity-nesting community.

Common name	Scientific name	Code	Guild
Brown-headed Nuthatch	*Sitta pusilla*	BHNU	Weak primary excavator
*Carolina Chickadee	*Poecile carolinensis*	CACH	Weak primary excavator, secondary cavity-nester
*Chimney Swift	*Chaetura pelagica*	CHSW	Secondary cavity-nester
*Downy Woodpecker	*Picoides pubescens*	DOWO	Primary excavator
Eastern Bluebird	*Sialia sialis*	EABL	Secondary cavity-nester
Great Crested Flycatcher	Myiarchus crinitus	GCFL	Secondary cavity-nester
Hairy Woodpecker	Dryobates villosus	HAWO	Primary excavator
Northern Flicker	*Colaptes auratus*	NOFL	Primary excavator
Pileated Woodpecker	*Dryocopus pileatus*	PIWO	Primary excavator
*Purple Martin	*Progne subis*	PUMA	Secondary cavity-nester
Red-bellied Woodpecker	*Melanerpes carolinus*	RBWO	Primary excavator
Red-cockaded Woodpecker	*Dryobates borealis*	RCWO	Primary excavator
Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO	Primary excavator
Tufted Titmouse	*Baeolophus bicolor*	TUTI	Secondary cavity-nester
White-breasted Nuthatch	*Sitta carolinensis*	WBNU	Secondary cavity-nester
Wood Duck	*Aix sponsa*	WODU	Secondary cavity-nester

*Uncommon (low detection rates) and were not included in analyses

Table 2.4. Significant pairwise differences in the number of cavity-nesting bird species (n = 10) detected per point count between sites (n = 10). Differences are between the means for each pair.

Site pair	Difference	95% lower CI	95% upper CI	Adjusted *P*-value
AVAL - ARCA	-2.333	-4.181	-0.4849	0.0032
FOSH - ARCA	-2.400	-4.248	-0.5516	0.0021
WADE - ARCA	2.525	0.7057	4.334	0.0007
MELR - ARCA	3.097	1.088	5.106	0.0001
SINK - AVAL	3.097	1.088	5.106	0.0001
SUNN - AVAL	1.933	0.0849	3.782	0.0325
TTRS - AVAL	1.733	0.0432	3.462	0.04889
WADE - AVAL	4.858	3.039	6.678	<0.0001
MELR - FOSH	3.164	1.154	5.173	<0.0001
SINK - FOSH	3.164	1.154	5.173	<0.0001
SUNN - FOSH	2.000	0.1516	3.848	0.0228
TTRS - FOSH	1.800	0.0710	3.529	0.0341
WADE - FOSH	4.925	3.106	6.744	<0.0001
WADE - GREN	3.325	1.506	5.144	<0.0001
WADE - OSCE	3.625	1.584	5.666	<0.0001
WADE - SUNN	2.925	1.106	4.774	0.0004
WADE - TTRS	3.125	1.427	4.823	<0.0001

Table 2.5. Linear regression models between species-specific density estimates (n = 11 species) and each covariate, with corresponding parameter estimates, standard errors, and P-values. Statistically significant relationships are designated with an asterisk.

Species	Covariate	Parameter estimate	Standard error	*P*-value
BHNU	Snag density	-0.013	0.037	0.724
	RCWO cavities	0.038	0.027	0.205
	Percent forest cover	1.33	1.21	0.306
EABL	Snag density	0.094	0.028	0.009*
	RCWO cavities	0.071	0.025	0.024*
	Percent forest cover	3.64	0.822	0.002*
GCFL	Snag density	0.036	0.016	0.055
	RCWO cavities	0.029	0.014	0.060*
	Percent forest cover	0.978	0.636	0.163
NOFL	Snag density	0.016	0.008	0.068
	RCWO cavities	0.016	0.005	0.012*
	Percent forest cover	0.686	0.229	0.017*
PIWO	Snag density	0.005	0.002	0.036*
	RCWO cavities	0.003	0.002	0.164
	Percent forest cover	0.077	0.084	0.384
RBWO	Snag density	0.010	0.007	0.154
	RCWO cavities	0.005	0.006	0.387
	Percent forest cover	0.051	0.262	0.849
RCWO	Snag density	0.015	0.022	0.520
	RCWO cavities	0.045	0.010	0.003*
	Percent forest cover	1.71	0.539	0.013*
RHWO	Snag density	0.040	0.026	0.160
	RCWO cavities	0.003	0.024	0.893
	Percent forest cover	0.317	1.035	0.767
TUTI	Snag density	-0.000	0.010	0.963
	RCWO cavities	0.017	0.005	0.016*
	Percent forest cover	0.442	0.303	0.184
WBNU	Snag density	0.049	0.0235	0.0724
	RCWO cavities	0.047	0.017	0.023*
	Percent forest cover	1.70	0.832	0.075
WODU	Snag density	<0.001	<0.001	0.988
	RCWO cavities	<0.001	0.002	0.717
	Percent forest cover	0.020	0.010	0.848

Figures

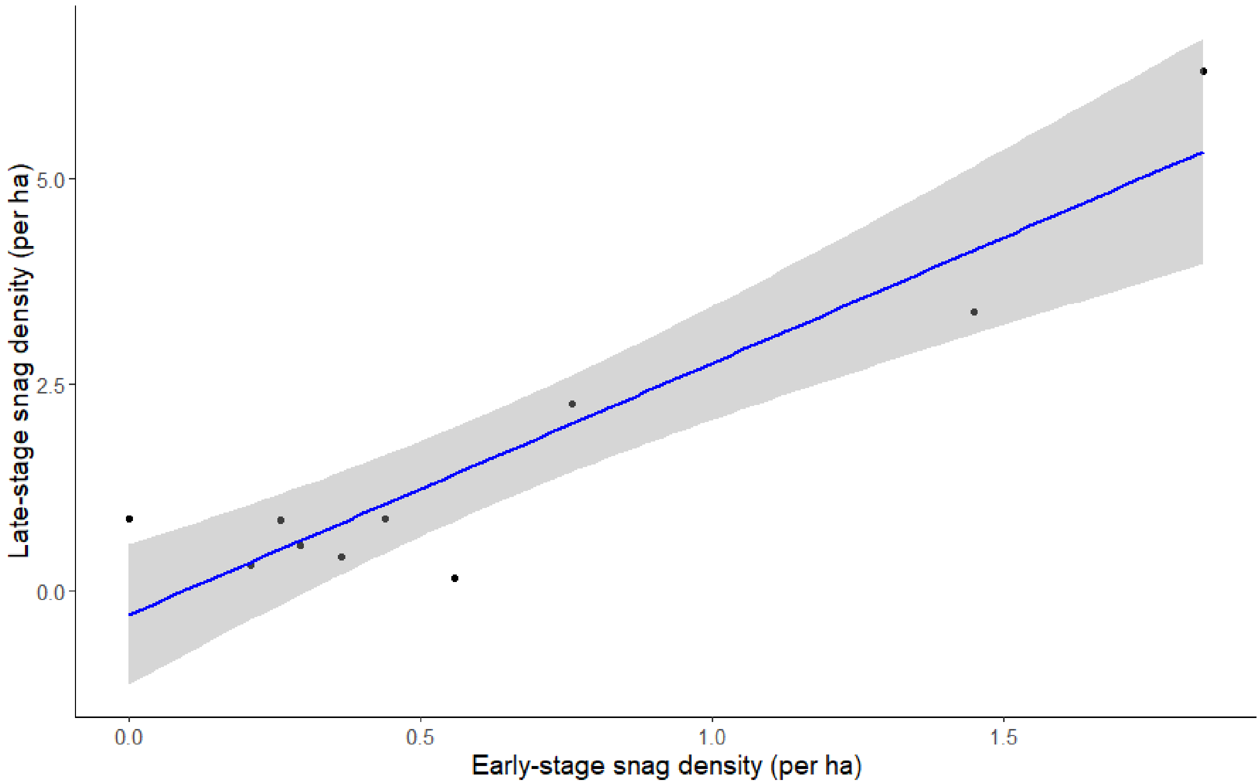

Figure 2.1. Pearson's product moment correlation of the relationship between early-stage snags and late-stage snags. The two snag types were highly correlated (R = 0.925, *P* < 0.001).

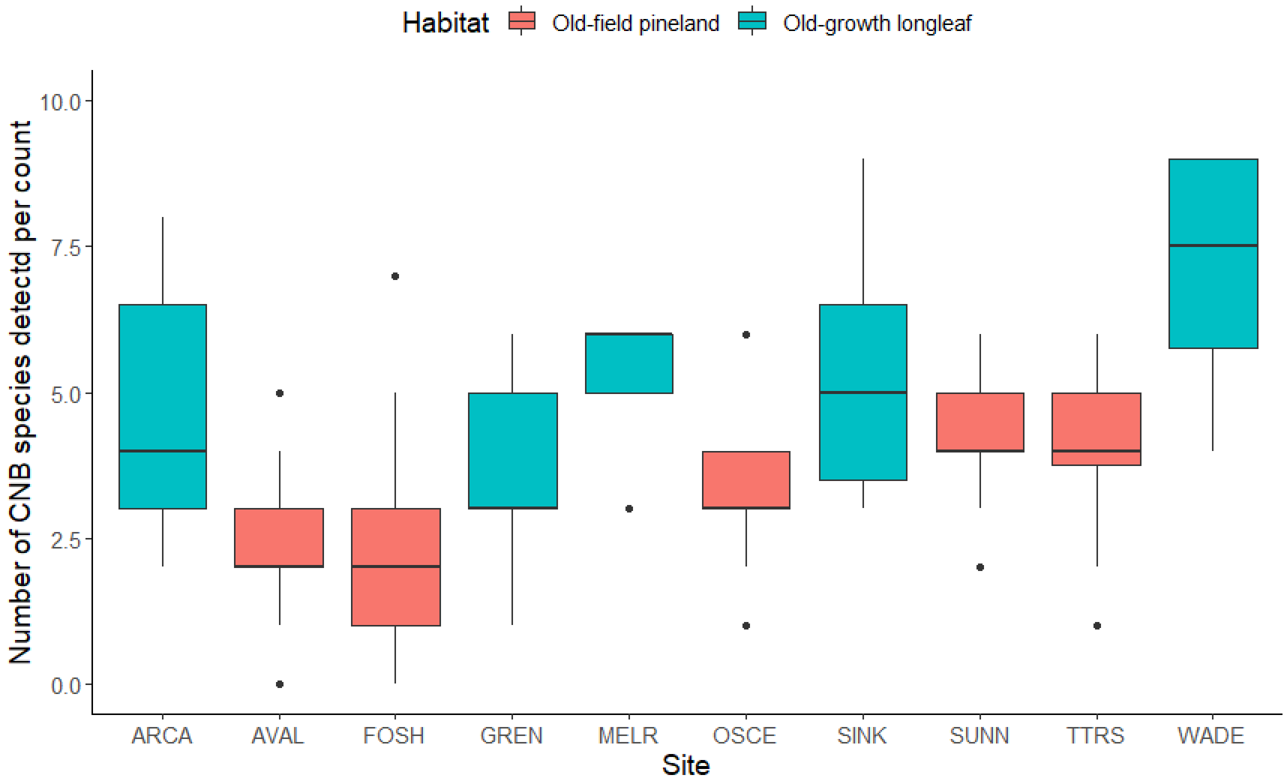

Figure 2.2. Boxplot of cavity-nesting bird species (n = 11) detected per point count across properties in old-growth longleaf pine forests (n = 5) and old-field pine forests (n = 5) in northwest Florida and southwest Georgia. See Table 2.1 for site acronyms.

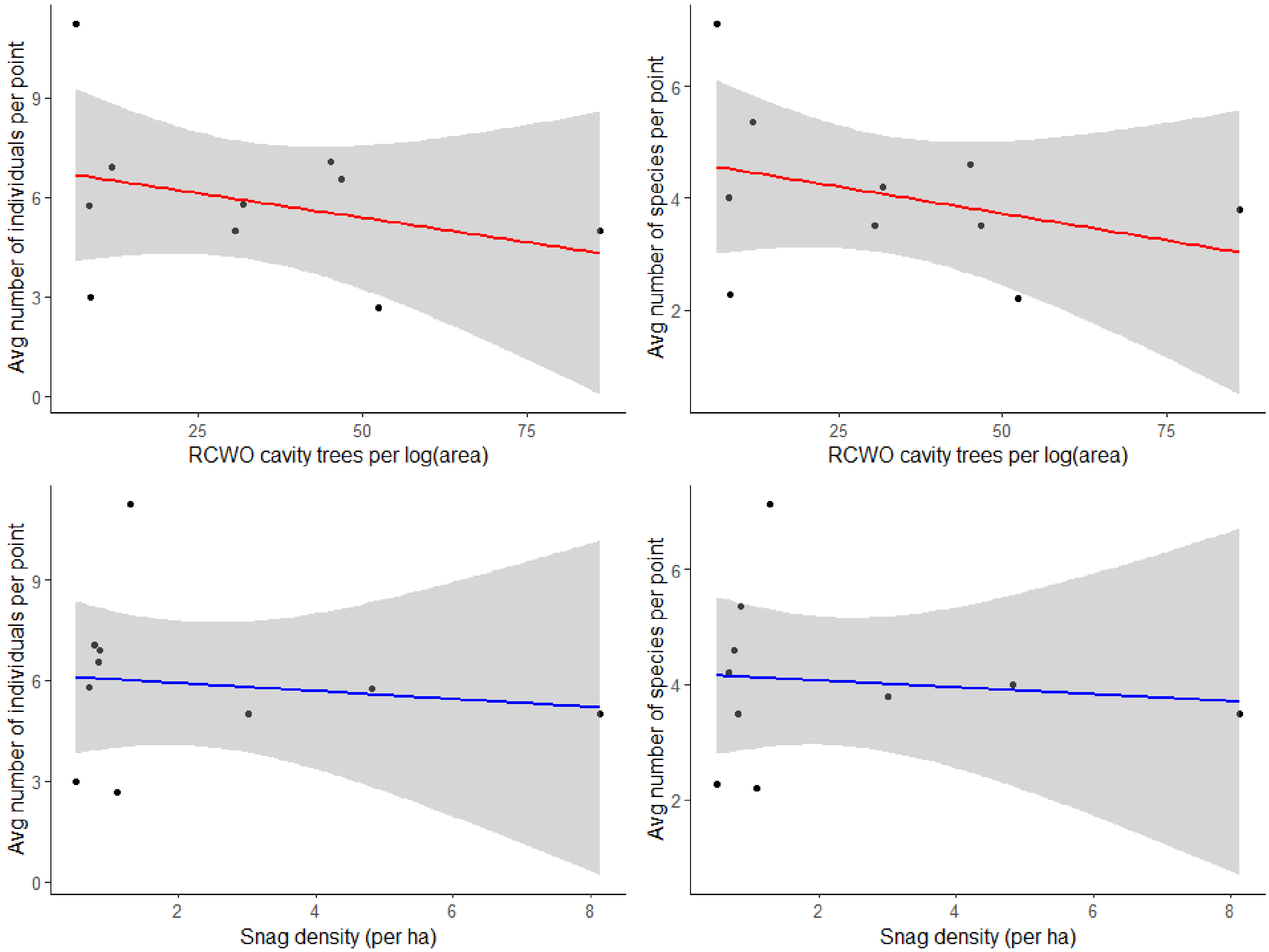

Figure 2.3. Linear regression models of the relationships between counts of individual cavity-nesting birds and number of bird species to the number of Red-cockaded Woodpecker (RCWO) cavities and snag densities surrounding count locations. Snag densities and Red-cockaded Woodpecker cavity trees per log area are representative of site-level estimates.

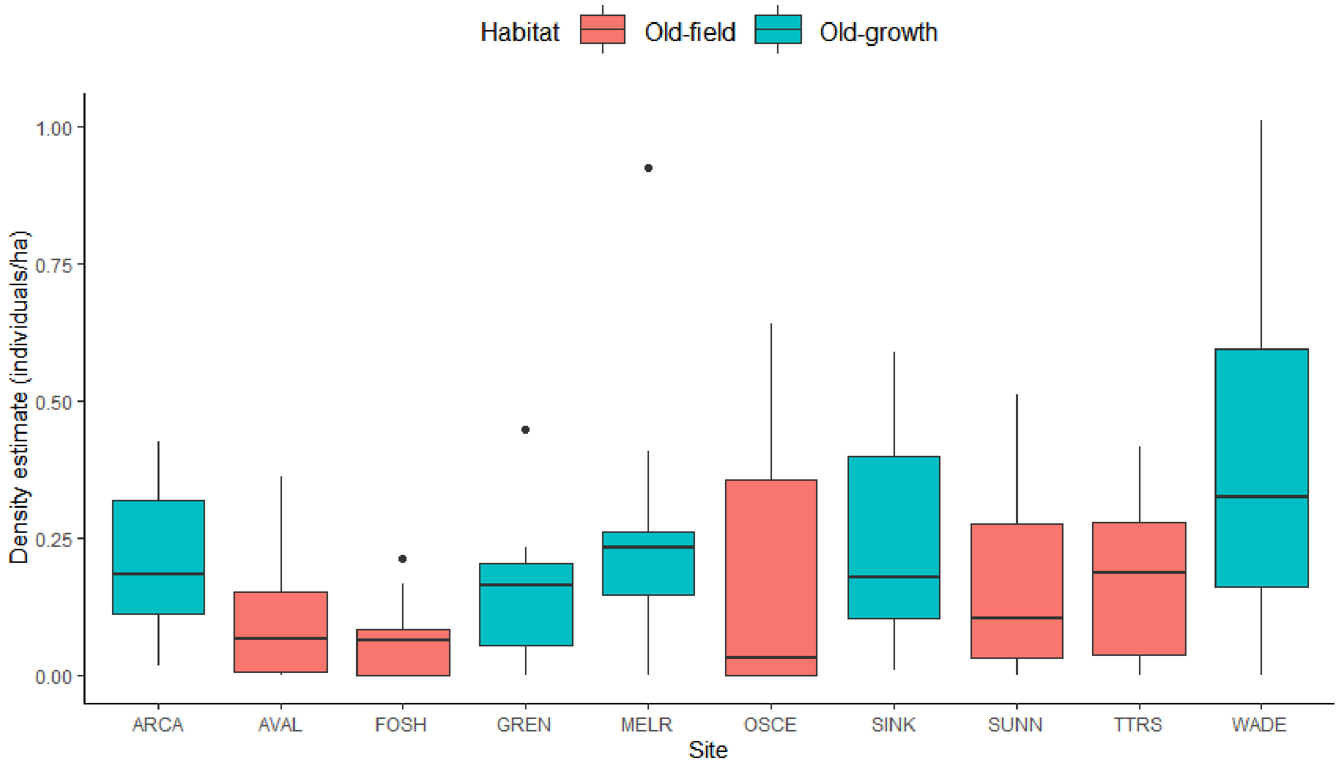

Figure 2.4. Combined density estimates of cavity-nesting bird species (*n* = 11) across old-growth longleaf pine forests (*n* = 5) and old-field pine forests (*n* =5) in northwest Florida and southwest Georgia. See table 2.1. for site acronyms.

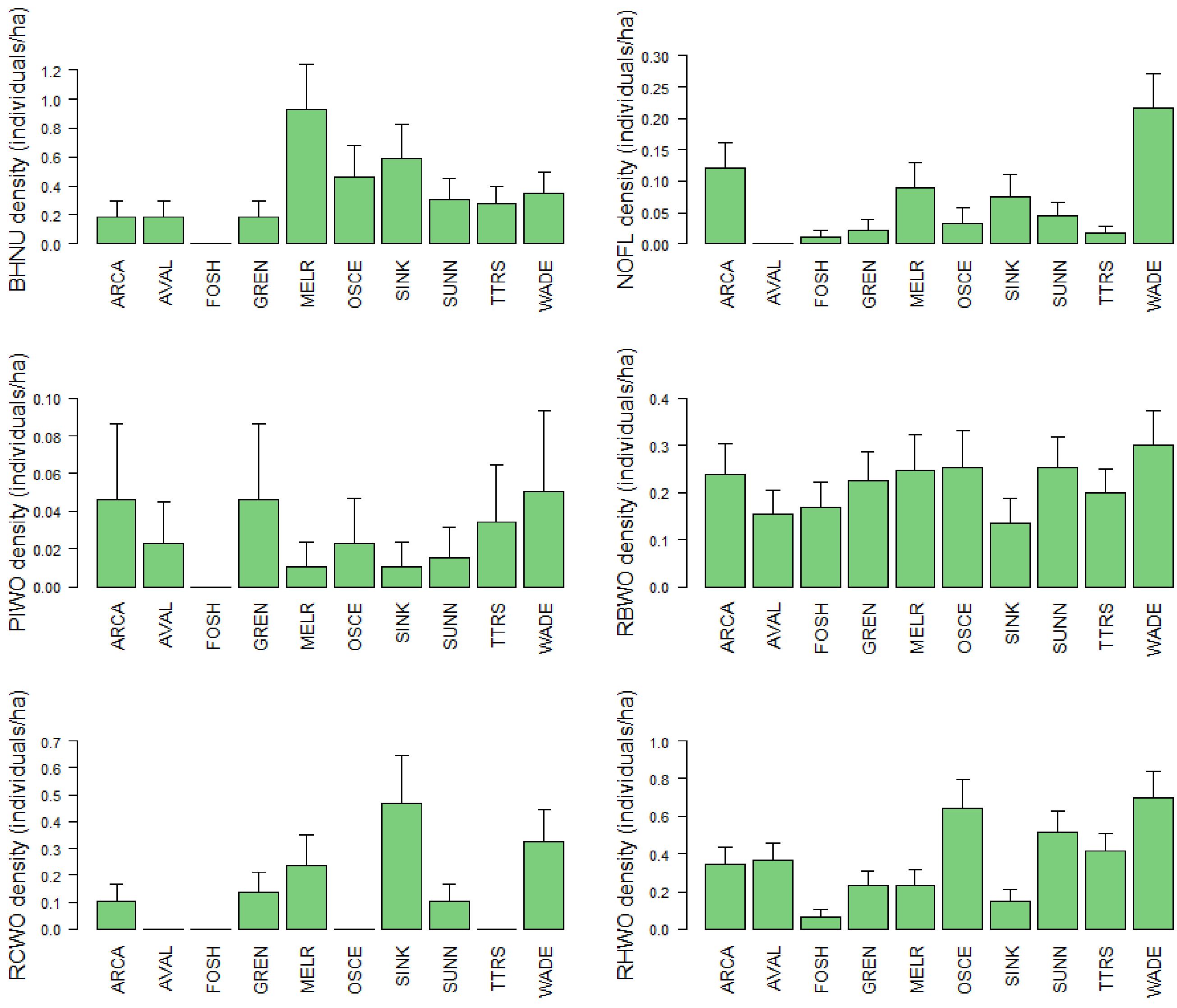

Figure 2.5. Density estimates of primary excavating species (*n* = 6; see Table 2.3 for acronyms of species) across southern pineland sites (*n* = 10) in northwest Florida and southwest Georgia (see Table 2.1 for acronyms of sites). Error bars represent standard errors.

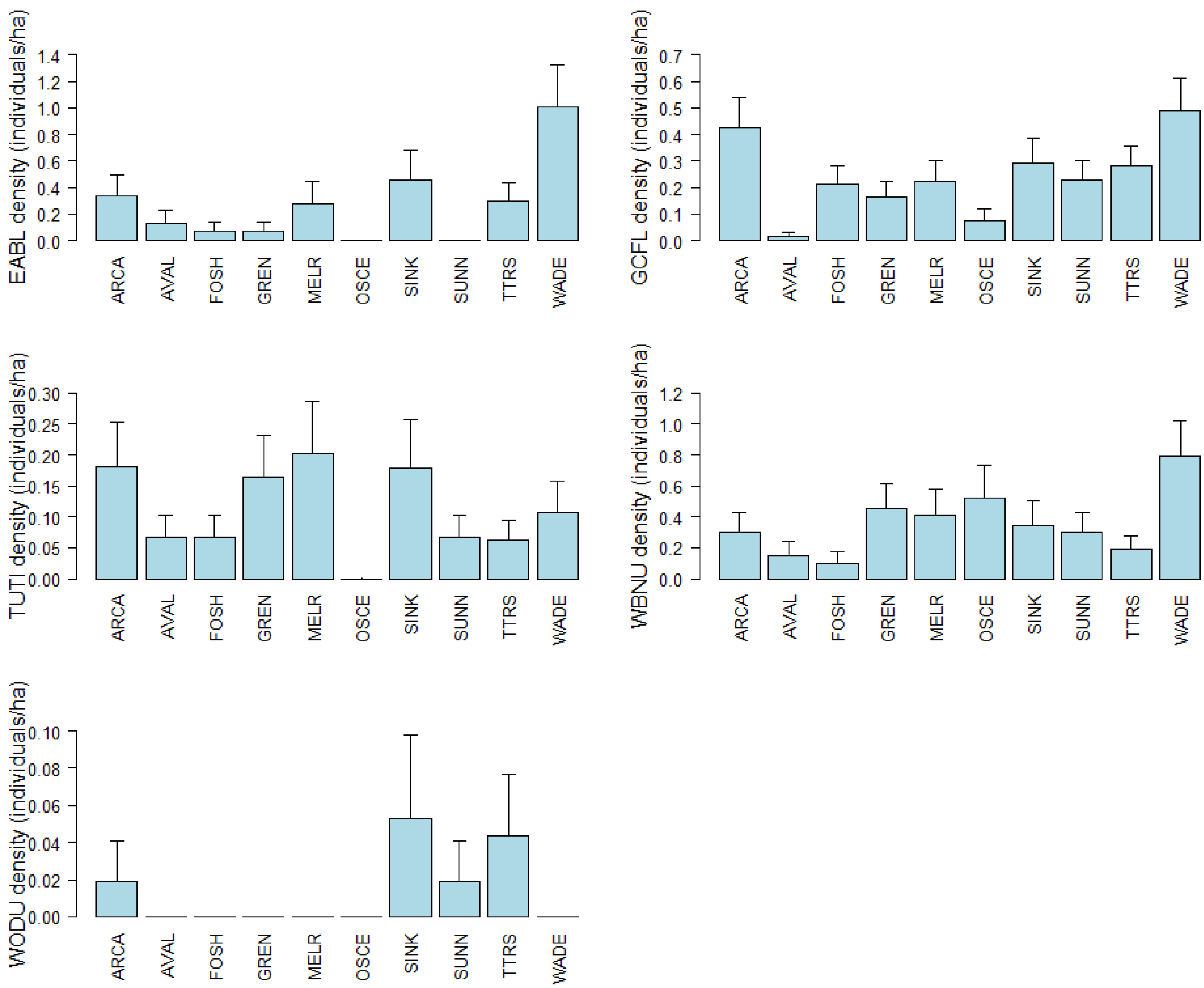

Figure 2.6. Density estimates of secondary cavity-nesting species (n = 5; See Table 2.3 for acronyms of species) across southern pineland sites (n = 10) in northwest Florida and southwest Georgia (see Table 2.1 for acronyms of sites). Error bars represent standard errors.

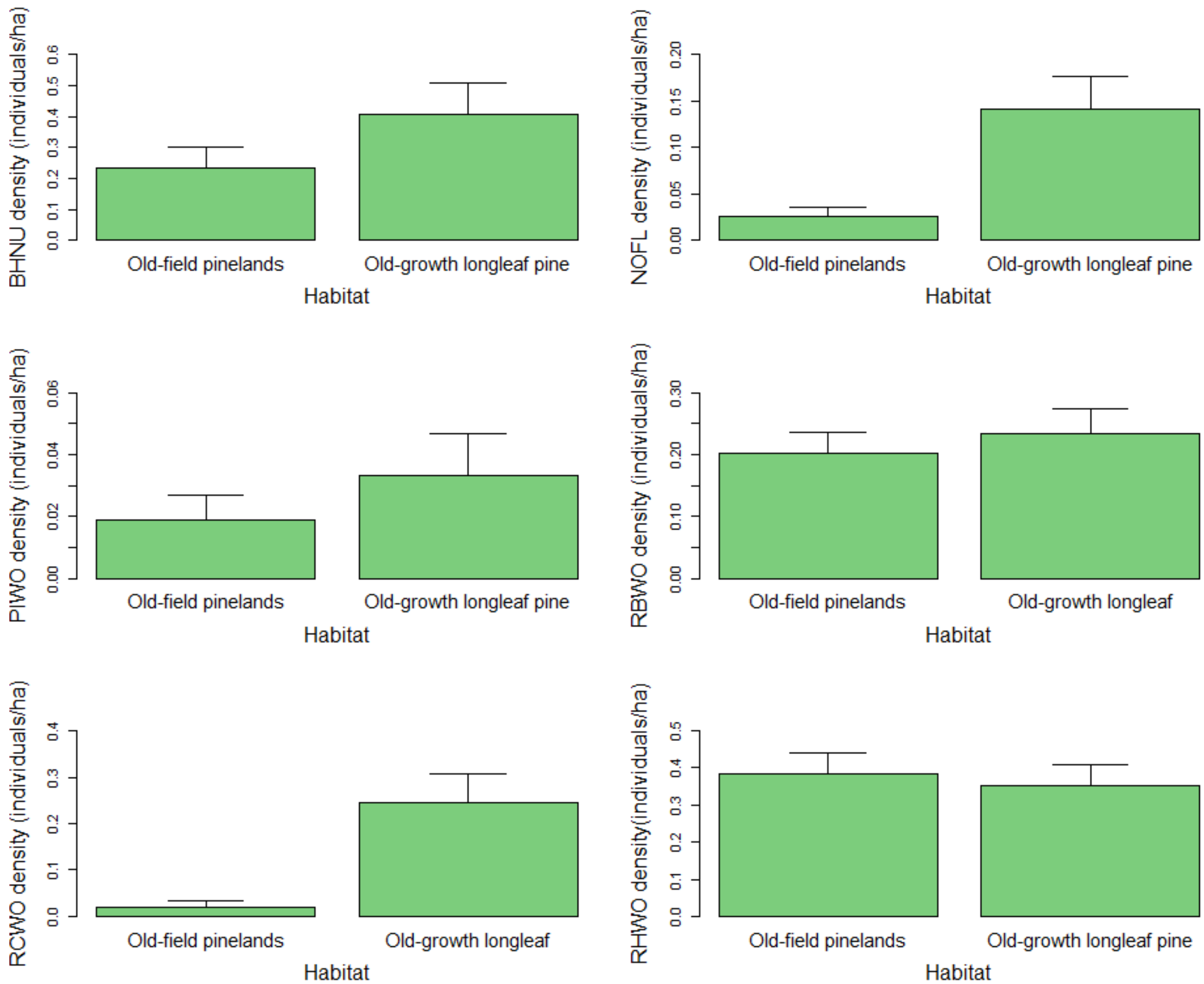

Figure 2.7. Density estimates of primary excavating bird species (n = 6; see Table 2.3 for acronyms of species) in old-field pine forests (n = 5) and old-growth longleaf pine forests (n = 5). Error bars represent standard errors.

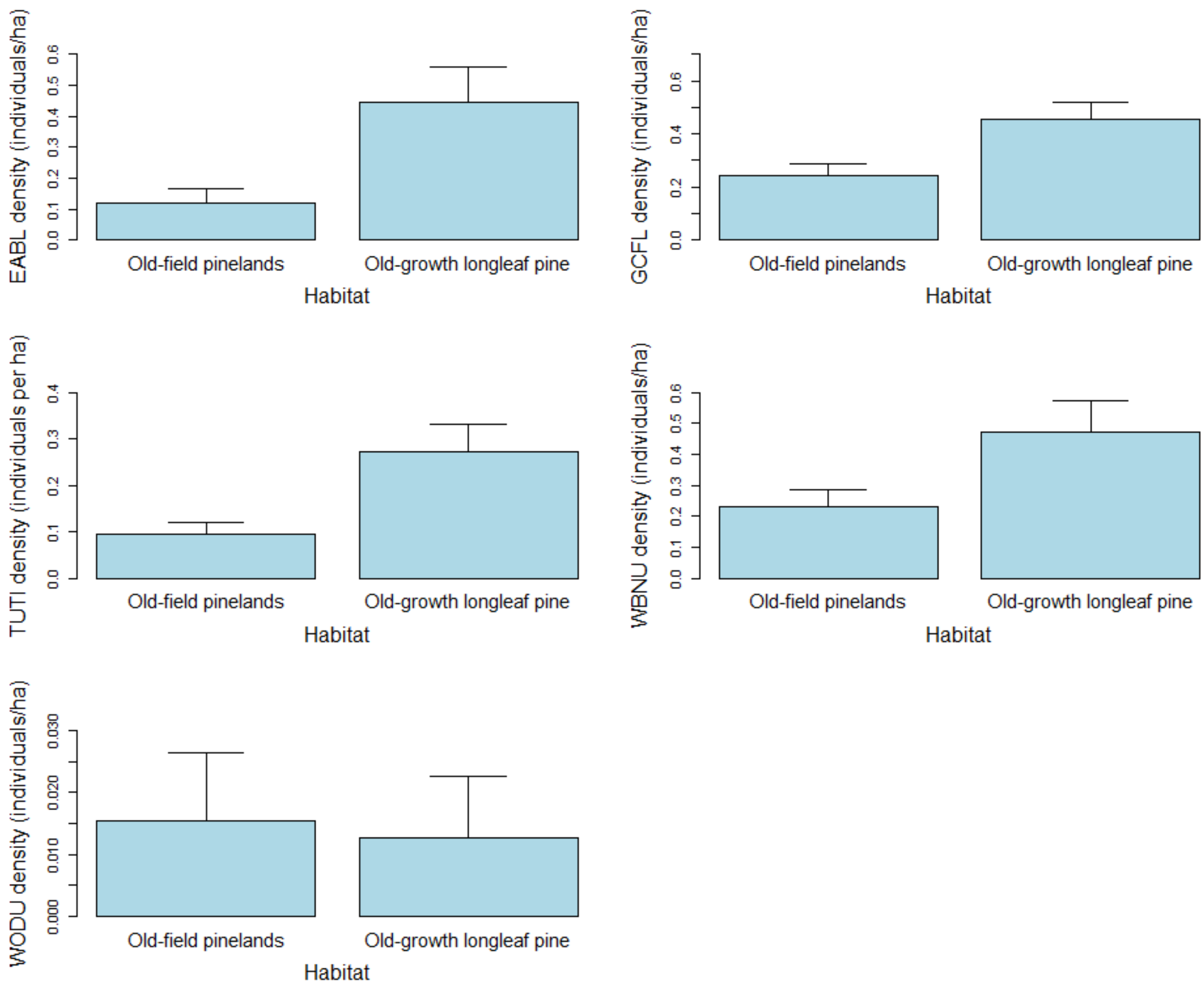

Figure 2.8. Density estimates of secondary cavity-nesting bird species (*n* = 5; see Table 2.3 for acronyms of species) in old-field pine forests (*n* = 5) and old-growth longleaf pine forests (*n* = 5). Error bars represent standard errors.

CHAPTER 3

NEST SITE PARTITIONING IN A CAVITY-NESTING BIRD COMMUNITY INHABITATING OLD-GROWTH LONGLEAF PINE FORESTS[1]

[1]Levy, H.E., Cox, J.A., Cooper, R.J. To be submitted to *The Wilson Journal of Ornithology*.

Abstract

According to competition theory, members of a community sharing similar resources will narrow their niche or utilize an exclusive portion of their niche to avoid interspecific competition via resource partitioning. Cavity-nesting bird communities provide an interesting system in which to study competition for nest sites and resource partitioning because of the ecological dependencies between species and degree of nest site reuse. Old-growth longleaf pine (*Pinus palustris*) forests are unique in they host an endemic keystone excavator, the Red-cockaded Woodpecker (*Dryobates borealis*), resulting in cavity abundances not typically seen in the younger pine forests that now dominate the region. In this study, we assessed nest site partitioning among members of the cavity-nesting community and identified species with high potential for interspecific competition in areas where nest sites are limiting. We predicted there would be a degree of partitioning among the community based on measured nest site characteristics and that larger species would outcompete smaller species for safer cavities. We measured 5 nest tree characteristics of 10 cavity-nesting bird species. We found evidence of nest site niche partitioning among the community based on selection of substrate type, tree decay, cavity height, diameter at breast height (DBH), and cavity location, but there was also substantial overlap between some species. We did not find evidence that body size drives partitioning in this community; instead, we observed distinct species groups based on substrate and snag decay selection. White-breasted Nuthatches (*Sitta carolinensis*), Tufted Titmice (*Baeolophus bicolor*), and Wood Ducks (*Aix sponsa*) used Red-cockaded Woodpecker cavities almost exclusively. Red-headed Woodpeckers (*Melanerpes erythrocephalus*), Red-bellied Woodpeckers (*M. carolinus*), and Northern Flickers (*Colaptes auratus*) frequently used snags of similar decay, but also commonly used Red-cockaded Woodpecker cavities. Brown-headed Nuthatches (*Sitta*

pusilla) and Eastern Bluebirds (*Sialia sialis*) most frequently used late-stage snags and may experience high nest site competition in areas where these snags are limiting. For managers interested in maintaining a high diversity and abundance of cavity-nesting bird species, we recommend snag retention or creation where snags are limiting for both large, mid-stage snags, and for short, late-stage snags. Conservation of large, unfragmented forest tracts for Red-cockaded Woodpeckers may be especially important to Northern Flickers, Red-headed Woodpeckers, and Brown-headed Nuthatches, three species of conservation concern in the region.

Introduction

Interspecific competition among species utilizing the same resources can limit the number of species that can coexist in a community. Some important mechanisms allowing for coexistence within a community include diet, resource, and habitat partitioning. A fundamental aspect of partitioning is that the resource in question is both limited and distributed across a gradient of quality or preference by individuals (Schoener 1974). Although there are numerous ways that habitat use can differ among species, habitat partitioning is often evaluated using nest site selection (e.g., Martin and Martin 2001, Kosinski and Winiecki 2004, Vierling et al. 2009, Martin 2015, Ye et al. 2019). Cavity-nesting bird communities provide a unique system to study nest site partitioning because of the ecological dependencies between species, degree of nest site reuse based on cavity longevity, and predicted limited quantity of high-quality cavities. Cavity-nesting bird communities interact through a complex web based on cavity creation and competition (Martin and Eadie 1999, Lawler and Edwards Jr 2002).

These communities often follow a keystone species-driven pattern of organization, in which one or a few excavators has the potential to influence richness and abundance of other species in the community (Martin and Eadie 1999). Cavity-nesting species fall into one of three guilds: primary excavators, weak primary excavators, and secondary cavity-nesters. Primary excavators and weak primary excavators are distinguished by the degree of tree decay necessary for excavation, with weak primary excavators requiring more advanced decay. Secondary cavity-nesters are completely dependent on existing cavities, resulting in strong ecological ties to primary excavators (Martin and Eadie 1999). These ties can be especially strong in conifer-dominated forests where naturally occurring cavities can be scarce (Bull et al. 1997). Suitable nest cavities are essential for reproduction and can ultimately limit population size if they are limiting. As a result, cavity-nesting birds often expend a significant portion of time and energy excavating or competing for nest cavities (Newton 1994). Cavities in snags may persist up to 20 years or more (Conner and Saenz 2005, Yamasaki and Leak 2006) and cavities in living trees may persist several decades, providing nesting resources for non-excavating species and the option for excavators to reuse cavities (Aitken et al. 2002).

Limited availability of high-quality cavities drives competition (Nilsson 1984, Newton 1994), especially among similarly sized species (Martin et al. 2004). However, cavity characteristics represent just one dimension of a species' niche in terms of nest site requirements (Holt 1987). Species using similar resources may avoid competition by narrowing their niche or by utilizing a part of their niche that minimizes overlap with other species (Colwell and Fuentes 1975). According to the nest site limitation hypothesis, excavators should be less constrained by cavity availability because they exhibit greater flexibility in nest placement (Martin 1993). However, even primary excavators may be limited if there are too few trees of appropriate decay and size classes for excavation (Li and Martin 1991). Secondary cavity nesters and some weak primary excavators generally occupy more broad nest site niches because of their dependency on existing cavities (Martin et al. 2004).

The potential for nest site partitioning has been documented in several cavity-nesting communities (e.g., Bull et al. 1986, Martin et al. 2004, Robles and Martin 2013), but limited nest site availability may drive continual competition even when partitioning is evident (Newton 1994). Interference competition, which involves direct and aggressive negative interactions, is common among cavity-nesting birds and may result in frequent and sustained interference competition; this may be a primary reason for decreased nest success in cavity-nesting species (Nilsson 1986), contrary to the widespread notion that cavity-nesting species have higher nesting success than open-cup nesters (Martin and Li 1992). Cavity quality is an important feature driving competitive interactions between excavators and secondary cavity-nesters (Robles and Martin 2013) because high quality cavities promote greater reproductive success (Newton 1994). One important feature of cavity quality is cavity height. Predation rates decrease strongly with increasing nest height for several cavity-nesting species (Nilsson 1984). Therefore, there may be severe competition for the safest cavities if high quality cavities are limiting on the landscape (Nilsson 1986). Competition may exclude less-dominant species from attaining high quality cavities, but there is often persistent competition among similarly sized species (Martin et al. 2004). Larger cavity-nesting species tend to outcompete smaller species, forcing the latter to use riskier cavities that may be more susceptible to nest predation. For example, Nilsson (1984) found that four cavity-nesting species in Sweden preferred nesting in higher cavities when they had the opportunity, but on average occupied decreasing cavity heights in order of decreasing dominance of each species.

Forest management also influences interspecific dynamics of the cavity-nesting bird community because of each species' dependence on dead and dying trees, making cavity-nesting birds particularly sensitive to forestry activities (Scott and Oldemeyer 1983). Snag removal and short harvest rotation are common forest management practices in southern pine forests that may exacerbate competition by reducing nest site availability (Blanc and Walters 2008b). As a result, cavity-nesting birds may face nest site limitations either directly through a lack of cavities, or indirectly through competition (Wiebe 2011). Accordingly, conservation of these communities through management requires understanding of how species-specific nest site requirements influences nest site limitation and interspecific competition (Bonaparte and Cockle 2017).

Mature, open longleaf pine (*Pinus palustris*) forests once dominated the Southeastern Coastal Plain (Landers et al. 1995). These forests currently occupy less than 5% of their original range and old-growth stands have been reduced to 0.00014% of their former extent (Varner and Kush 2004). Younger, even-age managed pine forests now dominate where longleaf historically thrived (Miller 2010). In old-growth longleaf pine forests, the endemic Red-cockaded Woodpecker (*Dryobates borealis*) acts as an ecosystem engineer, excavating cavities exclusively in living pines that are used by at least 24 other species (Jackson 1971, Conner et al. 1997, Loeb and Hooper 1997). Old-growth pine snags in these forests are large and longstanding, influencing cavity-nesting bird community composition and abundances (Miller and Marion 1995). Fire-maintained pine forests are typically considered to be cavity-poor due to a lack of hardwoods and frequent fires (Conner et al. 2001), however these conditions may be more typical of younger, heavily managed pine forests. Generally, frequent fire application does not affect densities of larger snags, though it may influence smaller snag densities (Perry et al. 2017). The presence of an endemic keystone excavator should result in higher cavity densities in older forests that may neutralize lower snag densities found in pine forests compared to hardwood and mixed-hardwood pine stands. Further, studies in other old-growth habitats have shown that environmental conditions may be more important than cavity-availability in constraining densities of cavity-nesting species because of the abundance of available cavities in these forests (Walankiewicz 1991, Lõhmus and Remm 2005, Remm et al. 2006, Aitken and Martin 2007, Robles et al. 2011).

The Red Hills physiographic region of northwest Florida and southwest Georgia contains some of the highest quality remaining old-growth longleaf pine stands (Cox et al. 2001) that support a rich assemblage of cavity-nesting bird species (Engstrom 1993). Old-growth longleaf pine forests contain many large trees (>50 cm diameter at breast height; DBH), long-lived large snags, large coarse woody debris, and patchily distributed age classes. Old-growth characteristics begin to develop around 120 years of age, with mature forests containing age classes > 150 years old and individual trees > 200 years old (Platt et al. 1988). The potential for community-level nest partitioning has previously been documented in longleaf pine forests and may explain how up to 14 cavity-nesting species can coexist in a relatively cavity-depauperate environment. However, the extent to which differences in decay dynamics can create sufficient niches, and how the modification of cavity resource availability affects interactions remains unexplored (Blanc and Walters 2008a). To address these gaps and provide management suggestions that will support a high diversity of cavity-nesters, we measured nest tree characteristics of ten cavity-nesting bird species in old-growth longleaf pine forests to assess nest site resource partitioning among members of the community and to identify species potentially subject to high degrees of competition based on amount of niche overlap. We predicted that (1) the community would demonstrate a degree of nest site niche partitioning based on substrate, decay class, DBH, cavity height, and cavity location but that (2) larger cavity-nesting birds would outcompete smaller species for higher and larger diameter (i.e., safer) cavities. Based on amount of nest site niche overlap, we identify species that may be subject to interspecific competition where cavity resources are limiting. We also discuss potential implications for managers interested in maintaining a high diversity of cavity-nesting bird species.

Methods

Study Sites

We conducted field work in the breeding seasons of 2018 and 2019 in the Red Hills physiographic region of southwest Georgia. We established eight 20-ha plots across 4 privately owned old-growth longleaf pine plantations in Thomas County based on the size of old-growth stands within each site: Greenwood Plantation (*n* = 4 plots), Melrose Plantation (*n* = 1 plot), Sinkola Plantation (*n* = 1 plot), and the Wade Tract (*n* = 2 plots). All sites are fire maintained on a 2-year return interval, resulting in a similar open-canopy forest structure with minimal hardwood components and patchily distributed age classes of pines. These plantations are predominantly clayhill, or upland longleaf pine forests characterized by scattered longleaf pine trees, the dominant tree, with a sparse mid-story of turkey oak (*Quercus laevis*) and a diverse ground cover of fire-adapted forbs and grasses such as wiregrass (*Astrida stricta*). Greenwood, Sinkola, and Melrose feature old-growth conditions where salvage operations are performed when mature trees are killed by lightning. This reduces the density and diversity of snag resources overall but provides a setting where Red-cockaded Woodpecker cavities are readily available (≥ 0.6 cavities per ha). Sinkola and Melrose are also managed for Northern Bobwhite (*Colinus Virginianus*), for which snags are sometimes removed to deter avian predators by reducing the number of perching sites. The Wade Tract, part of the larger Arcadia Plantations, is an 83 ha preserve considered to be the highest quality remnant longleaf pineland landscape in which there is no management other than fire application, resulting in higher snag densities (Varner and Kush 2004), that more likely reflects the historic landscape.

Data Collection

Nest searching was done on two to three transect lines (depending on the shape of the plot) placed 100 m apart on each of the 8 plots. Each plot was walked 1-2 times a week and the observer looked for any signs of nesting behavior by cavity-nesting birds. Behaviors included paired birds exhibiting territoriality against both conspecifics and other species, excavating cavities, lining nests, visiting a potential nest site, provisioning of partners or young, or removal of fecal sacs. Often, the observer strayed from the transect lines in pursuit of suspected nesting activity, but the entirety of the plot was covered during each visit. Once located, the substrate, DBH, height of the nest cavity entrance, and the location of the nest cavity (bole, limb or chimney [i.e., exposed on the top]) were recorded for each nest. We divided substrate into four categories: snags, Red-cockaded Woodpecker cavity trees, dead Red-cockaded Woodpecker cavity trees, and living pines. Snags were defined as any standing dead tree at least 1 meter tall and at least 10 cm in diameter. Living pines were those that contained cavities occurring either through natural decay (e.g., at the base of a fallen limb) or through unfinished woodpecker excavations. We used a decay classification system ranging from 1-8 for all standing dead trees, with 1 indicating a living tree, and 2-8 indicating dead trees with advancing stages of decay (Table 3.1).

Analyses

All nests were in either living or dead longleaf pine trees, the dominant substrate across all sites. We documented 11 cases of cavity reuse in 2019 (7.97% of all cases). Cavities that were reused were not included in descriptive statistics or subsequent analyses, resulting in 126 total unique nest cavities located in 2018 and 2019. All statistical analyses were performed using RStudio (RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA). RStudio is a wrapper for program R (R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/). For statistical tests, we used an alpha of 0.05.

To assess the presence and extent of niche partitioning, we employed a principal components analysis (PCA), a cluster analysis, and a similarity matrix to characterize general trends for each species along a gradient of nest site characteristics, including cavity height, DBH, and decay class. All nests were included in the PCA, which also included an ordination of the first two principal components. We then ran a cluster analysis of nest tree characteristics for species with ≥ 5 nests (which excluded White-breasted Nuthatches [scientific names of study species appear in Table 3.2] and Carolina Chickadees) using average linkage between groups. Results were then used to produce a dendrogram, depicting the similarities of nest tree characteristics among species. Covariates included median decay, minimum decay, maximum decay, average DBH, minimum DBH, maximum DBH, average cavity height, minimum cavity height, and maximum cavity height. A matrix of ecological similarity of cavity characteristics for all species with ≥ 5 nests (for greater accuracy in assessing relationships) was calculated using the mean Euclidean distances between species. Euclidean distance here serves as a proxy for niche overlap and partitioning (e.g., Rotenberry and Wiens 1980, Adamík et al. 2003) in which higher values indicate greater similarity among cavity characteristics between species. Following multivariate analyses, we used nonparametric Kruskal-Wallis tests to assess differences in species-specific nest site selection and to further identify differences in categorical variables not included in prior analyses such as substrate type and cavity location. Significant main effects were followed by a non-parametric post-hoc test, Dunn's Test of Multiple Comparisons, to assess differences among species groupings.

To assess the relationship between body size and cavity tree selection, we used linear regression models that included cavity height and DBH in addition to body size. We used mean body mass and body length as a surrogate for body size and acquired these measurements from the public Birds of North America database (https://birdsna.org). We used average male weights for all species, but we used only average female weight for Wood Ducks because males do not enter the cavity.

Results

General

Of the 126 nests found, nearly half (*n* = 62) were located in snags, followed by Red-cockaded Woodpecker cavities (*n* = 48), cavities in living pines (*n* = 11), and by dead Red-cockaded Woodpecker cavity trees (*n* = 5; Figure 3.1). Table 3.2. provides descriptive statistics of nests for each species. Cavities in living pines were either created naturally through fungal decay or by excavations initiated by a woodpecker, but these cavities occurred rarely and were not utilized often. Some cavity-nesting species used multiple substrate types, while others consistently used a single substrate. The three large primary excavators, Northern Flickers (*Colaptes auratus*), Red-headed Woodpeckers (*Melanerpes erythrocephalus*), and Red-bellied Woodpeckers (*M. carolinus*), either used living or dead Red-cockaded Woodpecker cavities or excavated cavities in snags. Northern Flickers used snags and Red-cockaded Woodpecker cavities roughly equally, whereas Red-bellied Woodpeckers used living or dead Red-cockaded Woodpecker cavity trees most of the time and Red-headed Woodpeckers used snags most of the time (Figure 3.1). Brown-headed Nuthatches (*Sitta pusilla*), the main weak excavator in this community, nearly always nested in snags (one pair nested in the decayed base of a broken limb on a younger pine). We documented only two Carolina Chickadee (*Poecile carolinensis*) nests, one of which was in an upright limb of a downed snag. Eastern Bluebirds (*Sialia sialis*) usually nested in snags, but also utilized fire scars that created open cavities low in the bole of large living pine trees. Great Crested Flycatchers (*Myiarchus crinitus*) showed a wider selection, using naturally decayed cavities in living pines, Red-cockaded Woodpecker cavities, and existing cavities in snags. Tufted Titmice (*Baeolophus bicolor*), White-breasted Nuthatches (*Sitta carolinensis*), and Wood Ducks (*Aix sponsa*) used Red-cockaded Woodpecker cavities exclusively.

The vast majority (84.9%) of nest cavities for most species were in boles of living and dead pine trees (Figure 3.2). Chimney cavities only occurred in decay class 7 and 8 snags and were used by both Brown-headed Nuthatches and Eastern Bluebirds. Fire scars that created shallow crevices at short heights in the boles of larger living pine trees were used exclusively by Eastern Bluebirds. Few nests were in limb cavities, likely because the width of limbs was not large enough and because these cavities are more susceptible to damage from strong winds and storms.

Because so many nests were in living trees, largely in Red-cockaded Woodpecker cavities (Figure 3.3), the most frequently observed decay class utilized for nests was decay class 1 (Table 3.3). We did not locate any nests in class 2 (freshly dead trees), and very few in class 3 (dead < 3 - 4 years). Class 5 (near complete loss of crown and bark) was the most utilized decay class for primary excavators that did not nest in Red-cockaded Woodpecker cavities, with number of nests dropping off again at class 6 (only intact bole remains). Classes 7 (soft wood, between 3 and 6 meters tall) and 8 (< 3 meters tall) were used almost exclusively by Brown-headed Nuthatches and Eastern Bluebirds, with nuthatches excavating the majority of cavities in these late-state snags.

We present measurements of cavity height and DBH for all nests found (Figure 3.4). Most species selected cavity heights between 10 and 20 meters in height, except Brown-headed Nuthatches and Eastern Bluebirds, which almost always used cavities less than 5 meters in height. Most species also selected larger diameter trees (ca. 40-50 cm).

Prediction 1: Nest Site Partitioning

The PCA included all nests located for all cavity-nesting bird species. Principal component 1 explained 67.4% of the total variance and principal component 2 explained 19.2% of the total variation (Table 3.4). Cavity characteristic relationships are plotted on the first two principal components (Figure 3.5). Plotted results depict two main groupings that did not overlap much, but species overlap was substantial within groupings. The first group contained Eastern Bluebirds and Brown-headed Nuthatches. Nest site selection of Brown-headed Nuthatches and Eastern Bluebirds corresponded with higher decay classes and lower cavity heights. The second grouping depicted substantial overlap between Red-headed Woodpeckers, Red-bellied Woodpeckers, Northern Flickers, Wood Ducks, and Tufted Titmice. Great Crested Flycatchers exhibited a broader niche that extended into both species' groupings. Nest site selection for these 6 species corresponded with higher cavity heights, lower decay classes, and larger DBH. For all nests, there were significant differences in selection of cavity location (χ^2 = 49.2.0, df = 9, P < 0.001), substrate (χ^2 = 44.4, df = 9, P < 0.001), tree decay (χ^2 = 61.2, df = 9, P < 0.001), DBH (χ^2 =31.2, DF = 9, P < 0.001) and cavity height (χ^2 = 70.7, df = 9, P < 0.001). Most of these differences were between Eastern Bluebirds and all other species and between Brown-headed Nuthatches and all other species (Table 3.5). However, Red-headed Woodpeckers and Red-bellied Woodpeckers displayed large overlap indicated by the PCA ordination with significant differences in substrate type ($P = 0.002$), with Red-bellied Woodpeckers nesting in Red-cockaded Woodpecker cavities more often than Red-headed Woodpeckers.

Cluster analyses among the seven species with ≥ 5 nests found produced 3 main groupings of species (Figure 3.6). The first grouping contained one weak excavator, Brown-headed Nuthatch, and one secondary cavity-nester, Eastern Bluebird. The second group included two excavators, Northern Flicker and Red-headed Woodpecker. The third group included one excavator, Red-bellied Woodpecker, and two secondary cavity-nesters, Wood Duck and Great Crested Flycatcher. We used these same seven species for the similarity matrix (Table 3.6). Brown-headed Nuthatches and Eastern Bluebirds had the highest similarity value. Most differences occurred between Brown-headed Nuthatches and all other species and Eastern Bluebirds and all other species, but there are also many similarities between the other species Red-headed Woodpeckers and Red-bellied Woodpeckers were not as closely linked by Euclidean distances as by other analyses, but this is likely explained by differences in the nest substrates used. Selection for snag characteristics was similar between the two species, but Red-bellied Woodpeckers used Red-cockaded Woodpecker cavities as substrates more than half of the time, while Red-headed Woodpeckers selected Red-cockaded Woodpecker cavities < 30% of the time.

Prediction 2: Influence of Body Size on Cavity Quality

Larger species did not nest in higher cavities than smaller species. There is a weak general trend across all nests found that, besides Brown-headed Nuthatches and Eastern Bluebirds, larger species utilize taller and larger cavities. Despite this weak trend, our prediction was not supported (Figure 3.7). We used cavity height and DBH as a proxy for cavity quality because both cavity height and DBH have been shown to be importance factors influencing nest predation, and we used both mass and body length as a surrogate for size. Body mass did not influence cavity height ($F_{1,5}$ = 1.4, R^2 = 0.07, P = 0.29) or DBH ($F_{1,5}$ = 0.91, R^2 = -0.02, P = 0.39). Body length also did not influence cavity height ($F_{1,5}$ = 3.4, R^2 = 0.29 P = 0.12) or DBH ($F_{1,5}$ = 1.9, R^2 = 0.13, P = 0.22), suggesting that size may not be an influential driver of niche partitioning in this community.

Discussion

Conservation of cavity-nesting bird species requires an understanding of interspecific interactions and interdependencies among guilds (Cornelius et al. 2008), yet most of our understanding of cavity-nesting species comes from studies of one or a few species in intensely managed stands (Newton 1994). Community-wide studies in natural conditions are necessary for investigating relationships and dynamics among members of cavity-nesting communities (Martin and Eadie 1999). In conifer dominated systems, where naturally occurring cavities are uncommon, excavation plays a critical role in creating cavities for secondary cavity users (Bull et al. 1997). Our findings also support this, as over 90% of all found nests were in excavated cavities, indicating the critical role primary excavators play in this ecosystem. Additionally, many of the nests found in snags were in large, mature pine snags, which are atypical of snags in many pine forests remaining in the southeast today (Blanc and Walters 2008a). The use of Red-cockaded Woodpecker cavities by several avian species in southern pine forests has been well-documented (Dennis 1971, Kappes Jr and Harris 1995, Kappes Jr 1997, Walters et al. 2004, Kappes Jr and Sieving 2011) and our study supports the importance of these cavity resources; seven out of ten cavity-nesting bird species and over one-third of all nests found were in Red-cockaded Woodpecker cavities. It can be expected that the presence of large, longstanding snags and remnant Red-cockaded Woodpecker cavities will influence cavity-nesting community interactions and that nest site selection will shift in the absence of these cavity resources.

In theory, competition should be less severe for species that (1) occupy a wide niche breadth and can adjust their niche in the presence of other species with which resources overlap, and (2) species that have very narrow niches that do not overlap with other species. Overall, there is evidence of both nest site partitioning and considerable overlap among at least some cavity-nesting bird species in our study. We found significant differences between several species in nest site selection based on substrate, DBH, cavity height, cavity location, and decay. We thus divide species into three main nesting categories: (1) those using Red-cockaded Woodpecker cavities, (2) those using mid-stage decay class snags (classes 4-6, with the majority occurring in class 5), and (3) those using late-stage decay class snags (classes 7-8, with the majority occurring in class 8). Because recently dead trees are difficult to excavate, earlier decay classes were not as widely used, with class 5 appearing to be an optimal decay class for woodpeckers.

Over half of all nests located were in Red-cockaded Woodpecker cavities, including nearly all Tufted Titmouse nests and all Wood Duck nests. Surprisingly, nearly all Red-bellied Woodpecker nests occurred in Red-cockaded Woodpecker cavities, with a few using mid-stage snags. Most Great-crested Flycatcher also used Red-cockaded Woodpecker cavities, but with some occurring at the site of a broken limb in living pines or an abandoned Red-cockaded Woodpecker excavation, and few occurring in late-stage snags. Northern Flickers either used Red-cockaded Woodpecker cavities or mid-to-late-stage snags. Red-headed Woodpecker frequently used mid-stage snags, with some occurring in Red-cockaded Woodpecker cavities.

Fire scars near the base of living pines can create natural cavities low in the bole of the tree, which were frequently used by Eastern Bluebirds. When they did not nest in these crevices, decay classes 7-8 were mainly used by Eastern Bluebirds and by Brown-headed Nuthatches. We did not obtain enough nesting information for Carolina Chickadees and White-breasted Nuthatches to discern substantial information on nest site selection. However, Leonard Jr (2005) has suggested strong ecological ties between Red-cockaded Woodpeckers and White-breasted Nuthatches, indicating the importance of old-growth longleaf pine ecosystem for this species.

In contrast to Martin et al. (2004), we found that the cavity-nesting bird community did not partition nest sites by body size. Rather, it appears that tree decay (which also relates to substrate type between living and dead trees) and cavity height were more critical components, suggesting that competition may be low in old-growth settings and not as dependent on species-specific dominance. Some secondary cavity nesters such as Great Crested Flycatchers and Eastern Bluebirds had a broader niche breadth than did primary excavators. Great Crested Flycatchers, which occupied the widest niche, nested in snags of varying heights, naturally occurring cavities in living trees, and in Red-cockaded Woodpecker cavities. In deciduous and mixed woodlands, Great Crested Flycatchers rely more on naturally created holes in trees than from woodpecker excavation, but the opposite is true in coniferous forests. Up to 73% of nests in slash and longleaf pine forests occurred in cavities excavated by other birds (Miller 2014). We found the same to be true on our old-growth sites, with the most nests occurring in excavated cavities, although these nests varied greatly in decay and in cavity height.

Most primary excavating species in our study used large snags. Larger diameter snags provide greater thermoregulatory stability (Wiebe 2011) and greater protection from predators (Gault et al. 2004). Old-growth forests typically contain taller trees and snags, allowing birds to excavate cavities at greater heights. Cavity height is a critical factor of increased nest success for many cavity-nesting species due to predation rates by ground-dwelling predators (Nilsson 1984). Larger snags also persist longer than smaller ones, providing longer-lived cavities (Bull 1983). These types of snags may not be common in other more intensively managed southeastern pine forests, but have shown to be extremely important factors influencing cavity-nesting abundances (Miller and Marion 1995). Similarly, Red-cockaded Woodpecker cavity heights in the Red Hills ($\bar{x}$ = 10.7 m; Tall Timbers Research Station, unpublished data) are higher than found elsewhere throughout the range ($\bar{x}$ = 7.4 m; reviewed in Shapiro 1983), which could contribute to higher nesting success.

Within the longleaf pine range, there are several ecotype classifications based on soil type, vegetation type, and forest structure (Peet and Allard 1993), and avian communities vary across this range, often by ecotype. Blanc and Walters (2008a) provided a similar assessment to this study in a sandhill old-growth longleaf pine forest; the community of birds is slightly different than in the clayhill ecotype. For example, American Kestrels (*Falco sparverius*) breed in the sandhills, but not in the clayhills and their assessment did not include species such as Wood Ducks and White-breasted Nuthatches, and had low detections of Brown-headed Nuthatches, Eastern Bluebirds, and Great Crested Flycatchers. Although Red-headed Woodpeckers and Northern Flickers nested less frequently in Red-cockaded Woodpecker cavities overall, species-specific nest site selection was similar between their study and ours.

Potential interspecific competition

We identified two groups of species with substantial overlap that may incur high degrees of interspecific competition for nests in cavity-limited areas: (1) species using Red-cockaded

Woodpecker cavities or mid-stage snags and (2) species using late-stage snags. Species in the first group include Red-headed Woodpecker, Red-bellied Woodpecker, Northern Flicker, and to a lesser degree, Great Crested Flycatcher, which infrequently used late-stage snags as well. All four species used both decay class 4-6 stage snags of similar diameter and cavity height, and commonly used Red-cockaded Woodpecker cavities. Species that exclusively or nearly exclusively used Red-cockaded Woodpecker cavities in our study may also be in competition where nest sites are limiting. However, Wood Ducks require large diameter cavity entrances, which typically occur in pine forests when Pileated Woodpeckers or Northern Flickers enlarged Red-cockaded Woodpecker cavities (Sisson and Engstrom 1993). Great Crested Flycatchers showed high variability in nest site substrates. Secondary cavity-nesters generally occupy wider niches because they are completely dependent on existing cavities (Martin et al. 2004). Two other species of secondary cavity-nesters, Tufted Titmice and White-breasted Nuthatches, may face more severe competition as they were both documented using unenlarged cavities, but we did not document enough nests to assess how wide their niches may be.

Red-headed Woodpeckers and Red-bellied Woodpeckers are similar sized species that are sympatric throughout much of their range (Jackson 1976). In our study, Red-headed and Red-bellied Woodpeckers generally preferred trees of similar decay, diameter, and excavated cavities at similar heights. Although all three woodpeckers commonly usurped Red-cockaded Woodpecker cavities, Red-bellied Woodpeckers used them most frequently, using living or dead Red-cockaded Woodpecker cavities in 83% of their nesting attempts, whereas Northern Flickers and Red-headed Woodpeckers used them 40% and 39% of the time, respectively. Nest date initiation is generally earlier in Red-bellied Woodpeckers than in Red-headed Woodpeckers (Ingold 1989). However, in the southern part of their range, Red-bellied Woodpeckers commonly exhibit double brooding, sometimes even triple brooding, resulting in greater potential for competition from phenological overlap. Red-headed Woodpeckers are often described as the most pugnacious of woodpeckers, and indeed often act as interspecific aggressors. In 85% of interactions with Red-bellied Woodpeckers, Red-headed Woodpeckers were the initiators (Ingold 1989) and in central Illinois during the winter, Red-headed Woodpeckers will displace Red-bellied Woodpeckers into different habitats and force other bark-foraging species to change vertical microhabitat use on trees (Williams and Batzli 1979). Additionally, after a winter storm shifted habitat selection in Illinois, Red-headed Woodpeckers moved into wintering habitats of Red-bellied Woodpeckers, causing a decline in numbers of the latter (Graber and Graber 1979). Red-bellied Woodpeckers are one of the most frequent Red-cockaded Woodpecker cavity kleptoparasites where their ranges overlap (Jackson 1978, Kappes 1993). Red-headed Woodpeckers and Red-bellied Woodpeckers share an almost identical range, and both often inhabit pine forests. Thus, it is possible that Red-headed Woodpeckers, which were abundant on our sites and have demonstrated extreme territoriality over Red-bellied Woodpeckers, outcompeted Red-bellied Woodpeckers for snags, resulting in increased use of Red-cockaded Woodpecker cavities by Red-bellied Woodpeckers. Nesting in Red-cockaded Woodpecker cavities may be riskier than excavation in snags because of sustained competition with Red-cockaded Woodpeckers and potentially lower nest success in these cavities (Kappes Jr and Sieving 2011).

Species in the second group include Brown-headed Nuthatches and Eastern Bluebirds. Late-stage snags (i.e., classes 7 and 8) comprised 94.4% of the total nests that nuthatches used and 75% of the total nests that bluebirds used. Where their ranges overlap, Brown-headed Nuthatches often aggressively chase Eastern Bluebirds, one of their most frequent nest competitors (Norris 1958, McNair 1984, Slater 1997). Entrance hole diameter and location may be one of the most important factors in deterring bluebird usurpation of nuthatch cavities (Stanback et al. 2019). In our study, Eastern Bluebirds often used cavities excavated by Brown-headed Nuthatches, although this may not necessarily infer competition. Brown-headed Nuthatches regularly excavate new cavities annually (J. Cox, Tall Timbers Research Station, personal communication), resulting in unused cavities for bluebirds to nest in. We also documented several instances of Brown-headed Nuthatches excavating chimney cavities, which were more susceptible to usurpation than cavities in boles because bluebirds can easily fit in chimney cavities. Because Brown-headed Nuthatches used these chimney cavities often, competition may be low enough for birds to feel safe utilizing riskier cavities. In addition to using old nuthatch excavations, bluebirds also nested in fire scars low in the boles of large living pine trees. Large diameter trees with frequent fire scars, which are likely less abundant in younger forest stands, may help alleviate competition by providing additional nesting substrates for bluebirds. Indeed, most interactions between Brown-headed Nuthatches and Eastern Bluebirds occur at atypical nest sites or in poor quality habitat (McNair 1984).

Species with high niche overlap should hypothetically distance themselves spatially to avoid direct competition. However, there were 4 instances of cavities in shared trees, also called condominium nesting (Salt 1985). Two occurrences were with a Northern Flicker and a Red-headed Woodpecker, one with a Red-cockaded Woodpecker and a Red-headed Woodpecker, and one with a Red-bellied Woodpecker and a Red-headed Woodpecker. Initially, a lack of suitable cavities should strongly influence shared tree cavities. However, there were multiple unused cavities throughout the landscape and upon observation of these cavities, there was minimal agonistic behavior, except when both birds were entering cavities at the same time. There is evidence that nesting in shared trees provides earlier detection of predators and can result in higher fledging rates than solitary nests (Mouton and Martin 2018).

Management implications

Older southern pine forests may not be cavity-poor habitats as McComb et al. (1986) once suggested based on studies of younger pine forests. The abundance of cavity resources in old-growth longleaf pine forests often supports abundances of species in decline in other parts of their ranges (Blanc and Walters 2008a) such as Northern Flickers, Red-headed Woodpeckers, and Brown-headed Nuthatches. The presence of Red-cockaded Woodpeckers influences abundances of Northern Flickers and the use of Red-cockaded Woodpecker cavities by flickers and Red-headed Woodpeckers has been documented by Blanc and Walters (2008b). They suggested that single-species management for Red-cockaded Woodpeckers, specifically the use of cavity entrance restrictors that restrict cavity enlargement, may be negative for Northern Flickers. Old-growth pine forest conditions are also important habitats for Brown-headed Nuthatches, which are considerably less abundant in young pine stands (typically <50 years of age; Dickson et al. 1980, Repenning and Labisky 1985). Longleaf savannas provide high quality habitat for Red-headed Woodpeckers, which prefer open habitat (Shackelford and Conner 1997). Consequently, managing for habitat conditions required by Red-cockaded Woodpeckers indirectly benefits several other cavity-nesting species through pine maturation, mid-story reduction, and frequent fire application.

While competition is a common theme in studies of cavity-nesting birds, competition should be low where nest site resources are not limiting. In this study, we did not directly examine nest site availability, which typically requires experimental manipulation, but a review by Wiebe (2011) suggested that the number of nest sites for cavity nesters in unmanaged, old forests is usually not limiting. This study represents one of the first such assessments restricted to old-growth longleaf pine forests, specifically in the clayhills. While old-growth conditions were present, our study sites also represent a gradient in snag numbers based on the salvaging of lightning struck trees ranging from very few snags (< 1 snag per ha) to an unmanaged (except for fire), old-growth preserve (> 6 snags per ha). Snag densities alone may not be good predictors of cavity availability. For example, the importance of decay to cavity-nesting birds supports a shifting view of tree management from a purely living-dead perspective to a gradient of decay (Blanc and Martin 2012). We suspect that birds in our study system were not limited overall based on the number of anecdotal unoccupied cavities in both snags and Red-cockaded Woodpecker trees, and thus interspecific competition for nest sites may not be as prevalent. Still, even in old-growth settings, for managers interested in maintaining a high diversity and abundance of cavity-nesting bird species, we recommend snag retention or creation where snags are limiting for both large, mid-stage snags, and for short, late-stage snags. Conserving these rare old-growth stands is of importance for the entire cavity-nesting community, as is allowing for maturation of younger pine stands. We also recommend studying cavity-nesting birds across other portions of the longleaf range in old-growth settings, where differences in community composition and cavity dynamics may affect species interactions, nest site selection, and demographics.

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Tables

Table 3.1. Description of decay classes used to characterize nest trees of cavity-nesting birds in the Red Hills region of southwest Georgia. Decay values range from 1-8, in which 1 indicates a living tree and 8 indicates the most decayed snag that was used by cavity-nesting birds.

Decay class	Description
1	Living tree
2	Recently dead (~1 year); still has most of its cones and needles
3	Dead < 3 years; obvious loss of cones, tertiary limbs begin decaying/falling
4	Loss of most tertiary limbs, most secondary limbs remain
5	Loss of almost all tertiary limbs and most secondary limbs
6	Broken-off top with only intact bole remaining
7	Bole shows obvious signs of decaying, between 3 and 6 meters off tall
8	Well decayed, bole not intact, often very charred, between 1 and 3 meters off ground

Table 3.2. Description of nests found (*n* = 126) for cavity-nesting bird species (*n* = 10) in the Red Hills region of southwest Georgia in located in 2018 and 2019. Species are broken 3 guilds based on nesting dynamics. *N* is the total number of nests found for each species. Median decay is presented with the range of decay classes used. Diameter at breast height (DBH) and cavity height are presented as means with standard errors (x̄ ± SD*)*.

Guild	Species	Scientific Name	Code	*n*	Decay	DBH (cm)	Cavity height (m)
Primary excavator	Northern Flicker	*Colaptes auratus*	NOFL	5	5 (1-6)	44.2 ± 13.3	14.42± 2.44
	Red-bellied Woodpecker	*Melanerpes carolinus*	RBWO	24	1 (1-5)	49.1 ± 11.7	15.6 ± 5.02
	Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO	37	5 (1-6)	43.03± 9.14	16.1 ± 4.74
Weak primary excavator	Brown-headed Nuthatch	*Sitta pusilla*	BHNU	17	8 (1-8)	32.1 ± 14.0	2.92 ± 1.85
	Carolina Chickadee	*Poecile carolinensis*	CACH	2	6 (4-8)	29.0 ± 17.0	12.85 ± 17.2
Secondary cavity nester	Eastern Bluebird	*Sialia sialis*	EABL	16	8 (1-8)	29.9 ± 3.68	3.34 ± 0.73
	Great-crested Flycatcher	*Myiarchus crinitus*	GCFL	14	1 (1-8)	51.0 ± 3.82	11.4 ± 1.90
	Tufted Titmouse	*Baeolophus bicolor*	TUTI	4	1	43.4 ± 4.98	10.7 ± 3.14
	White-breasted Nuthatch	*Sitta carolinensis*	WBNU	2	1	57.8 ± 9.70	12.2 ± 6.05
	Wood Duck	*Aix sponsa*	WODU	5	1	49.0 ± 4.78	21.4 ± 5.32

Table 3.3. Frequency (%) of nest cavity tree decay classes used by cavity-nesting bird species (*n* = 10). Percentages represent proportion of nests found for each species in each decay class. Species are divided into 3 guilds based on nesting dynamics. No nests were in decay class 2. *N* is the total number of nests found for each species.

Species	Decay Class								*n*
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	
Northern Flicker	40	0	0	0	20	40	0	0	5
Red-bellied Woodpecker	71	0	0	13	17	0	0	0	24
Red-headed Woodpecker	32	0	8.1	14	38	8.1	0	0	37
Brown-headed Nuthatch	5.9	0	0	0	0	0	24	44	17
Carolina Chickadee	0	0	0	50	0	0	0	50	2
Eastern Bluebird	0	0	0	25	0	6.3	6.3	0	16
Great-crested Flycatcher	86	0	0	0	0	0	0	14	14
Tufted Titmouse	100	0	0	0	0	0	0	0	4
White-breasted Nuthatch	100	0	0	0	0	0	0	0	2
Wood Duck	100	0	0	0	0	0	0	0	5

Table 3.4. Results of principal components analysis for 3 nest site characteristics of 10 cavity-nesting species (*n* = 126 nests). Principal components 1 and 2 describe 86.6% of the total variation.

Statistic		Principal component		
		PC1	PC2	PC3
Standard deviation		1.42	0.759	0.634
Proportion of variance		0.674	0.192	0.134
Cumulative proportion		0.674	0.866	1.00
Correlations of components to original variables				
	Decay	-0.596*	0.369	-0.714*
	DBH	0.593*	-0.400	-0.700*
	Cavity height	0.542*	0.840*	-0.017*

*Correlations of components > 0.5 indicate strong correlation of variables to each component.

Table 3.5. Post-hoc Dunn test results of pairwise species comparisons with at least one significantly similar nest site characteristic. Data was obtained from nests (n = 126) of cavity-nesting bird species (n = 10) located in 2018 and 2019. Asterisks indicate species pairings with $P < 0.05$.

Species comparison	Substrate	Decay	DBH	Cavity height	Cavity location
EABL-BHNU	0.069	0.109	0.396	0.425	<0.001*
CACH-GCFL	0.009*	0.030*	0.063	0.492	0.036*
CACH-NOFL	0.194	0.193	0.172	0.338	0.033*
CACH-RBWO	0.028*	0.031*	0.071	0.217	0.018*
CACH-RHWO	0.189	0.126	0.172	0.176	0.022*
CACH-TUTI	0.010*	0.021*	0.217	0.491	0.187
CACH-WBNU	0.012*	0.039*	0.046*	0.395	0.500
GCFL-NOFL	0.019*	0.094*	0.242	0.242	0.362
CACH-WODU	0.015*	0.018*	0.098	0.197	0.033*
BHNU-WBNU	0.003*	0.002*	0.001*	0.027*	0.079
GCFL-BHNU	<0.001*	<0.001*	<0.001*	<0.001*	0.203
NOFL-BHNU	0.133	0.011*	0.046	0.001*	0.171
RBWO-BHNU	<0.001*	<0.001*	<0.001*	<0.001*	0.063
RHWO-BHNU	0.050	<0.001*	0.005*	<0.001*	0.086
TUTI_BHNU	<0.001	<0.001	0.091	0.019	0.303
NOFL-WODU	0.043*	0.051	0.322	0.279	0.500
NOFL-WBNU	0.034*	0.108	0.143	0.460	0.033*
NOFL-TUTI	0.026	0.061	0.437	0.290	0.125
WODU-BHNU	<0.001*	<0.001*	0.012*	<0.001*	0.171
GCFL-EABL	0.001*	<0.001*	<0.001*	0.002*	<0.001*
NOFL-EABL	0.462	0.076	0.032*	0.002*	<0.001*
RHWO-WBNU	0.013*	0.100	0.084	0.286	0.022*
RHWO-WODU	0.007*	0.026*	0.202	0.463	0.431
EABL-WBNU	0.018*	0.009*	0.007*	0.034*	0.341
EABL-TUTI	0.008*	<0.001*	0.068	0.026*	0.027*
GCFL-WBNU	0.276	0.322	0.242	0.355	0.036*
RHWO-TUTI	0.004*	0.039*	0.493	0.093	0.096
RBWO-EABL	0.012*	<0.001*	<0.001*	<0.001*	<0.001*
RHWO-EABL	0.456	0.003*	0.002*	<0.001*	<0.001*
RBWO-WBNU	0.125	0.302	0.206	0.337	0.018*
WBNU-WODU	0.298	0.500	0.237	0.294	0.033*

WODU-EABL	0.013*	<0.001*	0.008*	0.002*	<0.001*
GCFL-RBWO	0.119	0.461	0.413	0.039*	0.292
RHWO-GCFL	<0.001*	0.032*	0.068	0.014*	0.374
RHWO-RBWO	0.002*	0.018*	0.066	0.351	0.375

Table 3.6. Correlation matrix of similarity values (complements of average Euclidean distance) for nest site characteristics of 7 cavity-nesting bird species (*n* = 121 nests). Higher values indicate higher cavity characteristic similarity between species. Only species with ≥ 5 nests located were included, which eliminated White-breasted Nuthatches, Carolina Chickadees, and Tufted Titmice.

Species	BHNU	EABL	GCFL	NOFL	RBWO	RHWO
EABL	0.850*					
GCFL	0.356	0.340				
NOFL	0.512*	0.516*	0.512*			
RBWO	0.311	0.294	0.767*	0.596*		
RHWO	0.484	0.474	0.604*	0.784*	0.703*	
WODU	0.225	0.208	0.645*	0.547*	0.783*	0.629*

*pairwise species with >0.5 similarity values

Figures

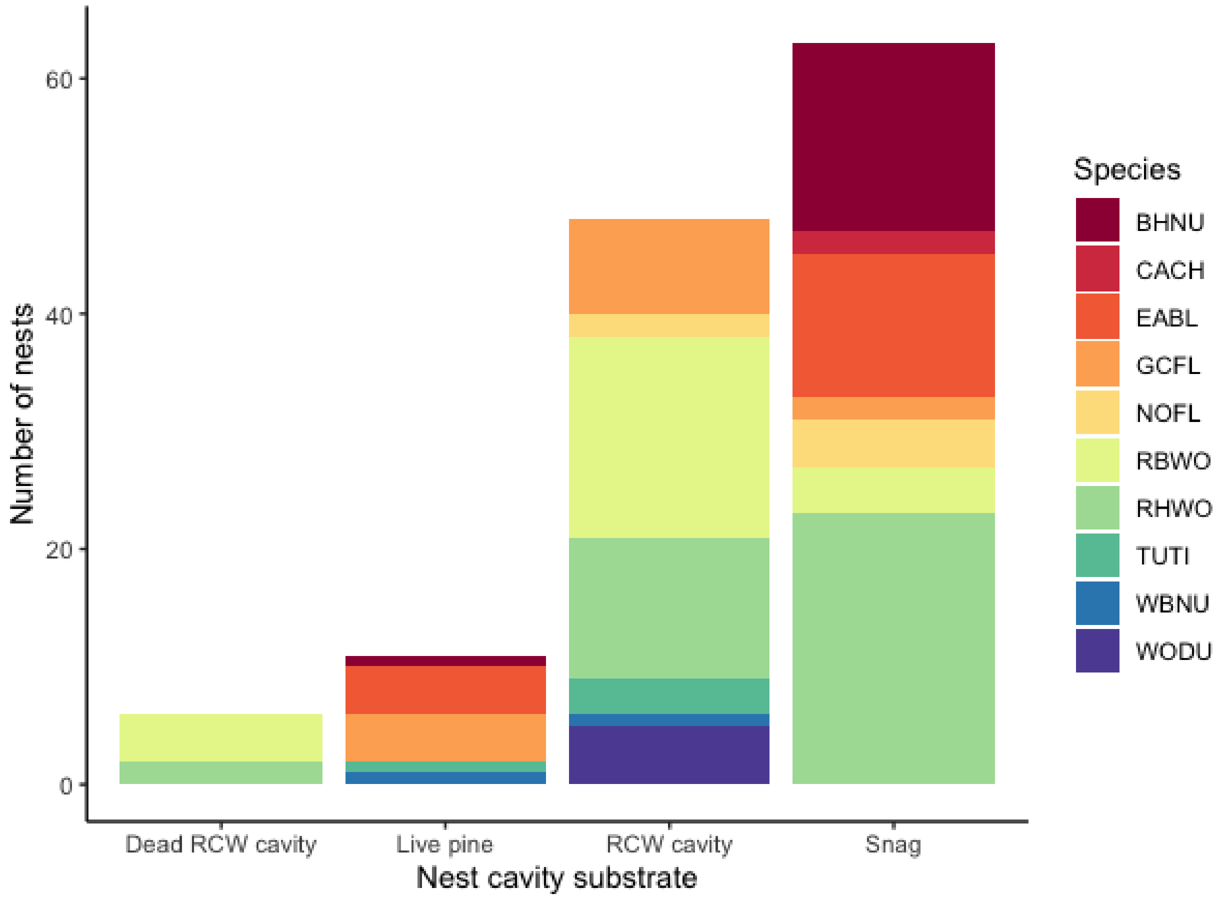

Figure 3.1. Number of nests (*n* = 126 total) by cavity tree substrates used by cavity-nesting bird species (*n* = 10) in old-growth longleaf pine forests of the Red Hills. We located 5 nests in dead Red-cockaded Woodpecker (RCW) cavity trees, 11 nests in live pine trees, 48 nests in Red-cockaded Woodpecker cavities, and 62 nests in snags.

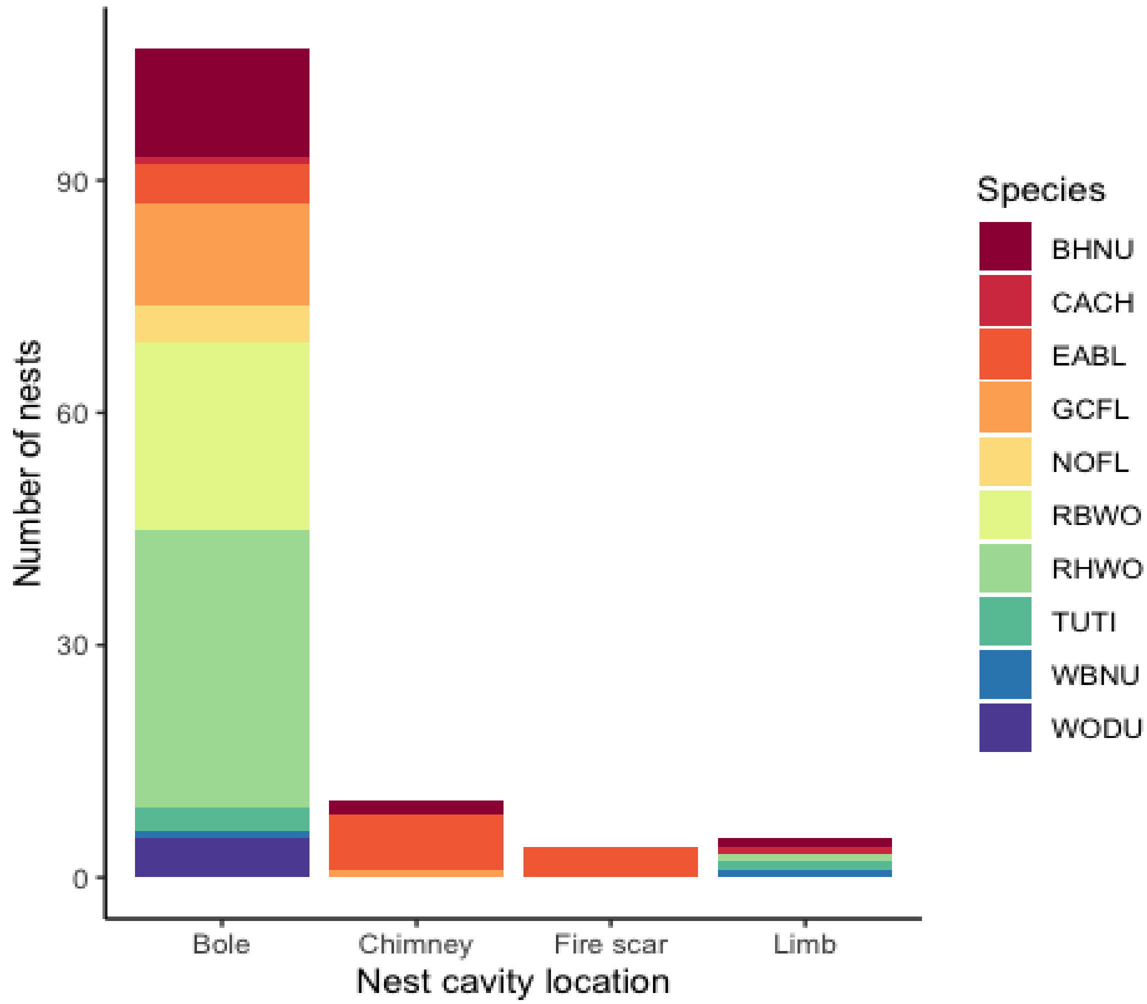

Figure 3.2. Number of nests (*n* = 126 total) by cavity location used by cavity-nesting bird species (*n* = 10) in old-growth longleaf pine forests of the Red Hills. Bole cavities (*n* = 107) are in the main trunk of the tree. Chimney cavities (*n* = 10) refer to cavities located at the top of well-decayed snags. Fire scar (*n* = 4) refers to previous fire events that created hollow cavities low in the bole of large pine trees. Limb cavities (*n* = 5) are in the limbs of living or dead trees, through either fungal decay or through woodpecker excavation.

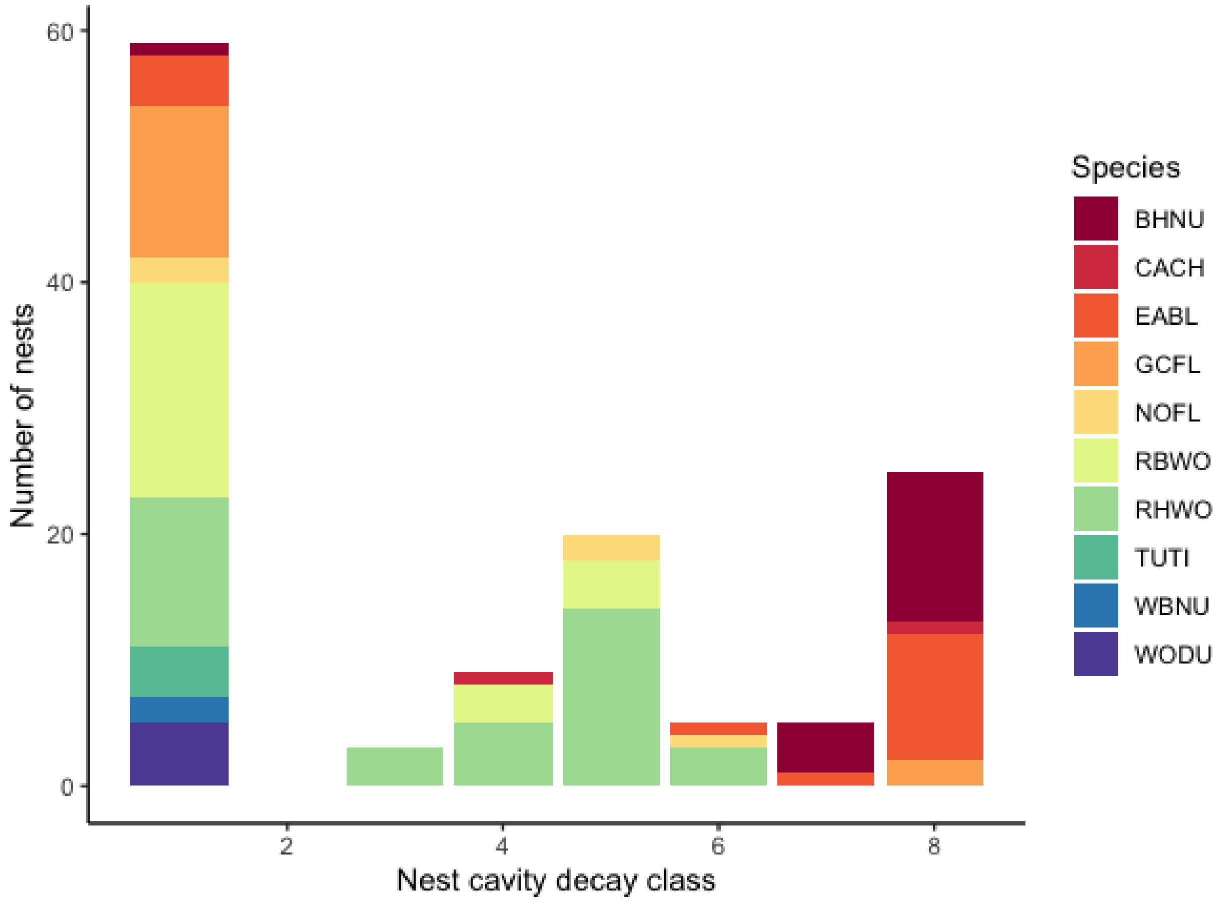

Figure 3.3. Number of nests (*n* = 126 total) by tree decay class for cavity-nesting bird species (*n* = 10) in old-growth longleaf pine forests of the Red Hills. Class 1 indicates a living tree, and classes 2-8 indicate dead trees of increasing decay. Class 1 includes nests in living Red-cockaded Woodpecker cavities trees, cavities in living pines created through fungal decay, and cracks low in the bole of fire scarred living trees. No nests were in decay class 2.

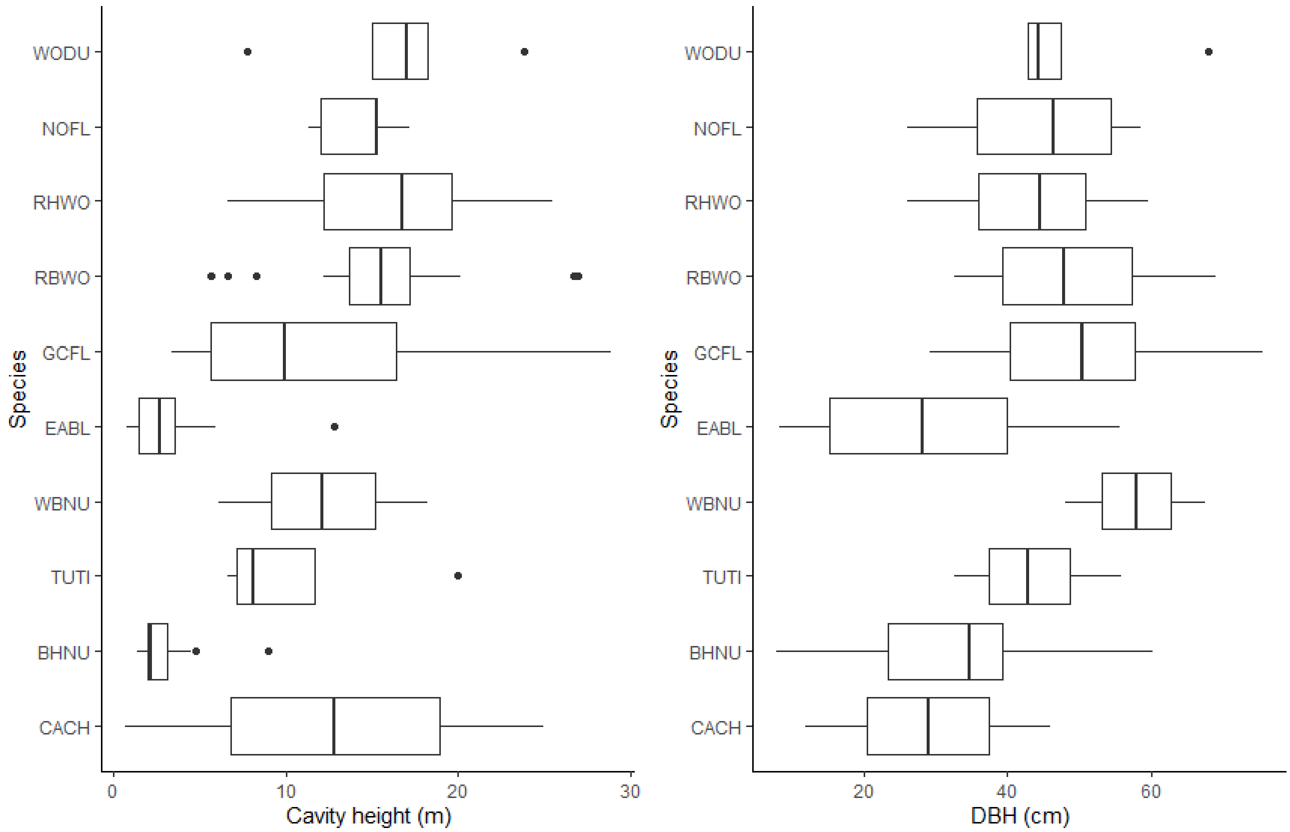

Figure 3.4. Boxplots of cavity height and diameter at breast height (DBH) measured for nests (*n* = 126) of cavity-nesting bird species (*n* = 10) in old-growth longleaf pine forests of the Red Hills. Species are arranged on the y-axis in descending order from greatest to smallest average mass (g).

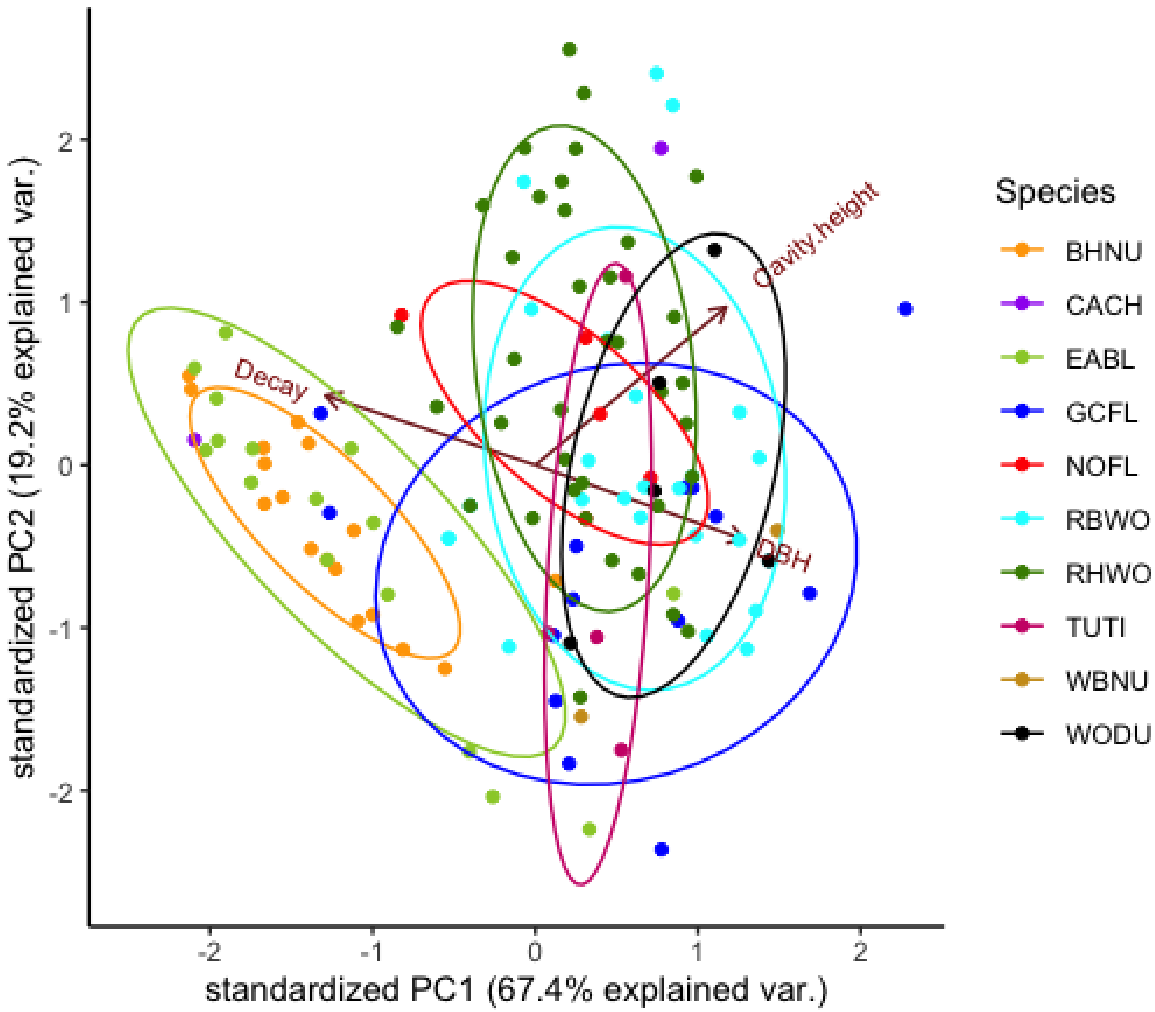

Figure 3.5. Two-dimensional ordination of the first two principal components, which included all nest cavities that were not reused between years (*n* = 126) for cavity-nesting bird species (*n* = 10). Cavity height and DBH are positively correlated with regards to the first component. Substrate and decay, unrelated to cavity height and decay class, are also positively correlated with regards to the first component.

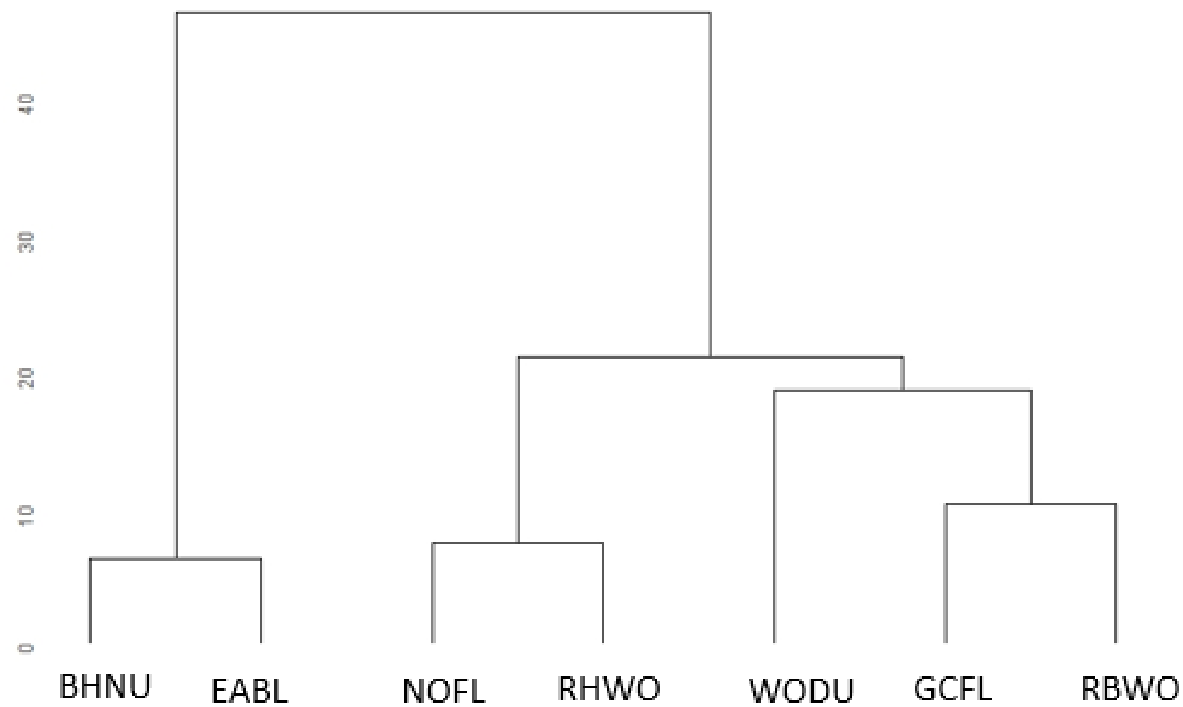

Figure 3.6. Dendrogram depicting results of a cluster analysis used to group cavity-nesting bird species (n = 7) on the basis of nest site similarities. Characteristics included median and mode decay, minimum decay, maximum decay, average DBH, minimum DBH, maximum DBH, average cavity height, minimum cavity height, and maximim cavity height. The least similar clusters have the largest distance between separating branches. Analyses included all species with ≥ 5 nests (n = 121 total nests).

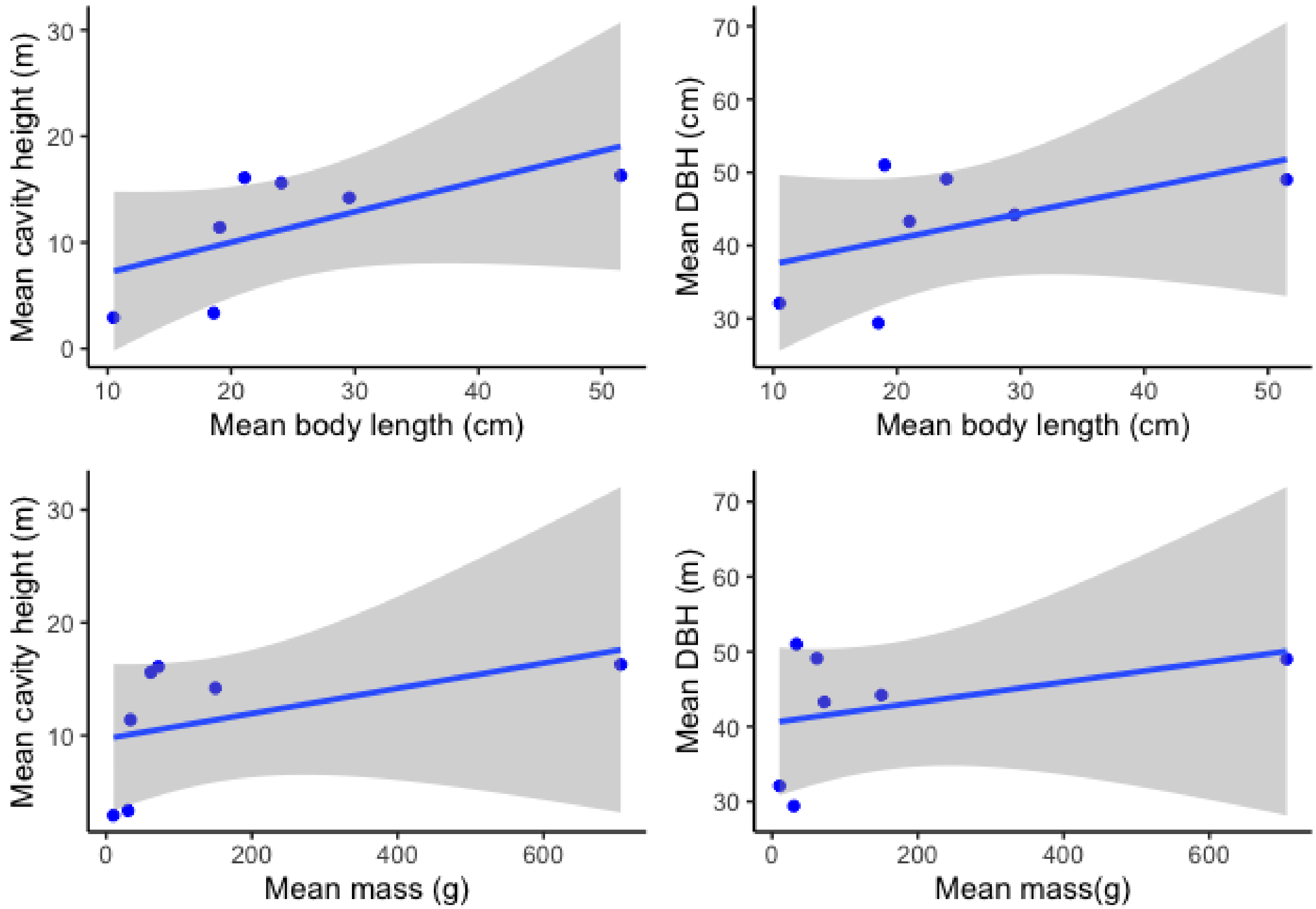

Figure 3.7. Linear regression of mean body mass and mean cavity height for 7 cavity-nesting bird species (left) and linear regression of mean body mass and mean diameter at breast height (DBH) relationships for cavity-nesting birds (right). Mean cavity height and mean DBH were recorded in 2018 and 2019 (*n* = 121 nests).

CHAPTER 4

CAUSES AND CONSEQUENCES OF RED-COCKADED WOODPECKER CAVITY USURPATION BY TWO COMMON KLEPTOPARASITES[1]

[1]Levy, H.E., Cox, J.A., Cooper, R.J. To be submitted to *Avian Conservation and Ecology*.

Abstract

The threatened Red-cockaded Woodpecker (*Dryobates borealis*) is a unique keystone excavator in mature southeastern pine (*Pinus* spp.) forests. Cavities excavated exclusively in live pine trees by Red-cockaded Woodpeckers are used by several other species as nest and roost sites. Interspecific cavity kleptoparasitism (i.e., the successful usurpation of completed cavities) can destabilize Red-cockaded Woodpecker populations because of the extended excavation time required to create suitable cavities in living pine trees. We investigated two potential drivers and recorded prevalence of Red-cockaded Woodpecker cavity kleptoparasitism in old-growth longleaf pine (*Pinus palustris*) forests of the Red Hills in southern Georgia during the breeding season of 2018 and 2019. We considered two competing but not mutually exclusive hypotheses: (1) limited local snag availability influences the frequency of kleptoparasitism events, or (2) nesting in Red-cockaded Woodpecker cavities promotes higher nest success than other types of available cavities. We related snag densities to prevalence of cavity kleptoparasitism and modeled nest success of Red-headed Woodpeckers (*Melanerpes erythrocephalus)* and Red-bellied Woodpeckers (*M. carolinus*), the two most common Red-cockaded Woodpecker cavity kleptoparasites on our sites. We pooled nest survival data from both species and related it to nest site characteristics. Proportion of kleptoparasitized cavities was relatively low overall ($\bar{x} = 0.15 \pm 0.02$) compared to similar assessments in other parts of the Red-cockaded Woodpecker's range. Snag densities and kleptoparasitism occurrences were not significantly related. The most supported model of kleptoparasite nest success included only cavity height as a predictor. Total nest success was lower in Red-cockaded Woodpecker cavities (0.35) than in snags (0.52), potentially due to differential predation from lower cavity height and inactive snake-deterrent resin wells. Results suggest that snag retention, a popular management tool, may alleviate but not

eliminate competition for Red-cockaded Woodpecker cavities. Maintaining habitat for Red-cockaded Woodpeckers will eventually provide a surplus of abandoned cavities and longstanding large snags, reducing competition over time. Our findings also suggest Red-cockaded Woodpecker cavities could serve as ecological traps for kleptoparasites if lower productivity leads to negative population growth, which may be an indirect mechanism regulating interspecific competition in the community. Further study of the potential costs and benefits of cavity kleptoparasitism is warranted, as well as potential habitat or reproductive drivers.

Introduction

Cavity-nesting bird communities interact through a hierarchical structure of primary excavators and secondary cavity-nesters, with the potential for strong interdependencies among members (Martin and Eadie 1999). Longleaf pine (*Pinus palustris*) forests host a rich assemblage of cavity-nesting species (Engstrom 1993a), but these forests have been eliminated from >95% of the original range (Outcalt and Sheffield 1996) with stands of old-growth occupying a mere 0.00014% of pre-settlement extent (Varner and Kush 2004). In old-growth longleaf pine forests, the Red-cockaded Woodpecker (*Dryobates borealis*) is a unique primary excavator that was once common throughout the Southeastern Coastal Plain, but faced large declines following extensive harvesting of pines and habitat degradation (Jackson 1971). Red-cockaded Woodpeckers play a crucial role in the cavity-nesting community as ecosystem engineers, being the only North American woodpecker to excavate cavities in live pines, the dominant substrate found within fire-maintained pine forests. Their cavities are subsequently used by over 24 species from several taxa as roost and nest sites (Harlow and Lennartz 1983, Kappes Jr and Harris 1995, Conner et al. 1997, Loeb and Hooper 1997). The unique life history and cooperative breeding system of the Red-cockaded Woodpecker is thought to be a direct product of the extended excavation time required for new cavities in live pines, which can take between 2 and 10 years. The cost of excavation is offset by the longevity of cavities in live pines (Conner and Rudolph 1995), which provide a long-lasting resource on the landscape, up to 15 years in longleaf pine trees (Harding III 1997, Conner et al. 2001). Extended excavation time and cavity availability make Red-cockaded Woodpeckers particularly vulnerable to cavity competition (Jackson et al. 1979, Conner and Rudolph 1995), especially in areas where cavities may be limiting due to population declines or reintroduction to younger forests.

Competition for cavities among the cavity-nesting bird community is driven by limitations in the number of high-quality cavities available that favor greater reproductive success (Nilsson 1984, Newton 1994). Nest characteristics that often influence fitness include microclimate, proximity to resources, and susceptibility to parasites and predators (Wiebe 2001). Competition may exclude less-dominant species from high quality cavities, though sustained competition can be frequent among similarly sized cavity-nesting birds (Martin et al. 2004). Secondary cavity-nesters are thought to face the greatest degree of nest site limitations because they cannot excavate and depend exclusively on existing cavities (Wiebe 2011). However, even primary excavators can be limited if there are too few snags of the appropriate size and stage of decay (Franzreb 1997, Schepps et al. 1999). Following the large decline of mature southeastern pinelands during the 19th and 20th centuries, overall potential for cavity competition is believed to have increased (Neal et al. 1992). Additionally, some forest management practices applied to southern pine forests feature snag removal and short harvest rotations, which further reduces overall cavity availability and exacerbates cavity competition (Blanc and Walters 2008b). Thus, cavity-nesting birds may face nest site limitations either directly through a lack of nest substrates or indirectly through competition for cavities (Wiebe 2011). Studies investigating the nest site limitation hypothesis have largely occurred in heavily managed and second growth pine stands in the southeast (eg., Scott 1979, Land et al. 1989, Caine and Marion 1991, Saab and Dudley 1998). Fewer have looked at community dynamics in old-growth systems (but see Blanc and Walters 2008a), which reflect the historic landscape of much of the southeast.

Characteristic features of old-growth longleaf pine forests include many large living trees (>50 cm diameter at breast height; hereafter DBH), large and longstanding dead trees (snags), and patchily distributed age classes. Typical old-growth characteristics develop around 120 years of age (Platt et al. 1988), and the average old-growth pine forests in Florida contain upper age classes of 100 – 350 years old (Landers and Boyer 1999). Old-growth pine snags are especially important because they can persist on the landscape for several decades and have strong influences on abundances of cavity-nesting species (Blanc and Walters 2008a). Fire-maintained pine forests are typically thought to be cavity-poor as a result of low tree, hardwood, and snag densities (Conner et al. 2001). However, old-growth forests may not be as cavity-depauperate as younger or more heavily managed forests. Mature southeastern forests that have supported sustained populations of Red-cockaded Woodpeckers for many decades contain surpluses of abandoned and enlarged Red-cockaded Woodpecker cavities that may be available for use by other cavity-nesting birds. The influence that abandoned and enlarged Red-cockaded Woodpecker cavities have on the community in old-growth settings is not well documented (Blanc and Walters 2008a).

Availability of suitable cavities for roost and nest sites is the most important limiting factor for most Red-cockaded Woodpecker populations (Ligon 1970). Cavities excavated by Red-cockaded Woodpeckers are in high demand by other species (Jackson 1978). Robust entrances and chamber walls theoretically make cavities in living pines higher quality resources than those in snags. Cavities in living pines may also host fewer parasites (Edworthy and Martin 2014). We use the term cavity kleptoparasitism throughout this paper to describe successful usurpation of Red-cockaded Woodpecker cavities by other cavity-nesting species (Kappes Jr 1997). Both primary and secondary cavity-nesting bird species usurp Red-cockaded Woodpecker cavities (Baker 1971, Jackson 1978, Harlow and Lennartz 1983, Rudolph et al. 1990a). Some kleptoparasites, such as the Pileated Woodpecker (*Dryocopus pileatus*) and Northern Flicker (*Colaptes auratus*), enlarge cavities, creating nest and roost sites for other larger secondary cavity-nesters, but enlarging almost always leads to permanent abandonment by Red-cockaded Woodpeckers (Walters 1991, Saenz et al. 1998). Other species, such as Red-headed Woodpeckers *(Melanerpes erythrocephalus)*, Red-bellied Woodpeckers *(M. carolinus)*, and southern flying squirrels *(Glaucomys volans)* are usually able to fit in un-enlarged cavities and actively compete with Red-cockaded Woodpeckers, which can reoccupy cavities that have not been expanded (Conner et al. 1997). Kleptoparasitism can negatively affect Red-cockaded Woodpeckers by preventing breeding opportunities if the nest cavity is usurped (Jackson 1978), reducing reproductive success (Ligon 1970, Jackson 1978). Additionally, interspecific cavity occupancy forces Red-cockaded Woodpeckers to roost in the open, making them vulnerable to depredation and weather (Rudolph et al. 1990a). Thus, Red-cockaded Woodpeckers exert a considerable amount of energy regularly defending their cavities (Jackson 1978). Though the frequency of kleptoparasitism is well documented across their range, less is known about drivers that influence these processes.

It would seem logical that greater densities of nest sites would result in reduced competition. For avian kleptoparasites, some recommend retaining high snag densities or adding artificial nest boxes to alleviate cavity competition by increasing nest sites available for competitors (Jackson 1978, Kappes Jr and Harris 1995, Loeb and Hooper 1997, Davis et al. 2005, Blanc and Walters 2008a), but this may just lead to overabundances of competitors that will eventually move into Red-cockaded Woodpecker cavities. Other studies have found very weak or no relationship between snag densities and kleptoparasitism, indicating a potential preference for nesting in Red-cockaded Woodpecker cavities (Harlow and Lennartz 1983, Everhart et al. 1993), but this hypothesis has not been well studied. Conversely, Blanc and

Walters (2008a) have suggested nesting advantages in snags over Red-cockaded Woodpecker cavities for some cavity nesting species based on occupancy rates alone.

We propose two ecological questions to investigate factors that may influence cavity kleptoparasitism in this system: (1) what habitat characteristics drive kleptoparasitism, and (2) what are the benefits of cavity kleptoparasitism over excavation? We studied usurpation of Red-cockaded Woodpecker cavities in old-growth longleaf pine forests of the Red Hills region of southwest Georgia. We formed two alternative but not mutually exclusive hypotheses: (1) Red-cockaded Woodpeckers in habitats with low snag densities would experience greater rates of cavity kleptoparasitism, which would suggest that nest site limitation drives kleptoparasitism. Alternatively, (2) nesting in Red-cockaded Woodpecker cavities promotes an advantage over nesting in snags because of cavity durability, suggesting that reproductive potential drives kleptoparasitism. We compared nest success of Red-headed Woodpeckers and Red-bellied Woodpeckers in Red-cockaded Woodpecker cavities and in cavities in snags, as these species were abundant on our study sites and were common Red-cockaded Woodpecker cavity competitors (Kappes Jr and Harris 1995, Kappes Jr 1997, DeLotelle et al. 2018). Additionally, as facultative kleptoparasites, they have the option to excavate cavities if there are suitable substrates, making them ideal candidates to better understand nest site limitations. Studying patterns of nest site limitation and use are critical to understand population ecology and evolution, especially how nest site use affects interspecific interactions (Lindell 1996). Last, we explore management implications of this research regarding the benefits of snag retention in these systems.

Methods

Study Area

The Red Hills physiographic region of northwest Florida and southwest Georgia encompasses an approximately 100,000 ha area that supports one of the largest populations of Red-cockaded Woodpeckers on private lands and the sixth largest population overall. Here, Red-cockaded Woodpeckers exist exclusively on private lands under conservation easements, where prescribed burning and sustainable timber salvaging are standard management practices, creating some of the best remaining examples of old-growth longleaf pine forests (Cox et al. 2001). To investigate cavity kleptoparasitism, we conducted fieldwork during the breeding season of 2018 and 2019 across 4 privately owned old-growth longleaf pine plantations in the Red Hills region: Greenwood Plantation, Melrose Plantation, Sinkola Plantation, and the Wade Tract of Arcadia Plantation. All sites are fire-maintained on a 1-2 year return interval, promoting an open forest structure and canopy, and consist predominately of longleaf pine in the over-story and fire-adapted grasses, such as wiregrass (*Aristida stricta*) and other herbaceous plants in the understory. Greenwood, located near the Ochlochnee River, is more mesic, containing forest floor species such as royal ferns (*Osmunda regalis*) and hooded pitcher plants (*Sarracenia minor*). Sinkola, Melrose, and the Wade Tract are more xeric and representative of the typical longleaf savanna. Greenwood, Melrose, and Sinkola are subject to varying degrees of sustainable timber salvaging and are managed for Northern Bobwhite (*Colinus virginianus*), which sometimes includes removal of snags used by avian predators. Thus, these sites were expected to contain lower snag densities than the Wade Tract, an old-growth preserve that is not subject to any management other than prescribed fire. We established eight 20 ha plots within the four plantations (*n* = 1 on Melrose and Sinkola, *n* = 4 on Greenwood, and *n* = 2 on the Wade Tract) for snag density sampling and nest searching and monitoring.

Snag and Red-cockaded Woodpecker Cavity Sampling

Within each of the 20 ha plots, we randomly placed ten 0.5 ha subplots that totaled one fourth of the plot area. We visited each subplot once in each year and recorded all snags present. We defined snags as standing dead trees with a minimum DBH of 10 cm and a minimum height of 1 meter. We averaged snag counts from each subplot to estimate snag density for each plot. We recorded snags in both 2018 and 2019 to investigate the influence of a major storm event; Hurricane Michael swept through as a category 3 storm in October 2018. Because we believed snag densities would decrease between years from extreme winds, it offered an opportunity to examine potential increases in kleptoparasitism if it were related to cavity density. As part of a monitoring study of the Red Hills population, Red-cockaded Woodpecker cavities are inventoried and catalogued on a recurring basis (Cox et al. 2001). The most recent inventory was completed in 2018. We determined cavity density by dividing the total number of cavities in each plot by the plot area.

Nest Searching and Nest Monitoring

In the breeding season of 2018 and 2019, we searched all plots for nests on a weekly basis and recorded all instances of heterospecific species occupying Red-cockaded Woodpecker cavities. Fieldwork in 2018 began in early May and fieldwork in 2019 began in early March to include earlier cavity-nesting species, such as Tufted Titmice (*Baeolophus bicolor*) and White-breasted Nuthatches (*Sitta carolinensis*), which are both cavity competitors of Red-cockaded Woodpeckers (Conner et al. 1997). We established 2-3 line transects for nest searching (depending on plot shape) that ran the length of each plot and were spaced ≥ 200 m apart. We used behavioral cues to detect nests, including nest defense, lining cavities, excavating, provisioning of mates or young, and removal of fecal sacs. Frequently, the observer strayed from the transect lines to pursue suspected nests, but the entirety of each plot was sampled during each visit.

Monitoring of Red-headed Woodpecker and Red-bellied Woodpecker nests occurred in the breeding season of 2019. Once nests were located, we monitored them on a 2-6-day interval. For nests where the cavity was less than 13.5 m in height, we used a wireless peeper camera (http://www.ibwo.org, North Little Rock, Arkansas, USA) mounted to a telescoping pole to investigate contents inside the cavity. For nests above 13.5 m, we conducted 15-25-minute behavioral observations to determine nesting status. Nests were considered failed if young were missing from the cavity at too young of an age to have fledged, if dead young were seen, or, for taller cavities, if the parents had not been seen visiting the cavity or acting defensively near the cavity on at least three consecutive observation days. Young were considered fledged if they were seen within 10 meters of the nest cavity on or soon after the suspected fledging date. We checked nests for fledglings at least three times before classifying the nest as failed. For each cavity nest tree, we measured the decay class, cavity and tree heights using a clinometer, DBH, and visually estimated the amount of bark remaining.

Data Analysis

We performed all descriptive statistics and analyses with RStudio (RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA), a wrapper for program R (R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/). We used a paired t-test to compare snag densities within plots between 2018 and 2019. We used two one-way analysis of variance (ANOVA) tests to assess differences in snag abundances in both years among sites followed by a post-hoc Tukey's honest significance test to identify differences between sites. Linear regression was used to examine the relationship between snag density on each plot and the proportion of Red-cockaded Woodpecker cavities usurped each year compared to the total number of available cavities. Proportions were transformed using the arcsine of the square root. A second linear regression was used to compare differences in snag densities and differences in kleptoparasitism occurrences between years to investigate post-hurricane effects.

We pooled nesting data to model nest success for Red-headed Woodpeckers and Red-bellied Woodpeckers since they are morphologically similar congeners (Ingold 1989) that are both common Red-cockaded Woodpecker cavity usurpers. We chose 5 nest site characteristics to measure as covariates: substrate (Red-cockaded Woodpecker cavity or snag), decay class, cavity height, tree height, and percent of bark remaining. Using measured nest site characteristics, we created a set of candidate models (Table 4). Generalized linear models with a logit link function in R (R library MASS, function logexp) were used to estimate daily survival and nest success (Hazler 2004, Shaffer 2004). The response variable was survival, and we specified the logit link function to restrict survival probabilities between 0 (nest failed) and 1 (nest survived), and to incorporate exposure days into survival probabilities (Hazler 2004). Covariates in the model were treated as fixed effects. We used an information-theoretic approach to rank a fully parameterized global model, its reduced forms, and a null model with Akaike's Information Criterion corrected for small sample size (AIC_c) and calculated the ΔAIC_c. The ΔAIC_c is the difference between the model with the lowest ΔAIC_c and each candidate model. Generally, ΔAIC_c scores between 0-2 represents significant model support, 4-7 represents less substantive support, and greater than 10 represents no support (Burnham and Anderson 2002). We calculated an 85% confidence interval for models with $\Delta AIC_c < 2$ (Arnold 2010).

To calculate nest survival, we estimated the number of days for the total nesting period from the literature and raised daily survival rate estimates to that power. For Red-bellied Woodpeckers, the incubation period lasts approximately 12 days from the laying of the last egg until hatchling of first egg in the clutch (Kilham 1961, Boone 1963, Jackson 1976) and fledging occurs 24-27 days after hatching (Kilham 1961). Incubation of Red-headed Woodpeckers lasts 12-14 days (Forbush 1925, Bent 1939, Skutch and Gardner 1985) and fledging occurs between 24 and 31 days after hatching (Bent 1939, Skutch and Gardner 1985). Thus, we used 38 days as an approximate estimate for total nesting period (Hudson and Bollinger 2013).

Results

Snags and Red-cockaded Woodpecker Cavity Kleptoparasitism

Snag densities within plots varied between 0.4 and 6.6 (mean ± SE, $\bar{x} = 2.45 \pm 0.56$) snags/ha in 2018 and 0.4 and 6.2 snags/ha in 2019 ($\bar{x} = 2.18 \pm 0.67$; Figure 4.1). Snag density was significantly lower in 2019 than in 2018 ($t_7 = 4.23$, $P = 0.003$), and snag densities were significantly different among sites in both 2018 ($F_{7,72} = 4.86$, $P < 0.001$) and 2019 ($F_{7,72} = 7.37$, $P < 0.001$). Most significant differences occurred between the Wade Tract and all other sites (Table 4.1). Red-cockaded Woodpecker cavity densities within each plot varied between 0.7 and 2.1 cavities per ha (Figure 4.2).

We recorded cavity usurpation by 7 avian species, in which Red-bellied Woodpeckers and Red-headed Woodpeckers were the most common kleptoparasites (Table 4.2). The proportion of cavities occupied by kleptoparasites varied between 0.03 and 0.31 in 2018 ($\bar{x}$ =

0.13 ± 0.03) and 0.07 and 0.25 in 2019 ($\bar{x}$ = 0.17 ± 0.04). In both years we found no relationship between snag densities and proportion of Red-cockaded Woodpecker cavities usurped (2018: R^2 = 0.007, $F_{1, 6}$ = 0.045, P = 0.84), (2019: R^2 = 0.003, $F_{1, 6}$ = 0.018, P = 0.90; Figure 4.3). Despite lower snag densities in 2019 post-hurricane, there was no relationship between the difference in snag densities and the difference in kleptoparasitism occurrences (R^2 = 0.027, $F_{1, 6}$ = 0.168, P = 0.70; Figure 4.4).

Red-headed Woodpecker and Red-bellied Woodpecker Nest Success

We located and monitored a total of 34 Red-headed Woodpecker and Red-bellied Woodpecker nests in the breeding season of 2019. For analyses, we only included the 27 nests for which fates were known (16 Red-headed Woodpeckers and 11 Red-bellied Woodpeckers). All nests occurred in live or dead longleaf pine trees. Of the 27 nests we monitored, 13 were in Red-cockaded Woodpecker cavities and 14 were in snags. Some of the nests in Red-cockaded Woodpecker cavities may have occurred in enlarged or abandoned cavities, but we included all nests because we wanted to estimate kleptoparasitism across the study area and determine the relative usage and importance of these cavities to other species. Because we used behavioral cues to determine nest stages for most of the nests, specific causes of failure for most could not be determined. Of the 27 nesting attempts, 14 nests (51.8%) failed to fledge at least one young. For nests that could be visually assessed, we had five cases of failure that could be inspected, of which we suspect two were due to snake predation (nest was completely empty), one due to another woodpecker or flying squirrel (broken egg shells were leftover), and two due to food availability or inexperienced parents (young dead inside the nest with no sign of predation attempts).

We pooled Red-bellied Woodpecker and Red-headed Woodpecker nest data for analyses to fit and rank 10 candidate models (Table 4.3). Of the 10 candidate models, the most supported model had 83.4% of the weight (Table 4.4), suggesting strong support (Burnham and Anderson 2002). That model had a main effect of cavity height, which positively influenced nest survival rates. Cavities that survived tended to be in higher nests (18.6 ± 3.27 m; $\bar{x}$ ± SD) than nests that failed (12.3 ± 3.91 m; Figure 4.5). The next top model (w_i = 0.09) was the global model, which contained all covariates. Although the model containing the interaction of cavity height and substrate had $\Delta AIC_c > 2$, it is important to note that Mayfield estimates of nest survival were substantially lower in Red-cockaded Woodpecker cavities (0.347) than in snags (0.512). Additionally, nests in Red-cockaded Woodpecker cavities tended to be lower in height (14.6 ± 2.88 m) than nests in snags (16.5 ± 5.92 m).

Red-bellied Woodpeckers had very low nest success compared to Red-headed Woodpeckers in our study. Our estimates of Red-headed Woodpecker nest success (0.61) fall within range of estimates derived (0.58-0.68) from other studies (Hudson and Bollinger 2013, Frei et al. 2015). However, Red-bellied Woodpecker nest success (0.11) was considerably low in our study compared to other studies (0.75-0.91; Johnson and Kermott 1994, Straus et al. 2011). Of Red-bellied Woodpecker nests monitored, 9 out of 11 occurred in Red-cockaded Woodpecker cavities, whereas only 4 out of 16 Red-headed Woodpecker nests occurred in Red-cockaded Woodpecker cavities.

Discussion

Cavity kleptoparasitism is a well-documented example of the complex interspecific interactions that take place within cavity-nesting bird communities. We tested two competing but not mutually exclusive hypotheses to explain cavity kleptoparasitism: (1) limited snag availability for nesting would influence kleptoparasitism occurrences, and (2) nesting in Red-cockaded Woodpecker cavities provides an advantage for usurpers, especially those that are facultative kleptoparasites. We did not find a relationship between snag density and kleptoparasitism. Both Red-bellied Woodpeckers and Red-headed Woodpeckers used Red-cockaded Woodpecker cavities despite abundant snags in sites like the Wade Tract, suggesting a potential preference for Red-cockaded Woodpecker cavities. Overall, avian cavity kleptoparasitism in both years was relatively low on our sites. The most supported model influencing nest success of the two most common kleptoparasites, Red-headed Woodpeckers and Red-bellied Woodpeckers, was cavity height, with nest survival increasing with cavity height. However, nest success in Red-cockaded Woodpecker cavities was substantially lower than in cavities in snags, suggesting they may be poor nest sites for kleptoparasites.

Influence of Snags and Nest Site Limitation

Fire-maintained pine forests are thought to be cavity-impoverished (Conner et al. 2001). Blanc and Walters (2007) reported densities of 5.2 – 8 snags/ha but considered these estimates to be atypically high. However, we report densities of up to 6.6 snags/ha in a fire-maintained, old-growth preserve. Red-cockaded Woodpecker cavities provide additional cavity resources that are typically not considered when assessing cavity-resources in pine systems. Original longleaf pine landscapes were probably not as cavity depauperate as many suggest. In fact, the number of abandoned Red-cockaded Woodpecker cavities historically available was considerable (Leonard Jr 2005) and competition for these cavities may have been mitigated by a large number of cavities in persistent snags and dead portions of live pines in old-growth forests (Davis 1931, Doren et al. 1993, Landers and Boyer 1999).

Cavity kleptoparasitism is thought to be strongly influenced by habitat quality, cavity availability, and population size; maintaining desired habitat conditions for Red-cockaded Woodpeckers, including promoting open, forests with prescribed fire and allowing maturation of pines will increase cavity availability in the long-term (Neal et al. 1992). Our sites are old-growth, open canopy pine stands with similar forest structure and mainly vary in snag and Red-cockaded Woodpecker densities. Reported kleptoparasitism rates by all species can be quite high, up to 46% in both South Carolina (Dennis 1971) and Texas (Rudolph et al. 1990a). Because of our sampling methods, we did not detect occupancy by flying squirrels. However, our average avian kleptoparasitism rate of 15% is still substantially lower than reported rates of 27% in South Carolina (Harlow and Lennartz 1983). In our study, we did not find a relationship between snag densities and kleptoparasitism, however all our sites had ≥ 0.4 snags per ha. In areas with more intense salvaging that results in even fewer snags, there is the potential for more severe nest site limitations, which might influence kleptoparasitism. This could be expected as nest site shortages tend to be more severe in regions of intensive management (Newton 1994). We recommend snag retention or creation in areas that may be extremely snag limited to provide additional nest sites.

Between 2018 and 2019, a category 3 hurricane hit the Red Hills. Cavity-nesting birds requiring large, mature trees and snags are particularly susceptible to hurricane effects (Wiley and Wunderle 1993). Despite lower snag densities following the hurricane, kleptoparasitism events did not significantly change between years, further suggesting that snag retention may alleviate, but not eliminate, kleptoparasitism. Although snag densities were lower in 2019, several live trees died during the hurricane from extreme winds. These trees may become suitable for woodpecker excavation in 3-8 years once the wood softens (Bull 1983), possibly resulting in minimal net losses of snags over time. Additionally, the loss of limbs on live trees and snags may create cavities or provide excavation opportunities for primary excavators (Torres and Leberg 1996). Strong disturbances therefore can both destroy and create snags, creating complex snag dynamics that are difficult to predict.

Nest Success of Cavity Kleptoparasites

Cavity height was the most important factor in determining nest success for Red-headed Woodpeckers and Red-bellied Woodpeckers. Cavity height is a critical factor that positively influences nest success in Red-headed Woodpeckers (Hudson and Bollinger 2013) and other cavity-nesting species (e.g., Rendell and Robertson 1989, Li and Martin 1991, Albano 1992). Increased predation from ground-dwelling species is often linked to lower nest success in lower cavities, presumably because they are easier to access than higher cavities (Nilsson 1984, Li and Martin 1991). Red rat snakes (*Pantherophis guttatus*) and grey rat snakes (*P. spiloides*) are common throughout the region and are one of the most frequent predators of cavity-nesting birds (Miller 2000, Kappes Jr and Sieving 2011). Experiments with grey rat snakes have shown that they are highly visual predators capable of perceiving nest provisioning that would allow them to preferably climb trees with active nests (Mullin and Cooper 1998). In Florida and southern Georgia pine forests, nest success of some cavity-nesting species is lower than that of their counterparts in northern regions, which has been attributed to high rates of snake predation (Miller 2000). Nests at lower heights, even those with smooth surfaces, are risky because the benefit of a potential prey item may outweigh the risk of falling (Hudson and Bollinger 2013).

We hypothesize the trend of lower nest success in Red-cockaded Woodpecker cavities may relate to differential nest predation by ground-oriented predators, specifically rat snakes based on cavity height and the drying of the snake-deterrent resin barrier on Red-cockaded

Woodpecker cavities. Rat snakes readily climb live trees, but Red-cockaded Woodpeckers have adapted to this predator by developing and maintaining an active resin barrier around the cavity hole that deters snakes (Jackson 1974). Several resin wells are associated with each cavity and are worked regularly so that copious resin flow persists, reducing accessibility by rat snakes (Ligon 1970, Dennis 1971). Red-cockaded Woodpeckers will also scale bark above and below the cavity entrance, producing a smooth surface that is difficult for snakes to climb (Rudolph et al. 1990b). Kleptoparasites do not maintain these barriers, and once a Red-cockaded Woodpecker no longer maintains the resin barrier, it dries within days and can make the usurper more susceptible to rat snake predation (Kappes Jr and Sieving 2011). Kappes Jr and Sieving (2011) found that Great Crested Flycatchers and Red-bellied Woodpeckers nesting in Red-cockaded Woodpecker cavities had higher rates of nest predation than nests in snags, which suggests that rat snakes potentially have an indirect positive effect for Red-cockaded Woodpeckers by depredating kleptoparasites more frequently and subsequently increasing cavity availability. It has been proposed that kleptoparasites may target Red-cockaded Woodpecker cavities with an active resin barrier to deter rat snake predation, (Kappes Jr and Sieving 2011), but this barrier would only serve its purpose for a short time and would not last the duration of the incubation stage. Conversely, rat snakes have difficulty climbing snags without bark, which have fewer surface irregularities (David 2009); increased bark smoothness negatively affects grey rat snake climbing ability in hardwood forests (Mullin and Cooper 2002). Red-headed Woodpeckers excavate cavities in bark-less snags in parts of their range (Ingold 1989), which may be a mechanism to lower nest depredation by rat snakes (Withgott 1994). The especially low nest success of Red-bellied Woodpeckers observed here stems in part from increased predation events in Red-cockaded Woodpecker cavities.

Conclusions, Implications, and Future Directions

Southern pine forests support a diverse community of cavity-nesting birds (Engstrom 1993b). Sites managed for Red-cockaded Woodpeckers promote more diverse and abundant avian populations than do mature forest sites without Red-cockaded Woodpeckers (Conner et al. 2002). The loss of high-quality old-growth habitat associated with Red-cockaded Woodpeckers has been linked to population declines in White-breasted Nuthatches (Leonard Jr 2005) and American Kestrels (*Falco sparverius*; Gault et al. 2004). These pinelands are also high-quality habitat for Red-headed Woodpeckers (Shackelford and Conner 1997), a species of conservation concern, and for a much broader avian community (Engstrom 1993a). In managed forests, snag retention is a useful management tool to alleviate competition by providing additional nest sites and promoting biodiversity (Hansen et al. 1991). Our results suggest that old-growth pine forests with abundant cavity resources (i.e., snags of various decay classes and Red-cockaded Woodpecker cavities) may alleviate nest site limitation and mitigate interspecific competition. In unmanaged, old-growth systems, the role of other ecological and environmental factors such as food supply and predation may be more important than cavity-availability in limiting cavity-nesting densities (Walankiewicz 1991, Wesołowski and Stawarczyk 1991, Newton 1994, Lõhmus and Remm 2005, Remm et al. 2006, Aitken and Martin 2007).

Kleptoparasitism of nest cavities from the standpoint of the usurper remains a relatively understudied aspect of avian ecology, especially for facultative kleptoparasites. There may be other environmental or biological drivers that were not tested in this study that drive kleptoparasitism, including microhabitat selection by Red-cockaded Woodpeckers that make their nest sites higher quality areas, or potential energy savings by circumventing costs of excavation. Because the costs and benefits of cavity kleptoparasitism are relatively unknown, if we liken cavity kleptoparasitism to cavity reuse, benefits over excavation may include earlier laying dates, larger clutches, and better body condition (Wiebe et al. 2007). For example, we observed a Red-bellied Woodpecker that nested in a Red-cockaded Woodpecker cavity and triple-brooded, a rare occurrence (Breitwisch 1977), though it failed each time.

A large focus of Red-cockaded Woodpecker management today focuses on preventing kleptoparasitism by expensive mechanical and labor intensive means, such as outfitting artificial nest boxes used to supplement population numbers with metal restrictor plates that prevent enlargement of cavity entrances (Carter et al. 1989). However, these plates only provide short-term success unless they are routinely managed and replaced (Wood et al. 2000) and cannot effectively exclude similarly sized competitors (Walters et al. 2004). Capsaicin, which evokes a burning sensation in mammals is an effective method to deter flying squirrels from cavities but requires repeated application (Meyer and Cox 2019). Kleptoparasites that do not enlarge or destroy cavities may pose only minor demographic effects on Red-cockaded Woodpeckers (Walters et al. 2004). Because Red-cockaded Woodpeckers can reuse the cavity, the period of competition is temporary. Competitors that enlarge cavities may limit the number of suitable cavities available for Red-cockaded Woodpeckers. We did not monitor Red-cockaded Woodpecker nest success on our sites, but based on long-term data, the Red Hills population is stable (J. Cox, Tall Timbers Research Station, unpublished data), suggesting that cavity competition has not negatively affected overall population growth. Though preventing competition is a large emphasis of Red-cockaded Woodpecker management, populations of kleptoparasites may be kept in check if Red-cockaded Woodpecker cavities pose an ecological trap relative to cavities in snags bereft of bark due to rat snake nest predation. This suggests that anti-snake management could result in unanticipated consequences if rat snakes indirectly positively affect Red-cockaded Woodpeckers (Kappes Jr and Sieving 2011). Although competitive interactions may be pervasive and important influences of Red-cockaded Woodpecker population dynamics in younger and more heavily managed pine forests where cavity resources are low, overall competition for cavities appears to be low in old-growth systems. Our findings warrant future work examining both environmental and ecological factors that drive kleptoparasitism as well as the influences and outcomes of differential nest success and the cost and benefits that influence cavity kleptoparasitism in this community.

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Tables

Table 4.1. Significant pairwise differences in snag density estimates between study plots (n = 8) across four private longleaf pine plantations in the Red Hills region of southwest Georgia in 2018 and 2019. Only pairs with significant differences in snag densities are included.

Pair	Difference in means	Lower Confidence Interval	Upper Confidence Interval	Adjusted P Values
WTW – GWNE	3.50	0.559	6.44	0.020
WTW – GWNW	3.90	0.959	6.84	0.010
WTE – GWSE	3.80	0.859	6.74	0.012
WTW – GWSE	4.90	1.96	7.84	0.002
WTE – GWSW	3.10	0.159	6.04	0.038
WTW – GWSW	4.20	1.26	7.14	0.007
WTE – MELR	4.80	1.86	7.74	0.003
WTW – MELR	5.90	2.96	8.84	<0.001
WTE – SINK	4.50	1.56	7.44	0.004
WTW – SINK	5.60	2.66	8.54	<0.001

Table 4.2. Occurrences of cavity-nesting species (n = 7) using Red-cockaded Woodpecker cavities in 2018 and 2019 across 4 private longleaf pine plantations in the Red Hills of southwest Georgia.

Species	Occupied in 2018	Occupied in 2019
Great Crested Flycatcher	4	4
Northern Flicker	2	1
Red-bellied Woodpecker	7	14
Red-headed Woodpecker	8	5
Tufted Titmouse	1	2
White-breasted Nuthatch	0	1
Wood Duck	2	3

Table 4.3. Candidate logistic exposure nest success models for Red-headed Woodpeckers and Red-bellied Woodpeckers based on nest site characteristics.

Model	Variables
Null	None
Differential species success	Species (Red-headed versus Red-bellied)
Substrate only	Substrate*(snag versus Red-cockaded Woodpecker cavity)
Species and substrate	Species + substrate
Nest site characteristics	Substrate + cavity height + tree height + DBH + %bark + decay
Tree decay	Decay + %bark
Cavity height	Cavity height
Decay and bark	Decay + bark
Cavity height * substrate	Cavity height*substrate (snag vs Red-cockaded Woodpecker cavity)
Global	All covariates included

*Nests in dead Red-cockaded Woodpecker cavity trees (*n* = 3) were treated as snags in the analysis

Table 4.4. Ranked logistic exposure nest success models results for nests (*n* = 27) of Red-bellied Woodpeckers (*n* = 11) and Red-headed Woodpeckers (*n* = 16). Akaike's information criterion (AICc; c = corrected for small sample size) was used to rank candidate models.

Model	Log likelihood	AIC_c	ΔAIC_c	Weight
Cavity height	-16.7	37.9	0.00	0.834
Global	-9.22	42.4	4.53	0.086
Cavity height*substrate	-16.5	42.8	4.89	0.072
Nest site characteristics	-16.0	48.1	10.2	0.005
Species only	-22.9	50.4	12.5	0.002
Substrate and species	-22.7	52.6	14.7	0.001
Null	-26.1	54.4	16.7	0.000
Substrate only	-25.6	55.7	17.8	0.000
Tree decay	-25.7	55.9	18.0	0.000
Decay class and bark	-25.7	58.2	20.5	0.000

Figures

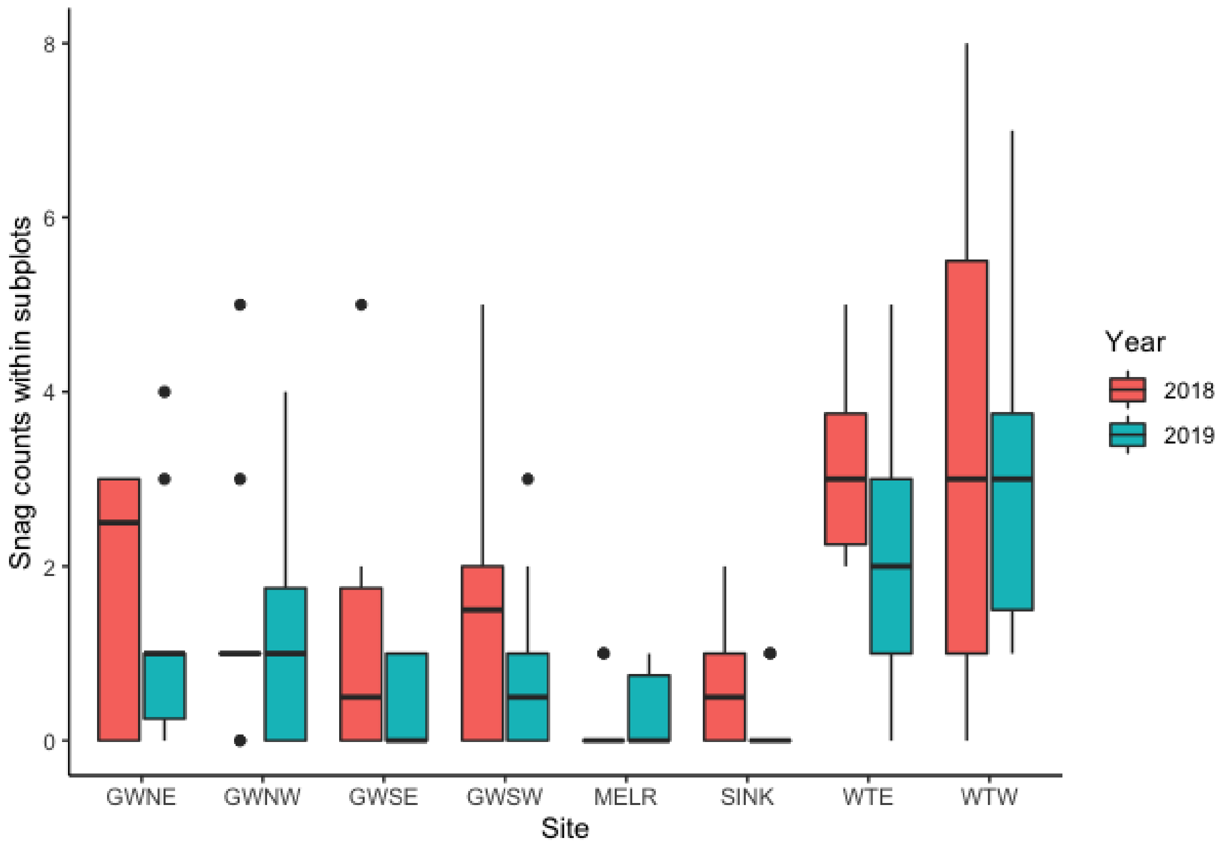

Figure 4.1. Number of snags recorded per plot in 2018 and 2019 within subplots (*n* = 10 each) recorded across sites (*n* = 8). Acronyms for subplots are as follows: GWNE = Greenwood northeast, GWNW = Greenwood northwest, GWSE = Greenwood southeast, GWSW = Greenwood southwest, MELR = Melrose, SINK = Sinkola, WTE = Wade Tract east, WTW = Wade Tract west.

Figure 4.2. Red-cockaded Woodpecker (RCWO) cavity densities on each plot (*n* = 10).

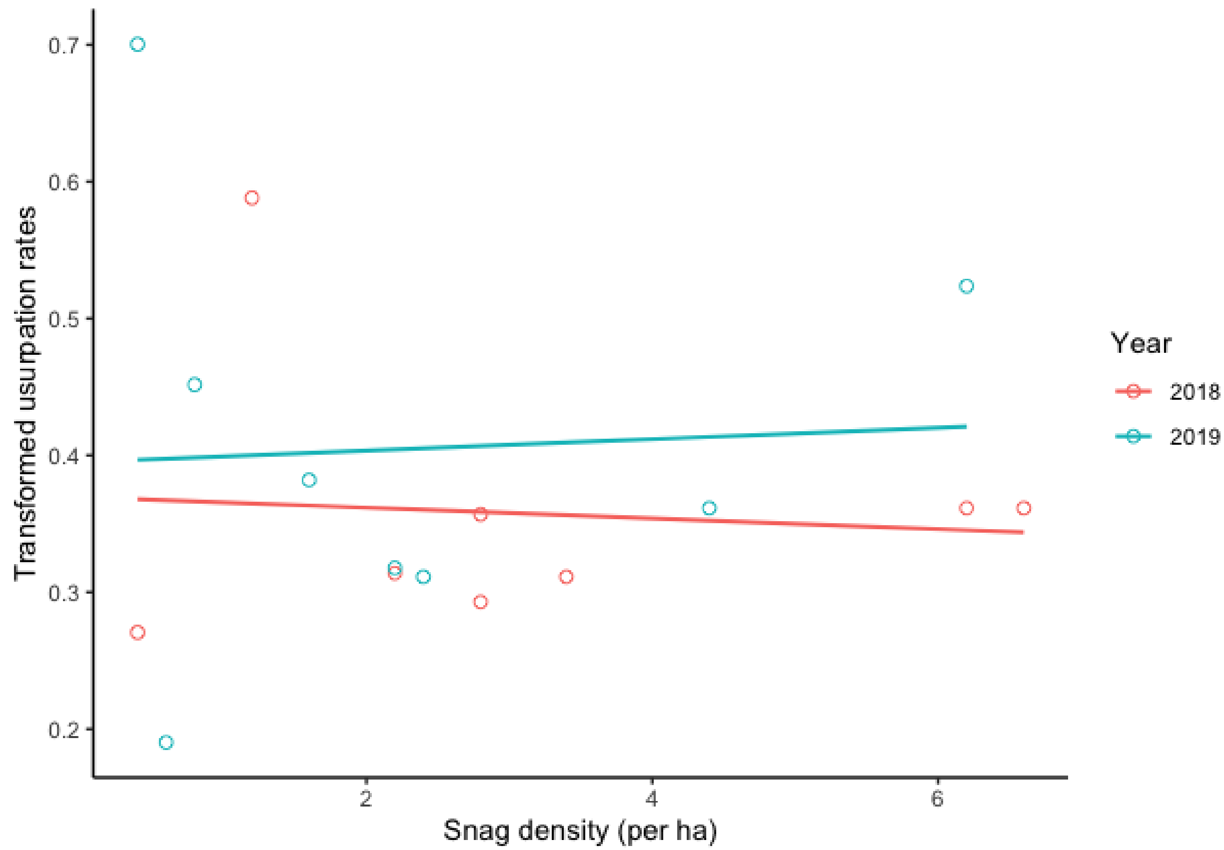

Figure 4.3. Linear regression of Red-cockaded Woodpecker kleptoparasitism rates and local densities. Relationships were not significant in either in 2018 ($R^2 = 0.007$, $F_{1, 6} = 0.045$, P = 0.839) or in 2019 ($R^2 = 0.003$, $F_{1, 6} = 0.018$, P = 0.898). Kleptoparasitism was calculated as the number of cavities occupied by heterospecific species divided by the total number of cavities available. Proportion rates were transformed using the square root of the arcsine.

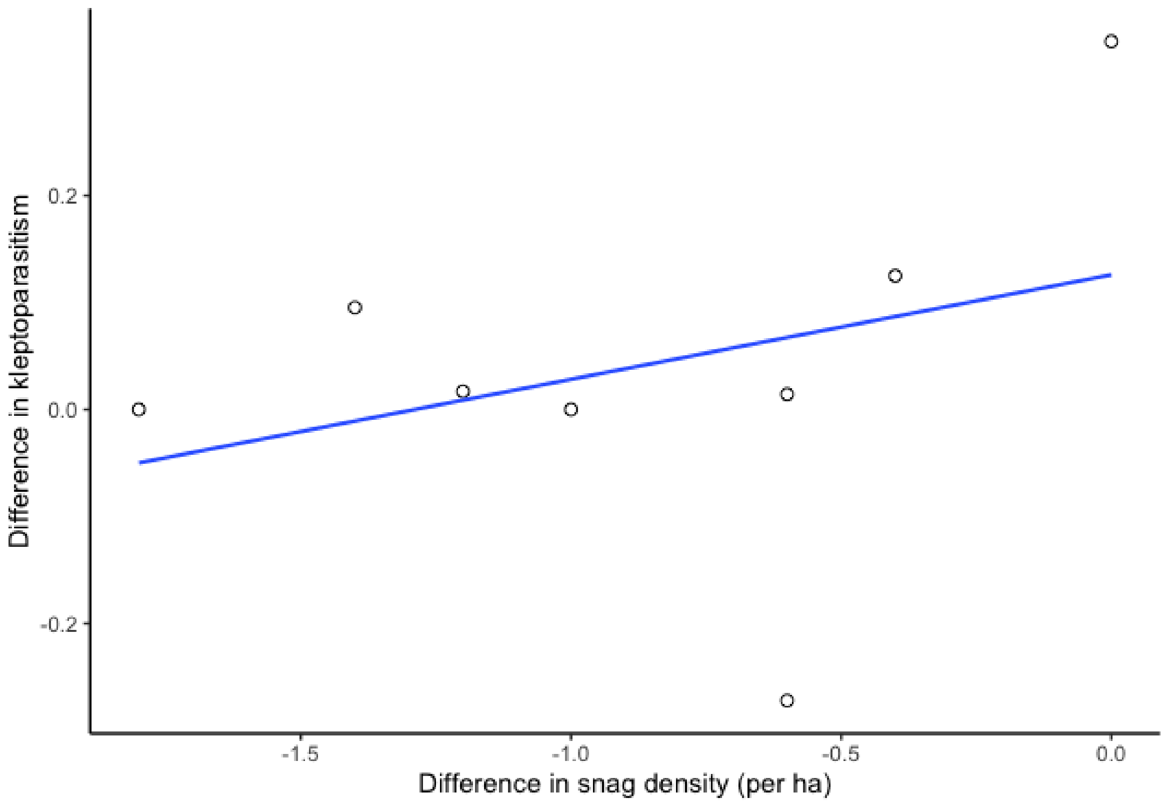

Figure 4.4. Linear regression of the relationship between differences in snag densities and differences in Red-cockaded Woodpecker cavity kleptoparasitism rates between years. Despite an overall decrease in snag densities, there was no significant difference in kleptoparasitism rates (R^2 = 0.11, $F_{1, 6}$ = 0.76, P = 0.42).

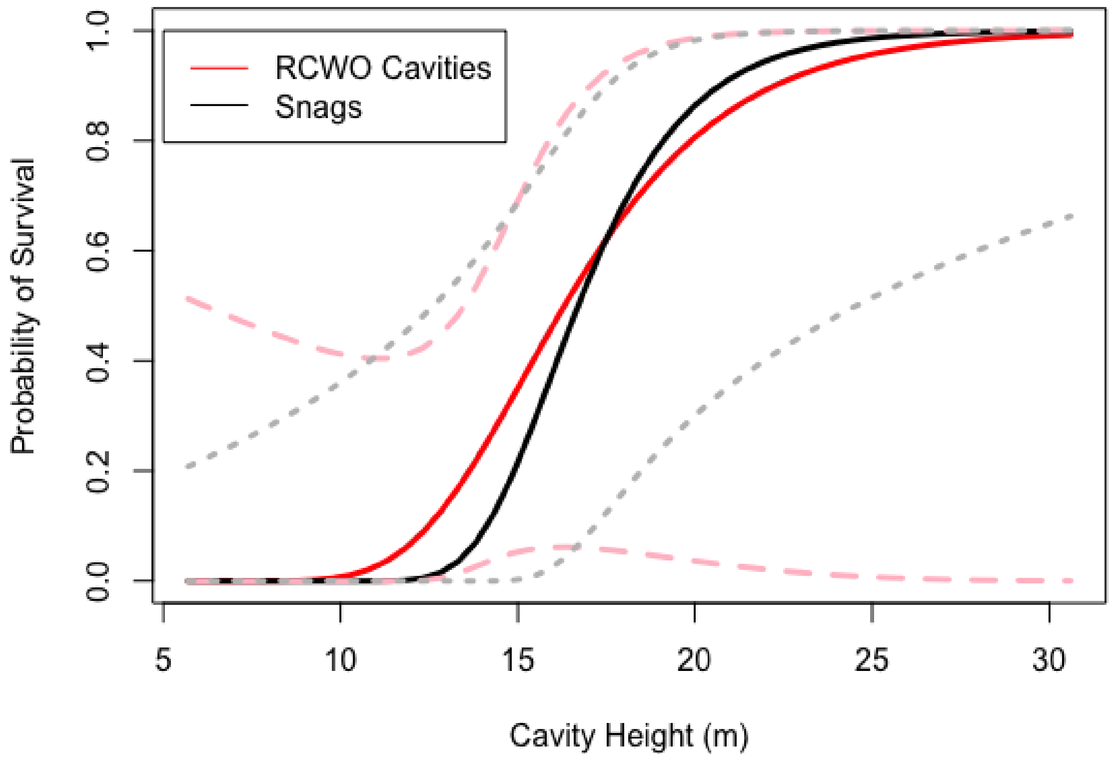

Figure 4.5. Combined Red-headed Woodpecker (*n* = 16) and Red-bellied Woodpecker (*n* = 11) nest success in Red-cockaded Woodpecker (RCWO) cavities and in snags in relation to cavity height. Gray dotted lines represent 85% confidence intervals for nest success in snags and red dotted lines represent 85% confidence intervals for nest success in Red-cockaded Woodpecker cavities.

CHAPTER 5

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Broadly, the goal of this thesis was to study the cavity-nesting bird community inhabiting old-growth longleaf pine forests of the Red Hills region, especially in relation to an endemic keystone excavator, the Red-cockaded Woodpecker (*Dryobates borealis*). This work presents the first such assessment of the cavity-nesting bird community in old-growth longleaf pine forests of the Red Hills physiographic region. We hypothesized generally that cavity-nesting bird dynamics would be influenced by the high density of Red-cockaded Woodpecker cavities on the study sites. The specific objectives were to: (1) assess how cavity-nesting bird richness and species densities shift in pine forests that are managed differently, (2) quantify nest site partitioning and potential for interspecific competition within the community, and (3) investigate Red-cockaded Woodpecker cavity kleptoparasitism by two common cavity usurpers: the Red-bellied Woodpecker (*Melanerpes carolinus*) and the Red-headed Woodpecker (*M. erythrocephalus)*.

We first documented species inhabiting these forests and identified potentially important characteristics in old-growth longleaf pine forests for cavity-nesting birds. Along a gradient of sites ranging from managed old-field pine forests to unmanaged old-growth longleaf pine forests, we found that densities of several cavity-nesting bird species had strong relationships to Red-cockaded Woodpecker cavities. The number of birds detected, and species detected per point count, were higher in old-growth longleaf pine sites than in old-field pine sites, as were total cavity-nesting bird density estimates and density estimates for several species. Red-cockaded

Woodpeckers and species that use their cavities were predictability more abundant on old-growth sites, and generalists (e.g., Red-bellied Woodpeckers) did not significantly differ between the two.

There were characteristics that we predicted would be important that had little influence on cavity-nesting bird richness and densities. Forest cover was not a significant predictor of density, but this was likely because the range of forest cover among study sites was relatively small. Surprisingly, we also did not find strong support for the influence of snag densities on cavity-nesting bird richness and abundances. However, using snag densities alone without regard to characteristics such as size and decay class may not provide enough detail to meaningfully relate to species that use those snags. Other important forest characteristics we recommend including in future assessments restricted to pine forests are pine and snag basal area. Unfortunately, due to the nature of working on private lands, we were not able to attain estimates of basal areas in this study. Additionally, spatial arrangement of snags (i.e., clustering) may be an important component of nest site selection and competition; clusters are attractive because of foraging opportunities (Raphael and White 1984, Li and Martin 1991), but territoriality may limit the number of individuals that can nest within the cluster (Bull et al. 1997).

To further investigate the importance of old-growth longleaf pine complexity for cavity-nesting birds, we studied similarity among species in nest cavity resources that were used during the breeding season and the potential for interspecific competition. Results indicate some evidence of nest site partitioning among distinct groups of cavity-nesting bird species, but there was high overlap among selected nest site characteristics among species within those groups. Based on these characteristics, we categorized species into three non-mutually exclusive groupings; (1) species using Red-cockaded Woodpecker cavities, (2) species using large, mid-stage decay snags, and (3) species using late-stage decay snags. This study demonstrated the critical importance of excavators for creating cavities, as over 90% of all nests found were in excavated cavities. Naturally occurring cavities via fungal decay are less common in coniferous forests than in hardwood forests (Bull et al. 1997).

Additionally, seven of the ten breeding cavity-nesting bird species in this study utilized Red-cockaded Woodpecker cavities, supporting their role as an important keystone species. The degree of niche overlap observed between species suggests the potential for high interspecific competition in forests where nest sites are limiting. Providing snags of various decay classes will help promote a diversity of species. For snag management, there is a potential trade-off between snag retention and Red-cockaded Woodpecker cavities, in which stands with high (> 1/ha) densities of cavities could be sufficient to decrease the number of snags needed. However, for species that infrequently use or do not use Red-cockaded Woodpecker cavities, typically the late-stage cavity users, conserving short-well decayed snags is essential.

Individual woodpeckers that did not use Red-cockaded Woodpecker cavities typically used large, mature pine snags. These snags have physical characteristics that are uncommon in younger forests, such as structural complexity, large boles, and proportion of heartwood to sapwood (Mitchell et al. 2009). Large snags also provide the opportunity for excavators to nest at greater heights, which tend to be more successful than cavities at lower heights because of differential depredation rates (Li and Martin 1991, Hudson and Bollinger 2013, Cockle et al. 2015)

Red-bellied Woodpeckers utilized Red-cockaded Woodpecker cavities at higher rates than any other species (ca. 71%). When they did not nest in Red-cockaded Woodpecker cavities, Red-bellied Woodpeckers nested in snags very similar to those used by Red-headed

Woodpeckers. These snags tended to contain little bark, had large DBHs (> 14 cm), and were relatively tall (> 14 m). Red-headed Woodpeckers utilized Red-cockaded Woodpecker cavities much less frequently than Red-bellied Woodpeckers. Based on studies of interspecific competition between the two species in other parts of the range in which Red-headed Woodpeckers were socially dominant (Williams and Batzli 1979, Ingold 1989), we hypothesized Red-headed Woodpeckers would outcompete Red-bellied Woodpeckers for higher quality cavities. Although snags theoretically provide less structural integrity than a cavity in a live tree, there is evidence to support higher rates of nest depredation for heterospecific occupants of Red-cockaded Woodpecker cavities (Kappes Jr and Sieving 2011), which was investigated further in chapter 4.

To study competition in the context of Red-cockaded Woodpecker kleptoparasitism, we formed two competing, but not mutually exclusive hypotheses that (1) limited snag densities would affect rates of kleptoparasitism (indicating nest site limitations), or (2) nesting in Red-cockaded Woodpecker cavities results in higher nesting success for two common kleptoparasites, Red-headed Woodpeckers and Red-bellied Woodpeckers. I found no relationship between rates of kleptoparasitism and snag densities across a gradient of sites that contained varying snag densities. The influence of snag densities on kleptoparasitism is contested in the literature, but our findings agree with Everhart et al. (1993), which initially suggested some unknown benefit of using Red-cockaded Woodpecker cavities based on occupancy rates. In this study, the most supported nest success model was cavity height, with predation rates decreasing at increasing heights. Although the most supported model of nest success for Red-headed Woodpecker and Red-bellied Woodpeckers was not substrate type, we found that nest success was lower in Red-cockaded Woodpecker cavities (0.35) than in snags (0.51). Red-cockaded Woodpeckers drill resin wells that surround active cavities. If these wells are not maintained, they dry up within days, rendering the occupant more susceptible to nest predation by rat snakes. This suggests that rat snakes indirectly positively affect Red-cockaded Woodpeckers by depredating nests of kleptoparasites (Kappes Jr and Sieving 2011). Additionally, Red-cockaded Woodpecker cavities in this study were lower on average than cavities in snags utilized by Red-headed Woodpeckers and Red-bellied Woodpeckers, and perhaps were more accessible by ground dwelling predators. We hypothesize that differences in nest success seen here is potentially due to differential nest depredation between snags and Red-cockaded Woodpecker cavities, which would suggest that Red-cockaded Woodpecker cavities are an ecological trap for nesting avian kleptoparasites. A study utilizing cameras on nest cavities of both substrates to identify nest predators would be necessary to evaluate this hypothesis,

Additional future work should broadly compare cavity-nesting bird communities and associated guilds across the longleaf pine ecotypes, which contain different community compositions. Species that use Red-cockaded Woodpecker cavities also vary across their range, which would result in nest niche shifts and differences in interspecific interactions and competition. Studies within the same longleaf ecotype comparing nest site diversity and abundances in old-growth and younger pine forests may highlight important resources in old-growth that can be mimicked in younger forests. More work quantifying nest success in the different cavity resources could elucidate which constitute high quality cavities for different species, especially regarding the differential-predation hypothesis.

Old-growth longleaf pine have become extremely rare with an estimated 3900 ha remaining, and much of this exists on private land. These forests face many challenges, including urbanization, land conversion, and fire suppression (Varner and Kush 2004). Understanding specific characteristics of old-growth forests that are important to cavity-nesting birds can help inform management of other forests by serving as reference sites (Lennartz and Lancia 1989). Continuing to promote habitat restoration on private lands is critical, as 83% of forested lands in the southeastern United States are privately owned (Brockway et al. 2005). Management on both private and public lands should encourage forest maturation and fire application at regular intervals (ca. 2 years; Stambaugh et al. 2011). This study can provide a reference baseline from which future work on specific nesting guilds, interactions, and nest success can stem. we hope the results of this work highlight the importance of these forests for cavity-nesting birds, and the critical role Red-cockaded Woodpeckers play in these forests.

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