

**Experimental study of an avian cavity-nesting community: nest webs, nesting ecology, and interspecific interactions**

by

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Experimental study of an avian cavity-nesting community: nest webs, nesting ecology, and interspecific interactions

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**Abstract**

Cavity-nesting communities are structured by the creation of and competition for cavities as nest-sites. Viewing these communities as interconnected ‘webs’ can help identify species interactions that influence community structure. This study examines cavity-nesting bird community interactions within the fire-maintained longleaf pine (*Pinus palustris*) ecosystem at Eglin Air Force Base, Florida. In chapter 1, I provide a background review of the ecology of my study system. In chapter 2, I use nest webs to depict the flow of cavity-creation and use at Eglin. I identified 2 webs into which most species could be placed. One web contained 6 species associated with pines. The second web contained 5 species associated with hardwoods. Red-cockaded woodpeckers (*Picoides borealis*) and northern flickers (*Colaptes auratus*) created most cavities used by other species within this community. In chapter 3, I describe snag densities and nest-site selection of the cavity-nesting bird community at Eglin. Large, mature pine snags were abundant, exceeding other reported densities for southern pine forests. Pine snags were heavily-used, despite the abundance of available red-cockaded woodpecker cavities in living pine. Hardwood snags accounted for 10% of nests found, and were used by 12 of 14 species. Diameters of nest-trees and available snags were below the range of optimal nest-snag diameters reported in other studies, indicating the need for site-specific snag management guidelines. In chapter 4, I combine a study of basic ecological principles with endangered species management to examine interactions within the cavity-nesting bird community at Eglin. I used a nest web to identify a potential indirect interaction between the red-cockaded woodpecker and large secondary cavity-nesters, mediated by the northern flicker. I used structural equation modeling to test a path model of this interaction. By experimentally manipulating cavity availability, I blocked links described in the model, confirming cavity creation and enlargement as mechanisms that influence this indirect relationship. I demonstrated that a red-cockaded woodpecker cavity-management technique could disrupt this indirect relationship by affecting northern flicker behavior, and provided an empirical example of how, in interactive ecological communities, single-species management can have indirect effects on non-target species.

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## **Attributions**

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Dr. Walters served as the chair of my doctoral committee. He contributed greatly to the design of this research and provided constructive input on all chapters of this dissertation.

Chapters 2, 3, and 4 are presented as separate manuscripts, on which Dr. Walters is a coauthor.

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# Chapter 1: General introduction

## Introduction

This dissertation describes a 4-year study of cavity-nesting birds inhabiting the fire-maintained longleaf pine (*Pinus palustris*) ecosystem on the Eglin Air Force Base reservation in northwest Florida. The study uses a combination of observational, experimental and modeling techniques to examine the relationships of the federally endangered red-cockaded woodpecker (*Picoides borealis*) with other members of the cavity-nesting bird community. During the first 2 years of the study, baseline data were collected on the relative abundance and nesting ecology of 14 species of cavity-nesting birds that breed in the longleaf pine sandhills, including the red-cockaded woodpecker. These observational data were used to determine the cavity-nesting bird community structure, identify nest resource availability and use, and generate a baseline estimate of cavity-nesting bird abundance. These data were then used to generate hypotheses about direct and indirect species interactions in the longleaf pine ecosystem, as well as which species had the potential to be impacted by management of cavities for red-cockaded woodpeckers. During the third year, the availability of red-cockaded woodpecker cavities was experimentally manipulated with standard and widely used cavity management techniques. Cavity-nesting bird abundance and nesting behavior were again monitored for the duration of the study to determine treatment effects. This research is presented as 3 separate manuscripts (chapters 2 - 4). Chapter 5 provides some additional results from the experimental study that were not presented in the manuscripts, and then summarizes the overall findings of my research. The current chapter provides a general background on the ecology of cavity-nesting birds, the longleaf pine ecosystem and the red-cockaded woodpecker.

## **Cavity-nesting birds**

A considerable number of bird species worldwide nest in cavities and cavity-nesting birds are a large component of many forest communities. Cavity-nesting communities are structured in such a way that community members interact through creation, use and competition for cavity nest and roosting sites. Primary cavity-excavators (PCEs), which include woodpeckers, excavate cavities in dead trees or in dead limbs of living trees, and many species excavate new cavities each year for their nest-sites. Cavity-excavators may be limited by the availability of dead or decaying wood (snags) suitable for cavity excavation (e.g., Haapanen 1965, Scott 1979, Mannan et al. 1980, Raphael and White 1984, Zarnowitz and Manuwal 1985, McComb et al. 1986, Schreiber and deCalesta 1992, Lohr et al. 2002). Snags may especially be limited in forests where management practices include the removal of dead or dying trees (McComb et al. 1986, Hansen et al. 1991). Weak cavity-excavators (WCEs), which include nuthatches and chickadees, use existing woodpecker cavities or excavate their own. Secondary cavity-nesters (SCNs) cannot excavate cavities and subsequently, can be limited by the availability of existing cavities (e.g., von Haartman 1957, Jones and Leopold 1967, Hamerstrom et al. 1973, Brush 1983, Haramis and Thompson 1985, Brawn et al. 1987, Brawn and Balda 1988, Gustafsson 1988; but see Waters et al. 1990, Brightsmith 2005). Thus, cavity-nesters exhibit a clear hierarchy, with some species depending partly or wholly on others for critical nesting resources.

Cavity-nesters have been widely studied and the role of woodpeckers as significant components of forests systems worldwide is becoming increasingly recognized (reviewed in Mikusiński 2006, Virkkala 2006). There are numerous descriptive studies of differences among species in resource use and of resource overlap (e.g., Conner and Adkisson 1977, Stauffer and Best 1982, Van Balen et al. 1982, Bull et al. 1986, Angelstam 1990, Sedgwick and Knopf 1990,

McFarlane 1992, Schreiber and deCalesta 1992, Ingold 1994, Dobkin et al. 1995, Sedgwick 1997, Shackelford and Conner 1997, Joy 2000). The niches (or areas of specialization) of cavity-nesting species have been studied from a foraging perspective (e.g., Bull et al. 1986, McFarlane 1992), as well as from a nest-site selection perspective (e.g., Conner and Adkisson 1977, Stauffer and Best 1982, Bull et al. 1986, Ingold 1994).

Studies on the role of snags in the cavity-nesting community have shown that the numbers and diversity of cavity-nesting birds increased with the density of snags available (e.g., Haapanen 1965, Mannan et al. 1980, Zarnowitz and Manuwal 1985, McComb et al. 1986, Schreiber and deCalesta 1992). Other studies showed that the densities of cavity-nesting birds declined following snag-removal (Scott 1979, Scott and Oldemeyer 1983, Raphael and White 1984, Lohr et al. 2002). Experimental studies have been conducted on the effects of cavity limitation on breeding bird density by increasing (via nest boxes) and decreasing available cavities (e.g., Jones and Leopold 1967, Hamerstrom et al. 1973, Dahlsten and Copper 1979, Brush 1983, Raphael and White 1984, Haramis and Thompson 1985, Brawn and Balda 1988). Few studies, however, have monitored the effects of cavity provisioning on breeding abundance, by before and after comparisons, changes in the treatment plot against those in a similar control plot, and with replication in several plots. Fewer still have directly examined the links among species or the mechanisms that structure these communities (Gutzwiller and Anderson 1988, Martin and Eadie 1999, Bonar 2000, Bednarz et al. 2004, and Martin et al. 2004). Cavity-nesting communities seem well suited to mechanistic community analysis, but they have not been well studied from this perspective.

It is well known that primary cavity-excavators provide resources critical for the survival and reproduction of many secondary cavity-nesting species. However, it is only in recent years

that researchers have started focusing on the connections and interactions within cavity-nesting communities, including the broad ecological context of how cavities are created and their role in supporting a functioning ecosystem (Bednarz et al. 2004). Martin and Eadie (1999) introduced the concept of the “nest web” as a theoretical framework by which to study cavity-nesting community structure. A nest web is similar to a food web, which is characterized by a central resource, a hierarchy of consumers of that resource, and links between species within and between levels of the hierarchy. The nest web, however, maps the interdependence of members of the cavity-nesting community based on cavity creation and use. Results from Martin and Eadie’s (1999) study identified the northern flicker (*Colaptes auratus*) as a potential keystone species within the cavity-nesting bird community in the Chilcotin Region of north central British Columbia, Canada. Since then, a pattern has emerged in other studies of cavity-nesters showing that 1 or 2 keystone species provide most cavities used in an ecosystem (Huss et al. 2002, Ripper 2002, Martin et al. 2004, Saab et al. 2004). Future community-wide studies are needed in additional types of forest systems to determine if this is a universal pattern.

In this study, I apply the concept of the nest web to the cavity-nesting bird community in the fire-maintained longleaf pine ecosystem of the southeastern United States. Of particular interest is the relationship of the red-cockaded woodpecker with other members of the cavity-nesting bird community in longleaf pine forests. Longleaf forests are dominated by living pine and generally have a low availability of hardwoods and snags, which provide the majority of suitable excavation sites for most woodpeckers (Allen 2001, Conner et al. 2001). In fact, fire-maintained longleaf pine forests have often been described as being a relatively “cavity-poor environment”. Still, there are over 15 species of cavity-nesting birds that breed in this ecosystem, 7 of which are primary cavity excavators. These 7 woodpecker species include the

northern flicker, red-bellied woodpecker (*Melanerpes carolinus*), red-headed woodpecker (*M. erythrocephalus*), downy woodpecker (*Picoides pubescens*), hairy woodpecker (*P. villosus*), pileated woodpecker (*Dryocopus pileatus*) and red-cockaded woodpecker. Of these species, the red-cockaded woodpecker is the only one capable of excavating cavities in the resource that dominates the historical landscape of the southeastern U.S. -- living pine. In fact, red-cockaded woodpecker cavities are considered a valuable resource in southern pine ecosystems and over 27 vertebrate species are known to use their cavities, including 4 of the 6 other woodpeckers noted above (Baker 1971, Beckett 1971, Dennis 1971, Hopkins and Lynn 1971, Jackson 1978, Harlow and Lennartz 1983, Rudolph et al. 1990, Loeb 1993, Kappes and Harris 1995, Conner and Dickson 1997, Loeb and Hooper 1997, Phillips and Gault 1997). Accordingly, the red-cockaded woodpecker has been described as the keystone species of fire-maintained southern pine ecosystems (Rudolph et al. 1990, Conner and Rudolph 1995, Conner et al. 2001, USFWS 2003, Costa and Daniels 2004).

### **The longleaf pine ecosystem and the red-cockaded woodpecker**

The red-cockaded woodpecker is a cooperatively breeding bird endemic to pine forests of the southeastern United States. This species lives in family groups which consist of one breeding pair and 0-3 helpers, typically offspring from previous years (Walters 1990). Red-cockaded woodpeckers excavate cavities in mature, living pine trees and use these cavities for nesting and roosting. Each family group typically maintains multiple cavity trees within their territory and these sets of cavity trees are termed clusters (Walters 1990).

Red-cockaded woodpeckers have strong ecological ties to fire-maintained habitat. This species is historically associated with pine-grassland habitats, particularly the longleaf pine

ecosystem, and the historic range of this once common bird coincided largely with that of this ecosystem (Fig. 1.1). The longleaf pine community once stretched from southeastern Virginia to eastern Texas and was among the most extensive ecosystems in North America, encompassing as much as 92 million acres (Landers et al. 1995). Natural fires historically occurred in these areas every 3 to 5 years on average, although frequency varied greatly across the southeast. The frequent occurrence of fire maintained an open, bunchgrass understory, sparse hardwood midstory and a diverse groundcover (Frost 1998). Within this ecosystem, the red-cockaded woodpecker developed a behavioral adaptation to the low density of snags and hardwoods (Jackson 1971) in that it excavates cavities in living pine trees, most often longleaf pine, which are highly resistant to fire. The red-cockaded woodpecker is the only bird in North America known to excavate cavities in live pine trees.

Conversion of longleaf pine forest to agriculture, timber plantations and urban development has resulted in major habitat loss over the past century (Wear and Greis 2002). Fire suppression in remaining forested areas has further degraded the longleaf pine ecosystem. Fire suppression became the general policy of government agencies through forest fire protection policies implemented in the 1920s. However, suppression of fire degrades red-cockaded woodpecker habitat by allowing a midstory of scrub-oaks (*Quercus* spp.) to develop. Encroachment of a hardwood midstory on cavity trees results in red-cockaded woodpecker territory abandonment, presumably because it allows predators, such as snakes, access to the cavities (Jackson 1978). Further degradation of habitat was caused by the elimination of old-growth trees due to short timber harvesting rotations and even-aged silvicultural techniques. This harvesting of timber every 20 to 40 years by clear-cutting prevents the occurrence of old-growth pines, which are necessary for red-cockaded woodpecker cavity excavation.

At present, approximately 1-3% of the original longleaf pine forests remain, most of which is degraded (Frost 1993, Ware et al. 1993, Costa and Daniels 2004). Because of this extensive habitat loss and degradation, the red-cockaded woodpecker declined greatly in numbers and was designated by the U.S. Fish and Wildlife Service (USFWS) as an endangered species in 1970 (35 *Federal Register* 16047, 13 October 1970). Since then, the red-cockaded woodpecker has been intensively studied. This species has been the subject of 4 symposia (Thompson 1971, Wood 1983a, Kulhavy et al. 1995, Costa and Daniels 2004), 2 books (McFarlane 1992, Conner et al. 2001) and countless journal articles. Research on the demography and sociobiology of the red-cockaded woodpecker (Walters et al. 1988, Copeyon et al. 1991) has identified carrying capacity, specifically availability of cavities and cavity trees, as the main factor limiting populations of this species. Management techniques geared towards increasing cavity availability have shown great success in stabilizing red-cockaded woodpecker populations (Walters 1991).

Red-cockaded woodpecker populations currently exist on 100 public lands and dozens of private lands distributed across the southeastern United States (USFWS 2003). Most of these populations are small and isolated. The current population level is estimated at 5,903 groups or 14,758 individuals, less than 3% of its estimated level at the time of European settlement (USFWS, *unpublished data*). The majority of these populations exist on public property such as U.S. Forest Service (USFS) lands and military bases.

### **Red-cockaded woodpecker cavities**

Red-cockaded woodpecker cavities, used for roosting and nesting, are excavated in old, large, living pine trees (Jackson 1994, Conner et al. 1995). Old trees are selected because 1) they

are more often infected with red heart fungus (*Phellinus pini*), which softens the heartwood and presumably makes excavation easier (Jackson 1994, Conner et al. 1995), and 2) they have sufficient heartwood for cavity excavation. Cavity trees are typically at least 80 - 120 years old (Jackson 1994). Cavity excavation in a living pine tree is labor-intensive and can take years to complete, as compared to a few weeks for other woodpecker species that excavate cavities in dead wood (Jackson et al. 1979, Conner and Rudolph 1995, Harding and Walters 2002, Harding and Walters 2004). Once a red-cockaded woodpecker cavity is excavated, however, it may remain in use for several decades. The formation of new red-cockaded woodpecker groups is uncommon. The high time-cost of cavity excavation appears to cause red-cockaded woodpeckers to compete for territories with existing cavities rather than form new groups (Walters et al. 1992). The fact that cavities are such 'valuable' real estate has been shown to play a significant role in the ecology and behavior of the red-cockaded woodpecker (Walters 1991).

The tendency of red-cockaded woodpeckers to use existing cavities, rather than excavate cavities in vacant habitat to form new territories, makes cavities a critical resource. Thus, the availability of cavities and cavity trees appears to be the primary limiting factor in red-cockaded woodpecker population growth. The loss of cavities (through hardwood encroachment) and cavity trees (through silvicultural practices) has greatly reduced the carrying capacity of red-cockaded woodpecker habitat. This reduction in carrying capacity, or ability of habitat to support a population, has been the major cause of decline in the red-cockaded woodpecker population in recent decades.

Over 27 species are known to use red-cockaded woodpecker cavities, indicating that the red-cockaded woodpecker may play a significant role in controlling the presence or abundance

of other cavity-nesting species in the longleaf pine ecosystem (USFWS 2003). Of the species known to use red-cockaded woodpecker cavities, some used unaltered red-cockaded woodpecker cavities (e.g., eastern bluebirds (*Sialia sialis*), tufted titmice (*Baeolophus bicolor*) and great-crested flycatchers (*Myiarchus crinitus*)), while others enlarge the cavities and / or cavity entrances prior to use (e.g., northern flickers and pileated woodpeckers). Other species such as the wood duck (*Aix sponsa*), American kestrel (*Falco sparverius*), eastern screech-owl (*Otus asio*) and eastern fox squirrel (*Sciurus niger*) use red-cockaded woodpecker cavities that are abandoned and enlarged. Even several species of reptiles, amphibians and insects use these cavities (Conner et al. 2001).

Species such as the eastern bluebird, southern flying squirrel (*Glaucomys volans*), and red-headed and red-bellied woodpeckers are considered kleptoparasites in that they may usurp an active cavity and thereby have a negative effect upon the red-cockaded woodpecker (Kappes 1997). Red-cockaded woodpecker cavity usurpation by other species has been well documented (Harlow and Lennartz 1983, Lennartz and Heckel 1987, Rudolph et al. 1990, McFarlane 1992, LaBranche and Walters 1994, Kappes 1997, Loeb and Hooper 1997). Rates of cavity usurpation may be inversely related to snag density within red-cockaded woodpecker clusters (Wood 1983b, Kappes and Harris 1995), although some studies have found mixed results (Harlow and Lennartz 1983, Everhart et al. 1993). Nonetheless, it appears that retention of snags in these forests could potentially alleviate usurpation pressure on red-cockaded woodpecker cavities and future studies in this area are needed.

Fire-maintained longleaf pine forests generally have a low availability of snags relative to other forest systems. Snag availability is further decreased by forest management practices in many southeastern forests which include removal of hardwoods and dead trees – the resources

that provide the majority of suitable excavation sites for most woodpeckers. The red-cockaded woodpecker may play an especially important role in providing nesting habitat in areas where snags are harvested. The prevalent use of red-cockaded woodpecker cavities by other species suggests that the red-cockaded woodpecker might play a vital role as an ecosystem engineer in the longleaf pine community, given its creation of nesting habitat for a wide range of species. However, the exact role of the red-cockaded woodpecker with the cavity nesting community, in terms of strengths and types of interactions, is yet to be explicitly tested and such testing is one of the goals of this study.

### **Current red-cockaded woodpecker management**

As a federally endangered species, the red-cockaded woodpecker is heavily managed using both ecosystem and single-species management techniques. Ecosystem management for the red-cockaded woodpecker includes prescribed burning, which is effective in maintaining the open midstory required by the red-cockaded woodpecker. The importance of the role of fire in the longleaf pine ecosystem was recognized in the 1980s (Frost et al. 1986) and prescribed burning is now considered one of the most critical and widely used management tools for the longleaf pine ecosystem. In fact, prescribed burning is well known for its positive effects on many fauna and flora of the longleaf pine community (Conner et al. 2001, Litt et al. 2001, Provencher et al. 2001, 2002, Allen et al. 2006).

On the other hand, little is known about the effects of single-species management for red-cockaded woodpecker on other cavity users. Single-species management includes provisioning of artificial cavities and use of cavity-restrictor plates. The development of techniques to construct artificial red-cockaded woodpecker cavities in living pines (Copeyon 1990, Allen

1991, Copeyon et al. 1991) arose from the identification of cavities as the limiting factor to red-cockaded woodpecker population growth (Walters et al. 1992), and metal restrictor plates were developed to prevent and repair the enlargement of red-cockaded woodpecker cavity entrances (Carter et al. 1989) by pileated woodpeckers and northern flickers. Both management techniques have contributed greatly to management of the red-cockaded woodpecker and have been widely and successfully used for the past decade (USFWS 2003). Since 1998, over 16,000 red-cockaded woodpecker cavities were provisioned (1,656 drilled cavities, see Copeyon 1990; and 14,604 insert boxes, see Allen 1991) and approximately 8,292 cavities were restricted (USFWS, *unpublished data*) (see Fig 1.2). Because insert boxes used for red-cockaded woodpecker management typically have restrictor plates built into the box, over 22,000 red-cockaded woodpecker cavities have been restricted in the southeastern U.S. If the red-cockaded woodpecker is truly a keystone provider of cavities in the fire-maintained longleaf pine ecosystem, then there is potential for impacts of red-cockaded woodpecker cavity management on other cavity-nesting species. Provisioning artificial cavities may have positive benefits for other cavity-users, but on the other hand, restricting cavities so that larger species cannot use them may have negative effects on some species. In fact, the nature of the relationships of the red-cockaded woodpecker with other cavity-users is poorly understood (USFWS 2003).

### **Project site**

Eglin Air Force Base (AFB), in the western Florida panhandle, encompasses 187,555 hectares in Okaloosa, Santa Rosa and Walton counties (Fig. 1.3). It is the largest forested military reservation in the United States and is the largest and least fragmented, single longleaf pine ownership in the Southeast (McWhite et al. 1999). Eglin is comprised of 6 major ecological

associations, with the majority of Eglin (78%) consisting of the Sandhills ecotype (McWhite et al. 1999). The sandhills community is characterized by scattered to dense longleaf pine, with a mid-story of mostly turkey oak (*Quercus laevis*) and a ground cover of various fire adapted forbs and grasses (Kindell et al. 1997). Red-cockaded woodpeckers inhabit this ecotype over the entire base (Walters et al. 2000), with 321 active red-cockaded woodpecker clusters and over 6000 cavity trees in 2005 (K. Gault, Eglin AFB, *personal comment*).

As part of an effort to stabilize and possibly increase the population on the eastern part of the base, which was declining in the early 1990s, various management techniques have been experimentally evaluated for their effectiveness (Walters et al. 2000, Walters et al. 2004a,b). One of these management techniques is the provisioning of artificial cavity sites, termed recruitment clusters, to induce new group formation. Since 1995, 925 artificial cavities were drilled in recruitment clusters at Eglin. In addition to recruitment cluster provisioning, cavity management is also conducted within existing clusters. Cavity management involves checking each active cluster each year to determine if four suitable, unenlarged cavities are available. If there are fewer than four cavities, additional cavities are provided, either by placing cavity restrictors on suitable but enlarged cavities, or drilling new artificial cavities. This practice is designed to prevent cluster abandonment by ensuring that all clusters are of sufficiently high quality (i.e. have enough suitable cavities). Within existing clusters, 327 new cavities were provisioned and over 300 cavity-restrictors were applied since 1995 (K. Gault, Eglin AFB, *personal comment*).

While cavity provisioning has been shown to be beneficial to the red-cockaded woodpecker, the impact of intensive cavity provisioning on other cavity-nesting species is currently unknown. The effect of cavity restrictors on the red-cockaded woodpecker has been

studied (Carter et al. 1989, Raulston et al. 1996, Wood et al. 2000, Walters et al. 2004a), however little is known about the impact of cavity restrictors on other cavity-nesting birds. Enlarged red-cockaded woodpecker cavities provide important habitat for many larger secondary cavity nesters (e.g., American kestrels, eastern screech-owls and fox squirrels). These larger species cannot use red-cockaded woodpecker cavities unless they have been enlarged by other woodpeckers, and red-cockaded woodpeckers will no longer use cavities that have been enlarged substantially. The process of enlargement creates a potential for indirect interactions between red-cockaded woodpeckers and larger secondary cavity nesters, mediated by other woodpecker species. Thus, while using restrictor plates may benefit the red-cockaded woodpecker by preventing cavity enlargement, this type of management may have a detrimental impact on these other, larger secondary cavity-nesters.

The Eglin reservation contains a large amount of old-growth longleaf pine (Varner and Kush 2001), and over 6,000 red-cockaded woodpecker cavity trees, of which over 1,700 are dead standing (Williams et al. 2006). In addition, Eglin has an atypical abundance of old-growth pine snags due to excessive tree mortality after the reintroduction of fire following years of suppression (Varner et al. 2005). Because Eglin land managers do not harvest dead trees, large, old-growth snags remain on the landscape. With both large number of red-cockaded woodpecker cavity trees and high snag availability, there seems to be no shortage of cavities on the reservation. Indeed, cavity-nesting birds comprise a major component of the bird community at Eglin. Due to its size, large amount of sandhills habitat, presence of red-cockaded woodpecker clusters (both active and abandoned), and high snag availability, Eglin is uniquely suited to large-scale cavity-nester studies that require replicate plots within longleaf communities (e.g., Walters et al. 2000, Litt et al. 2001, Provencher et al. 2001, 2002, Walters et al. 2004b).

## **Project overview**

The goal of this study is to describe the cavity-nesting bird community structure at Eglin and characterize the relationship of the red-cockaded woodpecker with other cavity-nesting birds using correlational, experimental and statistical modeling techniques. Relationships within the cavity-nesting community at Eglin, particularly those involving red-cockaded woodpeckers, are interesting for 2 reasons. First, there are concerns about the impacts of red-cockaded woodpecker management on other species, and about the impacts of other species on this endangered species. Second, red-cockaded woodpeckers may have exceptionally numerous and strong connections with other cavity-nesting species due to peculiarities of the longleaf pine ecosystem. In fact, several species normally considered primary cavity nesters seem to function instead as weak primary cavity nesters in longleaf pine forests (i.e., red-bellied woodpeckers, red-headed woodpeckers and northern flickers), using red-cockaded woodpecker cavities as well as excavating their own.

This dissertation consists of 3 manuscripts, which are presented in chapters 2-4. In chapter 2, I describe the structure of the cavity-nesting bird community in a fire-maintained longleaf pine ecosystem using 2 years of observational data. Specifically, I present “community webs” based on cavity-nesting bird abundance and nest data. These webs are used to provide a visual depiction of the community structure in relation to snag availability, red-cockaded woodpecker cavity availability, and the abundance of cavity-nesting bird species. In chapter 3, I describe snag availability and nest-site selection by 14 avian species that breed in the sandhills at Eglin. I compare these data to results from studies of other southeastern pine forests and discuss the implications for regional snag management guidelines. In chapter 4, I use a nest web depiction of Eglin’s cavity-nesting community to identify a potential indirect interaction between

the red-cockaded woodpecker and large secondary cavity-nesters, mediated by the northern flicker. I use structural equation modeling to test a path model of this interaction, using cavity excavation and enlargement as mechanisms which drive the relationship between these species. I then use experimental manipulation of cavity availability to block links described in the path model and test my predictions about cavity creation and enlargement as processes that influence community structure. In chapter 5, I present the results of an additional experimental study, in which I use experimental cavity-provisioning in living pine to test if this red-cockaded woodpecker cavity-management technique affects other members of the cavity-nesting bird community. Finally, I summarize the overall findings from this 4-year research project.

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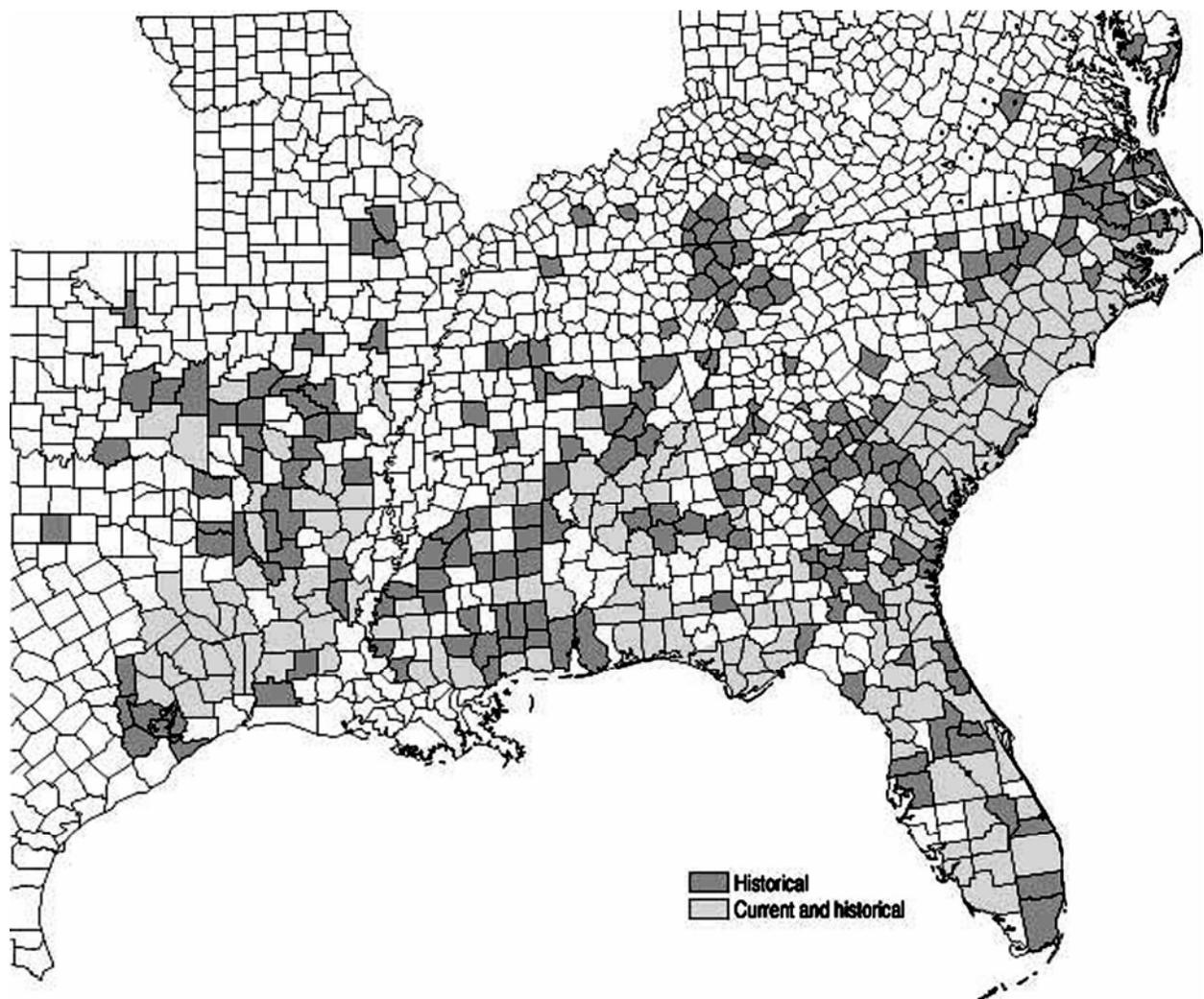
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**Figure 1.1.** Historical distribution of the red-cockaded woodpecker. From Costa and Walker (1995), <http://biology.usgs.gov/s+t/noframe/b240.htm>.



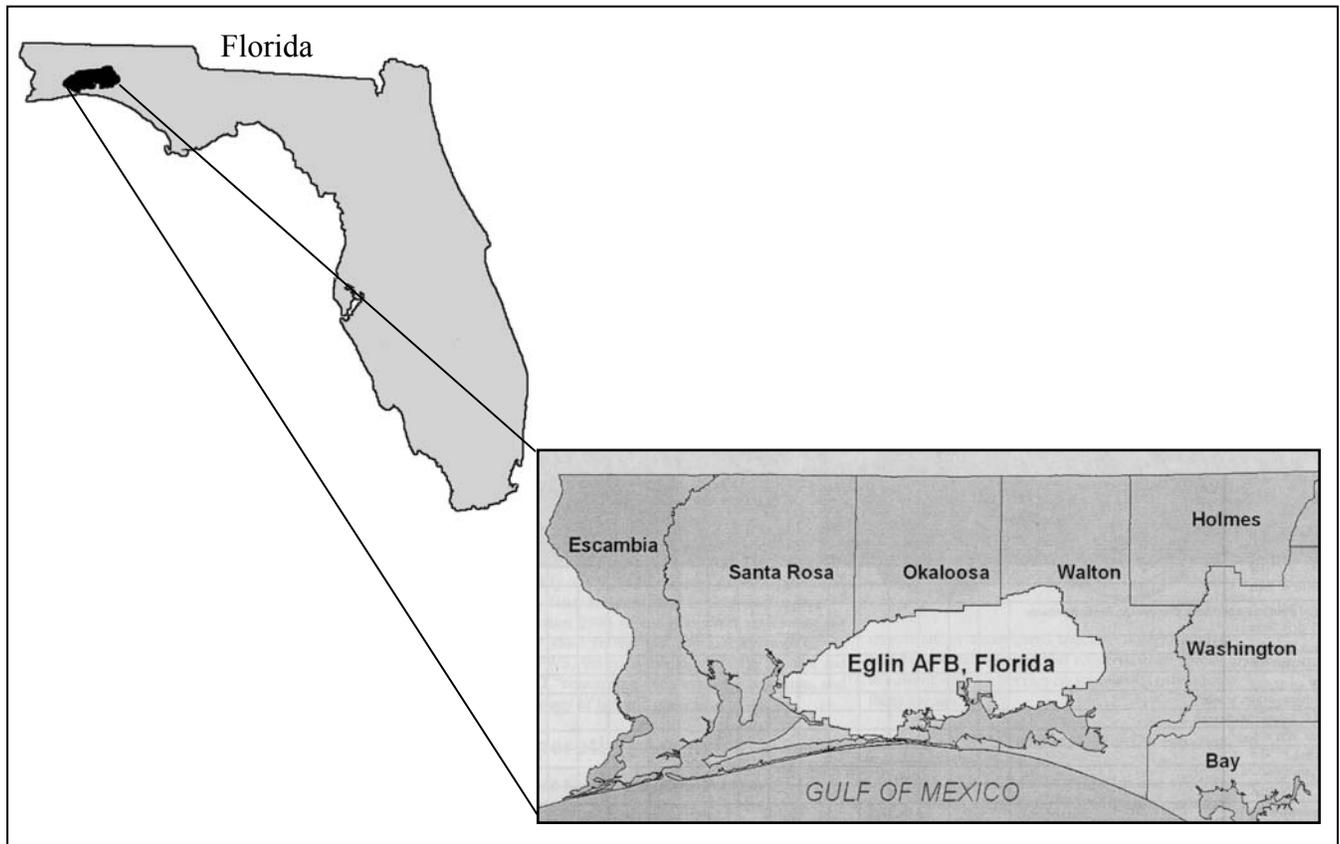
(a)



(b)



**Figure 1.2.** Metal restrictor plates used in red-cockaded woodpecker cavity management to (a) prevent enlargement of cavity entrances and (b) repair cavities with enlarged entrances. Photos taken by L. Blanc.



**Figure 1.3.** The project site: Eglin Air Force Base, Okaloosa, Santa Rosa and Walton counties, Florida. Map of Eglin adapted from D.O.D. 2002, Integrated Natural Resources Management Plan, Eglin Air Force Base.

## **Chapter 2: Cavity-nest webs in a longleaf pine (*Pinus palustris*) ecosystem**

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## **Abstract**

Cavity-nesting communities can be viewed as interconnected webs that interact through the creation of and competition for cavities as nest-sites. Using a web approach, we examined the cavity-nesting bird community of a northwestern Florida longleaf pine (*Pinus palustris*) ecosystem to depict the interconnections of cavity-creation and use, and identify species with potential to respond to cavity management for the endangered Red-cockaded Woodpecker (*Picoides borealis*). We identified two groups into which most cavity-nesting species could be placed. One group consisted of 6 species associated with pine snags and Red-cockaded Woodpecker cavities. The second group consisted of 5 species associated with hardwood snags. The majority of nests (60%) were found in large pine snags. The Red-cockaded Woodpecker and Northern Flicker (*Colaptes auratus*) created most cavities used by other cavity-nesters. The Northern Flicker was the primary creator of large cavities used by secondary cavity-nesters, through its excavation of cavities in snags and the enlargement of Red-cockaded Woodpecker cavities. Also, large secondary cavity-nesters were the primary users of Red-cockaded Woodpecker cavities. We identified 4 cavity-nesting species with potential to respond to Red-cockaded Woodpecker cavity management. The web dynamics of the cavity-nesting community documented in this study can 1) serve as a baseline for comparison to other communities where the absence of large pine snags may influence the relationship between species in their acquisition of nest-cavities and 2) provide a context for examining direct and indirect interactions between species, including those involving the Red-cockaded Woodpecker.

**Keywords:** cavity-nesting birds, community structure, nest web, northern flicker, red-cockaded woodpecker, snags.

## Introduction

Cavity-nesting species comprise a major part of forest bird communities throughout much of the world and are reliant upon the availability of cavity resources for nesting and roosting. Because cavity-nesting communities are often structured through the creation of, and competition for, cavity-nest sites (Martin and Eadie 1999, Martin et al. 2004), identifying strong relationships between cavity excavators and other cavity-users may be an important step in the effective management of cavity-nesting communities. Cavity-nesting communities are divided into several guilds which include primary cavity excavators (PCE), weak excavators (WCE) and secondary cavity-nesters (SCN). PCEs include woodpeckers, which typically excavate a new cavity each year for nesting and are limited by the availability of dead or decaying wood (snags) suitable for cavity excavation (Haapanen 1965, Scott 1979, Mannan et al. 1980, Raphael and White 1984, Zarnowitz and Manuwal 1985, McComb et al. 1986, Lohr et al. 2002). Weak excavators (e.g. nuthatches and chickadees) use existing woodpecker cavities or excavate their own. Secondary cavity nesters cannot excavate cavities and thus, can be limited by the availability of existing cavities (von Haartman 1957, Jones and Leopold 1967, Hamerstrom et al. 1973, Brush 1983, Haramis and Thompson 1985, Brawn et al. 1987, Brawn and Balda 1988, Gustafsson 1988). In recent years researchers have focused on the connections and interactions between species in cavity-nesting communities (reviewed in Bednarz et al. 2004). For example, Martin and Eadie (1999) introduced ‘nest-webs’ to visually depict the flow of cavity-use in a Pacific northwest forest system and as a result, identified the northern flicker (*Colaptes auratus*) as a keystone cavity excavator. Since then, additional studies have demonstrated that one or two keystone species provide most cavities used in an ecosystem (Bednarz et al. 2004). These findings suggest that community-wide studies in additional forest systems can serve to identify

potential keystone excavators and thus guide management efforts for cavity-nesting communities. In this study, we apply the nest-web concept to the longleaf pine (*Pinus palustris*) ecosystem to identify cavity-nesting bird community structure in relation to the red-cockaded woodpecker (*Picoides borealis*). The red-cockaded woodpecker is a heavily managed, federally endangered species and has been described as a keystone species and ecosystem engineer in the longleaf pine ecosystem, given its creation of nesting habitat for a wide range of species (Rudolph et al. 1990, Conner and Rudolph 1995, Conner et al. 2001, USFWS 2003, Costa and Daniels 2004).

The red-cockaded woodpecker is endemic to longleaf pine and other fire-maintained pine ecosystems, which have an open, savanna-like landscape dominated by living pine. The frequent occurrence of fire in these forest systems suppresses the development of a hardwood midstory and maintains a relatively low number of hardwoods and snags, which provide the majority of suitable excavation sites for woodpeckers (Ligon 1970, Allen 2001, Conner et al. 2001). Within these fire-maintained ecosystems, the red-cockaded woodpecker shows an adaptation to the low density of snags by excavating cavities in living pine trees. The red-cockaded woodpecker is the only bird in North America known to excavate cavities in live pine trees. Cavity excavation in a living pine tree is labor-intensive and can take years to complete, as compared to a few weeks for other woodpecker species that excavate cavities in dead and decaying wood (Jackson et al. 1979, Conner and Rudolph 1995, Harding and Walters 2002, 2004). Red-cockaded woodpeckers live in family groups and each group typically maintains multiple cavity trees (clusters) within their territory (Walters 1990).

Because red-cockaded woodpecker cavities are excavated in living pine, they provide a long-term nesting resource on the landscape for cavity-users, sometimes remaining in use for

several decades (Conner and Rudolph 1995). In comparison, the persistence of pine snags in the southeastern U.S. is highly variable, depending on species, diameter, cause of tree death and exposure to fire (e.g., Moorman et al. 1999, Miller and Marion 1995, Conner and Saenz 2005). Twenty-seven species are known to use red-cockaded woodpecker cavities, including 4 of 6 other woodpeckers that breed in longleaf pine forests (USFWS 2003).

The red-cockaded woodpecker is heavily managed using both ecosystem and single-species techniques. Ecosystem management for red-cockaded woodpecker habitat includes the use of prescribed burning and hardwood midstory-removal to maintain an open, pine-savanna landscape. Without frequent fire, encroachment of a hardwood midstory on cavity trees can result in red-cockaded woodpecker territory abandonment, presumably because it allows predators, such as snakes, access to the cavities (Jackson 1978). Single-species management for the red-cockaded woodpecker focuses on the provisioning and maintenance of cavities. The development of artificial cavities for the red-cockaded woodpecker (Copeyon 1990, Allen 1991, Copeyon et al. 1991) arose from the identification of cavities as the limiting factor to red-cockaded woodpecker population growth (Walters et al. 1992) and restrictor plates were developed to prevent and repair the enlargement of red-cockaded woodpecker cavity entrances by other woodpecker species (Carter et al. 1989).

In recent years, increasing attention has been placed on integrating an understanding of community interactions into red-cockaded woodpecker management (Kappes 1997, USFWS 2003, Kappes 2004, Walters et al. 2004). For example, managing red-cockaded woodpecker habitat has had positive effects on many fauna and flora of the longleaf pine community (Conner et al. 2001, 2002, Litt et al. 2001, Provencher et al. 2001a, Allen et al. 2006). Additionally, how habitat structure in this ecosystem (e.g., hardwood midstory development) and habitat

management for the red-cockaded woodpecker influence avian community structure has been studied (Shackelford and Conner 1997, Conner et al. 2002, Provencher et al. 2002, Allen et al. 2006). Little is known about how red-cockaded woodpecker cavities and snag cavity resource availability within longleaf pine forests influences cavity-nesting bird community structure, although it has been suggested that the distribution of suitable cavities may be a more important habitat feature to cavity nesters than vegetation structure alone (Allen et al. 2006). Identifying factors influencing cavity creation and use within the longleaf pine ecosystem is important for several reasons. First, there are concerns about potential negative impacts of heterospecific use of red-cockaded woodpecker cavities on this endangered species. Second, there are concerns about potential impacts of cavity management for the red-cockaded woodpecker on other species (USFWS 2003). However, the nature of the relationships of the red-cockaded woodpecker with other cavity users and how red-cockaded woodpecker cavity management affects other cavity users is poorly understood (USFWS 2003).

The goal of this study is to describe quantitatively the cavity-nesting bird community in a longleaf pine ecosystem with a focus on 1) examining the flow of cavity creation and use in this system, 2) determining if the abundance of other cavity-nesting birds is positively related to red-cockaded woodpecker cavity and snag availability, and 3) identifying species with potential to respond to red-cockaded woodpecker cavity management. Specifically, we use a nest-web approach (Martin and Eadie 1999) to visually depict cavity-nesting bird community structure in relation to cavity resource availability.

## Methods

### Study area

We conducted fieldwork in 2002 and 2003 on Eglin Air Force Base, located in the western Florida panhandle, U.S. Eglin is the largest forested military reservation in the U.S., encompassing 187,555 ha, and is the largest, least fragmented longleaf pine ownership in its region (McWhite et al. 1999). Approximately 78% of the Eglin reservation consists of longleaf pine sandhills (McWhite et al. 1999), characterized by scattered longleaf pine, with an open to sparse mid-story of turkey oak (*Quercus laevis*), and a ground cover of various fire adapted forbs and grasses (Kindell et al. 1997). Red-cockaded woodpeckers inhabit this ecotype over the entire reservation with over 300 active red-cockaded woodpecker clusters and 6,000 cavity trees in 2002 (K. Gault, Eglin AFB, *personal communication*). Thus, the Eglin reservation is well-suited to large-scale studies that involve replicate plots within longleaf communities.

Eglin contains an atypical amount of old-growth longleaf pine (Varner and Kush 2001), over 1,700 dead standing red-cockaded woodpecker cavity trees (Williams et al. 2006) and an abundance of old-growth pine snags resulting from the reintroduction of fire after years of fire suppression (Varner et al. 2005). As part of their habitat restoration process, Eglin land managers have also conducted hardwood midstory reduction through mechanical and herbicidal methods (McWhite et al. 1999). As a result, both hardwood and pine snags were abundant on some parts of the reservation, but in other parts, few snags were available, typical of many southeastern pine forests. Additionally, Eglin land managers do not harvest dead trees, and thus large, old-growth snags remain on the landscape as a resource for cavity-nesters. This provided

us with the opportunity to observe heterospecific use of Red-cockaded Woodpecker cavities in areas of varying snag densities.

## Methodology

In April 2002, we established 36 research plots, which we restricted to areas within the longleaf pine sandhills ecotype with mature pine and a relatively open midstory. We acquired the locations of all Red-cockaded Woodpecker cavity trees from Eglin's long-term management data set, which was updated annually through surveys and intensive year-round Red-cockaded Woodpecker population management. We then selected the 36 plots to reflect a broad range of snag densities and Red-cockaded Woodpecker cavity availability (between 0 and 43 red-cockaded woodpecker cavities per plot). We used the largest plot size possible (800 x 600 m) to accommodate the large territories of many cavity-nesting species in the study system, while minimizing the presence of roads and creeks within the plots. The large scale of our study plots (48 ha each) encompassed habitat patchiness inherent to this ecosystem and thus each plot contained a combination of pine savanna and some degree of hardwood midstory development. In each plot, we established a grid system to aid with distance estimation, general navigation and relocation of nests. The grid system consisted of 9 600-m transects located 100 m apart, with each transect flagged at 50-m intervals for visibility. We established twelve point-count sampling stations within each plot, with three stations located on each of four alternating transects. Point-count stations were located 200 m apart and were treated as sub-samples within each plot. The plot was a sampling unit.

We recorded the relative abundance (detections per survey) of birds at all sampling stations within each plot twice between 08 April and 21 June 2002 and 2003 using a point-transect count sampling technique, adapted for the open habitat (Provencher et al. 2002, Provencher et al. 2003). We sampled two plots (totaling 24 sampling stations) per morning within the first three hours after sunrise. We conducted an 8-minute point count at each sampling station during which we recorded species, time detected, vocalization type, location and movement within a 100-m fixed radius from the point center (Hutto et al. 1986). Two observers sampled simultaneously at point-count stations on alternating transects situated 200 m apart, and start-times for the point counts were synchronized. Birds detected by the two observers at the same time were not double-counted. The same two observers conducted the point counts during both years. In counts at each sampling station, we included birds detected as the observers moved between adjacent stations. This transect-count addition to the point-count sampling enabled us to account for birds fleeing ahead of the observers and may be appropriate for open habitat (Bibby et al. 1992). For each species and each round of sampling, we calculated relative abundance (detections per survey) by summing the total number of individuals detected at all 12 sampling stations in a plot. We then used the mean number of detections for the plot (across the two sampling rounds) as the measure of abundance for that season. In a previous study at Eglin, Provencher et al. (2002) found no substantial difference between a similar modified point-transect count method and standard point-count methodology, except for reduced variability in bird detection rates using the former method. Because, all study plots were in the same habitat type, observer bias was minimized by using the same two observers both years and double counts were minimized, we believe that our sampling methodology provides a measure of the relative abundance of birds occurring in all

study plots. Nonetheless, we emphasize that our measurement was used as an index of abundance, rather than an attempt to quantify breeding densities.

We conducted two rounds of nest searching per year in each plot (between 15 April and 30 June, 2002 and 2003). During each round, nest searching consisted of two separate efforts: one field crew that focused only on nests in Red-cockaded Woodpecker cavities and another field crew that focused on cavity-nests in snags. We located nests in Red-cockaded Woodpecker cavities by inspecting all Red-cockaded Woodpecker cavities within each plot once during each round of nest searching. We examined cavity contents with a Sandpiper Technologies Treetop Peeper (e.g., a camera mounted atop a telescoping pole), which enabled us to access cavities up to 15.3 m in height. In 2002, we conducted searches for snag-nests opportunistically. We located nests by walking along transects and observing breeding bird behavior in each plot twice during the season, and inspecting all snags for potential nest cavities. We examined the contents of potential nest cavities and marked nest trees with uniquely numbered aluminum tags. In 2003, we used the same searching methodology and also checked cavity nest trees from the previous year for nesting activity. In addition, we added a systematic time constraint to ensure equal amount of search effort on each plot. During each round of nest searching, we conducted searches for snag-nests on two plots per day, with two observers simultaneously. Over the entire season, each observer spent six hours nest-searching in each plot, totaling 12 person-hours per plot. In both 2002 and 2003, nests were also found incidentally, while conducting point counts. Nests found within 50 m of a plot were also recorded. The order in which plots were sampled and searched for nests was determined randomly within each of the two rounds of sampling, and then on the basis of obtaining access to restricted areas on Eglin. We rotated the starting order and observer assignment to transect within a plot across plot visits to minimize systematic

detection biases. We conducted point counts and nest searching under satisfactory weather conditions: good visibility, little or no precipitation and light winds (Martin 1997).

To record cavity resource (snag) availability, we established a 25-m radius vegetation plot at each sampling station in July of each year, totaling 12 per study plot (total area sampled per plot = 23 562 m<sup>2</sup>). We defined snags as dead, standing trees  $\geq 10.2$  cm diameter at breast height (dbh) and  $\geq 1.4$  m tall. We recorded numbers of snags in each vegetation plot, classified by type (pine / hardwood) and qualitative decay class: 1) living tree, 2) recently dead tree, most bark and branches and top of tree intact, 3) dead, >50% bark and branches intact, 4) dead, <50% bark/branches intact, top usually broken and 5) dead, no branches or bark, broken top, extensive decay. We calculated snag availability for each plot by summing stem data across all 12 sampling stations per plot, per year. In 2002, we recorded the number of old-growth longleaf pine on each vegetation plot as a habitat variable. Old-growth pine trees were identified by their characteristic gnarled, flat top morphology (Harper et al. 1997).

To detect any confounding between cavity resource availability and habitat condition (Martin and Eadie 1999), we measured an index of abundance for 2 sets of non-cavity-nesting birds based on their association with habitat condition of longleaf pine forests (i.e. degree of hardwood midstory succession). Specifically, we wanted to examine whether habitat condition was associated with the availability of each cavity resource type, including living red-cockaded woodpecker cavity trees, pine snags, and hardwood snags. Non-cavity-nesting species associated with an open midstory (NonCavOpen) included the Bachman's sparrow (*Aimophila aestivalis*), eastern meadowlark (*Sturnella magna*), and the loggerhead shrike (*Lanius ludovicianus*). Non-cavity-nesting species associated with a developing hardwood midstory

(NonCavMidstory) included the blue-gray gnatcatcher (*Polioptila caerulea*), Carolina wren (*Thryothorus ludovicianus*), and eastern towhee (*Pipilo erythrophthalmus*).

### Statistical analyses

Abundance and cavity resource data were non-normally distributed, therefore we used nonparametric statistics for all analyses. All statistical analyses were performed using SAS, Version 9.1 (2003; SAS Institute, Inc., Cary, North Carolina, USA). We used a significance level of  $P < 0.05$  in all tests. The use of Bonferroni corrections (Holm 1979) may not be appropriate in community-wide studies due to the large number of species and subsequent large number of significance tests required in these studies. In particular, the use of Bonferroni corrections in community-wide studies could hinder the ability to detect meaningful associations between species, simply due to the diversity of community (Moran 2003). For this reason, and because this study is the first exploratory step in a longer-term study of a community of 14 cavity-nesting species, we did not use a sequential Bonferroni correction.

We used a Mann-Whitney  $U$  test to determine if there was a significant difference in bird detections between years (i.e. high levels of annual variation). A significant difference occurred only for the eastern bluebird (*Sialia sialis*; Mann-Whitney  $U$  test,  $P = 0.02$ ,  $n = 36$ ), and thus this species was analyzed separately by year. The remaining data were pooled across both years. To test for confounding of cavity resource availability with habitat condition, we 1) correlated the abundance of each of the 2 non-cavity-nesting bird groups (NonCavOpen and NonCavMidstory) with pine snags, hardwood snags and red-cockaded woodpecker cavities in living pine. To determine if detections of cavity-nesting species within each plot was reflective of nesting effort,

we correlated the number of detections per plot with the number of nests found per plot for each species. All correlation analyses were conducted using a Spearman's correlation analysis.

We created an 'abundance web' diagram to visually depict the correlations of each species to red-cockaded woodpecker cavities, pine snags, hardwood snags, and other cavity-nesters. Values used in the abundance web were generated using a Spearman's partial correlation analysis. Because old-growth pine was significantly correlated with both red-cockaded woodpeckers ( $r = 0.43$ ,  $P < 0.001$ ) and their cavities ( $r = 0.55$ ,  $P < 0.001$ ), and with pine snags ( $r = 0.30$ ,  $P = 0.01$ ), we controlled for the effects of old-growth pine when correlating bird abundance with cavity resources, to remove the effects of old-growth pine as a habitat variable. Recently dead snags (class 2) were not included as cavity resources; such sites were not used for nesting by any of the cavity-nesting species during this study, presumably because the wood was not decayed enough for excavation (Conner et al. 1975, Scott 1979, Mannan et al. 1980, Schreiber and deCalesta 1992). We grouped the remaining snag classes (3, 4 and 5), which reflected usable snag resources, into pine and oak, and correlated these cavity resource groups with the abundance of each bird species. We then incorporated statistically significant associations into the 'abundance web' diagram.

Finally, we incorporated nest data into 2 nest web diagrams (Martin and Eadie 1999, and Martin et al. 2004), which reflect the flow of cavity-use between levels of PCEs, WCEs, SCNs and trees (cavity resources). Nest-webs included all nest cavities for which we could identify the excavator, either through known use of the cavity or reasonable estimation based on cavity characteristics. Nests used in the web include re-use of the same cavity across years, but not re-nesting attempts by the same species in the same cavity within the same year. Abundance webs and nest webs serve as alternative depictions of cavity-nesting bird community structure at Eglin.

When censusing it is possible to detect birds that are foraging, but not nesting, in the plot.

Basing a web on nest data provides a more definitive measure of which species actually use the plot for nesting, although it is possible to miss nests of species that are shy or stealthy or for which our nest searching methodology is not well suited. Thus, the abundance and nest webs should complement one another.

## Results

We detected 14 cavity-nesting species were detected during the censuses from 2002 - 2003 (Table 2.1, Fig. 2.3). Significant associations between these species and cavity resources are shown in the abundance web (Fig. 2.4). The abundance web reveals two groups into which most of the cavity-nesting species on Eglin can be placed. One group contains the red-cockaded woodpecker, brown-headed nuthatch (*Sitta pusilla*), eastern screech-owl (*Otus asio*), northern flicker, red-headed woodpecker (*Melanerpes erythrocephalus*), and southeastern American kestrel (*Falco sparverius paulus*), which are associated with pine snags and red-cockaded woodpecker cavities in live pines. The second group contains the Carolina chickadee (*Parus carolinensis*), downy woodpecker (*Picoides pubescens*), great-crested flycatcher (*Myiarchus crinitus*), red-bellied woodpecker (*Melanerpes carolinus*), and tufted titmouse (*Parus bicolor*), which are associated with hardwood snags. However, over half of the red-bellied woodpecker nests were found in pine snags and because this species was significantly correlated with a subset of pine snags (class 4;  $r = 0.26$ ,  $P = 0.03$ ,  $n = 72$ ), a dashed link was added to the pine web to indicate this relationship. The eastern screech-owl was rarely detected using our census methodology and thus, was not included in the pine abundance web, although nest data indicated this owl was a member of the pine group (see below). The eastern bluebird was associated with

the brown-headed nuthatch in 2002 ( $r = 0.51$ ,  $P = 0.002$ ,  $n = 36$ ), but had no significant associations with any other bird species or cavity resources in 2002 or 2003.

In 2002 and 2003, 432 cavity-nests were found, including nests of 13 of the 14 species of cavity-nesting birds (Table 2.2). A nest web illustrating cavity nest resource use at Eglin is shown in Figure 2.5, highlighting the proportion of nests for a given species found in particular resource type; SCNs are shown as using a cavity which was excavated by a particular PCE and PCEs are shown as using a particular tree type, regardless of whether that PCE was the excavator of the cavity. The nest web in Figure 2.6 shows the proportion of cavities excavated by a given species in each tree-type, regardless of which species was actually using the cavity for nesting at the time it was found. The Carolina chickadee is not shown in the nest web, as no nests were found for this species during the 2 years of this study. Only 1 eastern bluebird nest was found (in 2003), but we were unable to identify the excavator of the cavity and thus, it was also excluded from the nest web diagrams. The majority of nests were found in pine snags (60%, excluding cavities in dead red-cockaded woodpecker cavity trees,  $n = 260$ ). The second most commonly used resource was the living red-cockaded woodpecker cavity tree (27%,  $n = 116$ ), followed by hardwood snags (8%,  $n = 33$ ) and then dead red-cockaded woodpecker cavity trees (5%,  $n = 23$ ). These numbers were heavily influenced by the red-headed woodpecker, which was the most abundant cavity-nester detected in this study (37% of all nests found,  $n = 432$ ; mean 5.3 detections per plot) and used, almost exclusively, large pine snags with very little bark.

The red-cockaded woodpecker and northern flicker provided the greatest proportion of cavities used by other cavity-nesting birds in this system, relative to their nesting abundance (Fig. 2.5). Red-cockaded woodpecker nests accounted for only 15% of all nests found, but 33% of all nests were found in red-cockaded woodpecker cavities. Northern flicker nests accounted

for only 10% of all nests found, but 18% of all nests found were in cavities originally excavated by the northern flicker. The red-headed woodpecker excavated the majority of nest-cavities ( $n = 156$ ) at our study site; however, use of its cavities by other species was uncommon ( $n = 3$ ) (Fig. 2.5).

Most species detections were reflective of the nesting effort within each plot. Detections for 8 of the 14 species were significantly correlated with the number of nests found, including the southeastern American kestrel, downy woodpecker, great-crested flycatcher, hairy woodpecker (*Picoides villosus*), red-bellied woodpecker, red-cockaded woodpecker, red-headed woodpecker and tufted titmouse (Table 2.3). Detections for 3 species, the brown-headed nuthatch, northern flicker and pileated woodpecker (*Dryocopus pileatus*), were positively correlated with the number of nests found, but not significantly (Table 2.3). Correlations could not be computed for the remaining 3 species: the eastern bluebird and Carolina chickadee were frequently detected, but we found few or none of their nests, whereas we found many eastern screech-owl nests but rarely detected them in our censuses.

Neither of the non-cavity nesting bird groups (NonCavOpen or NonCavMidstory) were significantly associated with live red-cockaded woodpecker cavity trees ( $P = 0.79$  and  $P = 0.16$ , respectively;  $n = 72$ ), hardwood snags ( $P = 0.17$  and  $P = 0.89$ , respectively;  $n = 72$ ), or pine snags ( $P = 0.45$  and  $P = 0.43$ , respectively;  $n = 72$ ), indicating no confounding of habitat condition with cavity resource availability.

## Discussion

Classifying Eglin's cavity-nesting bird community into webs enables us to identify potentially important associations between the red-cockaded woodpecker and other cavity-

nesting species. The results of our community-wide study can contribute to red-cockaded woodpecker management in several ways, including examining the role of snags in structuring the cavity-nesting community at Eglin and the subsequent influence of snag availability on heterospecific use of red-cockaded woodpecker cavities, and identifying which species have the strongest associations with red-cockaded woodpecker cavities, and thus may be affected by red-cockaded woodpecker cavity management.

Our abundance web depicts 2 groups of cavity-nesting birds that occur in Eglin's sandhills ecotype, including (a) species associated primarily with pine snags and red-cockaded woodpecker cavities and (b) species associated with hardwood snags. To an extent, the birds in the pine and hardwood groups reflect habitat associations: most members of the pine web are known to be associated with open habitat and most members of the hardwood web are known to be associated with a hardwood midstory component (Shackelford and Conner 1997, Allen et al. 2006). For example, the association of the brown-headed nuthatch with red-cockaded woodpecker cavities is likely due to the former's foraging habits, rather than nesting resources, as brown-headed nuthatches forage primarily on large mature pine (Withgott and Smith 1998), which includes red-cockaded woodpecker cavity trees. However, the pine and hardwood grouping also reflects nest resource use. We believe that the abundance webs are also reflective of cavity-nest resource use for 3 reasons. First, there was no relationship between our measure of habitat condition and the 3 cavity resource types (red-cockaded woodpecker cavities, pine snags and hardwood snags), indicating that all 3 resource types were available to cavity-nesters regardless of habitat condition. Second, the abundance of cavity-nesting species was reflective of nesting effort within the study plots (Fig. 2.4). Third, the resource types of nests found for each species were generally reflective of the pine and hardwood groups shown in the abundance

web (Table 2.2). These results suggest that cavity resource type and availability may be influential in structuring the cavity-nesting bird community at Eglin.

Our results are consistent with other studies conducted at Eglin and elsewhere. Provencher et al. (2002) found no significant effect of hardwood midstory removal on the abundance of the Carolina chickadee, downy woodpecker, great-crested flycatcher, hairy woodpecker or pileated woodpecker. Allen et al. (2006) found the red-cockaded woodpecker, brown-headed nuthatch and red-headed woodpecker to be associated with open, upland longleaf pine, whereas the Carolina chickadee, great-crested flycatcher, northern flicker and red-bellied woodpecker were classified as generalist species (not significantly associated with either fire maintained or fire-suppressed habitat). Their results suggested that suitable cavity distribution may be more important to these cavity nesters than habitat condition alone. One exception may be the tufted titmouse, which is considered an indicator of hardwood midstory development in longleaf pine forests due to its negative response to red-cockaded woodpecker habitat management (Burger et al. 1998, Provencher et al. 2002). In our study, the tufted titmouse was negatively associated with both the red-cockaded woodpecker and its cavities ( $r = -0.30$ ,  $P = 0.01$  for both;  $n = 72$ ), suggesting that habitat structure may have a strong influence on the distribution of this species.

The hardwood group identified in this study likely reflects a minor and transitional group within the sandhills ecotype at Eglin. Relatively few nests were found in hardwood snags compared to pine snags and red-cockaded woodpecker cavities (Table 2.2). In addition, an abundance of hardwood snags was available at Eglin during this study, remnant of a hardwood midstory component that was killed with fire, herbicidal and girdling treatments used for red-cockaded woodpecker habitat management (Provencher et al. 2001a, 2001b). Many of these

hardwood snags were of sufficient diameter for cavity-excavation (>10.2 cm dbh), due to the years of fire suppression that preceded Eglin's midstory reduction efforts. Given the regular frequency of prescribed burning now conducted by Eglin land managers (D.O.D. 2002), these hardwood snags will likely not be replaced in similar numbers and sizes in the future.

The pine group is the numerically dominant group occurring in this study, with the majority of nests associated with pine snags and red-cockaded woodpecker cavity trees (Fig. 2.4, Table 2.2). The presence of old-growth pine snags at Eglin likely has a major influence on the dynamics of Eglin's cavity-nesting bird community, particularly those species in this pine web. Old-growth pine snags have large diameters and subsequent persistence over time (Miller and Marion 1995, Conner and Saenz 2005), making them a valuable resource for cavity-nesters. For example, Miller and Marion (1995) found that longleaf pine stands in Florida averaged twice the number of cavity-nesting birds with a snag density 40% lower than that of pine plantations, and attributed this to large, old and long-lasting longleaf pine snags. Indeed, the large old-growth pine snags at Eglin may account for one surprising aspect of this study, how little red-cockaded woodpecker cavities were used for nesting by other PCEs, WCEs and smaller SCNs.

The primary users of red-cockaded woodpecker cavities were large SCNs, including the eastern screech-owl and southeastern American kestrel. Of the eastern screech-owl and southeastern American kestrel nests found, 62% and 44%, respectively, were in cavities originally excavated by the red-cockaded woodpecker. In a previous study at Eglin, Gault et al. (2004) found 70% of southeastern American kestrel nests in cavities originally excavated by the red-cockaded woodpecker, although their nest searching effort focused on red-cockaded woodpecker clusters. At other sites in the southeast, frequent use of red-cockaded woodpecker cavities in living pine by other woodpecker species such as the red-bellied woodpecker and red-

headed woodpecker is well documented (Carter et al. 1989, Kappes and Harris 1995, USFWS 2003, Kappes 2004, Walters 2004, Walters et al. 2004). However at Eglin, red-cockaded woodpecker cavities accounted for only 6% of the PCE nests found. It is also surprising that no nests of smaller SCNs or WCEs were found in red-cockaded woodpecker cavities given their documented use of these cavities elsewhere (USFWS 2003). The uncommon use of red-cockaded woodpecker cavities by PCEs and small SCNs/WCEs at Eglin suggests that cavities in snags may have advantages over using existing red-cockaded woodpecker cavities in living pine, a possibility previously suggested by Kappes (2004).

The red-cockaded woodpecker and northern flicker were the main providers of cavities for other species at Eglin. The northern flicker was the primary creator of large cavities, through its excavation of new cavities in snags and enlargement of cavities originally excavated by the red-cockaded woodpecker in live pine. Northern flickers also occasionally enlarged red-headed woodpecker cavities (L. Blanc, Virginia Tech University, *personal observation*). In other locations, enlargement of red-cockaded woodpecker cavity entrances by other woodpecker species is common and generally pileated woodpeckers are considered the primary enlarger of these cavities (Jackson 1978, Walters 1991, Saenz et al. 1998, USFWS 2003). At Eglin, pileated woodpeckers do enlarge red-cockaded woodpecker cavity entrances, but only in a few areas on the reservation that have a strong mesic component (K. Gault, Eglin AFB, *personal communication*). In our study, we more frequently noted northern flicker enlargement and use of red-cockaded woodpecker cavities. In both the Southeast and the Pacific Northwest U.S., the pileated woodpecker has been referred to as the key provider of cavities required for nesting by large, secondary cavity-nesters (Saenz et al. 1998, Bonar 2000, Aubry and Raley 2002, Saenz et al. 2002, USFWS 2003), although this species produces few cavities relative to other PCEs

(Harestad and Keisker 1989, Martin and Eadie 1999, Bonar 2000). Given their greater numerical abundance, their tendency for cavity modification and the prevalent use of their cavities in this study, the northern flicker plays a greater role than the pileated woodpecker as a provider of large cavities for secondary cavity users at Eglin. This suggests that the northern flicker may be an important excavator in other fire-maintained southeastern pine forests as well, particularly in areas that don't have a strong mesic component. Elsewhere, the northern flicker has been identified as a significant excavator of large cavities used by secondary cavity-nesting species (Moore 1995, Martin and Eadie 1999, Martin et al. 2004, Saab et al. 2004), but that this role extends to the longleaf pine community was previously unappreciated.

#### Limitations of the data

It is likely that we underestimated the nesting effort of smaller SCNs and WCEs in this study due to timing and systematic limitations of our nest searching protocol. The nesting phenology of three species, the brown-headed nuthatch, Carolina chickadee and eastern bluebird (Gowaty and Plissner 1998, Withgott and Smith 1998, Mostrom et al. 2002), may be too early for our methods to produce a representative sample of nests during our study period. In addition, given our large plot-size and widely-spaced transects, our searching methodology may not have been well suited for locating nests in small, short snags, typical of these species. Therefore, we recommend that nest data on these smaller SCNs and WCEs be interpreted with caution.

Finally, the scope of this study is limited to the avian component of the cavity-nesting community at Eglin. Other cavity-users, in particular the southern flying squirrel (*Glaucomys volans*), regularly use red-cockaded woodpecker cavities and may influence cavity-use in this system (Kappes 2004).

## Conservation and management implications

Our results suggest that the red-cockaded woodpecker, through its cavity-excavation in living pine, may positively affect the abundance of the southeastern American kestrel, northern flicker and eastern screech-owl. They may also affect the abundance of other species such as red-headed woodpeckers, when suitable snags are not available on the landscape. We speculate that as snag availability at Eglin declines following years of ecosystem restoration and improvements in prescribed burning techniques, use of red-cockaded woodpecker cavities by this species will increase. Our results also suggest that the southeastern American kestrel and eastern screech-owl, the primary users of enlarged red-cockaded woodpecker cavities at Eglin, might be negatively affected by the use of cavity restrictor plates. The effect of cavity restrictors on the red-cockaded woodpecker has been studied (Carter et al. 1989, Raulston et al. 1996, Wood et al. 2000, Walters et al. 2004), however little is known about the impact of this management technique on species that require large cavities for nesting. Finally, our findings lend support to the hypothesis that retaining large pine snags on the landscape may indirectly benefit the red-cockaded woodpecker by reducing heterospecific occupation of red-cockaded woodpecker cavities (Kappes and Harris 1995, USFWS 2003).

The abundance of cavity resources at Eglin, in particular old-growth pine snags and red-cockaded woodpecker cavities, supports a number of cavity-nesting bird species that are in decline elsewhere. The southeastern American kestrel has declined by an estimated 82% since the early 1940's (McFarlane 1973, Hoffman and Collopy 1988) and is listed as threatened in the state of Florida (Wood 1996). However, this species is abundant at Eglin. In this study, 88% of southeastern American kestrel nests were in cavities originally excavated by the northern flicker

or red-cockaded woodpecker. Thus, these 2 excavators may play an important role as providers of cavities for large SCNs, such as the southeastern American kestrel.

The northern flicker has shown a large population decrease (>50%) in recent years and has been designated as a regional species of concern (Moore 1995, Panjabi et al. 2005). North American Breeding Bird Survey data from 1966 - 2005 indicate a 2% annual decline in the northern flicker throughout its range and a 5% decline in Florida, ranking it first among declining cavity-nesting species in the southeastern U.S. (Sauer et al. 2005). Conserving habitat for the northern flicker may be important given its role as a significant provider of large cavities for secondary cavity users.

The red-headed woodpecker, the most prolific cavity-nester in this study, is listed as a species of continental concern, showing decline in many parts of North America (Panjabi et al. 2005). The red-headed woodpecker is associated with mature, open woodland and clusters of snags resulting from catastrophic disturbance such as fire (Belson 1998, Smith et al. 2000). That longleaf savanna provides high quality habitat for this species is becoming more widely appreciated (Shackelford and Conner 1997, Belson 1998, Smith et al. 2000, Allen et al. 2006). The abundance of this species at Eglin appears to be closely tied to the availability of large pine snags for nesting. The highest detections of red-headed woodpeckers were in stands where clusters of large snags occurred due to overstory mortality from fire. Moreover, our study found almost exclusive use of pine snags by the red-headed woodpecker, consistent with other studies in Florida and South Carolina (Kilham 1977, Belson 1998, Lohr et al. 2002).

## Conclusions

In summary, this study provides a visual depiction of the relationship between cavity resources and cavity-nesting bird community structure within a fire-maintained longleaf pine ecosystem. The Eglin reservation supports a rich and abundant cavity-nesting bird community due to widespread availability of large pine snags and red-cockaded woodpecker cavities, both key resources for cavity-nesting birds in longleaf pine forests. Cavity-nesting species that are in decline elsewhere are abundant at Eglin and interspecific use of red-cockaded woodpecker cavities by other PCEs is not as prevalent as in many other southeastern pine forests. We propose that this is because PCEs are more dependent on red-cockaded woodpecker cavities in other areas than they are at Eglin, where the presence of large, mature pine snags provides an alternative nesting resource for these species. Indeed, the presence of numerous large pine snags makes Eglin unique among longleaf pine communities today and documenting the role of these snags in and importance to the cavity-nesting bird community is one of the most important results of this study. Another important finding was the identification of the northern flicker as a key provider of large cavities for large SCNs in this system. The dynamics of the cavity-nesting bird community on Eglin can be used as a baseline for comparison to communities elsewhere where the absence of large, old-growth snags may impose stress on the relationships between species and presumably increase competition between them. Additionally, the abundance and nest webs documented in this study can provide a context for examining direct and indirect interactions between species, including those involving the red-cockaded woodpecker.

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**Table 2.1.** Cavity nests found between April and July, 2002-2003 on Eglin Air Force Base in pine and hardwood (hdwd) snags, and live and dead Red-cockaded Woodpecker cavity trees. Species are presented in taxonomic order within guild, following the American Ornithologists Union Check-list of North American Birds, 7<sup>th</sup> edition (<http://www.aou.org/checklist/index.php3>).

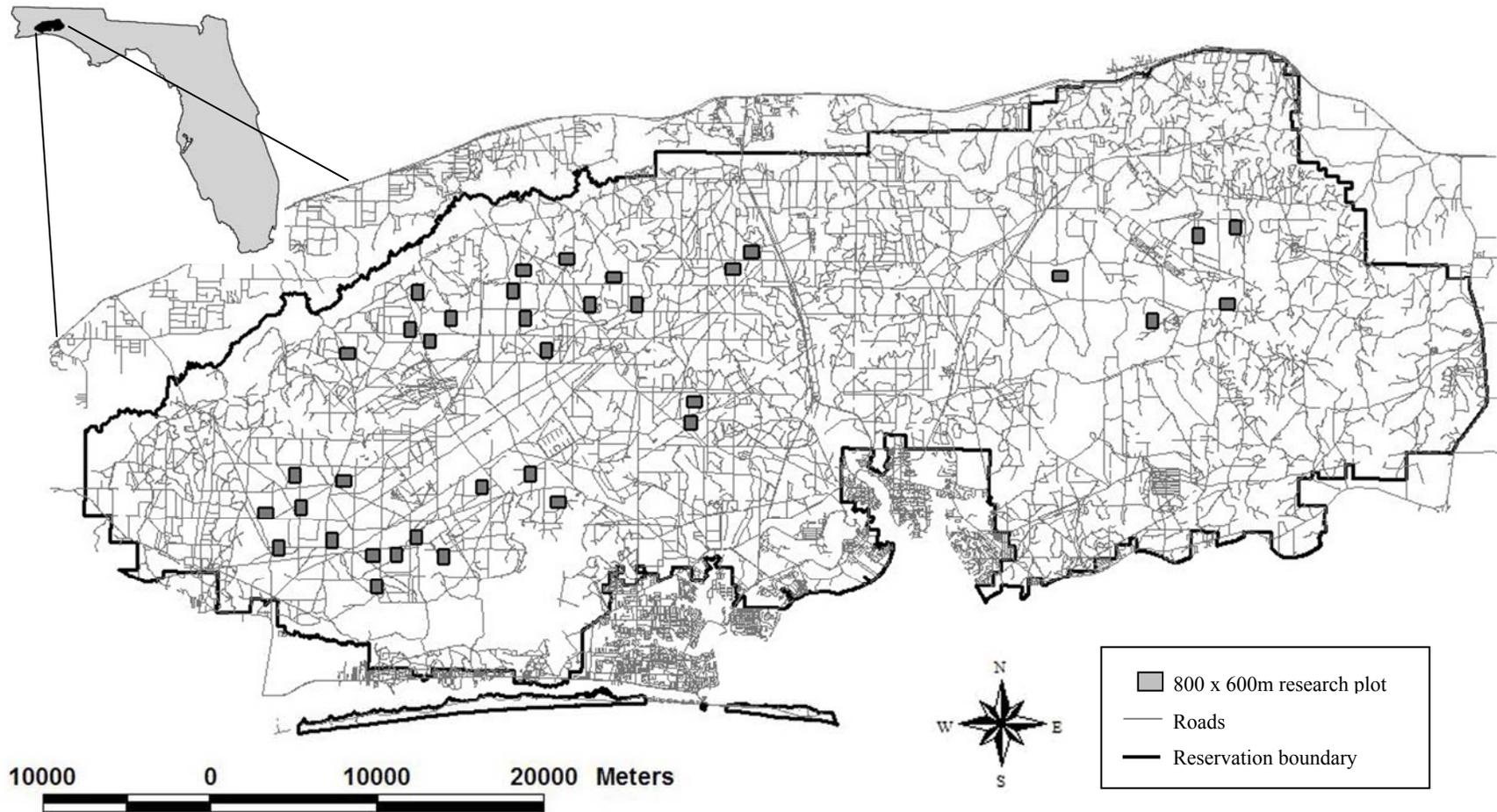
Scientific name	Common name	Snags		Red-cockaded Woodpecker cavity trees		No. nests found
		Pine	Hdwd	Live	Dead	
<b>Primary cavity excavators</b>						
<i>Melanerpes erythrocephalus</i>	Red-headed Woodpecker	153	0	1	4	158
<i>Melanerpes carolinus</i>	Red-bellied Woodpecker	22	11	7	1	41
<i>Picoides pubescens</i>	Downy Woodpecker	0	4	0	0	4
<i>Picoides villosus</i>	Hairy Woodpecker	0	2	0	0	2
<i>Picoides borealis</i>	Red-cockaded Woodpecker	0	0	63	0	63
<i>Colaptes auratus</i>	Northern Flicker	27	6	6	3	42
<i>Dryocopus pileatus</i>	Pileated Woodpecker	1	0	2	0	3
<b>Weak excavators</b>						

<i>Parus carolinensis</i>	Carolina Chickadee	0	0	0	0	0
<i>Sitta pusilla</i>	Brown-headed Nuthatch	0	2	0	0	2
<b>Secondary cavity-nesters</b>						
<i>Falco sparverius paulus</i>	Southeastern American Kestrel	50	0	25	14	89
<i>Otus asio</i>	Eastern Screech-Owl	5	3	12	1	21
<i>Myiarchus crinitus</i>	Great-crested Flycatcher	1	1	0	0	2
<i>Parus bicolor</i>	Tufted Titmouse	1	3	0	0	4
<i>Sialia sialis</i>	Eastern Bluebird	0	1	0	0	1
<b>Total</b>		260	33	116	23	432

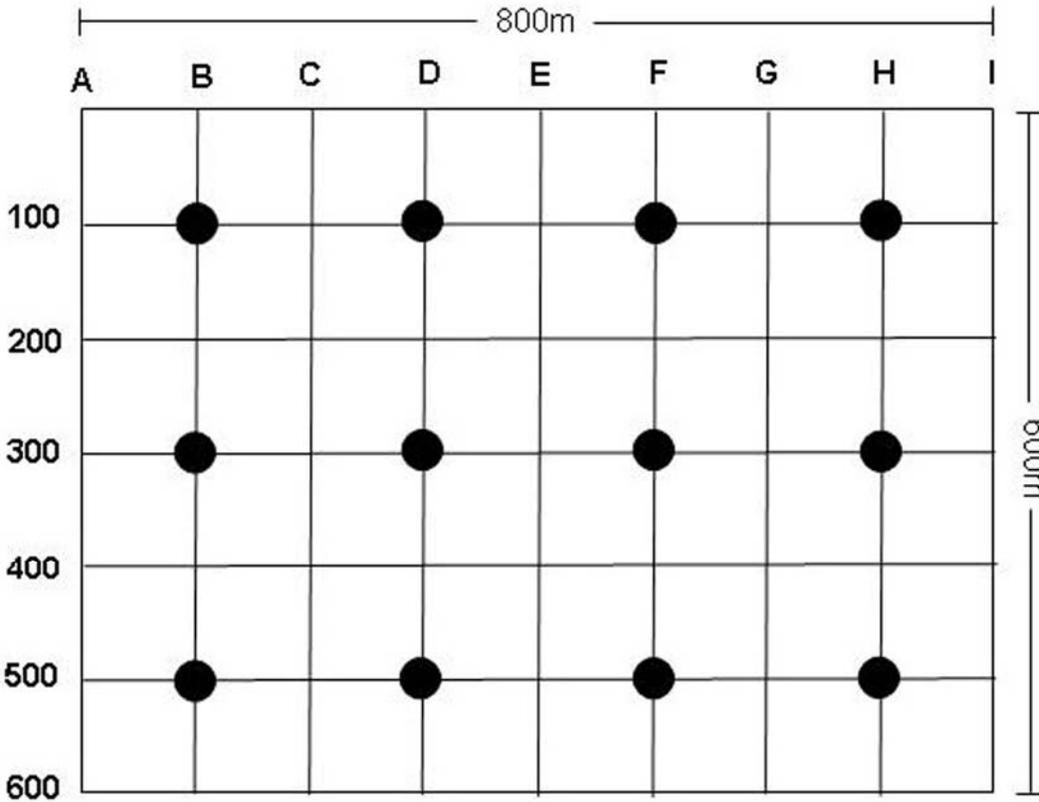
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**Table 2.2.** Correlation between number of individuals detected and number of nests found in each plot for each species between April and July 2002 - 2003 on Eglin Air Force Base, Florida. Because of lack of detections or nests found, correlations could not be computed for the eastern bluebird, Carolina chickadee and eastern screech-owl.

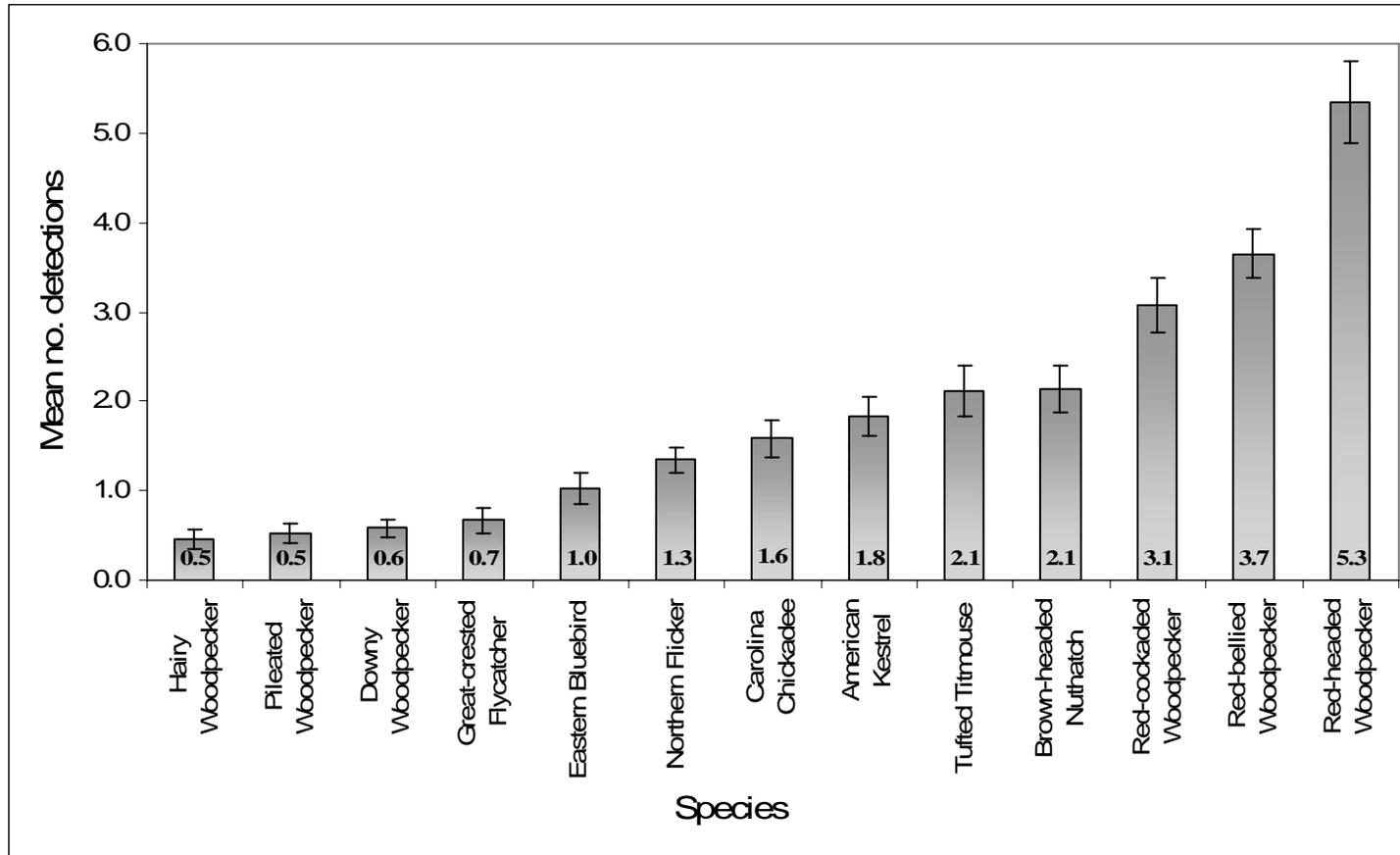
Species	Correlation coefficient	P-value
<b>Primary cavity-excavators</b>		
Red-headed Woodpecker	0.49	<0.001
Red-bellied Woodpecker	0.38	0.001
Downy Woodpecker	0.33	0.004
Hairy Woodpecker	0.33	0.004
Red-cockaded Woodpecker	0.79	<0.001
Northern Flicker	0.21	0.07
Pileated Woodpecker	0.21	0.07
<b>Weak excavators</b>		
Carolina Chickadee	--	--
Brown-headed Nuthatch	0.19	0.10
<b>Secondary cavity-nesters</b>		
Southeastern American Kestrel	0.65	<0.001
Eastern Screech-Owl	--	--
Great-crested Flycatcher	0.30	0.01
Tufted Titmouse	0.35	0.003
Eastern Bluebird	--	--



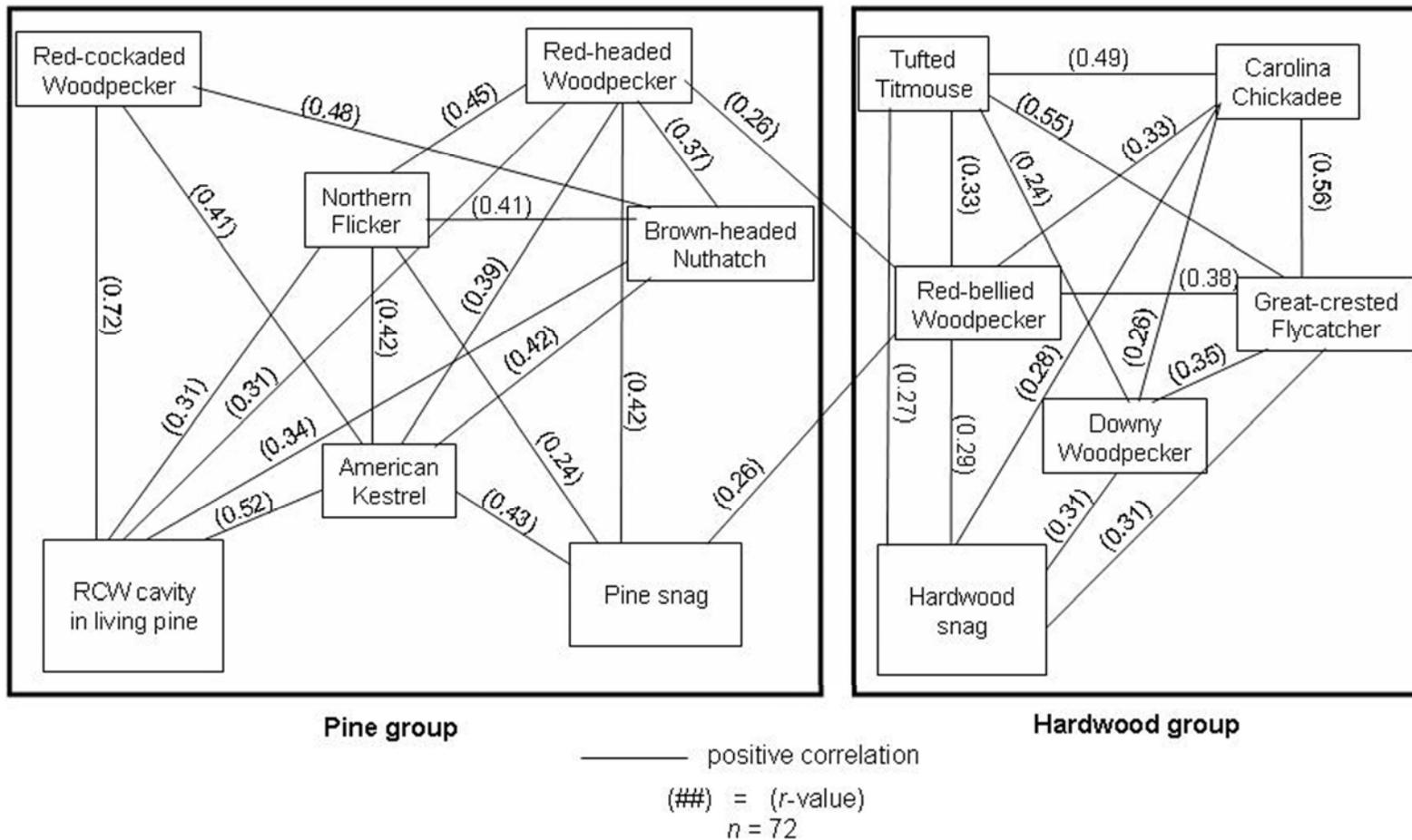
**Figure 2.1.** The location of the 36 research plots used in the cavity-nester study on Eglin Air Force Base, Okaloosa, Santa Rosa and Walton counties, Florida.



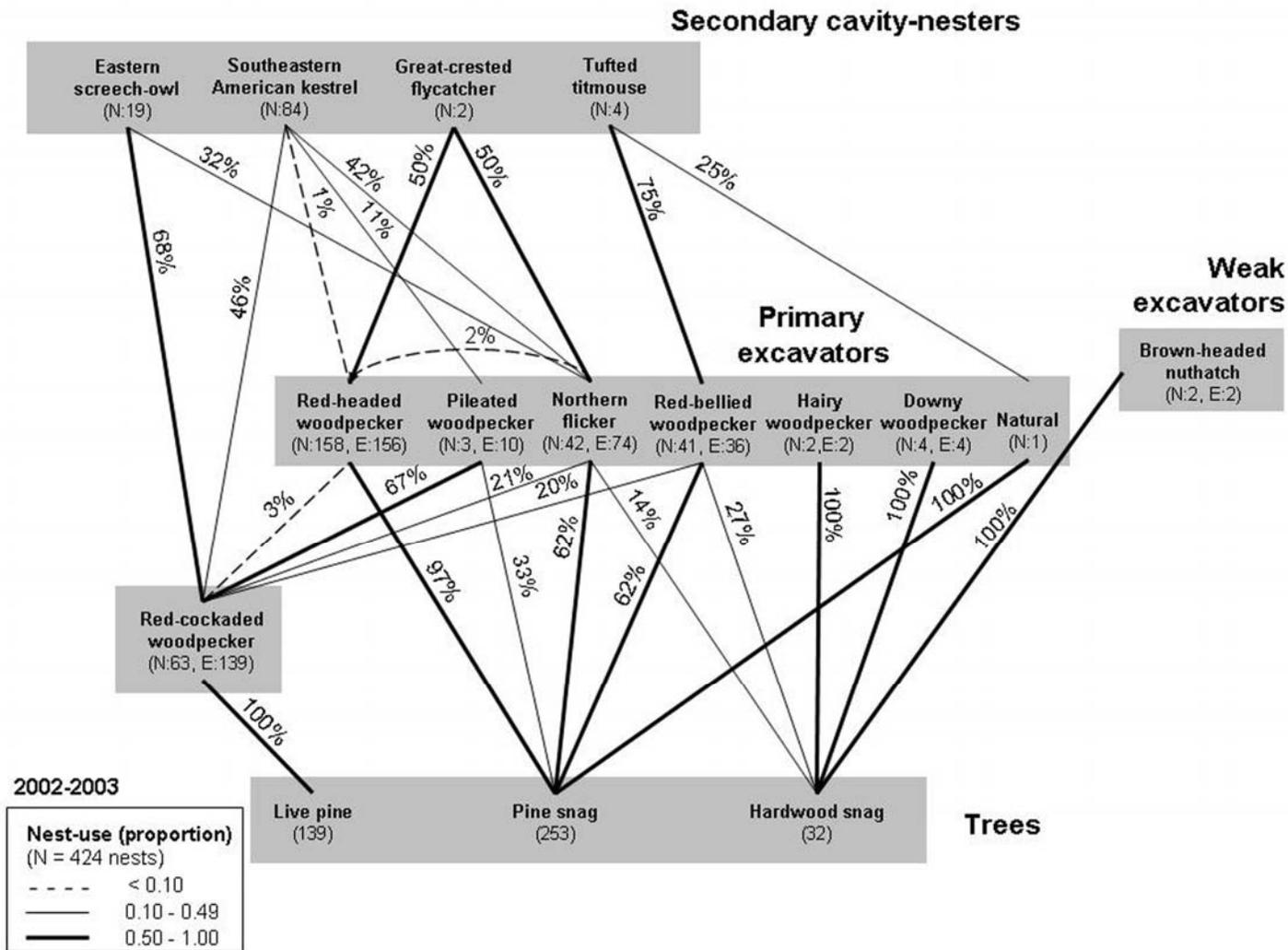
**Figure 2.2.** The layout of a research plot for the cavity-nester study on Eglin Air Force Base, Florida. Nine transects (labeled A-I), each 600 m in length, are spaced 100 m apart. Twelve census stations are located on alternating transects, spaced 200 m apart (indicated by the black circles). Due to landscape constraints, some plots have transects running north-south, while in other plots transects run east-west.



**Figure 2.3.** Detections (mean  $\pm$  SE) per 48-ha plot of cavity-nesting bird species on Eglin Air Force Base, Florida, based on point-counts conducted on 36 800 x 600 m plots from April through July 2002 - 2003. Species are ordered from lowest to highest number of detections per plot. Eastern screech-owls were only occasionally detected using our sampling methodology and thus are not included in this figure.

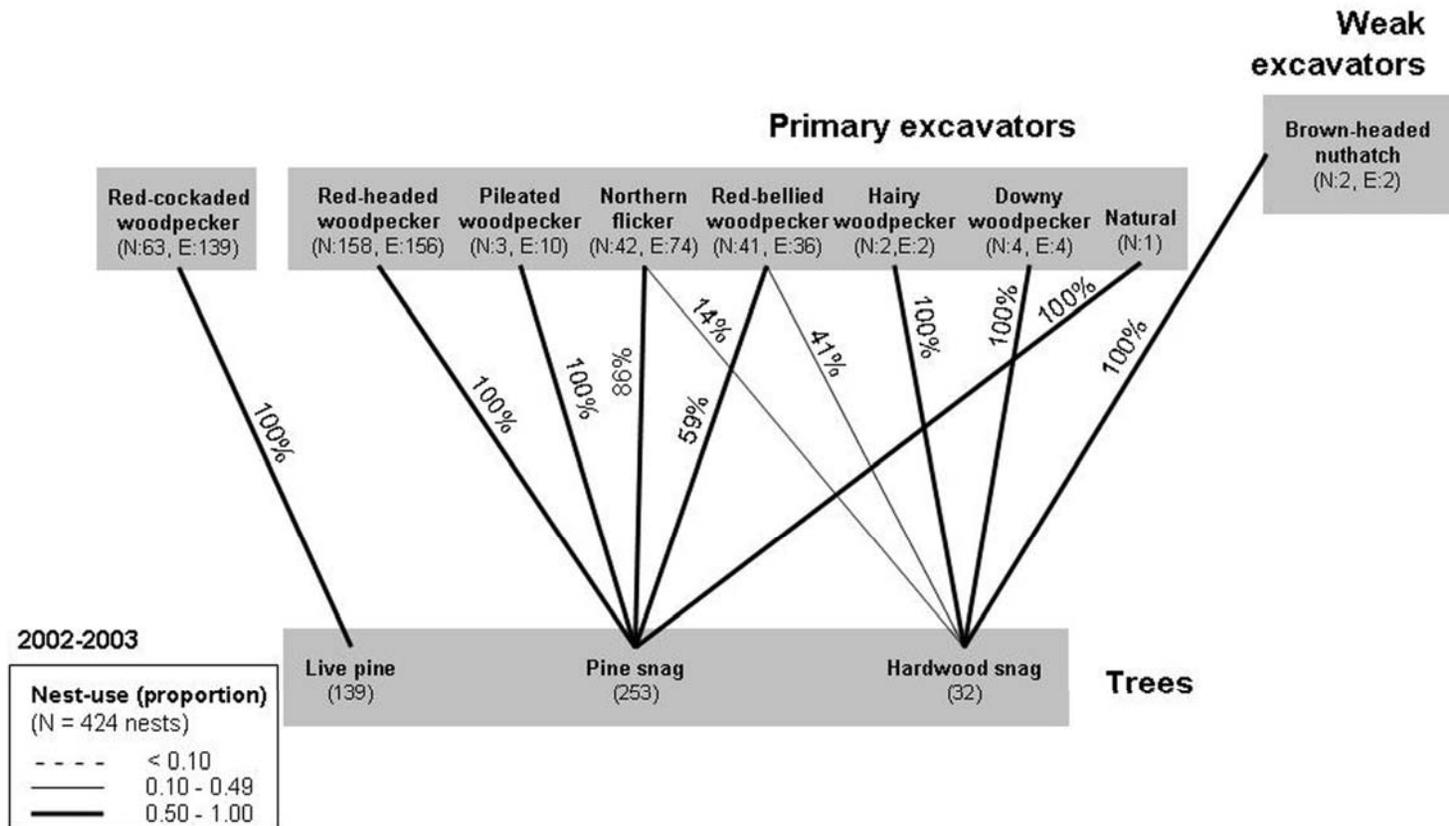


**Figure 2.4.** A bird-abundance web based on correlations of abundance data from Eglin Air Force Base, Florida, 2002 and 2003, pooled across both years. Numbers shown represent Spearman's partial correlation coefficients ( $r$ ), controlling for the number of mature pine. Only species that showed a significant correlation with a cavity resource are included in the web.



**Figure 2.5.** A nest web diagram highlighting nest resource use by the cavity-nesting bird community at Eglin Air Force Base, 2002 and 2003. N indicates the number of nests found for that species; E indicates the total number of all nest cavities excavated by that

species. Links between the secondary cavity-nester level and the primary cavity-excavator level represent the proportion of the secondary cavity-nester nests found in a cavity excavated by the indicated excavating species. Links between the primary cavity-excavator and tree levels reflect the proportion of that primary cavity-excavator's nests found in the connected tree resource. The link between the Northern Flicker and Red-headed Woodpecker indicates that 2% of Northern Flicker nests were found in cavities originally excavated by a Red-headed Woodpecker.



**Figure 2.6.** An excavation web diagram of the cavity nesting bird community on Eglin Air Force Base, 2002 and 2003. N indicates the number of nests found for that species; E indicates the total number of nesting cavities excavated by that species. Links between a primary cavity-excavator and the tree level reflect the proportion of all nest cavities excavated by that particular excavator in the tree resource.

## **Chapter 3: Snag-densities and cavity-nest site selection in a longleaf pine forest: implications for snag management**

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## Abstract

Snags are an important component of forested landscapes for cavity-nesting species. Despite wide-ranging and intensive silvicultural practices in southeastern pine forests, relatively little attention has been given to snag management in this region of the United States. A strong understanding of regional snag dynamics and cavity-nester requirements is essential to developing snag management guidelines. From 2002 - 2005, we documented snag densities and nest-site selection of the cavity-nesting bird community in an old-growth longleaf pine (*Pinus palustris*) forest located in the Florida panhandle. Pine snag densities ranged from 5.2-7.9 snags/ha. Hardwood snag densities ranged from 10.5-15.5 snags/ha. Mature pine snags within the 12.7-24.9 cm diameter class were the most abundant. Snag densities exceeded other reported densities and recommended guidelines proposed for southeastern pine forests. Cavity-nesters used trees with significantly larger diameters than what was available. With the exception of the red-cockaded woodpecker (*Picoides borealis*), which nests exclusively in living pine, cavity-nesters most frequently used large mature pine snags with little to no bark remaining (59% of nests found), despite the abundance of available red-cockaded woodpecker cavities in living pine. Although hardwood snags accounted for only 10% of nests found, these snags were used for either nesting or roosting by 12 of the 14 cavity-nesting species that occurred in this study. Cavity-nesters used hardwoods with significantly smaller diameters than pine. The diameters of nest-trees and available snags were below the range of optimal nest-snag diameters reported in other studies, indicating the need for regional or site-specific snag management guidelines. To avoid the inclusion of small pine snags that are insufficient for cavity-excavation, and the exclusion of small hardwoods that are suitable for cavity-nests, snag management guidelines for southern pine forests should differentiate between the two substrates when determining sufficient snag densities for cavity-nesting birds. We recommend that forest managers in the southeast retain existing snags on the landscape, and during harvesting operations, reserve a pool of large, mature pine trees for future snag recruits.

**Keywords:** cavity-nester, Florida, nesting ecology, *Picoides borealis*, *Pinus palustris*, snag management, southern pine forest, woodpecker.

## **Introduction**

Dead and decaying wood (snags) are critical components of forested landscapes, providing nesting, roosting, perching and foraging habitat for many wildlife species. Indeed, snags serve as the foundation of a web of cavity-nesting wildlife in forest communities (Martin and Eadie 1999). Snags are essential for woodpeckers to excavate tree cavities and because abandoned woodpecker cavities are regularly used by a broad range of birds, mammals, herpetofauna and insects, cavity creation may serve as a mechanism that influences community structure in forests worldwide (Martin and Eadie 1999, Virkkala 2006). In forests where naturally-occurring tree cavities are uncommon, woodpecker cavity-excavation may play a particularly important role in influencing cavity-nesting community structure. Guilds within cavity-nesting communities include primary cavity excavators (PCE), which typically excavate a new cavity each year for nesting (e.g., woodpeckers), weak excavators (WCE), which use existing woodpecker cavities or excavate their own, and secondary cavity-nesters (SCN), which cannot excavate cavities, and thus, rely upon the availability of existing cavities. In North America, at least 85 avian species nest in cavities (Scott et al. 1977).

Over 100 cavity-nesting bird species are in decline worldwide (reviewed in Eadie et al. 1998, Mikusinski 2006), largely due to loss of snags for cavity-nesting habitat. Because the number and diversity of cavity-nesting birds increase with snag density (Zarnowitz and Manuwal 1985, McComb et al. 1986, Brawn and Balda 1988, Land et al. 1989) and decline following snag-removal (Scott 1979, Scott and Oldemeyer 1983, Raphael and White 1984, Lohr et al. 2002), snags have been identified as an important part of managing forests for biological diversity (Sharitz et al. 1992, Martin and Eadie 1999, McComb and Lindenmayer 1999, Lohr et al. 2002). Snag management guidelines often focus on a number per acre prescription, however a growing body of literature emphasizes the influence of snag quality, as well as quantity, on

presence and abundance of cavity-nesting species (Miller and Marion 1995, Moorman et al. 1999, Jackson and Jackson 2004). Important qualitative factors of snags include diameter, tree species, stage of decay, diversity of snag-sizes on the landscape and method of the death or fungal infection (Mannan et al. 1980, Raphael and White 1984, Bunnell et al. 1999, Bunnell et al. 2002b, Farris and Zack 2005).

Despite wide-ranging and intensive silvicultural practices, little attention has been given to the importance of snags in pine forests of the southeastern United States. A number of studies in the Southeast have examined snag densities (Harlow and Guynn 1983, McComb et al. 1986, Miller and Marion 1995, Cain 1996, Moorman et al. 1999), and the relationship between some cavity-nesting species and snags (Conner 1978, Dickson et al. 1983, Land et al. 1989, Shackelford and Conner 1997, Lohr et al. 2002). Nonetheless, knowledge of the specific types of snags required by cavity-nesting birds in southern pine forests is still limited and, to our knowledge, no studies have documented cavity nest-site selection at the community level in southern pine forests.

Southern pine forests are dominated by living pine, with relatively few snags or hardwoods due to the historically low tree density and influence of regularly-occurring fire on the landscape (Conner et al. 2001). Nonetheless, these forests support 45 avian species that use snags for nesting, roosting or perching, including approximately 19 obligate cavity-nesting species (Hamel 1992). Efforts to manage for the exceptional biodiversity historically associated with southern pine forests (Bragg 2004, Engstrom and Conner 2006, Gilliam and Platt 2006, Mitchell et al. 2006) have focused primarily on prescribed burning, which benefits a diverse range of species (Conner et al. 2001, Litt et al. 2001, Provencher et al. 2001, 2002, Allen et al. 2006). Snags may serve as the next critical target for managing biodiversity in southern pine

forests, given the important role that dead wood plays in these forest communities (Lohr et al. 2002).

In this study, we examined avian cavity nest-site selection in a mature, longleaf pine (*Pinus palustris*) forest that recently experienced a pulse in tree mortality due to the reintroduction of fire after years of fire suppression. Subsequently, this forest contained a broad range of cavity resource types and sizes, including pine snags, hardwood snags and red-cockaded woodpecker (*Picoides borealis*) cavities in living pine. By documenting the nesting ecology of a cavity-nesting bird community in a mature, fire-maintained, snag-rich longleaf pine forest, we hope to develop a baseline upon which to examine how future changes in management of cavity resources may influence the structure of cavity-nesting bird communities in southern pine forests. In addition, we present estimates of snag availability within this pine forest and discuss implications for the development of snag management guidelines.

## **Methods**

### **Study Area**

We conducted fieldwork from 2002 through 2005 on Eglin Air Force Base, located on the western Florida panhandle, USA. Eglin is the largest forested military reservation in the United States (187,555 ha), and 78% of the land area consists of the longleaf pine sandhills ecotype (McWhite et al. 1999). This ecotype is characterized by a longleaf pine overstory, a relatively open mid-story of mostly turkey oak (*Quercus laevis*), and a ground cover of fire-adapted grasses and forbs (Kindell et al. 1997). Fourteen species of obligate cavity-nesting birds breed within the sandhills ecotype at Eglin (Table 3.1). Eglin contains a large amount of old-growth longleaf pine (Varner and Kush 2001), and over 6,000 red-cockaded woodpecker cavity

trees, of which over 1,700 are dead standing (Williams et al. 2006). In addition, Eglin has an atypical abundance of old-growth pine snags due to excessive tree mortality after the reintroduction of fire following years of suppression (Varner et al. 2005). Because Eglin land managers do not harvest dead trees, large, old-growth snags remain on the landscape. Just prior to this study, Eglin land managers conducted hardwood midstory reduction using mechanical and herbicidal methods (McWhite et al. 1999), resulting in an abundance of hardwood snags in a broad range of sizes. The presence of numerous large pine snags makes Eglin unique among longleaf pine communities today, and thus, makes it well suited for a large-scale study to develop baseline data on the ecology of cavity-nesting birds of the longleaf pine ecosystem.

## Methodology

In April 2002, we established 36 800 x 600 m research plots at Eglin. We restricted plots to areas within the sandhills ecotype that contained mature pine and a relatively open midstory. Each plot contained between 0 and 43 red-cockaded woodpecker cavities and natural variation in snag density. We conducted 2 rounds of nest searching in each plot within each season (between April and July, 2002 - 2005), and defined a nest as a tree cavity that contained either eggs or nestlings. We located nests by walking along transects in each plot, inspecting all red-cockaded woodpecker cavities in living pine, and all nest-snags with potential nest cavities. We inspected cavity contents using a camera mounted atop an extendable fiberglass utility pole (Treetop Peeper, Sandpiper Technologies Inc., Manteca, CA) which enabled us to access cavities up to 15 m in height. We also located cavity nests by observing breeding bird behavior and by checking tagged nest trees from previous years. For each nest, we recorded tree type (hardwood, pine), diameter at breast height (dbh), and cavity-height. We also

recorded the contents of all red-cockaded woodpecker cavities in each plot. We measured cavity-height using incremental height marks on the Treetop Peeper pole. We assigned nest trees to 1 of 5 decay classes: 1) living tree, 2) recently dead tree, most bark and branches and top of tree intact, 3) dead, >50% bark and branches intact, 4) dead, <50% bark/branches intact, top usually broken and 5) dead, no branches or bark, broken top, extensive decay. We established 12 25-m radius vegetation plots spaced 200 m apart within each study plot. In July of each year, we recorded the number of snags within each vegetation plot. We defined snags as dead, standing trees  $\geq 10.2$  cm and  $\geq 1.4$  m tall. For each snag, we recorded dbh, type (pine, hardwood) and decay class.

### Statistical Analyses

We analyzed nest and snag data using SAS, Version 9.1 (2003; SAS Institute Inc., Cary, North Carolina, USA). To calculate nest tree characteristics, we pooled nests across the 4-year period. Because other studies have indicated that reporting median characteristics of cavity-nest trees may be better suited for management guidelines (Bunnell et al. 2002a), we calculated medians, in addition to means, for tree diameters and cavity heights. For dbh calculations, we excluded duplicate nest-trees (i.e. re-use of the same tree or cavity by the same species) and snags that did not have a measurable dbh (i.e., when the lower portion of the tree was burnt to the heartwood, Fig. 3.1). We also excluded duplicate cavities for calculations of cavity heights. We calculated nest tree characteristics for both individual species and guilds. We calculated snag densities as follows: For each 25-m radius sampling station (0.196 ha), we calculated the number of hardwood and pine snags separately for each year. Using the 12 sampling stations as sub-samples within each research plot, we calculated the average number of snags per plot and

then averaged across plots for each year. Finally, we converted densities to a per-ha unit of measure. We calculated snag densities by tree type (hardwood, pine), and to facilitate comparison with other studies, we present snag densities for 6 dbh size classes (cm) (10.2 - 12.6, 12.7 - 24.9, 25 - 38.0, 38.1 - 48.0, 48.1 - 59.9, and >60).

We compared cavity-nester use versus availability of tree type (pine snag, hardwood snag, live pine) and decay class (1-5) using chi-square tests. In cases where the distribution of use was disproportionate to the distribution of availability ( $P < 0.05$ ), we compared one resource type (e.g., pine snag) to the remaining resource types (e.g., live pine and hardwood snags, pooled) to identify over- or under-proportional use of that particular resource. We compared cavity-nester use of tree diameters to availability using a *t*-test. We compared cavity heights and tree diameters of nests in pine to nests in hardwood using *t*-tests.

## Results

Between 2002 and 2005, we found 867 cavity nests for 14 species of cavity-nesting birds including 7 PCE's, 2 WCE's and 5 SCNs (Table 3.2). When examining nest tree characteristics, we included nests found outside of the research plots ( $n = 132$ ), to increase the sample. Use of cavity resources by cavity-nesters was disproportionate to availability ( $X^2 = 1452.3$ ,  $df = 2$ ,  $P < 0.0001$ ; excluding red-cockaded woodpeckers). Most cavity-nests occurred in pine snags ( $n = 551$  of 867, 64%) and living pine ( $n = 227$  of 867, 26%; Fig. 3.2). Hardwoods represented a smaller proportion of nests found at Eglin (live,  $n = 12$ , 1%; dead,  $n = 77$ , 9%; Fig. 3.2). Pine snags were used in over-proportion to their availability ( $X^2 = 764.5$ ,  $df = 1$ ,  $P < 0.0001$ ); hardwood snags were used under-proportionally ( $X^2 = 511.6$ ,  $df = 1$ ,  $P < 0.0001$ ). Red-cockaded woodpecker cavities in living pine were used under-proportionally ( $X^2 = 8.2$ ,  $df = 1$ ,  $P = 0.004$ ). All cavity-nests found in living hardwood and pine occurred within the bole of the tree. All

cavities in living pine were originally excavated by the red-cockaded woodpecker. Both pine and hardwood were used for nesting by 11 of the 14 species (Fig. 3.2). The red-cockaded woodpecker nested exclusively in living pine. Pileated (*Dryocopus pileatus*) and red-headed (*Melanerpes erythrocephalus*) woodpeckers nested only in pine, and downy (*Picoides pubescens*) and hairy (*P. villosus*) woodpeckers nested only in hardwood.

On average, 400 red-cockaded woodpecker cavities in living pine were inspected annually. Of the cavities that appeared to be viable (i.e., was not rotted or bottomless; annual mean = 383), 13% had nests, 52% of which were red-cockaded woodpeckers. The primary heterospecific users of red-cockaded woodpecker cavities in living pine were the American kestrel (*Falco sparverius*), eastern screech-owl (*Otus asio*), red-bellied woodpecker (*Melanerpes carolinus*), and northern flicker (*Colaptes auratus*), representing 34%, 24%, 19%, and 13% of all heterospecific nests in red-cockaded woodpecker cavities, respectively (Table 3.2). Large SCNs used red-cockaded woodpecker cavities in living pine over-proportionally ( $X^2 = 16.7$ ,  $df = 1$ ,  $P < 0.0001$ ). Use of red-cockaded woodpecker cavities by small SCNs and WCEs was rare, with only 1 nest of an eastern bluebird (*Sialia sialis*) over the 4-year period. Nine percent of other PCE nests were found in red-cockaded woodpecker cavities ( $n = 46$  of 508; Table 3.2) and the proportion of red-cockaded woodpecker cavities in living pine used by PCE's was significantly less than expected based on availability ( $X^2 = 21.0$ ,  $df = 1$ ,  $P < 0.0001$ ).

Cavity resource decay classes were used by cavity-nesting birds (excluding the red-cockaded woodpecker) disproportionately to what was available ( $X^2 = 508.7$ ,  $df = 4$ ,  $P < 0.0001$ ). Nest cavities in both pine and hardwood occurred most frequently in the level 4 (dead, <50% bark/branches intact, top usually broken) decay class trees ( $n = 446$  of 778, 57%;  $n = 42$  of 89, 47%, respectively). Excluding the red-cockaded woodpecker, which nest only in living pine,

PCEs used class 4 trees most frequently ( $n = 379$  of 508, 75%), in over-proportion to their availability ( $X^2 = 513.2$ ,  $df = 1$ ,  $P < 0.0001$ ). WCEs used only class 4 and 5 snags ( $n = 10$ ) (Fig. 3.3). Due to a small sample size ( $n = 10$ ), we were unable to assess WCE use of resources relative to availability. SCNs used the full range of decay classes (Fig. 3.3).

The average (cm; mean  $\pm$  SD) nest-tree dbh was  $34.5 \pm 7.4$  (median = 33.8 cm, Interquartile range (IQR) 29.4 – 39.4, range = 17.4 - 60) for pine and  $20.7 \pm 5.8$  cm (median = 20.3, IQR 17.3 – 24.5, range = 10.3 – 42.2) for hardwood. The average dbh (cm; mean  $\pm$  SD) of available snags at Eglin was  $24.9 \pm 8.8$  cm (median = 24.6, IQR = 17.9 - 31.1, range = 7.6 – 59.9) for pine and  $14.8 \pm 4.0$  (median = 13.8, IQR = 11.7 – 16.5, range = 10.2-46.2) for hardwood. Average nest-tree diameters were greater than what was available for both pine ( $t = -23.7$ ,  $df = 2358$ ,  $P < 0.0001$ ) and hardwood ( $t = -3.4$ ,  $df = 3961$ ,  $P < 0.0001$ ). The average (m; mean  $\pm$  SD) height of nest cavities was  $8.1 \pm 2.6$  (median = 7.8 m, IQR 6.2 – 9.8, range = 1.4 – 16.2) for pine and  $3.3 \pm 1.3$  (median = 3.1, IQR 2.3 – 4.0, range = 1.4 – 8.7) for hardwood. Both nest tree diameter and cavity height had high variation at the species level (Tables 3.3 and 3.4). Nests in hardwoods were in smaller diameter trees ( $t = -16.5$ ,  $df = 671$ ,  $P < 0.0001$ ) and had lower cavity heights ( $t = -17.0$ ,  $df = 763$ ,  $P < 0.0001$ ) than nests in pine (Figs. 3.4 and 3.5).

Annual pine snag densities at Eglin ranged from 5.2 snags/ha to 7.9 snags/ha (Table 3.5). Annual hardwood snag densities ranged from 10.5 snags/ha to 15.5 snags/ha (Table 3.5). Snags within the 12.7-24.9 cm diameter class were the most abundant (Table 3.6).

## **Discussion**

With the exception of the red-cockaded woodpecker, which nests exclusively in living pine, cavity-nesters at Eglin most often used large pine snags with little to no bark remaining

(59% of nests found). The predominant use of pine snags during this study, despite the abundance of red-cockaded woodpecker cavities, was surprising given the frequent heterospecific use of red-cockaded woodpecker cavities at other sites in the southeast (Carter et al. 1989, Kappes and Harris 1995, Kappes 2004, Walters 2004, Walters et al. 2004). Throughout this study, we noted many viable red-cockaded woodpecker cavities in living pine that went unused by birds for nesting (80 - 90% unused cavities annually), suggesting that cavities are not a limiting factor for cavity-nesting populations at Eglin. Southern flying squirrels (*Glaucomys volans*) were regular occupants of red-cockaded woodpecker cavities (10 - 20% of cavities annually). Because we often observed cavities containing flying squirrels early in the season that also had avian nests later in the same season, we considered these cavities to be available for use by cavity-nesting birds. Pine snags accounted for 73% of all non-red-cockaded woodpecker nests ( $n = 551$  of 752). Efforts to prevent heterospecific use of red-cockaded woodpecker cavities are common in managed populations throughout the southeast (USFWS 2003). The data presented here suggest that pine snags may have qualitative advantages over red-cockaded woodpecker cavities in living pine, and that retaining these snags on the landscape may reduce heterospecific use of red-cockaded woodpecker cavities. Other studies have found inconsistent relationships between snag availability and heterospecific use of red-cockaded woodpecker cavities (Harlow and Lennartz 1983, Everhart et al. 1993, Kappes and Harris 1995), and this may be due to qualitative differences in the available snags that were measured.

The availability of large, mature pine snags may be the critical factor influencing cavity-nest site selection observed in this study. Old-growth pine snags have large diameters and subsequent persistence over time (Miller and Marion 1995, Conner and Saenz 2005), making them a valuable resource for cavity-nesters (Moorman et al. 1999). Indeed, Miller and Marion

(1995) found that forested stands in Florida containing large, old and long-lasting longleaf pine snags averaged twice the number of cavity-nesting birds, despite having a snag density 40% lower than that of younger pine plantations.

One striking result in this study was that hardwood snags, often overlooked as a cavity-nesting resource in southern pine forests, were used for nesting by 11 of the 14 species, and as roosting sites for fledglings of an additional species, the red-headed woodpecker (L. Blanc, Virginia Tech University, *personal observation*). In addition, 8 out of 10 WCE nests were found in hardwood (Table 3.2), consistent with findings by Bunnell et al. (2002b). Current management and restoration regimes often eliminate hardwoods in the effort to create an open midstory, however, a small hardwood component may play an important role in supporting biological diversity in these forests (Johnson and Landers 1982, Zobrist et al. 2005). The results of this study, along with others (McComb et al. 1986, Cain 1996, Rosenstock 1998), suggest that retaining a small number of hardwood snags in southern pine forests may be important to cavity-nesters. Indeed, it has been suggested that a small hardwood component of scattered oaks was probably normal in historical, fire-maintained, longleaf pine forests (Landers and Boyer 1999, Engstrom and Conner 2006).

With the exception of red-cockaded woodpecker cavities in living pine, most cavity nests occurred in snags that were considerably decayed, often with very little bark and branching. PCEs were more flexible in their use of decay class than WCEs, which only used snags in the greatest stages of decay (Fig. 3.3). This variation in use of snag decay-classes for nesting likely reflects differences in the excavation ability of PCEs and WCEs. SCNs used the full range of decay classes (Fig. 3.3), possibly reflecting their reliance upon existing cavities.

Consistent with other studies (Zarnowitz and Manuwal 1985, Schreiber and deCalesta 1992, Dobkin et al. 1995), cavity-nesters nested in trees that were larger in diameter than what was available (Fig. 3.4). Nest-tree diameters at Eglin, particularly nests in hardwood snags, were smaller than previously reported diameters used to generate recommendations for snag management in the Southeast (Conner et al. 1983b, Harlow and Guynn 1983, McComb et al. 1986). We attribute this discrepancy to two causes. First, all three of these studies used the same source (Evans and Conner 1979) for nest-tree diameters in their calculations; it is unclear whether the source data, which was adapted for southern pine forests, included nests in hardwood snags. Second, pine trees at Eglin are relatively small in diameter compared to other southeastern pine forests, likely due to very low soil productivity in the sandhills (Provencher 1998). For example, pines >45 cm dbh are rare at Eglin, even in stands over 300 years old (Provencher 1998). Others have noted that pine forests in Florida could be expected to support 20 - 30% of average woodpecker populations found in other regions, due to inadequate densities of snags >25 cm dbh (Harlow and Guynn 1983, McComb et al. 1986).

Cavity-nesters used significantly smaller hardwoods than pine (Table 3.3). Other studies have noted that hardwoods can support the same bird species with a smaller dbh (Rosenstock 1998, Bunnell et al. 1999, 2002a, Boyland and Bunnell 2002). Hardwoods decay at younger ages and smaller sizes than pines due to their greater susceptibility to decay and faster rotting rates (Harmon 1982, Cain 1996, Bunnell et al. 1999), and thus, can provide suitable cavity-sites relatively quickly. In contrast, pine snags take longer to decay sufficiently for cavity excavation, however large sizes and slower decay rates enable them to persist longer than hardwoods (Bunnell et al. 1999).

Overall, snag densities at Eglin exceeded recommendations for southern pine forests (Harlow and Guynn 1983), and for Florida (McComb et al. 1986) (Table 3.6). Snags >38 cm dbh, however, were below recommended densities, likely due to the smaller diameter of trees attainable at Eglin (see above). Snag densities at Eglin are among the highest reported in southern pine forests (Harlow and Guynn 1983, Land et al. 1989, Miller and Marion 1995, Landers and Boyer 1999, Lohr et al. 2002), and similar to reported historical densities from the early 1900s (Landers and Boyer 1999). Moorman et al. (1999) reported similar snag densities for a loblolly (*Pinus taeda*) pine plantation >40 years old and a pine-hardwood forest >50 years old. Similar to Eglin, snags were rarely salvaged at their study site and most snags in pine plantation were large, mature trees that had been retained during harvesting operations (Moorman et al. 1999).

Our calculation of snag densities, based on dbh class, was complicated by large pine snags at Eglin for which the lower portion of the bole was burnt to the heartwood from fire exposure (Fig. 3.1). These snags are reported as an un-measurable size class in Table 3.6, but were frequently large enough to accommodate cavity-nests of American kestrels and northern flickers. In fact 16% of the nests found in pine snags ( $n = 86$  of 551) were in such trees, including nests of 20 American kestrels, 1 eastern bluebird, 14 northern flickers, 8 red-bellied woodpeckers and 43 red-headed woodpeckers. We contend that most of these snags fall in the 25.0 – 38.0 and 38.1 – 48.0 cm dbh size-classes.

Our findings emphasize two potential complications associated with the development of snag management guidelines. First, variation in forest productivity associated with soil characteristics and climate, which ultimately influences the number and characteristics of snags in different sites (Boyland and Bunnell 2002, Laudenslayer 2005), can make snag management

guidelines based on tree diameters in one region unrealistic elsewhere. Indeed, previously reported snag management recommendations for southern pine forests may be unsuitable for Eglin, given the smaller average dbh pine trees at Eglin relative to other southern pine forests. Second, qualitative differences between snag resource types, such as the suitability of hardwoods for cavity excavation at smaller diameters than pine, must also be factored in to snag management. In previous studies of southern pine forests, only Harlow and Gwynn (1983) differentiated between pine and hardwood snags when reporting densities, however they did not consider the different dbh requirements for use of hardwood and pine by cavity-nesters when calculating snag density recommendations. Our data indicate that such an omission could confound available snag resources, either by omitting small, but usable, hardwood snags or by including small pine snags that may not be suitable for cavity-excavation.

In recent years, researchers have focused on identifying and managing ecological processes that create suitable habitat for cavity-nesters (Bednarz et al. 2004, Jackson and Jackson 2004, Laudenslayer 2005). Laudenslayer (2005) recommended that management guidelines focus on processes underlying the flow of snag recruitment and loss to ensure continued functioning of forests over time. Others recommend maintaining a diverse range of tree size classes on the landscape to provide greater variability in snag recruitment and decay rates for cavity-nesters over the long term (Bunnell et al. 2002a). In southern pine forests, the 3 predominant types of cavity-resources may have very different recruitment and loss dynamics. Hardwood snags decay quickly relative to pine, but fall more quickly as well (Harmon 1982, Cain 1996, Bunnell et al. 1999). Pine snags take longer than hardwood to decay sufficiently for cavity excavation, but can remain on the landscape for 8 years or more in southern pine forests (Conner and Saenz 2005). A red-cockaded woodpecker cavity can take several years to

excavate, but can remain in use for several decades (Jackson 1994). The potential differences in decay dynamics among pine snags, hardwood snags, and living pine may provide a complementary range of cavity-resource recruitment and loss rates, and thus, maintain habitat stability for cavity-nesters within dynamic, fire-maintained southern pine forests. Of the 14 cavity-nesting species that occurred in this study, 8 used red-cockaded woodpecker cavities in living pine, 10 used pine snags, and 11 used hardwood snags. In addition, 6 of these species used all 3 cavity resources for either nesting or roosting, lending support to the possibility that the complementary dynamics of these different resources may have an important influence on cavity-nesting bird community structure, however further research is needed.

The need to develop snag management guidelines for the southeastern region is becoming increasingly important as demand for wood production grows. Snag densities are higher on public land and unmanaged forests than on privately owned land and pine plantations (McComb et al. 1986). Most forested land in the south is privately owned (89%, Wicker 2002), including approximately 12.5 million ha of intensely managed loblolly pine plantations (Sheffield and Dickson 1998). Over the next few decades, the land base for wood production in the southeast is expected to shift from natural forests to intensively managed loblolly pine plantations, with the area of pine plantations projected to increase by up to 67% in 2040 (Allen et al. 2005, Ware and Greis 2002). However, managed plantations typically lack the diversity of tree sizes and abundance of snags essential to cavity-nesting species (Hansen et al. 1991). Subsequently, there are concerns about maintaining biological diversity in southern pine forests (Noss 1988, Bragg 2004, Zobrist et al. 2005). As an important component of forest ecosystems (Virkkala 2006) and general indicators of forest biodiversity (Mikusiński et al. 2001), woodpeckers, and the snag resources they rely upon, must be integrated into forest management plans if the maintenance or

restoration of biodiversity is a goal. Although a number of techniques have been proposed for snag and nest-box creation in southern pine forests (Caine and Marion 1991, Conner et al. 1983a, b, Conner and Saenz 1996), retaining existing snags is likely a more practical management goal, requiring less labor and money than snag-creation or nest-box placement. Indeed, a growing body of research indicates that retaining a pool of large, mature pine trees as future snag recruits may provide a more effective management alternative to creating a large number of small, young pine snags that may not be well-suited for cavity-excavation.

### **Management implications**

Understanding factors that can complicate snag management is crucial to the successful development and application of management guidelines. Our results highlight several important areas of consideration when developing snag management guidelines, including 1) integrating nest-site selection and tree-size availability from the local scale into management guidelines, 2) differentiating between snag resources that show qualitative differences in cavity-nester use, such as the differences between hardwood and pine snags presented here, 3) retaining a supply of large, mature pine trees for future snag recruitment as part of a long-term management strategy, and 4) maximizing the retention of existing snags on the landscape.

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**Table 3.1.** Cavity-nesting bird species that breed in the sandhills ecotype on Eglin Air Force Base, Florida, based on a study conducted from 2002 - 2005. Species are presented in taxonomic order within guild, following the American Ornithologists Union Check-list of North American Birds, 7<sup>th</sup> edition (<http://www.aou.org/checklist/index.php3>).

Scientific name	Common name	Guild
<i>Melanerpes carolinus</i>	Red-bellied woodpecker	Primary excavator
<i>Melanerpes erythrocephalus</i>	Red-headed woodpecker	Primary excavator
<i>Picoides pubescens</i>	Downy woodpecker	Primary excavator
<i>Picoides villosus</i>	Hairy woodpecker	Primary excavator
<i>Picoides borealis</i>	Red-cockaded woodpecker	Primary excavator
<i>Colaptes auratus</i>	Northern flicker	Primary excavator
<i>Dryocopus pileatus</i>	Pileated woodpecker	Primary excavator
<i>Parus carolinensis</i>	Carolina chickadee	Weak excavator
<i>Sitta pusilla</i>	Brown-headed nuthatch	Weak excavator
<i>Falco sparverius</i>	American kestrel	Secondary cavity-nester
<i>Otus asio</i>	Eastern screech-owl	Secondary cavity-nester
<i>Myiarchus crinitus</i>	Great-crested flycatcher	Secondary cavity-nester
<i>Parus bicolor</i>	Tufted titmouse	Secondary cavity-nester
<i>Sialia sialis</i>	Eastern bluebird	Secondary cavity-nester

**Table 3.2.** Nests found between April and July 2002 - 2005 at Eglin Air Force Base, Florida.

Numbers include re-use of the same cavity across years, but not re-nesting attempts by the same species in the same cavity within the same year. All cavities in living pine were originally excavated by the red-cockaded woodpecker. Species are presented in taxonomic order within guild (primary cavity excavators, weak cavity excavators, and secondary cavity-nesters).

Species	Hardwood		Pine		Total
	Dead	Live	Dead	Live	
<i>Melanerpes carolinus</i>	24	4	34	21	83
<i>Melanerpes erythrocephalus</i>	0	0	301	9	310
<i>Picoides pubescens</i>	7	3	0	0	10
<i>Picoides villosus</i>	5	1	0	0	6
<i>Picoides borealis</i>	0	0	0	115	115
<i>Colaptes auratus</i>	11	2	66	14	93
<i>Dryocopus pileatus</i>	0	0	4	2	6
<i>Parus carolinensis</i>	4	0	0	0	4
<i>Sitta pusilla</i>	4	0	2	0	6
<i>Falco sparverius</i>	2	0	123	38	163
<i>Otus asio</i>	10	1	17	27	55
<i>Myiarchus crinitus</i>	1	0	1	0	2
<i>Parus bicolor</i>	6	1	2	0	9
<i>Sialia sialis</i>	3	0	1	1	5
Total	77	12	551	227	867

**Table 3.3.** Median diameter at breast height (cm) of pine and hardwoods used by cavity-nesting birds at Eglin Air Force Base, FL from 2002 - 2005. Data are based on 673 nests (588 pine, 85 hardwood) and do not include re-use of the same tree by any species, or snags without a recordable dbh. Species are presented in taxonomic order within guild (primary cavity excavators, weak cavity excavators, and secondary cavity-nesters).

Species	Pine dbh (cm)				Hardwood dbh (cm)			
	<i>n</i>	Median	IQR	Range	<i>n</i>	Median	IQR	Range
<i>Melanerpes carolinus</i>	41	36.0	31.2-39.0	24.1-49.5	26	22.1	20.3-25.5	15.7-42.2
<i>M. erythrocephalus</i>	231	30.1	26.9-33.7	17.4-59.1	0	--	--	--
<i>Picoides pubescens</i>	0	--	--	--	10	17.3	13.8-17.7	11.5-24.2
<i>P. villosus</i>	0	--	--	--	6	16.4	15.7-17.1	14.6-20.3
<i>P. borealis</i>	86	39.2	35.5-42.0	21.7-55.3				
<i>Colaptes auratus</i>	62	35.0	30-39.8	20.1-47.2	12	20.7	19.1-23.6	18-30.4
<i>Dryocopus pileatus</i>	5	36.6	35.9-38.1	35-45.3	0	--	--	--
<i>Parus carolinensis</i>	0	--	--	--	4	11.9	10.9-14.7	10.5-16.9
<i>Sitta pusilla</i>	2	21.6	18-25.2	18-25.2	4	15.6	11.75-18.45	10.8-18.5
<i>Falco sparverius</i>	118	37.4	31-42.1	20-57.9	2	25.7	20.3-31.1	20.3-31.1
<i>Otus asio</i>	39	38.7	33.6-42.2	28.1-60	10	25.6	21.3-29.7	18.1-31.1
<i>Myiarchus crinitus</i>	1	23.3	23.3-23.3	23.3-23.3	1	26.6	26.6-26.6	26.6-26.6
<i>Parus bicolor</i>	2	29.7	29.4-29.9	29.4-29.9	7	18.4	17.8-23.3	10.3-25.9
<i>Sialia sialis</i>	1	43.6	43.6-43.6	43.6-43.6	3	16.4	10.9-14.7	10.9-17.2

**Table 3.4.** Median height (m) of avian nest-cavities at Eglin Air Force Base, FL from 2002 - 2005. Data are based on 765 nests (677 pine, 88 hardwood) and don't include reuse of the same cavity by the same species. Species are presented in taxonomic order within guild (primary cavity excavators, weak cavity excavators, and secondary cavity-nesters).

Species	Pine (m)				Hardwood (m)			
	<i>n</i>	Median	IQR	Range	<i>n</i>	Median	IQR	Range
<i>Melanerpes carolinus</i>	50	9.9	7.3-12.2	3.8-15.8	28	3.9	3.2-4.4	1.4-8.7
<i>M. erythrocephalus</i>	304	8.2	6.7-10.3	3.6-15.2	0	--	--	--
<i>Picoides pubescens</i>	0	--	--	--	10	3.0	2.7-4.2	2.3-7.6
<i>P. villosus</i>	0	--	--	--	6	3.4	3.1-3.8	2.1-4.4
<i>P. borealis</i>	70	6.5	5.8-8.2	2.4-11.3				
<i>Colaptes auratus</i>	74	7.0	5.6-8.9	2.3-12.5	13	2.8	2.2-3.3	1.7-5.6
<i>Dryocopus pileatus</i>	5	6.5	5.7-11.0	4.4-11.5	0	--	--	--
<i>Parus carolinensis</i>	0	--	--	--	4	2.0	1.5-3.2	1.4-3.8
<i>Sitta pusilla</i>	2	2.5	1.8-3.2	1.8-3.2	4	2.0	1.9-2.6	1.9-3.0
<i>Falco sparverius</i>	129	7.6	6.4-9.4	1.7-16.2	2	3.9	2.1-5.6	2.1-5.6
<i>Otus asio</i>	38	6.8	5.9-8.2	2.7-11.6	10	2.5	1.9-3.5	1.8-4.1
<i>Myiarchus crinitus</i>	1	12.5	12.5-12.5	12.5-12.5	1	2.6	2.6-2.6	2.6-2.6
<i>Parus bicolor</i>	2	4.2	1.4-6.9	1.4-6.9	7	2.9	2.4-4.4	1.7-4.9
<i>Sialia sialis</i>	2	4.8	3.4-6.2	3.4-6.2	3	1.5	1.4-2.6	1.4-2.6

**Table 3.5.** Average (mean  $\pm$  SE) snag densities (stems/ha) on the 36 study plots at Eglin Air Force Base, Florida between 2001 and 2005. All snags  $>10.2$  cm dbh and  $>1.4$  m in height were recorded annually at 432 permanent sampling stations located within 36 study plots.

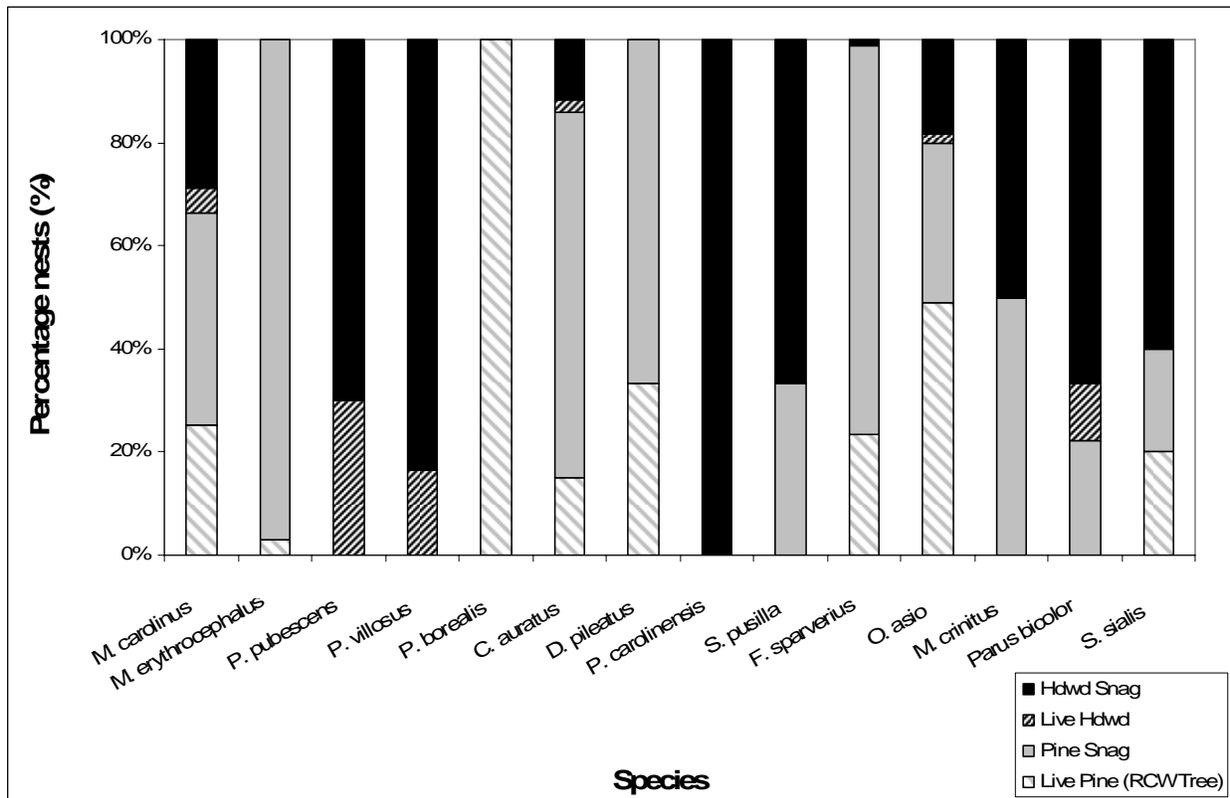
	2002	2003	2004	2005
Hardwood	13.9 (1.6)	15.5 (3.4)	10.6 (1.9)	10.5 (2.1)
Pine	7.9 (0.9)	8.0 (1.8)	5.2 (0.6)	5.2 (0.7)
Combined	21.8 (1.1)	23.5 (1.8)	15.8 (1.0)	15.7 (1.1)

**Table 3.6.** Snag densities at Eglin Air Force Base, Florida, compared to recommended dbh size class densities from other studies in the southeastern U.S. To facilitate comparison, recommendations from other studies are presented here in a per-ha format. Values for Eglin are means across 4 years. Snag data were recorded annually at 432 permanent sampling stations located within 36 study plots. The “un-measurable” size class is comprised of snags for which dbh could not be measured due to fire damage on the lower portion of the tree. Values with an asterisk indicate size classes that were combined in McComb et al. (1986).

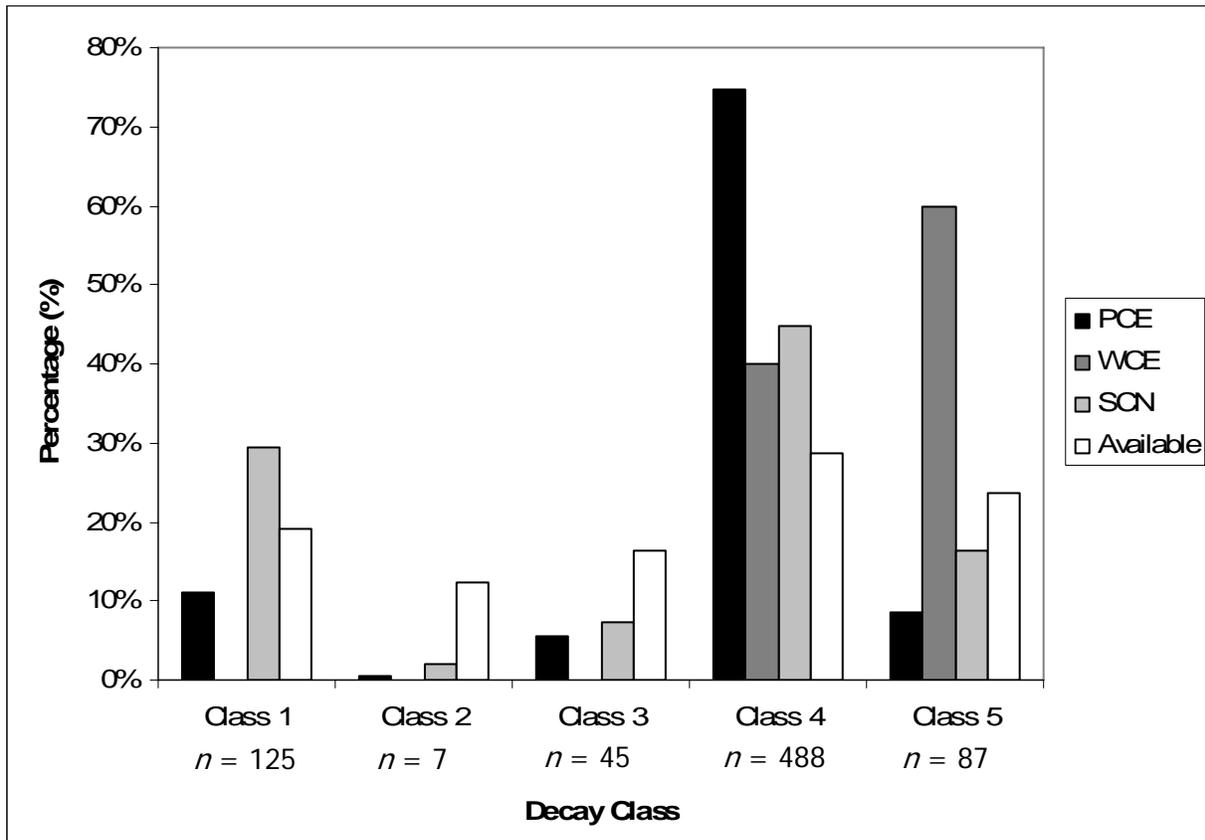
Dbh class (cm)	Harlow and Guynn (1983)	McComb et al. (1986)	Eglin Air Force Base		
			Pine	Hardwood	Combined
Un-measurable	n/a	n/a	1.36	1.19	2.55
10.2 - 12.6	n/a	n/a	0.47	3.96	4.43
12.7 - 24.9	0.91	3.00	2.19	7.04	9.23
25.0 - 38.0	1.05	2.10*	2.16	0.28	2.44
38.1 - 48.0	1.00		0.36	0.01	0.37
48.1 - 59.9	0.13	0.20*	0.04	0.00	0.04
60+	0.02		0.00	0.00	0
Total >12.7	3.11	5.30	4.75	7.32	12.07
Total overall	3.11	5.30	6.58	12.48	19.06



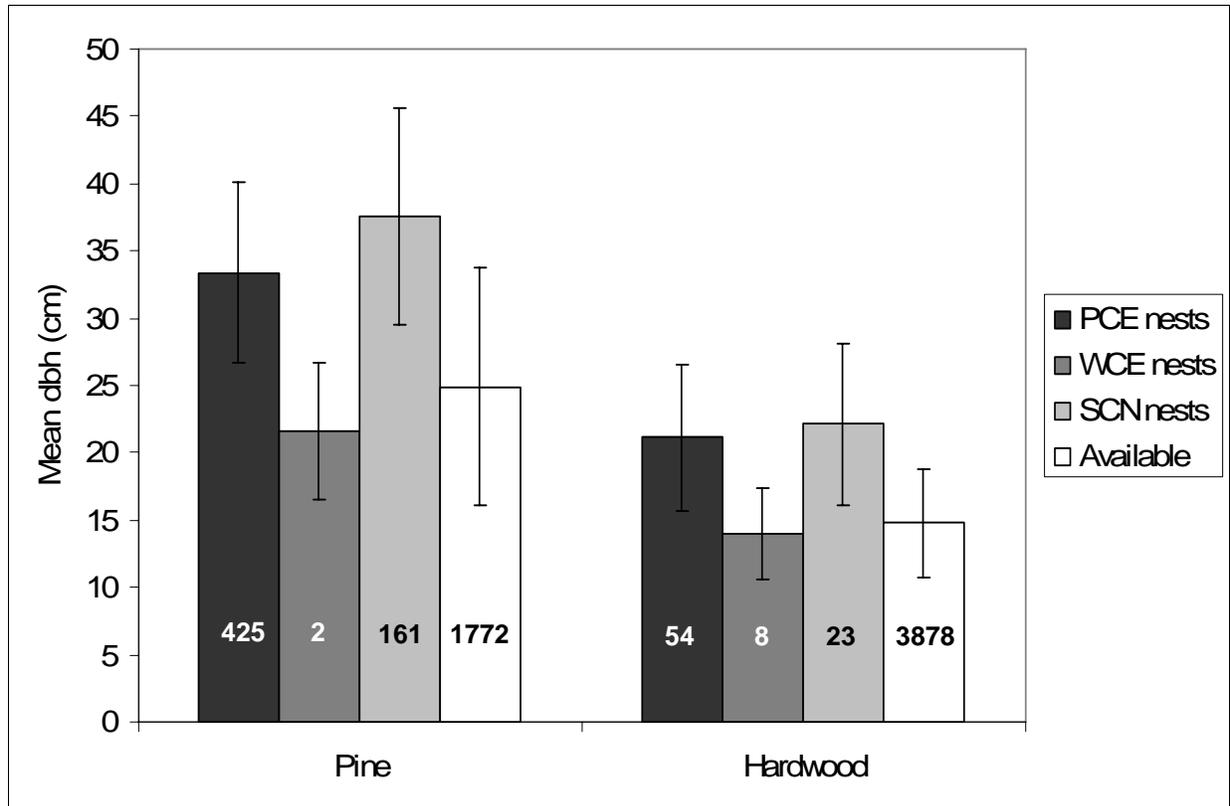
**Figure 3.1.** Two longleaf pine snags, both suitable for a nest cavity, but with an un-measurable dbh due to fire damage. The photo on the left shows the Sandpiper Technologies Treetop Peeper raised for inspection of a nest cavity. Photos taken by L. Blanc.



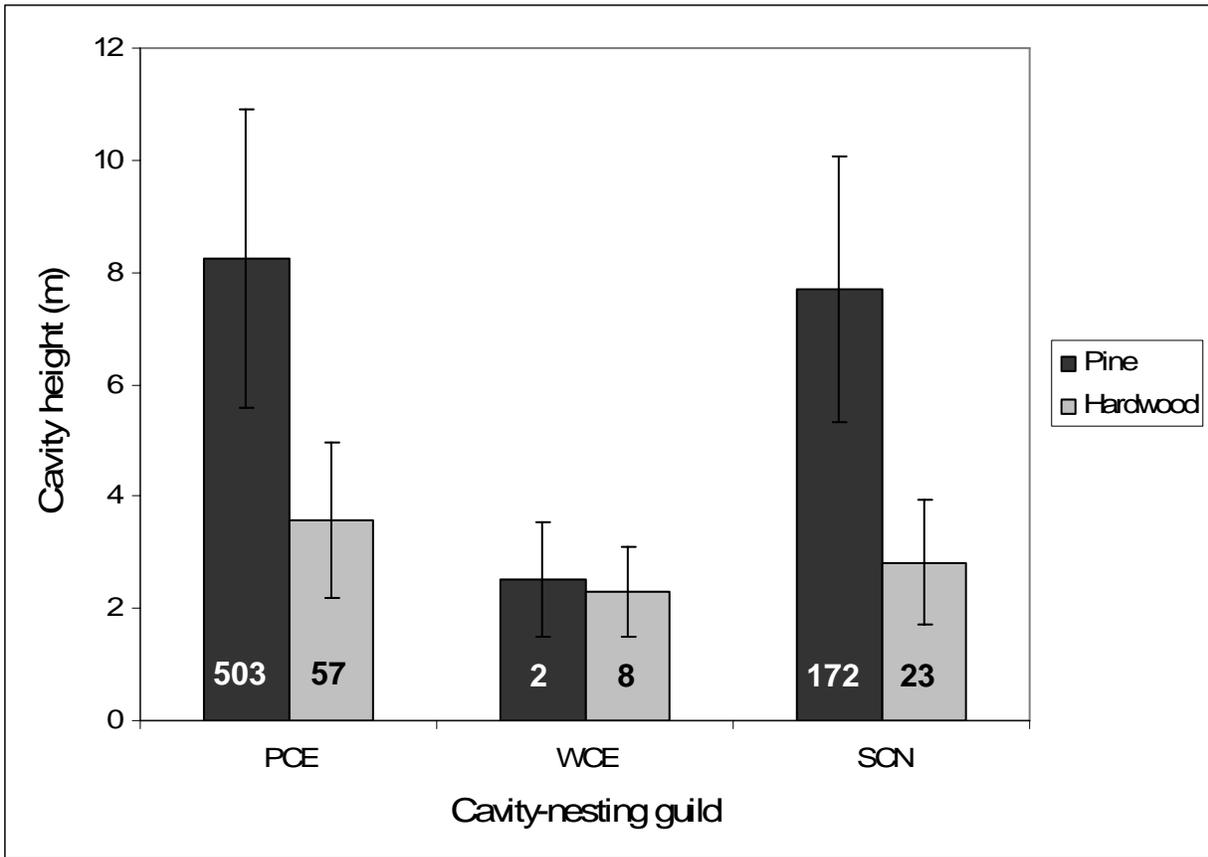
**Figure 3.2.** Distribution of cavity-nests across substrate type by 14 avian species at Eglin Air Force Base, Florida between 2002 and 2005 ( $n = 867$ ). Species are presented in taxonomic order within guild (primary cavity excavators, weak cavity excavators, and secondary cavity-nesters).



**Figure 3.3.** Distribution of cavity-nests across decay class levels, compared to cavity-resource availability at Eglin Air Force Base, Florida between 2002 and 2005. Data are based on 752 nests and do not include re-nests within the same year. Red-cockaded woodpecker nests, which use living pine exclusively, are excluded from these data. Decay classes are defined as: 1) living tree, 2) recently dead tree, most bark and branches and top of tree intact, 3) dead, >50% bark and branches intact, 4) dead, <50% bark/branches intact, top usually broken and 5) dead, no branches or bark, broken top, extensive decay. Because decay class distributions were comparable for hardwood and pine, both cavity-resource types were combined. Data are presented by guild (primary cavity excavators (PCE), weak cavity excavators (WCE) and secondary cavity-nesters (SCN)).



**Figure 3.4.** Mean dbh (cm; mean  $\pm$  SD) of pine and hardwood cavity-nest trees, including available pine and hardwood, at Eglin Air Force Base, Florida between 2001 and 2005. Nest trees are presented by cavity-nesting guild. Data are based on 673 nests (588 pine, 85 hardwood) and 5,650 snags sampled over the 4-year period. Nest data do not include a) re-use of the same tree by any species, or b) snags that did not have a recordable diameter at breast height. Numbers within bars indicate sample size. Data are presented by guild (primary cavity excavators (PCE), weak cavity excavators (WCE) and secondary cavity-nesters (SCN)).



**Figure 3.5.** Mean height (m; mean  $\pm$  SD) of cavities in pine and hardwoods used for nesting by cavity-nesting guilds at Eglin Air Force Base, Florida between 2001 and 2005. Data are based on 765 nests (677 pine, 88 hardwood), and do not include re-use of the same cavity by the same species. Numbers within bars indicate sample size. Data are presented by guild (primary cavity excavators (PCE), weak cavity excavators (WCE) and secondary cavity-nesters (SCN)). Data on general cavity availability (and thus, cavity heights) and are not available for comparison.

## **Chapter 4: Cavity excavation and enlargement as mechanisms for indirect interactions in an avian community**

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## **Abstract**

Direct and indirect species interactions within ecological communities may play a strong role in influencing or maintaining community structure. Complex community interactions pose a major challenge to predicting ecosystem responses to environmental change because predictive frameworks require identification of mechanisms by which community interactions arise. Cavity-nesting communities are well suited for mechanistic studies of species interactions because cavity-nesters interact through the creation of and competition for cavity nest-sites. In this study, we use a cavity nest web as a predictive framework for identifying potential indirect species interactions within a cavity-nesting community. From 2002 - 2005, we monitored abundance and nests of cavity-nesting birds in the longleaf pine (*Pinus palustris*) ecosystem. Using a nest web approach, we identified a potential indirect interaction between the red-cockaded woodpecker (*Picoides borealis*) and large secondary cavity-nesters, mediated by the northern flicker (*Colaptes auratus*). We used structural equation modeling to test a path model of this interaction, using cavity excavation and enlargement as mechanisms which drive the relationship between these species. Through experimental manipulation of cavity availability, we blocked links described in our model, confirming cavity creation and enlargement as processes that influence community structure. We found that a single-species management technique could potentially disrupt this indirect relationship by affecting northern flicker cavity-excavation behavior. This study is the first demonstration of how experimental cavity manipulation can be used to test inferred processes derived from a nest-web and highlights the need to understand how mechanisms underlying species interactions can complicate ecosystem responses to environmental change.

**Keywords:** cavity-nester, *Colaptes auratus*, community structure, indirect interactions, *Pinus palustris*, nest web, *Picoides borealis*, structural equation modeling.

## **Introduction**

Ecological communities consist of assemblages of species that interact with each other and the abiotic environment. These interactions occur with varying degrees of complexity and can play a strong role in influencing community structure (Krebs 1994). The need to develop a better understanding of how species interactions affect community structure has received increasing attention with the growing need to predict future impacts of environmental change on species and their associated ecosystems (Kareiva et al. 1993, Stachowicz 2001, Wootton 2002, Parmesan and Yohe 2003, Soulé et al. 2003, Parmesan and Galbraith 2004). Currently, a major challenge is to develop predictive frameworks for complex ecosystems, particularly when there is potential for indirect species interactions and unanticipated indirect effects of environmental change (Walther et al. 2002, Wootton 2002, Burns et al. 2003, Parmesan and Galbraith 2004). Indirect interactions occur among 3 or more species, where a species can, through a direct interaction with one species, indirectly affect the abundance of another species that it does not interact with directly. Many studies have documented examples of these effects in different systems (Strauss 1991, Wootton 1993, 1994a, 1994b, 2002, Menge 1995), but still little is known about the relative importance of indirect effects in structuring communities, particularly in terrestrial systems. An important next step to understanding complex community interactions is to document mechanisms or processes by which indirect effects arise.

Cavity-nesting communities interact through the creation of and competition for cavity nest sites (Martin and Eadie 1999). These communities consist of a hierarchy of tree resources, cavity excavators and secondary cavity users, forming a type of interaction web (Paine 1980) structured by cavity resource availability. Thus, cavity creation and subsequent use may serve as a mechanism through which indirect interactions can arise within cavity-nesting communities.

In recent years, cavity excavation has been proposed as a potential keystone process within forest communities (Bednarz et al. 2004). Cavity-nesting community structure and the connections within these communities can be visualized with the use of a theoretical framework based on empirical data, called a nest web (Martin and Eadie 1999), which can be used to identify the species and links that are most influential in the dynamics of community composition or structure. One advantage of visualizing the community as a web is that it provides a predictive framework for identifying potential direct and indirect species interactions.

In this study, we use a combination of nest web development, structural equation modeling (SEM) and experimental manipulation to examine interactions between the federally endangered red-cockaded woodpecker (*Picoides borealis*) and other cavity-nesting birds of a fire-maintained longleaf pine (*Pinus palustris*) ecosystem. SEM is a powerful statistical tool that enables the investigation of a priori hypotheses about interactions between complex systems of variables (Kline 1998, Grace 2006). Of particular use to studies in community ecology is the ability of SEM to evaluate path models, which can be used to represent direct and indirect relationships between multiple species (Grace and Pugsek 1998, Pugsek and Grace 1998). Indeed, SEM is especially well suited for studies of cavity-nesting communities because a key mechanism that structures these communities, cavity creation, may be measured and experimentally manipulated.

Fire-maintained longleaf pine forests are dominated by living pine, with relatively few snags (i.e. dead trees) or hardwoods due to the historically low tree density and influence of regularly-occurring fire on the landscape (Conner et al. 2001). Current forest management practices such as snag removal and short harvest rotations further reduce snag availability. Subsequently, suitable excavation sites for most woodpeckers can be limited in fire-maintained

southern pine forests. The red-cockaded woodpecker is the only species in this forest system that excavates nest cavities in the most abundant substrate in this system, living pine. The regular use of red-cockaded woodpecker cavities by other species creates the potential for direct and indirect interactions between the red-cockaded woodpecker and other cavity-nesters. Over 27 vertebrate species are known to use red-cockaded woodpecker cavities, and thus, the red-cockaded woodpecker has been referred to as a keystone species within fire-maintained southern pine forests (USFWS 2003). Usurpation and use of these cavities by other species has been well documented; however, the relationship of the red-cockaded woodpecker with other cavity-nesting species is poorly understood (USFWS 2003). Enlarged red-cockaded woodpecker cavities provide nesting habitat required by large secondary cavity-nesters, particularly in fire-maintained areas that have few large hardwoods and snags. Species that are known to enlarge red-cockaded woodpecker cavity entrances include the northern flicker (*Colaptes auratus*) and pileated woodpecker (*Drycopus pileatus*) (USFWS 2003). This process of cavity enlargement provides a mechanism for indirect interactions between red-cockaded woodpeckers and large secondary cavity-nesters, mediated by other woodpecker species. While cavity enlargement may benefit secondary cavity-nesters, it is often considered detrimental for the red-cockaded woodpecker, which will abandon greatly enlarged cavities (USFWS 2003).

Both ecosystem and single-species techniques are heavily used for managing red-cockaded woodpecker populations. Single-species management focuses on the creation of red-cockaded woodpecker cavities in living pine (Copeyon 1990, Allen 1991, Copeyon et al. 1991) and the repair and prevention of red-cockaded woodpecker cavity enlargement using metal restrictor plates (Carter et al. 1989). Red-cockaded woodpecker ecosystem management benefits many fauna and flora of the longleaf pine community (Conner et al. 2001, 2002, Litt et al. 2001,

Provencher et al. 2001, Allen et al. 2006); however, little is known about the effects of red-cockaded woodpecker cavity management on other cavity users. In recent years, there has been increasing focus on incorporating community interactions into red-cockaded woodpecker management (Kappes 2004) and concern about potential impacts of metal restrictor plates on secondary cavity-nesters that use enlarged red-cockaded woodpecker (USFWS 2003). Studies of impacts of restrictor plates on the red-cockaded woodpecker have been conducted (Raulston et al. 1996, Wood et al. 2000, Walters et al. 2004); however, no studies have examined the impacts of restrictor plates on other species.

For the purpose of clarity and flow, we present this study in 2 parts. In part 1, we use a nest web to visualize potential direct and indirect interactions within the cavity-nesting community of a longleaf pine forest. We then use structural equation modeling to assess a path model of relationships identified in the nest web. In part 2, we use the experimental application of red-cockaded woodpecker cavity restrictor plates to test links within the path model.

## **Part 1: Nest webs and structural equation modeling**

### **Study site and methods**

We conducted this study at Eglin Air Force Base, the largest forested military reservation in North America (187,555 ha). Eglin, located in the western Florida panhandle, contains a large number of old-growth longleaf pine and over 6,000 live and dead red-cockaded woodpecker cavity trees. During the study period, Eglin had an atypically high number of large pine snags due to tree mortality from the reintroduction of fire after many years of fire suppression (Varner and Kush 2001, Varner et al. 2005). Seventy-eight percent of Eglin's reservation consists of the Sandhills ecotype (McWhite et al. 1999), characterized by scattered longleaf pine, with an open

to sparse mid-story of turkey oak (*Quercus laevis*), and a ground cover of various fire-adapted forbs and grasses (Kindell et al. 1997). Given the size of the reservation, Eglin is well-suited for large-scale studies requiring replicate plots within longleaf communities, such as the study presented here.

In April 2002, we established 36 800 x 600 m research plots at Eglin (Fig. 4.1). We restricted plots to areas within the sandhills ecotype that contained mature pine and a relatively open midstory. Within each plot, we established a grid system to aid with navigation and relocation of nests and designated 12 census stations at 200-m intervals along alternating transects (Fig. 4.1). Census stations were considered sub-samples within each plot and each plot was a sampling unit. We acquired the locations of all red-cockaded woodpecker cavity trees from Eglin's long-term management data set, which was updated annually through surveys and intensive year-round red-cockaded woodpecker population management. Each plot contained between 0 and 43 red-cockaded woodpecker cavities and a range of snag densities.

We used a point-transect count census technique, adapted for the open habitat at Eglin, to record the relative abundance of cavity-nesting birds within each plot between 08 April and 21 June, 2002–2005 (Provencher et al. 2002). Each year, we conducted 2 rounds of censusing on 2 plots per morning within 3 hours after sunrise (totaling 24 census stations). Censuses consisted of 8-minute point counts at each sampling station during which we recorded species, time detected, vocalization type, location and movement within a 100-m fixed radius from the point center (Hutto et al. 1986). Counts included birds detected while moving between adjacent stations. Two observers censused simultaneously at stations on alternating transects (Fig. 4.1), and synchronized start-times for the point counts. Birds detected by both observers were not double-counted. This transect-count addition to the censusing accounted for birds fleeing ahead

of the observers and is considered appropriate for open habitat (Bibby et al. 1992). We calculated relative abundance by summing the detections at each census station within a plot for each round and then averaging the detections across the 2 sampling rounds. Our measurement was used as an index of abundance across years, rather than an attempt to quantify breeding densities.

In 2002, we conducted nest searches on all plots opportunistically. We located nests in red-cockaded woodpecker cavities by inspecting all cavities within each plot at least once between 15 April and 30 June. We located nests in snags by walking along transects in each plot, inspecting snags for potential nest cavities and observing breeding bird behavior. We examined cavity contents with a camera mounted atop a telescoping pole (Treetop Peeper, Sandpiper Technologies Inc., Manteca, California, USA), which enabled access to cavities up to 15 m in height. To ensure equal amount of search effort on each plot, we adopted a more systematic nest-searching schedule from 2003 to 2005. We conducted 2 rounds of nest searching per year in each plot between 15 April and 30 June, and during each round, one crew focused on red-cockaded woodpecker cavities and a second crew focused on snags. During each round of nest searching, we searched for snag-nests on 2 plots per day, with 2 observers simultaneously, beginning at sunrise. Each observer spent 6 hours nest-searching in each plot, totaling 12 person-hours per plot during each field season. We inspected the contents of all red-cockaded woodpecker cavities once during each round of nest searching. For each of the 2 rounds of sampling, we randomly determined the order in which plots were censused and searched for nests and modified this schedule when necessary for obtaining access to restricted areas on Eglin. To minimize systematic detection biases, we rotated observer assignment to transects within each plot across the 2 rounds.

In July of each year, we measured snag availability within 25-m radius vegetation plots, established at the 12 census stations within each research plot. We defined snags as dead, standing trees  $\geq 1.4$  m tall and  $\geq 10.2$  cm in diameter at breast height (dbh). We recorded the number and dbh of snags within each vegetation plot, classified by pine or hardwood. To calculate snag availability within a research plot each year, we summed stem data across all 12 sampling stations within the plot.

We constructed a nest web using all nest cavities found from 2002 to 2005 for which we could identify the excavator ( $n = 736$ ) through known use of the cavity or reasonable estimation based on cavity characteristics. We included re-use of the same cavity across years, but excluded re-nesting attempts in the same cavity within the same year. We then developed a path model to depict relationships identified in the nest web. Because systematic nest-searching protocol began in 2003, we used only data from 2003 to 2005 in the path model. Observational units consisted of each research plot from each year ( $n = 92$ ), excluding plots with experimental manipulations from the concurrent study on large cavity availability ( $n = 16$ , see part 2 below).

We developed and tested our path model using AMOS (v. 5.0, SPSS Inc., Chicago, Illinois, USA), which uses maximum likelihood to examine the overall model fit of to the observed variance-covariance matrix. We log transformed the data to meet assumptions of normality and linear relationships, and assessed model fit using a chi-square analysis (significant at  $P > 0.05$ ) and root mean square error approximation (RMSEA, significant at  $P < 0.05$ ). We also used the Comparative Fit Index (CFI; Bentler 1990), which assesses the improvement of model fit over the fit of the “null” or independence model (generally acceptable at  $CFI > 0.90$ ), and Akaike Information Criterion (AIC; Akaike 1987), which factors in the degree of model parsimony.

## Results: nest web and path modeling

Our nest web indicates several key relationships within the cavity-nesting community at Eglin (Fig. 4.2). The primary creator of large cavities at Eglin was the northern flicker, which excavated cavities in snags and enlarged red-cockaded woodpecker cavities in living pine. The primary users of large cavities were the southeastern American kestrel (*Falco sparverius paulus*) and eastern screech-owl (*Otus asio*), both large secondary cavity-nesters. Approximately half of large secondary cavity-nester nests were found in red-cockaded woodpecker cavities and half were found in cavities in large pine snags (dbh >20 cm), the majority of which were excavated by the northern flicker. Our nest web indicates a relationship between pine snags, red-cockaded woodpecker cavities, northern flicker cavities, and large secondary cavity-nesters.

Our path model is a conceptual model depicting the role that red-cockaded woodpecker and northern flicker cavities play in creating nesting habitat for large secondary cavity-nesters (Fig. 4.3). In this model, large secondary cavity-nester nests are predicted by large cavity availability, which includes enlarged red-cockaded woodpecker cavities and large cavities in snags. We used northern flicker presence (sum of northern flicker nests and abundance) as a surrogate measure of northern flicker cavity excavation and enlargement behavior. Red-cockaded woodpecker cavity availability is predicted by the abundance of red-cockaded woodpeckers (which excavate the original cavities) and northern flickers (which enlarge cavity entrances). Northern flicker presence is predicted by pine snag availability. All links within the model were significant ( $P < 0.01$ ), except for that between ‘Northern Flicker Presence’ and ‘Enlarged RCW Cavities’ ( $P = 0.069$ ). The model explained 35% of the variation ( $R^2$ ) in large secondary cavity-nester nests and fit the observed data ( $X^2 = 5.8$ ,  $df = 5$ ,  $P = 0.33$ ; RMSEA =

0.04; CFI = 0.99; AIC = 25.79). When we removed the non-significant link between ‘Northern Flicker presence’ and ‘Enlarged RCW Cavities’, model fit was reduced ( $X^2 = 9.0$ ,  $df = 6$ ,  $P = 0.17$ ; RMSEA = 0.07; CFI = 0.97; AIC = 27.03). When we modified the model to include only pine snags >20 cm dbh (potential nest trees), the model fit to observed data improved ( $X^2 = 5.0$ ,  $df = 5$ ,  $P = 0.41$ ; RMSEA < 0.01; CFI = 1.0; AIC = 25.03). In addition, the link between pine snags and northern flicker presence became significant at  $P = 0.001$ , and the standardized partial regression coefficient for this link increased to 0.32; all other values in the model remained the same.

## **Part 2: Experimental study**

### **Methods**

A concurrent experimental study enabled us to test the relationships shown in our path model. By using metal restrictor plates to repair existing enlarged red-cockaded woodpecker cavities and prevent cavity enlargement by the northern flicker, we blocked 2 links within the model, including a) the link between enlarged red-cockaded woodpecker cavities and northern flicker presence and b) the link between enlarged red-cockaded woodpecker cavities and large secondary cavity-nesters. We randomly selected 8 plots for experimental manipulation along with 8 control plots. Control and treatment plots did not differ significantly in the availability (mean  $\pm$  SD) of enlarged red-cockaded woodpecker cavities ( $5.5 \pm 2.1$  and  $7.9 \pm 3.4$ , respectively;  $t$  test,  $t = 1.7$ ,  $df = 14$ ,  $P = 0.11$ ) or pine snags ( $23.8 \pm 16.6$  and  $14.8 \pm 8.5$ , respectively;  $t$  test,  $t = -1.36$ ,  $df = 14$ ,  $P = 0.20$ ) prior to experimental manipulation. Between September 2003 and January 2005, we installed metal restrictor plates on all inactive and enlarged red-cockaded woodpecker cavities within experimental plots ( $n = 135$  cavities).

Because our systematic protocol for nest searching began in 2003, and experimental treatments were completed after the 2004 season, the experimental portion of this study consists of 2003 (pre-treatment) and 2005 (post-treatment) data.

To control for annual variation, we used the amount of change in abundance and number of nests found in each plot between 2003 and 2005 to determine if there was a treatment effect. For each plot we subtracted pre-treatment from post-treatment values and used a Mann-Whitney *U* test to detect significant differences in the amount of change between treatment and control plots. We predicted that the application of restrictors would cause a reduction northern flicker and southeastern American kestrel abundance, but that this effect would be weakened if snags were available as an alternative nesting resource. Because the eastern screech-owl was rarely detected using our census methodology, we did not make predictions about their abundance. We predicted that the application of restrictors would cause a reduction in the number of large secondary cavity-nester and northern flicker nests found in red-cockaded woodpecker cavities. For nest data analyses, both large secondary cavity-nesting species were grouped together. All data were analyzed using SAS, Version 9.1 (2003; SAS Institute Inc., Cary, North Carolina, USA). Because our a priori predictions were directional, one-tailed tests were used, with a significance level of  $P < 0.05$ .

### **Results of experimental study**

There was no difference between the change in northern flicker abundance in experimental and control plots (Mann-Whitney *U* test,  $P = 0.42$ ; Fig. 4.4). Northern flicker nests found in red-cockaded woodpecker cavities decreased in experimental plots, although not significantly more than in controls (Mann-Whitney *U* test,  $P = 0.11$ ; Fig. 4.5). There was a

significant increase in northern flicker nests found in snags in experimental plots (Mann-Whitney  $U$  test,  $P = 0.01$ ; Fig. 4.5), indicating a switch to the use of snags. Southeastern American kestrel abundance decreased in experimental plots, although not significantly more than in controls (Mann-Whitney  $U$  test,  $P = 0.40$ ; Fig. 4.4). There was a significant reduction in large secondary cavity-nester nests found in red-cockaded woodpecker cavities (Mann-Whitney  $U$  test,  $P = 0.01$ ) in experimental plots (Fig. 4.6); however, there was no change in large secondary cavity-nester nests found in snags (Mann-Whitney  $U$  test,  $P = 0.38$ ; Fig. 4.6). Finally, there was an increase in red-cockaded woodpecker abundance (Mann-Whitney  $U$  test,  $P = 0.08$ ), but no significant difference in number of red-cockaded woodpecker nests (Mann-Whitney  $U$  test,  $P = 0.10$ ) in experimental plots relative to controls.

## **Discussion**

Through the use of a nest web, structural equation modeling and experimental manipulation, we identified the processes of cavity creation in living pine and enlargement of these cavities as mechanisms by which an indirect relationship arises between the red-cockaded woodpecker and large secondary cavity-nesters. The use of metal restrictor plates to remove existing enlarged red-cockaded woodpecker cavities and hinder cavity enlargement behavior of the northern flicker resulted in a reduction of large secondary cavity-nester nests found in red-cockaded woodpecker cavities in living pine (Fig. 4.6) and caused the northern flicker to switch to snags for nesting (Fig. 4.5). Pine snags were atypically abundant at Eglin during this study, ranging from 5.2 stems/ha to 8 stems/ha annually (L. Blanc and J. R. Walters, Virginia Tech University, *unpublished data*), and provided alternative nesting resources for cavity-nesters; these nesting alternatives apparently buffered the impact of restrictor plates. The use of snags for

nesting is contingent upon the ability to find existing cavities in snags or excavate new cavities. The northern flicker, capable of cavity-excavation, has greater flexibility than secondary cavity-nesters in switching to the use of available snags when red-cockaded woodpecker cavities are restricted. This flexibility seems to be reflected in our experimental results. These results suggest that red-cockaded woodpecker cavity creation and enlargement may be important processes within the longleaf pine ecosystem when snags are scarce.

The red-cockaded woodpecker indirectly improves the habitat of large secondary cavity-nesters by influencing the excavation behavior of northern flickers. The presence of red-cockaded woodpecker cavities facilitates the ability of northern flickers to excavate in living pine, a behavior not found in forests where red-cockaded woodpecker cavities are absent. This change in northern flicker excavation behavior enhances nesting habitat for large secondary cavity-nesters, and thus, may cause an increase in large secondary cavity-nester abundance. This interaction may be described as a trait-mediated indirect interaction in which one species (the red-cockaded woodpecker) indirectly affects the abundance of another species (large secondary cavity-nesters) by altering the behavior of a third species (northern flicker) or by altering the environmental context of an interaction between two other species (a forest in which the northern flicker can excavate into living pine) (Wootton 1993, Werner and Peacor 2003). In a recent review, Werner and Peacor (2003) argue that indirect interactions based on modification of traits (e.g., behavior) may be highly important and widespread phenomena within ecological communities, and in some cases, may have a greater influence on community dynamics and structure than indirect interactions based on modification of species densities. A better understanding of these complex community interactions and their underlying mechanisms can potentially improve our ability to predict community response to environmental change.

Our path model shows 2 pathways through which red-cockaded woodpeckers and northern flickers can create nesting habitat for large secondary cavity-nesters. The first pathway represents the creation and enlargement of red-cockaded woodpecker cavities in living pine; the second pathway represents the creation of large cavities in pine snags. We propose that retaining snags in southern pine forests, particularly snags of sufficient diameter for nesting by large species, can ensure that the second pathway of the model remains intact (Large pine snags → Northern flicker presence → Large secondary cavity-nester nests). Maintaining this pathway may mitigate potential negative impacts of metal restrictor plates on large secondary cavity-nesters, particularly in small, managed red-cockaded woodpecker populations where restrictor plates may be critical to the maintenance of a limited number of cavities.

This study provides an empirical example of how, in ecological communities where complex species interactions occur, single-species management can have indirect impacts on non-target species. In some cases, these indirect effects may have broader implications for conservation management. For example, the southeastern American kestrel, which was indirectly affected by the use of metal restrictor plates in this study, is listed as threatened in the state of Florida (Wood 1996). In addition, Simberloff (1998) suggested that metal restrictor plates may impact the declining Sherman's fox squirrel (*Sciurus niger shermani*). Negative impacts of red-cockaded woodpecker cavity management on these declining species may conflict with ecosystem management goals of the Endangered Species Act of 1973. Understanding the mechanisms or processes that create suitable habitat for a broad suite of species within a larger associated community may ultimately improve our ability to effectively design conservation management strategies (Paine 1995, Simberloff 1998, Soulé et al. 2003). Indeed, Soulé et al. (2003) propose that biodiversity conservation should include the protection of critical

interspecific interactions, a goal that necessitates the integration of theoretical ecology into conservation management strategies (e.g., Walters 1991). In this study, we demonstrate how a study of basic ecological principles can inform conservation management and concomitantly, how the application of a management technique can aid in the study of basic ecological principles.

Because tree cavities serve as roosting and nesting habitat for a broad range of birds, mammals, herpetofauna and insects, the process of cavity creation may serve as a mechanism that influences community structure in forests worldwide. Woodpeckers have long been recognized as an important component of forest ecosystems (Virkkala 2006) and may be used as general indicators of forest biodiversity (Mikusiński et al. 2001). The structured, nest-web characteristic of cavity-nesting communities makes them well suited for studies of complex community interactions because mechanisms that structure these communities seem to be clear and testable through experimental manipulation. Indeed, the experimental study presented here is the first demonstration of how cavity manipulation can be used to test inferred processes derived from a nest web. The findings presented here highlight the need to develop a better understanding of how mechanisms underlying species interactions can influence community structure and ultimately mitigate or exacerbate community responses to future changes in environmental conditions.

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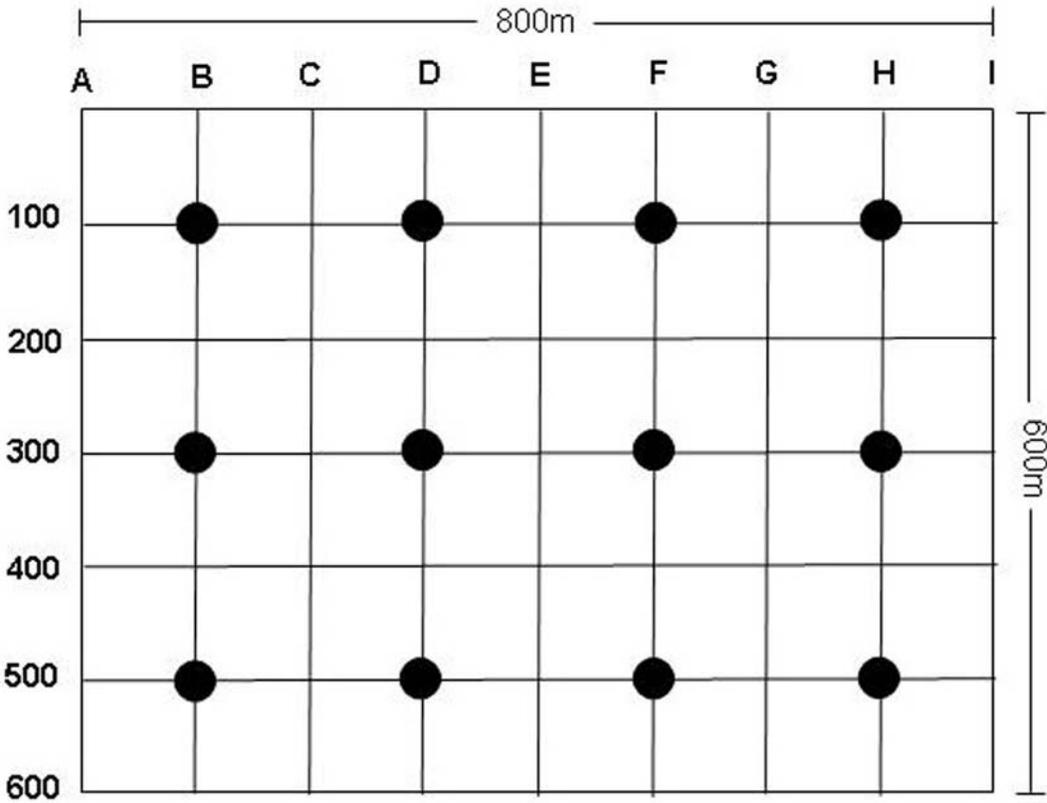
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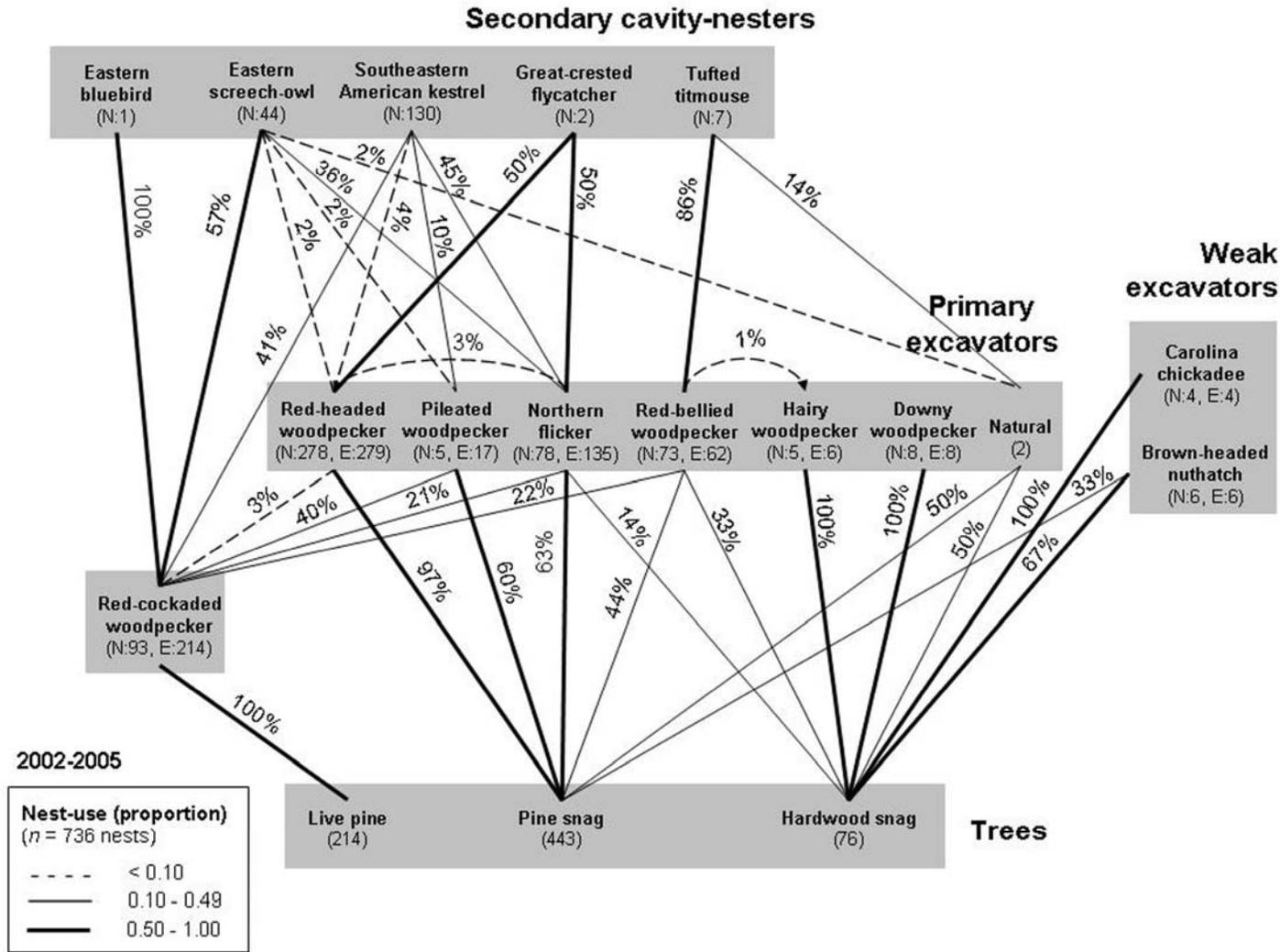
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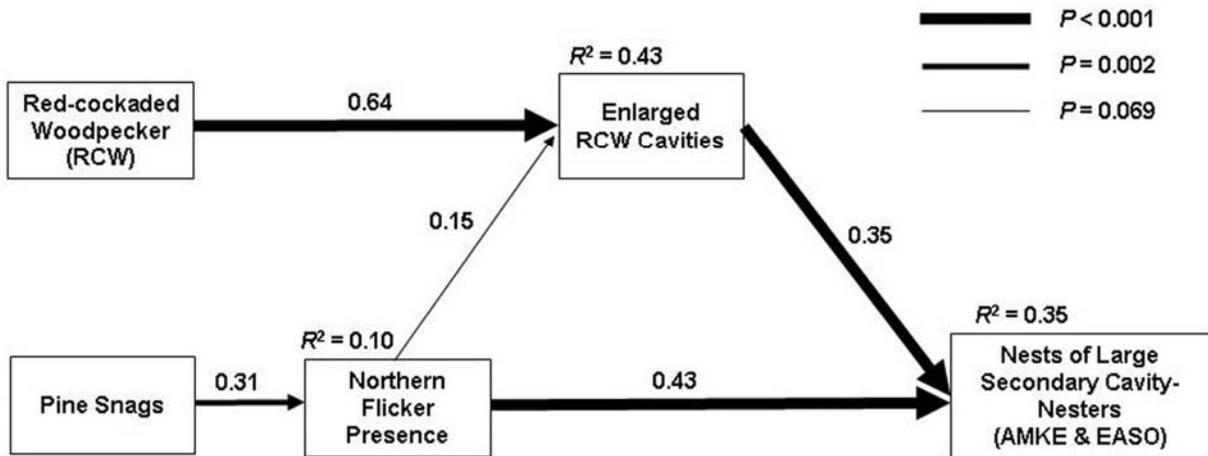


**Figure 4.1.** Diagram showing the layout of a research plot for the cavity-nester study on Eglin Air Force Base, Florida. Nine transects (labeled A-I), each 600 m in length, are spaced 100 m apart. Twelve census stations are located on alternating transects, spaced 200 m apart (indicated by black circles).

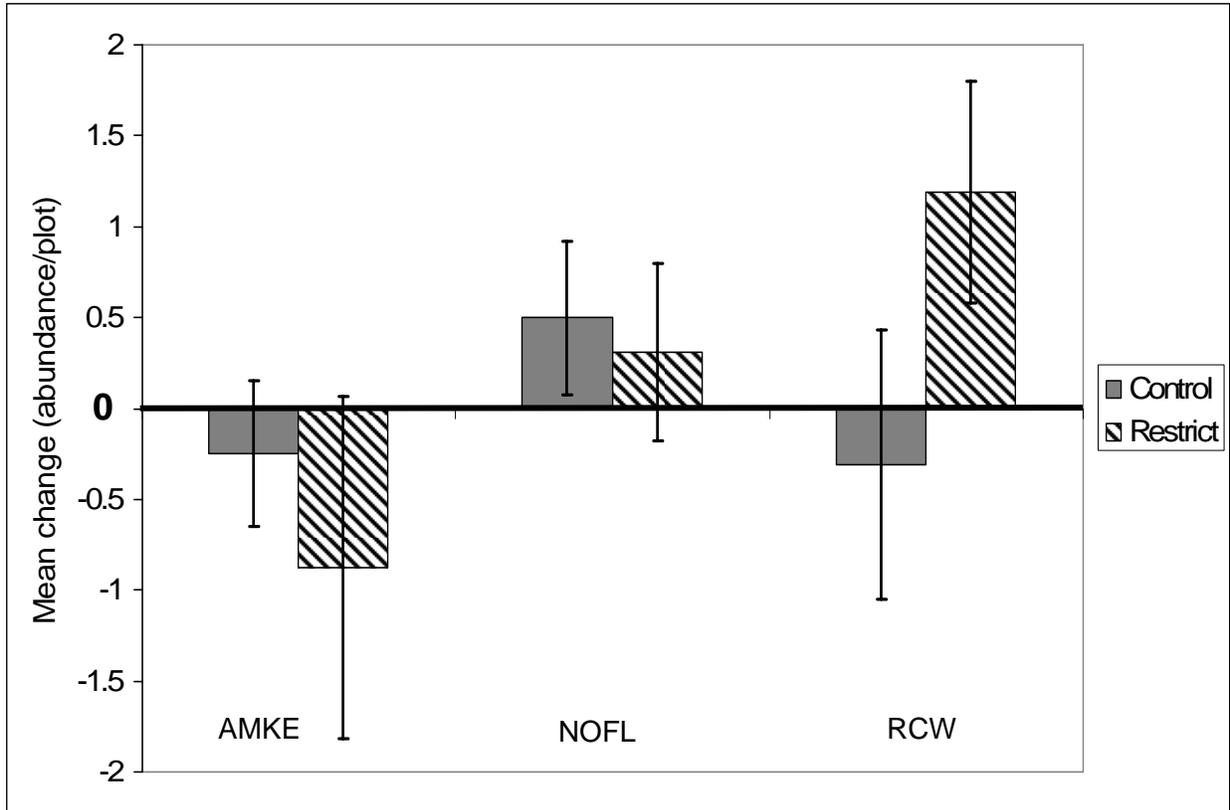


**Figure 4.2.** A nest web diagram highlighting the flow of cavity creation and use within the cavity-nesting bird community at Eglin Air Force Base, Florida. N indicates the number of nests found for that species; E indicates the total number of nest cavities excavated

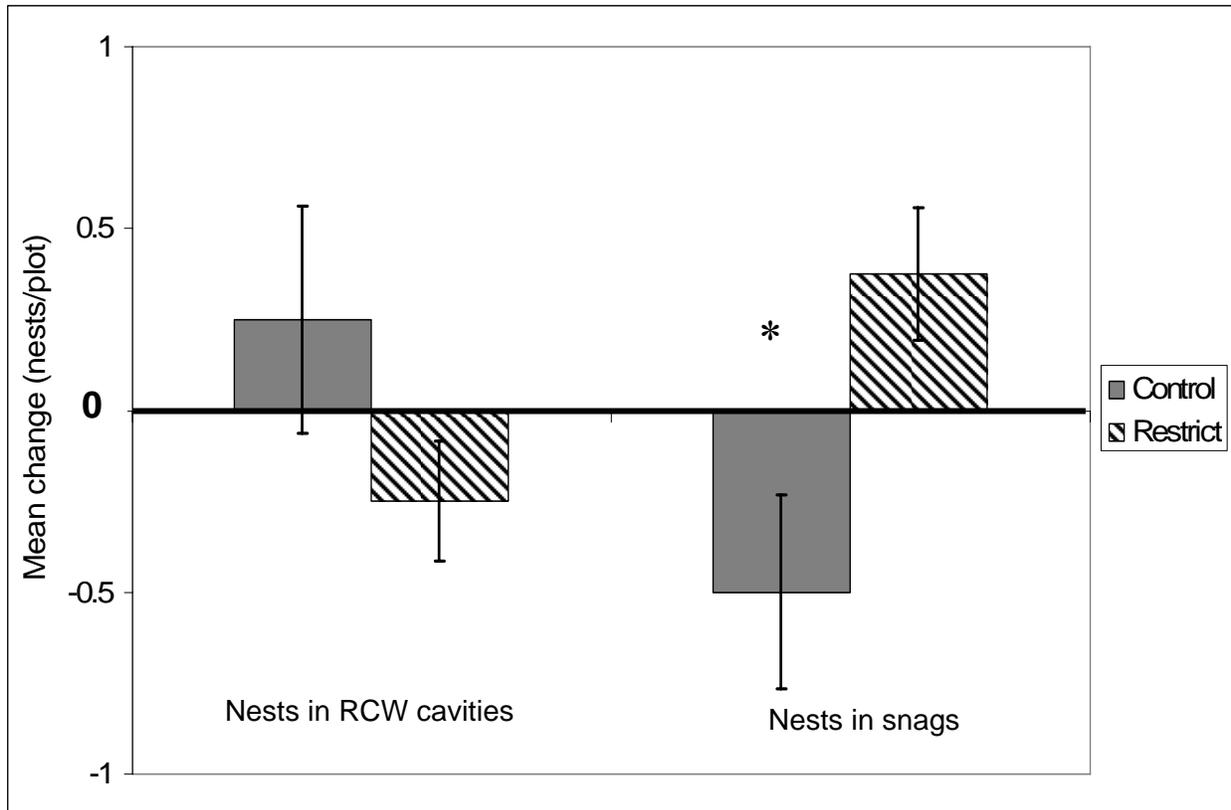
by that species. Links between the secondary cavity nester (SCN) level and the primary excavator (PCE) level represent the proportion of SCN nests found in a cavity that was excavated by the indicated PCE. Links between the PCE and tree level show the proportion of PCE nests found in that tree resource. The link between northern flicker (NOFL) and red-headed woodpecker (*Melanerpes erythrocephalus*, RHWO) indicates that 3% of NOFL nests were found in cavities originally excavated by a RHWO.



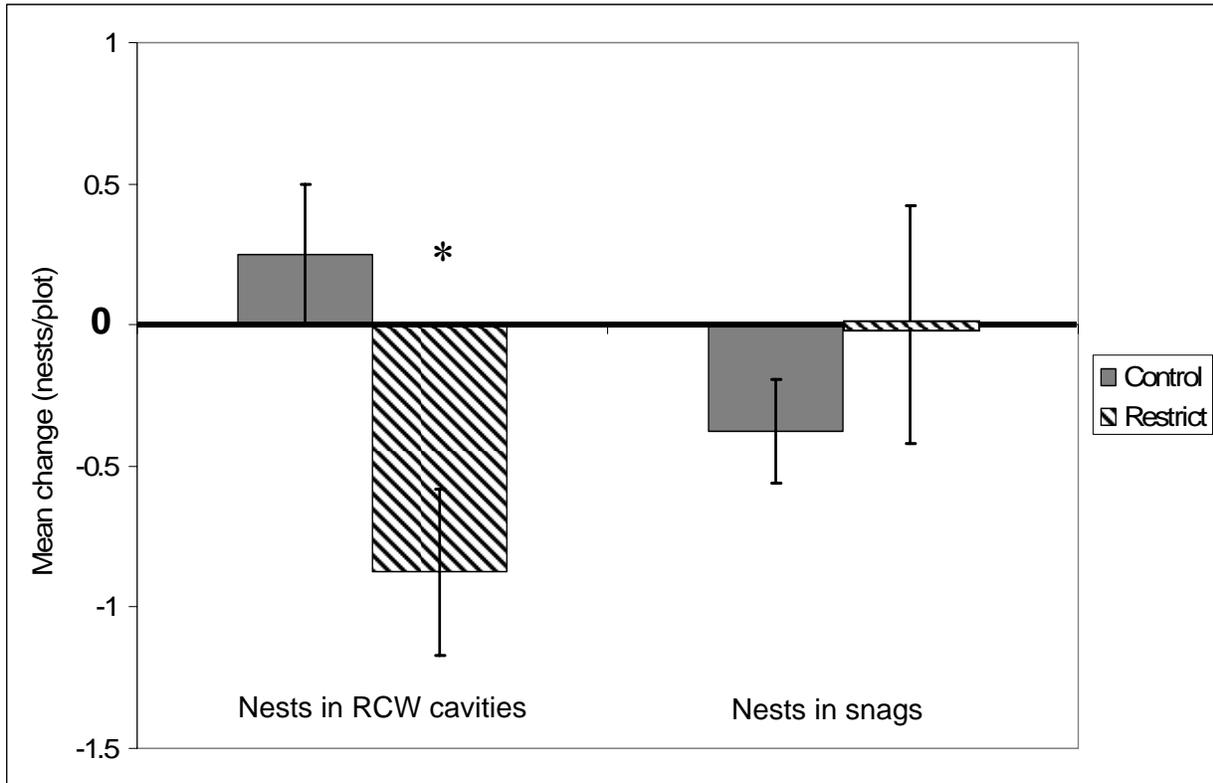
**Figure 4.3.** A conceptual path model depicting the relationships among red-cockaded woodpecker (RCW) cavities, pine snags, the northern flicker and large secondary cavity nesters (LSN). LSNs include the southeastern American kestrel (AMKE) and the eastern screech-owl (EASO). Arrows in the model reflect hypotheses about causal relationships between variables. Numbers above each arrow indicate the standardized partial regression coefficient showing the direct effect of an independent variable on the adjacent dependent variable in the model. This model fit the observed data ( $X^2 = 5.8$ ,  $df = 5$ ;  $P = 0.33$ ; RMSEA = 0.04; CFI = 0.99).



**Figure 4.4.** Change (mean  $\pm$  SE) in the relative abundance of the northern flicker (NOFL), red-cockaded woodpecker (RCW) and southeastern American kestrel (AMKE) at Eglin Air Force Base, Florida, in control (CONTROL,  $n = 8$ ) and experimental (RESTRICT,  $n = 8$ ) plots from 2003 to 2005, following application of metal restrictor plates on RCW cavities.



**Figure 4.5.** Change (mean  $\pm$  SE) in the number of northern flicker nests found in control (CONTROL,  $n = 8$ ) and experimental (RESTRICT,  $n = 8$ ) plots at Eglin Air Force Base, Florida, from 2003 to 2005, following application of metal restrictor plates on red-cockaded woodpecker (RCW) cavities. An asterisk indicates a significant difference ( $P < 0.05$ ) between control and experimental plots.



**Figure 4.6.** Change (mean  $\pm$  SE) in the number of large secondary cavity nester nests (southeastern American kestrel and eastern screech-owl) found in control (CONTROL,  $n = 8$ ) and experimental (RESTRICT,  $n = 8$ ) plots at Eglin Air Force Base, Florida, from 2003 to 2005, following application of metal restrictor plates on red-cockaded woodpecker (RCW) cavities. An asterisk indicates a significant difference ( $P < 0.05$ ) between control and experimental plots.

## **Chapter 5: Summary and Conclusions**

### **Research conducted**

The goal of this study was to describe cavity-nesting bird community structure in an old-growth longleaf pine (*Pinus palustris*) ecosystem and characterize the relationship of the federally endangered red-cockaded woodpecker (*Picoides borealis*) with other cavity-nesting birds using correlational, experimental and statistical modeling techniques. I conducted this 4-year study at Eglin Air Force Base, located in the northwest Florida panhandle, from 2002 through 2005.

One goal of this study, not presented in earlier chapters, was to experimentally test if cavity-provisioning in living pine, a commonly-used red-cockaded woodpecker management technique, affects other species within the cavity-nesting community at Eglin. It was not included in earlier chapters for purposes of clarity and flow, but is presented in this final chapter.

### **Additional experimental study: cavity provisioning in living pine**

#### **Introduction**

The construction of artificial red-cockaded woodpecker cavities in living pines (Copeyon 1990, Copeyon et al. 1991) is a widely-used management technique that has contributed greatly to management of the red-cockaded woodpecker (USFWS 2003). The development of this cavity-management technique arose from the identification of cavities as the limiting factor to red-cockaded woodpecker population growth (Walters et al. 1992). Since 1998, over 16,000 red-cockaded woodpecker cavities have been provisioned (USFWS, *unpublished data*). Because red-cockaded woodpecker cavities are used by many other species, provisioning artificial cavities may have positive benefits for other cavity-users. At Eglin, 3 species used normal-sized

red-cockaded woodpecker cavities (i.e. 2-inch entrance diameter), including the red-bellied woodpecker (*Melanerpes carolinus*), red-headed woodpecker (*Melanerpes erythrocephalus*), and eastern bluebird (*Sialia sialis*). In addition, 4 species enlarge or used enlarged red-cockaded woodpecker cavities, including the southeastern American kestrel (*Falco sparverius paulus*), eastern screech-owl (*Otus asio*), northern flicker (*Colaptes auratus*) and pileated woodpecker (*Dryocopus pileatus*). I predicted that increasing the number of red-cockaded woodpecker cavities would have a positive effect (i.e. increased abundance and nests) on those species that use normal-sized red-cockaded woodpecker cavities and, over time, positively affect those species that enlarge or use enlarged red-cockaded woodpecker cavities.

## Methods

This experimental study was conducted at the same time as the experimental study described in chapter 4. For details on plots setup, and censusing and nest-searching methodology, please refer to that chapter. For this study, I selected 11 plots for cavity addition, which originally contained an average (mean  $\pm$  SD) of  $1.8 \pm 2.2$  living red-cockaded woodpecker cavity trees. I designated 11 additional plots, with an average (mean  $\pm$  SD) of  $2.5 \pm 3.1$  red-cockaded woodpecker cavity trees as controls. Experimental and control groups had a comparable range of snag densities. From November 2003 through January 2005, I experimentally manipulated the availability of normal-sized red-cockaded woodpecker cavities using the cavity drilling technique. In each of the experimental plots, approximately 12 red-cockaded woodpecker cavities were drilled, depending on availability of drillable trees. On average (mean  $\pm$  SD),  $12.0 \pm 1.3$  cavities were constructed in each treatment plot, totaling 132 cavities. Experimental manipulations were completed just prior to the 2005 field season.

Because the systematic protocol for nest searching began in 2003, and experimental treatments were completed after the 2004 field season, the experimental portion of this study consists of 2003 data (pre-treatment) and 2005 data (post-treatment).

Many of the focal species in this study have large territory sizes and thus, I found relatively few nests per species within each plot. Additionally, many species nested in large pine snags, which were relatively abundant in many of the plots, thus reducing the sample of nests found in red-cockaded woodpecker cavities. Due to the small sample size of nests found, I grouped species together into 1) those that enlarge or use enlarged cavities (LCN), 2) those that use unaltered red-cockaded woodpecker cavities (NCN) and 3) those that do not use red-cockaded woodpecker cavities (OCN). I analyzed effects of the treatments on red-cockaded woodpeckers separately.

#### Statistical analyses

To control for annual variation, I used the amount of change in abundance and number of nests found in each plot between 2003 and 2005 to determine if there was a treatment effect. For each plot I subtracted pre-treatment from post-treatment values and used a Mann-Whitney *U* test to detect significant differences in the amount of change between treatment and control plots. For nest data analyses, the large secondary cavity-nesting species (southeastern American kestrel and eastern screech-owl) were grouped together. Because my a priori predictions were directional, one-tailed tests were used, with a significance level of  $P < 0.05$ . All data were analyzed using SAS, Version 9.1 (2003; SAS Institute Inc., Cary, North Carolina, USA).

## Results

I found 219 cavity nests in the 22 drill study plots in 2003 (pre-treatment) and 2005 (post-treatment) combined, including cavity nests in both snags and live red-cockaded woodpecker cavity trees. Data are shown in Table 5.1 by bird size grouping (LCN, NCN, OCN, or RCW), nest resource (live red-cockaded woodpecker cavity tree or snag) and treatment (drill or control). As predicted, there was a significantly greater increase in both abundance (Mann-Whitney  $U$  test,  $P = 0.04$ ) and in number of nests (Mann-Whitney  $U$  test,  $P = 0.02$ ) of red-cockaded woodpeckers on the treatment plots relative to control plots following addition of cavities (Fig. 5.1 and 5.2). There was no difference between the change in LCN (Mann-Whitney  $U$  test,  $P = 0.25$ ) or OCN (Mann-Whitney  $U$  test,  $P = 0.38$ ) abundance on experimental plots and control plots following addition of cavities (Fig. 5.1). The change in NCN abundance was different between experimental and control plots, although not significantly (Mann-Whitney  $U$  test,  $P = 0.07$ ). There was no significant difference between experimental and control plots in the change in number of nests following addition of cavities for the LCN, NCN or OCN groups (Fig. 5.2).

## Discussion

Drilling cavities in living pine trees had a clear effect on the species that excavates such cavities, the red-cockaded woodpecker, resulting in an increase in both abundance and nests. There was no indication of any impacts on any other species of providing artificial cavities for red-cockaded woodpeckers. By August 2005, 25% of the newly drilled cavities had red-cockaded woodpecker activity, 9% were showing signs of cavity enlargement and one contained a red-headed woodpecker nest. These data suggest that larger responses to the treatment may occur eventually, and that the time scale of the current study was too short to see the full effects

of the manipulation. Response times to manipulations in terrestrial systems often take many years (Power et al. 1996). Therefore I hope to resample the plots again in 2010 to assess long-term impacts.

## **Conclusions**

Cavity-nesting communities are structured by the creation of and competition for cavities as nest-sites. Viewing these communities as interconnected ‘webs’ can help identify species interactions that influence community structure, and subsequently, direct natural resource management efforts towards key species. Using a nest web approach to depict the flow of cavity-creation and use at Eglin Air Force Base in Florida, I identified 2 webs into which most cavity-nesting species on Eglin can be placed. One group contains the red-cockaded woodpecker, brown-headed nuthatch (*Sitta pusilla*), eastern screech-owl, northern flicker, red-headed woodpecker, and southeastern American kestrel, which were associated with pine snags and red-cockaded woodpecker cavities in live pines. The second group contains the Carolina chickadee (*Parus carolinensis*), downy woodpecker (*Picoides pubescens*), great-crested flycatcher (*Myiarchus crinitus*), red-bellied woodpecker, and tufted titmouse (*Parus bicolor*), which were associated with hardwood snags. The red-cockaded woodpecker and northern flicker created most cavities used by other cavity-nesters. The northern flicker was the primary creator of large cavities used by secondary cavity-nesters, through its excavation of cavities in snags and the enlargement of red-cockaded woodpecker cavities. Large secondary cavity nesters were the primary users of red-cockaded woodpecker cavities. I identified 4 cavity-nesting species with potential to respond to red-cockaded woodpecker cavity management, including the

southeastern American kestrel, northern flicker and eastern screech-owl and red-headed woodpecker.

Snags are a critical component of forested landscapes for cavity-nesting species, and a strong understanding of regional snag dynamics and cavity-nester requirements is essential to developing snag management guidelines. I examined snag densities and cavity-nest site selection at Eglin Air Force Base from 2002 – 2005. Large, mature pine snags were abundant at Eglin, exceeding other reported densities and recommended guidelines proposed for southeastern pine forests. Pine snags were heavily-used by cavity-nesting birds, despite the abundance of available red-cockaded woodpecker cavities in living pine. Hardwood snags accounted for only 10% of nests found, but were used for either nesting or roosting by 12 of the 14 cavity-nesting species that occurred in this study. Almost all species used smaller diameter hardwoods than pine. The diameters of nest-trees and available snags fell below the range of optimal nest-snag diameters reported in other studies, indicating the need for regional or site-specific snag management guidelines.

Enlarged red-cockaded woodpecker cavities provide important habitat for many larger secondary cavity nesters (e.g., American kestrels, eastern screech-owls and fox squirrels). These large species cannot use red-cockaded woodpecker cavities unless the cavities have been enlarged by other woodpeckers, and red-cockaded woodpeckers will no longer use cavities that have been enlarged substantially. The process of cavity-enlargement creates potential for indirect interactions between red-cockaded woodpeckers and large secondary cavity-nesters, mediated by other woodpecker species. I used structural equation modeling to test a path model of this interaction, using cavity excavation and enlargement as mechanisms which drive the relationship between these species. Through experimental manipulation of cavity availability, I

blocked links described in the path model, confirming cavity creation and enlargement as processes that influence community structure. I found that a cavity-management technique used for the red-cockaded woodpecker, the application of metal restrictor plates, could potentially disrupt this indirect relationship by affecting northern flicker cavity-excavation behavior. These findings provide an empirical example of how, in ecological communities where complex species interactions occur, single-species management can have indirect impacts on non-target species.

Cavity-nesting communities may serve as good model systems for integrating studies of basic ecological principles into conservation management strategies (e.g., Walters 1991). Because tree cavities serve as roosting and nesting habitat for a broad range of birds, mammals, herpetofauna and insects, the process of cavity creation may serve as a mechanism that influences community structure in forests worldwide. Woodpeckers have long been recognized as an important component of forest ecosystems (Virkkala 2006) and can be used as general indicators of forest biodiversity (Mikusiński et al. 2001). Much management is conducted for cavity-nesting birds, as at least 100 cavity-nesting bird species have declined worldwide (Eadie et al. 1998). Such management may provide excellent opportunities for studies of theoretical community ecology. Indeed, understanding the mechanisms or processes that create suitable habitat for a broad suite of cavity-nesting species within a larger associated community may ultimately improve our ability to effectively design conservation management strategies. However, biodiversity conservation that includes the protection of critical interspecific interactions necessitates the integration of theoretical ecology into conservation management strategies. In this study, I provided an example of how a study of basic ecological principles can

inform conservation management and concomitantly, how the application of a management technique can aid in the study of basic ecological principles.

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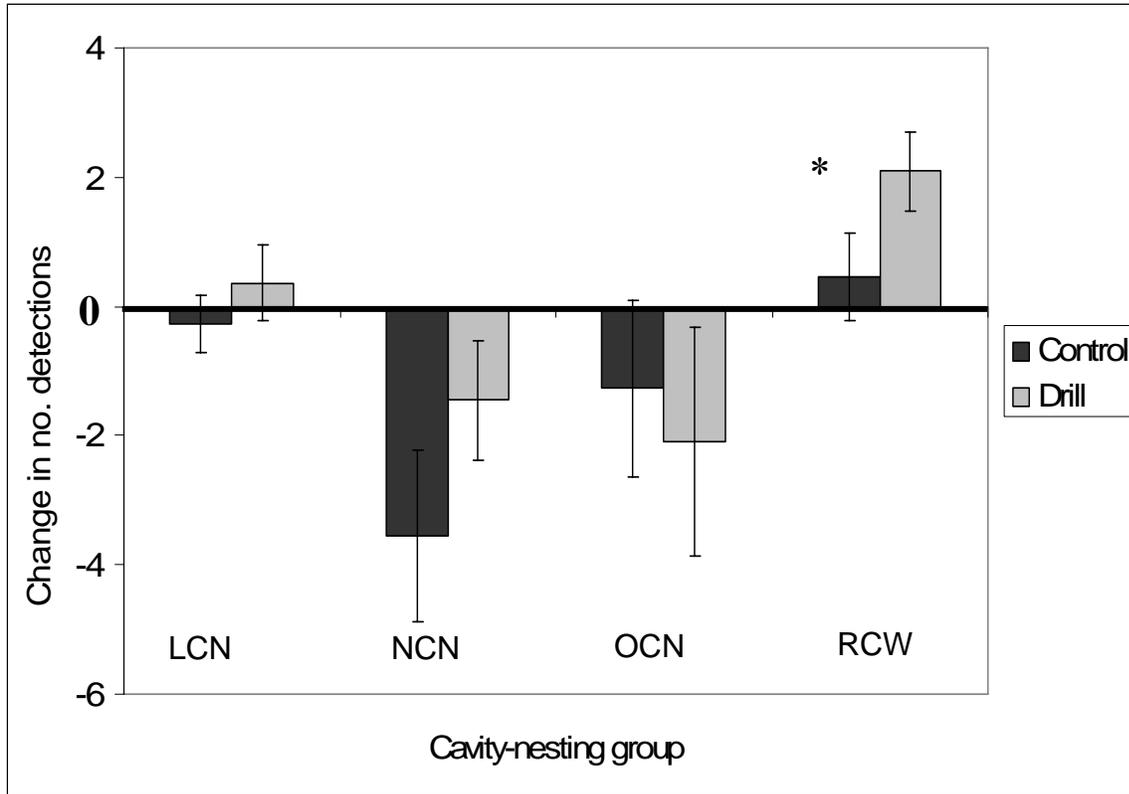
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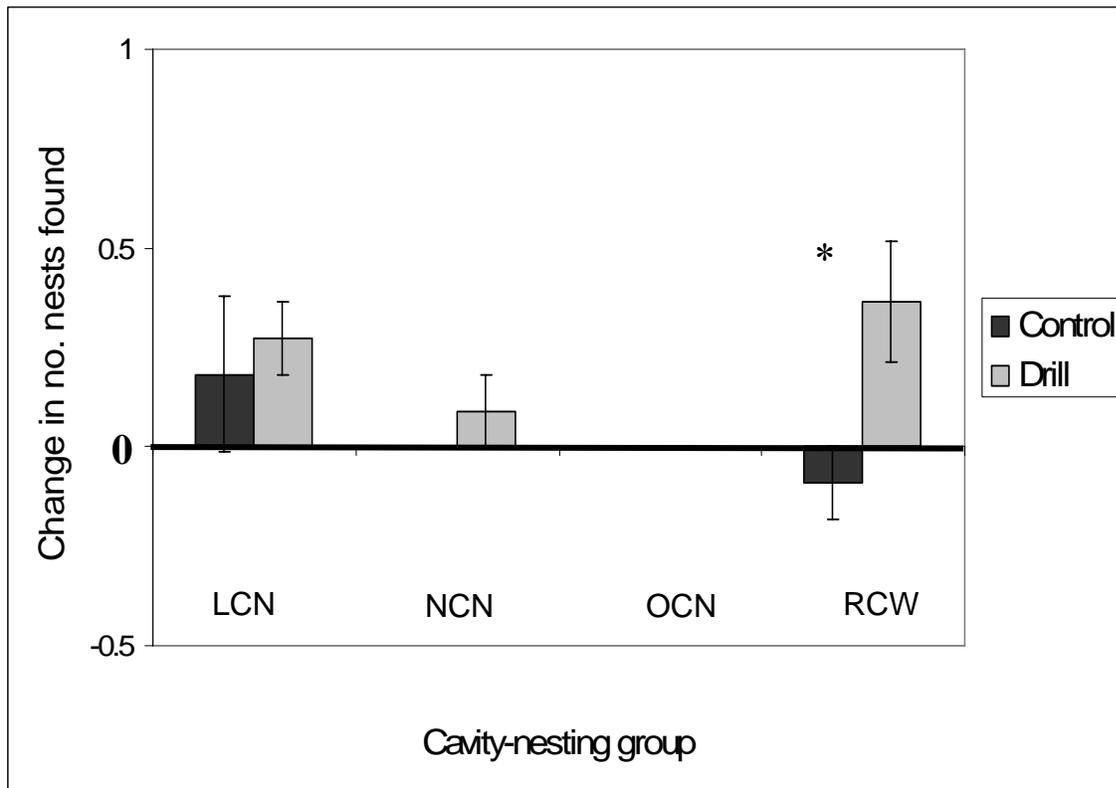
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**Table 5.1.** Nests found in 2003 and 2005 on 22 plots in the cavity addition experiment at Eglin Air Force Base, Florida. Data are shown by bird size grouping (LCN, NCN, OCN and RCW) and nest resource (live RCW cavity tree vs. snag) for both control and experimental (Drill) plots. The LCN group includes species known to use enlarged RCW cavities at Eglin; NCN includes those species that used normal-sized RCW cavities; OCN include other cavity-nesters that do not use RCW cavities.

Group	Treatment	Nests in RCW cavities (2003)	Nests in RCW cavities (2005)	Nests in snags (2003)	Nests in snags (2005)	% Nests in RCW cavities (2003)	% Nests in RCW cavities (2005)	% Nests in snags (2003)	% Nests in snags (2005)
LCN	Control	2	4	19	20	9.5	17	90.5	83
LCN	Drill	0	3	14	12	0	20	100	80
NCN	Control	0	0	34	25	0	0	100	100
NCN	Drill	0	1	29	32	0	3	100	97
OCN	Control	0	0	2	4	0	0	100	100
OCN	Drill	0	0	2	3	0	0	100	100
RCW	Control	3	2	0	0	100	100	0	0
RCW	Drill	2	6	0	0	100	100	0	0



**Figure 5.1.** Changes (mean  $\pm$  SE) in the relative abundance (detections per plot) of cavity-nesting birds in response to addition of artificial cavities for red-cockaded woodpeckers (RCWs), on control and treatment (drill) plots at Eglin Air Force Base, Florida. The LCN group includes species known to use enlarged RCW cavities, NCN includes species that use normal-sized RCW cavities, and OCN includes cavity-nesters that do not use RCW cavities. An asterisk indicates a significant difference between control and experimental plots.



**Figure 5.2.** Changes (mean  $\pm$  SE) in the number of nests found in red-cockaded woodpecker (RCW) cavities in control and treatment (drill) plots following addition of artificial cavities at Eglin Air Force Base, Florida. The LCN group includes species known to use enlarged RCW cavities, NCN includes species that use normal-sized RCW cavities, and OCN includes cavity-nesters that do not use RCW cavities. An asterisk indicates a significant difference ( $P < 0.05$ ) between control and experimental plots.