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THE RED-COCKADED WOODPECKER: INTERACTIONS WITH FIRE, SNAGS, FUNGI, RAT SNAKES AND PILEATED WOODPECKERS

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Abstract.—Red-cockaded woodpecker (*Picoides borealis*) adaptation to fire-maintained southern pine ecosystems has involved several important interactions: (1) the reduction of hardwood frequency in the pine ecosystem because of frequent fires, (2) the softening of pine heartwood by red heart fungus (*Phellinus pini*) that hastens cavity excavation by the species, (3) the woodpecker's use of the pine's resin system to create a barrier against rat snakes (*Elaphe* sp.), and (4) the woodpecker as a keystone cavity excavator for secondary-cavity users. Historically, frequent, low-intensity ground fires in southern pine uplands reduced the availability of dead trees (snags) that are typically used by other woodpecker species for cavity excavation. Behavioral adaptation has permitted red-cockaded woodpeckers to use living pines for their cavity trees and thus exploit the frequently burned pine uplands. Further, it is proposed that recent observations of pileated woodpecker (*Dryocopus pileatus*) destruction of red-cockaded woodpecker cavities may be related to the exclusion of fire, which has increased the number of snags and pileated woodpeckers. Red-cockaded woodpeckers mostly depend on red heart fungus to soften the heartwood of their cavity trees, allowing cavity excavation to proceed more quickly. Red-cockaded woodpeckers use the cavity tree's resin system to create a barrier that serves as a deterrent against rat snake predation by excavating small wounds, termed resin wells, above and below cavity entrances. It is suggested that red-cockaded woodpeckers are a keystone species in fire-maintained southern pine ecosystems because, historically, they were the only species that regularly could excavate cavities in living pines within these ecosystems. Many of the more than 30 vertebrate and invertebrate species known to use red-cockaded woodpecker cavities are highly dependent on this woodpecker in fire-maintained upland pine forests.

The red-cockaded woodpecker (*Picoides borealis*) evolved in a landscape where frequent, low-intensity fires burned within upland southern pine ecosystems. The fires reduced the numbers of hardwoods, and it is suggested that they also reduced the numbers of dead trees (snags) relative to their abundances in hardwood stands along riparian areas and bottomlands (Conner et al. 2001a). Hardwood snags, which serve as typical cavity trees for many woodpecker species in this scenario, were probably scarce. It was in this landscape that the red-cockaded woodpecker adapted to excavating cavities in live pine trees.

The extended length of time required to excavate cavities in live pines and the subsequent rarity of completed cavities in this ecosystem appear to be closely linked to the evolution of cooperative breeding in the red-cockaded woodpecker (Walters et al. 1988; 1992; Conner & Rudolph 1995). Cavities for nesting and roosting in living pines require a long time to excavate (Conner & Rudolph 1995; Harding & Walters 2002) and are so rare across the pine forest landscape that it is to the advantage of young woodpeckers, particularly young males, to forego dispersal and defer breeding until a breeding slot opens up in their natal cluster of cavity trees or a nearby cavity-tree cluster (Walters et al. 1992). These young woodpeckers from previous nesting efforts remain with the breeding pair and assist in subsequent nesting efforts by incubating eggs, feeding and brooding young, excavating cavities, and helping to defend the group's territory (Ligon 1970; Walters et al. 1988; Conner et al. 2001a).

In this paper a scenario is suggested by which historically frequent, low-intensity ground fires in southern pine uplands reduced the availability of dead trees (snags) that are typically used by woodpeckers for cavity excavation. Standing dead trees were more abundant in the more mesic hardwood sites where other species of woodpeckers are abundant. Behavioral adaptations permitted red-cockaded woodpeckers to excavate cavities into living pines for nesting and roosting. Thus, red-cockaded woodpeckers exploited the frequently burned pine uplands (Conner et al. 2001a), where the rarity of more typical cavity-excavation sites in dead branches and dead trees historically excluded or decreased the abundance of other woodpecker species in the southeastern United States because they typically do not make cavities in live pines (Conner et al. 1975; Kilham 1983). Discussion is also presented on how the woodpecker's adaptation to pine ecosystems has benefited other species by creating cavities in a relatively cavity-barren landscape.

THE INTERACTION OF FIRE WITH UPLAND PINE LANDSCAPES

Fossil pollen records indicate that fire-maintained pine ecosystems began to spread from peninsular Florida approximately 12,000 years ago and arrived at the western extreme of their distribution in Texas about 4,000 years ago (Webb 1987). This expansion was permitted by the retreat of the Laurentide ice sheet of the Wisconsin glaciation to the north (Conner et al. 2001a). Bartram (1791) described the original longleaf pine (*Pinus palustris*) forests as nearly unbroken expanses of widely spaced pines within a sea of grass. Fire, which burned in both the winter and growing season, was an integral part of the spread of pine ecosystems (Bonnicksen 2000; Conner et al. 2001a). Historically, frequent fires were ignited primarily during dry periods by lightning, Native Americans, and early settlers (Catesby 1731; Michaux 1802). The frequent fires burned day and night and meandered across the landscape until they encountered sites too isolated or too wet to burn (Frost 1993; Glitzenstein et al. 1995). The fires killed invading hardwoods in the upland pine ecosystem and maintained the herbaceous ground cover that consisted primarily of grasses and forbs (Jackson et al. 1986; Glitzenstein et al. 1995). Throughout the South, fallen pine needles and dried grasses served as fuel for the ground fires, which burned every one to three-plus years (Landers 1991; Glitzenstein et al. 1995; Bonnicksen 2000). Michaux's (1802) observations indicate that longleaf pine forests which occupied seven-tenths of the landscape in the Carolinas were burned annually.

Because hardwoods were rare in well-burned pine uplands (Chapman 1909; Platt et al. 1988; Frost 1993), live pines and pine snags were the primary sources of potential nest sites for woodpeckers. Although low-intensity ground fires may burn existing snags created by lightning and bark beetle (*Dendroctonus* sp., *Ips* sp.) infestation, they typically do not generate sufficient heat to kill pines, which would create new snags (Conner 1981; Conner et al. 2001a). Therefore, it is suggested that even pine snags may have been scarce in southern pine ecosystems.

INTERACTION OF RED-COCKADED WOODPECKERS WITH FUNGI

The use of living pines as sites to excavate cavities for nesting and roosting resulted in an increase in the length of time required for the woodpeckers to make a cavity. Most woodpecker species in eastern North America can excavate a new cavity in a dead, decayed snag in two to four weeks (Conner et al. 1975; 1976; Kilham 1983). Pileated woodpeckers (*Dryocopus pileatus*) can excavate a cavity in 23 days in the eastern United States, but excavation time can take three to six weeks in the Pacific Northwest (Bull & Jackson 1995). Downy woodpeckers (*Picoides pubescens*) can excavate a complete cavity in two weeks, whereas hairy woodpeckers (*Picoides villosus*) can take up to four weeks (Kilham 1983). Red-bellied woodpeckers (*Melanerpes carolinus*) typically can excavate a completed cavity within two weeks (Shackelford et al. 2000) and red-headed woodpeckers (*Melanerpes erythrocephalus*) within three weeks (Jackson 1976). Cavity excavation by northern flickers (*Colaptes auratus*) can take up to four weeks (Burns 1900). Lawrence (1967) observed that average cavity excavation time for northern flickers was 12.1 days, hairy woodpeckers 19.7 days, downy woodpeckers 16.0 days, and yellow-bellied sapsuckers (*Sphyrapicus varius*) 19.7 days.

Because red-cockaded woodpeckers use living pines for cavity trees, where the heartwood is often not decayed (Conner & Locke 1982), cavity excavation may require numerous years (Conner & Rudolph 1995). Unlike snags, which often have decayed sapwood and heartwood, the sapwood of live pines is not decayed (Conner & Locke 1982), and red-cockaded woodpeckers have to excavate through 8 to 16 cm of solid wood (Conner et al. 1994). Increasing sapwood thickness and the presence of flowing pine resin that seeps from the wound caused by cavity excavation further complicates the process and slows the rate of excavation (Conner et al. 1994; Conner & Rudolph 1995; Conner et al. 2001a). If resin flow is abundant, the woodpeckers typically must wait for the resin to crystallize before recommencing excavation, again, increasing the time required for cavity excavation (Conner & Rudolph 1995). Cavity excavation rates in red-cockaded woodpeckers may be influenced by the availability of suitable cavities (Harding & Walters 2002). As the need for cavities increases within a group of woodpeckers, the birds may accelerate their excavation activities (Conner et al. 2002).

Although red-cockaded woodpeckers can excavate a completed cavity into a pine with undecayed heartwood and sapwood (Conner & Locke 1982), the presence of red heart fungal (*Phellinus pini*) decay in the heartwood has an influence on the time required to excavate a complete cavity (Conner & Rudolph 1995). Red-cockaded woodpeckers are able to detect the presence of the fungus within the boles of the pines and actively select pines with red heart fungal decay for cavity trees (Conner & Locke 1982). Red heart fungus enters the heartwood of pines via broken branch stubs (Conner & Locke 1982; Conner et al. 2004). After gaining access to the heartwood of a pine, at least 15 to 20 years of growth and decay within the heartwood are required before the fungus produces a sporophore (conk) on the bole of the pine (Conner et al. 2004). This same 15- to 20-year time period is required for the fungus to decay a minimally sufficient diameter of heartwood (12 cm; Conner et al. 2004) for a woodpecker cavity. Although the age of the pine appears to be the primary factor associated with increasing frequency of heartwood decay (Conner et al. 1994), tree spacing and growth rate also have an influence (Conner et al. 2004). Older pines tend to have higher frequencies of heartwood decay and pines growing slowly in diameter prune lower branches more slowly and appear to have higher frequency of heartwood decay (Conner et al. 2004). Increased time during the natural limb pruning process allows more time for spores to infect wood tissue.

As red heart fungus decays the heartwood it softens the wood, and decayed heartwood is more easily excavated than sound heartwood. The presence of decayed heartwood can decrease the time required for cavity excavation by 1.3 years (Conner et al. 1994). Even with heartwood decay present in many cavity trees, an average of 1.8 years in loblolly (*Pinus taeda*) (n = 9 excavations), 2.4 years in shortleaf pines (*P. echinata*) (n = 12 excavations), and 6.3 years in longleaf pines (n = 12 excavations) is required to fully excavate a cavity (Conner & Rudolph 1995). Many red-cockaded woodpecker cavity trees are lost annually to bark beetles, lightning, wind action, and enlargement by pileated woodpeckers (Conner et al. 1991). Thus, the availability of pines infected with red heart fungus may determine whether red-cockaded woodpeckers have a sufficient number of useable cavity trees available for nesting and roosting in a given year.

Interaction of Red-cockaded Woodpeckers with Resin and Rat Snakes

Adaptation to contending with resin that flows from living pines when cavities are excavated has affected the interaction between red-cockaded woodpeckers and rat snakes (*Elaphe* sp.) and enhanced the survival of the woodpecker. Southern pines produce and maintain pine resin (gum) within an elaborate system of canals and ducts that extends from the pine's needles down into its roots. Resin is a mixture of primarily light resin oils (monoterpenes), which serve as solvents, and the heavier resin acids (diterpenes), which give the resin its viscous and sticky nature (Hodges et al. 1977).

The resin system in pines has evolved as their primary defense against bark beetles (Hodges et al. 1979). When bark beetles attack, the pine flushes the wound with resin and if sufficient resin is present, the attacking beetles are "pitched out." A similar response occurs when red-cockaded woodpeckers initiate cavity excavation. If resin flow is very high, it will temporarily interfere with cavity excavation as noted previously.

Red-cockaded woodpeckers nesting and roosting in living pines are extremely vulnerable to predation by rat snakes (Neal et al. 1993). Predictable, long-term use of individual cavities allows the local snake population to learn the location of cavities (Neal et al. 1993), and living pines with intact bark are easily climbed by rat snakes (Rudolph et al. 1990b). However, red-cockaded woodpeckers derive substantial protection from rat snakes by taking advantage of resin produced by pines to establish a resin barrier that prevents access to cavities by rat snakes. As cavities approach completion, red-cockaded woodpeckers excavate a series of small (1-2 cm) wounds into the cambium on the pine's bole around and above and below their cavity entrance. These wounds, termed resin wells, are pecked daily by the woodpeckers and the repeated pecking causes continuous wounding of the xylem-cambial boundary, keeping a stream of clear, fresh pine resin flowing from the wells and down the pine's bole. Multiple resin wells on a healthy cavity tree create a substantial barrier of sticky fresh resin that serves as a deterrent to climbing rat snakes (Ligon 1970; Jackson 1974; Rudolph et al. 1990b). However, repeated wounding of cavity trees over several years can decrease the ability of the pines to produce resin (Conner et al. 2001b) and pines with inadequate resin flow are abandoned by the woodpeckers (Conner & Rudolph 1995). Red-cockaded woodpeckers must continue to excavate new cavities to replace cavities with inadequate resin barriers and cavity trees lost to mortality factors or cavity enlargement by other woodpeckers.

Red-cockaded woodpeckers can detect how much resin a pine can produce (Conner et al. 1998). The socially dominant breeding male red-cockaded woodpecker selects the cavity tree that produces the most resin for his roost cavity. It is the breeding male's roost tree that usually becomes the breeding pair's nest tree. By selecting the cavity tree with the highest resin yield, the nesting effort of the breeding pair seems to receive the highest protection possible from rat snake predation (Conner et al. 1998).

RED-COCKADED WOODPECKERS AS A KEYSTONE CAVITY EXCAVATOR

In the historic fire-maintained upland pine ecosystems of the South where pines existed nearly as a tree monoculture (Chapman 1909; Platt et al. 1988; Frost 1993), red-cockaded woodpeckers were the only woodpeckers able to excavate complete cavities in living pines regularly (Ligon 1970; Conner et al. 2001a). Reports of other North American species of woodpecker excavating cavities in live portions of living pines in the eastern United States are extremely rare or nonexistent (Bent 1939; Reller 1972; Conner et al. 1975; Jackson 1976; Kilham 1983). Red-cockaded woodpeckers historically were and continue to be a keystone species because they are the primary woodpecker species to provide cavities for more than 30 other wildlife species within fire-maintained pine ecosystems of the South (Table 1).

If dead trees were rare because they were consumed by the frequent ground fires, other woodpecker species and cavities created by them were likely also rare. Data on woodpecker species use of well-burned open pine habitats versus mixed pine-hardwood habitats support the argument that other woodpecker species were less abundant in the historic fire-maintained pine forests of the South than in habitats where hardwoods were present (Shackelford & Conner 1997). Detections of pileated woodpeckers (mean number detected per 3.5 ha plot sector) were 33% higher (0.85 per plot visit versus 0.64) in infrequently burned pine-hardwood forest habitats than in more regularly burned longleaf pine habitats. Detections of red-bellied woodpeckers and northern flickers were 24% higher (1.56 per plot visit versus 1.26) and 75% higher (0.35 per plot visit versus 0.20), respectively, in pine-hardwood versus open pine habitats. The differences in the abundance of other *Picoides* were even more extreme. Detections of hairy and downy woodpeckers were 350% higher (0.27 per plot visit versus 0.06) and 2300% higher (0.24 per plot visit versus 0.01), respectively, in pine-hardwood versus open pine habitats. In contrast, a mean of 0.46 red-cockaded woodpeckers were detected per plot visit in the open pine habitats whereas none was detected in the pine-hardwood habitats (Shackelford & Conner 1997).

Support for this suggestion that red-cockaded woodpeckers likely were and continue to be a keystone cavity provider for other cavity nesters in well-burned, fire-maintained southern pine ecosystems comes from the abundance of observations of other species using red-cockaded woodpecker cavities. Numerous vertebrate and invertebrate species are known to use red-cockaded woodpecker cavities (Table 1). Because so many other cavity-nesting species are dependent on red-cockaded woodpeckers for cavities, forest biodiversity would suffer substantially in the absence of this endangered woodpecker in fire-maintained pine ecosystems of the South. Several species, such as red-bellied and red-headed woodpeckers and southern flying squirrels appear to compete actively with red-cockaded woodpeckers for intact cavities (Jackson 1978; Neal et al. 1992; Kappes & Harris 1995). The fact that red-

Table 1. Vertebrate and invertebrate species observed using unenlarged and enlarged red-cockaded woodpecker cavities in the southeastern United States.

Cavity occupant	References for observation
Birds	
American kestrel (*Falco sparverius*)	(Rudolph et al. 1990a)
Brown-headed nuthatch (*Sitta pusilla*)	(Jackson 1978)
Carolina chickadee (*Poecile carolinensis*)	(Beckett 1971)
Eastern bluebird (*Sialia sialis*)	(Baker 1971; Jackson 1978)
Eastern screech-owl (*Otus asio*)	(Baker 1971; Conner et al. 1997)
European starling (*Sturnus vulgaris*)	(Dennis 1971; Jackson 1978)
Great crested flycatcher (*Myiarchus crinitus*)	(Baker 1971; Conner et al. 1997)
Northern flicker (*Colaptes auratus*)	(Baker 1971; Dennis 1971)
Pileated woodpecker (*Dryocopus pileatus*)	(Baker 1971; Jackson 1978)
Red-bellied woodpecker (*Melanerpes carolinus*)	(Dennis 1971; Jackson 1978)
Red-headed woodpecker (*M. erythrocephalus*)	(Baker 1971; Beckett 1971)
Tufted titmouse (*Baeolophus bicolor*)	(Baker 1971; Beckett 1971)
White-breasted nuthatch (*Sitta carolinensis*)	(Baker 1971)
Wood duck (*Aix sponsa*)	(Baker 1971)
Mammals	
Eastern gray squirrel (*Sciurus carolinensis*)	(Dennis 1971; Jackson 1978)
Evening bat (*Nycticeius humeralis*)	(Rudolph et al. 1990a)
Fox squirrel (*Sciurus niger*)	(Baker 1971; Jackson 1978)
Raccoon (*Procyon lotor*)	(Loeb 1993)
Southern flying squirrel (*Glaucomys volans*)	(Baker 1971; Beckett 1971)
Reptiles and amphibians	
Broad-headed skink (*Eumeces laticeps*)	(Conner et al. 1997)
Five-lined skink (*Eumeces fasciatus*)	(Jackson 1978)
Gray treefrogs (*Hyla versicolor* & *H. chrysoscelis*)	(Jackson 1978; Conner et al. 1997)
Rat snake (*Elaphe obsoleta*)	(Baker 1971; Dennis 1971)
Arthropods	
Ants	(Conner et al. 1997)
Honey bee (*Apis mellifera*)	(Dennis 1971; Jackson 1978)
Moths (Lepidoptera)	(Conner et al. 1997)
Mud daubers (Sphecidae)	(Conner et al. 1997)
Paper wasps (3 *Polistes* sp.)	(Dennis 1971; Rudolph et al. 1990a)
Spiders	(Conner et al. 1997)

headed and red-bellied woodpeckers, two woodpeckers that normally are primary excavators, regularly use red-cockaded woodpecker cavities for nesting over a wide geographic area (Neal et al. 1992) provides compelling evidence of the keystone role red-cockaded woodpeckers play in upland pine ecosystems. Red-bellied woodpeckers have been reported using red-cockaded woodpecker cavities more than any other species of bird throughout the South.

Pileated woodpeckers enlarge the entrance to red-cockaded woodpecker cavities such that they are no longer useable by the endangered woodpecker (Carter et al. 1989). Red-cockaded woodpeckers likely do not use these enlarged cavities because of their increased vulnerability to predators and competitors. Once a cavity entrance is enlarged, however, larger secondary cavity users, such as the American kestrel, eastern screech-owl, northern flicker, fox squirrel, raccoon, and wood duck, are able to use the cavity (Table 1).

Anthropogenic forces have greatly altered the southern forest landscape over the past 150 years (Frost 1993; Conner et al. 2001a). Exclusion and suppression of fire from fire-maintained ecosystems and conversion of pine forests to other land uses have occurred southwide. Such changes have permitted hardwood species to invade the previously open pine uplands and likely increased the availability of dead trees across the previously pine-dominated landscape. Snags do not always ignite under modern day prescribed fire conditions, especially when nearly all burns are conducted during winter under cool, humid conditions when the risk of wildfire is low. These changes have permitted other species of woodpeckers to be in closer proximity to red-cockaded woodpeckers than they were historically (Saenz et al. 2002). A serious consequence of this change is the high rate of damage done to red-cockaded woodpecker cavities by pileated woodpeckers (Conner et al. 1991; Conner & Rudolph 1995; Saenz et al. 1998; 2002). The rate of damage is so severe that many red-cockaded woodpecker populations suffer an annual net loss of useable cavities. In Texas, red-cockaded woodpecker populations on the Angelina National Forest averaged an annual net loss of 4.6 useable cavities over a 10 year period (Conner et al. 1991; Conner & Rudolph 1995). The loss of cavities to tree death (57 cavity trees) was roughly equal to the loss due to pileated woodpecker enlargement (55 cavity trees).

Red-cockaded woodpeckers could not have evolved in the fire-maintained pine ecosystems of the South if they suffered such a loss rate historically. They would have lost cavities faster than they could have excavated them. Pileated woodpecker abundance and their current rate of cavity destruction likely are elevated above what occurred in the South in the historic fire-maintained pine ecosystems of pre-Columbian times. Testing this hypotheses would be somewhat problematic in present day landscapes. Because of the large home range of a pileated woodpecker pair and red-cockaded woodpecker group, large tracts (5,000+ ha) of unbroken well-burned longleaf pine forest that are not fragmented from a timber-type and land-use perspective and still contained populations of red-cockaded woodpeckers would be needed to test the hypotheses. Such landscape conditions are now only a historic memory (Frost 1993; Conner et al. 2001a).

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