CHAPTER 8

CAVITIES, CAVITY TREES, AND CAVITY COMMUNITIES

THE RED-COCKADED WOODPECKER CAVITY TREE: A VERY SPECIAL PINE

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Abstract: The adaptation of red-cockaded woodpeckers (*Picoides borealis*) to fire-maintained southern pine ecosystems has included the development of behaviors that permit the species to use living pines for their cavity trees. Their adaptation to pine ecosystems has also involved a major adjustment in the species' breeding system to cooperative breeding, probably in response to the extended time period required to excavate a completed cavity in a living pine and the relative rarity of completed cavities for nesting. The characteristics of live pines make them variable in their suitability as cavity trees, leading to the evolution of selection behavior among woodpeckers. Red-cockaded woodpeckers require a very special type of pine for their cavity tree. Potential cavity trees must be sufficiently old because only older pines have heartwood of sufficient diameter to physically house a woodpecker cavity without breaching the resin producing sapwood. Older pines also have a larger diameter of heartwood higher in the pine, permitting higher cavity placement, well away from frequent fires. Older pines also have a higher occurrence rate of red heart fungus (*Phellinus pini*), which decays the heartwood allowing cavity excavation to proceed more quickly. The potential cavity tree also needs to have relatively thin sapwood, which reduces the time the woodpeckers must spend excavating through living xylem tissue that exudes sticky pine resin when pecked. Red-cockaded woodpeckers scale loose bark from the bole of their cavity trees and excavate resin wells above and below cavity entrances. These behaviors create a resin barrier that is very effective in deterring predation by rat snakes (*Elaphe* spp.). Thus, the ability of pines to produce adequate resin is also important to the woodpecker. Red-cockaded woodpeckers can detect the pine's ability to produce resin and select pines that are high producers. Higher yields of resin likely create better barriers against rat snakes. The socially dominant breeding male red-cockaded woodpecker selects the cavity tree that produces the most resin for its roost tree, which during spring becomes the group's nest tree. Our recent research suggests that red-cockaded woodpeckers also select pines with particular resin chemistries. High concentrations of diterpenes may increase resin viscosity, stickiness, irritability, or other factors that may be important for creating a barrier against rat snakes.

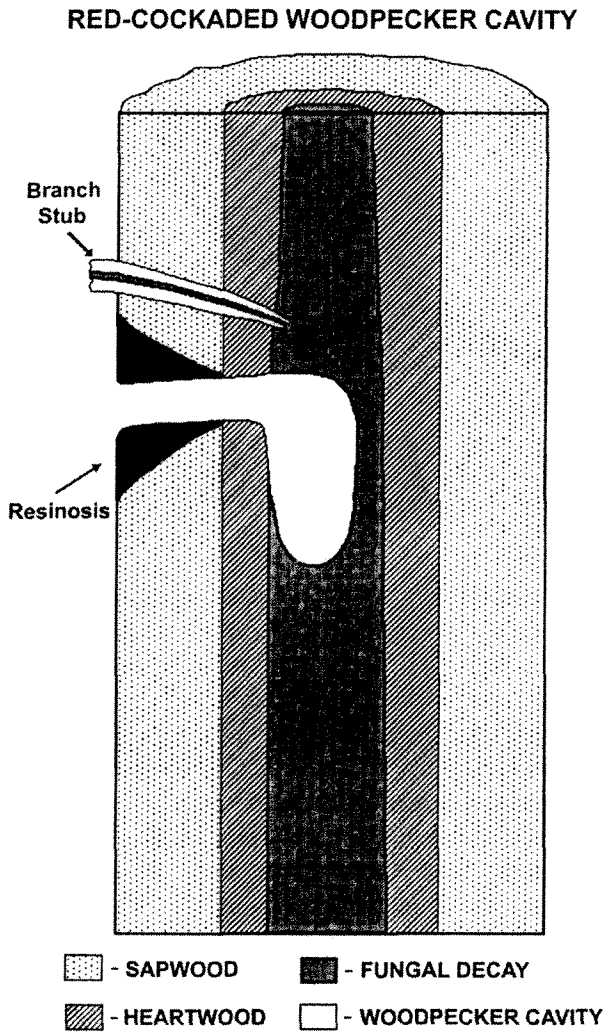

Figure 1. Diagram of a red-cockaded woodpecker cavity showing a vertical section of a cavity tree with adequate heartwood diameter, thin sapwood, and a column of decay resulting from an infection with red heart fungus (*Phellinus pini*). Inoculation of the heartwood with red heart fungus occurs through a branch stub and after about 12 to 15 years, sufficient decay has occurred to facilitate excavation. Crystallization of resin (resinosis) occurs around the cavity entrance.

Key words: cavity tree, pine resin, rat snakes, red heart fungi, red-cockaded woodpecker.

It has been suggested that the frequent, low intensity fires that historically burned within upland southern pine ecosystems might have reduced the numbers of hardwoods and dead trees (snags) relative to their abundances in hardwood stands along riparian areas and bottomlands (Conner et al. 2001*a*). In this scenario traditional hardwood snags, as sites for woodpecker cavity trees, were probably scarce. Under those conditions, live pines and pine snags may have become the primary source of potential nest sites for woodpeckers. Because frequent, low intensity fire also takes a high toll on pine snags and typically does not kill live mature pines to make new snags, we suggest that even pine snags may have been scarce. It was in this landscape that the red-cockaded woodpecker likely evolved behaviors associated with making cavities in live pine trees and tree preferences developed.

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*a*, 1992*a*; Walters 1990*a*; Copeyon et al. 1991; Conner and Rudolph 1995*a*). Cavities for nesting and roosting take so long to excavate and are so rare across the pine forest landscape that it is to the advantage of young woodpeckers, particularly young males, to 'stay at home' and defer breeding until a breeding position becomes available in their natal cluster or a nearby cavity-tree cluster (Walters et al. 1992*a*).

Adaptation to use live pines is not a simple matter and there are good reasons why it is a rare adaptation. Inherent problems in using live pines create variation in the suitability of trees and increase the evolutionary pressure for developing selection among pines. Thus, cavity selection has become very specialized. The characteristics of pines selected by red-cockaded woodpeckers for cavity trees are important for several reasons, some of which relate to factors that hasten the cavity excavation process and others that relate to defense of cavities against rat snakes (*Elaphe* spp.). Here we examine the multiple characteristics that appear to be important to red-cockaded woodpeckers when they select a pine for cavity excavation.

CAVITY TREE AGE

Red-cockaded woodpeckers require old pines for cavity trees for a variety of reasons, most of which relate to age factors that hasten the cavity excavation process (Jackson and Schardien-Jackson 1986, Conner and O'Halloran 1987). Most forests where red-cockaded woodpeckers occur currently do not have adequately aged pines and each year the woodpeckers continue to select the oldest pines available for cavity excavation

(Rudolph and Conner 1991). Until the south-wide deficit of old pines is corrected through time, management of woodpecker populations will require use of artificial cavity technology (Copeyon 1990, Allen 1991) to maintain woodpecker populations through the cavity tree shortage bottleneck (Costa and Escano 1989). Artificial cavities will be necessary because certain required features simply do not occur in young pines, chief among these are desirable heartwood to sapwood ratios and fungal decay.

Heartwood and Sapwood Characteristics

Red-cockaded woodpeckers need pines with adequate heartwood diameter to physically house the excavated cavity (Clark 1992, Conner et al. 1994). Heartwood is formed in the center core of the pine as the tree ages and living xylem (sapwood) ceases to actively transport water and minerals up the tree. Typically, new increments of heartwood are formed each year as new annual increments of sapwood xylem tissue are produced at the cambial zone under the bark. Soil quality and competition for nutrients and light directly affect pine diameter growth, rate of xylem growth, and the rate at which living xylem (sapwood) is converted to heartwood (Kramer and Kozlowski 1979). Typically, heartwood diameters are greater in the lower boles of pines than in higher regions of the bole. Only when pines exceed 90 to 120 years of age are sufficient diameters of heartwood available to physically house a cavity in the upper regions of the bole (Clark 1992, Conner et al. 1994). In longleaf pines (*Pinus palustris*) the trees typically must exceed 150 years in age before sufficient heartwood is present in the bole within the crown of the pine to permit cavity excavation (Conner et al. 1991, 2001*a*).

The importance of high cavity placement in the boles of pines is often not fully appreciated. Pine resin is highly flammable. Daily excavation at resin wells (discussed below) produces streams of flammable pine gum on the bole. Resin flowing from resin wells around cavities that are excavated in pines where adequate heartwood is present only in the lower regions of the bole is easily ignited by the frequent fires required to maintain the ecosystem (Conner and Locke 1979). If sufficient heartwood is present in the upper regions of the pine's bole, woodpeckers can excavate cavities in the upper region of the bole and in the crown portion of the bole. There is less risk of fire ignition of resin flow when cavities are excavated in the higher regions of the pine's bole (Conner and O'Halloran 1987, Conner et al. 1991). This is important for a species that lives in a fire-maintained ecosystem where the cavities are a critical resource (Walters 1990*a*, Conner and Rudolph 1995*a*) and are easily destroyed by fire (Conner and Locke 1979).

In addition to large heartwood diameter, red-cockaded woodpeckers prefer pines with certain sapwood characteristics (Figure 1). When red-cockaded woodpeckers begin to excavate into the living sapwood to make the entrance tube of a cavity, sticky pine gum (resin) flows from the wound site. A creamy white "icicle" of resin usually appears below the excavation site during this period as resin flows from the wound, runs down the bole of the pine, and crystallizes. Sapwood is living xylem tissue, it is usually about 8 to 15 cm thick, and actively transports resin to the wound site. During the time period when woodpeckers are excavating the cavity entrance tube through the sapwood, they must contend with fresh flowing resin at the wound site and often wait up to several weeks for it to crystallize (resinosis) before they can continue excavation (Figure 1). Thus, the thickness of the sapwood is important for cavity tree selection, and red-cockaded woodpeckers select pines with relatively thin sapwood for their cavity trees (Conner et al. 1994). The period of time required to excavate a cavity entrance tube is shorter in pines with thinner sapwood, because the entrance tube will be shorter and there will be fewer intervals spent waiting for resin to crystallize. This is an important point for a species that regularly faces an inadequate supply of cavities for nesting, roosting, and the formation of new breeding groups. Cavity excavation time is directly affected by the thickness of the sapwood and the ability of the pine to produce resin.

Pine age affects sapwood thickness. Older pines tend to have thinner sapwood than young and middle-aged pines. As pines age they tend to convert living xylem (sapwood) to heartwood at a higher rate than younger pines. Thus, older pines with a higher ratio of heartwood diameter to sapwood thickness provide ideal conditions for red-cockaded woodpecker cavity excavation.

Red Heart Fungus Decay of the Heartwood

The presence of red heart fungus (*Phellinus pini*) in the heartwood has a significant influence on the time required to excavate a completed red-cockaded woodpecker cavity. Red heart fungus enters the heartwood of pines via broken branch stubs (Conner and Locke 1982, Conner et al. 2004b, Figure 1). 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 and Locke 1983, Conner et al. 2004b). The sporophore appears to grow on the exterior of the pine's bole at the branch stub where the fungus initially entered the heartwood. This same 15- to 20-year time period is required for the fungus to decay a minimally sufficient diameter of heartwood for a woodpecker cavity. As the fungus decays the heartwood it softens the wood, and decayed heartwood is more easily excavated than sound heartwood. Thus, the presence of decayed heartwood significantly decreases the time required for cavity excavation (one-tailed t-test, $P = 0.0285$) (Conner et al. 1994). Red-cockaded woodpecker cavities are often excavated about 2 cm below the site where the fungal sporophore grows on the bole of the pine (Conner et al. 2004*b*), suggesting that woodpeckers may sometimes exploit the decayed branch stub to decrease the time required to excavate a cavity entrance tube. 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 and Locke 1982, Hooper et al. 1991*b*).

As with large heartwood diameter and thin sapwood thickness, the occurrence of heartwood decay is positively related to pine age. The entrance of red heart fungus into a pine's heartwood is related to when and how quickly larger diameter branches undergo natural pruning as the pine grows. Extensive heartwood decay can exist in the lower boles of pines as young as 50 years (Conner et al. 2004*b*), but more typically pines must reach 90 (Hooper et al. 1991*b*) to 120 years of age (Conner et al. 1994) before sufficient decay has occurred within the bole to benefit red-cockaded woodpeckers. Thus, older pines are needed by the woodpeckers to provide potential cavity trees with suitably decayed heartwood.

Many pines selected by red-cockaded woodpeckers for cavity excavation appear to have undergone periods of growth suppression due to competition with other pines followed by a release from competition and increased diameter growth (Conner and O'Halloran 1987). Periods of suppressed growth followed by periods of free growth may affect natural pruning rates of lower branches on pines and facilitate inoculation of pines with *Phellinus pini*. Additional research is needed to explore relationships between pine growth history and infection rates of red heart fungus in pines.

THE PINE TREE RESIN SYSTEM

In addition to age, the suitability of a tree depends on its pine resin system. Southern pines actively produce and maintain pine oleoresins within an elaborate resin canal and duct system that extends from the pine's needles down into its roots. Resin is produced in pine needles and in the cells lining the canals and ducts. Resin is a complex mixture of primarily light resin oils (monoterpenes), which are highly volatile and serve as solvents, and the heavier resin acids (diterpenes), which give the resin its viscous and sticky nature (Zinkel et al. 1971, Hodges et al. 1977). This resin system appears to have evolved in pines as their primary defense against bark beetles (Hodges et al. 1979).

The Importance of High Resin Yield

When bark beetles attack a pine and begin to chew into the cambium, the pine responds by pumping preformed resin to the wound site in an effort to 'pitch' the attacking beetles out. A very similar response occurs when red-cockaded woodpeckers excavate sapwood. If resin flow is very high, it will temporarily interfere with cavity excavation, as mentioned above, but it also provides protection for the cavity. When the cavity approaches completion, red-cockaded woodpeckers begin to excavate a series of wounds into the cambium on the pine's bole around and above and below the cavity entrances. These small wounds, termed resin wells, are tended daily by the woodpeckers and repeated pecking causes continuous wounding, keeping a stream of clear, fresh pine resin flowing from the wells and down the pine's bole. Multiple resin wells create a substantial barrier of sticky fresh resin that serves as a significant deterrent to climbing by predatory rat snakes (*Elaphe* spp.) (Jackson 1974, Rudolph et al. 1990*b*). The importance of pines that can produce a sustained high yield of pine resin as red-cockaded woodpecker cavity trees is obvious—when woodpeckers excavate and maintain resin wells, such cavity trees can produce a better barrier against rat snakes.

The importance of this resin barrier for defense of nest and roost cavities against rat snakes suggests that it would benefit red-cockaded woodpeckers to be able to distinguish between good and poor resin producers. Recent research suggests that red-cockaded woodpeckers can detect the ability of a pine to produce resin and likely use that ability to aid in cavity tree selection (Conner et al. 1998*b*). The socially dominant breeding male red-cockaded woodpecker appears to be able to

determine which active cavity tree currently being used by the woodpecker group produces the most resin, and selects that cavity tree for his roost tree. The breeding male also tends to select a newly completed cavity in a new cavity tree, likely because those cavities are in pines that are high resin producers. After multiple years of use, resin yield from cavity trees appears to decline, making them less acceptable to the woodpeckers (Conner et al. 2001*b*). Selection of cavity trees with high resin yields decreases the probability of being preyed upon by a climbing rat snake relative to other woodpecker group members. This selection by the breeding male has further significance because it is within his roost cavity that the breeding female lays her eggs. Thus, by selecting the cavity tree with the highest resin yield, the nesting effort of the breeding pair receives the highest protection possible from rat snake predation. Selection of pines based on resin yield ability likely occurs during 2 possible time periods: first, when the pine is initially excavated and resin flows from the cavity start, and second, during daily pecking at new and existing resin wells.

As mentioned above, daily excavation of resin wells over multiple years can affect the ability of a pine to produce resin. The decreasing yield of resin from cavity trees over time can affect the susceptibility of the cavity tree to bark beetle attack (Conner et al. 2001*b*), and likely also the ability of the tree to provide sufficient resin to maintain a barrier against rat snakes. After about 7 years of continuous use by red-cockaded woodpeckers, 24-hour resin yield from longleaf pine cavity trees dropped from a yield of more than 30 ml of resin down to about 2 ml (Conner et al. 2001*b*). Over a 5-year period of use by red-cockaded woodpeckers, 24-hour resin yield from loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pine cavity trees declined from about 3 ml to about 0.5 ml (Conner et al. 2001*b*).

These data strongly suggest that the higher value placed on longleaf pine cavity trees over loblolly and shortleaf pine cavity trees is because of longleaf pine's ability to sustain higher yields of resin over longer time periods (Hodges et al. 1979). Because longleaf pine can sustain high yields of resin over many years, it is the ideal pine species for red-cockaded woodpecker cavity trees (Conner et al. 1998*b*). In addition, because of their resin producing characteristics, longleaf pines live longer than loblolly and shortleaf pines (Wahlenberg 1946), are less susceptible to bark beetle infestation (Conner et al. 1991, Conner and Rudolph 1995*b*), and provide a better resin barrier against climbing rat snakes (Rudolph et al. 1990*b*, Conner et al. 1998*b*).

Selection for Special Resin Chemistries

Red-cockaded woodpeckers may be able to detect more about pine resin than just the ability of the pine tree to produce a sufficient yield. Recent research using a gas chromatograph to detect various chemical components of pine resin suggests that the woodpeckers may be able to taste or sense resin texture to select pines with particular resin chemistries for their cavity trees (R. N. Conner et al., U.S. Forest Service, unpublished data). Preliminary data indicate that pines selected by red-cockaded woodpeckers for natural cavity excavation have higher concentrations of isopimaric, paulustric, and levopaulustric resin acids than do pines selected by biologists for artificial cavity insert installation or matched control trees. The precise function of these particular resin acids is not fully understood; however, we suggest that they may function to enhance the flow dynamics, stickiness, or even irritability of the extruded resin and thus ultimately enhance the deterrence of rat snakes.

SUMMARY

The red-cockaded woodpecker cavity tree is a special pine. The pine's age, growth history, wood characteristics, presence of heartwood decay, and resin system are properties important to the red-cockaded woodpecker. The ideal pine for cavity excavation is old, has relatively thin sapwood and a large diameter of heartwood well into the bole in the crown. It has been infected by red heart fungus for at least 15 years and can produce a sustained high yield of resin when wounded. The pine may also need to have a specific resin chemistry that enhances the ability of resin flowing from resin wells to coat the pine's bole and remain sticky, creating an effective barrier against rat snakes.

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