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ECOLOGICAL RELATIONSHIPS BETWEEN FUNGI AND WOODPECKER CAVITY SITES

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Abstract. The presence of rotted wood is often noted in descriptions of woodpecker nest and roost sites, and ornithologists have found that certain fungi and species of woodpeckers, such as the red heart fungus (*Phellinus pini*) and Red-cockaded Woodpeckers (*Picoides borealis*) are intimately linked. The relationship assumed is usually one of woodpecker dependence or preference for partially decayed wood in which to excavate cavities, but the woodpecker is also sometimes suggested as a vector for the fungus. In this paper we review such associations and describe patterns evident among woodpecker nest sites that suggest microclimatic and microhabitat characteristics favoring fungal colonization of trees, woodpecker-favorable responses of trees to fungi, and ultimate use of the trees for woodpecker cavity excavation. Factors that favor fungal invasion and tree use by woodpeckers include tree species, growth history, site characteristics such as proximity to water and exposure to sun or shade, nature and position of tree injury, local climate, forest age and species composition, fire frequency, and human management activities. Woodpecker cavity height and entrance orientation may be related to the dispersal dynamics of fungi, which in turn may be related to forest vegetation, thermal, and hydric characteristics.

Key words: *cavity, fungi, nest-site correlates, nest-site selection.*

Relaciones Ecológicas entre Hongos y Cavidades de Pájaros Carpinteros

Resumen. En las descripciones de los nidos y dormideros de los carpinteros, muchas veces se menciona la presencia de madera podrida. Los ornitólogos han encontrado que ciertos hongos y especies de carpinteros, como el hongo *Phellinus pini* y el carpintero *Picoides borealis*, están íntimamente ligados. Usualmente se supone que el carpintero depende de o prefiere la madera en cierto estado de descomposición para excavar las cavidades, pero a veces también se sugiere que el carpintero es el vector del hongo. En este trabajo revisamos estas asociaciones y describimos patrones evidentes entre los sitios de nidificación de los carpinteros que sugieren (1) que existen características micro-climáticas y micro-ambientales que favorecen la colonización de los árboles por parte de los hongos, (2) que los árboles responden a los hongos de modo favorable para los carpinteros y (3) que los carpinteros usan luego los árboles para excavar las cavidades. Los factores que favorecen la invasión de los hongos y el uso de los árboles por parte de los carpinteros incluyen la especie de árbol, la historia de crecimiento, las características del sitio tales como la proximidad al agua y la exposición al sol o a la sombra, el tipo y posición del daño que presenta el árbol, el clima local, la edad y composición de especies del bosque, la frecuencia de fuego y las actividades antrópicas de manejo. La altura y orientación de la entrada de las cavidades de los carpinteros pueden estar relacionadas con la dinámica de dispersión del hongo, la cual a su vez puede estar relacionada con las características térmicas, hídricas y de la vegetación del bosque.

INTRODUCTION

Woodpeckers generally choose nest and roost sites in dead or partially dead trees, and ornithologists have often linked these sites with the presence of fungal decay (Jackman 1975). While acknowledging the general use of decayed wood for cavity excavation, some have also suggested that woodpeckers may regularly excavate nest and roost cavities in sound wood (e.g., Short 1979, Conner and Locke 1982). Excavation of a cavity in sound wood is a difficult and time-consuming task that woodpeckers generally seem to avoid. Woodpecker cavity excavation is a compromise among multiple factors associated with timing, ease of excavation, and vulnerability to predation or weather. The presence of fungi and degree of decay they have caused are important factors that affect this trade-off in cavity excavation. In this paper we focus on the com-

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plexity of relationships among woodpeckers, wood-decaying fungi, and the trees in which woodpeckers excavate nest and roost cavities.

Among woodpeckers, the nest cavity is used as a roost by the male, old nest cavities are often used as roosts by both males and females, and both sexes also regularly excavate roost cavities independent of nest cavities. Active, abandoned, and usurped woodpecker cavities also support large communities of other organisms, giving woodpeckers and their cavities pivotal roles in ecosystem dynamics (e.g., Kilham 1971, Daily et al. 1993, Martin et al. 2004).

There can be significant differences between nest cavities and roost cavities (e.g., in Pileated Woodpeckers [*Dryocopus pileatus*]; McClelland and McClelland 1999, Bull et al. 1992, Bull and Jackson 1995), because the nest must provide a safe receptacle for eggs and altricial nestlings, whereas the roost cavity provides refuge for a bird that can cling to vertical surfaces. The roosting bird does not need a bottom to its cavity, and the long cylinder caused by advanced fungal decay allows woodpeckers to have roosts with multiple entrances and escape routes. The roles of fungi in facilitating cavity excavation are similar for nest and roost cavities and we include both types in our discussions here. Roost cavities (e.g., those of Pileated Woodpeckers in western redcedar [*Thuja plicata*]; Parks et al. 1997) and rarely nest cavities (e.g., of Northern Flicker [*Colaptes auratus*]; JAJ, unpubl. data) are sometimes created by fungal decay with only limited woodpecker excavation.

Many woodpeckers can excavate a cavity in somewhat decayed wood within about two weeks, essentially the time required for nest construction in open-nesting passerines (Jackson 1976b, Moore 1995, Jackson and Ouellet 2002, Walters et al. 2002). To select the most decayed and hence most quickly excavated site could (1) increase the risk of predation to a predator ripping the nest cavity open, and (2) increase the risk of cavity loss due to excessive wind. To take longer to excavate a nest might mean squandering reproductive energies by (1) expending more energy during excavation, (2) increasing the risk of predation during cavity excavation, or (3) forgoing the opportunity for renesting should the first nest be lost.

Most woodpeckers take advantage of wood softened, but not extensively rotted, by wood-decaying fungi, but many factors influence this balance. For example, a high fire frequency in natural southeastern pine forests favors cavity excavation by Red-cockaded Woodpeckers in living pines rather than in more fire-vulnerable dead trees. These are excavated through sound sapwood and can take more than four years to complete (Fig. 1; Jackson et al. 1979).

FIGURE 1. Section through a Red-cockaded Woodpecker cavity that had been excavated in a living loblolly pine (*Pinus taeda*). Note the intact sapwood and the stained heartwood that has been decayed by *Phellinus pini*, and the extent to which the cavity contours are limited to the decay. Photo by JAJ.

WOODPECKER CAVITY-SITE AND CAVITY-TREE CHARACTERISTICS

The trees selected for cavity excavation and the position of woodpecker cavities within them play important roles in cavity quality. The differences between nest sites of woodpeckers in dead trees and nest sites in the trunk or living limbs of live trees are very important because of (1) cavity-site differences that reflect differential niche use among species, (2) differences in characteristics of the cavities excavated, and (3) differences in the fungus-tree relationships that facilitate cavity excavation. We will focus on differences in fungus-tree relationships.

Important cavity-site parameters relative to selection of a site for excavation include: (1) trunk or limb diameter, (2) cavity height and tree growth history, (3) cavity entrance orientation, (4) position relative to other limbs, foliage, and epiphytes, (5) tree species, (6) tree age, (7) nature, extent, and position of tree injuries, (8) whether the tree is alive or dead, and (9) local habitat and microclimate. Our goal is to foster an understanding of the possibilities of involvement of multiple factors in cavity-site selection and interrelationships between woodpeckers and fungi. In the discussion below we briefly characterize the significance of each parameter and identify potential relationships between the parameter and tree-decaying fungi.

Trunk or limb diameter. The diameter of a trunk or limb used for cavity excavation by a woodpecker is limited by the size of the bird; a Downy Woodpecker (*Picoides pubescens*) may use a limb as small as 12 cm in diameter (Ritchison 1999), whereas the Ivory-billed Woodpecker (*Campephilus principalis*) may have required limbs of 35–40 cm diameter (Tanner 1942, Jackson 2003). Smaller limbs generally take less time to grow and are much more abundant within a given tree; thus larger birds are increasingly limited by this single cavity-site parameter. Smaller woodpeckers, such as the Downy, may use larger limbs for cavity excavation, but in doing so, risk cavity loss to larger woodpeckers (Jackson and Ouellet 2002). For the smallest of woodpeckers, sapwood-decaying fungi may be of great importance, but as the ratio of heartwood to sapwood increases with limb diameter, woodpeckers have an increasing dependence on heartrot fungi.

Cavity height and tree-growth history. The higher the cavity above ground, the less vulnerable it would seem to be to predation from terrestrial predators. On the other hand with increasing height above ground, (1) limb diameter decreases, limiting cavity size and the thickness of wood insulating and protecting the cavity, (2) limbs are more vulnerable to wind and lightning, and, (3) to the extent that higher cavities are more in the open, birds approaching the cavity may be more vulnerable to aerial predators.

Considering these differing selective pressures, one might expect species-specific or habitat-specific optimum cavity heights to vary. We suggest that such variation in cavity height may be related to the dynamics of fungal colonization of trees. There is a strong relationship between tree height and cavity height, and tree height varies among species, localities, and with physical conditions under which trees grow (Horn 1971, Zimmerman and Brown 1971). For example, many open-grown trees tend to undergo little natural pruning, and thereby provide few sites (branch stubs) for invasion by heartwood-decaying fungi and for cavity excavation. As a result of competition for light, trees of many species grown within a forest tend to be taller and undergo more natural pruning, hence providing more branch stubs, more opportunities for invasion of heartrot fungi, and thus more potential woodpecker cavity sites.

Cavity entrance orientation. Several authors have identified species- and region-specific differences in the orientation of woodpecker cavity entrances. For example, Red-cockaded Woodpeckers have significantly more cavities opening to the south and west than to other directions (Dennis 1971, Jackson 1994). In Colorado, Yellow-bellied Sapsucker (*Sphyrapicus varius*) entrances opened predominantly to the south (Inouye 1976). In Colorado (Inouye 1976) and British Columbia (Wiebe 2001), Northern Flicker nests opened predominantly to the south, but in Ohio there was no pattern to flicker cavity orientation (Ingold 1994). In Ontario, 54% of 89 cavities of four species of woodpeckers had a general southern orientation (Lawrence 1967). In Virginia, these same species showed a predominant cavity orientation to the east-northeast (Conner 1975). The preferential orientation of nest-cavity entrances is suggested to have potential thermal advantages for eggs, nestlings, and adults (e.g., Wiebe 2001), with little attention paid to other possibilities. In riparian aspen woodlands, Dobkin et al. (1995) found overall cavity-entrance orientations toward woodland edges; primary and secondary cavity-nesting species that foraged outside of aspen woodlands were more likely to use cavities oriented toward woodland edge compared with cavity nesters that foraged within riparian woodlands. We suggest here that cavity orientation might also be related to patterns of spore dispersal and fungal colonization of trees. For example, prevailing winds from the southwest in the southeastern United States might favor deposition of spores on the southwest side of the tree, possibly influencing cavity entrance orientation of Red-cockaded Woodpeckers. Similarly, a branch or stub above a woodpecker nest may provide an avenue for fungi to enter the tree and soften the heartwood, thus making it easier for the woodpecker to excavate a cavity.

Tree species. Perhaps the two best-known tree species–fungus–woodpecker associations are the Red-cockaded Woodpecker and its association with several species of southern pines and the heartrot fungus *Phellinus pini* (Affeltranger 1971, Jackson 1977, Conner et al. 1976, 1994, Conner and Locke 1982), and the associations involving sapsuckers, aspens, and the heartrot fungus *Phellinus igniarius* (Shigo and Kilham 1968, Kilham 1971, Daily 1993, Hart and Hart 2001).

Tree age. Older trees tend to have larger trunks and limbs, and thus are more suitable for the cavities of larger woodpeckers. Older trees have had more time for injury and invasion by fungi, weakened defenses against invasion, and greater time for fungal development. The Red-cockaded Woodpecker is dependent on older pines for all of these reasons (Jackson et al. 1979, Jackson and Jackson 1986).

Nature, extent, and position of tree injuries. The source of tree injury greatly influences fungal development (Shigo and Larson 1969). Natural pruning as a result of shading, limb breakage from snow or ice, crown fires, and limbs, broken by wind, expose heartwood to fungal invasion that results in stem rot and favors woodpecker excavation. Broken vertical or near-vertical limbs expose a cross-section of the limb or trunk and provide optimum access to the vascular tissue, allowing saturation of the broken stub by water and a large site for fungal invasion. This environment is conducive to rapid fungal decay and sites for woodpecker cavity excavation (Fig. 1, 2; Jackson 1976a). Larger wounds provide greater opportunity for microbial and fungal invasion from air or water-borne propagules.

In the western United States, periodic crown fires may be essential for the survival of Lewis's (*Melanerpes lewis*), Black-backed (*Picoides arcticus*), and American Three-toed (*P. dorsalis*) Woodpeckers (Saab and Vierling 2001, Kotliar et al. 2002). Such fires kill many trees and often kill the tops of others, thus forming the snags that these species need for nest and roost sites.

FIGURE 2. The stub of an American elm (*Ulmus americana*) used in three successive years for nest cavities by a pair of Red-bellied Woodpeckers in Kansas. Successive cavities are below previous cavities, following the progression of fungal decay downward that is characteristic of top rot. Photo by JAJ.

Injuries unassociated with branches are less likely to result in heartwood invasion. Injuries at the base of a tree, such as caused by ground fires, mechanical injury caused by logging or other human activity, and beaver (*Castor canadensis*) damage, are more likely to promote butt or root rot (Fig. 3) that can lead to tree fall before fungal decay higher on the trunk provides sites for cavity excavation. Such injuries only occasionally lead to growth of the fungal decay to a height suitable for woodpecker excavation.

Whether the tree or limb is alive or dead. A dead tree or limb is more susceptible to decay than a living limb, because it cannot mount a defense against a specific fungal invasion. In a dead tree or limb, decay becomes more general and results in easily excavated cavities that deteriorate within a few months or years. Fungal invasion of a living trunk or limb can lead to

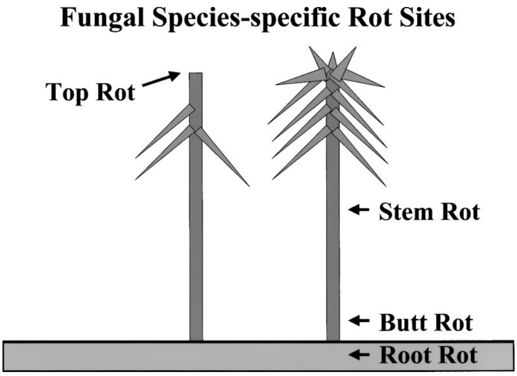

FIGURE 3. Graphic illustration of locations of site-specific fungal decay that can be of significance to woodpecker cavity excavation. Top rot characteristically occurs when a trunk or branch is broken and provides an abundance of woodpecker cavity sites. Such cavities are often quickly lost to continued decay; successive cavities in the same trunk are typically placed below previous cavities. Stem rot (specifically heartrot), usually enters through a branch stub; such areas can be compartmentalized and provide cavity sites in rotted wood that are surrounded by sound sapwood. Butt rot can sometimes grow upward to provide cavity sites, with successive cavities in the same trunk excavated above previous cavities due to upward progression of decay. Root rot generally leads to early windthrow of a tree, thus limiting its use for cavity excavation.

compartmentalization of fungal rot in sapwood, creating a pocket of rot suitable for cavity excavation surrounded by strong wood, thus resulting in a more protected, more durable cavity.

A tree that dies before being invaded by heartrot fungi provides little immediate opportunity for woodpecker cavity excavation. However, saprophytic fungi invade after the tree's death, and progression of decay often makes the tree suitable for cavity excavation within months to a few years. Several authors (Keen 1955, Thomas et al. 1979, Cline et al. 1980, Maser 1991, Morrison and Raphael 1993, Dickson et al. 1995, Doyon et al. 1999) have described easily observed stages of tree decay from death to tree fall, allowing correlation of cavity excavation with the phenology of tree decay. In general, larger dead trees remain standing and useful to woodpeckers and secondary cavity users for many more years than smaller trees (Morrison and Raphael 1993), but the phenology of tree decay plays out at different rates depending on tree species, age, size, climate, microclimate, and other factors. For example, in the Sierra Nevada of California, dead pines (*Pinus*) stood longer than dead firs (*Abies*), and trees killed by fire fell sooner than those dying of other causes in unburned plots (Morrison and Raphael 1993).

Utility of a tree for cavity excavation initially increases as insects and microorganisms invade and facilitate invasion by fungi. Once fungal decay has begun, a progression of woodpecker species may use the tree for cavity excavation, beginning with species known for their excavation abilities (typically ones who use excavation as a major method of securing food; e.g., Pileated, Ivory-billed, Hairy [*Picoides villosus*] Woodpeckers). The progression continues with woodpecker species less capable of excavation (species that make less use of excavation in securing prey; e.g., flickers, Lewis's, Red-bellied [*Melanerpes carolinus*], Red-headed [*Melanerpes erythrocephalus*], Downy Woodpeckers). As sapwood decay results in extensive sloughing, woodpecker cavity excavation declines and ceases as decay leads to tree disintegration and fall.

Local habitat and microclimate. Establishment of fungi and other decay organisms is greatly facilitated by a moist or humid environment. Blume (1961) noted a strong relationship between woodpecker nesting sites and proximity to water, but Lawrence (1967:62) suggested, ''the relationship between water, swamps, and wet places and the woodpeckers' nesting sites is not one of bird and habitat, but of water and its influence upon the inner condition of the trees.'' Thus trees in riparian or high precipitation areas support rapid fungal development. A tree within a forest is buffered from the heating influence of the sun and drying influence of the sun and wind, whereas a tree in the open is exposed to greater heat and drying.

CONSEQUENCES OF CAVITY NESTING IN THE PROCESS OF TREE DECAY

Excavations (including both cavities and foraging activities) by a woodpecker are like many other injuries to a tree in that they can provide an avenue for invasion by microorganisms that decay wood (Farris et al. 2004). Many more cavities are started than completed, and cavity starts may be avenues for infection that provide for future cavity excavation (Short 1982). Woodpeckers may also be vectors of decay-promoting organisms, infecting sites they excavate with hyphae or spores that adhere to bill or feathers

(Jackson 1977, Farris et al. 2004). While possible, compared to wind dispersal of spores, the woodpecker role as a vector may be insignificant (but see Farris et al. 2004). Examination of tissues around Red-cockaded Woodpecker cavity starts suggested that branch stubs, and not the cavity starts, were the entrance pathway for heartrot fungi (Conner and Locke 1982).

A cavity provides a nest or roost that is protected from weather and from many predators, but only so long as it is sound. Most woodpeckers only make use of a cavity for a single season or year, although nests in subsequent years are often nearby, even in the same nest tree. At first the brooding adults or roosting male may chip at the walls of the cavity, adding clean chips to the bottom, but this activity soon ceases (Jackson 1976b). As nestlings mature, efficiency of nest sanitation declines (Jackson 1976a). Excrement, fragments of eggshells and membranes, food, and feathers accumulate on the bottom, providing a fertile environment for growth of fungi, bacteria, and a host of small arthropods and other creatures, including both parasitic and commensal organisms.

The nest cavity of many woodpeckers (e.g., Red-bellied Woodpecker, Jackson 1976a) is a mess at fledging and increased fungal growth may make cleaning and rehabilitation of the cavity uneconomical. However, many species occasionally reuse a nest cavity and those that often reuse cavities (e.g., Lewis's, Golden-fronted [*Melanerpes aurifrons*], Red-cockaded Woodpeckers) may be a bit more fastidious and typically clean a cavity and enlarge it with each successive use (e.g., Husak and Maxwell 1998). We suggest that nest cavities of larger species of woodpeckers may be less likely to be reused as woodpecker nest sites as a result of the increased potential for rain entering the cavity entrance and hastening the rate of fungal decay.

NOT ALL SNAGS ARE CREATED EQUAL

Most woodpeckers display preference for snags. Studies tend to use either a narrow working definition of ‘‘snag’’ as a standing dead tree (e.g., Scott 1978, Cline et al. 1980, Raphael and White 1984, Rosenberg et al. 1988), or a broader definition that includes live trees with a dead top or dead limbs (Thomas et al. 1979). We use the broader definition, but limit the definition to the dead part of the tree (we do not refer to the live part of a tree as a snag, just the dead portion). As an example of the limits of the narrow definition, in the Sierra Nevada of California, Raphael and White (1984) found that only 7% of available trees were standing dead trees, but that 72% of nest cavities were in them, suggesting that 28% of nest cavities were in living trees. There is considerable ambiguity in the literature in that some nests reported in live trees are likely in dead limbs of live trees. We encourage greater detail to assure clarity in reporting nest sites of cavity-nesting birds.

Deterioration of wood is a complex process that may begin with bacteria and other microorganisms (Maser 1991), although basidiomycetes may also begin the decay process (J. Bednarz, pers. comm.). Early invaders weaken defenses that allow further invasion by fungi that, by weakening the wood, provide invasion opportunities for arthropods and excavation opportunities for birds. The rate of decay varies with tree and fungal species, presence and action of other microorganisms, extent of arthropod activity, temperature, humidity, and presence or absence of chemicals that inhibit or enhance the activity of fungi.

Decay begins with an injury or a broken branch due to natural pruning, can vary in rate and extent of progression, and is often isolated or compartmentalized (Shigo 1979, 1984). The progression of decay in a living tree often is not evident to human observers, often only becoming evident years later when the fungus produces a conk (i.e., sporocarp, or spore-producing structure) on the outside of the tree. Decay in snags has been categorized by a succession of clearly evident external stages in the transition from recently dead tree to well-decayed stump (Maser et al. 1979, Thomas et al. 1979, Cline et al. 1980, Raphael and White 1984, Maser 1991, Doyon et al. 1999).

Our understanding of the progression of decay within trees has been greatly facilitated by the work of Alex Shigo (e.g., Shigo and Kilham 1968, Shigo and Larson 1969, Shigo 1979, 1984, see also Conner et al. 1976). Shigo has championed an understanding of the relationship between fungal decay of wood and host trees that is important to the quality of a woodpecker cavity. In a living tree, fungi and other microorganisms enter through any kind of wound. The larger the wound, the greater the invasion and potential for fungal colonization; the smaller the wound, the greater potential that the tree will be able to seal the site of the wound to prevent fungal development. In a process called compartmentalization, the living tree closes off infected sapwood, isolating the infection in much the way that a leaking submarine might isolate a compartment to save the vessel. The isolation includes both physical and chemical barriers to the spread of fungal growth that persist as the sapwood becomes heartwood. Physical barriers include blocking of the xylem vessels with gum and other tree products. Chemical barriers include compounds such as tannins and phenols that are toxic to some microorganisms. The nature and extent of compartmentalization varies among tree species, thus contributing to varying levels of suitability for woodpecker cavity excavation. A woodpecker cavity in a well-compartmentalized pocket of decay is surrounded by sound wood, and is thus more secure from predators and longer lasting.

In contrast to cavities excavated into the compartmentalized decay formed by fungal invasion of the sapwood of a living tree, a healthy tree that dies and is then invaded by saprophytic fungi will undergo rapid decay of the entire tree. New cavities in dead trees lack the protective enclosure of sound wood and the durability provided by encapsulated decay. On the other hand, successive cavities can be excavated in concert with the slow progression of saprophytic decay. Thus Red-bellied (Fig. 2) and Pileated Woodpeckers may use the same snag for three or more successive years (Conner 1974, Conner et al. 1975, Jackson 1976a), excavating a new cavity just below the cavity of the previous year as the fungal decay grows down from the broken top where it easily entered the tree. Similarly, successive nests of sapsuckers in quaking aspen (*Populus tremuloides*) are often above previous cavities, a result of upward growth of the heartrot from its entrance through an injury at the base of the tree (Daily 1993, Hart and Hart 2001, Walters et al. 2002).

NOT ALL FUNGAL DECAY IS EQUAL IN FACILITATING WOODPECKER CAVITY EXCAVATION

Although wood-decaying fungi include more than 1700 species, the most important are members of the Phylum Basidiomycota, and the largest group important for woodpecker cavity excavation seems to be the family Polyporaceae, particularly some members of the genus *Phellinus*. We make this statement with the caveat that relatively few studies have clearly linked specific fungi with decay associated with woodpecker cavities (Table 1), but with the knowledge that the species of *Phellinus* associated with woodpecker cavity excavation are also very widespread and linked to a diversity of host trees. Wood-decaying fungi are often specific in their use of tree species, tissues, and sites of entrance.

Those fungi important for woodpecker cavity excavation are typically heartrot fungi that invade trees through branch stubs and injuries high on the trunk of a tree. Those taxa that infect the heartwood of living trees provide the safest nest sites for cavity nesters. Because these heartrot fungi are selective in their site of growth (the dead heartwood) they do not kill the tree; hence such trees not only provide sites for safe nest cavities, they can do so for decades.

Susceptibility to fungal heartrot varies among tree species, seems to increase with age of a tree, requires the presence of wounds that provide an avenue for infection, and requires the presence of spores or other propagules of heartrot fungi in the air or water, or associated with an animal vector, at a site of potential infection. These factors and others come together to create conditions that determine the location of heartrot and thus the prime sites for woodpecker cavity excavation.

Some tree species (e.g., baldcypress [*Taxodium distichum*]; Campbell and Clark 1960) can inhibit or combat fungal infection through production of defensive chemicals such as phenols and tannins while the tree grows to seal off the injury. In many species these chemicals continue to counter fungal decay for some time after the death of the tree, and wood of such trees is often highly valued because of this decay resistance.

Forest pathologists have divided wood decay fungi into two functional groups based on their appearance: white rots and brown rots (Alexopoulos and Mims 1979). Both can create conditions that facilitate woodpecker cavity excavation. White rots decompose both cellulose and lignins in wood, reducing the wood to a spongy texture. Brown rots decompose cellulose, leaving the darker lignin behind. Major wood-decaying fungi associated with woodpecker nest cavity excavation (e.g., *Phellinus pini, P. igniaris, Spongipellis pachyodon*) are white rots; the fungus *Oligoporus sericeomollis* that has been as-

TABLE 1. Examples of heartrot fungi that have been associated with woodpecker cavity excavation. Information on tree hosts was gleaned from Hepting 1971, Allen et al. 1996, and indicated sources.

Heartrot fungus	Principal tree hosts	Relative importance for cavity excavation	References
Phellinus pini	pines	high	
Phellinus igniarius	aspen, maple, alder, birch, apple, dogwood, locust, etc.	high	Shigo and Kilham 1968, Kilham 1971, Winternitz and Cahn 1983
Phellinus tremulae	known only from aspen; recently separated from *P. igniarius* and probably included in references for that fungus	high	
Spongipellis pachyodon	hardwoods	possibly high	Conner et al. 1976
Fomitopsis officinalis		unknown	McClelland and McClelland 1999
Oligoporus sericeomollis	western redcedar	unknown	Parks et al. 1997
Oligoporus placentus	western larch	unknown	Parks et al. 1996
Coniophora puteana		unknown	Parks et al. 1996
Gloeophyllum sepiarum		unknown	Parks et al. 1996
Stereum sanguinolentum	western pines, hemlock, spruce, fir, larch, tamarack, alder	unknown, a heartrot of mature trees	Parks et al. 1996
Phaeolus schweinitzii		unknown, normally a butt rot	Conner and Locke 1982

sociated with Pileated Woodpecker roost cavities is a brown rot.

DISPERSAL AND COLONIZATION OF HEARTROT FUNGI

Heartrot fungi may grow hidden within the heartwood of a host tree for years before producing a fruiting body known as a conk (typically recognized as a hard bracket or shelf fungus) on the surface of the tree. Once present, perennial conks can continue to grow and produce spores for many years. Factors influencing the phenology of conk production and the timing and duration of spore production, spore release, and spore dispersal are poorly understood (Alexopoulos and Mims 1979).

Although the primary mode of dispersal of heartrot fungi seems to be through wind-blown spores, insect and vertebrate vectors also accomplish some dispersal. We suggest that spore dispersal may also be facilitated by thermals generated by fire or solar heating of adjacent habitats, or by obstruction currents generated by natural or anthropogenic factors. Anthropogenic landscape alterations that change airflow patterns may dramatically influence dispersal of heartrot fungi. For example, construction of a parking lot adjacent to a forested area or even a clearcut within a forest might result in thermals that would carry spores high into the air, thus facilitating long-distance dispersal. Similarly, construction of tall buildings near a forest could result in obstruction currents that would also carry spores upward.

Because spores and hyphae capable of infecting a tree are carried by the wind, the potential for infection might be predicted to increase with (1) the size of the wound, (2) increased airflow at the height of the wound, and (3) increased airflow striking the wound. Wind patterns within a forest likely influence spore dispersal and deposition on wounds. Vegetation surfaces exert frictional resistance that impedes and directs airflow (Kittredge 1948, Fitzjarrald and Moore 1995), thus there are general patterns of increased wind speed with increasing height above vegetation surfaces, decreased wind speed within a forest with increased stand and foliage density, and variable currents influenced by deflection from vegetation surfaces (Raupach and Thom 1981, Rosenberg et al. 1983, Parker 1995). These factors could contribute to a higher occurrence of fungal infection along forest edges, and hence a higher density of cavities along edges.

Based on discussions in Kittredge (1948) and Fitzjarrald and Moore (1995), we present a graphic model that suggests that within an open southern pine forest, air movement patterns might favor fungal spore dispersal and deposition just below the lowest branches (Fig. 4). The top of the canopy, like the surface of the ocean, creates friction, slowing airflow. Within the canopy airflow is reduced, but includes downward and upward currents as a result of airflow deflection. Below the canopy, at the height of the most recent natural pruning, the forest may be relatively open, allowing increased airflow, again with minor upward and downward currents as a result of deflection. The forest understory again serves to diminish airflow, and air movement is minimal close to the ground. We suggest that this model, which fits both coniferous and broadleaf forests, favors the entry of heartrot fungi at the highest, most recently fallen branch stubs. Thus it seems not to be coincidental that Red-cockaded Woodpeckers generally excavate their cavities just below the lowest limbs of these pines (Jackson 1994, Bowman and Huh 1995). However, it may be much more difficult for human observers to locate cavities in the forest canopy, such that data available on nest heights may be biased.

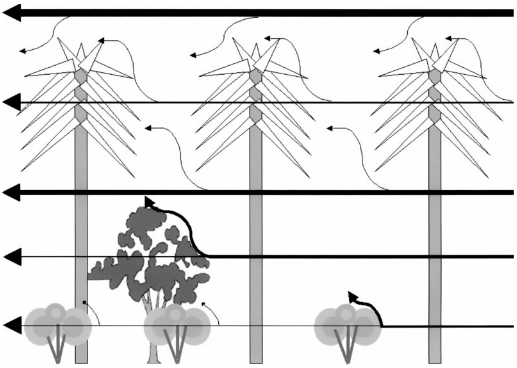

FIGURE 4. Graphic model of wind movements that might influence fungal spore dispersal through a forest habitat. Thinner arrow shafts suggest decreased air movement; scale of arrow shaft thickness is intended only to show relative change. Areas that receive the most wind are likely places for spore establishment, and so may be especially likely places for cavities to be excavated. Based on data summarized in Kittredge 1948.

CONSERVATION EFFORTS AND ALTERATION OF FUNGAL ECOLOGY BY MODERN FORESTRY

In the primeval forest, an old-growth tree might have been invaded successfully by wood-decaying fungi many times, forming many pockets of encapsulated decay, thus providing optimal conditions for woodpecker cavity excavation. In today's younger forests, trees are generally harvested before they become susceptible to heartrot fungi. Those that die before harvest (at a young age), begin the process of general decay, but provide sites suitable for woodpecker excavation for only a short interval in the progression of decay.

Recognizing that a single fungal conk might release millions of spores in a short time and that spores may be carried globally by the wind, it is also true that (1) the abundance of spores in the air would vary with the number of conks producing them, and (2) the concentration of spores and other fungal propagules in the air must decline with distance from their source. Nearly continuous virgin forest, such as the historic southeastern pine (*Pinus* spp.) forest of North America, has been seriously fragmented by clearing of forest and altered by cutting of old growth. Heartrot fungi and cavity excavation interfere with economic use of the heartwood of forest trees. Thus humans have tried to eliminate such fungi and to harvest trees before they normally become infected with heartrot. To what extent are human influences altering the natural processes of fungal ecology that facilitate cavity excavation by woodpeckers?

With increased mechanization of forestry, widespread clearcutting, and cutting of snags for firewood, concern for the loss of forest wildlife stimulated efforts to retain snags, and, ultimately, to create snags. Various methods have been used to produce snags that have been invaded by fungi and in which woodpeckers have excavated cavities. These have included: girdling (Conner, Kroll, and Kulhavy 1983), injection of herbicides (e.g., 2,4-D, Conner et al. 1981, Conner, Kroll, and Kulhavy 1983, Dickson et al. 1995; picloram, McComb and Rumsey 1983), cutting of trees a few meters above ground (Morrison et al. 1983), and combinations of treatments such as topping with dynamite or chainsaws, injection of herbicides, and treatment with beetle pheromones to promote infestation of tree-killing beetles (Bull et al. 1981, Bull and Partridge 1986). In western conifers, herbicide-injected trees died and often fell before being used by woodpeckers; trees topped by chainsaw and pruned of branches died quickly, provided the artificial snags most often used for cavity excavation, and stood longer than snags created by other means (Bull and Partridge 1986).

Establishment of the association between the red heart fungus (*Phellinus pini*), old growth pines, and Red-cockaded Woodpecker cavity excavation (e.g., Affeltranger 1971, Jackson 1977, Jackson et al. 1979), led researchers to investigate the potential for artificially infecting trees with the fungus (Conner and Locke 1983). By drilling a hole into the heartwood of a young pine and inserting a dowel on which red heart has been cultured, researchers have bypassed the tree's sapwood defenses and successfully initiated heartrot. Similar inoculation efforts with fungi in hardwoods have also been successful (Conner, Dickson, and Williamson 1983, Huss et al. 2002).

Other, more direct efforts to provide roost and nest cavities for woodpeckers have demonstrated that populations might be sustained and even enhanced by construction of artificial cavities, thus precluding the need for heartrot (Allen 1991, Copeyon et al. 1991). Although such efforts are labor-intensive and costly, artificial cavity construction is an important tool for managing endangered species in crises. It is not, however, a long-term, naturally sustainable answer, and there are other problems introduced with use of artificial cavities, including stress placed on the living pines used for artificial cavities for Red-cockaded Woodpeckers, and sometimes greater vulnerability to predators (Jackson 1994, Conner et al. 1998).

RESEARCH NEEDS

Among the take-home messages of this review and questions deserving further attention we offer the following: (1) Our understanding of tree-decaying fungi is lacking in many parameters relevant to the development of sites optimal for woodpecker cavity excavation. What stimulates production of fungal conks and release of spores? What is the phenology of fungal spore dispersal and invasion of trees? What are the dispersal dynamics of the spores of heartrot fungi? Do physical factors such as fire, thermals, and air currents within and near a forest influence fungal dispersal as we have suggested? As old growth forests have been fragmented by conversion of forestlands to other uses or converted to short-rotation plantations, how has the potential for development of heartrot suitable for woodpecker cavity excavation changed? (2) Our knowledge of specifics about woodpecker–fungus interactions is minimal. Is there validity in our model suggesting that woodpecker cavity height and orientation might be related to physical factors that influence fungal spore dispersal and fungal invasion of wounds? How does a woodpecker identify a site for cavity excavation? Although we are beginning to learn about cavity tree selection (e.g., Conner and O'Halloran 1987), we do not know how a specific cavity site is selected. The intimate association of fungal decay and woodpecker cavity excavation suggests that woodpeckers may be able to detect decay, and the presence of a conk on a tree or differences in resonance may be used as external indicators of a suitable site. But many uncompleted cavity starts in sound wood might be evidence that the process is largely trial and error. (3) Descriptions of woodpecker nest sites are often ambiguous. Many authors refer to nests in ''live trees,'' failing to indicate whether the nest is in a dead limb or stub or in a living branch; thus our understanding of nest-site needs and flexibility in woodpeckers is somewhat clouded. While cavity height is often given, tree height is often not provided. The habitat context of woodpecker nest sites often is not provided. We hope that by providing some discussion of the potential significance of woodpecker cavity parameters we will stimulate others to look more closely at habitat and community interactions and thus fill in these gaps in our understanding.

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