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THE ROLE OF FORAGING WOODPECKERS IN THE DECOMPOSITION OF PONDEROSA PINE SNAGS

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Abstract. We investigated the relationship between foraging woodpeckers and the decomposition of ponderosa pine (*Pinus ponderosa*) snags in the central and southern Cascades of Oregon and northern California. Our main objectives were (1) to compare the relative sapwood density of 4-year-old pine snags receiving varying levels of woodpecker foraging; and (2) to determine if woodpeckers were carriers of wood-inhabiting fungi. Snags used as foraging sites by woodpeckers had lower wood densities than snags that did not exhibit foraging sign. Additionally, wood-inhabiting fungi were recovered in significantly greater frequencies from the bills of woodpeckers than a comparison of non-cavity-nesting species. These results suggest that woodpeckers may contribute to the mechanical degradation of wood through foraging activities and the dispersal of a collection of fungi that likely participate in the process of decay for ponderosa pine snags. The complexity of these ecological interactions should be considered when planning snag management in coniferous forests.

Key words: cavity nesters, fungi, Picoides, Pinus ponderosa, *sapwood, snags, woodpeckers.*

El Papel de Forrajeo de los Carpinteros en la Descomposición de Tocones de *Pinus ponderosa*

Resumen. Investigamos la relación entre las actividades de forrajeo de los carpinteros y la descomposición de tocones de *Pinus ponderosa* en el centro y sur de las Cascades de Oregon y el norte de California. Nuestros objetivos principales fueron (1) comparar la densidad relativa de la albura de tocones de pino de 4 años de edad afectados por distintos niveles de forrajeo por parte de los carpinteros; y (2) determinar si los carpinteros transportaron hongos de la madera. Los tocones usados como sitios de forrajeo por los carpinteros tuvieron densidades de madera menores que los tocones que no presentaron señales de forrajeo. Adicionalmente, los hongos de la madera fueron encontrados con mayor frecuencia en los picos de los carpinteros que en especies que no nidifican en cavidades. Estos resultados sugieren que los carpinteros pueden contribuir a la degradación mecánica de la madera mediante las actividades de forrajeo y la dispersión de una variedad de hongos que probablemente participan en el proceso de descomposición de los tocones de *P. ponderosa*. La complejidad de estas interacciones ecológicas debería ser considerada a la hora de planear el manejo de los tocones en los bosques de coníferas.

INTRODUCTION

Standing dead trees (snags) with cavities are a critical ecological component of Western coniferous forests. Snags provide foraging, roosting, and nesting sites for numerous species of birds, mammals, reptiles, amphibians, and invertebrates (Thomas et al. 1979, Bull et al. 1997). Central to the primary excavation of nest cavities, and thus the management and conservation of cavity-nesting wildlife species, are woodpeckers. Most species of woodpecker excavate nest cavities on an annual basis, providing the cavity-nesting community with a continuous supply of nesting and roosting sites (Aitken et al. 2002). The specific factors that lead to cavity excavation in certain snags are not well understood. Previous research suggests that the quality of snags, as determined by the size and type of decay, may be more important than the sheer abundance of snags in determining the value of habitat for cavity-nesting wildlife (Jackson 1977, Bull et al. 1997, Conner et al. 2001). For example, Zack et al. (2002) found that fewer than 20% of more than 1700 snags sampled in northeastern California contained nest cavities.

Most woodpecker species tend to excavate nest cavities in snags containing decayed wood.

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This has led several authors to suggest that decomposition by fungi may be a prerequisite for nest excavation by many woodpecker species (Conner et al. 1976, Jackson 1977, Harris 1983, Bull et al. 1997, Conner et al. 2001, Jackson and Jackson 2004). Others have hypothesized that woodpeckers not only depend on wood-decay fungi to create suitable nest cavities, but that they may actually play a role in fungal colonization and dispersal. In their search for insect prey, foraging woodpeckers (particularly those of the genus *Picoides*) puncture the bark and fragment the underlying sapwood. These feeding behaviors may provide potential infection sites for airborne spores or create microhabitat conditions favorable for wood-decaying organisms (Otvos 1979, Ostry and Anderson 1998). Consistent with this notion, Conner, Jones, and Jones (1994) observed that hardwood snags with higher levels of woodpecker foraging tended to have higher incidences of decayed wood, and Jackson (1977) hypothesized that the characteristic flaking of tree bark by foraging Red-cockaded Woodpeckers could facilitate red heart fungal invasion in loblolly pine (*Pinus taeda*). Woodpeckers may also influence snag decomposition through the transmission of fungal spores. Ostry and Anderson (1998) hypothesized that woodpeckers were directly responsible for vectoring fungal mycelium from hypoxylon cankers in northeastern aspen forests.

Combined, these observations suggest that foraging woodpeckers, through their interaction with insects and tree pathogens, may play an active role in creating suitable nesting habitats by promoting wood decay. A number of studies have independently examined the interrelationships between bark and wood-boring beetles and foraging woodpeckers (Otvos 1970, Kroll and Fleet 1979, Murphy and Lehnhausen 1998) or nesting woodpeckers and decaying snags (Raphael and White 1984, Milne and Hejl 1989, Bull et al. 1997), but no published studies have simultaneously examined the potential synergistic relationships among bark and wood-boring beetles, foraging woodpeckers, and decay fungi that eventually lead to cavity generation.

The possible influences of woodpecker foraging activities on subsequent snag decomposition, and therefore future nest site quality, have gone largely unexplored. The purpose of our long-term research is to provide a better understanding of how foraging woodpeckers interact with snag decay processes in ponderosa pine ecosystems. In this paper we address two research questions: (1) how does relative sapwood integrity differ with varying levels of woodpecker activity in ponderosa pine snags, and (2) do woodpeckers carry decay fungi? We begin by reviewing key processes involved in the death and decay of ponderosa pine as they relate to the potential influence of foraging woodpeckers.

BACKGROUND

While the death of a tree can be a multifaceted process resulting from complex interactions between biotic and abiotic factors (Harmon et al. 1986, Franklin et al. 1987), for the purposes of this discussion we focus on cambium-consuming insects (bark beetles of the family Scolytidae, genera *Dendroctonus* and *Ips*) active in ponderosa pine ecosystems. *Dendroctonus* beetles can kill both healthy and weakened trees depending on the local environmental conditions. These insects kill via a mass invasion where thousands of individuals bore through the bark and lay their eggs in the cambium (Furniss and Carolin 1977, Paine et al. 1997). The eggs produce larvae, and eventually pupae, that contribute to the tree's death by consuming the living cambium and limiting the flow of carbohydrates through the phloem (Furniss and Carolin 1977). Furthermore, when adult beetles bore through the bark, they often inoculate the tree with wood-staining fungi which may contribute to the tree's death by blocking nutrient and water transport in the sapwood and food transport in the phloem (Whitney 1982). Once the tree has died, a suite of wood-boring beetles (families Buprestidae and Cerambycidae) invade the tree and begin to feed in the outer sapwood (Furniss and Carolin 1977).

This sapwood layer in ponderosa pine, which can comprise from 50–75% of the tree's volume, is often considerably decayed within a few years after tree death (Lowell and Cahill 1996, Bull et al. 1997) and is the location of most woodpecker nests (Bull et al. 1997). This pattern of wood composition, decay, and nest placement in ponderosa pine is in contrast to most conifers, where the ratio of sapwood to heartwood is much lower and nest cavities are placed within the interior, decayed heartwood (Conner, Rudolph, et al. 1994, Bull et al. 1997, Conner et al. 2001). Furthermore, mechanisms of fungal invasion be-

tween these two wood types differ. Generally, heartwood decay inoculates a tree through diseased roots, or puncture wounds deep enough to penetrate through the sapwood (Rayner and Boddy 1988). In contrast, sapwood decay organisms generally invade through superficial wounds in the bark and outer sapwood (Rayner and Boddy 1988).

The potential influence of *Picoides* woodpeckers on the decomposition of ponderosa pine sapwood begins as they respond to dying trees by foraging on the larvae and pupae of bark beetles and subsequently on wood-boring beetles. Woodpeckers are the primary vertebrate predators of these insects (Otvos 1965, 1970, Koplin 1972) and feed intensively within the bark and outer sapwood. As foraging woodpeckers begin to penetrate the bark and wood in search of prey, they may significantly alter the structure and microhabitat in localized areas of a snag and potentially facilitate invasion by wood-colonizing fungi. Our research aims to better understand these interactions in ponderosa pine.

METHODS

STUDY AREAS

We collected data at two separate sites on the Ochoco National Forest (44°22′N, 120°7′W) and at Blacks Mountain Experimental Forest, Lassen National Forest (40°44′N, 121°9′W) in the central and southern Cascades of Oregon and California, respectively. Interior ponderosa pine (*Pinus ponderosa* var. *ponderosa*) was the dominant species at both locations. The Ochoco site had a minor component of Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*), while the higher elevations of the Lassen site contained a large component of Jeffrey pine (*Pinus jeffreyi*), with scattered inclusions of white fir (*Abies concolor*) and incense-cedar (*Libocedrus decurrens*). Elevation ranged from 2275 m on the Ochoco site to 2730 m on the Lassen site. Resident woodpecker species of interest included the White-headed (*Picoides albolarvatus*), American Three-toed (*P. dorsalis*), Black-backed (*P. arcticus*), and Hairy (*P. villosus*) Woodpeckers. Other woodpecker species (i.e., Northern Flicker [*Colaptes auratus*], Pileated Woodpecker [*Dryocopus pileatus*], and three species of *Sphyrapicus* sapsuckers) were also present, but are generally not major predators of bark and wood-boring beetles in ponderosa pine.

SAPWOOD INTEGRITY

To evaluate the effect of woodpecker foraging on sapwood decomposition, we made use of an experimental population of 99 ponderosa pines intentionally infested with bark beetles (using pheromone bait packets) in 1998 as part of a related long-term study examining snag demography and wildlife use (Farris et al. 2002). Each tree in the population has been monitored yearly since 1999 to document death, and to quantify bark and wood-boring beetle use, woodpecker foraging, and structural decomposition over time. Because not all 99 of the treated trees were dead after the first year of the experiment, we selected a subsample of 25 of the oldest snags (4 years since death) for this study (mean diameter at breast height = 69.6 ± 14.3 cm [SD]). During August 2001, we visited each of these 4-year-old snags and recorded the following variables in a 15-cm-radius circle randomly located at three separate azimuths (separated by 120°) around the bole at a height of 1.4 m: wood density, the presence of woodpecker foraging, and the presence of bark beetle activity.

Wood density was quantified using a resistograph engineered by Instrument Mechanic Labor, Inc. (Kennesaw, Georgia). This instrument, powered by a cordless drill, is designed to accurately detect decay and defects in trees and wooden structures. The resistograph inserts a very fine drill (approx. 3 mm in diameter) into the wood at a constant rate. As the drill enters and passes through the tree, it encounters variable resistance which reflects the structural condition of the cell walls. This variation causes the drill to either increase or decrease the amount of torque applied to the drill shaft (Dunster 2000). These variations in torque are stored in an internal data-logger, which can be interpreted as wood density readings at each mm of drilling depth and used in subsequent statistical analyses (Fig. 1).

We evaluated woodpecker foraging activity by recording the presence of visible puncture holes in the bark within a 15-cm-radius circle centered on the resistograph sample point. Additionally, because insects can influence wood decomposition through the introduction of fungi (Rayner and Boddy 1988) and could be a confounding factor in our analysis, we also recorded the presence of bark beetle activity by looking for exit holes on the bark (an indicator of suc-

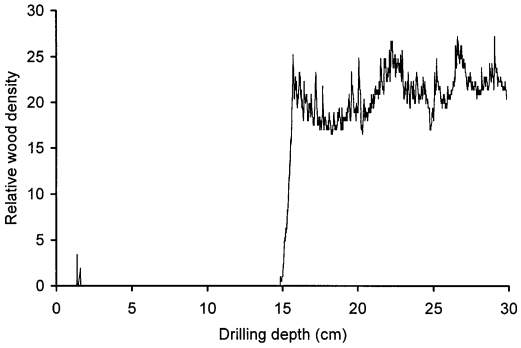

FIGURE 1. An example of computerized output from a resistograph illustrating the changes in wood density with drilling depth along the radius of a 60-cm-diameter ponderosa pine snag on the Ochoco National Forest, Oregon. In this case, the spikes in the outer 0–3 cm represent bark, cm 4–15 represent the relatively decayed sapwood, and cm 16–30 represent the intact heartwood.

cessful beetle exploitation) within the same 15-cm-radius sample area.

BIRD-FUNGI SAMPLING

During the summer of 2001 (mid-May to mid-July), we systematically searched for *Picoides* woodpecker nests within sixteen 150-ha study plots located on the Lassen site. Upon location of an occupied woodpecker nest, we monitored activity every three days using a pole-mounted camera inserted into the cavity. Once the nestlings reached a minimum age of 1 week and the parents began to feed them frequently, we captured the adults using mist nets. Because most of our nests were located relatively low to the ground (≤10 m), we were able to set up mist nets approximately 5–10 m from the nest in a V-shaped pattern with the apex centered on the nest cavity. Adults were captured as they returned to the cavity to feed nestlings. In order to reduce nest abandonment, we captured only one adult from each pair and continued to monitor these nests until they fledged.

When a bird was captured and removed from the net we swabbed the bill with a sterile culture swab (BBL™ Culturette™ 260210, Becton Dickinson & Company, Franklin Lakes, New Jersey) before release. For comparison to woodpecker samples, we set up mist nets within the same study plots and captured non cavity-nesting species (finches, juncos, kinglets, etc.) and repeated the above process.

Each sample swab was wiped back and forth across the surface of a sterile agar-based selective isolation medium (Huss et al. 2002) designed to promote the growth of decay and pathogenic fungi, while deterring growth of common contaminants (e.g., bacteria, fast-growing fungi). This particular medium consisted of a mixture of 20 g of dehydrated malt extract broth, 20 g of agar, 0.2 g of pentachloronitrobenzene (PCNB), and 1 L of distilled or deionized water. This medium was sterilized by autoclaving at 15 psi at 121°C for 15 min. After cooling to 50–60°C, 2 mL of a filter-sterilized antibiotic stock solution (20 000 units mL^{-1} of penicillin and 80 000 units mL^{-1} of streptomycin in distilled or deionized water) and 1 mL of benomyl solution (i.e., 0.1% benomyl in 100% ethanol) were incorporated into the medium. Swabbed culture plates were incubated at room temperature and checked periodically for fungal growth. After isolation of fungi became apparent, fungal material (e.g., mycelium, spores, yeast cells, etc.) were aseptically transferred to malt extract agar in slant culture tubes or petri dishes. Malt extract agar was used from then on as the growing and culture maintenance medium.

Fungal growth was transferred to slides, teased apart for identification under a microscope and mounted in lactophenol with cotton blue stain (Larone 1995). A variety of literature sources and identification keys were consulted in diagnosing all fungal specimens and cultures to the lowest taxonomic category possible (Rayner and Boddy 1988, Rippon 1988, Larone 1995, Barnett and Hunter 1998). Unlike many filamentous fungi, which possess unique cellular organization, structure, and spore morphology, yeast species are not readily identified based on microscopic characteristics. We were often able to identify yeasts to the genus or species level base on the outcome of certain physiological tests (Huss et al. 2002).

STATISTICAL ANALYSIS

We used the resistograph to drill to the center of each snag, thus providing a wood density profile of both the sapwood and heartwood. However, because cavity nests in ponderosa pine are typically placed within the sapwood, and the sapwood of ponderosa pine generally constitutes 50–75% of the tree's volume (Bull et al. 1997), we needed to drill to depths of at least 14 cm on our smallest snag (55 cm in diameter at

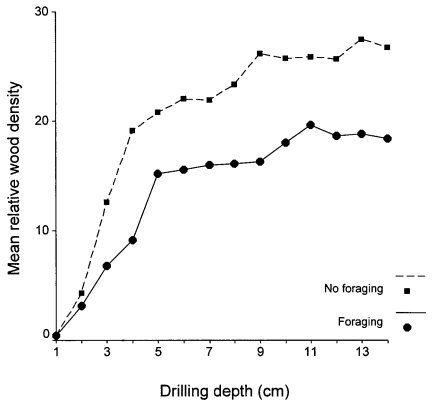

FIGURE 2. Mean relative wood density at increasing sapwood depth for ponderosa pine snags with and without woodpecker foraging activity from Ochoco National Forest, Oregon. The outer 0–2 cm represents bark; cm 2–14 represent sapwood. Data are marginal means from repeated measures ANOVA that included beetle and woodpecker use classes as main effects, and sample azimuth as a covariate.

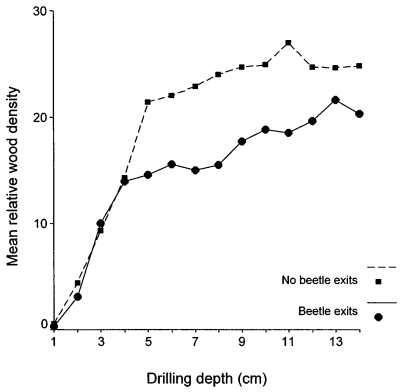

FIGURE 3. Mean relative wood density at increasing sapwood depth for ponderosa pine snags with and without beetle use from Ochoco National Forest, Oregon. The outer 0–2 cm represents bark; cm 2–14 represent sapwood. Data are marginal means from repeated measures ANOVA that included beetle and woodpecker use classes as main effects, and sample azimuth as a covariate.

breast height [dbh]), and a maximum of 25 cm on our largest snag (99 cm dbh) to ensure an accurate depiction of the sapwood density along the radial axis. Consequently, for simplicity and standardization, we truncated our resistograph measurements at 14 cm for the purposes of this analysis. Additionally, this depth encompasses the range of horizontal nest depth measurements for our largest onsite nest excavator, the Northern Flicker (Wiebe 2001, Baicich and Harrison 1997) and was therefore likely to depict the wood segment most woodpeckers in the study area would need for nest excavation.

Because the resistograph measures wood density as it drills into the snag, measures of increasing depth are likely to be interdependent. Consequently, we used repeated measures ANOVA, with depth at 1-cm intervals as the repeated measure, to analyze differences in wood density among two main effects (woodpecker foraging and beetle use), and one covariate (sampling azimuth). In this manner, we could test the effects of both woodpecker foraging and beetle activity while accounting for the possible effect of sample azimuth on our measurements. Because we decided to standardize our measures by truncating our sapwood radii to 14 cm, we did not consider tree diameter as a covariate for this analysis. To test whether the presence of fungal organisms was related to bird group (cavity versus non-cavity-nesting species) we used contingency table, chi-square analysis. SPSS Version 11.0.1 was used to conduct all statistical evaluations (SPSS 2001).

RESULTS

WOODPECKER FORAGING AND SNAG DECAY

Main effects of woodpecker foraging and beetle activity, plus the covariate of sampling aspect, were analyzed concurrently among all 75 samples ($n = 25$ snags). Only the main effect of woodpecker foraging was significant ($F_{1,70} = 4.7$, $P < 0.03$), with foraging areas having significantly softer wood than areas without foraging (Fig. 2). Wood hardness also tended to differ with beetle use in a similar manner (Fig. 3), but the differences were not significant ($F_{1,70} = 3.00$, $P > 0.08$). Additionally, the interaction between woodpecker foraging and beetle activity appeared to be fairly strong ($F_{1,70} = 3.7$, $P < 0.06$), suggesting that the simultaneous action of woodpeckers and beetles might affect wood density. Finally, the sample azimuth did not affect wood density ($F_{1,70} = 2.6$, $P > 0.11$).

BIRD-FUNGUS RELATIONSHIPS

We captured 53 birds: 26 cavity nesters and 27 non-cavity-nesters (Table 1). In order to boost our sample sizes of cavity nesters, we included captures of Red-breasted nuthatches (*Sitta canadensis*) and Mountain Chickadees (*Parus gambeli*) in our analysis. Pearson chi square

TABLE 1. Detection frequencies of filamentous fungi sampled from the beaks of six non-cavity-nesting and five cavity-nesting bird species captured on the Lassen National Forest, California.

Species	*n*	Detection frequency[a]
Non-cavity nesters		
Ruby-crowned Kinglet (*Regulus calendula*)	2	0.00
Yellow-rumped Warbler (*Dendroica coronata*)	2	0.00
Western Tanager (*Piranga ludoviciana*)	1	0.00
Dark-eyed Junco (*Junco hyemalis*)	12	0.17
Cassin's Finch (*Carpodacus cassinii*)	9	0.22
Red Crossbill (*Loxia curvirostra*)	1	0.00
Class total	27	0.15
Cavity nesters		
Hairy Woodpecker (*Picoides villosus*)	7	0.57
White-headed Woodpecker (*Picoides albolarvatus*)	6	0.50
Black-backed Woodpecker (*Picoides arcticus*)	7	0.57
Mountain Chickadee (*Poecile gambeli*)	1	1.00
Red-breasted Nuthatch (*Sitta canadensis*)	5	0.80
Class total	26	0.62

[a] Proportion of species sample testing positive for filamentous fungi presence.

analysis revealed that the presence of fungal organisms was related to capture group ($\chi^2_1 = 12.3$, $P < 0.001$). The cavity-nesting group tested positive for the presence of fungi 62% of the time, while these were found in only 15% of the non-cavity-nester samples (Table 1). The most common microorganisms isolated from both bird classes were unicellular fungi (yeasts), followed by several genera of filamentous or hyphal fungi (Table 2). In general, the cavity-nesting group contained a more diverse group of organisms including both unicellular yeasts and filamentous fungi, while the non-cavity-nester group tended to contain more yeasts than fungi (Table 2).

DISCUSSION

Our data show a correlation between high levels of woodpecker foraging and low levels of sapwood density in ponderosa pine snags. In addition, wood-inhabiting fungi were isolated from woodpecker bills in greater frequencies than would be expected by chance. The combination of these two observations is intriguing and suggests that woodpeckers may promote fungal invasion and sapwood decay in two ways. First, woodpecker foraging strategies may cause structural damage to young snags that facilitates fungal invasion and promotes successful sapwood decay. Second, the birds themselves may serve as important vectors of fungal spores, yeast cells, or hyphae that have the potential to decompose wood. Areas subjected to high levels of woodpecker foraging may therefore be more likely to decay and provide suitable substrates for subsequent cavity excavation. Given the localities where woodpeckers are likely to forage for food, these results may not be surprising; however, this observation under this set of ecological conditions has not been previously documented to our knowledge. The potential ability of woodpeckers to disperse fungi provides possible benefits to fungi, beetles, and woodpeckers, but whether this is a coevolved relationship or an incidental phenomenon with secondary ecological consequences is unknown.

We suggest that the physical act of woodpecker foraging punctures the bark and fragments the underlying wood structure in a way that likely promotes fungal colonization. Empirical data on the association between woodpecker foraging and wood integrity is limited. Our results are consistent with Conner, Jones, and Jones (1994), who observed a similar relationship between woodpecker foraging and relative wood hardness in hardwood snags in Texas. Woodpecker foraging strategies can range from superficial flaking or scaling to deep excavations that penetrate the outer sapwood (Fig. 4). In the process of foraging for bark beetles, woodpeckers typically use a scaling technique (Bull et al. 1986, Murphy and Lehnhausen 1998) that removes successive layers of bark and permits capture of larvae, pupae, and emerging adults as

TABLE 2. Detection frequencies of fungal and yeast genera isolated from the beaks of 27 non-cavity-nesting and 26 cavity-nesting birds captured on the Lassen National Forest, California.

Genus	Microorganism type	Detection frequency[a]
From non-cavity nesters		
Alternaria	filamentous fungi	0.11
Ulocladium	filamentous fungi	0.04
Unknown	yeast	0.22
Cryptococcus	yeast	0.11
From cavity nesters		
Cladosporium	filamentous fungi	0.19
Mucor	filamentous fungi	0.12
Acremonium	filamentous fungi	0.08
Trichoderma	filamentous fungi	0.08
Alternaria	filamentous fungi	0.04
Fusarium	filamentous fungi	0.04
Penicillium	filamentous fungi	0.04
Sporothrix	filamentous fungi	0.04
Cryptococcus	yeast	0.15
Rhodotorula	yeast	0.08
Torulopsis	yeast	0.08
Trichosporon	yeast	0.04
Unknown	yeast	0.04
Candida	yeast	0.04

[a] Proportion of samples within a class testing positive for the specified genus. A single sample may contain multiple genera.

they bore from the cambium out through the bark. As a snag is invaded by wood boring beetles, woodpeckers begin to excavate larger holes that can penetrate several cm or more to pupae and larvae galleries in the cambium and outer sapwood (Bull et al. 1986, Murphy and Lehnhausen 1998). Both disparate foraging techniques (particularly the latter) likely improve microhabitat conditions that facilitate sapwood decay fungi due to increased exposure of the sapwood. Moreover, they could increase the likelihood of fungal colonization by direct spore transfer from beak to wood or by air-dispersed spores.

Although snags used by foraging woodpeckers in our study were clearly associated with softer sapwood, the possibility exists that woodpeckers select foraging sites that have already been softened by bark beetles and associated fungi. Several species of bark beetles disperse members of the phylum Basidiomycota (Whitney and Cobb 1972) that can cause mechanical and enzymatic destruction of wood leading to brown rot (removal of hemicellulose and cellulose) or white rot (removal of cellulose and lignin; Rayner and Boddy 1988, Huss et al. 2002). Presence of basidiomycetes could soften the wood prior to the woodpeckers' foraging activities in some cases. However, the most commonly vectored organisms associated with bark beetles typically represent ''microfungi'' that are generally not responsible for structural decomposition, but consume cellular contents resulting in a staining of the wood (Rayner and Boddy 1988). Moreover, existing data from our study areas show that woodpeckers forage most intensively on snags during the first year of death when the outer sapwood is still relatively dense and intact (Farris et al. 2002; KLF, unpubl. data). We propose the most likely explanation is that a combination of bark beetle invasion and subsequent woodpecker foraging activity provides more favorable conditions for fungal invasion and subsequent wood decay.

Our analysis suggests that the interaction between bark beetles and woodpeckers could be an important factor affecting wood density. This potential interaction is intriguing, but the manner in which we collected data precluded us from simultaneously evaluating woodpecker foraging and bark beetle activity in more depth. We measured bark beetle activity by recording the presence of exit holes on the bark (Fig. 4). Because the presence of exit holes indicates successful development of eggs laid in the cambium by the original invading female (Furniss and Carolin 1977), higher numbers of exit holes should represent greater success of the overall brood. However, when woodpeckers forage in an area they tend to flake off or puncture the bark as they capture the young larvae, pupae, and adult beetles exiting the tree. In these instances we likely missed recording the presence of beetles even though they were in the sample area prior to capture by the foraging woodpecker. Such bias could have underestimated the actual effect of bark beetles on wood decomposition in our analysis.

In addition to the structural influence woodpeckers may have on wood decomposition, the cavity nesters sampled in this study carried bacteria, yeasts, and fungi in greater frequencies than non-cavity nesters. This suggests that foraging woodpeckers may contribute to the spread of these microorganisms throughout the forest. While we were not able to isolate any of the basidiomycete species associated with woodpecker nest cavities in other studies (Conner,

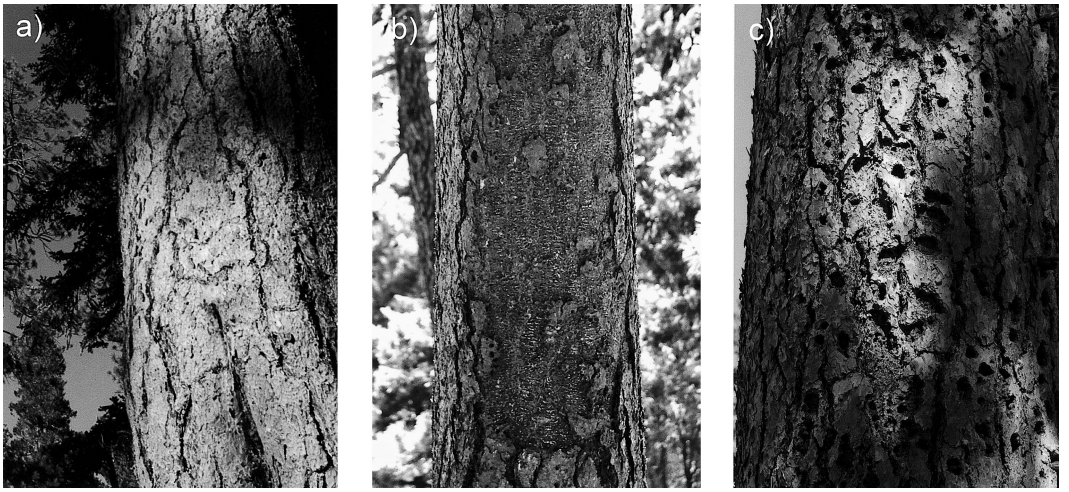

FIGURE 4. Examples of various bark conditions in ponderosa pine trees and snags: (a) undisturbed bark of a living tree, (b) an area of a snag extensively scaled by woodpeckers to retrieve emerging pupae and young adult bark beetles, (c) holes on a snag excavated by woodpeckers in search of wood-boring beetle larvae in the sapwood (photographs by SZ).

Rudolph et al. 1994, Huss et al. 2002), the ecological importance of the microorganisms we did isolate from the woodpeckers should not be overlooked. The species identified in this study precede or coexist with the colonization of the most common wood-decomposing basidiomycetes (Mercer 1982, Rayner and Boddy 1988) and may help to expedite decay. For example, Blanchette and Shaw (1978) found that coniferous wood decayed considerably faster when bacteria and yeasts worked in conjunction with basidiomycetes than wood containing basidiomycetes alone.

Of the yeast genera identified, *Candida, Cryptococcus*, and *Rhodotorula* are among the most common indigenous microorganisms found in soil (Atlas and Bartha 1998). The filamentous fungi tended to be represented by hyaline or nonpigmented to lightly pigmented fungi (species of *Mucor*, *Fusarium*, *Alternaria*, *Sporotothrix*, *Acremonium* [=*Cephalosporium*]) or by dematiaceous or darkly pigmented species of *Ulocladium* and *Alternaria*. All of these fungi probably have the capacity to decompose certain components of wood to varying degrees, and could be associated with soft rot in ponderosa pine. All of these fungi are commonly found in decaying plant and other organic debris and could conceivably be picked up by the birds while foraging, but these could also represent indigenous components of the natural microbial community on the body of birds. The sampled fungi are common in the environment and are mostly saprophytic, although *Alternaria* and *Fusarium* species can act as fungal pathogens on some types of plants (Agrios 1997). Species of *Fusarium* and *Trichoderma* are also capable of decomposing cellulose (Rayner and Boddy 1988), and could therefore be responsible for some sapwood decay.

Our combined results suggest a possible link between bark and wood-boring beetle colonization, woodpecker foraging activity, and phloem and sapwood decomposition in ponderosa pine. Sample areas used by foraging woodpeckers had significantly softer sapwood than areas without foraging evidence. Whether this correlation was a result of the birds alone or a combination of other biological factors (e.g., bark and wood-boring beetle activity) requires more research. Additionally, we recovered wood-inhabiting fungi from cavity nesting species in greater frequencies than non-cavity-nesting species. Many of the isolated microorganisms have been shown to significantly aid in decomposition in conjunction with other fungi. Additional research is needed to validate these implied relationships and to determine whether similar processes occur in other forest types and geographic regions. This study complements previous research in ponderosa pine suggesting that woodpeckers are intricately linked to the temporal process of snag

decomposition, relying on recently dead snags for foraging, and after significant decomposition, for their nesting requirements (Farris et al. 2002, Shea et al. 2002).

Clearly, the process of a ponderosa pine snag becoming a cavity-bearing structure depends upon numerous interdependent factors throughout the entire decay cycle. Consequently, we feel that the effective conservation and management of viable snags in Western coniferous forests lies in the management of the inherent processes (bark beetles, woodpeckers, decay fungi). If woodpeckers do facilitate sapwood decay in ponderosa pine, forest management strategies must recognize and maintain this process. Simply providing an adequate number of snags in a given area may not ensure that the snags will decay in such a way that leads to eventual cavity excavation by woodpeckers. An improved understanding of the roles of woodpeckers, bark beetles, and decay processes as they relate to snag dynamics and wildlife use may provide a valuable management perspective.

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