

Woodpecker Foraging and the Successional Decay of Ponderosa Pine¹

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Abstract

In 1998 we initiated a long-term study investigating the relationships between woodpecker foraging and snag decay processes in interior ponderosa pine forest communities located in Oregon and California. We describe temporal changes in snag structure and quantify both woodpecker foraging activity and relative sapwood decay in 144 ponderosa pine snags, ranging in age from 1 to 9 years (time since death). Preliminary results indicate that temporal changes in snag characteristics were reflective of both inherent insect activity and woodpecker foraging quality. Statistical analysis revealed no significant difference in cumulative woodpecker foraging abundance as snags aged, indicating that woodpecker foraging activity occurred primarily in the younger aged snags. Additionally, there was no correlation between woodpecker foraging intensity and relative sapwood decay. These results offer insights into the interactive biology of bark beetles, woodpeckers, and fungi in the decomposition of ponderosa pine.

Introduction

Woodpecker foraging and nesting ecology is closely tied to insect infestations and tree decomposition stages. Foraging woodpeckers tend to select trees and snags containing high levels of bark and wood boring insects (Baldwin 1960, Kroll and Fleet 1979, Otvos 1965), whereas nesting woodpeckers generally require pockets of older, decayed wood that permit nest excavation (Bull 1983, Bull and others 1997, Conner and others 1976, Harris 1983). In fact, Conner and others (1976) and Miller and Miller (1980) suggested that some form of wood decay is a prerequisite for nest excavation by most species of woodpecker. While the characteristics of snags utilized by woodpeckers for nesting have been studied widely, relatively little is known about structures associated with foraging (Bull and others 1997, Conner and others 1994, Steeger and others 1996). Moreover, the potential influences of foraging

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woodpeckers on snag decomposition characteristics, and therefore subsequent nest site quality, have gone largely unexplored.

In the interior ponderosa pine forests of the western United States, woodpeckers are commonly associated with dead or dying trees where they feed upon bark and wood boring beetles. In their search for prey, they puncture bark surfaces and fragment the underlying wood, thereby altering local microhabitat conditions. Otvos (1979) suggested that such behavior may actually expedite the process of snag decay by creating vectors for the colonization of wood decay organisms. Additionally, Conner and others (1994) observed that hardwood snags which received relatively more foraging activity by woodpeckers tended to have higher incidences of decayed wood. Considering that most species of woodpecker in North America require some form of wood decay for nest excavation, potential interrelationships between foraging activities and the spread of decay fungi in snags are intriguing.

Because organisms that promote sapwood decay tend to rapidly colonize dying conifers (Harmon and others 1986, Mercer 1982, Rayner and Boddy 1988), early patterns of snag utilization are likely central to understanding the relationship between woodpecker use and subsequent decay dynamics. Several researchers have reported concentrated foraging activity by some woodpecker species within the first few years of tree death (Bull 1983, Bull and others 1986, Murphy and Lehnhausen 1998, Steeger and others 1996). However, few have quantified foraging intensity across a spectrum of decay classes, or elucidated the relationships between foraging woodpeckers and subsequent snag decay dynamics.

Addressing such ecological questions requires the use of large populations of known age snags. Consequently, researchers often rely on snags produced in naturally occurring perturbations such as wildfires, insect outbreaks, or windthrow events, but this may prove problematic in many cases because the exact time and mode of death may be attributed to several underlying sources. Because the biological decay activity of a tree is directly related to both the timing and cause of its demise, it is easy to envision how controlling these two variables can greatly aid in the reduction of long term error. In this study, we made use of an experimental population of snags intentionally infested with bark beetles (using pheromone baits) as part of a separate, long-term entomological study. As a result, the exact date and mode of mortality were known, which narrowed the range of possible decay pathways and permitted us to better examine the effects of foraging woodpeckers on subsequent snag decay processes.

The purpose of this research was to investigate the dynamic relationship of foraging woodpeckers and ponderosa pine decay. Specifically, we wanted to identify the structural changes in ponderosa pine throughout the decay sequence, determine the decomposition stages used most intensely by foraging woodpeckers, and examine the effect of these foraging activities on sapwood decomposition.

Study Area and Methods

The study was conducted on three National Forests in the Cascade Range: the Lassen located in northeastern California and the Ochoco and Deschutes National Forests in central Oregon (*fig. 1*). Interior ponderosa pine (*Pinus ponderosa* var. *ponderosa*) was the dominant species at all three locations. The Oregon sites had a minor component of both Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies*

concolor var. *lowiana*), while the higher elevations of the Lassen site contained a large component of Jeffrey pine (*Pinus jeffreyi*), with scattered inclusions of white fir and incense-cedar (*Libocedrus decurrens*). Elevations ranged from 2,275 meters on the Ochoco National Forest to 2,730 meters on the Lassen National Forest. Resident woodpecker species of interest included the white-headed (*Picoides albolarvatus*), downy (*P. pubescens*) three-toed (*P. tridactylus*), black-backed (*P. arcticus*), hairy (*P. villosus*), and pileated woodpeckers (*Dryocopus pileatus*). Other woodpecker species (i.e., northern flicker [*Colaptes auratus*] and three species of *Sphyrapicus* sapsuckers) were also present, but do not typically feed on decaying pines.

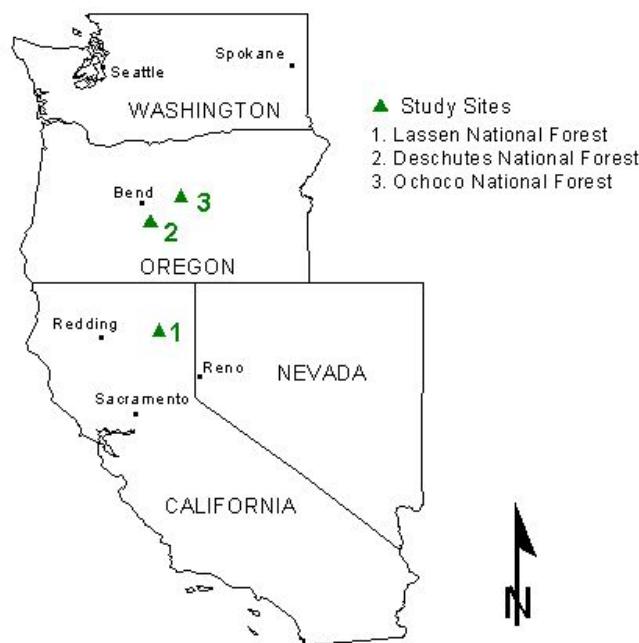


Figure 1—The three snag data collection areas in central Oregon and northeastern California.

Methods

Because snag decomposition is a slow and variable process, charting structural and biological changes directly requires very long periods of time. One recognized alternative is to use a chronosequence of snags with known dates of origin for reconstructing temporal patterns of decay. Between the three forests, we developed a chronosequence consisting of 144 snags ranging in age from 1 to 9 years. Snags on the Ochoco and Deschutes sites were created by bark beetles responding to pheromone baits in 1998 and 1997, respectively. Snags on the Lassen site were sampled from two separate populations. Half were baited with bark beetle pheromone in 1993 and the remainder were sampled from a large population of naturally occurring snags with known ages. All 144 snags, which ranged from 40 to 130 centimeters in diameter, were sampled between 1 June and 31 August 1999.

To document structural and biological changes in the snags across the chronosequence, seven age-dependant variables were visually recorded. These

included: foliage color (green, lime green, yellow, red), foliage retention (expressed as percent of needles remaining), bark retention (expressed as percent remaining), bark integrity (tight or loose, as indicated when the bark was punctured), presence of woodpecker nest cavities, presence of bark beetle pitch tubes, and type and quantity of beetle exit holes. Because the phenology of beetles foraging on ponderosa pine follows a distinct chronology, the size and shape of holes left in the bark when beetles exit the snag are indicative of particular families, and are therefore useful indicators of decay progression (Patrick J. Shea, pers. comm.). Using this information, we were able to classify and quantify exit holes of three taxonomic families in chronological order of tree infestation: Scolytidae (“primary” invaders), Buprestidae (“secondary” invaders), and Cerambycidae (“secondary” invaders).

To compare woodpecker foraging activity across snag ages, we developed a foraging intensity index based on the cumulative number of foraging excavations per square meter. Foraging intensity was quantified on each snag using a 30x spotting scope and counting all visible foraging excavations from a distance of 30 meters on a randomly selected azimuth. Counts were cumulative and did not distinguish between current season and previous years’ foraging evidence. The surface area surveyed was calculated and divided into the number of observed foraging “hits,” resulting in a standardized index of foraging hits per square meter of snag surface.

As a relative indicator of sapwood softness, we used a six-joule Proceq Pilodyn wood tester (Crown 1978, Sprague and others 1983). The Pilodyn compresses a spring loaded steel pin into the sapwood with a constant force, measuring penetration depth in millimeters. On each snag, at a height of 1.3 meters, we removed a square piece of bark measuring 4 centimeters² at each of the four cardinal directions. This permitted the Pilodyn direct access into the sapwood, which was measured with the Pilodyn three times at each exposed site to compute an average penetration in millimeters for 12 strikes per snag. Before bark removal, we quantified woodpecker foraging within the immediate area by counting foraging hits in a 15x15 centimeter area.

Because snags were sampled from two differing sources (bark beetle killed and unknown mortality causes) and considering that the mode of tree death likely influences subsequent woodpecker foraging activity and decay dynamics, we divided the data into two subsets, based on mortality agent, prior to analysis. We used simple linear regression to evaluate the relationships between woodpecker foraging, and both snag age and sapwood softness.

Results

Visual decay characteristics changed directionally with increasing snag age along the chronosequence (*table 1*). In general, foliage color tended to turn from dark green to lime or yellow within the first year and was red by year 2. Needle retention dropped to an average of 85 percent within the first year and 14 percent by year 2. By year 3 all snags had completely lost their foliage. Bark retention was 100 percent until year 4, then fell to between 90 and 95 percent for the remainder of age classes. However, 50 percent of the sampled snags had loose or sloughing bark by year 4 and all snags had loose bark by age 6.

Table 1—*Structural decay characteristics of 144 ponderosa pine snags across 10 age classes in the central and southern Cascades of Oregon and northeastern California, 1999.*

Snag Age Class	Mean/std. dev. age class			Percent of age class exhibiting described feature					
	Foliage Color ¹	Pct needles Remaining	Pct bark Remaining	Loose Bark	Pitch Tubes	Exit holes			Nest Cavities
						Scolytidae	Buprestidae	Cerambycidae	
0	Green	100/0	100/0	0	0	0	0	0	0
1	Lime	85/23	100/0	0	97	93	71	0	0
2	Red	13.5/24	100/0	0	92	100	90	23	0
3	n/a	0/0	100/0	50	75	100	100	100	50
4	n/a	0/0	95/5	71	75	100	100	100	50
5	n/a	0/0	90/7	75	50	100	100	100	50
6	n/a	0/0	90/19	100	50	100	100	100	71
7	n/a	0/0	90/0	100	50	100	100	100	100
8	n/a	0/0	90/14	100	50	100	100	100	100
9	n/a	0/0	90/29	100	13	100	100	100	100

¹ Color means calculated using 1 = green, 2 = lime, 3 = yellow, 4 = orange, and 5 = red.

The presence of beetle pitch tubes, which indicates either past or present beetle infestation, was highest during the first year, with 97 percent of sampled snags exhibiting tubes. This proportion gradually decreased over time, with only 13 percent of the snags having old tubes remaining by age 9. Ninety-three percent of 1-year-old snags exhibited exit holes created by members of the family Scolytidae, and this figure increased to 100 percent by the second year. Secondary beetles of the families Buprestidae and Cerambycidae emerged during the first and second years, respectively. Ninety percent of 1-year-old snags had Buprestid exits, but no visual evidence of Cerambycid emergence. By the second year, 100 percent of the snags showed signs of Buprestid emergence, while Cerambycid beetles emerged from only 23 percent of the snags. By the third year, 100 percent of the snags showed evidence of both beetle families. Nest cavities showed up in 50 percent of the snags by the third year, 71 percent by year 6, and all snags had cavities by year 7.

Initial linear regression analysis revealed no significant increase in woodpecker foraging intensity between beetle killed snags and those with unknown causes of mortality. Additionally, because t-test comparisons revealed similar slopes for each set ($p = 0.001$), the two data sets were combined for all subsequent analyses. Further regression analysis on the entire set of snags yielded similar results, with no increase in woodpecker foraging intensity as snags aged (*fig. 2*). The slope of the regression line did not significantly differ from zero ($p < 0.0001$), indicating that most woodpecker foraging activity took place in the early stages of decay. Sapwood softness was not linearly related to the amount of woodpecker foraging (*fig. 3*).

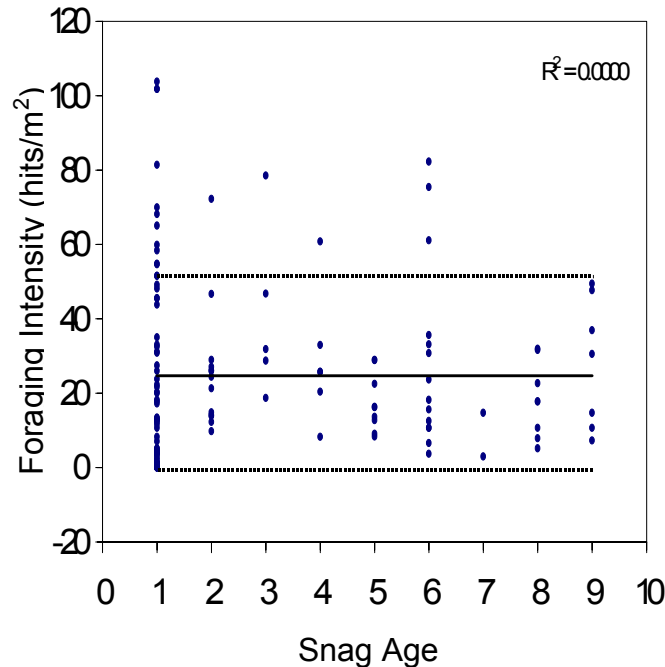


Figure 2—Linear regression analysis of cumulative woodpecker foraging intensity and snag age from 144 snags sampled on the Deschutes and Ochoco Forests in central Oregon and the Lassen National Forest in northeastern California, 1999. Dashed lines indicate 95 percent confidence intervals.

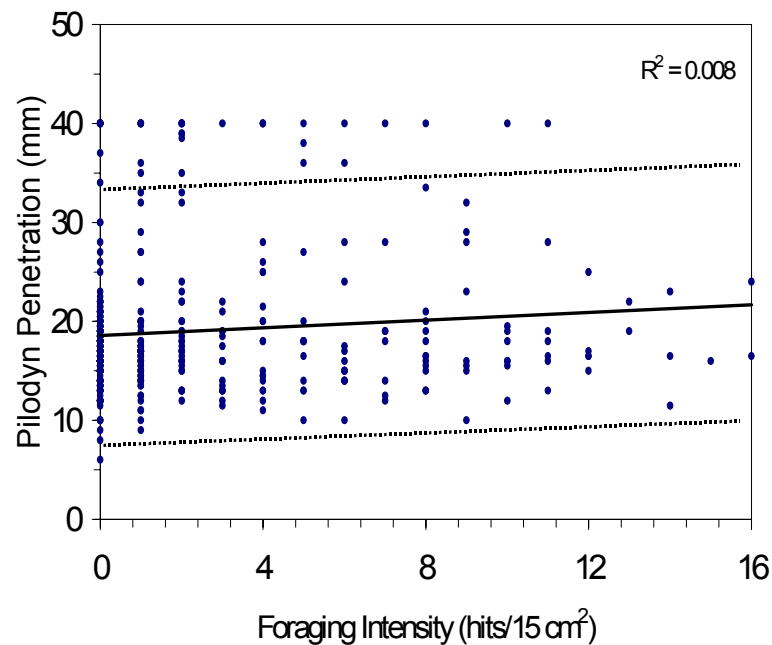


Figure 3—Linear regression analysis of woodpecker foraging intensity and sapwood softness as indicated by pilodyn penetration measured from 144 snags sampled on the Deschutes and Ochoco Forests in central Oregon and the Lassen National Forest in northeastern California, 1999. Dashed lines indicate 95 percent confidence intervals.

Discussion

The decay characteristics exhibited in this snag population show similarities with those described by other authors (Bull 1983, Raphael and Morrison 1987, Steeger and others 1996). However, we discretely defined snag decay characteristics to better reflect their value to foraging woodpeckers. For example, the commonly used decay classifications put forth by Thomas and others (1979) and Steeger and others (1996) broadly categorize snags on the basis of bark retention, needle, twig, and branch presence. Although these classifications are useful for defining suitable nest substrates, they probably do not reflect the more subtle changes in woodpecker foraging value resulting from early fluctuations in arthropod populations. We found that needleless snags were generally only 3 years old and would fit into decay category 1 (first category under “dead”), using established classification systems (Bull and others 1997, Steeger and others 1996, Thomas and others 1979). However, examination of beetle phenology data from our study areas (using exit holes as guidelines) suggests that most 3-year-old snags are probably past the peak of bark and wood boring beetle activity, and therefore less likely to be used by foraging woodpeckers. Consequently, a highly valuable foraging stage may be masked by current classifications. Maintaining high quality woodpecker foraging habitat may require modifications of current snag classifications to account for early stages of snag decay.

Woodpeckers in the study areas appear to concentrate their foraging activity within the first few years of tree death. This period coincides with the densest populations of bark and wood boring beetles, as evidenced by the appearance of beetle exit holes. These findings agree with what is currently known about the diets of *Picoides* woodpeckers that specialize on bark and wood boring beetles (Otvos 1965, 1970, 1979). Similar temporal foraging patterns have been documented in the literature (Bull 1983, Bull and others 1986, Parks 1999, Steeger and others 1996), especially in areas of epidemic beetle outbreaks (Amman 1984, Baldwin 1960, Kroll and Fleet 1979, Otvos 1965), or as a response to a localized perturbation such as windthrow (Wickman 1965) and fire (Murphy and Lehnhausen 1998).

Although these data appear to reinforce the notion that foraging woodpeckers concentrate their use on younger snags, it is based on a chronosequence of snag decay. Substituting space (in the sense of different geographical areas or individual snags) for time requires an inherent assumption regarding the temporal pattern of the foraging activity. When we sampled older snags, we assumed that the visible foraging sign took place in the early stages of the tree’s demise. This may be a reasonably safe assumption considering the rapid, abundant, response of both beetles and woodpeckers to a dying tree. In general, the activities of both groups within the early stages of tree death is so intense, it numerically overwhelms further evidence of subsequent beetle-woodpecker activities. However, because each individual snag was not followed yearly from death, we cannot unequivocally determine at what point along the decay sequence the foraging took place. To gain accurate insight into the relationships between foraging woodpeckers and snag decay, it is critical to have a long term data set in which each snag is followed and woodpecker foraging is quantified yearly from the time of death. We hope to rectify this problem over time as our data set grows, but until then these results should be interpreted accordingly.

Finally, these data did not reveal any pattern between the intensity of woodpecker foraging and the relative degree of sapwood decay. There could be several explanations for this particular finding, two of which relate to the use of the

Pilodyn as a sampling tool, and one that has to do with woodpecker foraging ecology. First, in addition to the effects of climate, aspect, and microhabitat differences, live trees compartmentalize invading bacteria and fungi, thus isolating these organisms to localized areas, creating a patchy mosaic of sound and decayed wood (Shigo 1984). Our survey methods were only designed to measure sapwood decay in one small localized, radial area, but as demonstrated by Shigo (1984), wood decay is spatially variable in nature, thereby making our measures with the Pilodyn a hit or miss procedure. This is evidenced by the often highly variable Pilodyn readings even within a small, 1 cm² area. Although one measure may have hit sound wood, another just a few millimeters away might have produced a clearly decayed reading. Our selected method of decay quantification was somewhat limited considering this fine-scale variability.

A second possible reason for our inability to detect a relationship between woodpecker foraging intensity and sapwood decay could be explained by a phenomenon known as “case hardening.” Mercer (1982) noted that the outer 3-4 centimeters of sapwood is frequently harder than more interior points due to weathering and drying of the snag surface. The Pilodyn had a maximum extension of 40 millimeters. Consequently, it may not even have been penetrating the truly soft areas of the wood. It is clear that the Pilodyn has limitations for this purpose, yet several researchers have found Pilodyn measures comparable to those of specific gravity (Conner and others 1994, Sprague and others 1983) and wood density (Crown 1978). We are currently exploring various options to better detect and quantify relative sapwood decay on a more universal scale.

Finally, we believe that the foraging ecology of woodpeckers could have a marked effect on the dynamics of wood decomposition, thus affecting our ability to accurately quantify an interrelationship. Methods of food procurement differ between woodpecker species and could play a role in whether the wood is exposed to decay fungi. For example, several species of woodpecker are thought to predominantly “scale” for primary bark beetles, while others “excavate” for secondary wood boring beetles. Scaling behavior involves striking the bark at an angle to “scale” away the outer surfaces. This behavior rarely penetrates the wood, its purpose being to exploit food resources just under the bark’s surface. In contrast, excavation involves creating large holes into the bark and wood (usually in pursuit of wood boring organisms) which significantly alters the microhabitat of the sapwood. It is easy to envision how this excavation behavior might facilitate more rapid fungal colonization by providing greater access points into the snag’s interior.

Because particular species of woodpecker are thought to specialize in certain foraging behaviors, interspecific population dynamics in the area of an individual snag could alter the rates of sapwood fungal invasion. For example, the three-toed woodpecker generally forages using the scaling technique (Bull and others 1986, Murphy and Lehnhausen 1998), whereas species such as the hairy and black-backed woodpeckers are relatively stronger excavators (Bull and others 1986). If a given area had relatively larger populations of “scaling” species, then decay rates could be less pronounced due to the relatively minor substrate manipulations created by this foraging strategy.

These preliminary results offer some insights into the dynamic relationship of woodpecker foraging and ponderosa pine decay, yet our sampling methods need refinement to more accurately quantify the potential effect of foraging woodpeckers on snag decay processes. In particular, a better method of quantifying sapwood decay

is needed. We are currently engaged in exploring these methodological issues and hope to further investigate the interactive biology of bark beetles, woodpeckers, and fungi in the decomposition of ponderosa pine.

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