Woodpecker-snag interactions: an overview of current knowledge in ponderosa pine systems[1]

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Abstract

Standing dead trees (snags) with cavities are a critical ecological component of western coniferous forests. These structures provide foraging, roosting, and nesting habitat for numerous species of invertebrates, amphibians, reptiles, birds, and mammals. Snags may be created through a variety of interrelated processes including wildfire, drought, insects and disease. However, dead trees containing excavated cavities are primarily the result of nest excavation by woodpeckers. While the specific factors leading to cavity generation in certain snags is not well understood, the manner in which a tree dies likely plays a significant role. We provide an overview of woodpecker-snag interactions in relation to the major modes of tree mortality in ponderosa pine. Of particular interest is the effect of mortality agent on the temporal patterns of snag decomposition, woodpecker foraging use, and woodpecker cavity excavation. Generally, snags created by bark beetles, and/or fire decay fastest, and experience the greatest foraging and nesting use by woodpeckers. Consideration of these interrelationships may aid in snag management.

Introduction

Standing dead trees (snags) are important to the structure and function of western coniferous forests (Bull and others 1997, Harmon and others 1986, Thomas and others 1979). These structures provide critical habitat for numerous organisms, contribute to nutrient cycling, and influence forest productivity (Harmon and others 1986). Dead trees containing excavated cavities are of particular importance to many species of snag-dependant wildlife and are a primary focus of forest management guidelines in the western coniferous forests (Bull and others 1997, Thomas and others 1997). Snags may be created through a variety of interrelated processes including wildfire, drought, insects and disease; however snags containing cavities are primarily the result of nest excavation by woodpeckers. Once abandoned, woodpecker cavities provide important foraging, roosting, and nesting sites for numerous species of birds, mammals, reptiles, amphibians, and invertebrates (Thomas and others 1979, Bull and others 1997).

The factors that determine which snags are selected for cavity excavation by nesting woodpeckers are complex and poorly understood. Several authors have

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suggested that the quality of snags, as determined by the size and type of decay, may be more important than the quantity of snags on the landscape when determining the value of habitat for cavity-nesting wildlife (Bull and others 1997, Conner and others 2001, Jackson 1977, Jackson and Jackson 2004). In ponderosa pine forests, Zack and others (2002) found that fewer than 20 percent of pine and fir snags sampled in northeastern California contained nest cavities. Additionally, Ganey and Vojta (2004) reported that only 17 percent of snags contained cavities in ponderosa pine forests of Arizona. These figures suggest current management guidelines which focus solely on snag quantity (e.g. snags/hectare) may not adequately reflect habitat requirements of nesting woodpeckers.

Ponderosa pine (*Pinus ponderosa* P.& C. Lawson) is a particularly important snag species for cavity-nesting birds due to its relatively large volume of sapwood, which often decays quickly and provides suitable sites for nest excavation (Bull and others 1997). In mixed-conifer stands, ponderosa pine is often preferred over other tree species by nesting woodpeckers (Bull and others 1997, Bate 1995, Dixon 1995, Haggard and Gains 2001, Hutto 1995, Lehmkuhl and others 2003, Zack and others 2002). Moreover, recent research in ponderosa pine suggests that the foraging activity of woodpeckers during the first few years of snag's life may influence subsequent decomposition of the sapwood by promoting decay organisms associated with nest cavity excavation (Farris and others 2004). While the snag requirements of nesting woodpeckers have been studied widely, relatively little is known about the structures associated with foraging (Bull and others 1997, Conner and others 1994, Steeger and others 1995), which may prove to be instrumental to the creation of future nesting habitat. Foraging woodpeckers respond to snags originating from various modes of mortality, and the manner in which a tree dies likely has a large influence on its eventual use by woodpeckers and subsequent wildlife species.

The objective of this paper is to provide an overview of woodpecker foraging and nesting behavior as it relates to snags originating from each of the major mortality agents in ponderosa pine systems. We will begin with a brief outline of how foraging and nesting woodpeckers respond to snags created by wind, lightning, and diseases. This will be followed by a more detailed discussion of responses of woodpeckers to fire and bark-beetles, two mortality agents that have been extensively studied. Finally, we will discuss woodpecker use of artificially created snags, as these structures are becoming a common management tool in some forests. Of particular interest throughout our discussion is the effect of each mortality agent on the timing of woodpecker use and snag attrition.

Mortality Agents

There are numerous mortality agents that act to create snags in ponderosa pine forests. Major agents of tree mortality in forested ecosystems have been outlined by Harmon and others (1986) and Rose and others (2001) and include: wind, fire, insects, diseases, competitive suppression, senescence, flooding, landslides, lightening, and volcanic events. Distinguishing between proximate and ultimate causes of tree death can be problematic and it is likely that mortality agents rarely act independently of one another. For example, fires can weaken trees both structurally and physiologically leading to windthrow, insect attack, or disease inoculation. For the purposes of this review, we will treat each mortality agent independently.

Wind

Wind events can kill trees by uprooting and snapping the bole, or breaking large branches. This agent can act on large scales during events such as severe wind storms or hurricanes, or on a smaller scale by killing single or small clusters of trees. In western North America, wind events are typically severe and contribute to a larger proportion of snag creation on the west side of major mountain ranges such as the Cascades or Sierra Nevada, or in coastal forests where as many as 70 percent of the stems may be killed (Greene 1984, Harmon and others 1986). In contrast, only 15-20 percent of trees are killed by wind in interior ponderosa pine forests (Avery and others 1976). Depending on the distribution of tree sizes in the affected stand and subsequent insect colonization after wind events, the resultant snags and downed logs may be useful for woodpeckers as both foraging and nesting sites. Wichmann and Ravn (2001) documented large influxes of Scolytid beetles following a windthrow event in spruce forests. Wickman (1965) reported both foraging and nesting use of wind damaged ponderosa pine by Black-backed Woodpeckers (*Picoides arcticus* Swainson) foraging on Cerambycid beetles in northeastern California.

Lightning

Lightning can kill trees by shattering or exploding the tops or entire boles. It can also damage trees, resulting in a narrow furrow of disturbed bark and sapwood spiraling around the bole from the top to the butt of the tree (Scharpf 1993). This often results in dead and decaying wood which may be colonized by insects (Bull and others 1997), subsequently attracting foraging woodpeckers (Bull and others 1997). Additionally, these pockets of dead wood can serve as cavity sites for nesting woodpeckers (Bull and others 1997).

Disease

There are numerous diseases which affect ponderosa pine. Scharpf (1993) outline 7 major categories: needle diseases; cankers; diebacks and galls; rusts; mistletoes; root diseases; and rots. The responses of foraging and nesting woodpeckers to trees with these diseases present, or snags created by them, is largely unknown. From the perspective of woodpecker use perhaps the greatest influence these diseases may have is in weakening and/or killing trees which facilitates the invasion of bark and/or wood-boring beetles, the major prey of foraging woodpeckers. Trees weakened or killed by disease may also provide nesting habitat depending on internal decay patterns.

Insect Mortality

There are numerous species of bark beetles which act as mortality agents in ponderosa pine systems. Most common are members of the genera *Dendroctonus* and *Ips*. These insects typically attack weakened or suppressed trees, but at epidemic levels, they can overcome even healthy trees, resulting in patches of mortality that contribute to both vertical and horizontal diversity in forest structure. These beetles are an important source of prey for many woodpecker species: particularly those of the genus *Picoides*. Woodpeckers of this genus respond dramatically to outbreaks of these insects and have been suggested as control agents for endemic insect populations. For instance, Murphy and Lehnhausen (1998) noted a four fold increase in Hairy (*P. villosus* Linnaeus), Three-toed (*P. dorsalis* Baird), and Black-backed Woodpeckers (*P. arcticus* Swainson) following a bark and wood-boring beetle outbreak in Alaska. Several authors have suggested that woodpeckers may be important regulators of bark beetle populations: especially at endemic levels (Kroll and Fleet 1979, Kroll and others 1980, Koplin and Baldwin 1970, Koplin 1972).

Picoides woodpeckers forage most intensively on ponderosa pine infested by bark-beetles during the first 1 to 3 years after invasion (Farris and others 2002). Bark beetles of the genus *Dendroctonus* are the primary prey items of woodpeckers during the first year following tree death (Farris and others 2002, Shea and others 2002). During the second and third years following the tree's demise, phloem and xylem consuming insects of the families Buprestidae and Cermabycidae provide additional prey for woodpeckers (Farris and others 2002, Shea and others 2002).

Ponderosa pine killed by bark beetles, once adequately decayed, may also serve as nesting sites for woodpeckers. Little information exists examining the nesting preferences of woodpeckers in ponderosa snags specifically originating from bark beetle activity; however it is likely that many of the snags examined in several studies were influenced by bark beetles. In general, woodpeckers nesting in ponderosa pine select snags that are larger in diameter and of advanced decay (Bull and others 1997, Bate 1995, Dixon 1995).

Recent evidence suggests a potential relationship between nest excavation in beetle-killed ponderosa pine and previous foraging use by woodpeckers during the early stages of snag decay. Zack and others (2002) determined that nest excavation was more likely on snags with an extensive history of foraging activity by both beetles and woodpeckers. Additionally, Farris and others (2004) documented the influence of foraging woodpeckers on the decomposition of ponderosa pine. Snags that were used by foraging woodpeckers experienced significantly greater sapwood decay than unused snags. Additionally, more than half the woodpeckers sampled in this study carried wood-decaying fungi on their beaks. These findings suggest that woodpeckers may influence snag decomposition through their foraging behavior that can structurally degrade the wood and passively introduce the wood decaying fungi required for subsequent nest cavity excavation.

Snag longevity following insect attack is variable and is likely dependent on site-specific factors such as soil characteristics, snag size, and local microclimate (Landram and others 2002; Laudenslayer, this volume). On average, the half-life (amount of time it takes for half of the population to fall) of ponderosa and Jeffrey pine snags in the southern Cascades of California is 5 to 6 years for small (13-36 cm [5.2-14.3 in] dbh) snags and 7 to 8 years for large (> 38 cm [15 in] dbh) snags (Landram and others 2002). However, the authors don't distinguish between fall rates of snags of various origins (e.g. fire versus beetle kill). Mitchell and Preisler (1998) found that the half-life of lodgepole pine killed by the mountain pine beetle in central Oregon to be 8 years, with snags falling as early as 3 years after death.

In summary, the temporal patterns of snag use by woodpeckers following beetle kill events are concentrated within the first 1 to 8 years. Foraging is most intense within the first 1-3 years after tree death, while nesting activity begins around year 5. Snags begin to fall during this same period and may be an indication that snags killed by beetles don't stand long enough to serve as useful nest sites in some instances (*fig. 1*).

Fire

Historically, fire was likely the most common mortality agent in ponderosa pine forests, and is the most widely studied means of tree death in terms of evaluating woodpecker response. Fire can directly kill and weaken trees through crown scorch, cambial girdling, and root damage (Harmon and others 1986). The effects of fire are highly variable and typically depend on the type of burn, its intensity, topography, and forest type. In ponderosa pine forests, fires historically burned at frequent intervals and low intensities (Agee 1993). However, management activities common during most of the 20th century including timber harvest, livestock grazing, and fire suppression, have altered both the structure and function of many of today's forest stands, resulting in an increase in the number, size, and severity of fires (Allen and others 2002). Typically woodpeckers respond dramatically to both large and small scale fires where they find an abundance of insect prey and decaying snags suitable for nesting. However, the specific patterns of woodpecker use are likely dependent upon the severity of the fire and whether trees are killed directly or experience a prolonged weakening and death from other associated mortality agents such as bark beetles.

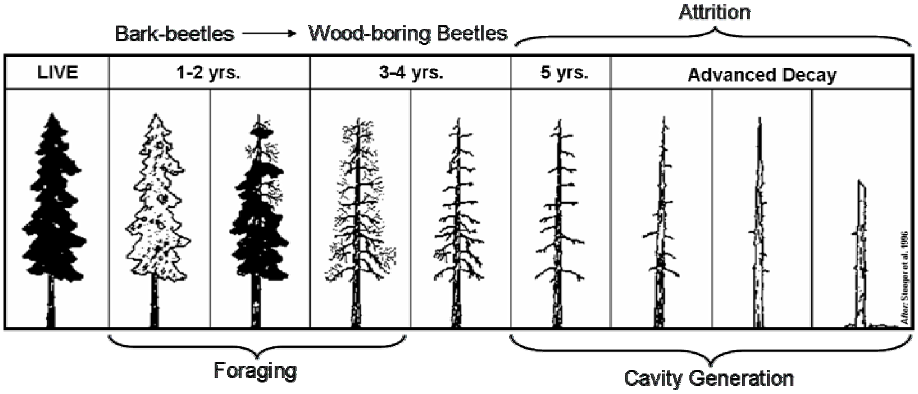

Figure 1—Generalized conceptual model of temporal woodpecker use and attrition of snags created by bark beetles in ponderosa pine. Foraging activity is most intense during the first 3 years following death and corresponds to the insect types active within the snag. Cavity generation and snag attrition both begin after approximately 5 years. The shading of the trees in this figure illustrates changes in foliage color from a healthy green (far left shaded black), fading to yellow (second panel shaded as light grey) and dead and shedding red needles (third panel shaded as black with gaps of needle loss). Schematic patterned after Steeger and others 1995).

Foraging woodpeckers, particularly those of the genus *Picoides* respond immediately to post-fire areas where they typically prey on bark and wood boring beetles that invade dead and dying trees (Farris and Zack in press, Murphy and Lehnhausen 1998). This foraging period is generally brief, lasting only 2-3 years after the fire, before most of the beetle prey has been exhausted (Farris and Zack in press, Murphy and Lehnhausen 1998). As decay progresses in subsequent years, insects such as carpenter ants and termites become important prey for other species of woodpecker, such as the pileated. In general, snags selected by foraging woodpeckers within burned areas are typically large in diameter (Kreisel and Stein 1999, Murphy and Lehnhausen 1998), and of moderate fire damage (less than 50 percent of the bole burned) (Murphy and Lehnhausen 1998). However, some studies have demonstrated woodpecker use of both small and large diameter snags in post-fire environments (Hutto 1995, Horton and Mannan 1988, Haggard and Gains 2001), suggesting that other variables, such as fire damage, tree species, bark thickness, timing, and insect activity may be important factors.

Nesting woodpeckers typically use post-fire environs relatively later than foraging woodpeckers. For example, models created by Lehmkuhl and others (2003) for ponderosa pine in the eastern Cascades of Washington predicted nest cavities to most likely occur between 5 and 25 years post-fire. Note that these were cumulative numbers across a chronosequence of wildfires so the exact timing of excavation and occupancy was unknown. In contrast, the models of Saab and others (2004) predicted nest occupancy to be highest during the first 5 years, with cavities showing up as early as 2 years after the burn. Snags selected as nesting sites are generally larger in diameter than the average available snag (Bull and others 1997, Lehmkuhl and others 2003, Saab and Dudley 1998, Saab and others 2004).

Snag longevity following fires is variable and likely dependent on numerous, site-specific factors such as fire severity, soil characteristics, snag size, and local microclimate (Landram and others 2002; Laudenslayer, this volume). Everett and others (1999) found that 50 percent of the small (<23 cm [9.1 in] dbh) ponderosa pine fell or broke to heights less than 1.5 meters (4.9 feet) during the first 7-12 years following fires in the eastern Cascades of Washington. Larger ponderosa pine (>41 cm [16.1 in] dbh) were scarce in their study areas, but of the few present, 79 percent remained standing 60 years post-fire. In Colorado, Harrington (1996) documented ponderosa pine snags falling as early as 3 years following fire. Morrison and Raphael (1993) found a 68 percent decline in snags 18 to 23 years following a fire event in the eastern Sierra Nevada of California, but do not distinguish between pine and fir. In northeastern California, Laudenslayer (2002) did not observe any snags fall during the 7 year study period, but did document top breakage after 5 years. Farris and Zack (in press) found 20 percent of Jeffrey pine snags fell 4 years following a fire event in the southern Cascades of California. There is conflicting evidence regarding the relative attrition and decay rates of ponderosa compared to other conifers such as white-fir. Landram and others (2002), Morrison and Raphael (1993) and Raphael and White (1984) all found that both ponderosa and Jeffrey pine fell at more rapid rates than white-fir. In contrast, one study in the southern Cascades of California noted greater persistence of Jeffrey pine as compared to white-fir following fire (Farris and Zack in press). Additionally, Lowell (1996) and Farris and Zack (in press) both noted more pronounced wood decay in white-fir compared to ponderosa and Jeffrey pine following fire, which may lead to more rapid attrition.

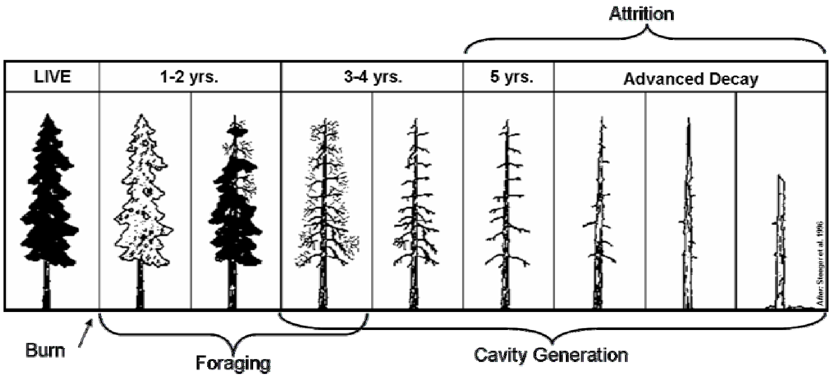

Figure 2—Generalized conceptual model of temporal woodpecker use and attrition of snags created by low to moderate intensity fire in ponderosa pine where most of the trees are weakened and eventually infested with bark and wood boring beetles. Foraging activity is most intense during the first 3 years following fire, while cavity generation can overlap this period and last for several years following the burn event. Fire-killed trees generally begin to fall about 5 years after death. Schematic adapted after Steeger and others 1995).

In summary, the temporal patterns of snag use by woodpeckers following fire events are concentrated within the first 1-5 years, but can extend to 15 years following wildfire. Foraging is most intense within the first 1-3 years after the burn and nesting activity overlaps the later stages of foraging and extends throughout the life of the snag. Attrition and advanced decay typically starts around 5 years after the burn, but can occur as early as 3 years (*fig. 2*). These generalizations are for low-moderate severity fires in which bark and wood-boring beetles play an active role.

Artificial Creation

Methods of artificial snag creation are becoming a tool to meet snag management guidelines in areas lacking suitable snag densities. Creation methods vary and include the use of insect pheromones (Shea and others 2002), mechanical girdling (Shea and others 2002, Hallett and others 2001), girdling through basal burning (Parks and others 1999), mechanical topping (Hallet and others 2001), and topping using explosives (Bull and others 1981). Typically, the motivation for creating snags is to provide nesting habitat, so few studies have evaluated the quantitative use of these artificially created structures as foraging substrates. In ponderosa pine 3 creation methods have been well documented: girdling, topping, and pheromone baiting.

In eastern Washington, foraging woodpeckers showed no preference between topped and girdled snags (Hallet and others 2001). Parks and others (1999) documented equal amounts of woodpecker foraging on ponderosa killed by basal burning and mechanical girdling in New Mexico. Shea and others (2002) documented a greater use of pheromone-baited trees as compared to girdled trees for two types of woodpecker foraging strategies aimed at two distinct types of insects. In their study, all trees that were baited with western pine beetle pheromone, exhibited woodpecker “flaking” (superficial removal of successively thin layers of bark to procure pupae and emerging adult bark beetles) within a few months after treatment, while none of the girdled trees showed evidence of flaking; suggesting that bark beetles were not present or were too rare to exploit in the girdled snags. In contrast, evidence of woodpecker foraging “excavations” (distinct holes created in the bark that often penetrate through to the tree’s sapwood created in pursuit of wood-boring beetles) were recorded on snags in both treatment types, but in much greater densities on the pheromone baited snags as compared to the girdled snags; suggesting that these structures provided a more productive foraging medium for woodpeckers.

Nesting woodpeckers tended to prefer topped trees versus girdled trees in Washington (Hallett and others 2001), while Parks and others (1999) documented greater nest use in mechanically girdled snags versus trees killed using basal burning methods, or a combination of girdling and burning. In the Southern Cascades, 44 percent of pheromone baited snags contained woodpecker nest cavities 6 years after treatment, while none of the girdled trees were used by nesting woodpeckers (Shea and others 2002). However, 2 years later, 14 percent of the girdled snags contained cavities and the use of baited snags increased to 50 percent (Shea unpublished data).

Decay and attrition of snags created by the three methods are variable and once again, likely dependant on local site conditions. Most authors cited “decay” as the breaking of branches off the bole, the loss of bark, or advancement between the standardized decay stages outlined by Thomas and others (1979) or Cline and others (1980). Hallet and others (2001) found that topped trees tended to decay slower than girdled trees, but have little data specific to ponderosa pine and do not speculate on fall rates. In New Mexico, 97 percent of the girdled trees remained standing while only 68 percent of the basally burned trees remained standing 4 years after treatment. After 6 years, standing girdled trees declined to 72 percent, while basally-burned trees declined to only 36 percent. In northeastern California, 16 percent of the pheromone baited trees had fallen, while only 12 percent of the girdled trees fell or broke to heights less than 1.5 meters (4.9 feet) 6 years after treatment (Shea and others 2002).

Summary and Implications

Several factors determine how and when snags are utilized by foraging and nesting woodpeckers. These include the mode of mortality, time since tree death, and snag size. In terms of foraging, woodpecker utilization of snags appears to be most concentrated within the first three years of tree death, especially on snags originating from bark-beetles and/or a combination of bark beetles and low/moderate severity fires. Snags created artificially through girdling or topping are used less intensively for foraging. Moreover, peak foraging activity in artificially snags typically occurs after the first two or three years of snag creation. This disparity is likely due to differences in the sequence of insect infestation. Greater insect diversity and abundance have been reported in naturally created snags compared to snags created artificially by girdling (Shea and others 2002).

In comparison to foraging woodpeckers, snag utilization by nesting woodpeckers appears to be concentrated in older snags with some level of decay. Importantly, intensive foraging by woodpeckers in young snags may facilitate future cavity excavation by promoting wood decomposition through a combination of structural damage to the wood and the transfer of tree decaying fungi. The manner in which a snag is created seems to have an effect on the timing of cavity excavation in ponderosa pine. Snags decay to cavity-bearing structures fastest in burned areas, as soon as 2 to 3 years after the fire in some cases. Bark beetle killed trees provide nesting habitat as early as 5 years after death, while girdled trees can take as long as 6 to 8 years. Snag size is another predictor of cavity generation with larger snags more likely to eventually contain nest cavities. However, it is important to note, that a very small fraction of available snags actually contain cavities excavated by woodpeckers; suggesting the need for more consideration of mortality agent.

Snag attrition rates are highly variable and tend to depend not only on the mode of mortality, but also on local site conditions. In general however, the fastest recorded attrition was in instances of fire-killed trees, which fell as early as 4 years after the fire. These patterns may be directly related to the severity of fire damage on individual trees and the history of post-fire beetle use. Generally, snags that experience greater use by both bark and wood-beetles attract foraging woodpeckers, which serve to further degrade the wood integrity and can lead to faster decay rates than trees that don’t experience these same use patterns. However, there are instances where trees that experience extremely severe fire damage stand for extended periods of time and are not used by either beetles or woodpeckers. Trees killed by insects, independent of fire, stand slightly longer than those affected by both fire and insects simultaneously. Insect-killed snags begin to fall between 5 to 6 years after death. This can be problematic, as these snags may fall before they can provide nesting habitat. Snags created artificially by topping or girdling tend to stand longer than either fire or insect killed trees. This may be due to the relatively less use of these trees by beetles and woodpeckers, which can contribute to expedited decay of these structures (Farris and others 2004).

These temporal trends in woodpecker use and snag decomposition patters are paradoxical. Trees killed by bark beetles alone, or in association with fire serve as high quality foraging habitat and seem most likely to contain future nest cavities. However, these same structures are likely to fall more rapidly than snags originating from sources of mortality that don't attract beetles and foraging woodpeckers in similar intensities (e.g. artificial creation methods such as mechanical girdling or topping).

Classically, snag management has been driven by the objective to provide nesting habitat for snag-dependant species such as woodpeckers. Many of the strategies have centered on the notion that snags simply needed to be large enough and in adequate densities in order to be useful for most wildlife species. As illustrated through this review, recent information suggests that managing quantity while ignoring quality may not be sufficient. In particular the following 5 principles should be considered:

1. Snag recruitment and attrition is a dynamic process that is dependent on characteristics of individual sites.
2. Snags are an ephemeral resource on the landscape (e.g. half of all ponderosa snags may fall within 8 years of death).
3. Not all snags are useful to wildlife (a small fraction of standing snags are actually used by cavity-nesting wildlife).
4. The manner in which a tree dies affects its subsequent use by beetles and woodpeckers.
5. Foraging use by both beetles and woodpeckers appears to play a significant role in the decay dynamics, cavity excavation patterns, and standing life span of a snag. These interactions likely influence future use by subsequent snag-dependent wildlife species.

Consideration of these important sources of variability in snag ecology and woodpecker use may help improve snag management in ponderosa pine forests.

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