

# The Pileated Woodpecker as a Keystone Habitat Modifier in the Pacific Northwest<sup>1</sup>

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## Abstract

We propose that the pileated woodpecker (*Dryocopus pileatus*) is a keystone habitat modifier in the Pacific Northwest. It is the largest woodpecker in this region and the only species that forages primarily by excavating; only pileateds are capable of creating large cavities in hard snags and decadent live trees. A wide array of species, including many that are of management concern in the Pacific Northwest, use old pileated nest and roost cavities. In addition, pileateds provide foraging opportunities for other species, accelerate decay processes and nutrient cycling, and may facilitate inoculation by heart-rot fungi and mediate insect outbreaks. Because of the potential keystone role of pileated woodpeckers in Pacific Northwest forests, it may be appropriate to give special attention to their habitat needs in forest management plans and monitoring activities.

## Introduction

A keystone species is an organism that has a significant influence on the ecosystem it occupies that is disproportionately large compared to its abundance or biomass (Power and others 1996, Simberloff 1998). In other words, a keystone is a relatively uncommon species that is functionally linked to the persistence of an array of other species and plays a critical role in the organization and/or functioning of the ecosystem. The term “keystone species” was first introduced by Paine (1966, 1969) to describe a starfish that maintained the organization of a rocky intertidal community by selectively preying on a mussel that would otherwise have been competitively dominant and prevented numerous other species from coexisting. Not all species that exert strong influences on an ecosystem are considered keystones; for example, the primary tree species in a forested ecosystem would be considered an “ecological dominant” rather than a keystone species, because its effects are a function of its importance in the ecosystem (Power and others 1996). Keystones may or may not influence ecosystem structure and function through trophic interactions, as in Paine's original example involving starfish and mussels; five broad categories of keystone species were described by Mills and others (1993), including keystone predators, prey, mutualists, hosts, and habitat modifiers.

The usefulness of the keystone species concept in ecology and conservation has been questioned recently (Mills and others 1993), but others (deMaynadier and

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Hunter 1994, Power and others 1996, Simberloff 1998) have argued strongly for its continued usage, largely because of its potential application to management and the conservation of biodiversity. Power and others (1996) suggested that if keystone species can be identified in threatened ecosystems, critical areas should be set aside to maintain keystones, rather than focusing management efforts solely on endangered species or “hot spots” of biodiversity. There is also concern that the current focus of ecosystem management on ecological processes, rather than on individual species, could result in a loss of biodiversity without detectable changes in key processes (Simberloff 1998, Tracy and Brussard 1994).

Simberloff (1998) argued that the conservation approach most likely to unite the best features of single-species and ecosystem management is to focus management efforts on keystone species because it involves explicit consideration of the mechanisms that underlie ecosystem function and structure. Unlike indicator, umbrella, or flagship species, keystones are functionally linked to a suite of other species; thus, management for the persistence of keystone species benefits other species by maintaining key ecosystem functions or structures. Furthermore, by studying keystone species and their role in ecological processes, we can significantly improve our understanding of ecosystems, identify ways to maintain or replace various functions, and increase the efficiency and success of conservation efforts.

## The Pileated Woodpecker as a Keystone Habitat Modifier

Keystone habitat modifiers, also called “ecosystem engineers” (Lawton and Jones 1995), are species whose activities substantially alter the physical structure of the environment, influencing both available habitat for other species and various ecosystem processes (Mills and others 1993, Simberloff 1998). Examples include the beaver (*Castor canadensis*), because its dam-building and feeding activities create habitat for many other species and alter hydrological processes, channel geomorphology, biogeochemical pathways, and community productivity (Naiman and others 1986, Pollack and others 1995); the Brazilian termite (*Cornitermes cumulans*), because the large, abundant, and uniquely structured mounds it produces support a wide array of both obligate and opportunistic users (Redford 1984); and various species of burrowing animals, because their activities have a profound influence on available habitat for other species, and on microbial activity, soil fertility, the structure of plant communities, and sediment stability (Meadows and Meadows 1991).

We propose that the pileated woodpecker is a keystone habitat modifier in the Pacific Northwest, because the effects of its excavations on habitat for many other species and on various ecological processes are both large and unique. The importance of woodpecker cavities to a broad array of secondary cavity-using species (those that use cavities but do not create them) has long been recognized by ecologists and forest managers (Balda 1975, Conner 1978, Davis and others 1983, Neitro and others 1985, Thomas and others 1979), but the unique contribution of pileated woodpeckers to cavity creation and ecosystem function has received little attention (Machmer and Steeger 1995). To provide a focus for discussing management implications that may result from this designation, we have limited our evaluation of management prescriptions to those on USDA Forest Service lands administered under the Northwest Forest Plan (i.e., within the range of the northern

spotted owl [*Strix occidentalis caurina*] in western Washington and Oregon and northwestern California; Anonymous 1994a, Tuchmann and others 1996).

## **The Ecological Role of Pileated Woodpeckers in the Pacific Northwest**

### ***Nesting, Roosting, and Foraging Requirements***

The pileated woodpecker resides year-round in a variety of forested habitats. About the size of a crow, it is the largest woodpecker in the western United States, ranging from 40-49 cm in length and 250-350 g in body mass; males are 10-15 percent heavier than females (Bull and Jackson 1995). The pileated woodpecker is a primary cavity excavator and, because of its large size, selects correspondingly large (generally  $\geq 65$  cm d.b.h. in the Pacific Northwest) snags or live trees with heartwood decay for nesting and roosting. Pileateds generally occupy mid- to late-successional forests where such structures are abundant, but they also occur in younger forests with large remnant trees and snags. Their diet consists primarily of wood-dwelling ants and beetle larvae, but other insects, fruit, and nuts are eaten when available (Bull 1987). Pileated woodpeckers excavate new nest cavities each year and exhibit strong selection for nest trees on the basis of tree diameter and the structural quality of the wood. Trees containing relatively sound wood in the early stages of decay from heart-rot fungi are preferred, presumably because soft wood in advanced stages of decay cannot support the large nest cavities of pileated woodpeckers (Harris 1983). Before selecting a final nest site in the spring, pileated woodpeckers often excavate multiple cavity-starts (Bent 1939, Bull and Meslow 1988, Hoyt 1957, McClelland 1977). Cavity-starts we found in western Washington were in various stages of completion; several had dimensions similar to active nest cavities and others, though not as large, were deep enough to function as potential nesting or roosting habitat for some secondary users.<sup>3</sup> Pileateds roost individually at night or during inclement weather in hollow trees to reduce the incidence of predation and conserve heat; roost chambers are large and generally have multiple openings to provide escape routes from predators (Bull and Jackson 1995).

### ***Creating Habitat for Secondary Cavity Users***

Pileated woodpeckers provide nesting and roosting habitat for secondary cavity users through three processes: excavation of nest cavities and cavity-starts, excavation of openings into roost cavities, and foraging excavations. Over 20 species of secondary cavity users occurring in the Pacific Northwest have been documented nesting or roosting in old cavities or openings excavated by pileated woodpeckers (*table 1*). The common merganser, silver-haired bat, fisher, and American marten were included as species of concern in the Final Supplemental Environmental Impact Statement for management of late-successional forests within the range of the northern spotted owl (Anonymous 1994b); the bufflehead, flammulated owl, and Vaux's swift are on priority or sensitive species lists in Washington and Oregon (Anonymous 1995, Marshall 1992); and the northern flying squirrel is a primary prey of the northern spotted owl (Forsman and others 1984).

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<sup>3</sup> Unpublished data on file, Pacific Northwest Research Station, Olympia, Wash.

The Pileated Woodpecker as a Keystone Species—Aubry and Raley

**Table 1**—Bird and mammal species known to use cavities, entrance holes, or foraging holes excavated by pileated woodpeckers in coniferous forests of the western U.S. and Canada. All species listed occur within the management area of the Northwest Forest Plan (Anonymous 1994a).

Species	Location
Wood duck ( <i>Aix sponsa</i> )	Western Montana, western Washington <sup>1,2</sup>
Common goldeneye ( <i>Bucephala clangula</i> )	Western Montana, Alberta <sup>1,3</sup>
Bufflehead ( <i>Bucephala albeola</i> )	Western Montana, Alberta <sup>1,3</sup>
Hooded merganser ( <i>Lophodytes cucullatus</i> )	Western Montana <sup>1</sup>
Common merganser ( <i>Mergus merganser</i> )	Western Montana <sup>1</sup>
American kestrel ( <i>Falco sparverius</i> )	Western Montana <sup>1</sup>
Flammulated owl ( <i>Otus flammeolus</i> )	Northeastern Oregon <sup>4</sup>
Western screech-owl ( <i>Otus kennicottii</i> )	Western Montana <sup>1</sup>
Northern pygmy-owl ( <i>Glaucidium gnoma</i> )	Western Montana <sup>1</sup>
Boreal owl ( <i>Aegolius funereus</i> )	Western Montana, central Idaho <sup>1,5</sup>
Northern saw-whet owl ( <i>Aegolius acadicus</i> )	Western Montana, western Oregon, western Washington <sup>1,6,7</sup>
Vaux's swift ( <i>Chaetura vauxi</i> )	Northeastern Oregon, western Washington <sup>7,8</sup>
Hairy woodpecker ( <i>Picoides villosus</i> )	Western Montana <sup>1</sup>
Northern flicker ( <i>Colaptes auratus</i> )	Western Montana, eastern Oregon, western Washington <sup>1,9,7</sup>
Brown creeper ( <i>Certhia americana</i> )	Western Montana <sup>1</sup>
Silver-haired bat ( <i>Lasionycteris noctivagans</i> )	Northeastern Oregon <sup>10</sup>
Big brown bat ( <i>Eptesicus fuscus</i> )	South-central British Columbia <sup>10</sup>
Douglas' squirrel ( <i>Tamiasciurus douglasii</i> )	Western Washington <sup>7</sup>
Red squirrel ( <i>Tamiasciurus hudsonicus</i> )	Western Montana, northeastern Oregon <sup>1,8</sup>
Northern flying squirrel ( <i>Glaucomys sabrinus</i> )	Western Montana, northeastern Oregon, western Washington <sup>1,8,7</sup>
Bushy-tailed woodrat ( <i>Neotoma cinerea</i> )	Northeastern Oregon <sup>8</sup>
Ringtail ( <i>Bassariscus astutus</i> )	West-central Oregon <sup>11</sup>
American marten ( <i>Martes americana</i> )	Western Montana, northeastern Oregon <sup>1,9</sup>
Fisher ( <i>Martes pennanti</i> )	Southwestern Oregon <sup>12</sup>

<sup>1</sup> McClelland 1979, <sup>2</sup> Bortorff 1999, <sup>3</sup> Bonar 1997, <sup>4</sup> Bull and others 1990, <sup>5</sup> Hayward and others 1993, <sup>6</sup> Mellen 1999, <sup>7</sup> Unpublished data, <sup>8</sup> Bull and others 1992, <sup>9</sup> Bull and others 1997, <sup>10</sup> Betts 1999, <sup>11</sup> Farrell 1999, <sup>12</sup> Aubry and others 1997.

Several characteristics of pileated woodpeckers and the cavities they excavate are unique among woodpeckers in the Pacific Northwest. Both the entrance hole and nest cavity of pileated woodpeckers are larger than those of other woodpeckers (table 2); thus, pileated excavations may provide the majority of suitable tree cavities for larger mammals and birds. For example, in southwestern Oregon, female fishers typically used old pileated woodpecker cavities for natal den sites (Aubry and others 1997); based on our field observations and video taken at den sites, fishers would be unable to enter tree cavities with smaller openings. In northeastern Oregon, flammulated owls preferred pileated woodpecker cavities over flicker cavities for nest sites, possibly due to the larger cavity size and higher placement of the cavity in the tree bole (Bull and others 1990). In central Idaho, 18 of 23 boreal owl nests found were in pileated woodpecker cavities (Hayward and others 1993). Because boreal owls need large cavities and appear to prefer relatively high nest sites, Hayward and others (1993) recommended that management for boreal owl nesting habitat include management provisions for pileated woodpeckers. Eastern gray squirrels (*Sciurus carolinensis*) and raccoons (*Procyon lotor*) were observed using red-cockaded woodpecker (*Picoides borealis*) nests after the entrance and cavity were enlarged by pileated woodpeckers (Dennis 1971), and in British Columbia, buffleheads nested in cavities that had greater volume and larger entrance holes than those used by smaller secondary cavity-nesting species (Peterson and Gauthier 1985). In addition, some species may lay bigger clutches in cavities that have a larger floor area (Rendell and Robertson 1989).

**Table 2**—Average dimensions of nest cavities for 12 woodpecker species occurring within the management area of the Northwest Forest Plan (Anonymous 1994a). Data are compiled from Terres (1980) except where noted.

	Entrance hole size (cm)	Cavity depth (cm)	Cavity width (cm)
Species with broad distributions within the management area of the Northwest Forest Plan:			
Pileated woodpecker <sup>1</sup>	9.0 x 12.0	57	21
Northern flicker <sup>2</sup>	6.3 x 7.0	30	15
Hairy woodpecker	3.8 - 5.0	25 - 38	?
Red-breasted sapsucker ( <i>Sphyrapicus ruber</i> )	3.1 - 3.8	35	?
Downy woodpecker ( <i>Picoides pubescens</i> )	3.1	20 - 30	?
Species with limited distributions within the management area of the Northwest Forest Plan:			
Lewis' woodpecker ( <i>Melanerpes lewis</i> ) <sup>3</sup>	5.0 - 7.6	23 - 76	13 - 20
Black-backed woodpecker ( <i>Picoides arcticus</i> )	3.8 - 5.0	25	?
White-headed woodpecker ( <i>Picoides albolarvatus</i> ) <sup>4</sup>	3.8 - 5.0	20 - 38	9 - 13
Acorn woodpecker ( <i>Melanerpes formicivorus</i> ) <sup>5</sup>	4.0	22 - 70	15
Species whose distribution is primarily east of the Cascade crest:			
Three-toed woodpecker ( <i>Picoides tridactylus</i> )	3.8 - 5.0	25	?
Williamson's sapsucker ( <i>Sphyrapicus thyroideus</i> ) <sup>6</sup>	4.2	20 - 27	9 - 13
Red-naped sapsucker ( <i>Sphyrapicus nuchalis</i> )	3.1	20	10

<sup>1</sup> Bull 1987, <sup>2</sup> Erskine and McLaren 1972, <sup>3</sup> Tobalske 1997, <sup>4</sup> Garrett and others 1996, <sup>5</sup> Koenig and others 1995, <sup>6</sup> Dobbs and others 1997.

In the Pacific Northwest, pileated woodpeckers typically locate nest cavities high in the bole of both snags and live trees (Aubry and Raley 1995, Bull 1987, Madsen 1985, McClelland 1979, Mellen 1987). Several studies have suggested that nest cavities located high off the ground may reduce the incidence of nest predation. Observed predation by raccoons on yellow-bellied sapsucker (*Sphyrapicus varius*) nests was attributed to the cavities being too shallow or too close to the ground (Kilham 1971), and higher cavities increased the reproductive success of tree swallows (*Tachycineta bicolor*) by reducing the probability of predation (Rendell and Robertson 1989).

Pileated woodpeckers are strong excavators capable of creating nest cavities in sound wood of both snags and live trees (Bull 1987, Christy 1939, Harris 1983). The sill width (an indicator of cavity wall thickness) of nest cavities in northeastern Oregon averaged 6 cm (Bull 1987), and two cavities we measured in western Washington had sill widths of 5.7 and 6.9 cm.<sup>3</sup> The sills of yellow-bellied sapsucker and northern flicker cavities in central British Columbia averaged 5.1 and 1.9 cm, respectively (Erskine and McLaren 1972), suggesting that pileated woodpecker cavities may have thicker walls than those of other woodpeckers. Thicker cavity walls decrease the rate of thermal conduction, which increases heat retention within the cavity (Betts 1998, Desch and Dinwoodie 1996, McComb and Noble 1981). In addition, cavities surrounded by a thick shell of sound sapwood provide better protection from predators, such as raccoons and black bears (*Ursus americanus*) that climb trees and break open nest cavities (Conner 1977, Conner and others 1976, Daily 1993, Erskine and McLaren 1972, Kilham 1971). These characteristics also increase the structural integrity of the cavity and reduce the likelihood that the tree will break at the cavity (Bull 1987, Harris 1983). Thus, nest cavities and cavity-starts excavated by pileated woodpeckers may provide more protection from potential predators, have greater longevity, and provide habitat for secondary users over a longer period of time than those excavated by other woodpeckers.

Hollow chambers in snags and live trees, which are created by the process of heartwood decay, are important to a wide array of bird and mammal species for nesting, roosting, denning, and resting (Bull and others 1997). Openings excavated into hollow trees by pileated woodpeckers for roosting enable secondary cavity users to access tree hollows they would otherwise be excluded from (i.e., the tree does not have a broken top or other natural openings that provide access to the hollow interior). In northeastern Oregon, radio-tagged pileated woodpeckers used an average of seven roost trees within a 3-10 month period (Bull and others 1992). In western Washington, pileateds also used an average of seven roost trees during an 8-month period, and one individual used 29 different roost trees during the 3 years we radio-tracked it.<sup>3</sup> However, because birds were not tracked daily in either study, the actual number of roost trees used by pileated woodpeckers each year is probably much higher. For each individual to have an adequate number of roost sites within its territory, it would need to excavate openings into several new roost sites each year. Thus, tree cavities that are used as nesting, roosting, and resting sites by other species are being created or made available by pileated woodpeckers throughout the year.

Lastly, the foraging excavations of pileated woodpeckers may also create important microhabitats for other species. Pileateds excavate deep into heartwood to reach carpenter ants (*Camponotus* spp.). These excavations may create openings into the decaying bole of snags and live trees that provide access to hollow chambers that are used by other species for nesting or roosting. For example, in south-central

British Columbia, a maternal colony of big brown bats was located in the hollow interior of a ponderosa pine (*Pinus ponderosa*) snag that they accessed through an opening created by a foraging pileated woodpecker (Betts 1999). Furthermore, foraging excavations that do not access hollow chambers can still be deep enough to provide roosting habitat for smaller cavity-users, such as the hairy woodpecker and brown creeper (McClelland 1979).

### ***Providing Foraging Opportunities for Other Species***

The pileated woodpecker is the only species that excavates extensively into sapwood and heartwood for invertebrate prey. Other Pacific Northwest woodpeckers are relatively weak excavators that typically locate prey by scaling bark, pecking substrates without penetrating the subcambial layers, surface gleaning, ground foraging, or hawking (Bull and others 1986; Conner 1979, 1981). Thus, pileated foraging excavations enable other species to prey on invertebrates that would otherwise be unavailable to them. Downy and hairy woodpeckers have been documented following foraging pileateds and gleaning or pecking in freshly excavated areas as soon as the pileateds leave (Bull and Jackson 1995, Christy 1939, Maxson and Maxson 1981).<sup>3</sup> Commensal foraging has also been observed between pileated and red-bellied woodpeckers (*Melanerpes carolinus*), northern flickers, and Williamson's sapsuckers (Bull and Jackson 1995).

### ***Accelerating Decomposition and Nutrient Cycling***

Pileated woodpeckers directly and indirectly accelerate wood decomposition and, ultimately, nutrient cycling by physically breaking apart sound and decayed wood as they excavate nest and roost cavities and forage for invertebrate prey and by exposing wood in live trees, snags, and logs to insect attack and fungal infection. Although pileated woodpeckers will obtain food by other methods, they are primarily excavators (Bull and Holthausen 1993, Bull and Jackson 1995, Conner 1979). A single foraging excavation can be large, often measuring 10-20 cm wide, >30 cm long, and extending deep into the heartwood (Christy 1939). One bird observed for 2 hours excavated two holes 15-cm deep with openings 15 x 15 cm and 15 x 25 cm in size (Christy 1939). In coastal forests of western Washington and Oregon, pileated woodpeckers forage mainly on standing dead and live trees, and only occasionally on downed logs (Aubry and Raley 1992, Mellen 1999); this differs from observations made by Bull (1987) in northeastern Oregon, where logs comprised a major proportion (36 percent) of foraging substrates used by pileateds. Thus, pileateds may have a greater impact on the decomposition of standing wood in coastal regions of the Pacific Northwest than in interior areas.

### ***Facilitating Inoculation by Heart-rot Fungi***

When woodpeckers excavate in dead wood, they expose new sites to insect attacks and fungal infection; additionally, it has been suggested that woodpeckers may facilitate the inoculation of live, healthy trees by heart-rot fungi (Otvos 1979, Parks 1999). Wood softened by heart-rot is essential for nest-cavity excavation by most woodpeckers (Conner and others 1976, Daily 1993, Kilham 1971), and heartwood decay in live, standing trees is the process by which hollow chambers in both trees and logs are formed (Bull and others 1997). Airborne spores of heart-rot fungi invade living trees through wounds that expose the heartwood to infection (Bull

and others 1997). Pileated woodpeckers are capable of creating cavities in live trees with no decay (Bent 1939, Harris 1983). Almost half of the cavity-starts we located in western Washington were in live trees, and most were deep enough to have penetrated the heartwood (Aubry and Raley 1992). Thus, it is possible that pileateds create wounds in healthy trees that become infection courts for heart-rot fungi.

### ***Mediating Insect Outbreaks***

The importance of woodpeckers in the control of insect populations, especially beetles, has long been recognized (Otvos 1979). Woodpeckers are adapted to forage on a variety of substrates and can access insect prey in the crevices of rough bark that are unavailable to other avian predators (Jackson 1979a). In addition, because most woodpeckers are non-migratory, they are the primary avian insectivores during the winter months (Jackson 1979b); predation on overwintering arthropods is believed to reduce the potential of population increases during the following year (Jackson 1979b, Kroll and Fleet 1979).

When woodpeckers scale bark or excavate into wood for insects, there are both direct and indirect effects on prey populations. Woodpeckers affect insect mortality rates through direct consumption. Indirect effects include altering insect microhabitats, increasing parasite densities, and exposing remaining prey to consumption by both vertebrate and invertebrate predators (Machmer and Steeger 1995, Otvos 1979). Woodpecker foraging physically alters tree and log surfaces by reducing bark thickness or removing bark and sapwood, potentially exposing remaining insects (particularly broods) to extreme temperatures and desiccation. These changes in microclimatic conditions can be significant mortality factors for beetles and other arthropods (McCambridge and Knight 1972, Otvos 1979). Woodpecker foraging activity changes bark color, which may also influence its thermal properties and suitability as arthropod habitat (Jackson 1979b). Scaling, by reducing bark thickness, exposes remaining insect broods to parasites with short ovipositors (Machmer and Steeger 1995, Otvos 1979). For example, in the central Sierra Nevada in California, parasites were observed swarming over sites that had recently been scaled by woodpeckers and ovipositing through the thinned bark layers (Otvos 1970).

Whether pileated woodpeckers have a greater impact on insect populations than other woodpeckers has not been investigated, but they are clearly the best-adapted species for digging larvae and pupae out of bark, sapwood, and heartwood, regardless of the stage of wood decay. Carpenter ants generally comprise >50 percent of pileated woodpecker diets (Beckwith and Bull 1985, Jackman 1975), but during outbreaks, beetles may comprise a higher percentage of the diet (Bull 1987, Kroll and Fleet 1979). In Texas, pileated, hairy, and downy woodpeckers significantly reduced numbers of overwintering pupae and brood adults of the southern pine beetle (*Dendroctonus frontalis*) (Kroll and Fleet 1979). We commonly found larval Coleoptera in pileated woodpecker scats in western Washington (Aubry and Raley 1996), and in Montana, pileateds commonly foraged on both carpenter ants and wood-boring beetles (McClelland 1979).



## Implications for Management Under the Northwest Forest Plan

Regulations pursuant to the National Forest Management Act of 1976 require that each National Forest identify “management indicator species” (MISs) to focus management attention on a species, species group, or habitat element to improve resource production, population recovery, maintenance of population viability, or ecosystem diversity (Anonymous 1984). Prior to the implementation of the Northwest Forest Plan (NWFP) in 1994 (Anonymous 1994a), the pileated woodpecker was an MIS for mature and old-growth forest conditions on all National Forests currently managed under the NWFP. Each Forest was required to establish a series of pileated woodpecker habitat areas that included both tracts of mature and old-growth forest and minimum densities of large snags (Anonymous 1986). To evaluate the effectiveness of these habitat areas, monitoring of occupancy and population trends was also required (Anonymous 1982).

The Northwest Forest Plan represents an ecosystem management strategy designed to provide for long-term ecological integrity throughout the range of the northern spotted owl, and includes specific provisions for late-successional reserves in both upland and riparian areas, as well as the retention of snags for cavity-nesting birds in lands open to timber harvesting (matrix lands). With the implementation of the NWFP in 1994, pileated woodpecker habitat areas were no longer maintained on most National Forests within the range of the northern spotted owl because it was believed that standards and guidelines (S&Gs) in the NWFP were adequate to maintain viable populations of pileated woodpeckers on federal lands.<sup>3</sup> Standards and guidelines in the NWFP for green-tree, snag, and log retention in timber harvest units on matrix lands in Forest Service ownership are summarized in *table 3*. Monitoring is a key component of management strategies in the NWFP and includes three types: implementation monitoring to determine if S&Gs are being followed, effectiveness monitoring to determine if they are achieving desired results, and validation monitoring to determine if underlying assumptions are sound (Anonymous 1994a).

Because of the potential keystone role of the pileated woodpecker in the Pacific Northwest, it may be appropriate to give special attention to their habitat needs in forest management plans and monitoring activities. Standards and guidelines for green-tree retention in the NWFP were strongly influenced by the Species Analysis Team’s recommendation to emphasize clumped green-tree and snag retention in harvest units (Anonymous 1994b). Because of safety concerns associated with retaining large, hard snags or decadent live trees in harvested areas (Hope and McComb 1994, Styskel 1983), the Team believed that retaining green trees in relatively large patches would provide the best opportunities for preserving such structures in harvest units (K. Aubry, personal observation). However, there are few data to indicate that pileated woodpeckers will use large snags in harvest units, regardless of their context. Several studies in western Washington and Oregon have documented nesting by smaller woodpeckers in both natural and artificially created snags in clearcuts (Chambers and others 1997, Mannan and others 1980, Morrison and Meslow 1983, Schreiber and deCalesta 1992, Zarnowitz and Manuwal 1985), but nesting by pileateds in remnant snags or decaying live trees in clearcuts has not been reported.

**Table 3**—Key Forest Service standards and guidelines for retention of green trees, snags, and logs during timber harvest on matrix lands in the Northwest Forest Plan (Anonymous 1994a).

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**Emphasize green-tree and snag retention in matrix management**

- Retain at least 15 pct of the harvested area as green trees.
- Retain 70 pct of those green trees in aggregates 0.2-1.0 ha in size. Retain the remainder as dispersed structures, either as individual trees or aggregates <0.2 ha in size.
- To the extent possible, aggregates and dispersed retention should include the largest, oldest live trees, decadent or leaning trees, and hard snags occurring in the unit. Patches should be retained indefinitely.
- As a minimum, snags are to be retained within the harvest unit at levels sufficient to support species of cavity-nesting birds at 40 pct of potential population levels based on published guidelines and models.
- To the extent possible, snag management within harvest units should occur within the areas of green-tree retention.

**Provide specified amounts of coarse woody debris in matrix management**

- In western Washington and Oregon north of and including the Willamette National Forest, leave 240 linear feet of logs per acre  $\geq 20$  inches in diameter. Logs <20 feet in length cannot be credited toward this total. In western Oregon south of the Willamette National Forest, leave 120 linear feet of logs per acre  $\geq 16$  inches in diameter and 16 feet long.
  - Decay class 1 and 2 logs can be counted towards these totals. Down logs should reflect the species mix of the original stand.
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We do not know if pileateds will nest or roost in suitable snags or decadent live trees located within 0.2-1.0-ha retention patches, but available data are not encouraging. We could find only one study on the use of remnant patches in regeneration harvests by pileateds. Gyug and Bennett (1995) conducted surveys for nesting pileated woodpeckers in coniferous forests of southeastern British Columbia on three 160-ha study plots including a clearcut, a clearcut with remnant patches about 1 ha in size, and an intact forest; experimental treatments were applied 25-30 yr prior to the study. Five pileateds were detected in the unharvested control, but none was found in either the clearcut or patch-retention treatment. Thus, regardless of the number of snags specified in management models, it is uncertain whether harvested areas will provide nesting or roosting habitat for pileated woodpeckers prior to the reestablishment of late-successional forest conditions.

Implementation monitoring has involved field visits to 109 randomly selected harvest sites since 1996 (Alverts and others 1997, 1998, 1999). Although data presented in these reports indicate a high level of compliance with S&Gs overall ( $\geq 95$  percent), compliance with green-tree and snag retention S&Gs was generally lower. Snag and green-tree retention S&Gs were a source of considerable confusion for project personnel during all 3 years of monitoring, due to differing interpretations of the S&Gs, lack of consensus on definitions, lack of data on snag levels needed to support species of cavity-nesting birds at 40 percent of potential population levels, and the difficulty of maintaining “legacy” trees when operators are commonly confronted with safety concerns and operational constraints.

Clarifying S&Gs for green-tree and snag retention and providing additional guidance on their implementation would ensure that timber harvest administrators share a common understanding of their intent relative to ecosystem management and

possess reliable strategies for implementing them on the ground. Although compliance with most relevant S&Gs is documented thoroughly in implementation monitoring reports, many of the details that will influence both the short- and long-term habitat quality of harvest units for pileated woodpeckers are not. For example, no data are collected on the number of large snags or decadent live trees that were preserved in the unit, how many were in aggregated vs. dispersed green-tree retention areas, or how many snags were created from living trees to meet minimum snag requirements. The inclusion of such information in implementation monitoring activities would greatly improve our ability to evaluate the habitat quality of harvested areas for pileated woodpeckers and other species associated with late-successional forest conditions (*table 1*).

Effectiveness monitoring under the NWFP is currently focused on late-successional and old-growth forests, aquatic and riparian ecosystems, northern spotted owls, and marbled murrelets (*Brachyramphus marmoratus*); monitoring strategies for other late-successional species are still being developed (Mulder and others 1999). Because of the large number of potential species in the latter category, Noon (1999) recommended that a “focal species” approach be used, and suggested that the keystone species concept may be useful for selecting ecological indicators for the Northwest Forest Plan. Because of its potential role as a keystone species in the Pacific Northwest and its strong association with large snags and decadent live trees, the pileated woodpecker may be a particularly appropriate ecological indicator for effectiveness monitoring of species associated with late-successional forest conditions. Other issues to address in effectiveness monitoring might include the prevalence of new pileated woodpecker nest cavities in clearcuts and retention patches, the relative abundance of pileated woodpecker cavities and foraging excavations in different forest types and moisture regimes, and occupancy levels and population trends in managed vs. unmanaged landscapes.

Several studies have recently been initiated to test or re-evaluate some of the assumptions in the NWFP (Aubry and others 1999, Marcot and others 2002), but we are not aware of any new or planned field studies of pileated woodpeckers within the management area of the NWFP. When validation monitoring strategies for the NWFP are formalized, it may be appropriate to include empirical evaluations of S&Gs for green-tree and snag retention relative to the habitat needs of pileated woodpeckers and of the model used to develop habitat management prescriptions for pileated woodpeckers in westside forests (Neitro and others 1985, p. 141-145). Lastly, habitat management strategies for woodpeckers in the Pacific Northwest are based on the assumption that viable populations can be maintained in managed landscapes by providing nesting snags at 40 percent of potential population levels (Thomas and others 1979, p. 72), yet this assumption has never been evaluated empirically.

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## References

- Alverts, Bob; Horton, Al; Mehrhoff, Loyal; Stone, Brian. 1998. **Results of the FY 1997 implementation monitoring program.** Portland, OR: Regional Implementation Monitoring Team, Regional Ecosystem Office; 62 p.
- Alverts, Bob; Horton, Al; Stone, Brian. 1997. **Results of the FY 1996 (pilot year) implementation monitoring program.** Portland, OR: Regional Implementation Monitoring Team, Regional Ecosystem Office; 46 p.
- Alverts, Bob; Hsin, Liang; Horton, Al; Shon, Fay; Mehrhoff, Loyal; Stone, Brian. 1999. **Results of the FY 1998 implementation monitoring program.** Portland, OR: Regional Implementation Monitoring Team, Regional Ecosystem Office; 25 p.
- Anonymous. 1982. **National Forest System land and resource management planning.** Federal Register 47(190): 43026-43052.
- Anonymous. 1984. **Wildlife, fish, and sensitive plant habitat management.** Title 2600, Amendment No. 48. Washington, DC: Forest Service, U.S. Department of Agriculture.
- Anonymous. 1986. **A report on minimum management requirements for forest planning on the National Forests of the Pacific Northwest Region, USDA Forest Service.** Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture; 12 p.
- Anonymous. 1994a. **Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl.** Portland, OR: Forest Service, U.S. Department of Agriculture, and Bureau of Land Management, U.S. Department of Interior.
- Anonymous. 1994b. **Appendix J2: results of additional species analysis. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth related species within the range of the northern spotted owl.** Portland, OR: Forest Service, U.S. Department of Agriculture, and Bureau of Land Management, U.S. Department of Interior.
- Anonymous. 1995. **Priority habitats and species list: habitat program.** Olympia, WA: Washington Department of Fish and Wildlife; 24 p.
- Aubry, Keith B.; Amaranthus, Michael P.; Halpern, Charles B.; White, James D.; Woodard, Brenda L.; Peterson, Charles E.; Lagoudakis, Cynthia A.; Horton, Alan J. 1999. **Experimental design of the DEMO study: evaluating the ecological and social effects of different levels and patterns of green-tree retention in harvest units.** Northwest Science 73(Special Issue): 12-26.
- Aubry, Keith B.; Raley, Catherine M. 1992. **Landscape-level responses of pileated woodpeckers to forest management and fragmentation: a pilot study.** Progress Report: 1990 and 1991. Olympia, WA: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 73 p.
- Aubry, Keith B.; Raley, Catherine M. 1995. **Ecology of pileated woodpeckers in managed landscapes on the Olympic Peninsula.** Annual Report FY 1995. Olympia, WA: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 61-64.
- Aubry, Keith B.; Raley, Catherine M. 1996. **Ecology of pileated woodpeckers in managed landscapes on the Olympic Peninsula.** Annual Report FY 1996. Olympia, WA: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 70-74.
- Aubry, Keith B.; Raley, Catherine M.; Catton, T. J.; Tomb, Gregory W.; Wahl, Fred E. 1997. **Ecological characteristics of fishers in southwestern Oregon.** Annual Report FY 1997. Olympia, WA: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 72-77.

- Balda, Russell P. 1975. **The relationship of secondary cavity nesters to snag densities in western coniferous forests.** Technical Bulletin 1. Albuquerque, NM: Southwestern Region, Forest Service, U.S. Department of Agriculture; 37 p.
- Beckwith, Roy C.; Bull, Evelyn L. 1985. **Scat analysis of the arthropod component of pileated woodpecker diet.** The Murrelet 66(3): 90-92.
- Bent, Arthur Cleveland. 1939. **Life histories of North American woodpeckers.** Bulletin No. 174. New York, NY: Dover Publications, Inc.; 334 p.
- Betts, Burr J. 1998. **Roosts used by maternity colonies of silver-haired bats in northeastern Oregon.** Journal of Mammalogy 79(2): 643-650.
- Betts, Burr J. [Letter to Keith B. Aubry]. 1999 November 5. Located at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia, WA.
- Bonar, Rick [Letter to CAVNET internet discussion group]. 1997. Located at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia, WA.
- Bottorff, James, Biologist, Washington State Department of Natural Resources, Olympia, WA. [Conversation with Catherine M. Raley]. 30 March 1999.
- Bull, Evelyn L. 1987. **Ecology of the pileated woodpecker in northeastern Oregon.** Journal of Wildlife Management 51(2): 472-481.
- Bull, Evelyn L.; Holthausen, Richard S. 1993. **Habitat use and management of pileated woodpeckers in northeastern Oregon.** Journal of Wildlife Management 57(2): 335-345.
- Bull, Evelyn L.; Holthausen, Richard S.; Henjum, Mark G. 1992. **Roost trees used by pileated woodpeckers in northeastern Oregon.** Journal of Wildlife Management 56(4): 786-793.
- Bull, Evelyn L.; Jackson, Jerome A. 1995. **Pileated woodpecker (*Dryocopus pileatus*).** In: Poole, Alan; Gill, Frank B., editors. The birds of North America, No. 148. Philadelphia, PA: The Academy of Natural Sciences; 24 p.
- Bull, Evelyn L.; Meslow, E. Charles. 1988. **Breeding biology of the pileated woodpecker: management implications.** Res. Note PNW-RN-474. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 8 p.
- Bull, Evelyn L.; Parks, Catherine G.; Torgersen, Torolf R. 1997. **Trees and logs important to wildlife in the Interior Columbia River Basin.** Gen. Tech. Rep. PNW-GTR-391. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 55 p.
- Bull, Evelyn L.; Peterson, Steven R.; Thomas, Jack Ward. 1986. **Resource partitioning among woodpeckers in northeastern Oregon.** Res. Note PNW-444. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 19 p.
- Bull, Evelyn L.; Wright, Anthony L.; Henjum, Mark G. 1990. **Nesting habitat of flammulated owls in Oregon.** Journal of Raptor Research 24(3): 52-55.
- Chambers, Carol L.; Carrigan, Tara; Sabin, Thomas E.; Tappeiner, John; McComb, William C. 1997. **Use of artificially created Douglas-fir snags by cavity-nesting birds.** Western Journal of Applied Forestry 12(3): 93-97.
- Christy, Bayard Henderson. 1939. **Northern pileated woodpecker.** In: Bent, Arthur Cleveland. Life histories of North American woodpeckers. New York, NY: Dover Publications, Inc.; 171-189.

- Conner, Richard N. 1977. **The effect of tree hardness on woodpecker nest entrance orientation.** *Auk* 94(2): 369-370.
- Conner, Richard N. 1978. **Snag management for cavity nesting birds.** In: Workshop proceedings: management of southern forests for nongame birds. Gen. Tech. Rep. SE-14. Asheville, NC: Southeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; 120-128.
- Conner, Richard N. 1979. **Seasonal changes in woodpecker foraging methods: strategies for winter survival.** In: Dickson, James G.; Conner, Richard N.; Fleet, Robert R.; Kroll, James C.; Jackson, Jerome A., editors. The role of insectivorous birds in forest ecosystems: proceedings of the symposium; 1978 July 13-14; Nacogdoches, TX. New York: Academic Press; 95-105.
- Conner, Richard N. 1981. **Seasonal changes in woodpecker foraging patterns.** *Auk* 98(3): 562-570.
- Conner, Richard N.; Miller, Orson K., Jr.; Adkisson, Curtis S. 1976. **Woodpecker dependence on trees infected by fungal heart rots.** *Wilson Bulletin* 88(4): 575-581.
- Daily, Gretchen C. 1993. **Heartwood decay and vertical distribution of red-naped sapsucker nest cavities.** *Wilson Bulletin* 105(4): 674-679.
- Davis, Jerry W.; Goodwin, Gregory A.; Ockenfels, Richard A., technical editors. 1983. **Snag habitat management: proceedings of the symposium.** Gen. Tech. Rep. RM-99. Ft. Collins, CO: Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 226 p.
- deMaynadier, Phillip; Hunter, Malcolm L. 1994. **Keystone support.** *BioScience* 44(1): 2.
- Dennis, John V. 1971. **Species using red-cockaded woodpecker holes in northeastern South Carolina.** *Bird-banding* 42(2): 79-87.
- Desch, H. E.; Dinwoodie, J. M. 1996. **Timber: structure, properties, conversion and use.** 7th ed. Binghamton, NY: Haworth Press; 306 p.
- Dobbs, R.C.; Martin, T. E.; Conway, C. J. 1997. **Williamson's sapsucker (*Sphyrapicus thyroideus*).** In: Poole, Alan; Gill, Frank B., editors. The birds of North America, No. 285. Philadelphia, PA: The Academy of Natural Sciences; 20 p.
- Erskine, A. J.; McLaren, W. D. 1972. **Sapsucker nest holes and their use by other species.** *Canadian Field-Naturalist* 86(4): 357-361.
- Farrell, Terry, Biologist, Oregon Department of Fish and Wildlife, Roseburg, OR. [Telephone conversation with Keith B. Aubry]. 19 October 1999.
- Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. 1984. **Distribution and biology of the spotted owl in Oregon.** *Wildlife Monographs* 87: 1-64.
- Garrett, Kimball L.; Raphael, Martin G.; Dixon, Rita D. 1996. **White-headed woodpecker (*Picoides albolarvatus*).** In: Poole, Alan; Gill, Frank B., editors. The birds of North America, No. 252. Philadelphia, PA: The Academy of Natural Sciences; 24 p.
- Gyug, Les W.; Bennett, Stephen P. 1995. **Bird use of wildlife tree patches 25 years after clearcutting.** In: Bradford, Peter; Manning, Todd; l'Anson, Bill, editors. Wildlife tree/stand-level biodiversity workshop proceedings; 1995 October 17-18; Victoria, BC. Victoria, BC: British Columbia Ministry of Forests and BC Environment; 15-33.
- Harris, Roger D. 1983. **Decay characteristics of pileated woodpecker nest trees.** In: Davis, Jerry W.; Goodwin, Gregory A.; Ockenfels, Richard A., technical coordinators. Snag habitat management: proceedings of the symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 120-128.

- Hayward, Gregory D.; Hayward, Patricia H.; Garton, Edward O. 1993. **Ecology of boreal owls in the northern Rocky Mountains, U.S.A.** Wildlife Monographs 124: 1-55.
- Hope, Sharon; McComb, William C. 1994. **Perceptions of implementing and monitoring wildlife tree prescriptions on National Forests in western Washington and Oregon.** Wildlife Society Bulletin 22(3): 383-392.
- Hoyt, Sally F. 1957. **The ecology of the pileated woodpecker.** Ecology 38(2): 246-256.
- Jackman, Siri Marion. 1975. **Woodpeckers of the Pacific Northwest: their characteristics and their role in the forests.** Corvallis: Oregon State University; 147 p. M.S. thesis.
- Jackson, Jerome A. 1979a. **Insectivorous birds and North American forest ecosystems.** In: Dickson, James G.; Conner, Richard N.; Fleet, Robert R.; Kroll, James C.; Jackson, Jerome A., editors. The role of insectivorous birds in forest ecosystems: proceedings of the symposium; 1978 July 13-14; Nacogdoches, TX. New York; Academic Press; 1-7.
- Jackson, Jerome A. 1979b. **Tree surfaces as foraging substrates for insectivorous birds.** In: Dickson, James G.; Conner, Richard N.; Fleet, Robert R.; Kroll, James C.; Jackson, Jerome A., editors. The role of insectivorous birds in forest ecosystems: proceedings of the symposium; 1978 July 13-14; Nacogdoches, TX. New York; Academic Press; 69-93.
- Kilham, Lawrence. 1971. **Reproductive behavior of yellow-bellied sapsuckers I. Preference for nesting in *Fomes*-infected aspens and nest hole interrelations with flying squirrels, raccoons, and other animals.** Wilson Bulletin 83(2): 159-171.
- Koenig, Walter D.; Stacey, Peter B.; Stanback, Mark T.; Mumme, Ronald L. 1995. **Acorn woodpecker (*Melanerpes formicivorus*).** In: Poole, Alan; Gill, Frank B., editors. The birds of North America, No. 194. Philadelphia, PA: The Academy of Natural Sciences; 24 p.
- Kroll, James C.; Fleet, Robert R. 1979. **Impact of woodpecker predation on over-wintering within-tree populations of the southern pine beetle (*Dendroctonus frontalis*).** In: Dickson, James G.; Conner, Richard N.; Fleet, Robert R.; Kroll, James C.; Jackson, Jerome A., editors. The role of insectivorous birds in forest ecosystems: proceedings of the symposium; 1978 July 13-14; Nacogdoches, TX. New York; Academic Press; 269-281.
- Lawton, John H.; Jones, Clive G. 1995. **Linking species and ecosystems: organisms as ecosystem engineers.** In: Jones, Clive G.; Lawton, John H., editors. Linking species and ecosystems. New York, NY: Chapman & Hall; 141-150.
- Machmer, Marlene M.; Steeger, Christoph. 1995. **The ecological roles of wildlife tree users in forest ecosystems.** Land Management Handbook 35. Victoria, BC: BC Ministry of Forests; 54 p.
- Madsen, Sarah J. 1985. **Habitat use by cavity-nesting birds in the Okanogan National Forest, Washington.** Seattle; University of Washington; 113 p. M.S. thesis.
- Mannan, R. William; Meslow, E. Charles; Wight, Howard M. 1980. **Use of snags by birds in Douglas-fir forests, western Oregon.** Journal of Wildlife Management 44(4): 787-797.
- Marcot, Bruce G.; Mellen, Kim; Livingston, Susan A.; Ogden, Cay. 2002. **DecAID: wildlife component.** In: Laudenslayer, William F., Jr.; Shea, Patrick J.; Valentine, Bradley E.; Weatherspoon, C. Phillip; Lisle, Thomas E., technical coordinators. Proceedings of the symposium on the ecology and management of dead wood in western forests. 1999 November 2-4; Reno, NV. Gen. Tech. Rep. PSW-GTR-181. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; [this volume].
- Marshall, David B. 1992. **Threatened and sensitive wildlife of Oregon's forests and woodlands.** Portland, OR: Audubon Society of Portland; 66 p.

- Maxson, Stephen J.; Maxson, George-Ann D. 1981. **Commensal foraging between hairy and pileated woodpeckers.** *Journal of Field Ornithology* 52(1): 62-63.
- McCambridge, William F.; Knight, Fred B. 1972. **Factors affecting spruce beetles during a small outbreak.** *Ecology* 53(5): 830-839.
- McClelland, B. Riley. 1977. **Relationships between hole-nesting birds, forest snags, and decay in western larch-Douglas-fir forests of the northern Rocky Mountains.** Missoula: University of Montana; 495 p. Ph.D. dissertation.
- McClelland, B. Riley. 1979. **The pileated woodpecker in forests of the northern Rocky Mountains.** In: Dickson, James G.; Conner, Richard N.; Fleet, Robert R.; Kroll, James C.; Jackson, Jerome A., editors. *The role of insectivorous birds in forest ecosystems: proceedings of the symposium; 1978 July 13-14; Nacogdoches, TX.* New York: Academic Press; 283-299.
- McComb, William C.; Noble, Robert E. 1981. **Microclimates of nest boxes and natural cavities in bottomland hardwoods.** *Journal of Wildlife Management* 45(1): 284-289.
- Meadows, Peter S.; Meadows, Azra, editors. 1991. **The environmental impact of burrowing animals and animal burrows.** Oxford, UK: The Zoological Society of London; 349 p.
- Mellen, Teresa Kim. 1987. **Home range and habitat use of pileated woodpeckers, western Oregon.** Corvallis: Oregon State University; 96 p. M.S. thesis.
- Mellen, Teresa Kim, Wildlife and Forest Program Ecologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Mt. Hood National Forest, Sandy, OR. [Telephone conversation with Catherine M. Raley]. 20 October 1999.
- Mills, L. Scott; Soulé, Michael E.; Doak, Daniel F. 1993. **The keystone-species concept in ecology and conservation.** *BioScience* 43(4): 219-224.
- Morrison, Michael L.; Meslow, E. Charles. 1983. **Avifauna associated with early growth vegetation on clearcuts in the Oregon Coast Ranges.** Res. Paper PNW-305. Portland, OR: Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 12 p.
- Mulder, Barry S.; Noon, Barry R.; Spies, Thomas A.; Raphael, Martin G.; Palmer, Craig J.; Olsen, Anthony R.; Reeves, Gordon H.; Welsh, Hartwell H., technical coordinators. 1999. **The strategy and design of the effectiveness monitoring program for the Northwest Forest Plan.** Gen. Tech. Rep. PNW-GTR-437. Portland, OR: Pacific Northwest Research Station, Forest Service; U.S. Department of Agriculture; 138 p.
- Naiman, Robert J.; Melillo, Jerry M.; Hobbie, John E. 1986. **Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*).** *Ecology* 67(3): 1254-1269.
- Neitro, William A.; Mannan, R. William; Taylor, Douglas; Binkley, Virgil W.; Marcot, Bruce G.; Wagner, Frank F.; Cline, Steven P. 1985. **Snags (wildlife trees).** In: Brown, E. Reade, technical editor. *Management of wildlife and fish habitats in forests of western Oregon and Washington: part 1.* Publ. R6-F&WL-192. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture; 129-169.
- Noon, Barry R. 1999. **Scientific framework for effectiveness monitoring of the Northwest Forest Plan.** In: Mulder, Barry S.; Noon, Barry R.; Spies, Thomas A.; Raphael, Martin G.; Palmer, Craig J.; Olsen, Anthony R.; Reeves, Gordon H.; Welsh, Hartwell H., technical coordinators. *The strategy and design of the effectiveness monitoring program for the Northwest Forest Plan.* Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 49-68.
- Otvos, I. S. 1970. **Avian predation of the western pine beetle.** In: Stark, R. W.; Dahlsten, Donald L., editors. *Studies on the population dynamics of the western pine beetle,*



*Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae). Berkeley, CA: University of California, Division of Agricultural Science; 119-127.

- Otvos, Imre S. 1979. **The effects of insectivorous bird activities in forest ecosystems: an evaluation.** In: Dickson, James G.; Conner, Richard N.; Fleet, Robert R.; Kroll, James C.; Jackson, Jerome A., editors. The role of insectivorous birds in forest ecosystems: proceedings of the symposium; 1978 July 13-14; Nacogdoches, TX. New York; Academic Press; 341-374.
- Paine, Robert T. 1966. **Food web complexity and species diversity.** American Naturalist 100: 65-75.
- Paine, Robert T. 1969. **A note on trophic complexity and community stability.** American Naturalist 103: 91-93.
- Parks, Catherine G., Research Plant Pathologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, La Grande, OR. [Telephone conversation with Catherine M. Raley]. 20 October 1999.
- Peterson, Barbara; Gauthier, Gilles. 1985. **Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia.** Wilson Bulletin 97(3): 319-331.
- Pollock, Michael M.; Naiman, Robert J.; Erickson, Heather E.; Johnston, Carol A.; Pastor, John; Pinay, Gilles. 1995. **Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins.** In: Jones, Clive G.; Lawton, John H., editors. Linking species and ecosystems. New York, NY: Chapman & Hall; 117-126.
- Power, Mary E.; Tilman, David; Estes, James A.; Menge, Bruce A.; Bond, William J.; Mills, L. Scott; Daily, Gretchen; Castilla, Juan Carlos; Lubchenco, Jane; Paine, Robert T. 1996. **Challenges in the quest for keystones.** BioScience 46(8): 609-620.
- Redford, Kent H. 1984. **The termitaria of *Cornitermes cumulans* (Isoptera, Termitidae) and their role in determining a potential keystone species.** Biotropica 16(2): 112-119.
- Rendell, Wallace B.; Robertson, Raleigh J. 1989. **Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities.** Condor 91(4): 875-885.
- Schreiber, B.; deCalesta, D. S. 1992. **The relationship between cavity-nesting birds and snags on clearcuts in western Oregon.** Forest Ecology and Management 50: 299-316.
- Simberloff, Daniel. 1998. **Flagships, umbrellas, and keystones: is single-species management passe in the landscape era?** Biological Conservation 83(3): 247-257.
- Styskel, Edward W. 1983. **Problems in snag management implementation—a case study.** In: Davis, Jerry W.; Goodwin, Gregory A.; Ockenfels, Richard A., technical coordinators. Snag habitat management: proceedings of the symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 24-27.
- Terres, John K. 1980. **The Audubon Society encyclopedia of North American birds.** New York, NY: Alfred A. Knopf; 1109 p.
- Thomas, Jack Ward; Anderson, Ralph G.; Maser, Chris; Bull, Evelyn L. 1979. **Snags.** In: Thomas, Jack Ward, technical editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: Forest Service, U.S. Department of Agriculture; 60-77.
- Tobalske, Bret W. 1997. **Lewis' woodpecker (*Melanerpes lewis*).** In: Poole, Alan; Gill, Frank B., editors. The birds of North America, No. 284. Philadelphia, PA: The Academy of Natural Sciences; 28 p.
- Tracy, C. Richard; Brussard, Peter F. 1994. **Preserving biodiversity: species in landscapes.** Ecological Applications 4(2): 205-207.

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- Tuchmann, E. Thomas; Connaughton, Kent P.; Freedman, Lisa E.; Moriwaki, Clarence B. 1996. **The Northwest Forest Plan: a report to the President and Congress.** Portland, OR: USDA Office of Forestry and Economic Assistance; 253 p.
- Zarnowitz, Jill W.; Manuwal, David A. 1985. **The effects of forest management on cavity-nesting birds in northwestern Washington.** *Journal of Wildlife Management* 49(1): 255-263.