

How Dead Trees Sustain Live Organisms in Western Forests¹

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Abstract

Dead wood contributes to biological richness as substrate, cavity sites, foraging sites, and shelter or cover. In the Pacific Northwest, 69 vertebrate species commonly use cavities, 47 species respond positively to down wood, and prevalence of both uses is related to natural fire regimes. Almost 80 percent of nests of weak excavators are in dead trees; strong excavators make greater use of live trees. Most bat roosts are in dead trees, whereas carnivores use mostly declining, living trees. Selection of both cavity and foraging sites is governed by decay patterns. Some species prefer large pieces of down wood. Management implications are discussed.

Introduction

Dying trees, snags, and down wood are common in unmanaged forests and required by many species, including fungi, cryptogams, invertebrates, and vertebrates (Berg and others 1994, Harmon and others 1986). We focus on vertebrates, and note contributions to non-vertebrates only briefly. We also focus on the Pacific Northwest, which we define as Alaska, Alberta, British Columbia, Washington, Oregon, Idaho, Montana, and northern Nevada and California. References to other regions are included to indicate trends where forestry has been practiced longer, or where particular species are well documented.

As concern for sustaining all organisms has grown, interest in natural disturbance regimes as models for guiding forest practices has also increased (Attiwill 1994, Hunter 1993). We first examine relations among natural fire regimes and vertebrates that use dead wood. We then review the diverse uses forest-dwelling organisms make of dead wood under four broad categories: substrate, cavity sites, foraging sites, and shelter or cover (down wood). We finish by noting management implications.

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Natural Disturbance Regimes and Use of Dead Wood

Fire is the major natural agent of disturbance in Pacific Northwest forests, and natural fire regimes differ among forest types, influencing the amounts of dead wood present (Agee 1993). We examined relationships of the forest-dwelling vertebrate fauna with natural fire regimes in the 12 forested biogeoclimatic zones of British Columbia, applying the approach of Bunnell (1995) to more recent data. We expected predictable differences. The proportion of species positively associated with down wood should increase as the fire-return interval increased and down wood accumulated. Cavity users should be negatively correlated with fire size, because size and intensity often are related, and fewer snags remain standing where fires are more intense.

The proportion of down wood users in the fauna increased with increasing fire-return interval, and proportions of bird and mammal cavity users decreased with increasing fire size (*table 1*). Species using down wood are mainly mammals (*appendix A*), and both numbers of species and proportions of mammalian users of down wood increased with increasing fire size. That is expected if larger, more intense fires create a more reliable supply of down wood. The number of species using cavity sites decreased significantly as fire return interval lengthened, and snags were created less frequently (*table 1*). Fire regimes vary with the precipitation regime, but associations between the vertebrate fauna and precipitation regimes were not found. The lack of relations with total precipitation suggests that fire regime had more influence on composition of the vertebrate fauna than precipitation itself (the two wettest types were also higher elevation and obscured any relationship between amphibian richness and precipitation).

Forest-dwelling vertebrate faunas appear to respond to amounts and duration of down wood as these are influenced by the natural disturbance regime, suggesting a mechanism for the differences in richness of dead wood users across broad forest types.

Table 1—Significant Spearman's rank coefficients among vertebrates using dead wood and mean annual precipitation, and characteristics of natural fire regimes in the 12 forested biogeoclimatic zones of British Columbia.¹

	Cavity users						Downed wood users			
	All		Birds		Mammals		All		Mammals	
	N ²	Pr ²	N	Pr	N	Pr	N	Pr	N	Pr
Precipitation								0.59*		
Fire Size		- 0.85**		- 0.75**		- 0.70*			0.66*	0.68*
Fire Return	- 0.58*		- 0.79**					0.83**		

¹ * = P < 0.05; ** = P < 0.01

² N = Number of species; Pr = Proportion of species in the native vertebrate fauna.

Dying and Dead Wood as Substrate

Dead wood makes its greatest contribution to biological richness as substrate for fungi, cryptogams, and invertebrates. There are no sharp distinctions between declining trees and snags as the most favored habitat. Some pendent lichens are common on both, but appear more abundant on snags (e.g., *Usnea longissima*, Berg and others 1994; *Letharia vulpina*, Bernes 1994). Berg and others (1994) reviewed

habitat requirements of 1,487 threatened forest-dwelling organisms in Sweden. Dying trees were favored habitat for 89 species of fungi and cryptogams and 252 species of invertebrates. Snags provided substrate for 21 percent of all threatened non-vertebrate species, including 36 macrofungi and cryptogam species and 266 invertebrates. Logs hosted more species. Berg and others (1994) estimated that about 30 percent of threatened cryptogams and macrofungi and 28 percent of the invertebrates were dependent on down wood.

The role of dead wood as substrate is less well known in the Pacific Northwest, but likely is similar to the role in Sweden. Of 636 lichen species reported from British Columbia 46 are largely restricted to old-growth stands (Goward 1999; Goward and others 1994). Goward and Arsenault (1997) reported a snag-specific community of lichens from Englemann spruce (*Picea engelmanni*; scientific names for most species are found in *appendix A*) and subalpine fir (*Abies lasiocarpa*) forests. At least 25 lichen species are found on decaying wood (data in Goward 1999, and Goward and others 1994). Of 93 forest-dwelling bryophytes reviewed by Vitt and others (1988) for the Pacific Northwest, 30 species (32 percent) preferentially grow on down wood that frequently is well rotted. Well-rotted logs also serve as foci for dispersal of mycorrhizal fungi critical to tree productivity (Maser and others 1978). Some “saprophytic” vascular plants (e.g., *Allotropa*, *Hemitomes*) rely upon mycorrhizal fungi that often are found in down wood for delivery of nutrients (Leake 1994). In British Columbia, 526 species of macrofungi are dependent on down wood, including some harvested commercially (Lofroth 1998). Because some vertebrates forage on fungi and insects in down wood, reductions of these food sources may appear higher in the food chain.

Features of logs considered to influence non-vertebrates include tree species, decay state, size, and distribution. Conifer logs are more durable than hardwood logs. Natural successions of cryptogams, fungi, and invertebrates on and in down wood (e.g., McCullough 1948, Söderström 1988) indicate the importance of a range of decay states. Larger logs provide better substrate than smaller logs for bryophytes and lichens, because larger logs last longer, have more surface area, and have higher, steeper sides that discourage ground-dwelling species from invading (Samuelsson and others 1994). Forest-floor bryophytes generally have very limited dispersal ability (Khanna 1964, Söderström 1987), and dispersal is from log to log for epixylic species. For these reasons, Samuelsson and others (1994) argued that logs should be close together, but not gathered into piles. Similarly, several small logs may provide more habitat than a single large log.

Dead wood is a critical substrate for hundreds of non-vertebrate species in the Pacific Northwest. Large, dispersed pieces of a range of decay states are preferred. Sustaining a range of decay requires sustained recruitment of down wood.

Dead Wood as Cavity Sites

Cavity sites are easily studied and hence well-documented. Foraging on snags is a year round activity, is less frequently studied, and less well known. Lack of cavity nesting sites has limited abundance of some birds in intensively managed forests (Angelstam and Mikusinski 1994, Newton 1994).

Because of the importance of heart rot for cavity sites, most nests of primary cavity nesters were in dead trees (*table 2*). Of 2,674 nesting records of weak

excavators, 2,154 (78 percent) were in dead trees (*table 2*). Although conifers are less prone to decay than most hardwoods, the proportion of dead trees used as nest sites by weak excavators did not change with the proportion of conifers used. Most strong excavators located < 50 percent of their nests in dead trees (*table 2*), but the proportion of nests in dead trees increased significantly with the proportion of conifers used (Bunnell and others 2002). That relationship explains apparently anomalous values in *table 2*. For example, in the largest sample for pileated woodpecker in *table 2* (Bull 1987; n = 105 nests) all available nest trees were conifers, and 99 percent of the nests were in dead trees. Conversely, another sample was gathered⁴ where hardwoods were available but scarce (< 10 percent of stems), but six of seven nest trees were living trembling aspen (*Populus tremuloides*). Dead trees were the main source of cavity sites for 16 of the 21 primary excavators (*table 2*). For most of the remaining species, dead trees were more commonly used as cavity sites when nests were in conifers. Weaker excavators largely restricted to conifers (e.g., Lewis's woodpecker, white-headed woodpecker) may be particularly threatened in managed, conifer forests, because trees do not become old enough for heart rots to develop. Both Lewis's and white-headed woodpeckers are designated 'at risk' in the Pacific Northwest (*appendix A*).

Table 2—Percentages of nests located in dead trees by strong and weak excavators of the Pacific Northwest.

	Pct dead	n ¹	Sources
Strong Excavators			
Yellow-bellied sapsucker	41.4	63	Scott and others 1980; BC Nest Records.
Red-naped sapsucker	24.0	557	Campbell and others 1990; Li and Martin 1991; C. Steeger ² ; W. Klenner and D. Huggard ³ ; K. Martin ⁴
Red-breasted sapsucker	55.3	132	Raphael and White 1984; Campbell and others 1990; Li and Martin 1991.
Williamson's sapsucker	59.3	303	Bull 1980; Scott and others 1980; Raphael and White 1984; Li and Martin 1991; Conway and Martin 1993; BC Nest Records.
Hairy woodpecker	62.4	190	Kelleher 1963; Bull 1980; Scott and others 1980; Raphael and White 1984; Campbell and others 1990; Li and Martin 1991; W. Klenner and D. Huggard ³ ; K. Martin ⁴ ; C. Steeger ²
Three-toed woodpecker	42.9	161	Scott and others 1980; Klenner and Huggard 1997; C. Steeger ² ; K. Martin ⁴ ; BC Nest Records.
Black-backed woodpecker	46.7	56	Bull 1980; Raphael and White 1984; C. Steeger (unpublished) ² ; BC Nest Records.
Acorn woodpecker	7.8	238	Scott and others 1980; Li and Martin 1991; Hooge and others 1999.
Pileated woodpecker	73.2	202	Bull 1987; Mellen 1987; Campbell and others 1990; C. Steeger ² ; W. Klenner and D. Huggard ³ ; K. Martin ⁴ ; K. Aubry and C. Raley ⁵

⁴ Unpublished data on file, British Columbia Ministry of Forests, Kamloops, British Columbia.

(table 2 continued)

	Pct dead	n ¹	Sources
Weak Excavators			
Lewis's woodpecker	62.4	367	Raphael and White 1984; BC Nest Records
Downy woodpecker	60.4	109	Scott and others 1980; Campbell and others 1990; Li and Martin 1991; C. Steeger ² ; K. Martin ⁴
White-headed woodpecker	97.4	123	Raphael and White 1984; Milne and Hejl 1989; Dixon 1995a; Dixon 1995b.
Northern flicker	55.9	717	Bull 1980; Scott and others 1980; Raphael and White 1984; Campbell and others 1990; Li and Martin 1991; W. Klenner and D. Huggard ³ ; K. Martin ⁴ ; C. Steeger ²
Nuttall's woodpecker	94.0	48	Miller and Bock 1972 (review within).
Black-capped chickadee	59.3	17	C. Steeger ² ; K. Martin ⁴
Mountain chickadee	65.8	433	Scott and others 1980; Raphael and White 1984; W. Klenner and D. Huggard ³ ; K. Martin ⁴ ; BC Nest Records.
Boreal chickadee	87.3	31	Peck and James 1987; Campbell and others 1997.
Chestnut-backed chickadee	58.0	132	C. Steeger ² ; BC Nest Records.
Red-breasted nuthatch	71.9	394	Raphael and White 1984; W. Klenner and D. Huggard ³ ; K. Martin ⁴ ; C. Steeger ² ; BC Nest Records.
White-breasted nuthatch	74.2	62	McEllin 1979; Scott and others 1980; Raphael and White 1984; Li and Martin 1991; Campbell and others 1997.
Pygmy nuthatch	78.0	331	McEllin 1979; Scott and others 1980; Raphael and White 1984; Li and Martin 1991; BC Nest Records.

¹Number of nest trees.

²Unpublished data on file, Pandion Ecological Research, Ltd., Nelson, BC, Canada.

³Unpublished data on file, BC Ministry of Forests, Kamloops Region, BC, Canada.

⁴Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

⁵Unpublished data for K. Aubry and C. Raley, sight unseen from Bull and Jackson (1995).

Figure 1 illustrates preferences by woodpeckers for trees in different stages of decay. Decay classes in figure 1 are those of Thomas and others (1979), and classes 1 and 2 represent healthy and declining, but living, trees. We used the electivity index of Ivlev (1961) to compare within studies, because it is largely symmetrical, ranging from -1.0 at complete avoidance to about +1.0 when all nests are in a particular category. Living conifers were not selected by either woodpeckers or cavity-using mammals (primarily red and flying squirrels). Living trembling aspen trees were used more in proportion to their availability, except by mammals that cannot excavate their own cavities. The most strongly preferred decay classes were recently dead trees (decay classes 3 and 4). Decay classes 4 and 5 of lodgepole pine (*Pinus contorta*) were strongly avoided because they were long dead, understory trees, too small to support cavities.

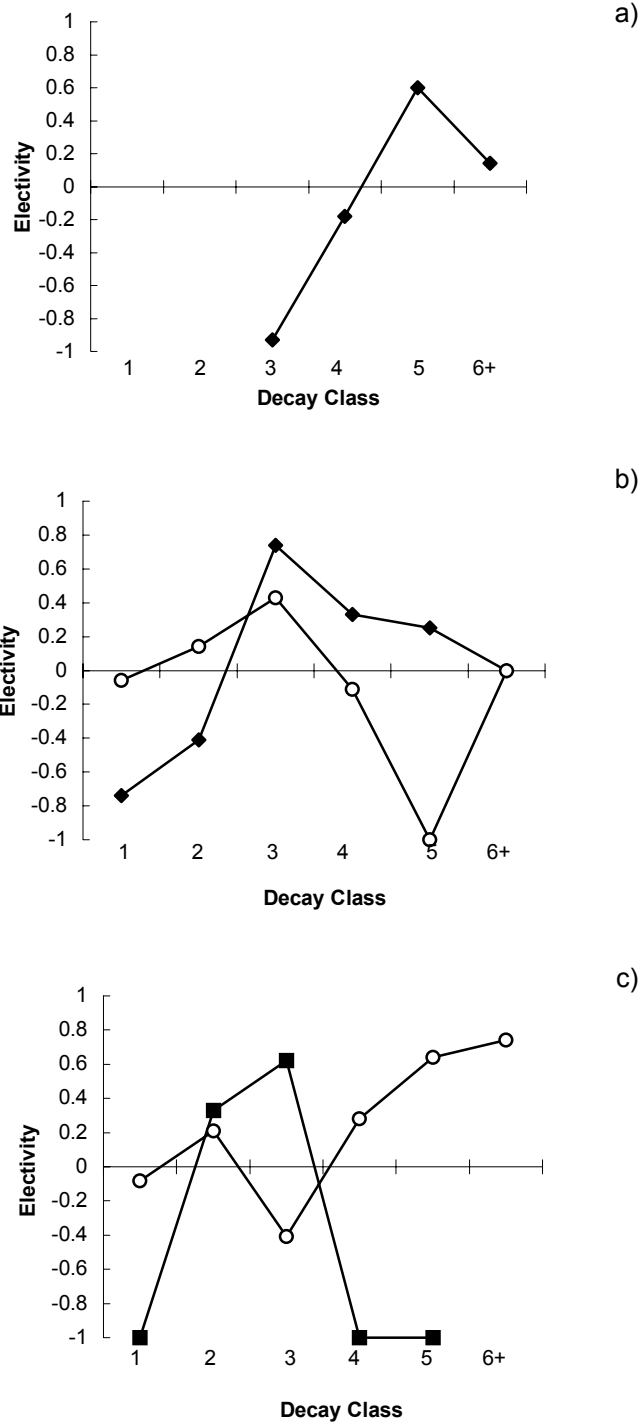


Figure 1—Apparent preference among decay classes shown by: a) woodpeckers nesting in conifers (data of Bevis 1996); b) woodpeckers nesting in Douglas-fir [◆] and trembling aspen trees [○] (data of Klenner and Huggard 1998); c) mammals in lodgepole Pine [■] and trembling aspen trees [○] (data of K. Martin unpublished). Preference evaluated by the electivity index of Ivlev (1961).

There are more secondary than primary cavity nesters (*appendix A*), but often 80 percent or more of their nest sites are created by primary nesters (Dobkin and others 1995, Li and Martin 1991, Schreiber and deCalesta 1992). Other nest sites are in cavities created by rot. For both forms of nest sites, dead trees are the major source of nesting opportunities. Several bat species also locate 70 to 100 percent of their roosts in dead trees (*table 3*). Less than 50 percent of denning trees of flying squirrels, American marten, and black bears were dead, indicating the importance of sustaining older trees with large rot pockets. Most black bear dens recorded from coastal forests of the Pacific Northwest were associated with wooden structures, including trees, logs, and stumps. Den sites in southern, inland forests also were commonly in trees (Bull and others 1996, Lindsay 1999). Mean sizes of den trees for mammals usually exceeded 50 centimeter (references of *table 3*). Amphibians and reptiles make occasional use of cavity sites (McComb and Noble 1981). Bunnell and Dupuis (1995) reported that snags used by amphibians were recently dead with sloughing bark.

Table 3—Percentage of denning and roosting sites located in snags and dead trees by mammals of the Pacific Northwest. Logs and stumps not included.

Species	Pct dead	n ¹	Sources
Bats			
Big brown bat	45.8	57	Rasheed and Holroyd 1995; Betts 1996; Vonhof 1996; Kalcounis and Brigham 1998; Rabe and others 1998.
California myotis	100.0	25	Vonhof 1996; Brigham and others 1997; Grindal 1997.
Fringed myotis	100.0	15	Rabe and others 1998.
Little brown myotis	63.2	23	Crampton and Barclay 1995; Rasheed and Holroyd 1995; Kalcounis and Hecker 1996; Grindal 1997.
Long-legged myotis	90.2	54	Rasheed and Holroyd 1995; Ormsbee and McComb 1998; Rabe and others 1998.
Northern long-eared myotis	42.9	7	Caceres 1997.
Pallid bat	100.0	3	Rabe and others 1998.
Silver-haired bat	72.0	50	Crampton and Barclay 1995; Rasheed and Holroyd 1995; Betts 1996; Campbell and others 1996; Vonhof 1996.
Southwestern myotis	0.0	2	Rabe and others 1998.
Western long-eared myotis	89.5	47	Caceres 1997; Grindal 1997; Vonhof and Barclay 1997; Rabe and others 1998.
Rodents			
Flying squirrel	32.1	627	Mowrey and Zasada 1984; Carey and others 1997.
Carnivores			
Black bear	32.1	249	Lindzey and Meslow 1976; Noble and others 1990; Immell and Boulay 1994; Akenson 1994; Bull and others 1996; Davis 1996; Lindsay 1999.
American marten	40.3	470	Spencer 1987; Martin and Barratt 1991; Jones and others 1997; Raphael and Jones 1997; Ruggiero and others 1998.

¹Number of denning or roosting sites.

Dying and Dead Trees as Foraging Sites

Long-term management of snag-using species requires provision of both foraging and cavity sites. Several studies suggest that cavity sites are less often limiting to cavity nesters than foraging habitat (Hutto 1995, Walankiewicz 1991, Welsh and Capen 1992). Given the relative lack of data for foraging sites, a key question is: are the kinds of trees that should be retained for foraging similar to those that provide nesting sites?

Among larger excavators, sapsuckers feed primarily on sap and insects associated with their sapwells. Northern flickers feed on ants on the ground (Bull and others 1986). Several woodpeckers feed primarily by flaking bark or probing after insect larvae in the cambium or sapwood. Pileated woodpeckers specialize on carpenter ants excavated from decayed sap- or heartwood (Bull and others 1986). For the latter two feeding techniques, decay state may reflect the likelihood of hosting preferred insects and the ease of excavating. It is less clear that size of tree should influence feeding preference, although duration of decay states and size of tree often are correlated. If decay state indicates foraging opportunities, we expect patterns specific to individual tree species, because species decay differently.

Figure 2 shows that conifers were avoided as feeding sites until they attained decay class 3 (recently dead). Their attractiveness as foraging sites then increased with further decay (see also Gyug and Bennett 1996), although that pattern differs among cavity-nesting species (Morrison and others 1987). In Englemann spruce-subalpine fir forests, three-toed woodpeckers strongly preferred recently dead snags (Klenner and Huggard 1997). Pileated woodpeckers use more decayed wood, provided it hosts carpenter ants (Bull and others 1992). Among conifers, Douglas-fir (*Pseudotsuga menziesii*) is a possible exception (*fig. 2*), and appears to become less attractive to woodpeckers once all bark is shed (decay class 6+). That may reflect Douglas-fir tending to rot from the outside in, so the sapwood becomes less favorable to breeding insects. On Bevis' (1996) study area, Douglas-fir was not sought as a foraging site (electivity = -0.04), and selection was shown only for western larch (*Larix occidentalis*) (electivity = 0.25). Douglas-fir snags also were not selected on Madsen's (1985) study site (electivity = -0.21), whereas western larch and ponderosa pine (*Pinus ponderosa*) were selected (electivity = +0.15 and +0.20, respectively).

Selection of trembling aspen followed a different pattern than for conifers. Foraging woodpeckers were indiscriminate in their use of decay classes 1 through 3 (apparently healthy to recently dead trees), but tended to avoid trees of decay class 4 or greater (*fig. 2*). Woodpeckers tend to use more of the smaller diameter trees when foraging than when nesting, especially when foraging on hardwoods (*fig. 3*).

We draw two broad points from comparisons of nesting and foraging sites. First, when foraging on conifers, woodpeckers select dead wood. The wood need not be standing, and several species forage on down wood when it is not snow covered (Bull and others 1997). Second, woodpeckers will use smaller trees when foraging than when nesting. Birds select similar decay states when foraging or nesting (compare *figs. 1, 2*), but smaller snags are used when foraging (*fig. 3*). The tendency for nesting trees to be larger than foraging trees makes biological sense: a cavity site must be large enough to contain an adult bird and its young; a foraging site need only be large enough to contain wood-boring larvae or ants. The trend is consistent across studies (e.g., Bevis 1996, Gyug and Bennett 1996). Small snags do not remain standing for

as long as large snags (Morrison and Raphael 1993), and may never be used as nest trees. Nonetheless, they do serve as foraging sites.

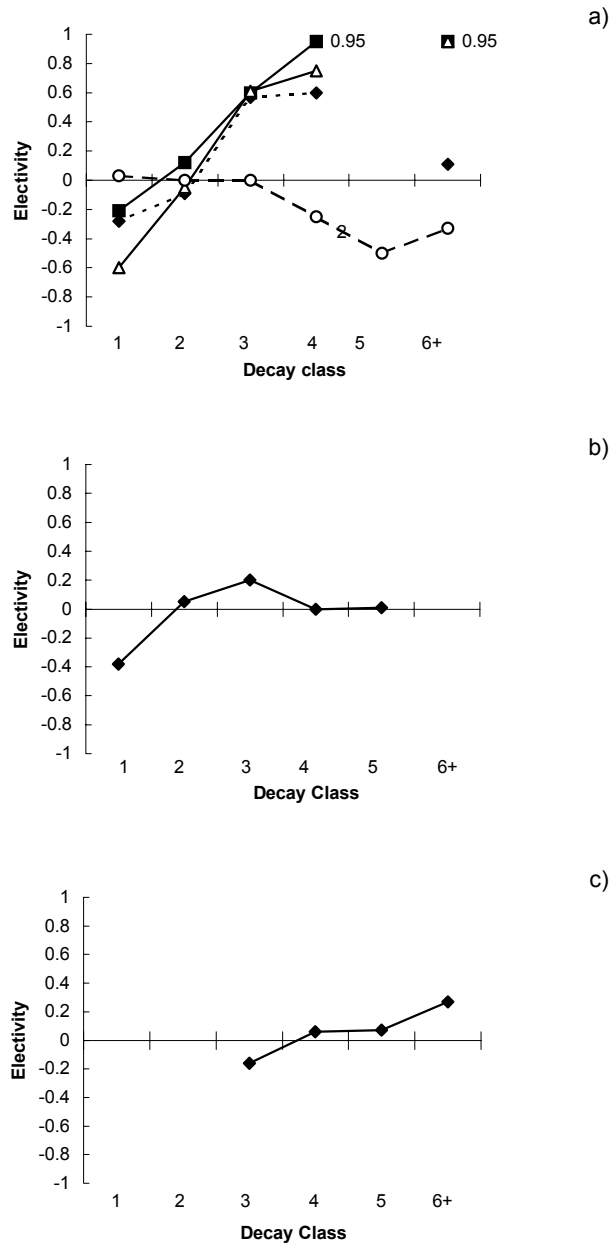


Figure 2—Apparent preference among decay classes shown by foraging cavity nesters. a) Woodpeckers foraging on Douglas-fir [—◆—], lodgepole pine [—■—], spruce [—△—], and trembling aspen trees [—○—] (from data of Klenner and Huggard 1998). b) Cavity nesting birds foraging on conifers (from data of Madsen 1985). c) Woodpeckers foraging on conifers (from data of Bevis 1996). Values of 0.95 represent instances where specific decay or size classes were sufficiently uncommon that they did not appear in the random sample of availability. Preference evaluated by the electivity index of Ivlev (1961). Decay classes of Thomas and others (1979).

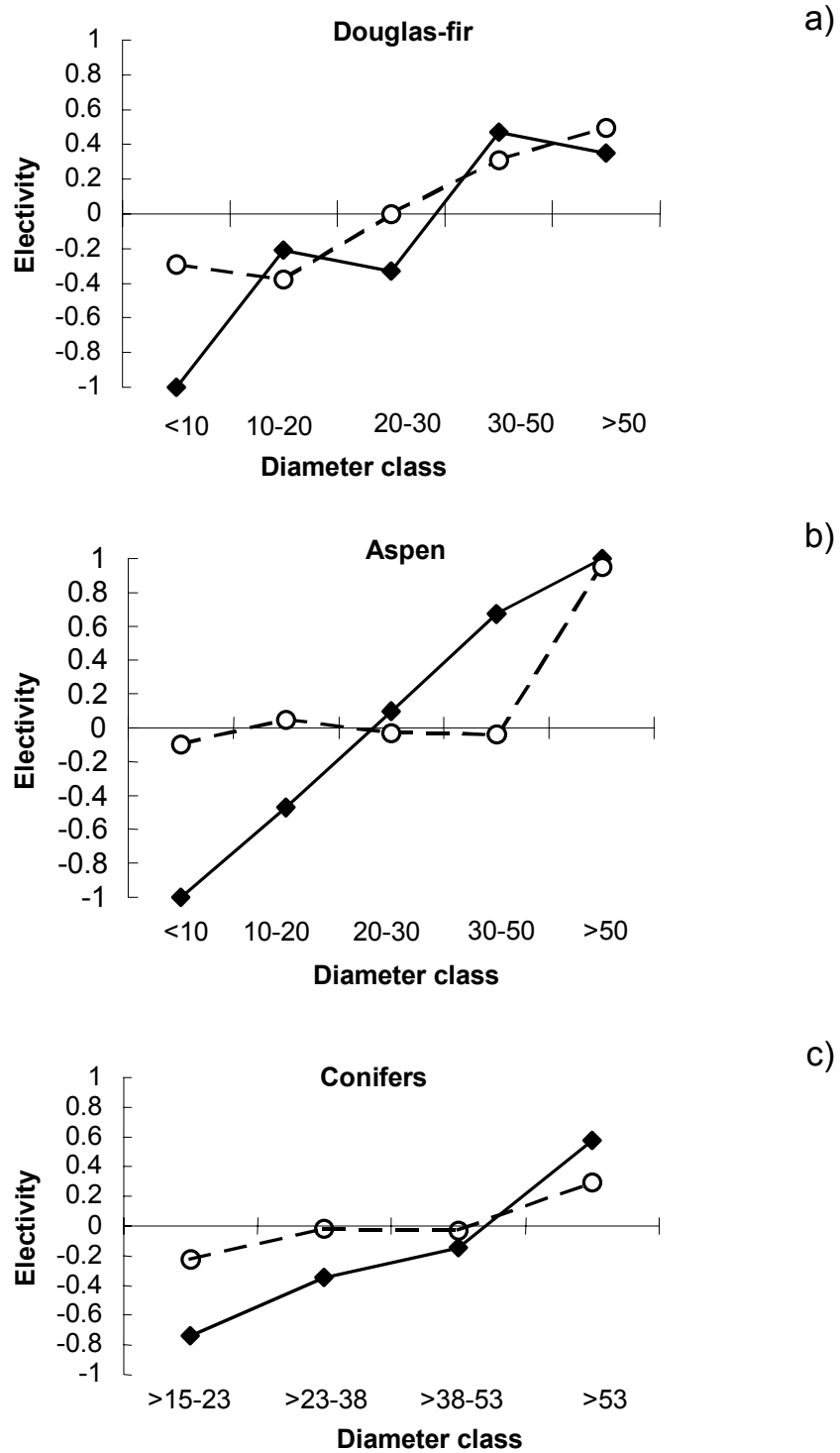


Figure 3—Comparisons of electivity shown by foraging [— ○ —] and nesting [— ◆ —] woodpeckers across diameter classes. Data for a) Douglas-fir from Klenner and Huggard (1998), b) Trembling aspen from Klenner and Huggard (1998), c) Conifers from Madsen (1985).

Some species foraging habitats are particularly difficult to incorporate into forest management. Both the black-backed and three-toed woodpeckers are specialized feeders commonly exploiting conditions after fires (Apfelbaum and Haney 1981, Hutto 1995). Three-toed woodpeckers feed primarily on larvae of bark beetles (Murphy and Lehnhausen 1998) that respond dramatically to forest fires, laying eggs in surviving trees and snags almost immediately after the fire. Adults emerge 2 to 3 years later, and secondary outbreaks appear rare. Although they do eat larvae of wood-boring beetles (Cerambycidae) in other snags, food is most abundant for these woodpeckers for only a 2- to 3-year, post-fire period. Black-backed woodpeckers specialize on larvae of wood-boring beetles that bore into the sapwood of fire- or beetle-killed trees. Populations of both woodpecker species are therefore irruptive and concentrated in areas of beetle-infested trees, and both are listed “at risk” in the Pacific Northwest (*appendix A*).

Kreisel and Stein (1999) found foraging woodpeckers in winter to be ten times more abundant in recently burned forest than in unburned forest. Hutto (1995) reported that 15 bird species occurred more frequently in burns than any other cover type, including four cavity nesters: hairy, three-toed, and black-backed woodpeckers, and the mountain bluebird. The black-backed woodpecker is the most vulnerable, because of its specialization on wood-boring larvae (rather than bark beetles or free-flying insects). In short, 15 bird species have recent burns as their favored habitat and at least one is dependent upon burns.

The problem for forest management is that beetle-infested stands provide the ideal (and possibly only productive) habitat for some woodpecker species. Numbers of black-backed woodpecker are much lower in older forests than among recent fire-killed trees so that even maintenance of old stands may not be a sufficient management tactic. Both fire suppression and salvage logging work to the detriment of the species. The life history of the black-backed woodpecker illustrates that commitment to maintaining all of biological diversity is also a commitment to sustaining some areas of dying and dead forest.

Dead Wood as Shelter and Cover

Dead wood on the ground influences vertebrate abundance and richness by providing:

- Necessary substrate, energy, and nutrients for many invertebrates and fungi upon which a wide range of amphibian, reptile, bird, and small mammal species depend for forage (e.g., Bull and others 1997, Maser and Trappe 1984; Rhoades 1986).
- Sheltered areas for reproduction in a range of vertebrates from salamanders to black bears, and cover from aerial predators (e.g., Corkran and Thoms 1996, Harestad 1991).
- A modified microclimate (cooler, moister, more stable temperature than surrounding habitat) that is essential to species that cannot tolerate extremes in temperature or humidity (several amphibians; Heatwole 1962).
- Runways for small mammals and display or lookout posts for birds (e.g., Bull and Henjum 1990, Lofroth 1998).

- Increased habitat diversity and aeration in water by forming riffles, small waterfalls, and pools, thereby creating habitat for amphibians and fish which are in turn fed on by other vertebrates.
- Structures exploited by near-aquatic vertebrates as cover, foraging sites, or basking (e.g., river otter [*Lontra Canadensis*], mink, painted turtles [*Chrysemys picta*]; Lofroth 1998).
- Access routes for predators, especially under snow cover (e.g., weasels, marten; Corn and Raphael 1992).

Among terrestrial vertebrates, strict dependence on down wood is most likely among species breeding in rotten wood (e.g., some salamanders). Other species, including shrews and several birds, forage on insects that are abundant in down wood and are often more abundant at sites with more down wood (e.g., Craig 1995, Waterhouse and Dawson 1999). Although several bird species opportunistically exploit down wood for nesting sites (e.g., blue grouse [*Dendragapus obscurus*] and ruffed grouse [*Bonasa umbellus*], Townsend's solitaire [*Myadestes townsendi*]), only one bird species relies largely on down wood for nesting opportunities—the winter wren (Waterhouse 1998). Opportunistic use can be high. For example, Campbell and others (1990) reported that 31 percent of blue grouse nests were alongside logs. Several mammal species, ranging from little brown myotis to black bears, use down wood as resting or denning sites, but most show flexibility across substrates. Rodents, snowshoe hare (*Lepus americanus*), gray wolf (*Canis lupus*), and wolverine (*Gulo gulo*) not only use down wood as maternal or resting dens but also use thickets or earth dens. Hagar and others (1995) estimated that 52 species of mammals in Oregon responded positively to greater amounts of dead wood. Among the 52, 40 were associated with logs as cover for themselves or their prey, but it has proven difficult to associate consistent positive responses in population size or fitness with abundance of down wood (Bunnell and Huggard 1999, Bunnell and others 1999b). We acknowledged that flexibility in *appendix A* by including only species for which a positive response appeared likely from current literature. By using that criterion, 12 to 18 percent of terrestrial forest-dwelling vertebrate species respond positively to increasing amounts of down wood in the 12 major forest types of British Columbia (Bunnell and others 1999b).

The strongest responses to down wood are among terrestrial-breeding salamanders (seven of eight salamander species in *appendix A*). Among habitat variables surveyed, down wood is most consistently related to abundance of terrestrial-breeding salamanders (reviews of Bunnell and others 1999b, deMaynadier and Hunter 1995). Some workers reported these salamanders to be associated with large pieces of down wood (Aubry and others 1988, Whitaker and others 1986). Corn and Bury (1991) found that densities of clouded and western redback salamanders were relatively constant per unit volume of down wood regardless of stand age, indicating the benefits of retaining down wood in younger stands. Other authors have documented positive responses of small mammals to down wood (e.g., Carey and Johnson 1995, Corn and others 1988, Gilbert and Allwine 1991), but results are highly variable within species and among locations. Bunnell and others (1999a) offered four reasons for the observed variability in response to down wood, of which the most troubling is that critical lower thresholds have not been reached.

Where forestry has been practiced longer than in the Pacific Northwest, many organisms are threatened by reductions in down wood (e.g., Anglestam 1997, Berg

and others 1994). Current evidence suggests that species dependent upon down wood in the Pacific Northwest are surviving on legacies of past practices, not the results of current practices (e.g., Bunnell and others 1997, Spies and others 1988). We believe that if current accumulations are not replenished, down wood accrued under past practices will decline, as will some species.

Management Implications

In the Pacific Northwest, 69 vertebrate species consistently seek cavities in dying or dead trees, and more use such cavities opportunistically. Another 47 or more species respond positively to increasing amounts of down wood (*appendix A*). The 90 species of forest-dwelling vertebrates in the Pacific Northwest listed as “sensitive” or “at risk,” include 30 species requiring cavities and 21 species strongly associated with down wood. (A definition of “forest-dwelling” is problematic, and we excluded species such as peregrine falcon (*Falco peregrinus*), Swainson’s hawk (*Buteo swainsoni*), and barn owl (*Tyto alba*) whose relationship with forest cover is marginal.) Thus, about 57 percent of listed vertebrate species are reliant upon or strongly associated with dead wood. Many more cryptogams, fungi, and invertebrates are dependent upon dead wood. Where the goal of management is to sustain or restore native biodiversity, forest practices must include ways of sustaining dead wood. Most managed stands have smaller volumes of dead wood than do unmanaged stands (Maser and Trappe 1984, Spies and others 1988). The trend is pronounced where forestry has been practiced longer. Angelstam (1997) reported that dead wood comprised 30-40 percent of the total wood volume in unmanaged stands and declined to about 20 percent after one rotation and to about 1 percent after several rotations of intensive fiber extraction. The trend is consistent with projections of Spies and others (1988) for the Pacific Northwest. Our review suggests that if managers desire to sustain biodiversity they should:

- *Ensure sustained provision of dying and dead wood*—Hundreds of species depend on dying and dead logs and trees. Where the goal is to sustain all of the biological diversity, patchwise retention incorporating all structures is helpful.
- *Retain trees and snags of both hardwoods and favored conifer species (larch, Douglas-fir, ponderosa pine), particularly where hardwood species are not abundant. Avoid creating monocultures of less preferred species, such as lodgepole pine*—Although they are favored nesting sites and provide the only substrate for some bryophytes, we cannot rely solely on more decay-prone hardwoods. The varied needs of forest organisms include well-decayed snags, large hollow snags, and snags with loose slabs of bark. Hardwood species will not accommodate all these needs, nor will any one species of conifer. Because conifers are longer-lived and provide a longer-lasting source of cavities than do hardwoods (Erskine 1977, Harmon and others 1986), they are more likely to sustain snags late into rotations. Conifer snags are required by species foraging on bark beetles and wood-boring beetles, and conifer logs last longer than do hardwood logs.
- *Retain a range of size and age classes of dead wood*—Where safety considerations eliminate older snags at harvest, managers should ensure that snags can develop through the rotation. Although larger diameters usually are selected by vertebrates, smaller snags and logs are used. The desirability of a

range of decay classes is well documented for bryophytes, insects, terrestrial breeding salamanders, and birds. Well-decayed snags present greater safety risks and are more easily retained in patches. Unless reserve patches are very large, recruitment of well-decayed snags must occur outside of reserve patches. Snags may never become well decayed if operational guidelines require snag-falling. Either no-work zones are required during subsequent entries, or silvicultural systems that do not require frequent entries should be employed in at least some areas. Well-decayed snags will not develop at all during a rotation if no trees die until late in the rotation. Retaining declining live trees, or recently-dead snags, ensures timely onset of decay.

- *Ensure that some large trees or snags are retained*—Although individual birds use a wide range of tree or snag sizes, they tend to select larger ones when available. Current data suggest that conifer cavity trees > 50 cm would accommodate most bird species, and most hardwood trees can be smaller (Bunnell and others 2002). Studies of vertebrate-forest relations have concentrated where trees are larger and more valuable, so existing data overestimate requirements where trees are smaller. A diameter > 30 centimeter will accommodate most bird species in less productive, inland forest types (Bunnell and others 2002). Some mammals select trees or snags > 50 centimeters in diameter (e.g., marten, black bear), and use down wood 50 to 150 centimeter in diameter (Davis 1996, Raphael and Jones 1997, USDA Forest Service 1996). Given how larger mammals use space, large pieces of down wood for such species can be well distributed across large areas. Large trees and snags provide nesting or denning sites longer than do small snags (Graham 1981, Morrison and Raphael 1993). However, smaller snags provide foraging sites, and many more foraging sites are needed than nesting sites.
- *Meet dead wood requirements for larger species in areas where the emphasis is not on intensive fiber production*—Binkley (1997) and Bunnell and others (1999a) reviewed economic and ecological advantages of zoning the intensity of fiber production. In some forest types, larger mammals prefer significant amounts (100 to 200 cubic meters/hectare or more) and sizes (> 50 centimeter diameter) of down wood (review in Lofroth 1993). Needs of those species are best provided in areas where late-successional attributes are being maintained. Provision of some large pieces of dead wood in forests where the dominant goal is fiber production may facilitate dispersal among areas of more favorable habitat.
- *Don't do the same thing everywhere*—Retention of trees in patches reduces safety risks of snag retention and windthrow (Coates 1997, Franklin and others 1997) and facilitates retention of a range of size and decay classes. It also concentrates recruitment of down wood. Debris piles are used by some vertebrates (Morris 1984, Raphael and Jones 1997), but scattered pieces of down wood favor other organisms. Dispersed retention of individual snags, or declining live trees intended to become snags, may be particularly advantageous for perching birds, and for territorial secondary users, such as, raptors and some small birds, but impact shrub nesters negatively by encouraging aerial predators (Vega 1993). Any single approach will disadvantage some group of species, so a range of practices is preferable if a range of species is to be sustained in an area.

- *Limit salvage logging after forest fires*—Fire suppression has reduced the area of recent burns favored by several vertebrates. If all vertebrates are to be sustained, salvage logging should not be performed over all burns, or the entire area of large burns.

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Appendix A—Native cavity and downed wood using vertebrates breeding in forests in the Pacific Northwest and their state or provincial status.

Common name	Scientific name	Cavity ²	DW ³	State or Province ¹				
				BC	AB	WA	OR	CA
Amphibians								
Pacific giant salamander	<i>Dicamptodon tenebrosus</i>		X	R				
Arboreal salamander	<i>Aneides lugubris</i>		X					
Black salamander	<i>Aneides flavipunctatus</i>		X				S	
Clouded salamander	<i>Aneides ferreus</i>		X				S	
Coeur D'Alene salamander	<i>Plethodon idahoensis</i>		X	R				
Ensatina salamander	<i>Ensatina eschscholtzii</i>		X					
Western redback salamander	<i>Plethodon vehiculum</i>		X					
Reptiles								
Western skink	<i>Eumeces skiltonianus</i>		X					
Western fence lizard	<i>Sceloporus occidentalis</i>		X					
Ruber boa	<i>Charina bottae</i>		X	B			S	
CA mountain kingsnake	<i>Lampropeltis zonata</i>		X					
Racer	<i>Coluber mormon</i>		X					
Ringneck snake	<i>Diadophis punctatus</i>		X					
Sharptail snake	<i>Contia tenuis</i>		X	R	S			
Birds								
Order								
Anseriformes								
Barrow's goldeneye	<i>Bucephala islandica</i>	S					S	
Bufflehead	<i>Bucephala albeola</i>	S					S	
Common goldeneye	<i>Bucephala clangula</i>	S						
Common merganser	<i>Mergus merganser</i>	S						
Hooded merganser	<i>Lophodytes cucullatus</i>	S						
Red-breasted merganser	<i>Mergus serrator</i>	S						
Wood duck	<i>Aix sponsa</i>	S						

(appendix A continued)

Common name	Scientific name	Cavity ²	DW ³	State or Province ¹				
				BC	AB	WA	OR	CA
Order Falconiformes								
American kestrel	<i>Falco sparverius</i>	S						
Barred owl	<i>Strix varia</i>	S			S			
Boreal owl	<i>Aegolius funereus</i>	S			S	S		
Flammulated owl	<i>Otus flammeolus</i>	S		B		S		
Northern hawk owl	<i>Surnia ulula</i>	S						
Northern pygmy-owl	<i>Glaucidium gnoma</i>	S		B		S		
Northern saw-whet owl	<i>Aegolius acadicus</i>	S		B				
Spotted owl	<i>Strix occidentalis</i>	S		R	T	T	T	
Western screech-owl	<i>Otus kennicottii</i>	S		R/B				
Order Apodiformes								
Vaux's swift	<i>Chaetura vauxi</i>	S						
Order Piciformes								
Acorn woodpecker	<i>Melanerpes formicivorus</i>	P						
Black-backed woodpecker	<i>Picoides arcticus</i>	P			S	S		
Downy woodpecker	<i>Picoides pubescens</i>	wP						
Hairy woodpecker	<i>Picoides villosus</i>	P		B				
Lewis's woodpecker	<i>Melanerpes lewis</i>	wP		B		S		
Northern flicker	<i>Colaptes auratus</i>	wP						
Nuttall's woodpecker	<i>Picoides nuttallii</i>	wP						
Pileated woodpecker	<i>Dryocopus pileatus</i>	P			S	S		
Red-breasted sapsucker	<i>Sphyrapicus ruber</i>	P						
Red-naped sapsucker	<i>Sphyrapicus nuchalis</i>	P						
Three-toed woodpecker	<i>Picoides tridactylus</i>	P					S	
White-headed woodpecker	<i>Picoides albolarvatus</i>	wP		R		S		
Williamson's sapsucker	<i>Sphyrapicus thyroideu</i>	P		R\B				
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>	P						

		State or Province ¹						
Common name	Scientific name	Cavity ²	DW ³	BC	AB	WA	OR	CA
Ash-throated flycatcher	<i>Myiarchus tyrannulus</i>	S						
Purple martin	<i>Progne subis</i>	S		R		S		
Tree swallow	<i>Tachycineta bicolor</i>	S						
Violet-green swallow	<i>Tachycineta thalassina</i>	S						
Boreal chickadee	<i>Poecile hudsonicus</i>	wP						
Chestnut-backed chickadee	<i>Poecile rufescens</i>	wP						
Mountain chickadee	<i>Poecile gambeli</i>	wP						
Plain titmouse	<i>Parus inornatus</i>	wP						
Siberian tit	<i>Parus cinctus</i>	wP						
Pygmy nuthatch	<i>Sitta pygmaea</i>	wP				S		
Red-breasted nuthatch	<i>Sitta canadensis</i>	wP						
White-breasted nuthatch	<i>Sitta carolinensis</i>	wP						
Brown creeper	<i>Certhia americana</i>	C		S				
Bewick's wren	<i>Thryomanes bewickii</i>	S						
House wren	<i>Troglodytes aedon</i>	S						
Winter wren	<i>Troglodytes troglodytes</i>	S	X					
Mountain bluebird	<i>Sialia currucoides</i>	S						
Western bluebird	<i>Sialia mexicana</i>	S				S		
Mammals								
Order Insectivora								
Common shrew	<i>Sorex cinereus</i>		X					
Dusky shrew	<i>Sorex monticolus</i>		X					
Pacific shrew	<i>Sorex pacificus</i>		X	R				
Pygmy shrew	<i>Sorex hoyi</i>		X					
Trowbridge's shrew	<i>Sorex trowbridgii</i>		X	B				
Order Chiroptera								
Big brown bat	<i>Eptesicus fuscus</i>	S						
California myotis	<i>Myotis californicus</i>	S						
Fringed myotis	<i>Myotis thysanodes</i>	S		B				
Hoary bat	<i>Lasiurus cinereus</i>	S						
Keen's long-eared myotis	<i>Myotis keenii</i>	S		R				
Little brown myotis	<i>Myotis lucifugus</i>	S						
Long-legged myotis	<i>Myotis volans</i>	S				S		

(appendix A continued)

Common name	Scientific name	Cavity ²	DW ³	State or Province ¹				
				BC	AB	WA	OR	CA
Northern long-eared myotis	<i>Myotis septentrionalis</i>	C		B	B	S		
Silver-haired bat	<i>Lasionycteris noctivagans</i>	S				S		
Southern red bat	<i>Lasiurus blossevilli</i>	S						
Yuma myotis	<i>Myotis yumanensis</i>	S						
Order								
Rodentia								
Creeping vole	<i>Microtus oregoni</i>		X					
Heather vole	<i>Phenacomys intermedius</i>		X					
Northern red-backed vole	<i>Clethrionomys rutilus</i>		X					
Southern red-backed vole	<i>Clethrionomys gapperi</i>		X	R/B				
Western red-backed vole	<i>Clethrionomys occidentalis</i>		X					
White-footed vole	<i>Phenacomys albipes</i>		X		S			
Columbian mouse	<i>Peromyscus oreas</i>		X					
Deer mouse	<i>Peromyscus maniculatus</i>		X					
Pinon mouse	<i>Peromyscus truei</i>		X					
Sitka mouse	<i>Peromyscus sitkensis</i>		X					
Douglas' squirrel	<i>Tamiasciurus douglasii</i>	S						
Least chipmunk	<i>Tamias minimus</i>		X	R				
Long-eared chipmunk	<i>Tamias quadrimaculatus</i>		X					
Northern flying squirrel	<i>Glaucomys sabrinus</i>	S						
Red squirrel	<i>Tamiasciurus hudsonicus</i>	S						
Sonoma chipmunk	<i>Tamias sonomae</i>		X					
Townsend's chipmunk	<i>Tamias townsendii</i>		X					
Western gray squirrel	<i>Sciurus griseus</i>	S				S		
Yellow-pine chipmunk	<i>Tamias amoenus</i>		X					
Order								
Carnivora								
Red fox	<i>Vulpes vulpes</i>		X					
Bobcat	<i>Lynx rufus</i>		X			S		
Lynx	<i>Lynx Canadensis</i>		X			S		
Ermine	<i>Mustela erminea</i>		X	R/B				
Fisher	<i>Martes pennanti</i>	S	X	B	S	S		
Least weasel	<i>Mustela nivalis</i>		X					

(appendix A continued)

Common name	Scientific name	Cavity ²	DW ³	State or Province ¹				
				BC	AB	WA	OR	CA
Long-tailed weasel	<i>Mustela frenata</i>			R	S			
American marten	<i>Martes Americana</i>	S	X				S	
Mink	<i>Mustela vison</i>		X					
Black bear	<i>Ursus americanus</i>	S	X	R				
Raccoon	<i>Procyon lotor</i>	S	X					

¹ R = red listed; B = blue listed; S = sensitive species; E = endangered species; T = threatened species; Sources include: Alaska Department of Fish and Game internet site as of July 1997 (www.state.ak.us/adfg/); British Columbia Ministry of Environment, Lands and Parks (1992, 1996); Alberta Environmental Protection Status of Wildlife internet site as of December 1996 (www.gov.ab.ca/env/fw/); Rodrick and Milner (1991) for Washington; Marshall and others (1996) for Oregon; and the U.S. Fish and Wildlife Service Division of Endangered Species internet site as of April 1999 for California. Other jurisdictions of the Pacific Northwest listed no species dependent upon cavity sites or downed wood.

² P = Primary Cavity Nester, wP = Weak Primary, S = Secondary Cavity Nester (obligate), C = Cave or Crevice; (may use cavities, especially during winter).

³ Uses downed wood for breeding and/or feeding; X = Strongly Associated.