

How Should We Spatially Distribute Dying and Dead Wood?¹

Fred L. Bunnell,² Mark Boyland,² and Elke Wind²

Abstract

We consider density and degree of aggregation of dead wood. Cavity nesters as a group respond asymptotically to snag density and attain half their maximum density at about 2.4 large snags/hectare. However, individual species show different responses, and there is no apparent effect of territoriality among smaller species. Dispersed retention of trees and snags strongly favors secondary cavity nesters and increases their abundance above that found in mature or old-growth forests; large patches favor primary nesters. Despite good operational and biological reasons for patchwise retention of dead wood, there are negative effects on some species.

Introduction

Many organisms rely upon dead wood (Bunnell and others 2002), and recent forest practices are exploring ways to sustain dead wood in managed stands (e.g., Anonymous 1995, Steventon and others 1998). There is a large literature on the sizes of dead trees and logs used by forest-dwelling organisms, but less is known about how that dead wood should be distributed within managed forests. We review relationships between forest-dwelling organisms and the amounts and distribution of dying or dead trees and dead wood on the ground. We focus on vertebrates, but briefly discuss other organisms that use dead wood. Our review is largely restricted to species of the Pacific Northwest defined as including 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 groups of species are well documented.

Density of Dying and Dead Trees

Richness and density of cavity-nesting birds are inconsistently related to snag densities. Studies surveying stands with many snags have obtained weak relations (e.g., Lundquist and Mariani 1991, Morrison and others 1987), while those including managed stands, in which some or all snags had been removed, have found stronger relations (e.g., Raphael and White 1984, Schreiber and deCalesta 1992). Bevis (1996)

¹ An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

² Professor, Ph.D. Candidate, and Research Technician, respectively, Center for Applied Conservation Research, Department of Forest Sciences, University of British Columbia, 3004-2424 Main Mall, Vancouver, British Columbia, Canada, V6T 1Z4. (e-mail addresses: fbunnell@interchange.ubc.ca, markbo@interchange.ubc.ca, and ewind@interchange.ubc.ca)

surveyed a range of stands from unmanaged to seed tree, and found the strongest predictor of red-breasted nuthatch (*Sitta canadensis*) and chickadee densities to be density of snags 25–50 centimeter dbh; $r^2 = 0.94$ and 0.83, respectively. These relationships may indicate nest site limitation, or they may reflect more productive foraging opportunities in stands with more snags (e.g., older stands with insect outbreaks versus thrifty managed stands).

Because rot within living trees is more common among hardwoods than among conifers, snag density is less important in hardwood stands. *Figure 1a* illustrates relationships for conifer stands with few hardwoods. Because much variation in cavity nester response to snag density is due to different size distributions of snags within stands, we limited estimates of snag density to larger snags that the birds use preferentially. Our diameter limits reflect the different sizes of preferred trees in coastal forests (about 50 centimeter dbh) and inland forests (30.5 to 38 centimeter dbh; Bunnell and others 2002). Bunnell and others (1999) fit a Michaelis-Menten relationship to the data (*fig. 1a*) under the assumption that the rate of response (cavity nesters density) was a function of the concentration of substrate (snags/hectare). The relationship implies an upper asymptote and a half-saturation constant. Response of the seven studies combined is asymptotic, with little additional increase in density of cavity nesters above about three large snags per hectare (*fig. 1a*). Estimated parameters were an asymptote of 2.42 cavity nesting pairs/hectare and a half-saturation constant of 2.37 snags/hectare with an r^2 of 0.53. That shape is expected among territorial species limited by other resources. As the snag density increases, other required resources become more important factors in limiting bird density until finally the scarcity of other resources are completely limiting the bird density. Birds present at 0.0 snags per hectare indicate that some species can nest in snags < 30 centimeter dbh (some of them hardwoods, unreported in data on conifers). The response is consistently expressed, and each individual study of *figure 1a* shows an initial increase in cavity-nester density with increasing snag density.

Relationships for some bird species appear more linear (*fig. 1b,c*). They suggest that competition for cavity sites is more strongly expressed within the entire cavity-nesting fauna than within the smaller species studied. Data of *figure 1c* also suggest that other habitat variables influence the response (compare data of Raphael and White 1984 with those of Cunningham and others 1980). We emphasize that smaller snags were present in all studies included in *figure 1*. Smaller snags are used as foraging sites, and foraging sites may be more often limiting than cavity sites (Walankiewicz 1991, Welsh and Capen 1992). More dead or dying wood than is required for nesting is needed to sustain all cavity-nesting species. Moreover, through provision of perching, foraging, and hawking sites, snags of all sizes tend to increase richness and abundance of birds other than cavity nesters (Dickson and others 1983, Scott 1979).

Species names mentioned in this text are taken from the following references: Plants—(Crittenden 1992); Birds—(Cannings and Harcombe 1990, Peterson and others 1993); Amphibians—(Cannings and Harcombe 1990); Mammals—(Cannings and Harcombe 1990, Whitaker 1993).

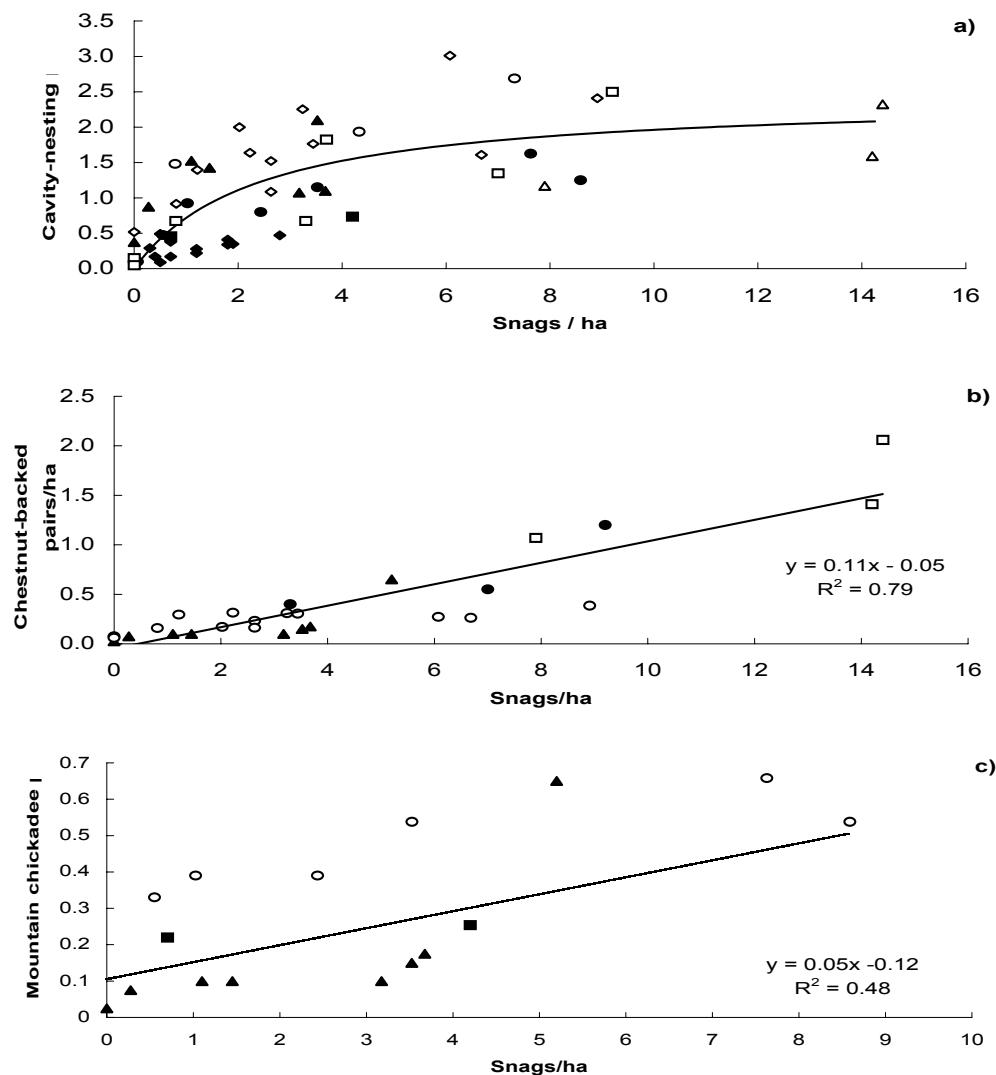


Figure 1—Density of cavity-nesting bird pairs versus snag density in primarily coniferous forests of the Pacific Northwest. Hollow symbols represent coastal forests; solid symbols are inland forest types. a) All cavity-nesting species. [○] = Carey and others 1991 (snags > 50 cm dbh); [▲] = Cunningham and others 1980 (snags > 30.5 cm dbh); [□] = Mannan 1977 (snags > 48 cm dbh); [■] = Mannan and Meslow 1984 (snags > 31 cm dbh); [◊] = Manuwal and Zarnowitz 1981 (snags > 51 cm dbh); [△] = Nelson 1988 (snags > 50 cm dbh); [●] = Raphael and White 1984 (> 38 cm dbh); [◆] = Steeger and Quesnel 1998 (snags > 50 cm dbh). Solid line is the fitted Michaelis-Menten relationship of the form cavity nesters per ha = 2.42 [asymptote] X (snags/hectare/ (snags/hectare + 2.37[half saturation constant])) (adapted from Bunnell and others 1999). b) Chestnut-backed chickadee pairs [▲] = Cunningham and others 1980 (snags > 30.5 cm dbh); [●] = Mannan 1977 (snags > 48 cm dbh). [○] = Manuwal and Zarnowitz 1981 (snags > 51 cm dbh); [□] = Nelson 1988 (snags > 50 cm dbh). c) Mountain chickadee (*Poecile gambeli*) pairs: [▲] = Cunningham and others 1980; [■] = Mannan and Meslow 1984; [○] = Raphael and White 1984.

Density of Downed Wood

The literature is least revealing of the appropriate amounts and distribution of downed wood. Of all habitat variables assessed, downed wood is the least consistently measured, and it is impossible to equate number of pieces, volume, and percent cover to extract broad patterns (e.g., Bunnell and Huggard 1999). In part, the variety of measurements reflects the fact that different ones are appropriate for different organisms: percent cover for some fungi, volume for terrestrial-breeding salamanders, and size for denning mammals. Although biologically appropriate, the variety prohibits synthesis. Moreover, when similar measurements exist, responses to downed wood within species are inconsistent, suggesting substitution with other habitat features, such as shrub cover (Bunnell and others 1999). Three broad points are evident from current data. First, hundreds of species in western forests are dependent upon decaying wood on the ground (Bunnell and others 2002). Second, volume of downed wood is important. That is most evident in data of Corn and Bury (1991) who reported that densities of clouded (*Aneides ferreus*) and western redback (*Plethodon vehiculum*) salamanders were relatively constant per cubic meter of downed wood, regardless of stand age. Third, some species seek out large pieces of downed wood, particularly marten (*Martes americana*), fisher (*Martes pennanti*), and black bears (*Ursus americanus*) (Bunnell and others 2002). Because these species also range more widely than most species using downed wood, required densities are probably low, provided scattered large pieces are accessible. In short, some downed wood is important for many species, and large pieces are critical to some.

Because different forest types grow and recruit different amounts of downed wood, it is misleading to transplant results. Initial studies have tended to focus on productive forests, which have little relevance to less productive forest types. What is clear is that size, decay class, and total amounts of downed wood have declined with the practice of forestry (e.g., Angelstam 1997, Spies and others 1988) to the detriment of many species (Berg and others 1994). In other words, we do not know what appropriate amounts are, but we do know we have not been recruiting enough downed wood (Bunnell and others 1997).

Distribution of Dying and Dead Trees

Effects of spatial arrangement of snags on cavity-nesters have received far less attention than the attributes of the individual nest trees (Swallow and others 1986). Dispersed retention of snags increased abundance and richness of secondary cavity nesters beyond that found in mature and old-growth forests, but abundance of primary nesters was much reduced (fig. 2). For primary cavity nesters, there are good reasons for retaining trees in patches. First, there is increased operational efficiency. Aggregated retention is safer during timber falling, especially when snags are retained, and windthrow is much reduced relative to dispersed retention or large clearcut edges (Coates 1997, Franklin and others 1997). Operational efficiency can also be gained in patches with a more desirable range of diameter and decay classes, that might prove difficult to select among the individual trees of dispersed retention. Aggregated retention also emulates natural patterns. Nests of primary excavators often are concentrated in dense patches of snags (Bull 1980, Lundquist and Mariani 1991, Raphael and White 1984). It is unclear whether this implies selection of dense patches for some associated value (e.g., social facilitation) or merely reflects the patchy way in which trees are killed by insects or disease. Cavity sites often are

concentrated where rots are concentrated in both hardwoods (e.g., *Phellinus* in aspen [*Populus tremuloides*] and birch [*Betula papyrifera*]; Merkens and others 1996), conifers (e.g., *Armillaria* in Douglas-fir [*Pseudotsuga menziesii*]), and lodgepole pine (*Pinus contorta*; Steeger and Hitchcock 1998).

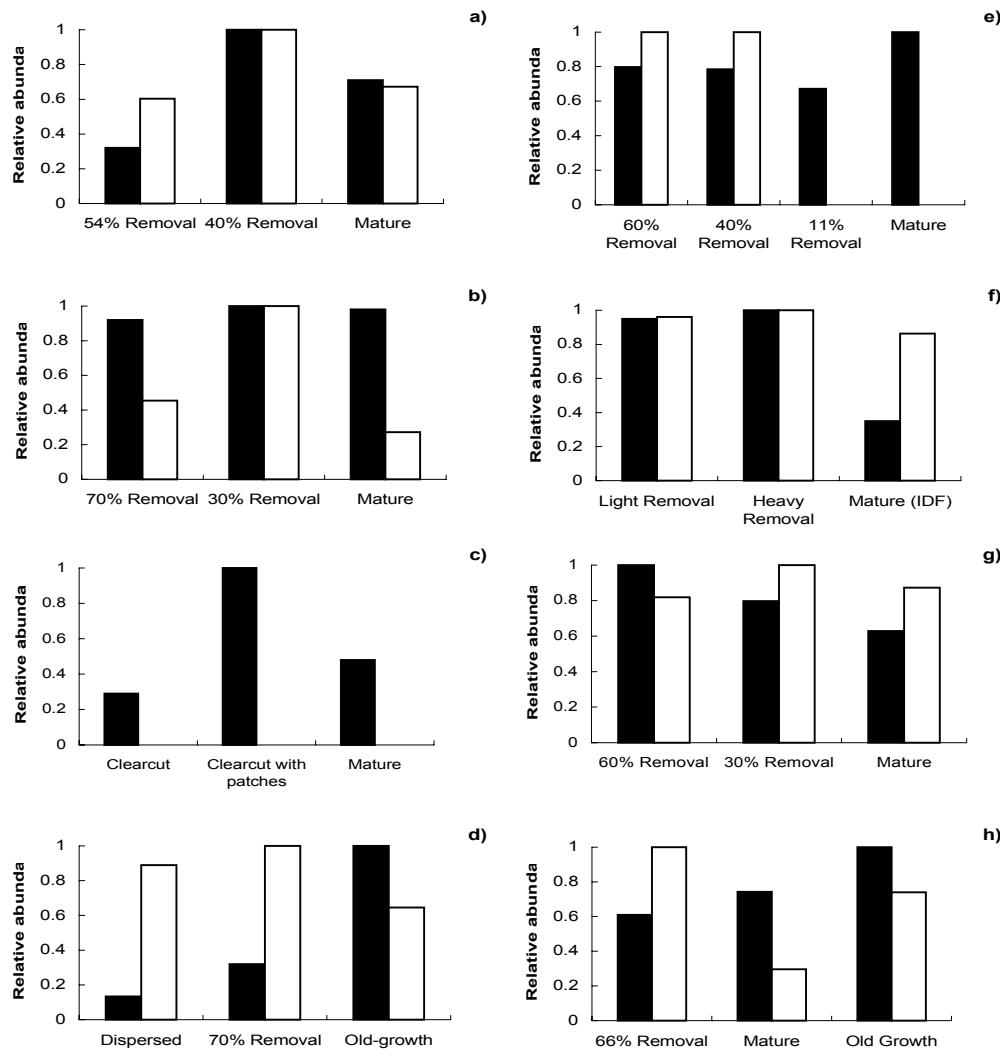


Figure 2—Relative abundance of primary [■] and secondary [□] cavity nesters in different forms of partial harvest. Data sources are a) Scott and Oldemeyer (1983) in Ponderosa pine (*Pinus ponderosa*). b) Steeger and Quesnel (1998) in interior Douglas-fir. c) Gyug and Bennett (1996) in interior western redcedar-hemlock; see text for patch sizes. d) Bryant (1997) in coastal western hemlock; dispersed retention retained about 25 trees per ha. e) Waterhouse and Dawson (1999) in interior Douglas-fir. f) Morgan and others (1989) in interior Douglas-fir; amount removed unspecified. g) Steventon and others (1998) in interior western redcedar-hemlock, h) Tobalske and others (1991) in western larch-Douglas fir.

The most compelling reason for aggregated retention of wildlife trees is that it has been shown to be effective when larger patches are retained. The utility of small patches appears undocumented, but Gyug and Bennett (1996) studied large seed-tree reserves in clearcuts 25 to 29 years after harvesting. Patches retained in the 160 hectare clearcut averaged 0.9 hectare (range 0.3 to 1.5 hectare); in the 1,000 hectare clearcut they averaged 3.6 hectares (range 1.6 to 18.9 hectares). Combined, the patches represented 7 to 10 percent of the gross area. In both clearcuts, more primary cavity nesters were detected in the patches than in the nearby forest, including pileated (*Dryocopus pileatus*) and hairy (*Picoides villosus*) woodpeckers. Current data also suggest that various silviculture systems that maintain some cover somewhere at all times (continuous-cover) are effective at sustaining cavity nesters (fig. 2).

Two broad patterns are evident. First, in all studies of figure 2, secondary cavity nesters were higher in areas experiencing some timber removal than in mature or old-growth forests. That increase likely reflects the fact that many secondary nesters forage more effectively in openings. Second, in most instances the abundance of primary cavity nesters was little affected by partial harvesting, and in some instances increased in abundance. That may reflect the fact that several primary excavators also favor small openings and edges (e.g., hairy woodpeckers; Klenner and Huggard 1998; northern flicker [*Colaptes auratus*], Campbell and others 1990; three-toed woodpecker [*Picoides tridactylus*], Klenner and Huggard 1997; and perhaps downy woodpecker [*Picoides pubescens*], Petit and others 1985). For three-toed woodpeckers, Klenner and Huggard (1997) noted that preferred nest sites were within 20 meters of an edge. If regulations encourage snag removal near edges, patches must be larger and continuous-cover systems will be less effective.

Distribution of Downed Wood

Downed wood can be provided by leaving slash or logs after harvest or by retaining trees to fall to the ground and become downed wood. Slash, including logs, can be either dispersed over the cutblock or aggregated into piles or windrows. More information is available on aggregated retention of downed wood than on dispersed retention.

Several species of small mammals use piles of both fine and coarse logging debris, including red-backed voles (*Clethrionomys* spp.), martens, and short-tailed weasels (*Mustela erminea*) (Lisgo 1999, Morris 1984, Raphael and Jones 1997). Jones and Raphael (1995) described 32 maternal den sites of marten in Oregon: 10 were in slash piles, 10 in logs, 6 in snags, 5 in live trees, and 1 in a stump. Using winter tracking, Gyug (1993, 1994) found that marten use of clearcuts without debris was very low compared to use of adjacent forests. Use of clearcuts with debris piles was significantly higher, but still lower than in adjacent forest. Isolated debris piles were not used by marten unless they were on a path of 135 meters or less between adjacent forest cover. Lisgo and others (2002) documented similar responses of weasels to debris piles in the boreal mixedwood of Alberta. Although marten and weasels hunted around debris piles, small mammal responses to debris were inconsistent. Gyug (1994) found that the presence and number of debris piles did not significantly increase the number of most small mammals. Red-backed voles were almost absent from clearcuts except in piles within 40 meters of forest edges, and only common shrews (*Sorex* spp.) were significantly more abundant when debris

piles were present. Lisgo and others (2002) found greater abundance of small mammals around slash piles than in clearcuts, particularly for red-backed voles. Benefits of piling logging residues remain unclear, because current data simply report higher densities of small mammals in piles than in clearcut areas without piles. Responses to dispersed downed wood have not been compared with aggregated downed wood.

For some organisms, dispersed retention of logging residues is advantageous. Because conditions of stable high humidity are favorable for bryophytes (Sharp 1939), particularly liverworts (Söderström 1988), the humidity and moisture content of logs are especially important to bryophytes (Andersson and Hytteborn 1991). Forest floor bryophytes generally have limited dispersal ability (Khanna 1964, Söderström 1987), and dispersal is from log to log. For these reasons, Samuelsson and others (1994) argued that logs should be close together, but not gathered into piles. It is probable that other organisms whose favored, or only, habitat is downed wood also are poor dispersers. Amaranthus and others (1994) and Carey and Johnson (1995) found that the abundance of truffles and truffle-like fungi, was related to the amount of forest floor covered by logs. More forest floor is covered if the logs are not piled. Encouraging truffles and truffle-eating mammals is a sensible thing to do if sustaining forest productivity is a goal (Harley 1969, Marks and Kozlowski 1973, Maser and others 1978). A dispersed distribution of downed wood would help to disperse both small mammals and mycorrhizae across the site.

There are tradeoffs between aggregating logging residuals or leaving it dispersed. Aggregations are used by several small mammals, both predator and prey. More evenly dispersed retention favors some fungi as well as bryophytes restricted to downed wood. Because there is not an unequivocal best way to distribute logging residuals, the wisest approach is not to do the same thing everywhere.

The other approach to providing downed wood is through dispersed or aggregated retention of living trees. Retained trees die a natural death and likely will have incurred fungal invasion. Natural cavities from heart rot are more likely, and invertebrates associated with some fungi are more likely to survive. Higher windthrow rates in dispersed retention hasten the provision of downed wood, but reduce the period when these trees can provide cavity sites. As well as reduced susceptibility to windthrow, aggregated retention of older trees (patches) has the advantage of immediate provision of downed wood. Additional advantages to aggregated retention are those noted with respect to cavity users, notably the provision of a range of decay and size classes. The disadvantage is that such provision is clearly not dispersed across the landscape. Species restricted to downed wood and that disperse poorly will be disadvantaged.

Implications to Management

From this review, we offer the following recommendations for the distribution of dead wood in managed forest:

- Maintain a target density of 2-3 large snags (> 50 or 30 centimeter diameter) per hectare, among 10-20 smaller snags per hectare through the rotation. However, ensure variation in densities, not an even distribution everywhere.

Cavity sites can become limiting, and there is a density below which species disappear (Campbell and others 1990, 1997; Newton 1994). Data of *figure 1* suggest

that in conifer types little is gained by sustained provision of more than about three large snags per hectare (> 50 centimeter dbh in coastal forests; > 30 centimeters in less productive forests). More smaller snags must be present, both as foraging sites and because some species find cavity sites in small snags. There are no applicable data, but we estimate 10 to 20 smaller snags per hectare as appropriate. In hardwood types, there is little need for a target density of snags, because most cavity nests are found in living trees. Providing for future recruitment of snags in coniferous stands is necessary to ensure that target densities are maintained through the rotation and after harvest. Suggested densities do not apply to each hectare of forest. Because of the diversity of organisms using snags, variability in density of snags must be maintained within and among stands.

- Amounts of downed wood?

Logs as small as 6 centimeters are favorable to shrews (Craig 1995), but in some forest types larger mammals prefer significant amounts (100 to 200 cubic meters/hectare or more) and sizes (> 50 centimeter diameter) of downed wood (review of Lofroth 1993). Current data suggest little more than small amounts are useful but that mammals such as marten, fisher, and black bear require scattered, large pieces, 50 to 100 centimeter diameter.

- Patches of 1-3 hectares will sustain some smaller species, even in extensive clearcuts.

Such patches sustain most, if not all, cavity nesters (*fig. 2*). Home ranges of some terrestrial-breeding salamanders and shrews are small enough (Craig 1995, Nussbaum and others 1983) that groups of individuals can be sustained within 1 hectare; 3 hectares will sustain groups of rodents (e.g., Mahon 1998, Thompson 1996). Retention of some logs on site would permit them to recolonize larger areas.

- Retaining snags in moderate-sized patches has several advantages. It should not, however, be the only distribution of snags used.

Retention of trees in patches helps reduce safety risks of snag retention, provided patches are large enough. Aggregates of 1-3 hectares are used by cavity-nesters in large openings, and are practical where snag-falling regulations permit snag retention within them. Aggregated retention also reduces risks of windthrow and provides diverse nesting opportunities over a range of size and decay classes. Although aggregating retention in moderate-sized patches has advantages, it should not be the only approach used. Dispersed retention of 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. Dispersed retention, however, may impact shrub nesters (Vega 1993) and should not be used everywhere.

Continuous-cover systems, such as individual tree selection, group selection and small (0.1-3 hectare) patch cut arrays have a number of benefits (*fig. 2*), and are of increasing operational interest (Vyse 1999). Openings of up to 3 hectares appear to have little effect on primary cavity nesters when 50 percent of the older forest is retained (Bryant 1997). However, repeated entries and need to fall snags in the surrounding forest can eliminate snags from large areas (Huggard 1997). Aggregated reserves should be considered for snag management in these systems.

- Meet dead wood requirements for larger species in areas where the emphasis is not on intensive fiber production.

The economic and ecological advantages of zoning intensity of forest practices (Binkley 1997, Bunnell and others 1999) suggests that needs of species requiring large amounts of dead wood are best provided in areas where late-successional attributes are being maintained. Most (perhaps all) of these species use clearcuts to forage and often find preferred food there, but must have denning sites nearby. Provision of large amounts of downed wood within clearcuts is incompatible with profit incentives of intensive fiber production.

Acknowledgments

Our research and synthesis was supported by Forest Renewal British Columbia, the Fraser River Action Plan of the Canadian Wildlife Service, Lignum, MacMillan Bloedel, and Western Forest Products. The manuscript benefited from reviews by Peter Arcese and Glen Dunswoth. This is publication R-40 of the Centre for Applied Conservation Biology, University of British Columbia.

References

- Amaranthus, Michael; Trappe, James M.; Bednar, Larry; Arthur, David 1994. **Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy.** Canadian Journal of Forest Research 24: 2157-2165.
- Andersson, Lars I.; Hytteborn, Hakan 1991. **Bryophytes and decaying wood—a comparison between managed and natural forest.** Holarctic Ecology 14: 121-130.
- Angelstam, Per 1997. **Landscape analysis as a tool for the scientific management of biodiversity.** Ecological Bulletin (Copenhagen) 46: 140-170
- Anonymous. 1995. **Sustainable ecosystem management in Clayoquot Sound: planning and practices.** Victoria, BC: Cortex Consultants; Scientific Panel for Sustainable Forest Practices in Clayoquot Sound; 296 p.
- Berg, Åke.; Ehnström, Bengt; Gustafsson, Lena; Hallingbäck, Tomas; Jonsell, Mats; Weslien, Jan 1994. **Threatened plant, animal, and fungus species in Swedish forests: distributions and habitat associations.** Conservation Biology 8: 718-731.
- Bevis, Kenneth R. 1996. **Primary excavators in grand fir forests of Washington's east Cascades and forestry on the Yakima Indian Nation, Washington.** In: Bradford, P.; Manning, T.; l'Anson, B., editors. Wildlife tree/stand-level biodiversity workshop proceedings; 1995 Oct 17-18, Victoria, BC. Victoria, BC: British Columbia Ministries of Environment and Forests; 77-86.
- Binkley, Clark S. 1997. **Preserving nature through intensive plantation management: the case for forestland allocation with illustrations from British Columbia.** Forestry Chronicle 73: 553-559.
- Bryant, Andrew A. 1997. **Effect of alternative silvicultural practices on breeding bird communities in montane forests.** Nanaimo, BC: MacMillan Bloedel Ltd.; 16 p.
- Bull, Evelyn L. 1980. **Resource partitioning among woodpeckers in northeastern Oregon.** Moscow, ID: University of Idaho; 109 p. Ph.D. dissertation.
- Bunnell, Fred L.; Houde, Isabelle; Johnston, Barb; Wind, Elke. 2002. **How dead trees sustain live organisms in western forests.** 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].
- Bunnell, Fredrick ; Huggard, David J. 1999. **Biodiversity across spatial and temporal scales: problems and opportunities.** Forest Ecology and Management 115(2/3): 113-126.
- Bunnell, Fredrick L.; Kremsater, Laurie L.; Wells, Ralph W. 1997. **Likely consequences of forest management on terrestrial, forest-dwelling vertebrates in Oregon.** Portland, OR: Oregon Forest Resources Institute; 130 p.
- Bunnell, Fredrick L.; Kremsater, Laurie L.; Wind, Elke 1999. **Managing to sustain vertebrate diversity in forests of the Pacific Northwest: relationships within stands.** Environmental Reviews 7: 97-146.
- Campbell, R. Wayne ; Dawe, Neil K.; McTaggart-Cowan, Ian; Cooper, John M.; Kaiser, Gary W.; McNall, Michael C.E. 1990. **The birds of British Columbia. Vol. 2. Diurnal birds of prey through woodpeckers.** Vancouver, BC: University of British Columbia Press; 514 p.
- Campbell, R. Wayne ; Dawe, Neil K.; McTaggart-Cowan, Ian; Cooper, John M.; Kaiser, Gary W.; McNall, Michael C.E. 1997. **The birds of British Columbia. Vol. 3. Passerines: flycatchers through vireos.** Vancouver, BC: University of British Columbia Press; 693 p.
- Cannings, R.A.; Harcombe, A.P. 1990. **The vertebrates of British Columbia. Scientific and English names.** Victoria, BC: Heritage Record No. 20, Royal British Columbia Museum; 110 p.
- Carey, Andrew B.; Johnson, Murray L. 1995. **Small mammals in managed, naturally young, and old-growth forests.** Ecological Applications 5: 336-352.
- Carey, Andrew B.; Hardt, M.M.; Horton, Scott P.; Biswell, Brian P. 1991. **Spring bird communities in the Oregon Coast Range.** In: Ruggiero, L. F.; Aubry, K. B.; Carey, A. B.; Huff, M. F., editors. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 123-144.
- Coates, K. David 1997. **Windthrow damage 2 years after partial cutting at the Date Creek silvicultural systems study in the interior cedar-hemlock forests of northwestern British Columbia.** Canadian Journal of Forest Research 27: 1695-1701.
- Corn, P. Stephen ; Bury, R. Bruce 1991. **Terrestrial amphibians in the Oregon Coast Range.** In: Ruggiero, L. F.; Aubry, K. B.; Carey, A. B.; Huff, M. F., editors. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 305-317.
- Craig, Vanessa J. 1995. **Relationships between shrews (*Sorex* spp.) and downed wood in the Vancouver watersheds, BC.** Vancouver, BC: University of British Columbia; 88 p. M.Sc. thesis.
- Crittenden, M. 1992. **Trees of the west.** Hancock House Publishers. Surrey, BC; 220 p.
- Cunningham, James B.; Balda, Russell P.; Gaud, William S. 1980. **Selection and use of snags by secondary and cavity-nesting birds of the ponderosa pine forest.** Res. Paper RM-RP-222. Fort Collins, CO: Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture; 15 p.
- Dickson, James G.; Conner, Richard N.; and Williamson, J. Howard. 1983. **Snag retention increases bird use of a clear cut.** Journal of Wildlife Management 47: 799-804.

- Franklin, Jerry F.; Berg, D.R.; Thornburgh, D.A.; Tappeiner, J.C. 1997. **Alternative silvicultural approaches to timber harvesting: variable retention harvest systems.** In: Kohm, K.A.; Franklin, J.F., editors. Creating a forestry for the 21st Century: the science of ecosystem management. Washington, DC: Island Press; 111-139.
- Gyug, Les W. 1993. **Furbearer and prey use of logging debris piles in clearcuts: progress report 1992/93.** Unpublished report. Victoria, BC: British Columbia Ministry of Environment, Lands and Parks; 25 p.
- Gyug, Les W. 1994. **Wildlife use of logging debris piles in clearcuts.** Unpublished report. Victoria, BC: British Columbia Ministry of Environment, Lands and Parks; 25 p.
- Gyug, Les W.; Bennett, Stephen P. 1996. **Bird use of wildlife tree patches 25 years after clearcutting.** In: Bradford, P.; Manning, T.; I'Anson, B., editors. Wildlife tree/stand-level biodiversity workshop proceedings; 1995 Oct. 17-18; Victoria, BC. Victoria, BC: British Columbia Ministries of Environment and Forests; 15-33.
- Harley, John L. 1969. **The biology of mycorrhizae.** Second Edition. London, UK: Leonard Hill; 334 p.
- Huggard, David. 1997. **Fall-down rates of subalpine fir snags at Sicamous Creek: implications for worker safety and habitat supply.** Extension Note 16. Victoria, BC: British Columbia Ministry of Forests Research Program; 6 p.
- Jones, Laurence C.; Raphael, Martin G. 1995. **Natural history and habitat use by American martens in a central Oregon lodgepole pine system.** 1995 annual report: ecology, management, and conservation of sensitive wildlife species. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 65-70 p.
- Khanna, Kuldip R. 1964. **Differential evolutionary activity in bryophytes.** Evolution 18: 652-670.
- Klenner, Walter ; Huggard, David J. 1997. **Three-toed woodpecker nesting and foraging at Sicamous Creek.** In: Hollstedt, C.; Vyse, A., editors. Sicamous Creek silvicultural systems project: workshop proceedings; 1996 April 24-25; Kamloops, BC. Working Paper 24/1997. Victoria, BC: Research Branch, British Columbia Ministry of Forests; 224-233.
- Klenner, Walter ; Huggard, David J. 1998. **Nesting and foraging habitat requirements of woodpeckers in relation to experimental harvesting treatments at Opax Mountain.** In: Hollstedt, C.; Vyse, A.; Huggard, D., editors. Managing the dry Douglas-fir forests of the southern interior: workshop proceedings; 1997 April 29-30; Kamloops, BC. Working paper 34/1998. Victoria, BC: Research Branch, British Columbia Ministry of Forests; 277-291.
- Lisgo, Kimberly A. 1999. **Ecology of the short-tailed weasel (*Mustela erminea*) in the mixedwood boreal forest of Alberta.** Vancouver, BC: University of British Columbia; 65 p. M.Sc. thesis.
- Lisgo, Kimberly A. 2002. **Summer and fall use of logging residue piles by female short-tailed weasels.** 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].
- Lofroth, Eric. C. 1993. **Scale dependent analyses of habitat selection by marten in the sub-boreal spruce biogeoclimatic zone, British Columbia.** Burnaby, BC: Simon Fraser University; 109 p. M.Sc. thesis.

- Lundquist, Richard W.; Mariani, Jina M. 1991. **Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range.** In: Ruggiero, L.F.; Aubry, K. B.; Carey, A. B.; Huff, M. F. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 221-240.
- Mahon, Todd E. 1998. **Response of small mammal populations to partial cuts and clearcuts in west-central British Columbia.** Burnaby, BC: Simon Fraser University, 87 p. M.Sc. thesis.
- Mannan, R. W. 1977. **Use of snags by birds, Douglas-fir region, western Oregon.** Corvallis, OR: Oregon State University; 123 p. M.Sc. thesis.
- Mannan, R. W.; Meslow, E. Charles. 1984. **Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon.** Journal of Wildlife Management 48: 1219-1238.
- Manuwal, David A.; Zarnowitz, Jill. 1981. **Cavity nesting birds of the Olympic National Forest, Washington.** Seattle, WA: Wildlife Science Group, College of Forest Resources, University of Washington; 144 p.
- Marks, Geoffrey C.; Kozlowski, Theodore T., editors. 1973. **Ectomycorrhizae – their ecology and physiology.** New York: Academic Press; 444 p.
- Maser, Chris ; Trappe, J. M.; Ure, D. C. 1978. **Implications of small mammal mycophagy to the management of western coniferous forests.** Transactions North American Wildlife and Natural Resource Conference 43: 78-88.
- Merkens, Markus; Darling, Laura; Booth, Barry. 1996. **Use and availability of wildlife trees in aspen stands of northeastern BC.** In: Bradford, P.; Manning, T.; I'Anson, B., editors. Wildlife tree/stand-level biodiversity workshop proceedings; 1995 Oct 17-18, Victoria, BC. Victoria, BC: British Columbia Ministry of Environment, Lands, and Parks, and Ministry of Forests; 35-44.
- Morgan, Kenneth H.; Wetmore, Stephen P.; Smith, G. E. J.; Keller, R. A. 1989. **Relationships between logging methods, habitat structure and bird communities of dry interior Douglas-fir, ponderosa pine forests of British Columbia.** Technical Report Series No. 71. Delta, BC: Pacific and Yukon Region, Canadian Wildlife Service; 48 p.
- Morris, Douglas W. 1984. **Patterns and scale of habitat use in two temperate-zone small mammal faunas.** Canadian Journal of Zoology 62: 1540-1547.
- Morrison, Michael L.; Timossi, Irene C.; With, Kimberly A. 1987. **Development and testing of linear regression models predicting bird-habitat relationships.** Journal of Wildlife Management 51: 247-253.
- Nussbaum, R. A.; Brodie, E. D. Jr.; Storm, R. M. 1983. **Amphibians and reptiles of the Pacific Northwest.** Moscow, ID: University Press of Idaho; 332 p.
- Nelson, S. Kim 1988. **Habitat use and densities of cavity-nesting birds in the Oregon coast ranges.** Corvallis, OR: Oregon State University; 157 p. M.Sc. thesis.
- Newton, Ian. 1994. **The role of nest sites in limiting the numbers of hole-nesting birds.** Biological Conservation 70: 265-276.
- Petit, Daniel R. Petit; Kenneth E.; Grubb, Thomas C., Jr.; Reichhardt, Lisa J. 1985. **Habitat and snag selection by woodpeckers in a clear-cut: an analysis using artificial snags.** Wilson Bulletin 97: 525-533.
- Peterson, R. T.; Mountford, G.; Hollom, P. A. D. 1993. **The Audubon Society field guide to birds of Britain and Europe.** Boston, MA; 261 p.

- Raphael, Martin G.; Jones, L. L. C. 1997. **Characteristics of resting and denning sites of American martens in central Oregon and western Washington.** In: Proulx, G.; Bryant, H.N.; Woodward, P.M., editors. *Martes: taxonomy, ecology, techniques and management*. Edmonton, AB: Provincial Museum of Alberta; 146-165.
- Raphael, Martin G.; White, Marshall 1984. **Use of snags by cavity-nesting birds in the Sierra Nevada.** Wildlife Monographs 86: 1-66.
- Samuelsson, J.; Gustafson, L.; Ingelog, T. 1994. **Dying and dead trees: a review of their importance for biodiversity.** Uppsala, Sweden: Swedish Threatened Species Unit; 110 p.
- 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.
- Scott, Virgil E. 1979. **Bird responses to snag removal in ponderosa pine.** Journal of Forestry 77: 26-28.
- Scott, Virgil E.; Oldemeyer, John L. 1983. **Cavity-nesting bird requirements and response to snag cutting in ponderosa pine.** In: Davis, J. W.; Goodwin, G. A.; Ockentels, R. A., editors. *Snag habitat management: proceedings of the symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99.* Fort Collins, CO: Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture; 19-23.
- Sharp, Aaron J. 1939. **Taxonomic and ecological studies of eastern Tennessee bryophytes.** American Midland Naturalist 21: 267-234.
- Söderström, Lars 1987. **Dispersal as a limiting factor for distribution among epixylic bryophytes.** In: Pócs, T.; Simon, T.; Tuba, Z.; Podani, J., editors. *Proceedings of the IAB Conference of Bryoecology; 1985 August 5-10; Akadémiai Kiadó, Budapest, Hungary. Symposia Biologica Hungarica 35:* 475-484.
- Söderström, Lars 1988. **The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in northeast Sweden.** Biological Conservation 45: 169-178.
- Spies, Thomas A.; Franklin, Jerry F.; Thomas, Ted B. 1988. **Coarse woody debris in Douglas-fir forests of western Oregon and Washington.** Ecology 69: 1689-1702.
- Steeger, Christof ; Hitchcock, Christine L. 1998. **Influence of forest structure and diseases on nesting habitat selection by red-breasted nuthatches.** Journal of Wildlife Management 62: 1349-1358.
- Steeger, Christof ; Quesnel, Harold 1998. **Impacts of partial cutting on old-growth forests in the Rocky Mountain trench: interim report.** Enhanced Forest Management Pilot Project, Report No. 9. Invermere, BC: Invermere Forest District; 9 p.
- Steventon, J. Doug ; MacKenzie, K. L.; Mahon, Todd E. 1998. **Response of small mammals and birds to partial cutting and clearcutting in northwest British Columbia.** Forestry Chronicle 74: 703-713.
- Swallow, Stephen K.; Gutiérrez, R. J.; Howard, Ronald A., Jr. 1986. **Primary cavity-site selection by birds.** Journal of Wildlife Management 50: 576-583.
- Thompson, R. L. 1996. **Home range and habitat use of western red-backed voles in mature coniferous forests in the Oregon Cascades.** Corvallis, OR: Oregon State University; 88 p. M.Sc. thesis.
- Tobalske, Bret W.; Shearer, Raymond C.; Hutto, Richard L. 1991. **Bird populations in logged and unlogged western larch/Douglas-fir forest in northwestern Montana.** Res. Pap. INT-RP-442. Logan, UT: Interior Research Station, Forest Service, U.S. Department of Agriculture; 12 p.

- Vega, Robyn M. S. 1993. **Bird communities in managed conifer stands in the Oregon Cascades: habitat associations and nest predation.** Corvallis, OR: Oregon State University; 78 p. M.Sc. thesis.
- Vyse, Alan 1999. **Is everything all right up there? A long term interdisciplinary silvicultural systems project in a high elevation fir-spruce forest at Sicamous Creek B.C.** Forestry Chronicle 75: 467-472.
- Walankiewicz, Wieslaw 1991. **Do secondary cavity-nesting birds suffer more from competition for cavities or from predation in a primeval deciduous forest.** Natural Areas Journal 11: 203-212.
- Waterhouse, Michaela J.; Dawson, Richard 1999. **Bird communities in Interior Douglas-fir forests.** In: Hollstedt, C.; Vyse, A.; Huggard, D., editors. Managing the dry Douglas-fir forests of the southern interior: workshop proceedings; 1997 April 29-30; Kamloops, BC. Working paper 34/1998. Victoria, BC: Research Branch, British Columbia Ministry of Forests; 90-112.
- Welsh, Christopher J. E.; Capen, David E. 1992. **Availability of nesting sites as a limit to woodpecker populations.** Forest Ecology and Management 48: 31-41.
- Whitaker, J. O. 1993. **The Audubon Society field guide to North American mammals.** Toronto, ON: Random House; 745 p.