

How Should We Spatially Distribute Dying and Dead Wood?¹

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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)

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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).

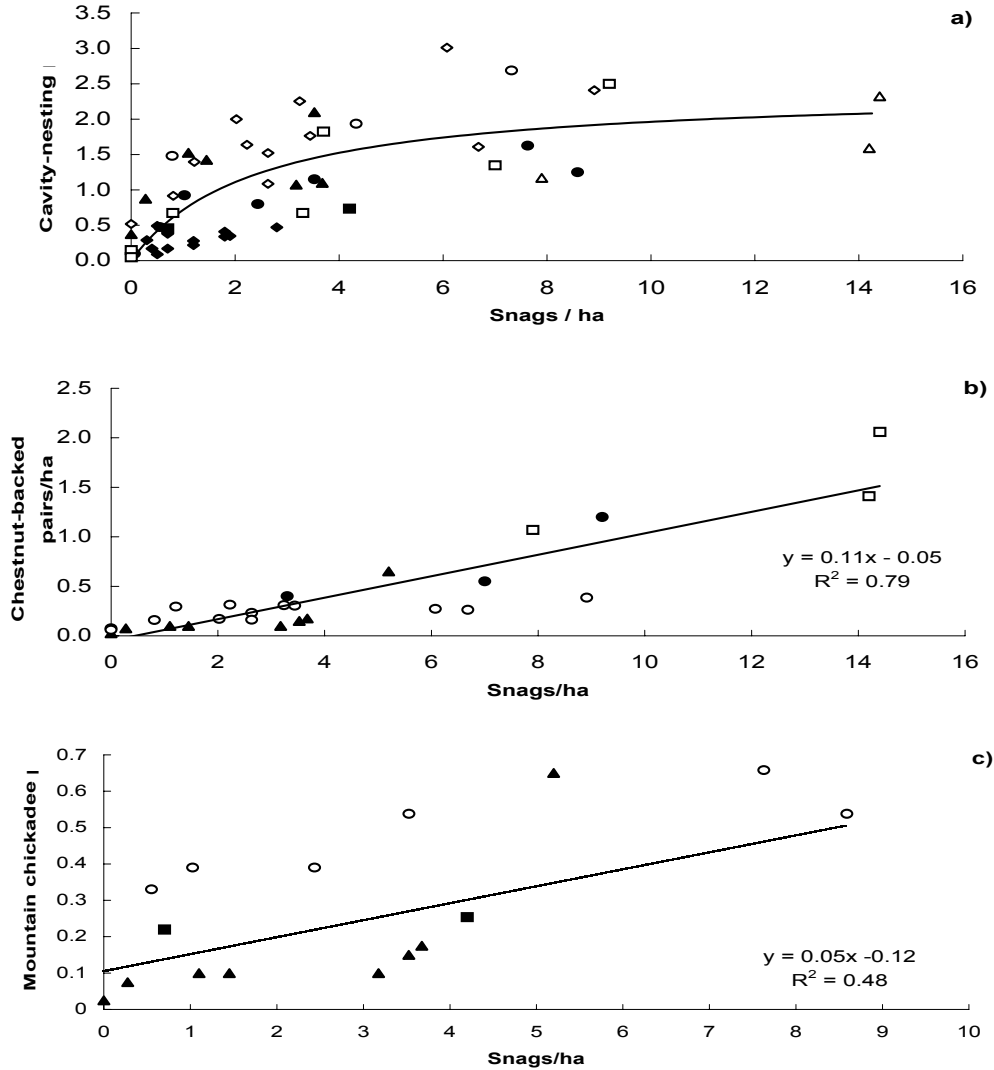


Figure 1—Density of cavity-nesting bird pairs versus snag density in primarily coniferous forests of the Pacific Northwest. Hollow symbols represent coastal forests; solid symbols are inland forest types. a) All cavity-nesting species. [O] = Carey and others 1991 (snags > 50 cm dbh); [▲] = Cunningham 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). [O] = 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; [O] = 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).

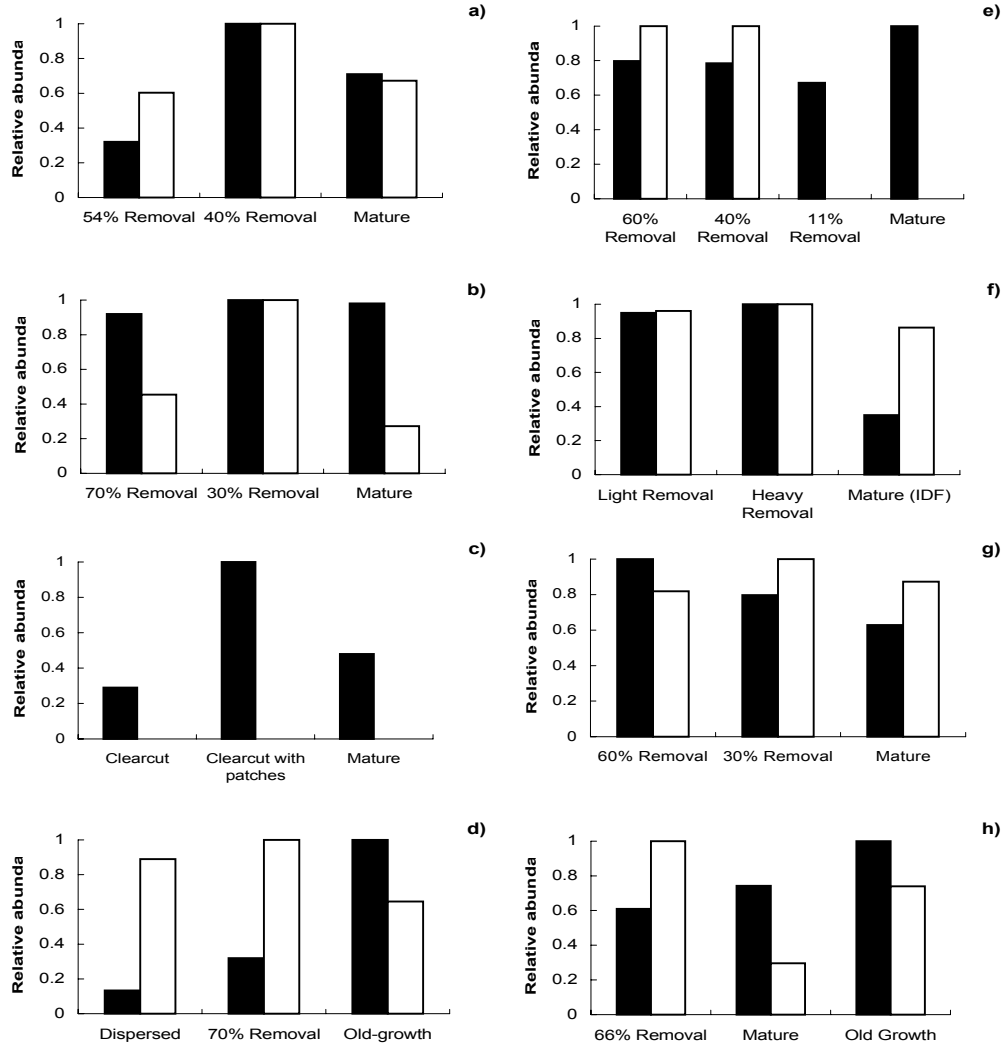


Figure 2—Relative abundance of primary [■] and secondary [□] cavity nesters in different forms of partial harvest. Data sources are a) Scott and Oldemeyer (1983) in Ponderosa pine (*Pinus ponderosa*). b) Steeger and Quesnel (1998) in interior Douglas-fir. c) Gyug and Bennett (1996) in interior western 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 Hyttborn 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 Kozłowski 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.

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