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Review Article

Sustaining Cavity-Using Species: Patterns of Cavity Use and Implications to Forest Management

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Abstract

Many bird and mammal species rely on cavities in trees to rear their young or roost. Favourable cavity sites are usually created by fungi, so they are more common in older, dying trees that are incompatible with intensive fiber production. Forestry has reduced amounts of such trees to the extent that many cavity-using vertebrates are now designated "at risk." The simple model of cavity use presented helps unite research findings, explain patterns of use, and clarify trade-offs that can, or cannot, be made in snag management. Predictions generated are tested using data from over 300 studies. Implications to forest management are derived from the tests, including the following: ensure sustained provision of dying and dead trees, retain both conifers and hardwoods and a range of size and age classes, sustain a range of decay classes, ensure that some large trees or snags are retained, promote both aggregated and dispersed retention of dead and dying trees, meet dead wood requirements for larger species where intensive fibre production is not emphasized, do not do the same thing everywhere, and limit salvage logging after tree mortality. The paper focuses on species breeding in the Pacific Northwest, but draws on data from throughout those species' ranges.

1. Introduction

Most cavities in trees begin with fungi. Because trees resist decay, it takes time for fungi to soften wood enough that cavity excavation by birds is possible. By that time, trees are often old and beginning to die. Old and dying trees reduce economic efficiencies within managed forests, so for decades we have sought to remove them. Our actions were successful, and cavity sites have been much reduced [1–3]. I focus on the Pacific Northwest of North America (PNW), here defined as Alaska, Yukon Territory, Alberta, British Columbia, Washington, Oregon, Idaho, Montana and northern Nevada, and California. Of the 67 vertebrate species commonly using cavities in the PNW, 20 (30%) are designated "at risk" or "potentially at risk." Where forestry has been practiced longer, the proportion of cavity users among forest-dwelling vertebrates designated "at risk" is higher [4].

I review kinds of cavity use, present a general framework of cavity use in the PNW, review key factors influencing cavity use, and interpret those in terms of management implications. Focus is on primary excavators, but all birds and mammals commonly using cavities are included. Summary tables and figures highlight regional differences: coastal forests (under maritime influence), subboreal plus boreal forest, and inland (all other forests). Common and scientific names follow the American Ornithologists' Union (birds) and British Columbia Conservation Data Centre (mammals).

2. Kinds of Cavity Use

Two broad groups of cavity users are distinguished: primary excavators, such as woodpeckers, that excavate their own cavities and secondary cavity users, such as bufflehead ducks (*Bucephala albeola*), tree swallows (*Tachycineta bicolor*), and northern flying squirrels (*Glaucomys sabrinus*), that use holes excavated by primary cavity excavators. Secondary users include species that seek a particular, often uncommon, form of natural cavity, such as brown creepers (*Certhia americana*), Vaux's swifts (Chaetura vauxi), and several bats plus opportunistic species that use cavities 50% or more of the time in some areas but not everywhere, such as black bears (Ursus americanus), porcupine (Erethizon dorsatum), and some bat and rodent species. In analyses following, such unconventional and opportunistic users are grouped with other secondary cavity users.

Primary excavators show different abilities to excavate. Two groups are recognized: species that forage by drilling, boring, or hammering into wood or soil and species that probe or glean bark, branches, and leaves to acquire prey. The former group is termed strong excavators. It includes most woodpeckers, sapsuckers, and the northern flicker (*Colaptes auratus*). Strong excavators are typically well-adapted for creating holes in trees and have reinforced skulls and ribs and chisel-like beaks [6]. Weak excavators include chickadees, nuthatches, and those woodpeckers that forage primarily by probing and gleaning, extracting seeds, or capturing insects in flight (e.g., acorn (*Melanerpes formicivorus*), downy (*Picoides pubescens*), Lewis's (*M. lewis*), Nuttall's (*P. nuttalli)*, and white-headed (*P. albolarvatus*) woodpeckers). Despite using cavities to nest, weak excavators are less well adapted to excavation than are species that drill into wood to forage, so often use cavities initiated by strong excavators. Strong excavators are generally large birds; weak excavators are mostly smaller species.

The larger species of strong primary excavators can act as keystone species, providing nest, den, and roost sites for other cavity-using species. If their requirements are lacking, secondary cavity users may be lost [7–11]. Similarly, sapsucker foraging activity creates feeding opportunities for many other species. At least 23 bird species, 6 mammal species, and numerous arthropods (9 orders and 22 families) have been reported feeding at sapsucker holes [12–14]. Woodpeckers also can sometimes constrain the abundance of forest "pest" insects [15, 16]. Loss of strong excavators would seriously disrupt forest ecosystems.

In the PNW, 67 vertebrate species use cavities more than 50% of the time, either generally or regionally; more species are opportunistic in their use of tree cavities. A small component of strong, primary excavators creates cavity sites for many more species (Figure 1). There are 22 primary cavity excavators and 45 secondary cavity users relying on hollows or cavities, not all of these excavated by birds. Only 9 species are strong excavators, affirming the role of strong excavators as keystone species. Most secondary users rely on holes excavated by primary excavators. The proportion of nest sites of secondary users excavated by other species ranged from 89 to 100% with one exception [7]; neither of two flammulated owl (*Otus flammeolus*) nest sites was excavated.

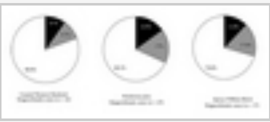

Figure 1: Proportions of strong primary excavators (black), weak primary excavators (gray), and secondary cavity users (white) among vertebrates using cavity sites in three biogeoclimatic zones of British Columbia: Coastal Western Hemlock, Ponderosa Pine, and Sitka Willow Birch (n = number of cavity–using species). Biogeoclimatic zones are described by [5].

Birds (48 species) and bats (11 species) represent 88% of species consistently or commonly using cavities. More bird than mammal species use cavities; mammals using cavities or hollows range in size from bats to grizzly bears (*Ursus arctos*). Other than for some bats and squirrels, mammal use of cavities is more opportunistic than it is for birds. Amphibians and reptiles also use cavities in snags and stumps opportunistically [17–19].

Larger snags provide more room and are longer lived, so provide greater opportunities for cavity use. The number of cavity-using species thus decreases with decreasing diameter of the dominant tree species. In the north, where trees are small (Spruce Willow Birch of Figure 1), the numbers of cavity users is much reduced.

Figure 1 excludes opportunistic cavity users that are included with secondary users in analyses following. Many of these are smaller birds and mammals that do not require cavities but will use them; some larger species (e.g., great horned owl, *Bubo virginianus,* and porcupine) also are opportunistic. In any forest type there also are a few individualist species that seek particular cavities not excavated by birds. Vaux's swifts, for example, nest and roost in hollow snags large enough that they can circle into and out of them [20]. Brown creepers, like some amphibians and reptiles, often nest or seek cover under slabs of loose bark [21]. Some cavity users (American martens, *Martes americana*; fishers, *M. pennanti*; black bears) are too large to rely on cavities excavated by birds. They rely on cavities formed by decay or fire. Such cavities are becoming uncommon, because old, large trees are increasingly uncommon.

3. Biology of Cavity Use and Associated Predictions

Hairy woodpeckers (*Picoides villosus*) need about 20 days to excavate their nest [22], as do yellow-bellied sapsuckers (*Sphyrapicus varius*) [23]. That is 20 days of hammering bill and head against wood in a small space, at rates of 100 to 300 times per minute [24]. There has to be some benefit to this behavior, and there is: cavity-using species benefit from the protection cavities, provide their young from predators, and shelter from weather in the nest, den, or roost. Because of their high-energy demands and sensitivity to temperature, bats often select cavities with favourable microclimates [25, 26]. For birds, the ideal cavity nest is located where the outer wood is hard to prevent predators from tearing open the nest, but the inner wood is soft to allow easy excavation. Soft inner wood may be required, due to the difficulty of chiseling wood in an enclosed space. Heart rots, preferably localized, are thus of prime importance. Generally, all primary excavators seek decayed heartwood [27–31]. Stronger excavators will chisel through sound wood to reach decay. For weak primary cavity nesters, harder outer wood is desirable to reduce predation, but these species are not adapted to excavating hard wood. They must either compromise with softened sapwood, or find existing holes in hard outer wood, such as those at dead branch stubs. The ideal cavity also should be high up a tree to avoid ground-dwelling nest predators, such as weasels (*Mustela*) and rodents.

The bole or branch, where the nest is located, must be wide enough to accommodate the animal and its eggs or young. Size of the cavity can affect productivity; several cavity-using species have been found to be more productive in larger nest boxes [32–35]. Together, these two factors (protection from predators and size) promote a preference for large diameter trees in which the bole is a suitable width at a greater height. When trees are sound, greater size also reduces the danger of the tree or snag breaking. The importance of softened heartwood also promotes preference for larger trees, because larger trees are usually older trees that have had time to experience heart rot. The search for decayed wood, appropriate stem diameter at the nest, and height above the ground explain many of the preferences documented for primary excavators.

Unlike primary excavators, excavating a cavity is not part of the breeding behaviour of secondary cavity users. With regard to cavities, secondary cavity users "take what they can get" with certain limitations. The most obvious limitation is that the cavity must be big enough. Mountain bluebirds (*Sialia currucoides),* for example, rely primarily on nests made by flickers, rather than those of the smaller woodpeckers or sapsuckers [11]. The nest also needs to be near the appropriate foraging habitat, which is not forest for many secondary cavity users (e.g., cavity-nesting ducks, swallows, bluebirds, American kestrels, *Falco sparverius*). Whereas primary excavators usually make or modify a new cavity each year, secondary users will return to the same cavity as long as it remains stable [36]. Because secondary users are relatively abundant compared to the primary excavators, competition for cavities can be intense [37, 38]. Where opportunities exist (e.g., holes at shed branches, stem breakage), secondary users seek more stable, living trees, but many end up using preexcavated holes in dead trees.

The preceding statement on the biology of cavity use provides a simple model or framework to unite research findings, explain patterns of observed use, and clarify trade-offs that can, or cannot, be made in snag management. The framework also generates expectations or predictions that can guide the questions posed in synthesis. Four broad predictions and associated corollaries were tested using attributes commonly employed to describe trees or snags used as cavity sites (tree species, size of tree, decay state, and snag density).

(1) Ability to excavate wood permits greater selectivity, with the range of sites used becoming broader from strong excavators through weak excavators to secondary users. Where possible, secondary users will use live trees.
(2) Strong excavators will select trees with less visible signs of decay than will weak excavators. Intense competition among secondary users will relegate most to use dead trees, where existing cavities are more common, rather than more stable, live trees.
(3) To attain desired protection, selection of tree species will reflect the tree's ability to compartmentalize decay. Deciduous trees more often contain internal rot surrounded by a sound outer shell than do conifers, so will be sought preferentially.
(4) The search for sufficient room and protection from predators will produce selection for the largest suitable cavity site available, as high above ground as possible. Strong excavators will enact selection more effectively.

4. Decay

The energy demands of excavation make softened wood or decay a dominating factor in selection of cavity sites. I review how decay is initiated, then examine patterns of use by primary excavators of cavities and secondary users.

4.1. Natural Disturbance and Decay

How a tree dies influences snag longevity and onset of decay. Research has identified tree species, tree size, decay stage, crown scorch, and stand density as major factors determining snag longevity [39–43]. Natural fire regimes influence the kinds and amounts of dead wood present [44]. The role of fire is apparent within the 12 broad forest types of British Columbia. Within forest types, the proportion of species using cavity sites decreased significantly with increasing fire size and intensity; species richness of cavity users decreased significantly as fire-return interval lengthened, and snags were created less frequently [45, 46]. Generally, snags created by fire fall sooner than do other snags. The species of snag has less effect on snag longevity than the method of creation and tree diameter [42]. Trees of larger diameter remain standing longer regardless of source of mortality, and pines (*Pinus*) stand longer than firs (*Abies*) [42]. *Pinus ponderosa* killed by fire remained standing longer than those killed by bark beetles [47–49]. Fire can encourage beetle attack by weakening the tree. Beetle-killed trees are more attractive to cavity nesters that tend to excavate nest sites in trees on which they have foraged [50].

Wounds influence the suitability of snags by encouraging different patterns of decay. Tops broken by wind or snow encourage nesting by species from black-capped chickadees (*Poecile atricapillus*) to spotted owls (*Strix occidentalis*). In conifers, decay occurs primarily in older live trees with defects in the outer sapwood, such as broken tops. Heart rots can create the hollow trees and hollow logs sought by Vaux's swift, American marten, fisher, and black bears. Large cavities result from a fire or a living tree's defense against fungi. A tree without decay that succumbs to windthrow will never become hollow. In most most temperate hardwoods, heart rots may not require a wound to enter, occur earlier than in conifers, and are common among otherwise healthy, young trees. In some species, sapwood decays at the same time as heartwood (e.g., Douglas-fir, *Pseudotsuga menziesii*, on wet sites), while in others, sapwood may not begin to soften until decades after the tree has died, and the centre has rotted (e.g., cottonwood and poplar, *Populus balsamifera* sbsp).

Because different agents of wounding or mortality create differ forms of decay and snags, local natural disturbances help explain the abundance of particular cavity-using species in an area. Usually, the forms of mortality are too varied to have predictive utility over large regions, but successful attempts to reduce specific forms of mortality can impact the fauna. Fire suppression in lodgepole pine (*Pinus contorta*) helped create the greatest insect mortality recorded in North America, with subsequent major impacts on bird species [51]. Similarly, harvest of potential nest trees before heart rot became prevalent would seriously impact Vaux's swifts. More generally, natural disturbance regimes can provide broad guidelines to the provision of cavity sites by revealing regional patterns in the onset of decay.

4.2. Species Patterns with Decay

Many decay agents are not readily visible in the field, so researchers classify decay of live trees and snags using a set of visual classes. Most researchers in the PNW follow the classification of [16]. Wood in classes 6 through 9 of that classification is too soft to be used by cavity nesters; the five harder classes are used here. Those classes are most simply defined as 1 (live), 2 (declining), 3 (dead, bark intact), 4 (dead, loose bark), and 5 (dead, no bark). Hardness of living trees and their resistance to excavation as determined mechanically is not consistently related to visual signs of decay [52], but broad patterns with visual signs of decay are evident (Figure 2).

Figure 2: Mean decay class of trees used by strong and weak primary cavity excavators and by secondary users in North America. Black bars represent conifers; grey bars are aspen; numbers in parentheses are sample sizes—the first number for conifers, the second for hardwoods. Decay classes of [16]. Data of [28, 55–66].

Primary Excavators

In North America, primary excavators, both weak and strong, often create 80% or more of their nest sites, relying on natural cavities for the rest [7, 9, 11, 53, 54]. Prediction 1 that strong excavators are able to select cavities in less decayed wood than can weak excavators is met (Figure 2).

When nesting in trembling aspen (*Populus tremuloides*), the weighted mean decay classes for strong and weak excavators are 1.9 (live) and 3.8 (dead), respectively. Visual estimates indicate more advanced decay when nesting in conifers: 2.8 and 4.8 for strong and weak excavators, respectively. Sapwood of aspen remains firm for years after tree death [67]. Even in forests dominated by conifers, large strong excavators (e.g., yellow-bellied sapsucker, *Sphyrapicus varius*, and pileated woodpecker, *Dryocopus pileatus*) preferentially nest in trembling aspen having decayed heartwood surrounded by sound sapwood [29, 55]. They use live and dead aspen relatively indiscriminately. Most pileated woodpecker nests in aspen are in live trees [68], affirming their ability to excavate live wood and the value of a sound sapwood shell. Conversely, weak excavators, such as boreal chickadee (*Poecile hudsonica*), nuthatches (*Sitta* spp.), downy, and acorn woodpeckers, do not excavate through hard sapwood shells. They seek dead trees or dead portions of living trees [46, 69, 70]. Among secondary cavity users, both birds and mammals tend to use less advanced stages of decay in hardwoods than in conifers (Figure 2). For waterfowl, too few decay classes for nest sites in conifers have been reported to permit comparisons with hardwood use.

More studies report whether a nest tree is living or dead than report decay class (Figure 3). Two points are clear. First, tree death provides nesting opportunities; 17 of 22 species in Figure 3 rely primarily on dead trees as nesting sites (decay class 3 and greater). The large portion of dead trees among cavity sites of all excavators emphasizes the importance of rot in determining nesting opportunities. In montane aspen stands, the number of nest holes was significantly and positively correlated with the percent of trees infected by *Fomes* (*Phellinus*) [71]. In coastal forests of the PNW, the marked preference cavity nesters show for western hemlock (*Tsuga heterophylla*) over western red cedar (*Thuja plicata*) has been attributed to the greater frequency of rot in hemlock [27, 72]. Woodpeckers may nest low in decay-resistant trees where butt rots are more prevalent than stem or top rots [27, 73]. In short, excavators create cavities where decay permits, and those trees are often dead.

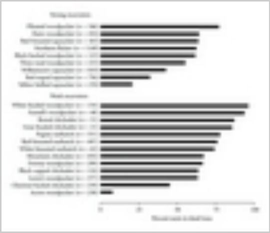

Figure 3: Percentage of dead trees used as nest sites by strong excavators and weak excavators of the Pacific Northwest (n = number of nest trees). Data of [8, 11, 28, 53, 55–57, 66, 70, 74–103].

A second point is that weak and strong excavators use trees differently. Across all 9 species of strong excavators in Figure 3, the interspecific average use of dead trees is 53.4%. Of 4403 nest trees used by strong excavators, 2229 (51.8%) were dead. Eleven of 13 species of weak excavators relied primarily on dead trees (Figure 3), even when more cavity-prone hardwoods comprised 80–100% of the nest sites. The acorn woodpecker is an exception that nests in live trees but seeks out dead limbs for cavity sites [87]. Excluding the acorn woodpecker, weak excavators located 70% (1831/2617) of their cavities in dead trees; the interspecific average across species was 74.8%. The abundance of suitable dead trees influences both groups, but weak excavators are less able to nest in living trees, and they are the larger group of species (Figure 1). Some small, weak excavators exploit advanced decay, even though it provides less protection. For example, 39 of 94 cavities excavated by chestnut-backed chickadees (*Poecile rufescens*) were close to the ground in rotting stumps [88].

The period that a snag remains firm enough to provide useful protection is shorter than the life of the snag. Analysis of preference for decay classes by comparing use to availability [46] showed the most strongly preferred decay classes were classes 3 and 4 (recently dead trees). How long a tree remains in these decay classes depends on cause of mortality, tree species, and site. Pileated woodpeckers used cavities in ponderosa pine (*Pinus ponderosa*) for 3–8 years after the trees were killed by fire [39].

Secondary Users

There are many more secondary users of cavities than primary cavity excavators (Figure 1). Dead trees provide most opportunities for secondary cavity users, whether cavities have been excavated by primary excavators or formed otherwise (Figure 4). The search for live trees and greater permanence is apparent as lower means in decay classes in Figure 2 (cavity sites in decay classes 1 and 2 are sought where available), but prior excavations and other natural cavities are more common in trees already dead (Figure 4).

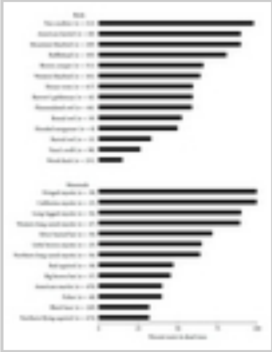

Figure 4: Proportion of dead trees used by secondary cavity users of the Pacific Northwest (n = number of nest trees). Data of [25, 60, 66, 70, 72, 75, 77, 94, 95, 98, 104–155].

Mammals denning in trees do not excavate cavities, so are more dependent upon natural cavities and rot patterns than are many birds. However, because competition for cavity sites is intense among secondary cavity-nesting birds, there is little difference in relative use of dead wood between them and mammals (Figure 4). The mean percent use of dead trees across mammal species is 63.0%, it is 60.4% for secondary cavity-nesting birds. Bats are least able to modify an existing cavity and show the strongest selection for dead trees (74.9% across the seven species). Other, larger mammals are more capable of modifying and enlarging an existing cavity in living trees so are less restricted to dead trees (38.4% across 6 species). These larger species require hollows too large to be created by birds.

Decay can create hollow, living trees, and ultimately, hollow logs through heart rot and loss of heartwood residues [156]. Less than 40% of denning trees of northern flying squirrels, American marten, American fisher, and black bears were dead, indicating the importance of sustaining older trees with large rot pockets (Figure 4). For example, most black bear dens recorded from coastal forests of the Pacific Northwest are associated with wooden structures, including trees, logs, and stumps [134, 157]. Den sites in southern, inland forests also are commonly in trees [133]. In dry inland forest, 20 of 23 den sites of radio-fitted black bears were associated with trees. Ten of these were entered through the treetop into hollow centres created by fungi [158]. Even coastal grizzly bears sometimes use hollows in living conifers or stumps [159].

Some birds also use hollow trees. All 60 Vaux's swift nests and roosts located in northeastern Oregon were in live or dead grand firs (*Abies grandis*) with hollow interiors [114]. Amphibians and reptiles use cavities rarely and opportunistically [18, 160]. Such use tends to occur in snags of decay class 3 and 4, when bark is loose and sloughing [17]. Their use of dying and dead trees is thus similar to that of the brown creeper, whose nests are almost always between the trunk and a loose piece of bark on a large, typically dead or dying tree [161].

Predictions 1 and 2 are met. Because strong excavators have more options, their cavity sites are more closely associated with more stable and preferable sites in live and recently dead trees (Figure 2). Decay classes used by weak excavators tend to be more advanced. The mean decay class of trees used by secondary users is relatively low (Figure 2), indicating a preference for living trees, but most cavity sites are found in dead trees (Figure 4).

5. Tree Species

The ideal cavity is in a stable, living tree. How a tree compartmentalizes fungal attack determines the likelihood of an ideal cavity. Broadleaved, deciduous tree species commonly isolate decay-softened wood inside a hard shell. When assessed by visual decay classes, broadleaved trees harbouring internal decay more often appear healthy (e.g., fully leaved) than do decayed conifers. Broadleaved tree species are conventionally termed "hardwoods." For a cavity-excavating bird, however, they are "softer" or better sites for excavation than are conifers (conventionally termed "softwoods"). The intact, outer sapwood shell provides stability and structure, with decayed wood a short distance beyond the shell. Conifers, however, often remain standing longer after death than do most hardwoods (large cottonwoods may be an exception). We thus expect (prediction 3) selection to be for live hardwoods when available and towards dead conifers when hardwoods are not available, with foraging preferences sometimes dominating. That expectation is met. Cavity nesters often chose hardwoods for 80–95% of their nest sites even where hardwoods comprised only 5–15% of the available tree stems [29, 53, 55, 162]. For bird species in Figure 2, conifer nest trees tended to exhibit more advanced decay by visual classes than did hardwood nest trees. Most conifers were dead.

Weak excavators are more often limited to dead trees (Figure 3), so availability of living hardwoods has greater influence on cavity site selection by strong excavators. Across 9 species of strong excavators, the percent of dead trees used declined significantly, as the percent of hardwood trees used increased ($P < 0.001$) [163]. The relationship accounts for much variability among the 46 studies aggregated in Figure 5. For example, in a large sample for pileated woodpeckers ($n = 105$ nests) all available nest trees were conifers, and 99% of the nests were in dead trees [57]. Conversely, where hardwoods were available but scarce (<10% of stems), 26 of 27 nest trees were in trembling aspen, more than 85% of them living [29]. Similarly, northern flicker selected snags for 33% of their nest sites when nesting in hardwoods ($n = 261$), increasing to 65% when nesting in conifers ($n = 141$) [77].

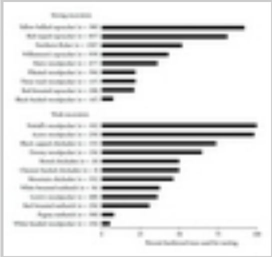

Figure 5: Percent use of hardwood by primary cavity excavators of the Pacific Northwest (n = number of nest trees). Data of [8, 11, 28, 53, 57, 58, 61–64, 70, 77, 79, 81–85, 87–93, 95–101, 103, 110, 164–185].

Selection for specific tree species as cavity sites has been evaluated for studies reporting both use and availability [163]. In the PNW, tree species selected disproportionately to their availability include trembling aspen, western larch (*Larix occidentalis*), and ponderosa pine. Trembling aspen is especially favoured. Several bat species also prefer to roost in aspen, probably because aspen is cavity prone [25, 60, 147]. In coastal forests, where aspen is lacking, primary excavators favour bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) disproportionately. Generally, lodgepole pine and the true firs (*Abies*) appear least favoured as cavity nesting sites [163]. However, a bird must feed itself before it can nest. Where black-backed (*Picoides arcticus*) and American three-toed (*Picoides dorsalis*) woodpeckers concentrate their foraging in beetle-ridden lodgepole pine, they also concentrate their nesting in lodgepole pine [164, 186]. In the absence of recent fires and beetle-infested trees, three-toed woodpeckers' primary habitat is mature or old-growth coniferous forests with an abundance of insect-infested snags or dying trees [187]. In old-growth Engelmann spruce (*Picea engelmannii*)-Subalpine fir (*Abies lasiocarpa*) forests all nests of three-toed woodpeckers were in Subalpine fir [165].

Although hardwoods are sought when available, use of hardwoods often is flexible. In the southern interior of British Columbia, all 243 nests of primary excavators found occurred in hardwoods, although hardwoods covered only 5% of the study area dominated by Douglas-fir [29]. In western Oregon, where hardwoods were scarce, the identical bird species nested mainly in Douglas-fir [188]. Flammulated owls show similar differences over their range. Cavities in oaks (*Quercus* spp.) and trembling aspen were used where they were prevalent [189–191]; elsewhere in its range, the owl nests in ponderosa pine and Douglas-fir [192–194]. Similarly, where large, hollow hardwoods were not available, all cavities used by Vaux's swift ($n = 58$) were in large grand fir [114].

Flexibility is not universal and is constrained by foraging requirements. Nesting of some weak excavators (e.g., white-headed woodpecker; pygmy nuthatch, *Sitta pygmaea*) is largely restricted to conifers (Figure 5). Throughout its range, only 14 of 256 white-headed woodpecker nests have been reported from hardwoods. The restriction is related to a diet high in pine seeds [8, 93]. The pygmy nuthatch shows a similar strong and almost exclusive preference for long-needled pine forests [195]. Restricted diets limit the acorn woodpecker and some sapsuckers (once trees leaf out) largely to hardwoods and other woodpeckers, such as black-backed and three-toed woodpeckers, to conifers (Figure 5). Weaker excavators, such as Lewis's and white-headed woodpeckers, that nest and forage in coniferous trees, are potentially threatened by forest practices, because the conifers in managed forests may not become old and decayed enough to permit excavation. Both Lewis's and white-headed woodpeckers are designated "at risk" in the PNW.

The general model predicts that selection of tree species should reflect the tree's ability to compartmentalize decay, frequently leading to selection of hardwoods. Foraging needs modify selection, but selection for cavity sites still reflects trees' species-specific decay patterns. In the PNW, that generally means hardwood species such as aspen, cottonwood, and birch (*Betula*) are preferred. Among hardwoods, primary excavators select decay-prone species over more decay-resistant species [196]. Fungi commonly invade live aspen, softening the heartwood, while the sapwood remains unaffected. Douglas-fir may be more abundant in the area but often decays from the outside in; that is, decay softens the sapwood before it affects the heartwood [197, 198]. By the time the heartwood is sufficiently decayed to allow excavation, outer layers of wood are sloughing. Smaller, weaker excavators, such as chickadees and nuthatches, sometimes have no choice but to use decay-softened sapwood [72, 88, 199]. Where hardwood species are not common, birds excavate more dead conifers. Rot patterns change both regionally and with the mix of tree species, impeding ready transfer of findings among areas. In coastal forests, western hemlock often harbours heart rot [200, 201], while the more decay resistant western red cedar can contain butt rots [27]. It appears to be the relative amounts of these fungi that shift nesting preferences between western hemlock and western red cedar. Similarly, where the root rot *Armilleria sinapina* creates butt rot in aspen, bat roosts may be as low as 10 cm above ground [202].

Preferences for hardwoods, coupled with regional differences in relative abundance of hardwoods, produce regional differences in use of hardwoods. These are illustrated for birds in Figure 5 and mammals in Table 1. The trend in declining proportions of hardwoods used by mammals as den or roost sites from boreal through inland to coastal forests reflects the relative abundance of hardwoods. Black bears are an exception; boreal hardwoods do not attain suitable diameters for bear dens. Without context, the data of Figure 5 do not make a strong case for selection of hardwood cavity sites by birds. Mean percentages of hardwoods as nest trees are 41.8% and 50.1% for strong and weak excavators, respectively. The context is that these species are using from 40 to 50% hardwoods as nest sites in forests where prevailing climate strongly favours conifers over hardwoods [230], and the large majority of the trees are conifer [163, 231]. Prediction 3, hardwood nest sites are sought preferentially, is affirmed.

Table 1: Regional use of standing hardwood trees as den, nest, and roost sites by mammals. Data of [25, 59–61, 128–130, 139, 140, 143, 144, 148–153, 203–229].

6. Size of Tree

The general model states that decay is the major influence on nest site selection, and susceptibility to decay is a major factor in tree species selection (Section 5). Decay, when "walled off" by living wood, provides the initial cavity site and protection. Size confers additional protection (height above ground) and room. The broad prediction 4 of the model embraces more specific corollaries about selection for size.

(i) Birds seek larger diameters (partly by seeking decay or older, larger trees; partly by seeking greater cavity height above ground).
(ii) Selection for taller heights will be less evident than for larger diameter (due to stem taper and many nest trees and snags having broken tops).
(iii) Larger bird species will tend to select larger, older nest trees (partly to seek more room, but primarily because they are better able to excavate so can pursue opportunities for greater protection in taller, larger trees).
(iv) For the same bird species, diameters sought in nest trees will be larger in conifers than in hardwoods (largely because conifers usually require longer periods to attain rot, during which they attain greater size).
(v) Relations between size of nest tree and size of species will be less apparent among secondary cavity users (because they "take what they can get").
(vi) No matter the animal's size, most den trees of mammals will be large, especially in conifers (because they rely greatly on natural cavities; trees are older, thus larger; height above ground may be less important for mammals because they are better able to defend themselves than are birds).

6.1. Diameter

I found 194 samples across 19 bird species that related nest tree diameter at breast height (dbh) to size of bird when nesting in either hardwood or coniferous trees. Larger diameter trees or snags are clearly preferred by cavity-nesting birds. In 30 of 31 comparisons, diameters of trees and snags used as nest trees were greater than the mean diameter of the available pool [232]. The same bird species does tend to use larger diameters when nesting in conifers than in hardwoods (Figure 6). For example, mean dbh of nest trees of pileated woodpeckers nesting in inland conifers was 79.3 cm, but only 54.2 cm in inland hardwoods; comparable values from coastal sites were 77.9 and 44.5. cm. Across all strong excavators, mean nest tree diameters in conifers were 82.2 cm on the coast and 53.7 cm inland. Comparable values when nesting in hardwoods were 45.9 and 36.8 cm. Values for weak excavators nesting in conifers were 86.8 cm on the coast and 55. 3 cm inland; when nesting in hardwoods, values were 45.4 cm and 38.4 cm.

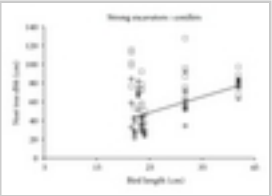

Figure 6: Mean diameter (dbh) of primary excavator nest trees or snags as a function of bird length (bill to tail length) in inland (○) and coastal forests (▫) of the Pacific Northwest. Regression lines for inland forests are shown; there were no significant regressions for coastal forests. Bird lengths from [234]. Data of [8, 11, 53–55, 57, 61–64, 68–70, 72, 74, 77, 79, 80, 82, 83, 86, 87, 91–94, 96–99, 103, 118, 162, 164–172, 188, 199, 235–251].

This pattern follows from patterns of rot. In the PNW, hardwoods generally rot at younger ages and smaller sizes than do conifers [197, 233]. Conifers, in particular, grow faster on the coast and attain larger sizes before rot has developed. The tendency for birds to select much larger conifers on the coast than in the interior affirms the pattern. Regional differences in size and growth rates are less for hardwoods, so interregional differences in size of hardwood trees used are less. Size of nest tree selected differs little between strong and weak excavators on the coast or inland.

Larger birds seeking larger trees is apparent only for inland forests (Figure 6). In coastal forests, there is little tendency for larger strong excavators to seek larger trees, because even the smallest of them sometimes excavate in very large trees. The latter observation suggests that coastal conifers attain large sizes before even small pockets of rot develop, again affirming the role of rot in nest tree selection. Both strong and weak excavators select larger conifers when nesting in conifers than when nesting in hardwoods. The tendency is stronger in small, weak excavators that require well-developed decay (Figure 6).

There is little relation between body size and secondary cavity nesters in conifers, but not in hardwoods (Figure 7). Even relatively small secondary nesters select large trees when nesting in conifers, there apparently is no need to do that in hardwoods. Nest tree diameters must be large enough to accommodate a cavity with room for an adult bird and nestlings, but sizes in conifers usually exceed that requirement. The selection of trees much larger than the size of cavity required reflects not only pursuit of height above ground, but age and the size at which heart rot develops. That occurs at younger ages and smaller sizes in hardwoods. Collated diameters of conifer nest trees of tree swallows ranged from 18 to 78 cm. Flammulated owls are only slightly larger than a sparrow, but nested in ponderosa pine averaging 57.7 cm dbh on southern aspects and 71.7 cm on northern aspects (data of [194]). The difference reflects greater rates of growth on north aspects, thus size at the age when rot appears. Pygmy nuthatches, flammulated owls, white-headed woodpeckers, and pileated woodpeckers all nest primarily in large ponderosa pine or Douglas-fir in at least some regions [57, 92, 192, 252], showing little relationship between size of bird and diameter of tree during nest site selection in conifers (Figures 6 and 7). I found few recorded diameters of conifer nest trees for larger species, such as waterfowl and the barred owl (*Strix varia).* Northern hawk owl (*Surnia ulula*), barred owl, bufflehead, hooded merganser (*Lophodytes cucullatus*), Barrow's golden eye (*Bucephala islandica*), and wood duck (*Bucephala islandica*) nests were recorded primarily in hardwood species.

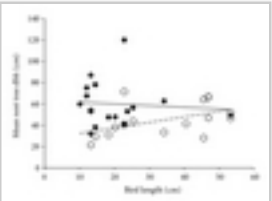

Figure 7: Mean diameter (dbh) of nest trees or snags used by secondary cavity nesters as a function of bird length (bill to tail length) in conifers (◆) and hardwoods (○) of the Pacific Northwest. Linear regression relationships are shown by a solid line for conifers (nonsignificant) and dotted line for hardwoods ($P < 0.01$). Bird lengths from [234]. Data of [11, 55, 61, 94, 97, 98, 104, 107, 115, 116, 120, 122, 155, 253–257].

Milling efficiency constrains the sizes of trees grown in managed forests. Optimal milling efficiency varies with mill configuration, but for most sawmills in the PNW the preferred maximum log diameter is from <45 to 50 cm [258]. That has been further lowered where salvage of trees killed by mountain pine beetles dominates the harvest. It has been suggested for inland forests that trees must be at least 23 cm dbh to provide a nesting site [236]. Most reported values exceed 23 cm dbh (Figure 6), but a few smaller mean values have been reported for black-capped and mountain chickadees (*Poecile gambeli*), red-breasted nuthatches (*Sitta canadensis*), and downy woodpeckers (*Picoides pubescens*), especially when nesting in hardwoods (Figure 6). Mean diameters of conifer nest trees in inland forests consistently exceeded 50 cm dbh for several species, including red-breasted (*Sphyrapicus ruber*), yellow-bellied and Williamson's sapsuckers (*Sphyrapicus thyroideus*), and pileated and white-headed woodpeckers. In all but one study, data for the northern flicker [97] and Lewis's woodpecker [245] also exceeded 50 cm dbh.

Of these species, only the white-headed and Lewis's woodpeckers are weak primary excavators, and several play keystone roles in particular regions. Three are candidates for designation or are designated "at risk" in portions of the PNW (Lewis's, pileated and white-headed woodpeckers), and one has two subspecies designated (Williamson's sapsucker). In coastal forests, some small birds (chestnut-backed chickadee, red-breasted nuthatch) consistently selected nest trees with a mean dbh >50 cm, indicating the strong role of age and decay in nest site selection by weak excavators (the chestnut-backed chickadee frequently nests in stumps when it cannot find large trees with rot). Habitat maintenance and milling efficiency are incompatible for some species.

Preferred roost trees also can exceed the maximum diameter for milling efficiency. Unlike nests, which often are excavated anew each year, roosts usually are sought in natural cavities. The average diameter of 123 pileated woodpecker roost trees was 71 cm [242]. Most of these were grand fir extensively decayed by Indian paint fungus (*Echinodotium tinctorium*). Pygmy nuthatches use communal roosts housing up to 100 birds during winter [259]. In Arizona, these roost sites averaged 73.2 cm dbh [252]. Similarly, the hollow trees or snags used by Vaux's swift must be large enough to allow the swift to fly up and down within the tree or snag. The mean dbh of 18 roost trees of Vaux's swift was 77 cm [260].

Mammals do select large trees for cavity sites (Table 2). Emphasis here is on implications to forestry, so only studies for which ≥40% of roosting or denning sites were in tree cavities, or bark fissures are summarized in Table 2. In some areas, species such as the red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel primarily use platforms or mistletoe brooms; some bat species (e.g., pallid bat, *Antrozous pallidus*, and fringed myotis, *Myotis thysanodes*) use a variety of substrates for roosting. For cavity or roost sites, even small bats use larger trees. Most studies of tree-using bats have found that species selected for larger diameters and greater heights than those of random trees [261]. Data of Table 2 extend that finding. One result is that diameters and heights selected vary with region, generally increasing from subboreal and boreal forests through inland forest, attaining their greatest values in the coastal forests where trees are largest (Table 2). The pattern reflects the age, thus size, at which common tree species develop heart rot or deeply furrowed bark.

Table 2: Characteristics of trees and snags used as denning and roosting sites by mammals, weighted means by species. Data of [25, 55, 59, 60, 123–130, 134–144, 146, 148–150, 152, 153, 162, 203–222, 262–306].

Differences in regional availability of large trees are most clear for the largest species in Table 2, black bear. Along the coast, from Vancouver Island south through Oregon, >95% of black bear dens were in large dead or dying trees and downed wood (Table 2 and [307]). In inland forests with trees of smaller stature, 69% of black bear dens were in wooden structures (Table 2). Mean dbh of hollow, black bear den trees is >100 cm in both coastal and inland forests. In boreal forests, only 12.3% of dens were in wooden structures. That value underestimates the significance of large trees to black bears. Of the 89 earthen den sites in boreal forest, 41% were under trees or stumps, 23% were under logs, and only 36% were directly into soil [300]. Grizzly or brown bears also use hollowed trees, though infrequently, in British Columbia [159] and Europe [308]. Most brown bear dens in Scandinavia were reported from ant hills and stumps [309].

Other than for the largest species, there is little relation between the size of tree selected and the size of the mammal. Bats use larger trees (Table 2), because they often use either natural hollows or cavities excavated by woodpeckers. The difference between hardwoods and conifers noted for birds applies (Figure 6). Diameters of bat roost trees on inland sites averaged 53.8 cm dbh ($n = 225$) for conifers and 48.1 cm for hardwoods ($n = 225$; Table 2). Six mammal taxa in Table 2 that use trees or snags >50 cm are listed as "sensitive" or "at risk" in the PNW (Keen's myotis, northern myotis, black bear (subspecies *Kermodei*), grizzly bear, fisher, and American marten).

Shape of the diameter distribution is more informative than the mean. Cumulative frequency distributions (CFDs) of snags tend to have long tails as small numbers of scattered large snags gradually accumulate (Figure 8). These tails raise mean values. That pattern is particularly evident in Figures 8(a) and 8(c). In coastal forests, active (used) snags were larger (height and diameter) than inactive or unused snags in old-growth areas ($P < 0.05$); snags in 70- to 100-year-old second growth were smaller than either active or inactive old-growth snags ($P < 0.01$) [27]. Only 14.7% of nest sites were located in snags <46 cm dbh (Figure 8(a)). Figure 8(b) illustrates the CFD of diameters of aspen nest trees over a range of about 15 to 55 cm dbh. Steep parts of the curves indicate the most sought diameters of nest trees in the region and are clearly evident in Figures 8(b) and 8(c). Most data on snag use are collected from unmanaged forests. Figure 8(d) compares nest trees selected by red-breasted nuthatches in managed and unmanaged forests of different tree species. The similarity of snag sizes selected suggests some governing relationship within the two disparate forest types.

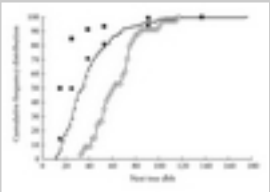

Figure 8: Cumulative frequency distributions (percent) of snag and nest tree measurements: (a) dbh of old growth snags without cavities (inactive, dotted line), old growth snags with cavities (active ○), and snags in younger stands, 70 (▪) and 100 (●) years of age (all inactive; data of [27, 310] for the Coastal Western Hemlock zone); (b) dbh of aspen nest trees in the Cariboo (data of K. Martin); (c) dbh of nest trees used by three species in unmanaged Interior Cedar-Hemlock: red-breasted nuthatch (▪), northern flicker (○), and red-naped sapsucker, *Sphyrapicus nuchalis* (▲) (data of C. Steeger and M. Machmer for the Interior Cedar-Hemlock zone); (d) dbh of nest trees used by red-breasted nuthatches in managed (▲) and unmanaged (○) stands (from [232]: Figure 2).

Three points are apparent. First, birds show a central tendency (steep portion of the CFD) when selecting nest tree diameters, even across different forest types (see also [28]). Second, because of the long tails in many distributions, this tendency is better reflected by medians (which typically are smaller than means), but means are more often reported. Third, minimum nest tree diameter is a poor management target, because it ignores the central tendency. A more appropriate management target would be to provide trees larger than the median diameter at which heart rot commonly accrues in that forest type.

6.2. Height

The fact that dbh of trees used for nesting may be much larger than the size of cavity needed by birds reflects the benefits of nesting high in trees to achieve greater protection from mammalian predators [113, 311]. In living trees, diameter and height usually are closely related. That is not true of snags because many have broken tops. Nonetheless, we expect cavity-nesting birds to seek out taller nest trees, both live and dead, from those available.

Taller snags generally are used disproportionately to their availability, but the mean height of nest trees exceeds that of the mean available only about half the time [232]. That occurs because many snags with broken tops are used. For example, in interior Douglas-fir, 14 of 20 nests of red-breasted nuthatches were within 2 meters of the top of decay class 4 Douglas-fir snags with broken tops; 21 of 22 nests in Englemann spruce-Subalpine fir forest were in similar class 4 Subalpine fir snags, broken off by heart rot and wind [232].

On the coast, mean reported nest heights averaged 16.9 m, 14.10 m, and 10.1 m for strong primary excavators, weak primary excavators, and secondary users, respectively. Comparable values from inland sites were 9.4, 8.9, and 7.4 m (e.g., Figure 9). Small, weak excavators often use soft substrate, commonly found in short, broken-topped snags or stumps. That tendency is most apparent among chickadees and accounts for some of the short nest tree heights in Figure 9(b). Larger excavators, both weak and strong, also occasionally use older, broken-topped snags or stumps (e.g., northern flickers, downy, black-backed, three-toed, and white-headed woodpeckers in Figures 9(a) and 9(b)). Secondary users most often nest close to the ground (Figure 9(c)). Reported tree or snag heights are naturally taller than nest heights. On the coast they were 25.2 m, 16.5 m, and 18.1 m for strong primary excavators, weak primary excavators, and secondary users, respectively. Comparable values for inland sites were 19.5 m, 12.5 m, and 16.1 m. The relatively tall tree heights for some secondary users reflects the use of cavities in larger taller trees by larger species such as kestrels and owls.

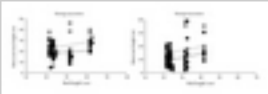

Figure 9: Mean height of primary excavator nest trees or snags and nests as a function of bird length (bill to tail) in inland (•) and coastal (▪) forests of the Pacific Northwest. All bird lengths from [234]. Regression lines are dotted for coastal forests and solid for inland forests. Data of [7, 8, 11, 29, 53, 55–58, 65, 69, 70, 72, 74, 75, 78–82, 84, 85, 87, 91–94, 98, 103, 108, 112, 169, 173–175, 188, 199, 238, 241, 242, 249, 312–323].

Among strong excavators, larger bird species locate their nests higher above ground ($P < 0.05$), and there is a tendency for larger birds to locate nests in taller trees and snags ($P < 0.05$), but there is great variability due to broken tops (Figure 9(a)). Across all species, however, nest height shows little relation with size of the bird ($r^2 < 0.10$). A general lack of relationship between bird size and nest height is expected, because stem taper means that larger cavities sought by larger birds cannot be as near the top of the tree as those of smaller birds. Management targets can be based on diameters alone.

7. Density and Distribution

There is little clarity on meaningful measures of density and distribution of trees for cavity nesters. Several issues, including scale, obscure appropriate metrics. For example, the area over which to measure density is ill defined and almost certainly a function of species-specific territory sizes, which themselves are a function of foraging opportunities; many cavity-using species use trees or snags for foraging as well as nesting (forage and nest trees have different attributes, but both are necessary); primary and secondary users of cavities usually forage differently; there are tradeoffs in the relative use of hardwoods and conifers, but researchers sometimes report only conifers; and numbers of snags in the immediate area of the nest tree likely overestimate requirements, because snags tend to occur in clumped patterns that do not extrapolate over large areas.

Predictions of expected responses are thus limited.

(i) Responses to density will be inconsistent and better exposed by extremes in simpler managed stands than in highly variable natural or near-natural stands.
(ii) Cavity nester density will be asymptotic against nest tree density and limited by factors other than snag density as snag density increases.
(iii) There will be little response to snag density in hardwood stands because a high proportion of living hardwoods contains heart rot.
(iv) Clumped distributions of nest trees (including snags) will better sustain primary excavators, because they are more likely to include foraging requirements.
(v) Many secondary users will favour dispersed retention because they forage in more open areas.

Density

Density of cavity-nesting birds is inconsistently related to measures of snag density. Generally, studies surveying natural stands with many snags obtain weak relations (e.g., 27, 61, and 316), while those including managed stands, in which some or all snags were removed, find stronger relations (e.g., [54, 70, 324]). In managed forests where snag density was high, there was no relation between cavity nester and snag density [325]. Including simpler managed stands in analysis is more revealing of snag effects than using only natural stands. Within stands ranging from unmanaged to scattered seed trees, density of snags 25–50 cm dbh was a strong predictor of red-breasted nuthatch and chickadee densities; $r^2 = 0.94$ and 0.83, respectively (mountain and chestnut-backed chickadees combined) [324]. Such relationships may indicate consistent nest site limitation or better foraging opportunities in stands with more snags (e.g., older stands with more insects versus thrifty managed stands).

Figure 10 illustrates relationships for stands dominated by conifers. Most variation in cavity nester response to snag density is due to sizes of the snags, so estimates of density were limited to larger snags that the birds use preferentially: ≥50 cm dbh for coastal forests and ≥30 cm for inland forests. Presence of an asymptote in density was evaluated by fitting a Michaelis-Menten relationship to data illustrated in Figure 10(a). That invokes the assumption that the rate of response (cavity nester density) is a function of the concentration of substrate (snags/ha). Response of the seven studies combined is asymptotic, with little additional increase in density of cavity nesters beyond about 3 large snags per ha (Figure 10(a)). That shape is expected among species limited by resources such as food, space, or nest sites. Birds present at 0.0 snags per ha indicate that some species can nest in snags <30 cm dbh (some of them hardwoods, unreported in data on conifers).

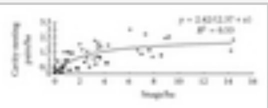

Figure 10: Density of cavity-nesting bird pairs versus snag density in primarily coniferous forests of the Pacific Northwest. Hollow symbols represent coastal forests; solid symbols are inland forest types. (a) All cavity-nesting species.[○] = [326]; snags >50 cm dbh]; [▲] = [118]; snags >30.5 cm dbh); ▫ =[327]; snags >48 cm dbh]; [▪] = [328]; snags >31 cm dbh]; [◊] = [329]; snags >51 cm dbh); [Δ]= [238]; snags >50 cm dbh]; [●]= [70]; >38 cm dbh); [⬩] = [330]; snags >50 cm dbh). Solid line is the fitted Michaelis-Menten relationship of the form cavity nesters per ha with asymptote = 2.42 and half saturation constant = 2.37 [adapted from [233]]. (b) Chestnut-backed chickadee pairs [▲] = [118]; snags >30.5 cm dbh]; [●] = [327]; snags >48 cm dbh]. [○] = [329]; snags >51 cm dbh]; ▫ = [238]; snags >50 cm dbh]. (c) Mountain chickadee pairs: [▲] = [118]; [▪] = [328]; [○] = [70].

The response shown in Figure 10(a) was consistently expressed: each individual study shows an initial increase in cavity-nester density with increasing snag density. That merely affirms large snags become limiting at densities of ≤1 per ha. The fact that the relation fits a Michaelis-Menten relationship implies that the response is consistent with limitation by substrate abundance. Small differences would shift the estimated half-saturation value between 2 and 3 large snags per ha. Relationships for some smaller individual bird species were more linear (Figures 10(b) and 10(c)). Territorial behaviour is only weakly expressed in the chestnut-backed chickadee but is evident in mountain chickadees. It is possible that competition for cavity sites is more strongly expressed within the entire cavity-nesting fauna, than within individual small species. However, data of Figure 10(c) also suggest that other variables may influence the response; at the same snag densities, data of [70] are consistently higher than those of [118]. During a mountain pine beetle epidemic, densities of both red-breasted nuthatches and mountain chickadees increased dramatically and linearly as beetles killed more conifers and provided more food. Once most of the conifers were killed, numbers of conifer snags continued to increase, but the numbers of beetles diminished and so did the nuthatches and chickadees [51]. Although the density of conifer snags increased greatly, the birds continued to nest primarily in aspen; food was a more influential variable than snag density.

Relations of Figure 10 are helpful to the extent that they reveal that low snag densities are limiting and suggest that about 2.5 large snags per ha support 50% of natural densities of cavity nesters. Current snag-retention guidelines for most North American forest types fall between 1 and 10 large snags/ha, converging around 6 to 7 trees/ha [331]. These guidelines derive primarily from work in the Blue Mountains of Oregon and are expected to sustain the full complement of cavity nesters ([16]: Appendix 22], [332]). Because of the great variation in the data, they differ little from the relationship of Figure 10.

There is a problem however. Although small and large snags are both important to cavity nesters, nesting densities usually correlate better with large snag densities than with densities of all snags. For example, in the coastal rain forest of British Columbia densities of all snags did not differ between old-growth sites and 70-year-old second growth (34.8 and 33.9 snags/ha, respectively [27]. Because many snags were larger in old growth, the proportion of snags used was about 12 times greater (16.0%, compared to 1.3% in second growth). Median diameter was about 18 cm dbh over all second-growth snags and 62 cm dbh for nest trees in old growth. Relations derived from the Blue Mountains and in Figure 10 address nesting, so focus on larger snags. Woodpeckers, however, tend to forage on several smaller snags rather than the single larger snag in which they nest. Smaller snags that represent foraging sites, but are inadequate for nesting, were present in all studies included in Figure 10 and undoubtedly influence the apparent response to snag density. Their abundance often is not reported. The number of small snags required, and the preferable distribution of snags remain obscure. The former is troubling because small snags are necessary foraging sites for many species. The latter can be evaluated by more integrative measures of retention (see below).

Data are few, but snag density appears less important in hardwood stands. In southern hardwood stands of Florida, cavity nester density increased with density of hardwood snags, though not as dramatically as in pine forests [333]; there was no increase in cavity nesters with a doubling in hardwood snags in mesophyll forest in Kentucky [334]. In mixed forests of hardwood and conifer, five of six cavity-nesting species increased dramatically during a mountain pine beetle epidemic and greater foraging opportunities [51]. Although the number of conifer snags increased dramatically, the birds continued to locate 95% of their nests in living or recently dead aspen. Densities of the five cavity nesters responding increased 5- to 6-fold with little change in density of hardwood snags. Black-capped chickadees, which did not change in density, forage primarily on insects found on living trees and showed no response to increasing numbers of beetles or conifer snag density until most trees were dead (when chickadees declined in abundance).

Distribution

Distribution has both spatial and temporal dimensions. From the broadest to finest scale, questions we ask about distribution of a resource are ordered. How do we sustain a continuous supply? Should actions be focused at the landscape level or within stands? How should within-stand efforts be distributed? How much is necessary? What kinds (e.g., sizes)?

Kinds and amounts (how much) were addressed above. Here we address the three broader questions noted. The broadest scale of distribution relates to planning for the sustained contribution of dying and dead wood. We know that if a 200-year-old tree is required 200 years from now, it must be planted now and subsequently reserved from harvest. Models that project the creation and duration of snags reveal projected shortfalls large enough to significantly impact cavity nesters [2, 3, 335]. For example, projections for managed Douglas-fir forest suggest 0.1 large snags per ha per decade [3], well below required levels of Figure 10. These models typically address the temporal scale and indicate that in managed stands snags are not being created or replenished fast enough to ensure a continuous supply. The solution appears simple—leave more trees to become snags. Solution becomes more complicated when we include the spatial scale. There often are landscape-level reserves or set asides (e.g., steep slopes, riparian areas, and reserves for a particular species) that contribute snags now and in the future. Trees and snags also may be retained within stands.

The challenge is then to determine what should be retained within stands, given landscape-level reserves and the natural rates of snag creation or fall, and how should within-stand retention be distributed? The kinds of bookkeeping and projection required are relatively simple, but we confront several challenges: (1) we usually do not have good estimates of rates of key processes (e.g., snag creation or tree mortality rates, snag fall down rates, and progression of decay or period when the snag is useful), (2) dead wood is a more transient habitat that many others and organisms are adapted to particular transient stages of decay (Figure 2 and [307]), (3) the diverse forms of tree mortality ensure stochasticity and a great deal of variation when amounts in natural stands are sampled [307, 336–338], (4) species using dead wood respond variably and may seek different sites for nesting and foraging, and, perhaps most challenging, (5) scale, which makes amount and distribution nearly inseparable. The same amount can be patchily or uniformly distributed. Patchily distributed amounts may have too little dead wood at local scales and what is local varies among species.

It is clear that many managed forests produce too few large nest trees, but once we choose to retain trees, the questions of where that retention should occur and what form it should take remain. Tolerance levels can help address the natural variation in measures of amount [339]. The issue of distribution remains. Retaining trees as landscape reserves or within harvest blocks have different costs. We need to know whether they also have different consequences. The shape of response curves relating cavity-nester abundance to proportion of forest retained permits evaluation of tradeoffs between stand- and landscape-level retention. The response of cavity nester abundance could be directly proportional to the proportion of forest retained, above or below proportional, or reveal potential thresholds (Figure 11).

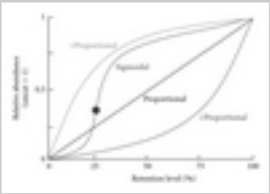

Figure 11: Examples of response curves with abundances greater than proportional, less than proportional, or proportional to retention levels, showing a sigmoidal or "soft threshold" relationship with retention levels. The dot on the sigmoidal curve shows the point of inflection. Adapted from [340].

The nature of the response curve has implications to the distribution of retention:

(i) Directly proportional to the amount of cover retained implies that within-stand and landscape-level retention contribute equally. The total abundance of the species in a landscape depends only on the total retention level, whether this is retained within stands or in landscape reserves or in a combination of the two.
(ii) Above proportional to the amount of cover retained indicates that within-stand retention during harvest is creating greater opportunities for the species within each stand. For example, in Figure 11 the >proportional response indicates that retaining 20% of trees in a cut block maintains a species at 40% of its abundance in uncut forest. That supports using retention in cut blocks at the stand level. For a given total amount of retention, stand-level retention maintains a greater abundance of the species across the landscape than would alternative strategies, such as retaining the same total amount in large reserves and clearcutting the harvested stands (all else being equal).
(iii) Total abundance less than proportional indicates that landscape-level retention is favoured because retention is less useful when "diluted" within individual cut blocks. For example, in Figure 11 the <proportional response indicates that 20% retention maintains the species at only 5% of its abundance in uncut forest. To sustain species showing such a response, it is better to allocate a given retention level to larger reserves, rather than stand-level retention (again, all else being equal).

The most helpful response to management would be a marked threshold response, that is, a sudden decline in a species' abundance when amount of a habitat variable drops below a particular value [341–343]. If well-defined thresholds were evident, they would help guide choices of target levels for retention [344]. However, the many sources of variability in natural systems means thresholds are more likely to occur as softer, sigmoidal-type relationships (Figure 11, [341, 343]). Whereas a hard threshold reveals a clear target value, a sigmoidal response or "softer" threshold suggests a mixed strategy of stand- and landscape-level retention, or of higher and lower retention levels in harvested areas. The practical point is whether the relationship has a point of inflection, where abundance changes from more to less rapidly increasing, as retention levels increase. For example, with 20% overall allocation to retention, the sigmoidal relationship in Figure 11 implies the best strategy would be to retain 35% in about half the stands with minimal retention in the rest.

In fact, most conceivable shapes of response appear in nature [345]. Few generalities are apparent among the 15 cavity-nesting species for which meta-analysis was possible: only 1 species (brown creeper in hardwoods) showed a response less than proportional to retention; 5 species showed neutral responses (these sometimes limited to particular seasons or regions); the majority profits from some within-stand retention. For some species, retention had no apparent effect until it reached levels from 15 to 20% of the original volume; others profited from some opening of the canopy. The combined response of 15 species plus 95% confidence intervals is illustrated in Figure 12.

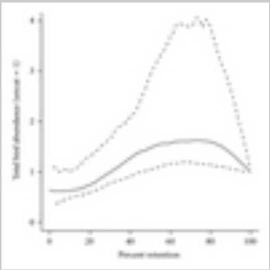

Figure 12: Combined response of 15 cavity-nesting species to percent forest retained. (a) Total abundance. (b) Similarity of the bird community in the retained forest to uncut controls. Methods of [340].

In Figure 12, the "community" is a composite of studies of 15 species [345], each standardized as 100% abundance in uncut forest. It shows that even small amounts of harvest eliminate some species, but over a wide range of retention most species are present, with a few species occurring much more commonly at high retention levels (openings <20% canopy cover). These few species—black-capped chickadee, mountain chickadee, downy woodpecker and red-breasted sapsucker—produce the wide confidence limits in abundance at higher retention levels. Clearly, some cavity nesters profit from opening of the canopy (abundance greater than that in uncut forest), and, other than for a few species, little is gained in abundance beyond 30% retention (Figure 12(a)). Collating data from several sources ensures wide scatter at the lower end, so confidence limits do not converge to near zero at zero retention. For example, northern flicker forages on the ground and is the only cavity nester for which confidence intervals do not contract towards zero abundance at zero retention at the stand level.

Even though desired amounts of retention vary across species, it is clear that all cavity nesters profit from some degree of retention. Retention silvicultural systems (e.g., green-tree retention and variable retention) contribute permanent retention—the trees will never be harvested. Other partial harvesting systems, such as regular or irregular shelterwoods, selection cuts, strip cuts, and group removals, often leave high levels of retention, but the trees are not intended to be retained permanently. Whatever the approach, trees retained within a treatment unit can be distributed in groups or as scattered individuals (dispersed retention) or as a mix of both.

Review of studies that permitted comparisons of forms of retention revealed three major patterns [346]. First, although dispersed retention of snags (high levels of removal) increased abundance and richness of secondary cavity nesters beyond that found in mature and old-growth forests, abundance of primary excavators was reduced (see also [347]). This response accounts for the increase in similarity of combined species at the highest levels of retention in Figure 12(b). Group retention better sustains primary excavators. In both logged and managed stands, nests of primary excavators often are concentrated in dense patches of snags or broken-topped trees for both strong and weak excavators [70, 72, 74, 244]. Woodpeckers also used snags in groups, even in an area where snags were uniformly distributed by salvage logging [186]. Likewise, there was no difference in nesting levels between clustered and scattered snags that had been created by topping, suggesting that some natural phenomenon was acting [315]. Trees, snags, and down wood typically occur in clumps [348]. It is unclear whether primary excavators seek dense patches of nest trees for some associated value or if it merely reflects the patchy way in which trees are killed by insects or disease.

Second, secondary cavity nesters were more abundant 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 and accounts for the increase in abundance at midlevels of retention in the combined response of Figure 12(a). Third, 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 [68], northern flicker [77], three-toed woodpecker [165], and perhaps downy woodpecker [349]). In central British Columbia, preferred nest sites for three-toed woodpeckers were within 20 meters of an edge [165].

In summary, it is apparent that snags can be limiting and that from 2 to 3 appropriately sized snags per ha appear to sustain about 50% of the natural cavity-nesting community locally (Figure 10). Individual species, however, show a variety of responses (Figure 12), with broad generalities apparent only between primary and secondary nesters. It is much less clear how much of the forest should have what snag densities. Sustained provision of habitat will differ among forest types, and the rates at which snags are produced, decay and fall. Estimating total snags required must recognize that smaller snags are used as foraging sites, and foraging sites are sometimes more limiting than cavity sites [350, 351]. More dead or dying wood than 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 [352, 353].

8. Management Implications

In forests of the PNW, most studies find significant correlations between snag density and the abundance of primary excavators (Figure 10 and review of [354]). Similar relations are evident for secondary cavity users [54]. Because we prefer that trees in managed forests do not die or become rotten, management is designed to reduce snag densities below natural levels [2, 3, 335]. One result is that a large portion of cavity-using species is listed "at risk," or "potentially at risk," globally [9] and in the PNW [46]. Over the past two decades, greater effort has been made to provide snags in managed forests (e.g., [355, 356]). Data collated here can help to guide those efforts. Comprehensive regional repositories for dead wood data and species using dead wood are available, such as DecAid for Washington and Oregon [357].

Major challenges to extracting management guidelines from available data are the fact that amounts and distribution of trees and snags are naturally interrelated, and that concern for old growth, particularly in the PNW, has focused research on older forests. The latter condition means that many studies report use based on a wide range of tree sizes; the results are "natural" but potentially inflate diameters required by the species. That is evident in regional differences in nest tree diameters (Table 1). The patterns of cavity use by birds and mammals extracted by this review cannot evade those challenges but still yields general guidelines to assist efforts at sustaining cavity-using species.

Implications following were derived from review of more than 350 studies of 67 cavity-using species occurring in the PNW. The regional focus was intended to restrict the number of species to a naturally occurring assemblage; data on use by a given species were incorporated no matter where the study occurred, including Eurasia. Varied locations act as independent samples of apparent use and preference. Even within the PNW, there are clear regional differences in patterns of nest or roost tree selection (Tables 1 and 2), much of it due to the relative abundance of hardwood and conifer species that are used differently (Figures 2, 5, 6, 7, and 9). Documenting biological reasons for regional differences within a general model aids extrapolation beyond the PNW.

8.1. Ensure Sustained Provision of Dying and Dead Trees

Many species depend on dying and dead trees and eventually logs (Figures 3 and 4). Snags come from living trees. If a species will need a 150-year-old tree that is required 150 years from now, that tree must begin growth now. Planning to sustain cavity sites must consider not just what is there now, but how that will be sustained. A practical way of providing sustained diversity of structure, including dead trees, is patchwise or group retention ([355]; e.g., Figure 12).

8.2. Retain Trees and Snags of Both Hardwoods and Favoured Conifer Species

Because hardwoods generally are preferred cavity sites (Figure 5) and provide favourable substrate at a younger age than do conifers, it is tempting to rely on hardwoods to meet cavity users' needs. Although they are favored nesting sites, we cannot rely solely on the more decay-prone hardwoods. Hardwoods are uncommon in many forests of the PNW and 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. Conifers are longer-lived and provide a longer-lasting source of cavities than do hardwoods [358, 359], so are more likely to sustain snags late into rotations. Moreover, conifer snags are required by species foraging on bark beetles or wood-boring beetles and conifer logs last longer than do hardwood logs. Favoured conifers include western larch, Douglas-fir, and ponderosa pine. Monocultures of less preferred species, such as lodgepole pine, should be avoided.

8.3. Sustain a Range of Decay Classes of Potential Nest Trees

A range of decay classes in standing trees is necessary to sustain biodiversity (fungi, arthropods, birds, and large mammals; e.g., Figure 2). The same is true for species using down wood [307, 360]. Regular inputs from harvest residues are important to maintain the total amount of down wood, but that input tends to be concentrated in a narrow range of decay classes. Retention helps sustain recruitment and ensure continual provision of different decay stages in standing and down wood. Given the patterns of succession among species on and within logs, gaps in recruitment should not greatly exceed 25 years [307]. Organisms in standing trees also use a range of decay classes (Figure 2) and similar recruitment intervals appear appropriate for sustaining standing decay. Some recruitment happens naturally within landscape-level reserves or set-asides (steep slopes, riparian areas, and reserves for particular species) and where retention is practiced. Sustained recruitment over large areas involves planning to avoid large gaps in size and decay stages as well as practices such as retention. Staggering harvest stages among adjacent stands helps sustain a variety of decay classes.

8.4. Retain a Range of Size and Age Classes

Large trees and snags provide nesting or denning sites longer than do small snags [42, 361]. However, smaller snags provide foraging sites, and many more foraging sites are needed than nesting sites. Although larger diameters usually are selected by vertebrates as cavity sites, smaller trees and logs are used. Where safety considerations encourage falling older snags during harvest, managers should ensure that snags can develop through the rotation. The desirability of a range of decay classes is well documented for bryophytes, insects, terrestrial breeding salamanders, and birds [1, 307]. 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. Retaining declining live trees, or recently-dead snags, ensures provision of later stages of decay.

8.5. Ensure That Some Large Trees or Snags Are Retained

Some large trees should be retained during both thinning and harvesting operations. Although individual species use a wide range of tree or snag sizes, they tend to select larger ones when available (Figures 6 and 7). In the PNW, studies of vertebrate-forest relations have been concentrated where trees are larger and more valuable, so existing data overestimate requirements where trees are smaller. Although data reveal many instances, particularly in coastal forests, where birds have selected larger trees, most species can be accommodated in managed forests by conifer cavity trees 50 cm dbh; hardwood trees can be smaller, and a dbh >30 cm accommodates most bird species in less productive, inland forest types [232]. However, those values appear too small for some bird species, including four designated "at risk" (Figure 6). Likewise, some mammals, including 6 taxa "at risk," select trees or snags >50 centimeters in diameter or use down wood from 50 to 150 cm in diameter [125, 134, 362]. A major implication is that stands managed intensively for fibre production often will not retain all cavity users. That implies some portion of the landscape should be left unmanaged. There is no unequivocal estimate of how much. While single target diameters are the simpler management target, tolerance intervals accommodate natural variation and the potential bias of large amounts of data collected from old growth forests [339]. Results of Figure 9 affirm that diameter is a sufficient guideline in assessing trees or snag suitability; height merits less attention.

8.6. Provide Both Aggregated and Dispersed Retention of Living and Dead Trees

Figure 10(a) suggests that relatively little is gained by providing more than 3 large snags per ha, but individual species may respond positively to greater snag densities (Figures 10(b) and 10(c). All forms of response in Figure 11 were observed, indicating that there is no single best approach. When targets are the cavity-nesting community, rather than a single species, about 30% retention maintains about 70% of community members (Figure 12(b)). The importance of variety in the distribution of retention applies equally to species reliant on downed wood [307]. If management for cavity users is to be effective at larger scales, approaches must be developed over a scale appropriate to the range of species affected and recruitment rates of snags, rather than individual land ownership.

8.7. Meet Dead Wood Requirements for Larger Species in Areas Where the Emphasis Is Not on Intensive Fiber Production

There are economic and ecological advantages to zoning the intensity of fiber production [363, 364]. In some forest types, larger mammals prefer significant amounts (100 to 200 m^3/ha or more) and large sizes (>50 centimeter diameter) of down wood (Table 2; [365]). Needs of such species are best provided in areas where late-successional attributes are being maintained. Provision of some large trees and pieces of dead wood in forests where the dominant goal is fiber production may facilitate dispersal among areas of more favorable habitat. Given the mobility of birds and patterns of larger mammals' use of space, large snags and subsequent pieces of down wood for such species can be well distributed across large areas.

8.8. Do Not Do the Same Thing Everywhere

Retention of trees in patches reduces safety risks of snag retention and windthrow [366, 367] and facilitates retention of a range of size and decay classes. It also concentrates recruitment of down wood. Some organisms favour piles of down wood, while others favour scattered pieces (review in [307]). 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 can impact shrub nesters negatively by encouraging aerial predators [368]. Any single approach will disadvantage some group of species, so a range of practices is preferable when a range of species is to be sustained in an area.

8.9. Limit Salvage Logging after Tree Mortality

Concern for biodiversity led to restrictions on green-tree harvest, particularly in the PNW. That in turn encouraged more complete harvest of dying and dead trees in areas subject to insect attack or fire kill. We learned two things. First, if all vertebrates are to be sustained in forests experiencing mortality to insects or fire, remaining standing dead trees should not all be logged. Review of more than 200 studies addressing forest harvest in beetle-killed forests [369] reported negative effects on bird, mammal, and fish species. Similar findings emerged from review of logging postfire areas [331, 370]. A second major point emerging from these reviews is that postdisturbance variation is so large that small-scale studies are unlikely to provide general principles for mitigating damage, beyond "do not take all dead trees and do not do the same thing everywhere."

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