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THE FORAGING ECOLOGY OF CAVITY-NESTING BIRDS IN YOUNG FORESTS OF THE NORTHERN COAST RANGE OF OREGON[1]

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Abstract. Cavity-nesting birds are important components of the avifauna in Pacific Northwest forests and are of special concern to land managers because of their reliance upon snags for nesting habitat. Because most research and management has focused on nesting habitat of cavity-nesting birds, the foraging ecology of cavity-nesting birds has generally been neglected. We studied the foraging ecology of the Chestnut-backed Chickadee (*Poecile rufescens*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), and Hairy Woodpecker (*Picoides villosus*) in 30- to 45-year-old, Douglas-fir (*Pseudotsuga menziesii*) forests of the Coast Range of Oregon. All four species were selective in their use of foraging substrates. Hardwoods were selected over conifers by Chestnut-backed Chickadees and Hairy Woodpeckers. In relation to randomly chosen live trees, Chestnut-backed Chickadees, Red-breasted Nuthatches, and Hairy Woodpeckers selected trees that were larger in diameter, and Brown Creepers selected trees with deeper furrows in the bark. Large diameter, heavily decayed snags and logs were selected for foraging by the Hairy Woodpecker. Foraging needs should be taken into account when managing habitat for cavity-nesting birds.

Key words: cavity-nesting, Certhia americana, *foraging ecology, habitat selection,* Poecile rufescens, Picoides villosus, Sitta canadensis.

INTRODUCTION

Cavity-nesting birds are important components of the avifauna in forests of the Pacific Northwest. Primary cavity-nesting species, birds that excavate cavities for nesting, are of special importance because they create cavities in dead wood that are subsequently used by many other species of wildlife. Cavity-nesting birds also play a key role in forest ecosystems as predators of forest pests (Knight 1958, Otvos 1965, Torgersen et al. 1990).

Most research and management approaches for cavity-nesting birds have focused primarily upon the relationships between cavity-nesting birds and snags used for nesting (Mannan et al. 1980, Neitro et al. 1985) and assume that maintaining adequate snags for nesting habitat for primary cavity-nesting species would also provide adequate foraging habitat for woodpeckers. Although woodpeckers sometimes do forage on the same types of snags that they use for nesting (Mannan et al. 1980), there is no information indicating whether management strategies that focus only on nesting habitat would provide adequate foraging habitat to support woodpecker populations. Furthermore, current management strategies rarely consider foraging needs of cavity-nesting species other than woodpeckers.

We studied the selection of foraging habitat and the foraging activities of Chestnut-backed Chickadees (*Poecile rufescens*), Red-breasted Nuthatches (*Sitta canadensis*), Brown Creepers (*Certhia americana*), and Hairy Woodpeckers (*Picoides villosus*) in young 30- to 45-year-old coniferous stands of the northern Coast Range of Oregon during the springs of 1995 and 1996. The objectives of our study were to quantify selection of foraging habitat and to describe foraging activities of cavity-nesting birds in young plantation forests.

METHODS

STUDY AREA

Four blocks of forest were selected for study, located approximately 14 km east of Tillamook, Oregon. Three stands, ranging in size from 25 to 45 ha, were located within each block. Densities of trees ranged between 150 and 700 trees ha^{-1}; trees averaged approximately 35 cm in diameter.

The study area burned during a series of in-

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TABLE 1. Categories used for describing locations of foraging by cavity-nesting birds. Vertical strata were used to describe bird use on live trees and snags and horizontal strata were used only to describe bird use on live trees.

Location	Definition
Vertical strata (relative to each individual tree)	
Lower bole	Lower half of the portion of the trunk lacking live foliage, or lower half of a snag
Upper bole	Upper half of the portion of the trunk lacking live foliage, or upper half of a snag
Lower crown	Lower half of crown of a live tree
Upper crown	Upper half of crown of a live tree
Top of snag	Top 0.25 m of a snag
Horizontal strata	
Bole	Main trunk of a tree or a snag
Short-dead branch	Dead branch < 1 m long
Long-dead branch	Dead branch ≥ 1 m long
Small-live branch	Living branch < 4 cm in diameter at location used by bird
Medium-live branch	Living branch 4 to 8 cm in diameter at location used by bird
Large-live branch	Living branch > 8 cm in diameter at location used by bird
Branch tip	Tips of living branches
Cone	Cone of a coniferous tree

tense fires between 1933 and 1951 that destroyed 140,000 ha of forest and left few live trees. The area was salvage logged, and most remaining snags were cut and left on the forest floor to reduce the potential for further fires. The area was replanted or seeded with Douglas-fir (*Pseudotsuga menziesii*) between 1949 and 1970. Today the forest is even-aged and dominated by Douglas-fir with patches of red alder (*Alnus rubra*). Western hemlock (*Tsuga heterophylla*), noble fir (*Abies procera*), and western redcedar (*Thuja plicata*) are present but rare. Common understory shrubs include vine maple (*Acer circinatum*), huckleberry (*Vaccinium* sp.), salal (*Gaultheria shallon*), and Oregon grape (*Berberis nervosa*).

PROCEDURES

We used focal animal sampling (Martin and Bateson 1986) to quantify activities of Chestnut-backed Chickadees, Red-breasted Nuthatches, Brown Creepers, and Hairy Woodpeckers engaged in foraging. We chose to study these four species because they were the only species of cavity-nesting birds present in adequate abundance to enable us to collect enough samples for use in analysis.

We located birds by sight and sound while walking transects spaced approximately 120 m apart, stopping for 3 min about every 120 m. Because independence between observations is critical to analysis of foraging data (Bell et al. 1990), we collected data on multiple individuals of a species only if distances between individuals observed during a given day exceeded 60 m for Brown Creepers and Chestnut-backed Chickadees, 100 m for Red-breasted Nuthatches, or 200 m for Hairy Woodpeckers. We used these criteria in addition to personal judgment to avoid collecting multiple observations of a single individual in a single day.

We made observations between 06:00 and 14:00 on days without heavy rain or wind, between 25 April and 10 July of 1995 and 1996. We attempted to distribute our sampling effort so that the number of foraging observations were roughly equally distributed among the stands. Because all species were more easily seen in stands with low densities of trees, we searched for cavity-nesting birds most frequently in stands with higher densities of trees.

We observed individual birds through binoculars and recorded observations using microcassette recorders. At the beginning of each observation, we noted the species of bird, the type of substrate (tree, snag, log, or shrub) being used by the bird, and the relative location of the bird on the substrate (Table 1). As the bird foraged, we noted when it changed substrates or locations within a substrate. We continuously recorded activities of individual birds from first observation until the bird flew from view or was joined by a conspecific. We later transcribed the data and determined the duration that individuals spent on different portions of the substrates to the nearest second.

We recorded characteristics of the substrates used for foraging and of the tree, snag, and log nearest to each of 30 randomly selected points in each stand. For each live tree, the species, foliage type (deciduous or coniferous), and dominance (dominant—occupying the tallest layer of the overstory; subdominant—not occupying the tallest layer of the overstory) were recorded. Diameter at breast height (dbh; 1.4 m) was measured to the nearest 0.1 cm and height was estimated using a clinometer. Depth of furrows in the bark was estimated to the nearest mm, based upon four measurements of the depth of the deepest furrow taken in each quadrant of the tree at a height of 1.4 m. The number of crown connections (number of trees whose crowns directly intermingled with the crown of the focal tree) and number of dead branches (as seen from the upslope side of the focal tree) were counted, and percent cover of bryophytes (mosses and lichens) was estimated visually.

For each snag and log, the species (if determinable), diameter (at 1.4 m height for snags and at the mid-point for logs), and percent cover of bryophytes were recorded. Height of snags was estimated visually, and length of logs was measured to the nearest 0.5 m. Snags and logs were classified as hard or soft. Hard snags and logs (adapted from Cline et al. 1980, snag decay classes 1 and 2) were freshly dead, still retained at least 70% of the bark, and had little decay of the wood. Soft snags and logs (adapted from Cline et al. 1980, snag decay classes 3–5) had been dead for a longer duration of time, had obvious signs of decay or softening of the wood, and frequently had little to no bark.

DATA ANALYSIS

We analyzed selection of foraging habitat for each species by comparing characteristics of live trees used for foraging to those of randomly chosen live trees. In addition, we compared characteristics of randomly chosen snags and logs to those used for foraging by the Hairy Woodpecker. The Hairy Woodpecker was the only species to use dead wood substantially for foraging. To avoid problems resulting from lack of independence between sequentially used substrates, we only analyzed data for the substrate foraged on for the longest duration of time (the focal substrate). Although Heij et al. (1990) suggest selecting the first or second substrate for use in statistical analysis, we felt that the substrate foraged on for the longest duration of time was most appropriate for our data set because this was the substrate on which the individual focused most of its foraging effort. For all observations, most of the birds (> 70%) were seen foraging on only one substrate.

We used logistic regression to examine selection of foraging substrates. We used stepwise, forward-selection procedures and drop-in-deviance tests to determine which variables significantly contributed to models that predict the probability of a substrate being used for foraging (Hosmer and Lemeshow 1989). If addition of a variable did not significantly reduce the deviance ($P \leq 0.05$), it was not included in the final model. We examined interactions between foliage type and all other variables for live trees, and between decay class and all other variables for snags and logs. We considered these interactions because of potential differences in foraging resulting from these substrate conditions. For example, percentage of bark might influence the likelihood of hard snags being selected for foraging by Hairy Woodpeckers, but might not influence selection of soft snags.

We used observations of birds foraging on focal substrates to supplement logistic regression analyses and to describe how birds foraged on substrates. For each observation, we recorded the vertical and the horizontal stratum of live trees and, for Hairy Woodpeckers, the vertical stratum of snags that was used for the longest duration of time by an individual bird. If a bird foraged for equal durations (± 2 sec) on multiple strata, each stratum was recorded and weighted proportionately. We used the percent frequency of these data to describe patterns of foraging for each species of cavity-nesting bird. Because we conducted separate analyses for each substrate type and omitted observations that had missing data for any variable examined, sample sizes for each analysis were smaller than the total number of foraging bouts.

RESULTS

All four species of cavity-nesting bird showed selectivity in use of foraging substrates. Chestnut-backed Chickadees foraged frequently on live trees (Fig. 1), and was the only species observed foraging on shrubs. When foraging on shrubs, they were observed exclusively, and about equally, on vine maple and huckleberry. Although Chestnut-backed Chickadees foraged

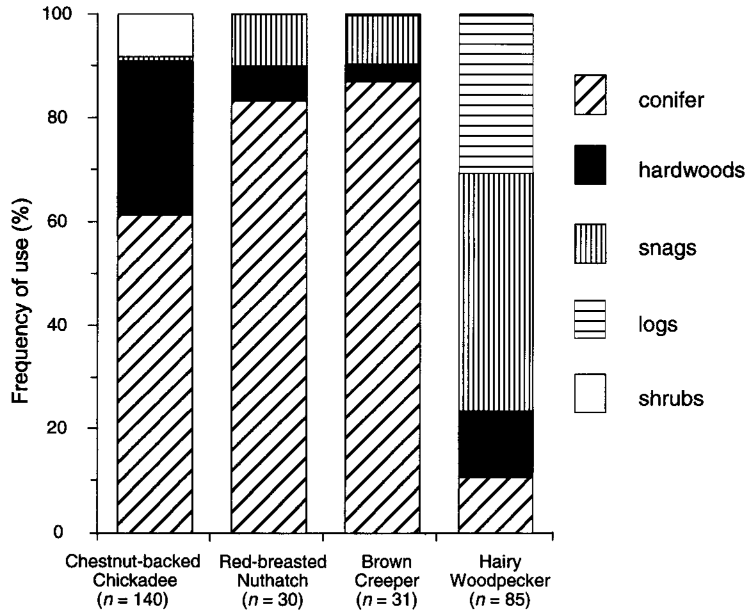

FIGURE 1. Use of substrates (% frequency) for foraging by cavity-nesting birds in young, 35- to 45-year-old, coniferous forests (n = total number of foraging bouts).

more frequently on conifers than on hardwoods (Fig. 1), they selected hardwoods over conifers in relation to their availability (Table 2). Chestnut-backed Chickadees also selected live trees in relation to their diameter, dominance, and percent cover of bryophytes (Table 2). When foraging on live trees, Chestnut-backed Chickadees foraged almost exclusively in the live crowns and more individuals foraged in the lower crown (53%) than in the upper crown (39%). We observed most chickadees foraging on small live limbs (60%) and branch tips (19%).

Red-breasted Nuthatches foraged mostly on live conifers, but occasionally used snags (Fig.

TABLE 2. Results of logistic regression analysis examining the selection of foraging substrates by cavity-nesting birds. For the variable "Foliage type," a value of 1 was used if the tree was coniferous and 0 if the tree was deciduous. For the variable "Dominance," a value of 1 was used if the tree was dominant and 0 if the tree was subdominant.

Species	Sample size (used/randomly chosen)	Substrate type	Variable selected	β ± SE	P
Chestnut-backed Chickadee	(115/323)	Live tree	Foliage type	−2.54 ± 0.37	<0.001
			Diameter	0.07 ± 0.01	<0.001
			Dominance	−0.84 ± 0.36	0.02
			Percent bryophytes	−0.03 ± 0.01	0.02
Red-breasted Nuthatch	(26/323)	Live tree	Diameter	0.05 ± 0.02	<0.01
			Canopy connections	−0.27 ± 0.12	0.02
Brown Creeper	(25/323)	Live tree	Furrow depth	0.16 ± 0.05	<0.01
			Canopy connections	0.30 ± 0.09	<0.01
			Dead branches	0.03 ± 0.01	0.04
Hairy Woodpecker		Live tree	Foliage type	−3.12 ± 0.59	<0.001
	(19/354)		Diameter	0.05 ± 0.02	0.02
	(38/348)	Snag	Diameter	0.02 ± 0.00	<0.001
		Log	Diameter	0.04 ± 0.01	<0.001
			Percent bryophytes	−0.02 ± 0.01	0.01

1), and selected live trees that had larger diameters and fewer crown connections than did randomly chosen live trees (Table 2). They foraged equally in all vertical layers of live trees, but foraged more frequently on long-dead limbs (55%) than on any other horizontal stratum.

Brown Creepers foraged mostly on live conifers (Fig. 1) and selected trees in relation to the depth of furrows in the bark, the number of crown connections, and the number of dead branches (Table 2). They foraged almost exclusively on the bole (98%) and spent more time foraging in the lower bole (67%) than in the upper bole (19%). Creepers also foraged in the lower crown (14%) but were never observed in the upper crown.

The only species to forage substantially on snags and logs was the Hairy Woodpecker (Fig. 1). When foraging on live trees, Hairy Woodpeckers selected deciduous over coniferous trees and selected trees that had larger diameters than did randomly chosen live trees (Table 2). They foraged in the lower bole (21%), upper bole (32%), and lower crown (47%), but never used the upper crown. On live trees, they most frequently foraged on dead limbs (47%) and on the bole (24%). Hairy Woodpeckers selected snags that had larger diameters than did randomly chosen snags, and selected logs that had larger diameters and lower percent cover of bryophytes than did randomly chosen logs (Table 2). Two types of snags and logs were generally abundant in our study area: small diameter snags and logs with little decay, and large diameter snags and logs with heavy decay (Fig. 2). Thus size and decay are confounded, and it is not clear whether Hairy Woodpeckers selected snags and logs in relation to diameter, state of decay, or both. Of the 29 Hairy Woodpeckers observed foraging on snags, 48% spent most of their time on the lower bole, 43% on the upper bole, and 9% on the tops of snags.

DISCUSSION

Chestnut-backed Chickadees, Red-breasted Nuthatches, Brown Creepers, and Hairy Woodpeckers showed selectivity in use of foraging substrates. Deciduous trees, large diameter conifers, large diameter heavily decayed snags, and large diameter heavily decayed logs were important components of foraging habitat.

Deciduous trees were an important foraging substrate both for a species that foraged primarily on live foliage (Chestnut-backed Chickadee) and for one that foraged mostly on dead wood (Hairy Woodpecker). Red alder, the most abundant deciduous tree species in our study area, may support a high diversity and abundance of arthropods (Furniss and Carolin 1977, Oboyski 1995). Many of the orders of arthropods found on red alder are important in the diet of adult and nestling Chestnut-backed Chickadees (Lepidoptera, Hymenoptera, and Hemiptera; Beal 1907, Kleintjes and Dahlsten 1992) and adult Hairy Woodpeckers (Coleoptera; Beal 1911, Otvos and Stark 1985). Schimpf and MacMahon (1985) found that arthropod density was higher in canopies of deciduous aspen forests than in canopies of coniferous forests. Although Schimpf and MacMahon (1985) did not know the biological basis behind the low numbers of arthropods in coniferous canopies, the relatively high concentrations of foliar-nitrogen (a limiting resource to many foliage-feeding arthropods; Mattson 1980, Waring and Cobb 1992) and the absence of thickened cuticles on leaves (Jackson 1979) may result in hardwoods being more suitable habitat for many species of foliage-feeding arthropods. Because abundance of arthropods may be higher on deciduous than on coniferous trees, deciduous trees within a conifer-dominated landscape likely provide valuable foraging habitat for cavity-nesting birds.

Diameter of live trees was an important predictor of use for foraging by Chestnut-backed Chickadees, Red-breasted Nuthatches, and Hairy Woodpeckers. As diameter increases, the surface area of the crown, bole, and branches increases (Biging and Wensel 1990, Maguire et al. 1991). As a consequence, there is more potential foraging habitat on a large diameter tree than on a small diameter tree. In addition, the more complex structure resulting from the increased surface area of the crown, bole, and branches may increase diversity of arthropods in large diameter trees. Thus, diameter of live trees may influence both the quantity and variety of prey items.

Large diameter conifers have more deeply furrowed bark and larger branches than do small diameter conifers (Jackson 1979, Mariani and Manuwal 1990). Depth of furrows in the bark of conifers has been hypothesized to strongly influence abundance of arthropods. Mariani and Manuwal (1990) found that depth of furrows in bark was positively related to the abundance of

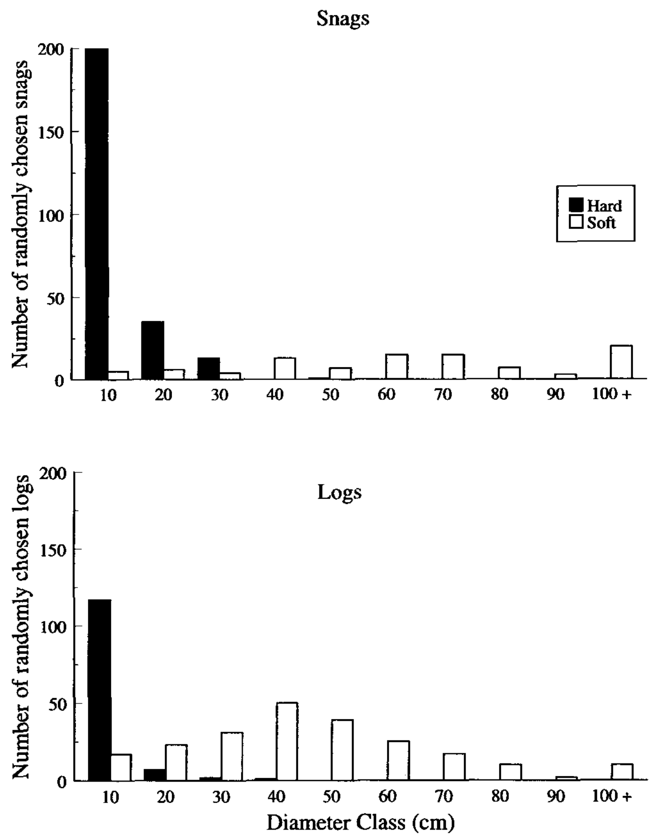

FIGURE 2. Size-class distribution of hard (decay classes 1–2: adapted from Cline et al. 1990) and soft (decay classes 3–5) snags and logs in the northern Coast Range of Oregon.

spiders and large, soft-bodied arthropods on tree boles. Our study demonstrates that depth of bark furrows influenced selection among conifers for foraging by Brown Creepers. It also is likely that depth of furrows influenced selection of specific foraging locations on a tree. Brown Creepers forage most frequently in the lower portion of trees (Franzreb 1985, Adams and Morrison 1993, this study), where the bark is most deeply furrowed.

In addition to deeply-furrowed bark, the presence and quantity of dead branches on conifers also may influence foraging activity by cavity-nesting birds. We frequently observed Brown Creepers foraging at the base, and Red-breasted Nuthatches and Hairy Woodpeckers foraging along the length, of dead branches. In addition, Brown Creepers selected trees that had more dead branches than did randomly chosen trees. Dead branches often had sloughing bark at their bases, and we frequently observed arthropods, especially spiders, residing under the sloughing bark. We suspect that trees with greater numbers of dead branches provide more habitat for arthropods and thus greater densities of prey than do trees with fewer numbers of dead branches. This is consistent with Jackson's (1979) hypothesis that dead branches provide important habitat for arthropods and significant foraging habitat for insectivorous birds.

Chestnut-backed Chickadees foraged disproportionately on subdominant trees. Subdominant trees are less vigorous and more susceptible to being attacked by foliage-feeding insects than are dominant trees (Barbosa and Wagner 1989). Although the reasons for the apparent preference of Chestnut-backed Chickadees for subdominant trees is not fully clear, the selection of subdominant trees may be a response to greater insect abundance on subdominant trees as compared to dominant trees.

Most small diameter snags and logs in our study area originated from the current cohort of trees and had very little decay, whereas all large diameter snags and logs originated from the previous cohort of trees and had moderate to heavy levels of decay (Fig. 2). Whereas small pieces of wood with little decay are mostly inhabited by low abundance of beetles (Coleoptera) and few other taxa, large diameter, highly decayed wood supports greater numbers of beetles and large colonies of carpenter ants (*Camponotus* sp.) and termites (*Zootermoptis* sp.; Maser et al. 1984, Harmon et al. 1986). Cline (1977) found that large diameter snags harbored more insects and insect larvae than did small diameter snags and that colonies of carpenter ants and termites most frequently occurred in large diameter, heavily decayed snags. We occasionally observed Hairy Woodpeckers capturing large larvae of beetles and carpenter ants on large diameter, heavily decayed logs.

Although our study did not directly address selection of stand types or microsites within a stand for foraging by cavity-nesting birds, our results suggest that selection may be occurring at these scales. Brown Creepers and Red-breasted Nuthatches selected live trees for foraging in relation to the number of adjacent trees whose crowns directly intermingled with the focal tree. Brown Creepers selected trees with more, and Red-breasted Nuthatches selected trees with fewer, crown connections as compared to the number of crown connections on randomly chosen live trees. Number of crown connections was confounded by the density of trees in a stand; trees in stands with high tree densities had more crown connections than did trees in stands with low tree densities. We observed most Brown Creepers in stands with high tree densities and observed most Red-breasted Nuthatches in stands with low tree densities. This was due in part to the patterns of abundance of Brown Creepers and Red-breasted Nuthatches and in part to the relative ease of viewing nuthatches in stands with low densities of trees (Weikel 1997). Because bird abundance and the corresponding number of samples collected are confounded with the number of crown connections within each density type, it is unclear at which spatial scale the birds were responding: the stand level (tree density), tree level (number of crown connections), or both. Our results suggest that Brown Creepers and Red-breasted Nuthatches may be selecting foraging sites at the stand level, but this should be examined further.

Arthropod abundance has been positively related to cover of bryophytes on live trees in boreal forests of Sweden (Pettersson et al. 1995). If the same relationships existed in conifer forests of the United States, we might have expected birds to select trees with a high percentage of cover of bryophytes. In contrast, Chestnut-backed Chickadees selected live trees that had relatively low percent cover of bryophytes. Similarly, Hairy Woodpeckers selected logs that had relatively low percent cover of bryophytes. Additional study is needed to determine the relationship between bryophytes and arthropods and the ramifications to foraging by birds. We believe that the observed relationships with percent cover of bryophytes may be spurious; percent cover of bryophytes may be correlated with some other unmeasured factor that is driving selection of foraging sites, such as microsite condition. Alternatively, abundance of arthropods may be positively correlated with bryophyte cover, but bryophyte cover may act as hiding cover for arthropods, thus limiting the availability of those arthropods to birds.

Management of nesting resources without regard to foraging resources is probably inadequate to provide habitat for cavity-nesting birds. We contend that in order to effectively manage habitat for cavity-nesting birds, foraging habitat, as well as nesting habitat, should be provided. In young conifer-dominated forests of the Pacific Northwest, patches of hardwoods, large diameter conifers, and large diameter snags and logs should be retained when logging. Legacy snags (large diameter snags from the previous stand) in young forests are especially important resources for cavity-nesting birds both as nesting (Mannan et al. 1980, Lundquist and Mariani 1991) and foraging substrates (Mannan et al. 1980, this study). These generally are the only large diameter snags available in young forests. Snags originating from the current cohort of trees in young forests are too small to provide adequate nesting sites for many species of cavity-nesting birds (Zarnowitz and Manuwal 1985, Nelson 1989). As a long duration of time (40 to 80 years or longer) will pass before the current cohort of live trees attain a diameter large enough to replace large diameter snags, it is especially important to retain large diameter snags and logs when harvesting and to extend harvest rotations to a duration that is long enough to allow trees to attain large diameters (> 50 cm).

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