SEASONAL DIFFERENCES IN FORAGING HABITAT OF CAVITY-NESTING BIRDS IN THE SOUTHERN WASHINGTON CASCADES

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Abstract. For each of four cavity-nesting bird species we compared winter and spring foraging habitat in second-growth (42–190 yrs) and old-growth (>210 yrs) stands in the western hemlock (*Tsuga heterophylla*) zone of the southern Washington Cascades. We measured the availability of live trees and snags and observed foraging birds in 48 stands during the breeding seasons of 1983 to 1986 and during the winters of 1983–1984 and 1984–1985. Although most species fed in large diameter (>50 cm dbh) trees more than expected in both seasons, the foraging methods as well as the tree portions used differed among species. In winter, Red-breasted Nuthatches (*Sitta canadensis*) shifted foraging activities inward to the trunk and to lower relative postions in trees. Brown Creepers (*Certhia americana*) and Hairy Woodpeckers (*Picoides villosus*) showed more subtle shifts in foraging location. Chestnut-backed Chickadees (*Parus rufescens*) differed from the other species in remaining in the outer branches and high in the crown profile of trees while feeding. Most species selected Douglas-fir (*Pseudotsuga menziesii*) trees in both winter and spring. Chickadees selected western hemlocks disproportionately in winter, but in spring they used tree species about as available. Relative use of dbh classes and tree species also differed between forest age classes for most species. The importance of large Douglas-firs to foraging birds appears to be related to abundance and diversity of prey species inhabiting its fissured bark.

Key Words: Seasonal differences; foraging; cavity-nesting birds; Cascade Mountains.

Seasonality is an important aspect of natural variation in temperate ecosystems that affects community structure and habitat use of birds (Fretwell 1972). For winter survival, permanent residents must be able to respond to changes in the distribution and abundance of food resources brought on by climatic changes (Gordon et al. 1968). Many authors have confirmed seasonal changes in patterns of habitat use and foraging activities in several bird species in other regions of North America (e.g., Stallcup 1968, Willson 1970, Austin 1976, Travis 1977, Conner 1981, Lewke 1982, Morrison et al. 1985, Morrison and With 1987). No study, however, has examined seasonal changes in foraging behaviors in the productive Douglas-fir (*Pseudotsuga menziesii*)/western hemlock (*Tsuga heterophylla*) forests of the Washington Cascades. Characterization of seasonal change is important not only in theoretical studies of niche overlap (or segregation) and community structure (Alatalo 1980), but also in forest management, because managers may have to provide for a different set of habitats for the needs of each species in the nonbreeding vs. the breeding season (Conner 1981). To the extent that intensive timber management changes the species composition and structure of forest stands, it may also affect the winter survival of resident birds.

Of particular concern are cavity-nesting birds, which typically nest in standing dead trees, or "snags," because snags are usually removed during timber harvesting. Birds may focus foraging activities on different species and sizes of trees from those used for nesting, and foraging activities may change seasonally, so characteristics of foraging habitats should not be overlooked (Conner 1980). Our objective in this study was to compare the foraging activities of cavity-nesting birds during winter and spring (breeding season) in old-growth and second-growth forests. Specifically, we examined seasonal changes in foraging behavior and location (both horizontal and vertical), as well as selection of different tree species, sizes, and conditions (in relation to availability).

STUDY AREA AND METHODS

The area studied was the southern Washington Cascades in the Gifford Pinchot National Forest (GPNF) and in Mt. Rainier National Park (MRNP). Forty-eight forest stands (25–30 ha each) representing second-growth (42–190 years old) and old-growth (200+ years old) forest age classes were selected as part of the vertebrate community studies of the USDA Forest Service's Old-Growth Wildlife Habitat Program (OGWHP) (Ruggiero and Carey 1984). All stands were within the Western Hemlock Vegetation Zone (Franklin and Dyrness 1973) and ranged in average elevation from 404 to 1218 m. Western hemlock was the most abundant tree species in old-growth, followed by Pacific silver fir (*Abies amabilis*), Douglas-fir, and western redcedar (*Thuja plicata*). Douglas-fir structurally dominated old-growth stands, however, as most of the largest trees (>100 cm dbh) were of this species. Douglas-fir was the most abundant species (in all size classes) in second-growth stands, followed by western hemlock and western redcedar.

Because winter access to many of the stands was limited, we selected a subset of eight stands in the southern part of the study area near the Columbia River Gorge for winter study (December through early March) in 1983–1984. The winter study was expanded in 1984–1985 to include eight additional stands in the northern portion of the study area. A more detailed description of the stands included in this study is found in Manuwal and Huff (1987) and Lundquist (1988).

FORAGING OBSERVATIONS

We observed foraging birds while conducting OGWHP studies during the winters of 1983–1984 and 1984–1985 and the springs (late April through June) of 1983 through 1986. The species analyzed, all permanent residents, included the following: Brown Creeper (*Certhia americana*), Chestnut-backed Chickadee (*Parus rufescens*), Hairy Woodpecker (*Picoides villosus*), and Red-breasted Nuthatch (*Sitta canadensis*). The observed foraging activities (≥2 s duration) of an individual bird on a single "host" (e.g., a tree, shrub, or log) comprised one foraging observation. Each observation ended when the bird flew to a new "host" or a time limit of 99 seconds was reached. In the springs of 1985 and 1986, up to five sequential observations were also taken on individual birds. Because of questions concerning independence (e.g., Morrison 1984a; Hejl et al., this volume; Bell et al., this volume), all but the initial observations were excluded from analysis. By attempting to monitor a bird's foraging activities on a single host for the maximum duration, and by establishing a minimum observation time of 2 s, we have attempted to minimize discovery (or visibility) bias, which may affect estimates of resource use (Bradley 1985). Loss bias may also be a problem (Wagner 1981a), but it may not be possible to avoid both biases simultaneously with one sampling method (Bradley 1985).

We recorded the following information on each foraging bird: species; sex and age class (where discernible); primary feeding behavior (e.g., gleaning, probing); horizontal part of tree or snag (i.e., trunk, or base, middle, or ends of branches); and vertical zone of the tree (e.g., upper, middle, lower crown, below crown), if applicable. Recorded attributes of the "host" included species, diameter breast height (dbh) class (10-cm intervals), condition (dead or alive, top condition), and position relative to the forest canopy (above, co-canopy, lower canopy, or understory). One exception to the above was during the first winter (1983–1984), when the dbh class of trees was recorded in 20-cm intervals. As a result, when analyzing use patterns in relation to tree availability (see below), we had to exclude observations in trees of dbh classes (e.g., 1–20 cm, 41--60 cm) that could not be placed in dbh categories to match those of the vegetation data.

VEGETATION SAMPLING

In analyses of resource selection, described below, we used vegetation data collected in 12 nested circular plots (0.05 ha, 0.2 ha) systematically located on each study stand. In the 0.05-ha plots, all live trees ≤100 cm dbh and all snags 10-19 cm dbh were tallied by tree species and dbh class. Live trees <10 cm dbh were tallied as well, but snags of this size were not, so we

excluded this size from the analyses. Stem counts in the 0.2-ha plots included live trees >100 cm dbh and snags ≥20 cm dbh by species and dbh class. We summarized the data in 11–50 and >50 cm dbh classes to obtain overal frequency distributions of trees (live and dead combined) in each forest age class (old-growth and second-growth).

DATA ANALYSIS

Various aspects of foraging behavior of birds have been shown to differ by sex and age class (Ligon 1968a, Jackson 1970, Austin 1976, Morrison and With 1987), among years (Root 1967; Grant and Grant 1980; Wagner 1981b; Szaro et al., this volume), and even within a season (Holmes 1966; Busby and Sealy 1979; Alatalo 1980; Hejl and Verner, this volume; Sakai and Noon, this volume). Unfortunately, our data samples were too small to analyze data comprehensively in multiway contingency tables (too many empty cells would have resulted) and to search for interactions among all these factors (e.g., by development of log-linear models, as in Hejl and Verner, this volume). Thus, we combined data for the two winters and four breeding seasons in analyzing seasonal changes in foraging patterns. In addition, the sexes of most species could not be distinguished in the field; this, together with limited data sets, prevented us from including intersexual comparisons in the analyses. Rather, we focused on the degree to which attributes of winter foraging by each species differed from foraging during the breeding season.

These analyses of seasonal shifts by each bird species were done separately for each attribute (i.e., behavior, horizontal location, vertical location) by means of two-way log-likelihood contingency tests of independence (G-tests). Log-likelihood G-tests are analogous to, and often preferred over, the Chi-square statistic (Sokal and Rohlf 1981:704, Zar 1984:52–53). We employed the Williams (1976) correction to the G-statistic to obtain a better approximation to the Chi-square distribution, even in cases with only one degree of freedom. This correction appears to be superior to the Yates correction for continuity in such cases (Sokal and Rohlf 1981).

Where sample sizes permitted, we also statistically evaluated the use (i.e., selection) of tree conditions (live or dead), size (dbh class), and tree species by each bird species in winter and spring separately by means of single-dimension log-likelihood G-tests. Expected frequencies for these analyses were calculated from tallies of trees and snags on the stands on which the foraging observations were made. Because the frequency distributions of size classes and species of trees differed between old-growth and second-growth, we evaluated use of trees by foraging birds separately in each forest age class. Low sample sizes for some bird species (see Results) prompted us to group some of the rarer tree species together for statistical analysis. Vegetation was summarized using the SPSSX computer package (SPSS 1986); log-likelihood G-tests were run using modifications of programs developed for the Hewlett-Packard HP-41CX hand calculator (Hewlett-Packard 1984.)

Estimates of minimum sample sizes required for statistical evaluation may vary considerably with the level of precision or confidence required (Sokal and Rohlf 1981; Petit, Petit, and Smith, this volume; Recher and
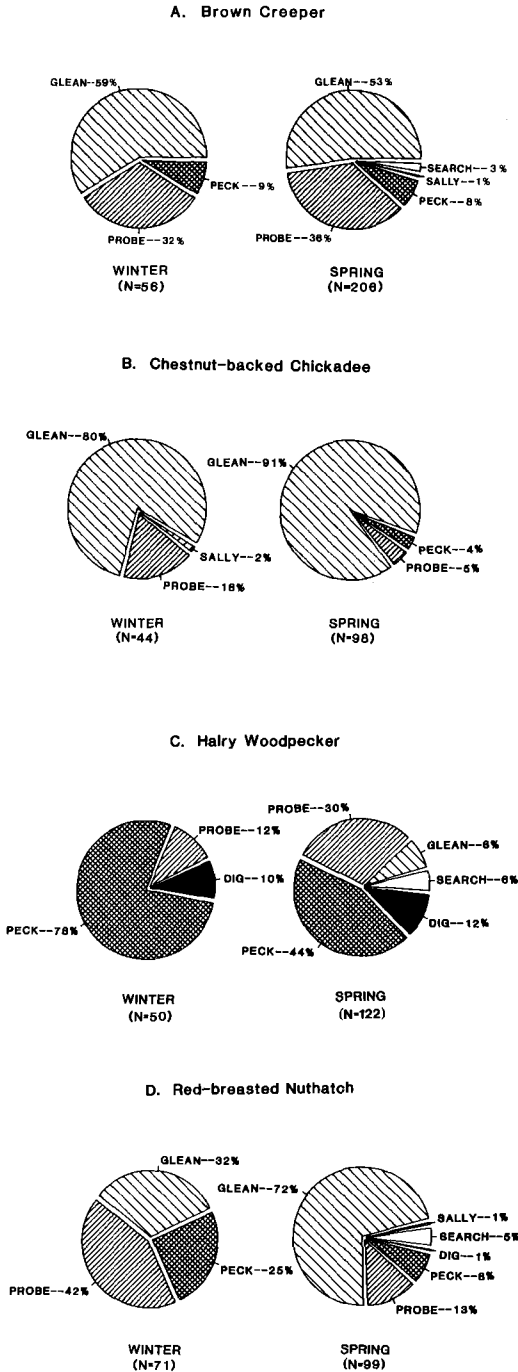
A. Brown Creeper

GLEAN--59%
PECK--9%
PROBE--32%
WINTER
(N=56)

GLEAN--53%
SEARCH--3%
SALLY--1%
PECK--8%
PROBE--36%
SPRING
(N=206)

B. Chestnut-backed Chickadee

GLEAN--80%
SALLY--2%
PROBE--18%
WINTER
(N=44)

GLEAN--91%
PECK--4%
PROBE--5%
SPRING
(N=98)

C. Hairy Woodpecker

PECK--78%
WINTER
(N=50)

PROBE--30%
PROBE--12%
DIG--10%
PECK--44%
GLEAN--6%
SEARCH--6%
DIG--12%
SPRING
(N=122)

D. Red-breasted Nuthatch

GLEAN--32%
PROBE--42%
WINTER
(N=71)

GLEAN--72%
PECK--25%
SALLY--1%
SEARCH--5%
DIG--1%
PECK--8%
PROBE--13%
SPRING
(N=99)

FIGURE 1. Primary foraging behaviors of four cavity-nesting bird species during winter and spring.

Gebski, this volume), as well as with the species and habitats studied (Morrison 1988). Although different rules have been suggested for goodness-of-fit tests, we followed the general rule commonly used in Chi-square tests that no expected frequency should be less than 1.0 and no more than 20% of the expected frequencies should be less than 5.0 in any test (Cochran 1954). In addition, in most cases our sample sizes for each species, season, and univariate attribute of foraging were above the minimum of 30 recommended by Morrison (1984a) for analysis of avian foraging behavior (but see Brennan and Morrison, this volume; Petit, Petit, and Smith, this volume). Where samples were near or below this minimum, the results were viewed as suspect and interpreted with caution.

RESULTS

PRIMARY BEHAVIORS

Brown Creepers, primarily bark gleaners, showed no seasonal shift in behavior (Fig. 1A). Chestnut-backed Chickadees, also gleaners of insects, but from foliage, probed more frequently in winter than in spring (P < 0.05) (Fig. 1B). Hairy Woodpeckers (Fig. 1C) and Red-breasted Nuthatches (Fig. 1D) shifted behaviors more substantially than the other two species. Both species pecked for food items more frequently in winter and nuthatches also probed more frequently in winter than in spring.

FORAGING LOCATION: HORIZONTAL AND VERTICAL

Creepers and chickadees showed no substantial horizontal or vertical shifts in foraging location between seasons, though creepers fed primarily in different locations in trees (Figs. 2A, 3A) than chickadees (Figs. 2B, 3B). The apparent relative decrease in trunk foraging by creepers (P < 0.001) and the increase in outer limb foraging by chickadees (P < 0.005) in winter, while statistically significant, could have been due to the great disparity in sample sizes between the seasons for each species. Hairy Woodpeckers foraged on the same portion of the trees (trunks) during both seasons (Fig. 2C), but they fed less frequently in the crown zones of trees and more frequently in snags without branches during winter than during spring (P < 0.0001) (Fig. 3C). Hairies rarely fed on logs in either season. Nuthatches shifted foraging locations most substantially between the sesons: they fed significantly more frequently further inward (Fig. 2D) and downward (Fig. 3D) in tree profiles during winter compared with spring (P < 0.0001 in both tests).

USE OF TREES IN RELATION TO AVAILABILITY

Tree condition. None of the four species shifted significantly their relative use of live or dead trees
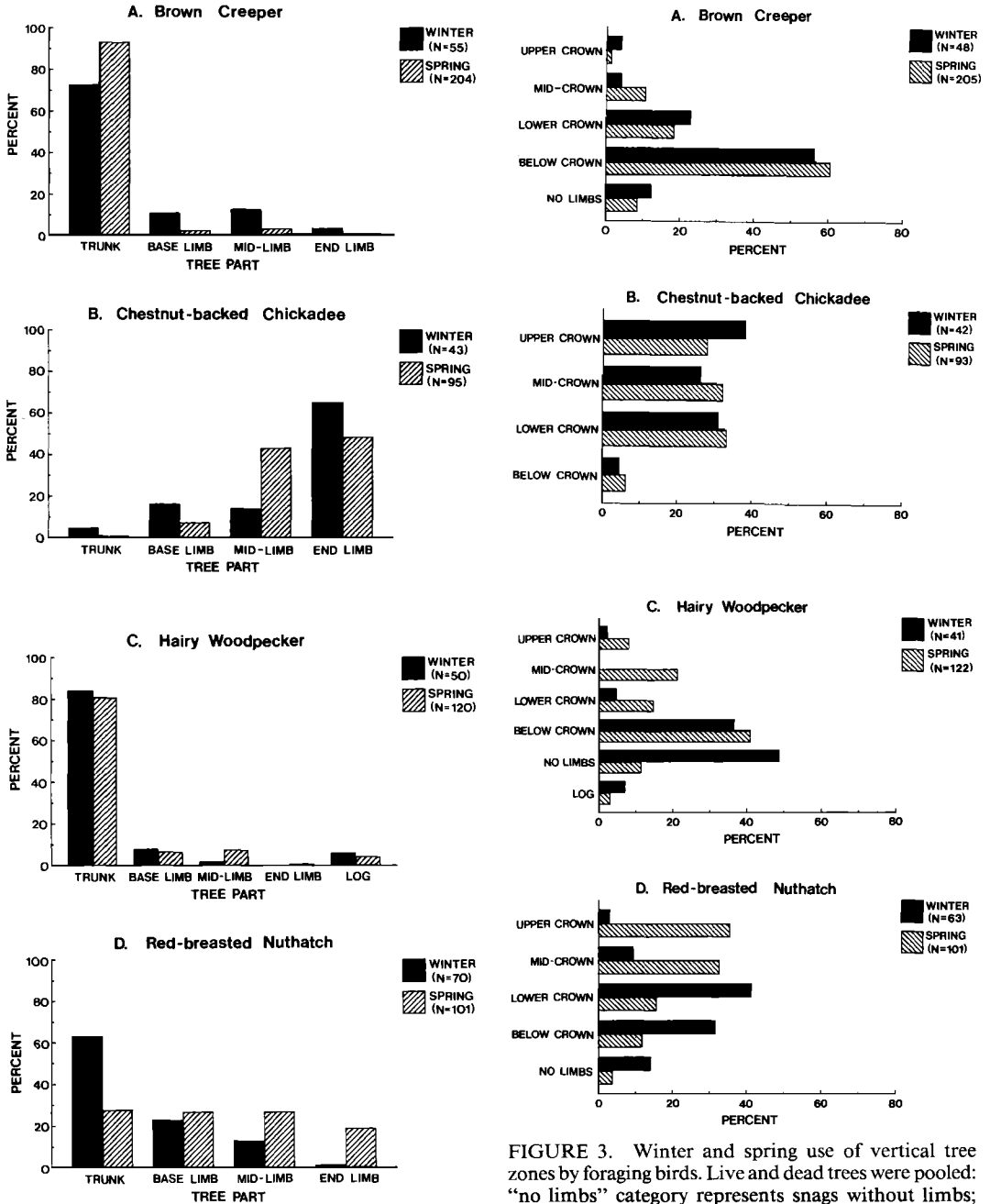
FIGURE 2. Winter and spring use of horizontal tree parts by foraging birds.

FIGURE 3. Winter and spring use of vertical tree zones by foraging birds. Live and dead trees were pooled: "no limbs" category represents snags without limbs; "logs" are fallen dead trees ≥ 10 cm diameter.

between seasons in old-growth (log-likelihood contingency analysis, df = 1, P > 0.05) (Fig. 4A). Sample sizes were generally too small in second-growth (Fig. 4B) to analyze seasonal shifts in growth (Fig. 4B) to analyze seasonal shifts in

resource use, but relative use of live and dead trees was similar to that in old-growth. Likewise, samples were too small to analyze resource selection for the winter data in second-growth (for all bird species).
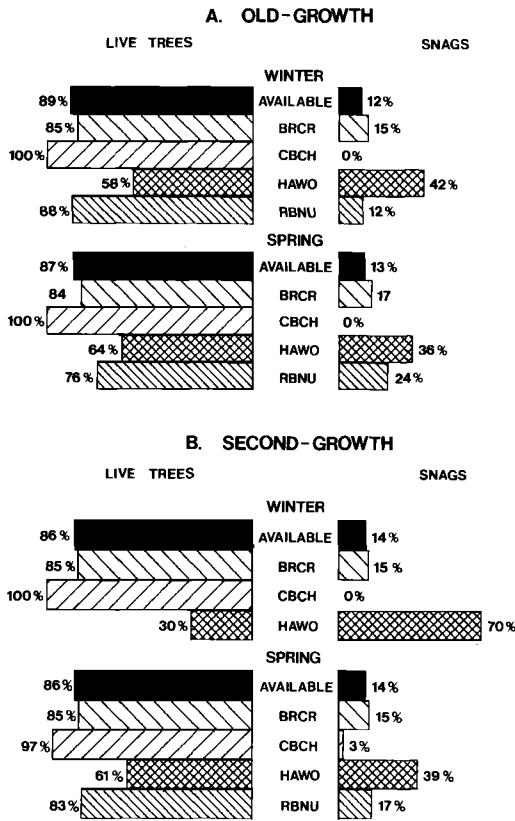
FIGURE 4.   Availability of live and dead trees (snags) and their use by foraging birds during winter and spring in both (A) old-growth and (B) second-growth stands. Live and dead trees <10 cm dbh, as well as logs, were excluded from the analysis. Bird species codes (Klimkiewicz and Robbins 1978) are as follows: BRCR, Brown Creeper; CBCH, Chestnut-backed Chickadee; HAWO, Hairy Woodpecker; RBNU, Red-breasted Nuthatch.
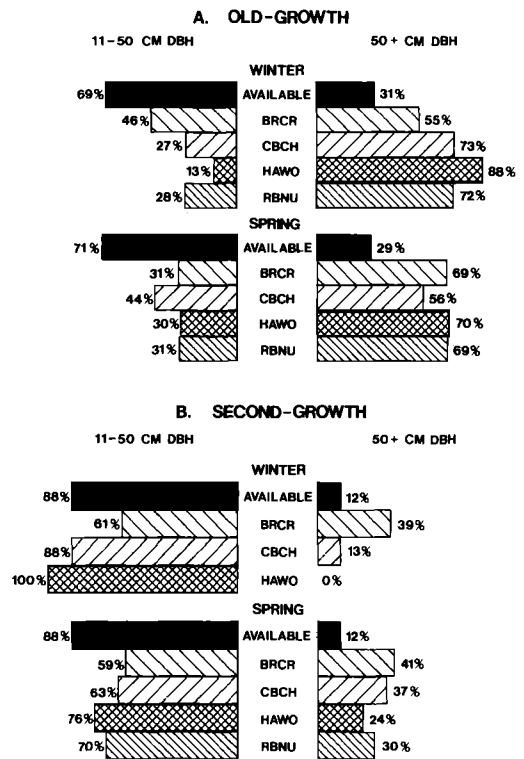

FIGURE 5.   Availability of tree diameter (dbh) classes and their use by foraging birds during winter and spring in (A) old-growth and (B) second-growth stands. Trees <10 cm dbh, as well as logs, were excluded from the analysis. Bird species codes are as in Figure 4.

Brown Creepers used live and dead trees in proportion to their availability in both forest age classes during both seasons (P > 0.05, all tests). Chickadees, which fed almost exclusively in live trees, appeared to select live trees over snags in all cases tested (G-tests, P < 0.005 in old-growth; P < 0.05 in second-growth [spring]). Hairy Woodpeckers, on the other hand, selected snags disproportionately in all cases tested (P < 0.001). Red-breasted Nuthatches used live and dead trees about as available in old-growth during the winter and in second-growth during the breeding season (P > 0.05). However, in old-growth during spring, nuthatches apparently selected snags over live trees as foraging substrates (P < 0.01) (Fig. 4A), despite the fact that no significant shift

was detected between winter and spring in the contingency analysis.

Diameter. In old-growth, no significant changes in relative use of tree dbh classes were noted for any of the bird species (Fig. 5A). All species fed in large trees (>50 cm dbh) significantly more than expected during both seasons (P < 0.01 for creepers, P < 0.005 for chickadees, and P < 0.001 for the others). While no seasonal comparisons could be made in second-growth, all bird species except Hairy Woodpeckers again selected large diameter trees disproportionately as foraging substrates (P < 0.01 for nuthatches, P < 0.001 for creepers and chickadees, and 0.05 < P < 0.10 for Hairies) (Fig. 5B). In contrast to old-growth, however, all bird species were observed primarily in smaller diameter trees (11–50 cm dbh) during both seasons in these stands.

Tree species. The Chestnut-backed Chickadee was the only bird species that significantly shifted relative use of tree species in old-growth stands between seasons (P < 0.05) (Fig. 6B). During the

A. Brown Creeper

B. Chestnut-backed Chickadee

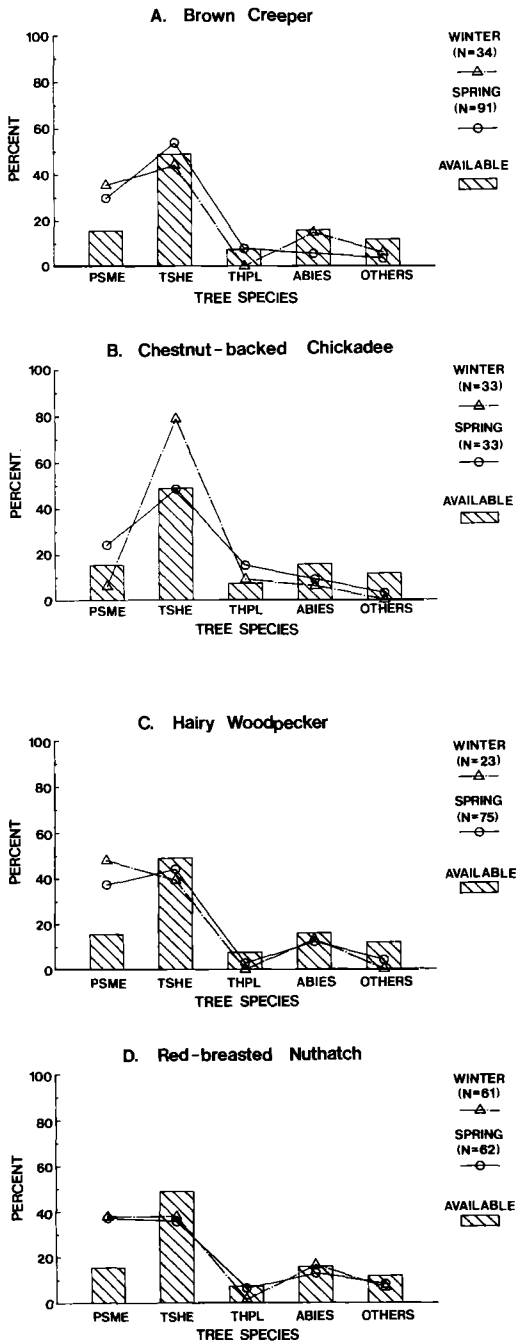## C. Hairy Woodpecker

D. Red-breasted Nuthatch

FIGURE 6. Availability of tree species and their use by foraging birds in old-growth stands during winter and spring. Trees <10 cm dbh, as well as logs, were excluded from the analysis. Tree species codes are: PSME, Douglas-fir; TSHE, western hemlock; THPL, western redcedar; ABIES, true firs, including Pacific silver fir, noble fir (*Abies procera*), and grand fir (*A. grandis*); OTHERS, including conifers such as Pacific
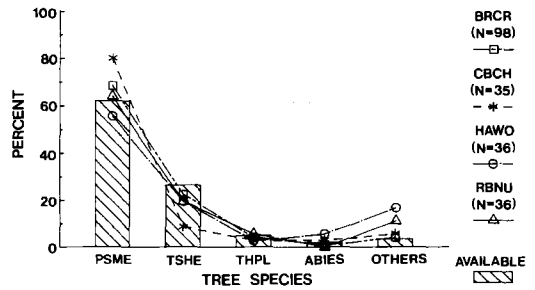
FIGURE 7. Availability of tree species and their spring use by foraging birds in second-growth stands. Trees <10 cm dbh were excluded from the analysis. Tree species codings are as in Figure 6.

breeding season they used tree species in proportion to availability, but during the winter they selected western hemlock significantly more than expected (P < 0.001). The other bird species all selected Douglas-fir disproportionately in old-growth during both seasons (P < 0.001 for Hairy Woodpeckers, and P < 0.01 for the others) (Figs. 6A,C,D). Again, no seasonal comparisons of tree species use could be made for the second-growth data, because of small winter samples. Interestingly, in contrast to old-growth, all bird species fed primarily in Douglas-fir during spring in second-growth (Fig. 7), but only chickades appeared to select this species significantly more than expected (P < 0.05).

DISCUSSION

Our results generally confirm seasonal changes in foraging activities, as other investigators have observed in other regions. Not surprisingly, analysis of foraging data pooled across seasons may then mask significant variation. Some of the shifts we noted may reflect differences in prey distribution on different tree parts in winter and spring. During spring, insects are constantly appearing and are readily available on all parts of trees. In winter, small branches, which have thinner bark and are more exposed to harsh weather conditions, provide fewer places for insects to survive (Jackson 1970, Travis 1977). Thus, we might expect resident birds to concentrate winter foraging activities on the tree bole or under the

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yew (*Taxus brevifolia*) and western white pine (*Pinus monticola*), and hardwoods such as vine maple (*Acer circinatum*), bigleaf maple (*A. macrophyllum*), red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*).

wood surface, and perhaps lower in tree profiles, than during spring.

However, the nature and degree of seasonal changes differed by species, depending upon the attribute in question. These differences may partly reflect evolved morphological differences among species and thus their relative abilities to extract prey items, which in turn determine which types of prey are exploitable (Kisiel 1972; Conner 1980, 1981). Of the species we studied, Hairy Woodpeckers were the most capable of finding prey beneath bark and bare wood surfaces. Their increased use of branchless snags in winter, and the increase in their pecking activities, probably reflected a shift toward prey items under the bark.

Nuthatches, which have smaller bills and are less able to extract subsurface prey, nevertheless can adequately chip bark pieces from tree trunks. In spring, they can exploit abundant insect populations in a variety of locations without resorting to more energetically-demanding means. In winter, these easily attainable foods were not available, so nuthatches concentrated activities on tree trunks and lower in the tree profile, where they pecked and probed more frequently. In Colorado pine forests, Stallcup (1968) noted similar seasonal changes by White-breasted Nuthatches (*Sitta carolinensis*) in winter.

Curiously, we found no shift inward and downward by Chestnut-backed Chickadees like that observed for nuthatches. Chickadees, adapted to foliage-gleaning, are less able to extract prey from bark or under wood surfaces than the bark-foraging species and probably focus on different food items. While the other species selected Douglas-fir in winter (and spring), chickadees markedly increased their use of western hemlocks. The specific benefits of western hemlock to chickadees are unclear, but their seeds (Manuwal and Huff 1987) might provide a reliable winter food for chickadees, which cannot compete with the other species for bark- and wood-dwelling prey. The need for quantification of potential food resources in both seasons is obvious.

Creepers, on the other hand, are bark specialists, highly adapted for removing prey items from crevices on tree trunks, a relatively more seasonally uniform source of food than other parts of trees (Jackson 1970). Thus, no substantial seasonal changes in foraging methods or location would be expected. The creepers' concentration on the lower bole then may have been due to visibility bias, even though our procedures should have minimized this problem. Other researchers (e.g., Willson 1970, Morrison et al. 1987b) have found that creepers concentrate activities on trunks and at lower relative heights than other bark-foraging species, particularly in winter.

Factors other than prey abundance may also have influenced seasonal shifts in foraging behavior and location. Grubb (1975, 1977, 1978) found that birds in deciduous woods foraged relatively lower in cold, windy periods, which mainly affected species using small outer branches. This may help explain the shifts that we observed in nuthatches. Hairy Woodpeckers and Brown Creepers, which already concentrated activities on trunks and foraged lower in trees than nuthatches in spring, may have been less affected in winter. Why chickadees remained in the outer branches is still unclear. Grubb (1975) suggested that birds may benefit from solar warming by foraging slightly higher when the sun is shining than during overcast conditions, even if air temperatures are lower with clear (but calm) skies. Because we observed birds during calm conditions and avoided severe weather in both seasons, we may not have witnessed its full impact.

The differences we observed strengthen the argument against treating all species within the same nesting or foraging guild together. The species we studied are all cavity or crevice nesters, and all but chickadees are bark-foragers. Analyzing data pooled over members of the same guild not only may lead to misleading conclusions with respect to resource selection by individual species (Mannan et al. 1984), but also may mask seasonal changes. While species may respond similarly to changes in food abundance or distribution within a season (e.g., Morse 1970; Hejl and Verner, this volume; but see Sakai and Noon, this volume), this is not consistently the case across different seasons (e.g., Conner 1981, this study). Management schemes based on the requirements of a single "indicator species" (e.g., Graul et al. 1976, Severinghaus 1981) or upon data pooled over all species in a guild (*sensu* Verner 1984) or over different seasons may therefore be inadequate.

The importance of large-diameter Douglas-fir to bark-foraging birds in winter (as well as spring) is probably due, in part, to its thick bark with deep furrows. Such trees may provide important places for insect larvae and pupae to overwinter (MacLellan 1959). Furthermore, Nicolai (1986) found that smooth-barked tree species in central Europe were dominated by a single arthropod species, whereas species with fissured bark had a higher density and diversity of arthropods, particularly spiders. Although we have no data on prey abundance during the winter season, Mariani and Manuwal (this volume) found that the relative abundance of bark-dwelling spiders and large, soft-bodied insects (several families) was highly correlated with bark furrow depth in Douglas-firs on our study sites during spring. Moreover, spiders were an important and con-

sistent component in the diet of Brown Creepers (Mariani and Manuwal, this volume).

Similarly, Morrison et al. (1985) attributed increases in winter bird use of incense cedar (*Calocedrus decurrens*) in California to the presence of an abundant prey clearly associated with its bark characteristics (relative to other tree species). They also noted use of significantly larger Douglas-fir, and Red-breasted Nuthatches increased relative use, albeit slightly, of Douglas-fir (all sizes pooled), in winter.

Our results with regard to forest age class, though incomplete because of inadequate winter samples, further caution against pooling data across sites differing in physiognomy, even within the same forest type (see also Szaro et al., this volume). Although all bird species appeared to select similar dbh classes and tree species in old-growth and second-growth in relation to availability, the proportions used differed with changes in the proportions of trees in the different categories. Because birds exhibited some plasticity in resource use, conclusions regarding resource selection based on data from any particular forest age class, or from pooled data, may be misleading.

We did not take into account variability among individual stands, which can be quite marked (Manuwal, unpubl. data). Also, frequency distributions, or densities, of trees may not be the most appropriate measure of resource availability. Measures such as total canopy volume, basal area, or bark surface area (Jackson 1979; Mariani and Manuwal, this volume) may be more representative. Nevertheless, our data revealed not only seasonal changes in relative use of resources, but also differences among the species, and at least the potential for selection of different kinds of trees by foraging birds in winter and spring. Future investigators should consider such factors when designing studies or formulating management plans.