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# The Vertical Occurrence of Small Birds in an Old-growth Douglas-fir-Western Hemlock Forest Stand

## Abstract

The vertical occurrence of the small bird assemblage (songbirds, small woodpeckers, nighthawks, and swifts) in a ~4 ha stand within the T.T. Munger Research Natural Area, a 500 yr old Douglas-fir-western hemlock forest, was quantified to characterize this assemblage and determine whether birds are vertically stratified within the canopy. We used a gondola suspended from a construction crane to count birds in a weekly series of vertically stratified fixed-area point counts, 5-min, 30 m radius, in the lower (0-20 m), mid (21-40 m) and upper (41-60+ m) canopy. Data are from 21 March 1996 to 21 March 1999, and included 121 survey days (mean 40 counts/yr, March-June 42, July-October 46, November-February 33). Twenty-nine species of birds were detected in the plots; the 20 most common were used for analysis. Fifteen of these species were detected significantly more often in one zone of the canopy. Timber foliage insectivores, air insectivores, timber seed-eaters, and most low understory herbivore-insectivores were stratified within the canopy. Bark insectivores (except brown creeper) and omnivore-scavengers (except gray jay), however, were not stratified within the canopy. The number of bird detections shifted to the upper canopy during winter. One species was generally restricted to the lower canopy, and five species were restricted to the upper canopy, whereas no species were found exclusively in the mid-canopy. The small bird assemblage of this old-growth forest stand was vertically and seasonally patterned and the vertical forest structure, particularly within the upper canopy, reflects these patterns.

## Introduction

Characterization of the vertical pattern of avian occurrence in a plant community is a key aspect of understanding terrestrial bird assemblages. Dunlavy (1935) recognized the term phyto-vertical distribution to describe the distribution of birds in any vegetation formation. He cited various examples of how ornithologists had defined the vertical zones in different vegetation and which birds occurred within these zones. Over the intervening 65 yr, ornithologists have quantified the vertical patterns of birds (MacArthur and MacArthur 1961, Anderson et al. 1979, Morrison et al. 1990). The vertical occurrence of bird species provides clues to the importance of vegetation structure, and provides a framework for more in-depth studies of avian biology and ecology.

Within the Pacific Northwest of North America, tree species composition (particularly broadleaf versus conifer), gaps, vegetation cover, canopy height, snags, branch architecture, bark texture, foliage type, arrangement and density, and stand age are important attributes for habitat selection by birds in natural forests (Sharpe 1996). Old-growth conifer forests are particularly important, because old growth trees have distinctive crown form, with well-developed branch structure, dead branches and tops, and epiphytic communities (Clement and Shaw 1999, McCune et al. 2000) that contribute to a complex and vertically organized food web (Carroll 1980). Nesting avian species that are known to have their greatest abundance in old-growth forests include hairy woodpecker (*Picoides villosus*), red-breasted sapsucker (*Sphyrapicus rubber*), pileated woodpecker (*Dryocopus pileatus*), Pacific-slope flycatcher (*Empidonax difficilis*), olive-sided flycatcher (*Contopus borealis*), red-breasted nuthatch (*Sitta canadensis*), winter wren (*Troglodytes troglodytes*), brown creeper (*Certhia americana*), chestnut-backed chickadee (*Poecile rufescens*), varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), red crossbill (*Loxia curvirostra*), evening grosbeak (*Coccothraustes vespertinus*), and Vaux's swift (*Caetura vauxi*).

Food resources and structure of temperate hardwood (broadleaf) forests differ from temperate conifer forests, which influences avian composition, use, and vertical occurrence (Jackson 1979, Sabo and Holmes 1983, Sharpe 1996). Conifers produce seed crops favored by nuthatches (*Sitta*), siskins (*Carduelis*), and crossbills (*Loxia*), whereas hardwood forests produce fruits and nuts favored by waxwings (*Bombycilla*), tanagers (*Piranga*),

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and thrushes (*Catharus, Turdus*) (Sharpe 1996). Conifer trees tend to have an excurrent crown architecture with a single main stem (Oliver and Larsen 1990), and the upper canopy becomes an aggregation of spire or columnar tops, separated in space, with age. Hardwood trees, on the other hand, generally have a more decurrent crown architecture with multiple stems in the upper crown (Oliver and Larsen 1990). This results in spreading crowns that are largest near the tops, and the upper canopy of hardwood forests can form a closed forest canopy due to the intersections of these crowns. Young conifer forests may also have a closed upper canopy, but old-growth Douglas-fir (*Pseudotsuga menziesii*) forests generally have an open upper canopy (Parker et al. 2002).

Within old-growth Douglas-fir forests the lower canopy encompasses the dim light zone (Parker 1997) and includes important resources such as the forest floor and soil, down logs, understory vegetation including berry and seed producing shrubs, lower boles of trees and snags, and all the associated arthropods that emerge from soil and forest floor. The mid canopy environment is within the transition light zone of Parker (1997), well above the understory vegetation, and foliage of shade tolerant species such as western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) is concentrated here (Parker 2002). Tree and snag boles, dead branches, heart rot of live trees, and intra canopy gaps are important structural elements. The upper canopy is in the bright light zone of Parker (1997), and is composed of the tops of the dominant and co-dominant tree cohort (Figure 1). Douglas-fir foliage predominates. Most of the conifer seed cones occur in this zone. There is extensive heart and top- rot, many dead tops, double tops, snags, and dead branches that provide habitat for cavity nesting birds and roosting birds, and food resources for wood foraging birds.

Old-growth Douglas-fir forests of the southern Washington Cascades are important winter habitat for resident birds (Manuwal and Huff 1987, Huff et al. 1991). Bark insectivores, timber foliage insectivores, low understory herbivore-insectivores, and timber seed-eaters are more abundant in old-growth than young and mid seral stages of Douglas-fir forests during winter (Huff et al. 1991). Characteristics of old-growth Doulgas-fir forests that may account for this are more reliable cone crop due to higher conifer species diversity, higher density of western hemlock, which is preferred by some foliage insectivores in winter and has a more regular cone crop, higher den-

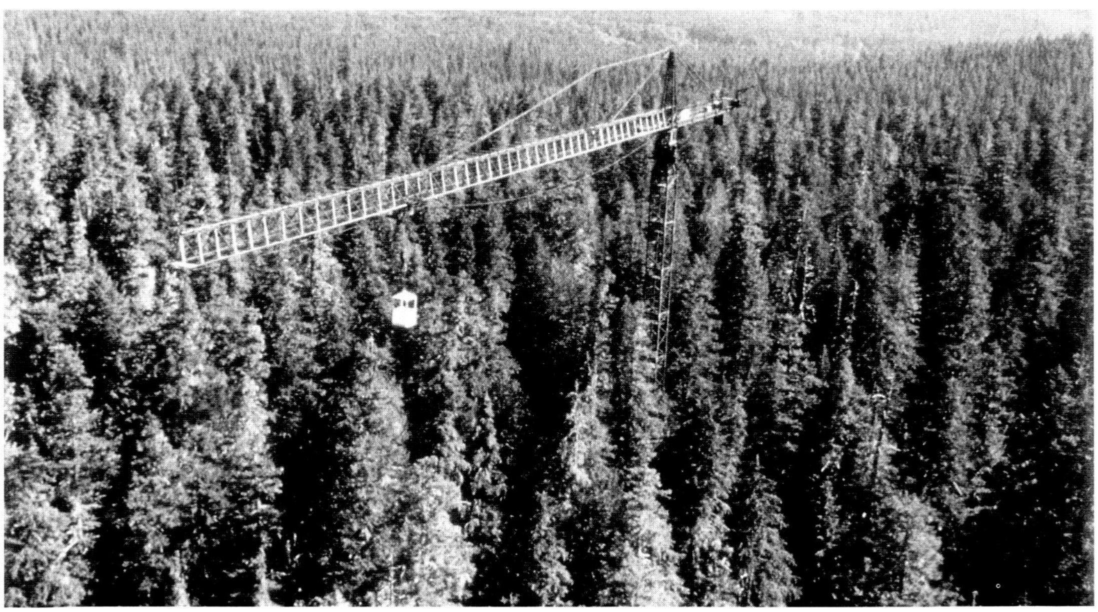

Figure 1. Photograph of the Wind River Canopy Crane, T. T. Munger Research Natural Area, Wind River Experimental Forest, near Carson, Washington. View is looking northeast, and includes old-growth forest surrounding the canopy crane and ~ 75 year-old forest in the background. Photo by Jerry F. Franklin.

sity and larger snags, and higher density of large diameter (>100 cm dbh) live trees.

Most research in vertical aspects of bird assemblages focus on foraging (Sabo and Holmes 1983, Airola and Barrett 1985, Morrison et al. 1990) and this is often limited to a small subset of the avian assemblage, such as cavity nesters (Lundquist and Manuwal 1990, Weikel and Hayes 1999). One study that took a broader perspective considered four eastern North American temperate forest stands in Tennessee and provided data that include vertical distribution (Anderson et al. 1979). About 40% of the avian activity was at the ground level, and the remainder of the activity was distributed uniformly through the canopy.

Old-growth Douglas-fir forests of the Pacific Northwest, with tall stature and complex vertical vegetation structure, provide challenges and opportunities for those who wish to observe birds in the mid and upper canopy strata. Research on the vertical organization of avifauna in these 50+ m forests is generally limited to studies by Lundquist and Manuwal (1990) on four resident cavity nesting species in 48 stands of young and old forests, and Shaw and Flick (1999) using a canopy crane for five resident species in one old-growth stand. Lundquist and Manuwal (1990) organized their observations of vertical foraging locations around individual tree crowns (upper crown, mid crown, lower crown, below crown, no limbs, logs), while Shaw and Flick (1999) organized their observations of vertical occurrence on whole forest canopy zones (upper, mid, and lower).

Lundquist and Manuwal (1990) found that brown creepers were most common in the below crown region, and this remained similar during spring and winter. Chestnut-backed chickadees were common throughout the crowns, slightly more common in the upper crown during winter, but generally similar between seasons. The hairy woodpecker was most abundant in the below crown area, with subtle seasonal shifts, and the red-breasted nuthatch was most abundant in the upper and mid-crown area in spring, with a distinct downward and inward shift in winter.

Shaw and Flick (1999) found the red crossbill was almost exclusively limited to the upper canopy, and this remained relatively constant throughout the year with some occurrence in the mid canopy in spring. The winter wren was limited to the lower canopy all seasons. The brown creeper and golden-crowned kinglet (*Regulus satrapa*) occurred throughout the canopy, but were most abundant in the mid canopy, and this remained so throughout the year. The chestnut-backed chickadee was most abundant in the upper canopy during spring and autumn, and most abundant in the mid-canopy during summer and winter.

Our objectives were to characterize the vertical occurrence of the small bird assemblage in a tall stature old-growth Douglas-fir forest stand. Previous work (Shaw and Flick 1999) using 2 yr of data (included in this study) indicated that five resident species are stratified in the canopy, and this stratification may shift with the seasons. This study focuses on 20 species, includes 3 yr of data, and attempts a more assemblage-wide analysis. We hypothesized that diurnal small birds will be stratified within the canopy, and that each species would be unevenly distributed within the canopy. In addition, we also asked whether these patterns shifted with seasons and whether the patterns we observed in this old-growth forest were similar to those reported for other temperate forests.

## Study Site

In 1995, a construction crane was installed in a 60+ m tall old-growth Douglas-fir-western hemlock forest in the southern Cascades, Washington, for use as a forest canopy observatory. The Wind River Canopy Crane (Figure 1) provides access to the entire vertical spectrum of the forest canopy. The crane jib (75 m) is 11.5 m above the tallest tree (63.5 m) and researchers can be lowered into the canopy in a gondola. The canopy crane was used to survey avian occurrence throughout the vertical profile of an old-growth forest stand. A major limitation in this approach is that only one forest stand is sampled. Therefore, any implications for forests in general will require further investigation.

The study site is a ~4 ha forest stand located at the Wind River Canopy Crane Research Facility (http://depts.washington.edu/wrccrf) in the T. T. Munger Research Natural Area (478 ha), Wind River Experimental Forest, near Carson, Washington at 371 m elevation. Mean annual precipitation is 247 cm, however, June, July and August receive only 5% of this total. Mean temperatures are 8.7°C annually, 17.0°C in July, and 0.0°C January. Snowfall averages 233 cm. The site is in the transient snow zone, where snowpack may not occur for the entire winter. Rain-on-snow, freezing rain, and high winds are common in winter (Franklin 1972).

The forest is a 500-yr old Douglas fir-western hemlock stand (Franklin 1972, Franklin and Dyrness 1988) with a significant component of western redcedar, Pacific yew (*Taxus brevifolia*), grand fir (*Abies grandis*), and Pacific silver fir (*Abies amabilis*). Total density of trees >5 cm diameter at breast height is 429 trees/ha, and basal area is 82.9 $m^2$/ha. Douglas-fir dominates the stand in height and basal area (35.0 $m^2$/ha), however, western hemlock dominates in density (224.0/ha >5cm dbh), and amount of foliage. The understory is dominated by vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), Alaska huckleberry (*Vaccinium alaskaense*), red huckleberry (*Vaccinium parvifolium*), and a variety of herbs, ferns, and bryophytes. Graminoids are rare. Coarse woody debris and snags are a significant component of the site.

The vertical structure of the forest is reflected in the light environment, which has been classified into three distinct zones: a lower dim zone to 12 meters, a mid canopy transition zone to 40 meters, and an upper canopy bright zone above 40 meters (Parker 1997). Leaf area has been estimated at 8.6 $m^2/m^2$, with about 20% of this in understory species (Thomas and Winner 2000). Maximum vertical structure occurs between 15 and 30 m, just above the dim zone (Parker 1997, Song 1998). The vertical structure also reflects the vertical organization of tree species (Song 1998, Ishii et al. 2000). Douglas fir, a shade intolerant species, dominates in the bright zone, which is composed of isolated crowns and groups of crowns with less foliage density in lower levels (Figure 1). The transition zone reflects the increasing abundance of western hemlock foliage, a shade tolerant species, with a few hemlocks reaching 50+ m. The shade tolerant western redcedar is most abundant in the transition and dim zone, with some tree tops reaching 50 m. Pacific silver fir, a shade tolerant species, predominates in the dim zone, especially in canopy gaps. Grand fir is less abundant, but has a higher percentage of trees reaching the bright zone.

The canopy supports over 2 metric tons/ha of epiphytic bryophytes and lichens that are vertically organized. The bryophytes dominate the dim light zone to about 15 m, the lower transition zone is dominated by cyanolichens to about 30 m, and the upper transition zone and bright zone is dominated by alectoriod and non-cyanolichens (McCune et al. 1997). The upper 2 m of the forest, particularly the dead tops of trees, have a unique community of lichens, which may be related to bird roosting, nutrient contributions, and transport of lichen propagules (McCune et al. 2000). The epiphytes reflect the changing microclimate conditions of the vertical profile of the forest. The upper canopy receives more light, UV exposure, greater amounts and speeds of wind, wider extremes of temperature and humidity, and generally more exposed conditions than the protected understory of the dim zone (Geiger 1965, Parker 1995).

The size and location of the Research Natural Area (RNA) and the landscape characteristics of the surrounding region, particularly an adjacent agricultural field, may affect the avian assemblages. No buffer exists against the agricultural edge 500 m south of the canopy crane. For this forest edge, effects of higher temperature, wind, and light, and lower humidity all attenuate individually (Chen et al. 1992, 1993). Maximum distance of the edge effect was about 200 m, leaving about 300 m of interior forest to the south of the crane site. Five hundred meters to the north of the crane site is a 75-yr old, logged and naturally regenerated Douglas-fir forest that was commercially thinned in 1993-1995, leaving a 50 m buffer of young forest on the edge of the RNA. To the east is a wetland about 350 m away. To the west is unbroken old-growth forest for about 1.5 km.

We observed European starling (*Sturnus vulgaris*) and common nighthawk (*Chordeiles minor*) in the open fields. The European starling nests in the old growth trees along the field edge, and in the buildings at the south end of the field. They feed in the fields, often in small flocks. They began attempting to nest on the crane in the second year (1997) after it was erected. We controlled the occurrence of these birds by shooting about 9-12 individuals each year. The common nighthawks nest in adjacent fields and feed over old growth. The birds consistently foraged over the old-growth, but did not exclusively use this habitat for foraging.

## Methods

### Field Methods

We took a simplistic approach to the vertical occurrence of birds by dividing the canopy into three equal zones. These zones reasonably reflect vertical forest structure differences that create the dim, transition, and bright light zone of Parker (1997). We then sampled these vertical zones weekly for 3 yr, by using fixed area point counts (Hutto et al. 1986, Manuwal and Carey 1991) from the gondola of the canopy crane to determine relative differences in composition and abundance of birds. Fixed-area point counts are generally used to compare the relative abundance of birds among sites such as young, mature, and old-growth forests (Manuwal 1991). In this case, we used the technique to describe the relative abundance of birds within three canopy strata of a tall forest stand.

A total of 121 surveys were conducted weekly from 21 March 1996 until 21 March 1999, averaging 40/yr. The canopy was divided in three vertical zones: lower canopy (0-20 m), mid canopy (21-40 m), and the upper canopy (41 m to under the jib of the crane, which varies from 69 m to 75 m with slope). Thirty-meter radius point count plots were conducted from the gondola at 10 m, 30 m, and 50 m, at approximately the mid-points of each canopy level. All birds seen or heard in the plot were noted during a 5 min period following a 3 min quiet down. The vertical series of plots was replicated in the four cardinal directions. Therefore, four point count plots were located in each canopy zone. Each vertical plot series was located 85 m horizontally from the tower of the crane, making the center of each plot series 120 m from the nearest plot series.

With only a 3-min quiet down between vertical plots, in a sequence of top to bottom, it is possible we counted the same bird more than once. Because the purpose of this study was to determine the relative occurrence of species by zone, the repeat counts do not matter. We only wanted to know whether a zone was used by a particular species of bird.

The totals from each canopy level were summed for each day, therefore the data represent 20 min of survey from each canopy level. Surveys began within 30 min of dawn, except from mid November through February when the surveys began during mid morning. Total time to complete the entire 12 survey plots took ~ 2.5 hr. Surveys were not conducted during snowfall, rainfall, high winds, or if lightning or thunder were detected. In addition, no other personnel were allowed on the site before or during avian surveys. The 30 m radius plot size was designed to insure that all birds in the plots were detected, because identifications can be especially difficult during the non-breeding season (Best 1981).

### Caveats of Using a Crane to Sample the Avian Community

Although the canopy crane provides access to observe the avian community, some aspects of the canopy crane may negatively affect the birds. General use of the site by people may influence the avian assemblage and its use of the canopy (Gurtzwiller et al. 1994, 1998). Minor noises are associated with operation of the crane, including an electrical transformer at the base 85 m from the point count plots, cooling fans on motors at the rear of the counterbalance jib 110 m from the point count plots, and a cooling fan on the trolly motor directly above the position of the gondola on the jib.

Each morning, prior to using the crane, a test lift is required by law. The gondola is lowered to the ground and inspected, at which time a test weight is attached to the gondola and the gondola is lifted back up to the highest possible point (67 m) to test a limit switch. The gondola is moved out to the end of the jib at 85 m, the jib is swung in a complete 360° revolution over the stand, then the gondola is lowered to the ground. This inspection and test lift takes about 45 min. Therefore, if dawn is at 0500 and the survey begins at 0515, then the test lift begins at 0430. Swinging the jib over the stand definitely affects birds in the upper canopy, but our attempts to quantify this effect have remained unsuccessful. In general, smaller birds seem to be less affected than larger birds.

### Analysis: Vertical Occurrence

The 20 most abundant species detected in vertical plots were used for analysis of vertical patterns. A Chi-square Goodness of Fit test (Zar 1999) was applied to test if their distribution among the three canopy levels was significantly different from random. The null hypothesis was that birds are equally distributed within the three canopy zones. The term stratified is used to describe the distribution of birds that are not equally distributed within the canopy. Finally, a proportional bar chart for the 20 most abundant species illustrated the vertical occurrence and the proportion of the total detections in each of the canopy zones.

## Analysis: Seasonality of Vertical Patterns

We defined seasons of the year based on weather and occurrence of birds for this site, and designated three seasons: early (March - June, total surveys = 42), late (July - October, total surveys = 46), and winter (November - February, total surveys = 33). The six resident species with counts of at least four in each of the three seasons were examined by use of proportional bar charts that helped evaluate how their distribution throughout the canopy changed with the seasons. These seasonal changes were further investigated with Analysis of Deviance, using a Poisson Error Structure and a Log link (Mathsoft 1998), which was used in an earlier analysis of five resident species (Shaw and Flick 1999). This particular regression method was chosen because of the count data structure. Histograms of the counts for each species revealed that counts were distributed with a high proportion of zeros and a long right tail, characteristic of Poisson Data. The main effects of season and level indicate if bird occurrence is evenly distributed over the year and over the canopy levels. The interaction term indicates whether the vertical distribution of the species changes with the seasons. Although no additional statistics were used, proportional charts were used to display the change in canopy use of the total number of birds detected in each zone.

## Results

### Vertical Occurrence of Species

Twenty-nine species of birds were detected in the fixed-area observation plots (Table 1). The most species, greatest number of guilds, and greatest

TABLE 1. Species list of birds detected in 30 m radius fixed-area observation plots during 121 surveys from March 21, 1996 to March 21 1999 at the Wind River Canopy Crane Research Facility. Code is the four letter species codes used in figures. Guilds codes are based on Manuwal (1991) and general literature: AI - Air insectivore, BI - Bark insectivore, LUHI - Low understory herbivore-insectivore, N - Nectarivore, OFGF - Open field ground feeder, OS - Omnivore-scavenger, TFI - Timber foliage insectivore, TFIO - Timber foliage insectivore-omnivore, TS - Timber seed-eater. Migration: NM = neotropical migrant, RM = regional migrant, R = resident. *not included in analysis because of insufficient detections in fixed radius plots.

| Species | Scientific name | Code | Guild | Migration |
|---|---|---|---|---|
| Common nighthawk | *Chordeiles minor* | CONI | AI | NM |
| Vaux's swift | *Chaetura vauxi* | VASW | AI | NM |
| Rufous hummingbird* | *Selasphorus rufus* | RUHU | N | NM |
| Red-breasted sapsucker | *Sphyrapicus rubber* | RBSA | BI | RM |
| Hairy woodpecker | *Picoides villosus* | HAWO | BI | R |
| Northern flicker* | *Colaptes auratus* | NOFL | BI | RM |
| Pacific-slope flycatcher | *Empidonax difficilis* | PSFL | AI | NM |
| Gray jay | *Perisoreus canadensis* | GRJA | OS | R |
| Steller's jay | *Cyanocitta stelleri* | STJA | OS | R |
| Violet-green swallow* | *Tachycineta thalassina* | VGSW | AI | NM |
| Chestnut-backed chickadee | *Poecile rufescens* | CBCH | TFI | R |
| Red-breasted nuthatch | *Sitta canadensis* | RBNU | BI | R |
| Brown creeper | *Certhia Americana* | BRCR | BI | R |
| Winter wren | *Troglodytes troglodytes* | WIWR | LUHI | R |
| Golden-crowned kinglet | *Regulus satrapa* | GCKI | TFI | R |
| Ruby-crowned kinglet* | *Regulus calendula* | RCKI | TFI | RM |
| Swainson's thrush* | *Catharus ustulatus* | SWTH | LUHI | NM |
| Hermit thrush | *Catharus guttatus* | HETH | LUHI | NM |
| American robin | *Turdus migratorius* | AMRO | LUHI | RM |
| Varied thrush | *Ixoreus naevius* | VATH | LUHI | RM |
| European starling | *Sturnus vulgaris* | EUST | OFGF | RM |
| Hermit warbler | *Dendroica occidentalis* | HEWA | TFI | NM |
| Western tanager* | *Piranga ludoviciana* | WETA | TFI | NM |
| Chipping sparrow* | *Spizella passerina* | CHSP | OFGF | NM |
| Dark-eyed junco | *Junco hyemalis* | DEJU | LUHI | RM |
| Black-headed grosbeak* | *Pheucticus melanocephalus* | BHGR | TFIO | NM |
| Red crossbill | *Loxia curvirostra* | RECR | TS | R |
| Pine siskin | *Carduelis pinus* | PISI | TS | RM |
| Evening grosbeak* | *Coccothraustes vespertinus* | EVGR | TS | NM |

number of total bird detections were documented in the upper canopy (Figure 2). A few species in each zone accounted for most of the observations (Figure 3). For example, the chestnut-backed chickadee accounted for 41% of the birds in the mid canopy and 38% of the birds detected in the upper canopy. In the lower canopy, the five most abundant species were more evenly distributed (Figure 3).

Fifteen of the 20 most common species were significantly more abundant in one level of the canopy (Table 2). The distributions of air insectivores, timber foliage insectivores, and timber seed eaters were stratified within the canopy, as were most of the low understory-herbivore-insectivores. The bark insectivores, except the brown creeper, and omnivore-scavengers, except gray jay (*Perisoreus canadensis*), were not stratified within the canopy. However, the absence of a detected canopy preference for the red-breasted sapsucker, hairy woodpecker, Steller's jay (*Cyanocitta stelleri*), and hermit thrush, may be a function of a small sample size (Table 2).

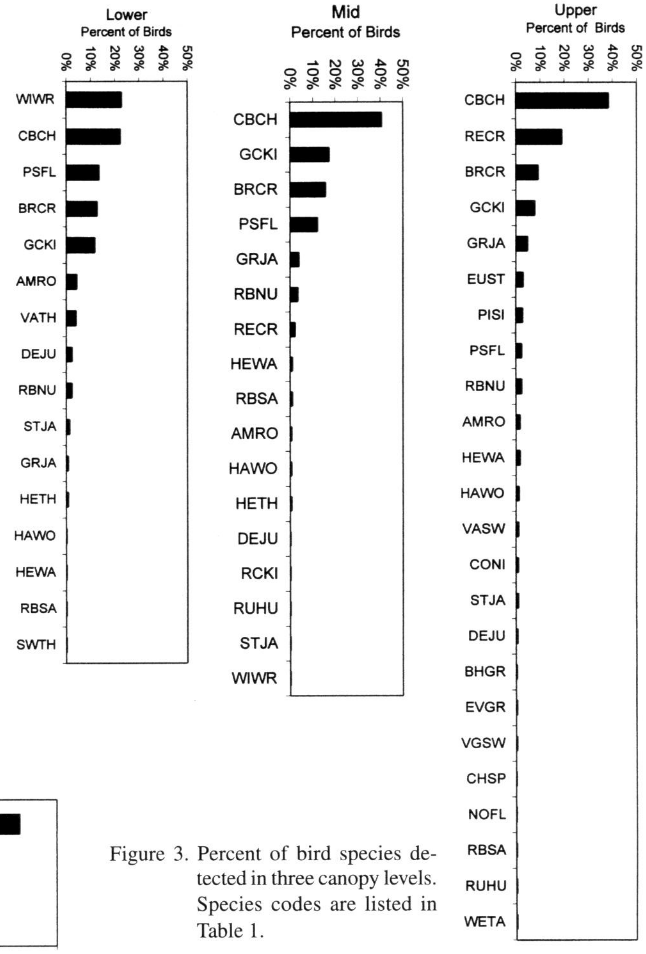


Figure 3. Percent of bird species detected in three canopy levels. Species codes are listed in Table 1.

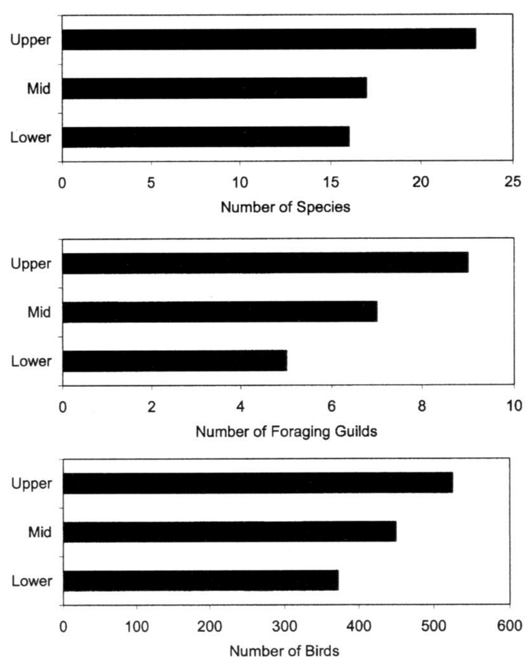


Figure 2. Distribution of number of species (A), number of foraging guilds (B), number of birds (C), in the low, mid, and upper canopy.

The forest stand was vertically used (Figure 4), with some species detected exclusively in the lower canopy, some only in the upper canopy, and some throughout the canopy. Species detected exclusively in the upper canopy were common nighthawk, Vaux's swift, European starling, and pine siskin (*Carduelis pinus*), whereas species most prevalent in the upper canopy were the hairy woodpecker, gray jay, red crossbill, hermit warbler (*Dendroica occidentalis*), and chestnut-backed chickadee (Table 2, Figure 4). The Pacific-slope flycatcher was most prevalent in the mid and lower canopy, the red-breasted nuthatch was most prevalent in the mid and upper canopy, whereas the red-breasted sapsucker, brown creeper, and golden-crowned kinglet were mostly detected in the mid

TABLE 2. Chi-square Goodness-of-Fit test to determine whether birds were evenly distributed in the three canopy levels, for the twenty most abundant birds in the research forest.

| Species | Number of birds Lower | Mid | Upper | Total | *P* |
|---|---|---|---|---|---|
| Unevenly distributed (*P* ≤0.05) | | | | | |
| Common nighthawk | 0 | 0 | 5 | 5 | 0.01 |
| Vaux's swift | 0 | 0 | 6 | 6 | 0.00 |
| Pacific-slope flycatcher | 50 | 54 | 13 | 117 | 0.00 |
| Gray jay | 3 | 17 | 26 | 46 | 0.00 |
| Chestnut-backed chickadee | 83 | 183 | 208 | 474 | 0.00 |
| Brown creeper | 47 | 71 | 49 | 167 | 0.04 |
| Winter wren | 85 | 1 | 0 | 86 | 0.00 |
| Golden-crowned kinglet | 43 | 78 | 42 | 163 | 0.00 |
| American robin | 16 | 3 | 9 | 28 | 0.01 |
| Varied thrush | 15 | 0 | 0 | 15 | 0.00 |
| European starling | 0 | 0 | 16 | 16 | 0.00 |
| Hermit warbler | 1 | 4 | 9 | 14 | 0.03 |
| Dark-eyed junco | 9 | 1 | 4 | 14 | 0.03 |
| Red crossbill | 0 | 10 | 103 | 113 | 0.00 |
| Pine siskin | 0 | 0 | 15 | 15 | 0.00 |
| Evenly distributed (*P* > 0.05) | | | | | |
| Red-breasted sapsucker | 1 | 4 | 1 | 6 | 0.22 |
| Hairy woodpecker | 1 | 3 | 7 | 11 | 0.08 |
| Red-breasted nuthatch | 9 | 15 | 13 | 37 | 0.47 |
| Steller's jay | 5 | 1 | 5 | 11 | 0.23 |
| Hermit thrush | 3 | 3 | 0 | 6 | 0.22 |

canopy (Table 2, Figure 4). The winter wren and varied thrush were detected in the lower canopy, while the hermit thrush was detected only in the lower and mid canopy. Finally, the Steller's jay, dark-eyed junco (*Junco hyemalis*), and American robin (*Turdus migratorius*) were prevalent in the lower and upper canopy, but not in the mid canopy (Table 2, Figure 4). The sum of the three timber foliage insectivores (chestnut-backed chickadee, golden-crowned kinglet, hermit warbler) is highest for the mid canopy and upper canopy (low - 127, mid - 265, upper - 259), as well as the sum of the four bark insectivores (brown creeper, red-

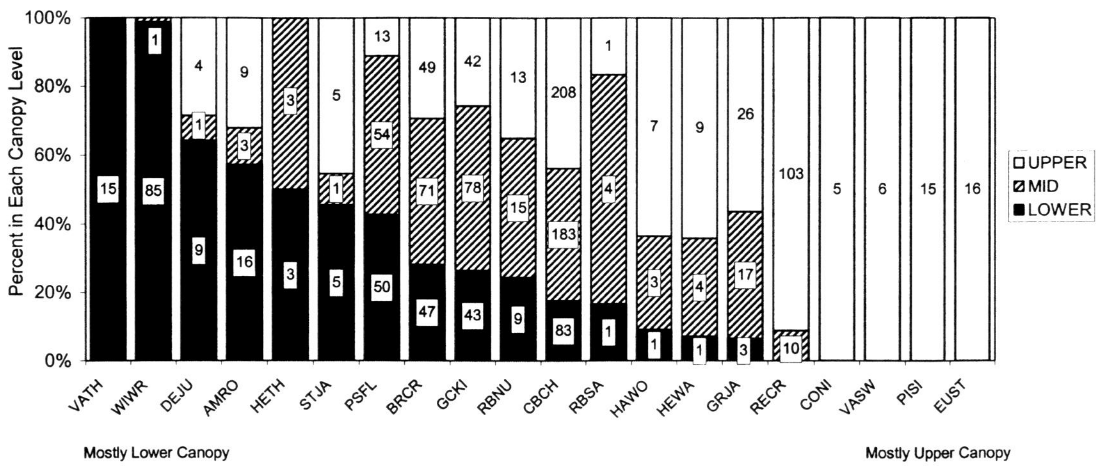


Figure 4. Proportional detections (percent of total) for of low, mid and upper canopy by twenty most abundant bird species. Species codes are listed in Table 1.

breasted nuthatch, hairy woodpecker, red-breasted sapsucker) (low - 58, mid - 93, upper - 70).

## Seasonality of Vertical Patterns

All six resident species were most abundant at one canopy level during each season, but the particular canopy level shifted for four of the species (Table 3, Figure 5). The brown creeper shifted downward in the winter. The red crossbill, chestnut-backed chickadee, and gray jay shifted upward

TABLE 3. *P* values for differences among canopy levels, seasons and the interaction for the six most common year round residents.

| Species | Canopy Level | Season | Canopy/Season Interaction |
|---|---|---|---|
| Gray jay | 0.00 | 0.46 | 0.04 |
| Chestnut-backed chickadee | 0.00 | 0.00 | 0.00 |
| Brown creeper | 0.05 | 0.00 | 0.00 |
| Winter wren | 0.00 | 0.00 | 0.80 |
| Golden-crowned kinglet | 0.00 | 0.00 | 0.07 |
| Red crossbill | 0.00 | 0.00 | 0.00 |

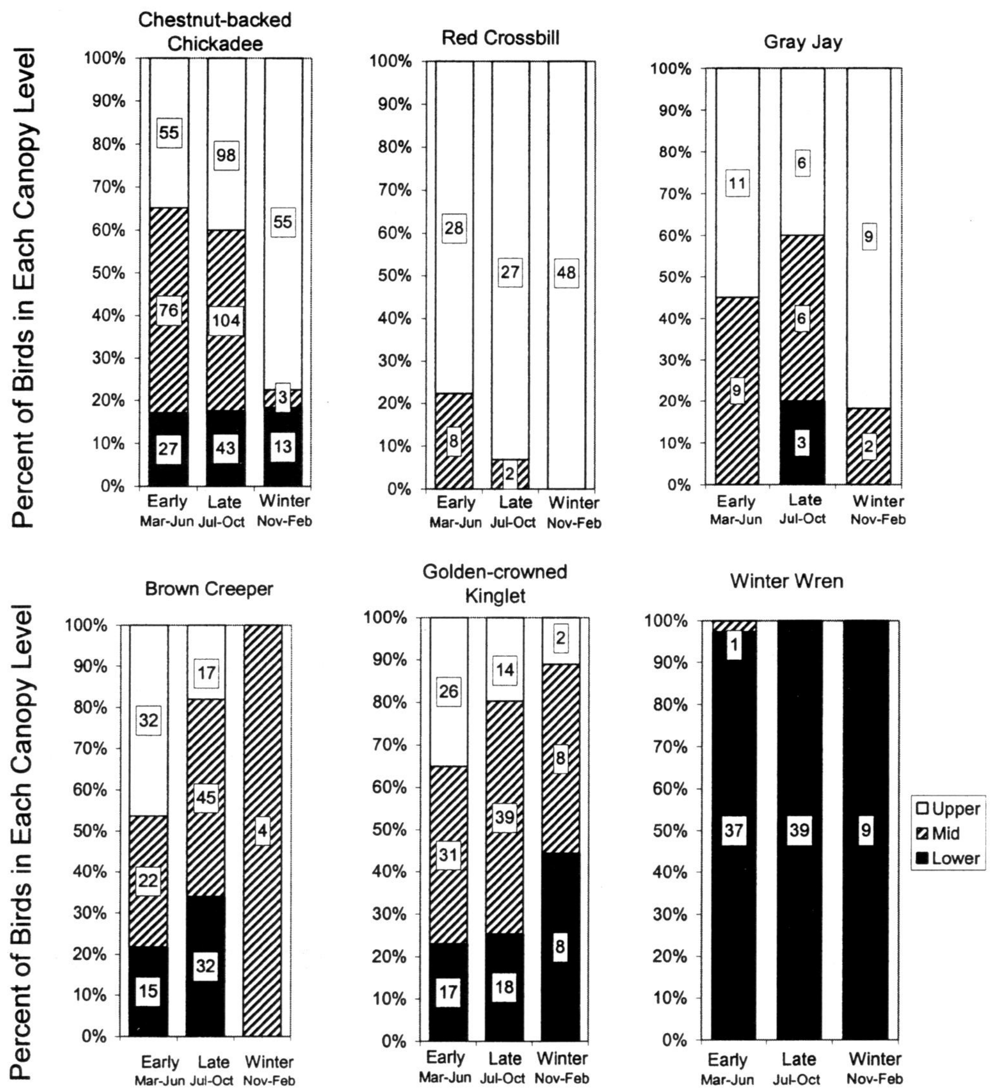


Figure 5. Proportional detections within the canopy during three seasons, early (March-June), late (July-October), and winter (November-February) by the six most abundant year-round residents.

during the winter. The winter wren was only detected outside the lower canopy zone once in a western redcedar tree at ~24 m (4 m above the zone division).

Three species had residual deviance larger than their residual degrees of freedom in the analysis of deviance, indicating over dispersion. This could be caused by an aggregated spatial distribution. These three species, chestnut-backed chickadee, golden-crowned kinglet, and red crossbill were often observed in flocks, especially outside the breeding season. The independence assumption is violated, and therefore the *P* values should be used only as general guidelines.

The total number of birds detected in each zone also shifted with the seasons (Figure 6). During the early season the mid and upper canopy were about equal with somewhat fewer birds detected in the lower canopy. During the late season detections were generally equal through the three canopy zones. However, there was a sharp shift upward during the winter, and a general lack of detections in the mid canopy.

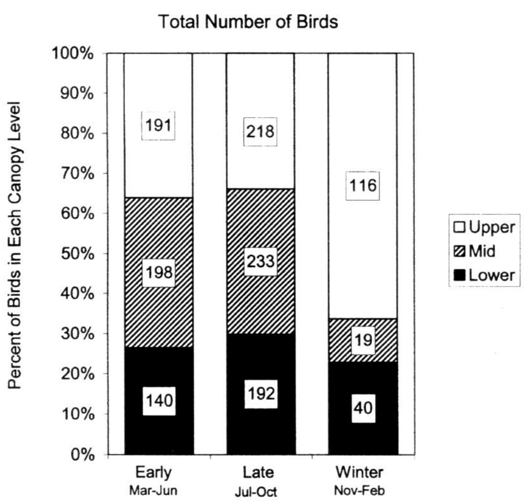


Figure 6. Proportional distribution of detection totals of birds within the three canopy levels by three seasons; early (March-June), late (July-October), and winter (November-February).

## Discussion

The diurnal small bird assemblage of the Wind River old-growth was characteristic of this forest type in the southern Washington Cascade Range (Manuwal 1991, Huff and Raley 1991, Huff et al. 1991, Lundquist and Mariani 1991), except for the European starling, which was attracted to the crane from the nearby (500 m) nursery fields. The small bird assemblage at Wind River was dominated by residents and regional migrants, with five (25%) common neotropical migrants present during May through August, a proportion similar to that noted by MacArthur (1959) for western Oregon forests in general. In northeastern forests (Sabo and Holmes 1983) and Sierran forests (Airola and Barrett 1985) of North America the resident species tend to exploit food resources that reflect winter feeding, such as arthropods on tree boles, twigs, and conifer foliage (and at Wind River, conifer seed), whereas the neotropical migrants tend to occupy more seasonal niches such as aerial (at Wind River: Vaux's swift, common nighthawk, Pacific-slope flycatcher), terrestrial (at Wind River: hermit thrush), and foliage (at Wind River: hermit warbler) insectivory.

The majority of birds (15 of 20 species) analyzed in this study were stratified within the canopy (Table 2, Figure 4). This stratification reflects their uneven distribution within the canopy, yet most species occurred throughout the canopy (Figure 3, 4). Canopy zone specialists were most common for the upper canopy. The only species generally restricted to the lower canopy was the winter wren. The varied thrush was not detected above the lower canopy but we have observed birds in the mid and upper canopy outside plot observation periods. None of the avian species was restricted to the mid canopy, although many species were most abundant there and this is a key zone for foliage insectivores and bark insectivores. Five species were generally restricted to the upper canopy in this stand, including common nighthawk, Vaux's swift, European starling, pine siskin, and red crossbill. The Vaux's swift nests and roosts in the old-growth, feeds in the upper canopy in mornings, but was often observed over fields and other forests, and very high above ground during later times of day. The pine siskin and red crossbill are wide ranging birds, using the old-growth forest for feeding and perhaps nesting.

The vertical occurrence of birds is reflected in the vertical structure of this old-growth forest stand. The moss dominated, dim light zone of the lower canopy, with berry producing shrubs, is characterized by low understory herbivore insectivores such as the winter wren, American robin, varied thrush, and dark-eyed junco (Figure 4).

However, the chestnut-backed chickadee, Pacific-slope flycatcher, golden-crowned kinglet and brown creeper were among the most commonly observed birds there (Figure 3), perhaps due to the abundance of conifer and vine maple foliage, deeply crevassed lower Douglas-fir boles, and flying insects. The mid canopy has the highest density of conifer foliage, and is characterized by foliage insectivores and bark insectivores (Figure 4). The Pacific-slope flycatcher was also abundant in this zone. This flycatcher was not commonly observed foraging in a classic sally-aerial flycatcher move, but mostly observed as a hyperactive, within crown forager, constantly moving among branches, epiphytes, and foliage. The upper canopy structure was open, with much space between tree crowns, dominated by Douglas fir, and characterized by dead wood and lichens. We detected the most hairy woodpeckers in this zone (Figure 4), although Lundquist and Manuwal (1990) detected hairy woodpeckers most commonly in the below crown zone. The greatest number of birds, and greatest diversity of species and guilds (Figure 2) were detected in the upper canopy, while aerial insectivores, timber seed eaters, foliage insectivores, and bark insectivores characterized the avian assemblage (Figure 3, 4). The complex and varied upper canopy of this old-growth forest is an important forest strata for biological diversity which has been little studied.

Of the six bird species examined for seasonal shifts in vertical occurrence in this study, the winter wren and golden-crowned kinglet did not shift zones with the seasons, whereas the chestnut-backed chickadee, red crossbill, and gray jay all shifted the bulk of their activity to the upper canopy, and the brown creeper was detected exclusively in the mid canopy. This compares to Lundquist and Manuwal (1990) who studied foraging locations and found chestnut-backed chickadees remained high in the canopy, red-breasted nuthatch shifted inward and downward, and hairy woodpecker and brown creeper did not shift vertical position of foraging during winter. Shaw and Flick (1999) used all four seasons to compare vertical occurrence and found chestnut-backed chickadees were most abundant in the upper canopy during spring and autumn, and most abundant in the mid-canopy during summer and winter.

In the Wind River forest, the total number of birds detected, as a percent of the total detections, shifted to the upper canopy in winter (Figure 6). The upper canopy may have more resources such as cavities, sun warmed foliage and tree boles, arthropods, and conifer seed, while the microclimate may be less severe during the day than the snow covered, humid understory. However, severe weather is known to depress the vertical foraging patterns of birds in winter (Grubb (1975, 1977), and we surveyed birds only on days with no rain, snow, or high winds. Therefore, we only have a snapshot of vertical occurrence on the more favorable winter days.

At Wind River, 4 of the species (20%) were detected most often in the lower canopy, 5 species (25%) in the mid canopy, 9 species (45%) in the upper canopy, while 1 species (5%) was equal in the low and mid canopy, and 1 species was equal in the low and upper canopy (Table 2). Sabo and Holmes (1983) provide data on mean height of foraging activity for woodpeckers and insectivorous birds in a northern hardwood forest (mean tree height 22 m) and a subalpine conifer forest (mean tree height 7 m). We divided the forest studied by Sabo and Holmes (1983) into thirds and determined the number of birds whose mean foraging height corresponded to low, mid, and upper canopy environments. Within the northern hardwood forest, 8 species (36%) had mean foraging heights in the lower canopy, 14 species (64%) in the mid canopy and 0 in the upper canopy. Within the subalpine conifer forest, 4 species (20%) had mean foraging heights in the lower canopy, 7 species (35%) in the mid canopy, and 9 species (45%) in the upper canopy. In the hardwood forests studied by Anderson et al. (1979), 40% of the avian occurrence was near the forest floor, and the remaining activity was evenly distributed through the canopy.

Although these three studies are a small sample size for comparisons, the vertical distribution of small birds in conifer forests appears to be skewed to the mid-upper canopy, bird distribution in hardwood forests tends to be skewed to the mid-lower canopy. A variety of factors is obviously involved, but the characteristic structural and resource differences between hardwood and conifer forests may play a leading role. The forest floor and soils in hardwood forests is generally more basic, and supports larger arthropods and earthworms, while the acidic soils and forest floor of conifer forests supports mites and smaller arthropods. The larger fruits and nuts of hardwood forests fall to the forest floor, where they, and their associated arthropods, may be fed on by low understory herbivore insectivores. This may increase the number of forest floor feeding birds in hardwoods as compared to conifer stands. The upper canopy of conifer forests is more open, and may be more suitable for a wider range of foraging guilds that move among and between the tree-tops and along the large main stems, than the upper canopy of hardwood forests. Temperate zone hardwood forests, on the other hand, with a closed forest upper canopy and small branches, have fewer foraging guilds in the upper canopy, decreasing the number of upper canopy birds relative to conifer forests.

In this tall stature old-growth forest, the vertical development of canopy structure provides a diversity of habitat elements and microclimate conditions, which are key to vertical canopy use by birds. This general relationship of bird species diversity and forest height diversity is well known in forest-avian research (Dunlavy 1935, MacArthur and MacArthur 1961, Willson 1974). However, the structure of the upper canopy of this old-growth forest leads to avian specialists occurring there in the breeding season, and the relative proportion of resident birds in the upper canopy increases in winter. The complex structure of old-growth Douglas-fir forests, particularly the upper canopy, is unique and important, requiring further vertically organized study to validate results from this single site research.

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