

ARE RESIDENT SONGBIRDS STRATIFIED WITHIN THE CANOPY OF A CONIFEROUS OLD-GROWTH FOREST?

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ABSTRACT. Resident songbirds of temperate coniferous forests survive throughout the year even though the resources within the forest change with the seasons. One aspect of that survival may be a generalist strategy that avoids vertical stratification of the canopy. Five small diurnal songbirds, Red Crossbill (*Loxia curvirostra*), Winter Wren (*Troglodytes troglodytes*), Brown Creeper (*Certhia americana*), Golden-crowned Kinglet (*Regulus satrapa*), and Chestnut-backed Chickadee (*Poecile rufescens*) were studied using the Wind River Canopy Crane from 21 March, 1996 to 20 March, 1998. Point counts were used to survey bird occurrence in low, mid-, and upper canopy positions. A three way Analysis of Deviance was used to test for significance of canopy level, season, and their interaction. All five species stratify the canopy, while all but the Winter Wren had population numbers shift with the season. Only the Chestnut-backed Chickadee and Red Crossbill had significant interaction terms, implying that they shift their abundance in canopy zones with the seasons. The Chestnut-backed Chickadee, Golden-crowned Kinglet, and Brown Creeper occurred in all zones of the canopy, even though they were most abundant in one particular zone during any given season, indicating a generalist ability.

Key words: songbirds, residents, canopy stratification, coniferous old-growth

INTRODUCTION

Vertical partitioning of forest habitat is common in forest birds and has been well studied, especially with regard to foraging ecology of insectivores in temperate forests (e.g., MacArthur 1958, Balda 1969, Anderson et al. 1979, Hutto 1981, Sabo & Holmes 1983, Airola & Barrett 1985). Vertical segregation of feeding zones is an important factor in the separation of species feeding activities (Cody 1974), and the concept of foliage height diversity has long been related to the diversity of bird species in any given forest habitat (MacArthur & MacArthur 1961, Willson 1974).

These concepts are especially interesting when applied to resident birds in temperate forests that experience four distinct seasons, because the resources and competitive relationships shift with the seasons (Anderson 1970, Lewke 1982). However, studies in tall stature (>50 m) coniferous forests are rare or absent because of the difficulty in accessing the entire vertical profile for observations.

We have attempted a simplistic assessment of habitat partitioning in an old-growth temperate coniferous forest by dividing the canopy into 3 equal vertical zones that reasonably reflect the

forest structure of the tall (60+ meter) stature forest. We then sampled avifauna by zone using point counts from the gondola of the Wind River Canopy Crane. We ask the question, "Are resident songbirds stratified within the canopy of a coniferous old-growth forest?" We predicted that resident songbirds would not stratify the canopy because the variability in the seasons would require a generalist strategy. The five most abundant resident songbirds at the study site were chosen for this analysis: Red Crossbill (*Loxia curvirostra*), Winter Wren (*Troglodytes troglodytes*), Golden-crowned Kinglet (*Regulus satrapa*), Brown Creeper (*Certhia americana*), and Chestnut-backed Chickadee (*Poecile rufescens*).

METHODS

Study Site

The study site is located at the Wind River Canopy Crane Research Facility in the Thorton T. Munger Research Natural Area in the Wind River Experimental Forest, southern Washington State, Cascade Mountains, at 355 meters elevation (45°49'13.76"N, 121°57'06.88"W). Mean annual precipitation is 2528 mm, and mean annual temperature is 8.7°C. The site is a classic four-season temperate coniferous forest with mean

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January temperature of 0°C and annual snowfall of 233 cm.

The forest is a 500 year old stand of *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*, with a lower canopy dominated by *Tsuga heterophylla*, *Abies* species, *Taxus brevifolia*, *Acer circinatum*, *Gaultheria shallon*, *Berberis nervosa*, *Vaccinium* species, and various herbs, ferns, and bryophytes typical of the *Tsuga heterophylla*/*Gaultheria shallon* plant association (Franklin & Dyrness 1973). *Pseudotsuga menziesii* dominates the upper canopy and is the tallest tree species in the forest (65 m), while *Tsuga heterophylla* dominates the mid- and lower canopy.

The vertical structure of the forest has been described by Parker (1997) and is bottom heavy, with the bulk of the foliage between 10 and 15 meters, although the canopy is 65 meters tall. The light environment indicates three vertical zones in the forest; a lower "dim" zone below about 12 meters, and mid-canopy "transition" zone between 12 and 40 meters, and an upper canopy "bright" zone. These zones also reflect the distribution of epiphytes, which occur in three vertical zones somewhat similar to Parker's light zones (McCune et al. 1997).

Field Work

Surveys of bird species were begun after the first day of spring in March 1996 and continued until first day of spring in March 1998 (the survey is continuing, but here report on these two years). Surveys were attempted weekly and a total of 84 surveys were accomplished over the two year period. The canopy was divided into three vertical zones; lower canopy, 0–20 meters, mid-canopy, 20–40 meters, and upper canopy, 40–60+ meters. Thirty meter radius point counts were conducted in the middle of each canopy zone from the gondola of the canopy crane, giving a plot which was 20 meters deep, and 60 meters in diameter. All birds observed or heard in the plot were noted during a five minute period following a three minute quiet down, although this paper discusses only five of the resident species. The plots were done approximately 85 meters from the center of the crane in the four cardinal directions, providing four point counts in each canopy zone. The totals from each zone were summed for any given survey day. During spring, summer, early fall, and late winter, the surveys occurred within ½ hour of sunrise. From mid-November through February the surveys occurred during mid-morning. Surveys were not conducted during snowfall or rainfall.

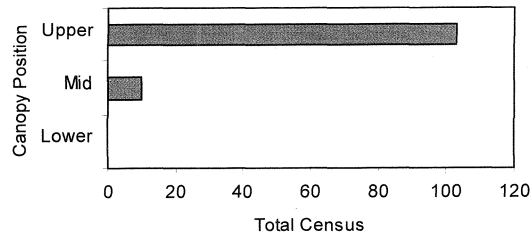


FIGURE 1. Total number of *Red Crossbill* individuals detected in the upper, mid-, and lower canopy zones for the survey period.

Data Analysis

The study consists of count data, with many zeros and low numbers, this suggests the use of a poisson model (with a log link) for the errors. To examine the nature of the data, histograms of the bird counts were made for the 5 species. These indicated skewed and long right-hand tails typical of poisson data. Poisson regression does assume independent events, that is, the occurrence of one event does not affect the occurrence of other events. This is not always appropriate for modeling bird behavior. This could cause inaccuracies in the tests, especially for birds such as *Loxia curvirostra*, that were often observed in flocks, and in these species, the tests should be treated as general guidelines.

Data was analyzed using a three way Analysis of Deviance (canopy level, season, and their interaction) based on a poisson model (S-PLUS 1998) and interaction plots were used to visualize the results. Chi-square contingency table analysis was not possible because of the occurrence of too many low expected frequencies. The design is slightly unbalanced, that is, spring (26) and summer (23) were sampled slightly more frequently than autumn (21) and winter (14). Therefore, the order of the factors has a slight effect on their *P* values. However, this change was small (on the order of $P = 0.0001$) and in no case did altering the order of the factors change a factor from significant to non-significant or vice versa.

RESULTS

Red Crossbills were observed mostly in the upper canopy, although they also occurred in the mid-canopy (FIGURES 1, 2). They stratify the canopy (*P* approaching 0), and population numbers shift with the season (*P* approaching 0). The interaction term was also significant (*P* also approaching 0) (FIGURE 2) indicating that they shift from being exclusively in the upper canopy during fall and winter, and also occur in the mid-

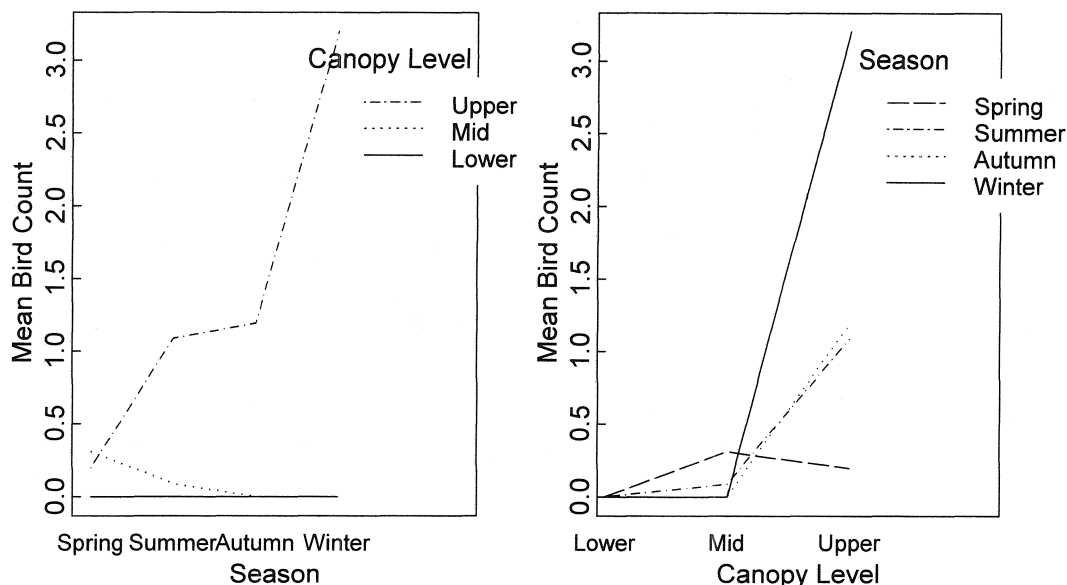


FIGURE 2. Interaction plots for Red Crossbill comparing mean bird count per survey day versus season and canopy level.

canopy during spring and summer. Only in spring were they observed in greatest abundance in the mid-canopy (FIGURE 2), where we observed them foraging on *Tsuga heterophylla* cones which occur lower in the canopy than *Pseudotsuga menziesii* cones.

The Winter Wren is a lower canopy specialist that was only detected once outside of this zone (FIGURES 3, 4). They stratify the canopy (P approaching 0), but their population numbers and/or detectability ($P = 0.054$) remain fairly stable throughout the year (FIGURE 4). The interaction term is not significant ($P = 0.937$) (FIGURE 4) indicating they do not shift zones with the seasons.

Brown Creepers were most abundant in the mid-canopy, but also occurred in the lower and

upper canopy (FIGURES 5, 6). They stratify the canopy ($P = 0.025$) and their population numbers strongly shift with the seasons (P approaching 0) (FIGURE 6). The interaction term is not significant ($P = 0.163$) indicating that although they occur throughout the canopy, they remain most abundant in the mid-canopy throughout the year, except in spring, when they occur most abundantly in the upper canopy (FIGURE 6).

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 (FIGURES 7, 8). They stratify the canopy (P approaching 0), and population numbers strongly shift with the seasons (P approaching 0) (FIGURE 8). The interaction term was significant (P approaching 0) indicating that their abundance in canopy zones shifts with the seasons (FIGURE 8). The Chestnut-backed Chickadee occurs in all canopy zones throughout the year, except in winter, when it was not detected in the lower canopy.

The Golden-crowned Kinglet was most abundant in the mid-canopy, but occurred in all canopy zones throughout the year (FIGURES 9, 10). They stratify the canopy ($P = 0.001$), and population numbers shift with the seasons (P approaching 0), their abundance being especially low in the winter (FIGURE 10). The interaction term was not significant ($P = 0.249$) indicating that they remain most abundant in the mid-canopy throughout the year, although they were ob-

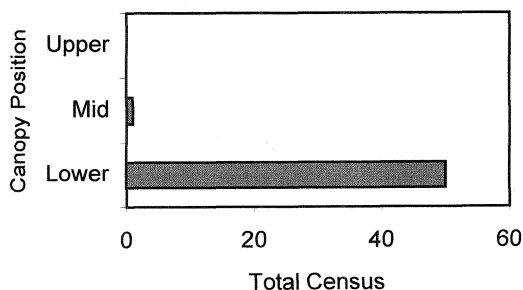


FIGURE 3. Total number of Winter Wren individuals detected in the upper, mid-, and lower canopy zones for the survey period.

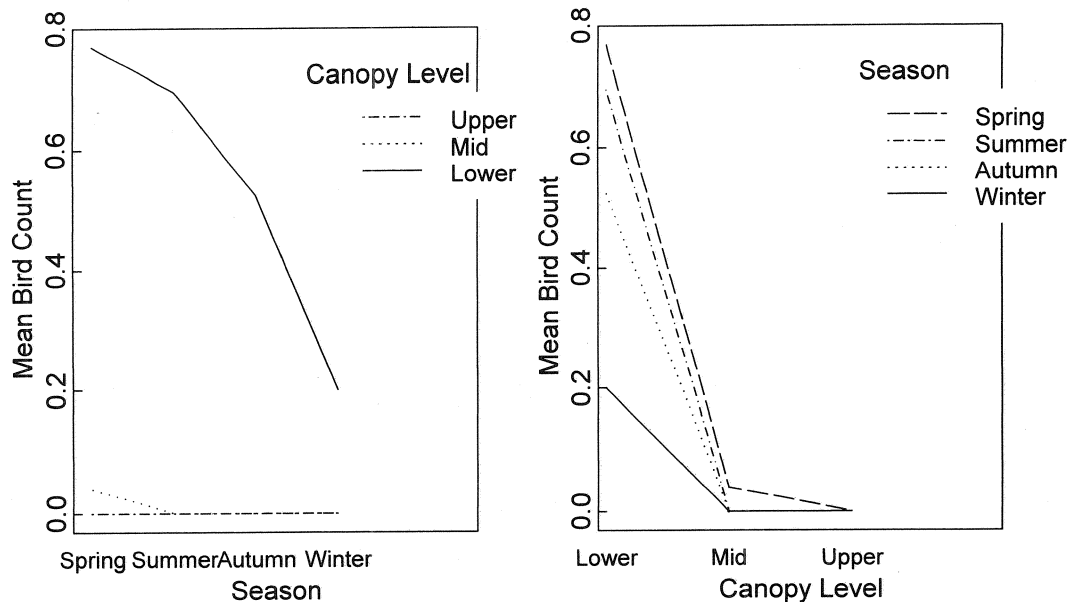


FIGURE 4. Interaction plots for *Winter Wren* comparing mean bird count per survey day versus season and canopy level.

served to be slightly more abundant in the lower canopy in winter (FIGURE 10).

DISCUSSION

All five species analyzed stratify the canopy, with two of the species significantly shifting levels with the seasons, and two others showing non-significant trends in shifting levels. Only the *Winter Wren* shows a highly specialized occurrence in one zone. Cody (1974) and Anderson et al. (1979) have noted that avian stratification by height is at a much finer scale near the ground. Birds also vary the range of heights used in forests with different heights. In this study, our techniques would mask any fine scale segregation of the lower canopy because we

considered everything below 20 meters the lower canopy.

Four of the five species show wide seasonal changes in detection numbers. The ability to detect birds varies with the season, and there is usually an optimal time during the year when an individual species can be detected (Best 1981). Therefore, it is possible that some of the population changes we show during the seasons are related to the fact that birds may be quieter, and not as easy to detect by ear during certain times of the year, especially when males are not singing or when flocking behavior is not occurring. However, to minimize this problem, we purposefully chose a small plot (30 m radius, 20 m deep).

The Red Crossbill is a "timber-seed eater" (Manuwal 1991) and specializes on conifer seed, including *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata* at Wind River. There are eight flight call types in North America (Adkisson 1996) and each are specialized on a different conifer. Type 3 specializes on *Tsuga heterophylla*, while Type 4 specializes on *P. menziesii* so that there may be more than one type at Wind River. Red Crossbills are wide ranging birds that only settle in one location when cone crops are abundant. Their vertical occurrence in a forest is closely tied to the vertical distribution of cones. *Pseudotsuga menziesii* has cones mostly in the upper canopy above 40 meters, while

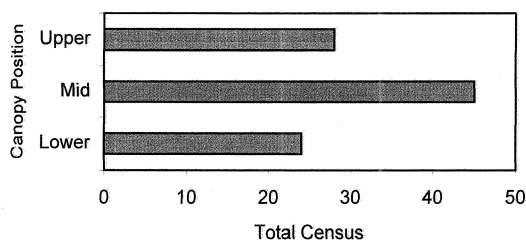


FIGURE 5. Total number of *Brown Creeper* individuals detected in the upper, mid-, and lower canopy zones for the survey period.

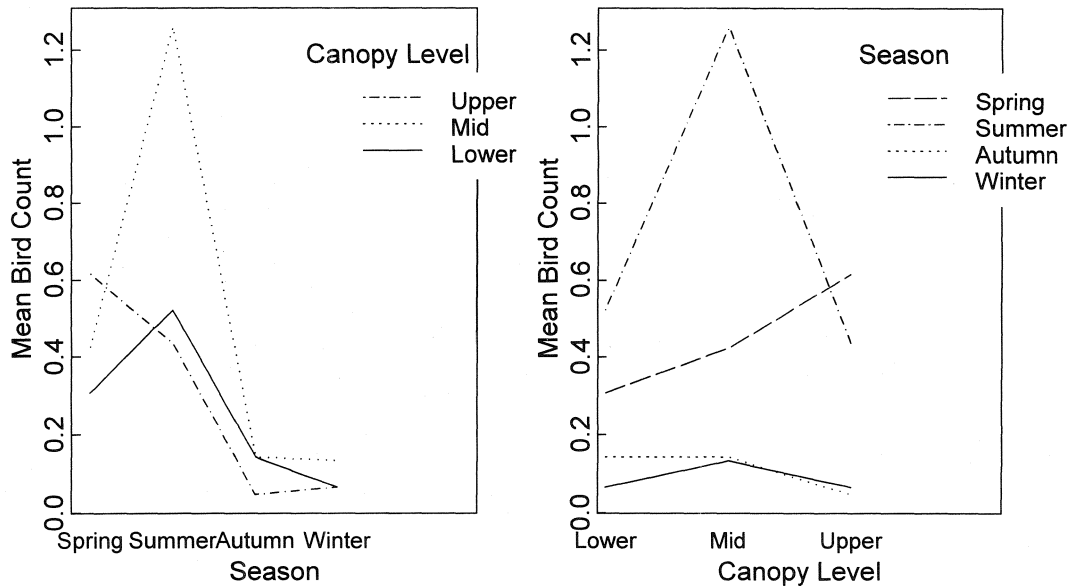


FIGURE 6. Interaction plots for the *Brown Creeper* comparing mean bird count per survey day versus season and canopy level.

Tsuga heterophylla and *Thuja plicata* have abundant cones in the upper and mid-canopy (during high cone years). Our observations indicate that the lowest numbers of birds occur in spring and summer, while these are the only seasons we observed birds in the mid-canopy. Although the Red Crossbill is a specialist, it has the generalist strategy to move geographically to where food is abundant (Adkisson 1996).

The Winter Wren (Kroodsma 1980) is a "low understory herbivore insectivore" (Manuwal 1991) which feeds on arthropods on the forest floor. It is a specialist in the lower canopy, rarely moving out of that zone. Sabo and Holmes (1983) observed Winter Wren foraging in New Hampshire (NE North America) and estimate mean foraging height in a northern hardwood forest at 1.7 m and in a subalpine forest at 0.2 m. In an earlier study of subalpine bird communities, Sabo (1980) ordinated birds along an

axis of arboreal to terrestrial and found that the Winter Wren was the most terrestrial of all birds studied.

The population numbers of Winter Wrens remained relatively stable throughout the year. Therefore, whatever resources the birds depended on also must remain reasonably stable also. This species was the only one of these five to have such a stable population in this stand.

The Brown Creeper is a "bark insectivore" (Manuwal 1991) that gleans arthropods off bark with a slightly curved bill (Davis 1978, Franzreb 1985, Mariani 1987). They are thought to prefer the tallest trees in a forest (Mariani 1987 observed them foraging on *Pseudotsuga menziesii* most abundantly), and are most commonly observed in the lower and mid-canopies. They have been observed to begin foraging on the lower tree bole and work their way up to the tops of the trees (Davis 1978, Franzreb 1985, Mariani 1987). However, at Wind River, we observed these birds most abundantly in the mid-canopy, while during spring we detected them mostly in the upper canopy. Davis (1979) has reported that singing males prefer upper treetop positions, and it may be that we were biased to singing males in our spring survey.

The Chestnut-backed Chickadee and Golden-crowned Kinglet are "timber foliage insectivores" (Manuwal 1991). The Chestnut-backed Chickadee gleans arthropods from needles, buds, and upper surfaces of branch twigs in an

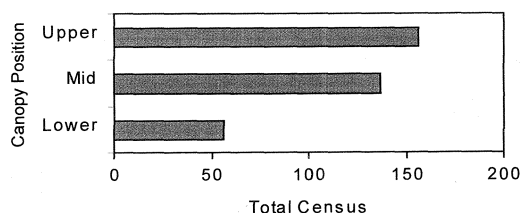


FIGURE 7. Total number of *Chestnut-backed Chickadee* individuals detected in the upper, mid-, and lower canopy zones.

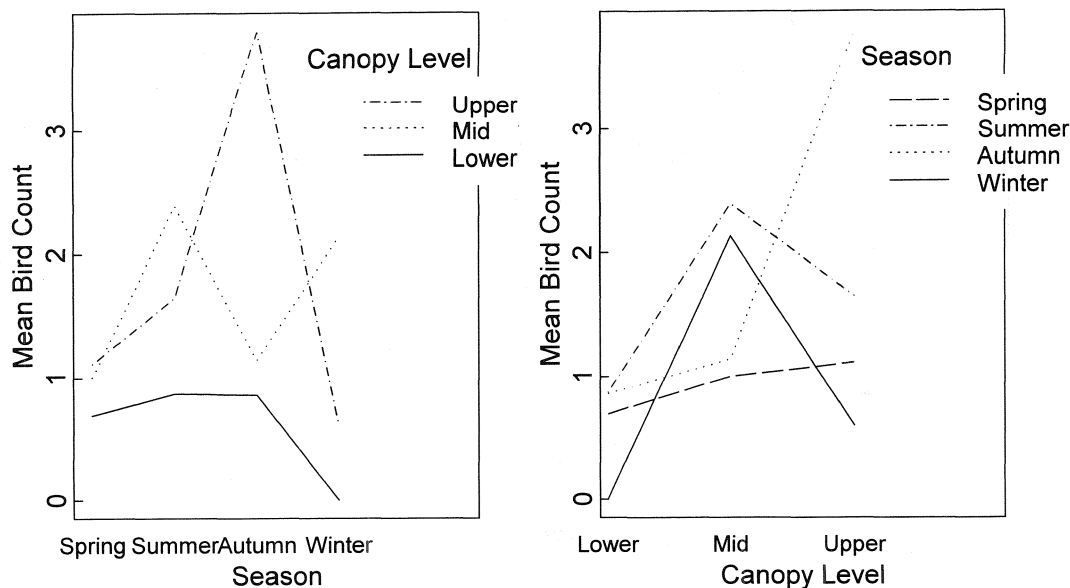


FIGURE 8. Interaction plots for the *Chestnut-backed Chickadee* comparing mean bird count per survey day versus season and canopy level.

upright stance (Sturman 1968), while the Golden-crowned Kinglet gleans from leaves and twigs and hovers and hawks to capture prey (Sabo 1980, Ingold & Galati 1997). These two bird species have very similar foraging strategies, both preferring conifers and forage primarily in foliage of the crowns (Airola & Barrett 1985). At the Wind River site, both species show presence throughout the entire canopy although the Chickadee is more abundant in the upper canopy and the Kinglet more abundant in the mid-canopy. However, in winter the Kinglet is most abundant in the lower canopy and the Chickadee is abundant in the mid-canopy. It appears that the two birds segregate the canopy with the Kinglets staying generally below the Chickadees. Ingold and Galati (1997) note several studies where Golden-crowned Kinglet foraging appears to be forced out of certain sites

by the presence of other competitor species, especially *Parus (Poecile)* spp.

The change in foraging height during winter by Golden-crowned Kinglets and Chestnut-backed Chickadees may be related to the weather. Grubb (1975, 1977) has studied weather dependent foraging behavior in wintering birds and found that wind velocity, temperature, and solar radiation all influence the foraging behavior of insectivores. In particular, birds were observed closer to the ground during lower temperatures and higher winds.

CONCLUSIONS

This was not a study on the foraging ecology of these birds, rather a simple point count of the occurrence of these five species in the three major zones of the forest. From this survey, however, we can conclude that each species does indeed stratify the canopy. The hypothesis that these birds would be vertical generalists is not entirely appropriate. However, of these five species, all but the Winter Wren show generalist strategies, either in the ability to move to another habitat or move in the vertical strata to find an appropriate microhabitat.

ACKNOWLEDGMENTS

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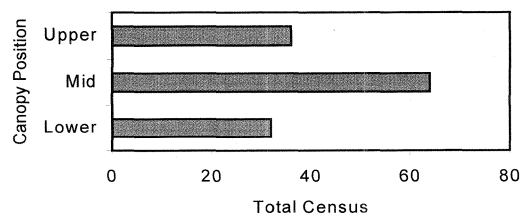


FIGURE 9. Total number of *Golden-crowned Kinglet* individuals detected in the upper, mid-, and lower canopy zones.

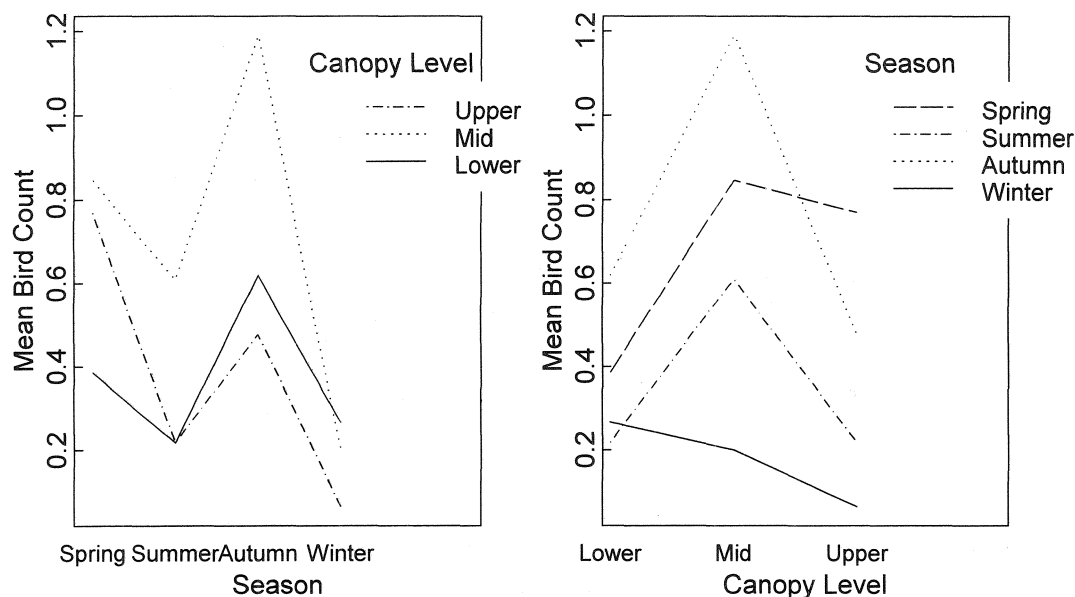


FIGURE 10. Interaction plots for the *Golden-crowned Kinglet* comparing mean bird count per survey day versus season and canopy level.

in the T.T. Munger Research Natural Area in Washington state USA. The facility is a cooperative scientific venture among the University of Washington, the USFS Pacific Northwest Research Station, and the USFS Gifford Pinchot National Forest. Elizabeth Freeman assisted with statistical analysis, and prepared the interaction figures.

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