

Running Head: AVIAN NEST SUCCESS IN FORESTS OF SW WASHINGTON

RELATIONSHIPS BETWEEN FOREST STRUCTURE AND AVIAN NEST SUCCESS IN
THE SOUTHWEST CASCADE MOUNTAINS OF WASHINGTON

REX SALLABANKS,^{1,3} AND TIMOTHY QUINN²

¹*Sustainable Ecosystems Institute, 1543 North Mansfield Place, Eagle, ID 83616 USA*

²*Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501 USA*

³ Present address: Nongame and Endangered Wildlife Program, Idaho Department of Fish and Game, 600 S. Walnut, P.O. Box 25, Boise, Idaho 83707 USA; E-mail: rsallaba@idfg.state.id.us

Abstract. Information on nesting behavior, nest-site selection, and nesting success of birds is lacking from forested landscapes of the Pacific Northwest. Moreover, we know little about the influence of forest management on songbird nesting success, and even less about the microhabitat requirements of breeding birds. To help meet these information needs, we initiated a two-year study in Douglas-fir (*Pseudotsuga menziesii*) - Western Hemlock (*Tsuga heterophylla*) forests of the southwest Cascade Mountains of Washington in 1998. We sampled 12 32 ha forest stands that were classified into one of three common forest treatments on the southwest Cascade Mountains landscape: (1) 8- to 12-year-old regenerating clearcuts ($n = 4$ stands); (2) 40- to 60-year-old managed forest that had been commercially thinned, but not yet clear-cut harvested ($n = 4$ stands); and (3) 150- to 270-year-old mature, naturally regenerated old growth forest ($n = 4$ stands). In each stand, we monitored nests of as many breeding bird species as we could find, and measured habitat characteristics both around nests and throughout study plots. Our specific study objectives were to: (1) describe nest-site characteristics of Pacific Northwest forest birds; (2) compare nesting success and productivity among three common forest treatments on the Cascades Mountains landscape; and (3) model species-specific nest-habitat relationships to identify habitat structural attributes that influence nesting success and productivity.

During the songbird breeding seasons of 1998–1999, we found and monitored 681 nests of 40 bird species. We used MANOVA to compare nest fate between years and among forest treatments for all nests combined. We found significant annual variation in nest success (success rates were higher in 1999), most likely due to annual variation in numbers of small mammalian nest predators. Nest fate did not vary among forest treatments, neither for all species and nests combined, or when Mayfield estimates of nest success were compared for individual species

(with one exception). The only exception was the Rufous Hummingbird (*Selasphorus rufus*), which experienced daily rates of nest mortality an order of magnitude higher in commercial thins compared to clearcut forests. Nest-site locations (e.g., nest height, nest-plant height, nest-tree diameter, and nest orientation), nest-site characteristics (e.g., number of branches supporting nests and nest cover by vegetation), and nest dimensions (inside and outside diameter and inside and outside height) were reported for 14 bird species.

For five focal species, the American Robin (*Turdus migratorius*), Song Sparrow (*Melospiza melodia*), Winter Wren (*Troglodytes troglodytes*), Pacific-slope Flycatcher (*Empidonax difficilis*), and Dark-eyed Junco (*Junco oreganus hyemalis*), we had sufficient sample sizes to examine nest-site selection quantitatively using a combination of linear and logistic regression. All species used sites with habitat characteristics that were different from characteristics available in the forest stands where their nests were located. In particular, we noted the apparent importance of woody structures such as rootballs and coarse woody debris on the forest floor as nesting habitat. Nesting productivity (number of young fledged per nest) of the Winter Wren was positively correlated with density of rootballs in commercial thins, and positively correlated with amount of coarse woody debris in old growth forests. In combination, our results suggest that birds nesting in managed forest landscapes of the western Cascade Mountains require structurally heterogeneous stands that offer a wide array of spatially-complex, small-scale microhabitat features. We recommend that forest managers leave (or even create) key forest structures that we have identified to be correlated with avian nest success and productivity, especially those that contribute to forest floor complexity such as rootballs and coarse woody debris. Finally, we urge researchers to conduct more studies of nesting birds in managed forests of the Pacific Northwest.

Key words: coarse woody debris, forest avifauna, forestry, nest-habitat relationships, nest monitoring, old growth forest, productivity, rootballs, silviculture, songbirds.

INTRODUCTION

Our knowledge of species-habitat associations in forests of the Pacific Northwest has improved throughout the past decade (e.g., Ruggiero et al. 1991 and references therein; McGarigal and McComb 1995; Carey and Kershner 1996; Hagar et al. 1996; Aubry et al. 1997; Hallett and O'Connell 1997; O'Connell et al. 2000; Pearson and Manuwal 2001; Sallabanks et al. 2001a, 2002). In the state of Washington, the Timber/Fish/Wildlife (TFW) program has funded two major wildlife studies: one that addressed the effects of forest stand age and fragmentation on wildlife ("landscape study"; Aubry et al. 1997), and the second that addressed wildlife use of forested riparian management zones of different widths ("RMZ study"; O'Connell et al. 2000). A major component of both studies was the collection of data on forest birds. While the landscape study used standard point-count methods (with 50- and 75-m radius point counts on the Westside and Eastside, respectively), the RMZ study employed small point-count plots (10, 15 m fixed-radius point count plots/replicate) in western Washington and thin transects (modified belt transects of 30 x 800 m/replicate) in eastern Washington to sample narrow strips of riparian forest. The Westside component of the RMZ study included nest monitoring but small sample sizes precluded the use of nest success as a measure of habitat quality (S. F. Pearson, pers. comm.).

The landscape study (Aubry et al. 1997) showed clear bird community patterns along a structural (forest age class) gradient and also concluded that the primary determinants of bird species richness and abundance appeared to be at the stand level rather than at the landscape level. Although Aubry et al. (1997) measured habitat characteristics of stands across a range of ages/stages, analyses of species association with habitat characteristics was limited to simple correlations between individual habitat variables and bird abundance. The RMZ study

(O'Connell et al. 2000) study was limited to mature upland and riparian forests and recently clearcut forest, and provided habitat relationships for numerous species, including the American Robin (scientific names in Appendix 1), Black-throated Gray Warbler, Pacific-slope Flycatcher, and Winter Wren.

While there have therefore been several studies of bird-habitat relationships in Washington state, including the western Cascades Mountains, all of them have relied upon measures of relative avian abundance to infer habitat quality. Even throughout the U.S., relatively few studies have identified specific relationships between structural attributes within forest stands and the nesting success of forest birds (Sallabanks et al. 2001b). Unfortunately, inferences about the actual quality of habitat can only be indirectly deduced from correlational wildlife surveys (Sallabanks and Quinn 2000). Moreover, without knowledge of which stand structures potentially operate as proximate mechanisms driving avian reproductive success, effective management recommendations lack an empirical basis for implementation (Marzluff et al. 2000, Sallabanks et al. 2000). Indeed, in a survey of forest managers throughout the Pacific Northwest, Arnett and Sallabanks (1998) reported that one of the highest ranked information needs is knowing which structural habitat features are of greatest importance to birds.

To begin to fill this information void for the region, we studied breeding bird communities during 1998 and 1999 in Douglas-fir (*Pseudotsuga menziesii*) - Western Hemlock (*Tsuga heterophylla*) forests of the southwest Cascade Mountains of Washington. We monitored nests and extensively sampled a wide array of habitat features in clearcut, commercially-thinned, and old growth forest treatments. Our specific study objectives were to: (1) describe nest-site characteristics of Pacific Northwest forest birds; (2) compare nesting success and productivity among three common forest treatments on the Cascades Mountains landscape; and (3) model

species-specific nest-habitat relationships to identify habitat structural attributes that influence nesting success and productivity. To enhance our study's applicability to current timber harvest practices, we end our paper with a discussion of how forest managers might influence the quality of habitat for breeding avifauna based upon the results from our study.

METHODS

Study area

Our study was conducted in the Douglas-fir - Western Hemlock zone (Franklin and Dyrness 1988) of the southwest Cascades of Washington. Data were collected in three principal forest types: (1) 8- to 12-year-old managed forest (regenerating clearcuts); (2) 40- to 60-year-old managed forest that had been commercially thinned, but not yet clear-cut harvested; and (3) 150- to 270-year-old mature, naturally regenerated old growth forest. Four replicates of each forest type were selected for study, spanning a variety of state, federal, and private ownerships (Sallabanks and Quinn 2000). Actual study plots were forest stands approximately 32 ha in size that matched these structural stage descriptions. We chose 32 ha because this was approximately equivalent to the maximum stand size available in our study area. While we would have preferred to work with larger plots (to increase sample points within stands), we could only work with what was available on the southwestern Washington Cascades landscape.

Criteria for selecting study plots

One goal of our study was to make inferences for as much of the forest (in structural stages described above) within the southwestern Cascades region of the Washington State Douglas-fir - Western Hemlock zone (e.g., the population) as possible. This would require that

study plots be randomly selected from all potential plots that constituted that population. To achieve this, we identified a population of suitable study plots and randomly selected from among that population, as long as our sample did not create logistical bottlenecks for field staff that had to conduct surveys at all plots. We controlled for major factors that could influence within-stand bird population dynamics, such as the amount and type of disturbance in the immediate vicinity of the study plot (stand), size of study plot, and disturbance history of the study plot. We recognized that there also were potentially important influences of longitude, latitude, and elevation on the composition of bird communities in forests of the western Cascades (e.g., Huff and Raley 1991) and controlled for such factors during plot selection where possible. In January of 1998, we began identifying potential study plots by working with state resource agencies and private timber companies. All study plots were as homogeneous as possible with respect to forest structural stage. Where necessary, we obtained permission from landowners to use privately owned land and were assured that the study plots would not be disturbed by forest management activities for at least two years.

Avian nesting success and productivity

From late April to early August 1998–1999, we sampled all 12 32 ha study plots for avian nest success and productivity. During each breeding season, we used standardized techniques to search for and monitor nests, emphasizing common forest bird species, in all study plots (Martin and Geupel 1993). All nests found were checked every three to four days and their fate recorded (i.e., successful, depredated, abandoned, parasitized, failed due to environmental conditions, disturbance by human observers, or fate unknown). We visited most nests on days when nestlings were predicted to fledge in order to remove uncertainty as to their true fate.

Types of nest predators (e.g., avian, mammalian, or reptilian) were identified where possible. We used mirror poles to check high nests (up to approximately 7 m high) and approached all nests on at least one occasion (typically upon first detection) to assess nest stage and clutch or brood size. Every attempt was made to minimize depredation events due to human visitation (e.g., Westmoreland and Best 1985, Major 1989). Because increased predation by avian predators is the main reason for reduced nesting success of birds disturbed by observers (Götmark 1992), we approached nests from different directions on each visit (to avoid leaving scent trails to nests) and only checked nests if Corvids and/or Brown-headed Cowbirds (*Molothrus ater*) were not present. Careful nest monitoring techniques such as these (see also Ralph et al. 1993) have been shown to effectively reduce the probability that visited nests were more likely to be depredated (Willis 1973, Gottfried and Thompson 1978).

Nest success and daily rates of nest mortality were calculated using the Mayfield method (Mayfield 1961, 1975) and modifications of Hensler and Nichols (1981). This method corrects for biases in the probability of nest survivorship that might result when nests are not observed on a daily basis throughout the entire nesting cycle. Mayfield nest success was calculated as the probability that a nest survived to fledge at least one host young and only nests with known fate and exposure period were included in these calculations. We considered the first observation day as the first day of incubation (if the nest was found before incubation began) or the day the nest was located (if the nest was located after incubation had begun). Nest success and daily rates of nest mortality were determined on a treatment level (by pooling nests among replicate study plots within treatments) for all species with ≥ 10 nests in at least two forest treatments. Prior to pooling nests, we tested for differences between years. For species with ≥ 10 nests in at least two forest treatments, we computed daily mortality across the nesting cycle as total number

of failures divided by total number of observation days pooled across all nests within a treatment (as in Donovan et al. 1995, Burke and Nol 2000). Daily survival was calculated as (1 - daily mortality) for each species in each treatment. Overall nest success was based on the estimate of daily success raised to the exponent that reflects average length of the entire nesting cycle (Mayfield 1975). Values for average length of the nesting cycle for each species examined were obtained from our own unpublished data from the region and the primary literature. We also partitioned total daily nest mortality into cause-specific components (e.g., daily predation mortality) as described by Donovan et al. (1995).

We calculated nesting productivity as the mean number of fledglings produced per nesting attempt by dividing the total number of young fledged by the number of nests monitored on a species by species basis (using the same suite of species previously identified for calculations of Mayfield nest success). Only nests for which we could determine the number of young that fledged were included in these calculations. Unlike estimates of Mayfield nest success and daily nest mortality, which require large sample sizes to achieve reasonable precision (Hensler and Nichols 1981), nesting productivity was determined on a plot level with plots representing replicates within each forest treatment.

Habitat sampling

For all nests found and monitored, regardless of species, we recorded data such as nest height, nest-plant species, nest-plant height, cover around the nest, and nest dimensions (where possible) using standard protocols modified from Martin and Conway (1994). For a subset of “focal species,” for which we expected larger nest sample sizes, we collected additional microhabitat data at and around each nest following protocols developed for forest stands by

Aubry et al. (1997) and Hallett and O'Connell (1997), with a few modifications from Sallabanks (1994, 1995). In 1998, focal species included Winter Wren ($n = 73$ nests), Dark-eyed Junco ($n = 46$ nests), and American Robin ($n = 31$ nests). In 1999, Song Sparrow and Pacific-slope Flycatcher were added to the list of focal species to yield nest-level habitat data for the following: Winter Wren ($n = 91$ nests), Dark-eyed Junco ($n = 30$ nests), American Robin ($n = 13$ nests), Song Sparrow ($n = 37$ nests), and Pacific-slope Flycatcher ($n = 25$ nests).

To sample habitat around each nest, we established an 11.3 m radius vegetation subplot centered on the nest. So as not to disturb birds from potential re-nesting attempts in the same nests, no nest-level habitat data were collected until at least 10 days following the end of the nesting cycle (for either successful or unsuccessful nests). At the center of each subplot, we measured slope with a clinometer, aspect with a compass, percent canopy cover using a moosehorn (Robinson 1947), and height to both the top and bottom of the canopy also using a clinometer.

Within each 11.3 m radius subplot, we sampled different components of the vegetation at three spatial scales: (1) a 0–2 m radius circle; (2) a 0–5 m radius circle; and (3) a 0–11.3 m radius circle. At the smallest spatial scale (0–2 m), we identified all forbs to species, estimated their stem diameter, and tallied individual stems by species. At the intermediate spatial scale (0–5 m), we identified all shrubs to species, estimated their stem diameter, and tallied individual stems by species. Also included at this scale were tree seedlings with diameters too small to measure at breast height (DBH). At the largest spatial scale (0–11.3 m), we did the following: (1) identified all living trees to species and measured individual tree DBH; (2) recorded all snags (standing dead trees) as we did live trees, recording species (whenever possible) and DBH; (3) sampled cut stumps by identifying tree species (again, whenever possible), as well as diameter (at the top of

the stump) and height; and (4) recorded numbers of rootballs (fallen trees with exposed root systems), regardless of size and tree species.

We also conducted ocular estimates of cover at the smallest scale (0–2 m) for the following cover types: (1) berry-producing deciduous shrubs <1 m in height; (2) broad-leaved evergreen shrubs <1 m in height; (3) other deciduous shrubs <1 m in height; (4) tree seedlings <1 m in height; (5) ferns; (6) leaf/needle litter; (7) moss; (8) bare soil; (9) rocks; (10) forbs; (11) grasses; (12) *Lobaria* lichen; (13) branches; (14) fine woody debris (e.g., twigs, decayed log fragments); (15) coarse woody debris (e.g., intact down logs); (16) cut stumps; and (17) other (e.g., saprophytes, above-ground roots, tree and snag boles). Ocular estimates were made to the nearest 5% independent of all other cover types. To increase accuracy, the 0–2 radius circle was divided into four quadrants and ocular estimates were conducted separately for each quadrant. To reduce observer bias, two observers performed the ocular estimates simultaneously and their data were averaged.

At the stand level, habitat sampling occurred systematically throughout all 12 study plots (six in 1998 and six in 1999) using similar protocols as conducted at nests. As part of a companion study, not reported on here (R. Sallabanks and T. Quinn, unpubl. data), we had established eight point count stations within each study plot at which we estimated relative avian abundance using point count surveys. All count stations were at least 200 m apart, at least 100 m from stand boundaries, and centered within stand interiors to the extent possible. To sample habitat at the plot level, we therefore established two 11.3 m radius subplots at each point count station for a total of 16 vegetation subplots per forest stand. The first subplot was centered over the count station center point, and the second was located 30 m from the station's center point in a random direction. Within each 11.3 m radius vegetation subplot, the same habitat

measurements were made as previously described for nests of focal bird species. Prior to analysis, habitat data from the two vegetation subplots at each point count station were averaged to yield eight replicates per forest stand.

For both nest-level and plot-level data, we combined habitat variables in order to make data analysis more tractable (i.e., decrease the number of potential dependent variables) and to eliminate variables that had a relatively large proportion of data cells with values of zero. The original data (150 variables) was collapsed into 27 variables, including slope, percent canopy cover, percent cover of each of broadleaf evergreen shrubs, berry producing shrubs, other deciduous shrubs, tree seedlings, ferns, herbs, coarse woody debris, fine woody debris, and other ground cover; and stem density of each of forbs, shrubs, small conifers, medium conifers, large conifers, giant conifers, small deciduous, medium deciduous, large deciduous, small stumps, large stumps, small snags, medium snags, large snags, giant snags, and rootballs (Appendix 2).

Data analysis

To first examine whether nest fate (i.e., successful, failed, or unknown) varied between years and among forest treatments, we used two-factor MANOVA with year and treatment as the main effects tested. We included all nests of all species ($n = 681$ nests of 40 species; Appendix 1) and the proportion of nests in each nest-fate category were arcsine transformed prior to analysis. We also used two-factor MANOVA to assess whether reasons for nest failure varied between years and among forest treatments. For this analysis, we classified all failed nests ($n = 230$ nests of 24 species) into one of five failure-reason categories (depredation, abandonment, environment [e.g., weather, lack of food, collapsed nest structure], disturbance by human observers, or unknown) and again analyzed arcsine-transformed data. Brood parasitism by the

Brown-headed Cowbird was never observed for any of the nests we monitored during our two-year study. For these analyses, we used $\alpha = 0.10$ to interpret statistical significance because of small sample sizes and associated low power (Schmiegelow et al. 1997, Pearson and Manuwal 2001).

Differences in daily nest mortality and daily predation mortality (daily nest mortality due to predation) among forest treatments were tested using program CONTRAST (Hines and Sauer 1989), which uses a modified Chi-square (χ^2) test (Sauer and Williams 1989). Prior to pooling for analysis of treatment effects, differences in daily nest mortality and daily predation mortality were compared between years using program CONTRAST and found to be nonsignificant ($P > 0.10$ in all cases). We used ANOVA to compare nesting productivity (mean number of fledglings produced per nest) among forest treatments, again following tests between years.

To examine relationships between habitat characteristics, nest placement, and the probability of nesting success, we considered the five (focal) species for which we had ≥ 25 nests after pooling data across years. We first used Chi-square tests to determine if aspects of nest sites were representative of the stand in which those sites were located. Observed counts (obs) were based on nest site locations and expected counts (exp) were based on a random selection of aspects from the stand in which those nests occurred. Aspect was classified into five groups, flat (slope of 0°), north ($316-45^\circ$), east ($46-135^\circ$), south ($136-225^\circ$), and west ($226-315^\circ$). Because expected values were measured at only eight points within a stand, we drew a sample of points with replacement from those eight points ($N(\text{exp}) = N(\text{obs})$) to generate an expected frequency of aspects for each forest stand (Manly 1991). Nest data for American Robin, Dark-eyed Junco, Pacific-slope Flycatcher, and Song Sparrow were pooled across treatments due to small sample sizes, whereas Winter Wren data were analyzed separately for commercial thins and old growth

forests. Similarly, we used a Chi-square test to determine if nest orientation was random. Nest orientation data were classified into north (331–30°), northeast (31–90°), southeast (91–150°), south (151–210°), southwest (211–270°), and northwest (271–330°), and then compared to a uniform distribution of counts across orientation classes. Again, we pooled nests for all species except Winter Wren across forest treatments due to small samples sizes. Winter Wren data were analyzed separately for commercial thins and old growth forests.

We used Mann-Whitney tests for comparing habitat at nest plots versus habitat at point count stations for the five focal species across all three treatments. Each treatment by bird species was analyzed separately.

We used stepwise linear regression to explore the relationship between the number of young fledged per nest and nest plot habitat characteristics; habitat variables included 27 variables (see Methods: Habitat sampling, above, and Appendix 2) plus nest site aspect and nest orientation. A separate regression was done for each species (i.e., American Robin, Dark-eyed Junco, Pacific-slope Flycatcher, and Song Sparrow), using data pooled across treatments (e.g., American Robin from all treatments were included in a single analysis). We had relatively large sample sizes for Winter Wren so we did three analyses, one each for Winter Wren in commercial thins, old growth, and pooled commercial thin and old growth treatments. Prior to analysis, we square-root transformed the habitat variables because examination of the winter wren data within commercial thin treatments (largest number of nests within a single treatment) showed that variable means were positively correlated with variance ($r = 0.92$; Zar 1996). We examined Pearson correlation coefficients between all pairs of 27 habitat variables before conducting the stepwise procedure. When correlation coefficients were >0.75 , one member of the pair was excluded from analysis. We kept for analysis those variables that were most closely related to

nesting substrate for a given species. When the choice between variables was unclear, we randomly chose a variable to exclude. The stepwise procedure began with no variables in the models, and at each step, added the variable with the smallest P -value (highest F -value) that was less than 0.10, and removed variables with P -value > 0.10 (Wilkinson et al. 1992).

Stepwise procedures remove cases (sample nests) that have missing data (e.g., missing a value for cover). In a large data sets like ours, missing data can result in the loss of many samples even before important independent habitat variables are identified in stepwise procedures. To avoid the loss of data, we did stepwise regression iteratively with respect to two variables, shrub density and forb density, which together often resulted in loss of up to 30% of the data for any given species. The first iteration began with all uncorrelated variables in the pool. If shrub or forb density were not identified as important, these variables were dropped and a second iteration was done to identify all potentially important variables.

Finally, we conducted a logistic regression for each species again by pooling data across treatments and years for all species except the Winter Wren, which was pooled across years but analyzed separately for commercial thins and old growth forests before being analyzed together. Nest success (i.e., >0 young fledged) or failure was the dependent variable and habitat characteristics were potential independent variables. Only habitat characteristics identified in the final stepwise linear regression above were included as independent variables in the logistic stepwise procedure. We used Mann-Whitney tests to compare habitat variables, identified by the regression, between successful and unsuccessful nests (microhabitat).

Because it is more likely to sample nests that are successful (i.e., have a longer time period for detection by researchers) than nests that have failed, technically the sample of nests used in our regression was not random. To overcome this issue, we searched for nests as early in

the nest-building stage as possible and monitored them throughout the breeding season. An alternative approach would have been to eliminate failed nests and conduct linear regression only on those nests that had fledged >1 young (based on the idea that all successful nests had similar exposure days). Unfortunately, this would have eliminated a large proportion of nests, made linear regression analysis impractical, and logistic regression impossible. Since our intent in performing the regression analyses was largely exploratory, we ignored the violation of the random assumption. As a result, our results should be interpreted cautiously.

RESULTS

Variation in nest fate between years and among forest treatments

During our two-year study, we found 681 nests of 40 bird species (Appendix 1). Pooling all nests of all species, MANOVA revealed that nest fate (i.e., successful, failed, unknown) varied significantly between years (Wilks' $\lambda = 0.60$, $df = 3$ and 16 , $P = 0.04$), but not among forest treatments (Wilks' $\lambda = 0.54$, $df = 6$ and 32 , $P = 0.11$; Fig. 1a). The interaction effect between year x treatment was nonsignificant (Wilks' $\lambda = 0.78$, $df = 6$ and 32 , $P = 0.66$). Univariate F -tests revealed that the proportion of nests that failed was significantly greater in 1998 compared with 1999 ($F = 5.35$, $df = 1$ and 18 , $P = 0.03$) and the proportion of nests that were successful was significantly greater in 1999 compared with 1998 ($F = 9.94$, $df = 1$ and 18 , $P = 0.006$).

Reasons for nest failure differed between years (Wilks' $\lambda = 0.40$, $df = 5$ and 13 , $P = 0.02$) and among forest treatments (Wilks' $\lambda = 0.26$, $df = 10$ and 26 , $P = 0.03$; Fig. 1b). The interaction effect between year x treatment was nonsignificant (Wilks' $\lambda = 0.50$, $df = 10$ and 26 , $P = 0.41$). Univariate F -tests suggested that all reasons for nest failure differed between years as

follows: failure due to depredation ($F = 5.94$, $df = 1$ and 17 , $P = 0.03$), abandonment ($F = 8.92$, $df = 1$ and 17 , $P = 0.008$), and the environment ($F = 3.37$, $df = 1$ and 17 , $P = 0.08$) was significantly greater in 1998 compared to 1999; failure due to human observers ($F = 10.07$, $df = 1$ and 17 , $P = 0.006$) and the proportion of nests that failed for unknown reasons ($F = 14.90$, $df = 1$ and 17 , $P = 0.001$) was significantly greater in 1999 compared to 1998. Only nests that failed due to disturbance from human observers varied significantly among forest treatments ($F = 2.99$, $df = 2$ and 17 , $P = 0.08$), occurring more frequently in old growth forest relative to clearcuts and commercial thins (Fig. 1b).

Nest success, daily nest mortality, and productivity

We had sufficient nest sample sizes (i.e., ≥ 10 nests in at least two forest treatments) to calculate Mayfield estimates of daily rates of nest mortality, daily survival, and overall nest success for 13 species of forest songbirds (Table 1). These data represented $>80\%$ ($n = 549$ nests) of all nests found and monitored during our two-year study. Because the primary reason for nest failure was predation (Fig. 1b), we also partitioned total daily nest mortality into that due specifically to predation (daily predation mortality). For five species with sufficient sample sizes, these rates of nest mortality could be compared between two forest treatments using CONTRAST analysis. With the exception of the Rufous Hummingbird, neither daily nest mortality nor daily predation mortality varied significantly among forest treatments for any species included in analyses (Table 2). For the hummingbird, the daily rate of nest mortality was almost an order of magnitude greater in commercial thins compared to clearcuts ($P = 0.01$; Table 2).

Combining nests together among the five species also yielded no differences in daily nest mortality or daily predation mortality among the forest treatments that we studied (Table 2). Relative to nest mortality due to predation, which accounted for almost 50% of nest failures, other cause-specific components of daily nest mortality (e.g., daily abandonment mortality) accounted for few nest failures and so were not analyzed. Nesting productivity did not differ among forest treatments for any of the 13 species examined, or for all species combined (Table 3).

Nest characteristics and nest-site selection

Nest-site locations (Table 4) and nest cover and nest dimensions (Table 5) for all species for which we found >10 nests ($n = 14$ species) are summarized. Nests of our five focal species (American Robin, Dark-eyed Junco, Pacific-slope Flycatcher, Song Sparrow, and Winter Wren) totaled 403 nests, each with ≥ 40 nests when combined across years. Of the 403 focal species' nests, 346 nests had complete data for inclusion in statistical analyses of habitat relationships. We found most nests ($n = 164$) for the Winter Wren. Four substrates, Douglas-fir, rootballs, hemlock, and vine maple (*Acer circinatum*), each provided nesting support for four focal species (Table 6). The most commonly used nesting substrates were Douglas-fir (51 nests), woody debris (43 nests), rootball (34 nests), and sword fern (*Polystichum munitum*; 33 nests).

Aspects of American Robin nest sites were similar ($P < 0.50$) to aspects available in the forests where those nests occurred (Table 7). The other four focal species tended to concentrate their nests at sites with northerly aspects, while avoiding southerly aspects (Table 7). The pattern was less clear for nest orientation. Dark-eyed Junco ($P = 0.040$) and Winter Wren ($P =$

0.051) tended to orient their nests in southerly directions, while nest orientation for other species was not different from uniform distribution across orientation classes (Table 8).

All species used sites with habitat characteristics that were different from characteristics available in the forest stands where those nests were located. In recently clear-cut forests, American Robins nested at sites that had less coarse woody debris cover ($P = 0.002$), and that had lower density of each of large deciduous trees ($P = 0.031$), large stumps ($P = 0.001$), small snags ($P = 0.003$), and medium snags ($P = 0.002$) than was available (Table 9). In commercial thinned forest, American Robins nested at sites that had less cover of each of broad leaf evergreen shrubs ($P = 0.007$) and fine woody debris ($P = 0.016$), and that had lower densities of each of small deciduous trees ($P = 0.049$), large stumps ($P = 0.010$), and small snags ($P = 0.003$; Table 9).

In recently clear-cut forests, Dark-eyed Juncos nested at sites that had less cover of each of canopy ($P = 0.000$) and tree seedlings ($P = 0.011$), and that had lower densities of each of shrubs ($P = 0.000$) and large deciduous trees ($P = 0.002$; Table 10). In commercially thinned forests, Dark-eyed Juncos nested at sites that had less cover of each of broad leaf evergreen shrubs ($P = 0.040$) and tree seedlings ($P = 0.010$), herbs ($P = 0.040$), and fine woody debris ($P = 0.000$), and that had lower densities of each of large deciduous trees ($P = 0.012$), and large stumps ($P = 0.016$; Table 10).

In commercially thinned forests, Pacific-slope Flycatchers nested at sites that had less cover of each of berry producing shrubs ($P = 0.000$) and tree seedlings ($P = 0.021$) and greater cover of fine woody debris ($P = 0.004$). In addition, flycatchers nested at sites with lower densities of large stumps ($P = 0.006$) and higher densities of giant snags ($P = 0.019$). In old growth forests, Pacific-slope flycatchers nested at sites with lower densities of each of medium

conifer trees ($P = 0.049$), large conifer trees ($P = 0.027$), and giant snags ($P = 0.006$) but with higher density of large conifer snags ($P = 0.003$; Table 11).

In recently clear-cut forests, Song Sparrows nested at sites that had less slope ($P = 0.001$), and less cover of each of tree seedlings ($P = 0.000$), coarse woody debris ($P = 0.000$), and other cover ($P = 0.000$), but more cover of berry producing shrubs ($P = 0.012$) and fern ($P = 0.000$). In addition, nests sites had greater densities of each of forbs ($P = 0.000$), shrubs ($P = 0.009$), small deciduous trees ($P = 0.002$), but lower densities of each of large stumps ($P = 0.001$) and large deciduous trees ($P = 0.000$; Table 12).

In commercially thinned forests, Winter Wrens nested at sites with less cover of each of other deciduous shrubs ($P = 0.045$), tree seedlings ($P = 0.001$), herbs ($P = 0.007$), and that had lower densities of each of large deciduous trees ($P = 0.009$) and large stumps ($P = 0.001$). In old growth forests, Winter Wrens nested at sites with less cover of each of canopy ($P = 0.002$), broad leaf evergreen shrubs ($P = 0.000$), tree seedlings ($P = 0.005$), coarse woody debris ($P = 0.022$), fine woody debris ($P = 0.001$), and other ($P = 0.021$). In addition, nest sites had lower densities of each of medium conifers trees ($P = 0.002$), large conifers trees ($P = 0.004$), large deciduous trees ($P = 0.020$), large stumps ($P = 0.000$), and large snags ($P = 0.009$; Table 13).

Influence of habitat structure on nesting success and productivity

We fitted a linear regression model for the American Robin that included density of large deciduous trees and giant snags ($F = 10.932$, $P = 0.000$; Table 14). The number of young per nest increased as the density of large deciduous trees and giant snags increased. The logistic regression model showed that the probability of American Robin nest success increased with increases in densities of large deciduous trees (Likelihood ratio $\chi^2 = 13.815$ $df = 2$, $P = 0.001$, ρ^2

= 0.245, Table 15). Sites with successful nests had significantly higher densities of large deciduous trees ($U = 117, P = 0.001$) than sites with failed nests (Table 16).

We fitted a linear regression model for the Dark-eyed Junco that included percent canopy cover ($F = 5.431, P = 0.023$; Table 14). As percent canopy decreased, the number of young fledged per nest increased. We found no relationship between nest success and canopy cover using logistic regression (Table 15; Log Likelihood $\chi^2 = 0.852$ $df = 1, P = 0.356, \rho^2 = 0.011$), although sites with successful nests had significantly less canopy cover ($U = 641.5, P = 0.034$) than unsuccessful nests (Table 16).

The fitted linear regression model for Pacific-slope Flycatcher suggested that number of young per nest increased with decreasing density of medium snags ($F = 5.932, P = 0.000$; Table 14). A logistic regression model was not done for this species due to small sample sizes.

We fitted a linear regression model for the Song Sparrow that included percent cover of fine woody debris ($F = 8.635, P = 0.006$; Table 14). The number of fledglings per nest decreased as percent cover of fine woody debris increased. Logistic regression showed that the probability of Song Sparrow nest success increased with decreases in percent cover of fine woody debris (Table 15). Sites with successful nests had significantly less cover of fine woody debris than sites unsuccessful sites ($P = 0.023$; Table 16).

Because we had relatively large sample sizes for Winter Wren, we analyzed this species by treatment (commercial thin and old growth) and then pooled across treatments. The fitted linear regression model for Winter Wren in old growth included percent cover of coarse woody debris ($F = 7.34, P = 0.009$; Table 14). Young fledged per nest increased with increasing coarse woody debris. However, we found no relationship between cover of coarse woody debris and Winter Wren nest success in old growth using logistic regression (Log Likelihood $\chi^2 = 1.65, df =$

1, $P = 0.199$). The fitted linear regression model for Winter Wren in commercial thinned forest included percent cover of other ground cover, and density of each of small deciduous trees and rootballs ($F = 4.808$, $P = 0.004$; Table 14). Number of young fledged per nest decreased as density of small deciduous trees and rootballs increased and as percent cover of other groundcover decreased. The probability of Winter Wren nest success in commercial thin forests increased with increases in small deciduous tree density and decreases in cover of other groundcover (Log Likelihood $\chi^2 = 11.100$, $df = 2$, $P = 0.004$). Successful nest sites had significantly lower cover of other groundcover ($P = 0.014$) than unsuccessful nest sites but there was no difference in density of small deciduous trees or rootballs between successful and unsuccessful nest sites. Finally, the fitted linear regression for Winter Wren across all treatments included density of small deciduous trees ($F = 5.781$, $P = 0.017$; Table 14), which was also included in the logistic regression model (Table 15; Log Likelihood $\chi^2 = 4.831$, $df = 1$, $P = 0.028$, $\rho^2 = 0.022$). The number of young per nest and nest success decreased with increases in density of small deciduous trees. There was no significant difference in small deciduous tree density between successful and unsuccessful nest sites ($P = 0.139$; Table 16).

DISCUSSION

Variation in nesting success

Our studies of nesting birds in Douglas-fir - Western Hemlock forests of the southwest Cascade Mountains of Washington yielded data on 320 nests of 32 species in 1998, and 361 nests of 35 species in 1999. Our analyses suggest that birds nesting in these forests experienced annual variation in nesting success that was consistent across forest treatments (i.e., all treatments experienced lower nest success [and productivity] in 1998 compare with 1999). A

combination of nest predation, abandonment of nests by adult birds, and environmental factors contributed to greater rates of nest failure in 1998 relative to 1999. Reasons for abandonment are unknown, and could be related to disturbance by predators and/or inclement weather, which in turn might have reduced food resources. In 1999, success rates were higher even though more nests were lost because of disturbance from human observers and for unknown reasons. Nest mortality due to predation has been documented by others to be the primary mechanism causing reduced nest success for forest birds (Ricklefs 1969; Martin 1993a, 1993b). Our results suggest the same is true for forest birds in the southwest Cascade Mountains of Washington where almost 50% of nest failures occurred due to predation events. We therefore suspect that the annual variation in nest fate observed during our two-year study reflected annual variation in numbers of nest predators. Our anecdotal evidence suggested that such predators were primarily small mammals, such as deer mice (*Peromyscus* spp.), northern flying squirrels (*Glaucomys sabrinus*), and/or Douglas squirrels (*Tamiasciurus douglasii*).

Despite annual variation in nest fate, the proportions of nests that were successful, that failed, and which had unknown fate were constant among forest treatments. This result was substantiated by our species-specific analyses, which indicated that of five species with sufficient sample sizes to compare Mayfield (1975) estimates of nesting success (daily rates of mortality and daily rates of predation mortality) among forest treatments, only one was found to differ. Combining all nests of the five species together yielded no differences in nesting success among forest treatments, and neither did nesting productivity (number of young fledged per nest) vary among forest treatments. The one species for which nesting success (daily rate of mortality) differed between treatments was the Rufous Hummingbird, which did far better in clearcuts than it did in commercial thins. To our knowledge, ours is the first study to compare nesting success

of birds among forest treatments in the Pacific Northwest and so comparison with other studies is not possible. Elsewhere, such as in the southeastern U.S., nesting success of forest birds was not found to be reduced in mid-rotation or single-tree selection stands of loblolly pine (*Pinus taeda*; Barber et al. 2001). Similar results are reported for silvicultural treatments (including clearcuts) in deciduous forests of West Virginia (Duguay et al. 2001). In general, there are few studies that have compared nesting success among forest treatments, but those that have typically report few effects when silvicultural treatments are embedded in a largely forested landscape (Sallabanks et al. 2001b).

It also is important to recognize that commercial thinning helps accelerate succession by promoting understory development. Harvest-aged stands that are not commercially thinned may be similar to the closed-canopy forests studied by Aubry et al. (1997) in western Washington. Aubry et al. (1997) showed that these forests typically have lower avian species richness and lower overall abundance of birds than clearcut, pre-canopy, and commercially-thinned harvest-aged forests. The fact that the stands we studied had been commercially thinned may therefore be one reason why we found few differences among forest treatments, at least between commercial thins and old growth forests.

The degree to which land-use practices might influence forest avifauna may depend on the contrast between vegetation types on the landscape. For example, agriculture (especially the development of farmland) is known to be detrimental to the reproductive success of many breeding birds (Andrén 1992, Fuller et al. 1995, Newton 1998) and has had a greater impact on populations of Neotropical migratory birds than any other human activity (Rodenhouse et al. 1995). On the other hand, silvicultural practices may be less influential because the forest edges that are created by silviculture are of lower contrast (less “abrupt”) over time (DeGraaf 1992,

Suarez et al. 1997), thereby reducing edge-related phenomena such as nest predation and brood parasitism (Rudnicki and Hunter 1993, Hanski et al. 1996, King et al. 1996). In addition, the effects of habitat loss by silviculture in a managed forest landscape may tend to “dissolve” at any one location over time as clearcuts or heavily thinned stands return to later seral stages (Hagan et al. 1996). Indeed, studies of fragmentation in industrial forest landscapes of northern Europe have generally not found forest patch size effects (Haila et al. 1989, Huhta 1998).

While we are cautious about interpreting results of analyses based upon small sample sizes, we nevertheless found little evidence to suggest that nesting success of birds in our study area varied among forest treatments. Of course, our analyses were limited to only five species, and we had insufficient sample sizes to compare nesting success among all three forest treatments for any species (because few species were distributed among all three treatments). Perhaps the lack of effects is related to small sample sizes and associated low power. On the other hand, perhaps it is related to the patchiness of the landscape and “softer” edges of silvicultural treatments as discussed above. To distinguish between these potential causes, we clearly need more studies of avian nest success in response to forest treatments in the western Cascades landscape. One way we also can address the potential impacts of forest management on nesting birds is to describe their habitat needs, the microhabitat in which they place their nests, and identify the habitat features that appear to influence nesting success. It is therefore to these matters that we turn our attention for the remainder of this Discussion.

Nest-site selection and nest-habitat relationships

Our results suggest that the focal species we studied (American Robin, Winter Wren, Song Sparrow, Pacific-slope Flycatcher, and Dark-eyed Junco) were selecting for specific habitat

characteristics at nesting sites that differ from nonnesting sites in the same forest stand (macroscale). In addition, it appears that successful nesting sites, as defined by those with production of one or more young and by total number of young produced, have different habitat characteristics than unsuccessful sites (microscale). We expected that differences in habitat at the macroscale would be easier to quantify than differences at the microscale since selection pressures at unsuccessful nesting sites must be relatively strong. Individual pairs have invested much energy into nesting by the time nests typically fail. One possible explanation for microscale differences in habitat is related to intraspecific dynamics. High bird densities may create a shortage of the “best” habitat (e.g., low predator density, high levels of resources), forcing less dominant individuals into suboptimal habitat where nest success is relatively low. If nest success were largely the result of stochastic effects rather than systematic effects, then differences in habitat characteristics at the microscale would theoretically be harder to quantify.

Differences in habitat characteristics at the macro and micro scale for a given species also appear to be treatment specific. For example, the American Robin had a number of characteristics, such as CWD, that differed by treatment at the macro scale. This pattern was repeated for the Winter Wren at both the macro and micro scales. Although small deciduous tree density was important to the Winter Wren in old growth forests and commercial thins, only other ground cover was important in commercial thins. Clearly, habitat suitability can be complex, and there may be many equally suitable sites that are based on very different combinations of physical and biological characteristics.

Perhaps the most surprising finding relative to nesting habitat was the use of rootballs as a nesting substrate. Despite the fact that rootballs are relatively rare on the landscape, four of five species used rootballs for nesting, and rootballs were the third most commonly used

substrate after Douglas-fir and woody debris, with a total of 34 nests across all species.

Rootballs were especially important to the Winter Wren and Dark-eyed Junco, which located 23 of 164 (14%) and 8 of 57 (14%) of their nests in this substrate, respectively. Rootballs, as opposed to woody debris, stumps, and live roots, are composed of soil, woody structures (roots), and often vegetation (i.e., forbs and shrubs), that may provide for more structural complexity and thus nesting opportunities for more species. For example, although Dark-eyed Juncos frequently nested on the ground, they never nested in woody debris, or living roots, but commonly used rootballs, suggesting that their use of rootballs may be related to the presence of soil.

Alternatively, rootballs may perhaps provide increased protection from predators. Another key finding is that Winter Wrens frequently use woody structures as nesting substrate. Of 164 nests analyzed, 112 (68%) occurred on woody structures (living roots, rootballs, snags, stumps and woody debris).

Except for the American Robin, the forest songbirds included in our analyses selected nest sites with northerly aspects while avoiding southerly aspects. While the reason for this pattern is unclear, it may be that birds select sites that minimize exposure to inclement weather that typically comes from the southwest in this part of Washington State. Interestingly, while the aspects of nesting sites were generally north, nest orientations (direction from the main stem of the nest tree) were southerly for species where there was a pattern (i.e., Dark-eyed Junco and Winter Wren). Orientation and nest site selection may represent a tradeoff between protection from inclement weather and maximizing insolation, but this hypothesis will require further study to elucidate.

Despite the fact that American Robins appeared to select nest sites with relatively low densities of large deciduous trees compared to random plots, the number of young produced per

nest and nest success were both associated with higher densities of large deciduous trees. This finding is counterintuitive and suggests a number of possible explanations. First, one or more of our results are in error. Alternatively, this species may be selecting nesting sites within a stand based on characteristics other than deciduous trees, or on densities of deciduous trees that meet some minimum criteria. Deciduous tree density may be related to soil moisture or other aspects of microclimate. For example, American Robins in old growth forests occur in greatest abundance at the wetter end of the moisture gradient (Manuwal 1991).

Our results for the Dark-eyed Junco are consistent with habitat association studies in the Pacific Northwest. Reproductive success, like relative abundance of this ground-nesting species, is associated with open canopy and clearcut forests (Aubry et al. 1997, Manuwal 1991). In addition to selecting open canopy forests, it appears that juncos may select sites within a stand that have relatively low cover of ground vegetation and presumably higher cover of mineral soil.

The vegetation characteristics for our regression analyses predicted only a small part of the variance associated with nesting success, a pattern similar to other bird abundance - habitat association studies (e.g., Huff and Raley 1991, Aubry et al. 1997). This unexplained variability may be the result of numerous possible causes (see Verner et al. 1986, pp. 207–258). In addition, predictions of habitat associations do not necessarily imply cause and effect (Rotenberry 1986). In some instances, the vegetation variables we measured had little direct biological meaning for nesting success. For example, small deciduous trees were negatively related to nest success of the Winter Wren, but the relationship between nest success and small deciduous trees is unclear. This variable is most likely associated with a complex set of stand or biological attributes associated with Winter Wren habitat that will require more study to elucidate. Where variables are more closely associated with nesting substrates, such as coarse

woody debris and rootballs for the Winter Wren, especially across different treatments, we can offer firmer conclusions about potential cause and effect relationships.

Management implications

Our study of nesting forest birds in the southwest Cascade Mountains of Washington has generated numerous relationships between habitat characteristics and nesting success that may be of value to forest managers. For five focal species, across a range of forest treatments and conditions, we have provided quantitative data on a number of forest structural attributes that appear to influence nest-site location, nesting success, and nest productivity (number of young fledged from nests). In all cases, we found birds to choose specific microhabitats that differ in terms of their structure from the macrohabitat at larger spatial scales (i.e., forest stands). We interpret this as evidence suggesting that forest birds require complexity and variation in habitat structure and plant species composition at relatively small spatial scales. Therefore, if forest managers can meet their timber harvest objectives, yet leave stands with heterogeneous microenvironments, from the forest floor to the overstory canopy, any deleterious impacts of forestry practices in breeding songbirds may be minimized. Of course, there are some species that nest in old growth forests, and which require old growth characteristics such as large trees and snags, closed overstory canopies, and large amounts of coarse woody debris to breed successfully. Such species, which were not included in our analyses because they were relatively uncommon on the landscape, would be negatively affected by most thinning operations in old growth stands despite the complexity of the forest post-harvest.

More specifically, the importance of rootballs and coarse woody debris was evident for several of our focal species. Both may provide some unique benefits to nesting birds that other

structures do not, such as increased protection from predators or improved microclimate (e.g., greater humidity, moisture, etc.). It might be possible to improve the quality of forest habitat for a variety of bird species simply by leaving (or even creating) greater densities of these important structures. Rootballs and coarse woody debris were especially important to one of the most common forest birds in the western Cascade Mountains, the Winter Wren. In old growth forest, where there was an abundance of coarse woody debris, wrens tended not to use rootballs and experienced greater productivity where there was more coarse wood on the forest floor. In thinned forest, on the other hand, wren productivity was not related to the amount of coarse woody debris, but instead to the density of rootballs. We suspect that in the absence of coarse woody debris in commercial thins, wrens switch their primary nesting substrate to rootballs. Although nesting success and productivity of the wren did not differ between commercial thins and old growth forest, it seems likely that thinned forests could only be improved for this species if both coarse woody debris and rootballs were made more available.

In conclusion, we hope our results offer forest managers some additional tools and increased flexibility with which to manage Douglas-fir - Western Hemlock forests of the Cascade Mountains with the needs of birds in mind. Where commercial timber harvest must occur, we encourage foresters to leave key structural attributes such as rootballs, coarse woody debris, and well-developed shrub understories. Forest floor complexity appears to be especially important for a number of bird species. Finally, we urge researchers to conduct more studies of avian nesting success and habitat relationships in the Cascade Mountains so that we may build on our understanding of what birds need to reproduce successfully in managed forest landscapes of the Pacific Northwest.

ACKNOWLEDGMENTS

This study was funded by Washington State Department of Natural Resources (DNR) as Personal Services Contract No. 98-037 between DNR and the Sustainable Ecosystems Institute, and Champion Pacific Timberlands, Inc. In particular we thank Cheryl Quade, Tami Grant, and Nikki Housh of DNR for administering this contract and providing project support from its inception. For logistical support in the field we thank Dr. Douglas Runde of Weyerhaeuser Company and Jessica Eskow of Champion Pacific Timberlands. Weyerhaeuser also provided two field vehicles. For providing access to study plots we are grateful to the following: Weyerhaeuser Company, Champion Pacific Timberlands, DNR, U.S. Forest Service, and the University of Washington Pack Experimental Forest. We also thank members of the Landscape and Wildlife Advisory Group (LWAG) for their support and advice throughout this project, especially Cheryl Quade and Dr. Daniel Varland for serving as the primary LWAG contacts. Finally, the following assisted with data collection: Nathan Blackburn, Jeanne Hammond, Robert Kaler, Greg Levandoski, Doug Milek, Anna Noson, Heidi Packard, Tom Parker, Peter Sanzenbacher, Jennifer Soules, Heather Wilson, and Julian Wood. We owe much of the success of this study to Tom Parker and Jennifer Soules, field team leaders in 1998 and 1999, respectively.

LITERATURE CITED

Andr n, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794–804.

Arnett, E. B., and R. Sallabanks. 1998. Land manager perceptions of avian research and information needs: A case study. Pages 399–413 in J. M. Marzluff and R. Sallabanks, editors. *Avian Conservation: research and management*. Island Press, Covelo, California, USA.

Aubry, K. B., S. D. West, D. A. Manuwal, A. B. Stringer, J. L. Erickson, and S. Pearson. 1997. Wildlife use of managed forests: a landscape perspective. Vol. 2: Westside Studies Research Results. Timber/Fish/Wildlife TFW-WL4-98-002.

Barber, D. R., T. E. Martin, M. A. Melchiors, R. E. Thill, and T. B. Wigley. 2001. Nesting success of birds in different silvicultural treatments of the southeastern U.S. pine forests. *Conservation Biology* 15:196–207.

Burke, D. M., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecological Applications* 10:1749–1761.

Carey, A. B., and J. E. Kershner. 1996. *Spilogale gracilis* in upland forests of western Washington and Oregon. *Northwestern Naturalist* 77:29–34.

- Degraaf, R. M. 1992. Effects of even-aged management on forest birds at northern hardwood stand interfaces. *Forest Ecology and Management* 46:95–110.
- Donovan, T. M., F. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* 9:1380–1395.
- Duguay, J. P., P. B. Wood, and J. V. Nichols. 2001. Songbird abundance and avian nest survival rates in forests fragmented by different silvicultural treatments. *Conservation Biology* 15:1405–1415.
- Franklin, J. F., and C. T. Dyrness. 1973. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon. 452 p.
- Fuller, R. J., R. D. Gregory, D. W. Gibbons, J. H. Marchant, J. D. Wilson, S. R. Baillie, and N. Carter. 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology* 9:1425–1441.
- Götmark, F. 1992. The effects of investigator disturbance on nesting birds. *Current Ornithology* 9:63–104.
- Gottfried, B. M., and C. F. Thompson. 1978. Experimental analysis of nest predation in an old-field habitat. *The Auk* 95:304–312.

Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* 10:188–202.

Hagar, J. C., W. C. McComb, and W. H. Emmingham. 1996. Bird communities in commercially thinned and unthinned Douglas-fir stands of western Oregon. *Wildlife Society Bulletin* 24:353–366.

Haila, Y., I. K. Hanski, and S. Raivio. 1989. Methodology for studying the minimum habitat requirements of forest birds. *Annales Zoologici Fennici* 26:173–180.

Hallett, J. G., and M. A. O'Connell. 1997. Wildlife use of managed forests: A landscape perspective. Final report Eastside studies. Department of Natural Resources Sciences and Zoology, Washington State University and Department of Biology, Eastern Washington University, Pullman, Washington.

Hanski, I. K., T. J. Fenske, and G. J. Niemi. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. *The Auk* 113:578–585.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bulletin* 93:42–53.

Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST - a general program for the analysis of several survival or recovery rate estimates. U.S. Fish and Wildlife Service, Fish and Wildlife Technical Report 24, Washington, D.C., USA.

Huff, M. H., and C. M. Raley. 1991. Regional patterns of diurnal breeding bird communities in Oregon and Washington. Pages 177–206 *in* Wildlife and vegetation of unmanaged Douglas-fir forests (Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords.). USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. 533 p.

Huhta, E., J. Jokimaki, and P. Helle. 1998. Predation on artificial nests in a forest dominated landscape - the effects of nest type, patch size, and edge structure. *Ecography* 21:464–471.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *The Auk* 96:651–661.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscapes. *Conservation Biology* 10:1380–1386.

Major, R. E. 1989. The effect of human observers on the intensity of nest predation. *Ibis* 132:608–612.

Manly B. F. J. 1991. Randomization and monte carlo methods in biology. Chapman & Hall, New York.

Manuwal, D. A. 1991. Spring bird communities in the Southern Washington Cascade Range. Pages 161–174 *in* Wildlife and vegetation of unmanaged Douglas-fir forests (Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords.). USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. 533 p.

Martin, T. E. 1993a. Nest predation and nest sites: new perspectives on old patterns. *BioScience* 43:523–532.

Martin, T. E. 1993b. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141:897–913.

Martin, T. E., and G. R. Geupel. 1993. Nest monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.

Martin, T. E., and C. J. Conway. 1994. BBIRD field protocol. Unpublished Report, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana. 39 p.

Marzluff, J. M., M. G. Raphael, and R. Sallabanks. 2000. Understanding why forest management may affect avian populations: mechanisms, experimental approaches, prioritization, and funding strategies. *Wildlife Society Bulletin* 28:1132–1143.

Mayfield, H. F. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.

Mayfield, H. F. 1975. Suggestions for calculating nesting success. *Wilson Bulletin* 87:456–466.

McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs* 65:235–260.

Newton, I. 1998. Bird conservation problems resulting from agricultural intensification in Europe. Pages 307–322 *in* J. M. Marzluff, and R. Sallabanks, editors. *Avian conservation: research and management*. Island Press, Washington, D.C., USA.

O'Connell, M. A., J. G. Hallett, S. D. West, K. A. Kelsey, D. A. Manuwal, and S. F. Pearson. 2000. Effectiveness of riparian management zones in providing habitat for wildlife. *Timber/Fish/Wildlife TFW-LWAG1-00-001*.

Pearson, S. F., and D. A. Manuwal. 2001. Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-fir forests. *Ecological Applications* 11:840–853.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. *Handbook of field methods for monitoring landbirds*. U.S. Forest Service General Technical Report GTR-144.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1–48.

Robinson, M. W. 1947. An instrument to measure forest crown cover. *For. Chron.* 23:222–225.

Rodenhouse, N. L., L. B. Best, R. J. O'Connor, and E. K. Bollinger. 1995. Effects of agricultural practices and farmland structures. Pages 269–293 *in* T. E. Martin, and D.M. Finch, editors. *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues*. Oxford University Press, New York, New York, USA.

Rotenberry, J. T. 1986. Habitat relationship of shrubsteppe birds: even good models cannot predict the future. Pages 217–222 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. Proceedings of an international symposium; 1984 October 7–11, Fallen Leaf Lake, CA. University of Wisconsin Press, Madison. 470 p.

Rudnicki, T. C., and M. L. Hunter. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57:358–364.

Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff (tech. coords.). 1991. *Wildlife and vegetation of unmanaged Douglas-fir forests*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285. 533 p.

Sallabanks, R. 1994. Bird-habitat relationships in Eastside industrial forested landscapes: Pilot studies in Idaho and Oregon. Unpublished Annual Report, Conservation Research Foundation, Boise, Idaho. 74 p.

Sallabanks, R. 1995. Avian biodiversity and bird-habitat relationships in conifer forests of the inland northwest: An ecosystem management approach. Unpublished Annual Report, Sustainable Ecosystems Institute, Meridian, Idaho. 150 p.

Sallabanks, R., E. B. Arnett, and J. M. Marzluff. 2000. An evaluation of research on the effects of timber harvest on bird populations. *Wildlife Society Bulletin* 28:1144–1155.

Sallabanks, R., and T. Quinn. 2000. Can we infer habitat quality from the results of wildlife surveys? Final Report TFW-LWAG6-01-001. Washington Department of Natural Resources, Olympia, Washington, USA.

Sallabanks, R., B. G. Marcot, R. A. Riggs, E. B. Arnett, and C. A. Mehl. 2001a. Wildlife of Eastside (interior) forests and woodlands. Pages 213–238 *in* D. H. Johnson, and T.A. O’Neil, managing directors. *Wildlife-habitat relationships in Oregon and Washington*, Oregon State University Press, Corvallis, Oregon, USA.

Sallabanks, R., E. B. Arnett, T. B. Wigley, and L. L. Irwin. 2001b. Accommodating birds in managed forests of North America: A review of bird-forestry relationships. *NCASI Technical Bulletin*, No. 822.

Sallabanks, R., R. A. Riggs, and L. E. Cobb. 2002. Bird use of forest structural classes in grand fir forests of the Blue Mountains, Oregon. *Forest Science* 48:311–321.

Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival and recovery rates. *Journal of Wildlife Management* 53:137–142.

Schmiegelow, F. K., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* 78:1914–1932.

Suarez, A., K. Pfenning, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. *Conservation Biology* 11:928–935.

Verner, J., M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. Proceedings of an international symposium; 1984 October 7–11, Fallen Leaf Lake, CA. University of Wisconsin Press, Madison. 470 p.

Westmoreland, D., and L. B. Best. 1985. The effect of disturbance on Mourning Dove nesting success. *The Auk* 102:774–780.

Wilkinson, L., M. Hill, J. P. Welna, and G. K. Birkenbeuel. 1992. *SYSTAT: the system for statistics*, Evanston, IL. SYSTAT, Inc.

Willis, E. O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. *The Auk* 90:263-267.

Zar, J. H. 1996. *Biostatistical analysis*. Third ed. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Appendix 1. Number of nests found and monitored for 40 bird species in forests of the southwest Cascade Mountains of Washington, 1998–1999.

Common Name	Alpha code	Scientific Name	Number of Nests Monitored (by Treatment†)			Total No. Nests Monitored
			Clearcut (n = 4)	Comm. Thin (n = 4)	Old Growth (n = 4)	
American Goldfinch	AMGO	<i>Carduelis tristis</i>	2	0	0	2
American Robin	AMRO	<i>Turdus migratorius</i>	21	23	4	48
Bewick's Wren	BEWR	<i>Thryomanes bewickii</i>	3	0	0	3
Black-headed Grosbeak	BHGR	<i>Pheucticus melanocephalus</i>	6	0	0	6
Blue Grouse	BLGR	<i>Dendragapus obscurus</i>	2	0	0	2
Brown Creeper	BRCR	<i>Certhia americana</i>	0	11	20	31
Chestnut-backed Chick.	CBCH	<i>Parus rufescens</i>	1	17	15	33
Cedar Waxwing	CEDW	<i>Bombycilla cedrorum</i>	13	0	0	13
Common Nighthawk	CONI	<i>Chordeiles minor</i>	1	0	0	1
Common Raven	CORA	<i>Corvus corax</i>	0	1	1	2
Common Yellowthroat	COYE	<i>Geothlypis trichas</i>	23	0	0	23

Dark-eyed Junco	DEJU	<i>Junco oreganus hyemalis</i>	25	47	8	80
Downy Woodpecker	DOWO	<i>Picoides pubescens</i>	0	0	1	1
Evening Grosbeak	EVGR	<i>Coccothraustes vespertina</i>	0	1	0	1
Golden-crowned Kinglet	GCKI	<i>Regulus satrapa</i>	0	1	0	1
Gray Jay	GRAJ	<i>Nucifraga columbiana</i>	1	1	0	2
Hairy Woodpecker	HAWO	<i>Picoides villosus</i>	3	4	6	13
Hermit/Townsend's Warb.	HETO	<i>D. occidentalis/townsendi</i>	0	1	0	1
MacGillivray's Warbler	MGWA	<i>Oporornis tolmiei</i>	3	2	0	5
Northern Flicker	NOFL	<i>Colaptes auratus</i>	1	2	1	4
Northern Pygmy-owl	NOPO	<i>Glaucidium gnoma</i>	0	1	2	3
Orange-crowned Warbler	OCWA	<i>Vermivora celata</i>	5	2	0	7
Pileated Woodpecker	PIWO	<i>Dryocopus pileatus</i>	0	2	1	3
Pacific-slope Flycatcher	PSFL	<i>Empidonax difficilis</i>	1	22	17	40
Red-breasted Nuthatch	RBNU	<i>Sitta canadensis</i>	0	4	5	9
Red-breasted Sapsucker	RBSA	<i>Sphyrapicus nuchalis</i>	0	0	2	2
Ruffed Grouse	RUGR	<i>Bonasa umbellus</i>	0	1	0	1
Rufous Hummingbird	RUHU	<i>Selasphorus rufus</i>	10	15	7	32

Song Sparrow	SOSP	<i>Melospiza melodia</i>	58	3	0	61
Spotted Owl	SPOW	<i>Strix occidentalis</i>	0	0	1	1
Spotted Towhee	SPTO	<i>Pipilo maculatus</i>	11	1	0	12
Steller's Jay	STJA	<i>Cyanocitta stelleri</i>	4	0	0	4
Swainson's Thrush	SWTH	<i>Catharus ustulatus</i>	3	5	1	9
Varied Thrush	VATH	<i>Ixoreus naevius</i>	1	2	16	19
Warbling Vireo	WAVI	<i>Vireo gilvus</i>	4	0	0	4
White-crowned Sparrow	WCSP	<i>Zonotrichia leucophrys</i>	4	0	0	4
Western Tanager	WETA	<i>Piranga ludoviciana</i>	0	3	0	3
Willow Flycatcher	WIFL	<i>Empidonax trailii</i>	15	0	0	15
Wilson's Warbler	WIWA	<i>Wilsonia pusilla</i>	1	3	2	6
Winter Wren	WIWR	<i>Troglodytes troglodytes</i>	3	121	50	174
All species combined			225	296	160	681

† "Clearcut" = 8–12 year-old regenerating clearcut forest; "Comm. Thin" = 40–60 year-old commercially thinned forest; "Old Growth" = 150–270 year-old old growth forest.

Appendix 2. Habitat variables used in analyses of nest location and nesting success for breeding birds in forests of the southwest Cascade Mountains of Washington, 1998–1999.

Variable	Units	Description
SLOPE	Degrees	Slope of the vegetation subplot
CNPYCVR	% cover	Percent overstory canopy cover
BLESHRB	% cover	Percent ground cover by broad-leaved evergreen shrubs <1 m in height
BPDSHRB	% cover	Percent ground cover by berry-producing deciduous shrubs <1 m in height
ODSHRB	% cover	Percent ground cover by other deciduous shrubs <1 m in height
TRESEED	% cover	Percent ground cover by tree seedlings <1 m in height
FERN	% cover	Percent ground cover by ferns
HERBS	% cover	Percent ground cover by herbaceous vegetation (includes forbs, grasses, <i>Lobaria</i> lichen, and moss)
CWD	% cover	Percent ground cover by coarse woody debris (includes down logs and stumps)
FWD	% cover	Percent ground cover by fine woody debris (includes leaf/needle litter and small branches)
OTHER	% cover	Percent ground cover by bare soil, rock, and other cover types (includes saprophytes, above-ground roots, tree and snag boles)
FORB	Stems/ha	Density of forb stems (all species combined)

SHRUB	Stems/ha	Density of shrub stems (all species combined)
S_CON	Stems/ha	Density of small-sized (0–10 cm DBH†) coniferous trees
M_CON	Stems/ha	Density of medium-sized (11–25 cm DBH) coniferous trees
L_CON	Stems/ha	Density of large-sized (26–60 cm DBH) coniferous trees
G_CON	Stems/ha	Density of giant-sized (>60 cm DBH) coniferous trees
S_DEC	Stems/ha	Density of small-sized (0–10 cm DBH) deciduous trees
M_DEC	Stems/ha	Density of medium-sized (11–25 cm DBH) deciduous trees
L_DEC	Stems/ha	Density of large- (26–60 cm DBH) and giant- (>60 cm DBH) sized deciduous trees
S_STUMP	Stems/ha	Density of small- (0–10 cm in diameter at top of stump) and medium- (11–25 cm) sized cut stumps
L_STUMP	Stems/ha	Density of large- (26–60 cm in diameter at top of stump) and giant- (>60 cm) sized cut stumps
S_SNAG	Stems/ha	Density of small-sized (0–10 cm DBH) snags
M_SNAG	Stems/ha	Density of medium-sized (11–25 cm DBH) snags
L_SNAG	Stems/ha	Density of large-sized (26–60 cm DBH) snags
G_SNAG	Stems/ha	Density of giant-sized (>60 cm DBH) snags
ROOTBALL	No./ha	Density of rootballs (all size classes combined)

† DBH = Diameter at Breast Height

Table 1. Mayfield estimates of daily nest mortality, daily nest survival, and overall nest success for 13 bird species studied in forests of the southwest Cascade Mountains of Washington, 1998–1999. Species are listed in descending order of total nest sample size. Scientific names in Appendix 1.

Species	Treatment†	No. nests‡	Exp. days§	Daily mortality	Daily survival (standard error)	Nest success¶
Winter Wren	Clearcut	3	58.5	0.0171	0.9829 (0.0169)	0.5710
	Comm. Thin	119	1396.5	0.0344	0.9656 (0.0049)	0.3209
	Old Growth	49	386.0	0.0570	0.9430 (0.0118)	0.1485
Dark-eyed Junco	Clearcut	25	297.5	0.0134	0.9866 (0.0067)	0.7275
	Comm. Thin	47	492.0	0.0244	0.9756 (0.0070)	0.5597
	Old Growth	8	66.5	0.0301	0.9699 (0.0209)	0.4879
Song Sparrow	Clearcut	58	503.0	0.0278	0.9722 (0.0073)	0.5151
	Comm. Thin	3	26.0	0.0769	0.9231 (0.0523)	0.1524
	Old Growth	0	0.0	--	--	--
American Robin	Clearcut	20	215.5	0.0650	0.9350 (0.0168)	0.1525
	Comm. Thin	21	208.5	0.0576	0.9424 (0.0161)	0.1902
	Old Growth	4	4.5	0.6667	0.3333 (0.2222)	0.0000
Pacific-slope Flycatcher	Clearcut	1	0.0	--	--	--
	Comm. Thin	22	314.0	0.0287	0.9713 (0.0094)	0.4119
	Old Growth	17	249.0	0.0402	0.9598 (0.0124)	0.2865
Rufous Hummingbird	Clearcut	10	246.5	0.0041	0.9959 (0.0040)	0.8745
	Comm. Thin	15	233.0	0.0386	0.9614 (0.0126)	0.2725

Brown Creeper	Old Growth	5	125.5	0.0159	0.9841 (0.0112)	0.5885
	Clearcut	0	0.0	--	--	--
	Comm. Thin	8	64.5	0.0465	0.9535 (0.0262)	0.2396
Common Yellowthroat	Old Growth	17	246.0	0.0041	0.9959 (0.0041)	0.8850
	Clearcut	22	177.5	0.0394	0.9606 (0.0146)	0.4126
	Comm. Thin	0	0.0	--	--	--
Chestnut-backed Chick.	Old Growth	0	0.0	--	--	--
	Clearcut	1	0.0	--	--	--
	Comm. Thin	11	145.0	0.0069	0.9931 (0.0069)	0.8238
Willow Flycatcher	Old Growth	9	180.5	0.0166	0.9834 (0.0095)	0.6254
	Clearcut	15	239.0	0.0209	0.9791 (0.0093)	0.5833
	Comm. Thin	0	0.0	--	--	--
Varied Thrush	Old Growth	0	0.0	--	--	--
	Clearcut	1	12.5	0.0000	1.000 (0.0000)	1.0000
	Comm. Thin	2	29.5	0.0339	0.9661 (0.0333)	0.3678
Cedar Waxwing	Old Growth	11	118.5	0.0422	0.9578 (0.0185)	0.2864
	Clearcut	13	220.0	0.0227	0.9773 (0.0100)	0.5134
	Comm. Thin	0	0.0	--	--	--
Spotted Towhee	Old Growth	0	0.0	--	--	--
	Clearcut	11	111.0	0.0541	0.9459 (0.0215)	0.2709
	Comm. Thin	1	21.0	0.0476	0.9524 (0.0465)	0.3177
	Old Growth	0	0.0	--	--	--

† “Clearcut” = 8–12 year-old regenerating clearcut forest ($n = 4$); “Comm. Thin” = 40–60 year-old commercially thinned forest ($n = 4$); “Old Growth” = 150–270 year-old old growth forest ($n = 4$).

‡ Total nest sample size (nests of known fate only).

§ Total number of exposure days pooled across all nests.

|| Mayfield adjusted daily rate of nest survival (maximum-likelihood standard errors in parentheses; Johnson 1979).

¶ Mayfield adjusted nest success (daily rate of nest survival raised to the exponent that reflects the length of the nesting cycle).

Table 2. Results of Chi-square tests of differences in daily nest mortality and daily mortality due to predation among forest treatments in the southwest Cascade Mountains of Washington, 1998–1999. Species are listed in descending order of total nest sample size†. Scientific names in Appendix 1.

Species	Mortality type	Daily rate of mortality (standard error) by forest treatment‡			Chi-square analysis§	
		Clearcut	Comm. Thin	Old Growth	χ^2 (df)	<i>P</i>
Winter Wren	Nest mortality	--	0.034 (0.005)	0.057 (0.012)	3.130 (1)	0.077
	Predation mortality	--	0.014 (0.003)	0.031 (0.009)	3.211 (1)	0.073
Dark-eyed Junco	Nest mortality	0.015 (0.008)	0.024 (0.007)	--	0.717 (1)	0.397
	Predation mortality	0.011 (0.007)	0.016 (0.006)	--	0.294 (1)	0.588
American Robin	Nest mortality	0.065 (0.017)	0.058 (0.016)	--	0.090 (1)	0.764
	Predation mortality	0.056 (0.016)	0.019 (0.010)	--	3.846 (1)	0.050
Pacific-slope Flycatcher	Nest mortality	--	0.029 (0.009)	0.040 (0.012)	0.538 (1)	0.463
	Predation mortality	--	0.013 (0.006)	0.016 (0.008)	0.090 (1)	0.764
Rufous Hummingbird	Nest mortality	0.004 (0.004)	0.039 (0.013)	--	6.622 (1)	0.010
	Predation mortality	0.000 (0.000)	0.017 (0.009)	--	3.568 (1)	0.059
All species combined¶	Nest mortality	0.025 (0.014)	0.037 (0.006)	0.160 (0.127)	3.500 (2)	0.174
	Predation mortality	0.017 (0.013)	0.016 (0.001)	0.054 (0.042)	0.933 (2)	0.627

† Only those species with ≥ 10 nests of known fate per treatment are included in analyses; for more details on nest sample sizes and Mayfield estimates of nest survivorship, see Table 1.

‡ “Clearcut” = 8–12 year-old regenerating clearcut forest ($n = 4$); “Comm. Thin” = 40–60 year-old commercially thinned forest ($n = 4$); “Old Growth” = 150–270 year-old old growth forest ($n = 4$).

§ Chi-square analyses conducted using program CONTRAST (Hines and Sauer 1989).

|| Daily rate of nest mortality is analyzed as failure due to any cause (nest mortality) and failure due specifically to predation events (predation mortality).

¶ Combined analysis of all four species conducted using Friedman ANOVA on mortality rates blocked by species (Zar 1996).

Table 3. Comparison of nesting productivity (mean number of fledglings produced per nesting attempt) for 13 bird species among forest treatments in the southwest Cascade Mountains of Washington, 1998–1999. Sample size (*n*) in parentheses refers to the number of forest stands in which data were collected. Scientific names in Appendix 1.

Species	Mean \pm SE (<i>n</i>) number of fledglings / nest by forest treatment [†]			Analysis of variance		
	Clearcut	Comm. Thin	Old Growth	<i>F</i>	df	<i>P</i>
Winter Wren	2.33 \pm 0.00 (1)	2.16 \pm 0.23 (4)	1.94 \pm 0.52 (4)	0.13	2, 6	0.88
Dark-eyed Junco	2.80 \pm 0.16 (3)	2.10 \pm 0.38 (4)	2.25 \pm 1.25 (2)	0.54	2, 6	0.61
Song Sparrow	2.63 \pm 0.26 (4)	1.33 \pm 0.00 (1)	--	7.22	1, 3	0.07
American Robin	0.74 \pm 0.53 (4)	1.48 \pm 0.42 (4)	2.00 \pm 2.00 (2)	0.61	2, 7	0.57
Pacific-slope Flycatcher	0.00 \pm 0.00 (1)	2.05 \pm 0.35 (4)	2.35 \pm 0.88 (4)	1.24	2, 6	0.35
Rufous Hummingbird	1.57 \pm 0.30 (3)	0.36 \pm 0.36 (2)	1.50 \pm 0.50 (2)	3.13	2, 4	0.15
Brown Creeper	--	3.65 \pm 0.76 (4)	4.60 \pm 0.71 (4)	0.84	1, 6	0.40
Common Yellowthroat	2.41 \pm 0.09 (2)	--	--	--	--	--
Chestnut-backed Chick.	0.00 \pm 0.00 (1)	3.08 \pm 1.35 (3)	4.48 \pm 1.02 (3)	1.78	2, 4	0.28
Varied Thrush	3.00 \pm 0.00 (1)	1.00 \pm 1.00 (2)	1.54 \pm 0.40 (3)	1.37	2, 3	0.38
Willow Flycatcher	2.03 \pm 0.28 (3)	--	--	--	--	--
Cedar Waxwing	2.28 \pm 0.38 (2)	--	--	--	--	--
Spotted Towhee	0.88 \pm 0.52 (4)	0.00 \pm 0.00 (1)	--	0.58	1, 3	0.50
All species combined [‡]	2.05 \pm 0.10 (4)	2.29 \pm 0.17 (4)	2.62 \pm 0.34 (4)	1.55	2, 9	0.26

† “Clearcut” = 8–12 year-old regenerating clearcut forest ($n = 4$); “Comm. Thin” = 40–60 year-old commercially thinned forest ($n = 4$); “Old Growth” = 150–270 year-old old growth forest ($n = 4$).

‡ Analysis of all species combined ($n = 641$ nests of 38 species).

Table 4. Nest-site locations of 14 bird species† studied in forests of the southwest Cascade Mountains of Washington, 1998–1999. Bird species' codes and scientific names are listed in Appendix 1. Values are means \pm standard error (with nest sample sizes in parentheses).

Bird Species	Nest Height (m)	Nest-plant Height (m)	Nest-tree Diameter‡ (cm)	Orientation of Nest from Main Stem (°)	No. Branches Supporting Nest	Diameter of Supporting Branches (cm)	Distance of Nest from Main Stem (m)
AMRO	8.09 \pm 1.34 (45)	17.67 \pm 2.16 (46)	34.17 \pm 9.13 (44)	179 \pm 16 (41)	2.36 \pm 0.16 (42)	2.21 \pm 0.34 (35)	0.23 \pm 0.10 (42)
BRCR	7.06 \pm 0.91 (31)	22.37 \pm 3.06 (31)	63.76 \pm 8.98 (31)	186 \pm 21 (30)	--	--	--
CEDW	2.08 \pm 0.12 (13)	5.59 \pm 0.33 (12)	7.40 \pm 0.98 (11)	219 \pm 25 (13)	3.00 \pm 0.25 (13)	1.32 \pm 0.17 (13)	0.30 \pm 0.10 (13)
CBCH	10.44 \pm 1.42 (33)	16.37 \pm 1.92 (33)	92.38 \pm 7.84 (32)	184 \pm 19 (33)	--	--	--
COYE	0.29 \pm 0.02 (21)	0.84 \pm 0.07 (21)	0.82 \pm 0.33 (4)	171 \pm 49 (5)	10.42 \pm 2.57 (19)	0.55 \pm 0.08 (19)	--
DEJU	0.10 \pm 0.03 (80)	0.76 \pm 0.15 (29)	--	197 \pm 13 (50)	--	--	--
HAWO	13.88 \pm 2.99 (13)	21.71 \pm 4.23 (13)	50.04 \pm 10.05 (13)	123 \pm 27 (13)	--	--	--
PSFL	3.52 \pm 0.76 (40)	21.54 \pm 5.88 (39)	65.33 \pm 15.58 (36)	198 \pm 18 (35)	2.80 \pm 0.48 (20)	1.70 \pm 0.35 (18)	0.10 \pm 0.06 (21)
RUHU	1.80 \pm 0.30 (32)	14.64 \pm 1.90 (32)	29.80 \pm 4.48 (32)	194 \pm 21 (31)	2.26 \pm 0.20 (31)	0.77 \pm 0.13 (30)	1.62 \pm 0.19 (30)
SOSP	0.47 \pm 0.04 (59)	1.28 \pm 0.11 (58)	2.82 \pm 0.91 (10)	214 \pm 22 (19)	6.70 \pm 0.73 (46)	0.61 \pm 0.06 (44)	0.03 \pm 0.02 (8)
SPTO	0.19 \pm 0.06 (12)	0.80 \pm 0.21 (11)	--	162 \pm 42 (4)	7.80 \pm 1.91 (5)	0.44 \pm 0.04 (5)	--
VATH	11.41 \pm 2.25 (19)	19.37 \pm 3.37 (19)	23.16 \pm 3.64 (19)	160 \pm 25 (19)	2.50 \pm 0.24 (16)	2.54 \pm 0.55 (12)	1.00 \pm 0.35 (19)

WIFL	1.05 ± 0.08 (15)	3.24 ± 0.59 (15)	4.61 ± 1.27 (11)	142 ± 46 (7)	2.71 ± 0.27 (14)	1.35 ± 0.33 (8)	0.41 ± 0.13 (9)
WIWR (cv)§	0.89 ± 0.07 (138)	6.56 ± 1.52 (131)	104.44 ± 11.52 (97)	180 ± 9 (131)	--	--	--
WIWR (ft)§	1.13 ± 0.39 (35)	5.70 ± 1.85 (34)	19.03 ± 5.76 (15)	199 ± 19 (29)	3.15 ± 0.30 (33)	1.17 ± 0.16 (33)	6.70 ± 5.65 (14)

† Only those species for which we sampled >10 total nests are included in analyses.

‡ Nest-tree diameter refers to diameter-at-breast-height (dbh) if nest tree was standing, or diameter at mid-point if nest tree was downed (e.g., for Winter Wren).

§ Winter wren nests are separated into two very different nest types: (1) “cavity” nests (cv), which were found under downed logs, in bark crevices, and in rootballs; and (2) “football” nests (ft), which were dome-shaped nests constructed of moss and placed low in the branches of live trees (often in the absence of downed logs and rootballs).

Table 5. Nest cover and nest dimensions of 14 bird species† studied in forests of the southwest Cascade Mountains of Washington, 1998–1999. Bird species' codes and scientific names are listed in Appendix 1. Values are means \pm standard error (with nest sample sizes in parentheses).

Bird Species	Overstory Canopy Cover at Nest Site (%)	Canopy Cover Directly Over Nest (%)	Side Cover Around Nest (Mean from N, S, E and W) (%)	Inside Diameter of Nest (mm)	Outside Diameter of Nest (mm)	Inside Height of Nest (mm)	Outside Height of Nest (mm)
AMRO	53.70 \pm 6.54 (43)	54.65 \pm 5.53 (43)	48.98 \pm 3.58 (44)	98.24 \pm 2.04 (21)	143.30 \pm 8.22 (23)	61.76 \pm 2.61 (21)	112.32 \pm 8.70 (22)
BRCR	87.84 \pm 2.43 (31)	94.13 \pm 4.35 (23)	71.79 \pm 3.82 (23)	--	--	--	--
CEDW	4.56 \pm 4.56 (9)	75.38 \pm 7.26 (13)	67.88 \pm 6.12 (13)	76.90 \pm 3.28 (10)	134.25 \pm 8.17 (12)	34.64 \pm 2.44 (11)	79.33 \pm 7.55 (12)
CBCH	70.90 \pm 5.66 (32)	99.89 \pm 0.11 (19)	68.61 \pm 2.49 (18)	--	--	--	--
COYE	0.00 \pm 0.00 (14)	94.50 \pm 2.23 (20)	95.24 \pm 1.66 (21)	55.14 \pm 1.32 (21)	87.48 \pm 2.65 (21)	42.00 \pm 1.09 (21)	75.76 \pm 2.82 (21)
DEJU	41.78 \pm 4.57 (80)	90.71 \pm 2.42 (78)	86.82 \pm 1.90 (79)	69.89 \pm 2.80 (66)	111.97 \pm 12.84 (65)	46.81 \pm 4.92 (64)	71.07 \pm 9.37 (15)
HAWO	52.85 \pm 11.80 (13)	100.00 \pm 0.00 (7)	68.39 \pm 4.44 (7)	--	--	--	--
PSFL	81.43 \pm 0.76 (40)	57.33 \pm 5.86 (40)	59.56 \pm 3.18 (40)	46.79 \pm 3.07 (21)	95.09 \pm 6.10 (22)	31.25 \pm 2.42 (20)	79.62 \pm 7.15 (21)
RUHU	66.00 \pm 7.18 (27)	81.45 \pm 4.84 (31)	41.69 \pm 5.08 (30)	29.54 \pm 0.92 (24)	48.48 \pm 1.28 (25)	14.95 \pm 1.22 (21)	36.41 \pm 2.53 (22)
SOSP	7.67 \pm 4.12 (36)	86.19 \pm 2.90 (58)	92.54 \pm 1.95 (58)	70.50 \pm 1.06 (58)	121.88 \pm 10.93 (59)	51.54 \pm 4.51 (59)	78.00 \pm 2.41 (59)
SPTO	28.75 \pm 15.97 (8)	82.55 \pm 9.05 (11)	75.00 \pm 10.36 (11)	78.89 \pm 3.06 (9)	127.89 \pm 5.81 (9)	57.67 \pm 5.82 (9)	86.89 \pm 10.80 (9)
VATH	83.37 \pm 7.62 (19)	54.21 \pm 8.27 (19)	30.33 \pm 5.60 (19)	93.50 \pm 8.46 (4)	166.00 \pm 12.98 (4)	50.75 \pm 4.15 (4)	145.50 \pm 21.79 (4)

WIFL	5.56 ± 4.96 (9)	79.33 ± 9.27 (15)	56.93 ± 8.73 (15)	53.92 ± 2.27 (13)	86.31 ± 3.78 (13)	32.46 ± 1.84 (13)	71.69 ± 4.99 (13)
WIWR (cv)†‡	70.18 ± 2.76 (136)	94.13 ± 2.23 (80)	78.34 ± 1.92 (80)	42.80 ± 7.05 (15)	92.84 ± 6.34 (31)	60.77 ± 3.48 (13)	103.06 ± 6.94 (31)
WIWR (ft)†‡	71.32 ± 4.28 (34)	58.26 ± 7.31 (34)	62.72 ± 5.47 (34)	39.64 ± 11.95 (7)	130.00 ± 4.31 (25)	73.33 ± 9.19 (6)	122.12 ± 5.98 (26)

† Only those species for which we sampled >10 total nests are included in analyses.

‡ Winter wren nests are separated into two very different nest types: (1) “cavity” nests (cv), which were found under downed logs, in bark crevices, and in rootballs; and (2) “football” nests (ft), which were dome-shaped nests constructed of moss and placed low in the branches of live trees (often in the absence of downed logs and rootballs).

Table 6. Nesting substrate of songbirds in forests of the southwest Cascade Mountains of Washington, 1998–1999. Data represent all nests found in three treatments (clearcut, commercially thinned, and old growth forests) pooled across two years. American Robin (scientific names in Appendix 1) = AMRO, Dark-eyed Junco = DEJU, Pacific-slope Flycatcher = PSFL, Song Sparrow = SOSP, and Winter Wren = WIWR.

Nesting Substrate	Bird Species					Total
	AMRO	DEJU	PSFL	SOSP	WIWR	
Forb						
<i>Digitalis purpureus</i>	0	1	0	0	0	1
<i>Epilobium angustifolium</i>	0	1	0	1	0	2
Gramminacea	0	5	0	0	0	5
<i>Polystichum munitum</i>	0	5	0	17	11	33
<i>Pteridium aquilinum</i>	0	0	0	1	0	1
Unknown forb	0	1	0	0	0	1
Shrub						
<i>Acer circinatum</i>	2	0	1	1	1	5
<i>Berberis nervosa</i>	0	1	0	0	0	1
<i>Corylus cornuta</i>	0	0	0	0	1	1
<i>Gaultheria shallon</i>	0	4	0	2	0	6
<i>Holdiscus discolor</i>	0	0	0	0	1	1
<i>Rosa gymnocarpa</i>	0	0	0	1	0	1
<i>Rubus spectabilis</i>	0	0	1	2	1	4
<i>Rubus ursinus</i>	0	1	0	0	0	1
<i>Vaccinium parvifolium</i>	0	0	0	1	1	2
<i>Vaccinium</i> species	0	1	0	0	0	1

Tree

<i>Abies amabilis</i>	0	0	0	0	1	1
<i>Acer macrophyllum</i>	1	0	0	0	5	6
<i>Alnus rubra</i>	4	0	3	0	2	9
<i>Populus balsamifera</i>	1	0	1	0	0	2
<i>Prunus species</i>	1	0	0	0	0	1
<i>Pseudotsuga menziesii</i>	30	0	3	2	16	51
<i>Thuja plicata</i>	0	0	1	0	3	4
<i>Tsuga heterophylla</i>	4	1	5	0	4	14

Other

Ground	0	22	0	0	3	25
Litter	0	3	0	5	2	10
Moss	0	2	0	0	0	2
Living root	0	0	0	0	9	9
Rootball	1	8	2	0	23	34
Snag	0	0	1	1	12	14
Stump	0	1	1	0	28	30
Woody debris	0	0	3	0	40	43

Grand Total	44	57	22	34	164	321
-------------	----	----	----	----	-----	-----

Table 7. Aspect of nest sites by bird species in forests of the southwest Cascade Mountains of Washington, 1998–1999. Observed counts (obs) are based on nest locations and expected counts (exp) are based on a random selection of aspects from the stand ($N_{(exp)} = N_{(obs)}$) in which those nests occurred. Data for American Robin (scientific names in Appendix 1), Dark-eyed Junco, Pacific-slope Flycatcher, and Song Sparrow were pooled across treatments due to small samples sizes, whereas Winter Wren data were analyzed separately for commercially thinned and old growth forests.

Bird Species	Nest Aspect					Statistic		
	Flat	North	East	South	West	χ^2	df	<i>P</i>
American Robin (obs)	6	10	4	12	12			
American Robin (exp)	5	11	4	16	8	3.29	4	<0.500
Dark-eyed Junco (obs)	6	36	11	12	11			
Dark-eyed Junco (exp)	6	22	13	26	9	17.20	4	<0.005
Pac.-slope Flycatcher (obs)	2	9	4	8	2			
Pac.-slope Flycatcher (exp)	1	2	3	12	7	30.74	4	<0.001
Song Sparrow (obs)	1	13	3	7	14			
Song Sparrow (exp)	1	4	3	16	13	26.39	4	<0.001
Winter Wren† (obs)	11	43	6	31	23			
Winter Wren† (exp)	21	17	5	50	20	52.13	4	<0.001
Winter Wren‡ (obs)	NA§	18	16	9	7			
Winter Wren‡ (exp)		11	9	18	12	16.48	3	<0.001

† Data from commercially thinned stands only.

‡ Data from old growth stands only.

§ No “Flat” aspect category existed for old growth stands.

Table 8. Nest orientation for five bird species in forests of the southwest Cascade Mountains of Washington, 1998–1999. Observed (obs) counts are based on actual nest location and expected (exp) counts are based on the assumption of equal distribution of nests by orientation category. Data for American Robin (scientific names in Appendix 1; AMRO), Dark-eyed Junco (DEJU), Pacific-slope Flycatcher (PSFL), and Song Sparrow (SOSP) were pooled across treatments due to small samples sizes within treatments. Orientation of Winter Wren (WIWR) nests in commercially thinned and old growth forests were not significantly different, so they were pooled for analysis.

Bird Species	Nest Site Orientation						Statistic		
	N	NE	SE	S	SW	NW	χ^2	df	P
AMRO (obs)	6	6	4	9	9	6			
AMRO (exp)	5.8	5.8	5.8	5.8	5.8	5.8	2.90	5	0.720
DEJU (obs)	6	11	4	8	15	4			
DEJU (exp)	8	8	8	8	8	8	11.75	5	0.040
PSFL (obs)	6	4	2	5	4	2			
PSFL (exp)	3.8	3.8	3.8	3.8	3.8	3.8	3.38	5	0.650
SOSP (obs)	6	4	2	5	4	2			
SOSP (exp)	3.8	3.8	3.8	3.8	3.8	3.8	NA†		
WIWR‡ (obs)	16	10	21	22	24	10			
WIWR (exp)	17.2	17.2	17.2	17.2	17.2	17.2	11.00	5	0.051
WIWR§ (obs)	9	5	7	14	3	10			
WIWR (exp)	8	8	8	8	8	8	9.50	5	0.091

WIWR (obs)	25	15	28	36	27	20			
WIWR (exp)	25.2	25.2	25.2	25.2	25.2	25.2	10.29	5	0.068

† Data was not analyzed due to small sample sizes.

‡ Data from commercially thinned stands only.

§ Data from old growth stands only.

|| Data from commercially thinned and old growth stands combined.

Table 9. Habitat characteristics of American Robin (*Turdus migratorius*) nest plots and random plots in clearcut and commercial thin forests of the southwest Cascade Mountains of Washington, 1998–1999. Habitat characteristics are defined in Appendix 2. *P*-values are not corrected for experiment-wise error rates.

Characteristic	Nest Plots			Random Plots			Mann-Whitney
	N	Mean	Std. Error	N	Mean	Std. Error	<i>P</i>
Clearcut							
SLOPE (degrees)	18	6.89	1.20	32	8.16	1.15	0.606
CNPYCVR (%)	18	12.39	6.66	26	8.04	3.62	0.896
BLESHRB (%cover)	18	6.94	2.23	32	3.46	1.21	0.169
BPDSHRB (%cover)	18	15.97	2.32	32	17.94	2.20	0.642
ODSHRB (%cover)	18	2.64	1.11	32	2.15	0.92	0.653
TRESEED (%cover)	18	7.57	2.91	32	6.27	1.29	0.266
FERN (%cover)	18	21.46	5.35	32	11.14	1.86	0.169
HERBS (%cover)	18	18.13	3.25	32	24.58	1.85	0.059
CWD (%cover)	18	4.31	1.96	32	11.21	1.97	0.002
FWD (%cover)	18	16.53	4.53	32	13.11	1.58	0.436
OTHER (%cover)	18	5.94	2.86	32	6.31	2.35	0.697
FORB (stems/ha)	18	47230.57	9491.30	32	42255.77	8209.80	0.390
SHRUB (stems/ha)	16	5928.34	1638.96	32	8844.76	1643.88	0.209

S_CON (stems/ha)	18	1393.45	423.46	32	1454.23	302.56	0.701
M_CON (stems/ha)	18	16.62	10.47	32	25.71	8.38	0.101
L_CON (stems/ha)	18	19.39	19.39	32	1.95	1.27	0.683
G_CON (stems/ha)	18	0.00	0.00	32	0.00	0.00	
S_DEC (stems/ha)	18	2008.83	579.68	32	1102.11	270.98	0.141
M_DEC (stems/ha)	18	11.08	5.42	32	12.47	9.45	0.358
L_DEC (stems/ha)	18	2.77	2.77	32	10.91	3.95	0.031
S_STUMP (stems/ha)	18	0.00	0.00	32	21.88	13.29	0.122
L_STUMP (stems/ha)	18	0.00	0.00	32	10.52	2.63	0.001
S_SNAG (stems/ha)	18	15.24	7.31	32	38.56	6.19	0.003
M_SNAG (stems/ha)	18	13.85	7.60	32	35.06	6.04	0.002
L_SNAG (stems/ha)	18	42.44	35.66	32	22.27	7.43	0.332
G_SNAG (stems/ha)	18	0.00	0.00	32	2.34	1.42	0.185
ROOTBALL (#/ha)	18	0.00	0.00	32	0.00	0.00	

Commercial thin

SLOPE	21	2.43	0.66	32	3.34	0.78	0.414
CNPYCVR	19	83.95	5.44	32	76.13	4.81	0.128
BLESHRB	21	4.64	2.07	32	10.00	2.11	0.007
BPDSHRB	21	9.70	2.61	32	10.63	1.31	0.150
ODSHRB	21	1.43	0.76	32	2.07	0.72	0.373
TRESEED	21	1.55	0.69	32	3.46	1.30	0.055

FERN	21	20.06	2.56	32	19.08	2.66	0.413
HERBS	21	19.88	2.11	32	24.02	2.88	0.604
CWD	21	5.95	1.20	32	5.02	0.78	0.535
FWD	21	32.02	3.22	32	21.91	1.65	0.016
OTHER	21	5.42	2.35	32	3.11	0.57	0.755
TOT_FORB	21	13964.4	4055.92	32	23713.82	5466.14	0.082
SHRUB_DEN	20	5041.87	1545.04	32	2608.07	449.69	0.211
S_CON	21	115.19	63.3	32	409.81	256.33	0.077
M_CON	21	61.73	16.47	32	39.34	7.45	0.352
L_CON	21	147.21	21.89	32	174.9	13.85	0.160
G_CON	21	24.93	6.66	32	30.77	6.18	0.575
S_DEC	21	24.25	14.22	32	777.85	447.87	0.049
M_DEC	21	20.18	7.22	32	10.13	4.09	0.287
L_DEC	21	15.43	5.57	32	28.83	7.88	0.329
S_STUMP	21	0.00	0.00	32	5.97	3.33	0.152
L_STUMP	21	13.06	4.75	32	28.83	4.99	0.010
S_SNAG	21	14.25	5.59	32	45.19	8.33	0.003
M_SNAG	21	39.18	7.21	32	24.15	4.37	0.150
L_SNAG	21	79.62	33.93	32	32.36	7.67	0.458
G_SNAG	21	4.75	2.19	32	4.28	1.33	0.690
ROOTBALL	21	2.37	1.65	32	0.39	0.39	0.307

Table 10. Habitat characteristics of Dark-eyed Junco (*Junco oreganus hyemalis*) nest plots and random plots in clear-cut and commercial thin forests of the southwest Cascade Mountains of Washington, 1998–1999. Habitat characteristics are defined in Appendix 2. *P*-values are not corrected for experiment-wise error rates.

Characteristic	Nest Plots			Random Plots			Mann-Whitney
	N	Mean	Std. Error	N	Mean	Std. Error	<i>P</i>
Clearcut							
CNPYCVR (%)	23	1.96	1.74	26	8.04	3.62	0.062
SLOPE (degrees)	23	9.78	2.11	32	8.16	1.15	0.932
BLESHRB (%cover)	23	6.20	2.30	32	3.46	1.21	0.971
BPDSHRB (%cover)	23	7.50	1.73	32	17.94	2.20	0.000
ODSHRB (%cover)	23	1.36	1.00	32	2.15	0.92	0.347
TRESEED (%cover)	23	2.50	0.67	32	6.27	1.29	0.011
FERN (%cover)	23	17.99	4.03	32	11.14	1.86	0.330
HERBS (%cover)	23	33.80	4.64	32	24.58	1.85	0.249
CWD (%cover)	23	8.42	1.75	32	11.21	1.97	0.407
FWD (%cover)	23	16.20	3.36	32	13.11	1.58	0.791

OTHER (%cover)	23	6.03	2.71	32	6.31	2.35	0.923
FORB (stems/ha)	23	36178.77	7637.43	32	42255.77	8209.80	0.676
SHRUB (stems/ha)	20	1858.87	427.83	32	8844.76	1643.88	0.000
S_CON (stems/ha)	23	1300.88	323.26	32	1454.23	302.56	0.707
M_CON (stems/ha)	23	80.21	34.73	32	25.71	8.38	0.815
L_CON (stems/ha)	23	1.08	1.08	32	1.95	1.27	0.495
G_CON (stems/ha)	23	0.00	0.00	32	0.00	0.00	
S_DEC (stems/ha)	23	315.53	75.46	32	1102.11	270.98	0.082
M_DEC (stems/ha)	23	2.17	2.17	32	12.47	9.45	0.313
L_DEC (stems/ha)	23	0.00	0.00	32	10.91	3.95	0.002
S_STUMP (stems/ha)	23	0.00	0.00	32	21.88	13.29	0.081
L_STUMP (stems/ha)	23	26.01	9.72	32	10.52	2.63	0.506
S_SNAG (stems/ha)	23	57.45	13.25	32	38.56	6.19	0.597
M_SNAG (stems/ha)	23	54.20	12.60	32	35.06	6.04	0.447
L_SNAG (stems/ha)	23	7.70	5.64	32	22.27	7.43	0.226
G_SNAG (stems/ha)	23	0.00	0.00	32	2.34	1.42	0.135
ROOTBALL (#/ha)	23	0.00	0.00	32	0.00	0.00	

Commercial thin

CNPYCVR	47	62.11	5.16	32	76.13	4.81	0.081
SLOPE	46	3.29	0.49	32	3.34	0.78	0.675
BLESHRB	47	7.63	1.86	32	10.00	2.11	0.040
BPDSHRB	47	13.48	2.01	32	10.63	1.31	0.845
ODSHRB	47	0.98	0.40	32	2.07	0.72	0.197
TRESEED	47	1.46	0.57	32	3.46	1.30	0.010
FERN	47	15.19	1.79	32	19.08	2.66	0.232
HERBS	47	33.92	3.26	32	24.02	2.88	0.040
CWD	47	5.21	0.94	32	5.02	0.78	0.231
FWD	47	15.98	1.88	32	21.91	1.65	0.003
OTHER	46	6.04	1.55	32	3.11	0.57	0.967
TOT_FORB	44	20550.83	3762.85	32	23713.82	5466.14	0.817
SHRUB_DEN	43	2955.01	584.88	32	2608.071	449.69	0.826
S_CON	46	249.10	149.23	32	409.81	256.33	0.134
M_CON	46	35.77	8.26	32	39.34	7.45	0.144
L_CON	46	169.63	13.66	32	174.90	13.85	0.729
G_CON	46	29.81	5.62	32	30.77	6.18	0.622
S_DEC	46	384.73	214.31	32	777.85	447.87	0.336

M_DEC	46	11.38	3.26	32	10.13	4.09	0.969
L_DEC	46	11.38	4.00	32	28.83	7.88	0.012
S_STUMP	46	2.77	2.77	32	5.97	3.33	0.171
L_STUMP	46	21.14	5.31	32	28.83	4.99	0.016
S_SNAG	46	52.03	9.45	32	45.19	8.33	0.815
M_SNAG	46	38.48	6.09	32	24.15	4.37	0.354
L_SNAG	46	61.74	23.98	32	32.36	7.67	0.254
G_SNAG	46	7.59	2.55	32	4.28	1.33	0.705
ROOTBALL	46	2.71	1.39	32	0.39	0.39	0.303

Table 11. Habitat characteristics of Pacific-slope Flycatcher (*Empidonax difficilis*) nest plots and random plots in commercial thin and old growth forests of the southwest Cascade Mountains of Washington, 1998–1999. Habitat characteristics are defined in Appendix 2. *P*-values are not corrected for experiment-wise error rates.

Characteristic	Nest Plots			Random Plots			Mann-Whitney
	N	Mean	Std. Error	N	Mean	Std. Error	<i>P</i>
Commercial thin							
SLOPE (degrees)	13	1.69	0.36	32	3.34	0.78	0.488
CNPYCVR (%)	13	80.92	8.13	32	76.13	4.81	0.142
BLESHRB (%cover)	13	6.37	2.82	32	10.00	2.11	0.061
BPDSHRB (%cover)	13	3.37	1.35	32	10.63	1.31	0.000
ODSHRB (%cover)	13	2.12	1.00	32	2.07	0.72	0.977
TRESEED (%cover)	13	0.77	0.59	32	3.46	1.30	0.021
FERN (%cover)	13	20.15	3.92	32	19.08	2.66	0.831
HERBS (%cover)	13	14.10	2.08	32	24.02	2.88	0.054
CWD (%cover)	13	4.13	1.30	32	5.02	0.78	0.371
FWD (%cover)	13	40.67	6.20	32	21.91	1.65	0.004
OTHER (%cover)	13	8.37	2.66	32	3.11	0.57	0.055
FORB (stems/ha)	12	17809.31	4778.25	32	23713.82	5466.14	0.722

SHRUB (stems/ha)	12	3066.29	884.94	32	2608.07	449.69	0.823
S_CON (stems/ha)	13	274.23	132.01	32	409.81	256.33	0.814
M_CON (stems/ha)	13	61.37	16.85	32	39.34	7.45	0.403
L_CON (stems/ha)	13	191.77	40.55	32	174.90	13.85	0.870
G_CON (stems/ha)	13	24.93	7.98	32	30.77	6.18	0.676
S_DEC (stems/ha)	13	107.73	49.62	32	777.85	447.87	0.785
M_DEC (stems/ha)	13	82.46	31.86	32	10.13	4.09	0.002
L_DEC (stems/ha)	13	65.20	24.53	32	28.83	7.88	0.209
S_STUMP (stems/ha)	13	9.79	9.79	32	5.97	3.33	0.919
L_STUMP (stems/ha)	13	7.67	3.32	32	28.83	4.99	0.006
S_SNAG (stems/ha)	13	11.51	5.37	32	45.19	8.33	0.007
M_SNAG (stems/ha)	13	42.19	13.65	32	24.15	4.37	0.357
L_SNAG (stems/ha)	13	273.82	142.99	32	32.36	7.67	0.294
G_SNAG (stems/ha)	13	17.26	5.19	32	4.28	1.33	0.019
ROOTBALL (#/ha)	13	1.92	1.92	32	0.39	0.39	0.483

Old growth

SLOPE	12	16.67	2.73	32	14.09	1.29	0.377
NEST_CNPYCVR	12	86.50	6.60	32	91.02	1.83	0.616
BLESHRB	12	6.67	3.21	32	8.22	1.72	0.192
BPDSHRB	12	1.77	0.89	32	2.32	0.45	0.176

ODSHRB	12	0.00	0.00	32	0.68	0.28	0.060
TRESEED	12	5.10	2.21	32	5.16	1.84	0.912
FERN	12	7.08	2.50	32	9.18	1.95	0.426
HERBS	12	12.60	4.06	32	9.71	1.58	0.979
CWD	12	8.54	1.62	32	11.89	1.98	0.510
FWD	12	44.69	3.40	32	47.60	3.02	0.477
OTHER	12	13.96	5.14	32	6.00	1.66	0.239
TOT_FORB	5	9071.78	5252.08	32	5846.91	1715.99	0.671
SHRUB_DEN	5	2393.62	516.24	32	1177.71	299.29	0.063
S_CON	12	1814.31	639.70	32	1002.65	313.52	0.426
M_CON	12	78.95	22.31	32	134.39	15.62	0.049
L_CON	12	87.26	18.02	32	153.86	17.88	0.027
G_CON	12	70.64	15.90	32	86.87	7.68	0.327
S_DEC	12	42.44	42.44	32	27.85	18.51	0.958
M_DEC	12	0.00	0.00	32	11.69	10.12	0.205
L_DEC	12	2.08	2.08	32	8.96	3.13	0.210
S_STUMP	12	0.00	0.00	32	5.97	5.97	0.540
L_STUMP	12	8.31	4.69	32	11.30	3.03	0.349
S_SNAG	12	14.54	3.71	32	8.96	3.27	0.059
M_SNAG	12	20.78	6.75	32	7.40	1.84	0.057
L_SNAG	12	169.76	158.54	32	159.83	40.45	0.003

G_SNAG	12	10.39	3.71	32	70.51	13.30	0.006
ROOTBALL	12	2.08	2.08	32	3.12	1.77	0.720

Table 12. Habitat characteristics of Song Sparrow (*Melospiza melodia*) nest plots and random plots in clear-cut forest of the southwest Cascade Mountains of Washington, 1998–1999. Habitat characteristics are defined in Appendix 2. *P*-values are not corrected for experiment-wise error rates.

Characteristic	Nest Plots			Random Plots			Mann-Whitney
	N	Mean	Std. Error	N	Mean	Std. Error	<i>P</i>
Clear-cut							
SLOPE (degrees)	36	4.33	0.96	32	8.16	1.15	0.001
CNPYCVR (%cover)	11	9.55	9.06	26	8.04	3.62	0.538
BLESHRB (%cover)	36	9.69	2.59	32	3.46	1.21	0.611
BPDSHRB (%cover)	36	26.22	2.48	32	17.94	2.20	0.012
ODSHRB (%cover)	36	0.73	0.26	32	2.15	0.92	0.492
TRESEED (%cover)	36	2.57	0.86	32	6.27	1.29	0.000
FERN (%cover)	36	23.75	2.57	32	11.14	1.86	0.000
HERBS (%cover)	36	22.59	2.88	32	24.58	1.85	0.261
CWD (%cover)	36	1.56	0.43	32	11.21	1.97	0.000
FWD (%cover)	36	11.65	1.50	32	13.11	1.58	0.522
OTHER (%cover)	36	0.35	0.18	32	6.31	2.35	0.000
FORB (stems/ha)	36	91336.71	8853.33	32	42255.77	8209.80	0.000

SHRUB (stems/ha)	34	15255.93	1990.71	32	8844.76	1643.88	0.009
S_CON (stems/ha)	36	728.55	56.40	32	1454.23	302.56	0.131
M_CON (stems/ha)	36	13.16	5.92	32	25.71	8.38	0.138
L_CON (stems/ha)	36	0.00	0.00	32	1.95	1.27	0.062
G_CON (stems/ha)	36	0.00	0.00	32	0.00	0.00	
S_DEC (stems/ha)	36	3469.47	693.30	32	1102.11	270.98	0.002
M_DEC (stems/ha)	36	5.54	4.88	32	12.47	9.45	0.318
L_DEC (stems/ha)	36	0.00	0.00	32	10.91	3.95	0.000
S_STUMP (stems/ha)	36	17.68	9.01	32	21.88	13.29	0.878
L_STUMP (stems/ha)	36	2.77	1.66	32	10.52	2.63	0.001
S_SNAG (stems/ha)	36	23.55	5.53	32	38.56	6.19	0.028
M_SNAG (stems/ha)	36	24.24	4.50	32	35.06	6.04	0.163
L_SNAG (stems/ha)	36	17.68	11.51	32	22.27	7.43	0.095
G_SNAG (stems/ha)	36	0.69	0.69	32	2.34	1.42	0.252
ROOTBALL (#/ha)	36	0.00	0.00	32	0.00	0.00	

Table 13. Habitat characteristics of Winter Wren (*Troglodytes troglodytes*) nest plots and random plots in commercial thin and old growth forests of the southwest Cascade Mountains of Washington, 1998–1999. Habitat characteristics are defined in Appendix 2. *P*-values are not corrected for experiment-wise error rates.

Habitat Character	Nest Level			Plot Level			Mann-Whitney
	N	Mean	Std. Error	N	Mean	Std. Error	<i>P</i>
Commercial thin							
SLOPE (degrees)	112	2.06	0.26	32	3.34	0.78	0.151
CNPYCVR (%cover)	111	71.72	2.86	32	76.13	4.81	0.766
BLESHRB (%cover)	114	9.56	1.42	32	10.00	2.11	0.132
BPDSHRB (%cover)	114	9.06	0.79	32	10.63	1.31	0.158
ODSHRB (%cover)	114	1.09	0.24	32	2.07	0.72	0.045
TRESEED (%cover)	114	0.86	0.18	32	3.46	1.30	0.001
FERN (%cover)	114	16.25	1.54	32	19.08	2.66	0.137
HERBS (%cover)	114	16.02	1.24	32	24.02	2.88	0.007
CWD (%cover)	114	11.55	1.25	32	5.02	0.78	0.214
FWD (%cover)	114	25.91	1.48	32	21.91	1.65	0.452
OTHER (%cover)	114	9.15	1.29	32	3.11	0.57	0.201
FORB (stems/ha)	112	21971.30	2338.44	32	23713.82	5466.14	0.952
SHRUB (stems/ha)	110	4840.47	664.21	32	2608.07	449.69	0.163

S_CON (stems/ha)	112	237.59	42.74	32	409.81	256.33	0.850
M_CON (stems/ha)	112	37.84	5.25	32	39.34	7.45	0.170
L_CON (stems/ha)	112	183.19	9.71	32	174.90	13.85	0.958
G_CON (stems/ha)	112	29.83	3.45	32	30.77	6.18	0.762
S_DEC (stems/ha)	112	352.40	99.89	32	777.85	447.87	0.608
M_DEC (stems/ha)	112	15.80	5.14	32	10.13	4.09	0.185
L_DEC (stems/ha)	112	15.80	3.95	32	28.83	7.88	0.009
S_STUMP (stems/ha)	112	7.96	3.34	32	5.97	3.33	0.471
L_STUMP (stems/ha)	112	17.36	2.83	32	28.83	4.99	0.001
S_SNAG (stems/ha)	112	33.17	4.15	32	45.19	8.33	0.070
M_SNAG (stems/ha)	112	31.83	3.61	32	24.15	4.37	0.697
L_SNAG (stems/ha)	112	63.77	12.67	32	32.36	7.67	0.376
G_SNAG (stems/ha)	112	10.91	1.97	32	4.28	1.33	0.492
ROOTBALL(#/ha)	112	4.01	1.21	32	0.39	0.39	0.170

Old growth

SLOPE	48	16.44	1.63	32	14.09	1.29	0.705
CNPYCVR	50	70.08	4.11	32	91.02	1.83	0.002
BLESHRB	50	1.30	0.36	32	8.22	1.72	0.000
BPDSHRB	50	1.18	0.29	32	2.32	0.45	0.005
ODSHRB	50	1.28	0.74	32	0.68	0.28	0.202
TRESEED	50	1.75	0.62	32	5.16	1.84	0.005

FERN	50	12.45	2.21	32	9.18	1.95	0.489
HERBS	50	15.34	2.11	32	9.71	1.58	0.087
CWD	50	17.50	1.95	32	11.89	1.98	0.022
FWD	50	32.56	2.78	32	47.60	3.02	0.001
OTHER	50	16.81	2.57	32	6.00	1.66	0.021
FORB	37	11291.23	4163.08	32	5846.91	1715.99	0.384
SHRUB	34	1235.75	198.93	32	1177.71	299.29	0.089
S_CON	49	659.99	115.31	32	1002.65	313.52	0.572
M_CON	49	82.93	12.85	32	134.39	15.62	0.002
L_CON	49	103.79	14.67	32	153.86	17.88	0.004
G_CON	49	70.21	7.04	32	86.87	7.68	0.053
S_DEC	49	103.93	103.93	32	27.85	18.51	0.150
M_DEC	49	4.07	3.59	32	11.69	10.12	0.170
L_DEC	49	3.05	1.87	32	8.96	3.13	0.020
S_STUMP	49	0.00	0.00	32	5.97	5.97	0.216
L_STUMP	49	1.53	0.86	32	11.30	3.03	0.000
S_SNAG	49	8.14	3.20	32	8.96	3.27	0.129
M_SNAG	49	10.68	3.63	32	7.40	1.84	0.609
L_SNAG	49	110.11	45.99	32	159.83	40.45	0.009
G_SNAG	49	44.77	10.07	32	70.51	13.30	0.053
ROOTBALL	49	2.54	1.09	32	3.12	1.77	0.784

Table 14. Results of stepwise multiple linear regression of number of square-root transformed (young fledged/nest) versus habitat characteristics in forests of the southwest Cascade Mountains of Washington, 1998–1999. All data were pooled across years and, in addition, data for American Robin (scientific names in Appendix 1), Dark-eyed Junco, Pacific-slope Flycatcher, and Song Sparrow were pooled across treatments due to small sample sizes. Habitat characteristics are defined in Appendix 2.

Species	N†	Source	Coefficient	Standard Error	Standard Coefficient	F	P	R ²
American Robin	38	Constant	0.150	0.278	0.000	0.538	0.594	0.348
		L_DEC	0.246	0.079	0.397	3.078	0.004	
		G_SNAG	0.402	0.143	0.361	2.801	0.008	
Dark-eyed Junco	73	Constant	2.869	0.2443	0.000	11.742	0.000	0.068
		CANCVR	-0.001	0.004	-0.261	-2.331	0.023	
Pacific-slope Flycatcher	12	Constant	3.218	0.542	0.000	5.932	0.000	0.141
		M-SNAG	-0.186	0.096	-0.376	1.944	0.064	
Song Sparrow	37	Constant	3.686	0.570	0.000	6.463	0.000	0.198
		FWD	-0.479	0.163	-0.445	-2.939	0.006	

Winter Wren (old growth)	49	Constant	0.091	0.759	0.000	0.121	0.904	0.135
		CWD	0.480	0.177	0.368	2.71	0.009	
Winter Wren (commercial thin)	110	Constant	2.715	0.364	0.000	7.469	0.000	0.118
		S_DEC	-0.033	0.013	-0.234	-2.578	0.012	
		OTHER	-0.240	0.100	-0.220	-2.39	0.018	
		ROOTBALL	0.225	0.111	0.186	2.024	0.045	
Winter Wren (All treatments combined)	161	Constant	2.332	0.174	0.000	13.434	0.000	0.034
		S_DEC	-0.028	0.012	-0.186	-2.404	0.017	

† Although sample sizes were ≥ 25 for all species, some records were omitted from analysis due to missing habitat data.

Table 15. Results of logistic regression of square-root transformed nest success (success or failure) versus habitat characteristics in forests of the southwest Cascade Mountains of Washington, 1998–1999. All data were pooled across years and, in addition, data for American Robin (scientific names in Appendix 1), Dark-eyed Junco, and Song Sparrow were pooled across treatments due to relatively small sample sizes. Data for Pacific-slope Flycatcher were not analyzed because of small sample sizes. Habitat characteristics are defined in Appendix 2.

Variable	Estimate	S.E.	<i>t</i>	<i>P</i>	Odds Ratio	Confidence Limits		Log Likelihood	ρ^2	<i>P</i>
						Upper	Lower			
American Robin								13.815	0.245	0.001
CONSTANT	-2.137	0.604	-3.540	0.000						
L_DEC	0.440	0.166	2.656	0.008	1.553	2.148	1.112			
G_CON	0.530	0.286	1.848	0.065	1.698	2.978	0.968			
Dark-eyed Junco								0.852	0.011	0.356
CONSTANT	1.598	0.443	3.606	0.000						
CANCVR	-0.006	0.007	-0.918	0.358	0.985	1.000	0.971			
Song Sparrow								5.062	0.112	0.024
CONSTANT	3.218	1.286	2.502	0.012						
FWD	-0.682	0.338	-2.019	0.044	0.506	0.980	0.260			

Winter Wren (Commercial thin)

CONSTANT	1.301	0.373	3.489	0.000				11.100	0.073	0.004
S_DEC	-0.034	0.016	-2.145	0.032	0.967	0.997	0.938			
OTHER	-0.272	0.109	-2.493	0.013	0.762	0.943	0.615			

Winter Wren (All treatments combined)

CONSTANT	0.453	0.176	2.582	0.010				4.831	0.022	0.028
S_DEC	-0.027	0.014	-2.026	0.043	0.973	0.999	0.948			

Table 16. Habitat characteristics at successful versus unsuccessful nest sites for songbirds in forests of the southwest Cascade Mountains of Washington, 1998–1999. All data were pooled across years and, in addition, data for American Robin (scientific names in Appendix 1), Dark-eyed Junco, and Song Sparrow were pooled across treatments due to relatively small sample sizes. Data for Pacific-slope Flycatcher were not analyzed because of small sample sizes. Habitat characteristics are defined in Appendix 2.

Habitat Characteristic	Successful Nest Sites			Unsuccessful Nest Sites			Mann-Whitney
	N	Mean	Std. Error	N	Mean	Std. Error	<i>P</i>
American Robin							
L_DEC (stems/ha)	15	21.60	7.24	28	3.56	2.47	0.001
Dark-eyed Junco							
CNPYCVR (%)	60	36.98	5.10	16	59.50	10.43	0.034
Song Sparrow							
FWD (%cover)	26	9.78	1.57	11	16.84	2.89	0.023
Winter Wren (old growth)							
CWD	27	4.19	0.31	23	3.64	0.30	0.306
Winter Wren (commercial thin)							
S_DEC	64	145.22	75.28	46	456.69	1.69.56	0.144
OTHER	66	7.10	1.56	46	12.35	2.22	0.014
ROOTBALL	64	4.67	1.74	46	3.25	1.66	0.538

Winter Wren (All treatments combined)

S_DEC (stems/ha)	93	93.94	52.15	68	383.83	136.61	0.139
------------------	----	-------	-------	----	--------	--------	-------

Figure Legend

Figure 1. Variation in nest fate (A) and reasons for nest failure (B) for 681 nests of 40 bird species found in three forest treatments in the southwest Cascade Mountains of Washington, 1998–1999. Nest numbers are indicated above each column.

