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Use of Small Streams and Forest Gaps for Breeding Habitats by Winter Wrens in Coastal British Columbia

Abstract

Few studies have examined the value of riparian areas adjacent to streams ≤ 10 -m wide as habitat for forest birds. In mature (80-120 yr) and young (40-60 yr) coastal forests of southern British Columbia, we examined the habitat values for male winter wrens of riparian areas adjacent to small streams and areas upslope of these streams. In both riparian and upslope areas, wrens preferentially located nests ($n = 47$) and song perches ($n = 77$) in disturbed sites with fewer trees than randomly located sites. Hydrological processes associated with streams, mortality of dominant canopy trees or uprooted trees can produce these disturbed sites. In mature forest, winter wrens chose stream banks and upturned root masses when available for building their nests with most nest substrates located within 5 m of small streams. In both young and mature forests, they also chose areas near small streams as locations for song perches. Winter wrens may use areas closer to streams when available because channel morphology, the associated heterogeneous forest structure, and microclimate likely provide optimal nesting and foraging habitat. Our research supports operational efforts by forest managers to conserve structures near small streams and in upslope areas because these structures maintain long-term habitat values for wildlife such as winter wrens.

Introduction

Riparian habitats provide resources to wildlife that complement those available in forested upslope habitats away from streams (Raedeke 1988). These include water, unique microclimate, and structurally diverse and disturbed sites. Such sites in forests are characterized by complex vertical vegetation structure associated with the riparian forest edge interfaces, and openings in the understory and overstory canopy (Gregory et al. 1991, Voller 1998). Openings in the overstory canopy that result from stream processes are called edaphic gaps (Lertzman et al. 1996). Mortality of standing canopy dominants and uprooted trees, referred to as gapmakers, also produce open and disturbed sites but these are called developmental gaps (Lertzman et al. 1996). Developmental gaps may contribute to the canopy opening above streams and in areas away from streams providing structural heterogeneity in the forest (Spies et al. 1990, Lertzman et al. 1996). Gaps have distinct micro-

climates in their understory because higher light intensities occur without shading from the overstory canopy. Furthermore, greater amounts of moisture accumulate because the canopy does not intercept rain and fewer roots remove water (Blake and Hoppes 1986, Schaetzl et al. 1989, Shure and Phillips 1991). Uprooting of trees can create pits that flood and drain poorly thereby becoming locally wet sites (Beatty and Stone 1986).

Few studies in the Pacific Northwest of North America have determined for forest birds the importance of riparian habitats of small streams relative to habitats upslope, and how best to manage these riparian habitats (Carey 1988, McGarigal and McComb 1992, Kinley and Newhouse 1997, Hagar 1999). As well, the transition in vegetation composition and structure from riparian areas upslope into the adjacent forest is often subtle in temperate and boreal forest stands, particularly when streams lack floodplains (Gregory et al. 1991, Naiman et al. 1993, Wiebe and Martin 1998). In British Columbia, this subtlety has obscured the need to manage habitats along small streams for terrestrial wildlife. Instead, placement of reserves or management zones is directed toward streams

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that are fish bearing or within community watersheds (B.C. Ministry of Forests and B.C. Ministry of Environment 1995). We therefore studied habitat selection by winter wrens, a common forest insectivore, to improve our understanding on how the forest surrounding small streams can provide habitat for wildlife.

The winter wren is significantly more abundant in old-growth forest compared to 40-80-yr second-growth in the south coast mainland region of British Columbia, but nearly absent from clearcut blocks of < 5-yr since harvest (Savard et al. *in press*). Yet age alone can be a poor criterion for managing habitats for wildlife (Rotenberry and Wiens 1980, Hayes et al. 1997, Waldien et al. 2000). In the Pacific Northwest, winter wrens are more numerous in structurally diverse stands (Carey et al. 1991, Hansen et al. 1995) and associated with riparian habitats (Barrows 1986, McGarigal and McComb 1992, Kinley and Newhouse 1997). Our main objective was to determine in the drier coastal temperate rainforest whether riparian habitats of small streams (≤ 10 m-wide, including seeps with surface water) are selected by male winter wrens for territories and nesting because of resources that differ from those available in upslope habitats away from streams.

Territories of birds include habitats that can provide food, nest sites, security cover, and shelter (Martin and Roper 1988). As well within these habitats, song perches are used by male winter wrens to advertise and defend their territory, to attract mates, and to advertise potential nests (Armstrong 1956, Garson 1980). Nest sites, as microhabitats within the territory, may be a major factor that influences placement of territories by birds (Matsuoka et al. 1997). Male winter wrens usually weave several nests from moss and twigs within available cavities in their territories (Armstrong 1956, Armstrong and Whitehouse 1977, Wesolowski 1983). Winter wrens in coastal British Columbia raise one or more broods from mid-April to mid-July and some males are polygynous (McLachlin 1983). Long-term habitat needs are important for winter wrens because they are site tenacious and can occupy the same territories in successive years. Streams and canopy gaps may be key criteria used by winter wrens to ensure they place themselves in high quality habitat for nesting or foraging (Fretwell and Lucas 1969, Cody 1981, Orians and Wittenberger 1991, Sodhi et al. 1999).

We used two approaches to study winter wrens. For one approach, we examined differences in habitat use by winter wrens observed in two seral stages. In 1996, we compared microhabitat used by winter wrens at singing locations between young structurally uniform forest (40-60 yr) and mature structurally heterogeneous forest (80-120 yr). We hypothesized that winter wrens should be positively associated with streams in both seral stages if characteristics unique to streams influence the spatial distribution of wrens. However, if streams only provide favorable habitats (e.g., structure) under particular conditions of disturbance history or stage of stand development, then the response of winter wrens to streams would likely differ between seral stages. We expected that the importance of riparian habitat for enhancing stand capability to support terrestrial wildlife such as the winter wren varies among stands, but is likely greater in structurally uniform forests. For our other approach, in the mature forest, we tested during 1995 and 1996 if winter wrens nested (nest substrates and nest sites) closer to small streams when available, and if the occurrence of nesting habitat is an important factor for selection of territories by males.

Study Area

Our study area was along south coastal British Columbia between Roberts Creek and Powell River (49°35'N, 123°38'W; elevation 350 to 550 m). Warm, relatively dry summers, and moist, mild winters, with little snowfall are typical in this region. The study area was mostly within the Coastal Western Hemlock Dry Maritime Subzone (CWHdm), although parts were transitional between the CWHdm and the Coastal Western Hemlock Submontane Very Wet Maritime variant (CWHvm1) (Meidinger and Pojar 1991, Green and Klinka 1994). The CWHdm is dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and lesser amounts of western redcedar (*Thuja plicata*). Douglas-fir is replaced by Pacific silver fir (*Abies amabilis*) in the transitional area. The forest understory is sparse and patchy, dominated by salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), and red huckleberry (*Vaccinium parvifolium*) or with Alaskan blueberry (*Vaccinium alaskaense*) in the transitional area. Streams in our study area were mostly ≤ 10 m-wide on gentle slopes (gradients < 11.5°). Generally, those with channels

5-10 m-wide had water throughout the breeding season, undercut banks along most of their length, gullied topography, and gaps in the overstory canopy along most of the stream course. Streams with channels < 5 m-wide were usually seasonal with sporadic undercut banks and few canopy gaps. Our definition of small streams included seeps with free surface water during the breeding season because sites with moist soils can also differ in stand structure, microclimate and associated plant and insect communities (Wesolowski 1983, Holmes and Robinson 1988, Tobalske et al. 1991, Sohdi et al. 1999). Over the past century, different forest harvesting regimes were used in our study area. The young forest stands regenerated after clearcut harvesting, whereas the mature forest stands originated after fire but had single tree selection harvesting for large diameter remnant redcedar. The study sites were on Crown Land (Timber Sale License area of the Small Business Forest Enterprise Program, British Columbia Ministry of Forests) and within Block 1 of Tree Farm License 39 of Weyerhaeuser Co. Ltd.

Methods

Winter Wren Sampling

We used two survey methods during the winter wren active breeding season from late April to early June, from sunrise to 4 hr after sunrise (Verner 1985). During 1996, in both young and mature forest, we used transects over the entire study area to locate singing winter wrens and their song perches (wren locations). In randomly selected stands from those accessible to us, we placed 500-m transects, a minimum of 400 m apart and parallel to the contours, to obtain a range of distances from streams \leq 10 m-wide. We conducted one survey along each transect and flagged all winter wren song perches that were detected within 150-m of either side of the line (our estimated maximum detection distance for winter wrens). If a singing wren moved from its song perch before we located the perch, we estimated its original location within 5 m. For each wren location, we randomly selected and flagged a location on the same transect within the 150-m boundaries. The sample of random locations provided an estimate of habitat available to winter wrens. Our methods did not account for possible non-breeding singing males or for individuals singing away from territories (Haila et al. 1989, Van Horne 1995).

During 1995 and 1996 in five study blocks of a south aspect, mature forest stand located at the Roberts Creek Study Forest, we mapped territories of winter wrens and identified their nest sites and nesting substrates. We randomly selected five streams, 5-10 m-wide, from those available in 1995 then we randomly located and centered on each a 12-ha (400-m-wide x 300-m-long) study block with a 25 x 25-m survey grid. Although centered on a stream 5-10 m-wide each study block included streams < 5 m-wide and seeps. This design facilitated examination of the spatial distribution of territories and nests in relation to streams 5-10 m-wide and < 5 m-wide. We included these < 5 m-wide streams because they are common in coastal forests and differ in structure compared to streams 5-10 m-wide. In 1996, we expanded the study blocks to 27-ha (600-m-wide x 450-m-long). We conducted 16-20 winter wren surveys each year in these study blocks recording all observations (visual, singing and counter-singing, mating displays, and nesting behaviors) (Verner 1985). Our mapping accuracy was improved by capturing (Falls 1981) and banding males in 1995 (24/35 territories) and 1996 (19/45 territories). We used two or three color-coded plastic bands in unique combinations and a numbered aluminum band provided by Environment Canada. During surveys, we located most nests through observations of displaying males or of birds carrying either nesting material or food (Martin and Geupel 1993). In addition, we located nests using searches focused in the vicinity of song perches in territories (Garson 1980). To minimize attracting predators to nests, we flagged 10 m from nests and measured habitat attributes after the young had fledged.

Habitat Measurements

We measured habitat attributes on transects at wren and random locations. Also, we measured habitat attributes at nests and in the five 27-ha study blocks at the 50 x 50-m points ($n = 315$; 65 per grid) on the 25 x 25-m survey grids. We measured slope and aspect at all sample locations. For wren and random locations, we used 0.20-ha slope-corrected circular plots and estimated percent overstory tree canopy cover (evergreen, deciduous, and combined) for dominant, codominant, intermediate, and total canopy classes. Using 0.01-ha slope-corrected circular plots, we estimated percent cover of herbs, ferns, shrubs

(individually and combined as total understory vegetation), moss, rock, exposed soil, and tree canopy (evergreen, deciduous, combined) in height strata (< 0.5 m, 0.5-2.0 m, ≥ 2.0 m, and total combined). At nests and 50 x 50-m survey grid points, we used slope-corrected nested circular plots. We measured understory vegetation for the stratum < 0.5 m-high in 0.002-ha plots and we used 0.01-ha plots for overstory canopy cover and understory vegetation in strata ≥ 0.5 m-high and total combined, and to count stems of trees and snags < 10 cm dbh. In addition to the above habitat attributes measured at wren and random locations, we estimated percent cover of deciduous and evergreen shrubs individually and combined, and we estimated percent ground cover (rock and duff). In 0.02-ha plots, we counted stems of trees and snags ≥ 10 cm dbh (Luttermerding et al. 1990) and numbers and types of upturned root masses as prime with loose soil and rootlets for nests or as other. We estimated percent cover of strata using the mean from two visual estimates of the vertical projection of the vegetation (Luttermerding et al. 1990).

To describe horizontal forest structure at all sample locations, we measured distance to the nearest stream (including noticeable seeps), the nearest upturned root mass, and mean distance to overstory canopy and understory canopy (≥ 0.5 m-high) trees and snags (Noon 1981, Morrison et al. 1992). Mean distance was calculated using a plotless method. Each location was divided into four 90° quadrants from a random orientation and the nearest distance to each of the attributes was measured in each quadrant. We used randomly placed line-intercept transects (Marshall et al. 2000) for estimating volume of downed wood by piece size diameter classes (2-6, 7-29, 30-49, 50-74, ≥ 75; and ≥ 50, ≥ 30, ≥ 7 cm) and decay/hardness classes (> 50% decay, blocky or soil wood; ≤ 50% decay hard, intact; and fresh). At wren and random locations, we used two 12.5-m line-intercept transects placed at a 90° angle for minimum effort. But we used three 12.5-m line-intercept transects placed in a randomly oriented spoke with 60° angles at the 50 x 50-m survey grid points and at the nest sites, also using these measures to estimate availability of nest structures. We calculated density of tree stems and snags per ha by diameter (< 10, 10-29, 30-49, 50-74, ≥ 75; and ≥ 50, ≥ 30, ≥ 10 cm dbh), canopy, and decay and hardness (hard outside or soft outside) classes.

Statistical Analyses of Song Perch Locations

We used an unbalanced, completely randomized, split-plot, factorial analysis of variance (Steel et al. 1997) (ANOVA) to determine whether winter wrens in young and mature forests placed their territories closer to streams than would be at random and to assess habitat selection at their song perches. We set our significance level at $P \leq 0.05$. We grouped transects within the same general area (usually a watershed) into blocks, and these blocks were nested within seral stage (10 blocks in young forest, 9 blocks in mature forest). The ANOVA determined which habitat attributes (response variables) had significant between group differences for a) the two seral stages (young and mature) and b) the two types of locations (wren and random). Seral stage was the whole-plot factor and location was the split-plot factor. The experimental units for the whole-plot factor were the blocks nested within seral stage. We eliminated habitat attributes that were infrequent across locations and one attribute for pairs of attributes that were highly correlated ($r \geq 0.70$) and had a similar ecological interpretation. A rank transformation was used on all habitat attributes to normalize the residuals. However, estimated least-square means and standard errors were calculated using the unranked data.

We used a logistic regression model to determine a resource selection function that identifies those habitat attributes that best convey the probability of a wren location in these forest stands (Brennan et al. 1984, Manly et al. 1993). The resource selection function $w(x_1, x_2, \dots, x_k)$ is directly proportional to the unknown resource selection probability function. It is estimated by modeling the conditional probability that an observation having a particular set of habitat attributes will be found at a wren location rather than at a random location, given that the observation is at one of the two locations (McCullagh and Nelder 1989, Manly et al. 1993). The habitat attributes used as covariates for the logistic regression model were those for which the ANOVA revealed significant differences in their amounts between wren and random locations. The logistic regression analysis proceeded in two steps. First, we used a mixed model logistic regression to determine whether seral stage had a significant effect on the conditional probability outlined above. The SAS macro GLIMMIX (Littell et al. 1996) was used to find

restricted (residual) pseudo likelihood (REPL) parameter estimates. The full model is:

$$\log \left(\frac{\tau_{ijk}}{1-\tau_{ijk}} \right) = \mu + s_i + a_{(ij)} + \beta_1 x_{1ijk} + \beta_2 x_{2ijk} + \dots + \beta_p x_{pijk} \quad [1]$$

where τ_{ijk} is the probability that an observation in a particular block and having a particular set of habitat attributes $\{x_1, x_2, \dots, x_p\}$ will be found in the wren location rather than the random location, given that it is one of these locations; μ is the overall intercept; s_i is the effect of seral stage ($i = 1, 2$); $a_{(ij)}$ is the random block effect $a_{(ij)} \sim N(0, \sigma_a^2)$ ($j = 1, 2, \dots, 19$), which is nested within seral stage; $\beta_1, \beta_2, \dots, \beta_p$ are the regression parameters, and the observations are indexed by $k = 1, 2, \dots, 148$. Following the non-significant effect of seral stage along with negligible block-to-block variability, we streamlined the model and incorporated all random and wren locations in a simple logistic regression. Non-significant habitat attributes were also dropped producing a simplified model with only $q \leq p$ regression parameters, where all parameters are defined as in Equation 1:

$$\log \left(\frac{\tau_k}{1-\tau_k} \right) = \mu + \beta_1 x_{1k} + \beta_2 x_{2k} + \dots + \beta_q x_{qk} \quad [2]$$

We will discuss [2] in the remainder of the paper, even though the actual resource selection function is of the form: $w(x_1, x_2, \dots, x_k) = \beta_1 x_{1k} + \beta_2 x_{2k} + \dots + \beta_q x_{qk}$.

Statistical Analyses of Nests and Nest Sites

We used log-likelihood Chi-square (G) tests and Bonferroni-adjusted Z-tests with 95% confidence intervals to test winter wren selectivity for nest substrates and nest substrate locations during 1995 and 1996 (Neu et al. 1974, Manly et al. 1993). We pooled nests from both breeding seasons because wrens reused nests between years. We pooled occupied and unoccupied nests because there were no identifiable criteria of unoccupied nests that distinguished them as dummy nests or as representing lower quality nest sites (Garson 1980, Wesolowski 1983). Males did not over-winter at the study area, therefore we reasoned the entire area was initially available each spring and we defined available habitat as the proportion of 50 x 50-m survey grid points ($n = 365$) within each category. If territoriality limits availability, we may have overestimated abundance of less common

attributes including stream channel and bank, upturned root masses, and remnant old cut stumps. To determine whether males selected for type of nest substrate, we used the following categories based on our field observations: logs; snags including nests behind bark, nests in a crevice, or nests in a remnant old cut stump; upturned root masses; stream banks; and branches on trees or snags. For testing whether nest locations selected by males were independent of distance to stream, we used five distance categories from streams and noticeable seeps (0-5, 6-10, 11-50, 51-100, 101-300 m). The 0-5-m category includes the influence of riparian channels on vegetation extended up to 5 m on each side of streams. The 6-10-m category is transitional between riparian and upslope areas. The 51-100-m category is differentiated from the 11-50-m and 101-300-m categories because 51 m is greater than the mean distance to water in the stand (50-m) and winter wrens were commonly observed to fly between locations up to 100 m apart.

For determining habitats selected by males at nests, we used Multivariate Analysis of Variance (MANOVA) (SAS Institute Inc. 1988; Tabachnick and Fidell 1989). We compared nest sites with non-nest sites within territories, defining non-nest sites as the closest (≥ 25 m) 50 x 50-m survey grid point within the territory that lacked nests. We randomly selected one nest in territories with multiple nests. For the analyses, we also needed to separate into different strata those nest sites in the channel and along the immediate edges of streams 5-10 m-wide (5-10-m channel) from the other nests beyond the 5-10-m channel (other). This ensured that the non-nest sites paired with nest sites of these larger channels had the same general characteristic forest structure and topography for measuring habitat selection within the territory. Therefore, we paired nest sites and non-nest sites by territory, year, and location (5-10-m channel, $n = 10$; other, $n = 37$). Habitat attributes within these pairs were used as the multivariate response because of the dependence between nest and non-nest sites occurring within the same territory in the same year. For the MANOVA, we tested for differences in amounts of habitat attributes between 5-10-m channel and other nest sites, and for differences between nest and non-nest sites. If an interaction for a particular attribute occurred between 5-10-m channel and other nest sites, then we tested for differences between nest

and non-nest sites within each of these categories separately, corrected for experiment-wise error. Residuals were examined for homogeneity of variance and normality. We reduced the number of habitat variables analyzed by eliminating one attribute of a pair of attributes that were highly correlated ($r \geq 0.70$) and had similar ecological interpretations.

Results

Song Perches

We identified 77 wren locations in 1996. Forty winter wrens were located along 9.12 km of transect in young forest compared to 37 along 9.30 km in mature forest. Fourteen percent (11 / 77) of the wren locations were estimated as within 5 m of the actual location and hence, for these we could not identify type of song perch structures. For the remaining 66 song perches, winter wrens used downed wood (9), upturned root masses (9), snags (30), and trees (18). We measured 75 random locations in young (37) and mature (38) forest.

Few of the habitat variables we sampled showed that the structure of the forest differed significantly between the two seral stages. Generally, young stands compared to mature stands had more closely spaced understory snags and root masses, less coverage of < 0.5 m-high vegetation, and a more prominent deciduous overstory component (Table 1). In contrast, wren locations compared to ran-

dom locations had overstory trees spaced farther apart and significantly less cover of vegetation < 0.5 m-high, including < 0.5 m-high shrub and moss (Table 1). From these findings, we infer that the lower strata likely had a combination of exposed mineral soil, rock, water, and downed wood. In both seral stages combined, we also observed that wren locations were significantly closer to streams than random locations although high variance was associated with this measure (Table 1). There was a significant interaction between seral stage and type of location for the total volume of downed wood ($P = 0.04$) suggesting its importance likely varied between seral stages. However, we did not detect any significant relationships between wren locations and volume of down wood for any piece size diameter class.

For the full mixed model logistic regression (Equation 1), we used mean distance to overstory tree (Over), cover of moss (Moss), cover of vegetation < 0.5 m-high (Veg), and distance to stream (Str). We eliminated shrub < 0.5 m-high because it is a component of vegetation < 0.5 m-high (Table 1). Seral stage did not have a significant effect in the model and it was eliminated from further analyses (Table 2). In the full model, both mean distance to overstory tree and cover of moss were significant at predicting the conditional probability that winter wrens would use a location in either seral stage (Table 2). The simple logistic regression best-fit model (Equation 2) also identified

TABLE 1. Results from split-plot ANOVA for differences between young ($n = 77$) and mature ($n = 75$) seral stages (main effect; $df = 1, 17$), and between wren ($n = 77$) and random ($n = 75$) locations (split-plot effect; $df = 1, 17$) using rank transformed habitat attributes for the ANOVA. Least-square means and standard errors were calculated using untransformed data.

Habitat attribute	Seral stage				Location type			
	Mean (SE)		Main effect		Mean (SE)		Split-plot effect	
	Young	Mature	F	P	Random	Wren	F	P
Distance to stream (m)	242 (87)	49 (91)	0.66	0.42	150 (64)	142 (64)	10.44	0.01
Mean distance to overstory tree (m)	3.6 (0.4)	4.8 (0.4)	3.82	0.06	3.9 (0.3)	4.5 (0.3)	11.77	<0.01
Mean distance to understory snag (m)	5.3 (0.8)	8.3 (0.8)	6.46	0.02	6.5 (0.6)	7.0 (0.6)	3.27	0.09
Distance to root mass (m) ¹	9.7 (1.4)	18.2 (1.4)	9.37	0.01	15.2 (1.4)	12.7 (1.4)	1.68	0.21
Deciduous overstory canopy cover (%)	21.8 (4.0)	3.3 (4.3)	25.77	<0.01	11.6 (3.4)	13.5 (3.4)	3.15	0.10
Vegetation cover < 0.5 m-high (%)	3.1 (0.9)	5.7 (0.9)	6.43	0.02	5.3 (0.8)	3.5 (0.8)	6.34	0.02
Shrub < 0.5 m-high cover (%)	3.1 (0.9)	5.0 (1.0)	3.86	0.07	4.8 (0.9)	3.2 (0.9)	4.29	0.05
Moss cover (%) ²	24.9 (7.0)	41.7 (7.4)	1.02	0.33	38.1 (5.4)	27.9 (5.5)	7.77	0.01

¹Sample size adjusted for 1 (distance to root mass) and 3 (moss cover) missing data points.

TABLE 2. Parameter estimates for the full model (Equation 1). Block-to-block variability is treated as a random factor. The intercept represents the mature seral stage and S represents the additional effect of the young seral stage over-and-above the mature seral stage. The estimate of the variance component is $\hat{\sigma}_b^2 = 0.000$.

Parameter ¹	Estimate	P
Intercept	-1.0851	0.12
Seral Stage	0.2679	0.54
Over	0.3706	0.01
Moss	-0.0100	0.05
Str	0.0001	0.86
Veg	-0.0400	0.26

¹Over = mean distance to overstory tree, Moss = cover of moss, Veg = cover of vegetation <0.5 m-high, and Str = distance to stream.

mean distance to overstory tree and cover of moss as the best predictors of male winter wrens using a location (Figures 1 and 2). The high Reduction of Deviance ($-2[\text{LogL}(\mu) - \text{LogL}(\mu, \beta_1, \beta_2)] = 13.958$, $P = 0.0009$) reflects the collective significance of these two factors. Both distance to stream and cover of vegetation < 0.5 m-high did not contribute significantly to the model. The non-significant Hosmer and Lemeshow Goodness of Fit statistic indicates closeness between predicted and observed probabilities, and suggests the model is a good fit. The logistic regression model shows that the greater the mean distance to overstory tree the higher the probability that winter wrens will use a location, with a maximum at ~15 m

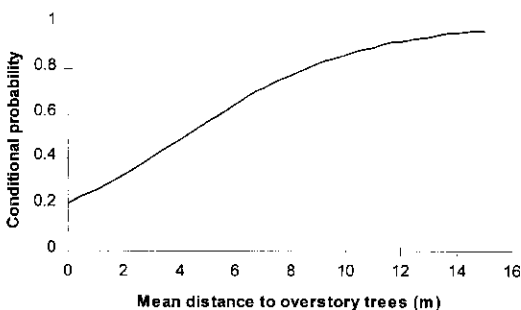


Figure 1. Predicted conditional probability (Equation 2) of a winter wren occupying a location: $\tau_k = e^{0.784 + 0.319 \cdot \text{over}_k + 0.017 \cdot \text{moss}_k} / (1 + e^{0.784 + 0.319 \cdot \text{over}_k + 0.017 \cdot \text{moss}_k})$ as mean distance to nearest overstory tree (over_k) changes from 0 to 15 m while moss coverage (moss_k) is held at its estimated mean (32%).

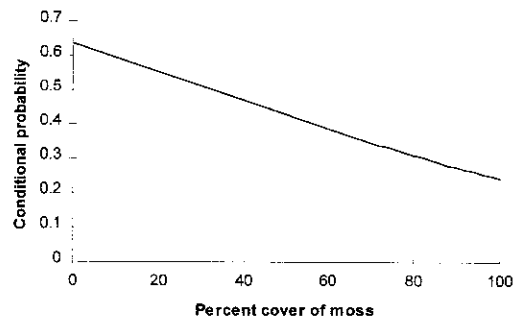


Figure 2. Predicted conditional probability (Equation 2) of a winter wren occupying a location: $\tau_k = e^{-0.784 + 0.319 \cdot \text{over}_k - 0.017 \cdot \text{moss}_k} / (1 + e^{-0.784 + 0.319 \cdot \text{over}_k - 0.017 \cdot \text{moss}_k})$ as cover of moss (moss_k) changes from 0 to 100% while mean distance to overstory tree (over_k) is held at its estimated mean (4.2 m).

(Figure 1). The negative relationship between wren locations and cover of moss has a smaller range of probability estimates for predicting a winter wren location (Figure 2). Wrens are more likely to occur in sites without moss.

Nests and Nest Sites

We found 99 nests during 1995 and 1996 of which 95 were associated with territories. Territories ranged in size from 0.37 to 2.38 ha. Some territories had multiple nests (22% in 1995 and 53% in 1996), some territories had single nests (35% in 1995, 47% in 1996) and in other territories, we were unable to find any nests (43% in 1995). Nests occurred at a range of heights in the understory of the forest (35 cm to 285 cm; mean heights 70 cm in stream banks to 190 cm on branches). Male winter wrens showed selectivity for type of nest substrate ($G = 124.9$, $P < 0.01$). Uprturned root masses and stream banks were used more than expected, logs and snags (bark, crevice, and stump) were all used in proportion to their availability, but branch substrates were used less than expected (Figure 3).

Males showed selectivity for streams ≤ 10 m-wide when building their nests ($G = 30.2$, $P < 0.01$; Figure 4), although streams < 5 m-wide tended to become dry by late May to early June. All nests in stream banks (12) and in upturned root masses (20) were ≤ 5 m from streams. Nests in other substrates occurred over a range of distances, but 52% were also ≤ 5 m from a stream (15 of 38 log nests, 16 of 23 snag nests including

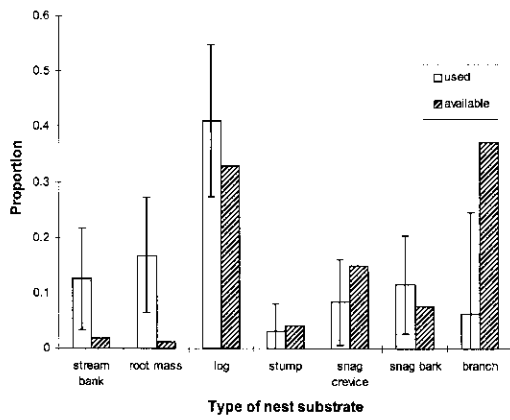


Figure 3. Proportions of substrates in which male winter wrens built nests compared to proportions of substrates available in the Roberts Creek Study Forest with 95% confidence intervals (Bonferroni-adjusted Z-tests, $K = 7$).

stumps, and 4 of 6 branch nests). Nests occurred in proportion to habitat availability in the 6-10-m and 51-100-m distance categories from streams. Fewer nests than expected were located in the 11-50-m category. Although some nests were > 100 m from a stream, few winter wrens tended to use these locations.

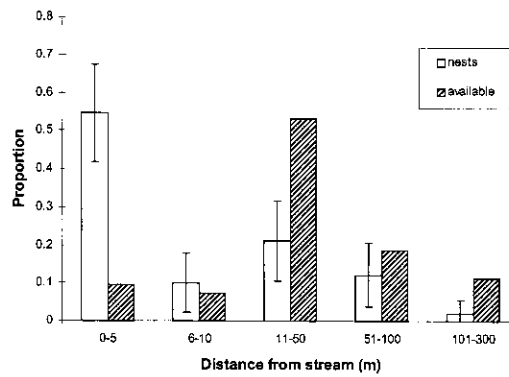


Figure 4. Proportions of winter wren nests and availability of habitat at different distances from streams in the Roberts Creek Study Forest with 95% confidence intervals (Bonferroni-adjusted Z-tests, $K = 5$).

Some habitat attributes differed between nest and non-nest sites, but these differences were not consistent for the 5-10-m channel nest sites and the other nest sites beyond the 5-10-m channels (Table 3). Compared to non-nest sites, nest sites beyond the 5-10-m channels had significantly fewer live stems (≥ 50 , 30-49, and ≥ 10 cm dbh classes), live stems and snags combined (30-49 cm dbh

TABLE 3. Mean habitat attributes at nest sites and paired non-nest sites (multivariate response) by habitat type (channel, i.e., 5-10-m and other, i.e., away from 5-10-m channels). Significant ($P \leq 0.05$) values from the MANOVA are presented separately by habitat type if an interaction was detected or pooled over habitat types if no interaction was detected.

Habitat attribute	Habitat type	Nest site		Non-nest site		MANOVA		
		Mean	SE	Mean	SE	df (n, d)	F	P
Downed wood 30 - 49 cm (m^3/ha)	Channel	140.6	28.4	77.6	18.8	1,9	4.45	0.06
	Other	94.7	13.0	127.1	11.9	1,36	4.50	0.04
Live stems 30 - 49 cm dbh (stems/ha)	Channel	115	20	85	22	1,9	0.89	0.37
	Other	99	11	232	27	1,36	24.96	<0.01
Live stems and snags 30 - 49 cm dbh (stems/ha)	Channel	145	25	110	27	1,9	1.15	0.31
	Other	137	14	257	27	1,36	27.63	<0.01
Live stems ≥ 50 cm dbh (stems/ha)	Channel	95	23	85	22	1,9	0.13	0.73
	Other	107	12	184	22	1,36	12.49	<0.01
Live stems ≥ 10 cm dbh (stems/ha)	Channel	400	47	325	62	1,9	0.871	0.36
	Other	481	40	727	40	1,36	27.91	<0.01
Live stems < 10 cm dbh (stems/ha)	Pooled	313	33	923	203	1,46	8.62	0.01
Live stems and snags < 10 cm dbh (stems/ha)	Pooled	505	51	1127	204	1,46	8.40	0.01
Live stems and snags ≥ 75 cm dbh (stems/ha)	Pooled	31	5	72	17	1,46	6.04	0.02
Live stems and snags ≥ 50 cm dbh (stems/ha)	Pooled	137	11	204	20	1,46	12.35	<0.01
Distance to upturned root mass (m)	Pooled	9.0	1.4	12.8	1.3	1,45	3.93	0.05
Deciduous shrub cover (%)	Pooled	5.4	1.0	3.4	0.6	1,46	5.02	0.03
Ground cover (%)	Pooled	82.0	2.2	88.5	1.0	1,46	7.55	0.01

class), and volumes of medium sized downed wood in the 30-49 cm diameter piece size class. Yet these densities of live stems and snags at the nest sites beyond 5-10-m channels were similar to those measured at both nest and non-nest sites in 5-10-m channel areas (Table 3). Seven additional habitat attributes also indicated differences between nest and non-nest sites using the pooled nest sites (Table 3). Nest sites compared to non-nest sites had fewer live stems (< 10 cm dbh class), live stems and snags combined (≥ 75 , ≥ 50 , < 10 cm dbh classes), and less exposed ground of duff and rock. Cover of deciduous shrubs was greater and root masses were closer to the nest substrate.

Discussion

Habitat Values of Small Streams

In both young and mature stands, the locations of song perches, thus territories of winter wrens were associated with streams (Table 1). Furthermore, the overall lack of interactions between seral stage and type of location indicated that winter wrens, independent of stand age and stage of seral development, selected a suite of habitat attributes to provide optimal habitat (Table 1). Winter wrens did not appear to use habitat differently as the forest developed from young to mature, and this finding further supports that age alone can be a poor criterion for managing habitats for wildlife (Rotenberry and Wiens 1980, Hayes et al. 1997, Waldien et al. 2000). Instead, occurrence and distribution of structural attributes and small streams with their unique characteristics, such as channel morphology (stream banks), influenced the spatial distribution of winter wrens in both seral stages of coastal temperate forests.

The heterogeneous forest structure associated with streams was important for providing winter wrens with nesting opportunities. Nests were located closer to streams relative to their availability (Figure 4) and wrens chose types of nest substrates (Figure 3) associated with small streams. Yet, wrens selected similar nest sites whether adjacent to streams 5-10 m-wide that had structurally distinct riparian areas including banks, overstory gap and vegetation or whether in other areas away from these 5-10-m channels (Table 3). However, fewer differences were apparent between the forest structure of nest and non-nest sites near streams 5-10 m-wide, than elsewhere

(Table 3). A male may build several nests in his territory, but fewer nests may be built in less favorable habitat (Armstrong 1956, Armstrong and Whitehouse 1977). Thus, when establishing their territories males may select for streams to obtain more nesting opportunities. In turn, the structure contributed by vegetation and terrain characteristics of streams 5-10 m-wide may offer more potential opportunities for wrens than do streams < 5 m-wide (Table 3). Other than nesting opportunities, factors that likely contribute to habitat selection of winter wrens are higher forage quality (Armstrong 1956, McLachlin 1983, Holmes and Robinson 1988, Van Horne and Bader 1990) and thermoregulation (Armstrong and Whitehouse 1977), and we hypothesize that riparian habitats may positively influence these factors (Waterhouse 1998).

Gaps in Upslope Habitats

Although winter wrens selected for song perches and nests nearer to streams when available, they also used habitats upslope of streams (Table 1, Figure 4). For example, stream location was not selected as a significant predictor of song perch location in the logistic regressions (Table 2). Thus, winter wrens use a range of habitat conditions for nesting and singing. The similarity between nest and song perch microhabitat patches is expected because males often use the nest substrate as a song perch when they are advertising the nest (Garson 1980).

Nests within territories, and song perches within the surrounding young and mature forest were at relatively open sites in the forest understory (Tables 1, 3). Our logistic regression model suggests winter wrens are more likely to sing in open sites because it was more probable that wrens would occur in locations with a 10-15 m mean distance to an overstory tree. In either the young or mature forest, this mean distance suggests a gap in the overstory canopy. However, our percent estimates of overstory canopy cover were not significantly lower at wren locations or nest sites compared to the surrounding forest. Therefore understory conditions associated with gaps may be more important for winter wrens because lateral branch growth diminishes the size of the overstory gap. The lack of moss cover and the significant association of upturned root masses with wren locations and nest sites confirm that wrens select disturbed sites.

Disturbed sites had stream banks or residual developmental gapmakers including snags, root masses, and downed wood available for nest substrates (Figure 4). During the breeding season in 1996, we observed that water collected in pits from uprooted trees turning these disturbed sites into locally wet sites. This process creates distinct microclimates (Beatty and Stone 1986, Schaetzl et al. 1989) and likely provides fine-scaled sites for foraging and nesting. The winter wren in other regions is associated with areas of localized disturbance that have canopy openings, downed wood, upturned roots, and with dense understory vegetation (Wesolowski 1983, Holmes and Robinson 1988, Carey et al. 1991, Tobalske et al. 1991). Thus, nest substrates and nest sites selected by winter wrens are often created through processes of succession and natural disturbance (Spies et al. 1990, Lertzman et al. 1996) and are linked directly to gaps. The structure and microclimate of developmental gaps provide alternate nesting and foraging habitats in upslope areas and further enhance the value of streamside habitats for winter wrens.

Although our research is limited to the winter wren, it is likely that other wildlife in the drier Coastal Western Hemlock Dry Maritime Subzone (CWHdm) benefit from the distinct habitat qualities of small streams including channel morphology, forest structure and microclimate that are associated with winter wrens. Reserve areas or aggregates of forest structure retained adjacent to small streams or seeps can be used to manage for streamside habitats. Some management options available in British Columbia for retaining forest structure and associated wildlife habitat within stands include retention of small patches of trees (wildlife tree patches) and riparian management areas that are established adjacent to streams (B.C. Ministry of Forests and B.C. Ministry of Envi-

ronment 1995, 1999). The area within 5 m of small stream banks was most important for nest sites of winter wrens, however, they also use areas beyond this narrow band next to stream banks. Hagar (1999) reported for the central Oregon Coast Range, that along first- to third-order streams, winter wrens in mature Douglas-fir/western hemlock riparian forest buffers >30 m wide approached minimum abundances comparable to those in unlogged forest.

Our research also exposes the value of canopy gaps and gapmakers as habitat sources in both riparian and upslope areas. Alternative silviculture systems can be used to retain or recruit structural features that mimic gapmakers (e.g., snags, logs, and uprooted trees). Removing small groups of trees (group selection) is one alternative for mimicking canopy gaps (Lertzman et al. 1996, Franklin et al. 1997). But prescriptions mimicking canopy gaps need to consider retention of structural features within the harvested area to also mimic the gapmakers. This retention is particularly important when group selection is cycled throughout the entire forest matrix and when the desired structural features have developmental periods longer than the rotation or are required in large numbers for biodiversity objectives (Franklin et al. 1997).

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