Chapter 17

Inland Habitat Associations of Marbled Murrelets in Western Washington

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Abstract: Little research has been done to quantify and describe the structural characteristics of forest stands that are associated with Marbled Murrelet (*Brachyramphus marmoratus*) nesting in the Pacific Northwest. Vegetation measurements and murrelet surveys to determine occupancy were conducted in stands located throughout western Washington. I used logistic regression to contrast stand attributes between occupied (n = 64) and unoccupied (n = 87) stands. The probability of occupancy of an old-growth stand increased with increasing total number of potential nest platforms, percent moss coverage on the limbs of dominant trees (≥81 cm d.b.h.), percent slope, the stem density of dominant trees, and the mean d.b.h. of western hemlock. The probability of occupancy of a stand decreased as lichen coverage on the limbs of dominant trees, stand elevation, and canopy closure increased. Mean detection rates and the percent of stands surveyed and verified as occupied declined sharply with an increase in elevation over 1,067 m, and for stands >63 km from salt water. The relationship of the number of potential nest platforms and elevation to the probability of occupancy was best explained by comparing the structural characteristics of old-growth trees for the five conifer species available for nesting. Land management activities that reduce or affect the number of potential nest platforms/ha, composition of low elevation conifers, moss cover on tree limbs, stem density of dominant trees (≥81 cm d.b.h.), or canopy closure, would reduce the quality of a site as nesting habitat for murrelets. Reproductive success should be used as a measure of habitat suitability in future studies by intensively studying occupied stands that have high detection rates of Marbled Murrelets and locating a sample of active nests to observe.

The research attempts to quantify and describe the structural characteristics associated with Marbled Murrelet (*Brachyramphus marmoratus*) nesting habitat have examined the general relationship between murrelet abundance and stand age, stand size, and tree size. A more specific model describing habitat is needed for a variety of reasons. A model would help (1) assess the relative impacts that forest management practices and associated activities will have on the quality of murrelet nesting habitat, (2) evaluate the relative suitability of a forest stand as nesting habitat for murrelets, (3) more accurately map suitable habitat, (4) understand how to speed the development of suitable habitat to meet long-term objectives for maintaining or increasing murrelet populations, (5) attempt to fashion habitat enhancement techniques or mitigation measures, and (6) plan future habitat research studies.

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Studies specifically addressing the forest habitat associations of Marbled Murrelets in Washington were initiated in 1990 and continued through 1993. A 1990 study examined the association of murrelets to four broad habitat categories and recorded the distribution and abundance of murrelets within an entire drainage basin, beginning at the Cascade crest and ending at its terminus with the Puget Sound (Hamer and Cummins 1990). An analysis of murrelet detection rates relative to the percent of old-growth forest available on the landscape was also conducted in this study. Studies from 1991 to 1993 focused on describing and analyzing the structural differences between old-growth stands occupied by murrelets and unoccupied old-growth stands. The results of these structural analysis are presented in this paper. In addition, a landscape analysis examining the attributes associated with stands occupied by Marbled Murrelets was completed in Washington in 1994 (Raphael and others, this volume).

Methods

Landscape Characteristics

Detection Rate Comparisons

For the comparison of Marbled Murrelet detection (murrelet detections/survey morning) and occupancy rates (number of stands surveyed and verified as occupied/number of stands surveyed) with respect to elevation, inland distance, and physiographic province, 262 old-growth stands were used. To investigate the effect of elevation on murrelet detection and occupancy rates, the mean detection rate and the percent of old-growth stands found occupied by murrelets were averaged for each 150-m interval in elevation ranging from 0 to 1,500 m. To determine the effect of inland distance on habitat use by murrelets, the mean detection rate and percent of old-growth stands verified as occupied were averaged for inland distances using 15-km intervals ranging from 0 to 95 km. The mean detection rate and the percent of stands surveyed and verified as occupied were also used as measures of the use of a region by murrelets. The physiographic provinces we used for data comparisons are those described by Franklin and Dyrness (1973). Of the 262 old-growth stands in this analysis, 132 stands occurred in the North Cascades Province, 32 in the South Cascades, 80 on the Olympic Peninsula, 8 in the Coast Range (southwest Washington), and 10 stands in the Puget Trough Province.

Inland surveys for Marbled Murrelets were conducted using standardized survey techniques developed by the Pacific Seabird Group Marbled Murrelet Technical Committee (Ralph and others 1994). Single observers visited each stand three or more times during the breeding season (1 May–5 August) recording observations during a 2-hour dawn survey period each visit. Mean detection rates for each stand were calculated by dividing the total number of detections by the number of survey visits. To standardize this calculation, stands with <3 visits were not used in the analysis. These stands would not have had enough survey effort to determine occupancy with sufficient likelihood. For sites with >4 visits, survey visits were removed by selecting those four visits that best represented the seasonal timing of surveys recommended by the Pacific Seabird Group survey protocol. This helped standardize the selection of surveys in order to equalize the survey effort between stands. Therefore, survey effort was standardized by using only three or four visits for each stand used in the analysis.

Occupied sites were defined as those stands with birds observed flying through the canopy, in or out of the canopy, birds observed landing or perched in trees, or stands with murrelets observed circling over the canopy (Ralph and others 1994). Occupied sites also included stands where nest platforms, murrelet egg shells, or juveniles had been found. Unoccupied sites included stands with birds present, but where no occupied or below canopy behaviors were observed, and stands where birds were not detected.

Stand Characteristics

Old-growth stands were included in the study if they met the definition of old-growth developed by the Washington Department of Wildlife Remote Sensing Program. Old-growth stands were defined as having at least 20 dominant overstory trees per hectare that were ≥81 cm diameter at breast height (d.b.h.). Co-dominant trees were ≥40 cm d.b.h. The presence of at least 2 canopy layers was also required.

Vegetation Quantification

A total of 38 attributes describing forest characteristics were used in the analysis (*table 1*). Observers were trained during a 3-day period to ensure forest variable measurements and estimates were performed consistently by all crew members. Vegetation data was not obtained from all the stands that were surveyed, therefore the sample size for the vegetation analysis was less than the number of stands used in the comparisons of mean detection and occupancy rates. Vegetation measurements were obtained from 64 occupied and 87 unoccupied old-growth stands located throughout western Washington for a total sample size of 151 stands.

The sample size of stands where vegetation data was collected was variable in each physiographic province (*table 2*). Old-growth stands in the North Cascades and Puget Trough Physiographic Provinces were selected systematically to represent a range of elevations, forest zones, and geographic areas. One to several stands were selected from each drainage depending on drainage size and access. Old-growth stands in the Olympic, South Cascades, and Coast Range Physiographic Provinces were selected in a opportunistic manner, primarily from a need to conduct surveys for Marbled Murrelets in certain stands because of impending forest harvest plans or other land management projects. The North Cascades and Olympic Peninsula physiographic provinces contained the largest proportion of sites because these provinces were areas where research had been conducted earlier and more intensively.

Because murrelet detection rates were found to decline with increasing inland distance, not all stands that were surveyed were used in the statistical analysis. Some stands may have possessed all the appropriate structural features required to produce suitable nesting habitat, but were unoccupied because the inland distance was too great. To avoid misinterpreting study results, only stands ≤61 km from salt water were used in the vegetation analysis. I arrived at this value by examining the relationship between murrelet abundance and the inland distance of stands.

Sites <0.8 km from salt water were not used in any analysis. Over the last three years a total of nine unoccupied sites have been located in Washington <0.8 km from salt water, with what appears to be excellent murrelet nesting habitat. This included five sites from southwest Washington and the Puget Trough, and four sites from the San Juan Islands. Murrelets may avoid using these stands because of their exposure to wind and coastal storms, or because of the presence of a higher number of predators such as gulls (*Larus* spp.), and crows and ravens (*Corvus* spp.).

Survey stations were located in or adjacent to old-growth stands with a minimum stand size of 50 ha. This is an area encompassed by a circle with a 0.4 km radius and was therefore the sampling unit used for the study. From field experience I felt that this would be the approximate area an observer could detect murrelets on the landscape, and also prevented the surveying of small old-growth stands in heavily fragmented areas. These smaller stands may have a lower abundance of murrelets because they lack a sufficient amount of habitat, rather than a deficiency in any particular structural feature of the forest. Stand size was not included as a variable in the study design. This was due to the large number of observation stations per stand needed to successfully measure this effect, and the large sample of stands required for the statistical design. Although the influence of stand size on murrelet abundance is a vital piece of information required by land managers, more extensive research will be needed to evaluate this variable. The mean stand size or age of the stands sampled was not determined.

The forest vegetation was measured using one 25-m radius plot for each old-growth stand being surveyed. The exact location of the plot was chosen by placing it in an area where flight behaviors below the canopy indicated possible nesting or, in other stands, in an area with the highest murrelet activity. For stands with no activity, the plot was located in an area with the highest stem density and largest basal area of old-growth trees. Therefore, even in areas with no activity, the highest quality old-growth available was selected to represent the stand thus establishing a conservative analysis.

Table 1—Definitions and units of measurement for each habitat variable used in the statistical comparison of occupied versus unoccupied murrelet stands in western Washington, 1991-92. A dominant tree was ≥81 cm diameter at breast height (d.b.h.)

Variable	Definition and units of measurement
Aspect	Major aspect of the plot in degrees
Basal area	Basal area (m^2) of all dominant trees (≥81 cm d.b.h.) in a 25-m radius plot
Canopy closure	Percentage of plot occupied by the crowns of live trees over 10 m in height
Canopy height	Mean tree height (m) of 10 trees measured per plot
High comp.	Percent composition of silver fir and mountain hemlock
Low comp.	Percent composition of Douglas-fir, western hemlock, western red cedar and Sitka spruce
Nest comp.	Percent composition of those tree species selected for nesting by murrelets in Washington and Oregon including Sitka spruce, Douglas-fir, and western hemlock
Silver fir comp.	Percent composition of silver fir
Sitka spruce comp.	Percent composition of Sitka spruce
Douglas-fir comp.	Percent composition of Douglas-fir
Western red cedar comp.	Percent composition of western red cedar
Western hemlock comp.	Percent composition of western hemlock
High d.b.h.	Mean d.b.h. (cm) of silver fir and mountain hemlock
Low d.b.h.	Mean d.b.h. (cm) of of Douglas-fir, western hemlock, western red cedar and Sitka spruce
Mean d.b.h.	Mean d.b.h. (cm) of all dominant trees measured per plot
Nest d.b.h.	Mean d.b.h. (cm) of tree species selected for nesting by murrelets in Washington and Oregon
Silver fir d.b.h.	Mean d.b.h. (cm) of silver fir
Sitka spruce d.b.h.	Mean d.b.h. (cm) of Sitka spruce
Douglas-fir d.b.h.	Mean d.b.h. (cm) of Douglas-fir
Western red cedar d.b.h.	Mean d.b.h. (cm) of western red cedar
Western hemlock d.b.h.	Mean d.b.h. (cm) of western hemlock
Mountain hemlock d.b.h.	Mean d.b.h. (cm) of mountain hemlock
Distance to saltwater	Closest distance (km) from the plot to salt water
Ecozone	Geographical areas of similar environments (Henderson and others 1989, 1991)
Elevation	Plot elevation (m).
Forest zone	A classification method for determining plant association based on vegetation series of tree species present (Henderson and others 1989, 1991)
Latitude	Latitude of the plot to the nearest minute
Mean lichen	The mean amount of lichen per plot based on an index of lichen coverage on the limbs of all dominant trees
Mean mistletoe	The mean amount of mistletoe per plot based on an index of mistletoe abundance (Hawksworth 1977)
Mistletoe number	The total number of trees/hectare infected with mistletoe
Mean moss	An index of moss coverage on the platforms of all dominant trees
Percent moss	The percent moss coverage on the limbs of all dominant trees in a plot
Platforms/ha	The total number of potential nest platforms/ha over 15 m in height and 18 cm in diameter
Platform total	The total number of platforms from all dominant trees measured within and outside the plot
Platforms/tree	Mean number of potential nest platforms per tree
Percent slope	Percent slope of plot
Slope position	Position of stand on slope: (1) lower 1/3; (2) middle 1/3; and (3) upper 1/3
Stem density	The number of dominant trees/hectare

Table 2—Sample size of stands used in the stepwise logistic regression analysis, listed by physiographic province and stand status.

Physiographic province	Number of sites	Stand status codes[1] 0	1	2	3	4	5	Total occupied	Total unoccupied
North Cascades	84	20	1	3	16	28	16	40	44
South Cascades	17	1	0	0	1	6	9	2	15
Olympic Mountains	45	3	1	1	13	20	7	18	27
Southwest Coast	5	0	0	1	3	0	1	4	1
Puget Trough	0	0	0	0	0	0	0	0	0
Total	151	24	2	5	33	54	33	64	87

[1] Stand status codes were: 0 = Marbled Murrelets observed circling the stand; 1 = nest platform was located; 2 = juveniles, eggs, or eggshell fragments were located; 3 = murrelets were observed flying in the canopy; 4 = murrelets were detected in the area; and 5 = no murrelets were detected. Occupied stands included status codes 0-3

Only dominant trees ≥ 81 cm in diameter were included in all vegetation measurements except for canopy closure and forest vegetation series. In addition, only conifer trees were included in the measurement for each variable, except canopy closure. To ensure that a large sample of tree measurements for each variable were recorded from each site, at least 20 trees were measured at each plot. If 20 trees were not available within the plot, the nearest dominant trees to plot edge were selected to be measured until 20 trees were recorded. Trees selected outside the plot were included in the calculations for mean tree d.b.h., total number of potential nest platforms, potential nest platforms/tree, lichen coverage, dwarf mistletoe (*Arceuthobium* spp.) infestation, moss (*Isothecium* spp.) coverage on potential nest platforms, and all tree species composition variables. Trees within the plot were used to calculate basal area, forest zone, vegetation series, canopy closure, mean canopy height, and all other measurements.

Ecozones, geographical areas of roughly similar environments, were delimited on the basis of the abundance and distribution of plant indicator species and are a general measure of the amount and kind of precipitation an area received. Ecozones were mapped in Washington by the USDA Forest Service (Henderson and others 1989, 1991). Ecozone 0 represented the wettest part of the study area (457 cm or more of annual precipitation), whereas ecozone 13 was the driest (less than 203 cm). Each plot was given an ecozone classification based on its location. The vegetation series and forest zone were identified for each plot using standard protocol and field guides (Henderson and others 1989, 1991). The latitude and distance to nearest salt water for each site was measured using topographic maps with a scale of 1:250,000. Latitude was measured to the nearest minute and distance to salt water to the nearest 0.4 km.

The number of potential nest platforms (platform total) for each tree was estimated from one point near the tree where the maximum number of limbs could be seen. The observer counted the number of limbs or structures >15 m in height and >18 cm in diameter directly along the tree bole. All structures were counted; the observers did not make judgments as to the suitability of the platforms for nesting. These measurements were chosen because all of the 18 nests found at the time the index was developed were >27 m in height with the majority of nest limbs >20 cm in diameter. Therefore, limbs >18 cm seemed a reasonable threshold to use for the index. To practice estimating whether tree limbs were >18 cm, limbs of known diameters were observed from a 30-m distance. A total count of all potential nest platforms in a tree was not possible, so this measurement was treated as an index. Mistletoe blooms located away from the tree bole were not counted as platforms, since their abundance was measured using another index. Mistletoe infestation was rated for each tree following an index developed by Hawksworth (1977). The number of trees infected with mistletoe (mistletoe number) were summed for each plot.

The percent cover of all epiphytes (moss and lichens separately) on the surface of the limbs of dominant trees was recorded for each tree by estimating the average cover for all limbs using five categories, including 0–20 percent, 21–40 percent, 41–60 percent, 61–80 percent, and 81–100 percent cover. Each tree was placed in a category and an average calculated for all trees in the plot for both lichen and moss coverage. Moss cover (mean moss) was estimated for potential nest platforms only. Lichen cover (mean lichen) on the surface of the limbs of dominant trees was estimated by averaging all the limbs of the tree. The average percent moss coverage (percent moss) on all the limbs of dominant trees in the plot were also estimated to the nearest 5 percent, as an additional measure of moss abundance.

Canopy closure was measured in a smaller 17.8-m plot by physically measuring all gaps in the canopy >4 m^2 in size.

This was accomplished by estimating the distance between gap edges as if the canopy created vertical shadows on the ground. Trees <9 m tall were not considered a part of the canopy. Mean canopy height was calculated from 10 dominant trees in the plot using a clinometer.

The percent composition and mean values for mean d.b.h., height, basal area, number of potential nest platforms, moss cover, lichen cover, and mistletoe abundance were calculated for each tree species present on each plot.

Statistical Model

Stepwise logistic regression was used to compare the structural characteristics of occupied and unoccupied old-growth stands in Washington. A predictive model for the binary dependent variable, defined as occupied and unoccupied stands, was developed to help define those forest characteristics associated with murrelet nesting habitat.

Logistic regression methods (SAS Institute, Inc. 1987) were used to develop a model for the binary dependent variable which was defined as occupied and unoccupied stands (Hosmer and Lemeshow 1989). Candidate independent variables were selected for inclusion in the model using the stepwise selection procedure. The *P*-value chosen for allowing a candidate variable to enter the model was 0.05. This value was also used as the criteria for retaining an independent variable in the model at the conclusion of each step.

For the statistical analysis, all 38 forest variables were treated as continuous variables except for forest zone. Forest zone was divided into two categories, high-elevation, and low-elevation zones. High-elevation zone included stands located in silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) zones. Low-elevation zone included stands located in the western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis*) zones. In addition, the variable ecozone was analyzed as a separate logistic stepwise model, because at a few sites the ecozone value could not be determined.

Principal Components Analysis (PCA) (SAS Institute, Inc. 1987) was used to create a correlation matrix of all variables and to consider more complex interdependencies among the independent variables. The correlation matrix was used to gauge the degree of association and interdependence between pairs of variables. This helped determine if one variable could be used in the logistic regression model as a substitute for another highly correlated variable. The PCA was not definitive in identifying higher order dependencies in these data.

Importance of Independent Variables

Four methods were used to subjectively evaluate the relative importance of each variable to the model's ability to predict occupancy and the importance of each variable in describing the differences between occupied and unoccupied sites. The first method was to examine the initial chi-square values of each variable before they entered the model. The second technique involved examining the step in which a variable was selected by the model. Variables selected earlier in the stepwise selection procedure had more power in explaining the variation between occupied and unoccupied sites than variables selected later in the procedure or variables not selected at all. The third method involved examining the final chi-square values for each variable used in the model. The last technique examined the stability of a variable as the stepwise selection procedure of the model progressed. Unstable variables experienced large fluctuations in chi-square value as each new variable was selected in the stepwise procedure, because of high colinearity with other variables used in the model.

Tree Characteristics

The mean structural characteristics of old-growth trees for the six conifer tree species available for nesting by Marbled Murrelets in Washington were calculated by pooling the values for each variable measured for each tree species across all plots. These variables included mean d.b.h., mean tree height, basal area, potential nest platforms/tree, percent moss coverage on limbs, percent lichen cover on limbs, and mistletoe abundance. This analysis was used to subjectively compare the structure and suitability of tree species in providing murrelet nesting habitat.

Results

Landscape Characteristics

Distance to Salt Water

Highest detection rates (5.9–9.5 detections/survey morning) in Washington occurred in intervals between 16 km and 64 km inland, but declined to 0.85 detections/ morning at distances >63 km from salt water (*fig. 1*). To date, 98.5 percent of all detections have been recorded <64 km inland, but this is partly due to the extensive survey effort that has occurred in this zone. The maximum distance at which birds were detected inland was at an occupied stand 84.1 km from salt water, located on Irene Creek near the Cascade River Drainage in 1992 and 1993. The next farthest occupied stands were located 72 km and 74 km inland. Of the known occupied stands, 36 percent (n = 31) were located more than 47 km from the ocean. Nests were located an average of 16 km inland, with a maximum distance of 34 km (n = 6). Of the old-growth stands located between 0 and 63 km inland, 20–54 percent were occupied (*fig. 1*). The percentage of occupied stands declined sharply after 63 km, with only 13 percent of stands occupied >63 km from the ocean.

Elevation

In Washington, detection rates declined sharply with an increase in elevation over 1,067 m (*fig. 2*). The highest detection rates, which ranged from 4.3 to 9.2 detections/ survey morning, were recorded between sea level and 1,067 m. Stands located above 1,067 m had mean detection rates

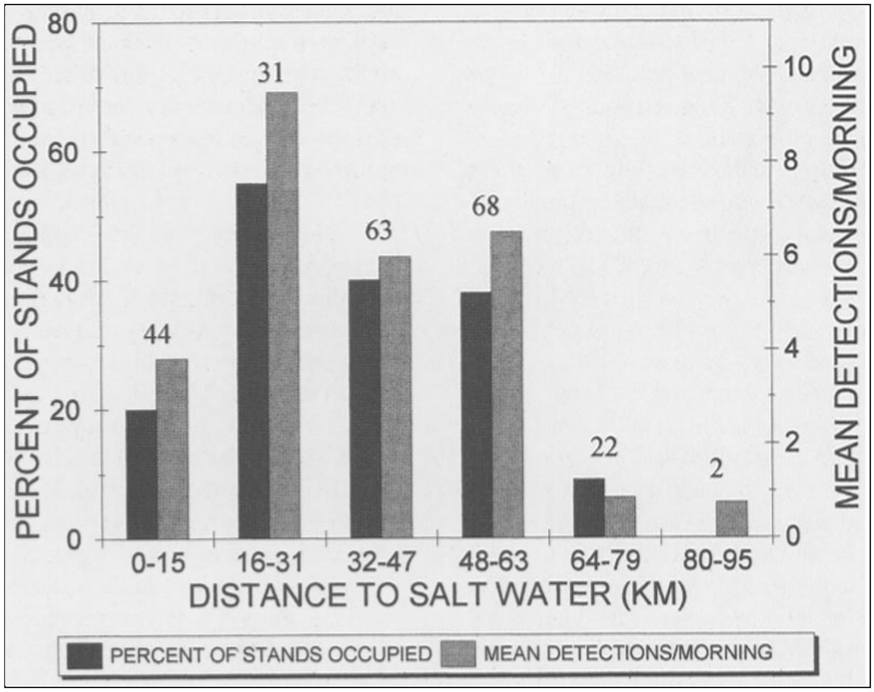

Figure 1—The percent of stands surveyed and verified as occupied, and the mean number of murrelets detected/survey morning, in relation to the distance of the stand from salt water. The sample of stands is from all the physiographic provinces in western Washington, 1991–93. Mean detection rates corresponded closely to occupancy trends.

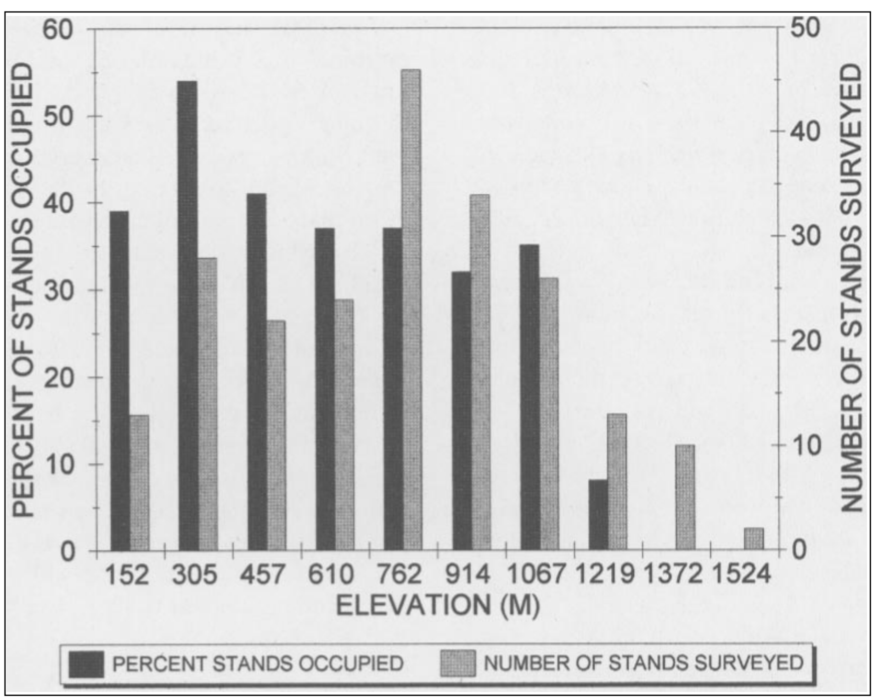

Figure 2—The percent of stands surveyed and verified as occupied in relation to stand elevation. The sample of sites is from all the physiographic provinces in western Washington, 1991–93.

<1.1 detections/morning. The highest occupied stand in Washington was located at 1,105 m in elevation, in the North Cascades Physiographic Province, near the upper headwaters of Crevice Creek. The highest occupied stand in the Olympic Peninsula Physiographic Province was located 1,025 m in elevation near Spot Lakes on the Hood Canal Ranger District, Olympic National Forest. The South Cascades physiographic province had an occupied stand 1,051 m in elevation, located 13 km south of Alder Lake in Lewis County, near the East Fork Little Creek drainage. More than 98 percent of all detections in Washington were recorded below 1,067 m in elevation.

Forest Type and Physiographic Province

Forest types surveyed in Washington included stands dominated by western hemlock, Douglas-fir, Sitka spruce, silver fir, and mountain hemlock. These stands commonly had a large component of western red cedar.

The mean detection rates for 229 old-growth stands were compared between the five physiographic provinces in Washington. The North Cascades Province had a mean detection rate of 23.5 detections/survey morning (n = 117 sites, $s.d.$ = 7.9) and 40 percent of the old-growth stands surveyed were verified as occupied. The Olympic Peninsula had a similar rate of 18.3 detections/survey morning (n = 67, $s.d.$ = 8.2) and a 37 percent occupancy rate of old-growth stands. The South Cascades had a detection rate of 12.5 detections/survey morning (n = 30, $s.d.$ = 15.7), and 10 percent of the stands surveyed were occupied. The Puget Trough had the lowest detection rate of any province, with 1.3 detections/survey morning (n = 7, $s.d.$ = 0, and no occupied stands, but the number of stands sampled was small. The Southwest Coast had the highest detection rate (90.1 detections/survey morning; n = 8, $s.d.$ = 7.4) and the highest occupancy rate (50 percent), but the number of old-growth stands surveyed was also small.

Stand Characteristics

Statistical Model

The results of the logistic regression model results from the 1994 study gave a total accuracy rate of 74.2 percent for a predicted probability of occupancy for each stand analyzed. The classification accuracy of occupied stands was 67.2 percent. The classification accuracy of unoccupied stands was 79.2 percent. Of the 32 stands with a predicted probability of occupancy >0.75, 74 percent were occupied. Of the 54 stands with a predicted probability of occupancy of <0.25, 93 percent were unoccupied. A total of 65 stands (43 percent) had probability values ≥0.25 and ≤0.75.

Eight forest variables were included in the model by the stepwise logistic regression procedure. These variables best predicted occupancy of a stand by murrelets (*table 3*). The stepwise selection procedure was completed in 10 steps.

The probability of occupancy of an old-growth stand increased with increasing percent topographic slope, total number of potential nest platforms/ha, stem density of dominant trees, mean d.b.h. of western hemlock, and the moss coverage (percent moss) on the limbs of dominant trees (*table 3*). The probability of occupancy of a stand decreased with increasing stand elevation, canopy closure,

Table 3—Stepwise Logistic Regression Model of Marbled Murrelet habitat in western Washington. The eight variables are listed in order of their probability values

Variable	Regression coefficient	Standard error	Wald Chi-square	Prob. > Chi-square
Intercept	–1.31820	1.6352	0.65	0.41
Percent slope	0.04360	0.0123	12.47	< 0.01
Platform total	0.04330	0.0151	8.19	< 0.01
Elevation	–0.00083	0.0003	8.16	< 0.01
Stem density	0.18590	0.0668	7.75	< 0.01
Canopy closure	–0.03340	0.0130	6.63	0.01
Western hemlock d.b.h.	0.01610	0.0065	6.18	0.01
Percent moss	0.02220	0.0093	5.72	0.02
Mean lichen	–0.58700	0.2726	4.64	0.03

and lichen coverage (mean lichen) on the limbs of dominant trees. Sites with a high probability of occupancy had a mean canopy closure of 86 percent.

Importance of Independent Variables

The step in which each variable was selected, the stability of variables through the stepwise procedure, the final chi-square values of variables used in the model, and the relationship between variables were used to subjectively assess the relative contribution of variables in predicting the probability of occupancy (*table 3*). The variables most correlated with occupancy of old-growth stands, included total potential nest platforms/ha, total percent moss cover on tree limbs, percent slope, mean d.b.h. of all dominant trees, mean lichen cover on tree limbs, stem density of dominant trees, elevation, canopy closure, mean d.b.h. of western hemlock, and percent composition of low elevation conifers.

Describing Low- and High-Quality Habitat

To begin to define what values would be considered to be the lower and upper thresholds for describing murrelet nesting habitat, the minimum, mean, and average values for each forest variable were calculated for occupied and unoccupied stands (*table 4*). Suitable murrelet nesting habitat was defined as sites with a high probability of occupancy. These stands had a mean topographic slope of 50 percent and were found at a mean elevation of 152 m. Stands with a high probability of occupancy also had a mean of 92 platforms/ha, a stem density of 50 dominant trees/ha (>81 cm d.b.h.), 83 percent canopy closure, 101 cm mean d.b.h. of western hemlock, 49 percent moss coverage on tree limbs, and a low index of lichen cover (*table 4*).

Stands with a high probability of occupancy (>0.76) had minimum values of 10 platforms/ha, 29 dominant trees/ha, 29 percent canopy closure, 85 cm mean d.b.h. of western hemlock, 5 percent moss cover, and 97 cm mean tree d.b.h.. These occupied stands were found at a maximum of 288 m in elevation.

Tree Characteristics

A comparison of old-growth tree characteristics for different conifer species in Washington indicated that old-growth Sitka spruce had most of the characteristics associated with known nest sites (Hamer and Nelson, this volume b). Sitka spruce had a higher mean d.b.h., taller height, higher number of platforms/tree, and higher moss coverage of the limbs than any of the five other conifers (*table 5*). On average, this species had more than two times as many platforms/tree than any other conifer species except Douglas-fir. Douglas-fir was second in having characteristics deemed suitable for murrelet use, with a similar number of platforms/tree as Sitka spruce, a large height, high mean d.b.h., but a low moss coverage on the limbs. Western red cedar ranked third as a suitable nest tree choice with a large mean d.b.h., high basal area, 1.4 platforms/tree, and one of the highest moss cover indexes. Western hemlock ranked fourth in the comparison but, as expected, has one of the highest mistletoe indexes of any tree species. Mountain hemlock ranked third and silver fir last. Both silver fir and mountain hemlock had a low mean d.b.h., low basal area, low number of platforms/tree, and a higher lichen index. Silver fir had an average of only 0.81 platforms/tree.

Discussion

Landscape Characteristics

Distance to Salt Water

Because murrelets forage at sea and only carry single prey items to the nest, but can nest at long distances from the coast, the energetic requirements of flying inland to incubate eggs and feed young, places a limit on their inland breeding distribution and use of inland forests. Even with the potential problems of energetic expenditure, Marbled Murrelets displayed a great tolerance for using nesting stands located up to 63 km inland from the ocean. Almost all the habitat in the North Cascades and South Cascades Physiographic Provinces is located >42 km inland because of rural development and intensive forestry practices within the Puget Trough. Even with these long flight distances, some birds were passing occupied stands to fly farther inland.

Breeding records also indicated that nesting is occurring at stands located long distances from salt water. A small downy chick was located on the ground along a trail on the east shore of Baker Lake in 1991, 63 km from the ocean (pers. obs.). Another downy chick was located 45 km inland at Helena Creek, in Snohomish County (Reed 1991). Six additional records of eggs, downy young, and fledglings found 29–55 km inland in Washington were compiled by Leschner and Cummins (1992a), and Carter and Sealy (1986).

Elevation

In general, stands found at higher elevations had a lower composition of conifer species reported to be used as nest trees. Murrelet nests have not been located in the higher elevation conifers such as silver fir or mountain hemlock in British Columbia, Washington, Oregon, or California, (Hamer and Nelson, this volume b). A negative association of murrelet abundance and stand occupancy to the occurrence of silver fir and mountain hemlock (high elevation tree species) is best explained by these species low mean d.b.h. and low number of platforms/tree (see Tree Characteristics). In addition, silver fir branches generally exit the trunk at sharp downward angles creating few level platforms.

Forest Type and Physiographic Province

All records of nests, eggs, eggshell fragments, and downy chicks in Washington have been associated with old-growth forests (n = 17) (Leschner and Cummins 1992a). In North America, fledglings have been found in a variety of unusual habitat types such as roads, airports, and rural areas (Carter and Sealy 1987b; Hamer and Nelson, this volume a). These

***Table 4—Mean values for occupied murrelet stands in Washington calculated using stands with a predicted probability of occupancy >76 percent (*n *= 25). Mean values for unoccupied stands were calculated using sites with a predicted probability of occupancy <14 percent (*n *= 44). Variables are listed in order of their initial chi-square score before step 1 of the model, with the eight variables used to develop the logistic regression model listed first. Final chi-square scores for the eight variables used by the model are listed in* table 3**

Variable	Predicted probability of occurrence	Mean	Minimum	Maximum	Probability > Chi-square
Percent slope	>0.76	49.9	3.0	90.0	0.05
	<0.14	35.1	3.0	75.0	
Platform total	>0.76	27.2	4.0	65.0	<0.01
	<0.14	7.3	0.0	29.0	
Elevation	>0.76	152.4	29.6	288.0	<0.01
	<0.14	271.4	27.9	445.8	
Stem density (trees/ha)	>0.76	50.0	29.0	89.0	0.05
	<0.14	39.0	0.0	84.0	
Canopy closure	>0.76	82.6	29.0	98.0	0.02
	<0.14	81.1	50.0	100.0	
Western hemlock d.b.h.	>0.76	100.8	84.7	136.2	0.02
	<0.14	98.3	56.5	135.2	
Percent moss	>0.76	49.1	5.0	82.0	<0.01
	<0.14	14.1	0.0	75.0	
Mean d.b.h.	>0.76	131.7	97.3	169.7	<0.01
	<0.14	103.3	58.7	183.0	
Low d.b.h.	>0.76	133.0	97.3	169.7	<0.01
	<0.14	107.0	58.8	183.0	
Platforms/ha	>0.76	92.0	10.0	183.0	<0.01
	<0.14	25.0	0.0	89.0	
Western redcedar d.b.h.	>0.76	153.9	91.4	247.5	<0.01
	<0.14	122.0	98.0	177.3	
Mean lichen	>0.76	1.4	1.0	3.1	<0.01
	<0.14	2.5	1.0	4.8	
Western red cedar composition	>0.76	45.1	5.9	100.0	<0.01
	<0.14	20.6	6.7	40.0	
Slope position	>0.76	1.6	1.0	3.0	<0.01
	<0.14	2.2	1.0	3.0	
Basal area	>0.76	14.3	4.2	28.4	<0.01
	<0.14	8.1	1.4	17.7	
Platforms/tree	>0.76	2.0	0.3	5.7	<0.01
	<0.14	0.8	0.0	3.2	
Canopy height	>0.76	53.6	37.2	69.3	0.01
	<0.14	45.8	26.1	71.3	
Low composition	>0.76	92.4	50.0	100.0	0.01
	<0.14	77.3	6.7	100.0	
High composition	>0.76	26.7	6.3	50.0	0.02
	<0.14	49.7	7.0	100.0	
Mistletoe number (trees/ha)	>0.76	15.0	5.0	39.0	0.03
	<0.14	10.0	5.0	25.0	
Distance to saltwater	>0.76	38.2	1.5	62.8	0.94
	<0.14	38.5	1.5	62.5	

Table 5—Summary of seven characteristics measured for six species of conifers available as nest trees by the murrelet in Washington state. Only trees ≥81 cm d.b.h. were measured. The mean, range, and sample size are shown. See text for moss and lichen cover categories

Variable	Tree Species					
	Sitka spruce *n* = 55	Douglas–fir *n* = 552	Western red cedar *n* = 347	Western hemlock *n* = 793	Mountain hemlock *n* = 54	Silver fir *n* = 234
D.b.h. (cm)	163.1 91–326	131.7 55–268	143.0 81–290	106.7 51–268	103.0 55–140	100.4 52–184
Height (m)	57.2 27–73	58.3 18–85	49.3 26–72	47.4 15–76	40.5 18–73	50.8 23–69
Basal area (m^2)	2.3 0.6–8.4	1.9 0–5.6	4.6 0.5–6.6	4.3 0.2–4.4	2.2 0.2–1.5	0.8 0.2–2.7
Platforms/tree	2.9 0–18	2.3 0–13	1.4 0–10	1.2 0–19	1.0 0–6	0.8 0–5
Moss index	2.8 1–5	1.5 1–5	2.2 1–5	2.0 1–5	1.1 1–2	2.4 1–5
Lichen index	2.5 1–5	2.0 1–5	1.2 1–5	1.7 1–5	2.6 1–5	2.2 1–5
Mistletoe index	0.2 0–5	0.1 0–2	0.0 0–3	1.1 0–6	0.1 0–3	0.2 0–4

records indicate that fledglings may travel some distance before becoming grounded.

Detection and stand occupancy rates increased with more older forest available on the landscape. For all provinces, the low detection and occupancy rates near the coast were probably due to the presence of large amounts of unsuitable or marginal habitat in the Puget Trough and near coastal lowland areas of the Olympic Peninsula. In a study encompassing the entire South Fork of the Stillaguamish River basin in northern Washington, significantly higher numbers of murrelets were observed in old-growth and mature forests than either rock/talus, clear-cut/meadow, or small saw/pole cover types (Hamer and Cummins 1990). Murrelet detection rates increased rapidly when the percentage of old-growth and mature forest cover types found within a 2,000-m-radius circle around each survey station made up more than 30 percent of the landscape. Mean detection rates for sites located in these areas ranged between 1 and 20 detections/morning ($\bar{x}$ = 5.7; *s.d.* = 5.8). All sites with <30 percent old-growth and mature forest cover had <1.5 detections/morning ($\bar{x}$ = 0.2; *s.d.* = 0.4). An analysis of the landscape features associated with occupied and unoccupied stands in Washington found that the amount of old-growth and large sawtimber available best predicted murrelet occupancy at the stand level (Raphael and others, this volume). Sites with a higher proportion of these mature forest classes were more likely to have evidence of nesting or occupancy than unoccupied sites.

Stand Characteristics

Statistical Model

Overall the model correctly predicted occupancy on about 74 percent of the sites. However, this success rate may be biased because the same sites that were used to build the model were used to test it. Because the model treats occupancy as a categorical variable, individual sites that scored near 0.5 were difficult to judge. In these cases it was more convenient to think of occupancy as a continuous variable where the higher probability scores indicated more suitable habitat and a higher probability of being occupied by murrelets. Errors in the classifications of stands could be due to several factors: (1) some stands determined to be unoccupied from field surveys may have actually been occupied; (2) it is possible in some instances that birds may be occupying stands of marginal habitat and; (3) the vegetation sampling for some stands may have been inadequate to accurately reflect the true structure of the stand. These potential problems could be avoided by increasing the number of survey visits to a stand used to determine occupancy and increasing the vegetation sampling effort. More vegetation information from a larger number of independent occupied and unoccupied stands needs to be collected to validate the model.

The results of the statistical model suggested that any land management activity that reduced or affected the number of potential nest platforms/ha, composition of low elevation conifers, moss cover on tree limbs, stem density of dominant trees, or canopy closure, would reduce the probability of occupancy of old-growth, and thus the suitability of an old-growth stand as nesting habitat for murrelets. Results from studies of murrelet habitat use to date have been derived from comparisons of stands occupied by murrelets to unoccupied stands, comparisons of stands receiving high use versus low use, or comparisons of nest trees and nest plots to random trees and plots. Although these can provide extremely useful descriptions and definitions of suitable habitat, they do not provide information on the habitat characteristics associated with successful nests. Information on the landscape and within-stand habitat characteristics that influence reproductive success is needed to fully understand murrelet nesting ecology and to model optimum habitat suitability for this species. Reproductive success should be used as a measure of habitat suitability in future studies by intensively studying occupied stands that have high detection rates of Marbled Murrelets and locating a sample of active nests to observe. A discussion of each variable used by the model follows.

Total Platforms—Results suggest that if any variable were to be used solely to assess habitat quality, total platforms would be the best indicator. More potential nest platforms within a stand mean more nesting and hiding opportunities and a higher diversity of nest choices for the murrelet. Although the total number of platforms was important, I currently have few measures of platform quality. A examination of the limb diameters of Marbled Murrelet nests indicated higher use and possible selection for platforms >35 cm in diameter (Hamer and Nelson, this volume b). Some stands may have an abundance of smaller potential nest platforms that are only 10-20 cm in diameter. These stands may be marginal nesting habitat because of the limitations of platform size. Future studies should include a measure of mean platform size when quantifying forest vegetation.

The total number of potential nest platforms would be especially important if nest platforms within a stand were limited, the number of nesting stands available on the landscape were limited, or intraspecific competition occurred for nest platforms within a given area. It is unknown whether platforms meeting all the requirements for nesting are limited in availability in a typical old-growth stand. It has been assumed that nest platforms may be unlimited in old-growth stands (Sealy 1974), but an understanding of the structural requirements needed for a platform to be used by murrelets is required before an analysis of platform availability is possible.

Total Moss—The presence of moss in the tree canopy was another important indicator of murrelet habitat. Although murrelets do not absolutely require moss as a nest substrate, the majority of nests have been located on moss (Hamer and Nelson, this volume b); the presence of moss may increase the number of potential platforms within a stand. Limbs with little or no moss coverage result in nest locations close to the trunk of a tree, which is usually the only area on a tree where debris such as needles and duff collect in sufficient quantities to form a thick substrate suitable for nesting, or where branches are large enough in diameter to create suitable nest platforms (pers. obs.). Other areas on the tree are usually too exposed to wind and other environmental influences to collect enough substrate to form a platform of suitable size. Thick mistletoe blooms are sometimes the exception to this observation. A high cover of moss creates a multitude of nest platform choices by providing substrate on many locations throughout a single limb, especially where there is suitable overhead cover and the limb is large enough to support a nest. In addition, the presence of a moss carpet essentially thickens the diameter of limbs, transforming limbs of marginal size into suitable nesting platforms. Moss is therefore related to the number of potential nest platforms of a stand. It is not known if one species of moss is preferred over others.

Mean D.b.h.—Although not selected by the final regression model, mean tree d.b.h. had one of the highest initial chi-square values (16.2) and the chi-square values showed high stability through the selection process. The mean number of platforms/tree increased rapidly with an increase in tree diameter from 50 to 200 cm (*fig. 3*). No increase in the mean number of platforms was evident for larger trees that ranged from 220 to 300 cm in diameter. Suitable platforms were most commonly found in stands with larger tree sizes, as evidenced by a correlation of total platforms to mean tree d.b.h. ($r = 0.60$), but the relationship of these two variables was complex. The presence of larger trees alone did not always explain the presence of nest platforms. In Washington, there were abundant examples of large trees >176 cm in diameter that contained no platforms. Other factors that can create platforms may include wind and insect damage, mistletoe brooms or other plant parasites, moss or larger quantities of duff, multiple overlapping tree limbs, natural limb deformities, and disease. Examples of 80-year-old stands of western hemlock that are heavily infested with mistletoe and occupied by murrelets have been found in Oregon (Nelson, pers. comm.). Therefore, total platforms was the best indicator of suitable murrelet nesting habitat because it directly measures the nesting structures required by this alcid, whereas mean tree diameter measures the availability of platforms indirectly and with less accuracy or predictability. Still, most agencies and private timber companies have measures of mean tree diameter available for their stands, but no measures of platforms or structure. In attempts to force the model to use mean tree diameter, the

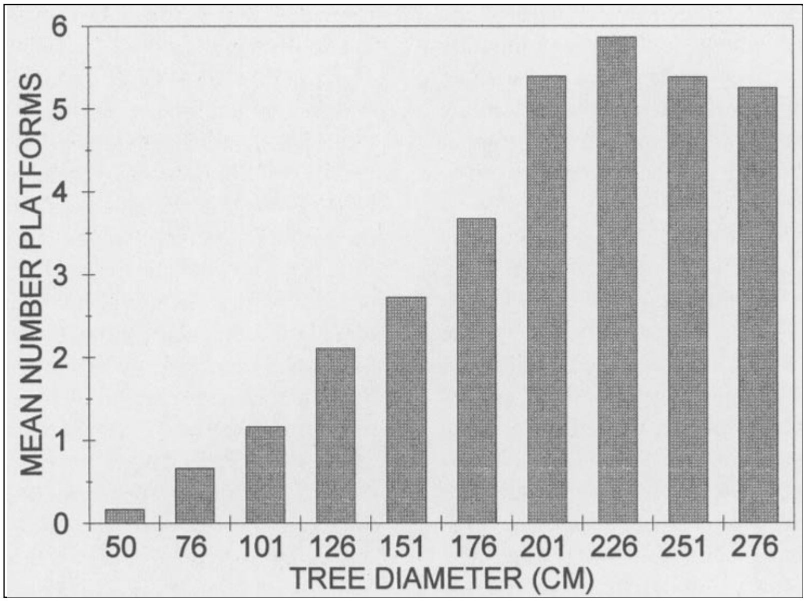

Figure 3—The mean number of potential nest platforms/tree in relation to tree diameter (25-cm intervals) for western hemlock, western red cedar, Douglas-fir, and Sitka spruce trees in western Washington, 1991–93. Trees (*n* = 1,860) were sampled from 151 stands.

model always re-selected a platform variable to replace mean tree diameter. Total platforms accounted for all the variation of mean tree d.b.h., but mean tree d.b.h. could not account for all the variation of total platforms. These results indicate that the structure of a stand is more important in predicting stand occupancy by murrelets than the size of the trees within the stand.

Mean Lichens—The percent cover of lichens on tree limbs was negatively correlated with the percent cover of moss (r = -0.23). Some common moss species such as *Isothecium* spp. require mild and wet conditions. These conditions are usually found at lower elevations in the Sitka Spruce and Western Hemlock Zones. Lichens such as *Alectoria* spp. and *Bryoria* spp. are most abundant at higher elevations where conditions are colder and dryer (Henderson and others 1989). These stands usually have a high percent composition of silver fir and mountain hemlock, which are not known to be used as nest trees by Marbled Murrelets in the Pacific Northwest. Therefore, it was not surprising that lichen cover was negatively related to the probability of occupancy.

Stem Density (trees ≥81 cm d.b.h.)—This variable was not correlated to any other variable to any great degree except basal area (0.63), but it can be assumed that in general, stands with a higher stem density of trees ≥81 cm d.b.h. would have a larger number of potential nest platforms/ha and higher canopy closures. A larger sample of stands in Washington with lower stem densities is needed to fully understand this variable and its effect on the probability of occupancy. Occupied stands with stem densities of only 5 trees/ha have been documented in Oregon (Nelson, pers. comm.)

Canopy Closure—It may be difficult for murrelets to locate and access nest platforms in stands with extremely high canopy closures, and the results of the analysis may reflect this because occupied old-growth stands still had mean canopy closures of 86 percent. A larger sample of stands with lower canopy closures is needed to fully understand this variable and its effect on the probability of occupancy. Nests located in stands with very low canopy closures may be subject to higher predation rates since corvids are the most common nest predator and locate prey almost entirely by sight. Stands with low canopy closures and low tree densities would be expected to have longer sight distances through the canopy. In these cases, murrelet nests would be easier to locate by visual predators.

Mean Diameter of Western Hemlock—Because the majority of trees infected with mistletoe were western hemlock and the mean d.b.h. of low-elevation trees was useful in assessing suitable habitat, the mean d.b.h. of western hemlock appears to combine the variation of these two factors into one variable.

Mistletoe Number—Stands that are infested with mistletoe may provide a higher number of nest platforms for murrelets. Mistletoe infects the branches of living trees, causing swelling, deformation, and brooming, which acts to thicken smaller diameter branches. This process can create suitable nest platforms from otherwise marginally-sized limbs. Thick secondary branching is characteristic of these mistletoe brooms that create dense overhead cover, a characteristic found at many murrelet nest platforms in Washington and Oregon (Hamer and Nelson, this volume b). In addition, mistletoe blooms help trap debris falling from the upper canopy, creating additional nesting platforms and platforms of larger size.

Describing Low and High Quality Habitat

In order to use the model to predict the probability of occupancy of an old-growth stand by murrelets, and thus judge the suitability of a stand as nesting habitat, it is necessary to obtain values for the 8 variables used by the model from the stand needing evaluation. The values for these variables can then be compared to the mean, minimum, and maximum values calculated for stands with a high probability of occupancy and stands with a low probability of occupancy (*table 4*). Using this comparison, a general sense of the suitability of a stand as nesting habitat can be obtained. In addition, by entering the values for the 8 forest characteristics into the formula shown below, the probability of occupancy can be calculated. Elevation should be entered in feet, stem density as the number of trees/25 m plot, mean d.b.h. of western hemlock in cm; and lichen, moss and canopy cover as percent total cover. First, the logistic regression model is used to predict $g(x)$ as follows:

$$g(x) = b_0 + b_1x_1 + b_2x_2 + ... + b_8x_8 \quad (1)$$

where,

b_0 is the intercept and, $b_1, ..., b_8$ are the logistic regression coefficients for each variable. These values are listed under the Regression Coefficients in *table 3*.

$x_1 , ..., x_8$ are the values for the independent variables measured at the stand in question and,

$g(x)$ is the predicted value of the logistic transformed probability of occupancy.

Then $g(x)$ is retransformed to estimate the probability of occupancy as follows:

$$P = \text{EXP}\ (g(x))/[1 + \text{EXP}\ (g(x))] \text{ where,} \quad (2)$$

P is the predicted probability of occupancy,

$g(x)$ is as defined in equation (1).

EXP is the exponentiation function, i.e.

$EXP^3 = e^3$ where e = 2.7183..., the base of natural logarithms.

It is important to recognize that this model was developed from a sample of old-growth stands and its reliability in other stands has not been evaluated.

Tree Characteristics

Because western red cedar ranked third in producing potential nest platforms and was indicated by the regression analysis to be helpful in assessing suitable habitat, nest-search parties should pay closer attention to this conifer. Western hemlock was rated lower as a suitable nest tree because of a lower platform abundance. Because observers did not count mistletoe brooms on the outer limbs of trees as potential nest platforms, the actual number of potential nest platforms/tree for western hemlock may be much higher.

Because murrelet surveys are often conducted in stands containing a mix of conifer species, it is difficult to use detection trend information from different stand types to confirm a preference for nesting in one type of conifer. In addition, not enough murrelet nests have been located, or located in a random manner, to determine whether birds are selecting particular tree species for nesting, especially since greater nest-search and survey effort have occurred in the Douglas-fir and Western Hemlock zones than in the Sitka Spruce zone. This comparison provides evidence that certain tree species are more likely to be used by murrelets than others.

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