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Multi-scale landscape and seascape patterns associated with marbled murrelet nesting areas on the U.S. west coast

Carolyn B. Meyer[1,*], Sherri L. Miller[2] and C. John Ralph[2]
*[1]Department of Botany, University of Wyoming, P.O. Box 3165, Laramie, WY 82071, USA; [2]Pacific Southwest Research Station, Redwood Sciences Laboratory, U.S. Forest Service, 1700 Bayview Dr., Arcata, CA 95521, USA; *Author for correspondence (e-mail: meyerc@uwyo.edu; phone: +1-307-766-2923; fax: +1-307-766-2851)*

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Abstract

Habitat for wide-ranging species should be addressed at multiple scales to fully understand factors that limit populations. The marbled murrelet (*Brachyramphus marmoratus*), a threatened seabird, forages on the ocean and nests inland in large trees. We developed statistical relationships between murrelet use (occupancy and abundance) and habitat variables quantified across many spatial scales (statewide to local) and two time periods in California and southern Oregon, USA. We also addressed (1) if old-growth forest fragmentation was negatively associated with murrelet use, and (2) if some nesting areas are more important than others due to their proximity to high quality marine habitat. Most landscapes used for nesting were restricted to low elevation areas with frequent fog. Birds were most abundant in unfragmented old-growth forests located within a matrix of mature second-growth forest. Murrelets were less likely to occupy old-growth habitat if it was isolated (> 5 km) from other nesting murrelets. We found a time lag in response to fragmentation, where at least a few years were required before birds abandoned fragmented forests. Compared to landscapes with little to no murrelet use, landscapes with many murrelets were closer to the ocean's bays, river mouths, sandy shores, submarine canyons, and marine waters with consistently high primary productivity. Within local landscapes ($\leqslant$ 800 ha), inland factors limited bird abundance, but at the broadest landscape scale studied (3200 ha), proximity to marine habitat was most limiting. Management should focus on protecting or creating large, contiguous old-growth forest stands, especially in low-elevation areas near productive marine habitat.

Introduction

Scale has become an important factor to consider when developing predictive habitat models for a species. Results can differ depending on the scale measured (Wiens et al. 1986). Often the largest spatial scales have been overlooked because of the difficulty of sampling intensively across large geographic regions. Due to its threatened status, the marbled murrelet (*Brachyramphus marmoratus*) has been surveyed inland with one common protocol during the last decade throughout a large geographic area. Therefore, with the aid of Geographic Information Systems (GIS), we used the unique situation of this seabird to assess the importance of spatial variables in predicting habitat use across multiple spatial scales in a very large geographic region: California and southern Oregon (where 36% of potential nesting habitat has been surveyed). Our objective was to discover which variables at which scales (from small forest patches to regional vegetation patterns) contributed most to our ability to predict murrelet habitat. Also, we tested for any delayed bird response to habitat change. Few studies have addressed the effects of past habitat conditions on present habitat use, particularly over large geographic areas. We believe our approach of combining several spatial scales and two temporal periods into one predictive function can serve as a model for broad-scale studies of habitat for other species.

The marbled murrelet also provides an excellent opportunity to develop methods to assess the importance of the spatial juxtaposition of two very different habitats: marine nearshore habitat and old-growth forests. Within California and Oregon, the bird spends most of its time foraging or resting on the ocean within 6 km of the shore (Ralph and Miller 1995). During the breeding season (March to September), it nests inland in old-growth forests or second-growth forests with remnant old, large trees (Hamer and Nelson 1995). The bird requires large trees to lay its single egg on a stout tree branch or other tree structure providing a suitable nest platform. Each day at dawn, the parents fly from the ocean to the nest to exchange incubation duties. After the egg has hatched, the parents fly to the nest several times daily to feed the chick (Nelson and Hamer 1995a). Nests can be located as far inland as 70 km from the coast (Ralph and Miller 1995). A species with such extensive daily movements is ideal for assessing spatial juxtaposition of habitats over large areas. The marine and terrestrial habitats must be integrated to build a murrelet habitat model. Once a model is developed, one can determine the relative importance of the terrestrial and marine habitats to bird abundance.

The rapid loss of old-growth forest nesting habitat in Washington, Oregon, and California led to the U.S. Fish and Wildlife Service listing the bird as a threatened species in 1992 (Miller et al. 1997). In the three states, much of the nesting habitat has also been fragmented (Hansen et al. 1991), which increases edge habitat and can potentially increase nest predation rates (Paton 1994) or create adverse microclimatic conditions (Chen et al. 1993). The effect of fragmentation on the murrelet is still not well understood, nor the role that small forest fragments play in the species' survival. For example, in Washington, Raphael et al. (1995) found murrelets occupied nesting landscapes with large, complexly-shaped old-growth patches. In contrast, Miller and Ralph (1995) found old-growth patch size did not affect inland occupancy of stands in California. On the Siskiyou National Forest, Oregon, Meyer and Miller (2002) found old-growth forest fragmentation had an adverse effect on the murrelet. Our current, more comprehensive study at multiple scales should improve our understanding of fragmentation effects.

To date, neither the bird's marine requirements nor the importance of the juxtaposition of high quality marine habitat with high quality terrestrial habitat are known, especially across large regional areas. A large study area is needed to capture the coarse-scale variability in the marine habitat quality (e.g., mapped mean chlorophyll concentrations remain the same over coastline lengths > 120 km). Because murrelets fly daily between nest sites and foraging areas, nesting habitat near marine areas containing abundant prey probably is at a premium. Therefore, a major objective of this study was to address both the effects of (1) forest fragmentation and (2) the proximity of terrestrial and marine habitats by quantifying habitat associations of the murrelet across a wide range of pertinent temporal and spatial scales. Because characteristics of individual old-growth patches used for nesting have been studied extensively (Grenier and Nelson 1995; Hamer 1995; Hamer and Nelson 1995; Miller and Ralph 1995), the major focus of our research was, by contrast, on the broad-scale landscape and seascape patterns. Fortunately, the location of our study area was ideal for our objectives because it occurs in the southernmost extent of the seabird's distribution (from Alaska down to Monterey Bay, California). In this region, the birds are less abundant and potentially more susceptible to extinction (Ralph and Miller 1995). Consequently, factors associated with bird abundance may be more easily identified.

In our multi-scale approach, we developed hypotheses at four spatial and two temporal levels. The spatial levels were the (1) old-growth patch, where the patch is defined as a contiguous area of a single mapped cover type; (2) landscape, defined as a mosaic of patch types, examined at four scales (50 to 3200 ha); (3) sub-region, defined as large areas encompassing both inland and marine habitats; and (4) region, defined as the range of the species in a large geographic area, specifically our study area. Recent bird use (from 1991 to 1997) was compared to forest conditions during two temporal periods: (1) the present period when murrelet surveys were conducted and (2) the mid-1980s.

Two bird metrics were used to test our hypotheses: occupancy (presence/absence) and bird abundance. Occupancy was evaluated to determine if birds might use an area for nesting, whereas abundance was evaluated because we felt it could relate more closely to habitat quality. The following hypotheses were tested:

1. At the patch level, we hypothesized murrelets

would more likely occupy old-growth patches that have the largest trees because such trees may have more platform branches available for nests. Nest sites within patches should be in areas protected from the wind, such as low elevation valley bottoms or gentle slopes near streams, and far from the disturbance of road or logging activity.

2. At the landscape level, we expected murrelets to occupy areas with relatively unfragmented and non-isolated old-growth forest. We expected the matrix (the vegetation surrounding the old-growth) to be contiguous, mature second-growth forest providing low contrast edge with the old-growth.
3. Within sub-regions, we hypothesized that murrelets would occupy landscapes located closer to nearshore areas of potentially high marine productivity, specifically river mouths, bays, potential upwelling sources (submarine canyons, promontories), kelp beds, and areas with cold water or high chlorophyll concentrations. Moreover, we hypothesized that the birds would nest closer to sandy beaches than other shoreline types because sand lance (*Ammodytes hexapterus*), a common fish in the murrelet diet, concentrate in nearshore areas with sandy bottoms (Burkett 1995).
4. At the regional level, we expected murrelets to be occupying cool, moist, vegetation zones that occur at low elevations near the coast and are strongly influenced by fog, similar to the findings on the Siskiyou National Forest, Oregon (Dillingham et al. 1995; Meyer and Miller 2002).
5. For the temporal scale, we hypothesized that bird use may show a time lag of at least a few years before responding to forest fragmentation. Birds may show such a time lag because of strong fidelity to their nest sites.
6. Finally, we expected landscapes with the estimated highest bird abundance to represent the above characteristics more consistently than areas that merely had one or more birds occupying the site.

Study area

The study area on the U.S. Pacific coast extends from Coos Bay in southern Oregon south to Point Lobos at the southern end of Monterey Bay, California, and from offshore up to 56 km inland (Figure 1). Elevation ranges from sea level to 1750 m. The study area is divided into (1) zones of vegetation that are strongly influenced by fog and (2) zones relatively uninfluenced by fog, based on the dominant vegetation (Atzet and Wheeler 1982; Agee 1993). In southern Oregon, the fog-influenced zones include the western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) zones described by Franklin and Dyrness (1973). The dominant species in the western hemlock zone is Douglas-fir (*Pseudotsuga menziesii*). In California, the fog-influenced zone is the redwood (*Sequoia sempervirens*) zone (Agee 1993). All other vegetation zones in the study area have little fog influence, are drier, and are east of the western hemlock vegetation zone in southern Oregon and usually, east of the redwood zone in California (Figure 1).

Methods

We prepared and analyzed data in several steps. First, we assembled all available data from inland (non-marine) surveys for murrelets in the study area. Second, we obtained available GIS databases in ARC/INFO (Environmental Systems Research Institute, Inc., Redlands, CA, USA, v. 7.1) and created GIS maps of old-growth forest and other cover types, marine features, topographic features, and climatic variables. Third, using the GIS, we calculated spatial and other habitat variables within landscape-sized circular sample plots (400-, 800-, 1600-, and 3200-m radius) placed over murrelet survey stations. Finally, we searched for relationships between the habitat variables and (1) murrelet occupancy or (2) murrelet abundance (number of bird detections) within the sample plots.

We used accuracy testing methods not often employed in landscape studies. Our large datasets allowed us the luxury of testing for accuracy of the statistical relationships using independent data. We set aside 20 to 30% of our murrelet locations to be used solely as validation plots to test our models. These plots were never used in model development. Additionally, these plots were separated into four geographic subsections to test if model accuracy remained high when applied to smaller areas within the study area.

Murrelet inland surveys

We assembled the results of 17,145 marbled murrelet surveys conducted at 9,362 stations by numerous investigators from 1991 to 1997. Survey stations were

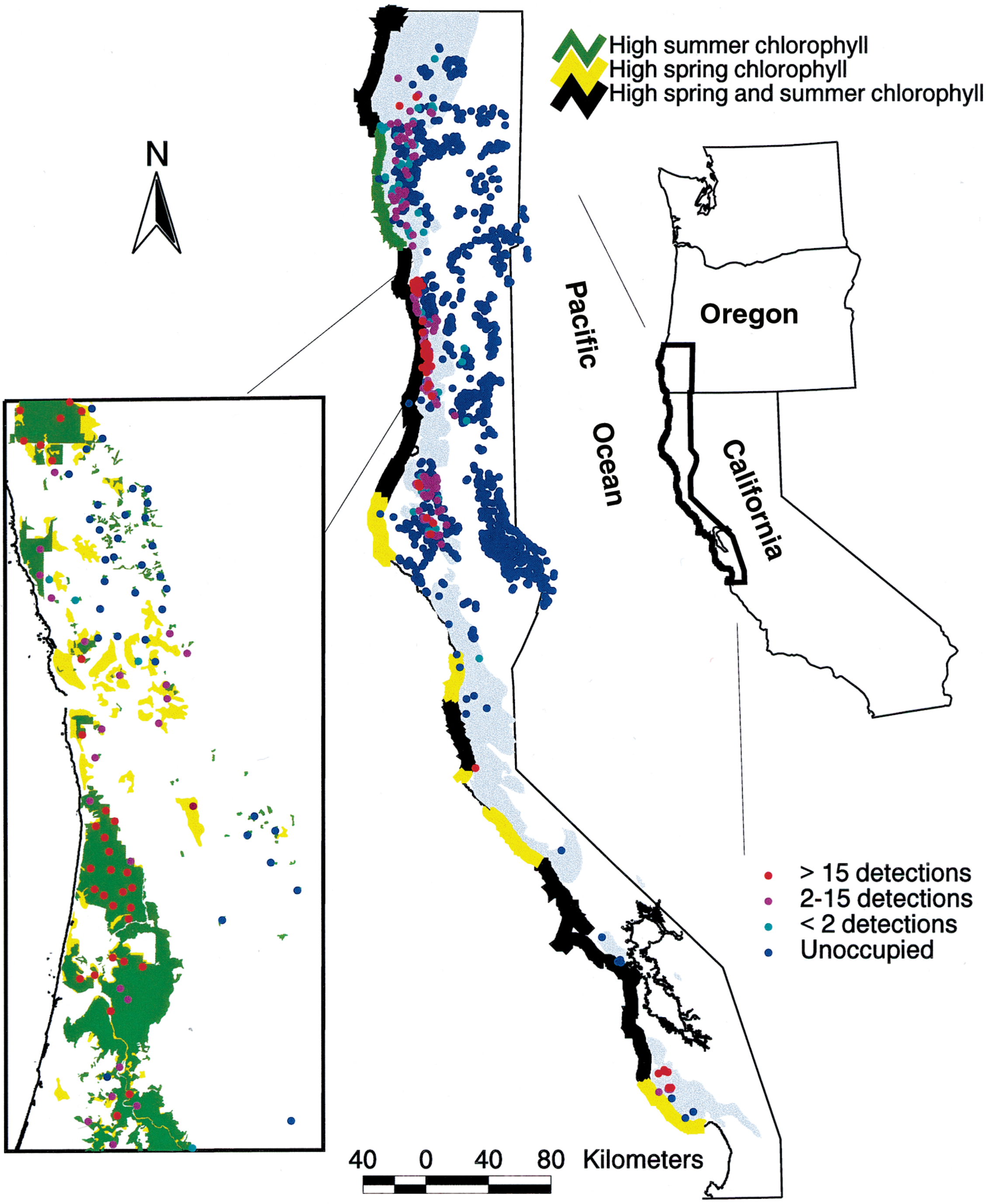

Figure 1. Marbled murrelet study area, showing the fog-influenced vegetation zone (California redwood and Oregon western hemlock zones in gray), nearshore areas with high summer and/or spring chlorophyll, and landscape plots with high (> 15 detections), medium (2–15), low (< 2), and zero (unoccupied) abundance of murrelets. Mean detections per survey were calculated in 800-m radius occupied plots. Inset gives an example of murrelet use of areas recently fragmented and areas fragmented in the past. Yellow patches were recently cut old-growth forest (since 1986) and green patches are what presently remains of the old-growth in the fog zone. Only green patches were surveyed for murrelets (some small ones are obscured by the abundance symbol). White areas were cut before 1986, so the small green patches with no adjacent yellow patches are the old-growth remnants of timber harvests before 1986. The ones with adjacent yellow patches were fragmented after 1986, and a number are still used by murrelets.

placed in potential murrelet habitat containing old-growth forest or second-growth forests with remnant old, large trees (some mature forests without an old-growth component were surveyed in Oregon). Each survey followed an established intensive survey protocol (Ralph et al. 1993). The protocol limits surveys to 15 April to 15 August, when bird activity in the nesting areas is highest. Stations were surveyed for two hours around dawn (starting 45 minutes before sunrise), and the number of birds seen or heard were recorded. Each visual or auditory observation of a single or group of birds flying together was considered one "detection". If a bird flew below the canopy, circled above the canopy, landed in the canopy, was stationary, or dropped broken eggshells around a tree, the station was classified as "occupied". Such behaviors indicate that the murrelets are probably nesting near the station, rather than flying over it toward another destination (Nelson and Hamer 1995a). Stations with birds detected, but with no nesting behaviors, were classified as "flyover", and stations with no murrelet detections were classified as "unoccupied". In a habitat patch (a contiguous area of habitat) where birds are truly present, four surveys are needed to detect birds at least 95% of the time in that patch (Miller and Ralph 1995). Thus, for "unoccupied" stations to be included in the study, at least four surveys must have been completed in the patch in which the station was located, if the patch was $\leqslant$ 50 ha. For patches > 50 ha, we subdivided the patch into 50-ha sections, and four surveys must have been conducted in each section.

Our study is a retrospective analysis of available survey data, where the sampling design varied from area to area. For almost half (7,863) of the surveys, researchers randomly or systematically placed stations within potential murrelet habitat. Although the locations of the rest of the surveys were determined by upcoming timber sales, those surveys were extensive and well-distributed within old-growth forest throughout the study area (see survey map in Meyer (1999)).

Vegetation databases

A single vegetation database of one map resolution was not available for the entire study area. To address our hypotheses, we used two different vegetation maps, referred to as GIS maps, that together covered the diversity of inland and offshore habitat conditions throughout the entire study area. The first map (called CA/OR map) combined two similar vegetation databases of very fine resolution (minimum mapping unit was a 25-m pixel = 0.06 ha), based on LANDSAT TM imagery: one for southern Oregon (Bureau of Land Management Western Oregon Digital Image Project, Portland, Oregon) and one for northern California that extended south to Point Reyes National Seashore just north of San Francisco (CTTF 1993, 84% accuracy for canopy cover, 94% for tree size in a subset of the area). This map did not include central California.

The second map did not include Oregon. For the second map (called CA map), the same vegetation database for northern California (CTTF 1993), but at a coarse resolution (4-ha minimum mapping unit), was combined with a coarse-resolution central California map that was based on aerial photography (Redwood Mapping Project by Larry Fox, Humboldt State University, CA). We modified the central California map by adding small old-growth redwood stands from aerial photographs to keep the minimum mapping unit at 4 ha.

Using the GIS, we classified cover types on the two maps as non-forest, freshwater, hardwood forests, and conifer forests. Forests were further divided into two canopy cover classes (class division at 40%) and four classes of tree diameter at breast height (dbh class divisions at 28, 61, and 91 cm for California, and 25, 52, and 77 cm for southern Oregon).

Our definition for "old-growth" was based on nest stand data from Hamer and Nelson (1995) and on our comparison of known old-growth areas to size and cover classes available in the satellite-derived vegetation databases. The old-growth class included coniferous forests having (1) total canopy cover $\geqslant$ 40% and (2) mean dbh $\geqslant$ 77 cm for Oregon and $\geqslant$ 91 cm for California.

Landscape-sized sample plots

We compared results for 400-, 800-, 1600-, and 3200-m radius sample "plots", centering these plots in concentric circles on the most central station of a cluster of survey stations. These plot sizes correspond to landscapes ranging from 50 to 3217 ha. We classified plots containing at least one occupied survey station as "occupied" plots with at least one flyover station and no occupied stations as "flyover", and plots with no murrelet detections as "unoccupied" (Figure 1). Because birds may either be nesting in "flyover" plots or just flying over the forest canopy heading elsewhere, the mean values of variables in "flyover" plots often fell between those of "occupied" and "unoccupied". Moreover, regression model fit and accuracy were decreased when "flyover" plots were combined with "occupied" plots. Therefore, we eliminated "flyover" plots from all regression analyses (they comprised < 10% of all plots). "Flyover" plots were included in this study only when evaluating the relative isolation of plots and when plotting bird distributions on maps. Overlapping plots were also removed to retain plot independence (unless overlap was under 5%), which reduced sample size as plot size increased. Final sample sizes for 400-, 800-, 1600-, and 3200-m radius plots (occupied and unoccupied) were 1013, 882, 563, and 246, respectively.

Not all occupied plots were included in our final analyses. Only 5 of 213 occupied plots were outside the fog zone, and all five were extreme outliers when entered in logistic regressions. Three of the outliers that were farthest from the fog zone were of questionable validity because a murrelet was detected only once (out of an average of 3 surveys) and other species can be mistaken for a murrelet. Although they were included in the accuracy assessment, we removed all five outliers from the final logistic regression models, which greatly improved the model fit.

Variables sampled

We recorded two metrics of murrelet use of forested areas: "occupancy" and "abundance". Occupancy is defined as the classification of a plot as either occupied or unoccupied. Abundance is the relative number of bird observations per survey in the plot. We used mean number of murrelet detections per survey in each occupied plot as the index to abundance. Following the methods in Miller and Ralph (1995), the mean number of detections per survey within each plot was standardized to adjust for the seasonal variation in number of murrelet detections (on average, detections peak in July; Miller and Ralph (1995); Jodice and Collopy (2000)). The number of surveys within individual plots averaged 6, 12, 23, and 53 for the 400-, 800-, 1600-, and 3200-m plots, respectively. Number of surveys increased in the larger plots because they included more old-growth patches that required surveying.

We quantified patch tree size by using the quadratic mean dbh of conifers in each patch found within a 400-m radius sample plot (using the 4-ha resolution database of the northern California timberland taskforce, CTTF 1993). The largest mean tree dbh of all the patches in the plot was recorded. We also noted if the patch was located in a national or state park. Within the landscape-sized plots, fragmentation and other spatial variables were calculated using FRAGSTATS (raster version, McGarigal and Marks (1995)). Fragmentation variables quantified were those that, when evaluated jointly, best presented a picture of whether or not the landscape was fragmented by logging (Mladenoff et al. (1993); McGarigal and Marks (1995); Table 1). In order to measure core area (interior habitat), we used distances to the edge of 50, 100, or 150 m.

To evaluate a time lag in response to fragmentation, we used a very coarse resolution 1985–1986 map of vegetation in the coastal region of California (Redwood Mapping Project, Humboldt State University) to determine if old-growth forest was present in relatively unfragmented blocks ($\geqslant$ 16-ha) during that period. Patches of old-growth forest highly fragmented before 1985–1986 were too small to identify on such a coarse-resolution map, but landscapes fragmented after that period still had large patches present on the map in 1985–86. In Oregon, we used the 1988 Siskiyou National Forest database (Congalton et al. 1993) and the Bureau of Land Management's record of harvest dates (M*S handbook, Medford District, Medford, Oregon) to identify relatively unfragmented old-growth forest present in 1988.

To estimate isolation, we noted if the distance from the center of a 400-m radius plot to the center of the nearest neighboring occupied or flyover plot was within 2, 5, 10, 15, or 20 km. Because survey effort was extensive, almost all plots had $\geqslant$ 2 neighboring plots within $\leqslant$ 5 km. From the center of each plot, we recorded (1) whether the plot was inside or outside the fog zone, (2) distance to nearest of each shoreline type, (3) distance to nearest marine and land features hypothesized to be important, and (4) values of topographic and climatic variables (Table 1).

Data analysis

We conducted multiple logistic regression analysis to predict probability of occupancy of a potential nesting area using occupied and unoccupied plots. We used multiple linear regression analysis to predict relative murrelet abundance using occupied plots only (SAS Institute (1990), SPSS version 8.0). Two methods were used to eliminate some of the many candidate variables before conducting these analyses. First,

Table 1. Habitat variables measured in inland circular plots in southern Oregon and California.

Fragmentation Variables (from FRAGSTATS)[a]

Percent of landscape in patch type (OG,OT[b])
Density of vegetation patches (no./100 ha)(OG,OT,L)
Mean core area per disjunct core (ha) (OG)
Percent of landscape in core area (OG)
Total edge per area (m/ha) (OG)
Density of edges (m/ha) (OG,OT,L)
Density of contrast-weighted edges (m/ha)(OG,L)
Mean and total shape index (OG,L)
Area-weighted fractal dimension (OG,L)
Percent of landscape in largest patch (OG,L)
Mean patch size (ha) (OG,L)
Mean nearest neighbor distance (m) (OG)
Density of core areas (no./100 ha) (OG,L)
Mean proximity index (OG)
Patch type interspersion and juxtaposition (OG,L)
Patch richness (L)
Shannon's diversity index (L)
Contagion (%) (L)

Topographic, Climatic, Zone, and Patch Variables

Elevation (m) (from 90 m DEM)
Slope (degrees)
Mean annual precipitation (cm)[c]
Mean maximum July air temperature (°C)[c]
Presence of unfragmented OG in mid-1980s
Presence in fog zone
Isolation > specified distance (2, 5, 10, 15 or 20 km)
Protected in national or state park
Mean tree dbh in patch (cm) (California only)

Distance Variables—distance (km) from plot center to nearest feature indicated

Ocean
Fine to medium-grained (0.06–12 mm) sandy beach (California only)
Nearshore (< 30 km) submarine canyons (from NOAA bathymetry)
Kelp beds
Major promontory
Streams (from 1:100,000 DLG)
High spring marine chlorophyll (mean from 1978–86 > 10 mg/m^3, from NASA CZCS, 18 km pixels)
High summer marine chlorophyll (mean from 1978–86 > 10 mg/m^3)
Spring/summer nearshore coldwater (< 10°C) areas (from NOAA AVHRR)
Major bay (Coos, Humboldt, Tomales, San Francisco)
Roads (from 1:100,000 DLG)

[a] Variable equations are in McGarigal and Marks (1995). A 400-m landscape border was used for edge variables (see Meyer (1999) for edge contrast codes), interspersion, and contagion. Variables not shown because they were eliminated during screening in all 16 analyses were distance to river mouths and various shoreline types (cliffs, rocky platforms, and coarse sandy, mixed, and gravel beaches). Data sources are described in more detail in Meyer (1999).

[b] OG = applies to old-growth, OT = other vegetation classes (seedling-sapling-pole, small, and medium-sized conifers; hardwoods), and L = entire landscape in plot.

[c] Precipitation and Oregon temperatures were from Daly et al. (1994). California temperatures were from interpolation (TIN) of 63 weather stations.

we discarded variables from consideration that were highly correlated with each other and yet, as a group had an insignificant relationship to the dependent variable. To do this efficiently, we reduced the candidate habitat variables to major principal components having eigenvalues > 1.0 and determined which of the resultant principal components were not significantly related to murrelet occupancy or abundance ($P > 0.05$) in a regression. We eliminated all variables that had high loadings (> 0.7) on those insignificant principal components. We did not use the principal components for any other purpose (they were not entered into the regressions to build our final models). Second, we eliminated one of a pair of variables (the least significant) if they were highly correlated ($r > 0.7$) and caused high multicollinearity. This screening reduced the original 63 variables down to 21 to 30 variables as candidates for the logistic regressions and down to 21 to 26 variables as candidates for the linear regressions. Because the number of candidate variables was still high and could lead to some being selected by chance, all models were validated with the independent datasets.

Habitat variables were entered into (1) stepwise logistic regression (using $P \leqslant 0.05$) to predict occupancy and (2) best subsets regression to predict abundance. Rather than relying solely on a stepwise procedure in the logistic regression, several regressions with the lowest Akaike's Information Criterion (AIC_c) of many regression combinations were evaluated. AIC_c is a maximum likelihood estimator corrected for sample size (Burnham and Anderson 1998). We also checked if variables at any one scale were unimportant. The final models selected were those that had a good Hosmer-Lemeshow test result (Hosmer and Lemeshow 1989) and the least misclassification of independent plots. The independent plots were randomly selected from the initial set of plots and are truly independent because they were never used to develop the final models. For linear regressions, the adjusted R^2 and Mallows' C_p (C_p estimates bias and random error to assess fit) were the criterion used to select the best subset of variables (following Neter et al. (1989)). Mean numbers of murrelet detections were $\log_{10}$- or square-root transformed (square-root for 3200-m radius plots) to meet parametric model assumptions of linearity, normality, and equal variances. We checked for interaction terms, but none improved the fit or accuracy of the models. Finally, we identified which was more limiting to murrelet abundance—inland (old-growth forest and topography) or marine habitat variables. In that analysis, we used only variables with very low intercorrelations with each other and compared their standardized regression coefficients and relative effects on R^2.

A variable may be important even if it is not selected in a regression, particularly if it is highly correlated to a variable in the model. To obtain a more a complete picture of a landscape with murrelets, highly intercorrelated sets of variables related to occupancy and abundance were identified. Habitat variables that were not in the final regression models, but were highly correlated with a habitat variable in the model ($r \geqslant 0.9$) were used to further interpret nesting landscape characteristics.

We also calculated the mean and variance of individual habitat variables to compare occupied and unoccupied plots as well as plots with high, medium, and low abundance of birds. We used these statistics to test whether fragmentation, elevation, and distance to nearest marine area with high productivity were lower and less variable in plots with abundant birds (> 15 detections per survey) than in occupied plots.

Finally, spatial autocorrelation among plots across the landscape was tested using Moran's I test of the residuals for both the CA/OR and CA logistic and linear regressions models (using S +, version 1.5). We used the inverse of the distance between the center of plots as the weighting statistic. We also constructed a variogram for each regression to find the distance at which autocorrelation became important and to adjust coefficients and standard errors (Cressie 1993) using a macro in Minitab (release 13.1), if autocorrelation was significant.

Results

As we will detail, we found several habitat characteristics were related to murrelet occupancy and abundance. Occupancy was most related to availability of low elevation, unfragmented old-growth forests within the fog zone that were close to highly productive marine areas. The important productive marine areas included areas with high chlorophyll concentrations, river mouths, bays, nearshore submarine canyons, and sandy beaches. Murrelet abundance was also related to the availability of old-growth forests located within national or state parks and away from roads. The abundance metric helped to further define the critical ranges for murrelets of some variables: elevation, distance to marine productivity, and old-growth forest fragmentation.

Regional distribution of murrelets

The regional distribution of plots classified as occupied was almost exclusively within the fog zone. The fog zone averaged lower elevations (394 vs. 876 m, SE = 12 m for both) and had cooler maximum July temperatures (24° vs. 30°C, SE = 0.14 and 0.18) than adjacent zones, although mean annual precipitation did not significantly differ (202 cm in fog zone vs. 184 cm, SE = 30 and 24). Even though about 60% of the 1,013 small plots (with a 400-m radius, and excluding "flyover" plots) were outside the fog zone, 98% of the 213 occupied plots were found inside the fog zone (Figure 1). Distribution of occupied plots was also limited by distance to the ocean and did not exceed 39 km, even when the fog zone extended further inland (maximum inland extent of the zone is 56 km). The farthest inland "flyover" plot with birds (no behaviors indicating nesting birds) was 59 km from the coast. Where found, birds were fairly abundant in the study area as the average number of detections observed per survey in occupied plots ranged between 11 to 13 (median = 4–6) over the plot sizes (SD = 14–19).

Occupied landscapes

Variables common to both maps
Using the occupied classification as an indication of where birds might nest, we found similar results using both GIS maps at the four landscape scales (Table 2). The habitat characteristics selected in the best logistic regression models were low elevation, close proximity to marine areas with high chlorophyll (Figure 1), proximity to other plots with murrelets, low old-growth fragmentation in the mid-1980s, and location within the fog zone. After the effects of other variables in the model were taken into account, murrelets were also occupying areas close to either submarine canyons or major bays (negative coefficient in Table 2).

Current old-growth characteristics
Variables that described current old-growth characteristics were predictive in the models Table 2. A set of additional old-growth variables not in the regressions were highly correlated ($r \geqslant 0.9$) with the set of old-growth variables in the models (mean proximity index, mean patch size, percent in largest patch, edge, total edge per area, percent in core area). Old-growth variables from both models indicated that murrelets were occupying areas that were less fragmented than unoccupied areas: they had larger and more core areas, more old-growth and large patches, more clumped patches (proximity index), and more edge (but less edge per area) (Figure 2, Table 2). The interior core areas most predictive of occupancy were 50 m (CA/OR map) or 100 m (CA map) from outer patch edges, distances selected over 150 m (Table 2).

In the smaller plots (400- and 800-m radius), either percentage in old-growth forest or the total amount of old-growth edge was often a very predictive variable (Table 2). In the larger plots (1600- and 3200-m radius), fragmentation and other spatial characteristics of old-growth became more important, as the old-growth in occupied plots had more and larger core areas, more complex shapes of large patches (area-weighted fractal dimension), and more contrasting edge. The contrasting edge result was unexpected, since more contrast would be expected to increase any adverse edge effects of fragmentation. However, it may be an indication that old-growth forests adjacent to recently clearcut areas are still used by murrelets loyal to the area.

Time lag effect
We found past old-growth characteristics were predictive (Table 2), indicating there was a time lag in the effect of fragmentation on occupancy. Presence of unfragmented old-growth forest in the mid-1980s was selected in almost all models, signifying this variable was very predictive of present-day (1991–1997) murrelet occupancy locations. Areas highly fragmented before the mid-1980s rarely contained murrelets today, yet areas highly fragmented after this period often contained murrelets (Figure 1).

Isolation effect
Murrelets were more likely to occupy plots within 5 km of other plots containing murrelets than plots more isolated from other murrelets (Table 2). Five km was the threshold distance most predictive of occupancy. Only 3% of occupied plots were isolated ($\geqslant$ 5 km) from other occupied or flyover 400-m radius plots. No occupied plots were > 11 km from another occupied or flyover plot.

Matrix characteristics
We expected that the matrix (the vegetation types around the old-growth forest) of occupied plots would be largely composed of contiguous blocks of older, second-growth forest. Indeed, we found that occupied plots had more medium-sized conifers (52–76 cm dbh in Oregon, 61–90 cm dbh in California) and a lower percentage (or at least fewer edges and patches) of the younger seral forest stages than unoccupied plots (Table 2). However, in one of the GIS maps (CA map in Table 2), the matrix was more fragmented in occupied plots, as we found occupied plots had fewer core areas in all patch types on the landscape as a whole (associated with more and smaller patches), even though the plots had a larger number of large, old-growth core areas. Thus, the matrix was responsible for the low number of core areas overall. Finally, matrix patch shapes were simpler in large occupied plots.

Marine habitat descriptions
Some of the marine variables selected in models of California alone changed when Oregon was included. For California, distance to high spring marine chlorophyll and submarine canyons was important (CA results in Table 2). When Oregon was included, distance to high summer chlorophyll and bays became important (CA/OR in Table 2). The importance of these marine features was not just due to a high correlation with distance to the ocean, at least when Or-

Table 2. Coefficients of predictor variables in logistic regression models of murrelet occupancy for southern Oregon (OR) and/or California (CA). Sample size (n_A = all plots, n_F = plots in fog zone only) is shown on the left and right of the forward slashes for the original and independent validation datasets, respectively. Accuracy$_F$ is the percentage of plots in which murrelet occupancy was correctly predicted in the fog zone and is also shown on the left and right of a slash for the original and validation datasets (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, and **** = $P < 0.0001$)

	Plot radius			
	400 m	800 m	1600 m	3200 m
CA/OR map – 0.06 ha resolution	*n_A = 691/295*	*603/256*	*418/110*	*185/46*
	n_F = 273/113	*227/101*	*164/46*	*70/20*
	Accuracy$_F$ = 84%/84%[a]	*85%/83%*	*89%/93%*	*88%/83%*
Variable				
Isolation > 5 km****	−4.5287	−4.4333	−4.2175	−6.3578
Elevation***	−0.0058	−0.0058	−0.0054	−0.0109
Unfragmented OG[b] in mid-1980s***	2.0855	1.7898	2.1667	4.7607
Seedling-sapling-pole (%) ***	−0.0675			
Edge density of OG patches***	0.0102			
High summer marine chlorophyll distance*	−0.0509	−0.0912	−0.0575	
Distance to major bay*		−0.0172		
Patch density of small hardwoods*		−0.0534	−0.0401	
OG and medium-sized conifer (%)****		0.0853		
Area-weighted mean fractal dimension of OG****			16.8966	
Landscape mean shape index**				−54.7987
Mean core area OG (50-m edge distance)*				11.2644
Fog zone[c]	6.3401	9.9915	7.9419	7.5119
Constant	−4.3211	−4.7755	−22.7642	65.4655
CA map - 4-ha resolution	*n_A = 480/208*	*405/165*	*288/73*	*127/36*
	n_F = 165/66	*125/51*	*93/29*	*44/13*
	Accuracy$_F$ = 85%/88%	*84%/80%*	*89%/93%*	*98%/92%*
Variable				
OG (%)****	0.0675	0.0824		
Elevation****	−0.0060	−0.0073		
Isolation > 5 km****	−3.8202	−8.0315	−3.8239	−5.6390
Unfragmented OG in mid-1980s*	1.7421	1.8316	1.7647	
High spring marine chlorophyll distance**	−0.0558		−0.0907	−0.0971
Landscape core area density (100-m edge distance)**			−1.2528	
Distance to submarine canyons*			−0.0979	−0.1217
OG core area density (100-m edge distance)****			6.9796	
Contrast-weighted edge density of OG****				0.6448
Edge density of patches of small conifers***				−0.0894
Fog zone**	8.3275	8.6234	13.9246	12.0732
Constant	−7.0774	−7.8344	6.0633	−1.0894

[a] To determine accuracy, the cutpoint (probability percentage) used to separate occupied from unoccupied plots was set at a value that produced the least misclassification of occupancy of the original dataset (ranged from 50 to 63%).

[b] OG = old-growth forest.

[c] At 3200-m radius, $P = 0.2794$ for the Fog zone coefficient, but $P < 0.01$ at the three smaller scales. Note: if just plots within the fog zone are modeled and fog zone is dropped as a variable, the regression coefficients in this table do not change except for the constants.

egon was included (correlations with distance to ocean were < 0.9). However, for California alone, many marine variables, including distance to ocean, were highly correlated to the selected model variable “distance to high spring chlorophyll”. These correlates ($r > 0.9$) indicated occupied plots in California

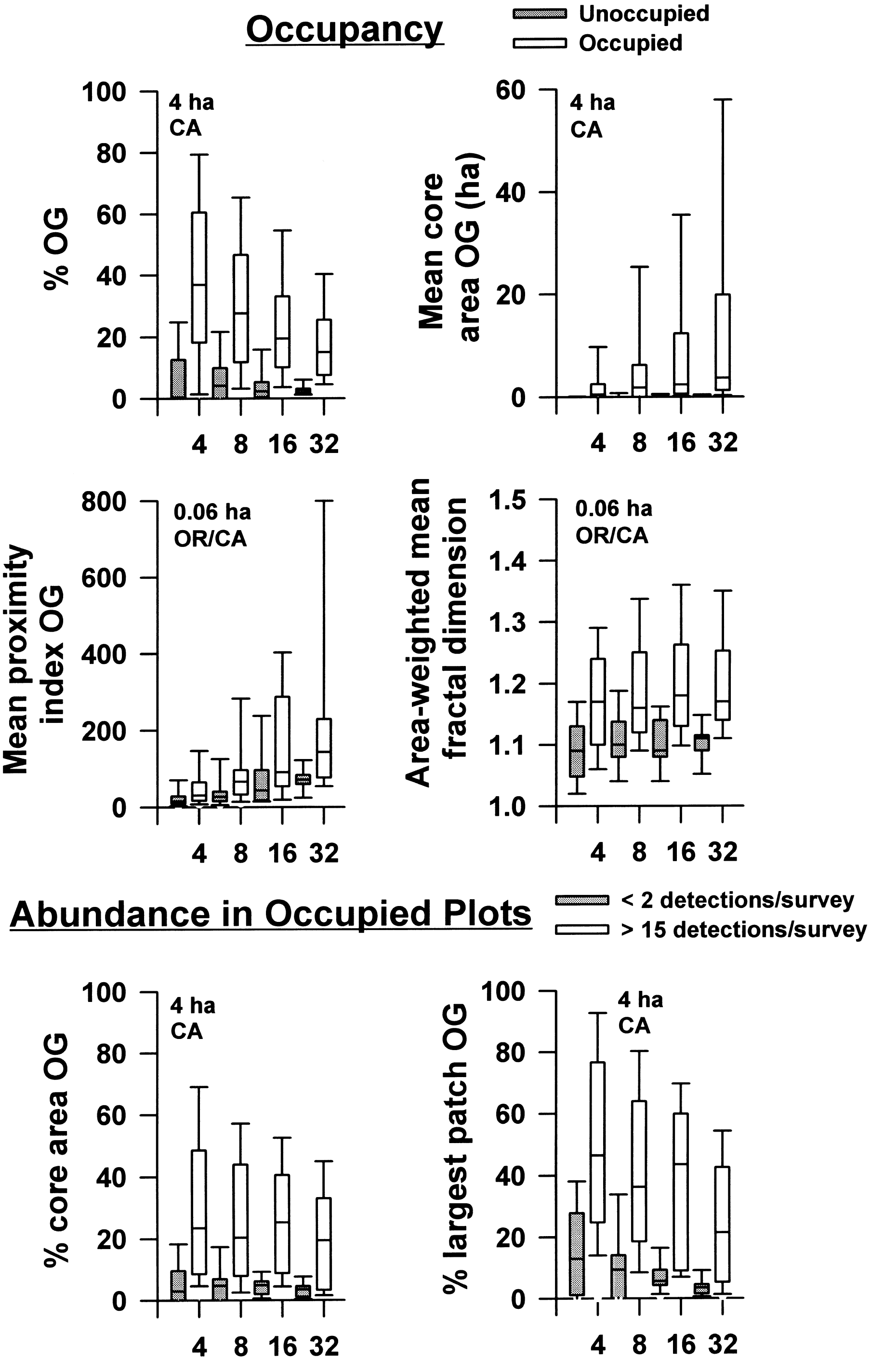

Figure 2. Distribution of some fragmentation variables in non-isolated plots within the murrelet nesting range using boxplots (median = line in box, 25th and 75th percentile = box ends, and 10th and 90th percentile = bar caps). Map resolution and area are in upper left corner of graph. OR = southern Oregon, CA = California, OG = old-growth. Core area has a 100-m (occupancy) or 50-m (abundance) edge distance.

Table 3. Coefficients of predictor variables in multiple linear regression models of inland murrelet abundance (mean detections per survey in occupied plots) in southern Oregon (OR) and/or California (CA). Sample size (n) is on the left and right of forward slash for the original and validation datasets, respectively. R^2 is also shown for the original and validation datasets on the right and left of a slash. (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, and **** = $P < 0.0001$)

	Plot radius			
	400 m	800 m	1600 m	3200 m
CA/OR map – 0.06-ha resolution	*n = 147/52*	*127/47*	*86/37*	*42/13*
	R^2 = 0.51/0.37[a]	*0.53/0.52*	*0.61/0.46*	*0.52/0.69*
Variable				
Elevation****	−0.0011	−0.0012	−0.0015	
Edge density of OG[b] patches**	0.0022	0.0027		0.0121
Protected in national or state park*	0.3543		0.3120	2.1550
High spring marine chlorophyll distance****		−0.0110		
Mean patch size OG****			0.3230	
Distance to road*			0.2840	
Landscape patch density**				−0.0103
Constant	0.6130	0.9188	0.5970	3.4097
CA map – 4-ha resolution	*n = 99/37*	*75/31*	*58/22*	*26/11*
	R^2 = 0.58/0.35	*0.66/0.52*	*0.71/0.71*	*0.77/0.79*
Variable				
Elevation***	−0.0009	−0.0012	−0.0016	
OG (%)****	0.0073			
High summer marine chlorophyll distance***	−0.0130	−0.0164	−0.0214	
Small conifer (%)**	−0.0084			
Edge OG per area OG***		−0.1150		
Protected in national or state park**		0.2686		
Largest OG patch (%)**			0.0091	
Patch density seed-sap-pole conifer**			−0.3340	
Distance to fine sand beach****				−0.1260
OG core area (50-m edge distance)(%)***				0.0750
Land in medium conifer (%)**				0.0413
Constant	1.1732	1.640	1.5244	3.5183

[a] Predicted abundance values of independent plots were regressed against observed values to assess R^2 for validation datasets.

[b] OG = old-growth forest.

were also relatively close to river mouths, sandy beaches, and the ocean.

Landscapes with abundant murrelets

Changes in variables and scale when using abundance

When we used abundance as our bird metric in multiple regression models to predict habitat, we found some differences in variables and scale. Many of the variables predictive of occupancy were also predictive of abundance, but two new variables became important: use of parks and farther distance from roads (Table 3).

Old-growth fragmentation

In contrast to occupancy results, when we used abundance as our metric in CA models, current old-growth fragmentation was much more important across all landscape scales except the smallest plot size (CA map in Table 3). In the larger plots, less edge per area, larger maximum patch sizes, and more total core area were more predictive than just percentage of the landscape in old-growth (CA map in Table 3, Figure 2). However, relative to such fragmentation variables, we found shape complexity of old-growth patches and edge contrast were not very predictive of abundance, although they were predictive of occupancy (Table 2). Total edge of old-growth in a plot was predictive in the models based on fine resolution maps (CA/OR map in Table 3) but not the coarse resolution maps. At the fine scale only, streams finely and extensively dissected the otherwise contiguous large blocks of old-growth that contained abundant murrelets.

Time lag and isolation

Two other variables differed when we used abundance instead of occupancy. First, a time lag in response to old-growth fragmentation was not important to abundance. Although present, birds were not abundant in recently fragmented forests. Second, isolation was not selected in models of abundance (Table 3).

Fragmentation and composition of the entire landscape

The effect of fragmentation of all patch types in the landscape within a plot was the opposite for abundance than for occupancy. As abundance increased, we found less fragmented landscapes as a whole: patch density was lower (Table 3) and mean patch size and contagion were higher, edges were fewer, and patch shapes less complex ($r > 0.9$ with patch density). In contrast, occupied plots often had more fragmented landscapes due to the fragmented matrix. The composition of the matrix in medium-sized conifer forest did shift in the expected direction between occupied and abundant-bird plots (from a mean of 17% in occupied to 21% in abundant plots, based on 1600-m radius, 4-ha-resolution plots).

Marine habitat

Comparing the maps of high chlorophyll areas (Figure 1), occupied plots were generally close to coasts with either high spring or summer chlorophyll, whereas plots usually had high bird abundance only if a nearby coast had high chlorophyll present during both seasons. The regression models further support such an observation. For example, in California, summer chlorophyll was generally more important for predicting abundance, whereas spring chlorophyll was more important for predicting occupancy. The opposite occurred when the GIS map included Oregon (compare Tables 2 and 3). Areas with high chlorophyll were scarce in the spring in Oregon, but where they did occur, nearby plots had a high abundance of murrelets (Figure 1). By contrast, in California, high chlorophyll areas were scarcer in summer, and plots with high abundance were close to these areas. Plots with high abundance were also close to fine sandy beaches (CA map in Table 3), areas closely associated with areas of high marine spring chlorophyll ($r > 0.9$).

Shift in variable means

By using abundance in addition to occupancy, we further refined the range of characteristics most important for high habitat quality. The mean or median value for variables in occupied plots usually shifted in our hypothesized direction in high abundance plots (> 15 detections per survey, Figure 3), and the variance decreased. For example, in the fog zone, mean elevation of occupied plots was about 400 m (standard deviation = 186), but in plots with abundant birds, it shifted to less than 200 m (standard deviation = 137). The direction of that shift was expected, because both the occupancy and abundance regression models indicated murrelet use should increase with decreasing elevation. If the variable means did not shift in the expected direction, the results would be more questionable. Similar predicted directional shifts in the means occurred for other variables: distance to high chlorophyll (from 23 to 9 km for spring chlorophyll), distance to fine sandy beach (from 14 to 9 km), and percentage in old-growth core area (7% to 19% for 3200-m radius plots, given a 50-m edge distance). Overall, the amount of contiguous old-growth forest required to support abundant murrelets was much greater than that required for occupancy. Threshold values of old-growth variables at which landscape plots (1600-m radius, 4-ha resolution) were always occupied were 20% of land in old-growth, 6% in core area, 12% in largest patch, one core area per 100 ha, mean patch size of 11 ha, and mean core area of 3 ha. For plots to always have abundant murrelets (> 15 detections per survey), such threshold values were 55% of land in old-growth, 19% in core area, 53% in largest patch, 2 core areas per 100 ha, mean patch size of 55 ha, and mean core area of 36 ha.

Accuracy of results

The percentage of plots with correctly predicted murrelet use was high for all the logistic regression models, ranging from 90 to 95%. Because it is easy to predict no occupancy in plots outside the fog zone, the accuracy of all plots within just the fog zone is of greater interest and was > 80% (Table 2). The independent validation data sets similarly had high accuracy within the fog zone for occupied, unoccupied (each evaluated separately), and all plots combined

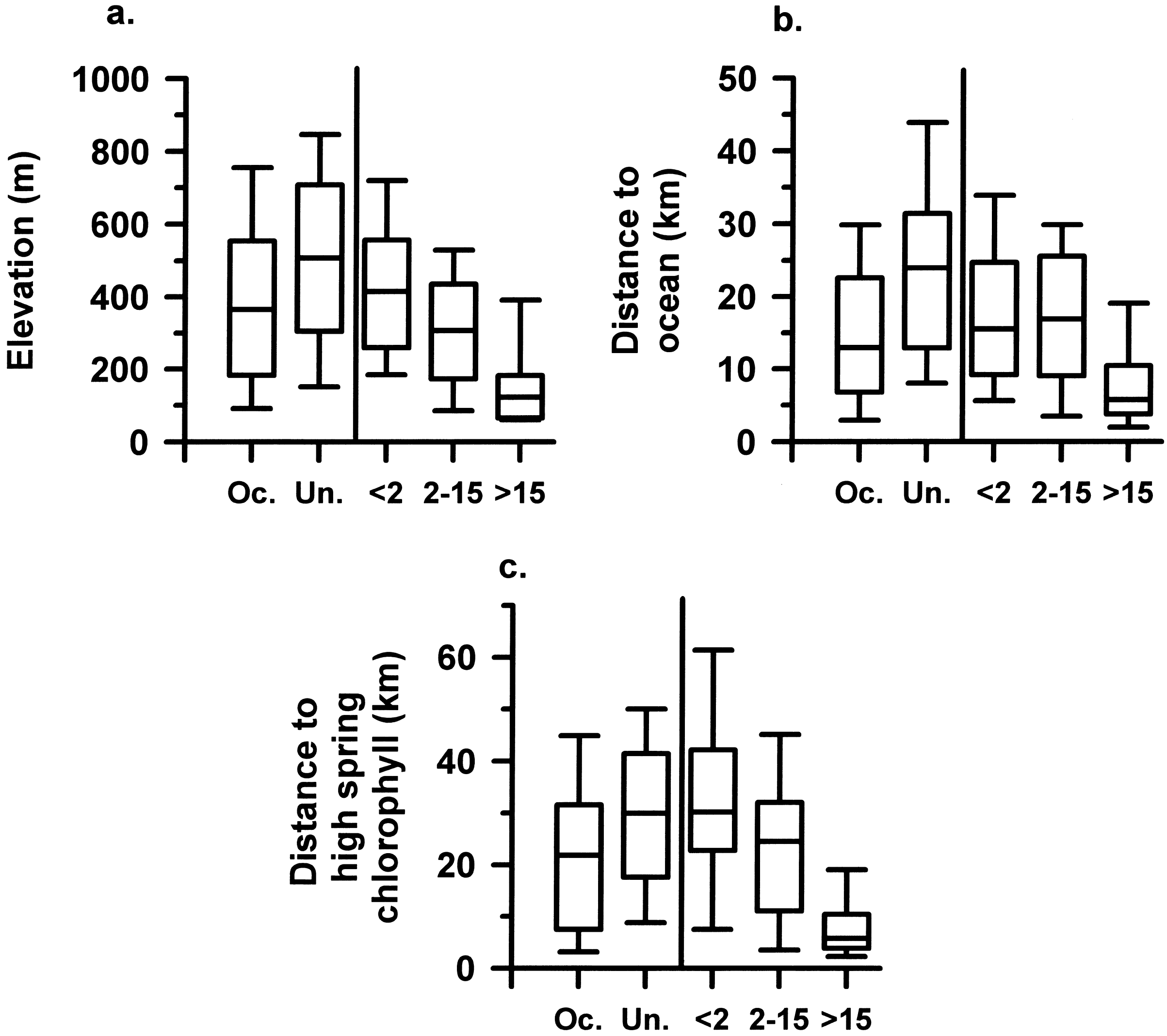

Figure 3. Distribution of elevation and two marine variables in occupied (oc.) and unoccupied (un.) plots compared to occupied plots that had high (> 15 detections per survey), medium (2–15), and low (< 2) murrelet abundance in the entire study area using boxplots (median = line in box, 25th and 75th percentile = box ends, and 10th and 90th percentile = bar caps). Note that distance to ocean does not separate medium and low abundance plots as well as distance to areas of high chlorophyll concentrations.

(always > 80%). Accuracy, as well as other measures of regression model fit (e.g., Nagelkerke R^2, see Meyer (1999)), tended to be best in the largest plot sizes, possibly due to the increased precision that results from having a larger number of survey stations. The accuracy of these models using the independent large plots was also relatively high when the data were divided into four geographic subsections of the study area. In that assessment, predictability, rated from 0 to 1 (random to perfect, using Somer's d; Somers (1962)), was mostly $\geqslant$ 0.8 in each subsection for 1600-m and 3200-m radius plots. In the linear regressions, variance in murrelet abundance explained by the habitat variables exceeded 70% for both the original and validation datasets using the coarse-resolution, 1600-m and 3200-m radius plots on the CA map but was lower at smaller plot sizes (see R^2 of CA map in Table 3) and using the CA/OR map (Table 3).

Only 400-m and 1600-m radius plots in the CA/OR abundance models had significant spatial autocorrelation ($P < 0.05$ for Moran's I and a variogram range > 0). Variograms indicated that the distance beyond which spatial autocorrelation became unimpor-

Table 4. Comparison of standardized coefficients and increase in R^2 among model variables in multiple linear regressions on murrelet abundance (multiple R^2 also shown).

	Plot radius							
	400 m		800 m		1600 m		3200 m	
Variable	Std. coeff.	R^2 inc.	Std. coeff.	R^2 inc.	Std. coeff.	R^2 inc.	Std. coeff.	R^2 inc.
CA map								
	Multiple R^2 = 0.48		*= 0.58*		*= 0.64*		*= 0.79*	
Elevation	–0.413	0.16	–0.451	0.18	–0.464	0.19	–0.269	0.06
Core area OG[a] (%) (50-m edge distance)	0.323	0.10	0.329	0.10	0.372	0.13	0.379	0.12
Distance to high marine summer chlorophyll	–0.269	0.06	–0.309	0.08	–0.275	0.07	–0.559	0.28

[a]OG = old-growth forest.

tant was about 9,000 m for 400-m radius plots and 21,000 m for 1600-m radius plots. The adjustments that would be required in the regression coefficients to account for the correlation were mostly minor, but generally standard errors increased. When tested with the new standard errors and coefficients, the model variables were still significant ($P < 0.05$) except for old-growth mean patch size in the 1600-m radius model ($P = 0.11$). Hence, the significance of this one variable was overestimated (CA/OR map, Table 3), and the results for the other models are more reliable.

Variables most limiting to murrelet abundance

We divided variables into three categories: topographic, marine, and old-growth. To assess which type contributed the most to murrelet abundance, we included one of each type (elevation, distance to high summer chlorophyll, old-growth core area) as independent variables in a multiple linear regression using the coarse-resolution CA map. Murrelet abundance in occupied plots (included original and validation plots combined) was the dependent variable. We considered the most limiting habitat variable the one with the largest absolute value of the standardized coefficient and the one that caused the largest change in R^2.

Of the three variables, distance to high marine chlorophyll had the highest absolute value of the standardized coefficient and increase in R^2 in 3200-m radius plots (Table 4). However, at all smaller plot sizes, elevation followed by the old-growth variable were potentially most limiting. Murrelet abundance appeared to be most limited by the availability of large landscapes (3200 ha) that contained local (50–800 ha) low elevation areas with abundant old-growth forest, and such large landscapes had to be close to marine waters with high primary productivity. The same results were found when we used the CA/OR map (using elevation, distance to high spring chlorophyll, and old-growth edge, Meyer (1999)).

Discussion

Patch characteristics

Tree size

In contrast to our prediction (hypothesis 1), mean tree size within old-growth forest patches was not very predictive of murrelet use after other variables were accounted for in the model. Old trees that are relatively small may still be large enough to provide suitable nest platforms, especially if branches are effectively thickened by epiphytes, litter, or mistletoe deformations (Hamer 1995). Nonetheless, mean dbh alone was significantly higher ($P < 0.05$, ANOVA) in occupied than in unoccupied plots in the fog zone (137 vs. 99 cm).

Elevation, parks, and roads

As hypothesized, elevation was an important factor in many models, although slope and proximity to streams were not. Most stations with abundant birds were below 200 m, below many of the ridges. Wind desiccation on ridgetops may reduce nesting by stunting growth of platform branches (Daniel 1942). Also as predicted, areas with abundant birds were farther from roads and more often in parks protected from logging. By contrast, we did not find any effect of these features on occupancy. Protection in parks was an important variable even when old-growth fragmentation or distance to roads was taken into account (1600-m radius, CA/OR model in Table 3). Many of the parks in the study area not only have large unfragmented patches of old-growth forest and low road density, but also relatively low disturbance. Although some observers have found that incubating adults and chicks did not abandon their nests following sharp, loud or prolonged noises including traffic (L. Long, personal communication), our study indicates that more research is needed on the effects of road or logging noise and other disturbances on nesting birds.

Present and past landscape characteristics

Old-growth fragmentation

As hypothesized (hypothesis 2), fragmentation and isolation of old-growth forest had an adverse effect on both murrelet occupancy and abundance. Fragmentation variables, such as old-growth core area, were more predictive than area of old-growth forest alone. Fragmentation effects were also most identifiable in the larger-sized landscape plots, which gave the most predictive models. As hypothesized (hypothesis 5), the effect of fragmentation on occupancy was not immediate. Murrelets more often occupied recently fragmented old-growth forest, as compared to forests fragmented before the mid-1980s. Not accounting for the time lag in response to fragmentation may be why Miller and Ralph (1995) did not find old-growth patch size affected murrelet occupancy. Their study area included many small fragments in recently harvested areas. In contrast to effects on occupancy, the effect of fragmentation on abundance appeared to be more immediate. Birds were often present, but the number of birds found in more recently fragmented forests (post-mid-1980s) during each survey was relatively low.

The adverse effect of fragmentation may result from increased predation on nests near old-growth forest edges, which could eventually cause the birds to abandon or disappear from small old-growth patches with high edge/area ratios. In our study, old-growth with large core areas over 50 or 100 m from the patch edge had higher occupancy and abundance than patches with little or no core area. The edge distance most predictive of murrelet abundance was larger than that (150 m) when habitat was more liberally defined as “old-growth plus residual forest” in southern Oregon and California (Meyer 1999). Actual nest data further supports that the adverse edge effect may extend up to 50 to 150 m into the patch. Of a sample of 77 murrelet nests, Manley and Nelson (1999) reported that 62% of murrelet nests > 50 m from an edge succeeded, whereas only 38% of those located closer to the edge succeeded. In British Columbia, none of 25 known nests > 150 m from edges failed from predation (I. Manley, personal communication).

Paton (1994) reported that mostly patches < 10 ha with < 4.7 ha of core habitat had high nest predation rates for a number of forest bird species, compared to larger patch sizes. His patch and core sizes are surprisingly similar to our finding that occupied plots had a mean patch size $\geqslant$ 11 ha and mean old-growth core area $\geqslant$ 3 ha. In addition to increased risk of predation, nest failure along edges may be increased by exposure to high heat or evaporative water loss, factors which may stress a coldwater-adapted seabird. Within old-growth Douglas-fir forests in Washington, Chen et al. (1993) found that edges had higher afternoon temperatures and lower humidity than interiors.

Our results for this study using just the California map were similar to results in our previous study on the Siskiyou National Forest in southern Oregon (Meyer and Miller 2002). Although in that study, we evaluated fragmentation of old-growth/residual habitat rather than just old-growth, the characteristics of variables predictive of high probability of occupancy in both studies were low old-growth fragmentation, low elevation, and close proximity to the coast, which had high summer chlorophyll concentrations.

Matrix composition and fragmentation

The matrix surrounding old-growth forest in occupied landscapes contained less young forest and more mature forest than unoccupied landscapes, but contrary to our hypothesis it was less contiguous in occupied landscapes. The composition of the matrix appeared to be more important to murrelets than the level of fragmentation of the matrix because the latter varied from analysis to analysis. For example, in landscapes with the most abundant murrelets, we found a more contiguous matrix was common, but such a result did not hold true for our occupied landscapes, occupied landscapes in Washington (Raphael et al. 1995), or for landscapes with abundant murrelets on the Siskiyou National Forest (Meyer 1999).

In Washington, the murrelet-occupied landscape as a whole had more complex shapes (Raphael et al. 1995), whereas ours had simpler shapes. Common to both areas were large old-growth forest patches and more abundant mature second-growth. We hypothesized that mature forest may reduce nest predation in old-growth habitat because, when adjacent to old-growth, such forest provides less edge contrast and hence may support fewer nest predators that prefer sharp edges. Recent research in Oregon suggests that murrelet nest predation rates are reduced in remote old-growth fragments surrounded by older regenerating forest than those surrounded by young berry-producing clearcuts (Marzluff and Restani 1999). However, in that study, fragments surrounded by clearcuts lacking berry-producing shrubs also had low predation rates. Moreover, in our study, we found high contrast edge of old-growth did not deter murrelets from using an area. More research is needed to fully understand the effects of nearby mature second-growth forest on nesting murrelets.

Sub-regional habitat characteristics

This was the first study of murrelets that examined the relationship of inland use of landscapes to many different marine environments across sub-regions. As expected (hypothesis 3), forest habitat used throughout the study area was generally closer to sandy beaches and certain types of marine areas with high productivity—specifically, bays, river mouths, submarine canyons, and areas with high spring or summer chlorophyll concentrations (an indicator of high primary productivity). These features have been shown to potentially concentrate murrelet prey (Burkett 1995; Hunt 1995; Pearcy and Schoener 1987; Schoenherr 1991). Other marine research in Oregon supports the importance of sandy shores, bays, and river mouths to murrelets (Strong 1995; Varoujean and Williams 1995).

Murrelets can have high energy expenditures flying daily to and from nest sites, which limits the inland distance of nests. Flight distances for all our occupied sites averaged 15 km from the ocean and 16 km from shores having high summer marine chlorophyll, which is farther than most alcids must travel from nest sites to foraging areas (Cody 1973). Distance travelled has a limit, however. The greatest distance for an occupied plot was less than 40 km, even where the preferred fog-influenced vegetation zone extended farther inland.

Regional habitat characteristics

As expected regional elevation trends and vegetation zone were important (hypothesis 4). No murrelets occupied zones or plots at elevations above 1,212 m in our study area. The ranges of the redwood and western hemlock zones, the zones that contained almost all the inland murrelet observations, do not extend much above 1,000-m elevation. Because fog typically flows through low elevation zones, the regional effect of elevation is probably related to fog influence. Foggy, coastal vegetation appears to provide a cool, moist, nesting environment for a seabird adapted to cold water conditions. The fog zone also provides larger trees than adjacent zones (Dillingham et al. 1995; Meyer 1999), and such trees may provide more abundant nest platforms. Notably, being in the fog zone appears to be more important than close proximity to the ocean. In California, old-growth stands of Douglas-fir close to the ocean and influenced by strong, desiccating winds flowing offshore (Zinke 1977) were unoccupied, whereas the adjacent more inland redwood stands within the fog zone were occupied. Energetic studies of the murrelet are needed to determine if heat or evaporative stress is an important factor in nesting distribution.

Occupancy and abundance metrics

Many of the habitat variables that explained occupancy also explained relative abundance in occupied plots and were consistent with our hypotheses. But as predicted (hypothesis 6), we found abundance a more precise and accurate measure of habitat quality than occupancy, which only evaluated absence versus presence of potential nesting birds. For example, old-growth fragmentation was less and consistently less variable in plots with abundant birds (> 15 detections per survey) than in occupied plots. Similarly, plots with abundant birds were at lower elevations and much closer to the ocean and productive marine areas than the average occupied plot.

In this discussion, we are assuming occupied landscapes represent areas used for nesting because birds exhibited behaviors that have been observed around nests. However, actual nests were not identified in the landscape (nests are extremely difficult to find), and we could be in error for some areas. Similarly, number of murrelet detections are not an actual count of individual nesting murrelets. The number of birds observed at a survey station often varies widely day to day (Jodice and Collopy 2000). Such high variability would be expected to make this index a poor predictor of habitat, yet the high accuracy of our large plot models in predicting murrelet detection levels suggests that number of detections averaged over large landscapes may reduce that variability and therefore serve as a useful index. Another potential problem with using murrelet detections as an index to abundance is that some birds observed in occupied plots may just be flying over the area to a more inland nest. Therefore, our "abundance" metric (but not the occupancy metric) may somewhat overestimate the importance of distance to productive marine habitat because the birds start flying inland on the coast and may be observed more often near these areas when flight paths are over old-growth. To reduce the problem of including landscapes that served as travel corridors, we deleted "flyover" plots from abundance analyses. Future studies of actual nest abundance could help confirm or refute our interpretation that inland habitat within 20 km of areas of high marine chlorophyll are used the most for nesting.

Even if detections are a good index to abundance of nesting murrelets, animal abundance is not always a good indicator of habitat quality (Van Horne 1983). Some of our habitat areas may be population "sinks" (murrelets are unable to replace themselves), and high abundance observed there could be from an influx of immigrants from nearby, more productive areas (Pulliam 1988). Such may be the case for small, old-growth patches located near large patches of high quality habitat. In small sample plots that capture only small patches and miss nearby large patches, the plot's habitat quality could be rated too high based on abundance. In the larger plots, the nearby large patch may be included, but the overall quality of the landscape would still be rated very high and not account for some of the low quality patches in the plot. Clearly, our methods do not adequately address spatial relationships of each individual patch within a plot, which could be a subject of future research. Instead, our methods provide insight into landscapes where birds are commonly observed and are possibly abundant. Future studies of fragmentation and distance to marine habitat using measures of bird fitness (i.e., breeding success and survival) could help define the actual habitat quality of such areas and demonstrate if the abundance measure we used is a good estimate of habitat quality.

Marine compared to inland habitat factors

At local scales of 50 to 800 ha, terrestrial habitat appeared to be more limiting to inland murrelet abundance than proximity to marine habitat (Table 4). Similarly, in the logistic regression functions on occupancy, inland variables were more significant than marine habitat variables across all plot sizes (Table 2). Marine primary productivity was the most limiting for murrelet abundance only when evaluated at the largest (and most predictive) landscape scale (3200 ha, Table 4), particularly in California. Thus, marine habitat conditions may set the stage for expected murrelet abundance over large areas inland, whereas the local terrestrial conditions may determine the relative abundance within portions of the large inland areas. Some areas where marine habitat proximity appears to have set the stage for murrelet abundance inland include: (1) near Point Arena in the central part of the California study area with its scarce nesting habitat, but high murrelet abundance (> 15 detections per survey in one drainage), possibly because of nearby marine areas sustaining both high spring and summer productivity; and (2) the southern portion of the Oregon study area, which had some good nesting habitat but relatively low nearby chlorophyll concentrations during the spring and correspondingly low bird abundance (Figure 1).

Importance of studying multiple temporal and spatial scales

Clearly, our results suggest that multiple spatial scales should be investigated for species that cover large areas or use spatially segregated habitat types. Four major spatial scales—local, landscape, sub-regional, and regional—all had variables with strong and important effects on murrelet use. Regional characteristics, such as fog zone, elevation, and maximum distance to the ocean were excellent delimiters of the nesting range of the murrelet. Sub-regional characteristics (distance to productive marine habitat and sandy shores) and landscape characteristics (old-growth fragmentation) helped further predict where murrelets were likely to be found or were abundant within the newly defined nesting range. At the local level, low areas below ridgetops, distance to roads, and location within parks added to our predictive capability. In contrast, many patch characteristics frequently studied by murrelet researchers such as mean tree dbh of old-growth forests, slope, aspect, and closeness to streams (Grenier and Nelson 1995; Hamer 1995), did not improve predictions of murrelet occupancy or abundance. If broad spatial scales across large geographic regions are ignored, habitat predictions can be weak.

Not just seabird studies, but many studies of wildlife habitat could benefit from our approach of combining into one model variables measured at vastly different spatial scales, from large, regional or statewide areas down to landscapes and local habitats. Most habitat studies have modeled only one of those scales or each separately, and thus are often unable to obtain predictive power as high as ours. Spatial modeling at different scales is particularly important for any species that has frequent and large within-season movements between different habitats. For example, many waterbirds use different types of wetlands and uplands over large areas (Haig et al. 1998), and proximity and quality of those habitats should be considered.

Our results also demonstrate that temporal effects are important to evaluate. The relatively recent history of logging accounts for why some heavily fragmented old-growth forests are still used today. When such temporal effects are ignored, one can easily interpret habitat use incorrectly and assume fragmentation does not affect murrelet use in some areas. To fully ascertain the deleterious effects of habitat loss or fragmentation over time, our study demonstrates that long-term monitoring of habitat and animal population changes is important for long-lived (more than a couple of years) species with high site fidelity, which includes many species of birds (Divoky and Horton 1995; Clark and Shutler 1999; Ganter and Cooke 1998), mammals (Labisky et al. 1999; Leptich and Gilbert 1989), and some reptiles and amphibians (Marvin 2001; Freilich et al. 2000). Fortunately, the present availability of satellite imagery and associated GIS variables can lend a great deal of information to the process of determining multiple-scale habitat relationships in both space and time.

Habitat recommendations

Our results indicate that management efforts in the study area, and probably elsewhere in the range of the species, should focus on protecting or creating large, contiguous blocks of old-growth forest, especially in low-elevation areas near productive marine habitat. Such habitat requirements of the murrelet appear to be fairly consistent across the study area. We believe that the regression models at the larger plot sizes can be used throughout the study area to predict occupancy and relative abundance with reasonable accuracy (> 80% for occupancy). The regressions can also be used to more fully understand the potential costs or benefits to murrelets of specific management scenarios within the study area. Future research should test whether landscape/seascape patterns observed in this study are applicable for other parts of the species' range. Also, more work should focus on studying the mechanistic factors, such as predation and microclimate, that might be producing the statistical relationships found in our study.

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