Use of Fragmented Landscapes by Marbled Murrelets for Nesting in Southern Oregon

C. B. MEYER*† AND S. L. MILLER†

*Department of Botany, University of Wyoming, Laramie, WY 82071-3165, U.S.A., email meyerc@uwyo.edu
†Pacific Southwest Research Station, U.S. Forest Service, 1700 Bayview Drive, Arcata, CA 95521, U.S.A.

Abstract: *As old-growth forest becomes more fragmented in the Pacific Northwest (U.S.A.), species dependent on large patches of old-growth forest may be at greater risk of extinction. The Marbled Murrelet (*Brachyramphus marmoratus*), a seabird whose populations are declining in North America, nests in such old-growth forests or forests with large remnant trees. Using logistic regression models on landscapes in southern Oregon, we addressed (1) whether old-growth forest fragmentation was associated with use of an area by murrelets and (2) whether proximity to certain marine features was associated with use of forest fragments by murrelets. On a geographic information system vegetation map derived from satellite imagery, we placed circular plots of 400-, 800-, 1600-, and 3200-m radius over surveyed inland areas occupied or unoccupied by murrelets. Within each plot, spatial and other land- and seascape habitat variables were calculated and regressed against murrelet occupancy. Murrelets generally occupied low-elevation inland sites in landscapes with relatively low fragmentation and isolation of old-growth forest patches, and these sites were close to the coast, river mouths, and a major bay. Almost all occupied landscapes occurred in a fog-influenced vegetation zone. Because nesting habitat with large amounts of interior forest is currently scarce in southern Oregon, management efforts should focus on protecting or creating large, contiguous blocks of old-growth forest, especially in areas near the coast.*

Uso de Paisajes Fragmentados para Anidación por el Mérgulo Marmoleado en el Sur de Oregon

Resumen: *Debido a que los bosques maduros están siendo más fragmentados en el Pacífico Noroeste (USA), las especies que dependen de parches grandes de bosque maduro pueden estar en un punto de mayor riesgo de extinción. El Mérgulo Marmoleado (*Brachyramphus marmoratus*) es un ave marina con poblaciones en disminución en Norteamérica que anida en estos bosques maduros o bosques con árboles grandes remanentes. Empleando modelos de regresión logística en paisajes del sur de Oregon, abordamos (1) si la fragmentación del bosque maduro estaba asociada con el uso del área por el mérgulo y (2) si la proximidad de ciertas características marinas estaban asociadas con el uso de fragmentos de bosque por el mérgulo. En un mapa de vegetación de GIS derivado de imágener de satélite, colocamos parcelas circulares de 400-, 800-, 1600- y 3200-m de radio sobre un área del interior ocupadas o desocupadas por mérgulos. Dentro de cada parcela, se calcularon y analizaron variables espaciales y otras variables terrestres y marinas en regresión contra la ocupación del mérgulo. Los mérgulos generalmente ocuparon sitios del interior de baja elevación en paisajes con relativamente poca fragmentación y aislamiento de parches de bosque maduro y estos sitios estuvieron cercanos a la costa, bocas de ríos y una bahía grande. Casi todos los paisajes ocupados ocurrieron en zonas de vegetación influenciadas por la neblina. Debido a que el hábitat de anidación con grandes cantidades de bosque interior es actualmente escaso en el sur de Oregon, los esfuerzos de manejo se deberían enfocar en la protección o creación de bloques de bosque maduro contiguos y grandes, especialmente en áreas cercanas a la costa.*

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Introduction

Within the Pacific Northwest (U.S.A.), only about 13–17% of the original old-growth forests that preceded European settlement remain (Booth 1991), and many have been fragmented (Harris 1984). Interior-restricted forest species are more likely to become extinct in such fragmented landscapes, causing a loss of regional biodiversity (Wilcox & Murphy 1985; Harrison & Fahrig 1995). For many species, habitat fragmentation not only causes a direct loss of habitat but also increases isolation of populations, decreases colonization, and increases mortality due to increased edge (Rolstad 1991; Lawton 1995). For interior-forest bird species, the increased edge often increases nest predation in the remaining breeding habitat (Paton 1994; Robinson et al. 1995) or creates a more adverse microclimate for nesting birds (Matlack 1993), which may lead to increased mortality and ultimately contribute to extinction of the species. It is often unknown, however, which bird species are interior specialists at risk of extinction. More research is needed to identify interior specialists dependent on habitats that are rapidly being fragmented.

A high-profile species in the Pacific Northwest that is closely associated with old-growth forests (defined by Franklin et al. 1986) and at risk of extinction is the Marbled Murrelet (*Brachyramphus marmoratus*). This seabird nests primarily on large, stout branches of large-diameter trees in old-growth forests or in old, remnant trees in second-growth forests (Hamer 1995; Hamer & Nelson 1995). In 1992 the bird was federally listed as a threatened species in Washington, Oregon, and California. Loss of nesting habitat from extensive timber harvest is believed to be one of the principal causes of the bird's apparent decline (Miller et al. 1997), but it is unknown whether fragmentation of such habitat is associated with the decline. If the murrelet is an interior specialist, preservation of small old-growth remnants may be less important for its recovery than preservation of large, contiguous blocks of old-growth forest with abundant interior habitat. Should we find that murrelet occupancy is associated with high amounts of interior habitat, the resultant habitat management directed toward the recovery of the murrelet might also maintain many other interior old growth–dependent species in the region, thus preserving regional biodiversity.

Habitat studies have been conducted on murrelet nest trees (Hamer & Nelson 1995) and on within-stand characteristics (Grenier & Nelson 1995; Hamer 1995; Miller & Ralph 1995), but the predictive capability of such habitat models has been relatively low. Studies at larger spatial scales that incorporate fragmentation across landscapes may be required to better predict murrelet habitat use. To date, only one murrelet study, conducted in Washington, has used many landscape-level spatial variables (Raphael et al. 1995).

A unique characteristic of this seabird is that it spends substantial time in two very different habitats: nesting in terrestrial forests and foraging in nearshore marine waters (Ralph et al. 1995). In Alaska, Kuletz et al. (1995) found murrelet occupancy to be highest in forests closer to heads of bays, but no studies in the conterminous United States have determined whether some potential nesting areas are used more than others due to their proximity to high-quality marine habitat that provides abundant food for nesting birds. Studies have addressed the importance of the proximity of old-growth forest to at-sea locations or densities of murrelets (Ralph & Miller 1995; Lougheed 2000), but our study is the first study to evaluate inland use of fragmented landscapes by murrelets while attempting to account for nearby marine habitat requirements. Our specific objectives were to develop predictive statistical habitat models that quantify the relationship of murrelet occupancy to forest fragmentation, and to account for the proximity of marine and terrestrial habitat and other important habitat variables.

Murrelet *occupancy* was defined to occur in a landscape when at least one bird was observed exhibiting a behavior that suggests it was nesting in the area (Ralph et al. 1994). A *patch* on the landscape was defined as a contiguous area of a single-mapped cover type, its minimum size being limited by the minimum mapping unit (grain size). A *landscape* (50–3217 ha) was defined as a mosaic of different patch types. *Old growth* was defined as inland (nonmarine) murrelet habitat and included forest patches unmodified by timber harvest and patches modified by harvest that contained at least 10% canopy cover in large, old remnant trees. We hypothesized that, during the breeding season (March to September), landscapes with occupancy would be found mostly in relatively unfragmented old-growth forest and contiguous landscapes in close proximity to marine areas with high primary productivity (kelp beds, cold-water areas, bays, river mouths, and potential upwelling sources such as submarine canyons and coastal promontories). Within old-growth patches, we expected more murrelets to nest at low elevations on gentle slopes near streams and far from roads. Such areas are potentially protected from high winds, may support the largest trees with many large "platform" branches (Hamer 1995) available for murrelet nests, and may receive less disturbance to nest sites from road activity. A study in northern California found that the lower portion of a slope was more likely to be used for nesting by murrelets (Miller & Ralph 1995). Also, old-growth forests in California valley bottoms usually had larger trees than ridgetops (Meyer 1999). Finally, murrelets were expected to occupy only regional coastal vegetation zones influenced by fog. Such moist areas often contain the largest trees (Dillingham et al. 1995; Meyer 1999) with the most potential nest-platform branches, and they may have the right climatic conditions for a coldwater-adapted seabird (Ralph et al. 1995).

Study Area

The study area was the Siskiyou National Forest, which is located predominantly in southern Oregon (Fig. 1). In this area, Franklin and Dyrness (1973) defined two potential natural vegetation zones: the fog-influenced western hemlock (*Tsuga heterophylla*) zone on the western side and the drier mixed-conifer/mixed-evergreen zone on the eastern side of the national forest. Within the southern two-thirds of the study area, the division between the two zones is defined by a major north-south ridge paralleling the ocean at approximately 800–1100 m in elevation. The vegetation change between zones is a response to less precipitation in the rainshadow of the ridge, the extent of the fog belt, and a decline in soil fertility (Dillingham et al. 1995). In the northern third of the study area, the fog-influenced western hemlock zone extends up to 51 km inland, whereas in the southern area it extends only from 20 to 28 km inland. Although referred to as the western hemlock zone, it is dominated by Douglas-fir (*Pseudotsuga menziesii*), the tree species most available for nests in the zone.

Methods

We obtained a geographic information system (GIS) vegetation database derived from Landsat thematic mapper imagery (Congalton et al. 1993) and mapped old growth and other cover types at a fine resolution (25-m pixel) in the study area. We also mapped marine and topographic features in the GIS. After mapping all murrelet survey stations in the study area, we calculated spatial and other habitat variables within landscape-sized circular plots that were placed over the point locations of survey stations. Finally, we looked for relationships between habitat variables and murrelet occupancy within the sample plots.

Murrelet Inland Surveys

From 1991 to 1997, the U.S. Forest Service conducted 4033 murrelet surveys at 3609 stations in potential murrelet habitat in the study area, where habitat was defined as mature (with or without an old-growth component) or old-growth coniferous forest or younger coniferous stands with deformations or structures suitable for nest-

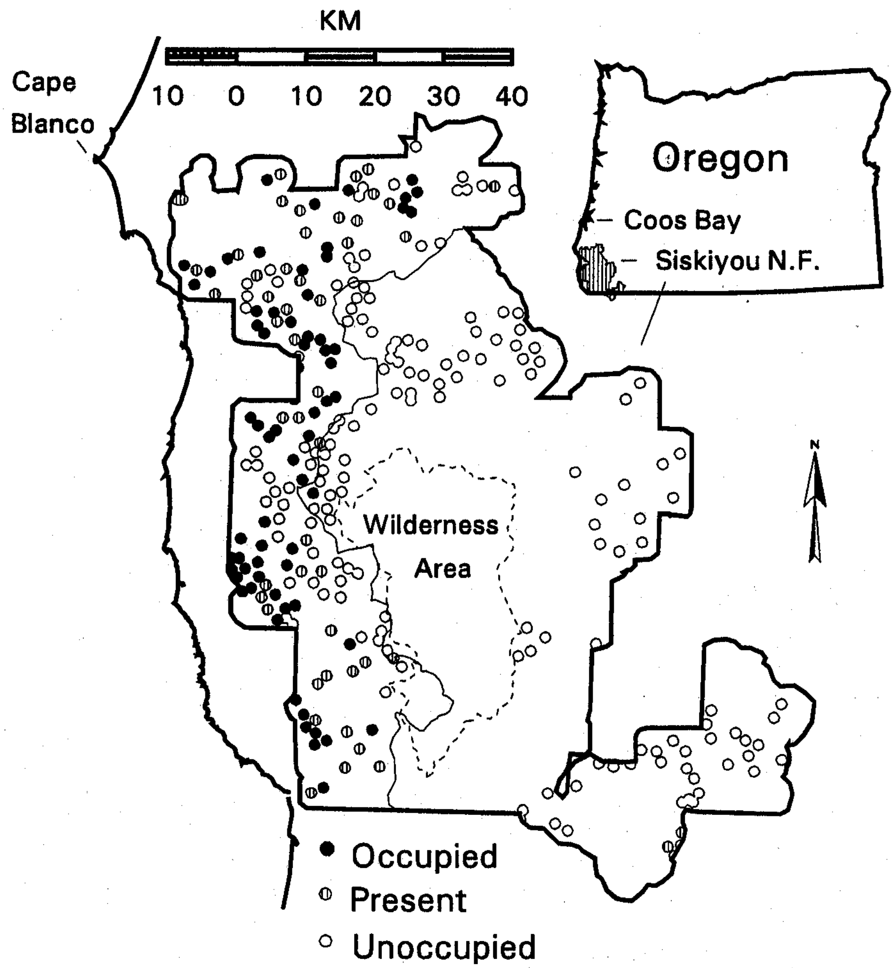

Figure 1. Marbled Murrelet occupancy status of 800-m-radius plots located in the Siskiyou National Forest in southwestern Oregon and northwestern California. To the left of the thin line is the western hemlock zone; to the right is the mixed-evergreen/ mixed conifer vegetation zone. Occupied plots are areas believed to be used for nesting.

ing (Dillingham et al. 1995). On average, one survey was conducted per 10 ha of habitat within areas targeted for logging. Wilderness areas, such as the center of the national forest, were not surveyed, and survey stations were not randomly selected. Thus, our study is a retrospective analysis of existing data, but survey coverage of potential habitat was fairly extensive and well distributed (Fig. 1). Surveys were conducted between 1 May and 15 August. Following an established, intensive survey protocol (Ralph et al. 1994), we surveyed each station for 2 hours around dawn and recorded the number of murrelet detections (visual or auditory observations of a bird or group of birds flying together). If a bird flew below the canopy, circled above the canopy, landed in the canopy, or was stationary, the station was classified as "occupied." Such behaviors suggest that murrelets are nesting in the stand rather than flying over it toward another destination (Nelson & Hamer 1995*a*). Stations at which birds were detected without behaviors indicative of nesting were classified as "present," and stations with no murrelet detections were classified as "unoccupied." In a habitat patch where birds are truly present, four surveys are needed to detect birds at least 95% of the time in that patch, whereas the probability of detection during a single visit is 0.527. Miller and Ralph (1995) found this probability rate realistic in California. Thus, to be included as an unoccupied plot, all surveyed unoccupied patches in the plot had a minimum of four surveys. The 1994 murrelet survey protocol (Ralph et al. 1994) says that the four surveys should be conducted for 2 years in a row to capture the annual variability in use of stations by murrelets. We did not use the eight survey criteria, so some of our unoccupied stations may have actually been occupied in some years.

Vegetation Database

Using ARC/INFO (Environmental Systems Research Institute, Inc., Redlands, California, v. 7.1), we classified cover types from the vegetation database as grassland, shrub, freshwater, hardwoods, and conifers (single and multistory). Forests were further divided into two canopy-cover classes (class division at 40%) and four tree size classes, where size-class divisions were 23, 54, and 82 cm diameter at breast height (dbh). Coniferous forests with <40% canopy cover were not separated by tree size and were grouped into one low-density forest class. Based on Hamer and Nelson (1995), the maps specifically defined murrelet habitat (old growth) as large, multilayered coniferous forests that had trees ≥82 cm dbh comprising at least 10% of the canopy cover, and in which total canopy cover was ≥40%.

The entire vegetation database was ground-truthed at 84% classification accuracy for old-growth forest, 62% for crown closure, and 47% for other size classes (Congalton et al. 1993; J. Teply, unpublished data). A second accuracy assessment that centered only on landscapes with old-growth habitat found similar old-growth forest accuracy (87%) but improved accuracy for crown closure (92%) and other size classes (88%) (S. Salmons, unpublished data), a level of accuracy acceptable for our purposes.

Landscape-Sized Sample Plots

The correct scale at which to measure forest fragmentation to predict murrelet nesting is unknown. Therefore, we compared results for plots of 400-, 800-, 1600-, and 3200-m radius, centering the nested plots of increasing size on the most central station of a cluster of survey stations (clusters within an approximately 800-m-radius area). We classified plots with at least one occupied survey station in the plot as occupied, plots with at least one present station and no occupied stations as present, and plots where birds were absent from every station as unoccupied (Fig. 1). Overlapping plots were visually identified and removed to retain plot independence (unless overlap was under 5%), which reduced sample sizes as plot size increased. The overlapping plots chosen for removal were those that lowered the sample size the least.

Initial analyses indicated that the nesting status of present plots was uncertain. Birds observed may either be nesting in these areas or flying overhead toward another destination, so the mean values of variables in present plots often fell between those of occupied and unoccupied plots. Moreover, the fit and accuracy of the regression model were decreased when present plots were lumped with occupied plots, so we eliminated present plots from all regressions. We included present plots only when evaluating the relative isolation of plots and when plotting bird distributions on maps.

Variables Sampled

We recorded occupancy as a measure of the use of nesting areas by murrelets. *Occupancy* was specifically defined as the classification status of a sample plot as either occupied (at least one occupied station in the plot) or unoccupied (no murrelet detections at any station in the entire plot). One survey was equal to one visit to a station. A station usually had only one visit, but some stations had more than one visit. The number of surveys within individual plots averaged 4, 9, 20, and 47 for the 400-, 800-, 1600-, and 3200-m plots, respectively. The number of surveys increased in the larger plots because they included more patches that required surveying. Also, because occupancy in a patch was often found after just one or two surveys (whereas at least four surveys were needed to classify unoccupied patches), on aver-

Table 1. Habitat variables measured in landscape-sized inland circular plots surveyed for Marbled Murrelets on the Siskiyou National Forest.[a]

Fragmentation variables (from FRAGSTATS)

Percentage of landscape in OGR	Percent area in largest patch (OGR,L)
Density of vegetation patches (no./100 ha) (OGR,L)	Mean patch size (ha) (OGR,L)
Mean core area per patch (ha) (OGR,L)	Mean nearest-neighbor distance (m) (OGR)
Percentage of landscape in core area (OGR,L)	Density of core area within patches (no./100 ha) (OGR,L)
Total edge per area (m/ha) (OGR)[b]	Richness of patch vegetation (L)
Density of patch edges (m/ha) (OGR,L)[b]	Shannon's diversity index (L)
Contrast edge index (OGR): mean contrast in vegetation height, assigned to borders and ranges from 0 to 1 (Meyer 1999)[b]	Contrast-weighted density of edges (m/ha) (OGR): edge density weighted by contrast edge index[b]
Interspersion and juxtaposition (OGR,L): quantifies unique patch type adjacencies to measure the extent a patch type is interspersed with other patch types[b]	Mean proximity index (OGR): quantifies size and distance of neighboring OGR patches to distinguish sparsely spaced, small OGR patches (low value) from clusters of large or closely spaced OGR patches (high value)
Mean area-weighted fractal dimension (OGR,L): quantifies shape complexity by dividing ln(area) into 2*ln(0.25*perimeter) for each patch and multiplying the resultant quotient by patch-area percentage	Contagion (%) (L): quantifies like pixel adjacencies by patch-type abundance to measure extent that patch types are clumped or interspersed[b]
Mean shape index (OGR,L): quantifies shape complexity of patch compared with a square (square = 1)	Isolation > 5 km: yes (1) or no (0) where distance is measured from plot center to nearest "occupied" or "present" plot

Distance variables (distance from plot center to nearest feature indicated)

Ocean (km)	Major bay (km): Coos Bay, just north of study area (Fig. 1)
	Submarine canyon (km): identified from National Aeronautic and Space Administration (NOAA) hydrographic and trackline survey data (1935–1995) for coastal waters within 30 km of shore
Spring/summer nearshore coldwater area (km): identified as coastlines regularly having ocean water at <10° C on NOAA advanced-very-high-resolution-radiometer satellite imagery (1.1-km resolution)	
Major promontory (km)	Kelp bed (km): identified on NOAA 1:200,000 nautical charts
River mouth (km): identified on a 1:100,000 U.S. Geological Survey (USGS) hydrographic digital line graph (DLG)	Road (m): identified on USGS 1:100,000 DLG
	Stream (m): identified on USGS 1:100,000 hydrographic DLG

Topographic variables

Elevation (m): from Defense Mapping Agency 90-m digital elevation model (DEM)	Slope (degrees): from 90-m DEM

[a]*Abbreviations: OGR, old-growth forest class; L, entire landscape in plot.*
[b]*A 400-m landscape border was added around each plot and included as part of the plot when this variable was calculated (all other variables were calculated with patches truncated at the plot boundary).*

age more surveys were conducted in unoccupied than occupied plots. Such variability in survey effort probably did not strongly bias the study results because survey effort was not significantly correlated with the habitat variables found to be important in this study. If anything, the greater survey effort expended in areas where murrelets were hard to find or absent biased the results in terms of making it easier to detect occupancy in marginal habitats than if we had surveyed occupied and unoccupied plots with equal effort. The resultant increase in the number of occupied plots with marginal habitat makes detecting habitat differences between occupied and unoccupied plots more difficult, so the bias strengthens our final conclusions about habitat differences.

Within the landscape-sized plots, we calculated fragmentation variables for each circular plot using FRAGSTATS (raster version; McGarigal & Marks 1995). We quantified fragmentation variables that, when evaluated jointly, best presented a picture of whether or not the landscape was fragmented by logging (Mladenoff et al. 1993, McGarigal & Marks 1995) (Table 1). *Interior habitat* was defined as core areas within patches that were >50 m from the edge of the patch (Nelson & Hamer 1995*b*). From the center of the plot, we recorded (1) the major vegetation zone, (2) distance to the nearest marine or land feature that we had hypothesized to be important, and (3) values of topographic variables (Table 1). To estimate isolation, we noted whether the distance from the center of the 400-m-radius (50 ha) plot to the center of the nearest neighboring occupied or present 400-m-radius plot was within 5 km. We chose 5 km to evaluate the effects of isolation of 50-ha areas across the landscape because murrelet occupancy is affected by isolation of such areas at that distance in California (Meyer 1999).

Data Analysis

Using occupied and unoccupied plots, we conducted stepwise logistic regression analysis to predict the probability of murrelet occupancy of a potential nesting area (Hosmer & Lemeshow 1989). Analyses were conducted with SPSS (Norusis 1997) or SAS (SAS Institute 1990). To decrease the number of candidate variables, the fragmentation variables were first reduced to major principal components having eigenvalues of >0.5. Using regressions, we determined which of the resultant principal components were not significantly related to murrelet occupancy ($p > 0.05$) and eliminated all variables that had high loadings (>0.7) on those insignificant principal components. Because we often found that individual habitat variables had stronger relationships to the birds than the principal components, we did not use the remaining principal components as candidates for the final models. We used only the variables highly correlated with the significant principal components. The least significant variable of a pair of highly correlated variables ($r > 0.7$) was also removed from the analysis to avoid high multicollinearity. This screening process reduced the number of candidate variables to 17 for the 400- and 800-m-radius models and to 14 for the 1600- and 3200-m-radius models. We further reduced the number for 1600- and 3200-m-radius models to 9 by eliminating all marine and topographic variables not selected in the 400- and 800-m models. Nevertheless, the high number of remaining candidate variables could increase the likelihood of some variables being selected by chance. To reduce this likelihood, we validated all models with independent data sets, obtained by randomly setting aside about 20–30% of the plots. These independent plots were used only to test how well the models performed. They were set aside before any of the models were built and were never used in the final models.

For logistic regressions, we selected the final set of habitat variables from the remaining candidate variables using the stepwise procedure with $\alpha = 0.05$. Rather than relying solely on the stepwise procedure, we evaluated three of the logistic regressions with the lowest Akaike's information criterion (AIC_c; Burnham & Anderson 1998) for each plot size. These three sets of regressions for each plot size are called model 1, 2, and 3. Based on its low AIC_c, its accuracy in classifying original and independent plots, and its consistency in variables across plot sizes, model 1 appeared to best fit the data.

We tested for spatial autocorrelation of the residuals of model 1 with Moran's I test in Splus (MathSoft 2000). We used the inverse of the distance between the center of plots out to 10 km as the weighting statistic. None of the regressions had significant spatial autocorrelation ($p > 0.05$). Also, the regressions did not have any significant interaction terms.

Just because a variable is not selected in a regression does not mean it is unimportant, particularly if it is highly correlated to a variable in the model. To obtain a more complete picture of a landscape with murrelets, we identified highly intercorrelated sets of variables related to occupancy. Habitat variables that were not in the final regression models but were highly correlated with a habitat variable in the model ($r \geq 0.9$; Neter et al. 1990) were used to further interpret characteristics of the nesting landscape.

Results

Only one of 46 occupied plots was not in the fog-influenced western hemlock zone. This plot was close to the zone, just east of the border (Fig. 1). Because of the virtual absence of occupied plots outside the fog zone, despite the intense survey effort in that area (106 plots surveyed out to 80 km inland), all regressions were developed only from the plots within the western hemlock zone.

Maximum inland distances for occupied and present plots combined tended to reflect the inland distribution of the boundary of the western hemlock zone (Table 2). Plots with only "presence" of birds (no "occupied" behaviors observed) were found almost up to the maximum inland distance of the western hemlock boundary in Oregon and beyond it on the southeastern edge of the national forest in northern California (Fig. 1). In contrast, the farthest distance from the coast of an occupied

Table 2. Mean (range) of distances to coast and elevation for 400-m-radius landscape plots surveyed for Marbled Murrelets and for the western hemlock zone in the Siskiyou National Forest, Oregon.

	Occupied	*Present*	*Unoccupied*	*Western hemlock zone*
Distance to coast (km)	16 (3–38)	18 (1–56)	23 (9–80)	22 (14–51)
Elevation (m)	418 (67–918)	407 (27–1090)	803 (122–1595)	503 (0–1120)

Table 3. Predictor variables (and coefficients for model 1) for the top three logistic regression models of Marbled Murrelet occupancy in the western hemlock zone in the Siskiyou National Forest, Oregon.[a]

	Plot radius (m)											
	400			800			1600			3200		
Variables[b]	*coefficient*	*SE*	p	*coefficient*	*SE*	p	*coefficient*	*SE*	p	*coefficient*	*SE*	p
Model 1												
mean proximity index of OGR										0.0520	0.0390	0.0005
elevation	−0.0065	0.0017	<0.0001	−0.0062	0.0018	<0.0001	−0.0110	0.0056	0.0013	−0.0141	0.0111	0.0210
ocean distance	−0.1161	0.0505	0.0126	−0.1380	0.0524	0.0009	−0.7253	0.3264	<0.0001	−0.8006	0.7399	0.0126
bay distance	−0.0402	0.0162	0.0071	−0.0405	0.0147	0.0050	−0.2074	0.1024	<0.0001			
mean core area of OGR	39.4858	19.5294	0.0012	20.1206	12.0850	0.0114	113.2020	69.2124	0.0010			
constant	9.5264	2.6087		9.9475	2.5691		41.7970	19.7691		17.7143	15.4877	
Model 2	OGR%, ocean distance, elevation			largest patch OGR, bay distance, ocean distance, elevation			landscape shape, ocean distance, elevation			edge contrast of OGR, ocean distance		
Model 3	bay distance, elevation			largest patch OGR, bay distance, ocean distance, elevation, stream distance			OGR%, ocean distance, elevation			landscape edge density, ocean distance		

[a]*Probability values based on the log-likelihood ratio test. The OGR is old-growth forest.*

[b]*Variable statistics are shown for first model only, which overall had the lowest AIC$_c$, the best predictive accuracy of both the original and validation datasets, and the most consistent variables from plot size to plot size.*

plot (38 km) was only 75% of the distance to the nearest zone boundary. When restricted to the western hemlock zone, unoccupied plot distances averaged a little farther inland than those of occupied plots (mean = 23 vs. 16 km). Mean elevations were generally lower in occupied or present plots (400 m) than the zone average (500 m) or than in unoccupied plots (800 m; Table 2). Such a difference held true even when unoccupied plots were evaluated just in the hemlock zone (in zone, unoccupied mean = 722 m).

The top three logistic regression models had many of the same variables across the four plot sizes (models 1, 2, and 3 in Table 3). Compared with unoccupied plots, occupied plots were at lower elevations and closer to the ocean and a major bay (Coos Bay, the only major bay near the study area). Occupied plots also had less fragmented old-growth forest (Fig. 2). In model 1, there was a larger mean core area of old growth than of unoccupied plots. Within the largest plot size (3200-m radius), close proximity of old-growth patches to other large old-growth patches was an important predictor of murrelet occupancy (Table 3). The following candidate variables were highly correlated ($r > |0.9|$) with the variables selected in model 1. Distance to river mouths was correlated with distance to coast ($r = 0.99$), percentage of land in old growth and density of old-growth core areas were correlated with mean core area (r varied from 0.88 to 0.95 over the plot sizes), and the area-weighted fractal dimension of old growth was correlated with the mean proximity index of old growth ($r = 0.96$). Based on these correlations, occupied plots were also closer to river mouths and had a higher percentage of land in old-growth core area, higher old-growth core-area density, and more complex shapes of large old-growth patches (higher area-weighted mean fractal dimension).

Models 2 and 3 often contained the variables of percentage of land in old-growth forest or in the largest old-growth patch, instead of mean core area of old growth (Table 3). Compared with unoccupied plots, occupied plots had more old-growth forest and were more strongly dominated by a large old-growth patch. For some plot sizes, these old-growth variables were too correlated with one another and could not be considered in the three competing models (although old-growth forest and mean old-growth core area never had $r > 0.7$). Other variables included in models 2 and 3 were distance to nearest stream, density and shape of landscape edge, and edge-contrast index of old-growth forest. Areas farther from streams that had low edge density and simpler shapes of all patches on the entire landscape, but high edge contrast of old-growth forest, had a greater probability of occupancy. Distance to nearest bay and elevation alone produced a good model (model 3, 400 m-radius plots) even though distance to nearest bay was dropped from some of the other top models (Table 3).

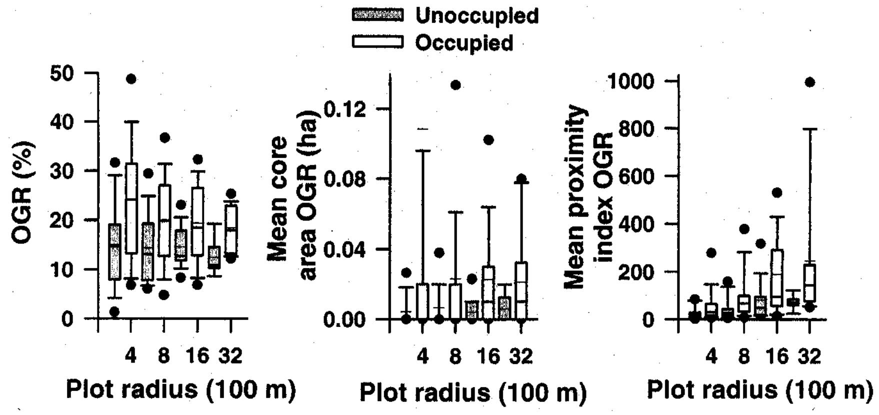

Figure 2. Distribution of fragmentation variables in occupied and unoccupied plots within the nesting range of the murrelet (in the western hemlock zone, ≤918 m elevation, ≤38 km from coast, and ≤144 km from Coos Bay). The median is the line in the box, twenty-fifth and seventy-fifth percentiles are box ends, tenth and ninetieth are bar caps, and fifth and ninety-fifth are outer dots. The mean is the thin line.

Accuracy of Results

Logistic regression models that fit the data well have a high Nagelkerke R^2 (high amount of maximum likelihood explained; Nagelkerke 1991) and a high value for the significance of the Hosmer and Lemeshow (1989) goodness-of-fit test statistic, $\hat{C}$. A comparison of the two measures of fit among plot sizes in model 1 showed that model fit was best at the two largest plot sizes (Fig. 3). Similarly, the models using large plots were generally better at predicting occupancy than models with small plot sizes (Table 4). The percentage of plots in which occupancy was correctly predicted in model 1 was high for all the plot sizes; accuracy was ≥82%. Prediction accuracy of the independent plots was similarly high (≥75%). Unoccupied and occupied plots had high accuracy (Table 4).

The overall accuracy of all three of the top models ranged from 75% to 100% (Table 4). Model 3, however, with 800-m-radius plots, was probably overfitted with too many variables. It was the only model that included distance to streams as a variable, and it had relatively poor accuracy of independent plots (76%), much lower than the original plots (90%). Although models 2 and 3, with 3200-m-radius plots, also had low accuracy of independent plots (75%) relative to original plots (90%), the sample size of the independent plots was too low (n = 4) to be of much use for model validation of these large plots. Conclusions for any of the top three models based on the 3200-m-radius plots alone are tentative at best. Yet this plot size was the only one that included mean proximity index, a variable that may not be predictive until the plot size is large enough to encompass larger distances between patches. The accuracy of the classification of independent plots for all the other top models was similar or better than that of the original plots.

Models that included percentage of land in old-growth forest as the old-growth variable generally had a slightly poorer fit to the data based on the AIC_c than models with mean core area, area in largest patch, or mean proximity index of old-growth forest (e.g., 26.1 for model 1 vs. 42.2 for model 3 in 1600 m-radius plots). But classification accuracy was almost as good when just the old-growth amount was substituted for the other old-growth variables (80–100% vs. 85–100% for original plots; 82.8–95% vs. 83.3–95% for independent plots). Thus, variables that included contiguity of the old-growth forest only slightly improved accuracy over a variable that measured only the amount of old growth.

Table 4. Sample sizes (n) and percentage of plots in which Marbled Murrelet occupancy was correctly predicted for the best logistic regression models within the western hemlock zone on the Siskiyou National Forest.[a]

	Plot radius (m)							
	400		*800*		*1600*		*3200*	
	n	*percent*	n	*percent*	n	*percent*	n	*percent*
Model 1[b]								
all plots	78/40	83/85	87/25	85/88	53/17	92/94	21/4	95/100
occupied	45/20	84/75	45/17	87/88	34/8	91/100	14/3	100/100
unoccupied	33/20	82/95	42/8	83/87	19/9	95/89	7/1	86/100
Range for models 1, 2, and 3								
all plots	78/40	78-85/80-87	87/25	83-90/76-88	53/17	85-92/94-100	21/4	90-95/75-100

[a] *Sample size (n) and accuracy for original and validation datasets are on the left and right of the slash, respectively. Cutpoints used that provided the least misclassification of plots were 0.48, 0.50, 0.65, and 0.50 for 400-, 800-, 1600-, and 3200-m-radius plots, respectively.*
[b] *Variables are shown in Table 3.*

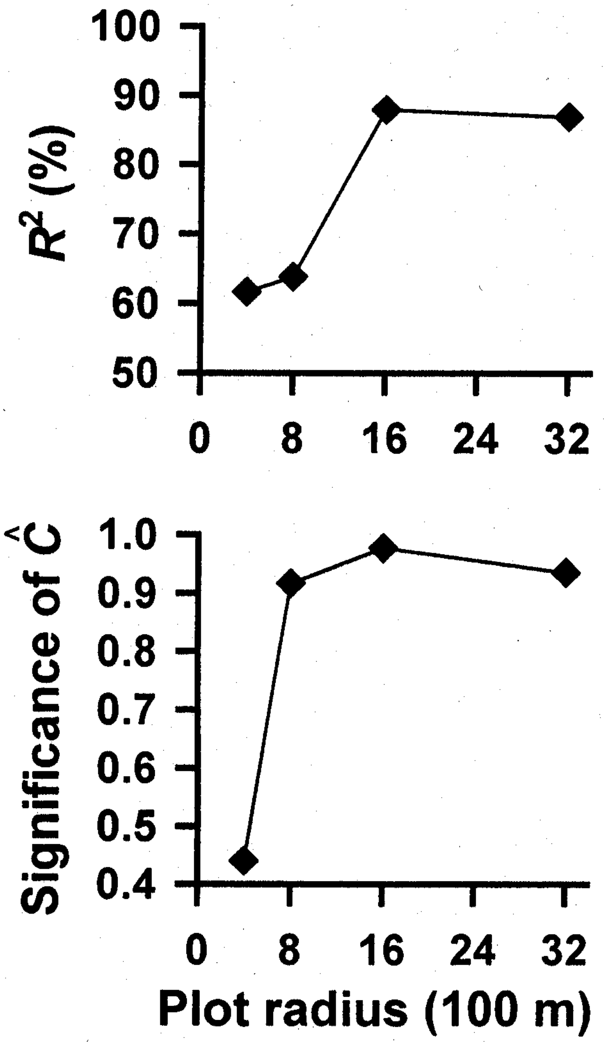

Figure 3. Statistics of model fit for logistic regressions on murrelet occupancy (using model 1 in Table 3). Specifically shown are the Nagelkerke's R^2 *and the significance of the Hosmer-Lemeshow statistic,* $\hat{C}$.

Compared with topographic and marine variables, old-growth variables moderately contributed to the accuracy of the best models, and the contribution was strongest for models based on the largest plots. When an old-growth variable was removed from the 3200-m-radius model, classification accuracy of all plots dropped 20%. For models with 1600-, 800-, and 400-m-radius plots, removal of old-growth variables decreased accuracy only by 3%, 3%, and 2%, respectively. Of all the variables in each model, elevation had the strongest effect on accuracy in 400- and 800-m-radius plots (dropped 7–11% without it), distance to ocean had the strongest effect in 1600-m-radius plots (dropped 6%), and mean proximity index of old growth had the strongest effect in 3200-m-radius plots (20% drop compared with 18% when distance to ocean was removed and 8% when elevation was removed).

Discussion

We assumed that occupied landscapes mostly represent areas actually used for nesting, because birds exhibited behaviors that have been observed around nests. Actual nests were not identified in the landscapes (nests are extremely difficult to find), however, so we could be in error for some areas. Nevertheless, many of our results supported our hypotheses. As predicted, occupied landscapes had less fragmented and isolated old-growth forest than unoccupied landscapes, were relatively close to the coast and associated river mouths, and were mostly restricted to the fog-influenced western hemlock zone. Proximity to Coos Bay (north of the study area), a potentially productive marine area, was also important. Contrary to our predictions, within-patch effects generally were not important except for elevation, which was lower in occupied than in unoccupied plots. Slope and distance to streams or roads did not affect murrelet occupancy.

Fragmentation Effects

Old-growth fragmentation appears to potentially have an adverse effect on use of a landscape by murrelets because a decrease in old-growth core area corresponded to a decrease in use of an area by murrelets. Both old-growth core area and old-growth percentage seem to be important, even though they were not highly correlated with each other. More studies are needed to separate the effects of amount compared to the contiguity of old-growth forest. Plots (1600-m radius) that were always occupied (potential nesting birds present, not necessarily abundant) required 28% of the plot to be in old growth, ≥0.03 ha for mean core area, and ≥12% in the largest patch of old growth. No such limits could be found to define areas that were always unoccupied, because some occupied plots had levels of old growth as low as those of unoccupied plots.

Fragmentation of old-growth forest may have an adverse effect on nesting because it reduces core habitat that is potentially more protected from predators than edge habitat (Paton 1994). Data on murrelet nests support our interpretation that reduced core area can eliminate or reduce the number of murrelets using an area. For a sample of 17 murrelet nests of known outcome across the murrelet's range, nest success was higher when nests were >50 m from the forest edge (Nelson & Hamer 1995*b*). In British Columbia, an additional 25 nests have been monitored and no murrelet nests >150 m from the edge failed due to predation (Manley & Nelson 1999). Such nest data suggest that edge effects may extend up to 150 m into the patch. Artificial murrelet nest experiments in Washington, however, showed similar rates of predation in fragmented and continuous stands (Marzluff & Restani 1999). An alternative explanation for the adverse effects of edge is that edge habitat is exposed to heat or high evaporative water loss on warm afternoons (Chen et al. 1993), which may stress a coldwater-adapted seabird.

In addition to having relatively large core areas, large occupied landscapes tended to have relatively complex old-growth shapes, high-contrast old-growth edge, and low edge on the entire landscape (more contiguous matrix). Natural areas dissected by streams often have larger old-growth patches with more complex shapes than areas with the numerous simple edge cuts of timber harvest (Mladenoff et al. 1993; Reed et al. 1996). Thus, occupied landscapes often contained the complexity of old-growth patch shape commonly found in natural landscapes. More research is needed to determine the importance of high-contrast old-growth edges. We expected murrelets to avoid such edges, where predators may be more abundant (Paton 1994).

In Washington, some landscape-level results were similar to ours when murrelet occupancy was evaluated with 800-m-radius coarse-resolution plots. In that state, the researchers found that occupied landscapes have more old-growth forest and larger, more complexly shaped old-growth patches than unoccupied landscapes. Contrary to our results, their occupied landscapes have more edge. Their landscapes also have a greater variety of cover types, which was not important in our study.

Mean proximity index, which indicates clumpiness of old-growth patches, was positively related to occupancy in the largest plot size in our study. Isolation of old-growth patches due to fragmentation may have a negative effect on nesting. Although the variable "isolation >5 km" was not selected in the regressions, only three occupied plots were >5 km from other plots with murrelets. As with many other species in the Alcidae family (De Santo & Nelson 1995), the results suggest that Marbled Murrelets may be a social nesting species, preferring to nest in loose groups or in patches that are not isolated. Murrelets have been found nesting within 1 km of each other (Naslund et al. 1995; Ralph et al. 1995).

Scale

The largest plot sizes provided the best regressions and may more fully capture the fragmentation characteristics of the landscape important to the murrelet. In particular, large plots provide large distances over which one can effectively calculate old-growth patch isolation (e.g., mean proximity index). Conversely, at the smallest plot size, local topography (elevation) was predictive of murrelet use but less predictive in the larger plots, which represent more regional elevation trends. Sample size for the largest plots was small, however, making the models based on those plots and the validation results less reliable. Model fit may have been best for the largest plot sizes partly because unoccupied plots represent large areas that are never or rarely used by murrelets. In contrast, smaller unoccupied plots were often intermixed with nearby occupied plots. Thus, classification of unoccupied plots may be less certain for the smaller plots. More research with larger sample sizes is needed to validate the importance of using large plots to assess fragmentation effects. The resolution of the vegetation map used in a study may not be important in determining fragmentation effects, because our results here with a fine-resolution map (25-m pixel) were similar to those with a coarse-resolution map (1.2-ha) of the Siskiyou National Forest (Meyer 1999).

Marine Habitat Proximity

Our results demonstrate that distance to elevation and marine features must be considered in models that evaluate fragmentation effects. Occupied inland habitat not only tended to be close to the coast and river mouths (42 river mouths were along the coast) but was also close to Coos Bay, the only major bay in the study area. The effect of the proximity of Coos Bay on occupancy is not obvious (Fig. 1) until elevation and core area of old-growth forest are also taken into account. Coos Bay and large river mouths have the potential for high food productivity because water-mass fronts formed by the influx of fresh water into the ocean in such areas can concentrate murrelet prey (Hunt 1995). Distance to Coos Bay was highly correlated ($r = 0.99$) to the Universal Transverse Mercator northing coordinate, however, which may indicate greater occupancy in more northern habitats on the national forest, rather than greater use of nesting areas near bays. Offshore murrelets generally become more abundant in a northward direction (Meyer 1999). More research is needed to separate the effects of latitude and distance to major bays.

Murrelet pairs exchange incubation duties every dawn and feed the chick several times a day early in the nesting stage (Nelson & Hamer 1995*a*). These flights incur high energy costs, particularly for nests distant from marine feeding areas. Consequently, murrelets were not found occupying areas >40 km from the coast, even when the western hemlock zone extended farther inland. Just north of the study area, the hemlock zone extended 56 km inland, yet the occupied plot farthest inland in that area was only 37 km (Meyer 1999). In contrast, occupied sites have been found as far inland as 84 km in the hemlock zone in Washington (Hamer 1995). The shorter limiting distance in our study area may be due to the stresses of hotter temperatures inland (especially outside the western hemlock zone) or lower marine productivity offshore compared to conditions in Washington. Although birds were detected 56 km inland in the study area, no nesting behaviors were observed in these areas despite many follow-up surveys. We hypothesize that they were nonbreeders.

Vegetation Zone and Elevation

Marbled Murrelets in the Siskiyou National Forest were generally not occupying areas inland of the fog-influenced western hemlock zone or above 1000 m. Dillingham et al. (1995) found the same result based on survey data for the national forest from the early 1990s. In other study areas, murrelets have also been observed mostly below 1000 m (Hamer & Nelson 1995; Miller & Ralph 1995; Raphael et al. 1995). Even below 1000 m, elevation is still important. The birds tend to not use ridgetops, which may be more windy and exposed to the elements.

We hypothesized that murrelets would use the western hemlock zone because it may have larger trees and a cooler, foggy climate that reduces heat stress. A small study in the national forest investigated differences in tree size between vegetation zones in areas close to the boundary (Dillingham et al. 1995) and found that old growth in the western hemlock zone contained larger trees (mean was 28 cm larger) than the mixed-evergreen/mixed-conifer zone. Hunter et al. (1998) did not find any birds inland of the fog zone in northern California, where the temperatures were quite warm (5.9-9.1° C warmer than where murrelets were found in the fog zone). Energetic studies of the murrelet are needed to determine if heat stress is an important factor in nesting distribution.

Management Applications

Overall, our study results suggest that management efforts to sustain or recover threatened murrelet populations on the Siskiyou National Forest should focus on maintaining or establishing large blocks of contiguous old-growth forest close to the coast, particularly in the north closer to Coos Bay. Such areas would maintain not only murrelets but also many other species that have similar requirements for interior old-growth habitat. Our models can also be used to create and compare murrelet habitat maps for various management alternatives on the national forest.

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