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STAND-SCALE HABITAT ASSOCIATIONS ACROSS A LARGE GEOGRAPHIC REGION OF AN OLD-GROWTH SPECIALIST, THE MARBLED MURRELET

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ABSTRACT.—We used two metrics, occupancy and relative abundance, to study forest stand characteristics believed to be important to a threatened seabird that nests in old-growth forests, the Marbled Murrelet (*Brachyramphus marmoratus*). Occupancy refers to murrelet presence or absence based on observed bird behaviors, while relative abundance refers to categories of low, medium, and high numbers of bird observations per survey in a forest stand. Within the murrelet's nesting range in California and southern Oregon, we measured habitat and climatic variables in all old-growth stands surveyed for murrelets between 1991 and 1997. The two bird metrics produced similar results. In California, murrelets most often occupied, or were abundant in, redwood (*Sequoia sempervirens*) stands with large trees (>100 cm diameter at breast height) located on gentle, low-elevation slopes or on alluvial flats close to streams. In stands of the less flood-tolerant Douglas-fir (*Pseudotsuga menziesii*) in southern Oregon, murrelets most often occupied, or were abundant on, gentle, low-elevation, west-facing slopes that were not close to streams. Murrelets tended to use areas farther from roads. The important climatic requirements for murrelet stands in both states were cool temperatures and high amounts of rainfall. *Received 24 November 2003, accepted 10 August 2004.*

The Marbled Murrelet (*Brachyramphus marmoratus*) is a species of seabird federally listed as threatened in California, Oregon, and Washington. It usually nests in large trees in old-growth or second-growth forests throughout most of its range, which extends from Alaska to central California (Ralph et al. 1995). Because of logging, its nesting habitat outside of Alaska has been shrinking rapidly (loss of 83–87% in the Pacific Northwest; Booth 1991), and much of what remains is fragmented (Hansen et al. 1991). Some research has been conducted on Marbled Murrelet habitat associations at the landscape and regional scales (Raphael et al. 1995, Meyer et al. 2002, Meyer and Miller 2002, Miller et al. 2002, Ripple et al. 2003), and a number of local studies (Hamer 1995, Hamer and Nelson 1995, Kuletz et al. 1995, Miller and Ralph 1995) have also addressed nesting habitat characteristics at the stand scale (here, we define a stand as a contiguous patch on the landscape that contains large, old trees; i.e., a patch of old-growth forest). However, no studies have systematically addressed local stand characteristics across a large geographic region. An advantage of a large-scale study is that it is more likely to encompass the full range of stand characteristics, including variation in climate. A comprehensive study in California and southern Oregon is particularly needed because the area is at the southernmost extent of the murrelet's distribution, where murrelets are less abundant and potentially susceptible to extirpation (~5,500 birds in our study area in 2000 compared with 13,100

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birds along a similar length of coastline to the north; Peery et al. 2004; M. H. Huff unpubl. data).

Habitat assessments for birds over large regions often are not possible for several reasons. First, usually many different investigators have conducted the bird surveys using a variety of methods; thus, the data are not comparable across the region. Second, large portions of the study area may not have been surveyed, creating substantial data gaps. Third, some survey methods that give the best habitat information, such as radio-telemetry, are too costly to conduct over large areas and only provide information at a local scale. Fortunately, due to its threatened status and careful coordination among investigators, our Marbled Murrelet study overcomes most of these limitations because the species was surveyed extensively via audio-visual techniques during the 1990s throughout California and southern Oregon by investigators using one common protocol. With the aid of Geographic Information Systems (GIS), we were able to compile all available audio-visual survey data and describe local characteristics of potential nesting habitat across a large region.

One limitation of our approach is that, unlike radio-telemetry methods being used in a few studies in British Columbia (e.g., Bradley and Cooke 2001; F. Huettmann unpubl. data) and California (R. T. Golightly pers. comm.), audio-visual surveys do not identify actual nest sites; rather, they identify potential nest sites based on bird behaviors indicative of nesting. Nevertheless, our extensive dataset of audio-visual surveys (>17,000) can provide complementary information on the distribution and associated habitat characteristics of birds observed inland across a large, bi-state area. Findings based on extensive analyses are currently needed to assist regional recovery and conservation efforts. When published, habitat results from more local nest studies will further enhance the interpretation of extensive studies such as ours by providing more insight regarding the quality and limitations of audio-visual surveys.

In other studies in California and Oregon, many stand-level variables such as mean tree diameter at breast height (dbh), aspect, slope, precipitation, temperature, and distance to nearest stream were of relatively lower significance compared to broader, landscape variables such as fragmentation and isolation (Meyer et al. 2002, Meyer et al. 2004). Nonetheless, managers are now focusing on these within-stand variables because they contribute additional information about local habitat characteristics important to the biology and conservation of murrelets. Clearly, landscape variables set the stage for the presence and abundance of murrelets, but local variables help clarify stand characteristics preferred by murrelets. For example, we would expect murrelets to more often use stands with the largest trees. Large trees potentially have more branches with platform-like structures available for nesting. Moreover, the nest stands might be in moist, cool areas protected from the wind, such as in low-elevation valley bottoms or on gentle slopes near streams—areas that may be ideal for a coldwater-adapted seabird that nests in the tree canopy (Ralph et al. 1995). To date, there have been no extensive studies to quantify and compare such stand characteristics across such a large area, nor has anyone systematically investigated the importance of precipitation and temperature in stand sites.

It has been suggested that results from presence/absence surveys can be extrapolated to predict population abundance by summing probabilities of use within territories over an area (e.g., Boyce and McDonald 1999). With that approach, only a presence/absence bird metric would be needed for our murrelet study. However, such an extrapolation requires knowledge of the size of the animal's territory. Not only is this unknown for the murrelet, but it is unknown whether Marbled Murrelets behave territorially. Thus, a second metric, relative bird abundance, was needed to complement presence/absence results. In this study we quantified murrelet use of a given stand with both metrics: occupancy (presence/absence) and relative abundance (hereafter, ''abundance'').

Our main objective was to characterize inland murrelet habitat at the stand level in California and southern Oregon, addressing possible differences in habitat selection between two states that have distinctly different vegetation types and climate. We also compared results using occupancy versus abundance.

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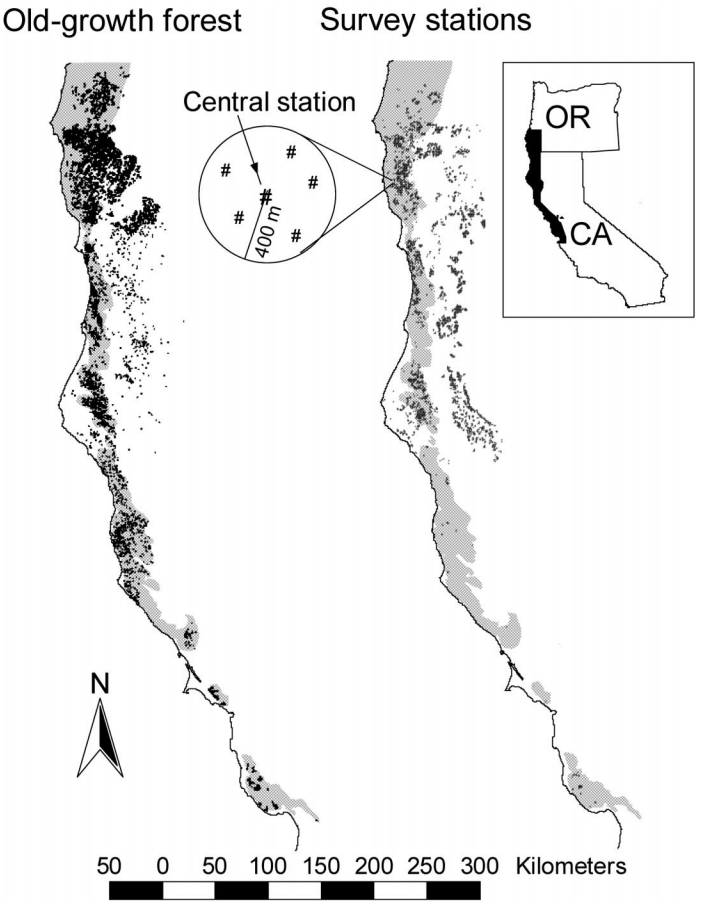


FIG. 1. Marbled Murrelet study area in California and Oregon showing old-growth forest stands (black areas, left map), and locations of all 1991–1997 survey stations (black areas, right map). Based on LANDSAT TM imagery, old-growth stands in California were those with mean tree diameter at breast height (dbh) >91 cm (dominated by redwood) and, in Oregon, mean dbh >77 cm dbh (dominated by Douglas-fir). We limited our surveys to the fog zone (gray shading), as birds were rarely found outside that zone. The inset illustrates one cluster of survey stations; the station at the center represents the ''central station,'' or the sampling unit in this study. All central stations were >800 m apart. Within a 400-m radius of each central station, we measured stand characteristics, murrelet occupancy (i.e., whether or not we observed ''occupancy behavior'' in at least one station in the circle), and number of birds per survey (averaged over the stations in the circle).

METHODS

Study area.—The study area encompassed the known nesting range of Marbled Murrelets in California and southern Oregon (based on Meyer 1999 and Meyer et al. 2002). This area extended from Coos Bay, Oregon, south to Monterey Bay, California, and inland up to 40 km from the coast. Because 98% of landscapes occupied by murrelets have been within fog-influenced vegetation zones (Meyer et al. 2002), we studied only those zones (Fig. 1). They included the redwood (*Sequoia sempervirens*) zone in California and the western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) zones in Oregon (Franklin and Dyrness 1973). Douglas-fir (*Pseudotsuga menziesii*) is the dominant tree species in the western hemlock zone and is the species most likely to be used as a nest tree, whereas, in California, redwood trees are used most often (Hamer and Nelson 1995). Based on Meyer et al. (2002), the criteria used to delineate the nesting range were further defined by elevation and distance to key marine

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features (see footnote in Table 1). Within this nesting range, average maximum temperature and annual precipitation were 25° C and 203 cm in California and 27° C and 297 cm in southern Oregon, respectively.

Sampling design and murrelet indices of use.—Our study is a retrospective analysis of available survey data, where the sampling design varied from area to area. Surveyors completed 17,145 surveys at 9,326 stations from 15 April to 15 August 1991–1997 (Fig. 1). Forty-six percent of the survey stations were randomly or systematically (in a grid) placed within potential murrelet nesting habitat that contained large platform-like branches; except for a few mature stands surveyed in Oregon, these were mostly found in stands of old-growth forest (hereafter referred to as stands). The remaining survey stations were placed in such habitat near proposed timber sales. The 2-hr surveys began 45 min before dawn according to a standardized protocol for intensive murrelet surveys (Ralph et al. 1994).

Because murrelets rarely used stands outside the fog-influenced vegetation zone, only the 7,616 surveys at 4,158 stations that were within that zone were included in our analyses. From that set of stations, 349 were selected as ''central stations'' (Fig. 1), each ≥800 m apart ($n = 133$ in Oregon and 216 in California). A central station was defined as the one nearest the center of the cluster of stations located within a small (<50 ha) stand or within a 50-ha section of a large stand (Fig. 1).

To determine occupancy, we classified a central station as either occupied or unoccupied based on murrelet behaviors indicative of nesting. A central station was considered occupied if any of the following behaviors were observed at any survey station within a 400-m radius (50 ha) of the central station: a bird flew below the canopy, circled above the canopy, landed in the canopy, was stationary in a tree, or broken eggshells were found (Ralph et al. 1994). Central stations with no murrelets observed or heard at any station within a 400-m radius were considered ''unoccupied.'' We deleted from the analysis any central stations where birds were seen or heard at a station within the 400-m radius, but occupancy status could not be verified (i.e., stations had birds ''present'' but no occupying behaviors were observed). To ensure 91% confidence that the remaining unoccupied areas with no birds seen or heard did not have murrelets ''present'' in the surveyed year, at least four surveys must have been conducted in 1 year within the 400-m radius area (based on an analysis in Evans Mack et al. 2003, Appendix A, p. 40) before the central station was assigned ''unoccupied'' status (otherwise it was deleted from the analysis). This confidence rate does not consider that the status of a site may change between years. Most of our stands were not surveyed in more than 1 year because the survey protocol initially did not require it. During the later years of this study, there was a change in the recommended number of surveys and years. To retain our ample data collected during the early years of our study, we used the early survey protocol and accepted that some of the unexplained variance in our models would be due to some unoccupied central stations actually being occupied in years they were not surveyed. Henceforth, the use of the term ''station'' in this paper will refer to the central station and its associated stand characteristics within the 400-m radius circle surrounding the central station (Fig. 1).

Our index of abundance was the total number of standardized bird detections observed during each survey averaged over all surveys conducted within 400 m of the central station. Each visual or auditory observation of a single bird or group of birds was considered one ''detection.'' In each state, the total number of detections was standardized by applying a multiplier to adjust for seasonal variations over time. On average, detections peak in July in both California (O'Donnell et al. 1995) and Oregon (Jodice and Collopy 2000). For the 12 consecutive 10-day periods starting with 15 April, the multipliers were 1.14, 1.81, 1.22, 1.36, 1.12, 1.40, 1.29, 0.93, 0.81, 0.59, 0.61, and 1.14. These multipliers are the ratio of the mean number of detections for the entire survey season divided by the mean for each 10-day period obtained from pooled surveys at three long-term (1989–1995) monitoring sites in northern California (Miller and Ralph 1995).

On average, six surveys contributed to the final mean number of murrelet detections assigned to a central station. Because differenc-

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TABLE 1. Means (±SD) of old-growth forest variables at stations occupied or unoccupied by Marbled Murrelets and at those with low, medium, or high murrelet abundance within the species' nesting range[a] in California and Oregon. Compared with unoccupied stations, occupied stations contained larger trees (dbh); were located on cooler, drier, lower-elevation sites; and had gentler slopes closer to streams. When compared with stations with low (<2) or medium (2–15) murrelet abundance, stations in California with the highest abundance (>15 detections per survey) were located in cooler, lower-elevation sites and those with gentler slopes closer to roads. In Oregon, occupied stations were at cool, low elevations with more west-facing aspects, but no variables differed significantly across abundance categories. Bold-faced values significant at $P < 0.05$ (Kruskal-Wallis test unless otherwise noted).

Variable	Occupancy			Abundance			
	Unoccupied	Occupied	*P*	Low	Medium	High	*P*
California	*n* = 85	*n* = 131		*n* = 21	*n* = 62	*n* = 48	
Mean tree dbh (cm)[b]	70 (49)	135 (38)	**<0.001**	124 (41)	138 (37)	138 (37)	0.25
Elevation (m)	423 (214)	235 (152)	**<0.001**	291 (148)	272 (157)	162 (117)	**<0.001**
Slope (°)	12 (7)	8 (7)	**<0.001**	10 (7)	10 (7)	4 (4)	**<0.001**
Distance to stream (m)	359 (291)	291 (289)	**0.034**	312 (350)	293 (263)	279 (299)	0.89
East-facing (sine aspect)[c]	−0.04 (0.77)	−0.04 (0.72)	0.94	−0.17 (75)	−0.02 (0.70)	−0.01 (0.74)	0.62
North-facing (cosine aspect)	0.01 (0.65)	0.01 (0.70)	1.00	0.01 (0.68)	0.01 (0.73)	0.00 (0.69)	0.99
Distance to road (m)	288 (321)	295 (375)	0.58	328 (305)	375 (409)	177 (330)	**<0.001**
Maximum temperature (° C)	26 (2)	24 (2)	**<0.001**	25 (2)	24 (2)	23 (2)	**0.011**
Annual precipitation (cm)	214 (44)	195 (35)	**0.010**	192 (31)	198 (34)	194 (39)	0.48
Southern Oregon	*n* = 62	*n* = 71		*n* = 27	*n* = 39	*n* = 5	
Elevation (m)	570 (241)	402 (187)	**<0.001**	413 (157)	396 (212)	389 (156)	0.79
Slope (°)	13 (6)	14 (7)	0.35	15 (9)	15 (6)	10 (6)	0.26
Distance to stream (m)	493 (310)	472 (404)	0.27	549 (401)	394 (379)	667 (550)	0.090
Distance to road (m)	415 (337)	426 (433)	0.74	380 (388)	448 (442)	505 (645)	0.83
East-facing (sine aspect)	−0.01 (0.70)	−0.33 (0.65)	**0.009**	−0.34 (0.64)	−0.35 (0.65)	−0.07 (0.85)	0.76
North-facing (cosine aspect)	0.08 (0.72)	0.15 (0.68)	0.58	0.08 (0.72)	0.16 (0.69)	0.19 (0.67)	0.42
Maximum temperature (° C)	27 (2)	26 (2)	**0.045**	26 (2)	27 (2)	26 (1)	0.86
Annual precipitation (cm)	303 (68)	291 (40)	0.22[d]	296 (46)	288 (37)	286 (40)	0.90

[a] In California, murrelet nesting range was defined as that part of the fog zone occurring at ≤880 m elevation, ≤42 km from marine areas with high spring chlorophyll, and ≤50 km from submarine canyons. In Oregon, nesting range was that part of the fog zone ≤918 m elevation and ≤38.5 km from marine areas with high summer chlorophyll. Only a few occupied stations were found outside these areas (Meyer 1999).

[b] Dbh values were available only from the northern border of California to Point Reyes National Seashore, yielding samples sizes (*n*) of 20, 60, and 42 for low-, medium-, and high-abundance stations, respectively.

[c] Some slopes in California were 0° (no aspect); thus, aspect $n = 82$ for unoccupied and 118 for occupied stations.

[d] *P*-value for *t*-test with unequal variances (Kruskal-Wallis, $P = 0.034$).

es between observers, daily survey conditions, or daily murrelet activity can cause murrelet survey results to vary, even when averaged over six surveys (Jodice et al. 2001), we assigned means to four levels of detections: zero, low (<2), medium (2–15), and high (>15), and used the categories, rather than the actual means, in our analyses. Such category boundaries are useful for showing differences in landscape variables (Meyer et al. 2002).

We assumed that the abundance metric was positively correlated to the number of nesting birds in a stand or section. To what extent this is true is unclear. The number of birds detected may be biased by the size of the forest canopy opening (Rodway and Regehr 2000), skill of the observer, weather, the flight path of the birds from the ocean to the nest site, or by the high variability in number of birds detected during each survey at a station (Jodice and Collopy 2000, Buckland et al. 2001, Jodice et al. 2001). Although the occupancy metric also can be biased by these factors, such problems probably would be associated with the abundance metric more than with the more robust occupancy metric (Rodway and Regehr 2000). Thus, we compared the interpretation of the results of the two methods to assess whether such biases might have occurred.

Forest stand variables.—We recorded elevation, slope, aspect (using 90-m digital elevation models), and distance to nearest stream or major road (identified with 1:100,000 digital line graphs) from each central station. To create linear variables from a circular distribution, aspect was divided into an east-west component using the sine of the aspect and a north-south component using the cosine of the aspect (in radians). Sine and cosine values range from 1 to −1, where positive values represent eastern and northern aspects and negative values represent western and southern aspects (Briggler and Prather 2003).

The annual precipitation and maximum temperature for the summer, averaged over the survey period (1991–1997), were measured at each station using PRISM (Parameter-Elevation Regressions on Independent Slopes Model) at a 4-ha resolution (Spatial Climate Analysis Service, Oregon State University, http://www.ocs.orst.edu/prism). This analytical model interpolates station data for monthly and annual climate, accounting for orographic, coastal, and hillslope exposure effects, and distributes such data onto a regular grid across the landscape (Daly et al. 2002).

The estimated mean dbh of canopy conifers in each stand was obtained for each station in northern California only (Point Reyes National Seashore to northern border) from a GIS database in ARC/INFO developed by the California Timberland Task Force (1993). Estimates of mean tree dbh for each stand on a 4-ha resolution GIS map were derived using remote sensing techniques (spectral signatures compared to ground observations) from LANDSAT Thematic Mapper (TM) imagery. Unfortunately, the expected accuracy of the mean dbh for each stand in our study was not available. However, this remote satellite approach was effective in identifying the size class >91 cm dbh (82.8% accuracy; California Timberland Task Force 1993), and the dbh datasets appeared reasonable given our knowledge of some areas. The quadratic mean diameter at breast height (QMD) was used to estimate the mean stand dbh. QMD is a measure applicable to the Marbled Murrelet because it emphasizes the dbh of large trees. The formula weights dbh by the percent tree cover (cover) contributed by that size tree:

$$\mathrm{QMD} = \frac{\sum_{i=1}^{n} \mathrm{dbh}_i^2 \cdot \mathrm{cover}_i}{\sum_{i=1}^{n} \mathrm{cover}_i},$$

where i is the i^{th} class of n dbh classes.

Statistical analyses.—We used either nonparametric Kruskal-Wallis tests or *t*-tests with unequal variances ($\alpha = 0.05$; Sokal and Rohlf 1981) to detect differences in mean ranks or means of forest stand variables (1) between occupied and unoccupied stations, and (2) among the abundance categories of occupied stations. Both tests identified almost the same set of variables as significant (one exception, shown in Table 1), even though many variables had highly skewed distributions (thus, the Kruskal-Wallis test was used for most comparisons). To evaluate whether abundance provided useful information beyond that provided by occupancy, stations with zero abundance (unoccupied stations already used in the occupancy analysis) were not included in the comparison of abundance categories.

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We used multiple logistic regression to predict murrelet use and assess the effect of habitat variables in combination. Binary logistic regression was used to relate occupancy to habitat variables. Ordinal logistic regression was used to relate murrelet abundance (zero to high categories) to the variables. Ordinal logistic regression creates three regressions with parallel slopes but different intercepts, where each category is contrasted with the highest abundance category. For the ordinal logistic regressions, we added the zero category to the other three abundance categories to include the full range of abundance levels.

For each regression analysis, we developed 15 candidate *a priori* model combinations that were the most biologically meaningful. We calculated Akaike's Information Criterion (AIC_c, corrected for sample size) for each model in SAS (SAS Institute, Inc. 1990). The models were ranked by ΔAIC_c, and the models with $\Delta AIC_c < 2$ (which had the highest Akaike weights) were selected as the best models (Burnham and Anderson 2002). Multicollinearity was not a problem (Neter et al. 1989) because no two variables were highly correlated (all $r < 0.6$); models also met the assumption of linearity (Neter et al. 1989).

The predictability of the logistic regressions was assessed by comparing Somers' *d* among the models. To calculate Somers' *d*, all possible pairs of stations are compared, where each in the pair is in a different category. For example, in the occupancy models, the proportion of such pairs in which the occupied station has a higher predicted probability of occupancy than the unoccupied station is recorded as the proportion of concordant pairs. This proportion is adjusted to range from −1 to 1. Zero is no correlation and 1 or −1 is perfect positive or negative correlation between observed and predicted occupancy (Harrell 2001).

RESULTS

Tree size.—In California, dbh was greater in occupied stands than in unoccupied stands (dbh data were unavailable for Oregon; Table 1). Only 54% of stations in the fog zone with mean dbh between 100 and 140 cm were occupied, whereas almost all (91%) stations with larger tree sizes were occupied (Fig. 2A). The majority (79%) of stations in the fog zone with mean tree dbh below 100 cm were not occupied. Mean dbh was much larger inside than outside of the fog zone (where occupied behaviors suggestive of nesting generally do not occur; Fig. 2B). At the occupied stations, dbh did not significantly differ across murrelet abundance categories (Table 1).

Elevation.—Occupied stations averaged 188 and 168 m lower in elevation than unoccupied stations in California and southern Oregon, respectively (Table 1). Elevation was lower at high-abundance stations in California ($P < 0.001$) but not in Oregon ($P = 0.79$; Table 1). The difference in elevation between stations with zero and high abundance (>15 detections per survey) was significant in both states (Kruskal-Wallis, $P < 0.001$).

Location in drainage.—Slope, aspect, and distance to nearest stream provide insight into locations within a drainage potentially used for nesting. In southern Oregon, location in the drainage did not differ between occupied and unoccupied stations, except that occupied stations were more west-facing than unoccupied stations (Table 1). In contrast, slope in California differed between occupied and unoccupied stands and across the three abundance categories; unoccupied stations had slopes (12°) that were three times steeper than the slopes of high-abundance stations (4°). Although occupied stations were significantly closer to streams (291 m) than unoccupied stations (359 m) in California, there was no difference among abundance categories in distance to stream (Table 1). In contrast to Oregon, aspect in California did not differ between occupied or abundance categories.

Distance to roads.—California stations with high bird abundance were significantly closer to roads than were stations with medium or low abundance, but distance to roads did not differ between occupancy categories. Road distance was not significantly related to occupancy or abundance in Oregon (Table 1).

Climate.—In California, occupied and high-abundance stations had cooler maximum summer temperatures than unoccupied stations (Table 1). Temperatures were 2° C cooler at occupied stations, and 3° C cooler at high-abundance stations. In southern Oregon, occupied stations were significantly cooler than unoccupied stations but temperatures did not differ among abundance categories. Precipi-

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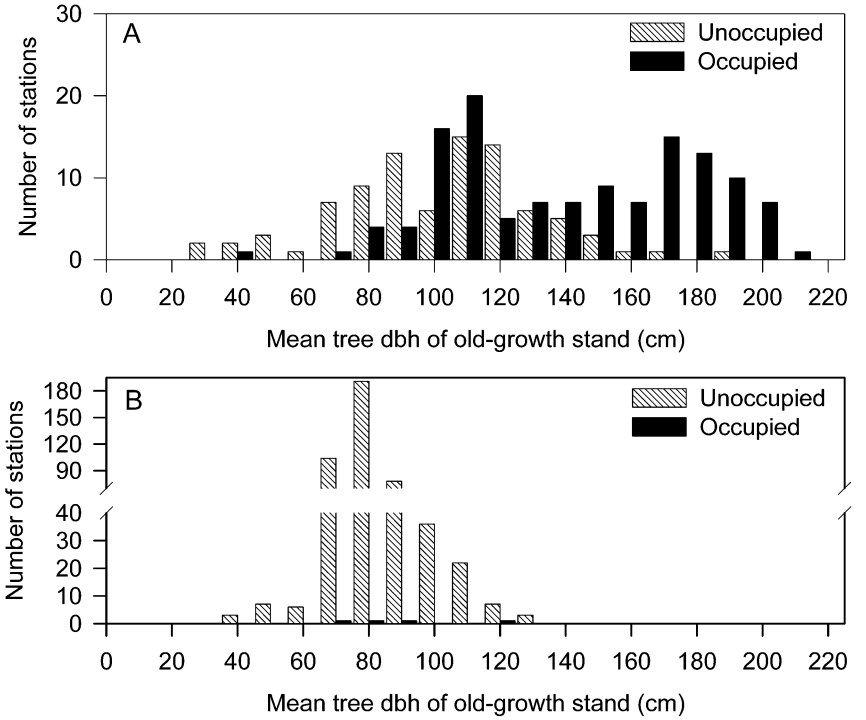


FIG. 2. From 1991 to 1997 in California, occupancy by Marbled Murrelets was highest in old-growth stands with a large mean tree diameter at breast height (dbh) of canopy trees, especially in the fog zone. A = inside fog zone, B = outside fog zone.

tation results were less clear. Precipitation was not significantly related to either occupancy or abundance in southern Oregon or to abundance in California. However, occupied stations in California were significantly drier than unoccupied stations.

Variables in combination.—The best binary logistic regression model in California (predicting occupancy) included tree size, maximum temperature, elevation, and precipitation (first model; Table 2). Based on Akaike weights, this model had about twice the support for being the best model compared with the two next-best combinations of variables (evidence ratios of the weights between two compared models ranged from 1.8 to 2.1); these models had the same variables but also included slope (second model) or distance to road (third model). All three models ($\Delta AIC_c < 2$; Table 2) indicate murrelets occupied stands on low-elevation, cool, moist, gentle slopes with large trees in areas farther from roads.

The best ordinal logistic regression (abundance) in California also included dbh, temperature, elevation, precipitation, and slope (first model; Table 3). Based on the evidence ratio, this model had 2.7× the support of the next-best model. Similar to the occupancy models, these models indicate that murrelets were most abundant in low elevation, cool, moist stands with gentle slopes and large trees. The predictability (Somers' *d*) of the occupancy models was higher than that of the abundance models (Tables 2 and 3).

The best binary logistic regression model for southern Oregon included elevation, east-west aspect, precipitation, and distance to stream, indicating that murrelets occupied sites that were often on low-elevation, high-precipitation, west-facing slopes far from streams (first model; Table 2). The next three best models of occupancy ($\Delta AIC_c < 2$) had about one-third less support for being the best model (Table 2).

The first four ordinal logistic regression models (abundance) for Oregon included elevation, east-west aspect, distance to stream, or

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TABLE 2. The top three (where $\Delta AIC_c < 2$) of the five best candidate binary logistic regression models—ranked in order of ΔAIC_c—indicate that stands occupied by Marbled Murrelets in California had larger mean tree dbh, lower elevations, cooler temperatures, greater precipitation, flatter slopes, and were farther from roads ($n = 207$) than unoccupied stands. In Oregon, the top four models ($\Delta AIC_c < 2$) indicate that occupied stands were on west-facing aspects at lower elevations with greater precipitation and were farther from streams ($n = 133$) than unoccupied stands. K = number of parameters.

Model	K	AIC_c	ΔAIC_c	Akaike weight	Somers' *d*
California					
Dbh, elevation, temperature, precipitation	5	143.97	0.00	0.334	0.866
Dbh, elevation, temperature, precipitation, slope	6	145.08	1.11	0.191	0.870
Dbh, elevation, temperature, precipitation, road	6	145.42	1.45	0.162	0.868
Dbh, elevation, temperature, precipitation, road, slope	7	146.34	2.37	0.102	0.872
Dbh, elevation, temperature, precipitation, stream	5	147.19	3.22	0.067	0.868
Southern Oregon					
Elevation, east, precipitation, stream	5	162.92	0.00	0.230	0.528
Elevation, east, precipitation	4	163.69	0.77	0.156	0.502
Elevation, east	3	163.90	0.98	0.141	0.486
Elevation, east, stream	4	163.90	0.98	0.141	0.498
Elevation, east, north, precipitation	5	165.45	2.53	0.065	0.498

precipitation in various combinations; Akaike weight did not strongly separate these models (Table 3). The fifth-best model, which included distance to road, had a lower Akaike weight but still had $\Delta AIC_c < 2$; thus, it is also a comparatively good model. Overall, the Oregon models had lower predictability than the California models (Somers' *d*; Tables 2 and 3).

DISCUSSION

Assuming that occupied stands are used for nesting, our study suggests that Marbled Murrelets prefer to nest in cool, moist, low-elevation stands of old-growth forest that contain the largest trees. Estimates of murrelet abundance within occupied stands added additional information on habitat requirements, often when the relationship between habitat

TABLE 3. The top model ($\Delta AIC_c < 2$) of the best five candidate ordinal logistic regression models—ranked in order of increasing ΔAIC_c—indicates that Marbled Murrelets in California were most abundant in stands with large trees at lower elevations, cooler temperatures, greater precipitation, and flatter slopes ($n = 207$). For Oregon, the top five models ($\Delta AIC_c < 2$) indicate that murrelets were most abundant in stands with west-facing aspects, lower elevations, greater precipitation, and which were farther from streams and roads than sites where murrelets were less abundant ($n = 133$). K = number of parameters.

Model	K	AIC_c	ΔAIC_c	Akaike weight	Somers' *d*
California					
Dbh, elevation, temperature, precipitation, slope	8	384.14	0.00	0.469	0.730
Dbh, elevation, temperature, precipitation, slope, road	9	386.15	2.01	0.172	0.730
Dbh, elevation, temperature, precipitation, slope, stream	9	386.32	2.18	0.157	0.730
Dbh, elevation, temperature, slope, stream	8	387.19	3.05	0.102	0.722
Dbh, elevation, temperature, precipitation, slope, stream, road	10	388.36	4.22	0.057	0.730
Southern Oregon					
Elevation, east	5	296.80	0.00	0.196	0.366
Elevation, east, precipitation	6	297.33	0.53	0.150	0.380
Elevation, east, stream	6	297.76	0.96	0.121	0.372
Elevation, east, precipitation, stream	7	297.77	0.97	0.121	0.389
Elevation, east, road	6	298.07	1.27	0.104	0.362

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variables and occupancy (presence/absence) was strong (Table 1). Overall, the interpretation of the results was similar, whether using the occupancy or abundance metric (Tables 2 and 3).

Tree size.—As expected based on previous research, murrelets in California most consistently used stands with the largest trees. As tree size decreased, stands were often unoccupied, especially those with mean dbh ≤100 cm. Other studies in Oregon, Washington, and Alaska have shown similar trends (Rodway et al. 1993, Grenier and Nelson 1995, Hamer 1995, Kuletz et al. 1995). Larger trees often have more potential nest platforms than smaller trees (Hamer 1995, Naslund et al.1995), although, as Hamer (1995) postulated, epiphytes on some smaller trees can effectively thicken branches, thus providing platforms for nest sites.

Slope position.—As predicted, murrelets in California most often used cool, moist, forests on gentle, low-elevation slopes near the bottom of drainages where the largest trees grow. Similarly, birds in southern Oregon used cooler and moister low-elevation areas, but not as low as in California. Unlike California murrelets, the Oregon birds tended to use west-facing slopes farther from streams, and the steepness of the slope was not important. The difference in slope position and distance from stream may be due to differences in dominant tree species used for nests between the two states. Unlike redwood trees, which grow largest along alluvial flats in California (Agee 1993), coastal Douglas-fir in Oregon is not adapted to flooding and does not grow well adjacent to streams (Stone and Vasey 1968). Thus, in Oregon, the best nest platforms may be in the largest Douglas-fir trees, which are farther from streams and higher on the hillside.

Data from other studies support our finding that forests with mostly flood-intolerant tree species may have more murrelet occupancy higher on the hillside—in contrast to forests with flood-tolerant tree species that may have the best nesting sites at lower elevation, on gentler slopes, and in flood-prone areas. In central Oregon just north of our study area, where the more flood-intolerant Douglas-fir was the dominant tree used by murrelets, occupied stands were mostly on the gentler slopes of middle and upper portions of hillsides (Grenier and Nelson 1995). In a Washington study that included areas dominated by flood-intolerant Douglas-fir trees, as well as other tree species used by murrelets that were more tolerant of flooding [western red cedar (*Thuja plicata*) and Sitka spruce; Duddles and Fitzgerald 1998], the probability of murrelet occupancy of a stand was highest on lower to middle portions of the hillside, and increased as slope increased (Hamer 1995). A study of 45 actual nest sites across the Pacific Northwest showed that, on average, nests were located on the lowest slopes in California, on the highest in Oregon, and on intermediate slope positions in Washington (Hamer and Nelson 1995), corresponding to the proportion of the dominant tree species that are flood-tolerant. Although there may have been a bias because areas were not randomly searched to locate nests, the trend in that nest study is suggestive.

One study does not support our finding that areas with flood-tolerant tree species have more murrelet use near the bottom of drainages. In a recent study of 157 actual nest sites in British Columbia forests near Desolation and Clayoquot sounds, murrelets avoided flat areas (F. Huettmann unpubl. data) even though the forests had many flood-tolerant species. It is difficult to compare our study area with British Columbia because slopes in our area are not as steep and the large avalanche chutes that are commonly found in British Columbia do not occur in Oregon and California. More research is needed to evaluate the relationships between tree size and number of potential nesting platforms in relation to position on slope and tree tolerance to flooding.

Elevation.—The apparent preference of Marbled Murrelets for nesting in relatively low-elevation sites (not necessarily at the bottom of valleys) appears to be fairly consistent across its range from Alaska to California (Rodway et al. 1993, Burger 1995, Grenier and Nelson 1995, Hamer 1995, Kuletz et al. 1995, Miller and Ralph 1995, Manley 1999). One might argue that lower-elevation sites tend to be closer to the coast, and, thus, increased use could be due to closer proximity to marine habitat. However, studies in California and southern Oregon have shown that low elevation is important even when prox-

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imity to marine habitat has been taken into account (Meyer and Miller 2002, Meyer et al. 2002).

For studies in which low elevation was found to be important to murrelet use, only Rodway et al. (1993), Miller and Ralph (1995), and this study clearly demonstrate that the elevation effect is related to slope position, with murrelets more often occupying stands at the bottom of local major drainages rather than occupying ridge tops. On a more regional scale, murrelets also may be responding to less favorable vegetation conditions that occur as elevation increases (Burger 1995, Hamer 1995). For example, in Washington and British Columbia, high-elevation trees such as silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) may be smaller and have fewer platform branches than trees that occur at low elevations—such as western hemlock, western red cedar, Douglas-fir, and Sitka spruce (Rodway et al. 1993, Hamer 1995). However, murrelets readily nested in high-elevation (>800 m) forests composed of mountain hemlock and yellow cedar (*Chamaecyparis nootkatensis*) in British Columbia (Manley 1999, Bradley 2002), even though they marginally preferred forests at elevations of <800 m (F. Huettmann unpubl. data). Although they may prefer lower elevations, murrelets readily use high-elevation forests.

Murrelets probably are responding to factors correlated to elevation, rather than to elevation itself. High elevations along ridge tops may be used less because branch growth needed to develop nest platforms may be less optimal (Daniel 1942), or wind damage may be higher. Also, fog—which provides cooler conditions for nesting birds and obscures a predator's view of nests—burns off more quickly on ridge tops.

Climate.—As predicted, murrelets used relatively cool forest stands with high amounts of precipitation (mostly rain). Although we hypothesized that such areas would be used by a coldwater-adapted seabird (Ralph et al. 1995), more use could also result if cool, moist environments promote more epiphyte growth on branches (i.e., suitable nest sites). In California, birds often occupied drier areas (Table 1), but once tree size was taken into account, the areas of greater precipitation had greater occupancy. In regard to temperature, other studies have shown that murrelets avoid warm areas, even where suitable nest sites are available (Dillingham et al. 1995, Hunter et al. 1998). Our study is the first to show that, even within the fog zone, murrelets appear to prefer moist areas with the coolest temperatures. Laboratory studies on the physiological tolerances of murrelets are needed to help validate this apparent preference.

Distance to roads.—When elevation was taken into account (Tables 2 and 3), regression analyses showed that sites used by murrelets were often farther from roads than sites without murrelets. We obtained this result even though birds might be detected more easily at survey stations near roads. In a previous study, wherein the level of fragmentation in old-growth forest was taken into account, murrelets were most abundant in sites farther from roads (Meyer et al. 2002). These results suggest that human disturbance and noise along roads may reduce murrelet use of an area.

Potential biases in indices based on audio-visual surveys.—We used occupancy as an index to murrelet nesting, and abundance as an index to number of nesting murrelets in a stand. These metrics may be poor proxies for nesting if they are biased by survey station placement. Rodway and Regehr (2000) showed that audio-visual survey sites near streams often have larger canopy openings than sites farther from streams, making it possible to detect more birds and more below-canopy flight or circling, two major behaviors used to classify a site as occupied. Consequently, detections may be upwardly biased in low-elevation valley bottoms with gentle slopes, even when the birds have no preference for using such areas. Moreover, murrelet abundance may be inflated if the birds use streams as travel corridors (Rodway and Regehr 2000). We detected higher occupancy and abundance in valley bottoms in California, possibly due to this bias; however, results in Oregon did not show the same trend. The lower predictability of our abundance models suggests that such biases and the high daily variability in number of detections made it more difficult to detect a significant relationship between abundance and habitat variables than between occupancy and the same variables. More actual nest sites need to be iden-

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tified in our study area using unbiased techniques, so that our results for occupancy and abundance, both of which are affected by detectability, can be compared with results of other studies.

In summary, our results suggest that recovery efforts for murrelets in our study area should focus on protecting cool, moist, low-elevation stands of old-growth forest with the largest-dbh trees, and that these areas should be far from roads. In California, redwood stands along alluvial flats adjacent to streams should be given high priority, and, in southern Oregon, the low-elevation Douglas-fir stands higher on hillsides should be given priority. This information, along with landscape and regional-level results from other studies, can help managers prioritize recovery efforts. More research is needed to establish the link between occupancy, abundance, and nest density to verify our conclusions.

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LITERATURE CITED

AGEE, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

BOOTH, D. E. 1991. Estimating pre-logging old-growth in the Pacific Northwest. Journal of Forestry 89: 25–29.

BOYCE, M. S. AND L. L. MCDONALD. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14: 268–272.

BRADLEY, R. W. 2002. Breeding ecology of radiomarked Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. M.Sc. thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

BRADLEY, R. W. AND F. COOKE. 2001. Cliff and deciduous tree nests of Marbled Murrelets in southwestern British Columbia. Northwestern Naturalist 82:52–57.

BRIGGLER, J. T. AND J. W. PRATHER. 2003. Seasonal use and selection of caves by the eastern pipistrelle bat (*Pipistrellus subflavus*). American Midland Naturalist 149:406–412.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.

BURGER, A. E. 1995. Inland habitat associations of Marbled Murrelets in British Columbia. Pages 151–161 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York.

CALIFORNIA TIMBERLAND TASK FORCE. 1993. The report of the California Timberland Task Force: submitted to the California legislature. Resources Agency of California, Sacramento.

DALY, C., W. P. GIBSON, G. H. TAYLOR, G. L. JOHNSON, AND P. PASTERIS. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22:99–113.

DANIEL, T. W. 1942. Comparative transpiration rates of several western conifers under controlled conditions. Ph.D. dissertation, University of California, Berkeley.

DILLINGHAM, C. P., R. C. MILLER, AND L. O. WEBB. 1995. Marbled Murrelet distribution in the Siskiyou National Forest of southwestern Oregon. Northwestern Naturalist 76:112–119.

DUDDLES, R. E. AND S. A. FITZGERALD. 1998. Managing western hemlock forests in the Oregon Coast Range. The woodland workbook: stand management, EC 1490, Oregon State University Extension Service, Corvallis.

EVANS MACK, D., W. P. RITCHIE, S. K. NELSON, E. KUO-HARRISON, P. HARRISON, AND T. E. HAMER. 2003. Methods for surveying Marbled Murrelets in forests: a revised protocol for land management and research. Pacific Seabird Group Marbled Murrelet Technical Committee, Corvallis, Oregon. Online at <http://www.pacificseabirdgroup.org/revMAMU_ISP_Jan_03.pdf> (accessed 1 September 2004).

FRANKLIN, J. G. AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. General Technical Report PNW–8. U.S. Forest Service, Pacific Northwest Station, Portland, Oregon.

GRENIER, J. J. AND S. K. NELSON. 1995. Relationship of Marbled Murrelets with habitat characteristics at inland sites in California. Pages 205–215 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

HAMER, T. E. 1995. Inland habitat associations of Marbled Murrelets in western Washington. Pages 163–176 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G.

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Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

HAMER, T. E. AND S. K. NELSON. 1995. Characteristics of Marbled Murrelet nest trees and nesting stands. Pages 69–82 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

HANSEN, A. J., T. A. SPIES, F. J. SWANSON, AND J. L. OHMANN. 1991. Conserving biodiversity in managed forests. BioScience 41:382–392.

HARRELL, F. E. 2001. Regression modeling strategies: with applications to linear models, logistic regressions, and survival analysis. Springer-Verlag, New York.

HUNTER, J. E., K. N. SCHMIDT, H. B. STAUFFER, S. L. MILLER, C. J. RALPH, AND L. ROBERTS. 1998. Status of the Marbled Murrelet in the inner north coast ranges of California. Northwestern Naturalist 79:92–103.

JODICE, P. G. R. AND M. W. COLLOPY. 2000. Activity patterns of Marbled Murrelets in Douglas-fir old-growth forests of the Oregon Coast Range. Condor 102:275–285.

JODICE, P. G. R., S. L. GARMAN, AND M. W. COLLOPY. 2001. Using resampling to assess reliability of audio-visual survey strategies for Marbled Murrelets at inland forest sites. Waterbirds 24:331–344.

KULETZ, K. J., D. K. MARKS, N. L. NASLUND, N. J. GOODSON, AND M. B. CODY. 1995. Inland habitat suitability for the Marbled Murrelet in southcentral Alaska. Pages 141–149 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

MANLEY, I. A. 1999. Behaviour and habitat selection of Marbled Murrelets nesting on the Sunshine Coast. M.Sc. thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

MEYER, C. B. 1999. Marbled Murrelet use of landscapes and seascapes during the breeding season in California and southern Oregon. Ph.D. dissertation, University of Wyoming, Laramie.

MEYER, C. B. AND S. L. MILLER. 2002. Marbled Murrelet use of fragmented landscapes for nesting in southern Oregon, USA. Conservation Biology 16: 755–766.

MEYER, C. B., S. L. MILLER, AND C. J. RALPH. 2002. Multi-scale landscape and seascape patterns associated with Marbled Murrelet nesting areas on the U.S. west coast. Landscape Ecology 17:95–115.

MEYER, C. B., S. L. MILLER, AND C. J. RALPH. 2004. Logistic regression accuracy across different spatial and temporal scales for a wide-ranging species, the Marbled Murrelet. Pages 94–106 *in* Resource selection methods and applications (S. Huzurbazar, Ed.). Omnipress, Madison, Wisconsin.

MILLER, S. L., C. B. MEYER, AND C. J. RALPH. 2002. Land and seascape patterns associated with Marbled Murrelet abundance offshore. Waterbirds 25: 100–108.

MILLER, S. L. AND C. J. RALPH. 1995. Relationships of Marbled Murrelets with habitat and vegetation characteristics at inland sites in California. Pages 191–215 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

NASLUND, N. L., K. J. KULETZ, M. B. CODY, AND D. K. MARKS. 1995. Tree and habitat characteristics and reproductive success at Marbled Murrelet tree nests in Alaska. Northwestern Naturalist 76:12–25.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1989. Applied linear regression models. Richard D. Irwin, Bunridge, Illinois.

O'DONNELL, B. P., N. L. NASLUND, AND C. J. RALPH. 1995. Patterns of seasonal variation of activity of Marbled Murrelets in forested stands. Pages 117–128 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

PEERY, M. Z., S. R. BEISSINGER, S. H. NEWMAN, B. H. BECKER, E. BURKETT, AND T. D. WILLIAMS. 2004. Individual and temporal variation in inland flight behavior of Marbled Murrelets: implications for population monitoring. Condor 106:344–353.

RALPH, C. J., G. L. HUNT, JR., M. G. RAPHAEL, AND J. F. PIATT. 1995. Ecology and conservation of the Marbled Murrelet in North America: an overview. Pages 3–22 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S Forest Service, Pacific Southwest Research Station, Albany, California.

RALPH, C. J., S. K. NELSON, M. M. SHAUGHNESSY, AND S. L. MILLER. 1994. Methods for surveying Marbled Murrelets in forests. Pacific Seabird Group Technical Paper 1.

RAPHAEL, M. G., J. A. YOUNG, AND B. M. GALLEHER. 1995. A landscape-level analysis of Marbled Murrelet habitat in western Washington. Pages 177–189 *in* Ecology and conservation of the Marbled Murrelet (C. J. Ralph, G. L. Hunt, M. G. Raphael, and J. F. Piatt, Eds.). General Technical Report PSW–152. U.S. Forest Service, Pacific Southwest Research Station, Albany, California.

RIPPLE, W. J., S. K. NELSON, AND E. M. GLENN. 2003. Forest landscape patterns around Marbled Murrelet nest sites in the Oregon Coast Range. Northwestern Naturalist 84:80–89.

RODWAY, M. S. AND H. M. REGEHR. 2000. Measuring Marbled Murrelet activity in valley bottom habi-

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tat: bias due to station placement. Journal of Field Ornithology 71:415–422.

RODWAY, M. S., H. M. REGEHR, AND J. P. L. SAVARD. 1993. Activity levels of Marbled Murrelets in different inland habitats in the Queen Charlotte Islands, British Columbia. Canadian Journal of Zoology 71:977–984.

SAS INSTITUTE, INC. 1990. SAS/STAT user's guide, ver. 6, 4th ed. SAS Institute, Inc., Cary, North Carolina.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry: the principles and practice of statistics in biological research, 2nd ed. W. H. Freeman and Company, San Francisco, California.

STONE, E. C. AND R. VASEY. 1968. Preservation of coast redwood on alluvial flats. Science 159:157–161.

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