Nesting Habitat Characteristics of the Marbled Murrelet in Central California Redwood Forests

LAUREN M. BAKER,[1] *University of California Berkeley, Department of Environmental Science, Policy & Management, Berkeley, CA 94720, USA*
M. ZACHARIAH PEERY,[2,3] *University of California Berkeley, Department of Environmental Science, Policy & Management, Berkeley, CA 94720, USA*
ESTHER E. BURKETT, *California Department of Fish and Game, Habitat Conservation Planning Branch, Sacramento, CA 95814, USA*
STEVEN W. SINGER, *Steven Singer Environmental and Ecological Services, Santa Cruz, CA 95061, USA*
DAVID L. SUDDJIAN, *David Suddjian Biological Consulting Services, Capitola, CA 95010, USA*
STEVEN R. BEISSINGER, *University of California Berkeley, Department of Environmental Science, Policy & Management, Berkeley, CA 94720, USA*

Abstract

*The marbled murrelet (*Brachyramphus marmoratus*) is a threatened seabird that nests in old-growth forests in the Pacific Northwest. Despite concern for this species, little has been published on murrelet nesting habitat in the coast redwood (*Sequoia sempervirens*) region. Here we present the first comprehensive study of marbled murrelet nesting characteristics in redwood forests based on confirmed nest sites. In this study, we 1) described habitat characteristics at 17 murrelet nest sites in the Santa Cruz Mountains, California, USA, located using radiotelemetry and visual searches, and 2) compared nest sites with random sites located in nearby stands and centered on trees ≥120 cm diameter at breast height (dbh [potential nest trees or PNTs]). All 17 nests were located in stands of old-growth redwood forest and the mean dbh of nest trees was 210 cm (SD = 91 cm). Eighty-two percent of nests (90% of telemetry-found nests) were in unharvested stands and 18%, all on private property, had been lightly harvested but did not contain significantly fewer trees ≥120 cm dbh than unharvested nest sites. Twelve of 15 (80%) nests for which we were able to locate the nesting platform were on limbs and the remaining 3 (20%), all in redwood trees, were located on broken tops. Nest trees were significantly larger than PNTs and tended to be Douglas-fir (*Pseudotsuga menziesii*) despite the fact that nest stands were dominated by redwoods, perhaps because of greater nest platform availability in Douglas-fir trees. Nest sites were located closer to streams, had a greater basal area of trees ≥120 cm dbh, and were located lower on slopes than random sites based on analysis of variance models. We classified 71% of nest sites correctly with a simple logistic regression model that included only nest tree dbh and distance to stream—a model that could be used by managers in the region to identify potentially suitable nesting habitat. Our findings indicated that murrelets in central California, USA, primarily use old-growth redwood stands for nesting but will use partially harvested stands if a significant residual component remains; stands that have experienced some harvest but retain old-growth characteristics should be considered potential murrelet habitat in redwood forests.* (JOURNAL OF WILDLIFE MANAGEMENT 70(4):939–946; 2006)

Key words

Brachyramphus marmoratus, *endangered species, habitat use, marbled murrelet, nesting habitat, old-growth redwood forest, Santa Cruz Mountains.*

Intensive timber harvesting has occurred in the coastal old-growth forests of the Pacific Northwest since the middle of the 19th century. Only 4% of the original old-growth coast redwood (*Sequoia sempervirens*) forest remains in California, USA (Fox 1989). As a result, some species of wildlife dependent on old-growth redwood forests have experienced large population declines (Noss 2000). One such species is the marbled murrelet (*Brachyramphus marmoratus*), a small seabird in the family Alcidae that forages at sea but nests on large tree limbs in coastal forests (Nelson 1997). Scientists generally believe that the logging of nesting habitat greatly reduced murrelet populations in California (Carter and Erickson 1992), and loss of nesting habitat was the primary reason the murrelet was placed on the federal threatened and state endangered species lists in California (Larsen 1991, U.S. Fish and Wildlife Service 1992). Two primary murrelet populations remain in the state; the larger population nests in remnant old-growth redwood forests in northern California and the smaller population nests in remnant old-growth redwood forests in central California.

Finding nests and characterizing nesting habitat is extremely challenging because the marbled murrelet prefers to nest high in large trees and exhibits secretive nesting behavior. Published literature has described only 4 murrelet-nest trees from California (Binford et al. 1975, Singer et al. 1991, 1995), although an additional 5 nest trees were pooled with data from other regions in a range-wide analysis of murrelet nesting habitat (Hamer and Nelson 1995). The more detailed studies of murrelet nesting habitat in the redwood region have used observations of birds flying beneath the canopy (Miller and Ralph 1995, Meyer and Miller 2002, Meyer et al. 2004), but inferences from such studies are limited because stands where murrelets are detected are not necessarily used for nesting. The recent development of capture and radiotelemetry techniques for seabirds (Whitworth et al. 1997, Newman et al. 1999) has greatly increased researchers' ability to locate and describe murrelet nest sites (e.g., Zharikov et al. 2006), but detailed analyses of murrelet nesting habitat in the redwood region based on known nests have not been conducted.

We present the first study of marbled murrelet nesting habitat characteristics in redwood forests based on confirmed nest sites that compares habitat use versus habitat availability, involves a

---

[1] *Present address: Center for International Environmental Law, Washington, D.C. 20036, USA*
[2] *E-mail: zpeery@mlml.calstate.edu*
[3] *Present address: Moss Landing Marine Laboratories, Moss Landing, CA 95039, USA*

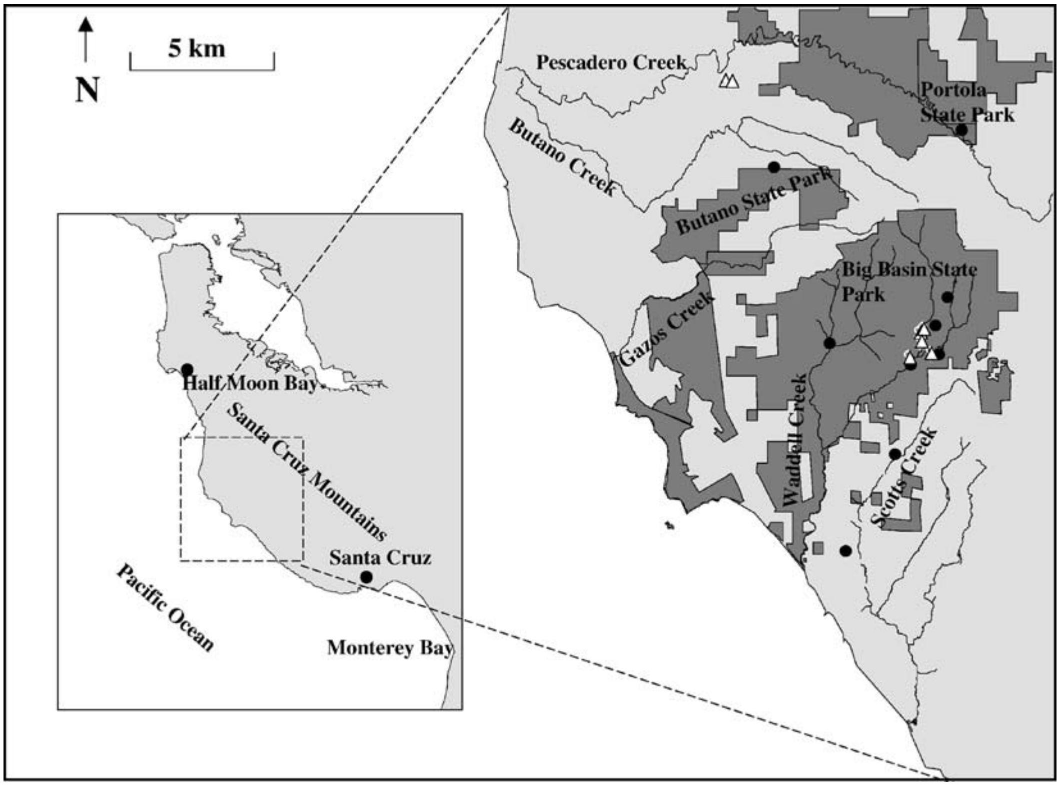

Figure 1. Study area and marbled murrelet nest locations in the Santa Cruz Mountains, central California, USA, 1989–2001. Dark circles represent nests found with radiotelemetry, and white triangles represent nests found visually.

detailed quantification of forest structure at the stand scale, and uses a relatively large number of nest sites. Using radiotelemetry and ground-based visual searches for nest sites in central California, we sought to 1) determine the frequency of murrelet nests in unharvested versus harvested redwood stands; 2) characterize murrelet nest sites at the stand, tree, and platform scales; and 3) identify important habitat characteristics by comparing habitat use to habitat availability at the tree and stand scales (Johnson 1980).

Study Area

We conducted the study in coast redwood forest in the Santa Cruz Mountains of central California, USA (Fig. 1). The Santa Cruz Mountains run from San Francisco to the Pajaro River (a distance of 119 km) and are part of the California Outer Coastal Range. Elevation ranges from sea level to 1,154 m. The redwood forest in this region is dominated by coast redwood in the overstory, but Douglas-fir (*Pseudotsuga menziesii*) is also present to a lesser degree. Hardwoods in the understory include tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), and California bay (*Umbellaria californica* [Zinke 1977, Sawyer and Keeler-Wolf 1995]). Logging of most original old-growth in the range occurred around 1900 (Singer et al. 1991, Noss 2000). Harvesting in the region from the late 1800s through the 1960s generally involved clear-cutting, including true clear-cutting, seed tree retention, and leaving small pockets of inaccessible timber (J. B. Bulger, personal communication; Evarts and Popper 2001). Most of the harvesting since the 1970s has been selective, which generally entails removing 25–30% of the total stems in the stand at 12- to 15-year intervals (J. B. Bulger, personal communication). There are currently less than 4,100 ha of old-growth redwood forest remaining in the Santa Cruz Mountains (J. B. Bulger, unpublished data), and many of the remaining old-growth stands are in state and county parks (Fig. 1). Smaller, isolated stands of old-growth redwood forest are located on smaller parks and on private property. Climatic conditions in the Santa Cruz Mountains vary from west to east because of high ridges that limit the penetration of maritime air masses and orographic effects. Our study sites were in the west half of the range where summer conditions are typically moderately cool with frequent low overcast or fog, and winter conditions are cool and wet. Average annual precipitation on the west side ranges from 70 cm on the coast (Davenport) to 147 cm at the summit (Ben Lomond Mountain; California Department of Water Resources 1982). Precipitation on the west side is mostly rain falling between October and May.

Methods

Locating Nests

We used a combination of radiotelemetry and ground-based visual searches to locate 17 marbled murrelet nests in the Santa Cruz Mountains (10 with radiotelemetry and 7 with visual searches). These nests constitute 17 of the 18 known nests in the region and include the nest trees described by Singer et al. (1991, 1995), but not the nest described by Binford et al. (1975). To locate murrelet nests with radiotelemetry, we captured and radiotagged murrelets in Año Nuevo Bay, California, USA, in April–June from 1997 to 2001 with a dip-net from a 4.5-m inflatable boat (Peery et al.

2004*a,b*). Radiotransmitters were attached using the subcutaneous anchor technique (Newman et al. 1999), were made by Holohil Systems Ltd. (model BD-2G, Carp, Ontario, Canada), and weighed 2.2 g with an expected life of 12–16 weeks. We tracked murrelets using aerial telemetry from a fixed-wing aircraft and ground-based telemetry from 4-wheel-drive vehicles outfitted with a null-peak antenna arrangement (Kenward 1987). We attempted to obtain at least one location at sea every 24 hours for each murrelet. If a radiomarked murrelet was not located at sea, we flew over all forested habitat in the Santa Cruz Mountains between Santa Cruz and Half Moon Bay to determine if the individual went inland to initiate incubation. When we detected a bird inland, we visited the forested area where the signal originated to locate the nest tree as soon as possible (usually the same day). We returned as soon as possible (usually early the following morning) to observe the nesting pair exchanging incubation duties in order to locate the exact nest site (Peery et al. 2004*a,b*). We detected radiomarked murrelets, or they had moved to at-sea areas far from nesting habitat (>250 km), on >95% of the days they carried a functioning radiotransmitter. Therefore, it is unlikely that we failed to detect many nests or that we biased nest locations towards forested areas with easy access.

We found 4 of the visually located nests during targeted nest searches and 3 of the visually located nests fortuitously. We conducted targeted searches during the breeding seasons in old-growth portions of Big Basin Redwoods State Park in 1989 and from 1991 to 1996 by placing observers around possible nest trees to watch for incoming murrelets from 1 hour before sunrise to 1 hour after sunrise (Singer et al. 1991, 1995; E. E. Burkett, California Department of Fish and Game, unpublished data). We selected possible nest trees based on tree size and the presence of suitable nest platforms, which we defined as any area within the live crown that was at least 18 cm in diameter, had some cover present, and was above the lower one-quarter of the live crown. We spent an average of 253 hours per year for the 7 years that we carried out targeted nest searches (SD = 316 hr), with a range of 51 to 831 hours per year. An observer conducting inland audiovisual surveys (Evans Mack et al. 2003) found 2 of the 3 fortuitously located nests because he witnessed predation events at the nest sites by common ravens (*Corvus corax*). Audiovisual surveys are a required component of timber harvest planning in any stand that has trees with suitable nest platforms. Surveyors have carried out audiovisual surveys in a large number of locations and range of habitats in the Santa Cruz Mountains. A third nest site was located by observing marbled murrelet eggshell fragments at the base of an old-growth tree below a suitable nest limb. We assumed that nests found with radiotelemetry constituted a random representation of murrelet nesting habitat, but the same may not be true for visually located nests because some searches were concentrated in old-growth habitat. We statistically compared habitat variables at nest sites located with radiotelemetry and visual techniques to determine if visually located nests were biased representations of nesting habitat.

Assessing Important Habitat Attributes

We employed a use-versus-availability study design to determine which habitat attributes murrelets used more than would be expected based on their availability (Johnson 1980). Nest sites constituted *used habitat* while randomly selected sites in the Santa Cruz Mountains were treated as *available habitat*. Each random site was paired with a nearby nest site and was placed in stands that contained at least a residual component of old growth. We defined *stands* as the 25-m-radius area surrounding a nest tree and *old growth* to be forest in a late seral stage in which the canopy is dominated by trees originating prior to about 1850 when significant logging began. By pairing nest and random sites and by excluding heavily harvested and pure second-growth stands, we attempted to determine which attributes within old-growth forests constitute important elements of murrelet nesting habitat. In doing so, we assumed that murrelets require at least a residual component of old growth for nesting.

Each random site was located within a 1-km radius of a nest site. To locate random sites, we randomly generated a series of Universal Transverse Mercator (UTM) coordinates and designated the closest tree to the first UTM coordinate with a diameter at breast height (dbh) of ≥120 cm as the center of the random site and the "potential nest tree" (PNT). We used a minimum of 120 cm dbh for PNTs because this measurement was approximately equal to the dbh of the smallest-sized tree expected to contain a suitable nesting platform in the Santa Cruz Mountains and was very similar to the minimum nest tree dbh (134 cm). If we did not locate a tree with a dbh of ≥120 cm in the area indicated by the randomly generated UTM coordinates, we searched for a PNT along a 150-m transect in a random direction. We used the first tree ≥120 cm dbh within 25 m of the transect line as the center of the random site. We excluded randomly generated locations that did not contain a residual component of old-growth and instead searched the next randomly located site until we located a suitable site.

Measuring Habitat Characteristics

We measured habitat variables at the nest-platform, nest-tree, and nest-stand scales. To measure stand-level characteristics, we centered a 25-m-radius plot (0.2 ha) on the nest tree or PNT. We measured dbh (cm) and determined the species of each tree >10 cm dbh within the plot. We also measured the dbh, height (m), canopy lift (distance to the bottom of the live crown; m), and crown diameter (m) of 5 randomly selected dominant and midstory trees within each plot. For analysis purposes, we grouped all trees within the 25-m-radius plots into 1 of 4 size classes based on their dbh: 10–60 cm ("small trees"), 60–90 cm ("medium trees" that consisted of large midstory to small dominant trees), 90–120 cm ("large trees" that consisted of old-growth trees; as defined by Miller and Ralph 1995), and >120 cm ("very large trees" consisting of old-growth trees that would qualify as PNTs in this study). Although not used for nesting by murrelets, we compared the basal area of small, medium, and large trees between nest and random sites because tree size may provide important habitat elements such as concealing nests from predators. We then calculated the basal area (m^2/ha) in each size class in each plot. We also measured the slope (%), aspect (°), position on slope (lower third, middle third, and upper third), number of canopy layers (for trees >10 m in height), and canopy cover (midstory, dominant, and total; %) at the center of the plot. Finally, we estimated the distance to nearest permanent stream (m), distance inland (km), and elevation (m) using range finders and topographic maps.

Some sites did not have measurements for the number of canopy layers, canopy cover, or for random midstory and dominant tree variables because we collected data prior to the establishment of habitat-characterization protocols.

At the nest tree scale, we measured the dbh (cm), height (m), canopy lift (m), crown area (calculated in m^2 from crown diameter along the cardinal directions), and number of platforms (limbs >10 cm in diameter) for all nest trees and PNTs. The limited data sites did not have measurements for the number of platforms, canopy lift, or crown area of the nest tree.

When feasible, we climbed nest trees and measured habitat characteristics at nest limbs and platforms including tree diameter at nest (cm), branch diameter at nest (cm), nest limb aspect (°), limb height (m), moss cover on all limbs (%), moss cover on the nest platform (%), lichen cover on all limbs (%), and lichen cover on the nest platform (%). We did not collect nest platform data for PNTs due to logistical constraints.

Data Analysis

Univariate analyses.—We used a chi-square analysis to compare categorical habitat variables such as harvest history, position on slope, and number of canopy layers between nest and random sites. We used a mixed-model analysis of variance (Littell et al. 1996) to compare continuous habitat variables between nest and random sites. Site classification (nest or random), method of locating the nest (visual or telemetry), and the interaction between site classification and method of location were treated as fixed effects, while site was treated as a random blocking effect. Method of location was included in the model to test for potential biases in visual searches, such as biases towards large trees and old-growth stands. We treated site as a random blocking effect to pair nest and random sites. Initially we included all factors in the model, then we systematically removed factors that were not significant in the following order: 1) the interaction between site classification and location method, 2) site classification, and 3) location method. We employed a 2-sample Watson–Williams test for circular data (Zar 1999) to compare aspect between nest and random sites. We assessed the normality of all continuous habitat variables using Shapiro–Wilk tests and transformed nonnormal variables using square root and $\log_{10}$+1 transformations. We considered P values of 0.05 to be significant for all statistical tests. We did not adjust critical values to account for multiple tests because 1) doing so would have resulted in low power to detect differences given our small sample size, and 2) our univariate analyses were exploratory and our intention was to identify habitat characteristics that were potentially important for murrelet nesting.

Logistic regression analyses.—We used logistic regression analysis (Hosmer and Lemeshow 2000) to develop a predictive model that could identify suitable nesting habitat for marbled murrelets. The basal area of large trees, the basal area of very large trees, total canopy cover, dbh of the nest tree, distance to stream, and slope were treated as independent variables and used to predict whether a site was a random or a nest site. We only used 2 basal area variables, the basal area of large trees and basal area of very large trees because 1) small and medium trees were not important in the univariate analysis, and 2) the basal area of large and very large trees was highly correlated with the basal area of individual species in these size classes. Variables not measured at all sites (random midstory and dominant tree variables, number of platforms, canopy lift and crown of the nest tree, and mid- and overstory canopy cover), that were circular (aspect), or exhibited little variation (elevation) were excluded. To restrict the number of candidate models, we first modeled all combinations of the basal area of large trees, the basal area of very large trees, and nest tree dbh separately from all combinations of slope, total canopy cover, and distance to nearest stream. We then explored a model that combined the most important variables from each of the 2 preliminary sets of models. We ranked competing models using Akaike's Information Criterion scores corrected for small sample size (AIC_c; Burnham and Anderson 2002).

We used a jackknifing procedure to determine the ability of the best logistic regression model to predict whether a site was a nest or random site. We conducted 34 sets of logistic regression analyses using the original data set with a unique observation removed. If the probability of the site being a nest was >0.50, we classified it as a nest site; otherwise we classified it as a random site.

Results

Distribution of Nest Sites with Respect to Landownership and Harvest History

We located 17 nest sites in the Santa Cruz Mountains (Fig. 1): 13 (76%) in California state parks and 4 (24%) on private property. Eight of 10 (80%) nests located with radiotelemetry and 5 of 7 (71%) nests located visually were in state parks. All nests were located in either unharvested (82%) or lightly harvested (18%), old-growth, coast redwood–Douglas-fir stands. Ninety percent of nests located with radiotelemetry and 71% of visually located nests were in unharvested forest stands, suggesting that we did not bias visually located nests towards or against unharvested stands. All 13 nest sites on state park lands were unharvested, but 3 out of 4 sites on private property had been harvested. Two harvested sites were logged over 50 years ago (J. B. Bulger, unpublished data) and one site was logged as recently as 10 years ago (M. Z. Peery, University of California Berkeley, unpublished data), all using individual tree selection harvesting techniques. Logging within all harvested stands had left a significant number of live trees and a significant component of residual old-growth trees (4–6 trees ≥120 cm dbh per plot). The number of very large trees in harvested nest plots ($\bar{x} = 5.3$, SD = 1.2) did not differ ($t_{16} = -0.48$, $P = 0.64$) from the number of very large trees in unharvested nest plots ($\bar{x} = 6.0$, SD = 2.3). Moreover, the dbh of very large trees did not differ ($t_{16} = 0.12$, $P = 0.91$) between partially harvested ($\bar{x} =$ 179 cm, SD = 50) and unharvested sites ($\bar{x} = 183$ cm, SD = 31). No difference in harvest history existed between nest and random sites ($\chi^2_1 = 0.66$, $P = 0.42$).

Habitat Characteristics and Selection at the Stand Scale

Nest sites were located an average of 9.0 km (SD = 2.9) from the coast, with a range of 1.7 to 16.2 km inland. All nest sites were on the bottom two-thirds of the slope, with 11 (65%) on the bottom third and 6 (35%) on the middle third of the slope. To ensure that expected values were ≥5 for the chi-square analysis comparing slope position between nest and random sites, we pooled sites on the middle and upper third of the slope. The distribution of nest sites with respect to slope position differed significantly from the

Table 1. Nest tree and site characteristics for 17 marbled murrelet nest sites and 17 random sites in the Santa Cruz Mountains, California, USA, 1989–2001.

	Nest sites			**Random sites**					
Habitat variable	$\bar{x}$	**SD**	***n***	$\bar{x}$	**SD**	***n***	***F***	***P***	**df**
Site characteristic[a]									
Elevation (m)[b]	280.4	86.7	17	314.7	109.3	17	1.03	0.32	1,32
Slope (%)[c]	48.9	25.7	17	47.5	24.1	17	0.03	0.87	1,32
Aspect (°)[d]	278.0	87.4	16	78.0	100.1	17	14.44	<0.01	1,31
Nearest stream (m)[e]	103.1	75.7	17	270.0	237.1	17	7.32	0.01	1,32
Dominant canopy cover (%)	29.6	11.9	14	30.1	11.0	17	0.31	0.58	1,26
Midstory canopy cover (%)	52.9	13.8	14	48.6	13.0	17	0.09	0.76	1,26
Total canopy cover (%)	65.0	16.5	17	69.8	8.8	17	1.12	0.30	1,32
Nest tree or potential nest tree characteristic									
Diameter at breast height (cm)[f]	209.5	90.6	17	165.7	47.1	17	4.63	0.04	1,32
Height (m)	56.6	11.9	17	51.4	14.2	17	1.33	0.26	1,32
Crown area (m^2)	125.6	59.2	13	105.1	58.9	17	0.82	0.37	1,24
Canopy lift (m)	21.7	6.8	14	18.8	7.2	17	1.08	0.31	1,26
No. of platforms	7.4	4.9	13	5.1	3.5	17	2.17	0.15	1,24

[a] Observations only included if a matching nest and random site were available.

[b] Random site effect significant at $P \leq 0.05$.

[c] Method of location significant at $P \leq 0.05$; visually detected nests had lower values than nests found with radiotelemetry.

[d] Watson–Williams circular distribution test used to compare aspect between nest and random sites (Zar 1984).

[e] Analysis conducted using square root transformation.

[f] Analysis conducted using log transformation.

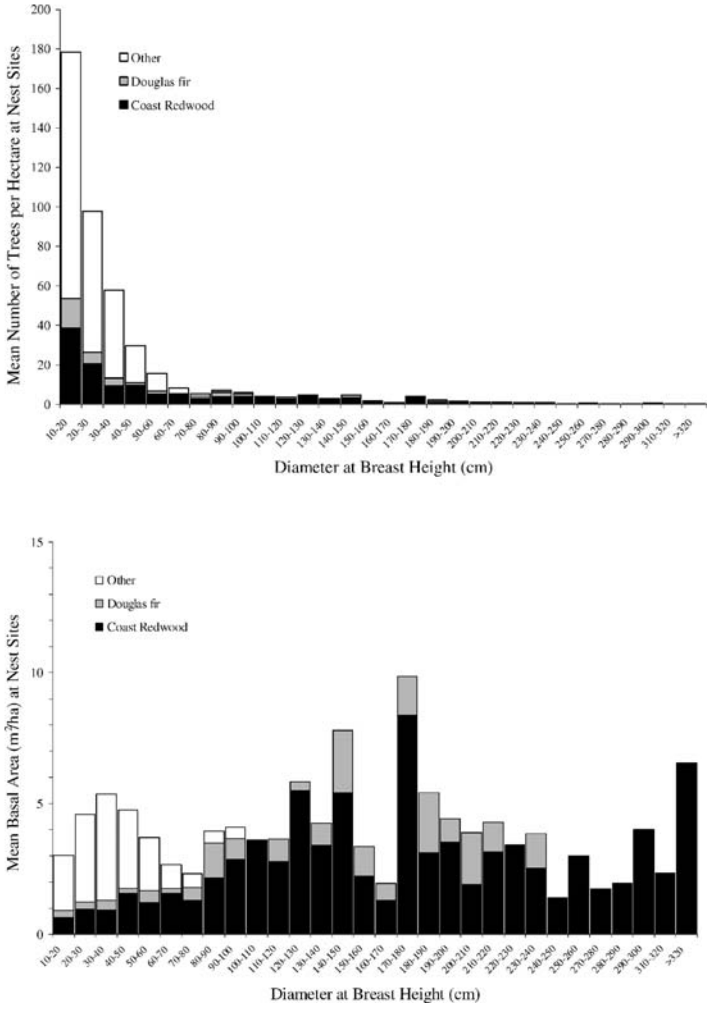

Figure 2. Trees at marbled murrelet nest sites in central California, USA, measured in 25-m-radius plots centered on the nest tree, 1989–2001. (a) Mean number of trees by size class and species, (b) mean basal area by tree species and size class. Species listed are coast redwood, Douglas-fir, and other.

random sites ($\chi^2_1 = 9.9$, $P < 0.01$), with 35% of random sites on the bottom third and 65% on the upper two-thirds of the slope. Nest sites were located significantly closer to streams than random sites ($P = 0.01$; Table 1). Nest and random sites were not different in percent slope, but differed significantly in aspect ($P < 0.01$), as nest sites generally faced west (Table 1). There was no significant difference in canopy cover between nest and random plots (Table 1). Nest and random sites had a minimum of 2 canopy layers and nest sites tended to have more canopy layers than random sites, but this difference was not significant ($\chi^2_1 = 2.5$, $P = 0.11$). Two of 4 cells in this chi-square analysis had expected values <5, and it is possible that we would have detected a difference with a greater sample size of nests.

Marbled murrelets generally nested in stands where coast redwoods dominated the total basal area, but most trees within nest stands were small tanoaks (Fig. 2). Although there were relatively few large trees in nest plots, 66% of the basal area at nest sites was in trees ≥120 cm dbh (Fig. 2). The basal area of very large trees in nest plots ($\bar{x}$ = 79.2 m^2/ha, SD = 43.6) was significantly greater than in random plots ($\bar{x}$ = 58.0 m^2/ha, SD = 47.4; $F_{1,32} = 4.42$, $P = 0.04$). The basal area of very large redwood trees tended to be greater at nest sites than at random sites (nest: $\bar{x}$ = 64.8 m^2/ha, SD = 47.1; random: $\bar{x}$ = 42.1 m^2/ha, SD = 37.8; $F_{1,32} = 3.70$, $P = 0.06$), but Douglas-fir trees did not follow this pattern (nest: $\bar{x}$ = 14.4 m^2/ha, SD = 12.0; random: $\bar{x}$ = 15.9 m^2/ha, SD = 22.5; $F_{1,32} = 0.33$, $P = 0.57$). No difference existed between nest and random sites in the basal area of any other size class or size class by species combination (all P values > 0.05). Nest sites did not have significantly more very large trees per hectare ($\bar{x}$ = 29.4, SD = 10.6) than random sites ($\bar{x}$ = 25.3, SD = 16.6; $F_{1,32} = 0.74$, $P = 0.40$), but the dbh of very large trees tended to be greater in nest sites ($\bar{x}$ = 180 cm, SD = 46) than in random sites ($\bar{x}$ = 157 cm, SD = 25; $F_{1,32} = 3.2$, $P = 0.08$). There were no significant differences between the height, lift, crown area, or dbh

Figure 3. Marbled murrelet nest platform on the broken top of an old-growth coast redwood tree. Note the egg, marked by the white arrow, in the middle of the picture beneath the epiphytic redwood sapling. (Photo by J. Spickler.)

of the 5 random dominant and subdominant trees measured for 13 nest and random sites (all P values > 0.05).

Habitat Characteristics and Selection at the Tree Scale

All 17 nests were found in very large conifers (mean dbh = 210 cm, SD = 91); 7 nests (41%) were in redwood trees and 10 (59%) were in Douglas-fir trees. Redwood ($\bar{x} = 244$ cm, SD = 135) and Douglas-fir ($\bar{x} = 186$ cm, SD = 30) nest trees did not differ significantly in dbh ($t_{16} = 1.33$, $P = 0.20$). However, Douglas-fir nest trees had a significantly greater number of platforms ($\bar{x} = 10.5$, SD = 3.4, $n = 8$) than redwood nests ($\bar{x} = 2.4$, SD = 1.1, $n = 5$; $t_{16} = 5.05$, $P < 0.01$). Of the 17 PNTs, 9 were in redwood trees (53%) and 8 were in Douglas-fir trees (47%). There was no significant difference in the proportions of the 2 species between nest trees and PNTs ($\chi^2_1 = 0.47$, $P = 0.49$). The mean diameter of nest trees was significantly greater than PNTs, which we randomly selected within old-growth forests and were at least 120-cm dbh (Table 1). The mean height, crown area, canopy lift, and number of platforms in nest trees and PNTs did not differ (Table 1).

Habitat Characteristics at the Platform Scale

We measured characteristics of 15 nest platforms from 14 nest trees (platforms for 3 of the 17 nest trees were not located and 1 tree was used twice for nesting). Twelve of the 15 (80%) platforms were located on limbs and 3 of the 15 (20%) platforms were created by broken tops (Fig. 3). All 3 broken-top nests were in redwood trees. The remaining 5 of 8 (63%) redwood nests and all Douglas-fir nests ($n = 7$) were on limbs. Mean diameter of the nest limb, including epiphyte cover, was 46.5 cm (SD = 12.1, $n = 12$) at the nest cup, with a range of 29–70 cm, and the mean diameter of the tree at the nest limb was 99.7 cm (SD = 28.6, $n = 11$). Mean limb height was 41 m (SD = 7.7, $n = 6$), mean limb aspect was 95° (SD = 100, $n = 13$), and mean nest limb length was 6.9 m (SD = 3.8, $n = 8$). Mean moss cover on nest limbs was 32.3% (SD = 35, $n = 10$) and mean moss cover on nest platforms was 27.2% (SD = 32.5, $n = 10$). Douglas-fir trees had significantly more moss cover ($\bar{x} = 59.0\%$, SD = 30.9, $n = 5$) than redwood trees ($\bar{x} = 5.6\%$, SD = 4.3, $n = 5$; $t_9 = 3.8$, $P < 0.01$). Mean lichen cover on all limbs was 16.1% (SD = 16.2, $n = 10$) and mean lichen cover on the nest platform was 5.8% (SD = 6.1, $n = 9$).

Table 2. Akaike's Information Criterion scores (AIC) for 16 logistic regression models predicting whether a site was a marbled murrelet nest site or a randomly measured site in the Santa Cruz Mountains, California, USA, 1989–2001.

Model	K^a	$\text{AIC}_c{}^b$	$\Delta\text{AIC}_c{}^c$
Nest Tree dbh[d] + Distance to Stream	3	42.43	0.00
Distance to Stream	2	44.31	1.88
Total Canopy Cover + Distance to Stream	3	46.19	3.76
Nest Tree dbh	2	46.41	3.98
Distance to Stream + Slope	3	46.66	4.23
BA[e] Very Large Trees	2	47.06	4.63
BA Large Trees + Nest Tree dbh	3	47.24	4.81
BA Very Large Trees + Nest Tree dbh	3	47.91	5.48
Slope + Total Canopy Cover + Distance to Stream	4	48.61	6.18
BA Very Large Trees + BA Large Trees	3	48.83	6.40
BA Very Large Trees + BA Large Trees + Nest Tree dbh	4	49.21	6.78
Intercept	1	49.26	6.83
Total Canopy Cover	2	50.26	7.83
BA Large Trees	2	50.44	8.01
Slope	2	51.50	9.07
Slope + Total Canopy Cover	3	52.47	10.05

[a] Number of parameters.
[b] AIC score corrected for small sample size.
[c] The difference in AIC_c scores between the best model and the model in question.
[d] Diameter at breast height.
[e] Basal area.

Multivariate Analyses

Multicollinearity was generally not an issue because the 6 independent variables used in the logistic regression analysis were uncorrelated (all $r < 0.35$) except for nest tree dbh and the basal area of very large trees ($r = 0.60$, $P < 0.01$). The logistic model that provided the best discrimination between nest and random sites contained nest tree dbh and distance to stream; it ranked 1.88 AIC_c units higher than the next best model, which only contained distance to stream (Table 2). The following equation describes the best model:

$$P = \frac{e^{7.85 \times \log(\text{NSTDBH}) - 0.18 \times \text{STMDST}^{1/2} - 15.50}}{1 + e^{7.85 \times \log(\text{NSTDBH}) - 0.18 \times \text{STMDST}^{1/2} - 15.50}},$$

where P was the probability that a site was a nest site, NSTDBH was the diameter of the nest tree (cm), and STMDST was distance of the nest to the stream (m). This model was the highest ranked model regardless of which observation we removed from the data set. Using the jackknifing procedure, we successfully classified 12 of 17 nest sites (71%) and 12 of 17 random sites (71%) with this relatively simple model.

Discussion

We found that unharvested and lightly harvested old-growth forest stands are the primary sources of nesting habitat for marbled murrelets in central California, and second-growth and heavily harvested (e.g., previously clear-cut) stands do not provide essential habitat features. This strong preference for old-growth forests at the nest tree and stand scales is consistent with the range-wide analysis conducted by Hamer and Nelson (1995) and corroborates results from counts of murrelets in inland habitats in California and other regions (Grenier and Nelson 1995, Hamer 1995, Miller and Ralph 1995, Meyer and Miller 2002, Meyer et al. 2004).

Inferences from our use-versus-availability analyses were limited by the sample size of nests ($n = 17$). Also, we compared nest sites to random sites instead of to unused sites, which could have compromised the power to detect important habitat characteristics (Garshelis 2000). Nevertheless, our nest-site characterization was based on 17 of the 18 known nests in central California, USA, and our use-versus-availability analyses allowed for some inferences to be made about murrelet habitat attributes. We found that nest sites were much closer to streams than would be expected based on randomly available sites within old-growth forests. Nest sites may have been located near streams because these sites afforded murrelets better access from at-sea flyways. Studies have found proximity to streams or other openings to be important for murrelet nesting in other regions as well (Hamer and Nelson 1995, Meyer et al. 2004, Zharikov et al. 2006). Murrelets also used very large trees ($\bar{x}$ dbh $= 210$ cm) for nesting that were significantly larger than the dbh of PNTs ($\bar{x}$ dbh $= 166$ cm). The large dbh of nest trees may also be an indicator for other important factors for murrelets at the nest limb, platform, and cup scales, such as increased nest concealment through increased vertical cover over limbs or a more favorable microclimate. Perhaps more importantly, large trees may harbor larger platforms or be older and have a higher incidence of limb and tree deformities, which we found to be important for murrelets. Finally, marbled murrelets selected stands characterized by greater basal area of very large trees, greater basal area of very large redwood trees, and a low position on the slope. The tendency for murrelets to nest in sites with greater basal area of very large trees suggests that, even within old-growth forests, murrelets select nest stands dominated by the largest trees.

Despite the importance of very large redwoods at the stand scale, more nests were located in Douglas-fir (59%) than in redwood trees (41%), possibly because Douglas-fir trees are more likely to contain suitable nesting platforms. Redwoods, even very large ones, had almost 4 times fewer limbs >10 cm than Douglas-fir nest trees and mean nest limb diameter was much greater for Douglas-fir than for redwood nests. When murrelets did nest in redwood trees, they often used broken tops (3 of 8 nests) instead of nest limbs. No literature has previously reported the use of broken tops, which may compose an important component of murrelet nesting habitat in redwood forests.

We did not find a difference in the number of potential nesting platforms between nest trees and PNTs. However, the presence of multiple suitable platforms does not necessarily indicate that a tree is suitable for nesting. Mean limb diameter was 59.8 cm, considerably larger than the 10-cm criteria used to identify suitable platforms during platform counts. Counts of limbs >10 cm, which are often used by managers to determine if a site is suitable for murrelet nesting, is probably not a useful index of nest-site availability in central California, USA, as the smallest nest limb we found was 29 cm in diameter.

Nesting habitat use by murrelets varies geographically because of regional differences in forest composition and structure, as well as murrelet behavior. For example, the majority of murrelet nests in British Columbia have been near natural and man-made forest edges (Burger 2002, Zharikov et al. 2006), whereas our nest sites were generally located in contiguous forests. Nevertheless, marbled murrelets appear to consistently select certain habitat features throughout much of their range, including locations low on the slope, close to streams, and a high basal area of very large trees (Hamer and Nelson 1995, Meyer et al. 2004, Zharikov et al. 2006).

Management Implications

Management for marbled murrelet nesting habitat in the Santa Cruz Mountains should protect unharvested and partially harvested stands of old-growth redwood forests, particularly those low on the slope and near streams. Our logistic regression model, which contained nest tree dbh and distance to stream, could be used by land managers to identify potential murrelet nesting for timber harvest and conservation planning. However, caution should be used when applying this model because 29% of nesting habitat would be incorrectly classified as nonhabitat and because of the small sample size of nests ($n = 17$) used to develop the model. Land managers could reduce the probability of a false negative (treating nesting habitat as nonhabitat) by conducting audiovisual surveys to determine occupancy status in areas not predicted to be nesting habitat.

Acknowledgments

Funding was provided by the California Department of Fish and Game, United States Fish and Wildlife Service, California State Parks, Big Creek Lumber Company, Pacific Lumber Company, and the University of California at Berkeley. We thank S. Newman for tagging all radiomarked murrelets and J. Takekawa, R. Golightly, and H. Carter for their invaluable leadership in the early stages of the radiotagging. We thank captains B. Wright and B. Pucinelli, Lieutenant D. Huckins, Lieutenant M. Crossland, Lieutenant K. Long, B. Delano, and the crews of the California Department of Fish and Game patrol boats, the *Bluefin* and the *Albacore*, for their assistance with captures. L. Heitz, R. VanBenthuysen, B. Cole, and B. Morgan piloted planes used to locate nests. We thank the many field assistants who helped locate and measure nest trees, including T. Poitras, S. Cooper, J. Rapp, J. Meyer, K. Bixler, C. Morrison, R. Steers, K. Cramer, J. McEntee, C. Neufeld, M. Fan, J. Erbe, and J. Tseng. We thank J. Bulger for sharing his knowledge of murrelets and the Santa Cruz Mountains; his assistance was invaluable during all phases of this project. We thank B. McCrary and Big Creek Lumber who provided housing and access to their property. G. Strachan, E. Burko, and H. Huenemann provided vital logistical support for the project, as did park staff at Año Nuevo, Big Basin Redwoods, Portola Redwoods, and Butano state parks. J. Spickler climbed nest trees and collected nest platform data.

Literature Cited

Binford, L. C., B. G. Elliott, and S. W. Singer. 1975. Discovery of a nest and downy young of marbled murrelet. Wilson Bulletin 87:303–319.

Burger, A. E. 2002. Conservation assessment of marbled murrelets in British Columbia: a review of the biology, populations, habitat associations, and conservation. Technical Report Series 387, Canadian Wildlife Service, Pacific and Yukon Region, British Columbia, Canada.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer-Verlag, New York, New York, USA.

California Department of Water Resources. 1982. Rainfall depth–duration–frequency for California. California Resources Agency, Sacramento, USA.

Carter, H. R., and R. A. Erickson. 1992. Status and conservation of the marbled murrelet in California. Proceedings of the Western Foundation of Vertebrate Zoology 5:92–116.

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, Arcata, California, USA.

Evarts, J., and M. Popper, editors. 2001. Coast redwood: a natural and cultural history. Cachuma, Los Olivos, California, USA.

Fox, L. J. 1989. A classification, map, and volume estimate for the coast redwood forest in California. Forest and Rangeland Resources Assessment Program, California Department of Forestry and Fire Protection, Sacramento, USA.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University, New York, New York, USA.

Grenier, J. J., and S. K. Nelson. 1995. Marbled murrelet habitat associations in Oregon. Pages 191–204 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service General Technical Report PSW-152, Albany, California, USA.

Hamer, T. E. 1995. Inland habitat associations of marbled murrelets in western Washington. Pages 163–176 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service General Technical Report PSW-152, Albany, California, USA.

Hamer, T. E., and S. K. Nelson. 1995. Characteristics of marbled murrelet nest trees and nesting stands. Pages 69–82 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service General Technical Report PSW-152, Albany, California, USA.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kenward, R. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. Academic, London, United Kingdom.

Larsen, C. J. 1991. Report to the Fish and Game Commission: a status review of the marbled murrelet (*Brachyramphus marmoratus*) in California. California Department of Fish and Game, Wildlife Management Division, Candidate Species Status Report 91–1, Sacramento, USA.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.

Meyer, C. B., and S. L. Miller. 2002. Use of fragmented landscapes by marbled murrelets for nesting in southern Oregon. Conservation Biology 16:755–766.

Meyer, C. B., S. L. Miller, and C. J. Ralph. 2004. Stand-scale habitat associations across a large geographic region of an old-growth specialist, the marbled murrelet. Wilson Bulletin 116:197–210.

Miller, S. L., and C. J. Ralph. 1995. Relationship of marbled murrelets with habitat characteristics at inland sites in California. Pages 205–218 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service General Technical Report PSW-152, Albany, California, USA.

Nelson, S. K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). Pages 1–25 *in* A. Poole and F. Gills, editors. The birds of North America, number 276. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and the American Ornithologists' Union, Washington, D.C., USA.

Newman, S. H., J. Y. Takekawa, D. L. Whitworth, and E. Burkett. 1999. Subcutaneous anchor attachment increases retention of radio-transmitters on Xantus' and marbled murrelets. Journal of Field Ornithology 70:520–534.

Noss, R. F. 2000. The redwood forest: history, ecology, and conservation of the coast redwoods. Island, Washington, D.C., USA.

Peery, M. Z., S. R. Beissinger, S. H. Newman, B. H. Becker, E. B. Burkett, and T. D. Williams. 2004*a*. Individual and temporal variation in inland flight behavior of marbled murrelets: implications for population monitoring. Condor 106:344–353.

Peery, M. Z., S. R. Beissinger, S. H. Newman, E. B. Burkett, and T. D. Williams. 2004*b*. Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. Conservation Biology 18:1088–1098.

Sawyer, J. O., and T. Keeler-Wolf. 1995. A manual of California vegetation. California Native Plant Society, Sacramento, USA.

Singer, S. W., N. L. Naslund, S. A. Singer, and C. J. Ralph. 1991. Discovery and observations of two tree nests of the marbled murrelet. Condor 93:330–339.

Singer, S. W., D. L. Suddjian, and S. A. Singer. 1995. Fledging behavior, flight patterns and forest characteristics at marbled murrelet tree nests in California. Northwestern Naturalist 76:54–62.

U.S. Fish and Wildlife Service. 1992. Determination of the threatened status for the Washington, Oregon, and California population of the marbled murrelet. U.S. Fish and Wildlife Service, Portland, Oregon, USA.

Whitworth, D. L., J. Y. Takekawa, H. R. Carter, and W. R. McIver. 1997. A night-lighting technique for at-sea capture of Xantus' murrelets. Colonial Waterbirds 20:525–531.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zharikov, Y., D. B. Lank, F. Huettmann, R. W. Bradley, N. Parker, P. P.-W. Yen, L. A. McFarlane Tranquilla, and F. C. Cooke. 2006. Habitat selection and breeding success in a forest-nesting alcid, the marbled murrelet, in two landscapes with differing degrees of forest fragmentation. Landscape Ecology 21:107–120.

Zinke, P. J. 1977. The redwood forest and associated north coast forests. Pages 679–698 *in* M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. 1988, Reprint. California Native Plant Society, Sacramento, USA.

Associate Editor: Block.