

# Predictive Model of Habitat Suitability for the Marbled Murrelet in Western Washington

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**ABSTRACT** The marbled murrelet (*Brachyramphus marmoratus*) is a small Pacific seabird with a breeding range that extends from the Aleutian Islands to central California. Throughout most of its breeding range, it uses mature and old-growth coniferous forests as nesting habitat. Although most murrelets seem to nest within 60 km of the coast, occupied nesting habitat has been identified as far as 84 km from the ocean in Washington state. Due to the extensive inland distances within which birds are known to breed, the area requiring surveys to identify breeding sites can be enormous. Therefore, the standard 2-year survey protocol can be expensive and time-consuming for forest management agencies and companies to administer. We developed a logistic regression model to determine whether a suite of forest structural characteristics could be used to reliably predict occupancy of a forest patch by marbled murrelets. We tested the performance of the final model using cross-validation procedures and a sample of independent sites. We used 50 sites surveyed for marbled murrelets to estimate the model, and 48 independent sites were available to test model performance. All 50 sites were on private forestland owned by Rayonier located in the western lowlands of Olympic Peninsula within the Sitka spruce and western hemlock transition zones. We sampled forest habitat at each site, and we collected information on 15 explanatory variables. The best-fitting logistic regression model contained variables that measured number of canopy layers ( $P < 0.001$ , approx. F test) and mistletoe (*Arceuthobium* sp.) abundance ( $P = 0.031$ , approx. F test). The model misclassified 2 of 33 (94% correct) unoccupied sites as occupied using a classification cut-off ( $c$ ) of  $c = 0.25$ . In the other direction, under cross-validation the final model misclassified 2 of 17 (88% correct) occupied sites as unoccupied. On a test of the model against an independent sample, using a classification cut-off value of  $c = 0.25$ , the final model correctly classified 36 of 48 sites (75% correct). The final model misclassified 3 of 31 occupied sites as unoccupied (90% correct). Use of predictive models could greatly reduce the amount of forest that requires surveys by screening out those sites with little probability of use and by focusing remaining effort on higher probability sites, resulting in a higher likelihood of identifying occupied sites and thereby more efficiently conserving marbled murrelet nesting habitat. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):983–993; 2008)

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The marbled murrelet (*Brachyramphus marmoratus*) is a small Pacific seabird with a breeding range that extends from the Aleutian Islands to central California, USA (Nelson 1997). Throughout most of this breeding range, the murrelet uses mature and old-growth coniferous forests as nesting habitat, and it forages primarily in nearshore environments (Nelson 1997). Most murrelets seem to nest within 60 km of the coast, although in Washington, USA, occupied nesting habitat has been identified 84 km from the ocean, and a grounded murrelet was found 100 km from the coast (Hamer 1995, Miller and Ralph 1995). The marbled murrelet was federally listed as threatened in Washington, Oregon, USA, and California in 1992 due to loss of nesting habitat and mortality from net fisheries and oil spills. The marbled murrelet is federally listed as threatened in Canada.

A primary difficulty in determining which habitat may be occupied at inland sites is the inability to detect murrelets at potential breeding sites in the forest ecosystem. Detecting birds at inland sites is extremely difficult due to poor visibility conditions during the dawn activity period; poor viewing conditions in closed canopy forests; and the species' cryptic plumage, small size, and fast flight speed (Nelson and Hamer 1995). To protect breeding sites, forest

managers conduct surveys in potential nesting habitat over 2 consecutive years to determine whether a site is occupied by breeding birds (D. Evans Mack, United States Forest Service, unpublished report). The standardized survey protocol to determine occupancy with a 95% confidence level can require  $\geq 18$  surveys at one site over a 2-year period (D. Evans Mack, unpublished report). Due to the extensive inland distances birds are known to breed, the area needing survey coverage can be enormous. Survey effort to determine site occupancy is therefore expensive and time-consuming.

Habitat models that reliably predict probability that sites are occupied using measurable forest structural characteristics can greatly reduce forestland acreage that require surveys by screening out sites with little probability of use. Predictive habitat models can also increase efficiency in locating occupied sites by identifying sites with high probability of use, thereby allowing forest managers to focus survey efforts at these important sites.

Although studies on habitat associations of marbled murrelets have compared use and nonuse areas (Meyer and Miller 2002, Meyer et al. 2002, Ripple et al. 2003), only a few have involved use of statistics to develop predictive models (Hamer 1995, Conroy et al. 2002, Bahn and Newsome 2002a); none of these were tested against an independent sample of observations to assess performance.

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Our goals were to first develop a habitat model using logistic regression to identify forest structural characteristics that may be used to reliably predict which forest patches may be occupied by marbled murrelets, and second to test model performance using both a sample of independent sites from the same study area and cross validation procedures.

## STUDY AREA

The study area was located in the western lowlands of Olympic Peninsula within the Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) transition zones (Franklin and Dyrness 1973, Henderson et al. 1989). Marbled murrelet survey sites were dominated by Sitka spruce, western hemlock, Douglas fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*). Many sites also contained a subcomponent of silver fir (*Abies amabilis*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). The western portion of the Olympic Peninsula has been influenced by a very wet, humid, maritime climate with precipitation ranging from 203 cm to 381 cm annually (Franklin and Dyrness 1973). Fog and clouds commonly contributed a substantial amount of precipitation as tree drip during summer. Snow accumulations were low and intermittent. Winter and summer temperatures were moderate, with January temperatures averaging 7° C and summer temperatures averaging 17° C (Franklin and Dyrness 1973). Average elevations ranged from 48 m along the coast to 1,477 m in eastern portions of the study area ( $n = 50$ ,  $\bar{x} = 408$  m,  $SD = 319$  m).

The landscape within the study area consisted of a mosaic of young (<80 yr), mature (80–75 yr), and mature–old-growth (>175 yr) stands (Henderson et al. 1989). Timber management, windthrow, fire, and mistletoe infestations greatly influenced forest structure and age composition in our study area and on the west side of the peninsula in general. In the past 200 years,  $\geq 10$  storms with hurricane force winds have hit the west coast of the Olympic Peninsula, with 2 storms having wind forces >241 km/hr (Henderson et al. 1989). Within the areas impacted by these winds, suitable murrelet habitat occurred where the original trees survived due to topographic effects. Fires also occurred in the study area, the largest and most recent being the Great Forks Fire, which burned approximately 13,350 ha in 1951 (Henderson et al. 1989). Historically, however, fires have generally been small (<405 ha), and they have occurred on southerly aspects at mid-elevations due to the drier conditions there (Henderson et al. 1989).

Dwarf mistletoe (*Arceuthobium* sp.) infestations were common in stands dominated by western hemlock. When mistletoe infects hemlock trees at a young age, it can create large brooms of branch growth and greatly enlarged limbs, both forming potential nest structures for marbled murrelets (Geils and Hawksworth 2002).

## METHODS

### Field Methods

In 1993 and 1994, we selected 14 sites for marbled murrelet surveys to identify suitable marbled murrelet habitat on land

owned by Rayonier, a private timber company. This site selection occurred before 1997 when Washington State Forest Practices rules were initiated to require nonfederal landowners to survey suitable marbled murrelet habitat [WAC 222-16-080(1)(j)(vi)(b)]. Between 1997 and 2002, we selected an additional 36 sites for survey based on Rayonier timber harvest plan needs and forest practices rules, which required surveys for sites with as few as 2 potential murrelet nesting platforms per acre. These sites represented a wide range of marbled murrelet habitat conditions across the study area (Table 1).

We conducted marbled murrelet surveys between 1993 and 2002 at 50 selected sites (Fig. 1; Table 2); we surveyed all sites according to the Pacific Seabird Group survey protocol available at the time we initiated surveys (C. J. Ralph, United States Forest Service, unpublished reports; D. Evans Mack, unpublished report). Each surveyed site had 1–6 survey stations. Surveys resulted in the following site status determinations: no detections, presence (murrelets heard or observed above tree canopy), or occupied (murrelets observed flying below or circling above tree canopy). After 1995, when we made a presence determination at a site, we increased effort to >10 surveys in each of 2 years to determine occupancy. For model development, we grouped sites with a determination of presence with sites with no detections and we classified both as unoccupied.

The survey protocol for marbled murrelets is a 2-stage sampling strategy (stopping early when no detections are made) that incorporates  $\geq 4$ , and an expectation of  $\geq 9$ , survey visits in each of 2 years to determine whether an individual site is occupied with 93–95% confidence (D. Evans Mack, unpublished report). With this strategy, we surveyed sites using 4–5 survey visits in each of 2 years (stage 1) until we detected murrelet presence. We then increased survey effort (stage 2) to  $\geq 9$  survey visits in each year to determine whether birds occupied the site. In addition, we increased survey effort (no. of surveys or no. of yr surveyed) at some sites to achieve other research objectives. Therefore, our survey effort varied from site to site depending on other research objectives and whether we detected presence, but all sites had  $\geq 93\%$  probability of detecting occupancy.

We sampled the forest habitat at each site using one of 2 methods, fixed radius plots or transects. We measured the same forest characteristics under both methods. We adopted the transect method in later years of the study to more thoroughly sample habitat at each site, especially sites with small patches of suitable habitat dispersed within larger forested areas.

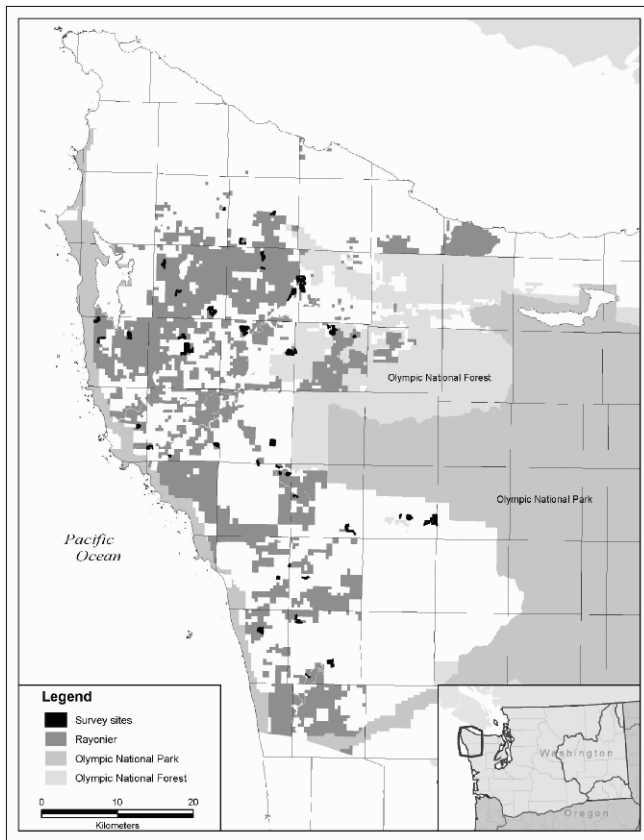
We sampled 13 sites by the fixed plot method between 1993 and 1996; sampling intensity averaged 5.3% (min. = 2.5%, max. = 15.0%,  $SD = 3.9\%$ ) of site area. We measured forest vegetation at each site in 3–9 ( $\bar{x} = 4.3$ ) 25-m radius plots (0.2 ha) located  $\leq 100$  m from survey stations by choosing a random direction and distance from survey station center.

We sampled 37 sites by the transect method between 1997 and 2002 (including one site that we originally sampled by

Table 1. Data<sup>a</sup> we used to build the predictive model of habitat suitability for marbled murrelet in western Washington, USA, 1993–2002.

Site no.	Canopy access	Canopy closure (%)	Canopy layers	Mean dbh (cm)	Mistletoe index	Moss cover (%)	% slope	Trees/ha 60-cm	Trees/ha 60-cm plat	Trees/ha 81-cm	Trees/ha 81-cm plat	Trees/ha 99-cm	Trees/ha 99-cm plat	Trees/ha mistletoe	Platforms/ha
48	2.0	83.6	2.0	91.8	2.0	25.8	4.0	28.9	16.0	17.5	12.4	7.2	6.2	10.3	34.5
121.1	1.3	96.6	1.6	74.7	0.0	50.4	0.7	5.1	0.2	1.2	0.1	0.3	0.1	0.0	0.3
121.2	1.9	96.0	2.1	81.7	1.1	49.3	13.5	15.0	2.3	5.2	1.1	1.9	0.5	3.4	6.1
154	2.2	87.6	2.9	75.9	1.5	69.0	7.2	18.8	3.3	5.5	1.7	0.7	0.2	4.8	4.7
169	2.5	94.8	2.5	92.2	0.1	78.9	2.1	12.8	2.5	5.6	2.4	2.5	1.5	0.3	13.5
176	2.3	86.3	3.4	93.6	1.5	43.0	15.0	24.5	8.5	10.1	6.6	5.3	4.4	6.9	29.1
178.1	1.0	82.3	1.0	78.1	0.0	6.4	6.0	30.9	0.7	12.4	0.7	0.0	0.0	0.0	0.7
32	3.0	85.0	4.8	114.8	1.5	50.8	6.0	17.0	12.4	9.8	8.8	6.7	5.7	5.7	62.9
52	3.0	82.3	3.0	85.8	2.1	45.3	22.0	33.7	10.3	16.5	8.3	5.5	5.5	11.7	19.9
77	3.0	85.4	4.8	119.1	0.2	11.7	8.0	34.7	18.9	25.1	16.8	17.9	13.8	0.3	41.6
97	3.0	90.6	3.3	122.0	1.8	54.1	25.0	14.4	9.6	8.9	6.9	7.6	6.9	5.5	29.6
108	3.0	85.7	3.7	85.1	1.3	36.3	11.0	24.7	13.8	10.3	7.6	6.9	5.5	6.9	30.2
126.1	2.7	86.8	3.1	80.1	2.6	49.7	10.8	23.0	5.1	5.9	2.9	2.6	1.8	11.1	11.8
126.2	2.7	86.0	2.9	82.3	2.5	64.2	15.1	26.4	9.4	8.8	5.1	3.6	2.5	11.7	20.4
126.3	2.5	86.8	2.9	83.1	2.1	70.7	14.7	29.4	11.0	9.5	6.4	4.1	3.2	12.3	25.0
180	2.0	83.8	3.0	88.0	1.5	25.3	27.0	33.0	9.8	16.5	7.7	8.3	6.2	8.8	19.1
189	3.0	92.6	5.0	85.6	1.5	44.9	12.0	28.9	13.8	15.1	9.6	6.2	4.8	9.6	37.1
214	3.0	86.1	3.0	114.7	0.5	26.6	28.0	28.9	15.1	26.8	14.4	17.9	13.8	1.4	33.7
215	3.0	80.1	4.8	130.0	0.1	16.2	15.0	35.1	24.4	27.5	23.7	19.9	19.2	0.3	87.3
222	3.0	89.9	4.0	87.4	0.7	43.7	2.0	20.6	6.2	10.3	6.2	4.8	3.4	2.1	17.9
25.091	1.3	97.1	1.8	84.0	1.4	72.4	7.2	11.6	4.3	5.4	2.5	2.1	1.1	3.2	9.6
26.167	1.7	98.7	2.0	73.0	1.2	78.9	7.5	8.1	1.9	1.9	0.9	0.0	0.0	0.6	3.1
26.170	2.3	93.8	1.9	78.9	1.4	95.0	11.1	19.6	7.1	6.2	2.9	1.8	0.8	2.9	19.6
26.171	1.8	89.0	1.7	74.6	2.1	55.7	10.2	8.7	4.5	2.0	1.5	0.3	0.3	3.4	9.5
27.151	2.5	89.0	2.3	89.0	0.4	80.6	3.5	9.5	0.7	3.8	0.5	1.2	0.2	0.2	0.7
27.168	1.8	93.9	1.4	73.6	1.3	59.0	11.8	6.9	2.2	1.4	0.8	0.1	0.1	1.9	5.7
27.184	2.7	93.3	1.3	82.9	0.7	97.1	5.0	19.4	5.0	8.3	3.1	2.5	1.3	1.9	15.2
27.189	2.8	90.8	1.3	75.2	2.7	68.2	8.8	6.1	3.9	1.7	1.7	0.0	0.0	3.9	23.9
28.205	2.0	95.6	1.4	83.8	1.6	64.0	8.6	2.8	1.1	2.2	1.1	0.0	0.0	1.1	1.1
28.226	2.5	93.7	2.1	79.1	1.8	92.6	0.7	24.4	12.1	9.7	5.9	2.1	1.6	7.7	31.3
29.342	2.5	94.5	1.3	83.8	1.9	99.6	32.5	21.7	6.1	9.7	4.2	2.5	1.7	7.5	16.9
29.426	2.1	95.2	1.8	80.1	0.9	87.3	19.2	17.1	4.2	5.7	2.2	2.4	1.0	2.8	13.9
29.430	2.6	96.0	1.7	83.5	1.5	73.3	16.2	11.8	5.9	5.5	3.6	0.9	0.9	2.7	25.0
29.431	2.0	96.2	2.0	83.1	2.4	97.8	28.3	7.5	3.1	3.6	1.9	1.1	0.6	3.3	17.2
30.402	2.2	94.8	2.3	80.0	2.3	90.4	25.6	14.6	8.3	4.9	3.3	1.6	1.3	5.5	37.2
30.403	1.2	98.6	2.0	85.4	0.1	66.2	4.2	16.3	1.9	8.8	1.9	4.1	0.9	0.0	3.8
30.474	2.0	92.3	1.5	81.7	1.3	83.6	4.7	10.0	3.5	3.0	1.7	1.4	1.0	2.4	14.6
30.506	1.9	96.5	1.7	79.6	1.2	96.7	15.0	14.7	3.8	5.3	2.5	1.3	0.8	2.7	12.9
31.057	1.9	83.0	1.3	72.9	0.7	83.2	30.5	5.5	2.6	1.4	0.9	0.2	0.2	0.8	6.2
31.204	1.7	92.4	1.6	78.6	0.6	91.4	12.3	11.5	2.9	3.4	1.9	1.6	0.8	1.0	9.8
31.206	2.1	92.1	2.6	83.7	0.1	83.4	7.0	11.9	1.3	4.4	0.9	1.6	0.6	0.0	4.7
27.178.1	1.7	95.0	1.7	80.2	1.1	74.4	5.5	8.1	2.4	3.0	1.3	1.0	0.6	1.7	8.0
27.181.1	1.8	97.3	2.0	77.2	1.5	56.5	8.2	13.5	3.2	2.7	0.9	0.6	0.0	2.4	5.0
27.181.2	1.0	98.1	2.0	0.0	0.0	0.0	7.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
29.241.1	2.2	94.2	1.8	80.3	1.4	86.0	13.6	22.0	8.6	8.8	4.2	2.6	1.2	5.3	30.7
29.241.2	2.4	93.7	1.7	78.6	0.4	92.4	21.8	18.2	3.0	6.6	1.8	1.9	0.6	1.2	8.3
30.507.1	2.0	96.5	1.8	77.1	2.4	97.8	6.9	15.6	10.3	4.7	3.4	1.3	0.6	6.9	33.8
30.507.2	2.4	94.2	1.8	81.1	1.2	91.3	19.7	17.4	4.8	6.8	2.4	2.4	1.0	4.2	16.2
29.473.1	2.7	94.8	3.3	87.2	2.8	50.8	38.0	23.3	16.5	12.0	10.2	5.7	5.3	13.0	82.6
29.473.2	2.5	95.2	3.0	89.2	2.2	50.9	69.4	12.7	9.8	6.2	5.7	3.6	3.5	5.8	45.3

<sup>a</sup> Variables are defined in Table 3.



**Figure 1.** Locations of marbled murrelet survey sites ( $n = 50$ ) we used to develop a model of habitat suitability on the northwest Olympic Peninsula, Washington, USA, 1993–2002.

the plot method), with a sampling intensity of 20% of site area. For each site, we placed a transparent overlay with grid spacing of 63.4 m  $\times$  63.4 m (a 0.4-ha grid) over a topographic map that contained site boundaries. We then plotted transect lines in an east–west direction along each grid on site maps for field use. Observers used these maps to traverse each transect line, 12.7 m wide, sampling all trees  $>61.0$  cm diameter at breast height. This method allowed us to evenly sample 20% of each hectare.

We conducted all other data collection in transects in 25-m radius (0.2-ha) circles located in every third grid cell along the transect line. The circular plot's center was located at the base of the first tree with platforms encountered or, for those grid areas with no platform trees, at the center of the grid cell.

For trees  $>61.0$  cm we 1) documented tree species, 2) measured diameter at breast height (to nearest 5 cm using a Biltmore stick), 3) estimated number of potential nest platforms, 4) estimated moss depth on limbs, 5) estimated moss cover on limb surfaces, and 6) estimated mistletoe (*Arceuthobium* sp.) abundance. We assessed the latter 4 variables from the vantage point that provided the best view of the tree crown.

We defined a potential nest platform (hereafter nest platform or platform) on a tree as any limb, deformity, mistletoe broom, or other structure  $>15$  m above the ground and approximately  $>18$  cm in diameter on a tree

$>61.0$  cm diameter at breast height (Hamer 1995). We counted only one platform on a branch even when several platforms were present on the same branch. We did not count branches or platforms at angles  $>45^\circ$ . To count platforms, the observer chose one point 8–30 m away from the tree where the tree crown was most visible. Because we made the platform count estimate from one point, and we counted only one platform per branch, values were indices of platform abundance and not estimates of the total number. If moss cover was present on a branch or limb deformity, we included it in the estimate of platform diameter. We used binoculars to help judge platform size, but we made final judgments with the naked eye.

We estimated average moss depth on each tree limb with the naked eye from the ground as trace or none (0), 0–1 cm (1), 1.1–2 cm (2), 2.1–3 cm (3), 3.1–4 cm (4), and  $>4$  cm (5). We estimated to the nearest 5% the average percent moss cover (0–100%) on the surface of all limbs of each sampled tree (Hamer 1995). We recorded mistletoe abundance (0–6) for each sampled tree following an index developed by Hawksworth (1977). Other plot-level data we took by fixed plot or transect methods included number of canopy layers, canopy access, percent slope, position of plot on slope, aspect, canopy closure, elevation, distance to nearest stream, and distance to ocean.

We estimated number of canopy layers (1–5) by counting the number of discrete tree crown layers present  $>5$  m in height within the plot. To help make this determination, we also examined the number of diameter classes of trees within the plot. We recorded canopy access, which measured flight access to and from the site by adult murrelets. To determine canopy access, we evaluated openness of the canopy and presence and size of gaps between adjacent trees. We classified canopy access as 1) difficult: closed canopy, high tree stem density, or low height class diversity; 2) low: some smaller openings in canopy, moderate tree stem density, and moderate height class diversity; 3) moderate: moderate sized openings in canopy are present, moderate tree stem densities, and higher height class diversity; and 4) high: large openings in canopy are common, lower tree stem densities, and high height class diversity.

We recorded 2 slope readings (%) from plot center using a clinometer. We recorded one upslope and downslope reading and averaged them. We recorded position of each plot relative to slope using topographic maps. We recorded slope position as 1) valley bottom, 2) lower one-third, 3) middle one-third, 4) upper one-third, and 5) ridge top. We recorded dominant aspect of the plot using a compass. We determined average percent canopy closure (0–100%) using a densiometer; we obtained the mean from 4 readings taken in each cardinal direction at a location 9 m in a random direction from plot center. We estimated distance to nearest stream from plot center in the field unless no stream was visible from the plot, in which case we measured distance from stream using topographic maps. We also measured stand size and distance to ocean.

**Table 2.** Legal location, occupancy status, and annual survey effort expended at 50 sites we used to develop a predictive model of habitat suitability for the marbled murrelet in western Washington, USA, 1993–2002.

Site no.	Legal location		No. of surveys by yr										Total surveys	Total yr	
	TWP-Range-Sec(s)	Status	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002			
48	30-14-20, 21, 29	Unoccupied		4	4									8	2
121.1	27-11-25	Unoccupied							10	10				20	2
121.2	27-11-25	Unoccupied							10	10				20	2
154	27-12-26	Unoccupied							6	10	10			26	3
169	27-11-25	Unoccupied							6	10				16	2
176	28-13-26	Occupied	13	15										28	2
178.1	28-14-30	Unoccupied		4	10									14	2
32	30-14-7	Occupied		4	4	10								18	3
52	30-13-24/25/26	Occupied		4	4	10		10						28	4
77	29-15-5	Occupied		4	10	10		16						40	4
97	29-15-11	Occupied		4	4	10								18	3
108	29-15-17	Occupied		4	4	10								18	3
126.1	29-14-15	Occupied						10	10					20	2
126.2	29-14-15/21/22	Occupied						10	10					20	2
126.3	29-14-15	Occupied		4	4			4	10					22	4
180	29-14-25	Occupied		4	4	10								18	3
189	28-14-32	Occupied		4	10	10								24	3
214	25-12-6	Occupied		5	4	10								19	3
215	25-13-10	Occupied		4	5	10								19	3
222	25-12-32	Occupied		4	6	10								20	3
25.091	25-12-27	Unoccupied								10	10			20	2
26.167	26-13-13; 26-12-18	Unoccupied									10	10		20	2
26.170	26-13-24	Unoccupied									10	10		20	2
26.171	26-12-20	Occupied								10	12			22	2
27.151	27-12-18	Unoccupied									10	10		20	2
27.168	27-11-25	Unoccupied								10	10			20	2
27.184	27-13-1/2	Unoccupied									10	10		20	2
27.189	27-11-27	Unoccupied								10	10			20	2
28.205	28-13-3/34	Unoccupied								10	10			20	2
28.226	28-15-24	Unoccupied									10	10		20	2
29.342	29-12-11	Unoccupied									10	10		20	2
29.426	29-12-3/4/9/10	Unoccupied									10	10		20	2
29.430	29-14-9/10	Unoccupied									10	10		20	2
29.431	29-12-4	Unoccupied									10	10	10	20	2
30.402	30-13-3/4/9	Unoccupied									10	10		20	2
30.403	30-13-9/10	Unoccupied									10	10		20	2
30.474	30-14-35/36	Unoccupied									11	12		23	2
30.506	30-12-18; 30-13-13	Unoccupied										10	10	20	2
31.057	31-13-14/15/22/23	Unoccupied									10	10		20	2
31.204	31-13-32	Unoccupied										10	10	20	2
31.206	31-14-13	Unoccupied									10	10		20	2
27.178.1	27-11-27	Unoccupied									10	10		20	2
27.181.1	27-13-01	Unoccupied									10	10		20	2
27.181.2	27-13-01	Unoccupied									11	10		21	2
29.241.1	29-13-5/8	Unoccupied									7	10		17	2
29.241.2	29-13-4/5/8/9	Unoccupied									6	10	11	27	3
30.507.1	30-12-18	Unoccupied										10	10	20	2
30.507.2	30-12-18/19	Unoccupied										10	10	20	2
29.473.1	29-13-13/24	Occupied												6	1
29.473.2	29-13-13; 29-12-18	Occupied												5	1

### Statistical Analysis

For analysis, we treated occupancy (and associated non-occupancy status) as a binary response variable. We built a logistic regression model to predict probability of occupancy given values of measured habitat variables (Table 3; Hosmer and Lemeshow 2000). Logistic regression modeled probability of occupancy  $\pi_i$  ( $0 < \pi_i < 1$ ) as

$$\ln\left(\frac{\pi_i}{1 - \pi_i}\right) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} \dots + \beta_p x_{ip}$$

where  $x_{i1}$  through  $x_{ip}$  were values of  $P$  measured forest characteristics and  $\beta_0$  through  $\beta_p$  were unknown coefficients. We estimated coefficients  $\beta_0$  through  $\beta_p$  by maximizing quasi-likelihood of the data, which included a term for extra-binomial variation (McCullagh and Nelder 1989). Before variable selection, we computed a correlation matrix to assess pairwise correlations among the 15 habitat variables we considered during analysis (Table 4). If we identified high correlation ( $>0.8$ ) between 2 variables, we eliminated one variable. We judged the variable we retained in each

**Table 3.** Variables we initially considered for use in a predictive model of habitat suitability for the marbled murrelet in western Washington, USA, 1993–2002.

Variable	Description
Canopy access	Average canopy access: 1 = difficult; 2 = low; 3 = moderate; 4 = high
Canopy closure	Average canopy closure: 0–100%
Canopy layers	Average no. canopy layers: 1–5, e.g., 1 = 1 layer, 2 = 2 layers
Mean dbh	Average dbh (cm) of trees with dbh > 81.3 cm
Mistletoe index	Average mistletoe index: scale of 0–6, with 0 = none, 6 = >50% infected
Moss cover	Average % cover of moss: 0–100% at 5% intervals
% slope	Average % slope: 0–100%
Trees/ha 60-cm <sup>a</sup>	No. trees/ha >60 cm dbh
Trees/ha 60-cm plat	No. trees/ha >60 cm dbh with >1 potential nest platform
Trees/ha 81-cm <sup>a</sup>	No. trees/ha >81.3 cm dbh
Trees/ha 81-cm plat	No. trees/ha >81.3 cm dbh with >1 potential nest platform
Trees/ha 99-cm <sup>a</sup>	No. trees/ha >99.1 cm dbh
Trees/ha 99-cm plat	No. trees/ha >99.1 cm dbh with >1 potential nest platform
Trees/ha mistletoe	No. trees/ha >60 cm dbh with mistletoe index of >3
Platforms/ha	No. potential nest platforms/ha

<sup>a</sup> Subsequently eliminated from consideration due to high correlation with other variables.

case to be more biologically justifiable than its eliminated counterpart.

We performed stepwise variable selection to select a final model from among all those that could have been built using uncorrelated variables (Tables 3, 4; Hosmer and Lemeshow 2000). We initiated the stepwise routine by estimating an intercept-only model (i.e., one that included  $\beta_0$  only). During subsequent forward steps, we individually added uncorrelated variables (Tables 3, 4) that were not already in the model to the current model, and we assessed their significance using an approximate F test (Venables and Ripley 1999). Approximate F tests compared changes in scaled model deviance when we removed a particular term to an F distribution with 1 and  $n - P$  degrees of freedom. We scaled changes in deviance by the Pearson estimate of extra binomial variation (McCullagh and Nelder 1989).

Based on recommendations in Bendel and Afifi (1977), Costanza and Afifi (1979), Lee and Koval (1997), and Hosmer and Lemeshow (2000), the most significant variable entered the model during forward steps provided its  $P$ -value was <0.15 (i.e.,  $\alpha_{\text{entry}} = 0.15$ ). Because a previously significant variable could become nonsignificant when we added another variable to the model, we took a backward look (deletion) step after each forward step. During backward looks, we deleted all variables with approximate F test  $P$ -values greater than  $\alpha_{\text{stay}} = 0.20$  from the model, and we put them back into the pool of variables and subsequently considered them for inclusion at a later step. Provided the model did not become unstable, forward and backward look step pairs continued until we could add no variables that met the  $\alpha_{\text{entry}}$  criterion.

**Table 4.** Correlation matrix<sup>a</sup> of explanatory variables considered for inclusion in the predictive model of habitat suitability for the marbled murrelet in western Washington, USA, 1993–2002.

	Canopy access	Canopy closure	Canopy layers	Mean dbh	Mistletoe index	Moss cover	% slope	Trees/ha 60-cm	Trees/ha 60-cm plat	Trees/ha 81-cm	Trees/ha 81-cm plat	Trees/ha 99-cm	Trees/ha 99-cm plat	Trees/ha mistletoe	Platforms/ha
Canopy access	1.00 <sup>a</sup>														
Canopy closure	-0.43	1.00 <sup>a</sup>													
Canopy layers	0.66	-0.47	1.00 <sup>a</sup>												
Mean dbh	0.60	-0.44	0.54	1.00 <sup>a</sup>											
Mistletoe index	0.28	0.01	0.01	0.03	1.00 <sup>a</sup>										
Moss cover	-0.05	0.51	-0.51	-0.12	0.22	1.00 <sup>a</sup>									
% Slope	0.23	-0.02	0.09	0.15	0.36	0.02	1.00 <sup>a</sup>								
Trees/ha 60-cm	0.49	-0.64	0.57	0.52	0.06	-0.40	0.09	1.00 <sup>a</sup>							
Trees/ha 60-cm plat	0.65	-0.51	0.71	0.62	0.24	-0.39	0.24	0.74	1.00 <sup>a</sup>						
Trees/ha 81-cm	0.52	-0.61	0.64	0.66	-0.12	-0.54	0.14	0.87 <sup>a</sup>	0.83 <sup>a</sup>	1.00 <sup>a</sup>					
Trees/ha 81-cm plat	0.61	-0.57	0.74	0.68	0.02	-0.52	0.18	0.74	0.94 <sup>a</sup>	1.00 <sup>a</sup>	1.00 <sup>a</sup>				
Trees/ha 99-cm	0.56	-0.54	0.72	0.71	-0.17	-0.54	0.16	0.69	0.83 <sup>a</sup>	0.92 <sup>a</sup>	0.94 <sup>a</sup>	1.00 <sup>a</sup>			
Trees/ha 99-cm plat	0.57	-0.58	0.73	0.70	-0.12	-0.57	0.19	0.67	0.86 <sup>a</sup>	0.91 <sup>a</sup>	0.96 <sup>a</sup>	1.00 <sup>a</sup>	1.00 <sup>a</sup>		
Trees/ha mistletoe	0.41	-0.28	0.31	0.10	0.77	-0.05	0.29	0.52	0.49	0.24	0.24	0.24	1.00 <sup>a</sup>	1.00 <sup>a</sup>	
Platforms/ha	0.61	-0.32	0.64	0.57	0.30	-0.25	0.35	0.50	0.88 <sup>a</sup>	0.62	0.81 <sup>a</sup>	0.66	0.72	0.42	1.00 <sup>a</sup>

<sup>a</sup> Correlations >0.8.

We assessed fit of the final model using the Hosmer–Lemeshow test (Hosmer–Lemeshow 2000). The Hosmer–Lemeshow goodness-of-fit test works equally well as other logistic regression goodness-of-fit measures (e.g., Receiver Operating Characteristic), but it is better known, easier to interpret, and provides a quantitative test of fit. The Hosmer–Lemeshow test assessed evidence for the null hypothesis  $H_0$ , which was that model fit is adequate, versus the alternative hypothesis  $H_A$ , which was that model fit is not adequate. Rejection of  $H_0$  in favor of  $H_A$  would imply that different or additional covariates were needed to adequately model the variation in occupied sites.

In addition, we assessed ability of the final model to accurately predict murrelet occupancy in 3 ways. First, we assessed the final model's ability to predict occupancy status of stands contained in the data set used to estimate the model. As part of this procedure, we plotted all predicted occupancy probabilities from the final model as a histogram to provide a visual representation of site classification. In addition, we reported the number of occupied sites predicted to be unoccupied (i.e., false negatives) and the number of unoccupied sites predicted to be occupied (i.e., false positives). Because we judged false negatives more detrimental than false positives, we classified a site as occupied if its predicted probability of occupancy was  $>0.25$ . Second, we used leave-one-out cross-validation to assess prediction accuracy for the same data set. The leave-one-out cross-validation procedure deleted one observation (i.e., one site), refitted the final logistic regression model on the remaining  $n - 1$  observations, estimated probability of a murrelet occupying the deleted site using the refitted model, and classified the site as either occupied or unoccupied based on this estimated probability. We compared the occupancy prediction for the deleted site to the known status of the deleted site and we reported false negative and false positive rates. We then added the deleted site back to the data set and continued the cross-validation procedure on other sites. Third, we tested our model against an independent sample of 48 sites that were surveyed for marbled murrelets by the Washington Department of Natural Resources (WDNR) in 1996 and 1997. Habitat assessments were conducted at these sites by WDNR using the same methods as those we used. All these sites were located within our study area and were on WDNR-managed lands. We used our final model to predict known occupancy of the WDNR sites, thereby assessing its classification accuracy on an independent data set.

## RESULTS

### Marbled Murrelet Surveys

We conducted 997 surveys at 50 sites on Rayonier ownership from 1993 to 2002 (Table 2); we surveyed sites 1–4 years ( $\bar{x} = 2.3$  yr,  $SD = 0.64$ ). We classified 17 sites as occupied and 33 as unoccupied. At occupied sites, we conducted 345 surveys, with an average survey period of 2.7 years ( $SD = 0.92$  yr); we completed 5–28 surveys per occupied site ( $\bar{x} = 20.3$  surveys,  $SD = 7.85$ ). Sites 29.473.1

and 29.473.2, both classified as occupied, had similar and low survey effort in comparison with other sites (Table 2). Surveyed in the last year of fieldwork for the study, these sites were the only occupied sites where we discontinued surveys once we made the determination of occupied. At unoccupied sites, we conducted 652 surveys with an average survey period of 2.1 years ( $SD = 0.23$  yr); we completed 8–27 surveys per unoccupied site ( $\bar{x} = 19.8$  surveys,  $SD = 3.04$ ; Table 2).

We sampled a large range of habitat conditions (Table 1). For example, potential nest platforms/ha ranged from  $<1$ /ha to  $>87$ /ha and number of trees/ha  $>81$  cm diameter at breast height with  $\geq 1$  nest platform ranged from  $<0.1$ /ha to  $>23$ /ha.

### Logistic Regression Model

Correlation was high ( $>0.8$ ) among the explanatory variables that measured the density of large trees without potential nest platforms (plat) to the density of trees in the same size class with platforms (Table 3). The variable trees/ha 60-cm was correlated with trees/ha 60-cm plat, trees/ha 81-cm with trees/ha 81-cm plat, and trees/ha 99-cm with trees/ha 99-cm plat (Table 4). High correlation implied that these 6 variables generally measured the same qualities of forest habitat and that some of these 6 could and should be eliminated. To reduce correlation, we eliminated the variables trees/acre 60-cm, trees/acre 81-cm, and trees/acre 99-cm from consideration because they were based solely on diameter at breast height, we and did not have associated potential nest platform counts. The remaining tree density variables trees/ha 60-cm plat, trees/ha 81-cm plat, and trees/ha 99-cm plat did include platform counts, and we considered them more relevant measures of murrelet nesting habitat. We considered these variables better predictors of site occupancy due to quantification of available potential nesting platforms.

At the first step of stepwise model selection, 10 of 12 variables were significant at  $P < 0.001$ , canopy access, canopy closure, canopy layers, mean diameter at breast height, moss cover, trees/ha 60-cm plat, trees/ha 81-cm plat, trees/ha 99-cm plat, trees/ha mistletoe, and platforms/ha (Table 5). At step 1 of the stepwise procedure (Table 5), variable trees/acre 60-cm plat entered the model because it had the lowest quasi-likelihood  $P$ -value. We subsequently removed trees/acre 60-cm plat during the backward look of step 2 (Table 5). During steps 2 and 3, variables canopy layers and mistletoe index entered the model and remained (Table 5). Not shown are  $P$ -values for steps 4 and 5, during which moss cover and trees/acre mistletoe entered the model before all variables failing the  $\alpha_{enter}$  criterion at step 6 (Table 5). We did not show steps 4 and 5 because we chose to stop model building after step 3 due to multiple instabilities introduced at step 4 (Table 5). When moss cover entered the model at step 4, the coefficients of canopy layers and mistletoe index changed by 10% and 70%, respectively, the coefficient of moss cover ( $-0.072$ ) contradicted our a priori notion that it should be positive, and the  $P$ -value for addition of trees/acre mistletoe changed from 0.956 (at step

**Table 5.** *P*-values derived from changes in the quasi-likelihood for all variables we considered in the marbled murrelet habitat suitability model during forward steps and backward looks of stepwise model building, western Washington, USA, 1993–2002.

Variable	Step 1 <sup>a</sup>		Step 2 <sup>a</sup>		Step 3 <sup>a,b</sup>	
	Forward	Backward	Forward	Backward	Forward	Backward
Canopy access	$2.70 \times 10^{-5}$		0.0131		0.7297	
Canopy closure	$9.97 \times 10^{-5}$		0.0745		0.1288	
Canopy layers	$1.04 \times 10^{-5}$		0.0030			$<0.01 \times 10^{-6}$
Mean dbh	$2.90 \times 10^{-5}$		0.0728		0.7355	
Mistletoe index	$8.07 \times 10^{-2}$		0.4114		0.0312	
Moss cover	$3.39 \times 10^{-4}$		0.1188		0.1946	
% slope	$2.89 \times 10^{-2}$		0.1421		0.3053	
Trees/ha 60-cm plat	$3.97 \times 10^{-6}$			0.2947	0.2947	
Trees/ha 81-cm plat	$9.52 \times 10^{-4}$		0.2278		0.3854	
Trees/ha 99-cm plat	$2.70 \times 10^{-5}$		0.0146		0.2999	
Trees/ha mistletoe	$9.49 \times 10^{-4}$		0.1564		0.2389	
Platforms/ha	$2.37 \times 10^{-5}$		0.8550		0.4718	
Action	trees/ha 60-cm plat added	none	canopy layers added	60-cm plat removed	mistletoe index added	none, stop

<sup>a</sup> Blank fields indicate *P*-value was not calculated.

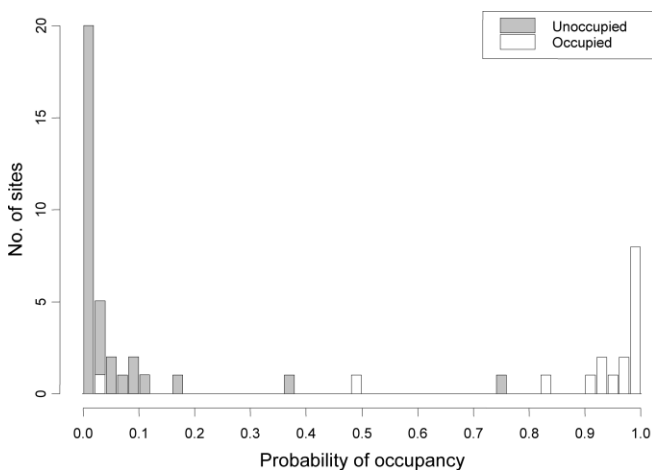
<sup>b</sup> Variable selection was stopped after step 3 due to instability and biologically questionable coeff. beyond step 3.

4) to 0.000 (at step 5). When trees/acre mistletoe entered the model at step 5, the coefficients of canopy layers, mistletoe index, and moss cover changed by 210%, 413%, and –245%, respectively. Such erratic behavior and biologically questionable coefficients indicated either complex collinearities among habitat variables or an extremely low level of leftover variation in model residual after step 3. We subsequently confirmed using classification results (Fig. 2) that the model at step 3 misclassified only 3 of 50 sites, an indication that little residual variation was left at that point.

The final murrelet logistic regression model at the end of step 3 was

$$\ln\left(\frac{\pi_i}{1 - \pi_i}\right) = -14.476 + 4.5663(\text{canopy layers}) + 1.6121(\text{mistletoe index}).$$

The estimate of extrabinomial variation for this model based



**Figure 2.** Distribution of estimated probabilities of occupancy from the predictive model of habitat suitability for the marbled murrelet in western Washington, USA, 1993–2002, for all sites in the data set we used to fit the model ( $n = 50$ ). Shading in the bars indicates actual occupied or unoccupied status of each site.

on the sum of Pearson residuals was 0.74, indicating no overdispersion; consequently, we set the overdispersion parameter to its nominal value of 1.0. Estimated standard error of the canopy layers coefficient was 1.4014, and the standard error of the mistletoe index coefficient was 0.9790.

The Hosmer–Lemeshow test indicated that the final model adequately fit the data ( $\chi^2 = 6.16$ ,  $df = 8$ ,  $P = 0.629$ ). Probability of occupancy predicted by the final model for sites in the current data set ranged from nearly 0 to nearly 1, with only 3 of 50 probabilities (6%) in the range 0.25 to 0.75, and only 6 (12%) in the range 0.1 to 0.9 (Fig. 2). The final model correctly classified 47 of 50 sites (94% correct) as either occupied or unoccupied using a classification cut-off of  $c = 0.25$  (Table 6; Fig. 2). The final model misclassified 2 of 33 unoccupied sites as occupied (94% correct; site no. 30.402 and 154) and 1 of 17 occupied sites as unoccupied (94% correct; site no. 26.171; Table 6; Fig. 2).

During drop-one-out cross-validation, the model correctly classified 46 of 50 sites (92% correct) as either occupied or unoccupied using a classification cut-off of  $c = 0.25$  (Table 7). The model misclassified 2 of 33 unoccupied sites as occupied (94% correct; site no. 30.402 and 154) and 2 of 17 occupied sites as unoccupied (88% correct; sites no. 214 and 26.171; Table 7).

When we tested our model against the independent sample of 48 sites surveyed by the WDNR, the final model

**Table 6.** Classification by the final predictive model of habitat suitability for the marbled murrelet in western Washington, USA, 1993–2002, using sites contained in the data set for estimation.

Actual status	Predicted status					
	Unoccupied		Occupied <sup>a</sup>		Total	
	No.	%	No.	%	No.	%
Unoccupied	31	94	2	6	33	100
Occupied	1	6	16	94	17	100

<sup>a</sup> A site was predicted occupied if its probability of occupancy, as predicted by the final model, was greater than  $c = 0.25$ .

**Table 7.** Results of leave-one-out cross-validation for the final predictive model of habitat suitability for the marbled murrelet in western Washington, USA, 1993–2002.

Actual status	Predicted status					
	Unoccupied		Occupied <sup>a</sup>		Total	
	No.	%	No.	%	No.	%
Unoccupied	31	94	2	6	33	100
Occupied	2	12	15	88	17	100

<sup>a</sup> A site was predicted occupied if its probability of occupancy, as predicted by the final model, was greater than  $c = 0.25$ .

correctly classified 36 of 48 sites (75% correct) using a classification cut-off of  $c = 0.25$  (Table 8). When our model predicted occupancy status of stands in the WDNR data set, the rate of relatively benign false positives was high (nearly 50%), but the critical rate of false negatives was low. The model misclassified 9 of 17 unoccupied sites as occupied (i.e., 53% false positives, or 47% correct), and 3 of 31 occupied sites as unoccupied (i.e., 10% false negatives, or 90% correct; Table 8).

## DISCUSSION

Correct classification rates for the final model were high, whether we tested the model using cross-validation procedures or used an independent sample of sites, with the final model correctly classifying 88% and 90% of the occupied sites as occupied, respectively. A site was predicted as occupied if its probability of occupancy was  $>0.25$ . Using a classification cut-off value of 0.5 would have produced similar results (Fig. 2). We used a low threshold value to minimize risk of false negatives, where an occupied site is predicted to be unoccupied, possibly never surveyed for marbled murrelets, and potentially harvested. Although using a low threshold may help locate and conserve occupied sites, in some models it could create additional false positives, where a number of unoccupied sites are predicted to be occupied and surveyed for additional time and expense, with no likelihood of detecting occupancy.

We chose to use a probabilistic approach versus the information theoretic approach to construct our model. There is a growing body of literature stating that the information theoretic approach is not appropriate for all situations (e.g., Guthery et al. 2005; Stephens et al. 2005). Our interpretation is that the information theoretic approach is not appropriate for exploratory analysis situations where prior hypotheses about effects are difficult or impossible to construct. Our foremost concern was derivation of a good predictive model for presence of marbled murrelet. As such, our analysis was exploratory in nature, and the stepwise approach we used was well suited for identifying the combination of strongest predictors from the set of predictors available to us.

Although some studies to date have correlated murrelet audiovisual detections to habitat features at the landscape and stand scale (Miller and Ralph 1995, Rodway and

**Table 8.** Classification by the final predictive model of habitat suitability for the marbled murrelet in western Washington, USA, of 48 independent sites surveyed by Washington Department of Natural Resources, 1996–1997.

Actual status	Predicted status					
	Unoccupied		Occupied <sup>a</sup>		Total	
	No.	%	No.	%	No.	%
Unoccupied	8	47	9	53	17	100
Occupied	3	10	28	90	31	100

<sup>a</sup> A site was predicted occupied if its probability of occupancy, as predicted by the final model, was greater than  $c = 0.25$ .

Regehr 2002, Bahn and Newsom 2002a), correlated digitally mapped landscape information to forest structural characteristics required by murrelets (Bahn and Newsom 2002b), or used radar detections to correlate murrelet numbers to landscape level variables (Burger 2001, Raphael et al. 2002), none have developed, as we have, a predictive model of habitat using within stand habitat features and tested these models for reliability in predicting site occupancy of marbled murrelets using an independent sample of sites. In a study of the multiscale landscape level features that best predicted murrelet occupancy in central and northern California, Meyer et al. (2002) used logistic regression models comparing occupied to unoccupied sites. Although the models were not tested, Meyer et al. (2002) found model accuracy in predicting occupancy was high ( $>80\%$ ) for all scales; classification accuracy was highest for the multiscale models using the patch, landscape, subregional, and regional scales. At the landscape scale, occupied sites were in less fragmented old growth, and they were less isolated from other occupied sites. In another landscape study, Ripple et al. (2003) used logistic regression to compare landscape patterns around 41 nest sites to a set of randomly located sites. Landscapes around nests were best distinguished from random sites by the combination of greater amounts of pole-young and mature-old-growth forests with less edge and more cohesive nest patch shapes. Although the models of Ripple et al. (2003) showed classification accuracies from 63% to 77% at the 0.50 probability level, they were not tested against an independent sample of sites. Hamer (1995) used logistic regression models to compare stand characteristics between occupied and unoccupied sites in northwestern Washington, USA. Probability of stand occupancy was positively associated with platform density, stem density of dominant trees, moss cover on limbs, slope, and presence of large diameter western hemlock. The final model correctly predicted occupancy at the 0.50 probability level in 74% of the sites; however, this model was also not tested. Conroy et al. (2002) found that murrelet nests were only found in habitat rated as “excellent” in a test of the landscape habitat model developed by Bahn and Newsom (2002b); habitat rated “excellent” had thicker epiphyte growth and had trees that were taller and significantly larger in diameter than trees in “good” or “sub-optimal” habitats.

Marbled murrelets are known to be highly mobile. In California, murrelets responded rapidly to small-scale variability in upwelling intensity and prey availability by shifting their foraging behavior and habitat selection within a 100-km area during the breeding season (Becker and Beissinger 2003). In addition, birds are known to fly great distances inland during the breeding season with birds detected as far as 56–88 km inland in Oregon and Washington (Nelson 1997). Although our analysis did not attempt to take into account oceanographic features that could also affect occupancy at inland nesting sites, our study area was small, 64 km north-to-south with the furthest inland study site 29 km from the ocean. Because of the small size of our study area, the proximity of our sites to the ocean, and mobile nature of the murrelet, we do not believe that we would have found any oceanographic variables to be strong predictors of site occupancy.

Measures of nest platforms, platform density, canopy access, mistletoe abundance, moss cover, and other murrelet habitat features are typically not available in stand inventory databases used by forest managers. Therefore, correct classification rates are typically low for many landscape scale studies due to the reliance on forest inventory data or digitally mapped forest information where the forest structural characteristics must be inferred from canopy characteristics using variables such as mean tree height, height diversity, or from data in forest inventory databases using variables like mean diameter at breast height or stem density of large-diameter trees. We needed no inference because we directly measured the within stand structural characteristics, thereby eliminating problems associated with poor correlations of forest inventory data or mapped forest information to the forest structural characteristics required by marbled murrelets.

Of the 4 tree density variables we tested, the variable trees/ha 60-cm plat may be a useful predictor of occupancy due to presence of mistletoe on younger age trees that create potential habitat even in younger aged stands in the western hemlock zone (Table 5). Mistletoe index may be a good predictor of site occupancy because it is not highly correlated to tree diameter, tree density, platform density, or other measures of forest structure (Table 4). Mistletoe creates deformities and brooms of branch growth, which are sometimes used as nest platforms. In a study of 29 murrelet nests at 5 sites within our study area, 28% were located on mistletoe-infected limbs (T. Hamer, Hamer Environmental, unpublished report). Besides creating large brooms, mistletoe also commonly increases the size of existing limbs, thus creating additional potential nest platforms (Geils and Hawksworth 2002).

Variables that measured canopy access by murrelets also were significant when considered singly (canopy access, canopy layers, and canopy closure); with canopy layers used in the final model (Table 5). These variables are indirect measures of the structural complexity of the canopy. Measurements of the degree of flight access by adults to platform-bearing trees and degree of canopy openness for

dispersing young may be good predictors of occupancy because murrelets are not well suited to flying in dense forests due to their high wing loadings and fast flight speeds. In addition, young fledge on their own after dusk and collisions with forest obstacles during their first flight to the ocean would likely ground them permanently, leading to starvation and death (Hamer and Nelson 1995, Nelson and Hamer 1995). Indeed, other models have also shown vertical canopy complexity to be an important explanatory variable (Bahn and Newsom 2002*b*, Conroy et al. 2002).

## MANAGEMENT IMPLICATIONS

Logistic regression models predicting site occupancy by marbled murrelets using within-stand characteristics can provide classification accuracies sufficient to reliably eliminate the need for surveys at sites with low probabilities of occupancy. In 1997, the WDNR Forest Practices Board adopted rules to protect murrelet habitat by requiring nonfederal landowners to conduct surveys in potential nesting habitat. From 1997 to 2002, Rayonier surveyed 36 new sites, of which 30 (83%) had probabilities of occupancy <25% and would not have been surveyed using the model approach, leading to substantial savings of cost and survey effort. Using the model, had those 30 sites been deemed unoccupied and subsequently disturbed by timber harvest, one occupied stand would have been logged. Use of models such as ours can increase the amount of forest screened for marbled murrelets, because stand suitability can be immediately assessed without a murrelet survey; time to conduct habitat assessments is minimal in comparison with time required for murrelet surveys under the 2-year survey protocol.

Construction and use of these models on other landscapes could focus survey efforts at those remaining sites that have higher probabilities of use by nesting murrelets. Focusing survey effort at these high probability sites should result in greater likelihood of identifying and conserving marbled murrelet occupied sites and nesting habitat.

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## LITERATURE CITED

- Bahn, V., and D. Newsom. 2002*a*. Can marbled murrelet use of nesting habitat be predicted from mapped forest characteristics? Pages 89–99 in A. E. Burger and T. A. Chatwin, editors. Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. Ministry of Water, Land and Air Protection, Victoria, British Columbia, Canada.
- Bahn, V., and D. Newsom. 2002*b*. Habitat suitability mapping for marbled

- murrelets in Clayoquot Sound. Pages 101–119 in A. E. Burger and T. A. Chatwin, editors. Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. Ministry of Water, Land and Air Protection, Victoria, British Columbia, Canada.
- Becker, B. H., and S. R. Beissinger. 2003. Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. *Marine Ecology Progress Series* 256:243–255.
- Bendel, R. B., and A. A. Afifi. 1977. Comparison of stopping rules in forward regression. *Journal of the American Statistical Association* 72: 46–53.
- Burger, A. E. 2001. Using radar to estimate populations and assess habitat associations of marbled murrelets. *Journal of Wildlife Management* 65: 696–715.
- Conroy, C. J., V. Bahn, M. S. Rodway, L. Ainsworth, and D. Newsom. 2002. Estimating nest densities for marbled murrelets in three habitat suitability categories in the Ursus Valley, Clayoquot Sound. Pages 121–137 in A. E. Burger and T. A. Chatwin, editors. Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. Ministry of Water, Land and Air Protection, Victoria, British Columbia, Canada.
- Costanza, M. E., and A. A. Afifi. 1979. Comparison of stopping rules in forward stepwise discriminant analysis. *Journal of the American Statistical Association* 74:777–785.
- Franklin, J. F., and C. T. Dyness. 1973. Natural vegetation of Oregon and Washington. U.S. Department of Agriculture Forest Service General Technical Report PNW-8, Portland, Oregon, USA.
- Geils, B. W., and F. G. Hawksworth. 2002. Damage, effects, and importance of dwarf mistletoes. Pages 57–65 in B. W. Geils, J. C. Tovar, and B. Moody, technical editors. Mistletoe in North American conifers. U.S. Department of Agriculture Forest Service General Technical Report RMRS-GTR-98, Ogden, Utah, USA.
- Guthery, F. S., L. A. Brennan, M. J. Peterson, and J. J. Lusk. 2005. Information theory in wildlife science: critique and viewpoint. *Journal of Wildlife Management* 69:457–65.
- Hamer, T. E. 1995. Inland habitat associations of marbled murrelets in western Washington. Pages 163–175 in C. J. Ralph, G. L. Hunt, J. Piatt, and M. Raphael, technical editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-152, Albany, California, USA.
- Hamer, T. E., and S. K. Nelson. 1995. Nesting chronology of the marbled murrelet. Pages 49–56 in C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, technical editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-152, Albany, California, USA.
- Hawksworth, F. G. 1977. The 6-class dwarf mistletoe rating system. U.S. Department of Agriculture Forest Service General Technical Report RM-48, Fort Collins, Colorado, USA.
- Henderson, J. A., D. H. Peter, R. D. Leshner, and D. C. Shaw. 1989. Forested plant associations of the Olympic National Forest. U.S. Department of Agriculture Forest Service General Technical Report R6-ECOL-TP 001–88, Portland, Oregon, USA.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression. Second edition. John Wiley and Sons, New York, New York, USA.
- Lee, K., and J. J. Koval. 1997. Determination of the best significance level in forward stepwise logistic regression. *Communication in Statistics* 26: 559–575.
- 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. 2002. Multi-scale landscape and seascape patterns associated with marbled murrelet nesting areas on the U.S. west coast. *Landscape Ecology* 17:95–115.
- McCullagh, P., and J. A. Nelder. 1989. Generalized Linear Models. Second edition. Chapman and Hall, London, United Kingdom.
- Miller, S. L., and C. J. Ralph. 1995. Relationship of marbled murrelets with habitat characteristics at inland sites in California. Pages 49–56 in C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, technical editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service General Technical Report PSW-GTR-152, Albany, California, USA.
- Nelson, K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). Pages 22–23 in A. Poole and F. Gill, editors. The Birds of North America. The Academy of Natural Sciences, and the American Ornithologists' Union, Washington, D.C., USA.
- Nelson, S. K., and T. E. Hamer. 1995. Nesting biology and behavior of the marbled murrelet. Pages 57–68 in C. J. Ralph, G. L. Hunt, J. Piatt, and M. Raphael, editors. Ecology and conservation of the marbled murrelet. U.S. Department of Agriculture Forest Service General Technical Report PSW-GTR-152, Arcata, California, USA.
- Raphael, M. G., D. Evans Mack, and B. A. Cooper. 2002. Landscape-scale relationships between abundance of marbled murrelets and distribution of nesting habitat. *Condor* 104:331–342.
- 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. 2002. Inland activity and forest structural characteristics as indicators of marbled murrelet nesting habitat in Clayoquot Sound, British Columbia. Pages 57–87 in A. E. Burger and T. A. Chatwin, editors. Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. Ministry of Water, Land and Air Protection, Victoria, British Columbia, Canada.
- Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. M. Del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology* 42:4–12.
- Venables, W. N., and B. D. Ripley. 1999. Modern applied statistics with S-Plus. Third edition. Springer, New York, New York, USA.

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