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RANKING HABITAT FOR MARBLED MURRELETS: NEW CONSERVATION APPROACH FOR SPECIES WITH UNCERTAIN DETECTION

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Abstract. An essential element in the conservation of rare species is the ranking of some aspects of habitat quality. We developed a method to rank the importance of individual habitat patches to Marbled Murrelets (*Brachyramphus marmoratus*) in 26 old-growth forest stands in northern California, using estimates of stand occupancy as an index of nesting activity. We used survey data collected in the stands from 1992 to 1997. The analysis was based on an adjustment that incorporates uncertainty of detection into a binomial model. Maximum likelihood estimators were used for the proportion P of the stands occupied by murrelets and the conditional probability p of detection with each visit to an occupied survey station, and bootstrapping methods were used for error estimates. We were able to rank a single stand most important, three other stands second in importance, and eight additional stands third in importance to murrelet nesting activity. For the murrelets in our study area, these results provided information useful in negotiations between government agencies and a private company in efforts to preserve some of the stands. Our methodology also has potential application for other flora and fauna of management concern, when sampling for presence or absence with uncertain detection. This technique can be applied at a variety of scales depending upon the species and habitat. Although conservation issues require consideration of many factors, including political, social, economic, and biological, our methods are helpful in providing science-based information from sample data to assist in the decision-making process.

Key words: Binomial model; Brachyramphus marmoratus; *California, USA; coastal redwoods; endangered species; habitat ranking; Marbled Murrelet; old-growth forest; presence–absence surveys; probability of detection;* Sequoia sempervirens; *uncertainty.*

INTRODUCTION

Species are generally distributed across a landscape in patches of suitable habitat. It is usually not possible in a conservation effort to preserve all patches containing a rare species. Therefore, it would be useful to prioritize habitat patches as to their relative importance to the species. We developed a method for ranking patches in a portion of northern California used by the Marbled Murrelet (*Brachyramphus marmoratus*).

The Marbled Murrelet is a seabird in the family Alcidae weighing 190–220 g, with a wingspan of 24–27 cm. Murrelets live and feed in the nearshore waters off the Pacific Coast of western United States and Canada, including Alaska. During the breeding season, April–August, it nests inland in old-growth, coniferous forests containing trees typically 200–1000 years old, while continuing to forage at sea, generally within 5 km of the shore. Nests are typically located on branches of large old-growth or late-seral-stage trees within 100 km of the ocean (Ralph et al. 1992). In northern California, nesting is particularly associated with coastal redwood (*Sequoia sempervirens*) and mixed redwood–Douglas-fir (*Pseudotsuga menziesii*) habitat, typically with high canopy cover and large trees. During the breeding season, murrelet plumage is cryptic in the forest: fewer than 300 nests have been discovered to date. Murrelet numbers have been estimated to be declining by 4–6% annually, especially in the southern portions of the species' range (Beissinger 1995). This perceived decline, which prompted, in 1992, its listing as a threatened species in California, Oregon, and Washington under the U.S. Endangered Species Act (Miller et al. 1997), is thought to be associated with loss of nesting habitat, high adult mortality, and low reproductive and breeding success rates. Remaining populations are believed to be ~14 300–25 400 birds in California, Oregon, and Washington (Huff et al. 2003), ~45 000–50 000 in British Columbia, and ~200 000–300 000 in Alaska (Ralph et al. 1995). Currently an offshore sampling design is being used to estimate the Marbled Murrelet population size. The sampling design was developed for the Northwest Forest Plan Marbled Murrelet Effectiveness Monitoring (Bentivoglio et al. 2002). The design was implemented in 2000, and the surveys have been conducted for four years. It is too early in this monitoring effort to estimate

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trends in the population, and the data are not compatible with prior monitoring designs.

Old-growth coastal redwood stands in southern Humboldt County, California are located on a mix of private and public lands. Some of these stands were the last large stands still in private ownership being managed for timber resources, and they contained Marbled Murrelet nesting activity. We report here information that was provided for consideration in the negotiations between the government and Pacific Lumber Company (PALCO) to preserve a portion of the stands in the region. The information was based on a new statistical methodology useful for analyzing presence or absence data of birds, animals, or plants, when the probability of detection with a survey visit is uncertain. This method provided approximately unbiased estimates for the extent of occupancy of the stands by Marbled Murrelets, a species whose nesting in California is closely associated with old-growth redwood forests (Miller and Ralph 1995).

Our objectives were to use an index of murrelet nesting activity to: (1) define habitat use in the old-growth forest throughout the study area by comparing estimates of occupancy and probability of detection among habitat types; and (2) based upon estimates of the area of occupancy of the stands and the probability of detection, rank the old-growth stands in order of their importance to the murrelet for nesting.

Methods

Survey protocol

Surveys of the old-growth stands were based primarily on the standardized protocol developed by the Pacific Seabird Group (e.g., Ralph and Nelson 1992, Ralph et al. 1994) for inland surveys. Because observers generally detect birds within 200 m of a survey station, the protocol prescribes that a station surveys ~12.15 ha (30 acres), the area of a 200 m radius circle centered on the station. Surveys began 45 minutes before sunrise and continued for two hours. Survey visits were distributed over the murrelet nesting season. For our study, stations were positioned throughout the old-growth habitat, providing a systematic survey of most of the stands.

Observers recorded the visible and audible detections of murrelets and the birds' behavior (vocalization type, flight path relative to the canopy, group or individual interactions). Station visits were assigned to one of three categories (Ralph et al. 1994): "occupancy," murrelets were present and exhibited nesting behavior (activity within the canopy or circling above the canopy); "presence," murrelets were present, but did not exhibit nesting behavior; and "absence," no murrelets were detected. Because individual murrelets cannot be identified during surveys, we could not reliably translate detections into distinct counts of individuals. Therefore, we estimated the proportion of each stand that was occupied by murrelets (cf. Seber 1982, 1986, Pendleton 1995). We used occupancy, rather than mean detection levels, as an index to describe the extent of murrelet activity in the stands.

Survey design

A regional data set from 1992 to 1997 was pooled for the analysis from surveys of stations, the sampling unit for analyses. We analyzed results from >3200 survey visits at 863 stations. The number of visits varied from a minimum of one per station at sites with four stations to eight or more surveys per station at sites with isolated stations.

The pooled data set resulted in a reasonably uniform distribution of stations throughout each of 10 habitat types in the 26 stands. Twenty-two of the stands were on PALCO lands (Fig. 1). We aggregated widely distributed, smaller fragments of residual old-growth on PALCO lands, as one of the 26 "stands" for purposes of the analysis, and designated it the "PALCO Remainder" stand. Additionally, we included four stands on Humboldt Redwoods State Park lands. We addressed the considerable variability in probability of detection and occupancy, as well as stand size, inherent in this pooled data set by stratifying by stand and habitat type. Thus we employed a stratified systematic sampling design with sample size proportional to the size of strata, providing (asymptotically) unbiased maximum likelihood estimates for the strata stand and habitat types as well as the aggregate population.

The habitat types were based on three criteria: (1) species types, i.e., redwood, Douglas-fir, or mixed redwood–Douglas-fir; (2) percentage of the stand covered by old-growth canopy (<50% or >50%); and (3) old-growth or residual habitat (partially harvested forest with remnant old-growth trees; see Fig. 2). This resulted in a stratification of the stands into $3 \times 2 \times 2 = 12$ habitat types. However, two of the habitat types, the old-growth, low-canopy redwood and the residual, high-canopy Douglas-fir, were not sampled because of the rarity of the habitat or the known absence of murrelets. Four other habitat types had no detections, so estimates of p were not achievable. We estimated P, the proportion of the stands occupied by murrelets, for 10 habitat types and p, the conditional probability of detection for each visit to an occupied survey station, for eight of the 10 sampled habitat types (Table 1).

Incorporating detectability into the binomial model

For the analysis, we incorporated detectability into the binomial model (Feller 1968, Johnson and Kotz 1969, Azuma et al. 1990, Hunter et al. 1998, Stauffer et al. 2002) using an adjusted binomial model. The binomial distribution $B(X; P, n)$ (Cochran 1977, Särndal et al. 1992, Thompson 1992) is described by the following probability distribution:

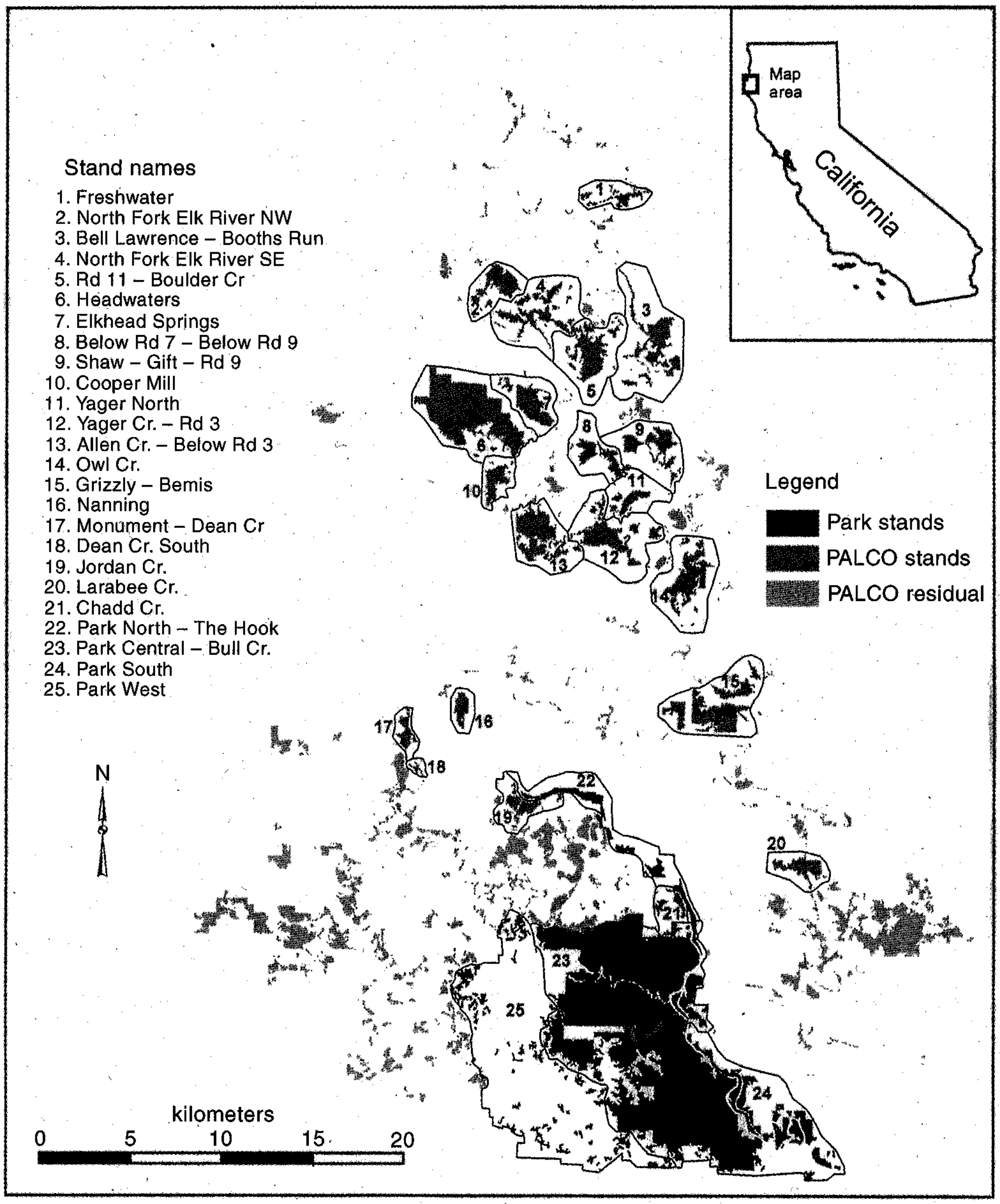

FIG. 1. The study area of 25 individual old-growth forest stands in northern California. Twenty-two of the stands are on Pacific Lumber Company (PALCO) lands. The widely distributed, smaller fragments of residual old-growth on PALCO lands were aggregated for analysis as a "stand" and were designated "PALCO Remainder." Four stands were in Humboldt Redwoods State Park.

$$B(X = x; P, n) = \binom{n}{x} P^x (1 - P)^{n-x}$$

where $\binom{n}{x}$ is the binomial coefficient $= n!/(x!(n - x)!)$; $X = x$ is the number of sampling units (i.e., our stations) with the species present (here, occupied); P is the probability of presence of the species at a sampling unit, representing the proportion of the survey area (in our case, the stand or habitat type) where the species is present; and n is the total number of units sampled. Note that the integer x (i.e., the number of occupied sampling units) can vary between 0 and n. The model assumes that P is constant throughout the stand or habitat type. The model also assumes that the sampling units are chosen independently with equal probability (i.e., simple random sampling). The binomial model implicitly assumes that there is complete certainty of detection if the species is present at a sampling unit.

We needed to account for the uncertainty of detection of the murrelets by adjusting the binomial model B into a model B_d that incorporates uncertainty of detection. The resulting adjusted binomial model $B_d(X; P, n, p, m)$ revises the binomial model $B(X; P, n)$ to incorporate uncertainty of detection, where P is the probability of

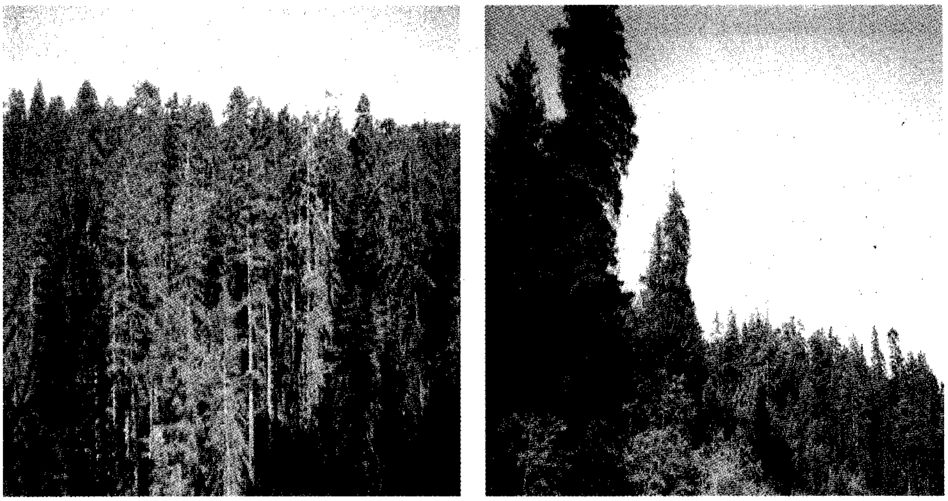

FIG. 2. Examples of old-growth (left) and residual (right) coastal redwood (*Sequoia sempervirens*) forests on Pacific Lumber Company lands in Humboldt County, California. The density of old-growth trees in the residual habitat type varies across the landscape.

presence; n is the number of units sampled; p is the conditional probability of detection of the species, if present, with one visit to a sampling unit; and m is the number of visits to the sampling units. The model is described by the probability

$$B_d(X = x; P, n, p, m) = \sum_{j \geq x}^{n} \binom{n}{j} P^j (1 - P)^{n-j} \binom{j}{x} \times p'^x (1 - p')^{j-x}$$

where $p' = 1 - (1 - p)^m$ describes the conditional probability of at least one detection, with m visits to a sampling unit, if the species is present. This distribution describes the probability B_d of x, the number of sampling units where the species is present and detected, as the sum of the probability of sampling j units when the species is present, successfully detecting it x times and failing to detect it $(j - x)$ times, where $j = x, x + 1, x + 2, \ldots, n$. The binomial coefficients $\binom{j}{x}$ count the number of combinations of such possibilities for each j. The equation represents the sum of the probabilities of all possible errors of not detecting the birds when they are present.

The $B_d(X; P, n, p, m)$ model incorporates uncertainty of detection by adding the two additional parameters p and m to the parameters P and n of the binomial model $B(X; P, n)$. It assumes that the sampling unit visits are independent binary events. It also assumes that the parameters P and p are fixed throughout a stratum. The B_d model is a special case of a compound binomial–binomial distribution (Johnson and Kotz 1969:194, Eq. 36). It can also be shown that $B_d(X; P, n, p, m) = B(X; P \cdot p', n)$, so that the B_d model is a special case of the binomial model. That is, the probability at the ith site, with m_i visits, is given by $P_i = P \cdot (1 - (1 - p)^{m_i})$ where P is the probability of presence and p is the probability of detection with one visit, given presence.

TABLE 1. Estimated proportional ($\hat{P}$) and absolute ($\hat{P}$·Area) amounts of area occupied by Marbled Murrelet in old-growth redwood–Douglas-fir forest habitat types, with detectability ($\hat{p}$), using maximum likelihood percentage estimates of P and p.

Habitat type	Area (ha)	No. stations (n)	Proportion of occupied area, $\hat{P}$ (%)	Absolute amounts of occupied area (ha)	Detectability $\hat{p}$ (%)
Old-growth, high-canopy, redwood	1123	63	54.4	611	81.3
Old-growth, high-canopy, redwood/Douglas-fir	6478	229	26.9	1743	71.2
Old-growth, high-canopy, Douglas-fir	500	56	0.0	0	NA
Old-growth, low-canopy, redwood/Douglas-fir	1774	33	8.7	155	33.1
Old-growth, low-canopy, Douglas-fir	547	45	0.0	0	NA
Residual, high-canopy, redwood	385	18	0.0	0	NA
Residual, high-canopy, redwood/Douglas-fir	263	18	25.7	68	29.0
Residual, low-canopy, redwood	2264	300	32.5	736	51.9
Residual, low-canopy, redwood/Douglas-fir	1667	41	8.9	148	86.4
Residual, low-canopy, Douglas-fir	6928	19	0.0	0	NA
Total	22 820			3461	

Note: NA indicates that p could not be estimated because there were no detections.

Analysis: maximum likelihood estimators for the adjusted binomial model B_d

We needed to estimate the proportion of occupancy to determine a ranking of the stands based on estimates of the area of occupancy by murrelets. We used maximum likelihood estimators (MLEs) for occupancy P and detectability p of the adjusted binomial model B_d developed by Max et al. (1995). They developed model estimators based on two sampling protocols for the Marbled Murrelet and the Northern Spotted Owl (*Strix occidentalis caurina*). The sampling protocol for the owl prescribes that visits to sites are concluded once a detection occurs or at the final visit, whichever comes first. The protocol for the Marbled Murrelet requires a fixed number of visits m, regardless of possible detections in earlier visits. The maximum likelihood estimators for the Marbled Murrelet protocol are given by

$$\hat{p} = \left(\frac{x}{n}\right)\left(\frac{y/x}{m}\right) \quad \text{when } y/x < \frac{m\left[1 - \left(\frac{n-x}{n}\right)^{1/m}\right]}{x/n}, \quad x > 0$$

$$= \text{not estimable} \quad \text{when } x = 0$$

$$= \tilde{p} \quad \text{otherwise}$$

and

$$\hat{P} = 1 \quad \text{when } y/x < \frac{m\left[1 - \left(\frac{n-x}{n}\right)^{1/m}\right]}{x/n}, \quad x > 0$$

$$= 0 \quad \text{when } x = 0$$

$$= \frac{x/n}{1 - (1 - \tilde{p})^m} \quad \text{otherwise}$$

with $\tilde{p}$ being the solution to

$$y = \frac{m\tilde{p}}{1 - (1 - \tilde{p})^m}.$$

In these formulas, y is the total number of visits with detections from all the visits to sampling units. Maximum solutions for some data sets may occur outside the parameter space ($0 \leq P \leq 1$, $0 \leq p \leq 1$). In this instance, given by the first two cases for each parameter estimator, Max et al. (1995) recommend use of the maximum value for the estimator within the parameter space.

Estimates for habitat types and stands

Maximum likelihood estimators for P and p, and their errors, were then applied to the 10 habitat types and the 26 stands (both in PALCO and state parks) in the regional survey area.

Habitat analysis.—To control for differences in survey effort within each habitat type, we divided the data set into subsets, each consisting of stations with equal numbers of visits, from two to 24 visits, in increments of one or more. We estimated P and p for each of these subsets. We then took averages of these estimates, weighted by sample size (the number of stations), to approximate the proportional amount of surveyed area for each subset in each habitat type. These weighted averages for P and p comprised the estimates for each habitat type. Two of the habitat types had no detections, so p could not be estimated. These estimated "proportional amounts of occupied area" and "detectability" are referenced in columns in Table 1.

Stand analysis.—For each stand, we divided the data set into subsets of stations associated with each habitat type, and within each habitat type, subsets of stations with equal numbers of visits. We estimated P and p for each subset of stations with equal numbers of visits of each habitat type in each stand, and took averages of these estimates, weighted by sample size. These weighted averages provided the estimates of P and p for the stands summarized in Table 2. For each stand, the estimates of P were multiplied by the amount of area to obtain estimates of total area occupied by the murrelets. The estimates of standard error were obtained by bootstrapping. Seven of the stands had no detections, so p could not be estimated.

We ranked the stands using estimates of total area occupied by murrelets (Table 2). We also included estimates of the risk of error (i.e., Type 1 error) for the ranking (Table 3), with individual paired comparison of the stands, based on a one-tailed t test (valid for $n\hat{P} \geq 5$ and $n(1 - \hat{P}) \geq 5$), where n is the sample size and $\hat{P}$ is the estimate of occupancy. Risk in the table refers to the probability of an incorrect ranking of the two stands compared. Managers considering the relative ranks of a collection of stands in the table can then obtain an approximation of the compounded risk of error, the risk of making one or more errors in the multiple comparisons, by adding the individual risks from all paired comparisons in the collection. For example, the maximum compounded risk of at least one error in the ranking of three stands in the table is the sum of the risks from three paired comparisons, the first stand with the second, the first stand with the third, and the second stand with the third.

Estimates of error using bootstrapping

Error was estimated using nonparametric bootstrapping (Manly 1997) on the sample data set. We bootstrapped, randomly resampling with replacement, each subset of murrelet stations with equal numbers of visits, in habitat types and in stands, using 5000 iterations. P and p estimates were calculated for each iteration. The bootstrap estimates of standard errors summarized in Table 2 were obtained by taking the standard deviations of the P and p estimates from the bootstrapping procedure.

TABLE 2. Ranking of the 25 stands and "PALCO Residual" by occupied area, based on percentage estimates of the proportion of occupancy ($\hat{P}$), detectability ($\hat{p}$), and occupied area ($\hat{P}$ × Area).

			$\hat{P}$ (%)		$\hat{p}$ (%)			Occupied area (ha)	
Rank	Stand	n	Estimate	1 SE	Estimate	1 SE	Area (ha)	Estimate	1 SE
1	Headwaters	48	60.2	8.0	77.6	2.0	1307.2	786.9	104.6
2	Park Central‡	130	17.3	2.9	96.2	0.5	3985.7	689.5	115.6
3	Allen Creek–Below Road 3	32	74.9	16.6	12.6	3.1	470.3	352.2	78.1
4	Elkhead Springs	25	78.4	14.7	45.3	4.3	275.3	215.8	40.5
5	Shaw–Gift–Road 9	28	60.5	27.9	17.8	10.8	287.0	173.6	80.1
6	Park South‡	62	3.3	2.3	100.0	0.0	4964.1	163.8	114.2
7	Park North‡	6	50.5	24.8	85.5	0.0	308.7	155.9	76.6
8	Road 11–Boulder Creek	20	43.6	27.0	45.9	4.3	352.9	153.9	95.3
9	Grizzly–Bemis	47	28.8	18.0	14.0	6.9	513.6	147.9	92.5
10	North Fork Elk River Southeast	23	38.6	18.3	70.0	0.9	346.6	133.8	63.4
11	Jordan Creek	20	73.4	14.9	9.7	4.0	173.5	127.3	25.9
12	Bell Lawrence–Booths Run	42	29.6	19.5	22.7	6.1	417.5	123.6	81.4
13	Cooper Mill	25	58.9	27.7	10.3	4.6	162.2	95.5	44.9
14	Owl Creek	33	21.9	28.4	6.0	3.9	389.5	85.3	110.6
15	Yager Creek–Road 3	24	19.4	14.6	25.5	3.6	405.9	78.7	59.3
16	Nanning	7	43.4	18.1	46.2	2.6	103.9	45.1	18.8
17	Below Road 7 & 9	26	12.0	8.3	7.1	2.8	196.6	23.6	16.3
18	Larabee Creek	8	12.9	16.8	100.0	0.0	173.3	22.3	29.1
19	Monument–Dean Creek	20	4.9	10.8	100.0	0.0	105.9	5.2	11.4
20	Freshwater	4	0.0	0.0	NA	NA	103.8	0.0	0.0
21	North Fork Elk River Northwest	6	0.0	0.0	NA	NA	221.1	0.0	0.0
22	Yager North	5	0.0	0.0	NA	NA	131.9	0.0	0.0
23	Dean Creek South	7	0.0	0.0	NA	NA	15.2	0.0	0.0
24	Chadd Creek	13	0.0	0.0	NA	NA	96.6	0.0	0.0
25	PALCO Remainder	203	0.0	0.0	NA	NA	6787.2	0.0	0.0
26	Park West‡	6	0.0	0.0	NA	NA	525.2	0.0	0.0

Note: NA indicates that p could not be estimated because there were no detections.
† Rank is based on occupied area.
‡ Park stands.

RESULTS

Estimates for habitat types

Estimates of proportions of occupancy ($\hat{P}$) and detectability ($\hat{p}$) for habitat types in the stands, based on the adjusted binomial model (B_d), are summarized in Table 1. The highest estimated proportion of occupancy occurred in old-growth, high-canopy redwood habitat, and was the habitat most associated with murrelet nesting activity. Residual, low-canopy redwood habitat was second in importance, and both old-growth and residual, high-canopy redwood–Douglas-fir habitats ranked next. Lowest in rank among the occupied habitat types were the old-growth and residual, low-canopy redwood–Douglas-fir habitats. The remaining habitat types had negligible amounts of area or small numbers of samples, except for the residual, low-canopy Douglas-fir habitat.

The estimates of detectability $\hat{p}$ (the probability of detecting at least one bird, if they were present, with one visit to a sampling unit) by habitat type (Table 1) were highest for both the redwood and redwood–Douglas-fir old-growth, high-canopy habitats and the residual, low-canopy redwood and redwood–Douglas-fir habitats, indicating that murrelets were most likely to be detected in these habitat types.

Estimates for the stands: proportion of occupancy

Three PALCO stands, Elkhead Springs, Allen Creek–Below Road 3, and Jordan Creek, had the highest estimated proportions of occupancy in the stands, all >70% (Table 2). A middle tier of seven stands had moderately high estimates, ranging from 39% to 61%: Shaw-Gift-Road 9, Headwaters, Cooper Mill, Park North, Road 11–Boulder Creek, Nanning, and North Fork Elk River Southeast. The remainder of the stands had lower estimates of proportion of occupancy, all <30%.

The estimated correlation between the proportion of occupancy ($\hat{P}$) and the detectability ($\hat{p}$) estimates was not statistically significant ($r = -0.19$, P value = 0.44). Hence, there was no statistical evidence to support the hypothesis of a linear relationship between the extent of occupancy of the stands and the detectability of the birds, if they were present.

Ranking of the stands

The Headwaters stand ranked most important, based on the estimate of total amount of area occupied by murrelets, with an estimated 787 ha occupied (Table 2). The compounded risk of at least one Type 1 error in ranking Headwaters above all the other PALCO stands below it was relatively low, <11% (i.e., adding all the risks, each <0.5%, from the 21 paired comparisons of Headwaters with the other PALCO stands in Table 3). The risk of error in ranking the Headwaters stand above the highest ranking Humboldt Redwoods State Park stand, Park Central, was 26.6%.

TABLE 3. Ranking of the 25 stands and "PALCO Residual" by occupied area, based on estimates of occupied area, with risks of Type I error for paired comparisons of the stand ranks.

Stand rank	Risk (%), compared with stand number													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1														
2	26.6													
3	<0.5	0.8												
4	<0.5	<0.5	6.0											
5	<0.5	<0.5	5.5	31.9										
6	<0.5	<0.5	8.7	33.4	47.2									
7	<0.5	<0.5	3.6	24.5	43.6	47.7								
8	<0.5	<0.5	5.4	27.5	43.7	47.3	49.3							
9	<0.5	<0.5	4.6	25.1	41.7	45.7	47.3	48.2						
10	<0.5	<0.5	1.5	13.8	34.8	40.9	41.2	43.0	45.0					
11	<0.5	<0.5	<0.5	3.3	29.1	37.8	36.2	39.4	41.5	46.2				
12	<0.5	<0.5	2.1	15.5	33.1	38.7	38.6	40.4	42.2	46.1	48.2			
13	<0.5	<0.5	<0.5	2.3	19.7	28.9	24.8	29.0	30.5	31.1	27.0	38.1		
14	<0.5	<0.5	2.4	13.4	25.9	31.1	30.0	31.9	33.2	35.2	35.6	39.0	46.6	
15	<0.5	<0.5	<0.5	2.8	17.0	25.4	21.3	25.2	26.4	26.3	22.6	32.8	41.1	47.9
16	<0.5	<0.5	<0.5	<0.5	5.9	15.2	8.0	13.1	13.8	9.0	0.5	17.4	15.0	36.0
17	<0.5	<0.5	<0.5	<0.5	3.3	11.2	4.6	8.9	9.3	4.6	<0.5	11.4	6.6	29.1
18	<0.5	<0.5	<0.5	<0.5	3.8	11.5	5.2	9.3	9.8	5.5	0.4	12.1	8.6	29.1
19	<0.5	<0.5	<0.5	<0.5	1.9	8.3	2.6	6.1	6.3	2.3	<0.5	7.5	2.6	23.6
20	<0.5	<0.5	<0.5	<0.5	1.5	7.6	2.1	5.3	5.5	1.7	<0.5	6.5	1.7	22.0
21	<0.5	<0.5	<0.5	<0.5	1.5	7.6	2.1	5.3	5.5	1.7	<0.5	6.5	1.7	22.0
22	<0.5	<0.5	<0.5	<0.5	1.5	7.6	2.1	5.3	5.5	1.7	<0.5	6.5	1.7	22.0
23	<0.5	<0.5	<0.5	<0.5	1.5	7.6	2.1	5.3	5.5	1.7	<0.5	6.5	1.7	22.0
24	<0.5	<0.5	<0.5	<0.5	1.5	7.6	2.1	5.3	5.5	1.7	<0.5	6.5	1.7	22.0
25	<0.5	<0.5	<0.5	<0.5	1.5	7.6	2.1	5.3	5.5	1.7	<0.5	6.5	1.7	22.0
26	<0.5	<0.5	<0.5	<0.5	1.5	7.6	2.1	5.3	5.5	1.7	<0.5	6.5	1.7	22.0

Note: See Table 2 for stand names (by rank), sample sizes, area, and P and p estimates.

Allen Creek ranked second among the PALCO stands, below the Headwaters stand and the Humboldt Redwoods State Park Central stand, with an estimate of 352 ha occupied, and the compounded risk of ranking it above all the other PALCO stands below it in the table of 34%. Elkhead Springs ranked third among the PALCO stands, with an estimate of 216 ha occupied. The compounded risk of at least one Type I error in ranking it above all the stands below it on the list was considerable. However, each of these three stands in this second tier of stands had a compounded risk of ranking it above the bottom seven stands in the table of <4% (i.e., each paired comparison had risk <0.5%).

A third tier of PALCO stands, Shaw–Gift–Road 9, Road 11–Boulder Creek, Grizzly–Bemis, North Fork Elk River Southeast, Jordan Creek, and Bell Lawrence–Booths Run, ranked next, with estimated amounts of occupied area ranging from 174 to 124 ha. The compounded risk of at least one error in ranking each of these stands with all stands below it in the table was high, but the compounded risk in ranking these stands above the seven stands at the bottom of the table was 4–46%.

The remaining stands below this third tier in the table all had <100 ha estimated to be occupied. Seven of these stands comprised a fourth tier of stands with estimates of occupied area >0. Four of these seven stands either had substantial amounts of area (>150 ha) or had limited amounts of compounded risk in comparison with the bottom seven stands in the table: Cooper Mill (risk <10.3%), Owl Creek (390 ha), Yager Creek–Road 3 (406 ha), and Below Road 7 & 9 (197 ha).

Of the four stands in state parklands, Park Central ranked second overall and two others, Park South and Park North, were ranked among the third tier of PALCO stands.

DISCUSSION

Occupancy and detectability in habitat types and stands

Our first objective was to look for differences in murrelet use by habitat type. Murrelet occupancy was most closely associated with redwood habitat. Mixed redwood–Douglas-fir habitat was of secondary importance. Old-growth and high-canopy-cover habitats were also associated with murrelet occupancy. No murrelets were detected in the purely Douglas-fir habitat.

Small estimates of error for detectability for the stands may be a result of several factors. Sampling effort for the stands (the number of surveys per station) was relatively high: 8–12 surveys for some stations. Habitat was relatively homogeneous by stand, for both large and small stands, resulting in similar visibility at stations within each stand. Additionally, detections at

TABLE 3. Extended.

Risk (%), compared with stand number										
15	16	17	18	19	20	21	22	23	24	25
29.4										
18.5	19.4									
19.7	25.6	48.5								
11.1	3.5	17.8	29.2							
9.2	0.8	7.4	22.1	32.5						
9.2	0.8	7.4	22.1	32.5	50.0					
9.2	0.8	7.4	22.1	32.5	50.0	50.0				
9.2	0.8	7.4	22.1	32.5	50.0	50.0	50.0			
9.2	0.8	7.4	22.1	32.5	50.0	50.0	50.0	50.0		
9.2	0.8	7.4	22.1	32.5	50.0	50.0	50.0	50.0	50.0	
9.2	0.8	7.4	22.1	32.5	50.0	50.0	50.0	50.0	50.0	50.0

isolated, small stands, such as Nanning, would likely be birds using that stand and not birds detected while traveling to a nearly stand; therefore, detection numbers between visits would be similar.

Contrary to our expectations, we found no evidence that occupancy and detectability were correlated. That is, habitat types and stands that had high occupancy levels, possibly indicating higher abundance levels, did not consistently exhibit higher levels of likelihood of detection. The higher percentages of canopy cover often thought to be associated with murrelet nesting (Miller and Ralph 1995) may tend to reduce the visibility essential for observing nesting behaviors in some stands, thus lowering the level of detectability. When utilizing only occupied detections for analyses, we think that the high estimates of detectability in some of the residual and low-canopy, old-growth habitats were at least partially due to the relative openness of the stands, resulting in enhanced visibility of the birds. Although murrelets were perhaps likely to be less abundant in some of these habitats, nesting behaviors were more likely to be observed. Other factors, such as predator abundance and nest density, also may have influenced occupancy of stands and confounded our results, but information for these variables was not available.

Avian species in many habitats show sensitivity to habitat fragmentation (Paton 1994, Faaborg et al. 1998, Walters 1998). Marzluff et al. (2000) suggest that rates of nest predation of artificial nests in murrelet habitat may be reduced when nesting stands are in complex landscapes of mixed, simple-structured, mature forest, and old-growth forest that generally contain fewer predators. Most old-growth and residual stands in our study area are fragments surrounded by recently logged or young forests. Although the more fragmented, smaller stands had lower occupancy proportions (P), we do not think that we can make direct inferences to the effect of fragmentation on predation rates based on the data collected in this study.

Multiple comparison vs. risk

Our second objective was to provide a ranking of the stands in order of their importance to the murrelets for nesting, based upon estimates of occupancy. We hoped to have a clear statistical delineation of the stands into groups of equal importance to the murrelet, for example one provided by a Bonferroni multiple-comparisons test at a pre-established experiment-wise level of significance. We were unable to statistically distinguish groups of stands that might be biologically different to the murrelets at a 5% level of significance. However, statistics in Tables 2 and 3 enabled us to examine rankings, based on estimates of area of occupancy, and to assess the risks of error, individual or compounded, of including or excluding any stand in a reserve designed on this basis.

Multiple comparison tests were designed for controlled randomized experiments, not observational studies such as ours. The results of a multiple comparison test would depend arbitrarily on the sample sizes and the particular test because stands did not correspond to "treatments," and null hypotheses of exactly equal parameters P's or p's were patently false. Any level of significance used for the test in this instance would have been arbitrary, imposed by the researchers and not by the decision makers. Caution against the inappropriate application of hypothesis testing for observational data has been well documented in the wildlife management and ecological literature (Burnham and Anderson 1998, Johnson 1999, Anderson et al. 2001), with recommendations on the use of estimates of parameters and error, instead of hypothesis testing. Our approach utilizes these estimates to provide an appropriate tool to help assess the risk of error when designing reserves.

Our ranking (Tables 2 and 3), providing scientifically based information for the negotiators, was one of many documents assisting them in reaching a decision regarding future status of the stands. It was important for the negotiators to be able to assess the relative risks of error in comparing alternatives, not to be bound by the inflexible dichotomous outcomes of a multiple comparison test. Estimates of occupancy and risk (Tables 2 and 3) allow managers to elect whether and where to take compounding of error into account when comparing stands in the table.

Robustness of the estimates

The adjusted binomial model used for the analysis was based on the assumption that the parameters P and p were constant throughout a stratum. Occupancy levels (P) and our ability to detect the birds (p) varied appreciably in this survey, both by habitat type (Table 1) and by stand (Table 2), so analyses were based on weighted estimates of the parameters P and p, assumed to be constant within these strata.

A study by Matsumoto (1999) concluded that estimators based on the adjusted binomial model were robust to moderate relaxation of the assumptions that the parameters P and p remain constant within strata. She demonstrated with computer simulation that power estimation from the model remained accurate, despite moderate amounts of variation of the population parameters (i.e., with standard deviations up to 50% of parameter values). Matsumoto conducted a Monte Carlo simulation study of the sensitivity of the power estimates from the Marbled Murrelet protocol for inland surveys in California, assuming extremely low levels of P at 1–10%, and p at 10, 25, and 50%. She allowed P and p to vary, using beta distributions centered at assumed fixed values for P and p, with standard deviations of varying magnitudes. Her results suggested that estimators based on the adjusted binomial model remain accurate, despite moderate relaxation of its assumptions of constant P and p.

Conclusions

In the final negotiated agreement between the federal and state government and the Pacific Lumber Company, Headwaters and Elkhead Springs stands, along with some adjacent and connecting habitat, were purchased as a public preserve in perpetuity. They comprised 1420 ha, with a 1620-ha buffer zone. Of the other stands, portions of nine others, a total of 3640 ha, were placed in five Marbled Murrelet conservation areas, to be preserved for 50 years, pending further review: Allen Creek–Below Road 3, Shaw–Gift–Road 9, North Fork Elk River Southeast, Bell Lawrence–Booths Run, Cooper Mill, Yager Creek, and Below Road 7 & 9. Owl Creek and Grizzly–Bemus have since passed into public ownership. The remaining 11 stands, some 8265 ha, were made available for timber harvesting, subject to the prescriptions of the PALCO Habitat Conservation Plan. Of the stands made available for harvesting, however, the prescriptions of the Habitat Conservation Plan place a majority of these areas into de facto preserves, such as riparian management zones and geologic areas of concern.

Detectability can be a concern for accuracy of estimates when field sampling for any flora or fauna species. The technique described here is entirely general and can be applied to other species when sampling yields presence–absence data to obtain estimates of the probability of presence or occupancy; i.e., the proportion of a region that is occupied by a species. The appropriate scale for ecological studies varies by taxa, habitat, and question, but our technique is not scale dependent. It is applicable to any scale: salamanders with a 1-m home range, invasive plants in a shortgrass prairie, or freshwater, benthic invertebrates.

The methodology presented here is innovative in separating the probability of occupancy P_o from that of apparent occupancy P_{ao},

$$P_{ao} = P_o \times P_d$$

by estimating both the probability of occupancy and the "nuisance" parameter, the probability of detection P_d. Thereby, it provided asymptotically unbiased estimates of the probability of occupancy. This idea of separating out estimates of the nuisance parameter, the probability of detection, has also been applied effectively to other indices of abundance such as estimates of counts or density (Williams et al. 2001:Chapter 12).

The estimates of occupancy for the stands and habitat types that we described in this manuscript provided science-based information useful in the negotiation for this agreement on the Marbled Murrelet. Conservation decisions are necessarily based on diverse criteria, including scientific, political, social, and economic issues or goals. Our technique for ranking habitat patches for this species provided important, scientific-based information using sample data that could be included in this decision-making process.

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