Research Report

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Using the low-level aerial survey method to identify Marbled Murrelet nesting habitat

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Abstract

Identifying and managing nesting habitat for the threatened Marbled Murrelet (*Brachyramphus marmoratus*) is difficult because it nests secretively, high in the canopies of large, old conifers of the Pacific Northwest. In British Columbia, low-level surveying from a helicopter is now a recommended standard method of assessing forested landscapes for key microhabitat features—such as availability of potential platforms and developed moss pads for nests, foliage cover above the nest, and accessibility—that are not distinguishable on air photos, satellite images, or forest cover maps. Using a sample of 111 nest sites and 139 random sites within forests greater than 140 years old and distributed across three study areas in south coastal British Columbia, we confirmed the effectiveness of the aerial survey method for classifying overall habitat quality of murrelet nesting habitat. The minimum map units were 3-ha patches. Overall, 40% of the 111 nest sites were in patches classed as Very High, 36% were in High, 15% were in Moderate, 6% were in Low, and 3% were in Very Low. Our ranking of habitat quality was most strongly influenced by estimates of platform availability and moss development. Using an information-theoretic approach, we identified that the Resource Selection Function scores of nest patches improved as elevation decreased, slope grade increased, and the proportion of emergent and canopy trees with mossy pads increased. We also confirmed that study area location affected the strength of model application. Our findings support the potential utility of the low-level aerial survey method for identifying or confirming Marbled Murrelet nesting habitat for land-management purposes.

KEYWORDS: *aerial survey,* Brachyramphus marmoratus*, classification, habitat quality, Marbled Murrelet, nesting habitat assessment, survey methods.*

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Introduction

The Marbled Murrelet (*Brachyramphus marmoratus*) is a small seabird (Family *Alcidae*) found in nearshore waters of the Pacific Northwest. Throughout most of their range, murrelets typically nest on thick mossy pads that have developed on large branches of older trees (Hamer and Nelson 1995; Nelson 1997; Manley 1999; Nelson and Wilson 2002). In British Columbia, forests less than 140 years old support few nesting murrelets, because these forests lack suitable canopy structures for nests. Most nest sites are found in forests greater than 250 years old (Burger 2002; Waterhouse et al. 2004). The declining areas of coastal old-growth forest in British Columbia has led to the listing of Marbled Murrelets as Threatened by the Committee on the Status of Endangered Wildlife in Canada (2000) and to efforts to manage their nesting habitat (CMMRT 2003).

Effective habitat management that is compatible with other forest resource use requires reliable mapping of the forest habitat in which murrelets are most likely to nest (British Columbia Ministry of Water, Land and Air Protection 2004). Studies at nest sites indicate that suitable nesting habitat generally includes: large, old trees; suitable platforms for nests on limbs or deformities within the canopy; some degree of foliage cover over the nest; and canopy gaps that allow flying murrelets to access nest sites (Nelson 1997; Burger 2002; CMMRT 2003). Not all large, old trees provide the necessary canopy structure that allows nesting. Consequently, habitat suitability mapping cannot rely solely on stand age and tree size as shown in forest cover mapping or air photo interpretation. Furthermore, a key requirement, potential nest platforms (defined as limbs or deformities > 15 cm in diameter, including epiphyte cover) are not visible in air photos and are not included in forest cover or other available Geographic Information System (GIS) resources (e.g., CMMRT 2003; Donaldson 2004; Waterhouse et al. 2008). Established methods used to assess canopy platforms involve ground-based observers (e.g., Manley 1999; Rodway and Regehr 2002; Burger and Bahn 2004), but these methods are both labour-intensive and biased by site accessibility (Bradley 2002; Bradley et al. 2004). Therefore, low-level aerial surveys using helicopters provide an alternative method for assessing forest canopy structures and for efficiently classifying and mapping potential murrelet habitat-nesting areas (Burger et al. 2004).

> *Our study tested the application of the low-level survey method in two regions of southern British Columbia, the Sunshine Coast and the west coast of Vancouver Island, and used nest sites previously located with radio-telemetry.*

Based on field testing and consultation with practitioners, standard methods for low-level surveys were developed (Burger et al. 2004) using environmental variables known to be linked to murrelet habitat requirements (Ralph et al. 1995; Nelson 1997; Burger 2002; CMMRT 2003). Briefly, the assessment ranks a range of canopy and topographic parameters, then provides a subjective ranking of the overall habitat quality using a six-class ranking system (Nil through Very High) (details in "Methods" section). Aerial surveys are usually undertaken in conjunction with other habitat-assessment methods, such as air photo interpretation or habitat algorithms, and are used either to confirm the quality of a specific forest area for murrelet management or to produce maps of habitat quality that will assist in management planning (Burger 2004). Our study tested the application of the low-level survey method in two regions of southern British Columbia, the Sunshine Coast and the west coast of Vancouver Island, and used nest sites previously located with radio-telemetry (Bradley 2002; Bradley et al. 2004; McFarlane Tranquilla et al. 2005).

Our study had three objectives. First, we tested whether nest sites could be effectively distinguished within the greater than 140-year-old forest (mature and old) by comparing habitat at nests with habitat at randomly selected points within the same landscapes. The assumption was that habitat murrelets actually use would best reflect the desirable qualities for nesting. (Cody 1985; Martin 1992). We inferred selectivity by murrelets for (or against) habitat of a particular class if nest sites occurred more frequently (or less frequently) within the class relative to the randomly selected sites (Jones 2001; Manly et al. 2002). These comparisons were made at two spatial scales: within patches (radius 100 m around the selected point or nest), and within the larger stand of similar forest surrounding the patch. Second, by comparing the habitat quality classes assigned to patches and stands, we examined whether the area of mapping unit would affect our ranking of habitat quality class, and if so, what implications this might have for describing and managing nesting habitat. Third, we evaluated the relationships between assessments made of the individually assessed environmental variables (e.g., tree size, moss development, and platform availability) and the overall habitat quality class for each site. This also allowed us to determine whether all assessed variables, or a subset of these, best predicted habitat suitability for nest sites.

Study areas

We analyzed data from three study areas: Desolation Sound and Toba Inlet, adjacent to each other on the Sunshine Coast (50°50' N, 124°40' W), and Clayoquot Sound on the west coast of Vancouver Island (49°12' N, 126°06' W). The Sunshine Coast region is characterized by three biogeoclimatic zones: Coastal Douglas-fir (0–600 m elevation), Coastal Western Hemlock (0–1000 m), and Mountain Hemlock (usually >1000 m) (Meidinger and Pojar 1991). Forests at lower elevations are dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and lesser amounts of western redcedar (*Thuja plicata*). Amabilis fir (*Abies amabilis*) becomes common at moister sites and with increasing elevation. The forest transitions into yellow-cedar (*Chamaecyparis nootkatensis*) and mountain hemlock (*Tsuga mertensiana*) in the Mountain Hemlock zone (Green and Klinka 1994). Forests on the Sunshine Coast are fragmented by mountainous topography, including steep cliffs and avalanche chutes (Zharikov et al. 2006), ongoing forest harvesting activities that date back to the early 1900s, fire disturbance (particularly in drier ecosystems), and some wind disturbance.

Clayoquot Sound is dominated by the wetter variants of the Coastal Western Hemlock and Mountain Hemlock zones. Sitka spruce (*Picea sitchensis*) is often found in wet sites of coastal floodplains. The windward hypermaritime variants of the outer coast of Clayoquot Sound commonly have bog forests and include a mixture of western hemlock, redcedar and yellow-cedar, amabilis fir, and small amounts of lodgepole pine (*Pinus contorta*) (Green and Klinka 1994). Forests in Clayoquot Sound are relatively continuous and uniform, except in the southwest portion of the study area, which is fragmented by forest harvesting, and in the northeast portion of the study area, which is mountainous.

Methods

Sampling

We used a two-sample design (i.e., use versus random). We evaluated habitat using 100 m radius plots centred on the sites defined as the patches. Nests were located by tracking radio-tagged murrelets on the Sunshine Coast from 1998 to 2001, and in Clayoquot Sound from 2000 to 2002 (Bradley et al. 2004; Zharikov et al. 2006). Nest samples from different years were combined on the assumption that habitat selection at the scale we tested was not detectably affected by inter-annual variations of other factors (e.g., food availability, climate; but see McFarlane Tranquilla et al. 2005). We used only nests at sites in forests older than 140-years and thus excluded 11 nests found in forest classed as less than 140 years old and six potential cliff nests (e.g., Bradley and Cooke 2001) for which platform structure assessments are not appropriate.

We compared known nest sites with sites at randomly located points in greater than 140-year-old-forest of each study area. We defined Study Area using a minimum convex polygon that encompassed all nests, plus a 5-km buffer. The buffer was approximately double the mean distance between the annual samples of known nests within the study areas (Zharikov et al. 2006). Inclusion of the buffer ensured that we could obtain a sample of random points that was at least equal to the number of nests.

We maintained a minimum spacing of 600 m between random points and ensured representation across the landscape and elevational gradient (Waterhouse et al. 2008). Elevation was calculated from a digital elevation model (Integrated Land Management Bureau 2007), and we retained it as an explanatory variable for the statistical analyses.

Aerial observations and habitat assessments

We used a Bell Jet Ranger helicopter and followed the methods of Burger et al. (2004). Flight routes were planned using GPS, a 1:85 000 topographic map, and 1:20 000 forest cover maps. Before data collection at a site, we confirmed GPS locations on pre-marked air photos. Sites were tested blind; that is, observers did not know whether the site was a nest or random point.

TABLE 1. Description of environmental variables and habitat quality classification used to assess nest and random patches by the low-level aerial survey method (adapted from Burger et al. 2004).

Variables	Description	Classes[a]
Large Trees[a]	% of canopy trees > 28 m tall	**Very High**, 51–100% **High**, 26–50% **Moderate**, 6–25% **Low**, 1–5% **Very Low**, ~1% **Nil**
Trees with Platforms[a]	% of canopy and emergent trees with potential nest platforms	
Moss Development[a]	% of canopy and emergent trees with obvious mossy pads on limbs	
Canopy Closure	% cover of overstorey canopy based on vertical projection of crowns on the ground, using the recommendations from the Canadian Marbled Murrelet Recovery Team (2003)	**Most Likely**, 40–60% **Moderately Likely**, 30 or 70% **Least Likely**, < 30%, > 70%
Vertical Complexity[b]	Vertical complexity and gappiness is subjectively ranked from least to highest, approximately matching the criteria used in air photo assessments of murrelet habitat	**Very High to Low**
Topographic Complexity[c]	Topographic features providing gaps and complexity to the forest (e.g., large boulders, rocky outcrops) ranked by subjective assessment	**Very High to Low**
Slope Grade	Steepness of slope grade at site	**Flat and gentle** **Moderate** **Steep**
Slope Position	Position on macroslope (slope assessed based on natural topographic breaks)	**Low and Valley Bottom** **Mid** **Upper and Ridge**
Patch Habitat Quality	Overall habitat quality ranked as a qualitative assessment considering occurrence and amount of all variables within the 100 m radius patch	**Very High**, 51–100% **High**, 26–50% **Moderate**, 6–25% **Low**, 1–5% **Very Low**, ~1% **Nil**
Stand Habitat Quality	As above, but overall habitat quality ranking of the stand (which varies in area) surrounding and including the 100 m radius patch.	

[a] Mod–Low refers to pooled Moderate, Low, and Very Low (~1–25% where applicable) for analysis (refer to Figure 1).

[b] Very High: Very non-uniform (> 40% difference leading trees and average canopy, very irregular canopy created by emergent trees, gaps, fallen trees); High: Non-uniform (31–40% height difference; canopy gaps often visible due to past disturbance; irregular canopy created by emergent trees, gaps, fallen trees); Moderate: Moderately uniform (21–30% height difference, some canopy gaps visible, evidence of past disturbance, a few emergent trees and obvious gaps); Low: Uniform (11–20% height difference, few canopy gaps visible, little or no evidence of disturbance, no emergent trees).

[c] A subjective assessment based on the effect of stand-level topography (e.g., slope, small rocky outcrops, avalanche chutes, large boulders) in creating small gaps and creating a complex canopy structure.

At each patch, the helicopter circled for 3–5 minutes. If patches or stands included young forest greater than or equal to 140 years old, or non-forested areas, the assessment was applied only to those portions of forest greater than 140 years old.

We classed environmental variables of patches using standard aerial survey criteria (Table 1; Burger et al. 2004). These variables are thought to describe habitat structure associated with cover (Canopy Closure, Vertical Complexity, and Slope Position, i.e., exposure), access into the stand (Vertical Complexity, Topographic Complexity, and Slope Grade), and nest platform availability for Marbled Murrelets (Large Trees, Trees with Platforms, Moss Development, and Slope Position, i.e., site productivity). After taking into consideration the classes of all the other parameters, we finally assessed the overall habitat quality of the patch (Patch Habitat Quality). Without making detailed assessments of each canopy parameter, we also subjectively classed the overall habitat quality of the stand surrounding the patch (Stand Habitat Quality). Stands included forest with relatively uniform age, species composition, and structure of trees, but were variable in area. Also, stands were broadly equivalent to polygons mapped for forest cover from air photos (Resource Inventory Committee 2002).

Data analysis

Statistical procedures used SAS 9.1 (SAS Institute Inc. 2003). Significance was evaluated using $\alpha = 0.10$, unless otherwise specified. We used a larger than customary level of significance to reduce the likelihood of a Type II error (i.e., not detecting real differences), which we felt could pose more risk to murrelet management than the occurrence of a Type I error. Using a suite of regression tools, we screened each variable and subsequently pooled classes of some variables to provide adequate sample sizes for analyses and pooled data among study areas where no effect was indicated (see methods in Waterhouse et al. 2008).

Determining habitat quality of nest patches and stands

We used a log-linear model (Agresti 1996) to determine if habitat quality differed according to Site Type (nest versus random point). This was done for both patches (Patch Type effect) and stands (Stand Type effect). From these models, we generated the predicted probabilities (Prob) that an observation belonging to one of the Site Types (nest or random point) would fall into any one of the habitat quality classes (e.g., Very Low through Very High).

Assessing habitat quality of patches compared to stands

To determine if overall habitat quality substantially differed depending on the area of forest classed, we used the Kappa statistic (κ) (Cohen 1960) to measure agreement between matched pairs of patch and stand (pooled nest and random samples: $n = 249$); full agreement equals 1 from a possible range of 0 to 1. Next, for those sites for which the habitat class of the patch differed from that assigned to the surrounding stand, we tested if the lack of agreement occurred more often between matched pairs at nest sites than between those at random sites (Chi-square test). We hypothesized that a lack of agreement would be greater for nest sites than for random sites if nesting murrelets selected smaller patches of higher-quality habitat within poorer-quality stands.

Determining relationships of environmental variables to patch habitat quality

To examine relationships between the environmental variables and the final habitat quality class of patch we used Spearman rank correlations (r_s) and the Mantel–Haenszel Chi-square test between ordinal variables (Mantel and Haenszel 1959).

Predicting nest patch habitat using resource selection functions

We determined which combination of environmental variables were the best predictors of nest patches using Akaike's Information Criterion adjusted for small samples (AIC_c) and Akaike weights (ω) to select logistic regression models (multiple or single) that best predicted Patch Type under our use–availability design (Burnham and Anderson 2002). We interpreted these models as Resource Selection Functions (Manly et al. 2002) that are proportional to the true probability of predicting Patch Type (i.e., nest patch). Please see Appendix for modelling details. We considered all variables identified a priori for field testing (Table 1) and included Study Area, Elevation, and any significant interactions indicated by the individual univariate analyses of the variables during screening. We reduced the potential for multicollinearity by excluding those variables highly associated based on Spearman rank correlations (if $P \leq 0.01$ and $r_s \geq 0.7$; Myers 1986), and retaining only the variable that best explained the differences between Patch Type.

Categorical predictors were parameterized using indicator or dummy variables that can take on values of 1 or 0 (Myers 1986, pp. 87–94). All but the final level of a predictor were assigned a dummy variable, so that the parameter estimate for each dummy variable conveyed the difference in the effect of a level compared to the effect of the final level. During model selection, all dummy variables of a categorical predictor were either kept in or dropped from the model. If the dummy variables associated with an interaction were included, then the dummy variables associated with both main effects were also included in the model. The "best" model had the minimum AIC_c and highest weight, and models that differed from it by less than 2 units in AIC_c scores were considered to have similar predictive ability (Burnham and Anderson 2002). Akaike weights were interpreted as approximate probabilities of the model, being the "best" from among those models examined (Anderson et al. 2000).

We initially assessed the "best" models based on the non-significant Hosmer and Lemeshow (2000) goodness-of-fit tests. Only then did we further examine fit of the "best" model in two phases. We used K-fold cross-validation (Boyce et al. 2002; Lillesand et al. 2004; see methods used Waterhouse et al. 2008) to assess the performance of each model for predicting Patch Type, where a strong positive Spearman rank correlation coefficient (r_s) between the predicted Resource Selection Function (categorized into bins) and the relative frequency of nests indicates good predictive performance (Boyce et al. 2002). Then, we determined the deviance reduction (ΔD) associated with each predictor variable by using (Chi-square) likelihood ratio tests (McCullagh and Nelder 1989; Guisan and Zimmermann 2000).

Results

Habitat quality of nest patches and stands

In the three study areas, we assessed 250 sites composed of 111 nest sites and 139 random sites (Table 2). We found that both nest and random patches centred on these sites (Patch Habitat Quality) and the stands surrounding the patches (Stand Habitat Quality) were distributed across five habitat quality classes (Figures 1a and 1b). Following pre-screening tests, we combined the Moderate, Low, and Very Low classes (hereafter Mod–Low) for testing habitat quality of patches and stands. Due to an interaction between Study Area and Patch Type ($\chi^2 = 6.23$, $P = 0.04$), we tested Patch Type separately by Study Area; whereas we pooled study areas for testing Stand Type due to non-significant differences (Study Area $\chi^2 = 1.60$, $P = 0.45$; Study Area × Stand Type $\chi^2 = 2.09$, $P = 0.35$).

Our tests of Patch Type (nests versus random) were significant for Desolation Sound ($\chi^2 = 4.88$, $P = 0.03$) and Toba Inlet ($\chi^2 = 9.22$, $P < 0.01$), but non-significant for Clayoquot Sound ($\chi^2 = 0.22$, $P = 0.64$). Most nests in all the Study Areas were classed Very High and High (approximately 70–80 %; Figure 1a). In Desolation Sound and Toba Inlet, nest patches, when compared to random patches, respectively occurred 1.6 and 3 times more often than expected in Very High quality habitat and similarly less often than expected in the Mod–Low

TABLE 2. Area, forest cover, and sample sizes for the three study areas.

Study Area	Total area (ha)	Forest > 140 years old (% of area)	Type of site	
			Nest (no. of sites)	Random (no. of sites)
Clayoquot Sound	1.82×10^5	53	31[a]	42
Desolation Sound	2.44×10^5	12	58	63[a]
Toba Inlet	1.89×10^5	20	22	34
Total patches			111	139

[a] One nest site and one random site were dropped for most analyses due to missing data.

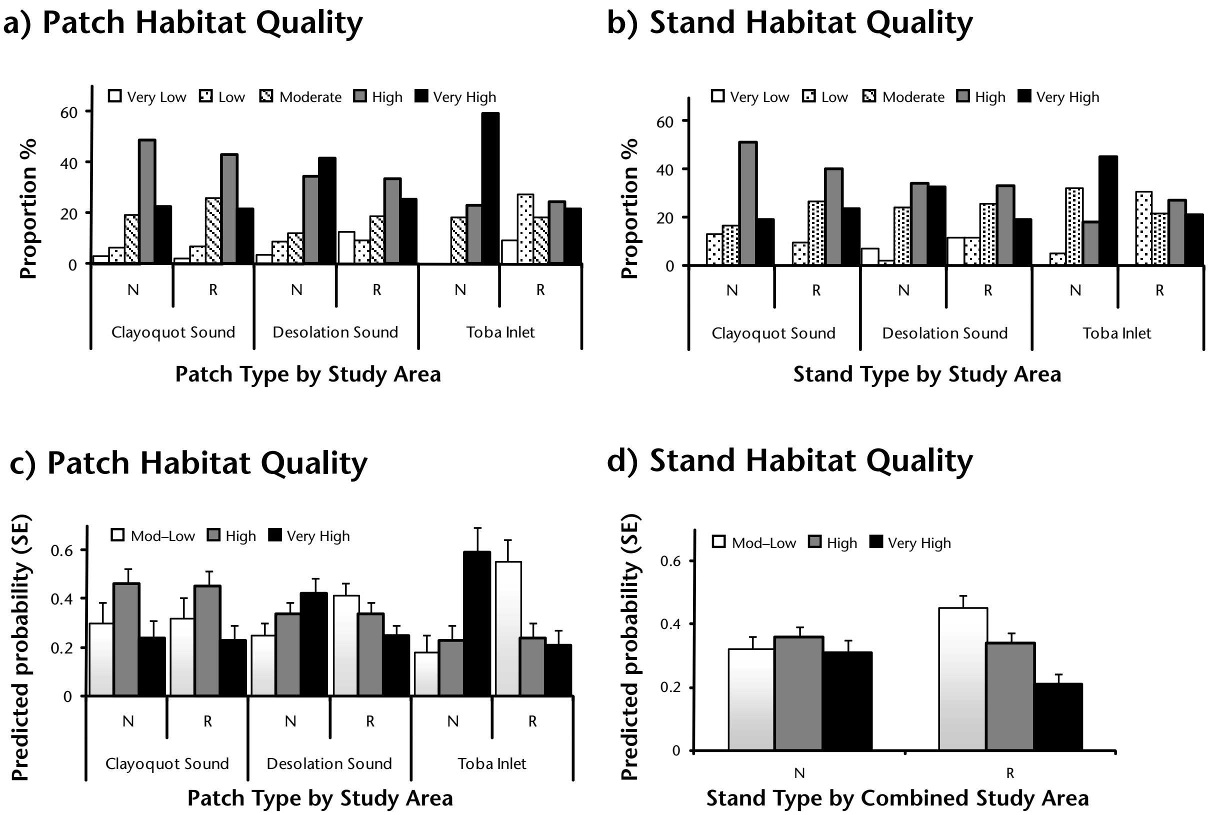

FIGURE 1. Proportions (%) by variable classes of nest (N) patches and of random (R) patches in each Study Area for Patch Habitat Quality (a) and Stand Habitat Quality (b) contrasted to the predicted probabilities and standard errors (SE) by variable classes (but using the combined Mod–Low as per Table 1) produced from reduced statistical models for Patch Habitat Quality (c) by Study Area and Stand Habitat Quality (d) for combined Study Areas.

habitat. (Figure 1c). For Stand Type, most nest stands (60–70 %) were also classed Very High or High (Figure 1b). Using the pooled Study Areas, our results were consistent with the Patch analysis ($\chi^2 = 5.13$, $P = 0.02$, Figures 1b, 1d); nest stands were 1.5 times more likely to be classed Very High than were random stands (Figure 1d), whereas those classed Mod–Low were similarly avoided (used 1.4 times less; Figure 1d).

Habitat quality of patches compared to stands

The habitat quality classes assigned to the patch and its surrounding stand were usually identical (75% of nest patches, $n = 111$; 73% of random patches, $n = 138$; 74% for pooled data, $n = 249$ with $\kappa = 0.65$, SE = 0.04). For those pairs that did not match ($n = 65$; 28 nest sites and 37 random sites) the difference was only one class, except for one pair with a larger difference. We found that significantly ($\chi^2 = 7.67$, $P < 0.01$) more of the nest patches were within stands assigned a lower habitat quality class (23/28; 82%) rather than a higher class (18%) compared to the random patches, which were as likely to be assigned a higher (18/37; 47%) or lower (53%) quality class than the surrounding stand.

Relationships of environmental variables to patch habitat quality

To examine relationships between the overall habitat quality and the environmental variables assessed at each patch, we pooled data from study areas. Overall patch habitat quality was strongly positively correlated with the occurrence of large trees, trees with platforms, and

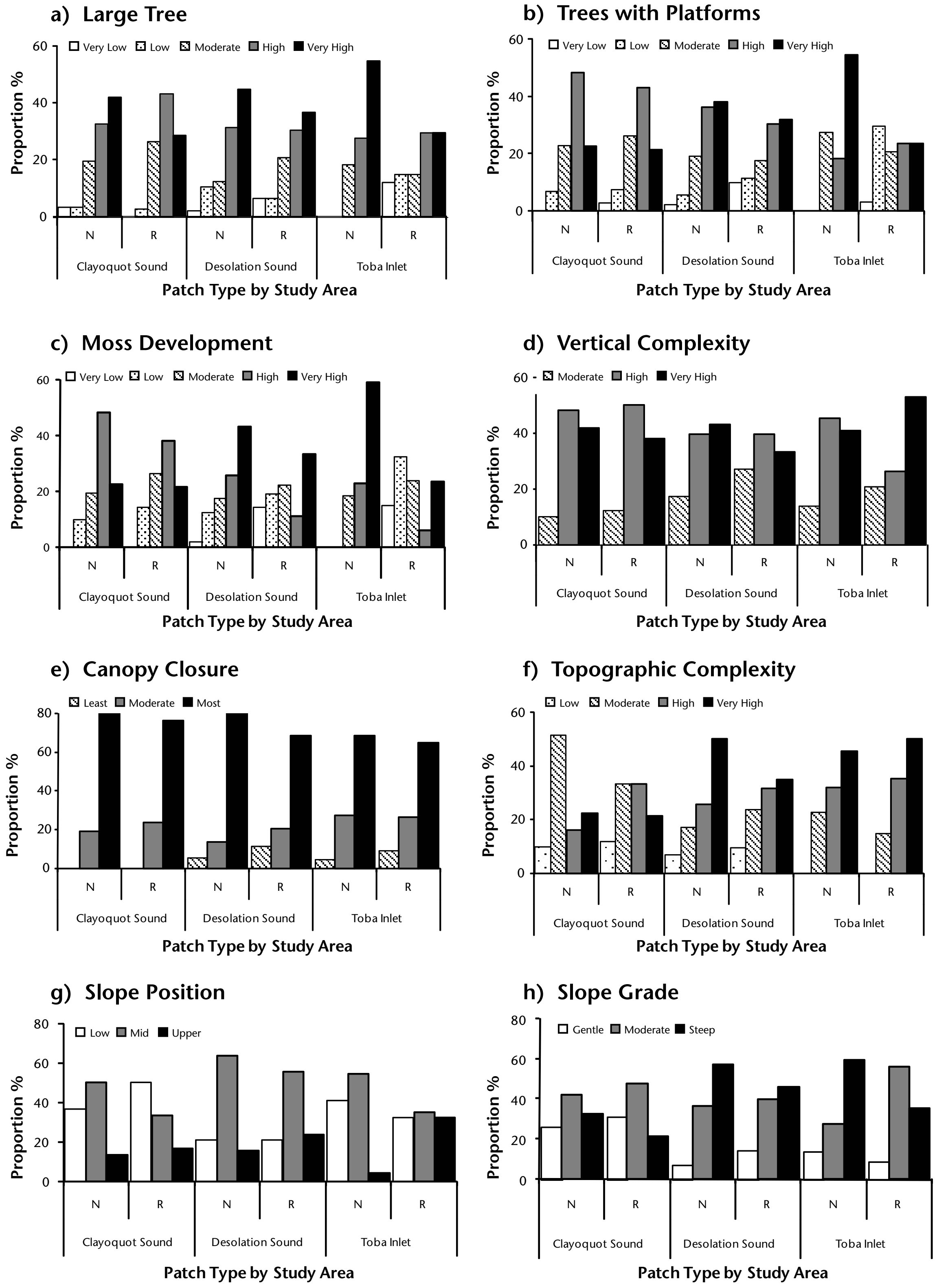

FIGURE 2. For each Study Area, proportions (%) of nest (N) patches and of random (R) patches by class for Large Trees, Trees with Platforms, Moss Development, Vertical Complexity, Canopy Closure, Topographic Complexity, Slope Position, and Slope Grade. Proportions of classes sum to 100% for each variable.

moss development (for each comparison: Spearman rank correlation, $n = 248$, $r_s = 0.75–0.91$, $P < 0.01$). Patch Habitat Quality was moderately correlated with vertical complexity (positive), slope position (negative), and elevation (negative) ($n = 248$, $r_s = 0.32–0.46$, $P < 0.01$), and weakly correlated with slope grade (negative) and topographic complexity (positive) ($n = 248$, $r_s < 0.21$, $P < 0.01$).

Predicting nest patch habitat using resource selection functions

In the greater than 140-year-old forest, we found that both nest and random patches fell within most of the possible classes of each environmental variable (Figure 2). Exceptions were that no patches were classed Nil for any variable, and no patches were classed Very Low for Topographic Complexity or as Low or Very Low for Vertical Complexity.

For model building, we excluded canopy closure as a candidate variable because most samples fell into the Most Likely class (Figure 2). We tested, separately, Large Trees, Trees with Platforms, and Moss Development because Spearman correlations suggested multicollinearity ($n = 250$, $r_s > 0.72$, $P < 0.01$). For the AIC_c analysis using Moss Development, Platform Trees, and Large Trees, following pre-screening, we combined the three lower classes into one (Mod–Low).

First, we tested models containing Moss Development, retaining Study Area because it had a significant effect on this variable ($\chi^2 = 19.55$, $P < 0.01$). We additionally retained all other variables including Elevation (thus the significant interaction term Study Area × Elevation), because the Spearman correlations among them were either significant but weaker (range $n = 248$ to 250, range $r_s = 0.13$ to 0.51, $P < 0.05$) or were not significant ($P > 0.05$ for Vertical Complexity and Slope Position, Vertical Complexity and Elevation). The analysis produced 160 models of which two appeared "best" for predicting nest patches (Table 3). Model 1 included Study Area, Moss Development, Slope Grade, Elevation, and Study Area × Elevation interaction. Model 2, which had a similar predictability (Δ $AIC_c < 2$), included these same variables plus Topographic Complexity. Only Vertical Complexity and Slope Position were excluded from the top models. Both models had reasonable fit based on a non-significant Hosmer and Lemeshow Goodness of Fit statistics (i.e., $P > 0.10$).

TABLE 3. Resource Selection Functions that predict Patch Type developed by using Akaike's Information Criterion adjusted for small samples (AIC_c) and weighting (ω_i). Top models were selected based on ΔAIC_c, with two top models identified using Moss Development.

Model	Variables	No. of variables (K)	AIC_c	ω_i
Model 1	Study Area Moss Development Slope Grade Elevation Study Area × Elevation	10	310.17	0.25
Model 2	Study Area Moss Development Slope Grade Elevation Study Area × Elevation Topographic Complexity	13	311.57	0.16
Model 3	Moss Development Slope Grade Elevation	6	313.14	0.08

The likelihood parameter estimates for Model 1 (Table 4) provided us with the influence of each variable on the Resource Selection Function score, which is proportional to the probability of nest patch use. The model yielded higher Resource Selection Function scores (assuming elevation is zero) at Toba Inlet than at Desolation Sound, and produced the lowest scores at Clayoquot Sound (Study Area effect). These scores: (1) increased if moss development was classed High or Very High (Moss Development effect); (2) decreased as elevation increased (Elevation effect); (3) declined most steeply with elevation in Toba Inlet and least steeply in Clayoquot Sound (Study Area × Elevation interaction); and (4) increased as slope gradient increased, where steep slopes were more likely and gentle slopes were least likely to have nest patches than were moderate slopes (Slope Gradient effect).

Model 2 had a similar interpretation, but the additional estimates from including Topographic Complexity were not significant. The estimates were difficult to interpret because nests were best predicted to occur in patches with Very High and Moderate complexities, followed by patches with Low complexity, and were least likely to occur in patches of High complexity. We therefore deemed Model 2 unreliable and focused further only on Model 1.

For Model 1 we used the K-fold cross-validation and confirmed that it had good predictive capacity ($r_s = 0.84$, $n = 10$, $P < 0.001$). We also determined that all variables included in Model 1 contributed significantly to explaining the deviance in the model (i.e., $P < 0.02$); the greatest change in deviance was explained by Elevation ($\Delta D = 20.57$), followed by Slope Grade ($\Delta D = 12.06$), Study Area × Elevation ($\Delta D = 9.13$), Moss Development ($\Delta D = 7.52$), and then Study Area ($\Delta D = 7.13$).

Next, we re-ran the AIC_c analysis using Trees with Platforms instead of Moss Development. We found that Trees with Platforms was retained as an explanatory variable in one of four top models only if Study Area, for which we had detected a significant pre-screening effect ($\chi^2 = 8.96$, $P < 0.06$), was excluded. Otherwise,

TABLE 4. Statistically significant predictions derived from the top-ranked binary logistic regression model (Model 1, Table 3) for separating Patch Type (nests versus random patches). Significance of the overall model was based on the reduction in deviance between an intercept-only model and a model with all predictor variables included (χ2 = 53.88, df = 9, $P < 0.0001$). All tests of variables or interactions shown here are based on 1 degree of freedom ($n = 248$).

Variable	Parameter estimate	Standard error	Likelihood ratio χ^2	P
Intercept	3.265	1.072	N/A	N/A
Moss Development				
Very High	0.564	0.379	2.22	0.14
High	1.064	0.377	8.22	0.004
Study Area				
Clayoquot Sound	−2.724	1.119	6.99	0.008
Desolation Sound	−2.244	1.083	4.98	0.0256
Elevation	−0.005	0.002	20.55	< 0.001
Elevation × Study Area				
Clayoquot Sound	0.004	0.001	7.50	0.006
Desolation Sound	0.004	0.001	7.99	0.005
Slope Grade				
Gentle	−1.435	0.472	.82	0.002
Moderate	−0.867	0.335	6.97	0.008

Trees with Platforms was not retained. Lastly we reran the analyses using Large Trees, for which the Study Area effect was non-significant ($\chi^2 = 0.80$, $P = 0.67$), and we found it was retained in two of five top models. Consistent with the AIC_c analysis for Moss Development, our analyses using Trees with Platforms and Large Trees also retained various combinations of these variables in the top models: Elevation, Slope Grade, Topographic Complexity, but also Vertical Complexity in the Large Tree AIC_c analysis.

Discussion

Classifying habitat quality

In support of using the low-level aerial survey method to assess Marbled Murrelet habitat, we found that murrelets selected nesting habitats in higher-quality classes and avoided those in lower-quality classes. This was found for both patches (100 m around nests) and the larger surrounding stands (usually tens or up to low hundreds of hectares). Overall, 40% of the 111 nest sites were in patches classed as Very High, 36% were in High, 15% were in Moderate, 6% were in Low, and 3% were in Very Low. Because we were comparing sites at nests with sites at random points within greater than 140-year-old forest, some proportion of the random sites also occurred in suitable nest habitat. Consequently, the differences between nest and random patches were less striking than expected; this is a common problem when comparing used habitat with random (Jones 2001; Manly et al. 2002). The small differences between nest and random patches (or stands) in the predicted probabilities of habitat quality (Figure 1c and 1d) and the considerable proportion of nests (24%) in patches classed as Mod–Low suggest that the classification's effectiveness for distinguishing all nest patches has limitations in the greater than 140-year-old forest stratum.

The aerial survey classification's greatest value for wildlife managers may be in its use to quantitatively rank and classify the potential value of one area relative to another, rather than to provide a threshold to identify suitable nesting habitat within the older forest stratum. The challenge in this application is that, given the lack of known relationships between habitat quality and occupancy or nest density (Burger 2004; Burger and Waterhouse 2009), we do not know to what extent one class supports higher densities of nesting murrelets than another class.

The low-level aerial survey method provided a regionally consistent method for identifying Marbled Murrelet nesting habitat in south coastal British Columbia. Despite some differences among study areas—that is, nesting habitat was more effectively distinguished on the Sunshine Coast (Desolation Sound and Toba Inlet) than on the west coast of Vancouver Island (Clayoquot Sound)—nest habitat patches had many similar characteristics among the regions based on those variables assessed by the aerial survey method. We suspect that nest patch selectivity was more easily detected on the Sunshine Coast because availability of suitable habitat is reduced there owing to historic disturbance and to effects of topography and elevation (Zharikov et al. 2006); that is, it is less likely on the Sunshine Coast that random points would fall within suitable habitat. In comparison, Clayoquot Sound has experienced far less habitat loss from logging and has more uniform coverage of suitable forest (Zharikov et al. 2006); consequently a higher proportion of random points might fall within suitable nesting habitat, thereby minimizing the differences between nests and random points.

Aerial assessments of habitat quality were sensitive to the area of forest assessed, even though agreement was high between the classes assigned to pairs of patch and forest stand (74% of these pairs had identical habitat quality class). Information can be lost as minimum mapping units increase in area (i.e., the grain at which the element is assessed increases) (Fassnacht et al. 2006), as shown by our comparison between smaller patches contained within often larger stands. Our result was of particular importance because we showed that, where there were differences between the habitat quality of the patch and surrounding stand at nest sites, the nests were disproportionately found in patches of habitat classed higher for habitat quality. Murrelets are likely selecting higher-quality patches for nesting within the overall forest matrix (Nelson and Wilson 2002). The minimum mapping unit currently applied for producing aerial survey habitat maps for murrelets in British Columbia is approximately 3 ha, with maps produced to 1:20 000 scale (Sue McDonald, Western Forest Products, pers. comm., November 2008). Based on our testing using 3-ha patches, if inventory sampling is applied uniformly during low-level flights, 3 ha should be adequate for identifying patches of higher-quality habitat.

Interpreting the Classification

Murrelets, as most other animals, likely exploit a wider range of habitats by using patches with a range of habitat characteristics (Guénette and Villard 2004). By broadly distributing themselves for nesting across the landscape, murrelets can perhaps better respond to factors such as the distribution of marine prey and predators. Research has shown that considering combinations of both structural and topographic variables improves the probability of detecting that a patch has nesting habitat value for murrelets (Bahn and Newsom 2002a, 2002b; Nelson et al. 2006; Zharikov et al. 2006). The habitat quality classification is intended to incorporate assessments of multiple forest structural and topographic variables (Burger 2004). Yet, the assessment of overall habitat quality made from the helicopter was, in practice, weighted by a few key forest structural features. The strong positive intercorrelations between the habitat quality classification and forest structure variables suggested that the final assigned habitat quality class was dependent on tree size, platform availability, and moss development while little weighting was attributable to topographic variables.

In contrast to the habitat quality classification, the Resource Selection Functions suggested that murrelet nest habitat was best distinguished from available habitat using topographic variables as well as forest structural variables. Moss Development, Slope Grade, and Elevation proved the best predictors of murrelet nesting habitat following our analysis approach using AIC_c. Mossy platforms are key forest structural features for supporting the nest (Nelson 1997; Burger 2002) and can be distinguished within the greater than 140-year-old forest by using aerial surveys. Although strongly intercorrelated, Large Trees and Trees with Platforms were less reliable predictors of murrelet nest habitat than Moss Development in the Resource Selection Functions. Slope Grade, retained as an aerial estimate of topography, is thought to describe site accessibility where steeper slopes may enhance a murrelet's ability to access stands by exposing entryways into the canopy (Bradley 2002). Although the best-fit models did not retain Slope Position, we suggest it may be beneficial to record this variable during aerial surveys because it may be help to eliminate stands on ridge tops that can be exposed to wind disturbance and are therefore less suitable for murrelets (Meyer et al. 2002, 2004). Elevation may influence murrelets' nest-site selectivity because low-elevation forests are often more productive (have larger trees) and are often closer to foraging areas used by murrelets (Burger 2002; Meyer et al. 2004; Nelson et al. 2006; Zharikov et al. 2006). More importantly, the model explained in part how nest patches may occur across a range of elevations and slopes where murrelets are able to access and use higher-elevation habitats or steeper slopes if platforms with moss pads are available.

We found only weak evidence that Topographic Complexity and Vertical Complexity, as assessed in aerial surveys, helped to predict murrelet nesting habitat. Their effectiveness for distinguishing habitat may be reduced if there is site-to-site variation in how murrelets discriminate stand access. Vertical Complexity can alternatively be assessed on air photos (Waterhouse 2002, 2008; Donaldson 2004). Canopy Closure, based on the lack of variability in our data, may not prove as useful a variable to collect during aerial surveys in the greater than 140-year-old forest stratum. In immature forests (< 140 years old), however, closed and uniform canopies might preclude murrelets from accessing canopy limbs (Waterhouse et al. 2002).

Conclusions and management implications

Low-level aerial surveys enable biologists to identify likely nesting habitat for Marbled Murrelets, as they focus on key habitat features (platforms and moss development) not discernable using lower-resolution tools such as aerial photographs or satellite images. When combined with knowledge of site topography, estimating availability of mossy platforms may prove one of the most useful indicators of the aerial survey. Aerial surveys can be used to rapidly classify and map large areas of forest, including forest with poor access for ground observers. If applied with a fine-scale resolution of approximately 3 ha, small patches of suitable habitat within a larger matrix of less suitable forest can be detected, and hence improve the accuracy of the classification. This information can be used to help identify candidate areas that meet habitat management objectives for nesting murrelets (e.g., Wildlife Habitat Areas; British Columbia Ministry of Water, Land and Air Protection 2004).

Our selectivity analysis supports the idea of focusing management for nesting murrelets on habitats classed Very High or High in aerial surveys. However, such higher-quality habitats might not be frequently found in some landscapes and a proportion of murrelets (approximately 25% in this study) do nest in some lower-quality habitats.

Low-level aerial surveys enable biologists to identify likely nesting habitat for Marbled Murrelets, as they focus on key habitat features (platforms and moss development) not discernable using lower-resolution tools such as aerial photographs or satellite images.

Consequently, wildlife managers may need to consider using lower-quality habitats (particularly those classified Moderate) to meet habitat management objectives. In such cases, and depending on management objectives, other methods could be applied to show evidence of murrelet use of these lower-quality habitats (e.g., radar or audiovisual surveys).

At the practical level, the current discrete six-class classification (Burger et al. 2004) could be replaced by the less subjective predictive Resource Selection Functions (i.e., producing continuous relative probabilities) (Boyce et al. 2002; Manly et al. 2002; Boyce 2006). We are cautious in overly interpreting our current Resource Selection Function results because our testing may be considered borderline exploratory, where the variables were selected a priori but the relationship between them was unknown. Further development of Resource Selection Functions would enable biologists to integrate stand-level metrics collected during aerial surveys with other stand and landscape metrics that relate to habitat selectivity (Bahn and Newsom 2002a, 2002b; Meyer et al. 2004; Zharikov et al. 2006). Such an approach could also help account for hierarchal or multistage habitat selection (Johnson 1980; Orians and Wittenberger 1991; Manly et al. 2002), which may be used by the Marbled Murrelet (Manley 1999; Meyer 2007).

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Appendix A

Using logistic regression to estimate a Resource Selection Function when the data consists of two samples: One of used and one of available sites

Following along the lines of Keating and Cherry (2004) and Manly et al. (2002):

$$P(\text{site has a nest} \mid \text{site is among the type types of samples drawn}, \mathbf{x}) = \frac{\frac{P_u}{P_a} P(\text{site has a nest} \mid \mathbf{x})}{1 + \frac{P_u}{P_a} P(\text{site has a nest} \mid \mathbf{x})}$$

where P_u and P_a are the sampling inclusion probabilities for the used and available sites respectively and $\mathbf{x}$ is a vector of explanatory environmental variables.

If we assume that the resource selection probability function has the form , where for all , then

$P(\text{site has a nest} \mid \mathbf{x}) = \exp(\boldsymbol{\beta}^{\mathrm{T}} \mathbf{x})$, where $\boldsymbol{\beta}^{\mathrm{T}} \mathbf{x} \leq 0$ for all $\mathbf{x}$, then

$$P(\text{site has a nest} \mid \text{site is among the two types of samples drawn}, \mathbf{x}) = \frac{\exp(\boldsymbol{\beta}^{*T}\mathbf{x})}{1 + \exp(\boldsymbol{\beta}^{*T}\mathbf{x})}$$

the first element of $\boldsymbol{\beta}^*$ is $\beta_0 + \log\left(\frac{P_u}{P_a}\right)$.

Keating and Cherry (2004) show that one way to ensure $\boldsymbol{\beta}^{\mathrm{T}} \mathbf{x} \leq 0$ for all $\mathbf{x}$ is for $P(\text{site has a nest}) \leq \frac{n_u}{n_a \exp(\boldsymbol{\beta}^{*T}\mathbf{x})}$

for all $\mathbf{x}$ in the population (where n_u and n_a are the size of the used and available samples, respectively).

Under these conditions, a logistic regression fit to the use-availability data (i.e., the dependent variable is coded as 1 when the site is used an 0 when the site it is available, along with the vector of explanatory variables) will be able to recover either: (1) the assumed resource selection probability function when P_u and P_a are known, or (2) a Resource Selection Function proportional to it when P_u and P_a and are unknown.

Test Your Knowledge . . .

Using the low-level aerial survey method to identify nesting habitat of Marbled Murrelets

How well can you recall some of the main messages in the preceding Research Report? Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. Low-level aerial surveys are most commonly used to assess:
    - A) Murrelet nest habitat
    - B) Murrelet nests
    - C) Habitat with nesting potential for murrelets

2. Low-level aerial surveys can be combined with
    - A) Air photo interpretation methods
    - B) GIS habitat algorithms mapping
    - C) Both of the above

3. One important low-level aerial survey habitat variable for identifying potential nesting habitat is:
    - A) Vertical complexity
    - B) Moss development
    - C) Canopy closure

ANSWERS

1. C 2. C 3. B