Research Report

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Using air photos to interpret quality of Marbled Murrelet nesting habitat in south coastal British Columbia

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Abstract

Reliable habitat assessment methods are needed to ensure the adequate management of Marbled Murrelet (*Brachyramphus marmoratus*) habitat in British Columbia. In two south coastal study regions, the Sunshine Coast and Clayoquot Sound, we evaluated the effectiveness of a qualitative habitat classification that uses air photo-interpreted forest structural characteristics for identifying and ranking habitat quality. Using a sample of 118 nest sites and 157 random sites within forests greater than 140 years old, we found that murrelets selected nest patches non-randomly with respect to forest characteristics. While selectivity varied between study regions, generally nest patches had taller and larger trees, exhibited more complex forest structure, and were located at lower meso-slope positions near large gaps or nearby edges. In addition, these patches were more often ranked higher in terms of habitat quality. However, we found that probable breeding success was greater in habitats classified as lower quality. Thus, further research is needed to understand our findings relative to other influences on breeding productivity, such as predators and hierarchal habitat selection. In summary, while our study supports the use of the current air photo habitat classification standards to improve identification and selection of murrelet nesting habitat for management, some modifications to these standards may be needed.

KEYWORDS: *air photo interpretation,* Brachyramphus marmoratus, *British Columbia, habitat management, habitat quality, habitat quality classification, habitat selection, Marbled Murrelet.*

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Introduction

The Marbled Murrelet (*Brachyramphus marmoratus*) is an Alcid seabird whose nesting habitat occurs in the older forests of coastal areas ranging from northern California to Alaska (Nelson 1997; McShane *et al.* 2004). Large, mossy tree branches (i.e., > 15 cm diameter), characteristic of older forests, provide nest platforms typically used by the murrelet (Ralph *et al.* 1995; Nelson 1997; Manley 1999). The loss of breeding habitat caused by the harvesting of these forests is identified as an immediate threat to the population of this species—the murrelet is officially listed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (2000). Therefore, the Province of British Columbia has prioritized management of murrelet nesting habitat (British Columbia Ministry of Water, Land and Air Protection 2004).

Directly managing known nesting habitat of this secretive bird is not feasible in British Columbia. Individuals are spread thinly throughout their extensive range (up to 50 km inland along most of the coastline; Burger 2002) and cannot easily be confirmed to use particular forest stands. Instead, management focusses on retention of potential suitable nesting habitat (British Columbia Ministry of Water, Land and Air Protection 2004). Accurate mapping of this habitat will help ensure that the Marbled Murrelet is adequately managed while reducing the potential for conflicts arising from multiple resource use. Tools such as air photos are recommended to help produce reliable and accurate habitat maps (British Columbia Ministry of Water, Land and Air Protection 2004).

Vegetation inventory maps derived through air photo interpretation are often used to describe wildlife habitats (e.g., Dussault *et al.* 2001; Boyce *et al.* 2002). Similarly, British Columbia vegetation inventory maps (Resource Inventory Committee 2002) are used to model wildlife habitat, including Marbled Murrelet habitat (Burger 2002). However, this vegetation cover information may not necessarily provide forest characteristics (such as those related to structural complexity) important for assessing murrelet habitat, or be delineated at a scale consistent with murrelet habitat use (Waterhouse *et al.* 2002). Addressing these concerns, Donaldson (2004) developed standard methods for directly interpreting air photos. These methods are used to identify and map occurrence of murrelet nesting habitat and to produce habitat maps.

Accurate mapping of suitable nesting habitat will help ensure that the Marbled Murrelet is adequately managed while reducing the potential for conflicts arising from multiple resource use.

Forest characteristics described on air photos are thought to be associated with murrelet nest structures, stand access, predator avoidance, and thermoregulation (Waterhouse *et al.* 2002; Waterhouse *et al.* 2004). Both traditional forest inventory variables (i.e., Tree Height, Crown Closure, and Vertical Complexity) as well as some novel variables specific to Marbled Murrelet life history requirements (i.e., Meso-slope, Gaps, Canopy Complexity, and Large Trees) are used in the standards (see Table 1) and assessed collectively to classify habitat quality (i.e., ranked very high to nil) (Donaldson 2004). This qualitative habitat classification follows the recommendations of the Canadian Marbled Murrelet Recovery Team (CMMRT) (2003). Habitats classified as higher quality are expected to have greater likelihood of use. Relative to lower quality habitats, they are thought likely to support a greater density of murrelets on a per-hectare basis if murrelets select nest sites independently of how habitat is spatially distributed (Burger 2004; Stauffer *et al.* 2004). The air photo method assesses habitats at the patch and stand level only. It does not incorporate a multi-scale pattern of habitat selection (Orians and Wittenberger 1991; Manly *et al.* 2002), although landscape (Meyer *et al.* 2002; Zharikov *et al.* 2006, 2007) and nest tree characteristics (Manley 1999) are also thought to influence nest-site selectivity. Nor does it directly account for factors external to forest structure that might influence habitat use, such as predators (Thomson 2006).

We focussed this study on forests greater than 140 years old (Forest > 140 years old) using a sample of 118 nest sites previously collected by telemetry methods from 1998 to 2002 in two regions in southern British Columbia: the Sunshine Coast and the west coast of Vancouver Island (Bradley 2002; Bradley *et al.* 2004; McFarlane Tranquilla *et al.* 2005).

TABLE 1. Airphoto interpretation method: variables described at 100-m-radius plots centred on the murrelet nest sites and random sites (adapted from Donaldson [2004] and Waterhouse *et al.* [2004])

Variable	Variable classes and definitions of classes
Airphoto Habitat Quality	• **High:** Forest > 28 m tall and ≥ 250 years old. Includes: – *Very High: Abundant large trees and large crowns, and excellent canopy structure; best habitat in study area.* – *High: Common and widespread large trees; very good canopy structure.* • **Moderate:** Forest usually 19.5–28 m tall and Forest > 140 years old; large trees with good crowns present, but patchy distribution. • **Low:** Includes: – *Low: Forest generally > 19.5 m tall or Forest > 140 years old; patchy and sparse large trees; poor canopy structure.* – *Very Low: Stands generally < 140 years old and < 19.5 m tall; large trees and complex canopy structure are sparse or absent.* – **Nil: (did not apply to our sample)*
Forest Cover (> 140 years old)[a]	• Proportion (%) of plot with Forest > 140 years old thought to provide potential nesting habitat. We infer if plots have < 100% cover that the nest site is closer to an edge.
Forest Cover (≤ 140 years old)[a]	• Proportion (%) of plot with Forest ≤ 140 years old, excluding non-vegetated and vegetated but non-treed portions of plot. We infer edges resulting from disturbance (e.g., clearcut or fire) from this variable.
Non-vegetated Cover[a]	• Proportion (%) of plot non-vegetated and non-treed. We infer natural edge owing to topography (e.g., rock outcrop) from this variable.
Vegetated Cover[a]	• Proportion (%) of plot vegetated but non-treed. We infer natural edge owing to disturbance or topography (e.g., avalanche chute) from this variable.
Tree Height	• Average estimated height (m) of the dominant, co-dominant, and high intermediate trees for the upper tree layer (Resource Inventory Committee 2002).
Large Trees	Dominant trees with large crowns ≥ 5 m above the canopy of the main stand. • **Prevalent:** > 20% of stems are above main canopy. • **Sporadic:** 3–20% of stems are above main canopy. • **None:** < 3% of stems are above main canopy. ** For testing mid-rearing success, the Sporadic and None classes combined or test invalid.*
Canopy Complexity	Estimate of overall variability of canopy structure and the distribution and abundance of large crowns and canopy gaps created by local topography (e.g., slope, hummock, and streams), vertical complexity, and (or) past stand disturbance (standing dead or down trees). • **High:** Well-distributed big crowns and canopy gaps creating a heterogeneous horizontal layer; optimum crown closure typically 40–60%. • **Moderate:** Fewer scattered large crowns. Varying numbers of canopy gaps, either well distributed or clumped, which result in greater variability in crown closures—typical range is 30–70%. • **Low:** Few or poorly distributed visible large crowns and closed forest with few canopy gaps (usually high crown closure), or few large crowns, but forest predominantly open (gappy, usually low crown closures).
Vertical Complexity	Describes uniformity of the forest canopy by considering estimates of the total difference in height of leading species and average tree layer height and gappiness. Three classes applied to the sample (Resource Inventory Committee 2002). • **Uniform:** 11–20% height difference. • **Moderately Uniform:** 21–30% height difference. • **Non-Uniform:** 31–40% height difference.

TABLE 1. Continued

Variable	Variable classes and definitions of classes
Large Gaps	Significantly visible openings (≥ 1 tree length wide) within the canopy. • **Present:** Occupies ≥ 5% of plot. • **None:** Occupies < 5% of plot.
Small Gaps	Smaller openings (< 1 tree length wide) within the canopy. • **Sporadic:** Gaps usually occupy 5–40% of plot, if applies includes None (< 5% of plot). • **Prevalent:** Gaps usually occupy > 40% of plot.
Ranked Crown Closure	Follows recommendations of the Canadian Marbled Murrelet Recovery Team (2003). Percent estimate of the vertical projection of tree crowns (upper layer) upon the ground (Resource Inventory Committee 2002), classified as: • **Most Likely:** 1 = 36–65% • **Moderately Likely:** 2 = 66–75% and 26–35%. • **Least Likely:** 3 = < 26% and > 75%. * *For testing mid-rearing success the Moderate and Least Likely classes combined or test invalid.*
Meso-slope	Relative position of plot within the local catchment area (~30 to 300 m vertical difference) (Luttermerding *et al.* 1990). • **Low:** Lower slope includes toe and flat. • **Mid:** Mid-slope. • **Upper:** Upper slope.

[a] From a measurement perspective, the cover estimates are not independent variables, because they are dependent on one another with their composition adding to 100%. We opted to treat these estimates as independent because they are evaluated separately and transformations would complicate their interpretation. They are not combined for analyses.

Our objectives were two-fold.

1. To test the effectiveness of both the individual air photo-interpreted forest characteristics and the habitat quality classification for predicting Marbled Murrelet resource selection (i.e., in terms of nest-site usage and nesting success) within Forest > 140 years old. We hypothesized that Marbled Murrelets have specific nest-site requirements (Cody 1981), and therefore they select nest sites that maximize breeding success and favour higher fitness (Van Horne 1983; Martin 1992). We limited our study to samples within Forest > 140 years old because other studies have already confirmed these older forests as the most probable habitat (Nelson and Hamer 1995; Burger 2002; Canadian Marbled Murrelet Recovery Team 2003). Therefore, we focus on structural differences of nesting habitat within these older forests rather than on age differences.
2. To evaluate which forest characteristics interpreted on air photos influence the classification of habitat quality, and whether these characteristics corresponded to the variables that best predict Marbled Murrelet resource selection. Where they did not, we recommend adjustments to the classification.

Study Areas

We analyzed data from three study areas identified by nearby ocean features. Desolation Sound and Toba Inlet are adjacent to and located on the Sunshine Coast at approximately 50°50' N, 124°40' W. Clayoquot Sound is located on the west coast of Vancouver Island at approximately 49°12' N, 126° 06' W.

The Sunshine Coast region includes three biogeoclimatic zones: the Coastal Douglas-fir (CDF), the Coastal Western Hemlock (CWH), and the Mountain Hemlock (MH) (Meidinger and Pojar 1991; Green and Klinka 1994). The forests are fragmented by mountainous topography, including steep cliffs and avalanche chutes (Zharikov *et al.* 2006). They are highly modified by ongoing harvesting activities, which date back to the early 1900s, fire disturbance, particularly in drier ecosystems, and some wind disturbance. Human and natural disturbances are more extensive at lower elevations, and they affect a larger proportion of Desolation Sound than Toba Inlet.

Forests around Clayoquot Sound are dominated by the wetter variants of the CWH zone and the MH zone including hypermaritime variants in the CWH zone on the outer coast (Meidinger and Pojar 1991; Green and Klinka 1994). Relative to forests on the Sunshine Coast, forests at Clayoquot Sound have incurred little disturbance. A portion of Clayoquot Sound overlaps the Vancouver Island Mountain Range (Strathcona Park); therefore, some forests in Clayoquot Sound are topographically fragmented. Forests on the windward side of the range (i.e., adjacent to the coast) are relatively continuous and pristine.

Methods

Sampling

Nests were located by tracking of radio-mounted birds, from 1998 to 2001 on the Sunshine Coast, and from 2000 to 2002 on the west coast of Vancouver Island (Bradley *et al.* 2004; McFarlane Tranquilla *et al.* 2005; Zharikov *et al.* 2006). Figure 1 shows an example of such nesting habitat and Figure 2 shows nest details.

Nest samples from different years were combined on the assumption that habitat selection at the scale we tested was not detectably affected by potential inter-annual variation of other factors (e.g., forage and climate, but see McFarlane Tranquilla *et al.* 2005). In our analyses of nesting success, we used mid-rearing success, determined from daily visitation activity by radio-marked birds at 10 days or later through the nesting stage (Bradley *et al.* 2004; Zharikov *et al.* 2006). We could not use fledging success because direct inspection of nest sites after breeding was biased due to limited ground access at many of the sites (Bradley *et al.* 2004).

Each study area was defined by delineating a minimum convex polygon encompassing known nest sites plus a 5-km external buffer. The buffer was approximately double the mean inter-nest distance for the study areas (see Zharikov *et al.* 2006), ensuring that we could obtain a sample of random sites in Forest > 140 years old that was at least equal to the number of nest sites.

Forest characteristics were estimated within 100-m radius plots centred on nest sites and random sites. Random sites were chosen from a set of points randomly located such that a minimum spacing of 600 m between points was maintained. This spacing provided for potential use of larger plots (e.g., 300-m radius plots) during future research (Waterhouse *et al.* 2004). Murrelet usage of random sites was unknown; therefore, our comparison was between used sites to those available, rather than the more powerful contrast of used versus unused sites (Manly *et al.* 2002).

Conrad Thiessen

FIGURE 1. Daniels River nest location. All nest sites located by radio-tracking in Desolation Sound, Clayoquot Sound, and Mussel Inlet can be viewed at: ***http://www.sfu.ca/biology/wildberg/mamuweb/welcome.htm***

Tom Ainsworth

FIGURE 2. Marbled Murrelet nest cup located at Daniels River.

Nest sites and random sites were situated in a range of elevations that varied among the three study areas from valley bottom to old scrub forest near the tree line. At Clayoquot Sound, nests ranged from 29 to 1191 m and random points from 27 to 1152 m; at Desolation Sound, nests ranged from 132 to 1386 m and random points from 60 to 1388 m; and at Toba Inlet, nests ranged from 6 to 1048 m and random points from 31 to 1600 m elevation. Elevation can influence stand structures such as tree height. By conducting a Kolmogorov-Smirnov goodness-of-fit test (D'Agostino and Stephens 1986), we therefore assessed whether the distribution of random points in each 100-m elevation contour was representative of area of Forest > 140 years old available within the same contour for each study area. Results indicated the elevational distributions of random points were representative of available area of Forest > 140 years old (Clayoquot Sound: $n = 17$ contours, $P = 0.45$; Desolation Sound: $n = 19$ contours, $P = 0.99$; Toba Inlet: $n = 19$ contours, $P = 0.53$).

Habitat Assessments

Thirteen variables, including a composite "Habitat Quality", were assessed by a certified photo interpreter (Table 1). Assessments were undertaken by first centring a 100-m radius plot on the site and estimating the proportions of Forest Cover > 140 years old, Forest Cover ≤ 140-year-old, Non-vegetated Cover, and Vegetated Cover (Table 1). Each of the other nine variables was then interpreted only for the portion of the plot classified as Forest Cover > 140 years old. Variables were either assigned an average value (i.e., Tree Height) or a class representing the average condition of the Forest > 140 years old (including Habitat Quality, Vertical Complexity, Canopy Complexity, Meso-slope, Large Trees, Large Gaps, Small Gaps, Crown Closure). Although some plots had less than 100% of Forest Cover > 140 years old, the values of the interpreted variables are not affected by the reduced area because air photo-interpreted plots of 3 ha or less in these coastal forest types are relatively homogenous. We used mid-scale (i.e., 1:10 000–1:20 000) air photos, mostly colour but some black and white, that were taken closest to the study year. For categorical variables with sparse representation, classes were combined—to facilitate statistical analyses—if the same trends and interpretation for the separate classes were indicated during preliminary analyses. Our results are limited to the interpretation of the variables with combined classes.

Statistical Analyses

Analyses were undertaken using SAS 9.1 (SAS Institute Inc. 2003). Unless specified otherwise, we evaluated for significance using $\alpha = 0.10$.

Predicting Resource Selection or Habitat Quality Class

First, we tested each air photo variable (Table 1) to determine whether the variable was associated with nest sites selected by murrelets (i.e., differences in Site Type: nest vs. random) as well as the association between these variables and Mid-rearing Success (i.e., differences between failed versus successful nest sites). We maintained Study Area and its interaction with Site Type (or Mid-rearing Success) as factors. In general, selectivity for a variable is inferred in our study if nest sites disproportionately occur in a particular class (or have greater amounts) of a variable relative to its availability; while avoidance is inferred if their occurrence is disproportionately less (or amounts lower) relative to availability (see Jones 2001; Manly *et al.* 2002). Mid-rearing Success is similarly interpreted, but using proportions of successful versus failed nest sites.

To test which variables differentiated between the three habitat quality classes, we pooled all samples, because application of the standard methods does not differ between type of site and study area. We also excluded from these tests the four cover variables (i.e., Forest Cover >140 years old, Forest Cover ≤140 years old, Vegetated Cover, and Non-vegetated Cover) because they are not used to classify Habitat Quality.

We analyzed continuous variables using an unbalanced, ranked analysis of variance (ANOVA), or fitted proportional odds regression models for ordinal variables, and polytomous logistic regression models for nominal variables (Agresti 1996). If the proportional odds assumption (e.g., parallel lines) was violated, an ordinal variable was then treated as nominal. If significant interactions occurred between Study Area and Site Type (or Mid-rearing Success), then we re-ran the analysis within each study area. For the polytomous and proportional odds models, we collapsed the models by first removing the interaction term if non-significant, then by removing Study Area if non-significant.

We assessed significant pair-wise differences for Study Area and Site Type (Mid-rearing) or Habitat Quality class by using custom contrasts that were functions of:

- the unranked-data, least-squares means (LSmeans) when using ANOVA; or
- predicted probabilities (Prob) when using logistic regression.

For categorical variables, the predicted probability represents the chance that an observation belonging to a specific class (e.g., Moderate Habitat Quality) will fall into one of the variable's categories (e.g., High Canopy Complexity). For the nominal logistic regression models, the predicted probabilities are identical to sampling proportions; however, for the proportional odds regression models, they will be slightly different due to the imposed model structure.

Determining Best-fit Predictor Models

We used Akaike's Information Criterion (AIC_c), adjusted for small samples, and Akaike weights (ω), to select models and identify which variables best predicted Site Type (i.e., a Resource Selection Function) and the Habitat Quality Classification (e.g., Manly *et al*. 2002).

We reduced the number of sets of predictor variables for testing in the multivariate models by only using variables that had indicated significant differences in univariate tests described in the previous section. Next, to address the potential of multicollinearity, we determined the Spearman rank correlations (r_s) between continuous and (or) ordinal variables (potential if $P \leq 0.01$ and $r_s \geq 0.7$; Myers 1986); the Mantel-Haenszel statistic between ordinal and nominal variables (potential if $P < 0.0001$; Mantel and Haenszel 1959); and the general association Cochran-Mantel-Haenszel statistic between two nominal variables (potential if $P < 0.0001$; Mantel and Haenszel 1959). We retained one of two similar variables by choosing the one for which no interaction with Study Area was indicated and (or), if possible, the one correlated with fewer other variables.

In the Resource Selection Function modelling of Site Type (nest vs. random), Study Area was included as a main effect, and interaction terms were included if they had highly significant effect(s) ($P < 0.05$) during univariate tests. During modelling of categorical predictors, all dummy variables of a 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 has minimum AIC_C and highest weight. Akaike weights are interpreted as approximate probabilities of the model being the best from among those models examined (Anderson *et al.* 2000); models having scores differing by less than two units are considered equal (Burnham and Anderson 2001).

We evaluated each top model for:

- the influence of outliers (i.e., the influence of each removed observation on the overall change in the regression estimates) by using CBAR plots in SAS's PROC LOGISTIC; and
- multicollinearity by examining whether parameter estimates had reasonable and acceptable values of tolerance (> 0.5) and variance inflation (VIF < 2.0), using the REG procedure of SAS (SAS Institute Inc. 2003).

We initially evaluated fit of the multiple logistic regression by using the non-significant Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000) for Site Type and by using the Pearson heterogeneity factor, χ^2 (McCullagh and Nelder 1989) for Habitat Quality classification. We then further evaluated predictive performance for Site Type using a K-fold cross-valuation procedure (e.g., Boyce *et al.* 2002), which better reflects model fit under use–availability designs.

For the K-fold test, we first applied a linear stretch transformation (Lillesand *et al.* 2004) that rescaled the predicted Resource Selection Function values from the model into pseudo-probabilities (between zero and one), which we separated into 11 sequential bins of equal size ($n = 25$) that represented the range of predicted values. Next, we divided our data into five random subsets of equal sizes and re-estimated the model parameters five times—once for each combination of four subsets, with the fifth withheld, then used to predict the Resource Selection Function values in the re-estimated model. A Spearman rank correlation coefficient (r_s) was calculated between the original bin midpoints and the (average) relative frequency of nests per bin—calculated from the five re-estimated models. Strong positive correlations are considered to indicate good predictive performance because more nests fall in higher probability bins (Boyce *et al.* 2002).

Results

We assessed forest characteristics and habitat quality of 118 nest sites and 157 random sites using air photos (Table 2). The three study areas varied in area, representation of Forest > 140 years old, and representation of nest sites and random sites (Table 2).

Nest-Site Selectivity

Ranked Crown Closure, Forest Cover ≤ 140 years old, and Non-vegetated Cover did not differentiate nest sites from random sites (Table 3). Significant differences for Site Type were detected with the remaining variables, but they were inconsistent between study areas (Table 3).

TABLE 2. Areal and sample representation of Forest >140 years old for comparisons of Site Type (nest and random) and Mid-rearing (Success or Failure)

Study Area	Total area (ha)	Forest > 140 years old (%)	Site Type: Nest (no.)	Site Type: Random (no.)	Mid-rearing: Success (no.)	Mid-rearing: Failure (no.)
Clayoquot Sound	182 000	53	32	54	18	11
Desolation Sound	244 000	12	62	69	35	21
Toba Inlet	189 000	20	24	34	15	7
Total			**118**	**157**	**68**	**39**

TABLE 3. Tests comparing Study Area and Site Type using two-way ranked ANOVA, or collapsed proportional odds or polytomous logistic regression models (i.e., non-significant Interaction term removed and if non-significant Study Area effect removed)

Model type	Dependent variable	Study Area[a]	Contrasts[b,c]	Site Type[a]
Polytomous		χ^2, P, (4 df)		χ^2, P, (2 df)
	Large Trees	14.03***	TB = (DS ≠ CS)	19.22***
	Large Gaps	5.08*	(TB ≠ CS) = DS	41.11***
	Small Gaps	*See Table 4*		
	Vertical Complexity	15.14***	DS ≠ (CS = TB)	7.21**
	Meso-slope	*See Table 4*		
	Ranked Crown Closure	Not applicable		3.94
		χ^2, P, (2 df)		χ^2, P, (1 df)
Proportional Odds	Canopy Complexity	*See Table 4*		
	Habitat Quality	*Not applicable*		3.98**
ANOVA	Tree Height	*See Table 4*		
	Forest Cover > 140 years old	*See Table 4*		
	Vegetated Cover	*See Table 4*		
	Forest Cover ≤ 140 years old	0.60		3.20
	Non-vegetated Cover	4.27		4.94

[a] *$P \leq 0.10$, **$P \leq 0.05$, ***$P \leq 0.01$.
[b] Statistically significant (≠) contrasts between study areas using $\alpha = 0.0333$.
[c] CS = Clayoquot Sound; DS = Desolation Sound; TB = Toba Inlet.

We detected the fewest relationships indicating nest-site selectivity at Clayoquot Sound (Table 4).

Compared to random sites, nest sites in all study areas had, on average, significantly taller trees and higher probabilities of having Prevalent Large Trees and High Canopy Complexity (Figures 3a–3c). Nest sites were also more likely to occur in Low Meso-slope positions while Mid and Upper positions were avoided. However, significant effects were indicated only for Desolation Sound and Toba Inlet, not for Clayoquot Sound (Figure 3d, Table 4).

Nest sites compared to random sites at Desolation Sound and Toba Inlet also had significantly less Forest Cover > 140 years old (Figure 4a), while significantly higher amounts of Vegetated Cover were detected at Desolation Sound nest sites only (Figure 4b). Large Gaps disproportionately occurred at nest sites for all three study areas (Figure 4c), which contrasted with the disproportionately sporadic occurrence of Small Gaps (Figure 4d). Nest sites were more likely to be classified as Moderately Uniform for Vertical Complexity, and less likely to be classified as Non-Uniform compared to random sites (Figure 4e). These latter two findings are consistent where Non-Uniform sites should have Prevalent Small Gaps. Murrelets selected for nest sites as classified by Habitat Quality (Table 3). Nest sites occurred more often in High Quality habitats and less often in Low Quality habitats with Moderate Quality habitats used in proportion to its availability (Figure 4f).

TABLE 4. Tests comparing Site Type or Mid-rearing Success at each Study Area following significant interactions between Study Area. Tests are based on ranked ANOVA, proportional odds or polytomous logistic regression models with 1 degree of freedom

			Study Area		
Effect	**Dependent variable**	**Model type and test statistic**[a]	**Clayoquot Sound**	**Desolation Sound**	**Toba Inlet**
Site Type	Forest Cover > 140 years old	ANOVA F	0.50	17.60***	7.15**
	Vegetated Cover		2.47	14.20***	2.44
	Tree Height		7.26***	3.27*	19.60***
	Canopy Complexity	Proportional odds χ^2	0.41	20.13***	4.17**
	Small Gaps	Polytomous χ^2	1.54	4.51**	11.41***
	Meso-slope[b]		1.15	7.44**	11.76***
Mid-rearing Success	Non-vegetated Cover	ANOVA F	1.47	8.39***	0.10

a $*P \leq 0.10$, $**P \leq 0.05$, $***P \leq 0.01$
b 2 df this test.

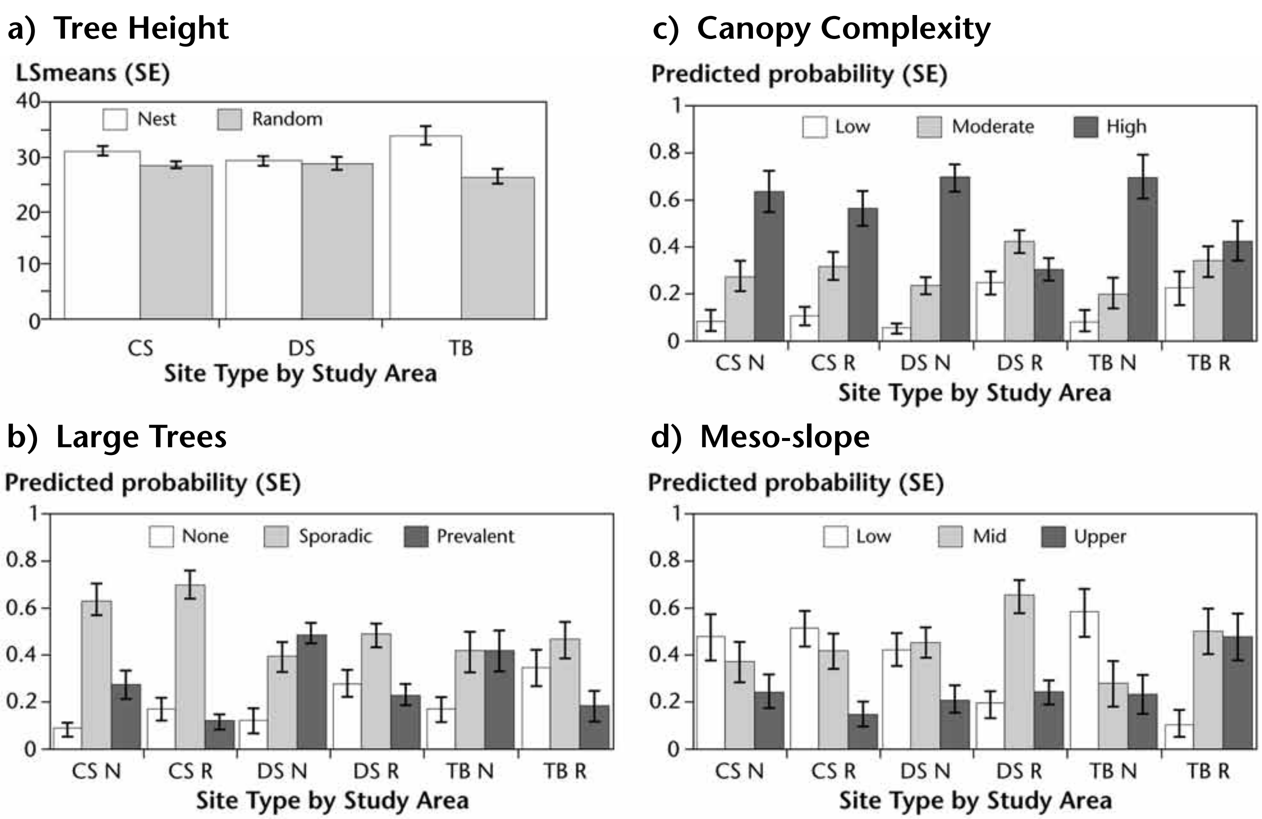

FIGURE 3. Least-square means (standard errors) of (a) Tree Height and predicted probabilities (standard errors) for occurrence of: (b) Large Trees; (c) Canopy Complexity; and (d) Meso-slope position for nest (N) sites and random (R) sites (Site Type) by Study Area (CS = Clayoquot Sound; DS = Desolation Sound; TB = Toba Inlet).

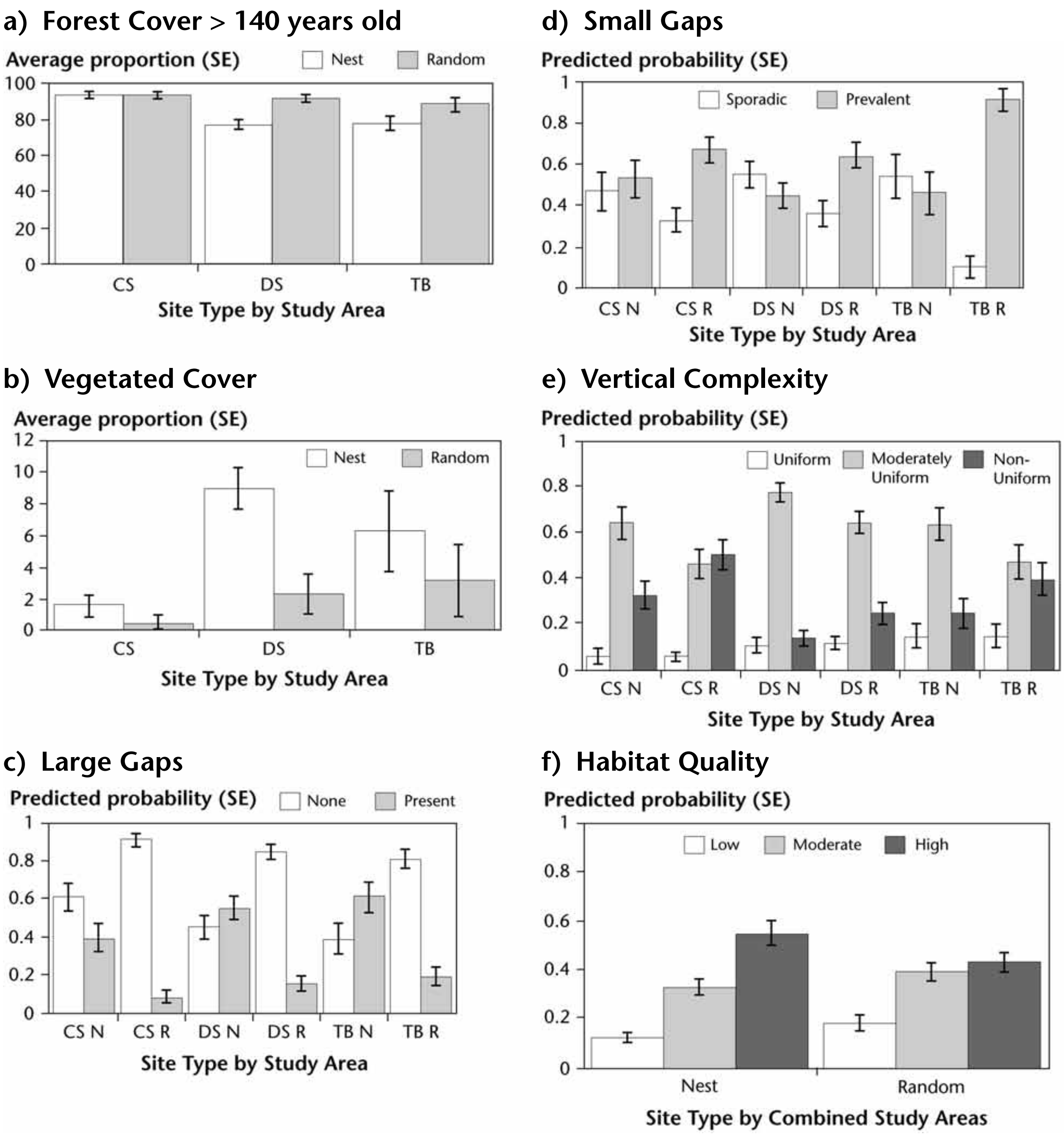

FIGURE 4. Least-square means (standard errors) of: (a) Forest Cover > 140 years old and (b) Vegetated Cover; and predicted probabilities (standard errors) for: (c) Large Gaps, (d) Small Gaps, (e) Vertical Complexity, and (f) Habitat Quality, for nest (N) sites and random (R) sites (Site Type) by Study Area (CS = Clayoquot Sound; DS = Desolation Sound; TB = Toba Inlet).

Nest-site Selectivity Resource Selection Function

For determining which variables might collectively best predict nest-site selectivity, we retained the following variables for model building: Forest Cover > 140 years old, Tree Height, Large Trees, Large Gaps, Small Gaps, Meso-slope, and the highly significant ($P < 0.05$) interaction terms between Study Area and Forest Cover > 140 years old, Tree Height, and Meso-slope. We excluded Vertical Complexity because of its potential collinearity with

Large Trees ($P < 0.0001$; i.e., fewer Large Trees as stands become Uniform), and we excluded Canopy Complexity for potential collinearity with Meso-slope ($P < 0.001$; i.e., Canopy Complexity decreases with Mid- to Upper slope positions). Vegetated Cover was excluded because a significant effect was indicated for Desolation Sound only (Table 4).

The best-fit top model of 280 possible combinations retained all variables, except the interaction term of "Study Area × Forest Cover > 140 years old" (Table 5). The next best model included this interaction term, and the AIC_c score differed by less than two which suggested the two models had similar predictive ability. We further evaluated the fit of the top model only (as the simpler of the two). We did not find that extreme outliers were indicated by the CBAR plots, or that Tolerance and VIF of parameter estimates supported potential collinearity within the model. The Hosmer and Lemeshow goodness-of-fit test ($\chi^2 = 12.35$, 8 df, $P = 0.14$) indicated the fit of the model was acceptable, and this result was supported by the K-fold cross-validation ($r_s = 0.94$, 1 df, $P < 0.0001$) indicating good predictive capacity. Based on the parameter estimates and significant chi-square tests of the model (Table 6), the model appears most applicable to Desolation Sound. Consistent with the univariate tests, it predicted that nest sites were more likely to occur in locations where small gaps are sporadic but where large gaps do occur and Large Trees are prevalent. In addition, nest sites were more likely to have less Forest Cover > 140 years old within a 100-m radius plot. The role of tree height also affected nest location, but its influence changed within a study area (i.e., based on the significant interaction).

TABLE 5. Number of parameters (K), Akaike Information Criterion (AIC_c), rescaled values (Δ_i) and weights (ω_i) indicating the three top-ranked models used to predict the dependent variable Site Type ($n = 274$)

Independent variables	K	AIC_c	Δ_i	ω_i
Study Area; Large Gaps; Small Gaps; Large Trees; Meso-slope; Tree Height; Forest Cover > 140 years old; Study Area × Meso-slope; Study Area × Tree Height	22	262.00	–	0.283
Study Area; Large Gaps; Small Gaps; Large Trees; Meso-slope; Tree Height; Forest Cover > 140 years old; Study Area × Meso-slope; Study Area × Tree Height; Study Area × Forest Cover > 140 years old	25	263.21	1.21	0.155
Large Gaps; Small Gaps; Large Trees; Tree Height; Forest Cover > 140 years old	11	264.84	2.83	0.069

TABLE 6. Binary logistic regression results for highest AIC_c-ranked model for predicting the dependent variable Site Type ($n = 27$, $\chi^2 = 113.30$, 16 df, $P < 0.0001$)[a,b]

Independent variable	Parameter estimate	Standard error	Wald χ^2	P
Intercept	1.21	2.76	0.19	0.66
Clayoquot Sound	1.54	3.32	0.22	0.64
Desolation Sound	5.03	2.99	2.82	0.09
Large Gaps, None	−3.03	0.55	30.64	< 0.0001
Small Gaps, Prevalent	−2.24	0.49	20.68	< 0.0001
Large Trees, None	−0.60	0.64	0.88	0.35
Large Trees, Prevalent	1.56	0.58	7.15	0.01
Meso-slope, Low	0.51	1.75	0.08	0.77
Meso-slope, Mid	0.08	1.35	0.00	0.96
Tree Height	0.15	0.10	2.21	0.14
Forest Cover > 140 years old	−0.04	0.01	8.68	0.003
Study Area × Meso-slope, Clayoquot Sound, Low	−3.24	2.01	2.58	0.11
Study Area × Meso-slope, Clayoquot Sound, Mid	−1.87	1.67	1.25	0.26
Study Area × Meso-slope, Desolation Sound, Low	1.36	2.05	0.44	0.51
Study Area × Meso-slope, Desolation Sound, Mid	0.03	1.58	0.00	0.99
Study Area × Tree Height, Clayoquot Sound	0.04	0.12	0.10	0.75
Study Area × Tree Height, Desolation Sound	−0.18	0.11	2.78	0.10

[a] All Wald tests are based on 1 degree of freedom.
[b] Test is based on the reduction in deviance between an intercept-only model and a model with all predictor variables included.

Successful Mid-Rearing Nest Sites

From the sample of 107 nest sites distributed over the three study areas (Table 2), we determined that 7 of 13 variables described sites more likely to be successful at mid-rearing stage (Table 7). Successful sites had significantly shorter trees and higher probabilities of Sporadic Large Trees; sites with taller trees and Prevalent Large Trees tended to fail (Table 7, Figures 5a and 5b). Success was more likely on Upper Meso-slopes and less likely on Mid Meso-slopes. Lower slopes showed no effect (Figure 5c). Successful nest sites also tended to be classified lower for Canopy Complexity, while nest sites with High Complexity more often failed (Figure 5d).

At Desolation Sound only, successful nest sites had significantly higher Non-vegetated Cover than failed sites. This trend was similar for Toba Inlet, but appeared opposite for Clayoquot Sound (Figure 5e). For all study areas, successful nest sites also appeared more likely to have some vegetated cover in the plot (Figure 5f). Nest sites in Non-Uniform Vertically Complex stands more often failed, while those in Moderately Uniform and Uniform stands more often succeeded at the mid-rearing stage (Figure 5g). Few nest sites were classified as Uniform ($n = 10$), and of these, none failed.

For the combined study areas, overall Habitat Quality produced an unexpected result: success at mid-rearing was less probable at High Quality sites than at Moderate and Low Quality sites, and although trends were similar among study areas, differences were least detectable at Toba Inlet (Table 7, Figure 5h).

Habitat Quality Classification

Predicting Habitat Quality Classes

Our tests confirmed that the three Habitat Quality classes significantly differed with respect to the representation and frequency of seven of the eight interpreted forest characteristics using the combined nest and random sites ($n = 275$). Sites classified as High usually contained taller and Large Trees, had High Canopy Complexity, and were located in Low Meso-slope positions (Table 8). Sites classified as Moderate tended to have mid-height trees and Large Trees and a mixture of Moderate to High Canopy Complexity, and they lacked a strong association with any one Meso-slope position (Table 8). Sites classified as Low had shorter trees and lacked Large Trees, had Moderate to Low Canopy and Vertical Complexity (i.e., tended to include Uniform stands), and often occurred in Mid to Upper Meso-slope positions. Furthermore, Low Quality sites exhibited a range of

TABLE 7. Final models comparing Study Area and Mid-rearing Success using two-way ranked ANOVA, or collapsed proportional odds or polytomous logistic regression models (i.e., non-significant Interaction term removed and if non-significant Study Area effect removed)

Model type	Dependent variable	Study area[a]	Contrasts[b,c]	Mid-rearing Success[a]
Polytomous		χ^2, P, (2 df)		χ^2, P, (1 df)
	Large Trees[d]	7.64**	CS ≠ (DS = TB)	4.01**
	Large Gaps	*Not applicable*		0.28
	Small Gaps	*Not applicable*		0.51
	Crown Closure	*Not applicable*		0.53
	Meso-slope	*Not applicable*		6.52**
Proportional Odds	Vertical Complexity	*Not applicable*		7.43*
	Canopy Complexity	*Not applicable*		5.57**
	Habitat Quality	4.56***	(DS = CS) ≠ TB	6.95*
		F, P, (2 df)		F, P, (1 df)
ANOVA	Tree Height	11.80***	DS ≠ CS ≠ TB	24.72*
	Forest Cover > 140 years old	6.37		2.22
	Forest Cover ≤ 140 years old	0.74		0.56
	Vegetated Cover	15.33***	(DS ≠ CS) = TB	17.10**
	Non-vegetated Cover	*See Table 4*		

[a] *$P \le 0.10$, **$P \le 0.05$, ***$P \le 0.01$.
[b] Statistically significant (≠) contrasts between study areas using α = 0.0333.
[c] CS = Clayoquot Sound; DS = Desolation Sound; TB = Toba Inlet.
[d] Large Trees 4 df for Study Area and 2 df for Mid-rearing Success.

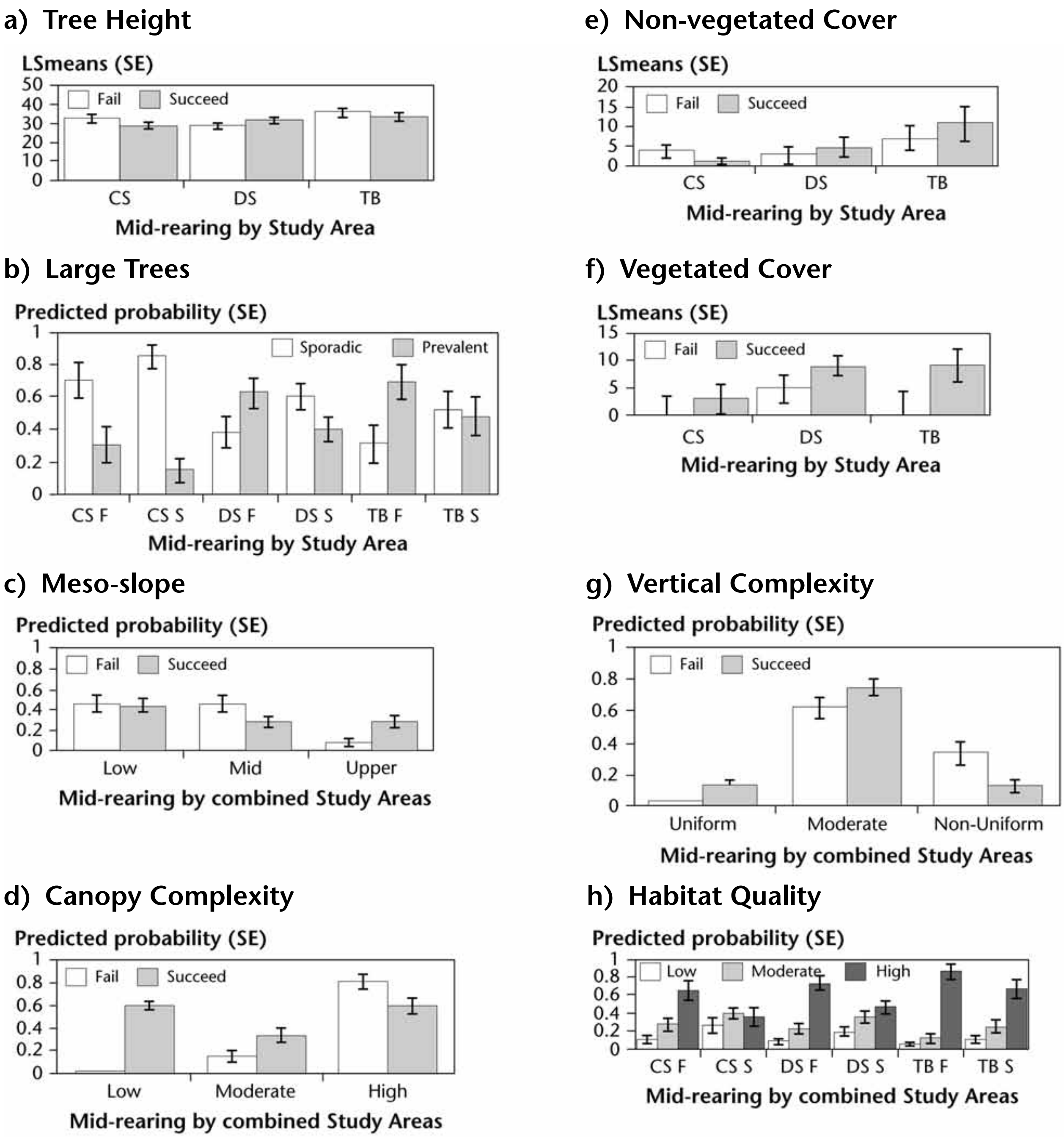

FIGURE 5. Least-square means (standard errors) of: (a) Tree Height; and predicted probabilities (standard errors) for occurrence of: (b) Large Trees, (c) Meso-slope position, (d) Canopy Complexity, (e) Non-vegetated Cover, (f) Vegetated Cover, (g) Vertical Complexity, and (h) Habitat Quality for failed (F) sites to successful (S) sites (Mid-rearing Success) for combined or each Study Area (CS = Clayoquot Sound; DS = Desolation Sound; TB = Toba Inlet).

crown closures (sparse to dense) and were associated with Large Gaps. Only one variable (Small Gaps) did not differ in its frequency between Habitat Quality classes (F = 2.35, 2 df, P = 0.31), which suggests this variable did not influence the ranking of sites.

We examined how forest characteristics could be combined to quantitatively describe the weightings and relationships considered in the qualitative habitat quality classification by building multiple regression models using Canopy Complexity, Large Gaps, and Tree Height. We

TABLE 8. Habitat variables significantly influenced by habitat quality classification, based on overall test of habitat quality class using ranked ANOVA or proportional odds or polytomous logistic regression models (n = 275)

Dependent variable	Levels of dependent variable	Overall test of habitat quality class[a]	Habitat quality class: High	Moderate	Low
		ANOVA F, P, (2 df)	LSMeans (SE)	LSMeans (SE)	LSMeans (SE)
Tree Height (m)	N/A	239.58***	33.8 (0.3)	27.4 (0.4)	20.2 (0.6)
		Proportional odds χ^2, P, (2 df)	Prob (SE)	Prob (SE)	Prob (SE)
Canopy Complexity	High	69.80***	0.78 (0.04)	0.37 (0.05)	0.15 (0.04)
	Moderate		0.18 (0.03)	0.45 (0.05)	0.43 (0.05)
	Low		0.03 (0.01)	0.18 (0.03)	0.42(0.07)
		Polytomous χ^2, P, (2 df)	Prob (SE)	Prob (SE)	Prob (SE)
Large Trees	None	34.89***	0.01 (0.01)	0.27 (0.04)	0.64 (0.07)
	Present		0.99 (0.01)	0.73 (0.04)	0.35 (0.07)
Vertical Complexity	Uniform	11.70**	0.04 (0.02)	0.12 (0.03)	0.21 (0.06)
	Moderately Uniform		0.62 (0.04)	0.62 (0.05)	0.55 (0.08)
	Non-Uniform		0.34 (0.04)	0.26 (0.04)	0.24 (0.07)
Large Gaps	None	11.43***	0.75 (0.04)	0.73 (0.04)	0.48 (0.08)
	Present		0.25 (0.04)	0.27 (0.04)	0.52 (0.08)
Ranked Crown Closure	Most	26.90**	0.86 (0.03)	0.68 (0.05)	0.43 (0.08)
	Moderate		0.13 (0.03)	0.20 (0.04)	0.26 (0.07)
	Low		0.01 (0.1)	0.12 (0.03)	0.31 (0.07)
Meso-slope	Low	40.35***	0.47 (0.04)	0.24 (0.04)	0.12 (0.05)
	Mid		0.46 (0.04)	0.44 (0.05)	0.38 (0.07)
	Upper		0.06 (0.02)	0.32 (0.05)	0.50 (0.08)

[a] *$P \le 0.10$, **$P \le 0.05$, ***$P \le 0.01$.

excluded Meso-slope, Large Trees, Vertical Complexity, and Ranked Crown Closure from the model because of high probability of association with Canopy Complexity ($P < 0.0001$). The best-fit predictive model of eight possible combinations ($k = 5$, $AIC_c = 250.327$, $\omega_i = 0.982$) included all three variables ($n = 275$, Reduction of Deviance $\chi^2 = 86.72$, 4 df, $P < 0.0001$, maximum rescaled $R^2 = 0.63$); however, it had a poorer than desirable fit based on a large heterogeneity factor (Pearson $\chi^2 \div$ df $= 3.6$), which indicated overdispersion possibly due to missing predictors or outliers. We examined the data for outliers and tried variations on the model, including fitting the alternate variables and Study Area, but could not improve model fit. This model suggested sites classified as higher quality had more complex canopies and taller trees, and that Large Gaps were absent.

Discussion

We used quantitative techniques to evaluate the effectiveness of the proposed standard methods for qualitative classification of Marbled Murrelet habitat using air photos (Donaldson 2004). First, we examined how well nest sites and a measure of their breeding success were predicted by photo-interpreted forest characteristics and an overall habitat quality classification. Then, we evaluated the effectiveness of the current classification for identifying nest habitat by comparing characteristics used in the classification to those which predicted nest-site selectivity.

Describing Nest-Site Selectivity from Forest Characteristics

Selection of nest patches (i.e., as represented by 100-m plots) by Marbled Murrelets was non-random. Marbled Murrelets selected for higher quality sites according to the ranked classification of Donaldson (2004). Using the nest-site selectivity Resource Selection Function, we demonstrated that quality of Marbled Murrelets nest sites is described by a suite of photo-interpreted forest characteristics—supporting the use of a habitat classification based on multiple forest characteristics.

Study area had an important influence on predicting the relationship between nest sites and habitat. Relationships were best described for the Sunshine Coast, particularly in the Desolation Sound area. We suspect selectivity for structural attributes may have been more easily detected on the Sunshine Coast because the availability of habitat was more limited, due to its past disturbance history and topography (Manly *et al.* 2002). Thus random sites would more often fall in poorer habitats on the Sunshine Coast compared to Clayoquot Sound with its extensive areas of available habitat. In addition, nest sites in Clayoquot Sound were biased towards later breeding birds that may be less experienced or more constrained in their site selection (McFarlane Tranquila *et al.* 2005). If late-nesters utilize nest sites of lower quality than early nesters, the Clayoquot Sound nest sample may under-represent use of high-quality habitat.

Using the air photo-interpreted variables, we confirmed that murrelet nesting habitats tend to be associated with more productive forest sites (Burger 2002; Rodway and Regehr 2002). Nest patches were selected that had taller trees and prevalence of Large Trees and higher Canopy Complexity. These structures may provide and (or) cue individuals into sites associated with adequate availability of nest platforms and variation in canopy structure for access and protective cover (Manley 1999; Nelson and Wilson 2002). We also detected selectivity for Low Meso-slope positions—which are often water-receiving, thus more productive for growing larger trees—while water-shedding upper slopes are usually less productive and grow smaller trees. Upper Meso-slopes could also be avoided by murrelets if they are wind-exposed and less habitable (Meyer *et al.* 2004).

The relationships we detected using the air photo-interpreted variables also support the suggestion that murrelets use sites that provide a balance between accessibility and cover (Manley 1999). On the Sunshine Coast, birds often selected for nest sites in closer proximity to edges (i.e., lower proportion of Forest Cover >140 years old and [or] in plots having Large Gaps); edges may provide flight access into the canopy or sub-canopy (Manley 1999, Bradley 2002). The higher representation of vegetated cover at these sites, instead of ≤ 140-year-old forest cover, also suggests these edges and gaps are mostly attributable to rock, windthrow, riparian areas, and avalanche chutes—the latter more typical of the Sunshine Coast. In contrast, nest sites were not selected with a prevalence of small gaps or non-uniform vertically complex stands that have more canopy openings and (or) poor stocking pattern (Resource Inventory Committee 2002). Instead, they were more likely to have sporadic small openings and be of Moderate Vertical Complexity. Moderate Vertical Complexity suggests some gaps and enhanced layering that potentially contributes to stand access and sub-canopy flight paths and development of large trees, while maintaining overstorey cover and thus providing protection to the nest. On the premise that murrelets seek a balance between access and cover, we would expect the role of small gaps for describing habitat may change in forests lacking large gaps and natural edges (see Waterhouse *et al.* 2007).

Classifying Habitat Quality of Nest Sites and Successful Mid-Rearing Sites

If murrelets behave adaptively and choose to nest in more productive habitat, we would expect consistent results for nest-site selectivity and breeding success (Jones 2001; Kristan 2003). Instead, the data from our study sites suggest that murrelets breed less successfully (at least to mid-rearing stage) in those sites for which we measured selectivity (i.e., High Quality sites and sites characterized by having higher value structure such as Prevalent Large Trees, taller trees, and High Canopy Complexity). However, our data suggest that murrelets choose and are successful at sites with characteristics associated with potential access to the nest site such as natural edge (inferred by Non-vegetated Cover or Vegetated Cover) and cover (i.e., as inferred by Moderate or Uniform Vertical Complexity). Predation is thought to be a main cause of murrelet nest failure (Nelson and Hamer 1995; Manley and Nelson 1999; Marzluff *et al.* 1999; Manley 1999; Raphael *et al*. 2002; Peery *et al.* 2004). We therefore hypothesize three predation-related reasons for our observed nonideal habitat selection (Arlt and Pärt 2007).

First, access into the stand and cover (from predators and for microclimate) are more important predictors of nest success than platform availability. Therefore, of the range of nest sites used by murrelets, those with access and cover are more likely to succeed.

Second, we may be observing hierarchal habitat selection (Manly *et al.* 2002) in which landscape-level selection for topographic features and older forest may supersede patch-level selection for specific forest structure characteristics. Studies by Bradley (2002) and Zharikov *et al.* (2006) that examined landscape-level selection using the same sample of nests from the Sunshine Coast, but different methods and variables (such as landscape metrics and forest age), found that successful mid-rearing nests had been initiated by earlier breeders and were associated with steeper locations at higher elevations. Bradley (2002) speculated that, on average, steeper locations at higher elevations may provide safer nests sites. The strong association of success with earlier breeders on the Sunshine Coast suggests that older birds disproportionately utilize safer sites, perhaps based on previous experience. In terms of our findings, forests at higher elevations and steeper locations will often have shorter trees (i.e., tree height is negatively correlated with elevation). Thus it is more likely that these sites would be classified as lower in habitat quality by air photo interpretation. But such sites may still contain more complex stand structure and larger trees relative to their topographic location and meet habitat needs of murrelets at the patch level.

Third, nest site selectivity may differ from productivity because murrelets are in an ecological trap—they select nest sites susceptible to failure owing to changes in external factors such as predators (Pulliam 1988; Kristan 2003). Greater predator distribution and densities along edge types associated with recent high levels of disturbance on the Sunshine Coast (Malt 2007) potentially support this hypothesis, but predator information is lacking for Clayoquot Sound. In addition, this study area has been less disturbed.

Given the inconsistency between the nest-site selectivity and mid-rearing findings and the uncertainties associated with covariance patterns of the latter (e.g., geographical attributes), we recommend continued evaluation of the effectiveness of the habitat quality classification based on the nest-site selectivity findings. This discussion assumes murrelets seek the best habitat available as described from patch-level forest characteristics, and ignores whether habitat quality or productivity may be altered by external factors such as predators (Kristan 2003). Consideration of a productivity component over and above selectivity awaits further delineation of geographical and landscape factors that may affect probable success in different areas (e.g., Malt 2007).

Refining the Habitat Quality Classification

The relatively small differences that we detected in the predicted probabilities between nest sites and random sites for Habitat Quality suggest that the classification methods may need refinement to improve predictability of nest habitats on air photos. Yet, we could not build a predictive model to determine how weightings were combined and assigned in the classification for the assessed variables. We suspect this poor fit may have occurred because the classification is applied using an informal decision-tree approach where some characteristics are considered based only on the occurrence of others. In other words, a linear model may not be sufficient to describe the intricacies of the classification process. For example, sites are usually first separated based on tree height because tree height can be most accurately evaluated by the interpreter. Then, depending on the height stratification, consideration is given to other characteristics such as crown closure. In this example, if the forests are shorter or younger, crown closure may be the next characteristic to be strongly considered because this characteristic can vary widely for these stands; whereas, if the forest is taller or older, crown closure may be only weakly considered because it tends to fall within the CMMRT's Most Likely category in these types of stands (A. Donaldson, pers. comm., January 2006).

Refining the standard methods criteria or weightings of criteria to tease out the few nest sites (14% of total) in the Low Habitat Quality class and reduce the number of sites in the Moderate class (30% of total; either by upgrading Moderate sites to High, or by downgrading to Low) would improve the overall effectiveness of the classification. After evaluating both the nest-site selectivity and Resource Selection Function results compared to the CMMRT (2003) recommendations (on which the classification is based), we suggest the following adjustments to the classification as applied within those ecosystems similar to those in our study areas:

1. give more weight to the prevalence of Large Trees and High Canopy Complexity, because size of trees relative to the overstorey canopy and occurrence of good canopy structure may be more important than tree height itself;
2. give a lower ranking to sites of Non-Uniform Vertical Complexity; and
3. do not rank habitats influenced by Large Gaps and natural edges lower if these features potentially provide for access and if cover is sufficient in the adjacent forest.

Management Implications

Recommendations

The results of our study lead us to make three main recommendations regarding the management of Marbled Murrelet habitat.

First, the nest-site selectivity Resource Selection Function confirmed that a suite of forest characteristics should be considered when classifying habitat from air photos, and that the quality of a potential site varies both with the weighting of these characteristics and the geographic location in which the habitat occurs. However, the nest site-selectivity Resource Selection Function developed for this study can not yet be directly tested or used for habitat mapping because we lack underlying databases with the same variables to model the function.

Second, the unexpected disparity between the attributes of selected nest sites and the attributes of successful mid-rearing nest sites suggests that biologists will need to further study how murrelets select habitats. More research is needed so that biologists can separate productive from non-productive habitat for murrelets (Marzluff *et al.* 1999; Malt 2007) and incorporate this information into land management.

Third, based on our findings we also suggest the standard methods need some flexibility. We recognize that some characteristics may differ in their utility because of differences in topography, disturbance history, biogeoclimatic ecosystem, or other factors. Although the general classification proposed by Donaldson (2004) is supported, it may be improved by:

- formalizing the approach for weighting the combined characteristics;
- adjusting how some characteristics are currently weighted in the classification (Tree Height) relative to others (e.g., Large Trees) at the same location;
- giving consideration to some additional characteristics (e.g., Large Trees); and
- combining Habitat Quality classes as in this study (i.e., Very High and High, and Low and Very Low) when seeking efficiencies in applying the air photo interpretation methods within the > 140-year-old forest stratum.

Challenges

One main challenge in further developing and applying the air photo habitat quality classification is that the lack of representation of any one particular characteristic within the > 140-year-old forest stratum may diminish, but not exclude, the potential suitability of a site for nesting habitat. Due to the multivariate nature of ecological relationships (Guénette and Villard 2004), species typically can occupy marginal habitats and rarely respond to occurrence of one variable. The nest-site selectivity Resource Selection Function accounts in part for this multivariate relationship by assigning a score that is proportional to the probability of use. However, we could not associate the habitat quality classes with a specific range of these scores, and the classes remain comparable only on a relative scale. Furthermore, no known relationship exists between habitat quality and occupancy such that a habitat quality threshold based on assessed characteristics can separate used from unused habitat (Burger 2004). In addition, the range of sites (Very Low to Very High) in which nesting murrelets were located in the study suggests the relationship is complex.

One main challenge in further developing and applying the air photo habitat quality classification is that the lack of representation of any one particular characteristic within the older forest stratum may diminish, but not exclude, the potential suitability of a site for nesting habitat.

One approach to addressing the unknown scale of the relative classes is to use expert opinion to choose an acceptable class threshold for defining suitable habitat. Currently for coastal British Columbia, land managers and biologists have informally considered all areas ranked Low to Very High on air photos as potential habitats. However, this approach ignores two findings:

1. that habitats of different classes have differing likelihoods of supporting a nesting murrelet; and
2. that a portion of the murrelet population will nest in habitats not captured by that threshold.

For example, in this study, nests were located over the range of habitat classes including the Very Low class. Even with improvements to the classification, we expect all potential nest habitats will not be distinguishable on air photos (Waterhouse *et al.* 2004); however, other efforts, such as ground surveys or low-level aerial surveys, could be undertaken to reduce uncertainty of whether suitable microhabitat structure occurs in areas ranked lower in quality on air photos (Resource Inventory Committee 2002; B.C. Ministry of Water, Land and Air Protection 2004; Burger *et al.* 2004a).

A second approach might be to use expert opinion to establish some relationship between density of murrelets and habitat quality class—for example, using a linear relationship in which density is proportional to habitat quality as indicated by radar work (Burger *et al.* 2004b); thus, more area of lower-ranked habitat would be set aside for the same number of birds managed in higher-ranked habitat. This approach would in part mitigate the risk that there is a lower likelihood of nest sites occurring in lower-quality habitats, and it would provide some flexibility in combining habitat areas to meet population targets.

Application of the Methods

We identify two uses for the information provided by the air photos habitat assessment methods. First, air photo interpretation can be directly applied using the standard methods to improve spatial accuracy of mapped polygons of suitable habitat, which are now produced by applying basic GIS habitat algorithms to forest cover maps. Second, information about the relative range of representation of differing qualities of habitat once mapped can be used to help identify candidate areas that meet different murrelet habitat management objectives (e.g., wildlife habitat areas; B.C. Ministry of Water, Land and Air Protection 2004).

Information about the relative range of representation of differing qualities of habitat once mapped can be used to help identify candidate areas that meet different murrelet habitat management objectives.

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Test Your Knowledge . . .

Using air photos to interpret quality of marbled murrelet nesting habitat in south coastal British Columbia

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. The Marbled Murrelet uses forests for:
   A) Foraging
   B) Nesting
   C) Both of the above

2. Which of these forest stand characteristics is thought to be associated with murrelet nesting habitat?
   A) Canopy complexity and vertical complexity
   B) Density of trees and snags
   C) Volume of downed wood

3. The air photo habitat classification can be used to improve identification of habitats for management of Marbled Murrelets and improve accuracy and reliability of habitat maps.
   A) True
   B) False

ANSWERS

1. B   2. A   3. A