MULTI-SCALE ANALYSES OF NEST SITE SELECTION AND FLEDGING SUCCESS BY MARBLED MURRELETS (*BRACHYRAMPHUS MARMORATUS*) IN BRITISH COLUMBIA

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ABSTRACT

I studied nesting habitat selection and fledging success by marbled murrelets, a seabird that nests in old-growth forests of high economic value, at two regions of southwestern British Columbia. At Clayoquot Sound, habitat occurs in larger stands, and murrelets selected steeper slopes and patches with more platform trees, and shorter trees, than at random sites. At Desolation Sound, where smaller forest stands predominate, patch scale variables were less important; increased canopy complexity in the patch, and wetter/cooler landscape aspects distinguished nests from random sites. In both regions, nests were often in “distinctive” trees, taller and with more potential platforms than others in the patch. Habitat features at multiple scales did not predict fledging success. Habitat quality as ranked by current remote methods (air photo interpretation, low-level aerial surveys) correlates with probability of use derived from stand-level habitat selection models, providing a quantitative assessment of their effectiveness as management tools.

Keywords: marbled murrelet; nesting habitat selection; Resource Selection Function; nest success; ground habitat plot; habitat suitability ranking;

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CHAPTER 1

PATCH SCALE NEST SITE SELECTION BY MARBLED MURRELETS (*BRACHYRAMPHUS MARMORATUS*)

1.1 Abstract

Marbled murrelet nests are difficult and costly to find. By using radio-telemetry of birds caught at sea, between 1998-2002 Simon Fraser University researchers located a sample of 157 Marbled Murrelet (*Brachyramphus marmoratus*) nests in two regions of southern British Columbia. I used ground habitat plots from these nest sites and a set of random habitat plots to describe nesting habitat selection for patch level habitat characteristics, using logistic regression models. These are the first for this species to use a relatively large sample of ground habitat plots and confirmed nest sites.

In the Clayoquot Sound region, density of platform trees and tree diameter have significant positive effects on the probability of nesting. Canopy height has a significant negative effect. In the more fragmented Desolation Sound, where most sites occurred in small patches (<300 ha), density of platform trees was not included in the best supported model. In both cases landscape-scale variables aspect and slope have positive effects in the models, while elevation has a neutral influence within the range 0–1210 m. For the first time, these models allow for habitat to be ranked according to the probability of use for nesting based on patch-scale variables measured on the ground. Ground-based habitat plots are expensive to carry out and inherently biased by limited accessibility to large portions of nesting habitat. The models presented here are therefore envisioned as a base

for validating remote methods (air photo interpretation and low-level aerial surveys) used to rank potential murrelet habitat for management, as well as provide a better understanding of how the probability of use varies with certain key patch scale habitat features such as the density of platform trees.

1.2 Introduction

The Marbled Murrelet (*Brachyramphus marmoratus*) is a northeastern Pacific seabird that in British Columbia depends almost exclusively on coastal old-growth forest for nesting habitat (Nelson 1997, Burger 2002). The species is classified as "threatened", listed under the Species at Risk Act in Canada and is currently afforded similar status in the United States. Loss of nesting habitat due to logging is considered one of the leading causes of population declines (Canadian Marbled Murrelet Recovery Team 2003). Identification and maintenance of quality nesting habitat is therefore a priority for conservation of the species (Burger 2002).

Current management guidelines for the conservation of marbled murrelet populations in British Columbia focus on protecting nesting habitat. Given the commercial value of timber in marbled murrelet habitat, there is major economic incentive to identify and protect habitat with the highest probability of use and nesting success. It is therefore important to identify forest structure components selected by marbled murrelets as well as how those components influence nest success. Due to the large area and often inaccessible nature of most of the potential murrelet habitat in the province, it is also important to develop efficient, relatively low-cost methods to identify suitable habitat remotely on a large scale. Current methods involve airphoto interpretation and low-level aerial surveys (Waterhouse et al. 2002, 2004, 2008, 2009).

Understanding characteristics of suitable nesting habitat for marbled murrelets is hampered by the extreme difficulty of locating nests. Nests are established primarily on platforms created by moss or duff on large branches of old growth conifers (Hamer and Nelson 1995, Nelson 1997). In British Columbia, these structures occur in stands at least 140 years old, and usually >200 years (Burger 2002). Nests occur at very low density (Conroy et al. 2002) over extensive tracts of often steep inaccessible terrain, making ground-based search methods impractical for large-scale application.

Audio-visual detections of behaviour associated with nest sites ("occupied detection", Paton 1995) are commonly used to assess habitat use (i.e., Hamer 1995, Kuletz et al. 1995, Rodway and Regehr 2002, Bradley et al. 2004), habitat selection (Hamer et al. 2008), or direct searches for actual nests (Manley 1999). Habitat inferences based on this method are limited because actual nest sites are not identified and success is unknown; occupied detections may involve prospecting behaviour, and detections can be biased towards gaps or edges where detections are more likely (Burger et al. 2000, Rodway and Regehr 2002).

Understanding habitat selection by marbled murrelets is essential to develop biologically meaningful habitat suitability models for management of forest nesting habitat. Evidence for habitat selection is based on disproportionate use of resources relative to their abundance (but see Van Horne 1983, Railsback et al. 2003). Selection, therefore, involves a comparison of ‘used’ to either ‘unused’ or ‘available’ habitat (Manly et al. 2002). It is not always possible to identify unused habitat; such is the case for the Marbled Murrelet, a species for which nests are difficult to locate and absence cannot, therefore, be readily confirmed. An alternate study design, by which relative probabilities of use may be determined, involves comparing used habitat to a set of random samples of available habitat (Manly et al. 2002).

In studies of habitat selection, it is important to carefully define available habitat at the appropriate scale (Johnson 1980, Jones 2001, Meyer 2007). Studies that address multiple scales are likely to yield more accurate and useful results (Meyer and Thuiller 2006, Meyer 2007). Scale-dependent habitat selection may be manifested in two ways, both of which affect availability: through hierarchical decisions and through hierarchical habitat structure. Habitat selection at one scale (i.e. nest tree) may be constrained by selection decisions already made by the species at coarser scales (i.e. territory, Johnson 1980, Jones 2001). In considering nest tree selection, available sites are limited by landscape-level decisions. Habitat itself may be structured hierarchically, such that features are correlated between scales (Kristan 2006). For example, selection for a specific structure within a tree may occur at the element (nest tree) scale. Distribution of that structure depends on the availability of suitable trees at the patch scale (here defined as ~0.2-2 ha area of forest), and landscape factors (i.e., elevation, moisture regimes) that affect distribution of suitable trees. Selection observed at one scale may therefore be a result of selection at smaller scales.

Previous studies of marbled murrelets have either used indirect evidence of nesting to infer habitat associations at the patch level, or employed remote methods (GIS, airphoto interpretation or low-level aerial surveys) to study habitat selection at larger scales. Studies of ground variables at the patch level (Hamer and Nelson 1995 range-wide, Hamer 1995 for Washington, Kuletz et al. 1995 for Alaska, Rodway and Regehr 2002 for Vancouver Island, Bahn and Newsom 2002b, Burger and Bahn 2004) compared occupied to unoccupied stands, identified through audio-visual detections, using forest variables measured in those stands. Bahn and Newsom (2002b) compared known habitat indicators to mapped forest variables to create a habitat suitability model that has recently tested favourably against a sample of known nests from the same area (V. Bahn, Wright State University and D. B. Lank, Simon Fraser University, personal communication). Studies using the nests located with radio-telemetry have investigated habitat selection and success at the patch level (using airphotos, Waterhouse et al. 2002, 2004), landscape level (Using GIS, Zharikov et al. 2006, 2007) and across scales (using low-level aerial surveys; Waterhouse et al. 2009). Manley (1999) used audio-visual detections and intensive ground surveys to locate real nests, comparing habitat variables at nest sites to those at random sites within the same patch.

Though results differ in some respects, five variables emerge from previous work as important marbled murrelet nesting habitat indicators at the stand level: mean diameter at breast height (DBH), density of large trees, density of potential platforms, and density of trees with platforms and canopy variation or complexity. At the landscape level, nests tended to be located on north aspects (F. H. Huettmann, University of Alaska- Fairbanks, unpublished data) and steeper slopes (Zharikov et al. 2006). Bradley (2002) and subsequent analysis (Zharikov et al. 2006, Zharikov et al. 2007) found that nests at higher elevations and on steeper slopes were associated with higher nest success. Results on habitat preferences with respect to elevation have been less consistent; while many studies have found preference for lower elevations, analysis of the nest dataset used here for Desolation Sound has produced conflicting results (Burger 2002).

In this study, I investigate nest site selection by marbled murrelets for stand-level variables across the landscape. Many of the studies mentioned above have described differences in habitat between used and either non-used or random sites. Although this design allows for analysis of habitat selection (Jones 2001), quantitative models are needed to determine probabilities of stand use and rank habitat since presence is impractical to confirm for all possible areas. In this study, I develop Resource Selection Functions (RSF; Manly et al. 2002), yielding an RSF score that is proportional to the probability of use for nesting. These models also show how the probability of use changes with habitat variables. The contribution of certain habitat features may be non-linear, resulting in 'thresholds' that may be used to refine existing habitat suitability rankings based on remote methods (low-level aerial surveys and airphoto interpretation; Canadian Marbled Murrelet Recovery Team 2003).

Finally, I investigate differences in habitat selection with patch size, as it may explain regional differences. Nesting data were available from two areas that differ in the extent of harvest of old growth forest. With commercial logging concentrated on more accessible valley bottoms, much of the remaining old growth forest habitat at one site, Desolation Sound (DS) is on steeper slopes or at higher elevations (Burger 2002), and is often very fragmented, while forests at Clayoquot Sound (CS) are more contiguous. It is reasonable to expect that the differing availability of potential nesting habitat will affect habitat selection observed in the two study regions, with selection for patch-scale variables dependent on the amount of available habitat.

1.3 Methods

1.3.1 Study area

This study took place in two regions on the southern coast of British Columbia, Canada that have large populations of marbled murrelets (Burger 2001, Hull et al. 2001): Clayoquot Sound (CS; 49°12’ N, 126°06’ W) on the west coast of Vancouver Island and Desolation Sound (DS; 50°05’ N, 124°40’ W) on the mainland (Figure 1.1). Both regions are mountainous, with forest cover naturally fragmented by steep topography, fjords and stream channels. Clayoquot Sound has a cooler and wetter maritime climate than Desolation Sound, with mean summer (April-August) temperatures of 11.9° and 13.4° C, rainfall of 720 mm and 300 mm, respectively. The two regions also differ in their extent of old growth forest loss, with over 80% loss of original old growth forest cover at Desolation Sound, compared to ~25% loss at Clayoquot (Zharikov et al. 2006). In both regions, human settlement is limited and habitat loss is mainly due to commercial logging in the last century.

1.3.2 Data sources

Nest habitat plots were collected by ground crews at nest sites located by radio telemetry at Desolation Sound (1999-2001; n = 43) and Clayoquot Sound (2000-2002, n = 27). Birds were captured at sea during the breeding season and fitted with radio transmitters. Radio frequencies were monitored from a helicopter, and when positions were located inland, incubation was inferred and the nest position marked on topographical maps and GPS (see Bradley 2002; Zharikov et al. 2006). Most nests fell within a 50 km radius of the capture location (Zharikov et al. 2006). This sample is considered geographically unbiased within the area and time-periods sampled (Bradley 2002, McFarlane Tranquilla et al. 2005).

However, many nests (76 out of 121 at DS and 8 out of 36 at CS) were inaccessible to ground crews and are therefore not included in this study. This non-random availability of nest points means that my results will be most applicable to other areas with comparable terrain, and should not be interpreted as reflecting ground conditions at the full range of sites used by murrelets in these regions.

Three different methods of ground vegetation survey were used in this study. “RIC” protocol (Resource Inventory Committee 2001, Resource Inventory Committee 2001) was used at all ground accessible nests as well as some random plots (n = 11 at DS). This method involves measuring DBH, (stem diameter at breast height), height, potential nesting platforms, and mistletoe and epiphyte development in all trees (>10 cm DBH) in a 25 m radius plot centred on the nest tree or a random tree in a randomly located plot. Field crews measured tree height using clinometers for a few trees in the plot, and used these as references to estimate others.

Most random plots were sampled at CS (2001) and DS (2004) following independent protocols (“SFU” protocol; F. H. Huettmann, unpublished data), which consisted of sub-sampling canopy trees within a 75 m radius of the centre. Species, DBH, and height were recorded for a randomly selected centre tree and its three nearest canopy trees, as well as any canopy trees found in 12 three-metre radius plots situated on four radial arms (two running along the slope contour from the centre, and two perpendicular to the slope) at 25 m intervals. Trees with at least one potential platform (“Platform Trees”) were counted over a 25 m radius (CS; similar to RIC protocol) or 75 m radius

(DS). At CS, additional 30 m x 30 m RIC protocol ground plots were available from a separate dataset (Bahn 1998, Bahn and Newsom 2002a). These plots were originally done for a different purpose and were not completely randomized, tending to be biased towards valley bottom. I sub-sampled 19 of these sites, stratified by valley location, with sample sizes selected such that the distribution of all CS random plots for valley location was similar to the distribution of the nest sample for CS.

Locations of random habitat plots were selected *a priori* using GIS software from old-growth forest across the landscape defined by nest locations (minimum convex polygon, Zharikov et al. 2006) within each region. Ground crews then sampled as many of those plots as possible using helicopter access. Steep terrain, geographic barriers or lack of safe nearby landing spots therefore limited access in a similar way as with nest sites. I retained only plots that sampled old growth forest and contained measures of at least five canopy trees.

1.3.3 Variables

I initially considered a set of variables based on availability throughout the dataset and results of previous habitat use studies (Table 1.1). Three of these (ASPECT, SLOPE and ELEV) are landscape variables in a GIS-based habitat selection study by F. H. Huettmann (personal communication) using the full set of DS nests (as opposed to the ground-accessible subset used here).

The variable ASPECT was categorized in two functional groups: “North” (N, including north, west, and flat aspects) and “South” (S, including south and east aspects). North and west aspects tend to receive less direct sunlight and more rainfall as prevailing weather systems are from the west, and would therefore be expected to have a positive effect on murrelet nesting habitat in terms of epiphyte development and cooler microclimate. Data on epiphyte development were available only for nest sites, recorded as epiphyte cover on the tree ranked in four categories (RIC 2001). Epiphyte categories did not differ among trees on north vs. west aspects (Pearson chi-square test: df = 1, χ^2 = 2.49 p = 0.12), nor on south vs. east aspects (df = 1 χ^2 = 0.31 p = 0.58). Significantly more trees with higher epiphyte cover occurred on north/west aspects compared to south/east (df = 1 χ^2 = 11.47 p <0.01. Only one nest site occurred on flat ground, and was therefore not included in the above analysis. Flat sites (n = 9) were grouped with north aspects as they occurred on valley bottoms which tend to be wetter and more shaded.

Although slope was measured on the ground at most sites, the data were missing for a number of sites. Therefore, I obtained slope from Digital Elevation Maps (Integrated Land Management Bureau (ILMB) 2000); the values used are the mean of the 25 m x 25 m cell containing the site and its eight neighbouring cells (see Zharikov et al. 2006).

I considered five ground variables for use in the model set (CANDBH, CANHT, CANCOMPL, DENCANSTEM and DENPLATR; Table 1.1). Since only canopy trees were measured at random plots (SFU protocol), the first four variables represent only the canopy trees within the plot. Previous studies (Bahn 1998, Rodway and Regehr 2002) found that canopy trees within the plot were the best predictors of use, and represent 94% of potential nesting trees in this dataset.

Potential nesting trees are reflected in the variable DENPLATR, the density of trees containing at least one potential nesting platform. This variable includes both subcanopy and canopy trees, though, as noted above, the vast majority are canopy trees.

The variable PATCHAREA was defined in ArcGIS 9 as the area of the old growth forest patch containing a site within 1 km radius buffer of that site (approximately 315 ha area). I verified each site visually to correct for non-contiguous patches within the buffer or for patches that extended beyond the buffer zone. Contiguous patches of old growth were defined regardless of forest cover polygon boundaries and narrow edges such as roads and smaller streams used by Zharikov et al. (2006) for analysis of patch area. Patches were categorized as Small (≤100 ha), Medium (101-300 ha), or Large (>300 ha). Patch size was not included in multivariate models since patch sizes were not well represented within each region (Figure 1.7). Differences in model performance (RSF scores) with patch size were investigated using non-parametric Mann-Whitney U-tests.

1.3.4 Comparison of protocols

As noted previously, two protocols, SFU and RIC, were used in sampling ground habitat. Both protocols were used at 61 nest sites, and I used these sites to compare the methods with respect to four variables of interest: CANDBH, CANHT, DENCANSTEM and DENPLATR. CANDBH, DENCANSTEM and DENPLATR were all found to differ significantly (paired t-test; $p < 0.01$) between protocols. The mean difference for CANDBH (RIC-SFU mean -6.69 cm ± 1.9 s.e.), however, did not seem biologically significant compared to the range of 34.2-166.3 cm (mean 80.4 cm) and 33.9-141.5 cm (mean 87.0 cm) for RIC and SFU protocols, respectively. Differences for DENCANSTEM were large (RIC-SFU mean -29.5 trees/ha ± 9.0), and I therefore dropped the variable from further consideration.

Values of DENPLATR measured over a 75 m radius were significantly and consistently lower than values measured over a 25 m radius at the same position (RIC-SFU mean 28.83 ± 3.7 s.e.; paired t-test $p < 0.01$). No other variable involved viewing every tree in the 75 m radius plot, and I suspect that a proper tally was often unfeasible over such a large area in challenging terrain, resulting in underestimation of the variable. An alternative possibility, that there are more platform trees in the immediate vicinity of nests, seems unlikely at this scale. Platform tree counts for a 25 m radius plot are the more consistent of the two methods, and account for all nest sites, all random sites at CS and a few random sites at DS. Eliminating 75 m radius sites, however, would eliminate almost all random sites at DS and therefore that entire region. I therefore used multiple imputations to permit unbiased estimation of missing data. Each missing observation was replaced with multiple (here, $m = 500$) plausible values based on a known relationship to existing data (Schafer 1997). I used PROC MI (SAS Institute Inc. 2003), with imputed values based on the linear relationship DENPLATR(25) = DENPLATR(75) and limited to the range of observed DENPLATR(25) over the entire dataset (0-150). This method was used to estimate only the variable DENPLATR, for 25 random sites at DS.

1.3.5 Data analysis

I used logistic regression models with binary (nest/random) response variable NEST (nest/random) to generate Resource Selection Functions. I built *a priori* models with plausible combinations of measured habitat variables to predict probability of nesting, and used an information-theoretic approach to select the best model(s) among the set of alternative candidates (Burnham and Anderson 2002).

The two regions included in this study differ in both climate and degree of fragmentation, factors that may affect habitat selection by murrelets (Zharikov et al. 2006, 2007). The distribution of certain habitat variables also differs between the two regions (Figure 1.4). I therefore applied the model set to CS and DS separately, as well as to the sites pooled from both regions ("Both"). Results for Both regions may help quantify patterns that are more general and generate a more widely applicable habitat selection model.

To simplify the model set (Table 1.2), I included or excluded landscape-level and tree variables as sets. Landscape level variables included ASPECT, ELEV and SLOPE, and support for these variables alone (Model 6) would suggest that patch-scale variables measured by ground-based observers are less important. The set of ground variables included CANDBH, CANHT and CANCOMPL. Support for this model (4) would indicate selection at the patch level. DENPLATR was included separately in models to help elucidate the importance of increasing availability of potential nest sites, within a patch, as indicated in previous studies (Manley 1999, Rodway and Regehr 2002). I tested all combinations of these variable-groups in the model set, as well as a null model that tested only the mean and variation inherent in the response variable. Support for this null model would indicate that variables other than those tested are responsible for variation observed. Three additional models included a quadratic term for CANHT and CANCOMPL to reflect the hypothesis of a non-linear relationship for these variables. These quadratic models (models 9-11) were relevant only to both regions combined.

Multiple Regression analysis assumes independence of variables (Zar 1999). Some degree of correlation can be expected with the variables used here, and has been indicated in previous studies. I checked for multicollinearity using the Variable Inflation Factor (VIF) in PROC REG (SAS Institute Inc. 2003), whereby a value >10 could indicate a problem (Neter et al. 1996). I used the mean of imputed values for each site for the variable DENPLATR at DS in this analysis. VIFs indicated no problem with multicollinearity, with values <3 for all variables in both CS and DS.

Sample sizes used here were relatively small (DS n = 72; CS n = 70), so I used Akaike's Information Criterion for small sample sizes (AICc). The global models for CS and both regions indicated overdispersion ($\hat{c}$ = 1.44, 1.62 respectively), so the Quasi-Likelihood AIC (QAICc) was used for those model sets (Burnham and Anderson 2002). I consider models in which AICc values differ from the best-fitting model by ≤2 (ΔAICc, Burnham and Anderson 2002) as well as AIC_w, which indicated relative support for a model from among a set of candidate models.

Models for DS that included DENPLATR were run using a partially imputed data set, consisting of essentially 500 data sets, each containing the imputed values. Model fit statistics for AIC, R^2 and predicted probabilities were averaged for each model. I used PROC MIANALYZE (SAS Institute Inc. 2003) to generate single, valid inferences for parameter estimates (β).

1.3.6 Model performance and analysis

I tested the performance of each top-ranked model using k-fold cross-validation (Boyce et al. 2002). RSF scores, proportional to the probability of use (Manly et al. 2002), scaled from 0 to 1, were output from the model and binned into sequential bins of equal size (CS/DS: 8 bins, n = 10-11; Both: 10 bins, n = 14-15). Higher scores were preferentially placed into the two larger bins (Wiens et al. 2008). The data set was then randomly partitioned (stratified by region) into five subsets. For each of the models I re-estimated model parameters, each time using a different combination of four subsets, reserving the fifth for model testing. Using Spearman rank correlation and χ^2, I compared the frequency of nest sites observed in the test set for each RSF bin (adjusted for bin size) to that expected based on the original model (Boyce et al. 2002).

I further tested the assumption that RSF scores are proportional to the probability of use by regressing observed versus expected bin values (Johnson et al. 2006). Properties of an RSF model that is proportional to the probability of use include an intercept close to zero, a slope (β_1) that is significantly different from zero and whose confidence interval includes one, a high R^2 value and a non-significant goodness of fit χ^2 (Johnson et al. 2006).

1.3.7 Model parameters

The odds ratio [OR = exp (β)] gives an indication of the effect of each variable within the model (O'Connell 2006). The percent change in the odds of success (i.e., the ratio P [nest]/P [random]) based on a one-unit change in the variable can be calculated as:

100 x (OR - 1) (O'Connell 2006)

Therefore variables with an OR = 1 have no effect on the model, while variables with an OR >1 have a positive effect on the probability of nesting, and OR <1 has a negative effect.

The change in the probability of use with select individual variables (CANDBH, CANHT, CANCOMPL and DENPLATR) is also of interest for habitat quality assessment. These ground variables had a significant effect in one or both of the regions. A set of simulated data points were created, wherein the variable of interest was varied across the range observed for all random sites, while all other variables were held constant at their mean value for all random sites. Predicted probabilities and 95% confidence limits were generated using the SCORE statement in PROC LOGISTIC (SAS Institute Inc. 2003) based on the model fit for the best model in each region. The result is a curve indicating the predicted probability of nesting at all intermediate levels of the variable.

1.4 Results

1.4.1 Ground habitat plots

Habitat selection models were created using 142 sites: 27 nest sites and 43 random sites at CS, and 37 nests and 35 random sites at DS. Sites at DS were located at elevations ranging from 5 to 1210 m. More than 50% of the nest sites in this region were located between 300 and 600 m. At CS, sites ranged from 0-1200 m, with most sites at mid elevations 300-900 m (Figure 1.2). The overall range of elevation was similar for both regions, but sites were not evenly distributed across all elevations and the distributions were somewhat different.

About 60% of both nest and random sites at CS were classified as "north" aspect. At DS, aspect of sites differed markedly, with 76% of nest sites and 48% of random sites at "north" aspects (Figure 1.3).

In both regions, the density of platform trees was higher at nest sites on average than at random sites (Table 1.3, Figure 1.4a), though the difference was much larger at DS. Diameter (CANDBH) of canopy trees was also consistently larger at all nest sites, though the difference was minimal (Figure 1.4b). Although canopy height was similar at nest and random sites for both regions combined (Figure 1.4c), differences were apparent when considering the regions separately. At CS, trees at random sites were taller, on average, than at nest sites. In contrast, trees at nest plots at DS were taller than those at random plots. Differences in canopy complexity also became more apparent when regions were considered separately (Figure 1.4d). While random plots at CS had greater canopy complexity than nest sites, complexity was much higher for nest sites at DS.

1.4.2 Model selection

The best models predicting nesting habitat selection differed between the three model sets (Table 1.4). For CS, Models 1 and 2 were strongly supported, with a cumulative $QAIC_w$ of 0.78. Model 1 is the global model, while Model 2 excludes Landscape variables. Tree variables appear in each of the top four models (Table 1.4a). There was very little support for Model 6 (ΔAICc >7), which includes landscape-level factors only.

For DS, in contrast, Models 5 and 4 collectively account for 72% of the total AIC_w in the models set (Table 1.4b). These two models both include Tree variables, again differing in the inclusion of Landscape. Density of platform trees does not appear in either of the two best-supported models. Model 6 (landscape only) receives very weak support (ΔAICc >7, $AIC_w = 0.01$) in this set.

The model set for Both regions consists of twelve models, and includes quadratic expressions for canopy height and canopy complexity. The five multivariate models that include density of platform trees (Models 1, 2, 3, 9 and 12) receive significant support (ΔQAICc <2; Table 1.4c), accounting for a total $QAIC_w$ of 0.85. Tree variables are present in four of the models, landscape in three and the quadratic term in two of the models, which differ very little in terms of $QAIC_w$. The Landscape-only model 6 receives moderate support with an $\Delta QAIC_w$ of 4.31 (Table 1.4c; Burnham and Anderson 2002).

1.4.3 Model analysis

All models that received significant support through AIC model selection tested well in k-fold cross-validation in terms of both performance and proportionality (Table 1.5). At CS, both Models 1 and 2 perform well in terms of rank correlation. A χ^2 test on the proportions for individual bins indicates the only significant deviation exists at very low RSF scores where nest frequency is very low (1 or 2 nests). Adjustments to bin composition might help (Boyce et al. 2002), but does not seem warranted here. Neither model differs significantly from a slope of 1 and intercept of zero, though model fit for Model 2 is slightly poorer and a significant χ^2 Goodness-of-Fit Test ($p < 0.05$) is the only deviation from the conditions outlined by Johnson et al. (2006). Since the two models receive support from both AIC and k-fold cross-validation methods, I obtained parameter estimates through model averaging, in which each model contributes according to its Akaike weight (Burnham and Anderson 2002). I compared the performance of the resulting averaged model to Models 1 and 2 in terms of RSF scores for nests at three different nest/random classification thresholds (>0.5, >0.65 and >0.8). The averaged model performed nearly as well as the best performing model 1 at the two lower thresholds, but scored half as many nests >0.8 than did model 1 (26% vs. 44%; Table 1.5). The averaged model also had larger 95% confidence intervals for parameter estimates. Given the proposed utility of these models in ranking commercially valuable habitat, the ability for a model to rank true nest sites very highly is especially important. I therefore consider model 1 the best, most practical model of this set for CS.

Both models 5 and 4 for DS have high Spearman rank correlation (r_s >0.9), indicating good predictive strength. Regression diagnostics are also very good for both models (Table 1.5), indicating a high degree of proportionality. Following model averaging and performance comparison methods for CS models, model 5 ranked slightly more nest sites at all levels than models 4 and the averaged model, but the difference was again most apparent for nests >0.8 (Model 5: 27%, averaged model 13%; Table 1.5). Parameter estimate confidence intervals were also larger in the averaged model. For the reasons stated for CS, I consider model 5 the best model from the Desolation Sound model set.

The four remaining models (1, 3, 9 and 12) test well in all respects with the pooled CS and DS data. Model averaging once again resulted in a model with larger confidence intervals, and much poorer predictive performance for nests ranked >0.8 (6%) compared to the best performing model 9 (20%). Model 9 scored more nests than the other three stable, AIC-ranked models at all three thresholds, and is therefore considered the best overall model for both regions.

Odds Ratios for the best supported model for each of the three data sets are presented in Table 1.6. The value represents the change in odds ratio P(nest)/P(random) with a unit increase in the variable. Odds ratios need to be considered in the context of their units and the overall range; the same odds ratio would indicate a much larger change for CANHT (in metres) than for CANDBH (in centimetres).

Based on the best models for each region, nest sites were consistently assigned high probability of use scores (Figure 1.5). In the combined model for both regions, nest and random plots showed a similar distribution of scores to that produced by region specific models.

Selection curves (Figure 1.6) indicate the effect of a patch-level variable on the RSF score. Density of trees with platforms shows a non-linear trend, with the increase in probability of use decreasing at densities greater than between 100 (CS) and 120 (all) trees per hectare (Figure 1.6a). This is equal to approximately 20-25 platform trees in a 25m hectare plot. This variable is not plotted for DS, since it was not present in Model 5.

While use shows a more or less positive linear trend with CANDBH, CANHT produces opposite trends at CS and DS. Probability of use decreases sharply in CS forests taller than about 40 m, while DS has a weakly positive trend. The quadratic function in Model 9 (All) produces a peak in use between about 30 and 42 m.

1.4.4 Stand size

The distribution of patch sizes was very different by region (Figure 1.7). At CS, all sites were in patches larger than 100 ha, and many were in contiguous forest >500 ha. At DS, all but 3 sites were ≤300 ha and 53% of all sites were in small patches of 100ha or less. RSF scores from habitat selection models did not differ between nests in medium (101-300 ha) and large patches (>300 ha), so these patch size categories were pooled for subsequent analyses and restricted to DS sites since no small sites occurred at CS. Both the DS-specific model 5 and the Both regions model 9 (for DS nests) tended to give higher RSF scores to nests in Medium/Large patches (Model 5: RSF: Mean 0.81 Median 0.81; Model 9: Mean 0.68 Median 0.76) versus nests in smaller patches (Model 5: RSF: Mean 0.57 Median 0.59; Model 9: Mean 0.53 Median 0.57); these differences were significant in both cases (Model 5: $U = 363$ $p = 0.002$; Model 9: $U = 326$ $p = 0.02$).

1.5 Discussion

1.5.1 Resource selection functions

This research was the first to create Resource Selection Functions (RSFs) based on ground plots at real nests and test their utility against landscape-level RSFs. In southern British Columbia, patch-scale variables were better predictors of marbled murrelet nest sites than landscape-level features. Models that included variables from both spatial scales were the most predictive.

The utility of Resource Selection Functions is their ability to predict relative habitat use for each site. Resource Selection Probability Functions (RSPF; Manly et al. 2002), yielding the predicted probability of use, cannot be obtained directly from a use-availability design due to unknown rates of contamination of the random sample by used sites (Keating and Cherry 2004). The RSF score is not necessarily proportional to the RSPF in all cases, and is not limited to the range 0 to 1 (Keating and Cherry 2004), but Johnson et al (2006) provide a method of testing proportionality. RSF scores used in this study ranged from zero to 1 and the scores for all models considered are shown to be proportional to the probability of use.

With an eye to conservation applications, the test of an RSF should be its predictive ability. The true test for any model is on an independent data set. Unfortunately, there are no other sets of known nest sites with habitat plots from the regions included in this study. In the absence of an independent data set, Boyce et al. (2002) recommend k-fold cross-validation for smaller sets of use-availability data. Tested models showed acceptable predictive ability; with high proportions of nest plots assigned a high probability of use (Figure 1.5).

I considered a limited number of ecologically relevant models for this study. Not all combinations of the available variables were considered, as this would have resulted in an unacceptably large model set. Tree and landscape variables are considered as a set, although some of these variables may not be as important in the final models. Excluding one of these variables within a group does not confer any advantage in terms of data availability or acquisition for future applications of these models. Ground variables are by no means easy to obtain, but the effort involved in obtaining any one of these is little less than that required to obtain the entire set.

1.5.2 Comparison of regions

Significant differences exist between the two study areas considered here, both in terms of climate and habitat availability. Previous studies at CS and DS that concentrated on a larger scale have also found differences in terms of habitat selection between the two areas (Zharikov et al. 2006, Waterhouse et al. 2009). This study shows that habitat selection does indeed differ between CS and DS, but that a single RSF can nonetheless describe habitat selection in both regions with reasonable predictive ability. Model 9, derived from pooled data, performed equally as well at CS and DS in terms of assigning high RSF scores to nest sites (Figure 1.5), when applied to each region independently. However, scores from region-specific models tended to be higher.

Both landscape and patch-scale variables have significant effects in these habitat selection models. With the exception of canopy complexity, all patch-scale variables considered here have significant effects within RSFs for CS and Both regions. Slope also has a significant positive effect in these models. At DS, aspect is the only variable to have a significant effect. All other variables have large confidence intervals that include 1 (no effect), a problem found in each of the top models for DS. Due to the uncertainties associated with parameters in the DS model 5, I restrict further discussion of variable effects within models to Both regions model 9 and CS model 1.

Previous habitat selection studies using this set of nests have failed to find strong selectivity at CS (Waterhouse et al. 2008) or had less predictive power (Waterhouse et al. 2009) than DS. It has been assumed that most habitats available at CS are suitable for nesting and that, as a result, murrelets are less “choosy”. The random habitat plots used in this study suggest this is not the case; platform trees, an essential component of nesting habitat, were absent in 23% of random sites (which are, therefore, unsuitable nesting habitat). There is also an apparent preference for shorter trees at CS, a finding contrary to previous research that I will discuss later.

Clayoquot Sound may also differ from DS in terms of the temporal breadth of the nest sample. The CS radio-telemetry nest sample was biased towards later breeders (McFarlane Tranquilla et al. 2005), which are likely to be less experienced than birds nesting earlier in the season. The nesting habitat represented in this study may therefore reflect habitat choices limited by previously occupied and perhaps higher quality, patches.

1.5.3 Accessibility bias

At DS, a larger proportion of all nests (about 40%) found by radio-telemetry were inaccessible by ground than at CS (Lank et al. 2003). F. H. Huettmann. (personal communication), using landscape variables available for all nests, concluded that inaccessible sites tended to be on steeper slopes and at lower-mid elevations and that this could create a bias in habitat selectivity studies based on ground accessibility. If patch-scale variables measured here co-vary with geographic parameters that affect accessibility, habitat selection models used here may not be representative of the entire landscape. I recognize that this bias affects this study and that results may not be applicable to the entire landbase available to nesting marbled murrelets in British Columbia. Although the magnitude of the bias is unknown, the accessible habitat to which these models apply is most representative of that used by current commercial logging, and therefore of higher immediate conservation value.

1.5.4 Stand size

Differences in habitat selection between regions may be due to the distribution of stand sizes. Medium and large stands account for just under half the sites at DS, but RSF scores for nests in larger stands were significantly higher from either the DS model, or the pooled Both model. The CS model, built using sites in predominantly large stands, also scored DS nest sites in medium/large stands higher than those in small stands.

Patch variables are more important in the models that perform better in regions with larger stands. Platform trees are patchily distributed (personal observation) and habitat quality is likely to vary within a large stand. Patch variables may therefore reflect cues used by prospecting murrelets to effectively narrow down the search for a nest site in landscapes where large stands predominate (L. W. Waterhouse, British Columbia Ministry of Forests and Range, personal communication). With less area to search in smaller stands, it may be just as effective to consider all potential nest sites.

Given the regional differences in fragmentation and total available habitat in this dataset, it is impossible to determine which aspect of the regions drives observed differences in habitat selection. My results do not suggest selection for certain stand sizes, since murrelets in either region were not presented with the full range of available stand sizes. Evidence from Desolation Sound suggests that murrelets do use small stands for nesting; these choices are likely constrained by the availability of habitat in the region and may not represent choices made under optimal conditions. Although Zharikov et al.

(2006) found that murrelets bred successfully in small patches at Desolation Sound, this pattern might result from covariation of stand size, altitude, and predator populations. All else being equal, predation risk is likely to be higher due to disproportionate edge effects in smaller patches (Malt and Lank 2007b). If further research indicates that habitat selection does differ with the degree of fragmentation in a given region, habitat quality assessments (see Chapter 4) could be adjusted accordingly. For example, in regions where small stands predominate, less emphasis could be placed on patch characteristics such as canopy height exceeding some minimum threshold.

1.5.5 Density of platform trees

The relationship of platform density at intermediate levels to the probability of nesting may be of particular interest to commercial logging interests, insofar as density of platform trees may be positively correlated to standing timber value. Habitat use studies have consistently identified higher densities of platform trees as a characteristic of nest sites (Burger 2002), even though murrelets are known to nest at low density (Conroy et al. 2002). Higher densities of nesting platforms are therefore unlikely to support a proportionally higher density of nests (Burger and Waterhouse 2009). Multiple potential nest sites may confer advantages in terms of decreased predation risk (Manley 1999) due to a dilution effect on searching predators (Martin 1993). It is considered more likely that nest predation is largely opportunistic (Malt 2007), so the magnitude of this effect, if any, is questionable. Another hypothesis is that prospecting murrelets cue in on patches with higher density of potential platforms as they are more likely to find a suitable nest from among the available choices. Increased platform availability may also allow re-use of a high-quality patch where re-use of the same nest site may be avoided due to increased risk of predation (Burger et al. in press). The effect that density of platform trees has on habitat suitability to murrelets is of particular interest. A minimum of one platform tree is a fundamental requirement of any potential nesting habitat, and availability of platforms is a substantial component of current habitat ranks based on low-level aerial surveys.

It is somewhat surprising that in Desolation Sound, models including the density of platform trees were not strongly supported by the data. This variable was imputed for most random sites at DS, which meant that average values were used and extreme values such as zero platform trees were less likely. It is worth noting that all habitat plots at DS (n = 4) with densities greater than 75 trees per hectare were nest sites. DENPLATR likely remains an important predictor of nesting habitat at DS even though it was not retained among the most parsimonious models for the region. Selection curves indicate that the relationship of DENPLATR to the probability of nesting is non-linear. Probability of nesting does not increase significantly at very high densities of platform trees. The densities at which this trend is seen however, occurs at the upper edge of the range of platform tree densities observed in the study areas. To the extent that platform tree density and commercial value of standing timber are positively correlated, the relationship of probability of nesting to density of platform trees may be of particular interest for management. This finding warrants further investigation, in terms of platform density in fragmented regions such as DS, as well as possible influence, if any, on breeding success.

1.5.6 Other variables

The ground variables used were important descriptors of nesting habitat in previous studies. Using inferred nest sites (Hamer 1995, Rodway and Regehr 2002) or a more localized design to measure selection, while Manley (1999) measured patch-scale habitat selection within the patch, pairing each nest site with a nearby random site.

The diameter of canopy tree stems (CANDBH), is correlated to stand age (Bahn and Newsom 2002a), though it does not appear to directly confer any direct advantage to nesting murrelets. Older trees are more likely to develop larger and more abundant platforms, and Manley (1999) found local selection for trees with more platforms and larger platform limbs. These features of larger, older nest trees may confer advantages in terms of nest success: nestlings and eggs are less likely to fall from larger platforms, and predator search efficiency may be reduced with more potential nesting platforms (Martin 1993, Chalfoun and Martin 2009). An analysis of fledging success using this set of nests found that both platform length and platform availability within the nest tree were associated with success at Desolation Sound (Chapter 2).

Canopy height appears to have opposite effects at DS and CS. At DS, overall canopy height of nest patches was taller than random patches, though the negative affect of this variable within the model was not significant. At CS, random patches were taller than nest patches, and canopy height was retained as a significant factor in the best model. Canopy height does not appear to be a limiting factor within old growth forests at CS; just 11% of random sites were shorter than the minimum height at nest patches. Figure 1.6 indicates a strong decline in probability of nesting for forests taller than about 40 m at CS. The quadratic term in the model for both regions results in a peak probability of nesting for forest patches between 30 and 40 m tall. The decreased suitability of very tall forests has not been found in previous research, and should therefore be viewed with some caution at this time. Indeed, most studies considering tree height show nests are often in the tallest trees of the patch (Manley 1999, Conroy et al. 2002, Chapter 3). This finding may be due to the temporally biased nest sample (McFarlane-Tranquilla et al. 2005) at CS, whereby late-breeders did not have access to taller, potentially higher quality stands. Although valley location was largely controlled for, it may be that random sites used in this sample inadvertently over-represented certain types of forest that happen to be taller. Despite this pattern, the absolute heights of trees utilized at Clayoquot Sound are within the ranges of previous work (Manley 1999, Burger 2002).

Canopy complexity did not have a consistently strong effect in any models. Canopy complexity may increase accessibility to the canopy for nesting murrelets (Burger 2002, Hamer and Nelson 1995), and may be correlated with other factors such as nest cover (Grenier and Nelson 1995, Hamer and Nelson 1995) and epiphyte growth (Bahn and Newsom 2002b). Various measures of canopy complexity are in use, depending on the method of interpretation. Rodway and Regehr (2002) use standard deviation of canopy height, the method chosen for this study due to information availability. Waterhouse et al. (2002) uses a measure of canopy complexity from air photos that includes forest gaps. More recently, Hamer et al. (2008) used “number of canopy layers” as a measure of complexity. In my study, proximity to edges or even small forest gaps (information that was not consistently available) may enhance accessibility independent of canopy complexity. Preference for steeper slopes, a significant effect in both CS and Both region models, may also confer accessibility advantages. Furthermore, the measure of canopy complexity used here reflects overall complexity of a 25 m radius plot, while access is only needed for a nest in a single tree in the plot.

1.5.7 Management implications

The competing hypotheses presented herein apply to old growth forests at Clayoquot Sound and Desolation Sound accessible to humans on the ground. Other habitat features, including moss development and canopy cover, shown to be important predictors of habitat use in the same regions (e.g. Rodway and Regehr 2002, Waterhouse et al. 2004, 2009), were not included in the present study due to limitations in their availability throughout the dataset. Nonetheless, these habitat selection models allow predictions of habitat use across a spectrum of habitat conditions. There is no evidence however, that habitat selection described here results in differences in marbled murrelet fledging success (Chapter 2), whereby nest success is independent of habitat quality according to the model. This simplifies management considerations, because habitat selection, which is easier to measure than productivity, should be a sufficient basis for decision making.

My results indicate that a multi-scale approach to understanding nesting habitat selection by marbled murrelets is warranted. Though habitat information at the landscape scale is more easily obtained and models apply to larger areas regardless of accessibility, landscape-only models in this study received very little support from the data when compared to models that incorporate patch scale variables measured on the ground. There is some evidence that habitat selection differs between Clayoquot Sound and Desolation Sound, possibly due to differences in stand size. Available stand sizes differ between the two regions, and this difference may affect habitat selection within the regions. This data gives no indication, however, of habitat preferences for stand size.

Acquiring ground habitat information such as that used in this study is extremely costly, subject to accessibility and impractical for widespread application in British Columbia where extensive potential habitat occurs over steep, topographically complex terrain. More efficient methods of assessing nesting habitat quality using airphoto interpretation and low-level aerial surveys have been developed and tested (Waterhouse et al. 2002, 2004, 2008, 2009). These methods are part of current management guidelines in the province and are used to rank habitat on a six-point scale. Ground-based habitat selection models will be used to validate these remote methods against habitat conditions more accurately measured by ground-based observers. Marbled murrelets share a limited and commercially valuable landscape with logging interests in British Columbia. This study is a step toward improving land-use decisions for conservation of murrelet nesting habitat.

1.6 Figures

Figure1.1 Map of study regions in south coastal British Columbia, showing nest (circles) and random sites (triangles).

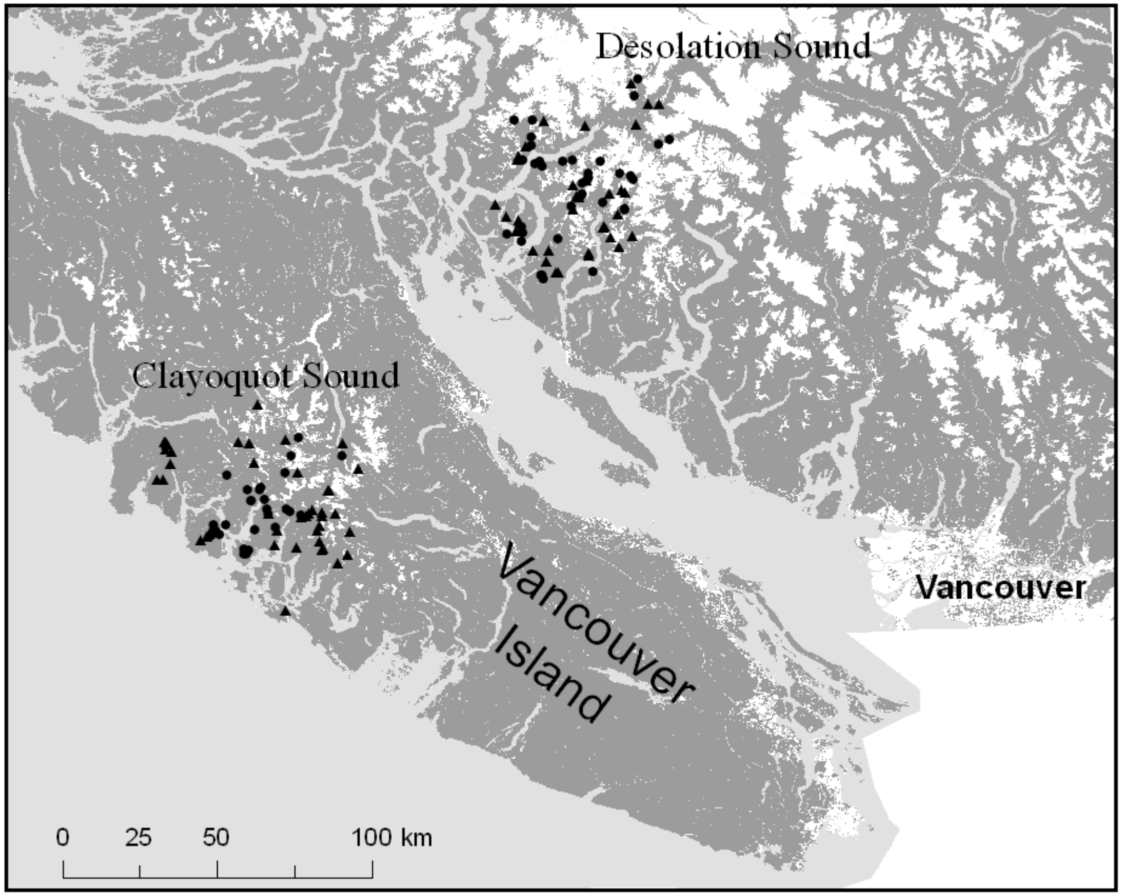
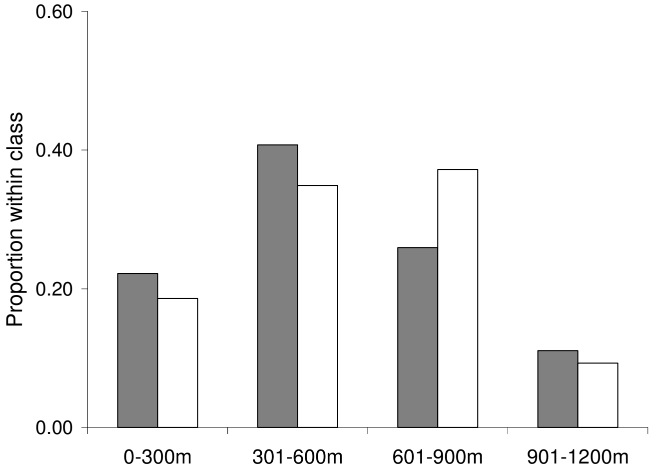


Figure 1.2 Distribution of elevation of sites at a) Clayoquot Sound (CS) and b) Desolation Sound (DS) by proportion of total. CS Nest n = 27, Random n = 43, DS Nest n = 37, Random n = 35.

a) Clayoquot Sound



b) Desolation Sound

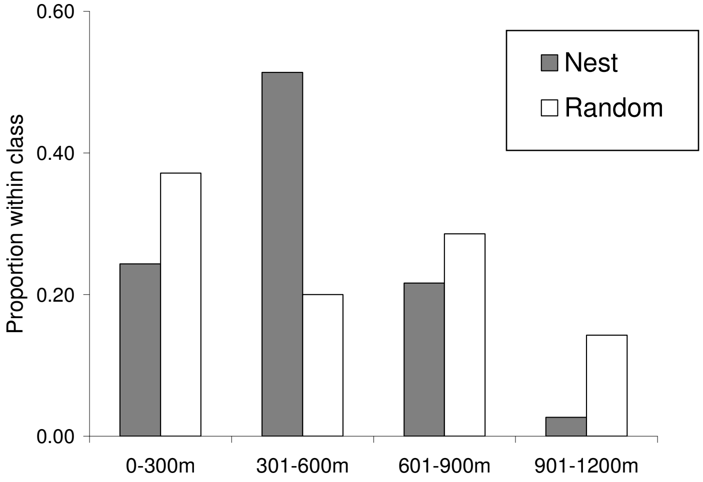


Figure1.3 A larger proportion of nest sites at Desolation Sound occurred on wetter "North" aspects**.** Aspects are grouped: South = south and east; North = north and west.

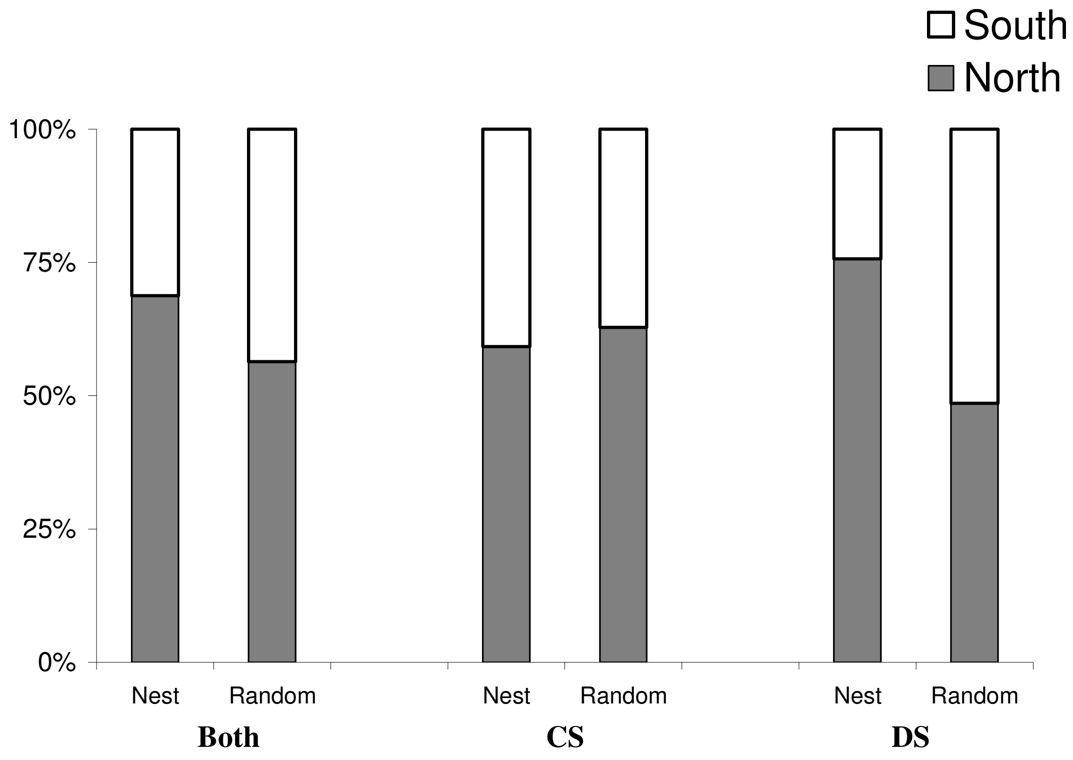


Figure 1.4 Mean values for ground variables: a) density of platform trees, b) diameter at breast height (DBH) of canopy trees, c) height of canopy trees, d) canopy complexity, the standard deviation of CANHT. Values are jittered on the x-axis for display purposes. Open = Random sites; Solid = Nest sites.

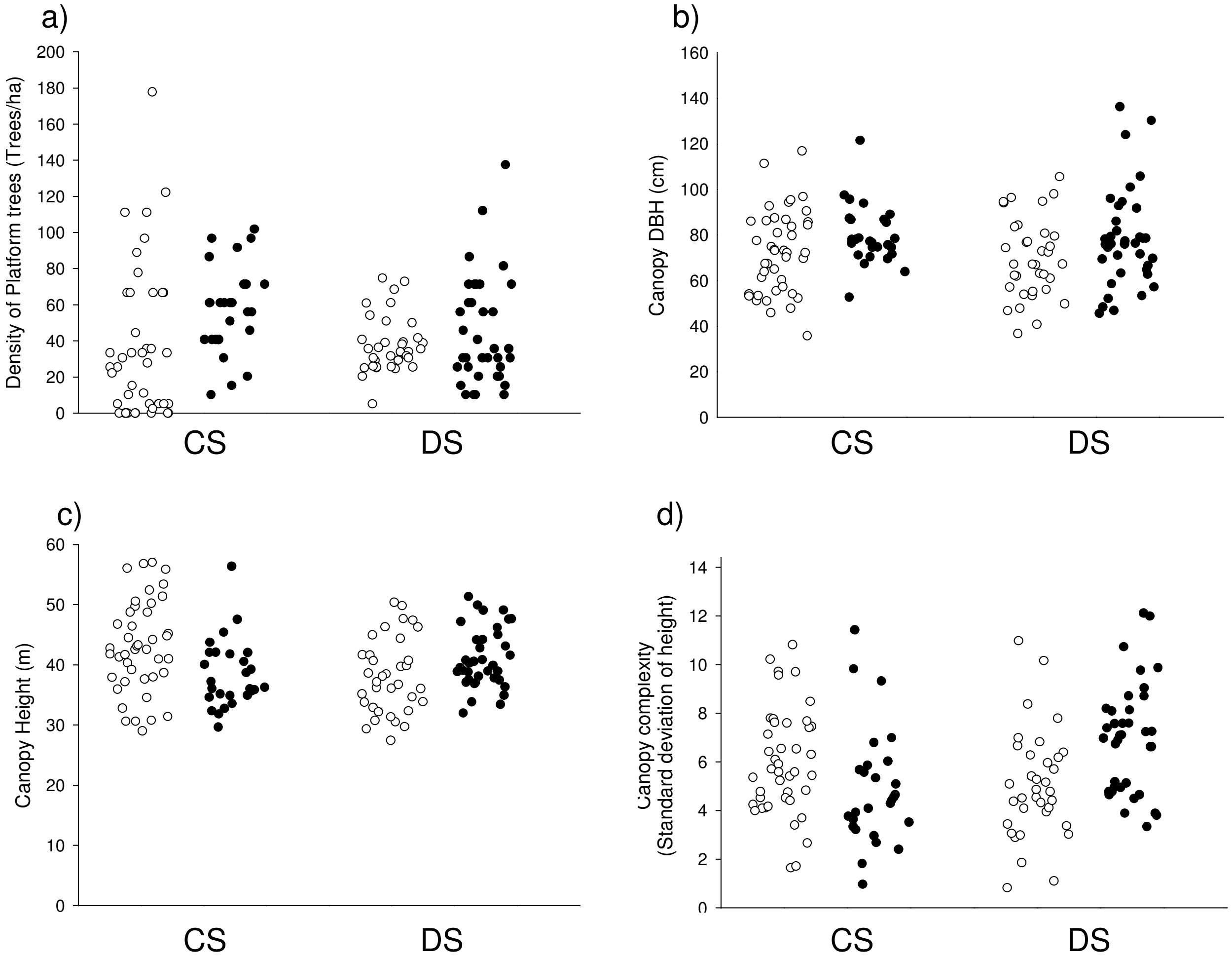


Figure 1.5 As expected, a greater portion of nest sites compared to random sites have higher RSF scores(predicted probability of nesting) for the best model for a) Clayoquot Sound, (b) Desolation Sound and (c) Both regions pooled. The model for both regions performs better when applied to CS than DS.

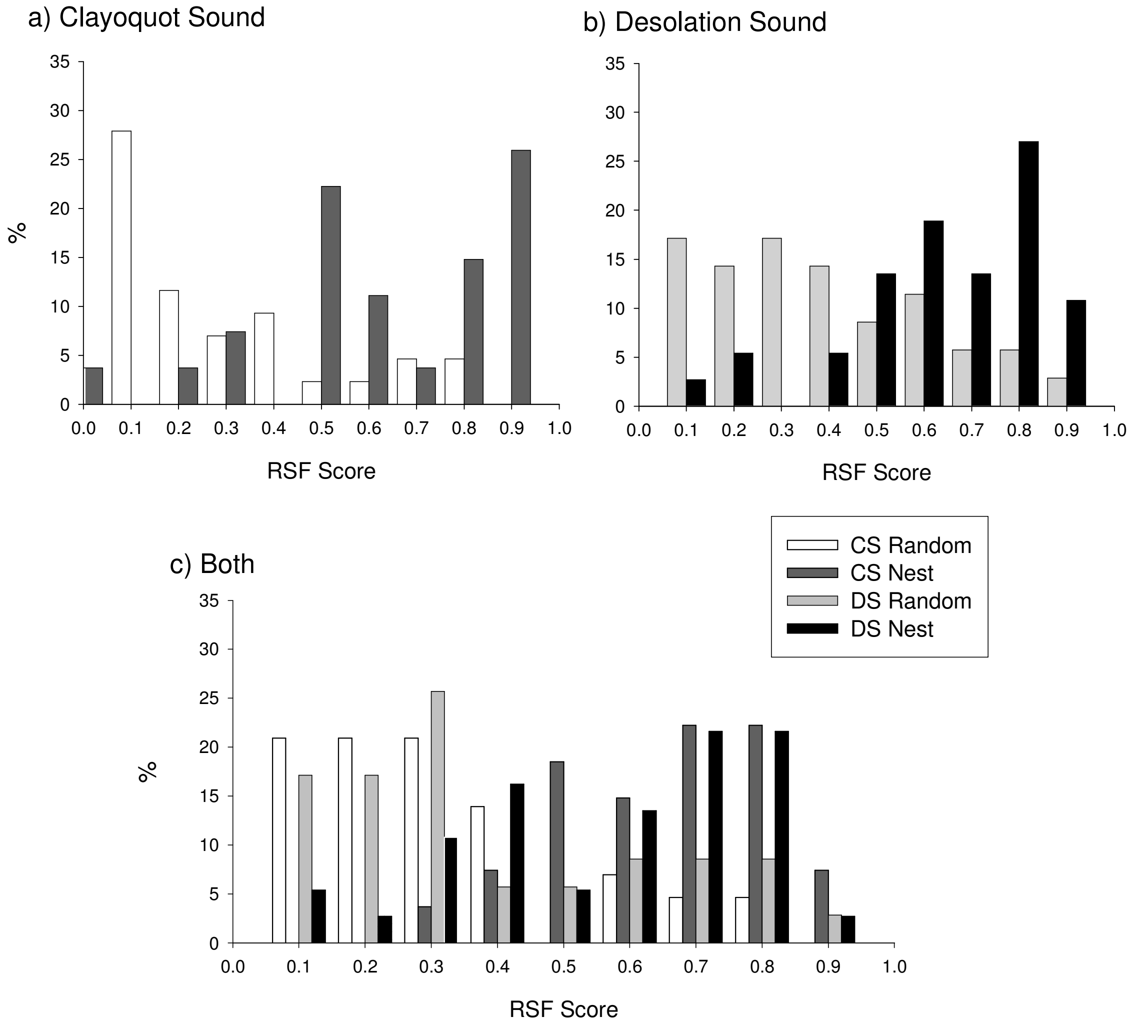


Figure 1.6 The predicted probability of nesting (RSF score) derived from the top model for each region, showing the effect of a single variable, with all other predictor variables held constant. a) Density of Trees with Platforms b) DBH of Canopy trees c) Canopy Height. Thin lines indicate 95% confidence limits.

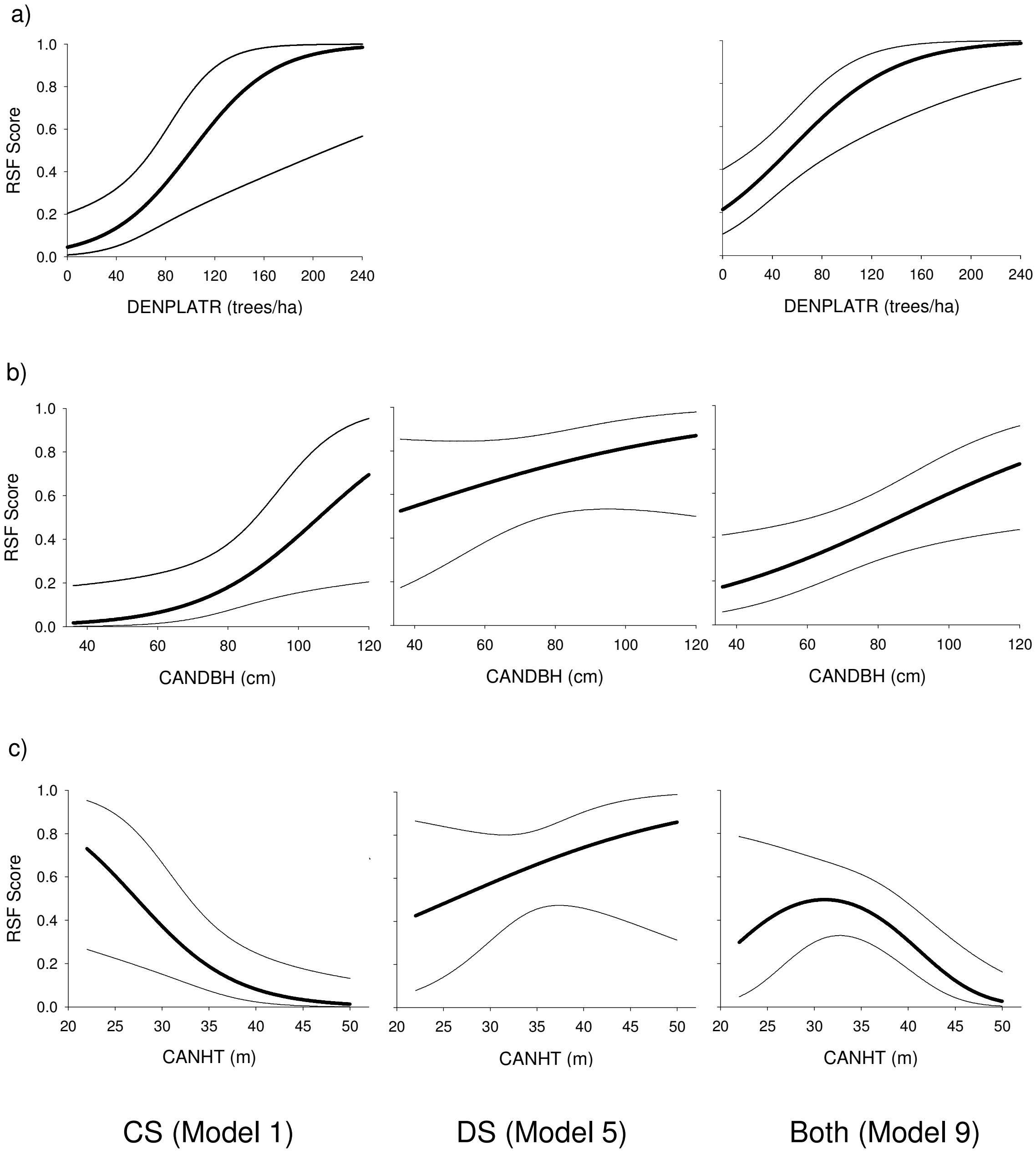
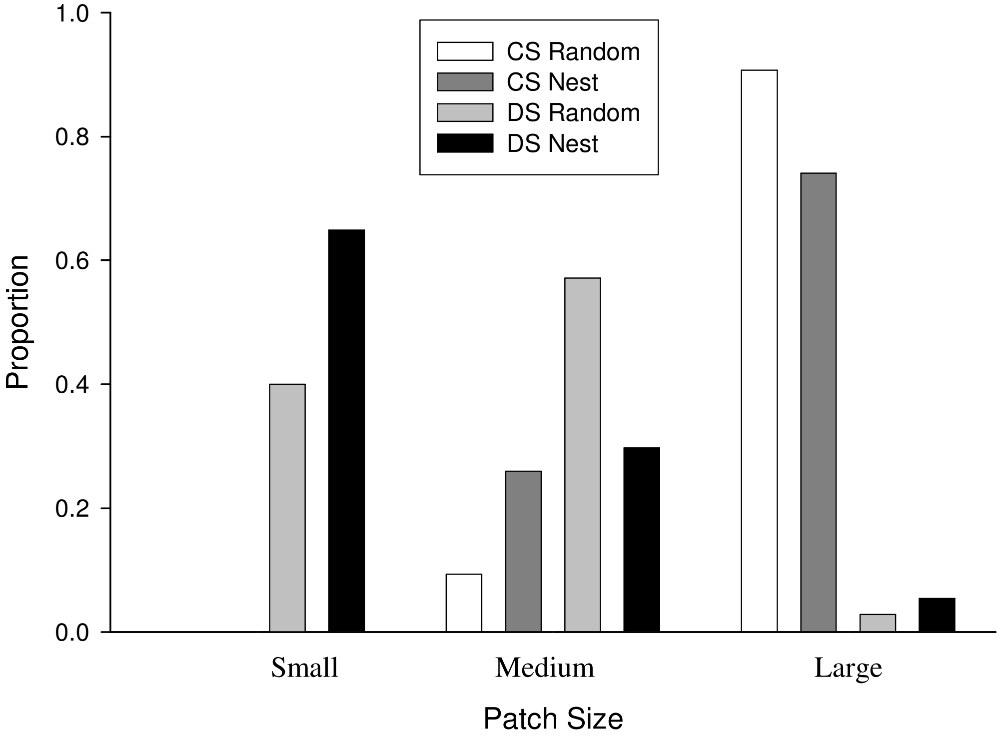


Figure 1.7 Patch size of plots. Most plots at CS were located in large patches (>300 ha), while DS plots were in small (≤100 ha) or medium (101-300 ha) patches. Total sites: CS random = 43, nest = 27; DS random = 35, nest = 37.



1.7 Tables

Table 1.1 Description of variables used for habitat selection modelling.

Variable Name	Description	Units of measurement	Scale
REGION	Desolation Sound or Clayoquot Sound	CS DS	
ASPECT	Slope aspect (North=226°-45°; South=46°-225°)	N S	Landscape
SLOPE	Slope, from Digital Elevation Model	degrees	Landscape
ELEVATION	Elevation (metres) measured on the ground	m	Landscape
CANDBH	Mean DBH (Diameter at Breast Height) of canopy trees	cm	Patch
CANHT	Mean height of canopy trees	m	Patch
CANCOMPL	Canopy complexity (standard deviation of CANHT)	m	Patch
DENCANSTEM	Density of canopy trees (all species	# per hectare	Patch
DENPLATR	Density of platform trees (trees with at least one potential nest platform)	# per hectare	Patch
PATCHAREA	Area of patch containing site. Small=0-100ha; Medium=101-300ha; Large=301+ha	S/M/L	

Table 1.2 The model set used to predict probability of nesting based on ground habitat variables. Variables were grouped according to the scale involved.

#	Model
1	DENPLATR + CANDBH + CANHT + CANCOMPL + ASPECT + ELEV + SLOPE
2	DENPLATR + CANDBH + CANHT + CANCOMPL
3	DENPLATR + ASPECT + ELEV + SLOPE
4	CANDBH + CANHT + CANCOMPL
5	CANDBH + CANHT + CANCOMPL + ASPECT + ELEV + SLOPE
6	ASPECT + ELEV + SLOPE
7	DENPLATR
8	(Null)
9[a]	DENPLATR+ CANDBH + CANHT + CANHT^2 + CANCOMPL + CANCOMPL^2 + ASPECT + ELEV + SLOPE
10[a]	CANDBH + CANHT + CANHT^2 + CANCOMPL + CANCOMPL^2 + ASPECT + ELEV + SLOPE
11[a]	CANDBH + CANHT + CANHT^2 + CANCOMPL + CANCOMPL^2

[a] Models with a quadratic term were applied only to the whole dataset (both regions combined)

Table 1.3 Range, mean and 95% confidence intervals for variables used in habitat selection models at Clayoquot and Desolation Sounds. N = 27, 43, 37 and 35 for CS nest, CS random, DS nest and DS random, respectively. See Table 1.1 for variable definitions.

Variable		Range	Mean	Confidence Interval
Clayoquot Sound				
CANDBH	Nest	52.7 - 121.5	79.8	74.9 - 84.7
	Random	35.8 - 116.9	72.4	67.1 - 77.7
CANHT	Nest	29.6 - 56.4	38.4	36.2 - 40.6
	Random	29.0 - 57.0	43.0	40.7 - 45.3
CANCOMPL	Nest	1.0 - 11.4	4.9	3.9 - 5.9
	Random	1.6 - 10.8	6.0	5.4 - 6.6
DENPLATR	Nest	10.2 - 101.9	57.2	48.0 - 66.4
	Random	0 - 177.8	36.4	23.9 - 48.9
SLOPE	Nest	6.6 - 57.6	30.8	25.7 - 35.9
	Random	3.2 - 48.5	23.0	19.5 - 26.5
ELEV	Nest	20 - 1120	501.6	383.4 - 619.8
	Random	0 - 1200	536.4	451.1 - 621.7
Desolation Sound				
CANDBH	Nest	45.6 - 136.3	78.1	71.2 - 85.0
	Random	36.7 - 105.5	69.6	63.9 - 75.3
CANHT	Nest	32.0 - 51.3	41.0	39.4 - 42.6
	Random	27.4 - 50.4	38.1	35.9 - 40.3
CANCOMPL	Nest	3.3 - 12.1	6.9	6.1 - 7.7
	Random	0.8 - 11.0	5.0	4.2 - 5.8
DENPLATR	Nest	10.2 - 137.5	44.2	34.6 - 53.8
	Random	5.1 - 74.8	37.9	32.8 - 43.0
SLOPE	Nest	1 - 51.5	2935	25.6 - 33.4
	Random	1 - 52.8	26.1	21.8 - 30.4
ELEV	Nest	5 - 910	430	361 - 499
	Random	10 - 1210	511.5	393 - 630

Table 1.4 Ranking of logistic regression models explaining nest habitat selection by marbled murrelets. Model number (#), number of estimated parameters (K), small sample Akaike's Information Criteria (AICc or QAICc), Akaike's weight (AICw) and Nagelkerke's R^2 (Nagelkerke 1991).

a) Clayoquot Sound (CS)

#	Model predicting nest vs. random site	K	QAICc	ΔQAICc	QAICw	R^2
1	**DENPLATR + CANDBH + CANHT + CANCOMPL + ASPECT + SLOPE + ELEV**	**8**	**57.80**	**0.00**	**0.56**	**0.55**
2	**DENPLATR + CANDBH + CANHT + CANCOMPL**	**5**	**59.66**	**1.85**	**0.22**	**0.38**
5	CANDBH + CANHT + CANCOMPL + ASPECT + SLOPE + ELEV	7	61.17	3.37	0.10	0.45
4	CANDBH + CANHT + CANCOMPL	4	62.66	4.88	0.05	0.27
3	DENPLATR + ASPECT + SLOPE + ELEV	5	62.89	5.08	0.04	0.32
7	DENPLATR	2	65.31	7.51	0.01	0.10
6	ASPECT + SLOPE + ELEV	4	66.75	8.95	0.01	0.17
8	Null	1	66.89	9.08	0.01	-

b*) Desolation Sound (DS)*

#	**Model predicting nest vs. random site**	**K**	**AICc**	**ΔAICc**	**AICw**	**R^2**
5	**Nest= CANDBH + CANHT + CANCOMPL + ASPECT + SLOPE + ELEV**	**7**	**92.98**	**0.00**	**0.40**	**0.36**
4	**Nest= CANDBH + CANHT + CANCOMPL**	**4**	**93.38**	**0.40**	**0.33**	**0.25**
1	Nest= DENPLATR + CANDBH + CANHT + CANCOMPL +ASPECT + SLOPE + ELEV	8	95.18	2.19	0.13	0.36
2	Nest= DENPLATR + CANDBH + CANHT + CANCOMPL	5	95.59	2.60	0.11	0.25
6	Nest= ASPECT + SLOPE + ELEV	4	100.62	7.64	0.01	0.14
3	Nest= DENPLATR + ASPECT + SLOPE + ELEV	5	101.06	8.08	0.01	0.17
8	Nest= Null	1	101.81	8.83	0.00	-
7	Nest= DENPLATR	2	102.42	9.44	0.00	0.03

c) Both Regions

#	Model predicting nest vs. random site	K	QAICc	ΔQAICc	QAICw	R^2
3	**DENPLATR + ASPECT + SLOPE + ELEV**	**5**	**117.20**	**0.00**	**0.20**	**0.20**
12	**DENPLATR + CANDBH + CANHT + CANHT^2 + CANCOMPL + CANCOMPL^2**	**7**	**117.32**	**0.23**	**0.19**	**0.25**
1	**DENPLATR + CANDBH + CANHT + CANCOMPL + ASPECT + SLOPE + ELEV**	**8**	**117.41**	**0.41**	**0.18**	**0.28**
9	**DENPLATR + CANDBH + CANHT + CANHT^2 + CANCOMPL + CANCOMPL^2 + ASPECT + SLOPE + ELEV**	**10**	**117.72**	**0.83**	**0.16**	**0.33**
2	DENPLATR + CANDBH + CANHT + CANCOMPL	5	118.68	2.49	0.10	0.18
6	Landscape	4	120.06	4.31	0.05	0.13
5	CANDBH + CANHT + CANCOMPL + ASPECT + SLOPE + ELEV	7	120.85	4.39	0.03	0.21
7	DENPLATR	2	121.10	5.68	0.03	0.05
4	CANDBH + CANHT + CANCOMPL	4	121.27	6.00	0.03	0.11
11	CANDBH + CANHT + CANHT^2 + CANCOMPL + CANCOMPL^2	6	122.16	6.07	0.02	0.16
8	Null	1	122.69	6.13	0.01	-
10	CANDBH + CANHT + CANHT^2 + CANCOMPL + CANCOMPL^2 + ASPECT + SLOPE + ELEV	9	122.85	8.05	0.01	0.24

Table 1.5 Top ranked models for each region showed good prediction success and proportionality to probability of use according to k-fold cross-validation. Significant rank-correlation indicates model prediction success Regression tests proportionality: models that are proportional to probability of use have zero intercept, β significantly different from zero and confidence interval including 1, high R^2 and insignificant χ^2 goodness of fit (Johnson 2006). Predictive performance (% sites with RSF score>x) is shown for each model as well as the averaged model for each set. * Parameter estimate is significantly different than zero (p <0.05).

		Rank correlation		**Regression**					**Predictive Performance (%)**		
Region	**Model**	r_s	*p*	**Intercept**	B_1	B_1 95% Confidence Interval	R^2	χ^2 p-value	**>0.50**	**>0.65**	**>0.80**
CS	1	0.964	0.0005	0.26	0.72*	0.39 – 1.04	0.87	0.87	78	52	44
	2	0.963	0.0005	-0.03	0.96	0.55 – 1.37	0.86	0.57	78	41	15
	Averaged								78	56	26
DS	5	0.929	0.0025	0.08	0.85*	0.46 – 1.25	0.83	0.10	78	54	27
	4	0.964	0.0005	-0.11	1.11*	0.69 – 1.53	0.88	0.67	65	43	16
	Averaged								78	49	13
Both	3	0.952	<0.0001	0.01	0.97*	0.61 - 1.33	0.81	0.76	58	25	6
	12	0.952	<0.0001	0.01	0.97*	0.78 - 1.16	0.94	0.98	63	39	9
	1	0.915	0.0002	0.09	0.92*	0.68 - 1.15	0.90	0.60	64	34	13
	9	0.818	<0.004	-0.03	0.93*	0.71 - 1.15	0.91	0.66	69	48	20
	Averaged								72	39	6

Table 1.6 Odds Ratios and 95% confidence intervals for final models. Odds Ratio for ASPECT represents the odds of a nest having a “north” aspect; odds of a “south” aspect are the reciprocal. Likelihood ratio tests indicate the significance of each variable within the model. * $p<0.05$ **$p<0.01$.

Variable	Odds Ratio	Confidence Interval
Clayoquot Sound	*Model 1*	
DENPLATR	**1.03****	1.02 - 1.04
CANDBH	**1.06***	1.03 - 1.09
CANHT	**0.83****	0.77 - 0.89
CANCOMPL	**0.89**	0.73 - 1.08
ASPECT (N)	**1.10**	0.763 - 1.61
ELEV	**1.00***	1.00 - 1.00
SLOPE	**1.10****	1.07 - 1.15
Desolation Sound	*Model 5*	
DENPLATR	**-**	
CANDBH	**1.02**	1.00 - 1.04
CANHT	**1.08**	0.99 - 1.17
CANCOMPL	**1.33**	1.14 - 1.56
ASPECT (N)	**2.49***	1.70 - 3.64
ELEV	**1.00**	1.00 - 1.00
SLOPE	**1.01**	0.99 - 1.03
Both Regions	*Model 9*	
DENPLATR	**1.02****	**1.02 - 1.03**
CANDBH	**1.03***	**1.02 - 1.04**
CANHT	**1.88***	**1.36 - 2.60**
CANHT^{2}	**0.99***	**0.99 - 0.99**
CANCOMPL	**0.82**	**0.56 - 1.20**
CANCOMPL^{2}	**1.03**	**1.00 - 1.06**
ASPECT (N)	**1.40**	**1.12 - 1.75**
ELEV	**1.00**	**1.00 - 1.00**
SLOPE	**1.03****	**1.03 - 1.07**

CHAPTER 2
USING HABITAT FEATURES AT MULTIPLE SCALES TO EXPLAIN FLEDGING SUCCESS AT MARBLED MURRELET NESTS IN SOUTHERN BRITISH COLUMBIA

2.1 Abstract

The marbled murrelet (*Brachyramphus marmoratus*) is a small alcid that nests almost exclusively in temperate old growth forests along the Pacific Coast of North America. Due to the extreme difficulty of locating marbled murrelets nests, data on fledging outcome of individual nests is scarce. I use a set of 58 nests from two regions of southwestern British Columbia (Clayoquot Sound and Desolation Sound) for which breeding outcome was confirmed by tree climbing at the end of the breeding season to investigate habitat features at multiple scales that may affect fledging success. Predation is the major cause of nest failure in this species, and success may depend on features that affect predator distributions and/or access to and concealment of the nest itself. This study is the first to investigate breeding success in murrelets using ground-measured variables and microhabitat features such as nest platform characteristics.

Although previous studies have shown that features at the landscape scale can explain variation in nest success in this species, these variables had little power predicting breeding success in this study, perhaps because the sample of nests was limited to those with ground accessibility. For the dataset available, the number of potential platforms within the nest tree, platform length and platform area were significant predictors of nest success at Desolation Sound. Such features may offer benefits to nesting marbled

murrelets in terms of reduced predator search efficiency, increased nest platform choice and nest access and concealment within the canopy. Univariate and multivariate analyses suggest weak detrimental effects of nesting near edges.

2.2 Introduction

The nesting habits of marbled murrelets (*Brachyramphus marmoratus*) are unique among seabirds. The species nests primarily on mossy platforms formed on large branches or deformities in large old growth trees of coastal forests (Nelson 1997). Commercial harvest of old growth coastal forests is thought to in part drive the decline of marbled murrelet populations throughout the species' range (Piatt et al. 2007). Protection of nesting habitat is therefore the focus of current management guidelines for the species in British Columbia (Burger 2002, Canadian Marbled Murrelet Recovery Team 2003).

Habitat, particularly breeding habitat, may have a large effect on an individual's fitness (Johnson 2007). Sustainable populations, therefore, depend on the availability of productive breeding habitat and effective management should include some indication of habitat productivity. Habitat selection models (see Chapter 1) aim to identify habitat selected by nesting marbled murrelets with the goal of identifying potentially suitable nesting habitat for possible protection. However, selection of a habitat for nesting does not necessarily reflect its fitness quality to an individual, or the Habitat Fitness Potential (Wiens 1989).

Since relatively few murrelet nests have been found, and nest outcome is rarely known, nesting habitat suitability models currently used to identify marbled murrelet nesting habitat in British Columbia do not include any measure of breeding success.

Nesting habitat selection can affect breeding success in a variety of ways (Clark and Shutler 1999). If habitats differ in fitness benefit (i.e., breeding success), and habitat selection is the result of adaptive behavioural decisions, one would expect selected habitat to also be the most productive. Zharikov et al. (2006) report that mid-chick rearing success is higher in smaller stands that were also more often selected by murrelets (but see Burger and Page 2007, Zharikov et al 2007b for a critical examination of these results). However, Waterhouse et al. (2008, 2009), using variables derived from airphoto interpretation, found evidence for apparently non-adaptive habitat selection by murrelets in Desolation (DS) and Clayoquot (CS) Sounds. If habitat selection appears maladaptive, it may indicate that murrelets are in an evolutionary trap (Schlaepfer et al. 2002), whereby changes have occurred such that poorer habitat retains or enhances habitat evaluation cues previously associated with more productive habitat. For example, easy access to the canopy via gaps in adjacent vegetation is important for both adults and fledging chicks (Hamer and Nelson 1995, Manley 1999). If proximity to gaps is preferred, clearcut edges, a relatively recent phenomenon with higher predator densities, may represent low quality habitat that retains the cues used by murrelets (Malt and Lank 2007b).

Marbled murrelet nests are notoriously difficult to locate and access. The outcome of nesting attempts by murrelets is relatively poorly understood, due to the difficulty of observing cryptic nests in the forest canopy. In a range-wide review of nest success, Nelson and Hamer (1995) reported 32.4% success, based on ground observations of 34 nests. When considering the 23 Pacific Northwest (excluding Alaska) nests in that sample, success was 39.1%. Ground-based observations of 68 nests at Desolation Sound

(Manley 1999) showed 33% success. Radio-telemetry at Clayoquot and Desolation Sounds was used to infer success to the mid-chick rearing stage for 137 nests (Bradley et al. 2004, McFarlane Tranquilla et al. 2005). This study, the most extensive of its kind for the species (Piatt et al. 2007) estimated overall success of 59.1% (Clayoqout 58.6, Desolation 65.7; Zharikov et al. 2006). Success was higher for ground inaccessible nests in this study (Bradley 2002), which may account for higher overall estimates of success compared to other studies where nests were located from the ground. Both methods are less likely to locate nests that failed in early incubation and may tend to overestimate success (Bradley et al. 2004). Hébert and Golightly (2007) suggest that murrelet nests may be particularly at risk to predation during early incubation as adults may be less attentive.

The most common cause of nest failure in marbled murrelets appears to be predation (Burger 2002). At DS, 86% of failed nests observed by Manley (1999) were depredated. Predators of murrelet nests include corvids such as ravens (*Corvus corax*), Steller's jays (*Cyanocitta stelleri*) and grey jays (*Perisoreus canadensis*); northern goshawks (*Accipiter gentilis*), and various other raptors (Burger 2002). Predation by arboreal mammals such as deer mice (*Peromyscus* spp.), tree squirrels (*Tamiasciurus* spp.) and northern flying squirrel (*Glaucomys sabrinus*) is suspected (Bradley and Marzluff 2003) and visits have been observed at artificial marbled murrelet nests (Malt and Lank 2007a). Other causes of failure include starvation, abandonment, and chick death (Nelson and Hamer 1995, T. Bloxton, USDA Forest Service, unpublished data).

Habitat characteristics of nest sites at multiple scales may reflect attempts by nesting murrelets to reduce predation. The nest itself is very low profile, consisting only of a depression in moss or duff substrate on the tree limb. Nests are occasionally situated on bare limbs with a surface sufficient to hold an egg (Nelson 1997). At the micro-site scale (“Nest”), nests tend to have high vertical and horizontal cover of overhead foliage, and are often located close to the tree bole, all of which may reduce visibility to predators (Nelson and Hamer 1995). At the element scale (“Nest Tree”), nests tend to be located in the canopy, on the upper portions of the tree canopy, where Nelson and Hamer (1995) suggest predators may be less active, although this was not supported by Masselink (2001). Preferences for stands with higher densities of “platform trees” (trees with at least one platform; Chapter 1, Rodway and Regehr 2002) may also reduce predator search efficiency by increasing the number of potential nest sites (Martin 1993, Chalfoun and Martin 2009). Characteristics of nest sites at patch and landscape scales are discussed in Chapter 1.

In this study I describe the habitat of successful and unsuccessful nests from the largest sample of real marbled murrelet nests with known outcome (Piatt et al. 2007). A function analogous to the Resource Selection Function (RSF) used in habitat selection is developed to describe the habitat features that contribute to success. Finally, I compare predicted probability of use derived from habitat selection models (Chapter 1) between successful and failed nests. If marbled murrelets were making adaptive habitat selection choices, I would expect nests with higher RSF scores to be more successful.

2.3 Methods

2.3.1 Study Area

This study took place in two regions of the southern coast of British Columbia, Canada: Desolation Sound (50°05’ N, 124°40’ W) on the mainland and Clayoquot Sound (49°12’ N, 126°06’ W) on the west coast of Vancouver Island (Figure 2.1). Both areas are mountainous with forest cover naturally fragmented by steep topography, fjords and stream channels. Clayoquot Sound has a cooler and wetter maritime climate than Desolation Sound, with mean summer (April-August) temperatures of 11.9° and 13.4°, rainfall of 720 mm and 300 mm, respectively. The two areas also differ in their degree of forest habitat loss, with over 80% loss of original old growth forest cover in Desolation Sound, compared to ~25% loss in Clayoquot (Zharikov et al. 2006).

2.3.2 Data Sources

Nest habitat plots were collected by ground crews at nest sites located by radio telemetry in Desolation Sound (1999-2001; n = 43) and Clayoquot Sound (2000-2002, n = 27). Birds were captured at sea during the breeding season and fitted with radio transmitters. Nest sites were located by helicopter when radio-tagged birds were found at an inland location on consecutive days. Ground crews accessed nest sites after the breeding season and climbers confirmed nest location, outcome and habitat features. Although 157 nests were located by radio-telemetry, many were inaccessible to ground crews and were therefore not included in this study. Since all nests used were observed directly, the measure of success in this study is inferred fledging, as opposed to “mid-chick rearing” success, used to describe the outcome of all nests found, regardless of accessibility (Bradley et al. 2004, Zharikov et al. 2006, Waterhouse et al. 2008).

Success was inferred by climbers based on evidence observed at the nest, described by Nelson (1997). Shell fragments, a distinct fecal ring and downy feathers indicate that the chick likely fledged. Direct evidence of failure was rarely observed, but when present included intact eggs, a chick carcass, or blood and permanent feathers in or near the nest. Failure was most often inferred by the absence of shell fragments (loss of egg) or an indistinct or absent fecal ring (loss of chick). This method is likely very accurate in determining fledging success, but does not offer consistent information on the timing or causes of failure.

Climbers also recorded habitat features at the nest, including nest platform dimensions, overhead foliage cover at the nest, platform height, and total potential platforms in the tree. Potential nesting platforms (typically mossy branches >15 cm diameter and >10 m above the ground) were counted within a 25 m radius of the nest tree, and other patch scale habitat features recorded using standardized protocol (Resource Inventory Standards Committee 2001).

Ground crews noted if forest edges were present within 50 m of the nest site, and edge type was classified *post hoc* using modified criteria based on Malt (2007). Edges were defined as natural if they were not the direct result of anthropogenic activity. Natural edge types included avalanche chutes, rivers, boulder fields or ocean shoreline. Natural openings less than 30 m wide were not considered as forest edges. Anthropogenic edges included roads, “hard” (recent clearcut) and “soft” edges (regenerating second growth forest; Malt and Lank 2007b). Since age was not known in this study, edges were defined on the basis of ground crew observations (i.e., “recent clearcut”, ”second growth” or “20-40 years old”). Ground crews recorded site elevation using GPS , while I obtained slope from Digital Elevation Maps (Integrated Land Management Bureau 2000).

2.3.3 Data Analysis

Since little is known about habitat features that may affect breeding success in marbled murrelets, I began by considering a large number of potential variables at the nest, nest tree, patch and landscape scales (Table 2.5). Landscape and patch scale (within 25 m radius of the nest) variables included those from habitat selection models (Chapter 1), as well as density of canopy trees (DENCANSTEM) and density of potential platforms (DENPLATFRM). Nest tree scale variables consisted of diameter of the bole at breast height (TRDBH), tree height (TRHT) and number of potential nesting platforms in the tree (TRPLATS). Height of nest trees was measured with a clinometer by ground crews and confirmed by climbers using a measured rope. Counts of platform abundance by climbers and ground crews are known to differ, with climber-based counts considered more accurate. Since all nest trees were climbed, climber-based counts were used for the variable TRPLATS, while ground-based counts were used for all trees (DENPLATFRM), regardless of whether they were climbed. Nest characteristics consisted of vertical foliage cover over the nest (VERCOV), which was measured following Manley (1999): exposed <33%, partial 34%-66%, covered >66%. Nest limb dimensions included nest limb diameter with moss measured at the location of the nest (DIANL), platform width (PLWID), length (PLLEN), area (PLATAREA) and depth of moss depression (PLDEP). The presence of an edge within 50 m (EDGE), year of breeding and the DATE (measured as days after April 1) of suspected initiation of breeding (“JD”, see Zharikov et al. 2006) were also analyzed.

I investigated univariate differences in these variables between regions and between successful and failed nests using independent samples t-tests (SAS Institute Inc. 2003) for continuous variables and Pearson chi-square tests for categorical variables. I visually assessed distributions of continuous variables for normality and natural log transformations were carried out for the following variables with non-normal distributions: CANHT, DENPLTFRM, TRPLATS and all Nest scale variables. For the variable PLLEN, for which there were large regional differences, I investigated within-species differences across regions to determine whether differences in platform length may be due to differential platform development in tree species.

I also took a multivariate approach, using logistic regression models to predict nest success in a design analogous to presence/absence design in habitat selection. Due to the large number of variables involved, including all possible combinations in logistic regression models would have increased the likelihood of selecting a spurious model. For logistic regression analysis, I chose variables with potentially significant univariate differences ($p < 0.2$) between fledged and failed nests for either region. These variables included EDGE, NLHT, TRPLAT, PLWID, PLLEN, and AREA. Variable inflation factors indicated that nest dimensions (PLWID, PLLEN, AREA) were highly intercorrelated (Variance Inflation Factor >10; Neter et al. 1996). To avoid multicollinearity, platform variables were combined in a principal component analysis. A single factor (PLAT1) with eigenvalue >1 was selected, with equal positive weight (0.5) for both PLLEN and AREA, and very weak weighting for PLWID (0.03). Since a number of apparently significant habitat variables different between regions for successful and failed nests, I applied models separately to CS and DS nests.

I initially considered all combinations of the four variables EDGE, NLHT, TRPLAT and PLAT1 as well as a null model, resulting in a set of fifteen models (Table 2.6). Support for the null model would indicate that factors other than those tested in the model set are responsible for variation in the response variable. Hosmer and Lemeshow Goodness-of-Fit tests were significant ($p < 0.05$) for several models, indicating poor fit; these models were removed from region-specific sets for subsequent analysis.

Sample sizes used here were relatively small (DS $n = 33$; CS $n = 25$), so I used Akaike's Information Criterion for small sample sizes (AICc). The global models for both regions combined indicated overdispersion ($\hat{c} = 2.80$), so the Quasi-Likelihood AIC (QAICc) was used for those model sets (Burnham and Anderson 2002). I consider models in which AICc values differ from the best-fitting model by ≤ 2 (ΔAICc, Burnham and Anderson 2002) as well as AIC_w, which indicated relative support for the model from among the candidate models.

Resource Selection Functions for selection at the landscape and patch scales were created for the set of nests considered here using ground habitat data (Chapter 1). I compared the RSF scores output from those models (one each for CS and DS and one for Both regions) for fledged and failed nests in the appropriate region(s). The mean RSF score, standard error and significance (Mann-Whitney U-test) are reported for each. I also compared the distributions of predicted probabilities using the Kolmogorov-Smirnov 2-sample test.

2.4 Results

Overall fledging success for this set of nests was 53% (n = 58). At CS, 13 out of 25 nests fledged (52%). Success could not be determined for two ground-accessible nests. Of the unsuccessful nests, one contained an intact egg with no embryo, predated remains of the radio-tagged adult were found in one nest, and four nests contained the predated remains of chicks. Cause of failure is not known for the remaining six unsuccessful nests. The minimum rate of predation at CS was therefore 20%. At DS, 18 out of 33 nests were successful to fledging (55%). Success was not determined at three nests, and tree data were not available for one other nest. Climbers found evidence for the cause of failure at five nests: two with intact eggs, two with chick predation and one intact deceased chick. The minimum rate of predation at DS was therefore 6%.

Nests were found in three years at each region. There was no significant difference in fledging success by year (Table 2.1) or slope aspect (Table 2.2), although power in these comparisons is limited. No anthropogenic edges occurred within 50 m of nests at CS used in this study (one of the nests for which success was not determined was near a road). The single ocean-edge nest was successful, while none of the three avalanche chute nests and two of five river-edge nests fledged a chick. Ten of 16 (63%) interior nests were successful. Success appears higher at interior sites than edges, but neither differed significantly from the overall success rate for CS (Table 2.3).

At DS, 4 nests were near anthropogenic edges (1 road, 1 hard, 2 soft); of these, only the nest near a road was successful. At natural edges, 2 of 5 river nests, 2 of 4 avalanche chutes and one ocean-edge nest were successful. Sixty three percent of 19 nests located more than 50 m from an edge ('Interior') were successful. As at CS, a higher proportion of interior nests than edge nests were successful, but the difference was not significant. This comparison approaches significance in the pooled sample (Table 2.3).

No nests occurred on exposed platforms at CS, while one exposed platform was used at DS. Partial and exposed nests were no less successful than nests on covered platforms (Table 2.4). Vertical cover was noted for all platforms in a subset of nest trees from both regions in this study. Nests in those trees were significantly more likely to occur on covered platforms than expected based on the available platforms (nests: n = 39, 80% covered; available: n = 748, 31% covered; $\chi^2 = 42.9$, df = 1, $p<0.01$).

At CS, fledged nests did not differ significantly from failed nests for any of the continuous variables used here (Table 2.5a). At DS, successful nests were on platforms that were significantly larger, and in trees with more platforms, than failed nests (Table 2.5b). A number of attributes at various scales differed between regions (Table 2.5). Differences in platform length were especially striking, with significantly longer platforms used for nesting at DS. Platform length differed among regions for the same tree species. Western hemlock (*Tsuga heterophylla*) was the only species with reasonable representation ($n \geq 5$) in each region, and platforms in these trees were significantly longer at DS (mean 167 cm ± 34 s.e., n = 8) than at CS (mean 52 ± 10 cm, n = 11; Mann-Whitney U-test U = 112.0, p = 0.009).

AIC model ranking gave significant support to the Null model for both CS and Both regions (Tables 2.7a, c); indicating that variation in fledging success is primarily due to variables not included in the model set. At DS, TRPLAT and PLAT1 factors, both together and on their own, comprise the top 3 models with a cumulative AIC_w of 0.54 (Table 2.7b). Model 12 (EDGE + TRPLAT + PLAT1) also receives significant support.

Distributions of predicted probabilities did not differ for any of the three models (Figure 2.2). At CS, predicted probabilities of nesting derived from landscape and patch level habitat selection models were slightly higher for successful nests compared to failed nests (0.72 ± 0.6 standard error versus 0.59 ± 0.9; Figure 2.2a), but the difference was not significant (U = 136, p = 0.29). At DS, successful nests differed very little from failed nests (0.69 ± 0.05 vs. 0.63 ± 0.05; U = 230, p = 0.38; Figure 2.2b). and failed nests had similar probabilities (0.63 ± 0.04; 0.59 ± 0.03, respectively; U = 718, p = 0.22, Figure 2.2c). Distributions of predicted probabilities did not differ for any of the three models (Figure 2.2).

2.5 Discussion

This study is the first to analyze ground habitat features at multiple scales around real marbled murrelets nests with known outcomes. In general, habitat features at successful nests varied little from those at failed nests; although significant differences were detected for two variables at the element and nest scale at DS. Multiple logistic regression models for CS and for Both regions suggest that factors not considered here, at other scales, or chance, are responsible for variation in predicting nest success. At Desolation Sound, nests that were successful to chick fledging were in trees with more potential nesting platforms and located on platforms that were larger than failed nests. Nest platforms at DS were generally much larger than platforms at CS, where I found no differences in nest parameters between successful and failed nests.

This study analysed the subset of nests that were accessible to crews on the ground. Previous work using the entire set of nests at DS found by radio-telemetry has found that breeding success from ground accessible nests (used here) was lower than estimates for all the nests (Bradley et al. 2004). The inability to detect such effects in this study might be due to the accessibility bias discussed earlier. Since measurements of the nest tree and platform are not available for inaccessible nests, it is not known how or whether this bias affects the results at the scales assessed here. However, this study describes productive habitat in the areas and types of potential murrelet nesting habitat that is economically most accessible to commercial harvest, and thus our results should be of value for forestry planning (Forest Practices Board 2008).

2.5.1 Causes of failure

Causes of mortality other than predation may be independent of forest nesting habitat conditions. No information is available on individual quality of nesting adults, nor on conditions at marine foraging sites, but breeding success did not differ by year, indicating no evidence for inter-annual effects. Depending on nest location, many murrelet parents may travel long distances. Hull et al. (2001) using the radio-telemetry nest set found that commuting distance (based on marine capture site) did not correlate with breeding success, within the range of 12.1-102.3 km that the Desolation Sound birds were commuting. Predation of adults or poor foraging conditions at sea may cause abandonment or reduced attendance (Blight et al. 1999). Adult experience and body condition, as well as offspring viability may also affect success rates. Although predation is widely suspected to be the leading cause of nest mortality, an unknown portion of predated nests may have experienced reduced attendance or abandonment, thereby increasing the risk of predation (Hébert and Golightly 2007). Many of these factors are likely to cause failure regardless of habitat at the nest site.

2.5.2 Effects of forest edges

My results suggest that modest detrimental edge effects exist. The univariate comparison (Table 2.3) approached statistical significance ($p = 0.08$), and "Edge" was retained in a supported multivariate model (Table 2.7). Proximity to edge is known to affect predator densities, and therefore is expected a priori to affect marbled murrelets nest success. Malt and Lank (2007b, in press) employed an experimental design using artificial murrelets nests in Southern British Columbia. Results of that study indicated that recent clearcut ("Hard") edges had higher rates of predation than nearby interior nests, while natural and regenerating ("Soft") edges were not found to have a detrimental effect. All three of the murrelet nests in this study located within 50 m of hard or soft edges failed, but the small sample size makes it difficult to draw conclusions. The effect of road edges on murrelet nesting was not considered by Malt and Lank (2007b, in press), and is poorly understood. A large number of nests in the sample were located near natural edges (Bradley 2002, for DS) in both regions.

Zharikov et al. (2006), using the entire radio-telemetry set of nests suggested that murrelets were able to successfully breed in close proximity to edges, and may even have better success near edges. However, since the spatial scale of differences found in that study was larger than the ~50-100 m into the forest considered likely for edge effects Burger (2002, Burger and Page 2007), Zharikov et al. (2007) suggested that the result might reflect spatial covariation of superior murrelet nesting habitat and forestry activity. Our methods also differed from that study: helicopter GPS positions for inaccessible nests were considered accurate to within 100 m (Bradley et al. 2004, Bradley and Cooke 2001), while Burger (2002) suggests that detrimental edge effects likely extend ~50-100 m into the forest. I used notes written by habitat crews that described the nearest edge within 50 m, regardless of GPS positional error.

2.5.3 Evidence for adaptive habitat selection

My study finds no evidence for adaptive or maladaptive habitat selection with respect to nest site variables. Habitat selection models from Chapter 1 were based on ground information at the patch level and select landscape factors. One model for each region (CS, DS, and Both pooled) was selected that best describes habitat selection in that dataset; these models were found to have good predictive power and yield an RSF score proportional to the probability of use as a nest site. If habitat selection is an adaptive process, successful nests would be expected to have higher probability scores than failed nests for the appropriate region-specific model. Based on this set of models, there is no evidence for or against adaptive habitat selection.

Previous work by Waterhouse et al. (2008) suggested that murrelets were actually using less productive habitat more often than expected, providing evidence for a potential evolutionary trap (Schlaepfer et al. 2002). providing evidence for a potential evolutionary trap (Schlaepfer et al. 2002). The accessibility bias, inherent in the present study using ground variables for this species, may account for differences in results, if Waterhouse et al.'s results were largely driven by inaccessible sites. However, I will consider other explanations.

I failed to detect significant differences between successful and failed nests for nearly all variables examined in this study. This set includes only actual nests that presumably reflect the habitat selection decisions made by nesting marbled murrelets. The absence of any difference between successful and failed nests may occur because all the nests have the necessary micro-habitat features required for success. Failure would then be due to factors other than nest micro-habitat. This would be the case if successful nesting habitat is not limiting, and one assumes that habitat selection is adaptive in terms of selecting productive habitat.

One potential example of this is vertical cover above nests (VERCOV), where most nests (80% at CS, 69% at DS; Table 2.4) were well covered. In a subset of nest trees, nests occurred on covered platforms more often than expected based on the distribution of platform cover classes for all available platforms in those trees. This indicates that selection, as observed by Manley (1999) may have already occurred for nests with high vertical cover.

2.5.4 Regional differences

Habitat at nest sites differed between CS and DS for a number of variables. At the patch scale, differences could result from differing habitat selection patterns. An analysis of habitat selection in these regions (Chapter 1) indicated strong selection for density of platform trees (DENPLATR) at CS only. While the density of platform trees for all available sites measured was not greater than at DS, nest sites at CS did have more platform trees. At DS, nests were also on larger platforms, and in taller trees with more platforms than at CS. In general, murrelets seem to use larger trees at DS. Forests may be more heterogeneous at DS than at CS; canopy complexity (CANCOMPL) is greater for nests at DS, where stronger selection for this attribute was also detected (Chapter 1).

2.5.5 Functions of variables with respect to fledging success

Manley (1999) found evidence for nest site selection at DS with respect to a number of the habitat variables considered here. Murrelet nests in that study tended to be in patches with more platform trees, although selection for density of platform trees was not found to be an important factor at DS in a more recent analysis of habitat selection at the landscape and patch scales (Chapter 1). Nest trees are often larger in terms of DBH, taller and have more potential nesting platforms than other trees (Manley 1999, Chapter 3). Within the nest tree, Manley (1999) found that nest platforms had larger area and more vertical cover than other potential nesting platforms. Each of these factors may confer benefit in terms of reduced predation or falling hazards (in the case of platform area) and would be expected to result in increased fledging success.

General characteristics of nest trees and platforms matched findings by Hamer and Nelson (1995) and Manley (1999). Platforms were on limbs that ranged in diameter (with moss) from 14-74 cm, and chicks fledged from nests on small limbs (14-20 cm) were able to successfully fledge chicks. All nests except for one had mossy substrate ranging in depth from 1.0-13.5 cm. One successful nest at CS was located on a bare branch 32 cm in diameter. This shows that potential platforms that might be considered 'suboptimal' due to their small size or lack of epiphytes are capable of supporting successful nests. This study provides no evidence, within the range used, that nesting success varies with limb diameter, platform width or substrate depth vary with nesting success. Platforms at DS were much larger than at CS in terms of both area and length, and both these were associated with increased fledging success. Differences in success based on platform area were mainly driven by platform length. The primary benefit to increased platform size has been considered mainly in terms of increased width/branch diameter (Nelson and Hamer 1995). Activity at the nest is mostly limited to a landing pad for provisioning adults (often a few cm distant from the nest cup) and the nest cup itself (Nelson and Peck 1995), although chicks become quite active prior to fledging and may pace the platform (Hamer and Nelson 1995). However, the length of platforms at DS (109 ± 20 cm and 162 ± 23 cm for failed and fledged nests, respectively) seems much longer than required for nesting activities. Long platforms may extend farther, and allow varying degrees of cover and access along their length. Both easy access and vertical cover over the nest are likely important components of success (Hamer and Nelson 1995, Manley 1999), and long platforms may offer both (L. W. Waterhouse, personal communication).

The finding that nest platforms at DS are much larger than those at CS is surprising. The differences do not appear to be due to observer bias (the same climber measured all platforms) or tree species. Western hemlocks, a tree species that supported a significant portion of nests in both regions (Chapter 3), had much longer nest platforms at DS than at CS. With no information on other available platforms I cannot state whether these regional differences are due to differential habitat selection or platform development.

Strong selection has been found for trees with more potential nesting platforms than neighbouring trees (Chapter 3) or available trees across the landscape (Manley 1999). My findings suggest that trees with more platforms also provide safer nest sites at DS. Manley (1999) proposed that such trees may provide a better selection of optimal nest sites, or that predator search efficiency is decreased. With more potential choices available, the likelihood of finding a high quality nest is improved. Nest predators also have more potential sites to choose from if they are actively searching for murrelets nests, thereby reducing their efficiency (Martin 1993, Chalfoun and Martin 2009). The latter hypothesis assumes that predators are searching for nests rather than encountering them opportunistically, which is more likely when nests occur at very low density as with this species.

2.5.6 Conclusions

Working with tree and nest level variables from the ground-accessible subset of the same nest data, this study found few differences, suggesting that site level habitat features that determine success were not limiting in this set of nests, and few if any birds were forced to use suboptimal (less successful) habitat. Studies at larger scales (Bradley 2002, Waterhouse et al. 2004, Zharikov et al. 2006, 2007a, Waterhouse et al. 2008) have found that factors such as timing, edges, proportion of young forest, elevation and slope correlate with breeding success. Ground accessibility bias or the scale and methods of measurement for certain variables may be responsible for the differences in findings. I suggest, however, that variations in landscape-level factors are in fact more important in determining fledging success in marbled murrelets than the variation in nest site characteristics among utilized sites. Larger-scale factors are best measured using remote methods (air photo interpretation and low-level aerial surveys; Chapter 4, Appendix 2, 3) rather than ground-based assessment. However, significant regional differences exist in nesting habitat observed at the patch scale, and certain features of the nest (area) and the nest tree (platform availability) may be important in some situations. Unfortunately, these smaller scale features are not practical to measure over large areas, but they may be correlated to patterns of tree growth and platform development in ways that are not yet well understood.

Current management for marbled murrelet nesting places high value on those habitats most often selected, and does not incorporate any measure of habitat productivity. However, selected habitat (disproportionately used versus available) may not always be the most productive for a number of reasons (Railsback et al. 2003). Since habitat selection may depend on the decisions of conspecifics (i.e., earlier nesters), intraspecific competition for nest sites could occur whereby individuals are excluded from certain patches of the highest quality habitat, leading to lower densities in more productive habitat, and producing discrepancies between “selected” and productive habitat. Having found few differences between tree and nest level factors of successful and failed nests, I can infer that at current murrelet nesting densities, intraspecific competition for sites may not be substantial at this scale of habitat choice.

For conservation, habitats that offer higher productivity, or higher habitat fitness potential (Wiens 1989) should be of most interest. The findings of this study indicate that fitness does not vary substantially with factors affecting nest-level habitat selection among utilized nest sites. Habitat fitness potential, would therefore, be proportional to selection, and using habitat selection models for management of breeding habitat is justified.

2.6 Figures

Figure 2.1 Map of study regions in south coastal British Columbia showing the locations of successful (circles) and failed (triangles) nest sites.

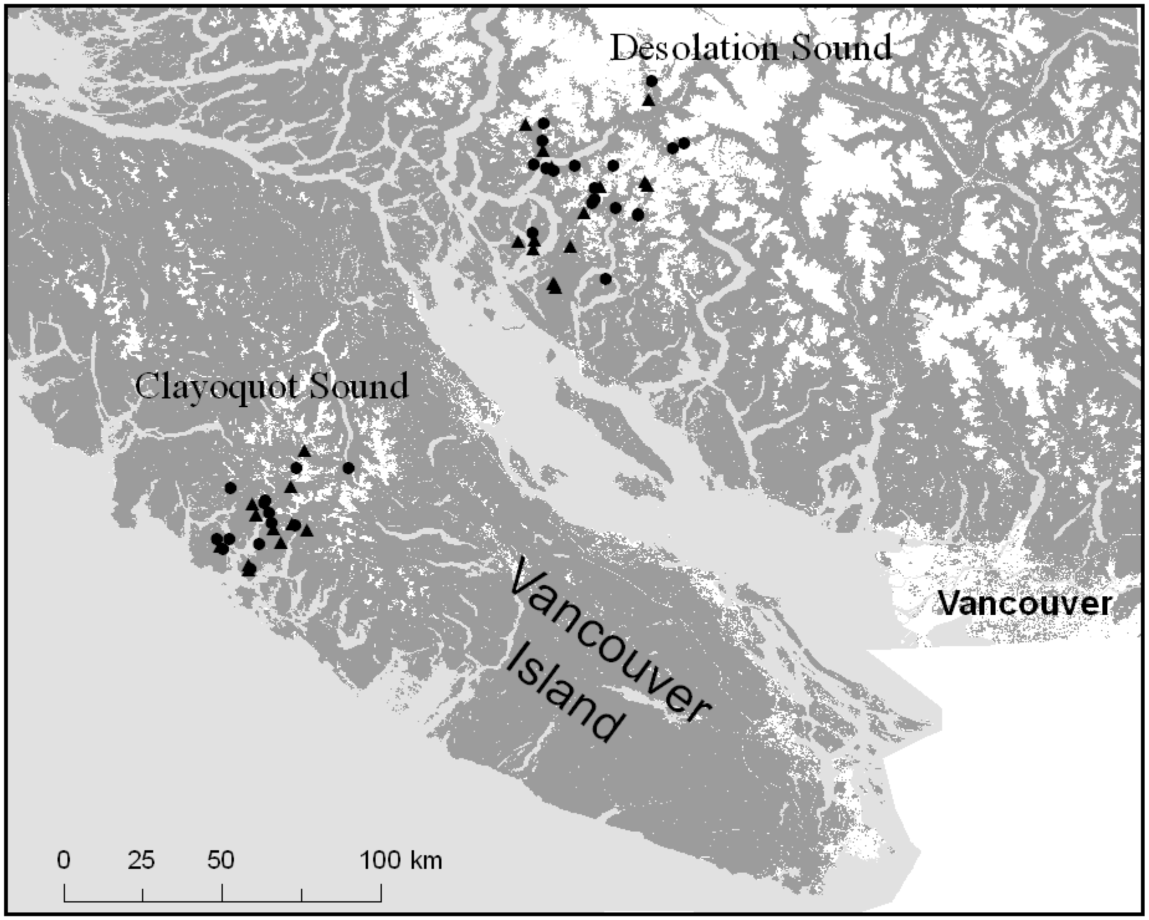
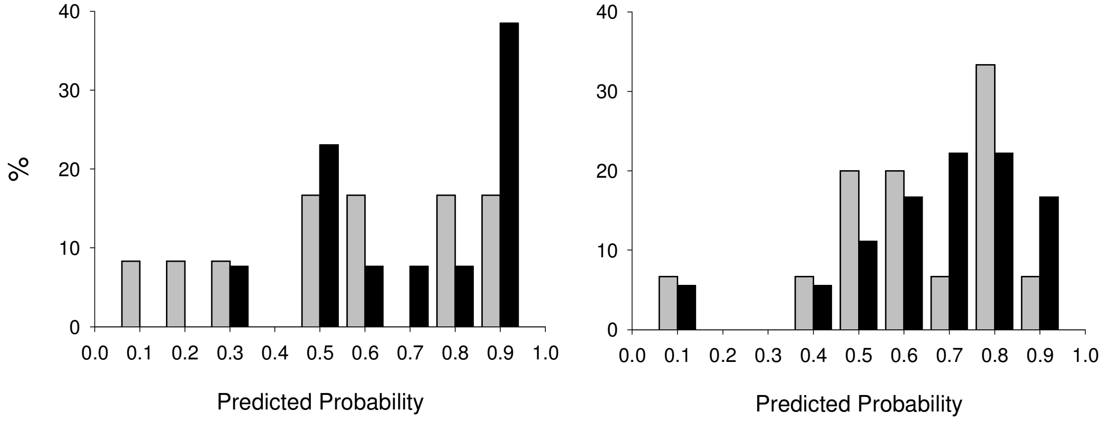


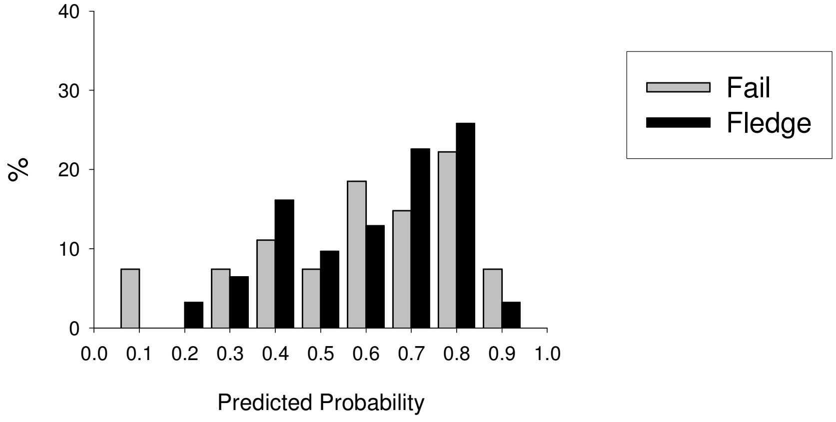
Figure 2.2 Fledged and failed nests did not differ in terms of predicted probabilities of nesting based on ground habitat selection models. CS: failed n = 12 fledge n = 13, Kolmogorov-Smirnov 2-sample test: KSa = 1.28, p = 0.08; DS: failed: n = 15 fledge n= 18, KSa = 0.43 p = 0.99; Both: n = 27, KSa = 0.64, p = 0.81.



a) Clayoquot Sound

b) Desolation Sound

C) All Regions



2.7 Tables

Table 2.1 Fledging success did not differ among years. χ^2 tests (df = 2) are reported.

Region		Fail	Fledge	χ^2	p
CS	**2000**	3	2		
	2001	3	5		
	2002	6	6	0.66	0.72
DS	**1999**	3	0		
	2000	3	7		
	2001	9	11	4.56	0.10

Table 2.2 Fledging success by slope aspect (N = North, E = East, S = South, W = West). χ^2 statistics (df = 1) and Fisher's exact probabilities are reported for each aspect class compared to the overall success rate.

Region		Fail	Fledge	χ^2	p
CS	**N**	4	4	0.92	1.0
	E	7	3	1.40	0.29
	S	1	3	0.74	0.6
	W	0	3	2.52	0.40
DS	**N**	5	3	0.74	0.45
	E	6	7	0.01	1.0
	S	0	2	1.60	0.50
	W	4	6	0.09	1.0

Table 2.3 Relationship between fledging success and proximity to edge within 50 m (χ^2 test, 1 df). Successful nests occurred less frequently at edges, and the pooled data shows a trend towards significant effects, though power is limited. For CS and DS, p-values from Fisher exact test are reported. χ^2 test (df = 1) is used for both regions combined.

Region		**Fail**	**Fledge**	χ^2	**p**
CS	**Edge**	6	3		
	Interior	6	10	-	0.23
DS	**Edge**	8	6		
	Interior	7	12	-	0.30
Both	**Edge**	14	9		
	Interior	13	22	3.14	0.08

Table 2.4 Fledging success did not differ with vertical cover above the nest. Exposed <33% cover above nest, Partial 33-66%, Covered >67%. Fisher's exact p-values are reported for CS and DS and χ^2 statistic for both regions pooled. At DS, one failed nests was exposed; for this analysis, exposed and pooled nests were combined.

Region		**Fail**	**Fledge**	χ^2	**p**
CS	**Partial**	3	2		
	Covered	9	11	-	0.64
DS	**Exposed/ Partial**	5	6		
	Covered	10	12	-	1.00
Both	**Exposed/ Partial**	8	8		
	Covered	19	23	0.11	0.75

Table 2.5 Fledging success did not differ for most continuous variables. Mean and standard error, U statistics and two-tailed p-values from Mann-Whitney U-tests are reported. * indicates variables that differed significantly between regions for either successful or failed nests (t-test, p<0.05). At CS, n = 25 for all variables except JD (n = 23). At DS, n = 33 for all variables. See text for variable abbreviations.

a) Clayoquot Sound

			Failed			**Fledged**				
Scale	**Variable Name**	**Units**	**Mean**	**±**	**s.e.**	**Mean**	**±**	**s.e.**	**t**	***p***
	DATE	Days after April 1	65	±	5	59	±	5	1.03	0.31
Landscape	ELEV	m	488	±	85	537	±	99	-0.38	0.71
	SLOPE	°	30.5	±	3.3	32.4	±	4.5	-0.33	0.74
Patch	DENPLATR*	Trees/ha	59	±	6	59	±	7	-0.02	0.98
	DENPLTFRM	Platforms/ha	229	±	41	226	±	30	-0.34	0.73
	CANDBH	cm	79	±	3	83	±	5	-0.64	0.53
	CANHT	m	35	±	2	33	±	2	0.59	0.57
	CANCOMPL*	m	4.9	±	0.7	5.0	±	0.7	0.02	0.98
Nest Tree	TRDBH	cm	95	±	11	121	±	12	1.60	0.12
	TRHT*	m	39	±	3	37	±	2	0.43	0.67
	NLHT*	m	27	±	3	27	±	2	0.16	0.87
	HTINTREE	% tree height	69	±	4	73	±	3	0.85	0.40
	TRPLATS*	*n*	18	±	3	13	±	2	1.12	0.27
Nest	DIANL	cm	30	±	4	29	±	3	0.23	0.82
	PLWID	cm	23	±	3	23	±	2	-0.26	0.80
	PLLEN*	cm	59	±	13	48	±	7	0.14	0.89
	AREA*	cm^2	1169	±	199	1109	±	222	0.00	0.99
	PLDEP	cm	4.6	±	0.4	4.7	±	1.0	0.13	0.89

b) Desolation Sound

Scale	**Variable Name**	**Units**	**Failed**			**Fledged**			**t**	***p***
			Mean	**±**	**s.e.**	**Mean**	**±**	**s.e.**		
	DATE	Days after April 1	58	±	5	55	±	3	0.62	0.54
Landscape	ELEV	m	429	±	69	455	±	41	-0.34	0.74
	SLOPE	°	27.6	±	3.6	31.1	±	2.9	-0.76	0.45
Patch	DENPLATR*	Trees/ha	40	±	6	45	±	8	0.49	0.63
	DENPLTFRM	Platforms/ ha	179	±	41	236	±	67	-0.76	0.45
	CANDBH	cm	76	±	5	78	±	5	-0.26	0.79
	CANHT	m	36	±	1	37	±	1	-0.61	0.55
	CANCOMPL*	m	6.8	±	0.6	7.1	±	0.5	-0.33	0.75
Nest Tree	TRDBH	cm	114	±	10	125	±	11	-0.73	0.57
	TRHT*	m	46	±	3	51	±	3	-1.19	0.24
	NLHT*	m	29	±	3.0	32	±	2	0.69	0.49
	HTINTREE	% tree height	64	±	3	64	±	3	-0.02	0.99
	TRPLATS*	*n*	19	±	3	28	±	3	-2.10	0.04
Nest	DIANL	cm	28	±	4	25	±	2	0.41	0.68
	PLWID	cm	19	±	1	23.4	±	2	-1.48	0.15
	PLLEN*	cm	109	±	20	162	±	23	-1.70	0.10
	AREA*	cm^2	2057	±	340	3667	±	514	-2.03	0.05
	PLDEP	cm	4.3	±	0.4	4.6	±	0.5	-0.05	0.96

Table 2.6 The model set used to explain fledging success for both CS (n = 25) and DS (n = 33).

#	Model
1	EDGE + NLHT + TRPLAT + PLAT1
2	EDGE
3	NLHT
4	TRPLAT
5	PLAT1
6	EDGE + TRPLAT
7	EDGE + NLHT
8	EDGE + PLAT1
9	TRPLAT+ PLAT1
10	TRPLAT + NLHT
11	TRPLAT + NLHT + PLAT1
12	EDGE + TRPLAT + PLAT1
13	EDGE + TRPLAT + NLHT
14	EDGE + NLHT + PLAT1
15	Null

Table 2.7 Ranking of logistic regression models explaining fledging success by marbled murrelets. Model number (#), number of estimated parameters (K), small sample Akaike's Information Criteria (AICc), Akaike's weight (AIC_w) and Nagelkerke's R^2 (Nagelkerke 1991) are listed. Models ranked based on AIC_w, with models in bold considered to have the most substantial support (ΔAICc $\leq$2). Models with significant Hosmer and Lemeshow Goodness-of-fit statistics were excluded.

a) Clayoquot Sound

#	Model	K	AICc	ΔAICc	AIC_w	R^2
15	**null**	**1**	**36.79**	**0.00**	**0.22**	**-**
4	**TRPLAT**	**2**	**36.83**	**0.04**	**0.21**	**0.12**
2	**EDGE**	**2**	**37.17**	**0.38**	**0.18**	**0.10**
6	**EDGE + TRPLAT**	**3**	**38.16**	**1.37**	**0.11**	**0.18**
5	PLAT1	2	38.89	2.10	0.08	0.01
10	TRPLAT + NLHT	3	39.31	2.52	0.06	0.12
7	EDGE + NLHT	3	39.56	2.77	0.05	0.11
12	EDGE + TRPLAT + PLAT1	4	41.02	4.23	0.03	0.18
13	EDGE + TRPLAT + NLHT	4	41.02	4.23	0.03	0.18
11	TRPLAT + NLHT + PLAT1	4	42.09	5.30	0.02	0.13
14	EDGE + NLHT + PLAT1	4	42.38	5.59	0.01	0.11
1	EDGE + NLHT + TRPLAT + PLAT1	5	44.17	7.38	0.01	0.18

b) Desolation Sound

#	Model	K	AICc	ΔAICc	AIC_w	R^2
9	**TRPLAT + PLAT1**	**3**	**43.86**	**0.00**	**0.24**	**0.30**
4	**TRPLAT**	**2**	**44.51**	**0.65**	**0.17**	**0.20**
5	**PLAT1**	**2**	**45.08**	**1.22**	**0.13**	**0.18**
12	**EDGE + TRPLAT + PLAT1**	**4**	**45.73**	**1.87**	**0.09**	**0.32**
6	EDGE+ TRPLAT	3	46.10	2.24	0.08	0.23
11	TRPLAT + NLHT + PLAT1	4	46.23	2.37	0.07	0.31
10	TRPLAT + NLHT	3	46.94	3.08	0.05	0.20
15	Null	1	47.60	3.74	0.04	-
14	EDGE + NLHT + PLAT1	4	48.11	4.25	0.03	0.25
1	EDGE + NLHT + TRPLAT + PLAT1	5	48.38	4.52	0.03	0.33
2	EDGE	2	48.53	4.67	0.02	0.05
13	EDGE + TRPLAT + NLHT	4	48.69	4.83	0.02	0.23
3	NLHT	2	49.36	5.50	0.02	0.02
7	EDGE + NLHT	3	50.72	6.86	0.01	0.06

c) Both regions

#	Model	K	QAICc	ΔAICc	AIC_w	R^2
15	**Null**	**1**	**30.69**	**0.00**	**0.26**	**-**
2	**EDGE**	**2**	**31.71**	**1.02**	**0.16**	**0.07**
5	**PLAT1**	**2**	**31.78**	**1.09**	**0.15**	**0.07**
4	**TRPLAT**	**2**	**32.47**	**1.78**	**0.11**	**0.02**
3	NLHT	2	32.75	2.06	0.09	0.01
6	EDGE+ TRPLAT	3	33.51	2.82	0.06	0.10
7	EDGE + NLHT	3	33.92	3.23	0.05	0.07
10	TRPLAT + NLHT	3	34.69	4.00	0.04	0.02
14	EDGE + NLHT + PLAT1	4	35.04	4.35	0.03	0.14
13	EDGE + TRPLAT + NLHT	4	35.80	5.11	0.02	0.10
11	TRPLAT + NLHT + PLAT1	4	36.22	5.53	0.02	0.07

CHAPTER 3
SELECTION OF NEST TREES BY MARBLED MURRELETS WITHIN OLD GROWTH FOREST PATCHES

3.1 Abstract

Understanding nesting habitat selection is of major interest to marbled murrelet (*Brachyramphus marmoratus*) conservation since the species nests in coastal old growth forests with high commercial value for logging. Habitat selection for this species has been studied at a variety of scales using ground and remote methods.

I investigated nest tree selection within a forest patch. Since marbled murrelet nesting activity is limited to a single tree, distinctive attributes of that tree may be important components of nest patch selection. Compared to neighbouring trees in the immediate surrounding patch, nest trees were often distinctive: they were typically taller, with a larger stem diameter, more potential nesting platforms and more moss than the average in the patch, and dispropotionately nest trees were the largest tree available within 25 metres. An analyses of platform usage as a function of the number of platforms per platform tree suggests that murrelets select platforms rather than platform trees per se. These findings emphasize the importance of single, large trees within a patch and have implications for habitat quality ranking by remote methods.

3.2 Introduction

Nesting habitat selection is a major topic of research on marbled murrelets. Loss of old growth nesting habitat has been identified as a major factor in population declines and management of nesting habitat is a key part of the recovery strategy for this threatened species in Canada (Canadian Marbled Murrelet Recovery Team 2003). Marbled murrelet nests are usually located on large limbs that offer a soft substrate of epiphytes (moss) or accumulated lichen and duff into which a depression is formed to hold a single egg (Nelson 1997). Limbs of sufficient size (typically >15 cm diameter including epiphyte cover if present; referred to as “platforms”) occur almost exclusively in old growth coniferous trees at least 140 years old (Burger 2002).

Nest site selectivity has been investigated at a variety of scales. At the landscape level, selection occurs for features that limit access and availability of nesting habitat (i.e., maximum distance to ocean and elevation; Burger 2002), topographic complexity (Waterhouse et al. 2004, 2009), and wetter north and west aspect (Chapter 1). Selection for forest patches within the landscape has also been shown. Mean tree size (stem diameter as well as canopy height), canopy structure and complexity, and the density of potential platforms and platform trees have been described as characteristics of habitat surrounding nest sites (Burger 2002 for summary). These habitat variables discriminate nest sites from available habitat (Waterhouse et al. 2004, Hamer et al. 2008, Waterhouse et al. 2008, 2009, Chapter 1) using either ground or remote (air photo interpretation, low-level aerial surveys) methods of habitat assessment. At the micro-site level, defined as a nest platform within the tree, Manley (1999) found that murrelets selected mossy platforms with greater vertical foliage cover above the nest. Both landscape and patch variables were retained in the best models in a recent multi-scale analysis of habitat selection (Chapter 1).

Selection for the nest tree within the patch, referred to as element-level selection (Manley 1999) or fourth order habitat selection (Meyer et al. 2007) is not well understood. Manley (1999) found that nest trees were taller and had more platforms than other trees in the forest patch surrounding the nest tree. At Clayoquot Sound, British Columbia, Conroy et al. (2002) found that five known nest trees had larger DBH, and more platforms than other trees in the valley. In Oregon, nest trees also had significantly larger DBH, more platforms and more moss than neighbouring trees (Nelson and Wilson 2002).

Between 1998 and 2002, SFU researchers located the largest set of nests for this species (Piatt et al. 2007) using radio telemetry in southern British Columbia (Bradley 2002, Bradley et al. 2004). This set of nests has been used for habitat selection studies of landscape features (Zharikov et al. 2006, Zharikov et al. 2007a), and nest patches using air photo interpretation (Waterhouse et al. 2004, 2008), low-level aerial surveys (Waterhouse et al. 2009) and using ground-based habitat data (Chapter 1). Although habitat selection at these larger scales is directly applicable to management questions and applies over a much greater area, murrelet activity is limited to a single tree within the patch or the landscape. If nest trees are distinctive from neighbouring trees in the patch, the presence of such distinctive trees may be an important characteristic of nest patches. For example, some of the nests located by radio telemetry were in large veteran trees within a matrix of otherwise unsuitable habitat (Zharikov et al. 2006), suggesting that in some cases characteristics of the single nest tree may be more important for selection than those of the surrounding patch.

In studies of habitat selection, it is important to appropriately define “available” habitat (Johnson 1980), and this is one important difference between the present study of element level habitat selection and that of Manley (1999), who compared pooled samples of nest trees to all other trees measured. I assume that selection is a hierarchical process (Battin and Lawler 2006) and that habitat selection has already occurred at the patch level and higher scales. Therefore, the available habitat in this study is defined as the patch surrounding the nest tree. I compare nest trees to all other canopy trees within 25 m and to the subset of those trees containing platforms. Several studies report that murrelets select trees with more platforms (Manley 1999, Conroy et al. 2002, Nelson and Wilson 2002). I examine usage versus availability of platforms among platform trees to look for evidence that this pattern results from selection for platform trees *per se*, as opposed to occurring simply because platform trees have more platforms. Finally, I investigate whether nest trees that differ from their neighbours are more productive in terms of fledging success than less distinctive trees.

3.3 Methods

The study took place at Clayoquot Sound (CS; 49°12’ N, 126°06’ W) and Desolation Sound (DS; 50°05’ N, 124°40’ W) on the southern coast of British Columbia. Nests sites were located by radio telemetry at Clayoquot Sound (2000-2002) and Desolation Sound (1999-2001). Breeding adults were fitted with radio transmitters at sea and monitored by helicopter for presence-absence patterns indicative of incubation (see Bradley et al. 2004, Zharikov et al. 2006). Although 157 nests were located, many were inaccessible to ground crews (n = 87), especially at DS, and are therefore not included in this study which requires on the ground sampling. One nest in lower portions of a deciduous tree (red alder, *Alnus rubra*) was omitted, as it was not representative of typical nest sites (Bradley and Cooke 2001). Ten sites where either habitat plot data was not available or the nest tree was not confirmed within the plot were also excluded. The study is thus based on 59 sites, some of which were missing epiphyte data; sample sizes are reported individually for these variables.

Ground vegetation surveys, measuring all trees (>10 cm stem diameter) in a 25 m radius plot centred on the nest tree were carried out at all ground accessible nests according to established "RIC" protocols (Resource Inventory Committee 2001). Fledging success was determined by climbers based on evidence observed at the nest, described by Nelson (1997). Shell fragments, a distinct fecal ring and downy feathers indicate that the chick likely fledged.

The variables investigated in this study include: the diameter at breast height (DBH; cm), tree height (m), number of potential nesting platforms, epiphyte cover on limbs (0 = none; 1 = trace; 2 = 1-33% cover; 3 = 34-66% cover; 4 = 67-100%), and epiphyte thickness (1 = sparse; 2 = intermediate; 3 = thick mats). Canopy height was measured using a clinometer for nest trees and certain other trees in the patch as a reference by which other tree heights were estimated. Nest tree height was often confirmed by climbers with measured ropes. For nest trees, both ground-based and climber counts were available for the number of potential platforms, and these were often quite different. Ground-based counts were used in all cases to allow comparison to other trees.

I consider a nest tree to be “distinctive” if it is significantly larger, or has significantly more platforms, moss, etc. than other trees in the plot. Since variables at many sites were not normally distributed and often had small sample sizes, non-parametric Sign tests were used to determine, for each variable, whether nest trees were significantly different from other trees in the plot. I used the weighted Z-method (Whitlock 2005) to obtain a measure of combined significance for each variable, with weight equivalent to the sample size of neighbouring trees in each plot. For comparisons involving only platform trees, I omitted any sites with very few other platform trees ($n \leq 5$), resulting in a smaller sample size of 42 for these analyses. I used Spearman rank correlations to investigate whether nest trees significantly different in one variable were likely to differ in other respects. Chi-square tests determined whether fledging success of “distinctive” nest trees differed from non-distinctive trees. I also investigated whether trees with more platforms were selected for or used proportionately to the overall availability of platforms. I used Kolmogorov-Smirnov 2-sample tests to compare the cumulative distribution of platforms in nest trees and all platforms relative to the number of platforms in a tree.

To determine whether epiphyte development depends on age or host species, I also investigated correlations whether epiphyte cover differs according to DBH or tree species. I used Pearson correlations to look for positive correlations between tree DBH and epiphyte cover. For tree species, I considered five species-groups to simplify analysis: Fir = amabilis (*Abies amabilis*; n = 175) and grand firs (*A. grandis*; n = 9); Cw = western red-cedar (*Thuja plicata*; n = 361); Fd = Douglas-fir (*Pseudotsuga menziesii*; n = 108); Hem = western (*Tsuga heterophylla*; n = 481) and mountain hemlock (*T.*

mertensiana; n = 16); Yellow cedar (*Chamaecyparis nootkatensis*; n = 100). Six Sitka spruce (*Picea sitchen*sis) were excluded from this analysis due to small sample size. I used ANOVA with Tukey post-hoc comparisons to investigate differences in epiphyte cover among species. All statistical analyses were conducted in SAS 9.1 (SAS Institute Inc. 2003).

3.4 Results

Nests occurred in western hemlock, mountain hemlock, Douglas-fir, western red-cedar, yellow cedar and amabilis fir (Table 3.1). Western hemlock and yellow cedar nest trees were notably smaller in terms of DBH and height than other species. Nest trees had, on average, a DBH of 118.4 cm ± 5.5 (standard error), were 43 ± 1 m tall and contained 8 ± 1 platforms. The number of trees in 25 m plots ranged from 5 to 50 (mean 21.0 ± 0.18 standard error), with a total of 1240 non-nest trees measured. The number of platform trees ranged from 5 to 25, with a mean of 10.7 ± 0.18. If murrelets chose nest trees at random, we would thus expect nest trees to have the most extreme values for variables about one in twenty times, or 5% compared with all trees, and one in 10, or 10%, when compared with platform trees.

Nest tree diameters averaged 42 cm greater than other trees in their plot. Nest trees had significantly greater diameters than other canopy trees at 38 (64%) sites (Appendix 1; Sign test: $p < 0.05$; weighted z-method for combined probabilities: $Z_w = -26.54$, $p < 0.0001$), and were the largest tree at 18 (31%) of sites. Nest trees were significantly larger than other platform trees at 36% of sites ($Z_w = -7.95$, $p < 0.0001$) with a mean difference of 21.0 ± 6.0 cm. Differences in DBH at DS were larger than at CS (Table 3.4), and this regional difference was marginally significant (Mann-Whitney U = 917.0, p = 0.08).

Nest trees were also taller, on average, than other canopy trees. Nest trees were significantly taller than other nearby canopy trees at 40 (68%) sites ($Z_w = -21.51$, $p < 0.0001$; Appendix 1). They were the tallest tree within 25 m at 21 (36%) sites, were significantly taller than platform trees in 45% of plots ($Z_w = -7.07$, $p < 0.0001$) with an average difference of 4.3 ± 1.1 m and nest trees were significantly shorter than other trees at three sites. The average difference between nest trees and neighbouring trees was significantly greater at DS (11 ± 1.6 m) than at CS (5 ± 1.3 m; U = 1001.0, p = 0.004).

There were more platforms in nest trees than other available trees at every plot used in this analysis. On average, nest trees had 8 more platforms than available trees (Figure 3.1c), and this did not differ between regions. In every case, the nest tree contained more platforms than the average number of platforms in other canopy trees in the plot. Compared to available trees within 25 m, nest trees had the most platforms in 29 cases (49%) and significantly ($p<0.05$) more platforms at 54 (92%) sites ($Z_w = -33.17$, $p < 0.0001$; Appendix 1). When considering only trees that contain at least one platform, nest trees had significantly more platforms at 62% of the sites ($Z_w = -14.16$, $p < 0.0001$). On average, nest trees contained 5 ± 0.7 more platforms than other platform trees in the plot.

On the platform level, nest trees did not have significantly more platforms than expected based on the number of platforms in available trees (Figure 3.2). Although it does appear that murrelets avoid using trees with very few platforms, we have no statistical support for selection for trees with more platforms; rather, platforms are used in proportion to their presence in trees.

Epiphyte cover and thickness were measured on 3 or 4-point scales, so differences are more difficult to detect. Nonetheless, nest trees had significantly more overall epiphyte cover than other trees at 40% of sites ($Z_w = -9.58$, $p < 0.0001$), and 15 of 53 (28%) nest trees ($Z_w = -19.25$, $p < 0.0001$) had significantly thicker epiphyte cover. Compared to platform trees, nest trees were as likely to have significantly more epiphyte cover (17%) than less cover (17%; n = 37; $Z_w = -0.99$, p = 0.16). Nest trees did have significantly thicker epiphytes than neighbouring platform trees at 13% (n = 32) of sites, for a combined significance of p = 0.003 ($Z_w = -3.04$).

Epiphyte cover is positively correlated to tree DBH (Pearson correlation r = 0.176, $p < 0.001$) and differs according to species (ANOVA F = 16.36 $p < 0.0001$). Western red-cedar have significantly (Tukey post-hoc tests, $p < 0.05$) more epiphytes than yellow cedar, and both cedar species have significantly less epiphyte coverage than any of the other species.

Nest trees tend to be distinguishable from other neighbouring trees with respect to more than one variable. Nest trees with a significantly larger DBH also tended to be significantly taller than other trees, and have more platforms and thicker epiphytes (Spearman rank correlation: $p < 0.05$; Table 3.2). Trees with more epiphyte cover also had thicker epiphytes, and the correlation between trees with more platforms and epiphyte thickness was marginally significant (p = 0.07). Similar results were seen when comparing only trees with platforms (Table 3.3).

Fledging success varied with only one variable at one site in the study. At CS, nests in trees with significantly more epiphyte cover and thickness than their neighbors were more likely to fail than nests in less distinctive trees (Figure 3.1). Fledging success did not vary with respect to any other variable in the study.

3.5 Discussion

3.5.1 Nest trees are distinctive

Nest trees can be distinguished from other trees in their immediate vicinity in terms of size, number of platforms and, to a lesser extent, epiphytes. Selection has been also been observed at the patch level for canopy height, DBH and density of platform trees (though trends differed somewhat between regions; see Chapter 1), indicating that selection for these variables may occur at both levels.

In a similar study of primarily high elevation nests (range 688–1260 m; mean 886 m) at DS, Manley (1999) found evidence of selection for taller nest trees with more platforms and greater DBH, even though definition of available trees differed somewhat from the present study. Conroy et al. (2002) also found that nest trees at CS had significantly larger DBH than other potential trees climbed, but did not differ in terms of height or platforms, particularly in better quality habitat.

Trees with a greater DBH have more platforms (Hamer 1995, Naslund et al.1995, Manley 1999, Rodway and Regehr 2002 for CS), likely due to tree age. The observed difference in DBH between nest trees and available trees in this study is most likely a product of selection for platform availability in the nest tree. When only platform trees are considered, many fewer sites showed a significant difference, and nest trees that had significantly larger DBH also tended to have more platforms.

Tree height is not well correlated to platform abundance (Manley 1999, this study). Nest trees were often much taller than other available trees, with an average difference amounting to almost 20% of the total height. Many studies have found that various measures of canopy complexity or height variability are important predictors of nest sites at the patch scale (Bahn and Newsom 2002b, Waterhouse et al. 2002, Waterhouse et al. 2004, Chapter 1). Use of nest trees that are significantly taller than surrounding trees likely offers easier access to the canopy, and may also provide a distinct ‘landmark’ to aid commuting adults in locating the nest.

Evidence of preference for epiphyte cover and epiphyte thickness in nest trees was weaker than for other variables, possibly due to the categorical nature of these variables. Epiphyte development is likely to vary greatly over a larger area due to climatic conditions, aspect and slope position. Since some degree of epiphyte development is usually necessary for platform development, one may expect that while the nest tree may have more epiphytes than other canopy trees, the difference may be much less when only platform trees are considered. Nonetheless, more than a quarter of nest trees considered here had significantly more epiphyte development than other platform trees. Variation in epiphyte cover within the patch is likely due to tree species, DBH and proximity to small watercourses where epiphytes often appear to more abundant (personal observation).

3.5.2 Preference for trees with more platforms

Although we usually discuss selection for trees, murrelets only use one platform. Within the patch, murrelets may select trees with preferred characteristics, select preferred nest platforms that happen to occur in certain trees, or some combination of the two.

Other studies (Manley 1999, Conroy et al. 2002, Nelson and Wilson 2002) have found evidence of strong selection for trees with more platforms over other available trees. Bahn (1998) notes that most nest trees known at that time had more than three platforms, and suggested that potential nest trees be limited to those with at least that many platforms. In this study, six nests (10%) occurred in trees with three or fewer platforms (Appendix 1). Additionally, at least two of the 52 nest trees in Manley's (1999) study had three or fewer platforms. Although the majority of nest trees in these regions have more than three platforms, Bahn's proposed criteria would miss a non-negligible portion of nest trees.

From a platform usage point of view, there is little support for disproportionate usage of platforms with respect to the number of platforms per tree (Fig 3.2), although as noted above, trees with fewer than e.g. three platforms may be avoided. Trees with more platforms are more likely to be used due to increased availability of platforms, rather than due to factors such as reduced predation risk (Manley 1999) or re-nesting advantages (Burger et al. in press).

As previously stated, while many characteristics of distinctive nest trees are correlated with numbers of platforms, significant differences in tree height are not. The value of platform trees as potential nest sites within a plot may be proportional to the number of platforms they contain, as well as a function of height relative to neighbouring trees.

3.5.3 Can element level selection explain apparent preferences for shorter stands?

A recent study of habitat selection based on ground data using the same set of nests (see Chapter 1) found that selection for certain patch scale variables differed between CS and DS. At CS, nest sites tended to have shorter average canopy height than available patches. Overall canopy complexity (measured as the standard deviation of canopy height) at CS was lower than at DS. If murrelets prefer to use trees that are taller than surrounding trees, such variability may not have been available at patches with taller trees.

3.5.4 Potential advantage of distinctive nest trees

Selection of distinctive trees may confer advantages to nesting murrelets in terms of nest access, relocating nests on future visits, or in selecting suitable micro-site features from among a number of potential platforms. While distinctive nest trees do not appear to confer an advantage in terms of fledging success, the finding does offer us further insight into the nesting habitat decisions made by marbled murrelets. From a management perspective, characteristics of the individual nest tree are important, and should be considered in habitat assessments. Murrelets may choose a nest tree that offers presumed high quality habitat not represented by the overall patch. Such considerations may be most important at the edges of the range of suitable habitat, such as high elevation habitats where suitably large trees occur at low densities.

3.5.5 Management implications

A hierarchical approach to marbled murrelet habitat assessment is currently recommended for British Columbia (Canadian Marbled Murrelet Recovery Team 2003), where ground assessments are not practical. Air photo interpretation and low-level aerial survey methods both consider presence and distribution of large trees (Burger 2004, Donaldson 2004, Waterhouse et al. 2004), based on observations made at nest patches using these methods. Individual nest trees could not be identified using these methods; this study confirms that nests, when present, are likely in those large trees and that the importance of these large trees should perhaps be emphasized within the criteria for determining habitat quality. These results may also be used to help direct tree-climbing nest searches (e.g. Conroy et al. 2002). The tree-climbing technique can be very inefficient when searching every potential platform tree (Conroy et al. 2002). Trees that are taller, have more platforms and more epiphytes than neighbouring trees within the patch are visually distinctive from the ground and are most likely to contain a nest if the patch is occupied.

3.6 Figures

Figure 3.1 Proportion of plots with distinctive nest trees. This does not differ across regions nor do successful nests tend to be in distinctive trees. A larger portion of failed nests were in trees with more epiphyte cover and thickness in Clayoquot Sound. CS success n = 16, fail = 11; DS success nests n = 17, fail n = 15.

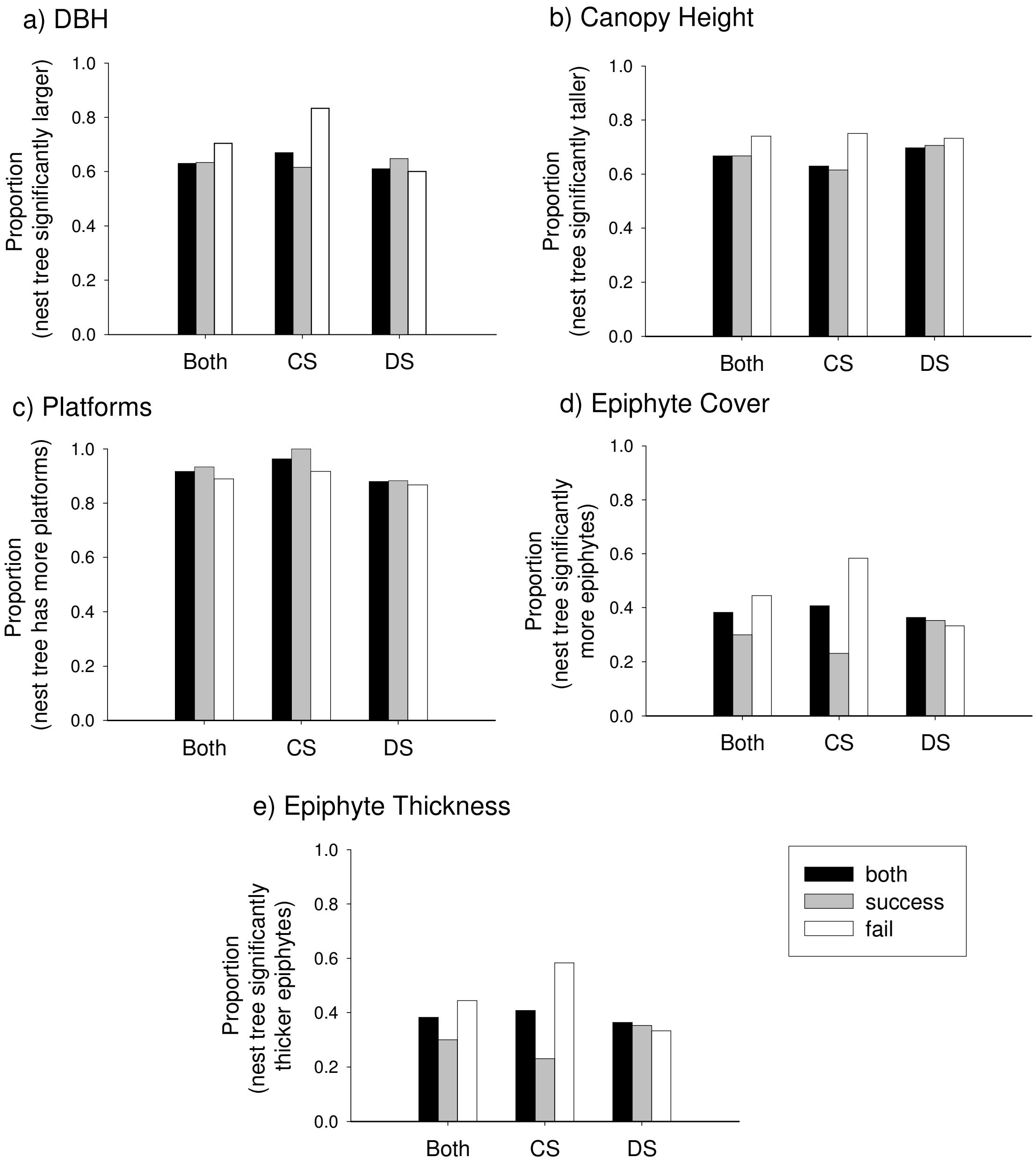
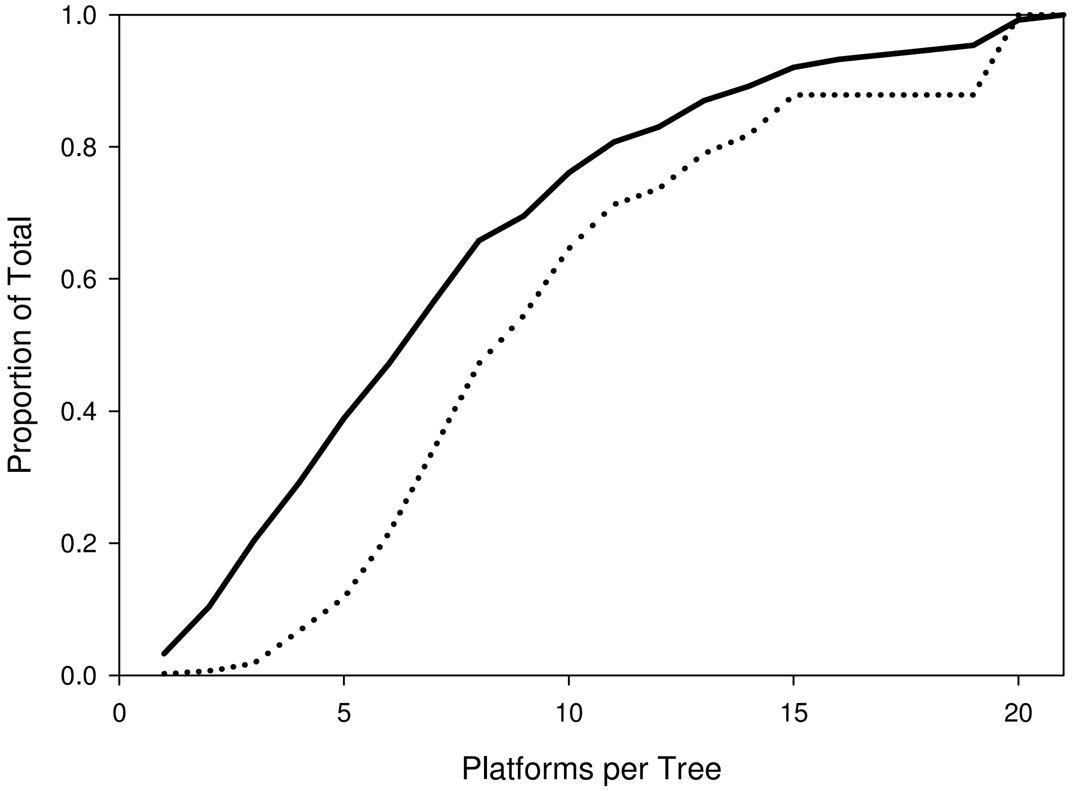


Figure 3.2 Cumulative proportion of total platforms (solid line) and platforms in nest trees (dotted line) as a function of trees with a given number of platforms. The distributions are not significantly different (Kolmogorov-Smirnov 2-sample test: KSa = 0.79 p = 0.33).



3.7 Tables

Table 3.1 Nests were found in a variety of tree species, with most in western hemlock and Douglas-fir. Nest trees had, on average, eight potential nesting platforms.

		DBH			Height			Platforms		
	n	Mean	±	s.e.	Mean	±	s.e.	Mean	±	s.e.
Western Hemlock	20	94.0	±	6.2	37	±	2	8	±	0
Mountain Hemlock	1	162.2			42			20		
Douglas Fir	16	137.9	±	7.2	48	±	2	8	±	1
Western Red Cedar	11	154.9	±	16.7	45	±	2	7	±	1
Yellow Cedar	6	89.8	±	10.8	32	±	2	8	±	2
Amabilis Fir	5	107.9	±	10.8	57	±	5	10	±	2
All	59	119.2	±	5.4	43	±	1.4	8	±	0.5

Table 3.2 Nest trees with a larger DBH than neighbouring trees also tended to be taller, have more platforms and thicker epiphyte growth. * Spearman rank correlation p <0.10 **p <0.05.

	DBH	Height	Platforms	Epiphyte Cover	Epiphyte Thickness
DBH		0.67*	0.40*	0.11	0.27*
Height			0.18	0.04	0.09
Platforms				0.12	0.23
Epiphyte Cover					0.33*
Epiphyte Thickness					

Table 3.3 Correlations between nest trees that are significantly different than neighbouring trees containing platforms for each variable. * Spearman rank correlation p <0.05.

	DBH	Height	Platforms	Epiphyte Cover	Epiphyte Thickness
DBH		0.52*	0.38*	0.24	0.29*
Height			0.03	0.26	-0.07
Platforms				0.30	0.43*
Epiphyte Cover					0.23
Epiphyte Thickness					

Table 3.4 Many nest trees had larger DBH, were taller, had more platforms or more/thicker epiphytes than neighbouring trees within 25 m. Sample sizes: canopy trees CS n = 27, DS n = 32 (epiphyte cover: CS n = 26, DS n = 32; epiphyte thickness: CS n = 25, DS n = 29). Platform trees CS n = 25, DS n = 19 (epiphyte cover: CS n = 21, DS n = 20; epiphyte thickness: CS n = 20, DS n = 18). *Combined significance $p < 0.05$ (weighted z-method; Whitlock 2005).

		All Canopy Trees			**Platform Trees Only**		
Variable	**Region**	**Mean Difference from nest tree**	**Nest tree Sig. different**	**Nest tree Highest ranked**	**Mean Difference from nest tree**	**Nest tree Sig. different**	**Nest tree Highest ranked**
		Mean ± s.e.	Sign Test p<0.05		Mean ± s.e.	Sign Test p<0.05	
DBH (cm)	CS	33.7 ± 6.2	67*	26	23.8 ± 6.8	41*	27
	DS	52.2 ± 8.3	63*	34	17.9 ± 10.4	32*	21
Height (m)	CS	5.0 ± 1.3	63*	30	2.8 ± 1.3	55*	32
	DS	11.2 ± 1.7	72*	41	6.0 ± 2.0	37*	32
Platforms	CS	6.6 ± 0.8	96*	44	4.8 ± 0.9	73*	36
	DS	5.9 ± 0.6	88*	53	4.5 ± 1.0	58*	42
Epiphyte Cover (categories; see Methods)	CS	0.4 ± 0.1	42	0	0.1 ± 0.1	29	0
	DS	0.4 ± 0.1	38	0	0.1 ± 0.1-	45	0
Epiphyte Thickness (categories; see Methods)	CS	0.6 ± 0.1-	76*	0	0.3 ± 0.1-	1*	0
	DS	0.7 ± 0.1-	52*	0	0.2 ± 0.1-	11*	0

CHAPTER 4
COMPARING METHODS OF ASSESSING HABITAT FOR MARBLED MURRELETS IN BRITISH COLUMBIA

4.1 Abstract

Assessing nesting habitat quality is an important step in establishing protected areas for marbled murrelets (*Brachyramphus marmoratus*) in old growth forest, and has been identified as a conservation priority for this threatened species. Actual nest locations for this species are extremely difficult to find, and direct assessment of habitat by ground crews is impractical and costly. Remote methods of habitat assessment using air photo interpretation and low-level aerial surveys from helicopters have therefore been developed and are currently employed in British Columbia (Burger 2004).

Resource selection functions discriminating between murrelet nests and random sites were developed based on old growth forest habitat characteristics measured by ground crews. The RSF score is proportional to the predicted probability of that site being used for nesting by marbled murrelets. Such fine-scale assessments of habitat are impractical for widespread use, but can be applied to validate remote assessment methods.

The probability of nesting based on ground data correlated with habitat quality ranked by existing standards for low-level aerial surveys correlated, but not to habitat ranks from air photo interpretation. Aerial habitat categories (Good and Moderate quality) were distinguished based on probability scores. Measures of platform density

estimated by low-level aerial surveys are roughly equivalent to the same attribute measured from the ground, and canopy closure estimates from air photos may be a reasonable predictor of platform availability. This study helps answer long-standing questions posed by land managers who use remote methods and provides a basis for refining these methods to improve marbled murrelet nesting habitat conservation. Success of model transferability to other regions in the province was mixed, possibly revealing shortcomings in the ground models and remote assessment methods.

4.2 Introduction

The marbled murrelet (*Brachyramphus marmoratus*) is a non-colonial seabird that depends on old-growth coastal forests for nesting habitat (Nelson 1997). The species is designated as Threatened in Canada (Committee on the Status of Endangered Wildlife in Canada 2002), with loss of forest nesting habitat identified as a primary cause for population declines (Canadian Marbled Murrelet Recovery Team 2003). In British Columbia, the species is on the red list of potentially endangered or threatened wildlife, and is an Identified Wildlife Species for protection under the Forest and Range Practices Act (B.C. Ministry of Water Air & Land Protection 2004), which enables protection of forest habitat in Wildlife Habitat Areas (WHAs).

In British Columbia, marbled murrelets nest primarily on large mossy branches (“platforms”) in trees up to 50 km inland (but usually <30 km inland; Burger 2002). Suitable platforms typically occur on old trees (>140 years) in mature or old seral forests with complex canopies and moist microclimates conducive to epiphyte development. Marbled murrelets appear to select nesting habitat with high densities of potential platforms, which offer clearer, more open access to the canopy through forest edges or gaps, complex canopy structure or steeper slopes (Chapter 1). Forests considered to provide the most suitable nesting habitat are typically older stands (>250 years) that usually have significant commercial harvest value. Effective habitat management must balance economic and conservation value, and decisions that will benefit from the best available understanding of marbled murrelet habitat quality.

With most murrelet nests situated high above the ground in the forest canopy (Nelson 1997), locating nests is very labour-intensive and often results in relatively small sample sizes, even when behaviour associated with nesting is used to infer nest location (Paton 1995). For practical reasons, nests located using ground based methods are often biased towards more easily accessible areas and gaps where audiovisual observations are possible. Selecting habitat for preservation of murrelets in British Columbia is therefore usually based on models of habitat use and habitat selection (Chapter 1) and, more recently, remote methods of habitat assessment (Burger 2004).

The Canadian Marbled Murrelet Recovery Team (2003) and the Province of British Columbia (B.C. Ministry of Water, Land and Air Protection 2004) recommend a multi-tiered approach to assessing habitat quality:

1. GIS mapping to identify habitat polygons of interest
2. Habitat algorithms
3. Air photo interpretation
4. Confirmation that suitable structure exists in selected habitat polygons using observations of occupancy or nesting, ground habitat surveys or low-level aerial (helicopter) surveys.

Habitat algorithms (based on forest cover and other GIS data) are used to map large-scale habitat features, though some algorithms include smaller-scale structure (e.g., density of potential platforms; McLennan et al. 2000). A number of algorithms have been applied to different regions of the province (Tripp 2001, Burger 2002). Algorithms have been validated against real nests (V. Bahn and D. B. Lank personal communication), ground transects (McLennan et al. 2000), and low-level aerial surveys (Hobbs 2003, Burger et al. 2005) with varying success. Even the best algorithms for a region may underestimate significant amounts of potential habitat (Burger 2004). A recent province-wide algorithm (Chatwin and Mather 2007) maps suitable habitat as forest polygons >140 years old, >28.5 m tall, <900 m elevation on the south coast and Vancouver Island (elevation constraints are lower in other regions) and within about 50 km of the ocean. Estimates using this model suggest that there are nearly 1.8 million hectares of potential marbled murrelet nesting habitat available in British Columbia, of which 22% is protected in some form (Douglas Bertram, unpublished report). The algorithm is dichotomous (unsuitable/suitable) and often misses habitat deemed suitable by airphotos or aerial surveys (L. W. Waterhouse, personal communication).

Airphoto interpretation can be used to rank forest polygons (minimum size usually 2-5 ha; Waterhouse et al. 2002) based on parameters such as vertical complexity, canopy height, stand age and canopy complexity (Donaldson 2004; Appendix 2). Habitat is ranked on a 6-point scale where 1 = Very High suitability and 6 = Nil, and important forest structures are absent (Burger 2004). Since this study took place within old growth forest where minimum potential habitat structures are present, category 6 is excluded and I refer only to the five categories that represent potential habitat. The habitat classification based on air photo interpretation has been tested using telemetry nest sites at Desolation Sound (DS) and Clayoquot Sound (CS) as well as nests from elsewhere in the province found using ground-based methods (Waterhouse et al. 2002, Waterhouse et al. 2004, Waterhouse et al. 2008).

The Canadian Marbled Murrelet Recovery Team (2003) recommends that the presence of structural features required for nesting (platforms and epiphyte cover) be verified by ground surveys or low-level aerial surveys. With such an extensive, often remote and mountainous landbase available for assessment, verification of habitat quality by ground surveys is either impractical and cost-prohibitive or impossible due to access constraints. Potential habitat identified by air photo mapping or algorithms is most often surveyed by helicopter (Burger et al. 2004). Features such as platform trees form a major component of the six-point low-level aerial survey habitat ranking scale (Appendix 3) similar to that used for airphoto interpretation.

Due to the high economic costs associated with protecting habitat and thereby removing it from the harvestable landbase, it is important to have a high degree of certainty that "highly suitable" habitat is most likely to be used for nesting. The difficulty of collecting ground habitat plots means that air photo and low-level aerial survey methods have not been compared to ground data. It is unknown how well habitat observed remotely by one of these methods reflects conditions "on the ground". This study is the first to ground-truth air photo and low-level aerial survey methods, and to associate a continuous-scale probability of use to each habitat rank.

Ground plots most accurately assess certain parameters known to affect nest site selection by marbled murrelets. Density of platform trees, in particular, is a key attribute found to characterize nest patches and distinguish them from other available sites (Hamer and Nelson 1995, Rodway and Regehr 2002, Manley 1999), and can only be directly measured from the ground or inferred by low-level aerial surveys, and not by remote sensing such as air photos or satellite imagery.

Resource Selection Functions (RSFs) were developed using ground-based habitat plots at nests and random sites in old growth forest at CS and DS (Chapter 1). These functions, one for each region and one combining both regions, produced an RSF score, proportional to the predicted probability of use, ranging from 0 to 1, for each plot. Habitat at many of these sites was independently ranked using the air photo interpretation and low-level aerial survey methods, collectively referred to as remote methods, as part of habitat selection studies (Waterhouse et al. 2002, 2004, 2008, 2009).

I compared the RSF probabilities to the remote habitat ranks to determine if higher ranked sites had higher probability of use, thus validating the remote classifications with ground data measures. Next, I examined relationships between variables measured on the ground and those estimated remotely to evaluate the effectiveness of remote methods at estimating actual habitat features such as density of platform trees. Finally, I investigate model transferability by applying the ground habitat selection models to other regions with novel remote datasets to determine if the relationships between remote and ground data have broader applicability to coastal British Columbia.

4.3 Methods

4.3.1 Classification validation

The study took place in two regions of Southern British Columbia: Clayoquot Sound (CS; 49°12’ N, 126°06’ W) on the west coast of Vancouver Island and Desolation Sound (DS; 50°05’ N, 124°40’ W) on the mainland (see Chapter 1, Figure 1.1). Both areas are mountainous with forest cover naturally fragmented by steep topography, fjords and stream channels. The two areas differ markedly in their degree of forest habitat loss, with over 80% loss of original old growth forest cover at Desolation Sound, compared to ~25% loss at Clayoquot (Zharikov et al. 2006, 2007a).

Nests were found using radio-telemetry, producing a relatively large, unbiased sample for the species (Bradley et al. 2004). Ground habitat plots (RIC 2001) were carried out in a 25 m radius plot (0.2 ha) at all nests that could be accessed by ground crews. Subsequent to the nest work, a set of random habitat plots (see Chapter 1 for methods) was collected in both regions. All habitat sites were located within old growth forest >140 years old, and represent the subset of potential nesting habitat that is accessible on the ground.

Ground habitat plots offer a quantitative measurement of size (height and diameter at breast height [DBH]), availability of potential nesting platforms and qualitative rankings of epiphyte cover and thickness for individual trees. Since they involve measurements by observers in the forest, ground plots are considered a more accurate, but also much more expensive and time consuming, method of assessing habitat compared to remote methods. Data from ground plots also represents forest characteristics in a very small area (generally 0.2 ha) and is less likely to reflect habitat quality in a heterogeneous stand.

Habitat selection models were developed using the set of ground habitat plots at nest and random sites. Since patterns of selection were found to differed between CS and DS, two separate region-specific models were developed as well as one model built using data from both regions pooled ("Both"). Resulting Resource Selection Functions produced an RSF score (ω_i), which can be interpreted as the predicted probability of nesting (Chapter 1) for each site ($0 \leq \omega_i \leq 1$).

Air photo interpretation involves interpreting forest attributes (Appendix 2) delineated from ≥1:20,000 scale air photos by experienced air photo interpreters (Donaldson 2004). Helicopter-based observers flying low over the forest canopy carry out low-level aerial surveys. Forest characteristics (Appendix 3) are rated and habitat quality classes assigned on the spot (Burger et al. 2004).

For the two studies by Waterhouse et al. (2008 ,2009), habitat at the remote research plots (air photo and aerial) was ranked from Class 1 to Class 5 and individual attributes described using ~100 m radius plots (Appendix 1, 2). Attributes at ground plots were described using 25 m radius plots (Chapter 1). Remote plots therefore described a larger area than ground plots used this study.

Sites for which both ground and remote methods surveys were available were matched. Most of the random sites available from remote methods were different from those used in developing ground RSF models (Chapter 1), though some sites at DS were the same (n = 23). Site locations for remote methods are less precise than those from the ground, since GPS locations were often obtained from moving helicopters. Sites with large differences (≥100 m) in elevation between remote and ground data, or those sites where age and/or crown closure did not correspond indicated a spatial mismatch was likely and were eliminated (n = 8). I used Spearman rank correlations to compare ground ω_i scores to habitat rank derived from either airphoto or low-level aerial surveys.

The percent of canopy trees with platforms is a key ranking criterion of low-level aerial surveys (Burger et al. 2004). A similar ground measure was available for most nest sites, allowing comparison of this variable between methods. On low-level aerial surveys, this variable is estimated on a 6-point non-linear scale based on observations made in a helicopter, rather than a measurement, as with ground surveys. Low-level aerial survey observations are therefore likely to be less precise (L.W. Waterhouse, personal communication). Ground measures of platform trees were therefore categorized according to the scale used for low-level aerial surveys, with values rounded to the nearest 5% (<20%) or 10% (≥20%).

I use Spearman rank correlations to investigate the relationship between density of platform trees and overall habitat quality ranked by either air photo interpretation or low-level aerial survey, as well as three air photo interpretation variables. Vertical complexity, canopy complexity (important predictors of nest sites; Waterhouse et al. 2002) and canopy closure are canopy attributes measured by air photo interpretation that may improve access for murrelets as well as influence platform development.

4.3.2 Model transferability

To test the transferability of the CS/DS habitat models, I obtained comparable ground data from other regions of coastal British Columbia. On the Central Coast, 13 sites in the Broughton Archipelago (50° 42 N 126° 32 W) and 23 sites in the Bella Coola and surrounding valleys (52° 21 N 126° 52 W) were available from an ongoing study of platform development (A. E. Burger, University of Victoria, personal communication). Ground data collected as part of another murrelet study (Malt and Lank in press) were available for southern British Columbia: the Nimpkish Valley on northern Vancouver Island (50° 13 N 126° 39 W; n = 29), Port Renfrew/Jordan River area of southwestern Vancouver Island (48° 30 N 124° 11 W; n = 22), and east Howe Sound on the Mainland (49° 38 N 123° 05 W; n = 12). That study investigated edge effects on artificial nest predation, and habitat sites were paired edge/interior within forests that contained at least one potential nesting tree. I randomly selected one plot (edge or interior) for each site for which habitat assessment data from low-level aerial surveys was available. Patches were ranked on the standard six-point scale using air photo interpretation (Central Coast) or low-level aerial survey (southern B.C. sites) methods and provided as ArcGIS files by the Species at Risk Coordination Office (British Columbia Ministry of Environment) and Terminal Forest Products (for east Howe Sound; Dave Marquis, Terminal Forest Products, personal communication).

4.3.3 Analyses

Spearman rank correlations were used to compare habitat quality ranks and RSF scores. Under the hypothesis that RSF scores are correlated to habitat quality, negative correlations would be expected, where higher quality, low-numbered habitat ranks would have higher RSF scores. Differences between habitat categories were investigated using ANOVA tests and Tukey post-hoc tests for comparisons of adjacent categories. The assumption of equal variances was confirmed with non-significant ($\alpha = 0.05$) Levene's Test for Homogeneity of Variances, and Welch's ANOVA (SAS Institute Inc. 2003) was used in the case of unequal variances. Mann-Whitney tests were used to compare differences between ranks where only two categories were available. I used SAS 9.1 (SAS Institute Inc. 2003) for statistical analyses.

4.4 Results

4.4.1 Air photo interpretation

Remote habitat assessments were available for 21 nest sites at CS, and 28 nest sites and 23 random sites at DS. Data from both methods were not available for random sites at CS. For the air photo interpretation method, most sites (89%) were ranked either High or Moderate; relatively few sites (9%) were considered Very High quality and just one site was ranked Low (Figure 4.1). Due to the limited sample size in some habitat ranks, Very High and High ranks (collectively referred to as Good) and Low and Very Low ranks (collectively referred to as Poor) were combined, for a total of three ranks, for some analyses. Some degree of heteroscedasticity is evident in these distributions, although Levene's test, which is robust to departures from normality (SAS Institute Inc. 2003) showed no statistical reason to reject the null hypothesis of homoscedasticity ($p > 0.50$).

At CS, nests were ranked either High or Moderate (Figure 4.1a) by air photo interpretation. RSF scores were not correlated to air photo habitat quality (Spearman rank correlation; $r_s = 0.14$, $p = 0.53$ High and Moderate did not differ in RSF scores (Table 4.1; Mann-Whitney U test: $U = 108$, $p = 0.53$). At DS, RSF scores were not significantly correlated with air photo habitat rank ($r_s = -0.23$, $p = 0.10$; Figure 4.1b) and mean RSF scores did not significantly differ. When ranks were combined into three classes, the rank-correlation was significant ($r_s = -0.31$, $p = 0.03$; Figure 4.1b), and Good habitat had significantly higher RSF scores than Moderate habitat (Table 4.1; ANOVA $F_{(2,48)} = 3.11$, $p = 0.05$; Tukey post-hoc test $p < 0.05$). For the pooled regional dataset (Both; Figure 4.1c), RSF score was not correlated to airphoto habitat rank, either individually (5 classes) or combined ($r_s = -0.13$, $p = 0.27$), and categories did not differ ($F_{(2,69)} = 0.79$, $p = 0.46$).

The density of platform trees in both regions pooled was not correlated to habitat quality ranks (Figure 4.2a; $r_s = 0.10$, $p = 0.46$), canopy complexity (Figure 4.3c; $r_s = 0.00$, $p = 0.99$) or to vertical complexity from air photos (Figure 4.3a; $r_s = 0.04$, $p = 0.71$). Crown closure ranks were significantly correlated to density of platform trees (Figure 4.3b; $r_s = -0.32$, $p < 0.01$), with Most Likely sites having significantly higher densities of platform trees than those in the Least Likely class encompassing the extremes of the range.

4.4.2 Low-level aerial surveys

Low-level aerial survey data was available for 20 nest sites at CS, and 28 nest and 23 random sites at DS. The aerial survey method ranked sites between 1 and 5. At CS, none of the sites were ranked Low or Very Low (Figure 4.4a). RSF scores did not correlate with habitat rank at CS (individual ranks: $r_s = 0.13$, $p = 0.60$) and RSF scores based on both DS (Figure 4.4b) and the Both regions (Figure 4.4c) models were significantly correlated to habitat rank (DS: $r_s = -0.57$, $p < 0.001$; Both: $r_s = -0.41$, $p = 0.0004$). At DS, habitat quality ranks were significantly different (ANOVA $F_{(4,46)} = 6.89$, $p < 0.001$), with category 1 Very High differing significantly from 2 High (Tukey test $p < 0.05$). Combined ranks were not significantly different ($F_{(2,48)} = 1.20$, $p = 0.30$). For Both sites, categories differed overall ($F_{(2, 66)} = 4.84$, $p = 0.002$), but there were no significant differences between adjacent categories, for either individual or combined habitat ranks.

For the proportion of canopy trees that contained platforms, ground data was available for 44 sites and fell into aerial survey categories 1 (>50%) through 3 (6-25%). Ground information was significantly correlated to the low-level aerial survey data for this variable (Table 4.2; Spearman rank correlation $r_s = 0.33$, $p = 0.03$). Categories matched for 57% of the sites, and where mismatches occurred, low-level aerial survey tended to underestimate platform trees relative to ground data. Low-level aerial survey categories for proportion of trees with platforms were not significantly correlated to actual density of platform trees ($r_s = -0.16$, $p = 0.17$). Two other low-level aerial survey measures were also correlated with the density of platform trees: proportion of large trees ($r_s = -0.26$, $p = 0.02$) and proportion of trees with mossy pads ($r_s = -0.23$, $p = 0.05$). Low-level aerial survey habitat ranks were correlated to density of platform trees (Figure 4.2b; $r_s = -0.30$, $p < 0.01$) and differences between High, Moderate and Low habitat classes are significant (ANOVA $F_{(2, 68)} = 3.08$, $p = 0.05$).

4.4.3 Model transferability

I compared the RSF scores for models developed from CS and DS, to polygon ranks from air photo interpretation on the Central Coast. Distributions among habitat ranks were skewed towards low quality habitat. A single site occurred in each of Very High and High quality habitat, 9 sites in Moderate and Low quality habitat, and 16 sites in Very Low quality habitat. RSF score from the CS and Both models were not correlated to habitat quality (Figure 4.5 a,c; Spearman rank correlation. Both: $r_s = -0.21$, $p = 0.21$; CS: $r_s = -0.04$, $p = 0.78$). RSF scores from the DS model were best correlated to air photo interpretation habitat rank ($r_s = -0.38$, $p = 0.02$), but the trend is not linear (Figure 4.5b).

Model transferability for sites in southern British Columbia using low-level aerial surveys varied among models and regions. At Howe Sound, 12 sites were available; one was in High quality habitat according to low-level aerial surveys, 3 in Moderate habitat and 8 in Low quality habitat. At Howe Sound, habitat rank was not significantly correlated to RSF scores for any model (Figure 4.6; Spearman rank correlation $p > 0.05$). The best fit for this region was to the Both model ($r_s = -0.51$, $p = 0.09$). In the Nimpkish Valley, 13 sites were in High quality habitat and 16 in Moderate habitat, and RSF scores were not correlated with habitat class ($r_s = 0.27$, $p = 0.15$) for the Both model, nor for either CS or DS specific models ($p > 0.15$). On Southwest Vancouver Island, there were 5 sites in High quality habitat, 9 sites in Moderate habitat and 8 sites in Low quality habitat, producing a significant correlation to RSF scores from each of the three models (CS: $r_s = -0.55$, $p < 0.01$; DS; $r_s = -0.41$, $p = 0.05$; Both: $r_s = -0.30$, $p = 0.03$). With all three regions combined, habitat quality and RSF scores were significantly correlated for the DS model ($r_s = -0.27$, $p = 0.03$) and categories were distinguishable (ANOVA F [4, 58] = 2.45 p =

0.02), with Poor quality habitat (4 and 5 pooled) significantly different from Moderate (Tukey post-hoc test $p < 0.05$). The correlation was not significant for the CS ($r_s = -0.12$, $p = 0.34$) or Both models ($r_s = -0.20$, $p = 0.11$). Combining ranks improved the fit for the Both model ($r_s = -0.26$, $p = 0.04$), with Moderate habitat having significantly higher RSF scores than Poor habitat (ANOVA $F_{(2,58)} = 5.40$, $p = 0.007$; Tukey post-hoc test $p < 0.05$).

4.5 Discussion

4.5.1 Ground-truthing remote methods

Habitat quality as rated by remote methods generally reflects ground habitat quality as rated by an earlier habitat selection model (Chapter 1). Although few variables used in remote methods bear a direct relationship to those included in ground habitat models, and landscape parameters are not directly considered by current remote methods, habitat quality ranked by low-level aerial surveys has a strong relationship with predicted probabilities of nesting, while the relationship was weaker for the airphoto habitat ranks. These observed relationships were transferable to some extent when applied to novel regions of the province.

These comparisons are based on habitat selection models developed for a set of nest and random habitat plots within old growth forest. The models were the best (i.e. the most parsimonious) from among the set of candidate variables and combinations considered. Few variables are directly comparable across methods, and the habitat selection models contain certain relationships that may or may not result in better approximations of marbled murrelet nesting habitat selection than the remote methods considered here. For example, models for Clayoquot Sound and for Both regions suggest that probability of nesting decreases with height of tall trees (>~40 m), while remote methods do not penalize very tall trees. The model for Desolation Sound has no consideration for availability of potential platforms, a key attribute for aerial surveys.

This study provides improved insight into how observations and habitat ranked from remote methods may relate to actual habitat conditions on the ground, despite differing scales. Ground habitat is measured in 25 m radius plots (0.20 ha), whereas air photos rank polygons (varying size, minimum 2 – 5 ha; Waterhouse et al. 2002) and low-level aerial surveys estimated habitat in 100 m radius plots (3.14 ha; Waterhouse et al. 2009, Burger 2004). Mismatches in the data may well be a result of these differing scales, where habitat quality averaged over a larger area may cause smaller patches of higher quality habitat to be downgraded. Positional errors, up to 100 m for these data (Bradley et al. 2004) may also have placed the ground plot in a different polygon from that estimated by remote methods. Waterhouse et al. (2009) recently compared low-level aerial survey ranks for 3 ha nest patches to the larger nest stand. Where habitat ranks differed, the smaller patch had the higher rank, suggesting that nests occurred in small patches of high quality habitat within the polygon. Scale differences may similarly affect this study. Although nest sites do tend to score higher than random sites in the same habitat quality rank, this result would be expected since the same nests were used to build the RSF models on which the score is based.

Habitat is ranked on a 5-point scale where 1 is Very High quality habitat and 5 is Very Low. The scale is non-linear, designed to emphasize differences in lower habitat quality (Burger 2004), and the relative quality of each category (i.e. High vs. Very High). The relationship to absolute and even relative nest densities remains unknown (Burger and Waterhouse 2009). Some comparisons are limited due to the relatively small size of the comparison dataset, and the limited distribution across habitat classes for air photo interpretation and low-level aerial surveys. I pooled classes 1 and 2 (Very High/High) and 4 and 5 (Low/Very Low) for some analyses, although this often did not improve the results. In all comparisons, some portion of suitable sites based on ground models is underestimated by remote methods.

4.5.2 Air photo interpretation

Air photo interpretation is currently a recommended method of assessing forest structure over large areas for potential marbled murrelet nesting habitat (Canadian Marbled Murrelet Recovery Team 2003). The method considers overall canopy structure, forest gaps and tree size that are associated with murrelet nesting (Donaldson 2004), but interpreters cannot observe key patch-scale features such as platform abundance that murrelets require.

Sites at CS were distributed in High or Moderate habitat classes, and the limited distribution may account for the lack of correlation observed for this region. Waterhouse et al. (2008), using air photo interpretation, found poorer selectivity for nest sites at CS compared to DS. This may be due to the limited variation in air photo interpretation variables such as vertical complexity that best discriminated nest sites from random sites in a previous study that was not limited to >140 year-old forest stands (Waterhouse et al. 2002). CS is less topographically complex than DS, which contributes to factors such as gap, edges and canopy complexity. Since the sample used for methods comparison at CS includes only nest sites, one would expect less variation in habitat suitability, and this finding provides some qualitative support for the validity of habitat ranks by this method. RSF models used to predict site usage at CS included canopy height as a negative effect. Avoidance of the tallest forests has not been observed previously, and this result may be due to sampling errors in the present study rather than biological reasons. This resulted in very low RSF scores for two nests sites in forests >45 m tall that were considered Very High quality habitat by air photo interpretation.

Ground models related more strongly to air photo habitat ranks at DS, where canopy complexity and vertical complexity variables observed on air photos proved good predictors of nest sites (Waterhouse et al. 2002). Estimates of canopy structure are perhaps better observed by remote methods, as ground workers may lack appropriate perspective. In ground models, canopy complexity (standard deviation of tree height in the plot) was greater at DS than at CS, and this variable was an important predictor of nesting in DS-specific models (Chapter 1; not to be confused with air photo variable of the same name). Some sites in all categories were ranked very low (<0.2) by ground models. These sites, mostly random sites that likely did not contain nests, were on south/east aspects, which received negative weighting in ground models, but are not considered in air photo interpretation methods.

When both regions are combined, and the ground-based model for both regions applied, Very High/High and Moderate categories did not differ, likely due to the effects of CS sites that were not predicted as well by air photo interpretation models (Waterhouse et al. 2008). Overall, probability of nesting tended to be lower for the same sites than when using the appropriate region-specific model.

4.5.3 Low-level aerial surveys

Low-level aerial surveys, though more expensive than air photo interpretation, can be a cost-effective method of surveying large areas of habitat for specific structures used by murrelets. Experienced observers in a low-flying helicopter can survey the occurrence of large trees, moss and potential platforms. The method, however, only allows for relatively crude estimates of these features compared to more accurate ground assessments where individual trees are measured.

At CS, four sites in very high quality forest varied greatly in terms of probability of nesting. Two of these sites were ranked very low by ground models because they were in very tall forests, as mentioned previously. If canopy height is artificially reduced in these sites to the mean value for the region, probability of nesting increases significantly to about 0.7 for both nest sites. The great majority of sites at CS were in class 2 (High), which limits interpretation of the comparison data.

At DS, ground models were able to distinguish between low-level aerial survey categories 1 and 2, and category 1 contained 79% of nest sites in the sample. This suggests that some low-level aerial survey variables are correlated to ground variables that were good predictors of nest sites at DS. The single largest effect in the DS model was aspect, which is not considered in low-level aerial surveys, but may co-vary with factors such as moss development; moisture regimes may be more aspect-dependent at DS, where the climate is drier, than at CS.

Many of the High quality sites with low RSF scores were on south/east aspects and had lower than average canopy complexity. Several of these sites were assigned higher RSF scores by the Both model, in which those variables have a smaller effect (Chapter 1). Another difference is platform trees, which are important components of both the aerial survey ranking method and ground models for Both regions, are not present in DS models. The low probability of nesting assigned to High quality habitat is therefore likely due to specific shortcomings in the ground-based habitat selection model for DS.

For all sites, using the combined model for CS and DS, probability of nesting correlates with low-level aerial survey habitat categories. Limited sample sizes in Moderate, Low and Very Low sample sizes may limit the power to detect differences between categories (i.e. Very High/High vs. Moderate).

4.5.4 Relative utility of habitat ranks

The relative utility of each habitat rank to nesting marbled murrelets (i.e. the expected relative or absolute nest density) is not well understood. Burger and Waterhouse (2009) pose four hypotheses for the relationship of density to habitat quality, and suggest that current evidence (Bahn and Newsom 2002, Waterhouse et al. 2007, 2008, 2009) supports the “modified threshold” hypothesis. Under this hypothesis, Very Low and Low quality habitats offer very limited nesting opportunities, Moderate has an intermediate utility, and High and Very High quality habitat offer similar, relatively high potential nest densities.

Though the radio-telemetry sample of murrelet nests used to generate RSF scores (Chapter 1) cannot be used to estimate absolute densities, the relative probability of a patch being used by nesting murrelets may offer one of the best quantitative measures of habitat quality currently available. In this study, only low-level aerial surveys offer some distribution in Low and Very Low habitat ranks, and therefore some opportunity to assess relative habitat quality across the full range of habitat quality. Very High and High quality habitat have very similar probabilities of nesting (RSF score) for both regions combined. At DS, comparisons for High quality habitat should be regarded with caution as previously discussed. In both cases, the largest difference between categories occurs between High (or Very High for DS) and Moderate habitat ranks. Moderate habitat is very similar to Low quality habitat, and Very Low habitat has slightly lower, but insignificant, probability of nesting. The results broadly support the Modified Threshold hypothesis (Burger and Waterhouse 2009), but suggest that Moderate and Low quality habitat may differ less than expected, although power is particularly limited for comparison of poorer quality habitat ranks.

4.5.5 Platform variables

Marbled murrelets select sites with higher densities of potential nesting platforms (Hamer and Nelson 1995, Manley 1999, Rodway and Regehr 2002). Density of trees with at least one platform is more accurately measured by ground crews than actual platform density, and had a significant positive effect in ground-based models for CS and Both regions. The proportion of canopy trees that contain platforms is the best approximation of this measurement available for remote methods (low-level aerial survey). Although this was not correlated with ground measures of platform tree density as a continuous variable, ground estimates of platform tree composition in relation to canopy trees is probably nonetheless the best match to aerial data. Where mismatches in categories occur in this data (Table 3.2), aerial surveys tend to underestimate platform trees relative to ground estimates in the High class (1). Comparisons at low densities are weak, since very few sites with ground-based data had low estimates for platforms. Inaccurately estimating platform abundance at low values would be most problematic, since platforms are an absolute requirement for suitability ranking by low-level aerial surveys (Canadian Marbled Murrelet Recovery Team 2003) and would result in either inclusion of unsuitable habitat or exclusion of suitable habitat. Since real murrelet nests tend to be in areas of higher platform abundance, such discrepancies are not likely to be a major problem.

Since platform tree content and other factors that contribute to platform abundance (large trees, moss development) are a major component of habitat ranks determined by low-level aerial surveys, it is not surprising that habitat rank is significantly correlated to the density of platform trees as observed from the ground (Figure 4.3b). Platform tree density is significantly correlated to proportion of large trees and to proportion of trees with moss, confirming that these variables are suitable surrogates for nesting platforms. Somewhat surprisingly, the ground-based density of platform trees (ground based) was not correlated with the proportion of trees with platforms estimated by aerial surveys, though the direct comparison of this variable previously discussed validates its use.

Potential nesting platforms and moss abundance cannot be observed on air photos, but are key attributes in ranking forest habitat for murrelets. Air photo variables that are correlated to density of platform trees would be of interest, and may assist in predicting platform abundance indirectly using air photos. Vertical complexity has been shown to be an important variable from previous air photo-based habitat selection studies (Waterhouse et al. 2002) and has been hypothesized to be related to platform development, but was not related to platform tree density as measured on the ground in this study. Canopy closure may influence access and nest cover, and habitat suitability ranks are significantly related to platform tree density. This indicates that observed avoidance of sites with canopy closure <26% and >75% may be a result of selection for platform density that has been observed in numerous other studies, but could not be shown for air photo interpretation.

4.5.6 Model transferability

Resource selection functions often apply only to the region for which they are developed (Boyce et al. 2002); therefore, lack of correlation to habitat ranks from other regions of British Columbia may indicate the regional specificity of the ground-based models.

On the Central Coast of British Columbia, few of the sites for which both ground and air photo interpretation data were available fell in Good quality habitat. Good quality habitat is available throughout the areas covered by ground plots, but the study design used for ground plots in that study did not place emphasis on high quality habitat, and accessibility was limited to sites with close proximity to roads (Bella Coola) or boat and shoreline access (Broughton Archipelago). As discussed previously, small patches of good quality habitat may also be missed by remote methods due to the larger scale of those assessments.

RSF scores in Moderate, Low and Very Low categories on the central coast varied between 0.05 and 0.95, and there was no correlation between habitat rank and probability of nesting. For the CS model in particular, RSF scores seemed to have a somewhat bimodal distribution, but inspection of the ground habitat attributes found no reason for this. Unfortunately, habitat attributes from air photo interpretation are not available for this region.

Trees are generally smaller at more northerly latitudes, and marbled murrelets nest in shorter trees in Alaska (Piatt et al. 2007, Hamer and Nelson 1995). Under current air photo interpretation methods, forest polygons of height class 3 or shorter (<28.5 m) can be assigned, at best, Moderate habitat quality. Though Donaldson (2004) suggests regional adjustments to height criteria, it is not known whether such adjustments were considered for air photo interpretation on the Central Coast. Based on ground data, 17 of the 34 sites in Moderate or lower habitat ranks were shorter than 28.5 m. However, 14 of those sites contained at least one platform tree (minimum density 11 trees/ha) and presumably had some potential as nesting habitat. It is possible that these sites would be ranked higher by low-level aerial surveys, especially if those platforms are visible from the air.

For comparisons to low-level aerial surveys in regions on the southern coast, sites on Southwest Vancouver Island were correlated with results for all three models. This was also the only region for which the full spectrum of habitat quality ranks was represented. Southwest Vancouver Island is similar to Clayoquot Sound in terms of topography, climate/growing conditions and habitat fragmentation, and showed the best correlation with the CS model. Two Very Low quality sites in this region were given relatively high RSF scores in all three models. Although data on habitat attributes from aerial surveys are not available, it is likely that large old trees were observed to be rare or absent at these sites (i.e., not old growth forest). This is surprising, since the study design for these plots (Malt and Lank 2007b, in press) required old growth patches at least 300 x 300 m (9 ha); such stands should have been delineated as separate polygons and visible for aerial surveys.

Data from Howe Sound are limited, with just 12 ground sites located mostly in Low quality habitat. All of the sites in this region were high elevation (800 – 1080 m), where trees are often slower growing and smaller than those at lower elevation. Ground RSF models may be more robust to potential nesting habitat at higher elevations, since many high elevation nests were used in ground models, particularly at DS (Chapter 1).

In Nimpkish Valley, Moderate habitat was very similar to High quality habitat in terms of probability of nesting. Ground plots for poorer quality habitat were not available with this dataset, as would be expected given that the study design required the presence of at least one potential platform in a plot (Malt and Lank 2007b, in press). Very High quality habitat sites had surprisingly low RSF scores, particularly with the CS model. Three of these sites contained very tall trees (>40 m), which, as previously discussed, reduces the probability of nesting under both CS and Both models. Three of the sites were also on south/east aspects, which would produce lower probabilities under all three models.

4.5.7 Conclusions

This study confirms that low-level aerial surveys provide better rankings of marbled murrelet habitat than air photo interpretation, corroborating previous findings (Waterhouse et al. 2007). Additionally, the step-down process of habitat selection recommended by the Canadian Marbled Murrelet Recovery Team (2003) should be applied with caution, since habitat deemed unsuitable by air photo interpretation may be suitable under low-level aerial survey methods, and similarly unsuitable low-level aerial survey habitat may be found to be suitable by ground surveys. As mentioned previously, habitat algorithms often miss large segments of potentially suitable habitat as well. It would appear that, although both are important tools in strategic landscape level planning, coarser-level methods of habitat assessment (i.e. algorithms, air photo interpretation) miss suitable habitat picked up by finer scales.

Both RSF models and remote methods for ranking habitat quality were developed based on habitat used for murrelet nesting. Habitats may well differ in their fitness potential (Wiens 1989), with nests in some habitat more likely to be successful than in others. Malt and Lank (2007b) suggest that proximity to certain types of forest edges may influence reproductive fitness. Habitats with higher fitness potential should be prioritized for conservation. However, ground RSF models used here do not reflect habitat fitness potential (Chapter 2) and Waterhouse et al. (2008) found evidence that higher quality habitats ranked by air photo interpretation had lower fitness. Recent findings using this set of nests (Chapter 2) suggest that fitness potential is proportional to the probability of use. Until the link between habitat quality and reproductive success is better understood, it is important to remember that the term habitat quality used herein refers to likelihood of use for nesting, regardless of fitness potential.

Air photo interpretation and low-level aerial surveys are useful tools for assessing habitat efficiently and cost effectively. Comparisons with ground models and data, though limited in the distribution of habitat classes, suggest that existing habitat ranks are roughly proportional to habitat selection observed by finer-scale ground models in the regions for which those models were developed. Comparisons to data in other regions suggest that ground models may be more broadly applicable, particularly if certain modifications regarding aspect and canopy height are considered. Although absolute nest densities within habitat ranks are still not available, this study offers some quantitative evidence for the quality of remote methods habitat ranks relative to one another.

4.6 Figures

Figure 4.1 Relationships between habitat quality derived from Air Photo Interpretation and probability of nesting (ωi) from ground based models. Bars indicate mean ω_i for each category. Solid circles = nests; open circles = random sites .

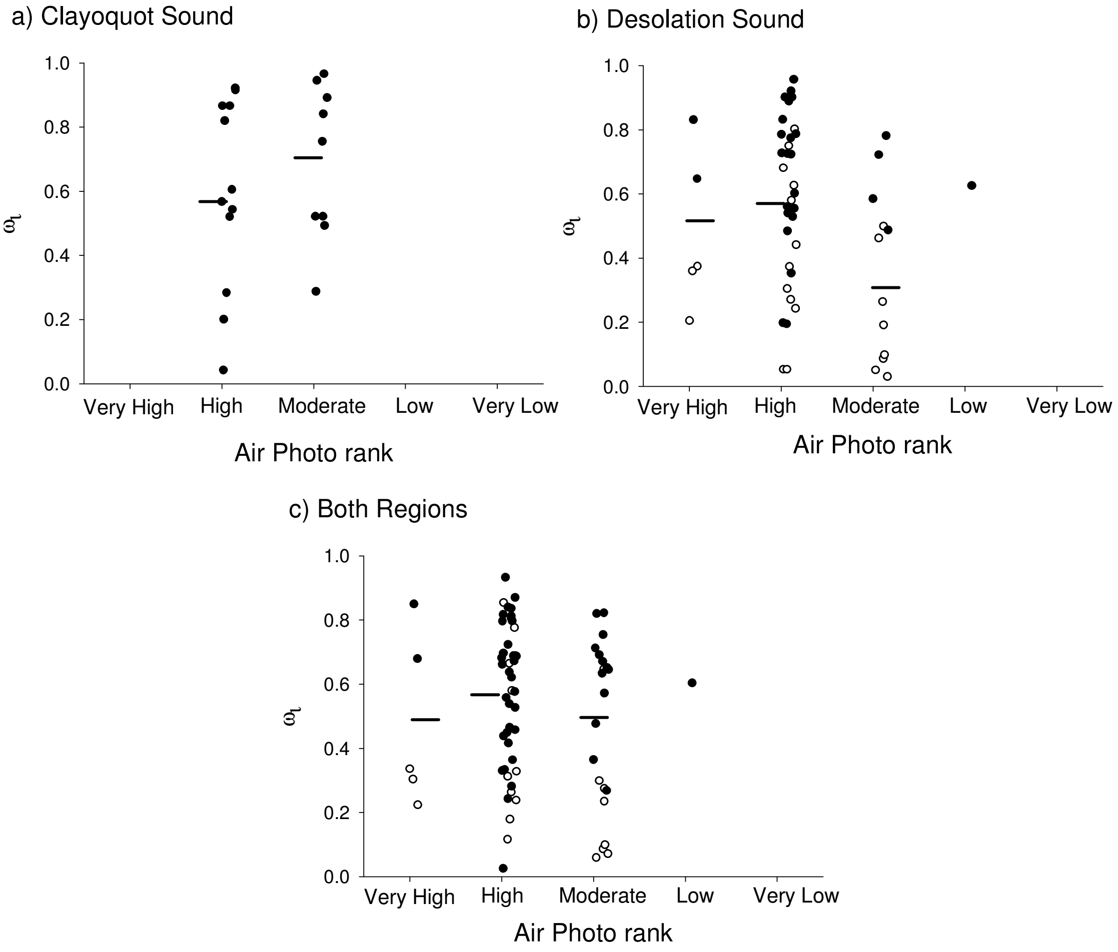
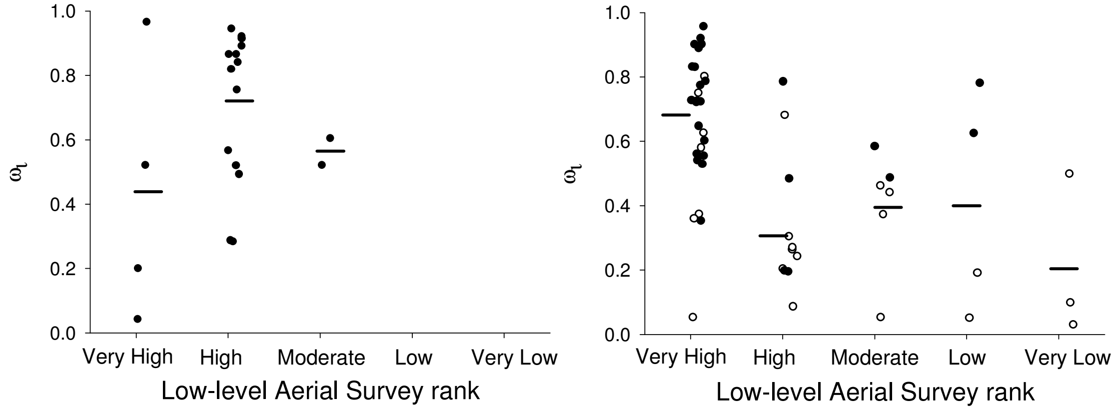


Figure 4.2 Relationships between habitat quality derived from Low-level Aerial survey and probability of nesting (ωi) from ground based models. Bars indicate mean ω_i for each rank. Solid circles = nests; open circles = random sites.


a) Clayoquot Sound

b) Desolation Sound

c) Both regions

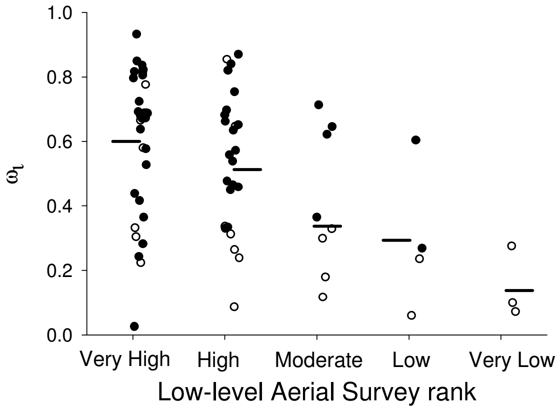
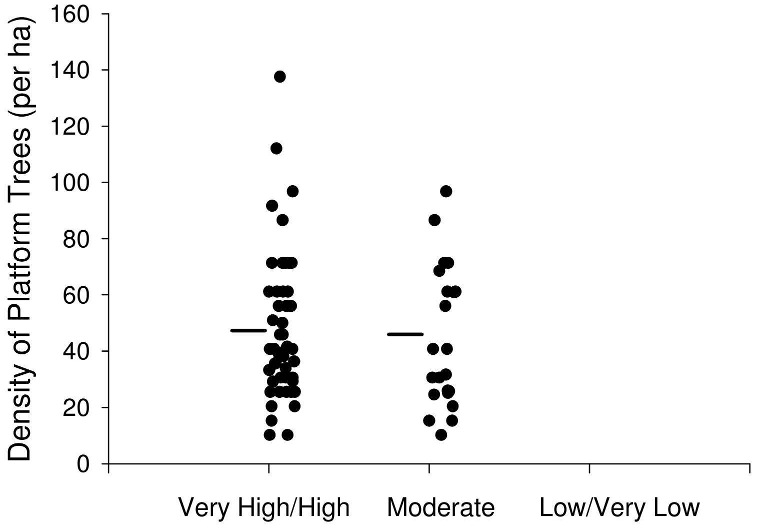


Figure 4.3 Density of platform trees (ground data) in each habitat class for a) air photo interpretation (Spearman rank correlation $r_s = -0.09$ $p = 0.46$) and b) low-level aerial survey $r_s = -0.31$ $p < 0.01$. Data points are jittered on the x-axis for display purposes. Bars indicate mean ω_i for each rank.

a) Air Photo Interpretation



b) Low-level Aerial Survey

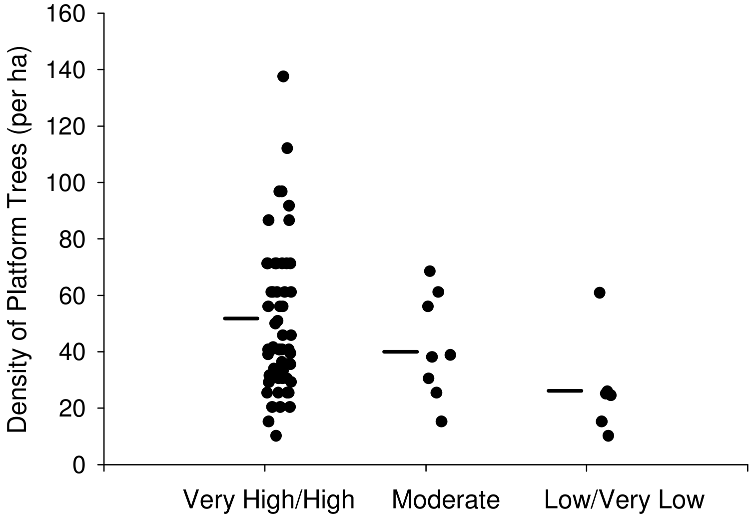


Figure 4.4 Crown Closure rank from air photo interpretation is correlated with density of platform trees (ground data). a) vertical complexity (Spearman rank correlation $r_s = 0.04$ $p = 0.71$), b) crown closure class $r_s = -0.32$ $p < 0.01$, c) Canopy complexity $r_s = 0.00$ $p = 0.99$. Data points are jittered on the x-axis for display purposes. Bars indicate mean ω_i for each rank.

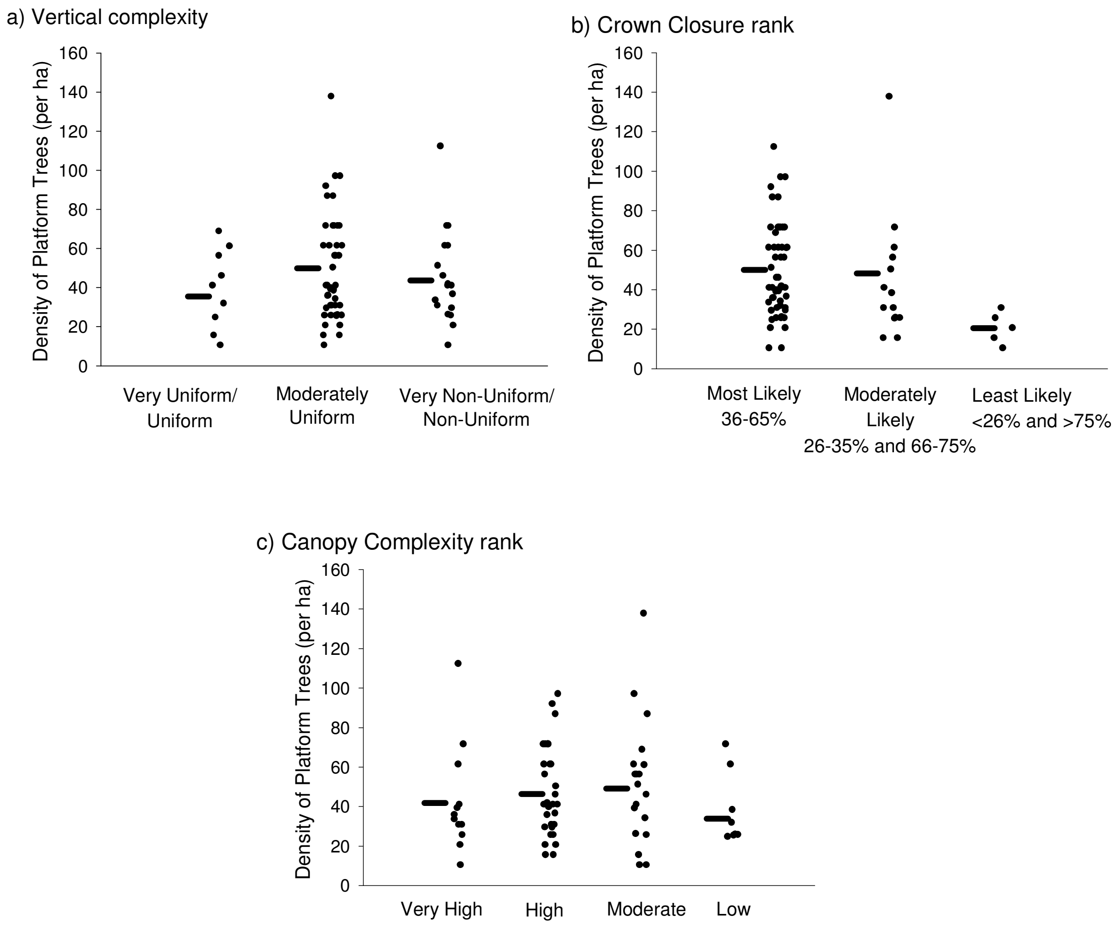


Figure 4.5 Ground plots on the Central Coast of British Columbia encompassed the full range of RSF scores, but tended to be ranked low by air photo interpretation. RSF scores from the DS model were correlated to habitat quality rank (Spearman rank correlation $r_s = -0.38$ $p = 0.02$). Bars indicate mean ω_i for each rank.

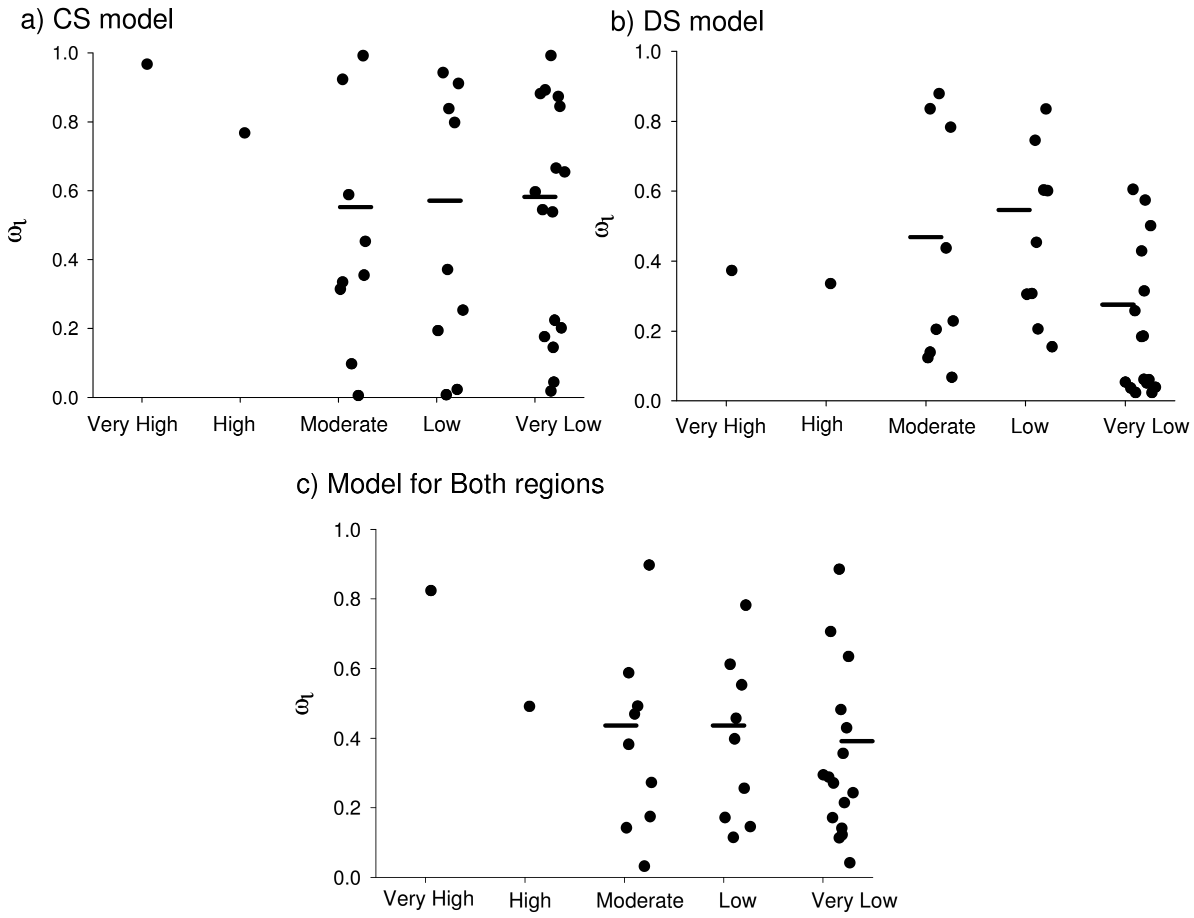
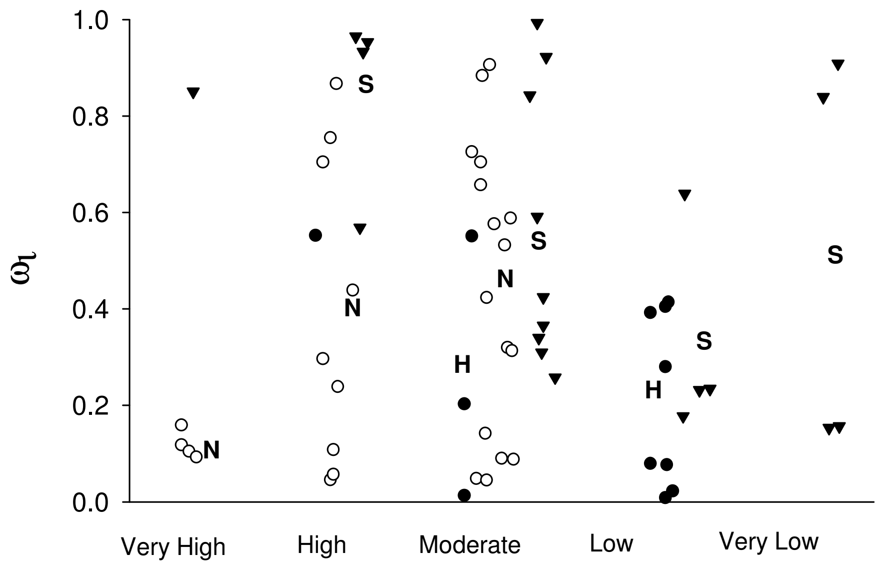
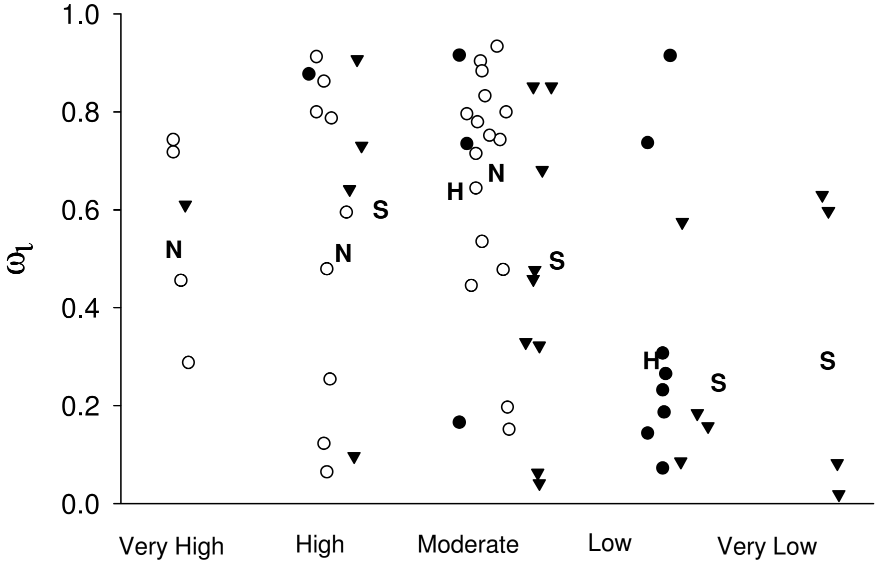


Figure 4.6 Habitat ranked by low-level aerial surveys compared to RSF scores for ground plots in three novel regions of southern British Columbia. Letters indicate mean value within each rank. Solid circles (H) = Howe Sound; open circles (N) = Nimpkish Valley; solid triangles (S) = Southwest Vancouver Island.

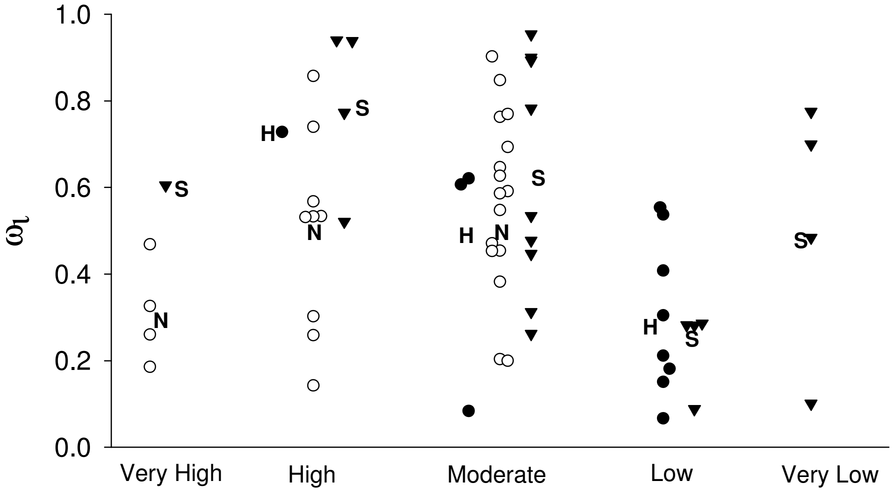
a) CS model



b) DS model



c) Model for Both regions



4.7 Tables

Table 4.1 Probability of nesting from each ground-based RSF model by habitat quality class for both air photo interpretation and low-level aerial surveys. Data reported as mean ± standard error (n).

Habitat Quality class		Probability of Nesting Mean± standard error (n)		
		CS	DS	Both
Air Photo Interpretation				
		-	0.48 ± 0.11 (5)	0.48 ± 0.12 (5)
1/2	High	0.60 ± 0.09 (12)	0.58 ± 0.05 (38)	0.55 ± 0.03 (50)
3	Moderate	0.69 ± 0.08 (9)	0.36 ± 0.08 (12)	0.47 ± 0.06 (21)
4	Low	-	0.63 (1)	0.60 (1)
Low-Level Aerial Survey				
1	Very High	0.43 ± 0.20 (4)	0.67 ± 0.04 (27)	0.60 ± 0.04 (31)
2	High	0.71 ± 0.06 (14)	0.34 ± 0.07 (11)	0.54 ± 0.04 (25)
3	Moderate	0.56 ± 0.04 (2)	0.40 ± 0.07 (6)	0.41 ± 0.08 (8)
4	Low	-	0.41 ± 0.17 (4)	0.29 ± 0.11 (4)
5	Very Low	-	0.21 ± 0.15 (3)	0.15 ± 0.06 (3)

Table 4.2 Percent of canopy trees that contain platforms. Comparison between ground and low-level survey methods. Spearman rank correlation $r_s=0.33$, $p=0.03$.

	Ground		
Low-level Aerial Survey	**1** 51-100%	**2** 26-50%	**3** 6-25%
1 51-100%	**12**	4	2
2 26-50%	8	**12**	-
3 6-25%	1	2	**1**
4 1-5%	-	1	1

APPENDICES

Appendix 1 Element scale features of nest trees and neighbouring trees within 25 m (mean ± s.e. reported). * indicates nest tree is significantly (Sign test p <0.05) larger/greater. # indicates nest tree was significantly shorter than neighbouring trees. Epiphyte cover: 0 = none, 1 = trace, 2 = 1-33%, 3 = 34-66%, 4 = 67-100%. Epiphyte thickness: 1 = sparse, 2 = intermediate, 3 = thick mats.

						Neighbouring Canopy Trees						Neighbouring Platform Trees					
				Epiphyte						Epiphyte						Epiphyte	
Site	DBH (cm)	Height (m)	Platforms	Cover	Thick	n	DBH (cm)	Height (m)	Platforms	Cover	Thick	n	DBH (cm)	Height (m)	Platforms	Cover	Thick
Clayoquot Sound																	
4.021	97	30	8	2	3	18	75 ± 5.0 *	33 ± 1.1	2 ± 0.6 *		*	9	88 ± 7.1	32 ± 1.0	3 ± 0.8 *		
4.022	158	38	7	4	2	23	86 ± 7.0 *	35 ± 1.0 *	1 ± 0.3 *	*	*	8	108 ± 11.8 *	36 ± 1.7	3 ± 0.4 *	*	
4.062	133	50	8	2	2	16	93 ± 16.7 *	38 ± 2.4 *	4 ± 1.3 *			11	107 ± 23.1 *	42 ± 2.8 *	6 ± 1.6 *	*	
4.072	112	38	3	4	3	38	75 ± 6.3 *	31 ± 0.6 *	2 ± 0.4 *	*	*	17	88 ± 11.9	32 ± 0.7 *	4 ± 0.5	*	
4.081	114	58	4	4	1	7	83 ± 8.2	33 ± 3.0 *	1 ± 0.6 *								
4.112	112	29	8	3	1	12	85 ± 6.9 *	35 ± 0.9#	4 ± 0.7 *			10	93 ± 5.5 *	36 ± 0.6 *	5 ± 0.6 *		
4.181	113	30	3	2	2	34	70 ± 4.9 *	32 ± 0.8	1 ± 0.2 *		*	8	81 ± 14.0	35 ± 2.0	3 ± 0.7	*	*
4.183	141	43	3	2	3	13	64 ± 4.8 *	31 ± 1.8 *	0 ± 0.3 *		*						
4.192	128	47	9	2	2	22	85 ± 7.2 *	37 ± 1.2 *	2 ± 0.5 *		*	11	85 ± 9.2 *	38 ± 1.8	3 ± 0.6		
4.232	162	42	20	3	3	9	86 ± 9.7 *	34 ± 1.9 *	3 ± 1.2 *			5	91 ± 14.1	36 ± 2.8	5 ± 1.7		
4.301	102	38	6	3	2	22	76 ± 6.8 *	31 ± 1.5 *	1 ± 0.3 *	*	*	9	78 ± 9.9	31 ± 1.2 *	2 ± 0.5 *		
4.311	55	30	10	4	3	25	75 ± 6.9	31 ± 0.6	1 ± 0.6 *	*	*	10	84 ± 11.4	32 ± 0.8 *	3 ± 1.4 *	*	
4.312	114	38	13	3	2	15	84 ± 8.1	31 ± 1.0	4 ± 1.2 *		*	11	95 ± 8.7	32 ± 1.3	6 ± 1.3 *		
4.312b	149	30	6	2	3	39	76 ± 4.6	28 ± 0.4	1 ± 0.3 *		*	15	100 ± 7.9	29 ± 0.6	3 ± 0.3 *		
4.323	227	49	8	3	3	17	115 ± 13.6 *	34 ± 1.1	2 ± 0.7 *	*	*	9	134 ± 21.8 *	33 ± 1.6 *	4 ± 1.0 *		
4.342	79	30	5	2	2	43	71 ± 5.0 *	26 ± 0.3 *	0 ± 0.1 *	*	*						
4.364	133	40	10	3	2	40	62 ± 2.8 *	33 ± 0.5 *	1 ± 0.3 *	*	*	12	68 ± 6.0 *	35 ± 0.8 *	4 ± 0.6 *		
4.402	63	30	15	3	3	20	71 ± 5.3 *	31 ± 0.7 *	1 ± 0.4 *		*	9	75 ± 7.9 *	31 ± 1.1 *	3 ± 0.6 *		

Appendix 1 Continued

						Neighbouring Canopy Trees						Neighbouring Platform Trees					
				Epiphyte						Epiphyte						Epiphyte	
Site	DBH (cm)	Height (m)	Platforms	Cover	Thick	n	DBH (cm)	Height	Platforms	Cover	Thick	n	DBH (cm)	Height (m)	Platforms	Cover	Thick
Clayoquot Sound																	
4.412	85	45	4	3	2	16	77 ± 6.1	38 ± 1.4 *	3 ± 1.2			6	94 ± 5.6	40 ± 1.7	8 ± 1.8		
4.431	118	32	9	2	3	38	54 ± 3.1 *	28 ± 0.8 *	2 ± 0.4 *		n/a	13	71 ± 3.2 *	30 ± 1.0 *	5 ± 0.6 *	*	n/a
4.492	117	32	5	2	3	16	76 ± 4.4 *	27 ± 0.8 *	1 ± 0.5 *		*	7	85 ± 4.8 *	28 ± 1.2 *	3 ± 0.7		
4.514	95	35	9	3	1	11	98 ± 13.0	33 ± 1.2	5 ± 1.3 *	n/a	n/a	7	95 ± 19.3	34 ± 1.4	7 ± 1.2	n/a	n/a
4.572	104	57	20	4	3	32	74 ± 4.5 *	46 ± 1.6 *	3 ± 0.9 *	*	*	16	84 ± 7.5	48 ± 2.5 *	7 ± 1.3 *		
4.681	55	24	5	3	3	11	68 ± 9.9	26 ± 1.3	1 ± 0.4 *	*	*	7	81 ± 12.9	26 ± 2.0	2 ± 0.4 *		
4.722	72	30	10	3	2	31	75 ± 6.5	35 ± 0.8#	2 ± 0.5 *			18	89 ± 8.3	37 ± 1.0 *	4 ± 0.5 *		
4.73	80	26	7	2	3	14	79 ± 7.1	25 ± 0.3	1 ± 0.3 *	*	*						
4.821	104	58	11	3	3	28	73 ± 3.6 *	49 ± 1.4 *	0 ± 0.0 *	*	*						
Desolation Sound																	
4.561	120	36	2	3	3	22	61 ± 7.8 *	29 ± 0.8 *	0 ± 0.1 *		*						
5.02	69	44	11	4	2	22	80 ± 6.3	42 ± 2.6	2 ± 0.6 *	*		13	93 ± 8.2	49 ± 3.2	4 ± 0.6 *		
5.053	125	56	20	4	3	14	137 ± 14.5	45 ± 2.9	1 ± 0.4 *	*	*	7	173 ± 13.2	52 ± 3.3	3 ± 0.4 *		
5.061	127	38	13	2	2	28	75 ± 4.7 *	33 ± 0.9 *	1 ± 0.3 *		*	10	92 ± 8.1 *	35 ± 1.5	3 ± 0.6 *		
5.071	49	26	7	4	3	20	73 ± 6.3	33 ± 1.2	5 ± 1.2	*	*	12	73 ± 7.5 *	33 ± 1.3 *	8 ± 1.3	*	
5.14	61	42	8	3	2	15	70 ± 6.1	36 ± 2.1 *	2 ± 0.4 *			10	77 ± 7.8	38 ± 2.8	3 ± 0.4 *		
5.17	175	48	5	2	2	8	83 ± 13.5 *	33 ± 2.6 *	0 ± 0.3 *								
5.19	139	51	4	4	2	14	70 ± 10.8 *	38 ± 2.0 *	0 ± 0.1 *	*	*						
5.192	85	40	10	3	3	10	68 ± 6.6	35 ± 1.2 *	2 ± 0.8 *								
5.222	153	44	6	2		5	126 ± 11.8	40 ± 1.7	2 ± 0.4 *		n/a	6	126 ± 11.8	40 ± 1.7	2 ± 0.4 *	*	
5.252	93	55	6	3	3	29	45 ± 2.3 *	33 ± 1.1 *	0 ± 0.1 *	*	*	11	46 ± 3.0 *	33 ± 1.4 *	1 ± 0.2 *	*	
5.252b	165	40	6	3	2	23	89 ± 11.3 *	32 ± 2.1 *	2 ± 1.0 *	*	*	5	174 ± 17.0	46 ± 5.6	8 ± 3.7		
5.254	110	45	7	2		12	49 ± 6.2 *	33 ± 1.8 *	0 ± 0.2 *		n/a						n/a

Appendix 1 Continued.

						Neighbouring Canopy Trees						Neighbouring Platform Trees					
				Epiphyte						Epiphyte						Epiphyte	
Site	DBH (cm)	Height (m)	Platforms	Cover	Thick	n	DBH (cm)	Height (m)	Platforms	Cover	Thick	n	DBH (cm)	Height (m)	Platforms	Cover	Thick
Desolation Sound																	
5.292	124	45	1	2	1	12	67 ± 9.5 *	32 ± 1.9 *	0 ± 0.1 *	*							
5.302	84	43	7	2	3	19	95 ± 8.8	38 ± 1.2 *	3 ± 0.7 *		*	13	101 ± 11.5	39 ± 0.8 *	5 ± 0.6 *	*	
5.381	75	41	7	4	3	27	77 ± 6.0	41 ± 1.5	3 ± 0.8 *	*	*	19	84 ± 7.8	43 ± 1.5	5 ± 1.0 *		
5.421	119	61	4	4	3	20	77 ± 5.9 *	45 ± 1.5 *	2 ± 0.6 *		*	11	94 ± 7.4 *	49 ± 1.5 *	3 ± 0.8	*	
5.472	191	71	4	3	3	17	72 9.4 *	38 2.3 *	1 0.3 *		*						
5.49	215	48	7	4	3	16	67 ± 13.7 *	37 ± 2.1 *	2 ± 0.6 *	*		5	117 ± 35.6	47 ± 2.5	5 ± 0.5		
5.491	111	45	9	3	2	21	92 ± 10.8	39 ± 1.7	1 ± 0.4 *			13	116 ± 13.1	43 ± 1.6	2 ± 0.6	*	
5.521	141	50	8	2	-	6	100 ± 13.0	40 ± 3.6	7 ± 2.2		n/a	5	105 ± 14.4	41 ± 3.8	8 ± 2.1 *	*	n/a
5.541	140	35	3	6	2	16	71 ± 8.6 *	29 ± 0.8 *	1 ± 0.6 *								
5.552	78	33	6	2	-	41	48 ± 2.6 *	40 ± 1.2#	0 ± 0.1 *								
5.571	137	58	4	4	2	11	66 ± 12.2 *	34 ± 1.7 *	1 ± 0.6 *	*							
5.582	121	45	10	2	3	24	42 ± 3.7 *	35 ± 1.4 *	1 ± 0.5 *		*						
5.592	76	43	7	3	3	32	52 ± 2.9 *	37 ± 0.8 *	1 ± 0.6 *		*	6	76 ± 7.8	40 ± 2.2	8 ± 1.7		
5.641	114	55	14	4	-	35	64 ± 3.6 *	39 ± 1.4 *	7 ± 1.0 *			25	72 ± 3.8 *	42 ± 1.2 *	10 ± 1.0 *	*	*
5.651	98	37	8	4	2	5	58 ± 12.6	29 ± 2.9	1 ± 0.6								
5.692	128	50	7	3	2	22	60 ± 5.5 *	34 ± 1.2 *	0 ± 0.3 *	*	*	2	103 ± 42.9	44 ± 11.5	4 ± 0.0		
5.742	104	75	8	2	3	39	55 ± 4.9 *	39 ± 1.3 *	2 ± 0.5 *		*	13	89 ± 8.2	47 ± 1.8 *	5 ± 1.0		
5.802	250	43	15	3	-	22	74 ± 7.7 *	31 ± 0.9 *	2 ± 0.6 *	*		13	88 ± 8.9 *	33 ± 0.9 *	4 ± 0.7 *	*	*
5.862	140	40	6	2	3	7	95 ± 21.9	32 ± 1.4 *	3 ± 1.1			5	110 ± 28.7	33 ± 1.7	4 ± 1.3		

Appendix 2 Airphoto interpretation method. Variables used and definition of categories. Adapted from Waterhouse et al. 2004 and Waterhouse et al. 2007.

Variable	Variable classes and definitions
Forest Cover >140 years old	Percent of plot with forest >140 years old (Class 8 and 9)
Forest Cover ≤140 years old	Percent of plot with forest ≤140 years old, excluding non-vegetated and non-treed portions
Non-vegetated cover	Percent of plot non vegetated and non-treed
Vegetated	Percent of plot vegetated but non-treed
Tree Height	Average estimated height of dominant, co-dominant and high intermediate tree layers
Large Trees	Dominant trees with large stems ≥5 m above main canopy layer **Prevalent.** >20% of stems are above canopy; **Sporadic.** 3-20% ; **None.** <3%
Canopy Complexity	Estimate of overall variability of canopy structure and distribution of large crowns and canopy gaps created by local topography, vertical complexity or stand disturbance **Very High/High.** Well distributed big crowns and gaps create heterogeneous layer. Crown closure typically 40-60% **Moderate.** Fewer scattered large crowns. Varying number of canopy gaps, well distributed or clumped with crown closure 30-70% **Low.** Fewer or poorly distributed large crowns and closed forest with few gaps, or predominantly open forest with few large crowns.
Vertical Complexity	Describes uniformity of forest canopy by considering estimates of total difference in height of leading species and average tree layer height. **Very Uniform/Uniform**. 11-20% height difference **Moderately Uniform** 21-30% height difference **Uniform**. 31-40% height difference

Appendix 2 Continued.

Variable	Variable classes and definitions
Large Gaps	Significantly visible openings (≥1 tree length wide) within canopy Present. Occupies ≥5% of plot; None. Occupies <5% of plot
Small Gaps	Smaller openings (≥1 tree length wide) within the canopy **None**. Gaps usually occupy <5% of plot; **Sporadic**. 5-40% of plot; **Prevalent**. >40% of plot
Ranked Crown Closure	Follows recommendations of the Canadian Marbled Murrelet Recovery Team (2003). Percent estimate of the vertical projection of the tree crowns (upper layer) upon the ground, classified as: **Most Likely**. 36-65% ;**Moderately Likely**. 66-75% and 26-35%; **Least Likely.** <26% and >75%
Meso Slope	Relative Position of plot within the local catchment area (~30 to 300 m vertical difference) **Low**. Lower slope includes toe and flat; **Mid**. Mid Slope; **Upper**. Upper Slope
Airphoto Habitat Quality	1=**Very High**. Forest >28 m tall and ≥250 years old; abundant large tree crowns , excellent canopy structure ; best habitat available. 2=**High**. Forest >28 m tall and ≥250 years old; Large trees are common and widespread, very good canopy structure. 3=**Moderate**. Forest usually 19.5-28 m tall and forest cover >140 years old., large tres with good crowns present, but patchily distributed. 4=**Low**. Forest generally >19 m tall or >140 years old. Patchy and sparse large trees with poor canopy structure. 5=**Very Low**. Stands generally <140 years old and <19.5 m tall; large trees and complex canopy structure are sparse or absent.

Appendix 3 Low-level aerial survey method: Variables used and definition of categories. Adapted from Waterhouse et al. 2004, 2007.

Variable	Variable classes and definitions	Ranking
Large Trees	% of canopy tres >28 m tall	**Very High**. 51-100% **High**. 26-50% **Moderate**. 6-25% **Low**. 1-5% **Very Low**. ~1% **Nil**. 0%
Trees with Platforms	% of canopy and emergent trees with potential nest platforms.	
Moss Development	% canopy trees with obvious mossy platforms.	
Canopy cover	% cover of over storey canopy based on vertical projection of crowns on the ground	**Most Likely**. 40-60% **Moderately Likely**. 30 or 70% **Least Likely**. <30% or >70%
Vertical Complexity	Gappiness and difference in tree heights; vertical complexity of the forest.	**Very High** **High** **Moderate** **Low**
Topographic Complexity	Topographic features providing gaps and complexity to the forest (e.g. large boulders, rocky outcrops)	
Slope Grade*	Steepness of slope grade at site	**Flat & Gentle** **Moderate** **Steep**
Slope Position*	Position on slope	**Low & Valley Bottom** **Mid** **Upper Slope and Ridge**
Aerial Patch habitat quality	Overall habitat quality ranking of the 100 m radius patch. Qualitative assessment based on above obseravations	1=**Very High** 2=**High** 3=**Moderate** 4=**Low** 5=**Very Low** 6=**Nil**
Aerial Polygon habitat quality	Overall habitat quality ranking of polygon (of varying area) surrounding and including the 100 m radius patch. Qualitative assessment based on above obseravations	

* Slope characteristics are recorded, but do not contribute to habitat ranking

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