PICKING PATCHES: WHAT IS THE UTILITY OF HABITAT FRAGMENTATION IN DETERMINING HABITAT USE BY LOCAL POPULATIONS OF THE MARBLED MURRELET, *BRACHYRAMPHUS MARMORATUS*?

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ABSTRACT

We investigated the utility of measures of landscape and matrix composition and configuration in determining local breeding abundance of marbled murrelets, as indexed by radar counts of breeding murrelets taken during breeding season, in three areas of coastal British Columbia: Southwest Vancouver Island, the South and Central mainland coast. Using an information theoretic approach, we tested whether models including landscape composition and configuration could better predict local murrelet abundance than models utilizing habitat area alone, and whether model selection varied between regions. Models including measures of landscape composition and configuration do better predict local murrelet abundance than those based on habitat area alone, and associations between landscape components and murrelet abundance differ among regions. Algorithms currently used to identify murrelet habitat as suitable or unsuitable for protection do not consider landscape context. We recommend refining these algorithms to include measures of landscape composition and configuration.

Keywords: marbled murrelet; habitat use; landscape composition; old-growth; matrix; edge effects; habitat fragmentation; GIS; mixed effects models.

DEDICATION

To my parents, Deborah Kannegiesser and Joe Cortese, for sharing your passion for the natural world and for always encouraging us to think critically about our impact upon it, and for my brother, who continues to be a great partner in exploration. Spending my early years hiking the mountains of the Cariboo-Chilcotin, catching minnows, and later full sized fish taught me the most important lessons that I have ever learned. I always knew that my life's work would be dedicated to preserving a piece of that peace you helped me to find in wild places and things. I feel so privileged to have a career I care so deeply about, which unites me with such committed and thoughtful people.

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1: INTRODUCTION

1.1 Landscape and management context

The influence of landscape composition and configuration on the viability of endangered species is a key consideration for land and wildlife managers, especially when species at risk are reliant on economically valuable habitat for survival (Franklin and Lindenmayer 2009). This is a pertinent issue in British Columbia (BC), where harvesting of forest habitat will continue, and currently 116 forest associated species are red listed (Ministry of Forests Lands and Mines (MFLM) 2010). Although habitat loss is the most pervasive threat to endangered species in Canada (Ventor 2006; Natural Resources Canada 2010), the fragmentation, or breaking up of continuous forest habitat into smaller patches (Fahrig 1997), can cause additional impacts (Andrén 1994), especially to avian species (Ferraz 2007; Mortelliti et al. 2010; Rittenhouse et al. 2010; Stephens et al. 2004). The additional impacts, or edge effects, resulting from the influence of the converted habitat, the matrix, on the remnant habitat patch, (Vergara and Hahn 2009) are still poorly understood (Ryall and Fahrig 2006), especially at the landscape scale (Ries et al. 2004). Improving our understanding of how landscape context affects habitat value for species is critical for sustainable forest management in British Columbia, where a large proportion of species diversity and species at risk are forest dependent (MFLM 2010).

The marbled murrelet (*Brachyramphus marmoratus*) is a Threatened old-growth habitat specialist (CMMRT 2003, Horn et al. 2009). Landscape context is a critical consideration in marbled murrelet management, as remaining coastal old-growth habitat is often fragmented and set within a matrix of mature-second growth, young forest, clear cuts and roads, which can create additional threats to the survival of murrelet adults and offspring (Burger 2002; Burger 2004b; Malt 2007). While associations between stand level characteristics and habitat used by murrelets are well documented (Burger 2002; CMMRT 2003; Piatt 2007), few studies have examined murrelet population responses to different habitat and matrix patterns at a landscape scale (Raphael et al. 2002b; Burger and Chatwin 2004; Meyer and Miller 2002). As harvesting of BC's coastal old-growth forests is likely to continue (CMMRT 2003; MFLM 2010), understanding how different arrangements of habitat composition and matrix configuration influence habitat use by marbled murrelets is key to their successful maintenance and recovery in Canada.

1.2 Marbled murrelet biology

Marbled murrelets are small diving seabirds whose range extends from the outer Aleutian Islands across Southern Alaska and as far South as central California (Nelson 1997; Piatt 2007). During the breeding season, marbled murrelets require both ocean to forage for food, and inland nesting habitat, usually located within 60 km of marine foraging grounds (Piatt 2007). In the summer, murrelets' diet consists primarily of small schooling fish including Pacific sand lance (*Ammodytes hexapterus),* northern anchovies (*Engraulis mordax*), Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus)* and osmerids (*Osmeridae*) (McShane et al. 2004). Habitat suitable for nesting in BC typically consists of large diameter, low elevation old growth conifers (typically >250 years old) with large limbs, and epiphyte mats on branches for nests (Burger 2002, Silvergeiter 2010). Variation in tree size, variable canopy structure and/or gaps in the forest that provide access to nests, are also features of suitable nesting habitat (Nelson 1997; Manley 1999; Burger and Bahn 2004; Burger 2002; Waterhouse 2002).

The greatest threat facing marbled murrelets is the loss of their specific old-growth forest nesting habitat (Hull 1999; Burger 2002; CMMRT 2003; Piatt 2007), of which an estimated 33-49% has been lost to industrial logging in BC (Piatt 2007). Several studies have shown significant correlations between available habitat area and murrelet abundance (Burger 2001; Meyer and Miller 2002; Meyer et al. 2002; Raphael et al. 2002; Burger 2002; Burger et al. 2004). In addition to reductions in the overall available nesting habitat, fragmentation can further affect murrelet habitat quality (Raphael et al. 2002b, Burger 2004b; Malt and Lank 2007, 2009). Fragmentation effects are driven by edge effects, which can be detrimental when edges experience higher rates of nest predation relative to interior areas (Andrén 1994; Paton 1994; Bartay and Baldi 2004). Increases in nest predation at edges may result from increases in predator density, activity or species richness at habitat edges (Chalfoun et al. 2002), or an increase in the detectability of nests at edges due to less nest site cover (Ratti and Reese 1988). Edge effects on murrelets can be direct, including thermal stress or dehydration to murrelet chicks (Binford et al. 1975), increased predation pressure on nests and adults (Malt and Lank 2007; 2009; Raphael et al. 2002b); or indirect, including changes to vegetative species and epiphyte cover required for nesting (Malt 2007).

Although there is general agreement on the suite of potential threats to murrelets at edges, there is equivocal evidence as to whether small patches and forest edges actually negatively impact marbled murrelet productivity (Raphael et al. 2002b; Zharikov et al. 2006, 2007; Burger and Page 2007). Some studies have found that samples of successful nests were significantly farther from edges than failed nests (Nelson and Hamer 1995; Manley 1999) and that proximity to clear-cuts and roads is an important predictor of nest success in BC and Oregon (Raphael 2002b). Recent research on the effect of edge type has also shown that murrelet nest predators are more abundant near hard edges (edge between old-growth patches and clear cuts) than soft edges (edge between regenerating forest and old-growth) (Malt and Lank 2007, 2009) and that nest site availability can be reduced by anthropogenic edges due to changes in microclimate (Malt 2007). However, other studies found no significant difference between the success of nests located near and far from edges (Bradley 2002; Zharikov et al. 2006, 2007) and that habitat fragmentation alone does not necessarily have a negative effect on murrelets unless associated with an increase in the abundance of predators (Zharikov et al. 2007). Murrelets also seem to nest disproportionately near both natural edges, such as streams and avalanche chutes, as well as anthropogenic edges like clearcuts and regenerating forest (Nelson and Hamer 1995; McShane et al. 2004; Zharikov et al. 2006, 2007). While there is debate regarding these results, the differences are likely due to variability in habitat availability, edge type and predation pressure.

1.3 Current management

In Canada, marbled murrelets have been federally listed as Threatened under the Species at Risk Act (SARA) by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This listing creates a legal requirement to develop a Recovery Strategy and Action Plan (SARA 2002), a task that falls on the Canadian Marbled Murrelet Recovery Team (CMMRT). The threatened status of marbled murrelets in Canada is based on evidence of past and continuing decline in their coastal old-growth forest nesting habitat, under the assumption that habitat area is a surrogate for population size (CMMRT 2003). A priority for federal and provincial recovery efforts is to maintain sufficient habitat to support the current geographic range and long term population viability of marbled murrelets throughout coastal British Columbia. The criterion for down-listing murrelets from Threatened to Special Concern is that the population and suitable nesting habitat does not decline from 2002 levels by more than 30% over three generations (30 years) (Burger 2002; CMMRT 2003).

The strategic goal in managing terrestrial habitat for marbled murrelets is achieving target areas of suitable habitat in each of six conservation regions (Figure 1 for conservation regions encompassed by our study) (CMMRT 2003). The CMMRT has outlined stand and landscape level habitat features important for nesting murrelets, as well as a methodology for selecting suitable nesting habitat consistently throughout BC (Burger 2004; CMMRT 2003). Current methods of estimating areas of suitable habitat, required to meet CMMRT population goals depend heavily on the existence of a predictable relationship between the number of birds in a given area and the amount of suitable habitat available (CMMRT 2003). This has been supported by positive correlations between areas of old growth forest and indices of murrelets (Burger 2001; Burger 2002; Burger et al. 2004; Meyer and Miller 2002; Meyer et al. 2002; Miller et al. 2002; Raphael et al. 2002). However, the precise nature of the relationship between murrelet abundance and available suitable habitat varies considerably in some areas of BC and remains uncertain for most regions, making it a source of uncertainty in marbled murrelet recovery policy (CMMRT 2003; Steventon et al. 2003).

Conflicting evidence regarding the influence of edge effects on murrelet productivity further hampers the establishment of habitat reserves, as there is uncertainty about the relative value of different sizes of forest patches for nesting murrelets (Zharikov et al. 2006; 2007; Burger and Page 2007). Refining our current understanding of how landscape context influences the suitability of remnant nesting habitat for the marbled murrelet will help reduce uncertainty in the current method of designating suitable habitat, and will assist in designation of habitat reserves required to meet recovery population targets (CMMRT 2003).

1.4 Goal

In this study, we test the value of habitat and matrix composition and configuration models for predicting local breeding population abundance of marbled murrelets, as indexed by radar counts of commuting birds taken during the breeding season. Using public and private forest cover data, updated with recent harvesting information, we analyse landscape composition and configuration in three regions of coastal British Columbia and make use of radar data not available for earlier analyses. Applying an information theoretic approach, we test whether models of landscape composition and configuration are useful in predicting local breeding abundance of the marbled murrelet and if adding measures of habitat fragmentation can better predict murrelet abundance than models utilizing habitat area alone. We also assess whether model selection, performance, and relevant variables and their effects, vary among regions, by running analyses separately for Southwest Vancouver Island and the Central and South mainland coast regions (Figure 1).

2: METHODS

2.1 Study area

We examined murrelet-habitat associations in three areas of coastal British Columbia: Southwest Vancouver Island, the Central Coast and South Coast areas of BC. Catchment areas (study areas) were located within Coastal Western Hemlock, Mountain Hemlock and Coastal Mountain-heather Alpine biogeoclimatic zones (Table 1, Figure 1) (Meidinger and Pojar 1991). The level of human disturbance varied between and within regions (Nelson et al. 2009). Forest cover data showed regional differences in the area of clear-cuts and the density of roads, Southwest Vancouver Island being the most disturbed and the Central Coast the most intact (Table 1). Catchments on Southwest Vancouver Island fell mostly within the West and North Vancouver Island conservation regions set out by the CMMRT, with the exception of two catchments, which extended into the East Vancouver Island conservation region. All catchments within the Central and South Coast areas fell within the CMMRT conservation regions delineated for these areas (Figure 1).

2.2 Marbled murrelet radar data

We used radar counts of marbled murrelets taken during breeding season. Radar stations were located at the mouths of drainages used as flyways (Peery et al. 2004) by murrelets for accessing inland nesting habitat from marine foraging grounds. The Canadian Wildlife Service (CWS) provided the radar data used in this study, assembled from a number of organizations. Radar data span 1996-2008 and sampling was uneven between study areas (Table 2). Uneven sampling was a result of the period over which data were collected and the multitude of agencies that collected the data, each having different sampling capabilities and priorities.

Topography that funnels murrelets through a central watershed entry point, as they leave marine foraging grounds bound for nesting habitat, produces more reliable radar counts compared to watersheds that have wide coastal access or multiple entry points (Burger 1997; 2001). We therefore selected radar monitoring sites for inclusion in this analysis based on topographic suitability of the site for monitoring with radar and assumed that murrelets used drainage mouths, where radar stations were located, for access to inland nesting habitat (Burger 2001; Burger 2004; Raphael et al. 2002). As we assumed that birds were remaining in the drainages upstream from the watershed entry points where radar stations were located, we excluded all sites with low topography and wide or multiple entry points, which could have permitted murrelets to cross ridges, violating this assumption. Catchments were comprised of watersheds that murrelets accessed from watershed entry points, topography and expert opinion (see Section 2.3). We assumed that murrelets did not cross ridgelines to gain access to adjacent drainages. Radio-telemetry studies in British Columbia provide evidence for the use of inlets, rivers and streams as pathways between marine resources and nest sites, with limited crossing between watersheds (Lougheed 1999).

All radar data were collected following Resource Inventory Standards Committee (RISC) guidelines for Marbled Murrelet population monitoring (Manley 2006). We analysed surveys conducted from the beginning of May through the end of July, most of which were conducted in the peak activity period, from May15 to July 15 (Manley 2006).

All radar units were tilted upwards at an angle of 25° following methodology described in Cooper et al. (1991), as tilted radar units detect more murrelets (Harper et al. 2004). The majority of surveys were performed on land at inlet mouths; however, a small number were performed from radar units stationed on boats near inlet mouths. We did not include inland radar sites (those located away from inlets) in the analysis, as these sites did not provide reliable estimates of birds entering catchments, due to their situation away from watershed entry points. As recommended by the CMMRT (2003), we used only pre-dawn counts of incoming birds, as dawn counts are higher and less variable than dusk counts (Manley 2006; Burger 2001; 2002; Cooper et al. 2001), and because pre-sunrise is known to be the peak activity period (Naslund and Odonnel 1995). Using pre-sunrise counts also eliminates the potential for a post-sunrise pulse, caused by birds taking a second trip or by non-breeding birds prospecting for nest sites (Burger 2001).

Weather, radar observer and precipitation are known to influence timing and detectability of murrelets (Naslund and Odonnel 1995), however due to the complexity of the models in our candidate set, we did not have sufficient sample size to include these covariates. Precipitation can obscure the detection of murrelets with marine radar (Manley 2006). Prior to 2006, RISC standards required excluding surveys with more than 10 minutes of rain during the survey (Resource Inventory Committee 2001). When RISC standards were updated in 2006, this restriction was changed such that surveys with rain clutter for more than ten minutes during peak activity periods were excluded. We followed the respective protocol for each period, excluding surveys with 10 minutes of rain pre-2006 and excluding surveys with rain during the peak period of activity in and after 2006.

2.3 Catchment definition

Catchments include all watersheds deemed to be used by murrelets censused at radar stations located at watershed entry points. The process of defining catchment areas requires extensive knowledge of the flight behaviours and pathways used by breeding murrelets. Because we utilized radar data collected over such a large spatial area, by a variety of sources, we defined catchments collaboratively with the assistance of field experts.

We began our catchment definition process by assessing the catchment boundaries used in Burger et al. (2004). Viewing Burger's 2004 catchment boundaries, and radar survey sites in GoogleEarth (Google Inc. 2009), we held telephone conferences with experts to collaboratively determine radar survey sites to exclude due to unsuitable topography, how to modify existing boundaries, and to define new catchments. Participation of field experts ensured catchment boundaries represented our best estimate of actual inland areas used by murrelets, and minimized the chance of including areas that would permit birds to cross between catchments. Based on a distribution analysis of distance of known nest sites from open ocean (J. Barrett, unpublished data), and following the CMMRT guidelines for habitat "most" and "moderately" likely to be suitable to murrelets, all catchments were distance limited to 40 km from watershed entry points, and for catchments close to marine waters the first 500m of land cover data were removed by buffering as these areas are considered to be less suitable to nesting murrelets (Burger 2002; CMMRT 2003).

2.4 Land cover data compilation

The base forest cover map used to measure landscape composition and configuration was created by combining five sources of land cover data in shape file format in ArcGIS 9.3 (ESRI Inc). To obtain a complete map of vegetation, topography, drainage systems, and human disturbance, we used public and private forest cover data, recent harvest information (where available), Terrain and Resource Inventory Monitoring (TRIM) roads and BC Freshwater Rivers Atlas (ILMB 2008).

2.4.1 Forest Cover

For Timber Supply Areas (TSAs), we obtained 1:20 000 Vegetative Resource Inventory (VRI) data from the Land and Resource Data Warehouse (LRDW). For areas under Tree Farm Licenses (TFLs), we obtained 1:20 000 private forest cover data from individual licensees. Both sources of data were comprised of spatial data layers for the collection, manipulation and production of forest inventory data, with accompanying textual attributes (MOFR 2006). We classified polygons based on the dominant land cover type and treed polygons based on the dominant tree species (Sandvoss et al. 2005). For TFL areas, spatial information on cutting that occurred after the last forest cover inventory was obtained from TFL holders, where available. If the recent harvest was within one of our study areas, the private forest cover data were updated with the recent harvest information.

2.4.2 Freshwater Rivers Atlas

We supplemented rivers information contained in public and private forest cover, with a 1:20 000 freshwater rivers atlas layer, containing all “double line” river polygons for BC (ILMB 2008). This layer includes streams down to approximately 10 meters in width (Malcom Gray, personal communication). While forest cover data from private licensees and provincial data have this resolution for streams, notable errors and omissions were discovered with respect to the spatial arrangement of waterways in both public and private forest cover data. To correct these errors, the combined private and public forest cover data were updated with the freshwater rivers layer, after the TRIM roads were added, using ArcGIS 9.3 (ESRI Inc.).

2.4.3 TRIM Roads

While public and private forest cover contained some roads, compared to 1:20 000 TRIM data, many roads were missing. We included all TRIM roads that fell within our study areas and which were not classified as overgrown. To accurately represent the impact roads have had on the spatial configuration of habitat within our study areas, we applied a buffer of 10m to all roads and allowed roads to break up otherwise contiguous habitat. In this way, we accounted for the habitat lost and habitat fragmentation caused by roads.

2.4.4 Missing Data

Comparable forest cover data were not available for some private land and parks areas. We excluded three catchments on Southwest Vancouver Island because there was a considerable amount (up to 17%) of unobtainable land cover data in these areas. Most of the missing data were on private land, with a smaller portion falling into Provincial parks. Missing data were less than 1% for remaining catchments in all regions.

2.5 Land Cover Data Combination

We combined land cover data in shape file format using ArcGIS 9.3 (ESRI Inc.). TSA and TFL forest cover data sources were combined first. For a small number of areas there was overlap between the TSA and TFL data, in these areas private forest cover data was used, as we had more recent harvest information for privately managed areas. Roads and streams were incorporated into combined public-private forest cover such that they detracted from habitat area and were allowed to break up otherwise contiguous habitat.

2.6 Landscape Variables Sampled

Each forested polygon was grouped into one of four distinct patch types based on the age of the dominant tree species for the polygon. The patch types included: clear-cuts (0-20 years), regenerating-young forest (21-140 years), mature-transitional (141-250 years) and old-growth (>250 years). The old-growth and mature-transitional age categories align with the CMMRT (2003) guidelines for habitat "most" and "moderately" likely to contain suitable murrelet nesting habitat. Initially, we categorized "young" forest as that aged 21-40 years and "regenerating" forest as aged 41-140 years, as in Malt (2007), however, we combined these age classes as they were highly correlated for some of our study regions (Pearson's correlation coefficient=0.96 for these age classes on Southwest Vancouver Island). Soft edge density was measured as the density of old-growth edge to young forest edge (21-40 years), since we were interested in further investigating edge effects identified by Malt (2007) at the landscape scale. We did not differentiate between coniferous and deciduous tree species when defining patch categories because some of the data for private land was missing the information required to do so. We considered this generalisation acceptable, as tree species have shown to be poor predictors of habitat use (CMMRT 2003; Nelson et. al 2009) and although rare, murrelets may nest in deciduous trees (Bradley and Cook, 2001). We decided *a priori* to focus experimental analyses on young *clearcuts*, *regenerating-young*, *mature-transitional* and *old-growth* (Table 3) forest areas as these structural stages appear to be the most relevant in predicting nest-site selection and reproductive success of marbled murrelets (Malt 2007; Zharikov et al. 2007).

It was not possible to determine the age composition of the forested landscape in each year for which we had radar data because historical harvest data were not readily available. We therefore projected forest ages in land cover data to 2001, as this was mid-way in the range of years for which we have radar data. We performed a sensitivity analysis to determine whether projecting ages to 2001 substantially changed the way forest habitat was categorized (see sensitivity analysis below). Forested polygons were then allocated to habitat patch types (Table 3), using the dominant age of the tree species in 2001. In addition to the age composition of the landscape, variables characterizing the configuration and elevation of habitat and matrix were measured in ArcGIS 9.3. We decided *a priori* on a set of 21 landscape metrics that were most relevant to our study questions, however we only included 15 of these in our candidate model set, as several of the variables were highly collinear (see Table 4 for descriptions of variables included and Appendix 2 for those excluded due to multicollinearity).

2.7 Sensitivity Analysis

To determine the effect of projecting all forest ages to 2001, we evaluated what percentage of the youngest two patch categories would have been classified differently if ages had been projected to the years in which radar data were collected, in each region.

We evaluated changes to the youngest two patch types as these were the smallest two age categories (before regenerating and immature were combined, which was done after landscape metrics were measured), with the highest potential for stands to switch between patch types. This sensitivity analysis showed that projecting stand ages to 2001 would result in classifying 1% or less of regional treed catchment areas differently than if age had been projected to years for which we have radar data. Based on this sensitivity analysis we concluded that projecting tree ages to 2001 would not substantially alter the age distribution among patch types.

2.8 Statistical Analyses

We grouped habitat variables into eight functional groups representing different general hypotheses regarding the effects of landscape structure on murrelet abundances. Functional groups included: area of most likely habitat *(old-growth*), moderately likely (*mature-transitional*) and potential habitat (see Appendix 1 for list of attributes included in this category), matrix composition (*regenerating-young* and *clear cut areas*), edge (*hard* and *soft edge density*), old-growth patch configuration (*old-growth nearest neighbour*, *old growth density*, *mean old-growth core area*) edge elevation (*proportion of hard* and *soft edge at low elevations*) and elevation of old growth (*mean slope of old-growth* and *proportion of old-growth at low elevations*) (Table 5). Variables in a group were always included or excluded together, which helped to reduce the size of the candidate model set and focus models on hypotheses of interest.

We measured a 21 landscape variables within each catchment. Because composition influences configuration and vice versa, there was multicollinearity between landscape variables (Smith et al. 2009). Multicollinearity refers to the situation where there are multiple correlated predictor variables (Craney and Surles 2002). If a variable is highly collinear with other variable(s), this indicates that most of the variation in that variable is explained by other covariates; this will inflate standard errors of parameters and can lead to erroneous conclusions (Graham 2003; Zuur et al. 2009b). As our objective was to determine which variables are driving habitat use by breeding murrelets, it was necessary to reduce multicollinearity by dropping some variables (Zuur et al. 2009b).

To assess multicollinearity, we examined Pearson's Correlation Coefficients (PCC) and the Variance Inflation Factor (VIF) for all desirable variable group combinations (Neter et al.1990). VIF indicates how much variance of the estimated coefficients is explained by the rest of variables in the model due to correlation among those variables (Craney and Surles 2002). We examined VIF scores for models developed by running all possible combinations of our variable groups. We examined models with VIF ≥ 10 for highly correlated variables that could be dropped (Craney and Surles 2002; Neter et al.1990; Smith et al. 2009; Lam, 2008). Following this methodology, we reduced landscape variables from 21 to 15. See Table 4 for variables included in models and see Appendix 2 for the list of variables that were dropped.

We investigated the relationship between local breeding population abundance of murrelets and habitat composition and configuration using a linear mixed effects model (lmer) applied in R© (R Development Core Team, 2008). We modelled habitat variables as fixed effects and included a random effect for *catchment* and *year*. Response data were overdispersed (variance response>mean) in all regions and we had partially crossed random effects due to year (see Table 2). We therefore applied a natural log transformation (log(count+1) for zero counts on the South Coast and Southwest Vancouver Island) to the response to allow application of the linear mixed effects model, which permitted the inclusion of random effects and the partially crossed nature of year (Bolker et al. 2008; Osborne 2002; Zuur et al. 2009; Zuur 2007). We included both linear and quadratic forms of survey date (date measured as number of days since May 1), as the peak period of nesting activity for murrelets is between May 15 and July 15 and we expected more murrelets to be commuting to nesting habitat during the peak activity period (Manley 2006).

We developed a set of 49 *a priori* candidate models representing alternative hypotheses of the potential effects of landscape structure on local breeding abundance of marbled murrelet, and ranked them using an information-theoretic approach (Table 6). We included all biologically relevant models with VIF below 10 in our candidate set. We included area of *old-growth* in every model assuming that it was important to murrelet habitat selection (Burger 2001; Meyer and Miller 2002; Meyer et al. 2002; Miller et al. 2002; Raphael 2006; Burger 2002; Burger et al. 2004; Burger and Waterhouse 2009). We also included *day*, day^2 and *percent land* in the radar beam (Table 4 for explanation of relevance) in every model as we hypothesized they would affect detection of murrelets. We always included the edge density variable group with the edge elevation group to permit meaningful interpretation of the elevation metrics, which were measured as proportions of total edge falling below the lower limit of the subalpine for each region (800m for the Central Coast and 900m for the South Coast and Southwest Vancouver Island).

We used an information-theoretic and multi-model inference approach to compare competing models in the candidate set and interpret results (Burnham and Anderson, 2002). We calculated Akaike's Information Criterion for small sample sizes (AICc), and the difference between AICc for the *ith* model and the model with the lowest AICc (ΔAICc). We also calculated the relative weight of evidence for each model (Akaike weight, ώ), interpreted as the probability that model *i* is the best model for the observed data, given the candidate set of models (Burnham and Anderson, 2002). We estimated the relative importance of each variable by summing the ώ 's over all models in which each variable group appeared. However, variable groups were not included equal numbers of times in candidate models (Table 5). Rather than correcting this imbalance, we chose to interpret relative importance values as they were, making the assumption that if a particular variable were important, it would have appeared in a top model. To reduce model selection bias and uncertainty, we calculated the model averaged parameter estimates and unconditional standard errors for all fixed effects (Burnham and Anderson 2002).

To assess how well our top models fit the data, we calculated a likelihood ratio based R^2 statistic (R^2_{LR}), defined as follows (Magee 1990, Sun et al. 2010, Kramer, 2010):

$$R^2_{LR}=1-\exp(-2/n(\log L_M-\log L_0)$$

where $\log L_M$ is the log-likelihood of the model of interest and $\log L_0$ is the log-likelihood of the intercept only model, and n is the number of observations. The R^2_{LR} is based on maximum likelihood estimation and is a good estimator of proportion variance explained (Sun et al. 2010, Kramer 2010).

We ran all models in each region with and without *day, day*^{2} and *percent land* in radar beam, to determine whether omitting these fixed effects would change model ranking. We also ran models with potential outlier counts for each region omitted to determine if these counts had high enough leverage to change model ranking (Zuur 2009). Excluding potential outliers did not change model ranking, and AIC values were lower with fixed effects *percent land in radar beam*, *day* and *day*^{2} included.

3: RESULTS

3.1 Model selection

The most parsimonious model of marbled murrelet habitat use differed among study regions (Table 6). However, in general, regional habitat use by marbled murrelets was associated mostly closely with the *area of old growth* forest, matrix composition, and the *density of hard* and *soft edges*. The proportion of variation explained by the top model in each region ranged from 11 percent on the South Coast to 35 percent on the Central Coast (R^2_{LR}) (Table 6). The best model in each region had Akaike weights (ώ) of < 0.95, suggesting that interpretation of a confidence set of models was more appropriate than interpretation based on a single best model (Burnham and Anderson, 2002).

In all regions the 95% confidence set of models ($\sum$ώ ≥ 0.95) (Burnham and Anderson 2002) contained old-growth configuration, edge, matrix composition, as well as likely and potential habitat area variable groups. Old-growth elevation and edge elevation metrics were also included in the 95% confidence set of models for the South Coast and Southwest Vancouver Island, but were excluded for the Central Coast. All models in the Central Coast that included the edge elevation variable group (EE) had AICc difference values (Δ_i) > 14, suggesting that models containing this variable group were relatively poor at explaining variation in counts of marbled murrelets in this region. All models in the 95% confidence set for Southwest Vancouver Island contained the edge variable group, indicating that *soft* and *hard edge density* were important factors in determining murrelet habitat use in this region.

Matrix composition appeared in the top four models for the South Coast ($\sum\acute{\omega}$ = 0.47) and the top six models in the Southwest Vancouver Island region ($\sum\acute{\omega} > 0.8$) and, although it was included in the confidence set of models for the Central Coast, models containing this variable group had large AICc difference values ($\Delta_i > 7$) indicating relatively poor fit. The edge density variable group was included in the top model for the Central Coast and Southwest Vancouver Island and in the second ranked model on the South Coast, suggesting the importance of this group among regions as well as within. Support for the likely habitat area variable group was strong on the Central Coast, as this variable group was included in the top three models (($\sum\acute{\omega} = 0.85$), and in almost half of the models comprising the 95% confidence set for this region. There was less consistent support for this habitat type on the South Coast and Southwest Vancouver Island, where it was included in only 27% and 15% of models comprising the confidence sets for these regions. The importance of old-growth configuration was also evident in the Central Coast region, appearing in 5 of 11 models in the confidence set, including the top two models ($\sum\acute{\omega} > 0.8$). Old-growth configuration appeared in 19% of models in the South Coast confidence set and 39% of those for Southwest Vancouver Island, but models containing this variable group did not have strong support in these regions ($\acute{\omega} < 0.035$) for all models containing this group in the South Coast and Southwest Vancouver Island.

Both edge elevation and old-growth elevation variable groups were included in the confidence set of models for the South Coast and Southwest Vancouver Island. However, there was support for the effect of elevation only on Southwest Vancouver Island, where the edge elevation group was included in nearly half the confidence model set, including the second best model (all models with old-growth elevation had $\acute{\omega} \leq 0.031$

for Southwest Vancouver Island and $\acute{\omega} \leq 0.025$ for the South Coast). Finally, potential habitat area was included in the confidence set of models for every region, but never appeared in a top model, and did not predominate in any confidence set, suggesting marginal support for this variable group.

3.2 Relative importance of variable groups

We calculated the relative importance (RI) of variable groups by summing Akaike weights for models in which the variable group appeared (Burnham and Anderson 2002). There was a large imbalance in the number of times each variable group was included in the candidate set, however, we chose to interpret the values as they were, rather than correcting for the imbalance, assuming that if a group were important, it would have been included in a top model. Relative importance of variable groups differed between regions. On the Central Coast, area of *mature-transitional forest* (likely habitat area group) and old-growth configuration were important for determining habitat use by murrelets with RI values of 0.89 and 0.84 respectively. However, old-growth configuration was included in the candidate set half the number of times the mature transitional group was, suggesting very high relative importance of old-growth configuration in this region. Matrix composition was the most important for breeding murrelets on the South Coast, with a RI value of 0.69, and even more important on Southwest Vancouver Island where it received a RI of 0.86. As only edge elevation and old-growth configuration variable groups were included fewer times in the candidate set than matrix composition, matrix was clearly important in determining habitat use on the South Coast and Southwest Vancouver Island, given unequal representation in the candidate set. The highest relative importance for any variable group was for edge density on Southwest Vancouver Island, where it received a RI of 0.99. Southwest Vancouver Island was also the only region where elevation effects were important with a RI of 0.45 for edge elevation. *Old-growth, day,* day^2 and *land* were included as fixed effects in every model in the candidate set, therefore their relative importance values are equal to 1.

3.3 Variable effects

3.3.1 Fixed effects

Model averaged coefficients for all regions indicated that marbled murrelets were associated with watersheds containing more area classified as old-growth forest, and strongly so on the Central Coast and Southwest Vancouver Island. The direction and magnitude of the remaining variable effects generally differed between the three study regions, therefore; effects are discussed separately for each region. Also, the large unconditional standard errors for some of the variables relative to their coefficients (Table 7) indicates considerable uncertainty regarding the true relationship for some variable groups, particularly for the old-growth elevation and potential habitat area groups. In describing effects of variables, we only considered effects of variables for which the magnitude of the parameter estimate was greater than the magnitude of the unconditional standard error (i.e. where $\beta/SE>1.0$). Coefficients that were smaller than their corresponding standard error were considered to have an uncertain effect, those that were >2xSE were considered strong effects.

For the Central Coast study region, murrelets showed a strong positive association with area of *old-growth forest*, but a strong negative association with area of *mature-*

transitional forest, *proximity of old growth patches* and *mean core area of old-growth* patches. Murrelets tended to use areas where, on average, old-growth patches were farther apart and smaller, and in this region *hard* and *soft edge density* were positively associated murrelet habitat use. On the South Coast murrelets showed a negative association with *regenerating-young* and *clear-cut area*. Similar to the Central Coast, murrelets breeding on South Coast were positively associated with *hard edge density*. For Southwest Vancouver Island, murrelets showed a strong positive association with area of *old-growth forest* habitat, *area of clear cuts* and *proportion of hard edge at low elevations* (below 900 m). Murrelets associated negatively with the *density of hard* and *soft edges*, the opposite of the direction of the effect in the other two regions

The relationship between local murrelet abundance and *day* was dome shaped for Southwest Vancouver Island, indicating that more murrelets used breeding habitat during the peak seasonal activity period. In contrast, the relationship between murrelet abundance and *day* was bowl shaped for the Central Coast, where high-count catchments were surveyed later in the season. Evidence for an effect of *land* on detection of murrelets was equivocal, as this variable received a positive value on the Central Coast, and a negative value on Southwest Vancouver Island, with no effect on the South Coast.

We examined QQ Normal and plots of observed versus fitted values for all candidate models in all three regions (Zuur et al. 2009; Zuur 2007) and determined that distributional assumptions generally were met. The South Coast and Southwest Vancouver Island Q-Q plots had longer lower tails than those for the Central Coast (Figure 3.2), where counts of zero were transformed using log (0+1). We accepted this structure, as mixed models are fairly robust to these types of minor distributional deviations (Verbeke and Lesaffre 1996).

3.3.2 Random effects

The variance of random effects differed between regions. On the Central Coast, the random variability attributed to *catchment* ranged from 0.25-0.91 and ranged between 0.02-0.08 for the random effect of *year*. For the South Coast, variation due to *catchment* ranged from 0.28- 0.77 and from 0.01-0.03 for *year*. Variance was apportioned differently in Southwest Vancouver Island, where *catchment* variance ranged from 1.0 (null model) to 0.23 and variance of *year* ranged between 0.09-0.16.

4: DISCUSSION

Uncertainty regarding the designation of suitable nesting habitat and the effect of differently sized habitat patches on marbled murrelet productivity have hampered protection of nesting habitat in British Columbia (CMMRT 2003; Dechesene-Mansiere 2004; Steventon et al. 2004). Refining our understanding of the ways in which landscape-level habitat measures influence habitat use by breeding murrelets will improve confidence in the current method of identifying areas of suitable nesting habitat and facilitate the establishment of reserves required to meet 2032 recovery population targets set by the CMMRT (CMMRT 2003). Our results clearly support the well accepted primary importance of old-growth habitat area, but provide analytical support for matrix composition and configuration as significant factors correlating with terrestrial habitat use by marbled murrelets. Top models in all regions included combinations of these variable groups and were ranked higher than models simply containing area of old-growth forest (Table 6). Our results further show that the best models for determining habitat use differ considerably between regions and that the effects of landscape components can vary between regions.

Total *old-growth area* had a consistently positive effect on habitat use by breeding murrelets among regions, with strong support for this effect on the Central Coast and Southwest Vancouver Island (Table 7). This straightforward finding is consistent with previous research (Burger 2001; Burger 2002; Burger 2004; Raphael et al. 2002; Burger and Waterhouse 2009) and supports the most fundamental tenant of management approaches (CMMRT 2003; Canadian Marbled Murrelet Nesting Habitat Recovery Implementation Group 2006). Since we included *old-growth area* in every model, we were unable to compare the relative importance of this variable with that of others.

The additional landscape components that best determined habitat use by breeding murrelets differed between regions, however, previous studies have also found differences in the variables best predicting murrelet habitat use among regions (Zharikov et al. 2006, 2007). Although the most important additional predictors of murrelet habitat use differed between regions, there was good support for the importance of hard and *soft edge density* across regions. Edge density appeared in the top model for both the Central Coast (RI=0.61, positive association) and Southwest Vancouver Island (RI=0.99, negative association) and the second best model for the South Coast, where it was also the second most important predictor of murrelet habitat use (RI=0.28, positive association). Matrix composition was an important predictor of habitat use on Southwest Vancouver Island (RI=0.86, positive association) and the most important on the South Coast (RI=0.69, negative association), but was not important on the Central Coast, where habitat composition and configuration (area of mature-transitional forest and old-growth configuration) and matrix configuration (i.e. edge) were most important. Interestingly, edge elevation was the only elevation group to receive noteworthy support, and was only important on Southwest Vancouver Island (RI=0.45, positive association) where it had a weak positive association with murrelet habitat use, indicating that more murrelets used catchments that had more hard edge at low elevations.

4.1 Regional associations between marbled murrelet habitat use and landscape composition and configuration

4.1.1 Central Coast

Murrelets on the Central Coast preferentially used catchments containing smaller patches of old-growth core area, which were farther apart and that contained less forest classified as *mature-transitional*. *Hard* and *soft edge density* were also positively associated with habitat use in this region. Working with data from nests located within several watersheds, Zharikov et al. (2006) found that murrelets at Desolation Sound, on the South Coast, nested in smaller than average habitat patches and closer to clear-cut edges than expected. Studies in Washington and Oregon have also found that areas occupied by murrelets contained higher amounts of forest edge and more complex shapes (Ralph et al. 1995) and had a higher edge contrast index (Meyer and Miller, 2002) than areas not occupied by murrelets. This apparently positive edge or fragmentation effect is unexpected if edge habitat is deleterious for murrelet nesting success, as commonly assumed in most of the literature (e.g. Burger 2001; Burger 2002; see Introduction), and as appears to be the case in our analyses for Southwest Vancouver Island. Among other potential causal mechanisms, this may reflect a preference for edges by murrelets (Nelson and Hamer 1995; McShane et al. 2004; Zharikov 2007), the parallel affinity of both murrelets and logging companies for old-growth forest (Zharikov et al. 2006), or a temporal lag, where despite increased predation near hard edges (Malt and Lank 2007, 2009), several years are required before birds abandon fragmented forests (Meyer et al. 2002). One possible explanation for the contrast in effect direction between the mainland and Southwest Vancouver Island site is that edge attraction does occur, but that predator populations, and therefore predator-driven edge effects, are less severe on the mainland.

The positive association of murrelets with watersheds containing more fragmented old-growth may also reflect landscape topography effects in this region. The mean slope of old growth stands on the Central Coast was significantly greater than the mean slope of old growth stands on Southwest Vancouver Island ($p= 0.00174$). Therefore, it is possible that natural edges created by slides and avalanches, which are more frequent on steeper slopes, occur often on the Central Coast, creating old-growth patches with less core area. Unfortunately, slides were not comprehensively mapped in the land cover data we obtained for this study, and the density of freshwater to old-growth edge was highly correlated with other variable groups (and was therefore excluded, see Appendix 2), preventing examination of natural edge effects. However, slides that were mapped did break up habitat and the density of freshwater: old-growth edge ranged from 0.2-2.24 m/ha on the Central Coast. In addition, natural edges dissected by streams often have more complex shapes than areas with the numerous simple edge cuts of timber harvest (Mladenoff et al. 1993; Reed et al. 1996). Old-growth dissected by streams, would then have a more convoluted edge boundary, which would result in less core area once the 50m edge buffer was removed. The prevalence of natural edges on the Central Coast, caused by streams, avalanches and slides may thus explain the affinity of murrelets for more skinny/irregularly shaped patches of old-growth. Additionally, natural edges show less negative edge effects than anthropogenic edges (Malt and Lank 2007, 2009).

Murrelets breeding on the Central Coast were also negatively associated with area of mature-transitional forest (141-250 years). This finding is contrary to previous, similar studies using this age category (Burger 2004), but is not entirely surprising given that stands with the structural elements required for nesting are usually greater than 200 years old (Hamer and Nelson 1995; Burger 2002, Waterhouse et al. 2002). Additionally, catchments containing the largest areas of old-growth had considerably smaller proportions of mature-transitional forest area and this habitat category was not well represented on the Central Coast (total area was <7% catchment area, compared to >19% total catchment area classified as old-growth). This is consistent with studies of landscape age distribution and natural disturbance regimes, which show that unmanaged coastal rainforest landscapes are dominated by old forest, with only a small proportion of the area in disturbed and recovering forests (Clayoquot Science Panel 1995; Lertzman et al. 2001; Lertzman et al. 1996). Similarly, Meyer and Miller (2002) found that landscapes occupied by murrelets tended to be dominated by old-growth. Given this, strong selection for area of old-growth forest may have contributed to the negative association for area of mature-transitional forest, due to the way habitat classes were distributed among catchments.

4.1.2 South Coast

There was a considerable degree of uncertainty in model selection on the South Coast, as evidenced by the large number of models in the 95% confidence set (Table 6) and lower R_{LR}^2. We therefore place less emphasis on drawing inferences from analyses in this region. For the South Coast, after *area of old growth*, matrix composition was the most important predictor of murrelet habitat use (RI=0.69) and associations were negative for both area of regenerating forest and area of clear-cuts. A negative association between *areas of clear cuts* and *regenerating forest* and abundance of marbled murrelets is expected based on previous studies showing linear or curvilinear relationships between area of suitable nesting habitat and abundance of marbled murrelets (Burger and Waterhouse 2009). Edge was the second most important predictor of habitat use in this region (RI=0.28) and as with the Central Coast, there was a positive association between habitat use and *hard edge density*, although this effect was very weak (β=0.115 and SE=0.110). Edge density was included in the candidate set 29 times, compared to 18 times for matrix composition, which further supports the importance of matrix composition in determining murrelet habitat use in this region.

The composition of our study areas may have contributed to the weak associations between murrelet abundance and measures of landscape composition and configuration on the South Coast. This region had the lowest percentage of overall catchment area that fell into our four patch types (~25% total catchment area). In contrast, a large proportion of our catchment areas were classified as alpine (>60%). It is possible that some drainages that were actually being used by murrelets, inventoried at South Coast radar sites, were excluded from this analysis during the catchment definition phase (due to topography), or as a result of distance limiting to 40 km from watershed entry points. If this was the case, revision of catchment boundaries may result in better model performance in this region.

4.1.3 Southwest Vancouver Island

Murrelets breeding on Southwest Vancouver Island showed a negative association with the *density of hard edges* and a strong negative association with the *density of soft edges*. The *density of hard* and *soft edges* was a more important predictor of murrelet habitat use on Southwest Vancouver Island than for any other region, a trend which was also true for the edge elevation (RI=0.45) and matrix composition variable groups

(RI=0.86). However, the edge variable group was included in the candidate set 29 times (compared to 18 and 14 times for matrix composition and edge elevation respectively) which may have inflated its relative importance somewhat.

The negative association between murrelet habitat use and edge density on Southwest Vancouver Island is expected based on most current opinions and opposite from the result we obtained on the Central Coast, indicating that the direction of these effects may vary regionally. In addition to the hypotheses discussed above, landscape structure may be involved (Table 6). Southwest Vancouver Island had the some of the most industrially fragmented catchments of all our study regions as well as some of the most intact. Generally, catchments North of Alberni Inlet were more intact and those South of it were more disturbed. There was therefore a large degree of variability in the level of fragmentation among catchments in this region (Table 1). The Central Coast, by comparison had the overall lowest percentage area classed as *clear-cut*, and *regenerating* and fragmentation was fairly even among catchments (see Table 1 for road density). Therefore, the difference in the direction of edge effects between these two regions may be at least partly explained by different levels of fragmentation. A potential causal mechanism for this is the existence of disturbance thresholds, beyond which detrimental edge effects become more pronounced (Laurence 1998; Fahrig 2001; Toms 2003). Nest predators that are attracted to edges due to increases in food availability, such as the presence of berry producing shrubs (Malt 2007), may be preferentially attracted to areas with more food. Areas with higher abundance of nest predators experience higher rates of nest predation (Malt 2007) and may be avoided for this reason by breeding murrelets (Meyer and Miller 2002).

Murrelets nesting on Southwest Vancouver Island also showed a positive association with the *area of clear cuts* and the *proportion of hard edge at low elevat*ions (below 900m), although the effect *for hard edge low* was fairly weak (β=0.152 and SE=0.110). Similar to results on the Central Coast, the positive association for *clear-cuts* may reflect the parallel affinity of both murrelets and logging companies for old-growth forest (Zharikov et al. 2006).

4.14 Influence of radar site

The presence of land in the radar beam can obscure the detection of murrelets, similar to clutter produced by waves and rain (Manley 2006). This occurs because any land within the radar beam appears as a solid mass on the radar screen, preventing the detection of moving objects, like murrelets. For this reason, we included the percentage of land falling within a 1 km radius circle around the radar station as a fixed effect in all models, hypothesizing that this variable may have an effect on the number of murrelets detected. The *percentage of land in the radar beam* had a negative association with local abundance of murrelets on Southwest Vancouver Island (β=-0.0.93 and SE=0.071), but a weak positive relationship on the Central Coast (β=0.106 and SE=0.103), and no effect on the South Coast. Although further studies will be required to confirm this result, positioning of radar stations such that there is less land within the radar beam may help to improve the detection of murrelets.

4.2 Summary and management implications

Our results clearly support the incorporation of components of landscape and matrix composition *and* configuration into models of habitat suitability, as well as the development of regional models of habitat suitability. In all regions, the best models of murrelet habitat use included combinations of habitat area and matrix composition and/or configuration, which ranked higher than models of old-growth habitat area alone. Currently, methods of identifying suitable habitat begin with the examination of GIS and/or habitat maps to identify and map habitat polygons under consideration for protection. This is followed by the application of habitat algorithms which rank habitat as suitable or unsuitable (CMMRT, 2003). A number of habitat algorithms have been developed, many of them regionally specific (reviewed in Burger 2002, see also Chatwin and Mather 2007). However, these have primarily been focused on: stand age, tree height class, canopy closure, vertical canopy complexity as well as site productivity index, elevation and distance of habitat from saltwater. This initial step is followed by two further classification techniques, using air photo interpretation, to identify murrelet habitat criteria related to forest canopy structure, and low-level helicopter surveys, which focus on canopy microhabitat features such as epiphyte cover and availability of potential nesting platforms (Burger et al. 2009).

Our results suggest the refinement of algorithms used in the identification of suitable habitat. Our results indicate that the habitat algorithms could be improved by incorporating landscape composition *and* configuration measures in the categorization of areas as either suitable, or unsuitable for nesting murrelets. Based on the results of this analysis, an initial recommendation would be to include measures of matrix composition and edge density in models used to determine habitat suitability. In addition, suitability models for the Central Coast may be improved by adding measures of old-growth configuration.

Further studies on the effects of landscape composition and configuration on local breeding abundance of marbled murrelets should be conducted to verify the results of this study. In particular, studies that simultaneously investigate the relationships between murrelet abundance and landscape structure as well as relationships between breeding success and landscape structure are needed to reveal causal relationships that are driving habitat use.

4.3 Study limitations and assumptions

One factor influencing the interpretation of our results is the assumption that murrelets that were counted flying into drainages, stayed within the catchment boundaries we associated the respective radar station. Information from British Columbia on the relationships between nesting and foraging areas, and routes used to commute between them are available from radio-tracking studies conducted around Desolation Sound, on the South Coast, and Clayoquot Sound, on Southwest Vancouver Island. The distributions of nest sites located relative to capture sites (Zharikov et al. 2006), and the pathways taken by birds moving between marine and terrestrial areas (Lougheed 1999) provide general support for our assumption. To decrease error due to unrepresentative data, we selected radar sites and defined the boundaries of our catchments to minimize the chance that murrelets would cross between study areas, using the best available information on murrelet flight paths, as well as expert field advice. As such, we believe that the combination of natural topographic barriers and placement of radar sites greatly reduced the chances of erroneously associating murrelets with the drainage they were entering and missing large numbers of murrelets entering catchments.

We assumed that counts of murrelets indicated levels of breeding activity, however we acknowledge that not all murrelets flying into catchment areas were actually nesting there. Some murrelets visiting forest habitat were likely non-breeders making prospecting trips (Burger 2001). There seems little reason to argue that non-breeders biased our results by selectively raising abundance in certain areas related to our analysis variables.

We assumed that harvested areas began to regrow immediately after harvesting. For example, if we had information that an area had been harvested in 1980, we would have categorized this area as regenerating-young in 2001. We recognise that the rate of regrowth differ among ecosystems and may not begin immediately, however, we felt that the age categories we applied acceptably accounted for this generalization, for the purposes of this study.

TABLES AND FIGURES

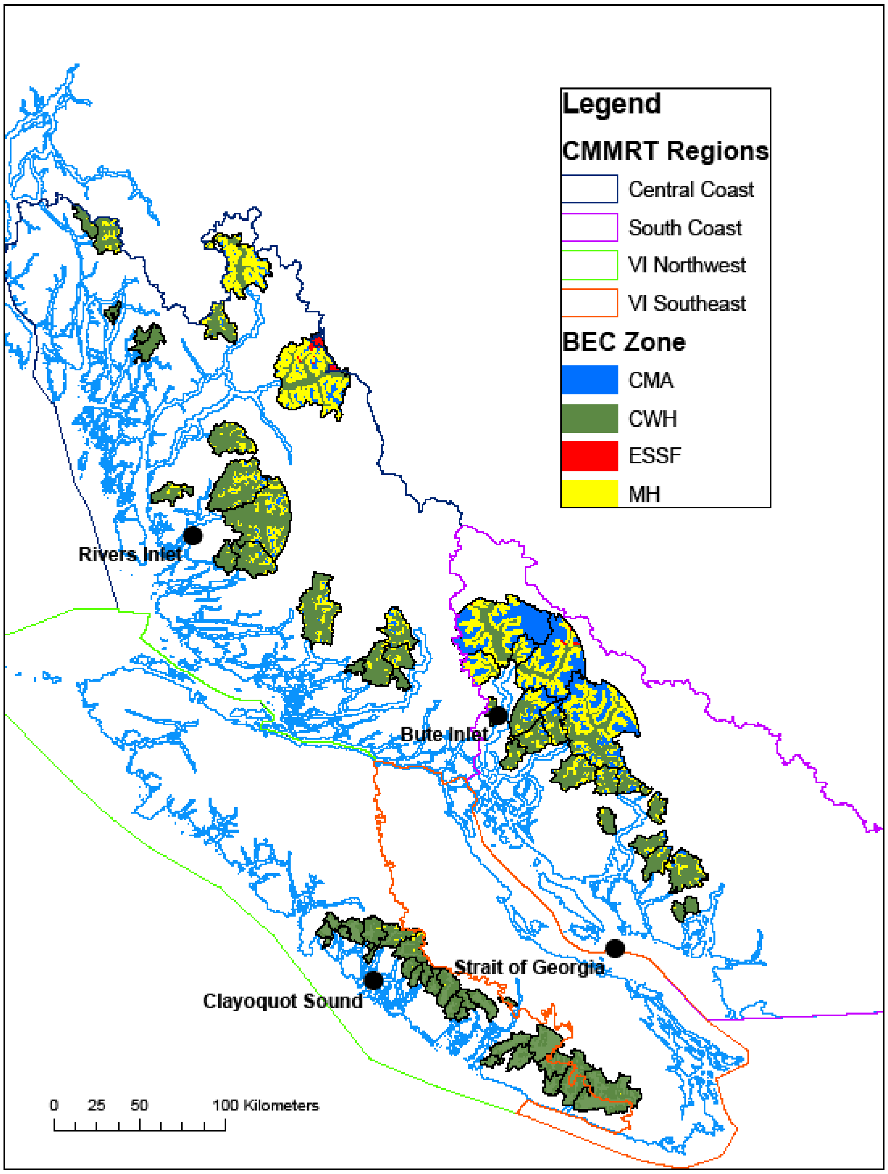

Figure 1. Study area (catchment) locations in three areas of coastal British Columbia, with respect to the Central Coast, South Coast, Northwest Vancouver Island (VI) and Southeast VI CMMRT conservation regions, and biogeoclimactic composition of catchments. Biogeoclimactic (BEC) zones include: Coastal Mountain-heather Alpine (CMA), Coastal Western Hemlock (CHW) Engelman-spruce Subalpine Fir (ESSF) Mountain Hemlock (MH).

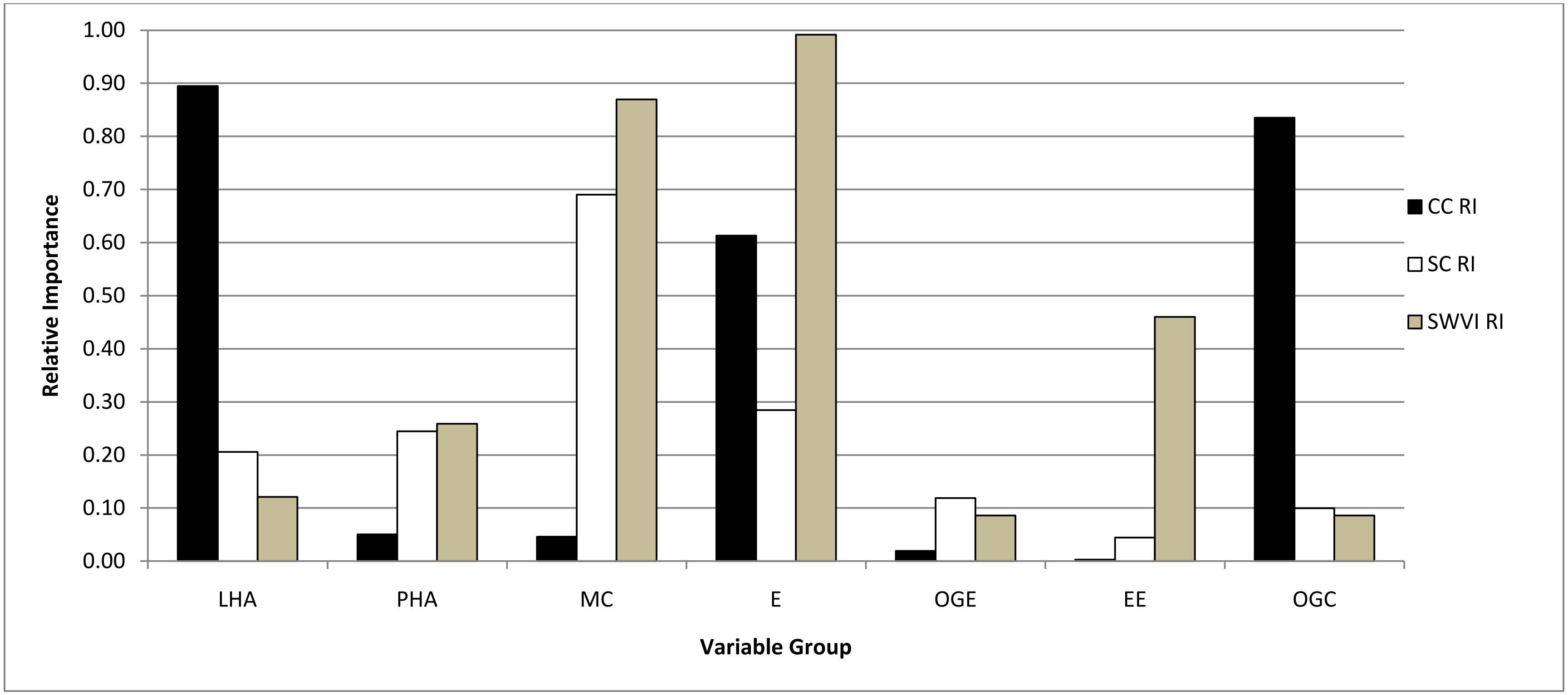

Figure 2. Relative importance of variable groups included in mixed model analysis of marbled murrelet habitat use in three regions of British Columbia; the Central Coast (CC), South Coast, (SC) and Southwest Vancouver Island (SWVI). MLHA= most likely habitat area, LHA= likely habitat area, PHA=potential habitat area, MC= matrix composition, E= edge density, OGE= old-growth elevation/slope, EE=edge elevation and OGC=old-growth configuration. See Table 5 for variables included in each functional group. Old growth area, day, day^2 and land were included as fixed effects in every model while year and catchment were modeled as random effects.

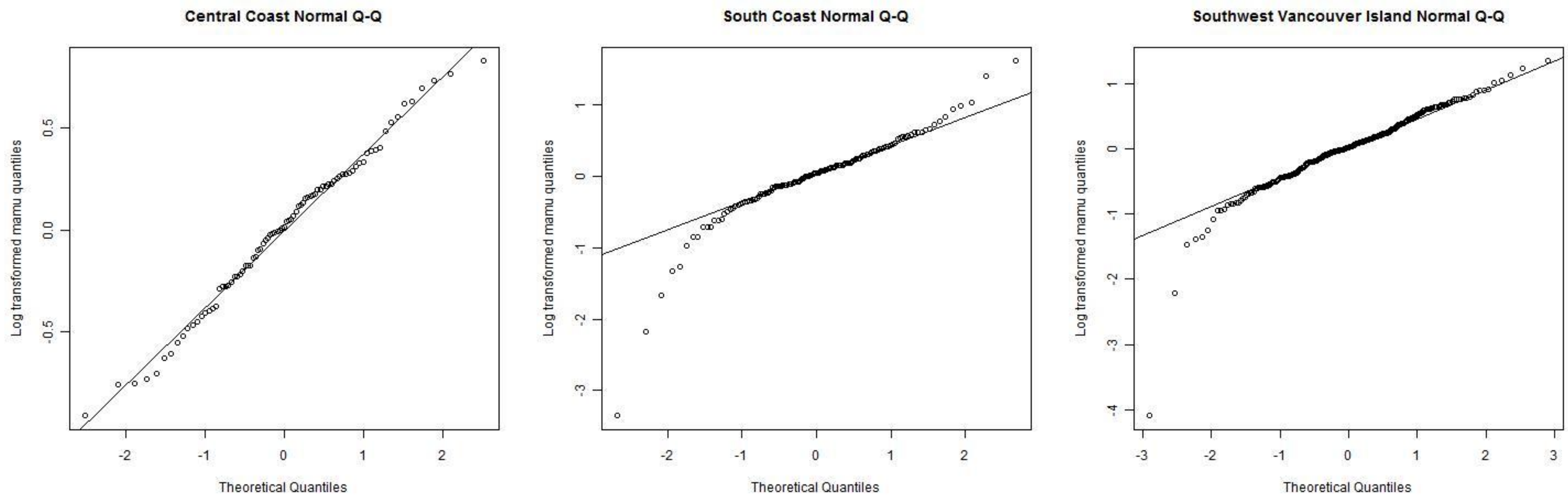

Figure 3. Normal Q-Q plots for log transformed counts of marbled murrelets (Log transformed marbled murrelet count quantiles) in three regions of coastal British Columbia; the Central Coast (CC), South Coast (SC) and Southwest Vancouver Island (SWVI). Counts of murrelets on the SC and SWVI were transformed using log(marbled murrelet count+1) as these regions had counts of zero for some surveys.

Table 1. Landscape composition of three regions in coastal British Columbia, the Central and South mainland Coast and Southwest Vancouver Island. Number of catchments per region, total area of: old-growth, mature-transitional forest, clear-cuts, regenerating-young forest. Average road density is shown with standard deviation (SD) in brackets, total catchment area and distribution of catchment areas among biogeoclimactic zones is also shown. Biogeoclimactic zones within study areas include Coastal Western Hemlock (CWH), Mountain Hemlock (MH), and Coastal Mountain-heather Alpine. The CC and SC also had under 1% in Engelmann Spruce-Subalpine Fir and the CC also had under 1% Boreal Altai Fescue Alpine

Region	Catchments/ region	Total old-growth area (ha)	Total mature-transitional area (ha)	Total clear-cut area (ha)	Total regenerating-young area (ha)	Average road density (SD) (m/ha)	Total catchment area (ha)	%CWH	%MH	%CMHA
Central Coast	20	147727	50730	9680	44639	0.67(0.80)	751293	47	25	26
South Coast	21	92026	20530	11962	68774	2.73(2.77)	781495	32	20	48
Southwest Vancouver Island	25	124286	13082	28683	43139	6.54(8.69)	258884	90	9	1

Table 2. Years of marine radar data and number of surveys for three regions of coastal British Columbia, Southwest Vancouver Island (SWVI) and the Central (CC) and South (SC) mainland coasts.

Region	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Total Surveys
CC			32								28		25	85
SC					51	29					27		27	134
SWVI	48	50	36	2			13	13	12	11	67	16		268

Table 3. Age categories corresponding to clear-cut, regenerating-young, mature-transitional, and old-growth patch categories. Age is that of the dominant tree species in 2001

Patch category	Age (years)
Clear cut	0-20
Regenerating-Young	21-140
Mature-transitional	141-250
Old-growth	>250

Table 4. Landscape composition and configuration variables measured in ArcGIS 9.3 which were used in this analysis, their descriptions, relevance to marbled murrelet and what component of landscape they quantify. See Appendix 2 for the variables that were dropped from the analysis due to multicollinearity.

Variable Name	Description	Relevance	What does it quantify?
Area of old-growth	Area of catchment that is > 250 years.	Characterizes composition of the landscape, which has been shown to influence occupancy (e.g., Burger 2001, Zharikov et al. 2007, Meyer et al. 2002) and predator abundance (Malt 2007).	Composition
Area of mature-transitional forest	Area of catchment that is 141- 250 years.		Composition
Area of regenerating-young forest	Area of catchment that is 21 -140 years.		Composition
Area of clear-cuts	Area of catchment that is < 20 years.		Composition
Non-productive forest habitat*	Areas classified as non-productive in TFL or TSA data. Represents the portion of the forested land base not currently considered to be valuable murrelet habitat.	Investigates the influence of habitat currently thought to be marginal on habitat selection by breeding murrelets. We include it because polygons categorized this way can have trees old enough to have the structural elements required for nesting. Murrelets have also been found to nest in habitats not considered to contain the structural elements required for nesting (Zharikov et al. 2006).	Composition
Old-growth patch density	Number of old-growth patches per unit area of catchment.	Characterizes level of fragmentation, where the number of patches per unit area increases as continuous habitat is broken into fragments. Note that this metric does not distinguish between size of the patches (e.g., a catchment with 5 small patches will have the same value as a catchment of equal size with 5 large patches).	Configuration
Mean old-growth patch core area	Mean interior area of old-growth patches after a 50m buffer edge (i.e., edge-effect area) is eliminated.	Smaller patches with greater shape complexity have less core area. Integrates patch size, shape and edge effect. The buffer can be a different size for different edge types. Raphael et al. (2002) found that the abundance of marbled murrelets increased with increasing core area.	Shape

Variable Name	Description	Relevance	What does it quantify?
Old-growth nearest neighbour	Mean nearest neighbour distance between old-growth patches in a catchment.	Addresses whether proximity of habitat patches influences murrelet abundance within a catchment. Raphael et al. (2002) found that abundance of marbled murrelets increased with proximity of habitat patches.	Configuration
Hard edge density	Density of old-growth | young clear-cut edge (length (m)of edge/catchment area (ha))	Addresses the influence of edge type on murrelet habitat selection. Predation risk to murrelet nests (Malt 2007) and nest site selection (Zharikov et al. 2006) have been correlated with edge type.	Configuration
Soft edge density	Density of old-growth | regenerating edge (21-40 years) (length of edge (m)/catchment area (ha))		Configuration
Proportion of old-growth at low elevations	Proportion of the total old growth occurring below the lower limit of BEC subalpine band for the region (800m for the CC and 900m for the SC and SWVI).	Investigates the influence of low vs. high elevation habitat on murrelet habitat use	Composition
Proportion of hard edge at low elevations Proportion of soft edge at low elevations	Proportion of hard and soft edge occurring below the lower limit of the BEC subalpine band for the region (800m for the CC and 900m for the SC and SWVI).	Investigates the influence of edge type on murrelet habitat selection at high and low elevations	Configuration
Mean slope of old-growth stands	Mean slope of old growth stands in each catchment	Investigates the influence of slope on murrelet habitat selection.	Configuration
% land in radar beam	Percentage of area that is land, falling within a 1km circular buffer around the radar station.	Interference from land and rain can obscure the detection of murrelets with radar (Manley 2006). This variable tests the effect of radar station location on marbled murrelet detections.	Influence of survey location

*See Appendix 1 for a list of polygon types included in the non-productive forest parch type/region.

Table 5. Variable groupings used to construct candidate model set. Groups were based on general hypotheses about how landscape composition and configuration affect local breeding population size of marbled murrelet. Variables in a group were always included together and the edge group was always included with the edge elevation group.

Functional group	Variables Included	Number of times group was included in candidate set (/49)
Most Likely Habitat Area (MLHA)	Old-growth area (ha)	49
Likely Habitat Area (LHA)	Mature-transitional area (ha)	19
Potential Habitat Area (PHA)	Non-productive habitat area (ha)*	22
Matrix Composition (MC)	Clear-cut area (ha)	
	Regenerating-immature area (ha)	18
Old-growth configuration (OGC)	Nearest neighbour	8
	Old-growth patch density	
	Mean core area of old-growth patches	
Edge (E)	Soft edge density	29
	Hard edge density	
Edge elevation (EE)	Hard-edge low	14
	Soft-edge low	
Old-growth elevation/slope (OGE)	Proportion old-growth low	20
	Mean slope old-growth	

*See Appendix 1 for a list of polygon attributes included in Non-productive forest patch type/region.

Models investigating the relationship between landscape composition, configuration, elevation and habitat use by local breeding populations of marbled murrelets. Models are represented by the variable groups that were included in each and have been numbered for easy reference. See Table 5 for variables included in each group.

Model #	MLHA	LHA	PHA	MC	E	OGC	EE	OGE
1	X							
2	X	X						
3	X		X					
4	X	X	X					
5	X			X				
6	X	X		X				
7	X	X	X	X				
8	X		X	X				

Model #	MLHA	LHA	PHA	MC	E	OGC	EE	OGE
1	X							
9	X				X			
10	X	X			X			
11	X	X	X		X			
12	X		X		X			
13	X			X	X			
14	X		X	X	X			
15	X					X		
16	X	X				X		
17	X		X			X		
18	X			X		X		
19	X				X	X		
20	X	X			X	X		
21	X		X		X	X		
22	X				X		X	X
23	X	X			X		X	X
24	X	X	X		X		X	X
25	X		X		X		X	X
26	X							X
27	X	X						X
28	X	X	X					X
29	X		X					X
30	X			X				X
31	X	X		X				X
32	X	X	X	X				X
33	X		X	X				X
34	X				X			X
35	X	X			X			X
36	X	X	X		X			X
37	X		X		X			X
38	X			X	X			X
39	X		X	X	X			X
40	X				X		X	
41	X	X			X		X	
42	X	X	X		X		X	
43	X		X		X		X	
44	X			X	X		X	
45	X	X		X	X		X	
46	X		X	X	X		X	

Model #	MLHA	LHA	PHA	MC	E	OGC	EE	OGE
1	X							
47	X				X	X	X	
48	X			X	X		X	X
49	X		X	X	X		X	X

Table 6. AICc ranking of models describing habitat use by breeding marbled murrelets in three regions (CC=Central Coast; SC=South Coast and SWVI=Southwest Vancouver Island) of coastal British Columbia. The number of parameters (k), AICc difference (Δ_i) and Akaike weights (ώ) and likelihood ratio based r squared (R^2_{LR}) for models that make up the 95% confidence set (∑ώ just ≥ 0.95) for each study region are shown. Functional groups included in each model are shown; see Table 5 for variables included in each model. Old-growth, day, day^2 and land were included as fixed effects in every model while year and catchment were modeled as random effects.

CC					SC					SWVI				
Model	**k**	**Δ_i**	**ώ**	**R^2_{LR}**	**Model**	**k**	**Δ_i**	**ώ**	**R^2_{LR}**	**Model**	**k**	**Δ_i**	**ώ**	**R^2_{LR}**
MLHA+LHA+OGC+E	14	0.00	0.589	0.35	MLHA+MC	10	0.00	0.213	0.11	MLHA+MC+E	12	0.00	0.273	0.34
MLHA+LHA+OGC	12	1.96	0.221	0.29	MLHA+MC+E	12	1.19	0.118	0.14	MLHA+MC+E+EE	14	0.45	0.218	0.35
MLHA+LHA	9	5.29	0.042	0.19	MLHA+PHA+MC	11	2.07	0.076	0.11	MLHA+PHA+MC+E	13	1.40	0.136	0.34
MLHA	8	5.91	0.031	0.16	MLHA+LHA+MC	11	2.37	0.065	0.11	MLHA+LHA+MC+E+EE	15	2.34	0.085	0.35
MLHA+MC	10	7.44	0.014	0.19	MLHA	8	2.37	0.065	0.06	MLHA+PHA+MC+E+EE	15	2.60	0.074	0.35
MLHA+PHA	9	7.52	0.014	0.17	NULL	4	2.39	0.064	0.00	MLHA+MC+E+OGE	14	4.33	0.031	0.34
MLHA+LHA+PHA	10	7.85	0.012	0.19	MLHA+LHA	9	3.38	0.039	0.07	MLHA+E+OGC+EE	15	4.43	0.030	0.35
MLHA+LHA+MC	11	8.35	0.009	0.21	MLHA+PHA+MC+E	13	3.47	0.037	0.14	MLHA+E+OGC	13	4.83	0.024	0.34
MLHA+MC+OGC	12	8.45	0.009	0.23	MLHA+OGC	11	3.79	0.032	0.10	MLHA+MC+E+EE+OGC	16	4.95	0.023	0.35
MLHA+MC+OGC	13	8.77	0.007	0.25	MLHA+MC+OGE	12	4.29	0.025	0.11	MLHA+LHA+OGC+E	14	5.00	0.022	0.34
MLHA+OGC	11	8.98	0.007	0.20	MLHA+LHA+PHA+MC	12	4.48	0.023	0.11	MLHA+PHA+MC+E+OGE	15	5.42	0.018	0.34
					MLHA+PHA	9	4.53	0.022	0.06	MLHA+PHA+E+OGC	14	6.82	0.009	0.34
					MLHA+MC+E+OGE	14	4.98	0.018	0.14	MLHA+E+EE	12	6.85	0.009	0.32
					MLHA+MC+OGC	13	5.02	0.017	0.13					
					MLHA+OGE	10	5.02	0.017	0.08					
					MLHA+MC+E+EE	14	5.09	0.017	0.14					
					MLHA+PHA+OGC	12	5.42	0.014	0.11					
					MLHA+E	10	5.49	0.014	0.07					
					MLHA+LHA+OGC	12	5.60	0.013	0.11					
					MLHA+LHA+PHA	10	5.65	0.013	0.07					
					MLHA+PHA+OGE	11	6.42	0.009	0.08					
					MLHA+E+OGC	13	6.42	0.009	0.12					
					MLHA+PHA+MC+OGE	13	6.45	0.008	0.12					
					MLHA+LHA+MC+OGE	13	6.74	0.007	0.11					
					MLHA+LHA+MC+E+EE	15	7.09	0.006	0.15					
					MLHA+PHA+OGE	11	7.33	0.005	0.08					

Table 7. Model averaged parameter estimates (β) and their unconditional standard errors from models of terrestrial habitat use by breeding marbled murrelets on the Central Coast (CC), South Coast (SC) and Southwest Vancouver Island (SWVI). Bolded β's are greater in magnitude than their respective SE, and shaded β's do not cross zero within their 95% confidence interval.

Covariates	**CC**		**SC**		**SWVI**	
	β	**SE**	**β**	**SE**	**β**	**SE**
Area of old-growth	**0.658**	0.217	**1.162**	0.719	**0.414**	0.179
Area of mature-transitional forest	**-0.539**	0.165	-0.019	0.049	0.004	0.029
Area of regenerating-young forest	-0.019	0.024	**-0.696**	0.405	0.079	0.247
Area of clear-cuts	0.011	0.016	**-0.184**	0.142	**0.359**	0.272
Non-productive forest habitat*	-0.006	0.016	0.008	0.043	0.024	0.049
Hard edge density	**0.187**	0.117	**0.115**	0.110	**-0.267**	0.203
Soft edge density	**0.135**	0.124	-0.013	0.112	**-0.514**	0.140
Proportion of old-growth at low elevations	0.005	0.007	0.004	0.020	0.000	0.010
Mean slope of old-growth stands	0.001	0.005	0.017	0.023	-0.002	0.009
Proportion of hard edge at low elevations	-0.001	0.001	0.008	0.011	**0.152**	0.110
Proportion of soft edge at low elevations	-0.001	0.001	-0.001	0.006	0.059	0.071
Mean old-growth core area per catchment	**-0.329**	0.153	0.023	0.029	-0.042	0.049
Old-growth patch density	0.063	0.196	-0.015	0.024	0.021	0.031
Old-growth nearest neighbour	**0.797**	0.247	-0.043	0.044	0.008	0.021
Day	**-1.304**	0.572	0.251	0.425	**1.658**	0.186
Day^2	**1.421**	0.538	-0.095	0.431	**-1.801**	0.187
% land in radar beam	**0.106**	0.103	0.065	0.089	**-0.093**	0.071

*See Appendix 1 for list of attributes included in non-productive forest category/region.

APPENDICIES

Appendix 1.

Table 8. Attributes, description, and data sources of the polygons types included in non-productive habitat class.

Region	Attributes included	Data source	Description
CC	AFold	VRI	Alpine forest>140 years old
	ISL	VRI	Island (usually within a large stream) – Assumed forested but not productive for harvesting
	NP_T	VRI	Polygons classified as NP in the NP_DESC field but TC, TB, or TM in the BCLCS_LV_4 field
	SCRUB	Private	Mature stand of less than 210 m3/ha.
	NSR04	Private	Productive but not satisfactorily restocked (disturbed 2004)
SC	AFold	VRI	Alpine forest>140 years old
	NP-T	VRI	Polygons from VRI data classified as NP in the NP_DESC field but TC, TB, or TM in the BCLCS_LV_4 field
	NSR	Private	Productive but not satisfactorily restocked (year of disturbance unknown)
	SCRUB	Private	Mature stand of less than 210 m3/ha.
SWVI	AFold	VRI	Alpine forest>140 years old
	Shrub forest	VRI	Polygons classified as shrub (less than 10% crown closure), but containing some treed area. Trees are>140 years old.
	NP-T	VRI	Polygons classified as NP in the NP_DESC field but TC, TB, or TM in the BCLCS_LV_4 field
	IS	Private	Island (usually within a large stream) – Assumed forested but not productive for harvesting
	NC	Private	Private data owner advised this polygon type had some potential for containing murrelet habitat in their TFL areas

Appendix 2.

Table 9. List of landscape composition and configuration metrics measured in ArcGIS that were excluded from the analysis due to multicollinearity, their descriptions, relevance, attributes and usage.

Metric	Description	Relevance	What does it quantify?	Status; dropped or combined
Area of regenerating-young forest	Area of catchment that is 21 -140 years.		Composition	Combined regenerating (41-140 yrs) and young (21-40 yrs); highly correlated in all regions: CC PCC=0.85, SC PCC=0.78, SWVI PCC=0.96.
Patch diversity	Diversity of patch types (based on age class described above) within a catchment, measured by Simpson's diversity index (0 = no diversity, 1 = all 5 patch types in equal abundance).	Characterizes the landscape matrix.	Composition	Dropped; high negative correlation with core area in SWVI PCC=-0.83
Mean old-growth patch perimeter:area ratio	Mean of [perimeter of the patch]/[area of patch] for all old-growth patches in the catchment.	Quantifies the shape of habitat patches within the catchment, with smaller values for regular (circular/square) patches and larger values as the patch becomes elongated.	Shape	Dropped correlated with mean old-growth nearest neighbour on the SC PCC=-0.75
Freshwater edge density	Density of old-growth │rivers and lakes (length of edge/catchment area)	Addresses the influence of edge type on murrelet habitat selection. Both predation risk of murrelet nests (Malt 2007) and nest site selection (Zharikov et al. 2006) have been correlated with	Configuration	Dropped; highly correlated with soft edge density on the SC (PCC=0.96)

		edge type.		
Interspersion and juxtaposition index	IJI approaches 0 when old growth is adjacent to only one other patch type and 100 when old growth is equally adjacent to all other patch types. This addresses interspersion of old-growth patches.	IJI characterizes the diversity of patches immediately surrounding an old-growth patch.	Configuration	Dropped; relevance of this variable to Murrelets is captured in hard and soft edge density metrics.
Road edge density	Length of roads/ unit area of catchment	Is a measure of human activity, disturbance, and road edge.	Configuration/human activity	Dropped; highly correlated with soft edge in the CC (PCC=0.88)
Proportion old-growth to freshwater edge at low elevations	Proportion of freshwater: old-growth edge occurring below the lower limit of the BEC subalpine band for the region (900m for the CC 800m for the Sc and SWVI)	Investigates the influence of edge type on murrelet habitat selection at high and low elevations	Configuration	Dropped; see above note for old-growth to freshwater edge

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