PICKING PATCHES: WHAT IS THE UTILITY OF HABITAT FRAGMENTATION IN DETERMINING HABITAT USE BY LOCAL POPULATIONS OF THE

APPROVAL

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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. M

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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

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

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

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

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.

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

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

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 th

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

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)

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)

structure,

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 considera 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*

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, 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

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

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

TABLES AND FIGURES

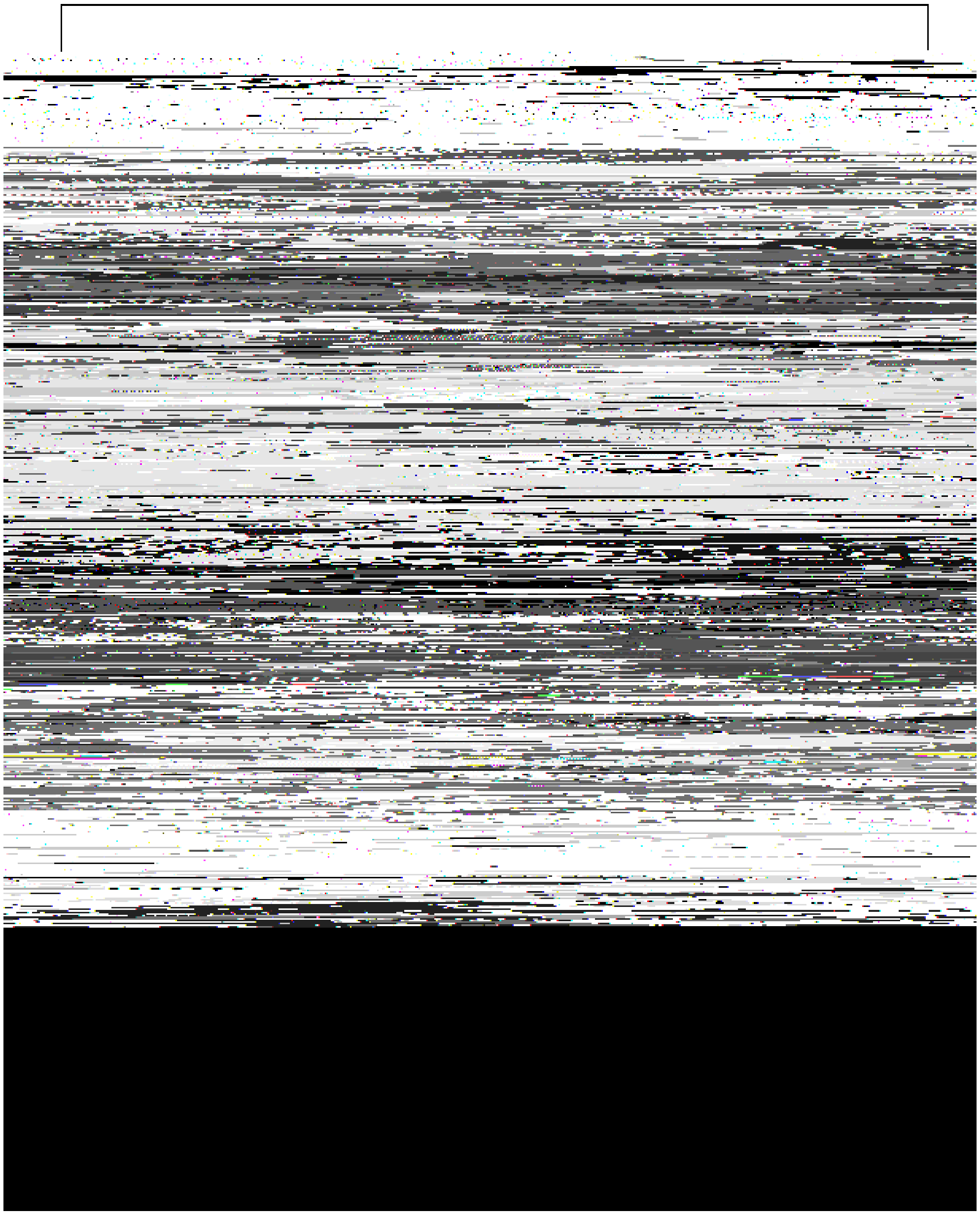

Figure 1. Study area (catchment) locations in three areas of coastal British Columbia, with respect to the Central Coast, South Coast, Northwest Vancouver Island (VI) and Southeast VI CMMRT conservation regions, and biogeoclimactic composition of catchments. Biogeoclimactic (BEC) zones include: Coastal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

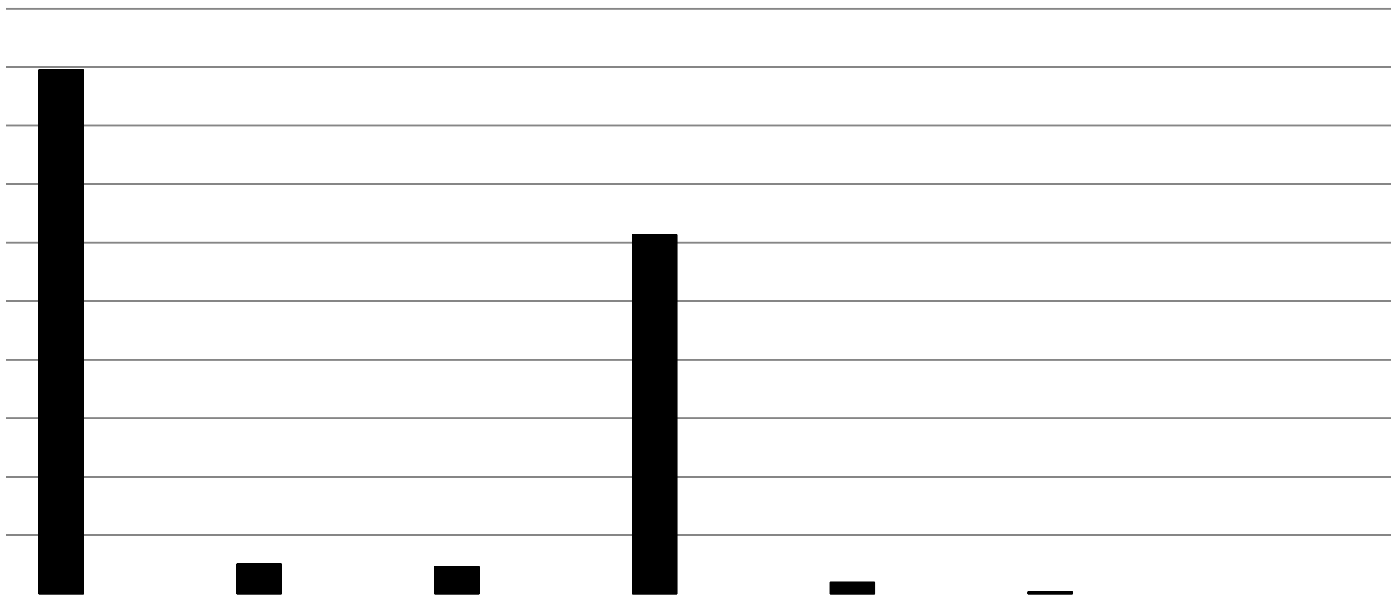

Figure 2. Relative importance of variable groups included in mixed model analysis of marbled murrelet habitat use in three regions of British Columbia; the Central Coast (CC), South Coast, (SC) and Southwest Vancouver Island (SWVI). MLHA= most likely habitat area, LHA= likely habitat area, PHA=potential 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.

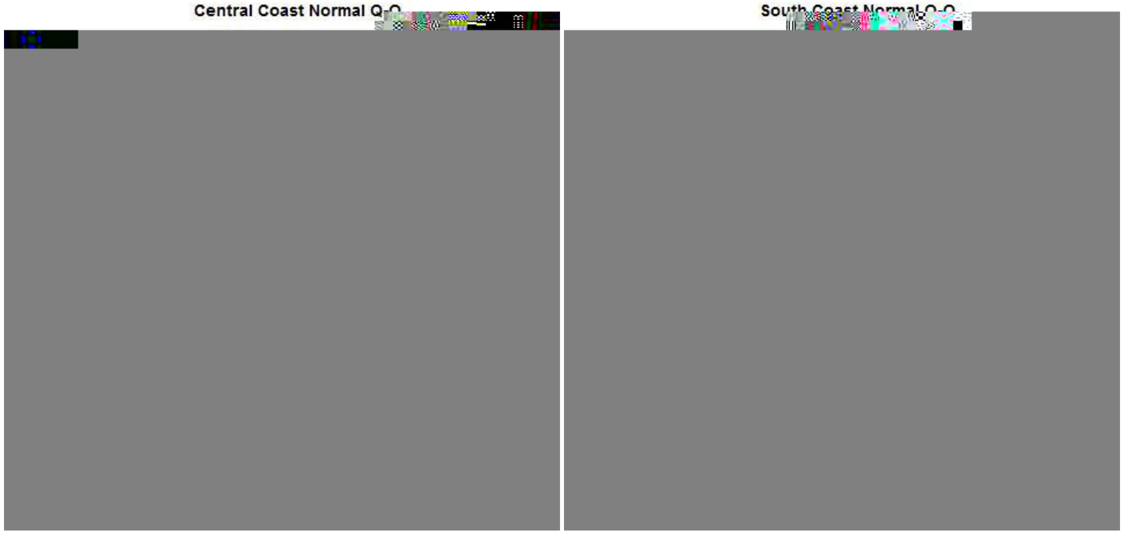

Figure 3. Normal Q-Q plots for log transformed counts of marbled murrelets (Log transformed marbled murrelet count quantiles) in three regions of coastal British Columbia; the Central Coast (CC), South Coast (SC) and Southwest Vancouver Island (SWVI). Counts of murrelets on the SC and SWVI were transformed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

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. P	

Model #	MLHA	LHA	PHA	MC	E	OGC	EE	OGE
1								

Model #	MLHA	LHA	PHA	MC	E	OGC	EE

Table

Table 7. Model averaged parameter estimates (β) and their unconditional standard errors from models of terrestrial habitat use by breeding marbled murrelets on the C

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		

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

		edge type.
Interspersion and juxtaposition index	IJI approaches 0 when old growth is adjacent to only one other patch	

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