Research article

Habitat selection and breeding success in a forest-nesting Alcid, the marbled murrelet, in two landscapes with different degrees of forest fragmentation

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Abstract

We studied habitat selection and breeding success in marked populations of a protected seabird (family Alcidae), the marbled murrelet (*Brachyramphus marmoratus*), in a relatively intact and a heavily logged old-growth forest landscape in south-western Canada. Murrelets used old-growth fragments either proportionately to their size frequency distribution (intact) or they tended to nest in disproportionately smaller fragments (logged). Multiple regression modelling showed that murrelet distribution could be explained by proximity of nests to landscape features producing biotic and abiotic edge effects. Streams, steeper slopes and lower elevations were selected in both landscapes, probably due to good nesting habitat conditions and easier access to nest sites. In the logged landscape, the murrelets nested closer to recent clearcuts than would be expected. Proximity to the ocean was favoured in the intact area. The models of habitat selection had satisfactory discriminatory ability in both landscapes. Breeding success (probability of nest survival to the middle of the chick rearing period), inferred from nest attendance patterns by radio-tagged parents, was modelled in the logged landscape. Survivorship was greater in areas with recent clearcuts and lower in areas with much regrowth, i.e. it was positively correlated with recent habitat fragmentation. We conclude that marbled murrelets can successfully breed in old-growth forests fragmented by logging.

Introduction

Studies of habitat selection conducted across large spatial scales (e.g., 'landscapes') are fundamental for conservation and management of species of special concern (Henske et al. 2001). Such studies are more valuable if they address landscape patterns of both the distribution (Fielding and Haworth 1995; George and Zack 2001; Boyce et al. 2002) and fitness measures of individuals (Pidgeon et al. 2003). Information on landscape-level patterns of individual fitness is critical for population

conservation (Jones 2001), but it may not be readily available for rare and difficult-to-census species (Green et al. 1997).

The marbled murrelet (*Brachyramphus marmoratus*) is a unique seabird (family Alcidae) that nests predominantly on thick mossy branches of old trees in coastal coniferous forests of the Pacific Northwest region of North America, from central California to western Alaska (Nelson 1997). Due to its secretive behaviour and difficult accessibility of nest sites, the first active nests of this species were not found until 1974 in the USA and 1993 in Canada (Nelson 1997). Extensive harvesting of old-growth forests along the Pacific coast and lengthy (>150 years) regeneration time of suitable nesting platforms, have resulted in substantial losses of the species' nesting habitat throughout its range (Garman et al. 1999; Burger and Bahn 2004). These losses resulted in designation of the marbled murrelet as a protected species throughout its range exclusive of Alaska (Nelson 1997).

Much of the ecological research on the marbled murrelet has focused on the links between fragmentation of its habitat and population abundance (Raphael et al. 2002). Small-scale (forest patch-level) characteristics of nest sites have also been well described (Nelson 1997; Raphael et al. 2002), and are used to select potential nesting habitat for protection (MWALP 2004). However, it is not known how nesting habitat selection and breeding success in this species relate to the characteristics of the surrounding 'landscape' (Nelson 1997; Raphael et al 2002; see also Ripple et al. 2003). Considering that forestry operations alter marbled murrelets' environment on a large scale (Garman et al. 1999; Burger and Bahn 2004), this is an important question because structurally similar patches may differ qualitatively depending on their surroundings (Henske et al. 2001).

Here, we examine habitat selection and breeding success in marbled murrelet populations from two areas in south-western Canada with different historical levels of forest fragmentation. We test whether the choice of a nest site and breeding success co-vary with the size of the nest patch and Euclidean distances to landscape features likely to produce 'edge effects' (Chen et al. 1995; Marzluff and Restani 1999) or influence nest site accessibility (Pennycuick 1987). Previous research has shown that the abundance of marbled murrelets is positively correlated with the amount of

unfragmented old-growth forest in coastal watersheds (Burger 2001; Meyer and Miller 2002; Meyer et al. 2002; Raphael et al. 2002). Within their range, marbled murrelets may also be more abundant and/or likely to nest in areas with low edge density (Meyer and Miller 2002; Ripple et al. 2003). However, other studies suggest positive selection for areas with high-contrast edges (Meyer and Miller 2002), canopy gaps (Manley 1999) and high vertical complexity (Waterhouse et al. 2004). Finally, these Alcids experience reduced nesting success ≤150 m from human-induced forest edges (Nelson and Hamer 1995; Manley 1999). Therefore, we hypothesize that if marbled murrelets select their nesting habitat to ensure successful breeding (Jones 2001), they will nest in larger than average old-growth patches, select for natural gaps in vegetation, but will avoid anthropogenic features fragmenting forest cover, and will have lower breeding success in the vicinity of anthropogenic edges. We address these hypotheses by analysing one of the largest available sets of confirmed nest sites, thereby removing the uncertainty associated with previously used inland audio–visual censuses (Rodway and Regehr 2000; Burger 2001) and potential other biases caused by pre-selection of nest search sites (Ripple et al. 2003).

Methods

Study area

The study was carried out on the mainland coast of British Columbia, Canada at Desolation Sound (50°05′ N, 124°40′ W) and on the west coast of Vancouver Island at Clayoquot Sound (49°12′ N, 126°06′ W) (Figure 1). Both areas accommodate large populations of marbled murrelets (Burger 2001; Hull et al. 2001) and are mountainous with steep cliffs, U-shaped glacial valleys, and numerous avalanche chutes and streams naturally fragmenting forest cover. Elevation ranges from the sea level to 2500 m at Desolation Sound (DS) and 2200 m at Clayoquot Sound (CS) and the terrain is more rugged at DS. The climate is warmer and drier at DS than at CS: mean summer (April–August) temperature and cumulative rainfall are 13.4 °C, 300 mm and 11.9 °C, 720 mm respectively. The old-growth forest of the lower slopes consists of western red cedar (*Tsuga plicata*), western hemlock
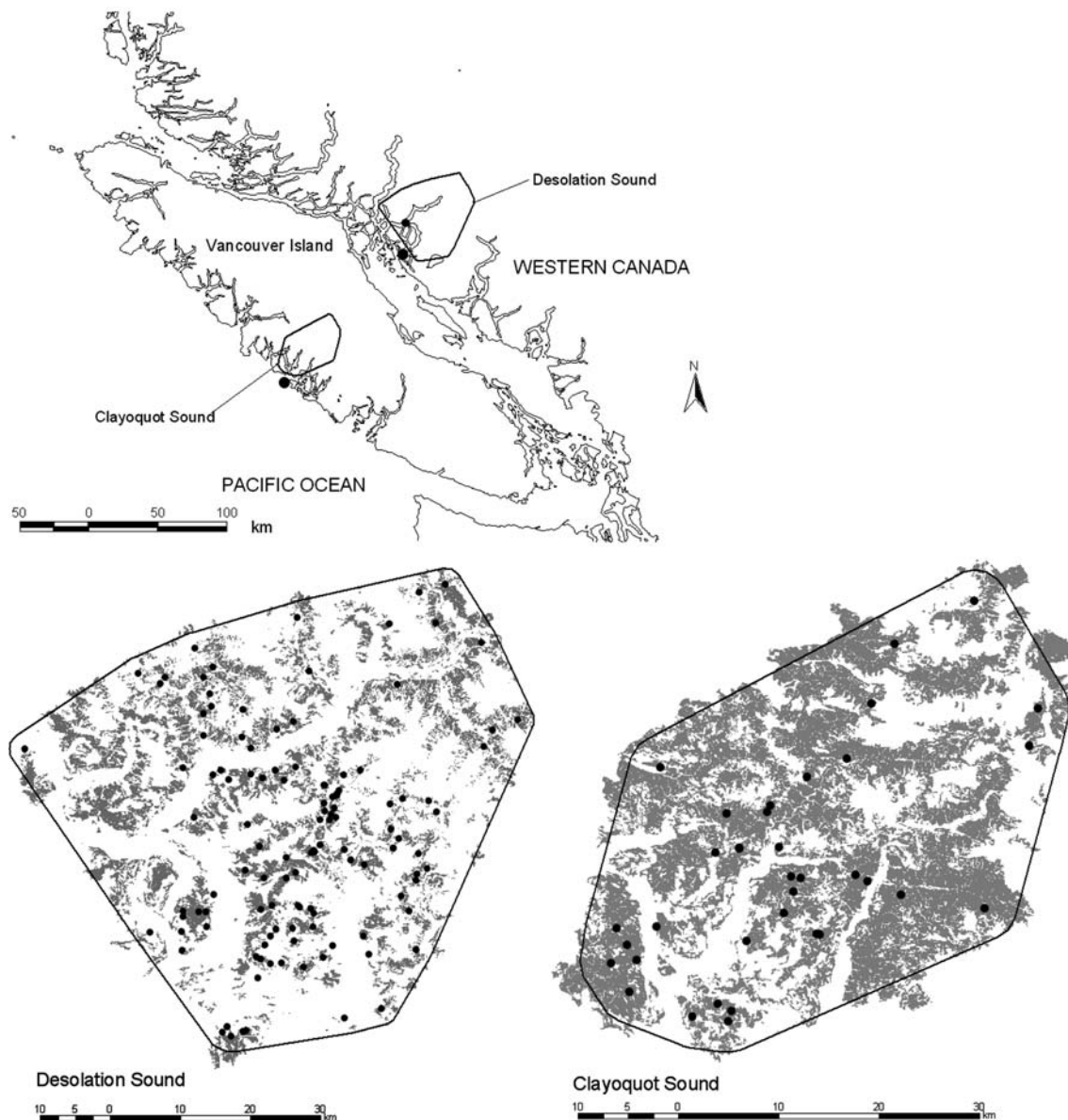
Figure 1. Location of the study landscapes relative to the coastline of south-western Canada. Dot-symbols represent at-sea capture sites (the smaller symbol at Desolation Sound is the secondary site in that area). Insets show the distribution of old-growth forest patches (grey shade) and nest locations (black dots) within the study landscapes.

(*T. heterophylla*), Douglas fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*). At DS, clearcutting started in early 20th century and it still continues. The loss of the original forest cover has been estimated at 80% (F. Huettmann et al. unpublished). In contrast, CS has few major clearcuts and logging roads. Commercial logging started there after 1954 and by 1998–1999 ≈25% of the original forest cover was harvested (D. Lank, unpublished).

Nest site mapping

An unbiased sample of nest sites was obtained by following a population of marked individuals. Murrelets were captured in late April–early June (DS, 1998–2001 and CS, 2000–2002) at their marine foraging areas (Figure 1) using a spotlighting technique (Whitworth et al. 1997). They were fitted with radio transmitters (Advanced

Telemetry Systems; Models 386, 394, and A460, 2.2–3.0 g, ≤2% murrelet body mass) attached with a subcutaneous anchor and glue (see Hull et al. 2001; Bradley et al. 2002, 2004 for further details). Following capture and tagging, birds were monitored using a helicopter and nests were located using radio-telemetry. During flights over the marine area, radio frequencies of all individuals were scanned until detected. When a bird could not be found at sea, incubation was suspected and flights were extended inland. Once a signal was detected inland, the nest location was photographed from the air, marked on a topographic map and its position was recorded using a Global Positioning System (Garmin GPS 48). If accessible from the ground, the nest location was confirmed by tree climbing. Nest coordinates were plotted in a Geographic Information System (GIS), and adjustments were made based on field reconnaissance when necessary. In total, 121 nests were located at DS and 36 at CS.

Breeding success

A pronounced faecal and down ring around the nest cup indicates successful fledging from a marbled murrelet nest (Nelson 1997). However, at DS only 45 nests could be climbed to confirm fledging because either the tree could not be located (five nests), or the site was too remote or dangerous to be accessed from the ground (71 nests). Therefore, following Bradley et al. (2004) we classified all nests as either active (successful) or failed using radio-telemetry data. A nest was considered active if radio-marked birds were visiting the site every 48 h through day 20 of the 30+ day chick rearing period. Otherwise it was considered failed. We termed this measure of breeding success 'mid-rearing success' (MRS). We emphasize that MRS is a surrogate of fledging success, since some nests classified as active probably failed at the final stages of rearing. However, MRS would predict breeding success patterns relative to the variables considered unless there was a strong temporal trend in failure rates, which was not the case (Bradley et al. 2004). Bradley et al. (2004) concluded that the estimates obtained only from ground-accessible nests would bias the breeding success low whereas the actual success in the population is closer to the MRS estimates because

inaccessible nests found at higher elevations and steeper slopes experienced better breeding conditions. Not all nests could be monitored through day 20 of chick-rearing, restricting MRS analyses to 108 nests. At CS, MRS data were available for 29 nests. Thus, breeding success was modelled only for DS; one-way ANOVAs with sequential Bonferroni corrections were applied to the CS sample since it was too small for modelling.

Spatial data compilation and definitions

Land-cover data were compiled from 1:20,000 terrain resource information (TRIM) and industrial forest cover maps and 1:250,000 baseline thematic land use (BTM) maps in ArcView 3.2 (ESRI Inc.). At DS, 24 nests occurred in areas for which no forest data were available. The land-cover within 1 km of each of these nests was classified from available aerial photographs following the standard government guidelines (Waterhouse et al. 2004). Current clearcut maps were produced from two LandSat 7 ETM images (resolution 30×30 m; DS, 13 August 2000; CS, 19 September 1999; Geogratis 2002) using eCognition (Definiens Imaging GmbH) for image processing (S. Steeby, M. Hall-Beyer and F. Huettmann, unpublished). Two types of clearcuts, 'hard-edge' (completely devoid of trees) and 'fuzzy-edge' (containing regrowth and <0.2 ha tree patches) were distinguished.

We defined as 'old-growth', forest with either the dominant or co-dominant coniferous tree species >140 years of age (all tree heights) for DS and >250 years (tree heights ≥15 m) for CS. These criteria encompass the current marbled murrelet habitat protection guidelines applied by the British Columbia government (MWALP 2004) and reflect the established tree- and stand-level nest site characteristics from the study areas (Manley 1999; Waterhouse et al. 2004). Thus the old-growth strata represent the true nesting habitat of the study species at both locations. 'Forest patch' represented an area of contiguous old-growth forest as delimited by streams and roads – features that fragment forest cover in real terms (Parendes and Jones 2000), but may not be accounted for in the available maps.

Different definitions of a 'landscape' exist (Bastian 2001). We defined as 'landscapes', minimum

convex polygons encompassing the distribution of all nest sites in each area with an external buffer (2.3 km, DS; 3.1 km, CS), representing the mean annual nearest-nest distance. Landscapes defined in this way (DS = 3.33×10^5 ha^2, CS = 1.52×10^5 ha^2) accounted for the distribution of individuals and are assumed to represent available terrestrial environment for the populations (Figure 1 insets). We defined as 'landscape features' spatially explicit elements of the environment, mapped in a GIS as polygons or polylines, representing geomorphological, vegetative and hydrological phenomena hypothesized to be relevant to habitat selection and breeding success of marbled murrelets.

Predictor variables

We used a distance-based (as opposed to composition-based) approach to study habitat selection and breeding success in the marbled murrelet (Conner and Plowman 2001). This was done because the landscape features of interest were both areal and non-areal and the scale at which breeding ecology of this species co-varies with landscape patterns is uncertain (Meyer and Miller 2002). We placed 1000 (DS) and 350 (CS) random points within the old-growth stratum of a landscape. We recorded forest patch area (PA, ha) for each nest and random site and measured Euclidean distance (to 0.01 km) to the nearest edge of the following features: (1) the nest/random site forest patch (PED), (2) three hard-edge clearcuts (HEC), (3) three fuzzy-edge clearcuts (FEC), (4) logging road (RD), (5) stream (STR), (6) subalpine area (SA), (7) cliff (CL), (8) glacier (GL) and (9) ocean (OC). Point-to-edge distances for the three nearest features (2) and (3) were measured to account for a possible density effect of logging operations on the birds. Distance to glaciers was included because of their effect on local vegetation patterns (Mizuno 1998), while distance to the ocean affects commuting costs between nest sites and foraging areas (Hull et al. 2001). To test for possible altitudinal and topographic effects, elevation above sea level (to 10 m, EL) and slope (to 1 °, SL) indices (and their quadratic terms) were derived for nest and random sites from a 25 × 25 m Digital Elevation Map by recalculating each cell to the mean of its 9-cell neighbourhood. Interaction terms between elevation and distance to hard-edge clearcuts and between slope and distance to stream were included in the habitat selection analyses. This was done because historically logging activities in the region progress from low-lying valleys to the higher ground (Garland et al. 1999) and slopes of glacial valleys are steeper than the watercourse terraces (Jonsson 1997). Also, for MRS analysis, the possible effect of the time of breeding was investigated by including the Julian date (1st April = 1, JD) of initiation of incubation.

Patch size selection

The size of an old-growth forest patch is an important criterion in designating protected sites for wildlife (George and Zack 2001), including the marbled murrelet (MWALP 2004). Hypothesizing that this habitat characteristic alone may provide a simple rule for identifying potential nest sites, the effect of PA on habitat selection was first analysed separately.

We approached the problem as follows. If there are k forest patches ($k = 10154$, DS; $k = 6868$, CS) each of an area a_i, $i = 1,\ldots, k$, and p_i is the probability of finding a nest in a given patch, then the number of nests per patch is a Poisson distributed variable with the mean $e_i = N p_i$ and the null hypothesis is where c is a constant estimated as $1/A$ ($A = \sum_i^k a_i$). The probability of finding a nest in a patch relative to a monotonic increase in its area, was determined using a Cramér-von-Mises W^2 statistic (Choulakian et al. 1994). The statistic compares the cumulative theoretical distribution with its estimate:

$$W^2 = N^{-1} \sum_{j=1}^{k} Z_j^2 t_j \qquad (1)$$

Here, if $S_j = \sum_{i=1}^{j} o_i$ and $T_j = \sum_{i=1}^{j} e_i$, then S_j/N corresponds to the empirical distribution in the continuous case, $Z_j = S_j - T_j$, $j = 1, \ldots, k$ and $t_i = (p_i + p_{i+1})/2$.

Distribution under null hypothesis was developed following a Monte Carlo procedure using the probabilities p_i calculated as above and the observed values o_i. We generated N random numbers from the uniform distribution between 0 and 1 and used these to allocate N nests in the k patches 1000 times, calculating the W^2 for each allocation. Kolmogorov–Smirnov $D_{\max}$-statistic was employed to determine the case with maximum

difference $|Z_j|$ between observed and predicted distributions. We ranked individual patches in the increasing order of area and plotted cumulative old-growth area versus the cumulative number of nests encompassed. It is expected that if no selection for a particular class size occurs, the resulting plot will represent a straight line ($p_i = ca_i$). Deviations above or below the neutral selection pattern will represent disproportionate use or avoidance respectively. Also, the distribution of patch areas binned in 10 classes selected by the birds was compared to a random distribution (1000 points) using goodness-of-fit tests.

Multiple modelling

We pooled the data across years for each study landscape because field methods were consistent and there were no strong annual differences in nest distribution (F. Huettmann et al. unpublished). Nest distribution within the landscapes was predominantly random: R-statistic (Clark and Evans 1954) was not significantly different from 1 in three years (1999–2001) out of four at DS and two years (2000 and 2002) out of three at CS. Otherwise it was clumped ($R = 0.77$, $p < 0.05$, $n = 23$; 1998, DS) or uniform ($R = 1.54$, $p < 0.05$, $n = 10$; 2001, CS).

We studied habitat selection by comparing the distributions of known (used) nest sites against a set of random available locations using generalized linear models (GLM, Statistica® 6.0) with binomial error distribution and a logit link-function. The same modelling technique was applied to distinguish between active and failed nests. Following preliminary data exploration (Eberhardt 2003), we constructed sets of 14 candidate habitat selection models (identical for DS and CS) and 16 mid-rearing success models (DS). Thirty five nests at DS were missing patch area (PA) and patch edge distance (PED) information. Therefore, DS habitat selection and MRS models that included PA and/or PED terms had 86 and 76 nest data points respectively. At CS, three nests were missing PA/PED data and these were replaced with the respective means.

Model selection, fit and predictive performance

Model selection was based on the Akaike's information criterion difference for small samples

($AIC_c\Delta$) and Akaike weights (ω). The lowest AIC_c score indicates the most parsimonious candidate model required to explain the observed data. Models with scores differing by ≤ 2 are considered similar regardless of the absolute magnitude of the AIC_c. AIC_c weights represent relative likelihoods of candidate models scaled to 1 (Burnham and Anderson 2002; Johnson and Omland 2004).

We calculated model fit for the best candidate models as % deviance explained, R^2, and the log-likelihood χ^2 statistic. The percentage deviance explained is low in logistic regression models (values 0.2 to 0.4 represent a good fit) due to the binary nature of the response variable. We used 95% confidence intervals of coefficients to evaluate the effects of predictors on the response variable. Inconsistent inference is likely when coefficients overlap zero. We used tolerance scores to check predictors within each model for multicollinearity and Cook's distance D to identify cases with unusually high influence (Hosmer and Lemeshev 2000).

Predictive performance of the best habitat selection models was evaluated using cross-validation. The datasets were divided into five random equal-sized subsets. Cross-validation was performed five times. Each time the model was trained on 80% of the data (four random subsets) and tested on the remaining 20%. Because the 'used' versus 'available' categories are not mutually exclusive (the used category is a subset of the available category), even best logistic regressions developed with such data may produce low probabilities for the 'used' events (Boyce et al. 2002). Therefore, absolute probabilities (p) of a site being a nest site were rescaled to relative probabilities ($\hat{p}$, 0 to 1) using a linear stretch transformation (Lillesand et al. 2004):

$$\hat{p} = \left(\frac{p(x) - p_{\min}}{p_{\max} - p_{\min}} \right) \qquad (2)$$

Here, $p(x)$ is the probability of a site being a nest site derived from the model and $p_{\max}$ and $p_{\min}$ are maximum and minimum probabilities in the nest dataset respectively. A Spearman rank correlation was then employed to assess the relationship between the relative probabilities of use for the withheld nest sites and their frequency within 10 probability bins representing the range of the predicted values. A model with good predictive performance will have a strong positive correlation

($\geq$0.8) as more nest sites would fall within higher probability bins (Boyce et al. 2002). Predictive performance of MRS models was evaluated using the probability threshold free ROC curve, where the area under the curve (AUC) is interpreted as the probability of a random nest from the active group receiving a greater score than a random nest from the failed group (Fielding and Bell 1997; Boyce et al. 2002).

Results

Habitat selection: patch area

At DS, marbled murrelets used old-growth patches disproportionately to their area ($W^2 = 0.59$, $p = 0.021$). They selected for $\approx$10 ha fragments ($D_{max} = 13.65$, $p = 0.021$, 9.8 ha fragment) and also $\approx$200 ha fragments (Figure 2). Splitting the distribution of individual patch areas into 10 bins (Figure 3) showed an identical pattern of two unequal peaks in selection for the smallest size class ($\leq$10 ha) and the intermediate size class (150–210 ha) (goodness-of-fit test, $\chi^2_9 = 29.30$, $p < 0.001$).

At CS, the mean size of patches containing at least one nest was considerably larger than at DS (397 ± 416 ha, $n = 26$ versus 108 ± 191 ha, $n = 78$). Distributions of the nest patch choices made by the birds were not significantly different from those available ($W^2 = 0.08$, $p = 0.69$ and $D_{max} = 4.46$, $p = 0.52$; goodness-of-fit test, $\chi^2_9 = 9.18$, $p = 0.42$) (Figures 2, 3).

Habitat selection: multiple analyses

Three DS models, 4, 9 and 12, (Table 1) performed well in describing habitat selection in marbled murrelets. A Spearman rank correlation across five cross-validation samples, however, indicated that model 4 had poor predictive capacity ($r_s = 0.398$, $p > 0.05$); predictive capacities of models 9 and 12 were similar ($r_s = 0.893$ and $r_s = 0.811$ respectively, $p < 0.001$). Both models suggested that marbled murrelets nested closer to streams and hard-edge clearcuts, at lower elevations, on steeper slopes and farther from the glaciers than expected. The interaction term between elevation and distance to
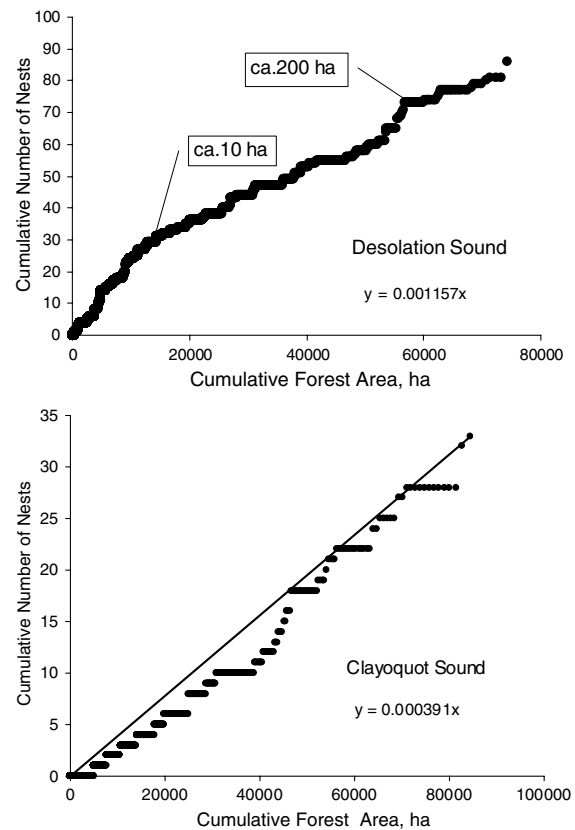

Figure 2. Cumulative plots of area under old-growth forest and the number of marbled murrelet nests encompassed. The linear trend represents a neutral selection for patch size ($p_i = c\alpha_i$). Boxes indicate the individual fragment sizes with the greatest deviation from the neutral trend.

hard-edge clearcuts in model 12 had a confidence interval that overlapped zero ($\beta = 0.0005$, CI $= -0.0001, 0.0009$) suggesting an inconsistent effect. We accepted the simpler model 9 ($R^2 = 0.115$, $\chi^2_6 = 87.80$, $p < 0.001$) as best describing habitat selection in marbled murrelets at DS (Table 2).

At CS, habitat selection in marbled murrelets was best described by model 14 ($R^2 = 0.115$, $\chi^2_5 = 27.1$, $p < 0.001$; $r_s = 0.682$, $p < 0.05$). Here, the birds nested closer to streams, hard-edge clearcuts and the seashore, on steeper slopes and farther from subalpine areas than expected (Table 2). Confidence intervals for the ocean and clearcut terms overlapped zero in this model suggesting inconsistent inference relative to these covariates, although the difference in the mean distances to the ocean was considerable.
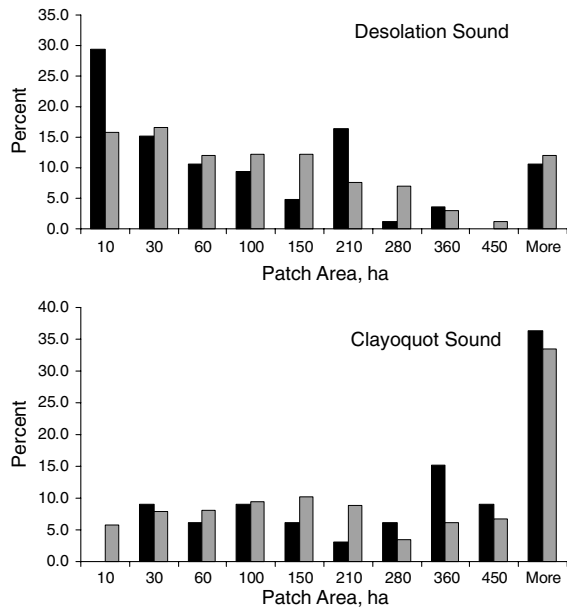
Figure 3. Percent frequency distribution of nest (black) and random (grey) forest patch sizes.

Mid-rearing success

At DS and CS 71 (of 108) and 17 (of 29) nests survived through day the 20 of chick-rearing period respectively. The difference in MRS between the two locations was not significant ($\chi^2_1 = 0.5$, $p = 0.48$). At DS, two models produced a strong fit to the MRS data and demonstrated high predictive

capacity: model 6 ($R^2 = 0.467$, $\chi^2_8 = 46.5$, $p < 0.001$, AUC $= 0.91$) and model 11 ($R^2 = 0.227$, $\chi^2_4 = 31.1$, $p < 0.001$, AUC $= 0.81$) (Table 3). In model 6, however, the patch edge distance covariate had an inconsistent effect ($\beta = -16.507$, CI $= -35.492$, 2.479). Participation of this term in the model resulted in the reduction of the modelling dataset from 108 to 76 nests. Therefore, we accepted the simpler model 11 as probably more robust in describing breeding success patterns in the population (Table 4). According to the model, successful breeders nested earlier in the season, closer to hard-edge clearcuts, farther from fuzzy-edge clearcuts and closer to subalpine areas than unsuccessful breeders.

At CS, none of the eight predictors participating in the DS breeding success models 6 or 11 differed significantly between the active and failed treatment groups (one-way ANOVA on $\log_e$-transformed data, $F_{1,27} < 4.19$, $p \geq 0.05$).

Discussion

Habitat selection: patch area

Forest patch size is highly important in habitat management and it is often used as a simple habitat conservation criterion (Garman et al. 1999; George and Zack 2001). Larger forest fragments

Table 1. Candidate habitat selection models with the numbers of predictor variables (k), AIC_c differences ($\varDelta$), and AIC_c weights (ω).

	MODEL		Desolation sound*			Clayoquot sound	
		k	AIC_c $\varDelta$	AIC_c ω		AIC_c $\varDelta$	AIC_c $\varDelta$
1	STR +HEC +PED	3	39.3	<0.001		11.9	0.002
2	STR +HEC +OC +PA	4	39.7	<0.001		4.5	0.077
3	STR +HEC +PA +PED	4	39.1	<0.001		9.5	0.006
4	STR +HEC +EL^2 +SL +PA^2**	7	0.0	0.807		12.1	0.002
5	STR +HEC +EL^2 +SL^2 +PA^2 +PED	9	2.9	0.193		15.1	<0.001
6	STR +OC +EL +SL	4	17.9	<0.001		4.3	0.085
7	STR +HEC +EL^2 +EL*HEC +SL	6	7.2	0.020		14.5	<0.001
8	HEC +FEC +RD	3	66.5	<0.001		13.1	0.001
9	STR +HEC +EL^2 +SL +GLA	6	2.4	0.225		5.9	0.040
10	STR +HEC +EL^2 +SL +SL*STR +EL*HEC***	7	436.4	<0.001		15.5	<0.001
11	STR +HEC +EL^2 +SL +EL*HEC +OC	7	9.0	0.008		9.3	0.007
12	STR +HEC +EL^2 +SL +EL*HEC +GLA	7	0.0	0.738		7.9	0.014
13	STR +HEC +FEC +EL +SL +RD +GLA +OC +SUB +CL	10	9.1	0.008		7.8	0.015
14	STR +HEC +SL +OC +SUB	5	36.2	<0.001		0.0	0.749

*AIC_c $\varDelta$ and AIC_c ω for DS models 1 to 5 and 6 to 14 were calculated separately since the models with PA/PED terms included only a subset of the data.

**If a quadratic term is shown, its linear counterpart is also included.

***Model adjusted for overdispersion.

Table 2. Parameters of the most parsimonious marbled murrelet habitat selection model at Desolation and Clayoquot Sounds including mean ± SD values of predictors for the nest and random sites.

Variable	Coefficient	95% CI	Nest*	Random*
DS				
Constant	−4.494	−6.998, −1.998		
Stream	−2.412	−4.188, −0.636	0.13 ± 0.14	0.17 ± 0.18
Hard-edge clearcuts	−0.274	−0.436, −0.111	1.89 ± 1.35	2.35 ± 1.46
Elevation	−0.004	−0.006, −0.002	700 ± 340	880 ± 380
Elevation^2	0.103	0.012, 0.193		
Slope	0.041	0.025, 0.057	39 ± 16	33 ± 13
Glacier	0.061	0.020, 0.101	6.51 ± 5.35	5.60 ± 4.76
CS				
Constant	−2.393	−3.856, −0.930		
Stream	−8.436	−13.385, −3.487	0.09 ± 0.07	0.14 ± 0.10
Hard-edge clearcuts	−0.194	−0.420, 0.032	2.49 ± 1.68	2.74 ± 1.74
Slope	0.048	0.014, 0.082	31 ± 12	28 ± 12
Ocean	−0.047	−0.105, 0.011	6.31 ± 8.10	9.37 ± 8.40
Subalpine area	0.107	0.022, 0.192	5.28 ± 6.26	3.79 ± 5.22

*Distances are in kilometres, elevation in metres, slope in degrees.

Table 3. Candidate mid-rearing success models for DS with the numbers of predictor variables (k), AIC$_c$ differences (Δ), and AIC$_c$ weights (ω).

	MODEL	k	AIC$_c\Delta$*	AIC$_c\omega$*
1	JD + STR + HEC + EL + SL + PA	6	24.7	< 0.001
2	JD + HEC + EL^2 + PA^2**	6	16.7	< 0.001
3	JD + HEC + EL + PA^2 + SA	6	8.1	0.017
4	JD + HEC + EL + PA^2 + OC	6	20.1	< 0.001
5	JD + PA^2 + PED	4	22.8	< 0.001
6	JD + HEC + FEC + RD + EL + OC + SA + PED	8	0.0	0.982
7	JD + EL + OC	3	6.8	0.027
8	JD + STR + HEC	3	8.0	0.015
9	JD + STR + OC	3	9.6	0.007
10	JD + STR + HEC + EL^2 + SL	6	9.0	0.009
11	JD + HEC + FEC + SA	4	0.0	0.836
12	JD + HEC + FEC + RD + EL^2 + SL	7	7.7	0.017
13	JD + HEC + EL + SL + GLA	5	6.4	0.034
14	JD + HEC + EL + SL + OC	5	8.2	0.014
15	JD + STR + HEC + EL + SL + GLA	6	8.4	0.012
16	JD + STR + HEC + EL^2 + SL + SA	7	6.7	0.029

*AIC$_c\Delta$ and AIC$_c\omega$ for DS models 1 to 6 and 7 to 16 were calculated separately since the models with PA/PED terms included only a subset the data.
**If a quadratic term is shown, its linear counterpart is also included.

Table 4. Parameters of the most parsimonious marbled murrelet mid-rearing success model at Desolation Sound including mean ± SD values of predictors for the active and failed nest sites.

Variable	Coefficient	95% CI	Active*	Failed*
Constant	5.307	2.688, 7.925		
Julian date	−0.073	−0.115, −0.032	54 ± 13	64 ± 13
Hard-edge clearcuts	−0.435	−0.802, −0.068	1.72 ± 1.21	2.35 ± 1.57
Fuzzy-edge clearcuts	1.418	0.268, 2.569	0.81 ± 0.54	0.69 ± 0.46
Subalpine area	−0.238	−0.411, −0.065	1.21 ± 1.94	2.76 ± 3.86

*Distances are in kilometres.

can support higher density, abundance and breeding success of a number of bird species (Henske et al. 2001) justifying their prioritisation for conservation. Indeed, based on abundance estimates alone, marbled murrelets appear to prefer larger old-growth patches for nesting (Burger 2001; Meyer and Miller 2002; Meyer et al. 2002). However, our analyses of the distribution of actual nest sites do not support this hypothesis.

At DS, marbled murrelets selected for smaller than average old-growth patches. In addition to those included in the patch size analysis, about one quarter of the nests located occurred in classes of habitats (young or secondary forest, regenerating burned areas) that do not possess structural elements necessary for nesting. These were likely located in small pockets of old-growth imbedded in an otherwise unsuitable habitat matrix (Nelson 1997). These fragments were not mapped for commercial purposes and their size, if defined, would have been at or below the lower range of patch sizes analysed. Thus, at DS, our results under-represent the usage of small patches. However, there is also a smaller peak in patch size selection reflecting high usage of average size fragments. At CS, a much less fragmented area, marbled murrelets used old-growth patches relative to their availability, as also found by Ripple et al. (2003) in Oregon.

An important implication of our results and the findings of Ripple et al. (2003) is that patch size is neither a consistent nor an important nesting habitat predictor in this species. Therefore, this criterion should not be applied for marbled murrelet habitat management on its own. Our findings also signify that marbled murrelets do not 'pack' into large patches even if their nesting landscape is highly fragmented. This means that although habitat loss will cause population declines (Kelson et al. 1995; Burger 2001), forest fragmentation per se, may have no immediate additional negative effect on the species.

Habitat selection: landscape characteristics

In the Pacific Northwest of North America, montaine riparian forests support a greater abundance of epiphytic mosses (Peck and Muir 2001), which form marbled murrelet nesting platforms (Singer et al. 1991) than do more upland areas. Thus, the observed tendency to nest close to streams and on steeper slopes in both landscapes could be related to enhanced nesting substrate there. Watercourses also serve as inland flyways in this species (Peery et al. 2004). However, the immediate access to a nesting branch will depend on gaps in adjacent vegetation (Manley 1999). Nelson (1997), Burger and Bahn (2004) and Waterhouse et al. (2004) reported high vertical complexity (difference in tree height) as an important attribute of marbled murrelet breeding habitat. Topographic complexity of terrain may enhance suitability of old-growth stands for the nesting murrelets by creating gaps and irregularities in canopy structure (Waterhouse et al. 2004), thus providing a plausible explanation for the selection for steeper slopes. Clear nest site access is also critical for fledging young who, if they collide with an obstacle and become grounded during their maiden flight, have slim chances of taking off again (Carter and Sealy 1987).

Murrelets nested farther from glaciers (DS) and subalpine areas (CS) than expected. However, in both landscapes these two variables were highly correlated (DS, $r_p = 0.80$, CS, $r_p = 0.90$, $p < 0.001$) indicating that one or the other could participate in the respective models. Both glaciers and subalpine areas, when they retain snow-fields, will produce a local cooling effect. As a result, forests located closer to glaciers and subalpine areas will have a shorter growing season (Mizuno 1998; Parish and Antos 2004) which in turn may translate into lower epiphyte abundance and poorer nesting conditions for the murrelets.

At least at DS, elevation acted on marbled murrelet habitat selection independently of the other variables. These birds occur from sea level to the altitudes exceeding 1000 m across their breeding range, but are most abundant at moderate elevations (200–800 m) (Nelson 1997). This pattern has been explained by favourable microclimatic (high humidity) and habitat (large tree size) conditions within this zone (Meyer and Miller 2002; Meyer et al. 2002; Burger and Bahn 2004). Our results confirm that the observed abundance patterns represent true nesting habitat selectivity relative to landscape topography.

Distance to productive marine areas is a strong predictor of regional marbled murrelet distribution patterns (Meyer and Miller 2002). The importance of this factor can be explained by both suitable climatic and habitat conditions near the

coast (Meyer et al. 2002), but also by energetic costs related to the commuting distance between nesting and foraging sites (Hull et al. 2001). We consider nest distribution at CS as consistent with these hypotheses (Table 2). At DS, marbled murrelets nested 30% farther from the ocean (8.83 ± 6.43 km) than at CS and this variable did not appear in the best models. The explanation here may be that there is insufficient suitable nesting habitat at DS near the coast because of century-long logging activities.

Contrary to our hypothesis, marbled murrelets at DS nested closer than expected to recent (≤ 15–20 years) clearcuts. Indeed, Ralph et al. (1995) and Meyer and Miller (2002) reported a higher amount of forest 'edge' and higher edge contrast index in areas occupied by marbled murrelets in Washington and Oregon respectively (but see Ripple et al. 2003). These findings imply that the same stands of old-growth forest may be equally attractive to marbled murrelets and logging companies. Thus stands used by the birds and clearcuts can be spatially correlated. Also, the murrelets do not seem to immediately respond to logging by abandoning their nest sites.

High breeding site fidelity in the Alcids is determined by the physical quality of a site and individual experience (Kokko et al. 2004). Therefore, marbled murrelets are likely to maintain their traditional sites as long as the stands retain suitable nesting structure and nesting is successful. Long-term deterioration of nesting conditions is an important consequence of habitat fragmentation and isolation (Brooks et al. 1999) and it may explain why in California and Oregon marbled murrelets occupied recently fragmented forests more often than stands fragmented a decade ago (Meyer et al. 2002). However, if breeding conditions deteriorate so as to affect individual fitness, a negative population trend is expected. A recent study found this not to be the case at DS (Cam et al. 2003) suggesting considerable resilience in the system. Also the overall proportions of successful nests were similar at the heavily fragmented DS and relatively intact CS.

Correlates of breeding success

Our results suggest a positive correlation between MRS and forest fragmentation, again implying that fragmentation itself does not immediately devalue the nesting habitat of these birds or, perhaps, that they respond adaptively to logging in their environment. Such breeding success pattern, matching the pattern of habitat selection, is unusual for an old-growth specialist especially when compared with many species from eastern North America (George and Zack 2001).

The main reason for nest failure in the marbled murrelet is predation by birds and possibly mammals (Nelson 1997; Raphael et al. 2002). Fragmentation of old-growth habitat will increase the risk of nest failure due to predation if the newly created habitat allows for a better detectability of nests (Friesen et al. 1999) or supports a greater population of potential predators (Marzluff and Restani 1999). It is not apparent that either would occur in our landscape.

Marbled murrelets have a highly cryptic coloration (Nelson 1997) and they commonly nest near canopy gaps and in the environments (stream-side forests) supporting a higher than average abundance of potential nest predators (cf., Saab and Vierling 2001). Therefore, creation of additional edges may not make the nests substantially more detectable.

Populations of potential nest predators rarely increase in forest landscapes managed for timber, in contrast to forests adjacent to human settlements or agricultural fields (Henske et al. 2001). This is because local predator populations will increase only if fragmentation produces a concurrent increase in the amount of their staple food supply (e.g., berries) and/or breeding habitat (Marzluff and Restani 1999; Raphael et al. 2002). In this study area clear-cutting is not associated with development of human habitation or agricultural fields. It is thus unlikely that recent forest fragmentation could create anthropogenic sources of food. At the same time, clear-cutting may have decreased the amount of nesting habitat for such known adult and nest predators of marbled murrelets as the northern goshawk (*Accipiter gentilis*), common raven (*Corvus corax*) and gray jay (*Perisores canadiensis*) and thus lower their abundance in recently logged areas (Raphael et al. 2002). However, as clearcuts overgrow and berry-producing shrubs become established there (Nielsen et al. 2004), their usage by nest predators may increase (Steller's jay *Cyanocitta stelleri*, Raphael et al. 2002), explaining the lower breeding success closer to old (fuzzy-edge) clearcuts.

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Marbled murrelet nests were located too far from subalpine areas to suggest a direct influence on the MRS. Distance to subalpine areas was mildly correlated with elevation ($r_p = -0.24$, $p = 0.01$) suggesting an underlying factor that co-varies with elevation. At DS, abundance of potential avian and mammalian nest predators of marbled murrelets decreases significantly with elevation (Bradley 2002). Thus, a lower abundance of predators at higher elevations may explain why the birds nested more successfully closer to sub-alpine areas.

As do many other species (Nettleship and Birkhead 1985; Hipfner and Gaston 2002), marbled murrelets displayed a strongly negative seasonal trend in the probability of breeding success. Presently there are insufficient data for the marbled murrelet populations in the study area or elsewhere to suggest whether this happens because of negative changes in the marine (Vermeer and Cullen 1979) or in the terrestrial environment (Hartman et al. 1997).

To conclude, nesting habitat selection in these populations of marbled murrelets co-varied with the landscape features influencing microclimate and habitat structure (streams, glaciers, subalpine areas, elevation), distribution of potential nest predators (recent clearcuts), travel distance (ocean) and access to nest sites (streams, hillslopes). Breeding success was likely driven by distribution patterns of potential nest predators, which themselves could be responding to local landscape characteristics (clearcuts and elevation). Marbled murrelets did not respond to habitat fragmentation by either selecting for larger patches or avoiding recent clearcuts. Our results imply that marbled murrelets can continue nesting in highly fragmented old-growth forests, successfully using patches ≥10 ha. However, we caution that breeding success in such areas may decrease as adjacent clearcuts overgrow.

Acknowledgements

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