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1. The marbled murrelet *Brachyramphus marmoratus* is a threatened Alcid nesting in old-growth coastal forests from central California to Alaska. Logging has greatly reduced the amount and altered the pattern of the species' nesting habitat. Landscape fragmentation effects on the breeding ecology of the species are poorly understood because of the inaccessibility of nest sites.
2. Using radio-telemetry, 157 marbled murrelet nests were located in two old-growth areas in British Columbia, Canada, with different logging histories. Probable breeding success was estimated from nest attendance patterns by radio-tagged parents. Information-theoretic and hypothesis-testing methods were used to model breeding distribution (used vs. random unknown sites) and success (successful vs. failed nests) within *c.* 50-km radius extents at a scale of 2·3-km radius landscapes. Intersite transferability of distribution models was tested.
3. Breeding distribution was positively related with old-growth patch proximity, edge density (natural and artificial) and contrast, proportion of landscape under old-growth or core habitat, and interspersion of old-growth patches; it was negatively related with

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Woodlands fragmented by logging vary in their capacity to support wildlife (Lichstein, Simmons & Franzreb 2002; Betts *et al*

during the nesting period (May–June) within 5 km offshore of the study areas (Fig. 1). Birds were radio-tagged

Tab 2. Variables used in analyses, their measurement units, definition and ecological relevance. Variables 1 and 2 describe the old-growth habitat area in a landscape. Variables 3–5 describe edge characteristics of a landscape relative to the old-growth forest class. Variables 6–9 describe landscape composition. Variables 10–12 reflect the distribution of old-growth patches in a landscape and their shape

No.	Variable (unit)	Acronym	Definition, ecological and conservation relevance
1	Core area percentage in a landscape (%)	CPL	Defined by the edge depth and quantifies the proportion of landscape occupied by interior old-growth forest. The amount of core habitat in a landscape is positively correlated with marbled murrelet occupancy* and watershed-level abundance (Meyer, Miller & Ralph 2002; Raphael, Mack & Cooper 2002)
2	Mean patch area (ha)	PA_{mn}	Greater patch size of old-growth has been associated with higher inland abundance (Meyer, Miller & Ralph 2002) but lower probability of nesting (Zharikov *et al*. 2006)
3	Total edge contrast index (%)	TECI	Quantifies edge contrast for the landscape as a whole as a percentage of the maximum possible. Earlier reports conflict in describing effects of edge contrast on occurrence of nesting marbled murrelets (positive, Raphael, Young & Galleher 1995; Meyer & Miller 2002; negative, Ripple, Nelson & Glenn 2003)
4–5	Edge density (m ha^{-1})	*E*	Quantifies the amount of edge in a landscape per unit area. Occupancy is higher in landscapes with more edge (Raphael, Young & Galleher 1995) whereas watershed-level abundance appears to be lower (Raphael, Mack & Cooper 2002). Current guidelines in BC call for preferential selection of forest patches with natural edges over artificial edges (MWALP 2004). Separate artificial (E_a) and natural (E_n) edge densities were calculated. Ocean was excluded from natural edge as old-growth forests adjacent to oceanic shores may be avoided by the birds (Burger, Bahn & Tillmanns 2000). The percentage of landscape under ocean was included as a composition variable (below)
6–9	Composition: percentage ocean, old-growth, clearcut and young forest	%Oc, %OG, %Logged, %YF, respectively	Forests of the coastal strip are avoided by the birds (Burger, Bahn & Tillmanns 2000); percentage old-growth and logged/young forest have, respectively, positive and negative effects on occupancy (Meyer, Miller & Ralph 2002) and watershed-level abundance in the species (Burger 2001)
10	Nearest neighbour distance (m)	NND	Quantifies the mean Euclidean distance to the nearest old-growth patch in a landscape. Proximity of patches is positively related to murrelet occupancy (Meyer & Miller 2002) and watershed-level abundance (Raphael, Mack & Cooper 2002)
11	Interspersion and Juxtaposition Index (%)	IJI	IJI approaches 0 when old-growth class is adjacent to only one other land-cover class and 100 when the old-growth is equally adjacent to and interspersed with all the other land-cover classes in a landscape. Murrelet occupancy is higher in more diverse landscapes (Raphael, Young & Galleher 1995).
12	Mean perimeter to area ratio (no unit)	PARA	Quantifies the mean shape of an old-growth patch in a landscape. PARA is minimal for regularly shaped (round) patches and increases as the shape becomes more irregular or elongated. Marbled murrelet occupancy is positively related to the complexity of patch shape (Meyer & Miller 2002). Predation rates may be lower in patches with low perimeter to area ratios (Raphael *et al*. 2002)

*Occupancy, frequently employed as a proxy of nesting in the marbled murrelet, refers to audiovisual detection of behaviour patterns associated with nesting.

amount of edge in a landscape. Edge contrasts between old-growth forest and clearcuts and streams were considered the sharpest (1·0) while those between old-growth and mature forest were considered the weakest (0·2) (Table 1). The contrast definitions were somewhat subjective, but followed generally accepted logic (McGarigal & McComb 1995; Harper *et al*. 2005). The outer boundary of a plot and the 'Not mapped' land-cover class were excluded from calculations.

Model selection and fit

Breeding distribution and success were studied by comparing the distributions of used nest plots to random plots with unknown usage and successful to failed nests, respectively, using binary logistic regressions. Nest/random plots and successful/failed nests were coded as 1/0.

Construction of candidate predictive models is always a challenge. When a species' ecology is poorly understood, a combination of information-theoretic and hypothesis-testing approaches to model building may be appropriate (Eberhardt 2003; Stephens *et al*. 2005). For marbled murrelets, old-growth area, old-growth edge density/contrast and landscape composition appeared to be the most important factors affecting breeding ecology 43(a)21(pe comppothesio71(wth]TJ -1 -1. (et al)Tj /F2 1 Tf 0 g 2 d)8
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relation was detected only in models 1–3 for year 1999 ($I \leq 0{\cdot}09$, $P = 0{\cdot}05$) and models 3–4 for year 2001 ($I \leq 0{\cdot}10$, $P = 0{\cdot}05$), suggesting that, in general, nests were not clumped beyond the level explained by landscape pattern.

Of the eight retained Desolation models, four (5–8) transferred well to Clayoquot (TI > 0·80). Based on their AUC values, the models that included edge metrics (1–4) performed better at Desolation, while those that included habitat area and landscape composition metrics (5–8) performed better at Clayoquot, but not as well as the edge metric models at Desolation. All Desolation models when applied at Clayoquot gave probability scores greater than 0·5 for both nest sites ($n = 36$, model average 0·57–0·95) and random sites ($n = 145$, model average 0·50–0·92), suggesting that most predictors (except for the percentage logged and Interspersion and Juxtaposition Index (IJI)) had the same direction of effect at either site (Fig. 2). Also, given the 0·5 probability threshold, different models produced very similar distributions of predicted used and unused landscapes in either study area (Fig. 3). When the preliminary models (Table 3) were reparametrized using Clayoquot data, they converged to two adequate models ($\chi^2 > 11{\cdot}7$, $P < 0{\cdot}003$), with structure and discriminatory performance similar to their Desolation counterparts (cf. Table 4):

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old-growth edge density and contrast, higher proportions of old-growth or core and logged habitat (only at Desolation), lower proportions of ocean, higher interspersion of old-growth patches (only at Desolation) and smaller average patch sizes than random. Three studies of marbled murrelets in coastal Washington, Oregon and California have employed similar landscape sampling (circular plots of 0·5, 2, 8 and 30 km^2) and analytical methods (Raphael, Young & Galleher 1995; Meyer & Miller 2002; Meyer, Miller & Ralph 2002) but used indirect (behavioural) evidence of nesting. They demonstrated that occupancy (probable nesting) by marbled murrelets was positively related to the proportion of landscape under old-growth forest or core habitat (plots ≤ 8 km^2), edge density (0·5 and 2 km^2), proximity of old-growth patches, land-cover diversity and edge contrast (30-km^2 plots), and negatively to the proportion of young forest in a landscape (8 km^2). Additionally Burger, Bahn & Tillmanns (2000) found a significantly lower frequency of nesting behaviours by marbled murrelets within the immediate coastal zone (250 m) than > 1·5 km inland.

Our results are surprisingly similar. This implies that the designation of protected nesting habitat areas for murrelets based on indirect observation is generally valid despite the associated uncertainties (Raphael *et al*. 2006). The major difference between our work and previous studies is that occupancy was predicted to be higher in landscapes with larger old-growth patches (Meyer & Miller 2002; Meyer, Miller & Ralph 2002; Raphael *et al*. 2006) while we detected the opposite trend at our sites. The difference may be both methodological and biological. Studies based on indirect nesting evidence may have preferentially sampled larger and more accessible tracts of forest (Raphael *et al*. 2006), while we analysed a full range of forest conditions used by the birds. Thus landscapes with small fragments supporting murrelets, as in our data set, may not have been surveyed in audiovisual studies. The fact that we allowed linear features to ‘break up’ otherwise contiguous forest could also have contributed to the difference. Also, the nesting distribution of marbled murrelets with respect to patch size at Desolation and Clayoquot may simply reflect local nesting conditions that genuinely differ from those further south.

Overall, our landscape selection patterns suggest a preference by these heavily wing-loaded, fast-flying birds to nest in areas where topography, vegetation structure and landscape pattern naturally ‘break-up’ forest cover, thus facilitating access to forest stands and individual nest trees (Burger & Bahn 2004; Zharikov *et al*. 2006). Logging, while decisively detrimental to the birds because of habitat loss, may have little add-on negative effect caused strictly by fragmentation, at least in the short term (but see Meyer, Miller & Ralph 2002).

landscapes and that 50% of our models (transferability index > 0·8) were able to predict adequately the occurrence of nesting marbled murrelets at two distinct sites.

Previous inferences about the effects of habitat fragmentation on habitat use in the marbled murrelet were mostly based on visual observations of nesting behaviour. Here, it is shown that the true nesting patterns of the birds correspond to those inferred from visual observations. Furthermore, our results fine-tune the existing guidelines by recommending, if necessary, protection of old-growth forests adjacent to recent clearcuts. Our models can aid in desktop classification of potential marbled murrelet landscapes throughout south-western BC and probably outside the region. However, we suggest application of different models, depending on the amount of remaining old-growth forest, to evaluate the consistency of predictions. A narrowed-down subset of

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