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Influence of landscape pattern on breeding distribution and success in a threatened Alcid, the marbled murrelet: model transferability and management implications

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Summary

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 coastal zone proximity and mean old-growth patch size. Breeding success was negatively affected by the edge contrast, coast proximity and proportion of young forest, probably reflecting the distribution of nest predators.

4. All distribution models discriminated well between used and random landscapes within the training area. Intersite model transferability was good for 50% of the models. The models less predictive of the training site (area under the curve 0·676–0·738) were more transferable, probably because at the training site, which had considerably less old-growth nesting habitat (18% of extent) than the testing site (55%), breeding distribution was driven by a different subset of predictors.

5. *Synthesis and applications.* Geographic information system (GIS) data were helpful in discriminating between landscapes known to be used by nesting marbled murrelets and those with unknown breeding status. Previous indirect inferences about landscape-level effects on breeding distribution in the birds were shown to correspond with their true nesting distribution. Our results suggest that habitat fragmentation *per se* need not have a negative effect on the birds beyond that as a result of habitat loss, unless associated with an increased abundance of predators. Our results fine-tune the existing habitat conservation guidelines by suggesting that protection of old-growth forest adjacent to clearcuts is important. We provide a means for desktop classification of marbled murrelet landscapes. We advise the application of several different models, depending on the amount of remaining old-growth forest, to evaluate the consistency of predictions.

Key-words: breeding success, *Brachyramphus marmoratus*, distribution, edge, marbled murrelets, model transferability, old-growth

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Introduction

Woodlands fragmented by logging vary in their capacity to support wildlife (Lichstein, Simmons & Franzreb 2002; Betts *et al*. 2006), depending on biotic and abiotic interactions among adjacent forest and non-forest landscape components (Chen, Franklin & Spies 1995; Harper *et al*. 2005). Because distribution and fitness of wildlife can be influenced by the pattern of the surrounding landscape, conservation actions in woodland ecosystems should be informed by models predicting the landscape-level distribution and fitness of individuals (Fielding & Haworth 1995; McGarigal & McComb 1995). It is equally important to assess the performance of distribution models outside the training environment (Vaughan & Ormerod 2005; Graf *et al*. 2006).

The marbled murrelet *Brachyramphus marmoratus* Gmelin is an Alcid that forages inshore and nests in coniferous old-growth forests of the Pacific north-west of North America (Nelson 1997). Marbled murrelet nests are notoriously difficult to locate because of their occurrence high in old-growth trees and placement in rugged terrain and the birds' secretive nesting behaviour (Bradley *et al*. 2004; Peery *et al*. 2004; Baker *et al*. 2006). Forest logging along the Pacific coast has produced substantial loss and fragmentation of murrelet nesting habitat (Raphael *et al*. 2002, 2006). Habitat loss, concurrent with perceived population declines, has precipitated habitat protection and listing of the species as threatened throughout its range, excluding Alaska (Nelson 1997).

Recent studies have focused on quantification of marbled murrelet populations (Bigger *et al*. 2006) and the impacts of deforestation upon them (Burger 2001; Meyer & Miller 2002; Raphael *et al*. 2002; Peery *et al*. 2004). Patch- and stand-level nest site selection has also been addressed (Burger & Bahn 2004; Baker *et al*. 2006; Zharikov *et al*. 2006). However, because of the paucity of known nest sites, effects of landscape pattern on the species' breeding ecology remain poorly understood (Raphael *et al*. 2002, 2006; Ripple, Nelson & Glenn 2003). It is also not known whether distribution models developed for one nesting population can inform conservation actions elsewhere.

In British Columbia (BC), Canada, current guidelines for the conservation of marbled murrelet nesting habitat stipulate protection of patches of coastal forest structurally suitable for nesting. Suitability is primarily defined by patch-level characteristics (tree age, height, presence of epiphytes) derived from digital forest inventories and aerial surveys. Only tentative consideration is given to the overall landscape pattern (MWALP 2004). Landscape pattern can influence individuals above and beyond the effect of breeding habitat *per se* (Lichstein, Simmons & Franzreb 2002; Betts *et al*. 2006) and much of that influence in fragmented forest landscapes is the result of the increased amount and contrast of forest edges (Harper *et al*. 2005).

This study used the largest available sample of marbled murrelet nests to examine the effects of landscape pattern on the species' breeding distribution and success in south-western BC. The same data set was used by Zharikov *et al*. (2006) to investigate the effects of patch size, location and topography on breeding distribution and success in the marbled murrelet. The current work focused on landscape-level effects, in particular of old-growth edge, on the species' breeding ecology, with the aim of enhancing current conservation guidelines. This study also assessed the spatial transferability of distribution models with an independent data set. The following questions were addressed. (i) Are the choice of a nest site and the outcome of a nesting attempt predicted by the pattern of the surrounding landscape? (ii) How do artificial and natural edges of the old-growth forest influence breeding distribution and success in the species? (iii) How do landscape-level distribution models developed at one site perform elsewhere?

Methods

STUDY AREA

The field work was carried out at Desolation (training site) and Clayoquot (testing site) Sounds in south-western BC in 1998–2001 and 2000–02, respectively (Fig. 1). Both areas, located 145 km apart, are mountainous (sea level to 2500 m at Desolation and 2200 m at Clayoquot), with glacial valleys, fjords and inlets. Avalanche chutes, streams, logging roads and clearcuts create numerous forest edges. The climate is warmer and drier at Desolation than at Clayoquot; mean summer temperature and cumulative rainfall are 13·4 °C and 300 mm, and 11·9 °C and 400 mm, respectively. The primeval vegetation at either site is/was dominated by coniferous old-growth forest comprising western red cedar *Tsuga plicata* Donn., western hemlock *Tsuga heterophylla* Sarg. and Douglas fir *Pseudotsuga menziesii* Franco. At Desolation, industrial-scale logging started early in the 20th century and continues at present. Approximately 80% of the original forest has been logged (F. Huettmann, unpublished data). At Clayoquot, large-scale logging commenced in 1954 and by 1993 15–25% of the old-growth cover had been harvested (Kelson, Manly & Carter 1995).

LAND-COVER DATA

Land-cover data were compiled in ArcGIS 9·0 (ESRI Inc., Redlands, CA) from current (1997–2000) 1 : 20 000 digital forest inventories (minimum mapping unit 0·1 ha) and stream and road layers maintained by the BC Ministry of Forests and private forest companies. From these data, we created raster maps of nine land-cover classes (Table 1) deemed important for marbled murrelets according to published sources (Nelson 1997; Burger, Bahn & Tillmanns 2000; Burger 2001; Meyer & Miller 2002; Raphael *et al*. 2002; Raphael, Mack & Cooper 2002; Ripple, Nelson & Glenn 2003; Burger & Bahn 2004; Meyer, Miller & Ralph 2004; Baker *et al*. 2006)

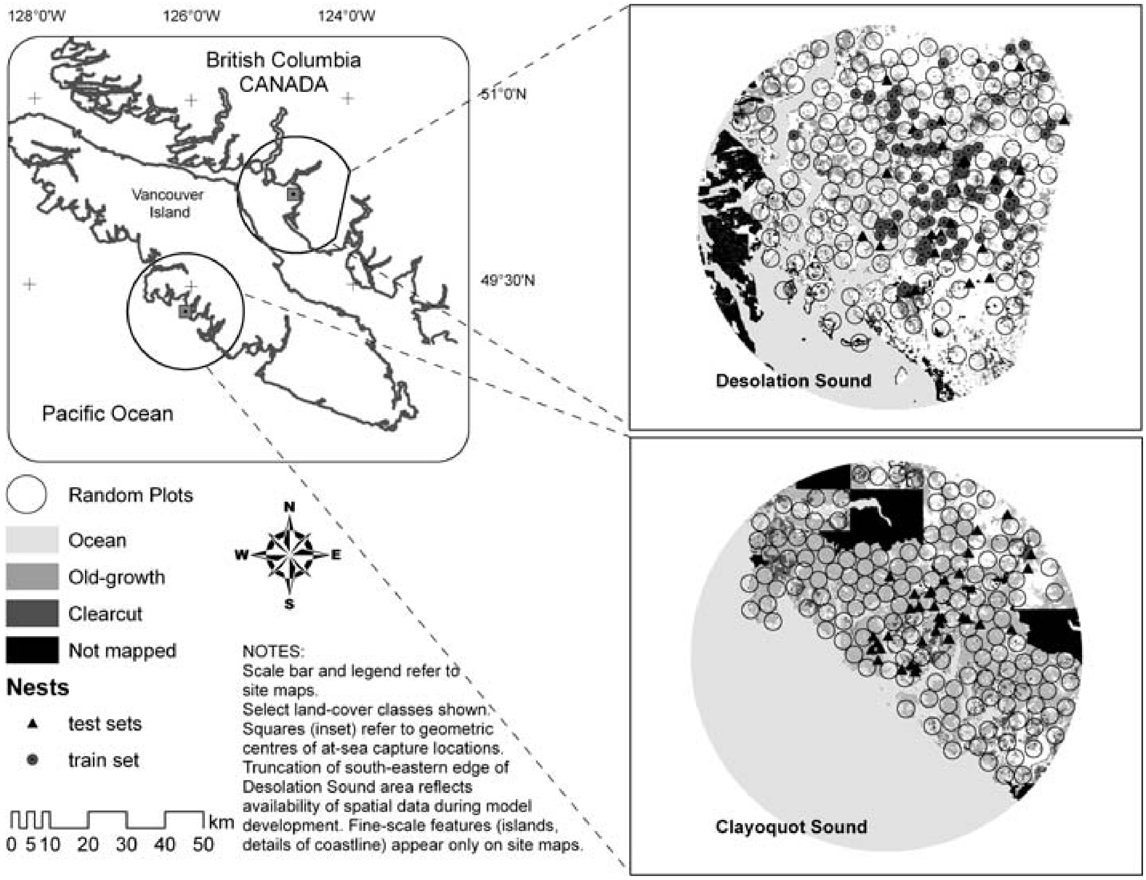

Fig. 1. Locations of the study areas, marbled murrelet nests and 2·3-km radius random plots in south-western British Columbia, Canada.

Table 1. Land-cover composition of the two *c.* 50-km radius study areas (Desolation and Clayoquot) with the respective edge depth (m) and edge contrast (0–1) values. Percentage ocean refers to the total extent; all other land-cover classes refer to the terrestrial component. Cliff, freshwater and alpine classes were considered as creating natural edges relative to old-growth forest. Young and mature forest, clearcut and 'brush and burn' (mostly the results of a silvicultural practice) land-cover classes were considered as artificial edges

Land-cover class*	Percentage	Edge depth	Edge contrast
1. Young forest (21–60 years)	9·2/2·9	30	0·7
2. Mature forest (61–140 years)	22·2/3·8	15	0·2
3. Old-growth forest (> 140 years)	17·7/55·2	0	0·0
4. Cliff, gravel, boulder	2·0/0·4	30	0·7
5. Freshwater (lakes, streams and rivers)	8·0/6·7	30	1·0
6. Clearcut (clearcuts, logging roads, ≤ 20-year-old regrowth)	5·4/6·9	60	1·0
7. Brush and burned areas	5·8/1·7	30	0·8
8. Alpine (includes subalpine)	20·5/9·7	30	0·6
9. Ocean	25·8/47·5	120	0·9
10. Not mapped	9·6/12·8	0	0·0

*Land-cover classification was validated at 92 random ground points at Desolation Sound in 2000–01. Ground points were classified as forest (all age classes combined), clearcut or non-forest (all non-forest land-cover classes combined). The overall classification accuracy was 83%, with producer accuracies for forest, clearcut and non-forest components of 89%, 100% and 33%, respectively.

and the current habitat conservation guidelines in BC (MWALP 2004). Raster resolution was 15 × 15 m, to prevent overemphasis on the prevalence of linear features (streams and roads) in a landscape (J. Sundé, personal communication). Linear features were allowed to dissect otherwise contiguous forest patches.

CAPTURE OF MURRELETS, NEST LOCATION AND BREEDING SUCCESS

Marbled murrelet capture, radio-tagging and nest location methods are detailed by Bradley *et al.* (2004). Briefly, marbled murrelets were captured prior to and during the nesting period (May–June) within 5 km offshore of the study areas (Fig. 1). Birds were radio-tagged and, once nesting started, searched for, inland, using helicopters. Some nests that failed early were not found; a nest had to persist for ≥ 4 days to have a > 50% chance of detection (details in Bradley *et al*. 2004). The initial spatial accuracy of nest locations estimated by Bradley *et al.* (2004) to ±50–60 m (i.e. an area no larger than 100 × 100 m) was subsequently improved to approximately 30 m following consultations with field crews and re-examination of mapped locations (F. Huettmann, unpublished data).

Nest locations were confirmed by ground crews where logistically possible. However, many nests (76 out of 121 at Desolation and eight out of 36 at Clayoquot) could not be accessed from the ground because of remote and/or dangerous terrain. Consequently, the fledging success could not be determined by direct examination of the faecal-ring at the nest. Instead, a nest was classified as successful (i.e. active) if radio-tagged birds were visiting the nest site regularly for at least 20 days of the *c.* 40-day chick-rearing period. Otherwise it was classified as failed. The 20th-day cut-off point was determined by logistics and resources (for more details see Bradley *et al.* 2004). This measure, termed 'mid-rearing success' (MRS), was used only as a proxy of breeding success because these data could be obtained regardless of a nest's accessibility, whereas true fledging success was known only for the physically accessible nests (a non-random subset of the data). In the final analyses, 108 nests from Desolation were used to model landscape-level effects on MRS. The Clayoquot sample of 29 nests with known MRS outcome was considered too small for a meaningful test of the effects of landscape pattern on breeding success.

LANDSCAPE SAMPLING

Extent of the available area

The nesting area potentially available to marbled murrelets was defined as a *c.* 50-km radius circle around the geometric mean of marine capture locations that encompassed all known nests (Fig. 1). This definition was based on the highest inland activity of marbled murrelets within 40–80 km of the coastline (Nelson 1997; Meyer, Miller & Ralph 2002, 2004; Raphael, Mack & Cooper 2002). Earlier, similar distribution results were obtained for the Desolation population relative to local topography whether a 50-km radius circle or a minimum convex polygon definition of the available area was used (F. Huettmann, unpublished data).

Sampling scale

Elsewhere, analyses of landscape patterns of inland distribution of the species at the level of 1·6- and 3·2-km radius plots provided more accurate models than smaller plots (Meyer & Miller 2002; Meyer, Miller & Ralph 2002). Nest spacing at Desolation was stable among the 4 study years (CV = 2·7%), with an overall within-year mean nearest nest distance (NND) of 4·6 ± 4·0 (SD) km. The NND was independent of the number of located nests (range 23–38) in a given year ($r_s = -0{\cdot}05$, $P = 0{\cdot}94$). At Clayoquot, fewer nests were located per year (eight, 10 and 18) because of a lower sampling effort; on average they were further apart (6·6 ± 4·2 km). However, the NND in the year with the highest sample size (2002, 18) was essentially the same as at Desolation (4·8 ± 4·2 km). Consistent with the earlier modelling exercises and the distribution of our sample of nests, landscape samples were defined as circular plots centred on nest/random locations with a radius of 4·6/2 = 2·3 km (16·5 km^2).

To enhance the contrast between known used and unknown (potentially unused) landscapes, the total available extent was sampled by placing as many non-overlapping random plots as the available extent permitted ($n = 145$ at either site). Each random plot was centred on a point in the old-growth stratum that lay outside any nest plot. Overlaps occurred among nest plots, but all were included into the analyses. In the absence of published evidence for either overdispersion or aggregation of breeding individuals, it was felt that excluding overlapping used plots could depreciate the ecological relevance of predictive models (de Solla, Bonduriansky & Brooks 1999). After model-fitting, deviance residuals were tested for autocorrelation with Moran's *I* adjusted for small distances (CrimeStat 3·0; The National Institute of Justice, Washington, DC) to test for departure from second-order stationarity in nest distribution (Betts *et al*. 2006).

LANDSCAPE AND EDGE VARIABLES

The landscape pattern of the used and random plots was quantified using Fragstats 3·2 (McGarigal & McComb 1995). Twelve landscape metrics were selected for analyses (Table 2). These metrics described landscape characteristics previously shown to be relevant to the ecology of marbled murrelets. However, they were not necessarily exactly the same metrics as used in other studies. The selected parameters were weakly intercorrelated ($r_p = 0{\cdot}6$) except for percentages of core habitat in a landscape (CPL) and old-growth habitat (%OG) ($r_p = 0{\cdot}95$). Consequently, the latter two predictors were never included together in a model. We defined as 'edge' only the interface between old-growth and any other land-cover class in the landscape. Edge depth, i.e. the extent of penetration of abiotic factors into an old-growth patch from the outside, was inferred from studies of vegetation and microclimatic gradients across the edges of coniferous old-growth forest (Chen, Franklin & Spies 1995; Burger, Bahn & Tillmanns 2000; Harper *et al.* 2005). This parameter determines the size of a core (interior) forest area. Edge contrast was defined by the relative steepness of the vegetation gradient between the old-growth forest and a given other land-cover class. This parameter weighs the contribution of a particular edge type (e.g. old-growth–clearcut) to the total

Table 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 of the species. Additionally, shape of old-growth patches and their proximity and position relative to other land-cover classes may be important (Table 2). Thus the 12 individual landscape metrics were grouped into four factors to test for the effects of habitat area (HA), edge (EDGE), landscape composition (LC) and old-growth habitat distribution and shape (DS) (Tables 2 and 3). Ten preliminary candidate models (plus the null) assessing individual and combined effects of these four factors on breeding distribution and success were parameterized (Table 3). At present it is not known whether or how these factors interact in their influence on the species. Therefore, when fitting preliminary models, both independent predictors and their first-order interactions were included. This step constituted the hypothesis testing part of our approach. Parameter coefficients were examined and those overlapping zero (95% confidence interval) were sequentially removed as not allowing for conclusive prediction (Johnson, Seip & Boyce 2004); coefficients of remaining parameters were adjusted accordingly. At this stage most models included one or two interaction terms that, as shown by test trials, overfitted the models and strongly reduced their generalizability (Vaughan & Ormerod 2005). This outcome was consistent with the suggestion that interaction terms in animal distribution models often represent local effects (Whittingham *et al*. 2007) and that models with simpler structures are likely to have better transferability (Ginzburg & Jensen 2004; Graf *et al*. 2006). As a precaution against model overfitting, we applied a more stringent selection procedure to interaction terms: only interactions that improved a model's Akaike's information criterion for small samples (AIC_c) by ≥4 points were retained. As an application of the information theoretic approach, final candidate models were ranked based on their AIC_c and Akaike weights (ω) (Burnham & Anderson 2002). Model fit was calculated as the log-likelihood χ^2 statistic. Range odds-ratios, i.e. the change in odds of the positive response over the full range of a given predictor, were calculated. Models were not overdispersed. Cook's distance *D* was used to identify and exclude cases with unusually high influence (Hosmer & Lemeshow 2000).

Table 3. Preliminary candidate models for predicting breeding distribution and success in the marbled murrelet with the number of independent parameters (excluding first-order interactions)

Model	Predictors
HA	2
EDGE	3
LC	4
HA + EDGE	5
HA + LC	5*
EDGE + LC	7
HA + EDGE + LC	8*
HA + DS	5
EDGE + DS	5
LC + DS	7
NULL	1†

*%OG was excluded as it is strongly correlated with CPL. †A random variable was fitted to the data. Inclusion of the NULL model in the best model subset would have been interpreted as lack of relevant predictors in the analysis.

MODEL EVALUATION

Distribution models

Discriminatory ability of distribution models was evaluated using the probability threshold-free receiver-operating curves (ROC) (McPherson, Jetz & Rogers 2004), where the area under the curve (AUC) represents the probability of a random positive case receiving a greater score than a random negative case. AUC values of > 0·8, 0·8–0·7, 0·7–0·6 and < 0·6 are usually considered as good, fair, poor and inadequate, respectively. A random selection of 90 nest and 90 random plots from Desolation was used to train distribution models, thus setting aside ≥25% of the data for internal model tests. Internal and external tests of discriminatory performance of the models were accomplished in four steps. (i) For each final distribution model, its data-optimized AUC (AUC_m) statistic was calculated. (ii) The model was then applied to the test subset using the inverse logistic transformation to generate a nest probability score *p* for each data point, where:

$$P = \left(\frac{1}{1 + \exp^{(-\log it)}}\right) \qquad \text{eqn 1}$$

(iii) The distribution of the proportion of true nests ($n = 31$) that received greater probability scores than random locations ($n = 55$) in the test subset was calculated by comparing each nest in the set to a randomly selected random plot 100 times. This distribution, denoted as AUC_i, represents an internal assessment of the discriminatory performance of the Desolation distribution models. (iv) Whether AUC_m belonged to the corresponding population of AUC_i values was determined by a *z*-score test.

External performance of the models was tested by repeating steps (ii) and (iii) on the geographically independent Clayoquot data (36 nests and 145 random plots). The distribution of the proportion of true nests in the data set that received greater probability scores than random plots, denoted as AUC_e, constitutes an external test of the discriminatory performance of the Desolation models. One-way, Desolation → Clayoquot, model transferability was assessed using a modification of the index proposed by Randin *et al.* (2006), where:

$$\mathrm{TI} = \frac{1 - (\mathrm{AUC}_i - \mathrm{AUC}_e)/0{\cdot}5}{1 + (\mathrm{AUC}_i - \mathrm{AUC}_e)/0{\cdot}5} \qquad \text{eqn 2}$$

TI = 1 when a model performs as well externally as it does internally.

Breeding success models

Performance of breeding success (MRS) models was evaluated using the ROC method on the same data as used for model development.

Results

DISTRIBUTION MODELS

Of the 10 preliminary distribution models, two were eliminated because the predictors for one group were not significant (HA + EDGE → EDGE; HA + LC → LC; Tables 3 and 4). At Desolation, marbled murrelets were more likely to nest in landscapes with a greater proximity of old-growth forest patches, higher artificial and natural old-growth edge density and contrast, and higher proportions of old-growth (or core) and logged habitat. The landscapes used were also characterized by higher interspersion of old-growth patches (among other land-cover classes) and smaller average old-growth patch size (as defined in this study; Table 4). These patterns suggested birds were overutilizing patchy forest and underutilizing the most extensively logged and remaining larger areas in this fragmented landscape. Birds were less likely to nest in landscapes with a higher proportion of ocean but, when nesting in the coastal zone, they selected landscapes with a higher than random density of natural edge (interaction term in model 2).

AIC weights gave the same order of model ranking as either AUC_m or AUC_i (respective r_s values 0·93 and 0·95, $P < 0{\cdot}001$). As expected, the data-optimized AUC_m values were higher than the corresponding AUC_i estimates (Table 4). However, the difference was not significant ($|\,z\text{-scores}\,| < 1{\cdot}96$), implying that all models could adequately predict the distribution of the murrelets within the model-training region. Testing each year separately, evidence of weak residual positive autocor-

Table 4. Ranking, according to the sample-adjusted Akaike information criterion difference and Akaike weights ($\Delta\mathrm{AIC}_c$ and $\mathrm{AIC}_c\omega$) and internal and external discriminatory performance of marbled murrelet distribution models. Parameters within models are listed in descending order of their impact on the response as defined by the range odds ratios given in the superscript. Inconclusive parameters (parentheses) are retained if they participated in interaction terms

	Model (logit =)*	$\Delta\mathrm{AIC}_c$	$\mathrm{AIC}_c\omega$	AUC_m†	AUC_i	AUC_e	TI
1	$-0{\cdot}032 \times \mathrm{NND}^{(1\times10{}^\wedge-10)} + 0{\cdot}093 \times E_a^{(104{\cdot}95)} + 0{\cdot}017 \times E_n^{(4{\cdot}77)} - 0{\cdot}395$	0·0	0·532	0·783	0·735 (0·064)	0·571 (0·064)	0·51
2	$0{\cdot}003 \times E_n \times \%\mathrm{Oc}^{(410{\cdot}26)} + 0{\cdot}095 \times E_a^{(111{\cdot}85)} + 0{\cdot}040 \times E_n^{(39{\cdot}07)} + (\%\mathrm{Oc})^{(3{\cdot}10)} - 2{\cdot}633$	0·5	0·415	0·790	0·723 (0·061)	0·573 (0·065)	0·54
3	$0{\cdot}089 \times E_a^{(85{\cdot}03)} + 0{\cdot}026 \times E_n^{(11{\cdot}17)} + 0{\cdot}039 \times \mathrm{TECI}^{(10{\cdot}52)} - 4{\cdot}982$	5·6	0·032	0·762	0·724 (0·061)	0·558 (0·062)	0·50
4	$0{\cdot}068 \times E_a^{(29{\cdot}63)} + 0{\cdot}040 \times \%\mathrm{OG}^{(16{\cdot}09)} - 0{\cdot}035 \times \%\mathrm{Oc}^{(0{\cdot}10)} - 1{\cdot}903$	6·6	0·020	0·769	0·700 (0·061)	0·623 (0·052)	0·74
5	$0{\cdot}051 \times \%\mathrm{OG}^{(33{\cdot}42)} + 0{\cdot}067 \times \%\mathrm{Logged}^{(7{\cdot}16)} - 0{\cdot}026 \times \%\mathrm{Oc}^{(0{\cdot}17)} - 1{\cdot}522$	14·0	0·001	0·738	0·680 (0·065)	0·627 (0·07)	0·81
6	$-0{\cdot}027 \times \mathrm{NND}^{(4\times10{}^\wedge-9)} + 0{\cdot}031 \times \mathrm{IJI}^{(10{\cdot}54)} + 0{\cdot}033 \times \%\mathrm{OG}^{(9{\cdot}50)} - 1{\cdot}568$	15·0	0·000	0·728	0·677 (0·061)	0·640 (0·065)	0·86
7	$-0{\cdot}031 \times \mathrm{NND}^{(3\times10{}^\wedge-10)} + 0{\cdot}031 \times \mathrm{IJI}^{(10{\cdot}20)} + 0{\cdot}031 \times \mathrm{CPL}^{(6{\cdot}10)} - 1{\cdot}013$	17·0	0·000	0·714	0·668 (0·063)	0·639 (0·064)	0·89
8	$0{\cdot}088 \times \mathrm{CPL}^{(181{\cdot}1)} - 0{\cdot}054 \times \mathrm{PA}_{mn}^{(0{\cdot}037)} - 0{\cdot}889$	29·3	0·000	0·676	0·646 (0·065)	0·663 (0·062)	1·07

*All models fitted the data adequately (log-likelihood $\chi^2 > 18{\cdot}2$, $P < 0{\cdot}0001$).

†AUC_m, AUC_i and AUC_e correspond to the intrinsic discriminatory performance of the model expressed in terms of area under the curve, its internal performance (SD) on independent training data (Desolation) and its external performance (SD) on independent testing data (Clayoquot), respectively. TI, transferability index, equals 1 when $\mathrm{AUC}_i = \mathrm{AUC}_e$.

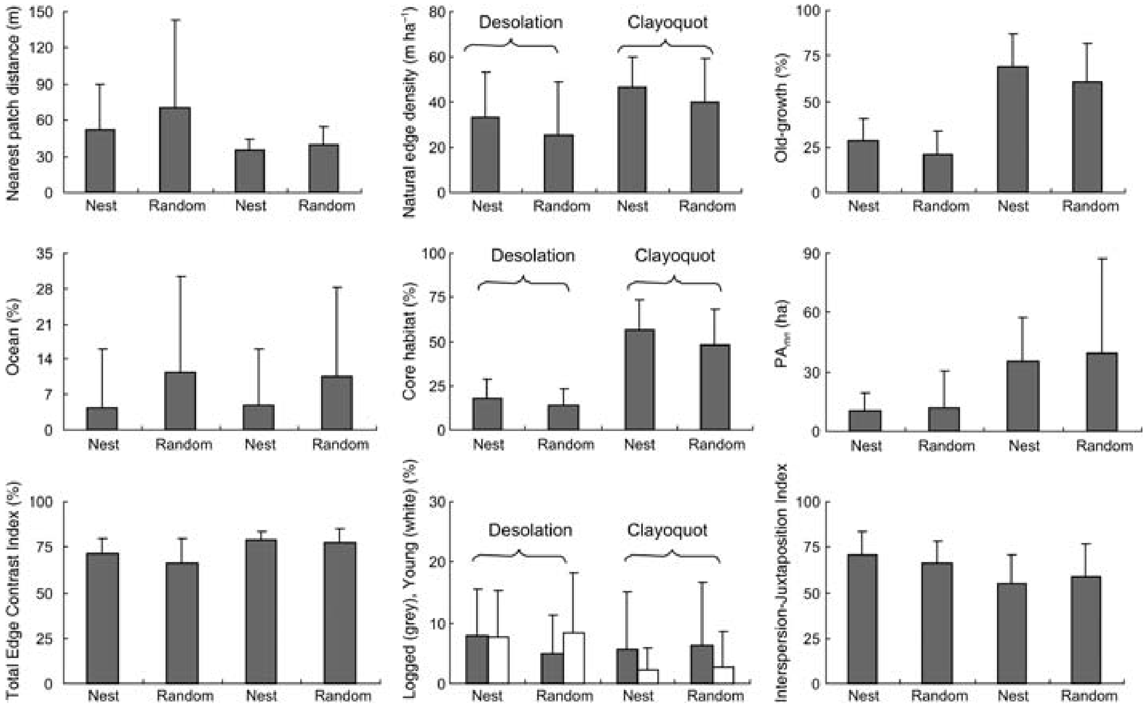

Fig. 2. Mean (SD) site and group differences for predictor variables.

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):

(i) $0{\cdot}016 \times \%\mathrm{OG} \times \%\mathrm{YF} + 0{\cdot}121 \times \%\mathrm{YF} + 0{\cdot}049 \times \%\mathrm{OG} - 4{\cdot}626$ ($\omega_i = 0{\cdot}83$, $\mathrm{AUC}_m = 0{\cdot}693$, respective range odds ratios 9×10^{11}, 127·59 and 55·23; cf. Desolation model 5); (ii) $-0{\cdot}020 \times \mathrm{PA}_{mn} + 0{\cdot}045 \times \%\mathrm{CPL} - 3{\cdot}011$ ($\omega_i = 0{\cdot}16$, $\mathrm{AUC}_m = 0.676$, respective range odds ratios 0·01 and 33·93; cf. Desolation model 8).

These models suggested that, at Clayoquot, murrelets nested in landscapes with higher than random proportions of young and old-growth forest, a greater proportion of core habitat and smaller average forest patch size. In used landscapes, the proportions of old-growth and young forest were independent, while in random landscapes there was a negative relationship between the two (interaction term model 1).

MRS MODELS

Mid-rearing success (Desolation only) could be adequately described by two models ($\chi^2 > 9{\cdot}2$, $P < 0{\cdot}003$):

(i) $-0{\cdot}069 \times \mathrm{TECI} - 0{\cdot}073 \times \%\mathrm{YF} - 0{\cdot}047 \times \%\mathrm{Oc} + 6{\cdot}494$ ($\omega_i = 0{\cdot}74$, $\mathrm{AUC}_m = 0{\cdot}711$, respective range odds ratios 0·01, 0·10 and 0·12); (ii) $-0{\cdot}078 \times \%\mathrm{YF} + 1{\cdot}339$ ($\omega_i = 0{\cdot}25$, $\mathrm{AUC}_m = 0{\cdot}653$, range odds ratio 0·09).

MRS was negatively associated with the total edge contrast index and the proportions of a landscape under ocean and young forest (Table 5).

Table 5. Mean (SD) values of the predictors of mid-rearing success of marbled murrelets at Desolation Sound

Variable	Successful ($n = 71$)	Failed ($n = 36$)
Total edge contrast index	70·4 ± 9·3	73·1 ± 6·6
% young forest	6·2 ± 6·6	11·2 ± 9·3
% ocean	3·2 ± 8·8	6·7 ± 13·1

Discussion

DISTRIBUTION MODELLING

Digital forest inventories are an important data source for wildlife conservation and management (Lichstein, Simmons & Franzreb 2002; Betts *et al.* 2006; Raphael

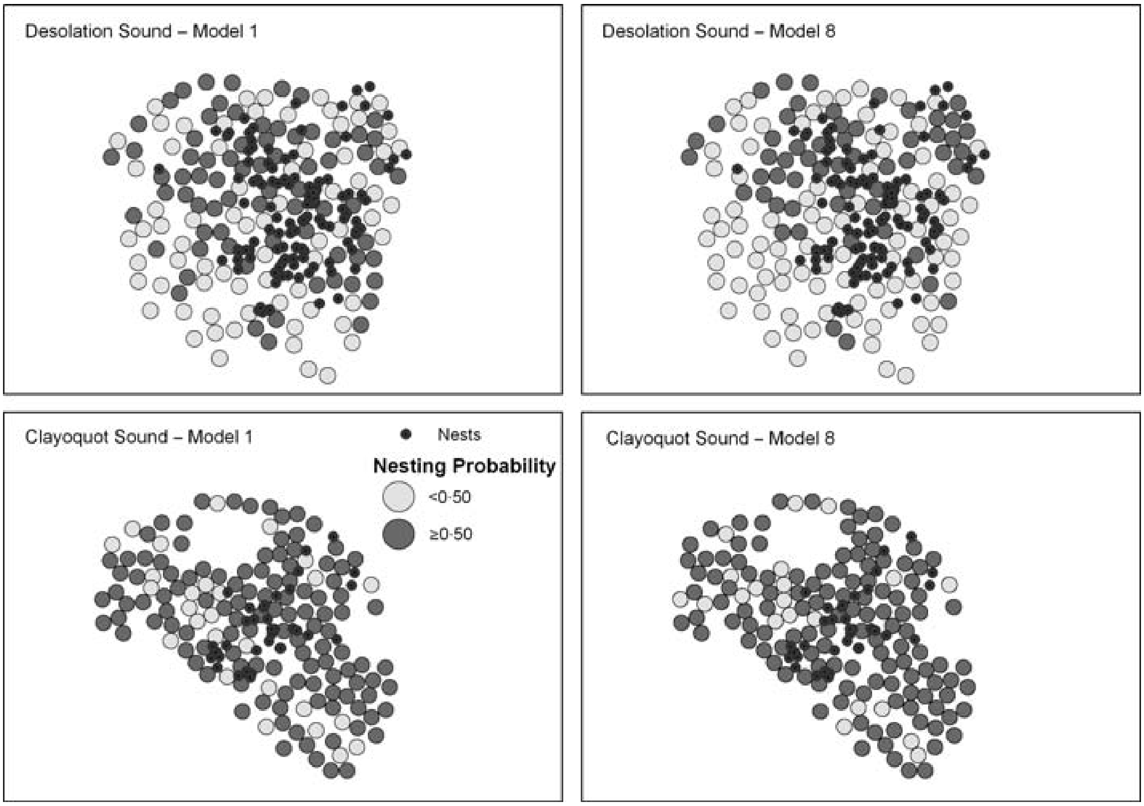

Fig. 3. Predicted probability of nesting of marbled murrelets in random landscapes at Desolation and Clayoquot, according to select models.

et al. 2006). We have shown that the pattern of old-growth landscape matters to nesting marbled murrelets, and that an improvement in selecting landscapes suitable for nesting by these birds can be achieved with geographical information system (GIS) data alone. Yet only 50% of our models transferred well to a different site. Other studies that have examined cross-regional model transferability (birds, Fielding & Haworth 1995; Graf *et al.* 2006; plants, Randin *et al.* 2006) have suggested differences in environmental characteristics as a major reason for decreased model performance between sites. This is because models tend to reflect dominant features of their training region, i.e. features that vary over a broad range of values and occur throughout the modelling extent (Fielding & Haworth 1995). In the context of forest fragmentation (forest songbirds, Betts *et al.* 2006) in more fragmented areas, animal distribution patterns are increasingly driven by fragmentation variables; at Desolation (18% of land under old-growth) these were patch proximity and forest edge density. In more intact areas, variables describing the overall amount of habitat come to the fore as more important predictors of distribution: extent of old-growth forest or core habitat and patch size at Clayoquot (55% of land under old-growth).

The distribution of nests in our 'available' extents suggests that more widespread bird-tagging would have placed additional used landscapes into what we considered as habitat with unknown status. This mutual non-exclusiveness of our used and random data sets is one explanation for the general weakness of the distribution models, particularly at Clayoquot. The other explanation is the strong dependence of marbled murrelets on local habitat structure (Burger & Bahn 2004; Baker *et al.* 2006). Because at Clayoquot there is more nesting habitat than at Desolation, most Clayoquot landscapes should fall higher along a suitability gradient than Desolation landscapes. It is thus not surprising that when Desolation models were applied at Clayoquot, most random landscapes were assigned high probabilities of nesting. Consequently the discriminatory performance of the models at Clayoquot was both poor (AUC < 0·7), because of much suitable habitat (Lichstein, Simmons & Franzreb 2002), and diminished relative to Desolation, where a clearer difference between suitable and unsuitable landscapes existed.

Importantly, the same two metrics describing habitat area (percentage core habitat and mean patch size) were equally predictive of murrelet distribution at both sites (model 8; Table 4). Thus the birds are more likely to nest in landscapes possessing more old-growth forest (Meyer & Miller 2002; MWALP 2004), as previously believed, but also favour sites broken up into smaller patches either naturally, as at Clayoquot, or in part artificially, as at Desolation (see also Zharikov *et al.* 2006).

HABITAT SELECTION: RANGE-WIDE SIMILARITIES AND DIFFERENCES

Marbled murrelets were more likely to nest in landscapes with greater clumping of forest patches, higher 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).

FITNESS CONSEQUENCES OF NEST SITE CHOICE

Within their distribution 'niche', marbled murrelets nested more successfully in landscapes with lower edge contrast and a lower proportion of landscape under young forest and outside the immediate coastal zone. The main agents of nest mortality in the marbled murrelet are corvids (Nelson 1997; Raphael *et al.* 2002; Peery *et al.* 2004). The lower edge contrast index in the landscapes with successful nests is indicative of both their location in areas with more low contrast alpine/subalpine–old-growth interface, and therefore at higher (> 800 m) altitudes (Zharikov *et al.* 2006), and further from the coastal zone. At Desolation, TECI was negatively correlated with percentage ocean ($r_p = -0{\cdot}54$, $P < 0{\cdot}01$), which in turn was negatively correlated with altitude ($r_p = -0{\cdot}57$, $P < 0{\cdot}01$); no other predictors displayed clear altitudinal trends. In south-western BC, Bradley (2002) found a negative altitudinal trend in abundance of potential corvid predators of marbled murrelet nests, while Burger, Bahn & Tillmanns (2000) reported a higher abundance of corvids along the 250-m coastal strip of old-growth than further inland. Also, studies in Washington State have suggested that the juxtaposition of old-growth and regenerating forest may represent optimal habitat for Steller's jays *Cyanocitta stelleri* Gmelin, an important predator of the murrelet nests (Marzluff *et al.* 2004; Marzluff & Neatherlin 2006). Thus it appears that breeding success in the marbled murrelet is driven by distribution of potential nest predators, which in turn is affected by the landscape pattern.

MANAGEMENT IMPLICATIONS

Other than preserving large contiguous blocks of forest, current conservation guidelines in BC recommend that protected marbled murrelet habitat areas (i) be embedded in heterogeneous landscapes and (ii) have natural edges but (iii) not hard anthropogenic edges (MWALP 2004). Our results on landscape heterogeneity (interspersion and juxtaposition index; Desolation) combined with those of Zharikov *et al.* (2006) on topography support the former two points but not the latter point. We found no evidence that the birds distinguish between landscapes with a prevalence of natural vs. hard artificial edges, nor that the two differ in terms of nesting success. Therefore old-growth fragments, particularly those outside the coastal zone that are adjacent to clearcuts, need not be discarded by habitat managers. As logged areas begin to overgrow, the suitability of adjacent old-growth patches may decline because of increased nest predator abundance. In murrelet reserves, this may necessitate the application of predator control measures (Marzluff & Neatherlin 2006; Raphael 2006).

SYNTHESIS AND APPLICATIONS

It is unlikely that models based on GIS data alone can make highly accurate predictions about the distribution of a species, such as the marbled murrelet, highly dependent on local habitat structure. However, it is encouraging that easily acquired GIS data are helpful in discriminating between suitable and unsuitable 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 suitable landscapes can then be surveyed from the air to check for the availability of nesting platforms, as is currently done by habitat managers (A. Burger, unpublished data). This approach could save both time and resources for selecting marbled murrelet habitat areas for conservation, thus contributing to the effort to arrest population declines in this unique Alcid.

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References

Baker, L.M., Peery, M.Z., Burkett, E.E., Singer, S.W., Suddjian, D.L. & Beissinger, S.R. (2006) Nesting habitat characteristics of the marbled murrelet in central California redwood forests. *Journal of Wildlife Management*, **70**, 939–946.

Betts, M.G., Forbes, G.J., Diamond, A.W. & Taylor, P.D. (2006) Independent effects of fragmentation on forest songbirds: an organism based approach. *Ecological Applications*, **16**, 1076–1089.

Bigger, D., Peery, M.Z., Chinnici, S. & Courtney, S.P. (2006) Efficacy of audiovisual and radar surveys for studying marbled murrelets in inland habitats. *Journal of Wildlife Management*, **70**, 505–516.

Bradley, R.W. (2002) *Breeding ecology of radio-marked marbled murrelets* (Brachyramphus marmoratus) *in Desolation Sound, British Columbia*. MSc thesis. Simon Fraser University, Burnaby, Canada.

Bradley, R.W., Cooke, F., Lougheed, L.W. & Boyd, W.S. (2004) Inferring breeding success through radiotelemetry in the marbled murrelet. *Journal of Wildlife Management*, **68**, 318–331.

Burger, A.E. (2001) Using radar to estimate populations and assess habitat associations of marbled murrelets. *Journal of Wildlife Management*, **65**, 696–715.

Burger, A.E. & Bahn, V. (2004) Inland habitat associations of marbled murrelets on southwest Vancouver Island, British Columbia. *Journal of Field Ornithology*, **75**, 53–66.

Burger, A.E., Bahn, V. & Tillmanns, A.R.M. (2000) Comparison of coastal fringe and interior forests as reserves for marbled murrelets on Vancouver Island. *Condor*, **102**, 915–920.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.

Chen, J., Franklin, J.F. & Spies, T.A. (1995) Growing season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications*, **5**, 74–86.

Eberhardt, L.L. (2003) What should we do about hypothesis testing? *Journal of Wildlife Management*, **67**, 241–247.

Fielding, A.H. & Haworth, P.F. (1995) Testing the generality of bird–habitat models. *Conservation Biology*, **9**, 1466–1481.

Ginzburg, L.R. & Jensen, C.X.J. (2004) Rules of thumb for judging ecological theories. *Trends in Ecology & Evolution*, **19**, 121–126.

Graf, R.F., Bollmann, K., Sachot, S., Suter, W. & Bugmann, H. (2006) On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions. *Ecography*, **29**, 319–328.

Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.-A. (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, **19**, 768–782.

Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*. John Wiley & Sons, New York, NY.

Johnson, C.J., Seip, D.R. & Boyce, M.S. (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology*, **41**, 238–251.

Kelson, J.D., Manley, I.A. & Carter, H.R. (1995) Decline of the marbled murrelets in Clayoquot Sound, British Columbia: 1982–1993. *Northwest Naturalist*, **76**, 90–98.

Lichstein, J.W., Simons, T.R. & Franzreb, K.E. (2002) Landscape effects on breeding songbird abundance in managed forests. *Ecological Applications*, **12**, 836–857.

McGarigal, K. & McComb, W.C. (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs*, **65**, 235–260.

McPherson, J.M., Jetz, W. & Rogers, D.J. (2004) The effects of species' range sizes on accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology*, **41**, 811–823.

Marzluff, J.M. & Neatherlin, E. (2006) Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biological Conservation*, **130**, 301–314.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P. & Handcock, M. (2004) Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology*, **85**, 1411–1427.

Meyer, C.B. & Miller, S.L. (2002) Use of fragmented landscapes by marbled murrelets for nesting in southern Oregon. *Conservation Biology*, **16**, 755–766.

Meyer, C.B., Miller, S.L. & Ralph, C.J. (2002) Multi-scale landscape and seascape patterns associated with marbled murrelet nesting areas on the US west coast. *Landscape Ecology*, **17**, 95–115.

Meyer, C.B., Miller, S.L. & Ralph, C.J. (2004) Stand–scale habitat associations across a large geographic region of an old-growth specialist, the marbled murrelet. *Wilson Bulletin*, **116**, 197–286.

MWALP (2004) *Marbled Murrelet Brachyramphus marmoratus*. Identified Wildlife Management Strategy. Ministry of Water, Land and Air Protection, Victoria, Canada. http://wlapwww.gov.bc.ca/wld/identified/accounts.html (accessed 1 November 2005).

Nelson, S.K. (1997) Marbled murrelet (*Brachyramphus marmoratus*). *The Birds of North America* (eds A. Poole & F. Gill), pp. 1–25. Academy of Natural Sciences and American Ornithologists' Union, Philadelphia, PA, and Washington, DC.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Burkett, E.B. & Williams, T.D. (2004) Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. *Conservation Biology*, **18**, 1088–1098.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.

Raphael, M.G. (2006) Conservation of the marbled murrelet under the Northwest Forest Plan. *Conservation Biology*, **20**, 297–305.

Raphael, M.G., Galleher, B.M., Huff, M.H., Miller, S.L., Nelson, S.K. & Young, R.D. (2006) Spatially explicit estimates of potential nesting habitat for the marbled murrelet. *Northwest Forest Plan: The First 10 Years (1994–2003). Status and Trends of Populations and Nesting Habitat for the Marbled Murrelet* (eds M.H. Huff, M.G. Raphael, S.L. Miller, S.K. Nelson & J. Baldwin), pp. 97–146. General Technical Report 650. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Raphael, M.G., Mack, D.E. & Cooper, B.A. (2002) Landscape-scale relationships between abundance of marbled murrelets and distribution of nesting habitat. *Condor*, **104**, 331–342.

Raphael, M.G., Mack, D.E., Marzluff, J.M. & Luginbuhl, J.M. (2002) Effects of forest fragmentation on populations of the marbled murrelet. *Effects of Habitat Fragmentation on Birds in Western Landscapes: Contrast with Paradigms from the Eastern United States* (eds T.L. George & D.S. Dobkin), pp. 221–235. Studies in Avian Biology No. 25. Cooper Ornithological Society, Camarillo, CA.

Raphael, M.G., Young, J.A. & Galleher, B.M. (1995) A landscape-level analysis of marbled murrelet habitat in western Washington. *Ecology and Conservation of the Marbled Murrelet* (eds C.J. Ralph, J.G.L. Hunt, M.G. Raphael & J.F. Piatt), pp. 177–189. Pacific Southwest Research Station, Forest Service, Albany, CA.

Ripple, W.J., Nelson, S.K. & Glenn, E.M. (2003) Forest landscape patterns around marbled murrelet nest sites in the Oregon coast range. *Northwestern Naturalist*, **84**, 80–89.

de Solla, R.S., Bonduriansky, R. & Brooks, R.J. (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, **68**, 221–234.

Stephens, P.A., Buskirk, S.W., Hayward, G.D. & Martínez del Rio, C. (2005) Information theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology*, **42**, 4–12.

Vaughan, I.P. & Ormerod, S.J. (2005) The continuing challenge of testing species distribution models. *Journal of Applied Ecology*, **42**, 720–730.

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D. & Freckleton, R.P. (2007) Should conservation strategies consider spatial generality? Farmland birds show regional but not national patterns of habitat association. *Ecology Letters*, **10**, 25–35.

Zharikov, Y., Lank, D.B., Huettmann, F., Bradley, R.W., Parker, N., Yen, P.P.-W., McFarlane-Tranquilla, L.A. & Cooke, F. (2006) Habitat selection and breeding success in a forest-nesting Alcid, the marbled murrelet, in two landscapes with different degrees of forest fragmentation. *Landscape Ecology*, **21**, 107–120.

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