



Research Papers

Patch Scale Nest-Site Selection by Marbled Murrelets (*Brachyramphus marmoratus*)

Sélection du site de nidification à l'échelle de l'îlot chez le Guillemot marbré (*Brachyramphus marmoratus*)

*Michael P. Silvergieter*¹ and *David B. Lank*¹

ABSTRACT. The Marbled Murrelet (*Brachyramphus marmoratus*) is a threatened alcid that nests almost exclusively in old-growth forests along the Pacific coast of North America. Nesting habitat has significant economic importance. Murrelet nests are extremely difficult and costly to find, which adds uncertainty to management and conservation planning. Models based on air photo interpretation of forest cover maps or assessments by low-level helicopter flights are currently used to rank presumed Marbled Murrelet nesting habitat quality in British Columbia. These rankings are assumed to correlate with nest usage and murrelet breeding productivity. Our goal was to find the models that best predict Marbled Murrelet nesting habitat in the ground-accessible portion of the two regions studied. We generated Resource Selection Functions (RSF) using logistic regression models of ground-based forest stand variables gathered at plots around 64 nests, located using radio-telemetry, versus 82 random habitat plots. The RSF scores are proportional to the probability of nests occurring in a forest patch. The best models differed somewhat between the two regions, but include both ground variables at the patch scale (0.2-2.0 ha), such as platform tree density, height and trunk diameter of canopy trees and canopy complexity, and landscape scale variables such as elevation, aspect, and slope. Collecting ground-based habitat selection data would not be cost-effective for widespread use in forestry management; air photo interpretation and low-level aerial surveys are much more efficient methods for ranking habitat suitability on a landscape scale. This study provides one method for ground-truthing the remote methods, an essential step made possible using the numerical RSF scores generated herein.

RÉSUMÉ. Le Guillemot marbré (*Brachyramphus marmoratus*) est un Alcidé menacé qui niche presque exclusivement dans les vieilles forêts de la côte nord-américaine du Pacifique. L'étude de son habitat de nidification exige des ressources financières importantes. En effet, les nids de guillemots sont très difficiles à trouver, de sorte que cette activité est coûteuse, conférant à la planification de l'aménagement et à la conservation un caractère incertain. Les modèles fondés sur des cartes du couvert forestier provenant de la photointerprétation ou encore sur des évaluations faites à partir de vols en hélicoptère à basse altitude sont actuellement utilisés pour classer l'habitat de nidification des Guillemots marbrés en Colombie-Britannique en fonction de sa qualité présumée. Cette approche repose sur la présomption que ce classement est corrélé à l'occupation des nids et à la productivité des guillemots. L'objectif de cette étude était de déterminer les meilleurs modèles pour prévoir l'habitat de nidification des guillemots dans la partie accessible au sol des deux régions étudiées. Nous avons élaboré des fonctions de sélection des ressources (FSR) au moyen de modèles de régression logistique, à partir de variables de peuplements forestiers récoltées au sol dans 64 parcelles contenant un nid (localisé par radiotélémetrie) et dans 82 parcelles tirées aléatoirement. Les valeurs prévues par les FSR sont proportionnelles à la probabilité d'occurrence d'un nid dans un îlot forestier. Les meilleurs modèles différaient légèrement entre les deux régions, mais

¹Simon Fraser University



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comprenaient des variables à l'échelle de l'îlot (0,2-2,0 ha), comme la densité des arbres contenant une plateforme, la hauteur et le diamètre des arbres, et la complexité du couvert forestier, et des variables à l'échelle du paysage, comme l'altitude, l'orientation et la pente. La collecte au sol des données de sélection du site de nidification n'est pas rentable dans un contexte d'aménagement forestier à grande échelle; la photointerprétation et les relevés faits à partir de vols à basse altitude sont des méthodes beaucoup plus efficaces pour classer la qualité de l'habitat à l'échelle du paysage. En conclusion, cette étude offre une méthode de validation au sol des méthodes à distance, étape essentielle réalisée au moyen des valeurs numériques générées par les FSR.

Key Words: *Brachyramphus marmoratus*; *habitat selection*; *Marbled Murrelet*; *nesting habitat*; *Resource Selection Functions*

INTRODUCTION

The Marbled Murrelet (*Brachyramphus marmoratus*) is a northeastern Pacific seabird that utilizes coastal old-growth forest between southeast Alaska and central California for nesting habitat (Nelson 1997, Burger 2002). The species is classified as "threatened" under the Species at Risk Act in Canada, and southern populations have similar status under the Endangered Species Act in the United States, recently reconfirmed (USFWS 2009).

Marbled Murrelet nests are extremely difficult to locate, therefore knowledge of nesting habits and habitat selection relies upon a relatively small sample of confirmed nest sites. Nests are established primarily on platforms created by moss or duff on large branches of old-growth conifers (Hamer and Nelson 1995, Nelson 1997). Nests must be sufficiently high enough in the tree to allow for stall landings and drop-off takeoffs, and ideally adjacent to forest canopy gaps (see reviews by Burger 2002, McShane et al. 2004, Piatt et al. 2007). In British Columbia, these structures occur in stands at least 140 years old, and with a higher probability of occurrence in stands > 200 years (Burger 2002). Nests occur at low densities (Conroy et al. 2002) over extensive tracts of often steep inaccessible terrain.

About 180 nests have been confirmed to date in British Columbia. Partly because of the difficulty of locating nests across a large landscape, land managers and conservation biologists in British Columbia have developed remote methods of habitat assessment, including GIS algorithms, air photo interpretation, and low-level aerial surveys

(Burger et al. 2009a). The attributes scored by these methods at the forest patch scale (~0.2 – 2.0 ha of similarly aged forest) rely on the scant ground data previously available from real nests, and audio-visual detections of behavior associated with nest sites ("occupied detection", Paton 1995), and modified with subsequent findings (Manley 1999, Chatwin 2002). These have been used to infer habitat associations, or selection, by comparing forest variables of occupied and unoccupied stands (Hamer 1995, Hamer and Nelson 1995 range-wide, Kuletz et al. 1995 for Alaska, Bahn and Newsom 2002a, Rodway and Regehr 2002 for Vancouver Island, Burger and Bahn 2004, Hamer et al. 2008 for Washington). Habitat quality inferences based on this method must be treated with some caution because actual nest sites are not identified and nest success is unknown. Occupied detections may include prospecting behavior, and be biased toward gaps or edges where detections are more likely (Burger et al. 2000, Rodway and Regehr 2002). However, Bahn and Newsom (2002b) compared nesting habitat indicators inferred from behavioral observations to mapped forest variables to create a habitat suitability model for Clayoquot Sound, which tested well against a sample of known nests from the same area (V. Bahn and D. B. Lank, *personal communication*). Manley (1999) used audio-visual detections and intensive ground surveys to locate a reasonably sized sample of real nests, and compared ground habitat variables at nest sites to those at random sites within the same patch.

Based on previous studies of habitat use (using occupied detections; Rodway and Regehr 2002, Hamer et al. 2008) and habitat selection and success at the patch level (using air photos; Waterhouse et al. 2004, 2008), five stand-level variables emerge

as indicators of Marbled Murrelet nesting habitat in British Columbia: mean diameter at breast height (DBH), density of canopy trees, density of potential platforms, density of trees with platforms, and canopy variation or complexity. At the landscape level, controlling for old-forest distributions, nests tend to be located at somewhat below average elevations (mean elevation at Desolation Sound: 748 m for nests, 840 m for old forest) on steeper slopes, and north aspects (Bradley 2002, Zharikov et al. 2006, 2007, Waterhouse et al. 2008). Waterhouse et al. (2008), in different analyses of the same data, found that nests at higher elevations and on steeper slopes had higher midfledging success. Landscape information can be easily obtained by remote methods, and habitat selection determined solely by landscape attributes is a tempting prospect for management.

Previous studies described differences in habitat between used and either nonused or random sites. Although this design allows for analysis of habitat selection (Jones 2001), quantitative models are needed to rank habitat based on probabilities of stand use, because presence is impractical to confirm for all possible areas. Because of the cost and logistics involved in accessing sites on the ground, we do not expect these methods to find widespread application. Rather, this study uses ground-based stand-level attributes from real nests and available sites to determine the relative importance of patch and landscape scales, and to provide a tool that may be used to help validate habitat suitability indices based on remote methods. We develop Resource Selection Functions (RSF; Manly et al. 2002) for ground-accessible landscapes in southern British Columbia. Our models are based on habitat characteristics measured on the ground at the largest sample of nest sites currently available for the species, comprising over 40% of the known nests in British Columbia, and comparing those to characteristics at random sites in the same regions, yielding probability of use for nesting at a site. The RSF scores we develop show how the probability of use changes with habitat variables, allowing us to answer the critical question of what murrelets select for in nesting habitat with greater certainty and detail than previous studies. For example, it is well established that forest stands utilized for nesting contain higher densities of platform trees than do random or unoccupied stands (Burger 2002). However, the shape of the relationship between platform density and probability of nesting has not been previously investigated because of lack

of data from ground plots. The contribution of variables may be nonlinear, producing ‘thresholds’ that may be used to refine existing habitat suitability rankings based on remote methods.

METHODS

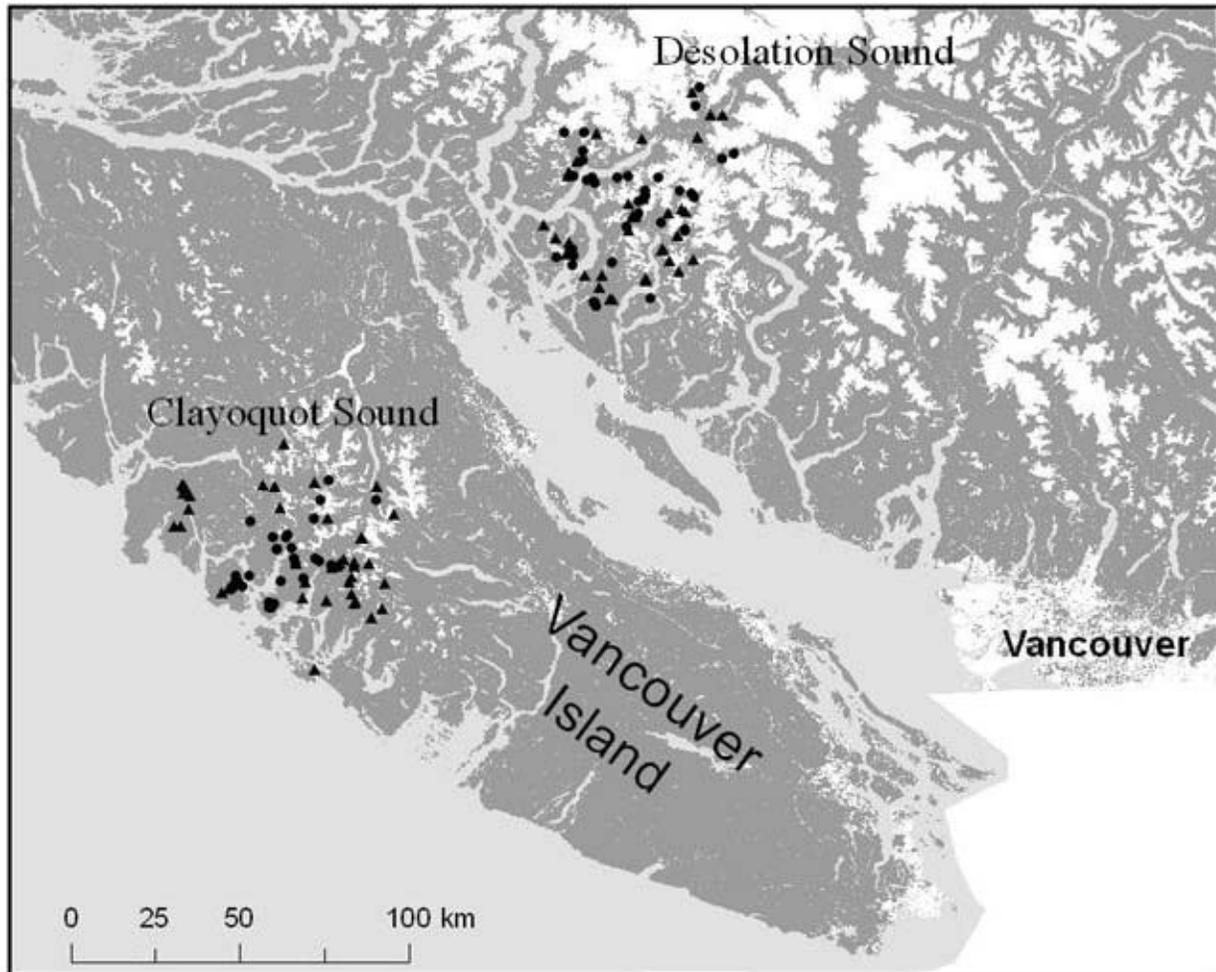
Study areas

We studied two regions on the southern coast of British Columbia, Canada, that support large populations of breeding Marbled Murrelets (Burger 2001, Hull et al. 2001): Clayoquot Sound (CS; 49° 12' N, 126°06' W) on the west coast of Vancouver Island and Desolation Sound (DS; 50°05' N, 124° 40' W) on the mainland (Fig. 1). Both regions are mountainous, with forest cover naturally fragmented by steep topography, fjords, and stream channels. Clayoquot Sound has a cooler and wetter maritime climate than DS, with mean summer (April-August) temperatures of 11.9° and 13.4° C, rainfall of 720 mm and 300 mm, respectively. The regions also differ in their extent of old-growth forest loss, with over 80% loss of original old-growth forest cover at DS, compared with ~25% loss at CS (Zharikov et al. 2006). As a result, remaining old-growth forest at DS is fragmented and tends to occur in small patches. Fifty percent of the DS sites in this study occurred in forest patches smaller than 100 ha; by contrast, all of the CS sites were in patches larger than 100 ha, and many were in large contiguous tracts of old-growth forest. In both regions, human settlement is limited and habitat loss is mainly due to commercial logging.

Data sources

Nest habitat data were collected by ground crews at plots surrounding nest sites located by radio telemetry (Bradley 2002, Zharikov et al. 2006) at DS (1999-2001; n = 43) and CS (2000-2002, n = 27). Many additional nests located (76 out of 121 at DS and 8 out of 36 at CS) were inaccessible because of steep terrain, geographic barriers, or lack of safe nearby helicopter landing spots. These sites could not be included in this study because ground habitat data were not available. Our results are thus most applicable to areas with comparable terrain, and should not be interpreted as reflecting ground conditions over the full range of nesting habitat used by murrelets in these regions.

Fig. 1. Map of study regions in south coastal British Columbia. Circles = nest sites; triangles = random sites.



Locations of random habitat plots were selected a priori within old-growth forest (>140 years) across the landscape defined by nest locations within each region (Zharikov et al. 2006). Ground crews sampled random plots using helicopter access, and as with nest sites, some preselected random plots were inaccessible.

At CS, additional ground plots were available from a separate dataset (Bahn and Newsom 2002a). Because these were not completely geographically randomized, we subsampled 19 sites stratified by valley location, with sample sizes selected such that

the distribution of all CS random plots for valley location was similar to the distribution of nests at CS.

Two methods of ground vegetation survey were used in this study. “RIC” protocol (Resource Inventory Standards Committee 2001) was used at all ground accessible nests as well as some random plots ($n = 11$ at DS). This method involves measuring stem diameter at breast height (DBH), tree height, potential nesting platforms, and mistletoe and epiphyte development in all trees (> 10 cm DBH) in a 25 m radius plot centered on the

nest tree or a random tree in a randomly located plot (30 m x 30 m for Bahn's additional CS plots). Tree height was measured by clinometer for a few widely-spaced reference trees in the plot, and estimated for others.

Most random plots were sampled at CS (2001) and DS (2004) following the "SFU" protocols (F. H. Huettmann, *unpublished manuscript*), which consisted of subsampling canopy trees within a 75 m radius of the center. Species, DBH, and height were recorded for a randomly selected center tree and its three nearest canopy trees, as well as any canopy trees found in 12 three-meter radius plots situated on four radial arms (two running along the slope contour from the center, and two perpendicular to the slope) at 25 m intervals. Trees with at least one potential platform, i.e., platform trees, were counted in a 25 m (CS; similar to RIC protocol) or 75 m radius (DS).

Variables

We considered a set of variables based on the results of previous habitat use studies and their availability throughout the dataset (Table 1). ASPECT was categorized as: "north" (N, including north, west, and flat aspects) or "south" (S, including south and east aspects). North and west aspects receive less direct sunlight and more rainfall, because prevailing weather systems are from the west, and would therefore be expected to have a positive effect on murrelet nesting habitat in terms of epiphyte development. Data on epiphyte development were available from nest sites, ranked in four categories (Resource Inventory Standards Committee 2001). Epiphyte categories did not differ among trees on north vs. west aspects (Pearson chi-square test: $\chi^2 = 2.49$, $df = 1$, $P = 0.12$), nor on south vs. east aspects ($\chi^2 = 0.31$, $df = 1$, $P = 0.58$). Significantly more trees with higher epiphyte cover occurred on north/west aspects compared with south/east ($\chi^2 = 11.47$, $df = 1$, $P < 0.01$). Flat sites ($n = 9$) were grouped with north aspects because they occurred on valley bottoms, which tend to be wetter and more shaded.

We obtained SLOPE from Digital Elevation Maps (Integrated Land Management Bureau 2000) using the mean of the 25 m x 25 m cell containing the site and its eight neighboring cells (Zharikov et al. 2006). Elevation was measured on the ground using GPS or altimeter.

We considered five ground-based patch-level variables in the model set (CANDBH, CANHT, CANCOMPL, DENCANSTEM, and DENPLATR; Table 1). Because only canopy trees were measured at random plots (SFU protocol), only these were represented in the first four variables. Previous studies (Bahn and Newsom 2002a, Rodway and Regehr 2002) found that canopy trees within the plot best predicted usage, and represent 94% of potential nesting trees in this dataset. In this study, canopy trees are the dominant and codominant trees in the patch. Potential nesting trees are reflected in the variable DENPLATR, the density of platform trees, including canopy and a small proportion of subcanopy trees. Because of differences in protocol, reliable data for this variable was not available for random plots at DS.

Comparison of protocols

Both SFU and RIC methods were used at a sample of 61 sites, to allow comparison. We assessed the comparability of variable values for CANDBH, CANHT, and DENCANSTEM, and DENPLATR. CANDBH, DENCANSTEM, and DENPLATR differed significantly (paired t-test; $P < 0.01$) between protocols. The mean difference for CANDBH (RIC-SFU mean -7 cm ± 1.9 SE), however, did not seem biologically significant compared to the range of 34-166 cm (mean 80 cm) and 34-142 cm (mean 87 cm) for RIC and SFU protocols, respectively. Though statistically significant, the authors were comfortable that a difference of 7 cm did not represent an important habitat difference, and was likely less than the field measurement error, considering the challenging terrain in which these measurements were taken. Differences for DENCANSTEM were large (RIC-SFU mean -29.5 trees/ha ± 9.0) and biologically significant. This variable was also correlated with CANDBH, and for these reasons was dropped from further consideration.

DENPLATR was significantly lower under SFU protocol (RIC-SFU mean: 28.8 platform trees/ha ± 3.7). We suspect this is because of the difference in plot sizes and the difficulty of viewing platforms in any trees within a 75 m radius. DENPLATR was therefore not included for analyses at DS, but was retained at CS.

A small number of trees were measured at some sites, particularly with SFU protocol. Subsampling

Table 1. Description of variables used for habitat selection modeling.

Variable Name	Description	Units of measurement	Scale
REGION	Desolation Sound or Clayoquot Sound	CS/DS	
ASPECT	Slope aspect (North=226°-45°; South=46°-225°)	N/S	Landscape
SLOPE	Slope, from Digital Elevation Model	° (Degrees)	Landscape
ELEVATION	Elevation (meters) measured on the ground	m	Landscape
CANDBH	Mean DBH (Diameter at Breast Height) of canopy trees	cm	Patch
CANHT	Mean height of canopy trees	m	Patch
CANCOMPL	Canopy complexity (standard deviation of CANHT)	m	Patch
DENCANSTEM	Density of canopy trees (all species)	# per hectare	Patch
DENPLATR	Density of platform trees (trees with at least one potential nest platform)	# per hectare	Patch

of the above mentioned sites showed that habitat measures for the plot were not significantly different when five or more trees were measured. For this reason we retained sites containing at least five canopy trees; those with fewer were excluded from our analyses.

Data analysis

We used logistic regression models with the binary response variable NEST (nest/random) to generate RSFs. We built a priori models with plausible combinations of measured habitat variables to predict probability of nesting, and used an information-theoretic approach to select the best model(s) among the alternative candidate set (Burnham and Anderson 2002).

The regions included in this study differ in both climate and degree of fragmentation, factors that may affect habitat selection by murrelets (Tranquilla et al. 2005, Zharikov et al. 2006, 2007). A combined model set including REGION and regional interaction terms (Table 2) strongly supported the hypothesis that relationships differed between regions (Table 3a). Given regional

interactions, we applied the model set 1-4 plus 9 and 10 to CS and DS separately, to develop more region-specific RSFs. This approach also permitted the use of DENPLATR as a variable in the CS model set (models 5-8).

To simplify the model set, we included or excluded landscape and patch-level variables as sets (Table 2). Support for landscape-level variables alone (Model 1) would suggest that patch-scale variables measured by ground-based observers are less important. Support for patch-level variables alone (Models 2, 5, 7, 9) would indicate selection at the forest patch level is most important. However, DENPLATR was included separately, for the CS region, because of its importance in previous studies (Manley 1999, Rodway and Regehr 2002). All combinations of these variable-groups were tested in the model set, as well as a null model (intercept only) that tests only the mean and variation inherent in the response variable. Support for the null model would indicate that variables other than those tested are responsible for variation observed. For combined regions, three additional models included a quadratic term for CANHT and CANCOMPL to reflect the hypothesis of a nonlinear relationship for these variables (models 9-11). The result is eight

Table 2. The model set used to predict probability of nesting based on ground habitat variables. Variables were grouped according to the scale involved.

Model	
1 ^{†,‡,§}	ASPECT + ELEV + SLOPE
2 ^{†,‡,§}	CANDBH + CANHT + CANCOMPL
3 ^{†,§}	CANDBH + CANHT + CANCOMPL + ASPECT + ELEV + SLOPE
4 ^{†,§}	(Null)
5 [‡]	DENPLATR
6 [‡]	DENPLATR + ASPECT + ELEV + SLOPE
7 [‡]	DENPLATR + CANDBH + CANHT + CANCOMPL
8 [‡]	DENPLATR + CANDBH + CANHT + CANCOMPL + ASPECT + ELEV + SLOPE
9 [†]	CANDBH + CANHT + CANCOMPL + CANHT ² + CANCOMPL ²
10 [†]	CANDBH + CANHT + CANCOMPL + CANHT ² + CANCOMPL ² + ASPECT + ELEV + SLOPE
11 [†]	REGION + ASPECT + ELEV + SLOPE + REGION*ASPECT REGION*ELEV REGION*SLOPE
12 [†]	REGION + CANDBH + CANHT + CANCOMPL + REGION*CANDBH REGION*CANHT + REGION*CANCOMPL
13 [†]	REGION + CANDBH + CANHT + CANCOMPL + REGION*CANDBH + REGION*CANHT + REGION*CANCOMPL + ASPECT + ELEV + SLOPE + REGION*ASPECT + REGION*ELEV + REGION*SLOPE
14 [†]	REGION + CANDBH + CANHT + CANCOMPL + CANHT ² + CANCOMPL ² + REGION*CANDBH + REGION*CANHT + REGION*CANCOMPL + REGION*CANHT ² + REGION*CANCOMPL ² + ASPECT + ELEV + SLOPE + REGION*ASPECT + REGION*ELEV + REGION*SLOPE
15 [†]	REGION + CANDBH + CANHT + CANCOMPL + CANHT ² + CANCOMPL ² + REGION*CANDBH + REGION*CANHT + REGION*CANCOMPL + REGION*CANHT ² + REGION*CANCOMPL ²

† Combined model set

‡ CS model set

§ DS model set

models applied to CS, four models applied to DS, and 11 models applied to the combined set.

We checked for multicollinearity using the Variable Inflation Factor (VIF) in PROC REG (SAS Institute Inc. 2003), whereby a value > 10 could indicate a problem (Neter et al. 1996). VIFs indicated little multicollinearity, with values < 3 for all variables in both CS and DS.

Sample sizes were relatively small (DS n = 72; CS n = 70), so we used Akaike's Information Criterion for small sample sizes (AIC_c). The global model for CS indicated over dispersion (c = 1.44, respectively), so the Quasi-Likelihood AIC (QAIC_c) was used for that model set (Burnham and Anderson 2002). We consider models in which AIC_c values differ from the best-fitting model by ≤ 2 (AIC_c; Burnham and Anderson 2002) as well as

Table 3. Ranking of the top four models for each region, with predictive performance of the top-ranked and averaged models. Models with significant support ($\Delta \leq 2$; Burnham and Anderson 2002) are in bold.

a) Combined								
Model #	K [†]	AIC _c [‡]	Δ^{\S}	$w_i^{ }$	R ^{2¶}	Predictive Performance [#]		
						> 0.5	> 0.65	> 0.8
13	14	173.43	0.00	0.89	0.42	75	52	27
12	8	179.55	6.03	0.04	0.28	-	-	-
9	6	180.10	6.67	0.03	0.24	-	-	-
b) Clayoquot Sound (CS)								
Model #	K [†]	QAIC _c ^{††}	Δ^{\S}	$w_i^{ }$	R ^{2¶}	Predictive Performance [#]		
						> 0.5	> 0.65	> 0.8
8	8	57.80	0.00	0.56	0.55	78	52	44
7	5	59.66	1.85	0.22	0.38	78	41	15
2	4	61.17	3.37	0.10	0.45	-	-	-
3	7	62.66	4.88	0.05	0.27	-	-	-
				Averaged Model		78	56	26
c) Desolation Sound (DS)								
Model #	K [†]	AIC _c [‡]	Δ^{\S}	$w_i^{ }$	R ^{2¶}	Predictive Performance [#]		
						> 0.5	> 0.65	> 0.8
3	7	92.98	0.00	0.54	0.36	78	54	27
2	4	93.38	0.40	0.44	0.25	65	43	16
1	4	100.62	2.19	0.01	0.36	-	-	-
4	1	101.81	8.83	0.01	-	-	-	-
				Averaged Model		78	49	13

[†] Number of parameters, including intercept.

[‡] Akaike's Information Criterion, corrected for small sample sizes.

[§] Increase in AIC over the best model.

[|] Akaike weight, the relative support for the model within the set.

[¶] Nagelkerke's R² (Nagelkerke 1991).

[#] For best and averaged models only; Predictive performance = % sites with RSF score > x.

^{††} Quasi-likelihood Akaike's Information Criteria, corrected for small sample sizes and over dispersion.

AIC_w , which indicated relative support for a model from among a set of candidate models.

Model and parameter performance and analysis

In region-specific model sets, multiple models received significant support from AIC_c . We therefore obtained parameter estimates through model averaging, in which each model contributes according to its Akaike weight (Burnham and Anderson 2002). Because we were most interested in model performance, we tested the performance of both AIC_c -selected models and averaged models in predicting nest sites. The same data set was used for testing because we did not have an independent data set with confirmed nest sites, nor was the original data set large enough to warrant setting aside data for testing. We report the proportion of nest sites that were assigned RSF scores > 0.5 , > 0.65 , and > 0.8 (where the RSF score represents probability of nesting).

To assess the effect of individual ground variables on probability of use, a set of simulated data points were created, wherein each continuous variable was varied at equal intervals across the feasible range for that variable, with all other variables held constant at their mean value for all random sites. Predicted probabilities of nesting and 95% confidence intervals were generated using the SCORE statement in PROC LOGISTIC (SAS Institute Inc. 2003) based on the model fit for the best model in each region. This produces a curve indicating the predicted probability of nesting throughout the range of the variable.

RESULTS

Ground habitat plots

Habitat selection models were created using 142 sites: 27 nest sites and 43 random sites at CS, and 37 nests and 35 random sites at DS. Sites at DS were located at elevations ranging from 5 to 1210 m, with more than 50% between 300 and 600 m. CS sites ranged from 0 to 1200 m, with most between 300

and 900 m. Slopes ranged from 3 to 58°. About 60% of both nest and random sites at CS were classified as “north” aspect compared with 76% of nests and 48% of random sites at DS.

The variables considered here differ with respect to nest/random sites, as well as between regions (Table 4). Of special note is the surprising result for canopy height at CS, where trees at random sites were taller than those at nest sites. This contrasts with the DS sample, as well as the results of numerous previous studies (summarized in Burger 2002).

In univariate logistic models, CANHT and CANCOMPL showed significant regional interactions (for both: Wald chi-square = 12.6, $df = 1$, $p < 0.01$). All other variables available for both regions did not have significant regional interactions.

Model selection

The best models predicting nesting habitat selection differed among the three model sets (Table 3). The combined regions model set includes quadratic expressions for canopy height and canopy complexity as well as regional interaction terms. Patch variables occur in two of the models, landscape in one, and the quadratic term in one of the models. Model 13, with landscape and patch variables as well as regional interaction received significant support with an AIC-weight (w_i) of 0.89.

For CS, models 8 and 7 were the best supported, with a cumulative w_i of 0.78. Model 8 is the global model, whereas model 7 excludes landscape variables. Patch variables appear in each of the top four models (Table 3b). There was very little support for model 1 ($\Delta AIC > 7$), which includes landscape-level factors only.

For DS, models 3 and 2 collectively account for 72% of the total w_i in the model set (Table 3c). These two models both include patch variables, with one model including landscape variables and the other not. Model 1 (landscape only) again receives very weak support ($\Delta AIC > 7$, $w_i = 0.01$).

Table 4. Mean and 95% confidence intervals for continuous variables included in models.

Variable	Region	Nest			Random		
		n	Mean	95%CI	n	Mean	95%CI
ELEV (m)	CS	27	501	378 – 625	43	536	449 – 624
	DS	37	430	359-501	35	512	388 – 635
SLOPE (°)	CS	27	30.8	25.4 – 36.4	43	23.0	19.4 – 26.6
	DS	37	29.5	25.4 – 33.6	35	26.1	21.6 – 30.6
CANDBH (cm)	CS	27	79.8	74.6 – 84.9	43	72.4	66.8 – 77.9
	DS	37	78.1	71.0 – 85.3	35	69.6	63.7 – 75.6
CANHT (m)	CS	27	33.4	31.1 – 35.7	43	37.6	35.2 – 40.0
	DS	37	36.7	35.2 – 38.2	35	33.0	30.9 – 35.0
CANCOMPL (m)	CS	27	4.9	3.9 - 5.8	43	6.0	5.3 – 6.6
	DS	37	6.9	6.2 – 7.7	35	5.0	4.3 – 5.8
DENPLATR (trees/ha)	CS	27	57.2	47.5 - 66.8	43	36.4	23.6 - 49.2
	DS	-	-	-	-	-	-

Model analysis

Because multiple models for each region received support from both AIC, we obtained parameter estimates through model averaging (Burnham and Anderson 2002). The resulting models had much lower predictive performance than any of the original models (Table 3) and were therefore not considered further.

The averaged model for each region model set performed nearly as well as the best performing models at the two lower thresholds, but scored less than 60% as many nests > 0.8 than did the original models. The averaged models also had larger 95% confidence intervals for parameter estimates. We use predictive performance, particularly at the highest threshold to distinguish the best predictive

model. Based on these criteria, we select as the top model the global models for each region: model 13 for both regions combined, model 8 at CS, and model 3 at DS.

Figure 2 indicates the effects of single variables on RSF scores. For patch variables, density of trees with platforms, available for CS only, shows a clear nonlinear trend, with the increase in probability of use slowing markedly at densities greater than 100 (Fig. 2a). This is equal to approximately 20 to 25 platform trees in a 25 m hectare plot. Although CANDBH shows a more or less positive trend with use in both regions, CANHT produces opposite trends at CS and DS. Probability of use decreases sharply in CS forests taller than about 40 m, whereas DS has a less positive trend. CANCOMPL shows a weakly negative trend at CS, a strong positive effect

at DS, and an increasing trend for the combined regions, with a slight dip at intermediate values due to the quadratic function.

Among the topographic variables, slope has a positive effect on probability of use in all three top models, with the strongest effect at CS. Probability of use decreases with elevation at CS, although it has a weakly positive relationship at DS.

DISCUSSION

Resource selection functions

This research is the first to create Resource Selection Functions (RSFs) based on ground habitat plots from known Marbled Murrelet nests. In southern British Columbia, models including both patch and landscape scale predictors were the best models. Model 1, containing only landscape-scale variables received minimal support in region-specific model sets, and had lower predictive performance compared with other top-ranked models for both regions combined, indicating that significant predictive ability is lost when habitat selection models do not include patch-scale variables.

The test of an RSF should be its predictive ability. Unfortunately, there were no suitable independent sets of known nest sites with habitat plots from the regions included in this study. One approach might have been to test models from DS against nests at CS (cf. Zharikov et al. 2007), but the limited size of our dataset and strong regional interactions precluded doing so. Instead, we tested the ability of the models to predict nest sites. If RSF scores are proportional to the probability of use, nest sites would typically have high RSF scores from a good predictive model. Random sites, which may have contained nests, are not diagnostic of model performance.

We considered a limited number of ecologically relevant models for this study to avoid an unacceptably large model set. Patch and landscape variables were considered as sets, although some of these variables may not be important in the final models. Excluding one of these variables within a group does not provide any advantage in terms of data acquisition for future applications of these models. Although ground variables are difficult to obtain, the high cost and logistics are involved in accessing the site; once there, the savings realized

by eliminating one or more of these variables would be negligible or nonexistent.

Accessibility bias

At DS, a larger proportion of all nests (~40%) found by radio-telemetry were inaccessible by ground compared with CS. Using landscape variables available for all nests, F. H. Huettmann, E. Cam, D. B. Lank, R. W. Bradley, L. Loughheed, N. Parker, L. McFarlane Tranquilla, C. Loughheed, Y. Zharikov, P. P.-W. Yen, and F. Cooke (*personal communication*) concluded that inaccessible sites tended to be on steeper slopes and at lower-mid elevations, which could create a bias in habitat selectivity studies based on ground accessible nests only. Accessibility was often based on factors outside the plot itself, such as steep terrain distance between the nearest access point and the plot.

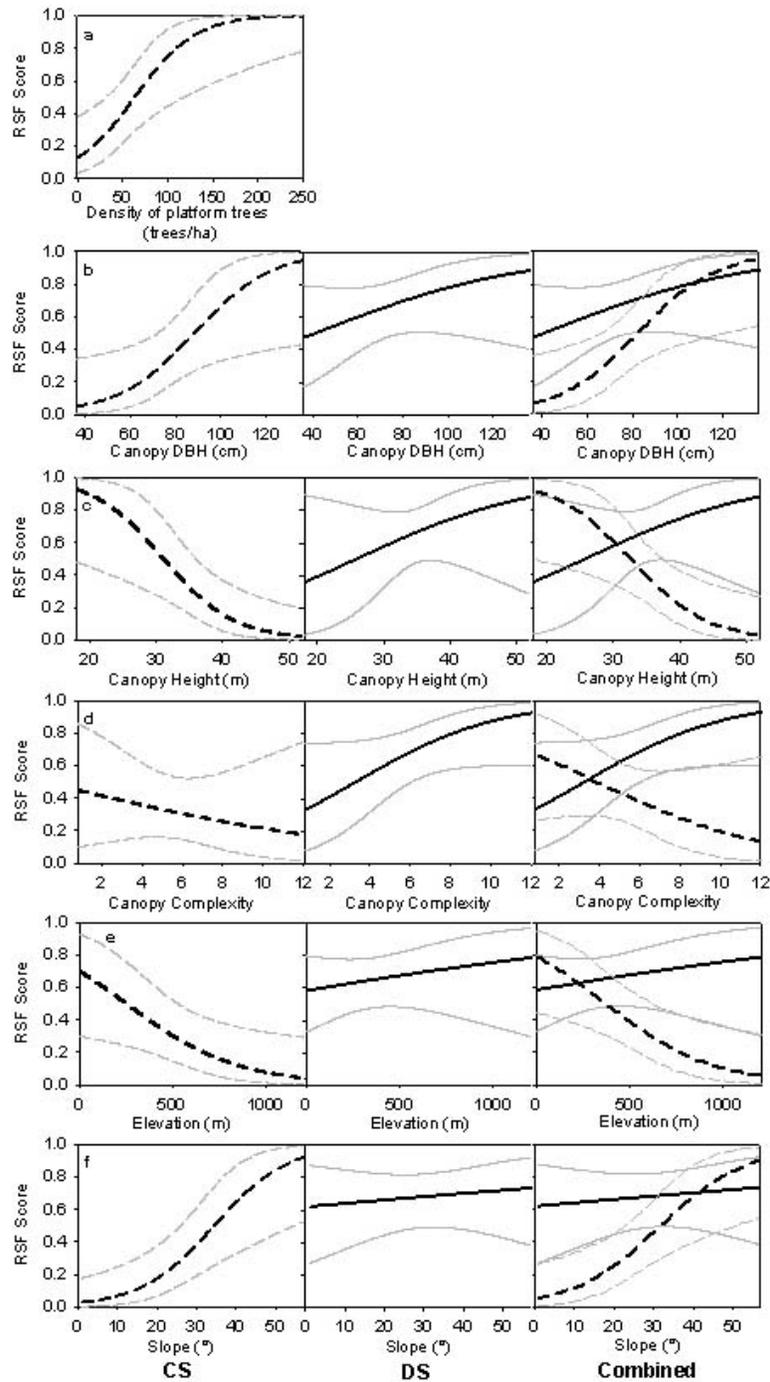
As stated earlier, our results apply to the portion of the landscape that is accessible on the ground. If the patch-scale variables measured here covary with geographic parameters that affect accessibility, our RSFs may not represent the entire local landscapes used by nesting Marbled Murrelets. However, the habitat where our models are directly applicable is representative of that most available for commercial logging, and therefore of most immediate conservation concern.

Comparison of regions

Significant differences exist between the two study areas considered here in terms of climate, logging history, and current habitat availability and fragmentation, as well as availability of platform density data for this study. Models including regional interactions received the strongest support, as expected, because CANHT and CANCOMPL had opposite effects at CS compared with DS. Thus, with respect to ground variables at least, regional modeling of habitat preferences will provide better predictability.

Each of the top models at CS included density of platform trees, a variable that was not available at DS. The next highest ranked models at CS that do not include density of platform trees are the top two models at DS (models 2 and 3). Density of platform trees is an important factor affecting murrelet nesting choices in CS. Unfortunately, the absence

Fig. 2. Plots of the Resource Selection Functions (RSF) Score (predicted probability of nesting) derived from the top model for each region, showing the effect of a single variable, with all other predictor variables held constant. a) density of platform trees b) DBH of canopy trees c) canopy height d) canopy complexity e) elevation f) slope. Grey lines indicate 95% confidence intervals; dashed lines = Clayoquot Sound (CS); solid lines = Desolation Sound (DS).



of similar data for DS prevents us from making inferences for that region. Differing degrees of harvest have resulted in smaller contiguous patches of old-growth forest at DS, which may affect habitat selection decisions with regard to platform density (Silvergieter 2009).

Model 13 for the combined data set is adequate at predicting nest sites in both regions, with 41% of nest sites at DS and 53% of nest sites at CS having an RSF score ≥ 0.7 (Fig. 3). For the region-specific models, 59% of nest sites at CS and 64% of those at DS had an RSF score higher than 0.7 (Fig. 3). The combined model, as expected, is not as good as region-specific models for describing habitat in those regions. The real benefit to a combined model would be in extending to other regions of the coast, an application that is limited by regional interactions. The highest ranked combined model that did not include regional interactions was model 3 ($AIC_w < 0.01$), that scored 27% of DS nests scored higher than 0.7, and only 15% of CS nests.

A single RSF thus does not describe habitat selection nearly as well as region-specific models. Previous studies at CS and DS that concentrated on a larger scale found differences in habitat selection between the two regions (Zharikov et al. 2006, Waterhouse et al. 2009). Specific to our data, opposing trends seen in canopy height and the omission of platform data may account for the difference, or it may be due to real differences in climate, forest harvest, or other features (Zharikov et al. 2006).

Previous habitat selection studies using this set of nests have failed to find strong selectivity at CS (Waterhouse et al. 2008) or had less predictive power (Waterhouse et al. 2009) than at DS. It has been inferred that most habitat available at CS is suitable for nesting and that consequently, murrelets there are less “choosy.” The random habitat plots used in this study suggest this is not the case. Platform trees, an essential component of nesting habitat, were absent in 10/43 (23%) of random sites at CS. There is also an apparent preference for shorter trees at CS, a finding contrary to previous research.

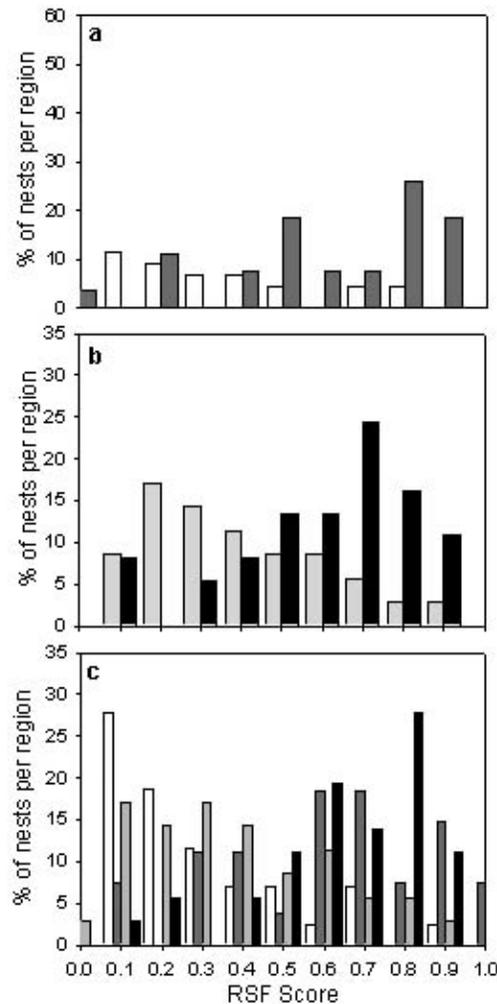
Density of platform trees

Figure 3 indicates that the relationship of DENPLATR to the probability of nesting is nonlinear. The probability of nesting levels off at the upper edge of the range of platform tree densities. This relationship is of particular interest for management because the forests with highest value for logging are also prime murrelet habitat, often characterized by the largest trees that tend to contain more platforms (W. Wall, D. Marquis, D. Lindsay, D. Byng, *personal communication*). A ranking of platform availability is a substantial component of current habitat ranks based on low-level aerial surveys. This curve is also biologically significant. A minimum of one platform tree is a fundamental requirement of any potential nesting habitat, but habitat use studies have consistently identified higher densities of platform trees as a characteristic of nest sites (Burger 2002). This is somewhat puzzling because murrelets are known to nest at low densities (Burger 2002, Conroy et al. 2002). Researchers have thus argued that higher densities of nesting platforms at the forest stand level are unlikely to support a proportionally higher density of nests (e.g., Burger and Waterhouse 2009). Our asymptotic curve is consistent with this argument for higher platform densities. At lower densities, multiple potential nest sites may increase the likelihood of finding a higher quality site, confer advantages by diluting predator search efficiency (“multiple nest site hypothesis”; Martin 1993, Chalfoun and Martin 2009), or allow reuse of the same high quality patch without reusing an old nest known to predators (Burger et al. 2009b). Despite these possibilities, although the sample size is not large, platform tree density did not correlate with measures of nesting success in this dataset (Silvergieter 2009).

Other variables

The diameter of canopy tree stems (CANDBH), although not likely to confer any direct advantage to nesting murrelets, is correlated with stand age (Bahn and Newsom 2002a). Older trees are more likely to develop larger and more abundant platforms, which may in turn affect nest success: nestlings and eggs are less likely to fall from larger platforms, and predator search efficiency may be

Fig. 3. A greater percentage of nest sites within each region have higher Resource Selection Functions (RSF) scores (predicted probability of nesting), compared with random sites for the best model for: a) Clayoquot Sound (random = white, nest = dark grey); (b) Desolation Sound (random = light grey, nest = black); and (c) Combined regions.



reduced with more potential nesting platforms (Martin 1993, Chalfoun and Martin 2009).

Canopy height appears to have opposite effects at DS and CS. At DS, overall canopy height of nest patches was taller than random patches, though the negative effect of this variable within the model was not significant. At CS, random patches were taller than nest patches; Figure 3 indicates a strong decline in probability of nesting canopy height at CS. Some random sites at CS had extraordinarily tall trees that were underrepresented at nest sites. The absolute

heights of trees utilized at CS are typical of those at DS and reported in previous work in the region (Manley 1999, Burger 2002). Canopy height does not appear to be a limiting factor within old-growth forests at CS; just 11% of random sites were shorter than the minimum height at nest patches. The quadratic term in the model for both regions results in a peak probability of nesting for forest patches around 30 m tall. A lower suitability of very tall forests has not been found in previous research, and should be viewed with caution. Studies consistently find that nest trees are among the tallest within a

patch (Manley 1999, Conroy et al. 2002, Silvergieter and Lank 2011).

Canopy complexity has been found to be an important indicator of habitat selection in previous studies (e.g., Waterhouse et al. 2002, Hamer et al. 2008) although methods of estimating the variable vary among studies. Canopy complexity in our study reflects overall complexity of a 25 m radius plot, and it did not have a consistently strong effect in any models and was not a significant factor in the CS and combined models. Complexity may be correlated with other factors not available in remote analyses, such as nest cover (Grenier and Nelson 1995, Hamer and Nelson 1995) and epiphyte growth (Bahn and Newsom 2002*b*). Canopy complexity may offer improved canopy accessibility (Hamer and Nelson 1995, Burger 2002), though overall complexity across the plot may not be strictly necessary because access is only needed for a nest in a single tree.

Overall, inference for landscape variables in this study should be taken in the context of the accessibility bias discussed above. Preference for steeper slopes may provide accessibility advantages and preferred nesting possibilities (Fig. 2f) although the strength of the effect differs between CS and DS. Using the complete dataset not limited by accessibility bias, Zharikov et al. (2006) found a preference for steeper slopes, and Bradley et al. (2004) noted that nest success was higher on steeper slopes. Results for elevation also differ between regions (Fig. 2e). These results reflect previously existing ambiguous results (see Burger 2002) with respect to these aspects of murrelet nesting habitat selection. Our models show that landscape variables in conjunction with ground variables are an important component of Marbled Murrelet habitat selection, but their specific contribution is perhaps better studied with other methods.

Management implications

The ground variables of significance in previous studies, based on inferred nest sites (Hamer 1995, Rodway and Regehr 2002) proved useful descriptors of nesting habitat in this study, providing support for their continued use in management applications. The shapes of relationships with particular variables, controlling for other factors, as shown in Figure 3, can be used to refine interpretations of these variables in habitat ranking

schemes. In our dataset, the best fitting habitat selection models differ between Clayoquot Sound and Desolation Sound, suggesting that region-specific models will have greater utility.

The models supported here apply directly to old-growth forests at Clayoquot Sound and Desolation Sound accessible to humans on the ground. Nonetheless, they provide predictions for habitat use across a spectrum of habitat conditions. The topographical stratum represented by this study corresponds to that most strongly impacted by conventional forestry operations, and thus the results should be most applicable to such areas of operational interest. Note, however, that nests in “inaccessible” areas may be affected in future with use of more expensive helicopter logging or other approaches.

Our results indicate that a multiscale approach to understanding nesting habitat selection by Marbled Murrelets is warranted. Though habitat information at the landscape scale is more easily obtained and models apply to larger areas regardless of accessibility, landscape-only models in this study received little support compared with models that incorporated patch scale variables measured on the ground. Acquiring ground habitat information is extremely costly. More efficient methods of assessing nesting habitat quality using air photo interpretation and low-level aerial surveys have been developed and tested (Waterhouse et al. 2002, 2004, 2008, 2009). These methods are part of current management guidelines in the province and are used to rank habitat on a six-point scale. One of the primary questions that remain regarding this system is the relative suitability of each category rank, particularly the two highest quality ranks (Burger and Waterhouse 2009). Ground-based habitat selection models can be used to validate these remote methods. For instance, relative numbers of potential nesting platforms, a key requirement of nesting habitat and an important component of RSF models at Clayoquot Sound, cannot be quantitatively measured by remote methods. This study assigns a relative probability of nesting for any site for which certain ground data are available, which can be compared with the habitat quality rank assigned to those sites by remote methods. A proper treatment of this comparison is outside the scope of this paper, but Silvergieter (2009) provides such a treatment using habitat selection models similar to those presented here.

Silvergieter (2009) also found that fledging success was independent of habitat selection described here. This simplifies management considerations because habitat selection, which is easier to measure than habitat productivity, should be a sufficient basis for decision making in terms of its relative impact on nesting murrelet productivity. Marbled Murrelets share a limited and commercially valuable landscape with logging interests in British Columbia. This study is a step toward improving land use decisions for conservation of murrelet nesting habitat.

Responses to this article can be read online at:
<http://www.ace-eco.org/vol6/iss2/art6/responses/>

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