APPLICATION OF RADAR SURVEYS IN THE MANAGEMENT OF NESTING HABITAT OF MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS*

ALAN E. BURGER[1], TRUDY A. CHATWIN[2], SEAN A. CULLEN[3], NORMAN P. HOLMES[4], IRENE A. MANLEY[5], MONICA H. MATHER[6], BERNARD K. SCHROEDER[7], J. DOUGLAS STEVENTON[8], JAMIE E. DUNCAN[9], PETER ARCESE[10] & ERVIN SELAK[10]

[1]*Department of Biology, University of Victoria, Victoria, British Columbia, V8W 3N5, Canada (aburger@uvic.ca)*
[2]*Ministry of Water, Land and Air Protection, Nanaimo, British Columbia, V9R 6R1, Canada*
[3]*Box 85, Roberts Creek, British Columbia, V0N 2W0, Canada*
[4]*P.O. Box 1234, Station A, Comox, British Columbia, V9N 7Z8, Canada*
[5]*RR 1 Site 4-C8, 5768 HaHa Creek Road, Wardner, British Columbia, V0B 2J0, Canada*
[6]*Box 497, Lantzville, British Columbia, V0R 2H0, Canada*
[7]*351 Howard Ave, Nanaimo, British Columbia, V9R 3R8, Canada*
[8]*Ministry of Forests, Bag 5000, Smithers, British Columbia, V0J 2N0, Canada*
[9]*Ministry of Sustainable Resource Management, Victoria, British Columbia, V8W 3E1, Canada*
[10] *Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada*

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SUMMARY

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We analysed counts of Marbled Murrelets *Brachyramphus marmoratus* made with radar in five independent studies at 101 watersheds in British Columbia, Canada, covering the northern, central and southern mainland and two areas on the west coast of Vancouver Island. Mean counts of murrelets totalled 18 129 birds (24%–33% of the estimated provincial population). We compared mean murrelet counts per watershed with habitat measures estimated from geographic information system (GIS) databases within the watersheds (total area > 2 million ha). Estimates of areas of apparently suitable habitat were derived from each original study, or by applying habitat algorithms recommended by the Canadian Marbled Murrelet Recovery Team, with (CMMRT-ELEV) or without (CMMRT-ALL) elevation constraints. General linear model analysis showed significant positive correlations between murrelet counts and areas of habitat, for all three habitat measures, in all five areas and for pooled data. The models consistently showed regional differences between the British Columbia Mainland and West Vancouver Island: murrelet densities were significantly higher in the latter region (respectively 0.045±0.039 and 0.090±0.060 birds per hectare of apparently suitable nesting habitat as defined by the CMMRT-ALL algorithm). Distance to likely foraging areas (estimated as the distance to the nearest open coastal water) was a significant covariate on the British Columbia Mainland, but not on West Vancouver Island. Our results give some confidence to the application of the CMMRT algorithms, but these algorithms and murrelet densities should be derived and applied separately for the British Columbia Mainland and West Vancouver Island.

Key words: *Brachyramphus marmoratus,* British Columbia, Marbled Murrelet, nest habitat, radar, wildlife management, geographic information system, GIS

INTRODUCTION

High-frequency marine radar has been successfully used to estimate and monitor local populations of Marbled Murrelets *Brachyramphus marmoratus* in diverse situations and is becoming a standard tool for these purposes across the species' range (Hamer *et al.* 1995; Burger 1997, 2001, 2002a; Cooper *et al.* 2001; Cooper & Blaha 2002). Radar is the method recommended for long-term monitoring of population changes and the effects of habitat changes in Canada [Canadian Marbled Murrelet Recovery Team (CMMRT) 2003].

Many of the advantages and limitations of radar as a census tool have been identified (Cooper & Hamer 2003). When positioned at the mouth of a watershed, radar provides a relatively consistent count of murrelets entering the watershed, especially if the birds are tracked over open water as they enter the forest. These counts can then be applied to analyse landscape-level associations between murrelets and available habitat. Two studies found significant positive correlations between the numbers of murrelets counted with radar and the areas of forested nesting habitat apparently available within the watersheds in Clayoquot Sound, British Columbia (Burger 2001), and on the Olympic Peninsula, Washington (Raphael *et al.* 2002). In addition, four other unpublished studies made in British Columbia showed similar patterns (Schroeder *et al.* 1999, Manley 2000, Cullen 2002, Steventon & Holmes 2002: summarized in Burger 2002b).

The purpose of this paper is to assess landscape-level habitat associations and densities across a wide geographic range by combining the data from the five studies completed in British Columbia. The information is valuable for management of the nesting habitat of Marbled Murrelets, which are listed as Threatened in Canada (CMMRT 2003).

A preliminary analysis using habitat data provided in the five study reports was made by Burger (2002b). That analysis was limited by the differences in habitat definitions used in the various studies. Despite more than a decade of intensive research, uncertainty still exists about how to reliably define and predict the forest habitat likely to be used by Marbled Murrelets within British Columbia (Burger 2002b, CMMRT 2003). The present paper expands the preliminary analysis by using consistent definitions of suitable habitat across the murrelet's range in British Columbia. We used the definitions of "most likely" and "moderately likely" nesting habitat of Marbled Murrelets in British Columbia as defined by the CMMRT (2003).

In general, Marbled Murrelets nest on large boughs providing nest platforms high in the canopies of mature (>140 years old) or old-growth (>250 years old) conifers (Ralph *et al.* 1995, Nelson 1997, Burger 2002b). Old conifers provide the height, canopy complexity, forest gaps, large boughs and epiphyte cover (generally mossy mats) apparently preferred by nesting murrelets. The species of conifers used vary with latitude, elevation and local biogeoclimatic conditions. In British Columbia, nesting by murrelets can be expected if the forests provide the structural components listed above; however, predicting the availability and extent of such forests from forest cover maps and geographic information system (GIS) data has proved difficult. Models and algorithms used to predict and map apparently suitable habitat have had only moderate success (Tripp 2001, Burger 2002b), hindering comparisons of radar counts with landscape-level habitat areas.

The specific goals of this paper are therefore:

- to examine the relationships between the numbers of Marbled Murrelets counted with radar at 101 watersheds and landscape-level habitat availability as defined by the CMMRT (2003)
- to compare the results with the patterns shown in these watersheds in the original study reports, using separate and somewhat different definitions of habitat
- to investigate regional differences in habitat associations and densities within British Columbia
- to discuss the value and limitations of comparing radar-based counts of murrelets with GIS-based habitat data.

METHODS

Study areas and sources of data

Five independent studies provided data. The number of stations in each subregion ranged from 18 to 25 (Table 1). The areas sampled in each study are called subregions here, to distinguish them from the larger conservation regions identified by the CMMRT (2003). On the northern mainland of British Columbia (hereafter North Coast), Steventon and Holmes (2002) did one to two surveys per station in one year (2001). On the central mainland (Central Coast), Schroeder *et al.* (1999) did one to two surveys per station in one year (1999). On the Sunshine Coast, southern mainland (South Coast), Cullen (2002) sampled watersheds in 2000 and 2001; most stations were sampled twice in both years. On the northwest coast of Vancouver Island (NW Vancouver Island), Manley (2000, unpubl. data) sampled watersheds in 1999 and 2001 (one to three surveys per station in each year). In Clayoquot Sound on the west coast of Vancouver Island, Burger (2001, 2002a) sampled watersheds over two to three years (1996–1998; usually two to three surveys per station in each season). Refer to each study for details of methods, station locations, definitions of habitat types, sources of habitat data and radar counts.

With the exception of three watersheds sampled by both North Coast and Central Coast studies, the areas sampled by each study did not overlap. Sample sizes in the present analysis differed slightly from those in the original studies because some watersheds were omitted or combined. The following stations included in the original study reports were omitted from the present analysis because the counts were made during prolonged rain (which masks birds on radar) or because the original authors, upon re-consideration, deemed the counts unreliable because the flight paths were too broad or ill-defined:

- North Coast: Chambers Creek
- Central Coast: Apple, Nekite and Walkum
- South Coast: Dakota and Rainy
- NW Vancouver Island: Sucwoa, Canton and Nuchalitz

Estimating the inland area in which Marbled Murrelets detected at a radar station are likely to be nesting (i.e. the catchment area) is difficult and obviously affects estimates of density (see "Discussion"). In the present analysis most of the catchment areas were those originally defined in the reports from each of the five studies. New information of flight paths and reconsideration of the topography led us to pool the data from some adjoining watersheds on NW Vancouver Island: Klashkish/East Creek, Artlish/Tashish, Amai/Kaouk and Tlupana/Nesook/Kleptee. In addition we corrected a few minor errors where secondary drainages had been inadvertently included or omitted in the original catchment areas.

Radar counts of Marbled Murrelets

The methods used in all five studies were similar. All used high-frequency X-band (9410 MHz) radar units with 2 m scanners mounted on shore-based platforms (Clayoquot Sound) or on a small vessel anchored close to the watershed mouth (all other studies). The radar unit used on the North Coast had a maximum output of 5-kW and the antenna was not tilted. The two units used in the other four studies were both 10-kW with antennas tilted upward by 12º: tests in Clayoquot Sound showed no significant differences in the counts made with these two units (Burger 2002a). Recent tests showed no significant differences in the abilities of 5-kW and 10-kW units to detect murrelets, but did show that in most situations tilted units were more likely to detect flying murrelets than non-tilted ones (Harper *et al.* 2004). Consequently, counts made with the non-tilted unit in the North Coast were likely to be underestimates, relative to the counts made in the four other studies (see also "Results").

In the present analysis we used the mean of the maximum annual counts of incoming (landward flying) murrelets recorded before sunrise at each station. Pre-sunrise counts of incoming murrelets generally provide the highest and least variable measure of murrelet numbers per watershed and also minimize multiple counts of murrelets making successive visits to nest sites (Burger 2001, 2002a). The North Coast surveys were treated differently because the sampling effort was less than in the other subregions, making

TABLE 1

Mean habitat parameters and murrelet densities from the five subregions sampled in British Columbia [a]

	North Coast	Central Coast	South Coast	NW Vancouver I.	Clayoquot Sound	Comparison among subregions (ANOVA)
Habitat measures [b]						
Watershed area (ha)	15 685±16 470 ab	34 847±32 442 a	38 983±46 978 a	9 458±9 052 b	7 927±5 449 b	F(4,96) = 5.62, *P* < 0.001
Area of Habitat2 per watershed (ha)	3 254±3 280 a	6 825±5 687 b	4 542±4 218 ab	3 822±3 121 ab	3 611±2 226 ab	F(4,96) = 2.81, *P* = 0.030
Habitat2 as % of watershed area	27.0±12.3 a	22.8±12.9 a	15.6±8.6 a	46.9±20.1 b	51.7±21.8 b	F(4,96) = 18.83, *P* < 0.001
Area of CMMRT-ALL habitat per watershed (ha)	1 935±2 187 a	6 531±4 321 b	3 930±3 755 ab	4 245±4 428 ab	4 247±3 176 ab	F(4,96) = 4.67, *P* = 0.002
CMMRT-ALL as % of watershed area	14.2±6.0 a	26.0±16.1 a	12.6±5.3 a	46.0±19.5 b	57.2±25.8 b	F(4,96) = 29.35, *P* < 0.001
Area of CMMRT-ELEV habitat per watershed (ha)	1 738±1 767 a	4 487±2 692 b	2 516±2 485 ab	4 073±4 246 ab	3 874±2 855 ab	F(4,96) = 3.67, *P* = 0.008
CMMRT-ELEV as % of watershed area	13.4±5.6 a	19.4±14.2 a	8.0±3.3 a	44.6±19.9 b	52.7±23.5 b	F(4,96) = 35.16, *P* < 0.001
Distance to inlet mouth (km)	34±17 a	37±30 a	40±25 a	10±6 b	6±6 b	F(4,96) = 12.30, *P* < 0.001
Distance to open sea (km)	78±38 a	66±35 a	61±22 a	18±9 b	18±8 b	F(4,96) = 21.86, *P* < 0.001
Murrelet counts and densities						
Total murrelet count	1826	3430	2421	5460	5194	
Density from Habitat2 (birds/ha)	0.027±0.017 a	0.046±0.059 a	0.035±0.029 a	0.088± 0.043 b	0.083±0.030 b	F(4,96) = 10.71, *P* < 0.001
Density from CMMRT-ALL habitat (birds/ha)	0.054±0.038 ab	0.031±0.026 a	0.046±0.047 a	0.090±0.054 b	0.091±0.068 b	F(4,96) = 6.25, *P* < 0.001
Density from CMMRT-ELEV habitat (birds/ha)	0.056±0.038 ab	0.045±0.041 a	0.071±0.069 ab	0.093±0.054 b	0.095±0.067 b	F(4,96) = 3.41, *P* = 0.012
Watersheds sampled (*n*)		25	21	19	18	18

[a] Subregions marked with the same letter (a, b, or c) had similar parameters; those with different letters were significantly different (ANOVA, with Tukey post-hoc test). Percentages were arcsine transformed before statistical analysis.

[b] The habitat measures were those from the original studies (Habitat2) and those defined by the Canadian Marbled Murrelet Recovery Team with (CMMRT-ELEV) or without (CMMRT-ALL) elevation restrictions. See "Methods."

that effort less likely to accurately capture maximum counts. Following Steventon and Holmes (2002), we used the maximum dawn count of either incoming or outgoing (seaward flying) murrelets for each North Coast station.

Habitat parameters

Original estimates of habitat

Each of the five studies independently estimated areas of habitat per watershed, using various algorithms applied to GIS databases. Here we include one of these categories (Habitat2 sensu: Burger 2002b) for comparison with more recent habitat data. Habitat2 was the algorithm found to be most likely to predict suitable nesting habitat in each study; it reflected measures being applied for management in each region (Burger 2002b:165). For NW Vancouver Island and Clayoquot Sound, the habitat was low-elevation mature (>140 years) and old-growth (>250 years) forest below 600 m (Manley 2000; Burger 2001, 2002a). For the South Coast, it was old forest (>250 years) with tree height class >19.5 m at all elevations (Cullen 2002). For the Central Coast the measure was mature and old-growth forest (as above) within tree height class >28.5 m at all elevations (Schroeder *et al.* 1999). For the North Coast a habitat suitability index was applied to weight the areas of forest in each age and size class (Steventon & Holmes 2002).

CMMRT habitat algorithm

The CMMRT habitat algorithm defined nesting habitat that fell within the categories Most Likely and Moderately Likely as defined by the CMMRT (2003). The habitat was defined as forest with these features: stand age class >140 years; tree height class ≥28.5 m; elevation restrictions (see below); and distance from the ocean 0.5–50 km. Most watersheds were within 30 km of the ocean and for the present analysis we restricted habitat to 0–30 km for all watersheds. We excluded forests within 0.5 km of the open sea because such areas apparently provide less suitable habitat for murrelets than those further inland (Burger 2002b). Elevation was identified as a key habitat element in British Columbia (CMMRT 2003), and we applied elevation in two models. The first model included all elevations (CMMRT-ALL) and the second (CMMRT-ELEV) applied the recovery team's recommendations for most likely habitat (elevation 0–900 m for Vancouver Island and 0–600 m for the British Columbia mainland; CMMRT 2003). The GIS coverage was insufficient to include stand index (a measure of timber productivity) and canopy crown closure, which were both identified as potentially important to murrelets in British Columbia (CMMRT 2003).

Estimates of the area that matched each habitat algorithm within the 101 watersheds sampled with radar were made using the GIS database maintained by the B.C. Ministry of Sustainable Resource Management in Victoria, B.C. That database was commissioned by the CMMRT and the provincial government for estimating and managing murrelet habitat across British Columbia. The database is derived from topographic, forest cover and biogeoclimatic mapping done by provincial ministries and local timber companies.

Habitat covariates

Two additional variables were included as covariates in our habitat models. Preliminary analysis indicated that the size of watersheds (irrespective of the amount of habitat they contained) might affect numbers of murrelets counted with radar (Burger 2001). Total watershed area was therefore considered a covariate. The distance that murrelets commute between nesting and foraging areas might affect their selection of nest sites (Whitworth *et al.* 2000, Hull *et al.* 2001). We did not know where all the murrelets counted with radar were likely to feed, but in general murrelets in British Columbia avoid foraging in deep inlets and fjords and are most often found in relatively shallow sheltered waters bordering the open sea (Burger 2002b). Consequently we considered two measures of likely commuting distance as covariates: distance from the radar station

TABLE 2
Mean habitat parameters and murrelet densities from the British Columbia Mainland and West Vancouver Island

	British Columbia Mainland [a]	West Vancouver Island	All areas pooled [a]	Comparison among regions (ANOVA)
Habitat measures				
Watershed area (ha)	29 159±34 849	8 828±7 514	21 690±29 684	F(1,96) = 11.88, $P < 0.001$
Area of Habitat2 per watershed (ha)	4 845±4 728	3 714±2 659	4 437±4 124	F(1,96) = 1.696, $P = 0.196$
Habitat2 as % of watershed area	22.5±12.5	49.4±20.8	32.2±20.5	F(1,96) = 61.22, $P < 0.001$
Area of CMMRT-ALL habitat per watershed (ha)	4 074±3 995	4 246±3 798	4 137±3 905	F(1,96) = 0.044, $P = 0.835$
CMMRT-ALL as % of watershed area	17.7±11.9	51.6±23.2	30.2±23.5	F(1,96) = 88.65, $P < 0.001$
Area of CMMRT-ELEV habitat per watershed (ha)	2 873±2 615	3 973±3 567	3 277±3 029	F(1,96) = 3.06, $P = 0.083$
CMMRT-ELEV as % of watershed area	13.8±10.1	48.7±21.8	26.6±22.8	F(1,96) = 116.50, $P < 0.001$
Distance to inlet mouth (km)	37.1±24.2	8.1±6.2	26.4±24.0	F(1,96) = 49.74, $P < 0.001$
Distance to open sea (km)	69.0±33.9	18.1±8.2	50.3±36.8	F(1,96) = 78.47, $P < 0.001$
Murrelet counts and densities				
Total murrelet count	7475	10654	18129	
Density from Habitat2 (birds/ha)	0.036±0.040	0.086±0.036	0.054±0.045	F(1,96) = 36.93, $P < 0.001$
Density from CMMRT-ALL habitat (birds/ha)	0.045±0.039	0.090±0.060	0.061±0.052	F(1,96) = 20.74, $P < 0.001$
Density from CMMRT-ELEV habitat (birds/ha)	0.058±0.051	0.094±0.060	0.071±0.057	F(1,96) = 10.06, $P = 0.001$
Watersheds sampled (n)		62	36	98

[a] Three North Coast watersheds that were also sampled in the Central Coast study were omitted from these pooled data (see text for details).

to the mouth of the inlet or fjord (Distance to Inlet Mouth) and distance from the radar station to the nearest open coastal water (Distance to Open Sea). Both were estimated as the minimum distances along waterways, assuming that murrelets flew over the sea between the radar stations and their foraging areas. These two distance variables were strongly correlated (Pearson r = 0.845, n = 101, P < 0.001) and we therefore used only Distance to Open Sea, which showed a slightly stronger effect on Marbled Murrelet counts, in our models.

Analysis

Models comparing radar counts of Marbled Murrelet (dependent variable) with habitat variables were tested using the general linear model (GLM) procedure in SPSS 11.5, with significance set at P < 0.05. The three habitat measures (Habitat2, CMMRT-ALL and CMMRT-ELEV) were tested separately, with and without including covariates (Total Watershed Area and Distance to Open Sea as defined above). In addition, because we found significant differences in several habitat parameters among the subregions, we also considered Location (British Columbia Mainland vs. West Vancouver Island; see "Results") as a fixed factor when using pooled data from all five studies. Each radar survey station and associated catchment area was treated as an independent sample. Fortuitously the five studies provided similar numbers of stations (18–25; Table 1), which simplified comparisons among them. Percentages were arcsine transformed (Zar 1996:282) before statistical analysis.

RESULTS

Murrelet counts and habitat areas

Data from 101 watersheds were used (Appendix 1, available at the *Marine Ornithology* Web site, http://www.marineornithology.org/). The sum of the mean murrelet counts in all watersheds was 18 129 birds, or 24%–33% of the estimated total population in British Columbia (55 000–78 000 birds; Burger 2002b). The catchment areas covered a total of 2 184 812 ha, of which 328 500–440 900 ha was considered suitable nesting habitat, depending on the algorithm used (Appendix 1).

Three watersheds were sampled by both the Central Coast (in 1999) and North Coast (in 2002) studies. The two studies provided identical maximum counts at the Aaltanhash station (38 birds in each study), but counts were higher in the Central Coast study at the Khutze (136 vs. 91 birds) and Green (201 vs. 73 birds) stations. The differences might have been due to the lack of tilting of the radar

TABLE 3
Results of general linear models[a] comparing the radar counts of Marbled Murrelets per watershed with habitat variables and covariables

Grouping of watersheds	Model: Habitat alone — Habitat measure	r^2	Habitat plus covariates[a] — Covariates selected	r^2
All British Columbia (98 watersheds)				
	Habitat2	0.157	Habitat2 Location Total watershed area	0.494
	CMMRT-ALL	0.265	CMMRT-ALL Location Total watershed area	0.531
	CMMRT-ELEV	0.410	CMMRT-ELEV Location	0.573
British Columbia mainlaind (62 watersheds)				
	Habitat2	0.244	Habitat2 Distance to open sea	0.385
	CMMRT-ALL	0.228	CMMRT-ALL Distance to open sea	0.352
	CMMRT-ELEV	0.254	CMMRT-ELEV Distance to open sea	0.357
West Vancouver Island (36 watersheds)				
	Habitat2	0.708	Habitat2 (no covariates selected)	0.715
	CMMRT-ALL	0.535	CMMRT-ALL (no covariates selected)	0.556
	CMMRT-ELEV	0.556 (no covariates selected)	CMMRT-ELEV	0.568

[a] Models were selected if P < 0.05

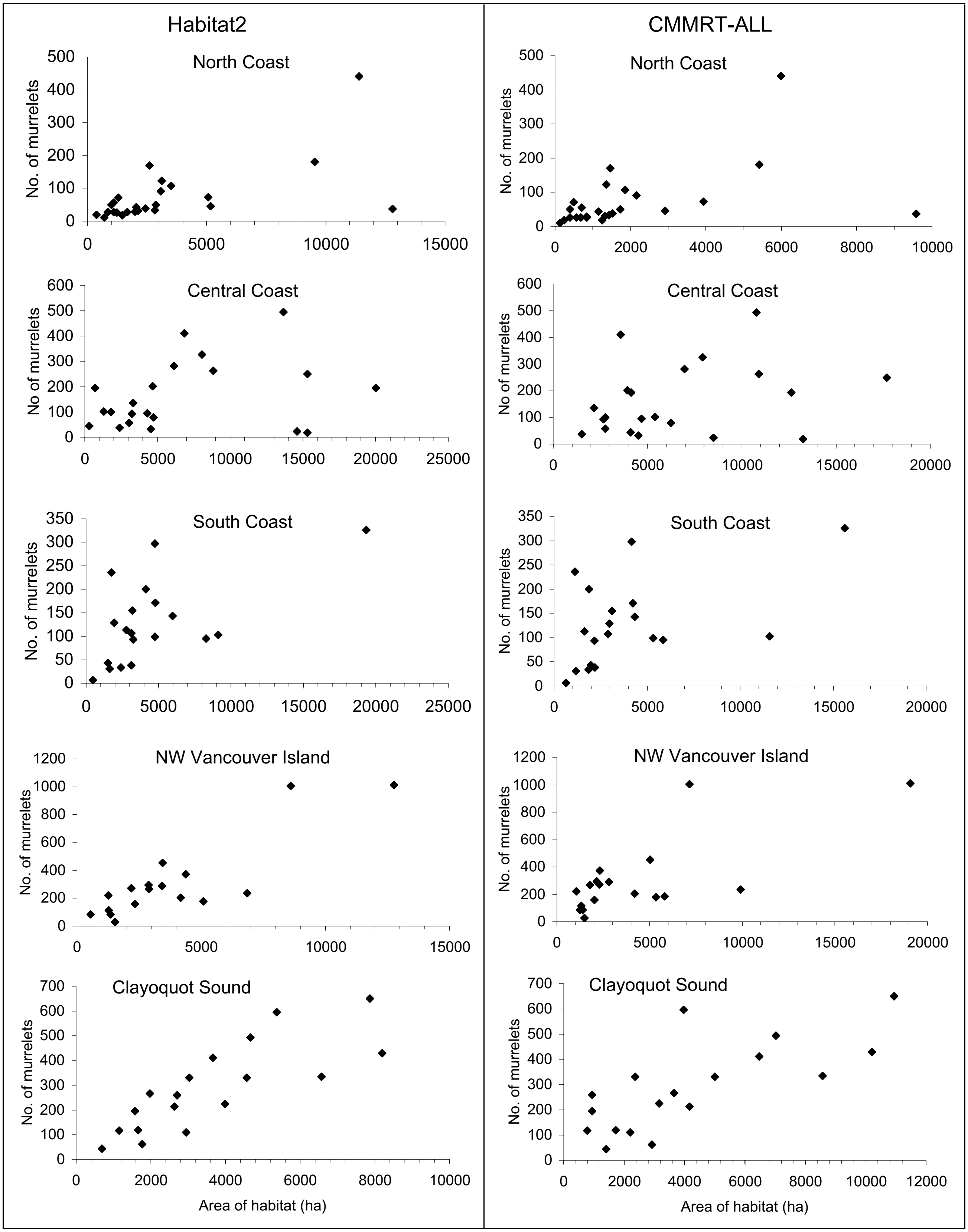

Fig. 1. Counts of Marbled Murrelets made with radar plotted against habitat area in five studies from British Columbia. Two habitat algorithms used to estimate the amounts of habitat are considered here: the original algorithms reported in each study (Habitat2, left column) and the habitat algorithm recommended by the Canadian Marbled Murrelet Recovery Team covering all elevations (CMMRT-ALL, right column). The third algorithm considered in this paper (CMMRT-ELEV) produced a similar scatter of points to CMMRT-ALL and is not shown here. Each point shows data from a single radar station and matching inland catchment area.

scanner in the North Coast study. The three North Coast data points were retained for the analysis within that subregion, but were omitted from the analysis for pooled data with other subregions.

Variations in habitat among subregions

Differences among the five subregions were found for most habitat parameters (Table 1). In general the subregions fell into two groups: West Vancouver Island (no significant differences between Clayoquot and NW Vancouver Island in any measures) and British Columbia Mainland (other three subregions, which were generally but not invariably similar to one another and usually different from the West Vancouver Island samples). Relative to the mainland, West Vancouver Island had smaller watersheds that were closer to likely foraging areas (distances to inlet mouths and open sea). For all three measures of habitat, watersheds on West Vancouver Island contained a significantly higher proportion of suitable habitat than the mainland watersheds, although the actual areas of habitat per watershed were similar. For subsequent analyses we pooled the data into two locations: British Columbia Mainland and West Vancouver Island (Table 2).

Landscape-level habitat associations

Comparison of the radar counts of Marbled Murrelets with the watershed habitat parameters revealed habitat associations at the scale of hundreds to ten thousands of hectares. Numbers of Marbled Murrelets per watershed were significantly correlated with the areas of habitat within the watersheds for all three measures of habitat (Table 3). Adding Total Watershed Area and Distance to Open Sea as covariates improved the predictability of the models for the pooled British Columbia data and for the British Columbia Mainland, but had a negligible effect for West Vancouver Island (Table 3). In all models the measures of habitat area had a far stronger effect on murrelet counts than the other covariates considered here. For the pooled British Columbia data, a significant effect of Location was seen (British Columbia Mainland differed from West Vancouver Island). Total watershed area was also selected in two of the three models, but that was likely because of the large differences in that measure between the two Locations (Table 2). Distance to Open Sea was selected in all three models for the British Columbia Mainland, but not for the pooled British Columbia data or for West Vancouver Island (Table 3).

When comparing the CMMRT habitat algorithms with (CMMRT-ELEV) and without (CMMRT-ALL) elevation constraints, we found little difference and no consistent trends in the strengths of association (as indicated by r^2 values) and in the covariates selected (Table 3). Those two habitat measures were strongly intercorrelated ($r = 0.94$, $n = 101$, $P < 0.001$) and in most watersheds very little apparently suitable habitat fell outside the elevation constraints considered here (compare areas of CMMRT-ALL and CMMRT-ELEV; Table 1, Appendix 1).

Plots of murrelet counts against areas of apparently suitable habitat showed considerable scatter, both within each study area (Fig. 1) and in larger pooled regions (Fig. 2). Count data were more scattered in the three British Columbia Mainland subregions than in

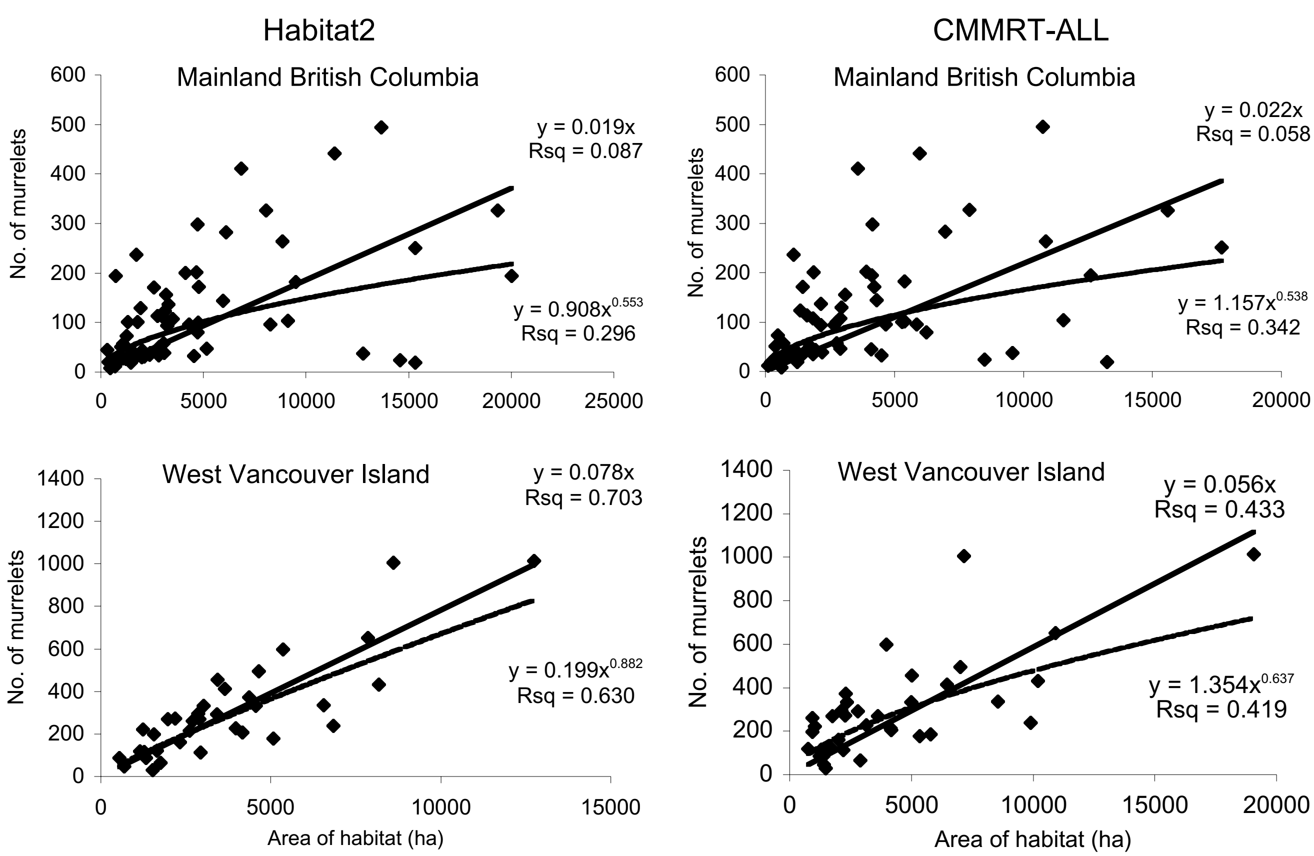

Fig. 2. Counts of Marbled Murrelets plotted against habitat area with data pooled into two regions: British Columbia Mainland and West Vancouver Island. Habitat types as in Figure 1. Each point shows data from a single radar station and matching inland catchment area. Linear regressions forced through the origin (solid lines) and power regressions (curved dotted lines) are plotted.

the West Vancouver Island samples. As shown by the GLM models (Table 3), some of this variability on the mainland was explained by Distance to Open Sea (used as a proxy for commuting distance). Three large mainland watersheds in particular (Kemano River on the North Coast and Kimsquit and Bella Coola on the Central Coast) provided relatively large areas of habitat, but had very low murrelet counts (mean values of 37, 18 and 23 birds, respectively). These three watersheds appear as obvious low outliers in Figs. 1 and 2: all three were at the heads of long inlets, a long way from expected foraging areas in open coastal sea (137 km, 142 km and 129 km, respectively). Another potential source of variability might be changes in habitat areas caused by clearcut logging not shown in older forest cover data in the GIS files.

Based on the preliminary analysis of these data (Burger 2002b), we compared linear with nonlinear regressions of the murrelet counts on habitat areas (Fig. 2). Linear equations (forced through the origin to more realistically deal with zero habitat) and power equations were the most consistent predictors of murrelet numbers. For Mainland British Columbia, power equations gave stronger correlations than linear equations did, but the reverse was true for West Vancouver Island. In general the linear and power equations produced very similar regression lines (Fig. 2). We did not explore the more complicated nonlinear models that might include habitat covariates.

Densities of murrelets

Densities of Marbled Murrelets (defined as birds per hectare of suitable habitat) varied significantly among the five subregions; the greatest differences were between the B.C. Mainland and West Vancouver Island (Table 2), with fewer differences within these groups (Table 1). Densities derived from the original habitat variables (Habitat2) were strikingly different from those derived from the CMMRT algorithms for the B.C. Mainland subregions, but less so for the two West Vancouver Island subregions (Table 1). Likewise, including elevation constraints in the CMMRT algorithm had marked effects on densities on the British Columbia Mainland but minor effects on West Vancouver Island (Tables 1 and 2).

DISCUSSION

Problems with estimating murrelet counts and catchment areas

Even in optimal locations, radar is unlikely to detect all incoming murrelets (Burger 1997, 2001, 2002a; Cooper *et al.* 2001; Cooper & Hamer 2003; Harper *et al.* 2004). All of our count data were therefore underestimates to some extent. We tried to minimize the effect by using the mean of the annual maximum counts for stations sampled more than once. The differences reported for two of the three stations sampled in both the North Coast and Central Coast studies might be attributed to the lack of tilting of the radar scanner in the former study, although the two studies reported identical maximum counts for the third station. The advantages of tilting the radar scanner to match the local flight paths of murrelets and increase the detectability of high-flying murrelets are discussed by Harper *et al.* (2004).

Determining the inland area in which Marbled Murrelets detected at a radar station are likely to be nesting (i.e. the catchment area) is difficult (Burger 2001, 2002a; Harper *et al.* 2004). In some situations murrelets might cross hills or mountain ridges, moving out of the immediate watershed where the radar station is located. Such movement would cause an underestimate of the catchment area and an overestimate of density (birds per hectare of habitat). Conversely, birds might enter the defined catchment area via flight paths not within the radar's radius. This problem occurs with open coastlines and low topography (Burger 1997, 2002a), but most of the sites sampled in the five studies had stations located at the heads of relatively narrow inlets, where the murrelets' flight paths were more constrained and likely to fall within the radar's radius.
Radar surveys undertaken by Harper *et al.* (2004 unpubl. data) indicate that some of the murrelets counted by Manley (2000, the present paper) on NW Vancouver Island were passing out of the catchment areas used here and probably nested in the central and eastern drainages of Vancouver Island. In particular, their surveys suggest that the very high counts made in the East and Klaskish valleys (mean of annual maximum counts: 1005 murrelets) included some birds that likely nested in the adjacent valleys to the east. The combined East/Klaskish watershed appears as a high outlier in some graphs (Figs. 1 and 2), suggesting that we underestimated the catchment area.

Although we acknowledge that our estimates of likely catchment areas are imperfect, we lack sufficient data on flight paths and likely nesting areas to be able to correct for situations where murrelets are crossing high ridges en route to adjacent valleys beyond the immediate drainage sampled with the radar. With the accumulation of additional radar count data and better understanding of the constraints upon commuting behaviour and nest site selection, we will be able to fine-tune our estimates of murrelet numbers, catchment habitat areas and densities.

Landscape-level habitat associations

Our analysis confirms the significant correlations between numbers of murrelets and areas of apparently suitable habitat in watersheds first reported by Burger (2001) and Raphael *et al.* (2002). Significant relationships were detected in each of the five studies considered in our analysis, whether using the original habitat parameters (e.g. Habitat2 reported here; see also other measures reported in the original studies) or the new algorithms recommended by the CMMRT (CMMRT-ALL and CMMRT-ELEV).

By themselves, habitat areas defined by CMMRT-ALL and CMMRT-ELEV within the catchment areas explained 27%–41% of the variability in murrelet counts in the 98 pooled samples from British Columbia (Table 3). Habitat areas explained a higher proportion of murrelet counts in the two West Vancouver Island subregions (54%–56%) than in the three British Columbia Mainland subregions (23%–25%). Inclusion of the covariate Distance to Open Sea with the habitat measures improved the British Columbia Mainland models (35%–36% of variation explained), but had negligible effects on West Vancouver Island.

The significant correlations between numbers of murrelets and areas of apparently suitable habitat estimated from the CMMRT algorithms in British Columbia provide support for the application of these algorithms for conservation and management as proposed by the recovery team (CMMRT 2003). The consistent and marked differences between the British Columbia Mainland and West Vancouver Island samples indicate that regional algorithms are more likely to succeed than those applied uniformly across the province. We have already identified commuting distance as a likely important factor for the highly indented mainland, whereas it appears to have negligible effect on West Vancouver Island (see also Burger 2001 for a similar conclusion for the Clayoquot Sound area). Other covariates are likely to emerge as important in the future (see below).

Our models represent preliminary attempts to incorporate a full range of habitat measures and covariables likely to affect the numbers of Marbled Murrelets using forested watersheds. As GIS information on forest cover, canopy structure, tree size and stand age improve, future models will undoubtedly provide stronger predictive power and give better insights into the factors affecting the numbers and distribution of nesting Marbled Murrelets. In particular, the effects of logging and fragmentation of nesting habitat need to be addressed.

Raphael *et al.* (2002) showed that radar counts of murrelets on the Olympic Peninsula, Washington, were significantly affected by proximity of habitat patches and amounts of edge at late-seral patches. Effects of fragmentation and proximity of habitat patches have been reported in other landscape-scale analyses of murrelet distributions (Raphael *et al.* 1995, Meyer & Miller 2002, Miller *et al.* 2002). Burger (2001) found that areas of clearcut and immature forest were significant negative covariates in multiple-regression models explaining radar counts of murrelets in Clayoquot Sound. We lacked complete coverage on clearcuts, immature forest, patch size and fragmentation for the wide range of watersheds covered in the present analysis, but should be able to include those factors in the future as GIS databases improve.

Better information on the likely flight paths and commuting distances of murrelets and the relative effects of marine (foraging) versus terrestrial (nesting) parameters will also lead to improved models. Estimates of murrelet numbers made with radar can also be improved with repeated sampling and careful consideration of the effects of weather.

Application of densities derived from radar counts

Densities derived from radar counts are estimated as birds per hectare of apparently suitable habitat in the catchment area. That method does not provide measures of nest densities (nests per hectare of habitat), because the radar counts include active breeders, failed breeders and non-breeding birds, all of which venture inland during the breeding season in variable proportions (Nelson 1997; Bradley *et al.* 2002, 2004). As a rough rule of thumb, there might be one nest for every three birds counted (taking into account non-breeders and having two breeders per nest). In British Columbia, population estimates and density calculations both use birds as the unit of population size, which avoids the problem of converting from birds to pairs or nests (CMMRT 2003).

Densities derived in this manner have great value in management and conservation. The approximate amount of nesting habitat required to support a known population of murrelets can be estimated. For example, populations of Marbled Murrelets to be maintained over the next 30 years have been proposed for each of the six conservation regions within British Columbia by the CMMRT (2003). Regional densities can be applied to estimate the areas of habitat needed in each region to meet the goals.

Conversely, the number of murrelets likely to be using a forested stand or landscape unit can be estimated from the area of habitat within such areas. For example, using the CMMRT-ELEV algorithm, it has been estimated that 399 200 ha of suitable habitat currently exist within protected areas (parks, ecological reserves, etc.) within the murrelets' British Columbia range (JED unpubl. data). Using the province-wide density derived from that algorithm (0.071 birds/ha; Table 2), we estimate that these protected areas support 28 343 birds, or 36%–52% of the estimated provincial population (Burger 2002b).

Reliable applications of density estimates depend on the consistency, accuracy and predictability of the algorithms used to define habitat. Given the regional and latitudinal variations in forest structure and habitat use (Ralph *et al.* 1995, Nelson 1997, Burger 2002b), the most reliable estimates will be obtained if both murrelet densities and areas of managed habitat are assessed using identical locally derived algorithms, ground-truthed for the landscape in which they are to be applied. Methods for testing algorithms and confirming habitat suitability using air photo interpretation (Donaldson 2004, Waterhouse *et al.* 2004) and rapid helicopter-borne field checks (Burger *et al.* 2004) are being refined in British Columbia.

CONCLUSIONS

Our analysis, covering 24%–33% of the estimated total population of Marbled Murrelets in British Columbia and 101 watersheds totalling over 2 million hectares, provides the most comprehensive application of radar counts for assessing habitat associations and densities for the species. Significant correlations between murrelet counts and estimates of suitable nesting habitat were found within each of the five sets of data, whether using the original habitat definitions provided by each study (Habitat2) or common algorithms recommended by the CCMRT (CMMRT-ALL and CMMRT-ELEV). The consistent correlations indicate that murrelet numbers are closely tied to available areas of breeding habitat—perhaps mediated in some regions by other factors, such as distance to foraging areas. These data suggest that reductions in the areas of suitable habitat by clearcut logging are likely to produce corresponding reductions in local breeding populations. No evidence exists that murrelets pack into reduced habitat patches in higher densities as habitat is lost from logging, but some evidence from Clayoquot Sound indicates that recently logged watersheds show reductions in murrelet numbers (Burger 2001). Repeated radar sampling at a widespread sample of watersheds, covering a range of timber extraction intensity could determine how murrelets respond to loss of nesting habitat (CMMRT 2003). Such information is crucial for the long-term management and conservation of this threatened species.

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