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Inland habitat associations of Marbled Murrelets on southwest Vancouver Island, British Columbia

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ABSTRACT. We used a combination of standardized audio-visual surveys, made over nine years, and vegetation analysis to determine habitat associations of Marbled Murrelets (*Brachyramphus marmoratus*) breeding in inland coniferous forests. Our study, in Carmanah-Walbran watersheds on southwestern Vancouver Island, British Columbia, covered extensive contiguous tracts (>16,000 ha) of apparently suitable habitat that supported a large breeding population of murrelets, a threatened species. Indicators of stand occupancy (circling and subcanopy flights) from audio-visual surveys were consistently associated with known nest habitat indicators (availability of platform limbs, cover and thickness of epiphytes on tree limbs, variable canopy structure). Both murrelet detections and nest microhabitat indicators were associated with a suite of macrohabitat variables, indicating that the most suitable habitat was low-elevation old-growth forest with widely spaced large trees. Biogeoclimatic productivity units, based on soil moisture and nutrient regimes, were useful proxies of habitat suitability, but tree species composition, timber volume, and tree height, variables commonly available in timber inventory maps, were not. Using two principle component factors derived from habitat characteristics, we clustered the 27 survey stations into three groups that differed significantly in occupied and subcanopy detections of murrelets and in nest habitat indicators. This is a useful method for combining multivariate measures for classifying and mapping habitat for murrelets.

SINOPSIS. **Asociación de habitats del interior por parte de individuos de *Brachyramphus marmoratus* en el suroeste de la isla de Vancouver, Columbia Británica**

Utilizamos una combinación de censos audiovisuales estandarizados a lo largo de 9 años de trabajo y de análisis de vegetación para determinar asociaciones de habitat e individuos de *Brachyramphus marmoratus* reproduciéndose en bosques de coniferos, del interior de Vancouver. El trabajo se llevó a cabo en la cuenca de Carmanah Walbran en el suroeste (de la isla antes mencionada) en Columbia Británica, y cubrió una área extensiva y continua (más de 16,000 ha) con habitat aparentemente adecuado para la especie en donde se encontró una población reproductiva del ave. Indicadores de áreas ocupadas (como vuelos en el subdocel) obtenidos de los censos audiovisuales estuvieron consistentemente asociados con indicadores de habitat (disponibilidad de ramas con plataformas, cubierta y grosos de epifitas en ramas, y estructuras del docel). Ambas, las detecciones de las aves e indicadores de microhabitat del nido resultaron estar asociados a una serie de variables del macrohabitat, lo que indcó que los habitats más adecuado son los bosques maduros de gran edad, con árboles espaciados y de baja elevación. Unidades de productividad biogeoclimática, basadas en la humedad del sustrato y régimen de nutriente fueron de gran utilizadad para determinar la adecuacidad del habitat. Sin embargo, la composición de especies de árboles, volumen de la madera, altura de los árboles (como variables comunmente disponibles en mapas de inventarios de bosques), no fueron de utilidad. Utilizando dos factores de componente principal derivados de las características del habitat, agrupamos las 27 estaciones examinadas en tres grupos que difirieron significativamente en la detección de lugares ocupados y de aves en el subdocel, como indicadores de habitat de anidamiento. Este es un método útil para combinar medidas multivariables para clasificar y trazar mapas de habitat utilizado por *B. marmoratus*.

Key words: *Brachyramphus marmoratus*, Marbled Murrelet, nesting habitat, Vancouver Island

Understanding the habitat requirements for an essential life-history phase, such as breeding, is a critical step in the conservation and management of threatened species. For Marbled Murrelets (*Brachyramphus marmoratus*), assessing nest habitat requirements is difficult because of the problems in locating a sufficient sample of nests. Throughout most of its range, this seabird nests high in large old-growth conifers and flies to and from nests in twilight (Ralph et al. 1995a; Nelson 1997). Relatively few nests have been found, and nest-habitat requirements are poorly known for most of its range (Hamer and Nelson 1995; Manley 1999; Burger 2002). This knowledge is urgently needed, because loss of nesting habitat from logging is the principal cause of this species' decline and the major threat facing existing populations (Ralph et al. 1995a).

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Locating nest sites using radio-telemetry is an effective method to identify nest habitat preferences of the Marbled Murrelet (Bradley and Cooke 2001; Bradley 2002), but the expense and logistics involved in this method have precluded its widespread application. Indirect measures of nesting activity, based on standardized audio-visual surveys, have become the primary protocol for identifying murrelet presence and stand occupancy (Ralph et al. 1994; Evans Mack et al. 2003), and, combined with measures of vegetation and topography, have been used to identify habitat use (Ralph et al. 1995b; Burger 2002).

We report on the relationships between audio-visual detections, direct measures of canopy microhabitat features known to be important to murrelets, and larger macrohabitat features suitable for mapping. Our goal was to identify the suite of characters likely to provide good nesting habitats at several spatial scales. In particular, we focused on characters useful for mapping suitable habitat at the landscape scale. Our results contribute to improving the identification and management of the nesting habitat of the murrelet.

The murrelet is listed as threatened in British Columbia, Oregon, and Washington, and as endangered in California (Nelson 1997). These jurisdictions have measures for preserving murrelet habitat, but the knowledge needed to identify and map suitable habitat remains incomplete. In British Columbia, where forest practices legislation permits logging of much of the existing habitat, identifying suitable habitat is especially critical to ensure that the type and areas of forest preserved are optimal for successful nesting. Although we focus on regional habitat requirements, our methods and results are applicable across the murrelet's range.

Our study was done in the Carmanah-Walbran watersheds on southwestern Vancouver Island. This area retains large contiguous tracts (>16,000 ha) of apparently ideal nesting habitat for murrelets, supports some of the highest known concentrations of murrelets, and is known to be used by nesting murrelets (Jordan and Hughes 1995; Manley and Kelson 1995; Burger 2002). By working in relatively undisturbed habitat, we hoped to avoid the bias associated with highly fragmented, logged areas, in which murrelets might often be forced to nest in suboptimal habitat. Studies in relatively undisturbed parts of a species range are more likely to reveal favored and productive habitats than studies in areas with greatly reduced habitat options (Caughley 1994).

METHODS

Study area. Our study area in the Carmanah Valley (6500 ha) and western Walbran Valley (9500 ha) included Carmanah-Walbran Provincial Park and a coastal strip of the Pacific Rim National Park (Fig. 1). The watersheds are in the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991). This zone contains most of the coastal old-growth forest in British Columbia, and supports a substantial portion of the Marbled Murrelet's breeding population (Burger 2002). In our study area the dominant trees were Sitka spruce (*Picea sitchensis*) (valley bottoms and coastal fringes), western hemlock (*Tsuga heterophylla*), western red-cedar (*Thuja plicata*) and amabilis (Pacific silver) fir (*Abies amabilis*). Many trees were 200–600 yr old and some dated >1000 yr old. Fires are rare, but blowdowns have created a few small patches of younger forests, which were not sampled in our study.

Survey methods. We recorded murrelet activities at 27 stations (Fig. 1) in 1991–1999 using fixed-station protocols (Ralph et al. 1994; RIC 1997). Survey stations were separated by >500 m and were treated as independent samples, because detections at the stations were unlikely to overlap. Stations were in creek beds or clearings in the forest to provide adequate views of the sky and enhance visual observations. Stations in creek beds were placed where creek noise was minimal. Observers sat semi-reclined on the ground looking up, to get the best view of the sky.

The 27 stations were sampled for an average of 4.8 yr (range 1–9 yr) and 20.8 surveys per station (range 3–79), for a total of 562 surveys. All surveys were made during the core of the breeding season when flight activities were high (mid-May through mid-July), and through most of the study we sampled each station three times per season, at 10–14 d intervals. Surveys began 60 min before sunrise and ended 60 min after sunrise, or 20 min after the last record of murrelet activity. No surveys were made in heavy rain. Data were recorded on tape recorders and transcribed to spreadsheets. Training of

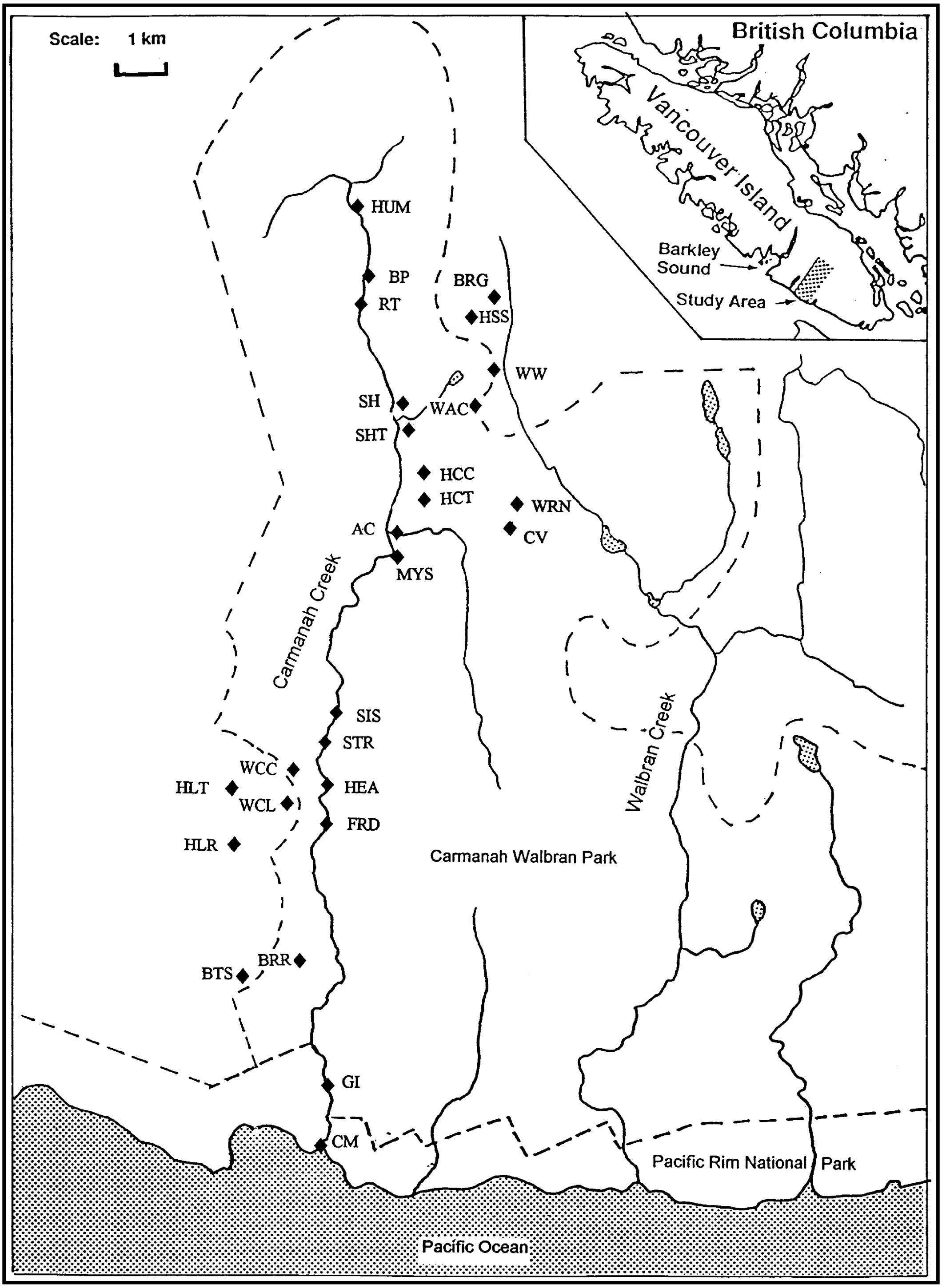

Fig. 1. Map of the study area in the Carmanah and Walbran valleys, southwest Vancouver Island, British Columbia, Canada. The diamond symbols show the locations of 27 stations used to survey activity of Marbled Murrelets and sample habitat plots.

observers in the recognition of flight patterns and vocalizations followed the accepted protocol (Ralph et al. 1994).

The unit of measurement for murrelet activity was the detection, defined as the sighting or hearing of one or more murrelets acting in a similar manner (Paton 1995). A subset of the detections, named occupied detections because they indicated near-nest behavior and stand occupancy (Paton 1995), included circling above or below the tree tops and all flights below the tree tops (subcanopy detections). Stationary calls, considered non-visual evidence of stand occupancy (Paton 1995), were negligible. Frequency of occupied detections per survey was used as an indicator of likely nesting activity, although the relationships between detections and numbers of birds, or number of nearby nests, are not known and are likely to be highly variable (Jodice and Collopy 2000; Jodice et al. 2001).

Average canopy closure (AVCC) was measured at each observation station from five overlapping photographs taken to cover the maximum area of sky. A 35-mm camera with a 28-mm wide-angle lens was mounted on a tripod at the observer's eye-level (60 cm above ground). One photo was taken vertically up, with the long axis of the picture parallel with the longest area of open sky. Four oblique photos were taken, each 15° below vertical and sequentially 90° horizontally displaced on the borders of the vertical photo. The photos were digitally scanned (Polaroid Sprintscan 35), and Optima 3.0 was used to estimate the percentage canopy cover in each image, with manual adjustment to separate vegetation and sky. The mean of the five images was used as the AVCC for each station.

Analysis of murrelet detections. Detections of Marbled Murrelets can be affected by date and weather (Rodway et al. 1993a,b; O'Donnell et al. 1995), although these factors sometimes explain little of the day-to-day variability (Jodice and Collopy 2000). Significant changes in the frequencies and chronology of detections have been found among years in Carmanah-Walbran (Burger 2000), and not all stations were sampled in every year. Preliminary analysis of our data showed that weather had less influence on detection rates than year and season, and that our sample sizes were insufficient to include year, season and weather as cofactors in ANOVA (Rodway and Regehr 2002). In order to generate multi-year measures of detection frequencies and minimize the effects of weather, season and year, we calculated indices of relative activity (IRA) for three sets of detections (total, occupied, and subcanopy). For each set we first calculated the mean rate of detections for each station during the core period in each season. Eleven stations, sampled annually for nine years (Burger 2000), were designated as primary stations, and their annual mean detection rates were used as a basis for comparison among all stations. The IRA was created for each station in each year by dividing the station's annual mean detection frequency by the mean for the 11 primary stations for that year. Thus, an index of 1 was equal to the mean of primary stations for that particular year, and values >1 and <1 were higher and lower than the primary mean, respectively. The IRAs for separate years were then averaged to produce an overall multi-year IRA for each station of total (IRATOT), occupied (IRAOCC), and subcanopy (IRASUB) detections. Treating stations rather than surveys as independent measures reduced sample size, but eliminated pseudoreplication and provided a more direct comparison with habitat characteristics.

Comparison of stations with and without evidence of occupancy is a common method of analysing audio-visual survey data (Ralph et al. 1995b). We did not include such analysis, because few stations showed no occupied detections (7/27), and several of these stations lacked the sample size needed to disprove occupancy (Evans Mack et al. 2003).

Habitat measures. We sampled habitat in 30 × 30 m quadrats. At creek-bed stations we sampled two quadrats, one on each side of the creek, and averaged the results. At all other stations we sampled a single quadrat placed along a random bearing from the station. To avoid edge ecotones, all quadrats were positioned >10 m from the edge of the opening used for the observation station. Within each quadrat we recorded the species, diameter at breast height (dbh), and height of each tree >10 cm dbh, and the number and dbh of large snags >5 m tall. Each tree height was estimated visually by 2–4 trained biologists, after using a clinometer to measure 2–4 representative trees in each plot. Canopy closure (percentage of projected canopy cover) was estimated by these biologists at 3–5 random points in the plot and then averaged. For each tree we recorded the number of potential nest platforms (limbs or deformities >15 m above ground and >18 cm in diameter, without assessing suitability as nest sites), scores for the estimated epiphyte cover on branches (moss, lichens and ferns, scored as 0, none; 1, trace; 2, 1–33% cover; 3, 34–66%; 4, 67–100%), epiphyte thickness on branches (0, absent; 1, sparse; 2, intermediate; 3, thick mats), and mistletoe infestation scored from 0 (absent) to 6 (heavy infestations) using the Hawksworth (1977) method. The mean of these measures was then calculated for each station.

Each quadrat was classified into stand-level biogeoclimatic categories (site series; Green and Klinka 1994), based on the topography, soil, vegetation physiognomy, and plant species composition. Our stations fell into five site series, within the CWHvm1 and CWHvh1 subzones. Variations among these site series were often subtle, and some of our stations had characteristics of two site series. Consequently we pooled the site series into productivity units, indicating expected growth rates of trees (Green and Klinka 1994:197). Our sites fell within the two highest of the four productivity units (classes I and II of Green and Klinka 1994; which we coded inversely as 2 [high] and 1 [moderate-high], respectively, to produce more intuitive correlations). Elevation, distance to the sea (measured along creek beds), and distance to the valley bottom were measured from 1: 20,000 topographic maps. Timber volume, estimated from aerial photographs and ground cruising, was obtained from industrial forest cover maps (Weyerhaeuser Ltd.).

Five micro-habitat measures, hereafter referred to as nest habitat indicators, were selected because they consistently occurred at murrelet nests at these latitudes (Hamer and Nelson 1995; Nelson 1997; Manley 1999), and appear to fill primary requirements for tree-nesting by murrelets (Burger 2002). These were vertical variability of the tree canopy structure allowing access for murrelets, which in our study was best measured by the SD of tree height (HGTSD); the availability of limbs providing potential nest platforms (platforms/ha; DENPLTF); the density of trees with two or more platforms (trees/ha; DENTR2PL); and the mean scores of epiphyte cover (EPILIVE) and epiphyte thickness (EPITHICK) on branches of living trees.

Data analysis. Codes and definitions of the variables used are given in Table 1. Statistical analysis was done using SPSS 10.0. The data on murrelet detections did not meet the requirements for parametric analysis (normally distributed and homoscedastic data), and neither logarithmic nor square-root transformations (Zar 1996) improved their normality. Accordingly we used nonparametric tests where possible. Some of the habitat data were not normally distributed, but were not transformed, for several reasons. Tests showed that transformations generally did not significantly alter any relationships or significance tests, but some of the biological and management value of the data were obscured by transformation. Transformation of independent (i.e., habitat) variables has less effect on least-squares regressions than transformations of the dependent (i.e., detection) variable (Zar 1996:346).

As a first step we looked for correlations among the five nest habitat indicators, the four measures of murrelet activity, and a range of habitat parameters, using Spearman rank correlation (Zar 1996). We also plotted these data to identify significant nonlinear relationships.

Because many of the habitat variables were intercorrelated, and in order to simplify the habitat measures for cluster analysis, we performed a principal component analysis (PCA). Principal components were included if eigenvalues were >1, and a scree plot was used to identify break-points separating the most important components from the rest. Cluster analysis was performed using Ward's method and squared Euclidean distance applied to the principal components. This produced clusters of stations with similar habitat characteristics. The value of such clustering was then tested by comparing measures of murrelet detections and the five nest habitat indicators among the clusters, using Kruskal-Wallace ANOVA and the Tukey posthoc test.

RESULTS

Nest habitat indicators compared with other habitat measures. The five indicators of nest habitat (HGTSD, DENPLTF, DENTR2PL, EPILIVE, and EPITHICK) were all significantly intercorrelated ($r_s > 0.40$, $N =$

Table 1. Codes and definitions of variables used to analyse habitat preferences of Marbled Murrelets.

Variable	Description
Measures of murrelet activity	
IRADET	Index of relative activity for all audio-visual detections
IRAOCC	Index of relative activity for occupied detections
IRASUB	Index of relative activity for subcanopy detections
Topographic variables	
DSEA	Distance to the ocean (km)
ELEV	Elevation in m above sea height (m)
Stand/tree variables	
AVCC	Mean canopy closure at observation site (percentage), from five photographs
CCPLOT	Mean canopy closure within the vegetation plot
DBHMN	Mean diameter of trees measured at breast height (dbh) in cm
DBHSD	Standard deviation of dbh (cm)
DENLARGE	Density of trees with dbh > 80 cm (trees per ha)
DENLIVE	Density of living trees with dbh > 10 cm (trees per ha)
DENSNAG	Density of snags per ha
HGTMN	Mean height of all trees (m)
HGTSD[a]	Standard deviation of tree height, indicating variable canopy structure (m)
PROD	Productivity unit drawn from site series according to Green and Klinka (1995)
TIMVOL	Timber volume from forest cover maps (m^3 per ha)
Species composition	
DENBA	Density of amabilis fir (trees per ha)
DENCW	Density of western red-cedar (trees per ha)
DENHW	Density of western hemlock (trees per ha)
DENSS	Density of Sitka spruce (trees per ha)
Microhabitat	
DENPLTF[a]	Density of potential platform limbs per ha
DENTR2PL[a]	Density of tress with two or more potential platform limbs (trees per ha)
EPILIVE[a]	Mean index of epiphyte cover on live trees
EPITHICK[a]	Mean index of epiphyte thickness
MISTLE	Mean mistletoe or other deformity score

[a] This measure also used as nest habitat indicator (see text).

27, $P < 0.05$, in each case), confirming their association with similar conditions within the tree canopy. All five nest habitat indicators were positively correlated with the density of Sitka spruce ($r_s > 0.40$, $N = 27$, $P < 0.05$, in each case), but negatively correlated with western red-cedar ($r_s > 0.52$, $N = 27$, $P < 0.01$, in each case). Measures of platform density (DENPLTF, DENTR2PL) were positively correlated with the density of large trees ($r_s = 0.43$ and $r_s = 0.49$, respectively; $N = 27$, $P < 0.05$ in each case). Epiphyte thickness was negatively correlated with canopy closure at the observation station ($r_s = -0.52$, $N = 25$, $P < 0.01$) and elevation ($r_s = -0.49$, $N = 27$, $P < 0.01$), but positively correlated with the mean dbh of trees ($r_s = 0.41$, $N = 27$, $P < 0.05$). All five nest habitat indicators, plus the density of western red-cedars and large trees, and distance from the sea, differed significantly when the stations were grouped into two biogeoclimatic productivity units (Table 2).

Comparison of murrelet detections with habitat measures. Occupied (IRAOCC) and subcanopy (IRASUB) detections differed significantly when grouped by biogeoclimatic productivity, but total detections (IRADET) did not (Table 2). Similarly, IRAOCC and IRASUB were positively correlated with all the nest habitat indicators except epiphyte cover, but IRADET was not (Table 3). IRAOCC and IRASUB showed positive correlations with the densities of large trees and Sitka spruce, but negative correlations with elevation. IRASUB

Table 2. Comparisons of Marbled Murrelet detection rates and values for nest habitat indicators between the two units of vegetation productivity. None of our stations was in low productivity vegetation.

	Productivity		Mann-Whitney test	
Variable	1 (Moderate-High)	2 (High)	*Z*	*P*
Marbled Murrelet detections				
IRADET	0.92 ± 0.49	0.97 ± 0.33	0.395	0.693
IRAOCC	0.30 ± 0.44	1.10 ± 1.21	2.439	0.015
IRASUB	0.09 ± 0.14	0.84 ± 0.73	3.218	0.001
Nest habitat indicators				
DENPLTF	160 ± 155	1418 ± 1006	3.208	0.001
DENTR2PL	29.8 ± 21.4	111.5 ± 63.1	3.247	0.001
EPILIVE	2.08 ± 0.85	2.89 ± 0.48	2.615	0.009
EPITHICK	1.40 ± 0.52	1.82 ± 0.43	2.122	0.034
HGTSD	13.0 ± 2.5	16.9 ± 2.8	3.158	0.002
Other habitat variables[a]				
DENCW	85.4 ± 99.9	13.2 ± 28.0	2.197	0.028
DENLARGE	69.2 ± 34.4	97.2 ± 29.6	2.279	0.023
DSEA	7.3 ± 4.5	12.7 ± 5.2	2.789	0.005
Number of stations	11	16		

[a] Only macrohabitat variables differing significantly between the productivity categories are shown. All other variables showed no significant differences ($P > 0.05$).

was positively correlated with mistletoe index and negatively correlated with densities of western red-cedar.

All measures of murrelet detections were negatively correlated with canopy closure at the observation site, AVCC (Table 3). This indicates a possible bias towards underestimating occupied detections, which were visual, at stations with small openings. Such conditions were typical of stations on slope forests, where there were no streamside gravel bars to provide large openings. Dealing with this potential bias is difficult because many habitat variables potentially important for murrelets were also highly correlated with canopy closure, and so controlling for canopy closure might in turn mask meaningful habitat relationships. With AVCC controlled, the correlations between murrelet detections and epiphyte thickness, density of Sitka spruce, elevation (except occupied detections), and density of large trees were no longer significant, whereas correlations with SD of dbh, densities of amabilis fir and western hemlock, and mean height became significant for some measures of detections (Table 3).

Most significant relationships were well described by linear correlations, although there was often wide scattering of data points (Fig. 2). The relationships between occupied detections (IRAOCC) and the availability of potential platforms (DENPLT and DENTR2PL) were, however, best described by a logistic step-function indicating a threshold in platform availability, below which there was little or no occupied activity, and above which occupied activity was relatively unaffected (Fig. 2). The Carmanah Giant site (GI) was an outlier, having unusually high levels of occupied detections.

PCA and grouping of stations using habitat variables. PCA was used to classify the stations and compare inter-related habitat variables collectively rather than individually. The first two principal components explained 48% of the variation in the overall matrix and were used for the next phase of analysis (Table 4). The first component characterised large, variable, widely-spaced, valley-bottom trees, and had high positive loadings from the mean and SD of tree diameter, SD of tree height, epiphyte cover and thickness, and density of Sitka spruce, and negative loadings from tree density and elevation. The second component had positive loadings from density of potential platforms, vegetation productivity, and density of amabilis fir.

Comparisons of stations grouped into habitat units. The first two PCA compo-

Table 3. Correlations between measures of Marbled Murrelet activity and habitat variables.

	Measures of murrelet activity					
	Uncontrolled ($N = 27$; Spearman correlation)			Controlled for AVCC ($N = 25$; partial correlation)		
Variables	IRADET	IRAOCC	IRASUB	IRADET	IRAOCC	IRASUB
Nest site indicators						
DENPLTF	0.099	0.573**	0.742**	−0.068	0.250	0.596**
DENTR2PL	0.149	0.527**	0.717**	−0.048	0.103	0.592**
EPILIVE	0.149	0.361	0.366	0.077	0.391	0.173
EPITHICK	0.145	0.579*	0.521**	−0.086	0.366	0.169
HGTSD	−0.015	0.495**	0.577**	−0.044	0.752**	0.419*
Other habitat variables						
AVCC	−0.428*	−0.676**	−0.571*			
CCPLOT	−0.341	−0.350	−0.265	−0.150	−0.120	−0.082
DBHMN	−0.040	0.199	0.116	−0.021	0.607**	−0.006
DBHSD	0.134	0.347	0.308	0.017	0.624**	0.127
DENBA	0.047	0.191	0.330	0.097	0.091	0.449*
DENCW	−0.046	−0.360	−0.446*	0.079	−0.249	−0.350
DENHW	−0.144	−0.292	−0.280	−0.203	−0.456*	−0.311
DENLARGE	0.182	0.405*	0.483*	0.215	0.171	0.357
DENLIV	−0.074	−0.057	−0.029	−0.093	−0.515*	−0.007
DENSNAG	−0.057	−0.067	0.025	0.098	−0.060	0.334
DENSS	0.342	0.574**	0.527**	0.150	0.227	0.326
DSEA	−0.128	−0.050	0.208	−0.121	−0.293	0.190
ELEV	−0.525**	−0.794**	−0.648**	−0.373	−0.474*	−0.336
HGTMN	−0.128	0.068	−0.046	−0.101	0.477*	−0.088
MISTLE	−0.093	0.218	0.439*	−0.157	−0.228	0.118
PROD	0.077	0.478*	0.631**	−0.036	0.330	0.529**
TIMVOL	0.096	−0.240	−0.101	0.095	−0.160	−0.090

* $P < 0.05$
** $P < 0.01$

nents were used to cluster the 27 stations, producing three clearly defined clusters (labelled 1 to 3 in Fig. 3): the first cluster included seven valley bottom stations in the lower Carmanah drainage (CM, FRD, GI, HEA, MYS, SIS and STR; Fig. 1); the second included valley-bottom stations in the mid- to upper-drainages (AC, BP, RT, SH, HUM, BRG and WW) plus a few nearby slope stations (SHT, WAC, HSS and WRN); and the third cluster included the remaining stations on slopes. The indices of murrelet activity (except IRADET) and values of nest habitat indicators differed significantly among the three groups (Table 5). Posthoc tests showed that the valley-bottom lower-drainage group (group 1) differed significantly in all measures (except IRADET) from the slope stations (group 3). The mixed valley-bottom/slope upper-drainage stations (group 2) were intermediate in all measures and sometimes differed significantly from groups 1 and 3.

DISCUSSION

Application and limitation of audio-visual detections. Audio-visual detections made during dawn surveys are widely used to assess occupancy, relative abundance, and habitat associations of Marbled Murrelets in inland nesting habitat (Ralph et al. 1995b; Nelson and Sealy 1995; Bahn 1998; Bahn and Newsom 2002; Rodway and Regehr 2002). Limitations in the application of audio-visual data for these purposes have been identified (Rodway et al. 1993a,b; Jodice and Collopy 2000; Jodice et al. 2001; O'Donnell et al. 1995; Rodway and Regehr 2000, 2002; Evans Mack et al. 2003), and our study contributes to the refinement of this

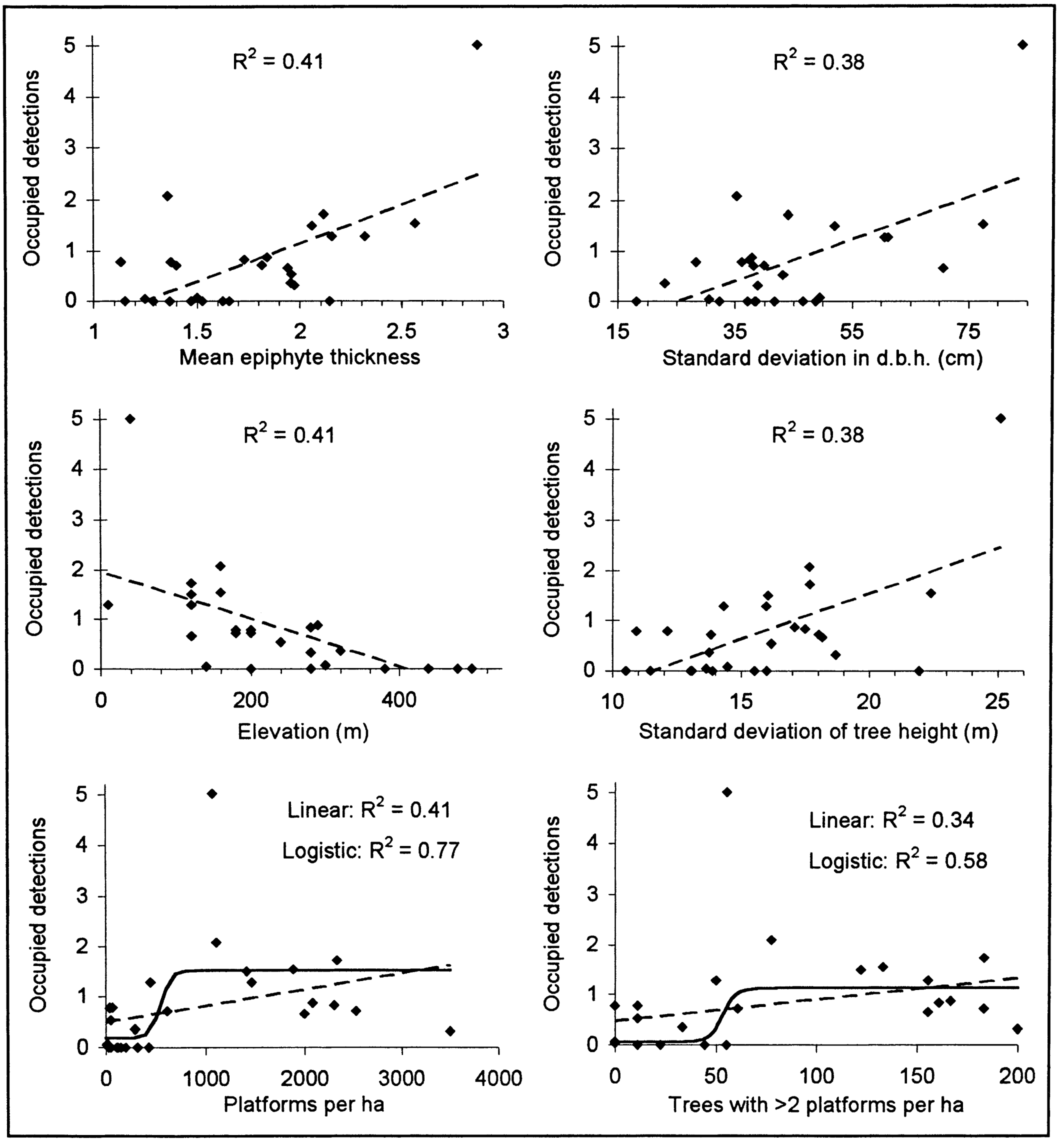

Fig. 2. Linear (dashed line) and nonlinear logistic (solid line) regressions of occupied detections of Marbled Murrelets plotted against six habitat variables.

method. Our method of combining multi-year data using the index of relative activity (IRA) provides a novel approach to minimize the variations due to weather, seasons, and annual effects, while focusing on the variations among the stations.

We confirmed that occupied detections (circling and subcanopy flights) or subcanopy detections alone were more realistic indicators of local activity and habitat association than total detections (Burger et al. 2000; Rodway and Regehr 2002). Total detections include purely auditory detections with undetermined flight paths, and visual detections of direct flights above the trees, which might involve passing birds not associated with the local habitat.

Occupied and subcanopy detections, however, are virtually all visual and hence influenced by visibility and canopy closure at the observation station (Rodway and Regehr 2000,

Table 4. Results of the principal components analysis, showing the loadings of the habitat variables on the first two principal components, and the correlation between these components and the IRA of occupied murrelet detections. Boldfaced values were used for interpreting and characterizing the components.

Variables	Component number 1	Component number 2
CCPLOT	−0.34	−0.03
DBHMN	**0.74**	−0.56
DBHSD	**0.76**	−0.24
DENBA	−0.11	**0.78**
DENCW	−0.50	−0.49
DENHW	−0.30	0.17
DENLARGE	0.44	0.24
DENLIV	−0.60	0.58
DENPLTF	0.54	**0.68**
DENSNAG	−0.35	0.36
DENSS	**0.69**	−0.13
ELEV	−0.56	−0.12
EPILIV	0.62	0.39
EPITHICK	**0.84**	0.16
HGTMN	0.56	−0.60
HGTSD	**0.77**	0.25
MISTLE	0.46	−0.01
PROD	0.53	0.59
TIMVOL	−0.13	0.22
Eigenvalue	5.9	3.3
Percentage of variance explained	30.9	17.1
Spearman correlation with murrelet detections		
IRADET	0.168	0.112
IRAOCC	0.637**	0.306
IRASUB	0.665**	0.518**

$^{**}P < 0.01$

2002). We found significant negative correlations between detections and the canopy closure at the stations (AVCC). Stations with low AVCC were typically valley-bottom gravel-bars and a few in roads at higher elevations. Controlling for AVCC reduced the correlation coefficients involving elevation (although the negative correlation with occupied detections was still significant) and eliminated significant correlations with density of large trees and with Sitka spruce, a dominant species bordering gravel bars on major creeks. Controlling for AVCC might therefore inadvertently eliminate variables concentrated on the valley bottom that might be biologically important for murrelets. For example, epiphyte thickness was significantly correlated with AVCC (Table 1). Therefore, controlling for visibility also controlled for a part of the variability in detections due to epiphyte thickness, an undesired side effect. Future studies should try to keep visibility constant among survey stations (Rodway and Regehr 2000). This was not feasible in our study since our stations were used for multiple purposes, and the paucity of roads and trails limited our options in selecting sites.

Valley-bottom surveys might overestimate murrelet activity if the birds followed creek beds as flight paths (Rodway and Regehr 2000). Radar surveys showed that flight paths were not necessarily associated with the creek bed in Carmanah Valley (Burger 1997). Furthermore, if most murrelets followed the creek up from the sea, then detection frequencies should have declined with increasing distance from the sea, as birds stopped at nest sites, but there was no evidence for this (Table 3). We conclude that there was no significant bias in our data due to flight paths along valley-bottom creeks.

Microhabitat canopy structures as nest

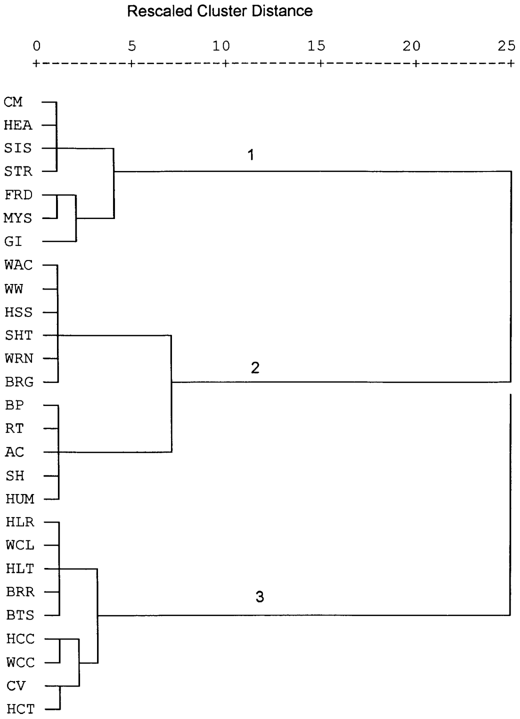

Fig. 3. Dendrogram showing the clustering of the 27 stations in Carmanah-Walbran on the basis of the first two Principle Components of habitat variables. See Fig. 1 for the station locations. The three major clusters are labeled 1–3.

indicators. Rodway and Regehr (2002) suggested that structural characteristics of trees provided more reliable indicators of murrelet habitat than audio-visual detections. Accordingly, in addition to audio-visual data we used five habitat features commonly found at tree nests of Marbled Murrelets as a second independent measure of habitat suitability. These nest habitat indicators were significantly intercorrelated, and most were significantly correlated with all detection measures and with many of the same macrohabitat features as the detection measures. Epiphyte cover (EPILIVE) was an exception, probably because even small trees had extensive moss cover in the wet Carmanah-Walbran forests. Epiphyte thickness (EPITHICK), indicating mossy mats found on older trees, was a more reliable habitat indicator there. Mistletoe deformities, used for a few nests in Oregon (Nelson 1997), were not reliable indicators of suitable murrelet habitat in our area or elsewhere in British Columbia (Bahn 1998; Manley 1999; Rodway and Regehr 2002).

Data from habitat plots seem to be essential for interpreting and applying audio-visual detection data (Bahn 1998; Rodway and Regehr 2002). A habitat suitability model combining audio-visual and habitat plot data (Bahn and Newsom 2002) provided similar results to a multivariate analysis of the habitat actually used for 45 murrelet nests found by telemetry in British Columbia (Waterhouse et al. 2002). This gives some confidence that indirect identification of nest habitat combining audio-visual, vegetation, and topographic measures is valid, within the range of habitat that is actually sampled.

Macrohabitat indicators of murrelet nesting. Audio-visual and canopy microhabitat data cannot be used to identify, map and manage nesting habitat at the landscape scale. Macrohabitat proxies, available from timber-inventory mapping and GIS databases, which are reliably associated with microhabitat indicators and nesting activity, need to be identified, both individually and, as in our PCA analysis, collectively.

Our study suggests that valley-bottom habitats provided better conditions for nesting than higher slopes. Occupied detections were higher in the valley bottom, even after controlling for visibility (AVCC), as discussed above. In our cluster analysis, valley-bottom stations in the lower drainage (group 1) had significantly higher occupied and subcanopy detections (but not AVCC), and higher values for platform density, epiphyte thickness, and epiphyte cover than stations on mid- or upper-level slopes (group 3), while the mixed group of slope and valley-bottom stations (group 2) were intermediate. The elevations sampled in Carmanah-Walbran (10–500 m) did not cover the full range used by Marbled Murrelets. In British Columbia murrelet nests located with telemetry have been found from sea level to 1500 m (most below 900 m), but where extensive low-elevation old growth remained, most were below 600 m (Burger 2002).

Negative associations of murrelet detections or measures of suitable habitat with elevation have been reported in many parts of the species' range (Hamer 1995; Rodway et al. 1993a,b; Rodway and Regehr 2002; Meyer and Miller 2002). In contrast, Bradley (2002) showed that

Table 5. Comparisons of Marbled Murrelet detection rates and values for nest habitat indicators among the three groups of stations in Carmanah-Walbran identified by cluster analysis. Groups with different letters (a, b) were significantly different (Tukey posthoc test).

Variable	Cluster group: 1 Valley bottom, Lower Carmanah	2 Walbran and Upper Carmanah	3 Slope sites	Kruskal-Wallis chi-square (df = 2)	ANOVA *P*
Marbled Murrelet detections					
IRADET	1.16 ± 0.23	0.98 ± 0.35	0.76 ± 0.49	4.11	0.13
IRAOCC	1.85 ± 1.42 a	0.60 ± 0.60 b	0.16 ± 0.26 b	12.67	0.002
IRASUB	1.08 ± 0.67 a	0.59 ± 0.69 ab	0.05 ± 0.09 b	12.55	0.002
Nest habitat indicators					
DENPLTF	1513 ± 633 a	1181 ± 1180 a	95 ± 91 b	14.010	0.001
DENTR2PL	123 ± 48 a	98 ± 65 a	20 ± 19 b	14.975	0.001
EPILIVE	3.12 ± 0.49 a	2.86 ± 0.44 a	1.75 ± 0.54 b	16.788	0.000
EPITHICK	2.23 ± 0.27 a	1.58 ± 0.30 b	1.29 ± 0.45 b	14.790	0.001
HGTSD	17.8 ± 3.6 a	15.5 ± 2.4 ab	13.2 ± 2.7 b	7.629	0.02
Canopy closure at station					
AVCC	20.8 ± 24.8	51.3 ± 27.7	51.9 ± 30.4	4.170	0.124
Number of stations	7	11	9		

breeding success increased with elevation in nests located by telemetry in Desolation Sound, possibly due to fewer predators at higher elevations. Most valley-bottom old-growth forests in Desolation Sound have been logged and are highly fragmented, but murrelets still seemed to under-utilize the higher elevation forests there (Burger 2002).

Distance from the ocean did not affect murrelet detections or habitat suitability. Our study area covered contiguous forest up to 22 km inland, which is well within the range of known nests (Nelson 1997).

Timber volume, tree size, and tree species composition are readily extracted from industrial timber-inventory maps. Timber volume was useful for identifying likely murrelet habitat elsewhere (Bahn 1998; Grenier and Nelson 1995; cf. Kuletz et al. 1995), but not in our study. Dense stands of tall, slender trees, typical of many slopes in Carmanah-Walbran, have timber volumes similar to the larger, widely spaced trees more suitable for murrelets. Mean tree height or diameter were indicators of suitable habitat in some studies (e.g., Kuletz et al. 1995; Hamer 1995; Grenier and Nelson 1995; Bahn 1998; Bahn and Newsom 2002), but not all (Manley 1999). In Carmanah-Walbran, where there is an abundance of tall trees, density of large trees (>80 cm dbh) was associated with potential nest platforms and occupied detections, but mean tree height and diameter (dbh) were not. Complex canopy structure, indicated by variable tree height (HGTSD) and platform density, seemed more important than tree size per se. Variable canopy structure and small openings were important habitat indicators in stands containing murrelet nests (Manley 1999, Waterhouse et al. 2002) and in other studies using similar methods to ours (Burger 2002).

Murrelets nest in several conifer species (Nelson 1997; Burger 2002). In our study murrelet detections and nest habitat indicators were correlated positively with densities of Sitka spruce and negatively with western red-cedar, with no consistent trends for western hemlock or amabilis fir. Tree species composition is best combined with other measures of forest structure (Bahn 1998; Rodway and Regehr 2002; Burger 2002).

Stations grouped by site productivity, associated with high moisture and soil nutrient regimes, showed consistent differences in occupied and subcanopy detections and nest habitat indicators. Productivity derived from biogeoclimatic information might therefore be useful for mapping potential habitat. Our samples did not include the two lowest productivity categories, typical of poor soils or bogs (Green and Klinka

1994), which seem unlikely to be optimal for murrelets.

Relationships with suites of habitat measures. Murrelets probably respond to a suite of proximate stimuli when selecting nest sites, and successful nesting depends on several ultimate habitat requirements. Many of these habitat parameters are closely interlinked, specifically the availability of large, well spaced trees with large, moss-covered boughs and variable canopy structures. PCA allowed us to derive components loaded with several such characters, and when the stations were clustered on the basis of these components, we found significant differences among the grouped stations. Our classification yielded three levels of habitat suitability with consistent ranking, whether tested with murrelet detections or the availability of nest habitat indicators. Similar multivariate approaches should be applied for classifying and mapping nesting habitats of Marbled Murrelets. Habitat variables, measured in the field and from maps and remote sensing, should include topography, tree size, canopy structure and complexity, platform and epiphyte availability, and to a lesser degree tree species composition.

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