
Effects of Habitat Fragmentation and Forest Edges on Predators of Marbled Murrelets and Other Forest Birds on Southwest Vancouver Island

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Abstract: We recorded the occurrence and relative abundance of potential predators of the threatened marbled murrelet (*Brachyramphus marmoratus*) in the Carmanah, Walbran, and Klanawa Valleys on southwest Vancouver Island, British Columbia. Data covering multiple years (1994–2000) came from two series of dawn surveys used to monitor murrelet activities (45 stations in total), and two series of point counts (190 stations). Steller's jays (*Cyanocitta stelleri*) were consistently the most common potential predator. Common ravens (*Corvus corax*) and red squirrels (*Tamiasciurus hudsonicus*) were also frequently encountered, but owls, accipiters, and falcons were rare. Northwestern crows (*Corvus caurinus*) and bald eagles (*Haliaeetus leucocephalus*) were rare at our inland stations, but other studies showed that they were common at the coast. The survey and point count data showed that the percent occurrence and relative abundance (individuals per survey) of Steller's jays, common ravens, and all predators combined were higher at stations bordering clearcuts and roads than at stations within interior forest or bordering streams. Highest counts were usually at sites frequently used by people. Predators were more abundant in the fragmented forests of the Klanawa Valley than in the less disturbed Carmanah-Walbran Valleys. In particular, counts of Steller's jays at road and clearcut edges were significantly higher in Klanawa than in Carmanah-Walbran. A pilot experiment using 40 artificial nest sites on tree boughs in old-growth patches in the Klanawa Valley revealed that eggs disappeared more rapidly near clearcut edges than in the interior forest. We conclude that predation risk at nests of marbled murrelets is likely to be higher near clearcuts and roads than in interior forest, and higher in fragmented landscapes than in relatively undisturbed old-growth forests.

Key Words: *Brachyramphus marmoratus*, marbled murrelet, predation, nesting, habitat fragmentation, logging, edge effects, corvids, Vancouver Island, British Columbia

Introduction

The marbled murrelet (*Brachyramphus marmoratus*) is a threatened species in Canada and is endangered or threatened in Washington, Oregon, and California (Ralph et al. 1995). The principal threat appears to be loss of nesting habitat in old-growth coastal forests, with additional

threats from gill nets, oil spills and the possibility of reduced prey linked with climate change (Ralph et al. 1995; Nelson 1997; Burger 2002). The production of fledged young by this species appears to be among the lowest in the Alcidae (De Santo and Nelson 1995). In a sample of 77 nesting attempts observed from Alaska through California, only 35% resulted in fledged young (Manley and Nelson 1999). On the Sunshine Coast, British Columbia (B.C.), two studies reported nesting success (fledgling per nest) of 33% (Manley 1999; $n = 68$ nesting attempts) and 46% (Cam et al. 2003; $n = 215$ tagged birds). The major cause of nest failure was predation of eggs, chicks, and, to a lesser extent, adults at nest sites (Nelson and Hamer 1995; Nelson 1997; Manley 1999; Manley and Nelson 1999).

Predation of the eggs and chicks of marbled murrelets by common ravens (*Corvus corax*), Steller's jays (*Cyanocitta stelleri*), and sharp-shinned hawks (*Accipiter striatus*) has been confirmed, and predation by great horned owls (*Bubo virginianus*), barred owls (*Strix varia*), American crows (*Corvus brachyrhynchos*), and gray jays (*Perisoreus canadensis*) is suspected (Nelson 1997; Burger 2002). Adult murrelets have been killed by bald eagles (*Haliaeetus leucocephalus*), sharp-shinned hawks, northern goshawks (*Accipiter gentilis*), peregrine falcons (*Falco peregrinus*) and common ravens (Nelson 1997; Burger 2002). Other species of crows, owls, accipiters, and falcons are also likely predators (Nelson 1997; Raphael et al. 2002). No mammals have been confirmed as predators at murrelet nests, but raccoons (*Procyon lotor*), marten (*Martes americana*), fisher (*Martes pennanti*), squirrels, and arboreal mice (*Peromyscus* spp.) are potential predators (Nelson 1997; Raphael et al. 2002; Bradley and Marzluff 2003). A 5-year study of predation at artificial murrelet nests in Washington and Oregon revealed that the principal predators of eggs were Steller's and Gray jays, while rodents (principally flying squirrels [*Glaucomys sabrinus*]) were probably the major predators of chicks (Raphael et al. 2002; Luginbuhl et al. 2001; Bradley and Marzluff 2003). Flying squirrels are not found on Vancouver Island, but red squirrels (*Tamiasciurus hudsonicus*) are known to be nest predators of forest birds and are likely to prey on murrelet eggs and chicks (reviewed by Burger 2002).

There is concern that the observed levels of predation at marbled murrelet nests might be unusually high as a result of fragmentation of forest habitat, increased edge effects, and increased densities of predators caused by logging and other human activities (Nelson and Hamer 1995; Ralph et al. 1995; Nelson 1997; Burger 2002). In general, the effects of fragmentation and forest edges on predation of forest-nesting birds are not consistent or well understood (Paton 1994; Haskell 1995; Marzluff and Restani 1999; Chalfoun et al. 2002; Batáry and Báldi 2004), and there have been few attempts to investigate these relationships in the coniferous forests of the Pacific Northwest. Evidence on the effects of forest edges and patch size on the breeding success of marbled murrelets is equivocal (Burger 2002): a range-wide review suggested that nests within 50 m of forest edges had lower success than nests in the interior forest (Manley and Nelson 1999), whereas a study of nests found with telemetry on B.C.'s Sunshine Coast found no effects of edge or patch size on breeding success (Bradley 2002). Given the high degree of fragmentation of logged watersheds, and the continued predominance of clearcut logging in coastal B.C., it is

important to know whether edge effects and fragmentation have significant impacts on sensitive forest-nesting species such as the marbled murrelet. Corvids (crows, ravens and jays) are of particular concern as nest predators (Andren 1992, 1995; Paton 1994; Marzluff and Restani 1999). Populations of corvids are increasing dramatically in much of the Pacific Northwest, including B.C. (Marzluff et al. 1994; Campbell et al. 1997).

We report on the occurrence, relative abundance, and spatial distributions of potential predators in coniferous forests of three watersheds on southwest Vancouver Island, B.C. Data used for this analysis were obtained as part of research conducted on marbled murrelets from 1994 through 2000 in the Carmanah and Walbran Valleys, and 1999 and 2000 in the Klanawa Valley. Large numbers of marbled murrelets are known to nest in inland old-growth conifers in these and adjacent watersheds (Burger 2002). In particular, we tested whether predators were more common at stations in or near clearcuts, roads, and camping and picnic sites than in the forest interior. Although our focus is on predation risk to marbled murrelets, our results help to assess the risks to other forest-nesting birds.

Methods

Study Areas

Our study areas included the Carmanah Valley (6500 ha), western Walbran Valley (9500 ha), and Klanawa Valley (24,200 ha) on southwest Vancouver Island. The three valleys have similar topography and climate, and 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). All of our survey stations were within the submontane very wet maritime subzone (CWHvm1), which occurs at 0–600 m elevation (Meidinger and Pojar 1991). Survey stations in the Carmanah and Walbran Valleys were within or bordering Carmanah-Walbran Provincial Park; most stations were in undisturbed, contiguous old-growth forest > 250 years old, but some were in regenerating clearcuts within the park (< 12 years since logging), in recent clearcuts bordering the park, or on roads (details below). The Klanawa Valley has experienced extensive clearcut logging for over 50 years and contains a mosaic of old-growth patches, second growth, and recent clearcuts, interspersed with many logging roads.

Potential Predators Considered

We considered eagles, falcons, accipiters, owls, corvids, squirrels, and mustelids to be potential predators of nesting murrelets and other forest-nesting birds. Red-tailed hawks (*Buteo jamaicensis*) and American kestrels (*Falco sparverius*), which catch prey on the ground, were not considered likely predators of murrelets or other forest-nesting birds.

Dawn Murrelet Surveys

During standardized audiovisual surveys for marbled murrelets (RIC 1997, 2001) we recorded the occurrence and relative abundance (individuals per survey) of potential predators. Surveys began 60 minutes before sunrise and continued for 60 minutes after sunrise, or 20 minutes after the last record of murrelet activity (usually within 2 hours of sunrise). The observers remained stationary throughout the survey, sitting in a semi-reclined posture to afford the best view of the sky. This was analogous to a prolonged point-count for sampling forest birds (Ralph et al. 1993). Data were recorded on tape recorders and transcribed to spreadsheets.

The observers had been trained to detect marbled murrelets and to identify potential predators by sight or sound. Most predators, and corvids in particular, have readily recognizable calls. Some predators were undoubtedly missed, and the occurrence and relative abundance reported here are minimum estimates. Because observers were focused on marbled murrelets, no attempts were made to estimate the distances to each predator heard or seen during surveys; hence, no estimate of absolute densities per unit of area was possible.

Murrelet survey stations were more than 300 m apart, 2–21 km from the coast, and accessed using hiking trails or logging roads. In most years, each station was sampled three times at intervals > 14 days, between 1 May and 7 August, with most surveys between 15 May and 16 July. Rain and logistic problems prevented some surveys from being conducted; consequently, sampling effort was not uniform in all years.

Two data sets from the murrelet surveys were analyzed for this paper. The first set consisted of predator occurrence and relative abundance recorded in 1994–1997 at 27 murrelet survey stations within the adjacent Carmanah and Walbran Valleys (see Burger and Bahn 2004 for station locations). Part of this data set has already been analyzed to show that predators were more abundant at coastal stations (20–250 m from the coastal forest edge) than at inland stations (1.5–21.0 km inland [Burger et al. 2000]). Our analysis therefore focused on inland stations 2.5–21.0 km from the coast. The degree of habitat disturbance at each station was classified as *high* (station bordering a clearcut logged within the past 12 years, or a road clearing) or *low* (more than 100 m from clearcuts or roads); there were no stations at intermediate distances. The frequency of human use, predominantly logging activities, camping, picnicking or hiking, was classified as *high* (people likely to be encountered several times a week) or *low* (people likely to be encountered at intervals of more than a week). Classifications were made independently by three observers, with 100% and 96% agreement in classifying disturbance and human use, respectively.

The second data set was comprised of records of predator occurrence and relative abundance in 1999 and 2000 at 14 inland murrelet stations in the Carmanah-Walbran watersheds (a subset of the ones sampled in 1994–1997) and 18 inland stations in the Klanawa Valley. The intent was to compare the relatively undisturbed Carmanah-Walbran (all stations within or bordering the Carmanah-Walbran Provincial Park) with the highly fragmented and disturbed Klanawa (all stations within managed forests with numerous roads, recent clearcuts, and young second-growth stands).

Point Count Surveys

We analyzed two sets of data from standardized 10-minute point counts. Methods followed Ralph et al. (1993), and details are given in Masselink (2001). Counts were made in the morning, and the occurrence and relative abundance (individuals per survey) of all forest birds, including all avian predators of marbled murrelets were recorded. No surveys were made during heavy rain or strong winds.

The first data set covered point counts within the Carmanah and Walbran watersheds (details in Masselink 2001). Stations were ≥ 250 m apart and located at forest edges (bordering recent clearcuts, roads, or rivers), at old-growth forest interior stations located 250 m from the adjacent edge stations, or at stations within recent clearcuts and > 125 m from any old forest. Each station was sampled seven times at roughly two-week intervals from 16 May through 31 August 1997.

The second data set covered point counts made in the Carmanah-Walbran (at different stations from those sampled by Masselink 2001) and Klanawa watersheds. Stations were ≥ 150 m apart and located at forest edges bordering recent clearcuts, roads, or rivers, and at adjacent sites in interior old-growth forest > 150 m from edges. Stations were sampled 2–3 times at intervals > 14 days between 18 May and 20 July 2000. Mammalian predators were also recorded in these surveys.

Experiment Testing Egg Predation

In 2001, one of us (M.J.K.) conducted a pilot experiment to test the effects of forest edge on the predation of eggs at artificial nests sites in old-growth trees in the Klanawa Valley. Chicken eggs (similar in size and shell thickness to eggs of marbled murrelets) were dyed to resemble those of the murrelet, and were placed in artificial nests made of moss pads and located on the limbs of forest trees, 2–5 m above ground level. Although this height was considerably lower than sites typically used by nesting marbled murrelets (Burger 2002), a telemetry study in Carmanah-Walbran showed that Steller's jays spent similar proportions of time at all vertical levels of the old-growth forest (Masselink 2001). We also saw ravens and squirrels foraging in the lower levels of the forest. Exposure of nests to predators at 2–5 m should, therefore, be similar to that experienced by the canopy-nesting murrelets.

Forty nests were tested. The nests were located along eight transect lines that were perpendicular to the forest edge. The nests were placed at 10, 40, 80, 130, and 200 m from the edge along each transect. Transects were 40–100 m apart, and located within old-growth stands (> 250 years old) bordered by recent clearcuts (8 years after logging). Nests were placed in position on 11 August 2001 and checked after 7 and 14 days. Mean eggshell thickness was 0.46 ± 0.11 (SD) mm ($n = 6$ eggs).

Statistical Analysis

Given the variability and non-normality of most of the data, we applied nonparametric tests (Kruskal-Wallis for analysis of variance, Mann-Whitney to compare means of two sets of data, and *G*-tests for frequencies), using SPSS 11.5. Differences were considered significant for $P < 0.05$. To test the effects of location and habitat of survey stations, we first calculated mean values of relative predator abundance (individuals per survey) for each station and then used each station as an independent sample.

Results

Murrelet Survey Data: Within Carmanah-Walbran

Steller's jays were by far the most common predator; mean annual occurrence was at 81% of stations and 50% of all surveys (Table 1). Common ravens were found at 32% of stations and in 10% of surveys. Three species of owls were fairly widespread, but less frequently encountered (annually at 10–17% of stations, and in 3–5% of surveys), and showed marked differences among years. Red squirrels were the only mammals reported during these surveys, and on average were recorded at 69% of stations and in 24% of surveys. All other predators were rare, in most years occurring in 1% or fewer surveys and at few stations (Table 1). Bald eagles and northwestern crows (*Corvus caurinus*), although common at coastal stations not included in this analysis (Burger et al. 2000), were rare or absent at inland stations. The only other potential predators seen outside the survey periods during our research were a solitary peregrine falcon seen twice in 1995, and 2–3 sightings of solitary marten in each year.

Relative abundance (individuals per survey) was used to test the effects of habitat disturbance (clearcut logging and roads) and human activity at the 27 inland stations (Table 2). We found a significant negative correlation between distance from the coast and the abundance of Steller's jays ($r = -0.43$, $P = 0.026$), common ravens ($r = -0.40$, $P = 0.039$), all birds ($r = -0.49$, $P = 0.009$), and all predators ($r = -0.46$, $P = 0.017$). There was, however, no significant difference in the distance from the ocean between disturbed and undisturbed stations (Mann-Whitney test, $Z = 0.72$, $P = 0.473$), or between stations with high or low human activity ($Z = 0.59$, $P = 0.554$).

Table 1. Annual variation in the occurrence of potential predators of marbled murrelets per murrelet survey station and per survey (all inland stations pooled) in Carmanah and Walbran Valleys, 1994–1997.

Species	Occurrence per station (%)					Occurrence per survey (%)				
	1994	1995	1996	1997	mean	1994	1995	1996	1997	mean
Bald eagle (<i>Haliaeetus leucocephalus</i>)	18.2	0.0	0.0	7.7	6.5	2.3	0.0	0.0	2.1	1.1
Cooper's hawk (<i>Accipiter cooperii</i>)	9.1	0.0	0.0	0.0	2.3	1.1	0.0	0.0	0.0	0.3
Unidentified accipiter (<i>Accipiter</i> sp.)	0.0	0.0	4.4	0.0	1.1	0.0	0.0	1.0	0.0	0.3
Merlin (<i>Falco columbarius</i>)	9.1	0.0	0.0	0.0	2.3	2.3	0.0	0.0	0.0	0.6
Unidentified falcon (<i>Falco</i> sp.)	0.0	0.0	13.0	0.0	3.3	0.0	0.0	1.0	0.0	0.3
Western screech-owl (<i>Otus kennicottii</i>)	27.3	28.6	13.0	0.0	17.2	4.5	5.8	3.0	0.0	3.3
Great horned owl (<i>Bubo virginianus</i>)	0.0	0.0	39.1	0.0	9.8	0.0	0.0	10.9	0.0	2.7
Northern pygmy-owl (<i>Glaucidium gnoma</i>)	18.2	0.0	13.0	30.8	15.5	5.6	0.0	3.0	9.3	4.5
Barred owl (<i>Strix varia</i>)	0.0	0.0	4.4	3.8	2.1	0.0	0.0	1.0	1.0	0.5
Northern saw-whet owl (<i>Aegolius acadicus</i>)	0.0	0.0	0.0	3.8	1.0	0.0	0.0	0.0	1.0	0.3
Unidentified owl	0.0	0.0	4.4	0.0	1.1	0.0	0.0	1.0	0.0	0.3
Steller's jay (<i>Cyanocitta stelleri</i>)	100.0	78.6	82.6	61.5	80.7	49.4	55.2	49.5	44.3	49.6
Gray jay (<i>Perisoreus canadensis</i>)	0.0	0.0	0.0	3.8	1.0	0.0	0.0	0.0	1.0	0.3
Northwestern crow (<i>Corvus caurinus</i>)	0.0	0.0	4.4	3.8	2.1	0.0	0.0	1.0	1.0	0.5
Common raven (<i>Corvus corax</i>)	27.3	71.4	21.7	7.7	32.0	5.6	27.6	5.9	2.1	10.3
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	100.0	71.4	56.5	46.2	68.5	39.3	19.5	19.8	15.5	23.5
Any potential predator	100.0	92.9	100.0	88.5	95.4	69.7	66.7	68.3	58.8	65.9
No. of stations	11	14	23	26	18.5					
No. of surveys						89	87	101	97	93.5

Compared with 19 undisturbed stations, the 8 stations at disturbed sites had significantly higher relative abundance of Steller's jays (Mann-Whitney test, $Z = 2.95$, $P = 0.003$), common ravens ($Z = 2.17$, $P = 0.030$), all birds ($Z = 3.06$, $P = 0.002$), and all predators pooled ($Z = 2.44$, $P = 0.015$), but no significant differences in abundance of owls (all species pooled; $Z = 1.08$, $P = 0.279$) or red squirrels ($Z = 1.79$, $P = 0.074$) (Table 2). Disregarding disturbance, we found significantly more common ravens at stations with high human activity ($Z = 2.33$, $P = 0.020$), but no other species or groups differed significantly between high and low human activity ($P > 0.05$ in each case). With the data separated into disturbed and undisturbed sites, the highest relative abundance of Steller's jays, common ravens, and all predators was consistently found at stations with high human activity, but the samples were too small for statistical testing. The mean relative abundance of all predators at disturbed stations with high human activity (2.2 ± 1.2 [SD] individuals per survey) was double that at undisturbed stations, whether they had high or low human activity.

Table 2. Mean relative abundance of potential predators recorded during dawn murrelet surveys at each station in Carmanah and Walbran Valleys, 1994–1997.

Station classification	Distance from ocean (km)	No. of surveys	Mean no. of predators per survey					
			all owls	Steller's jay	common raven	all birds	red squirrel	all predators
A) Disturbed stations								
High human use								
West Walbran Bridge	16.1	3	0.00	0.33	0.00	0.33	0.00	0.33
Lower Clearcut	17.7	32	0.16	1.37	0.35	1.93	0.07	2.00
Warden's Cabin Camp	5.8	13	0.39	1.25	0.88	2.62	0.00	2.62
Warden's Cabin Clearcut	5.4	13	0.44	1.90	0.57	2.91	0.08	2.99
Walbran South Bridge	9.8	3	0.00	2.30	0.33	2.63	0.67	3.30
Mean disturbed + high human use	11.0	12.8	0.2	1.4	0.4	2.1	0.2	2.2
SD	5.7	11.8	0.2	0.7	0.3	1.0	0.3	1.2
Low human use								
Bonilla Road	2.9	7	0.11	1.13	0.17	1.71	0.17	1.87
High Logging Road	4.6	6	0.56	0.69	0.00	1.52	0.00	1.52
West Walbran	13.8	24	0.06	0.90	0.13	1.12	0.34	1.46
Mean disturbed + low human use	7.1	12.3	0.2	0.9	0.1	1.4	0.2	1.6
SD	5.9	10.1	0.3	0.2	0.1	0.3	0.2	0.2
Mean all disturbed stations	9.5	12.6	0.2	1.2	0.3	1.8	0.2	2.0
SD	5.7	10.5	0.2	0.6	0.3	0.9	0.2	1.0

Table 2. Mean relative abundance of potential predators recorded during dawn murrelet surveys at each station in Carmanah and Walbran Valleys, 1994–1997 (cont'd).

Station classification	Distance from ocean (km)	No. of surveys	Mean no. of predators per survey					
			all owls	Steller's jay	common raven	all birds	red squirrel	all predators
B) Undisturbed stations								
High human use								
Bearpaw	16.6	28	0.00	0.13	0.00	0.13	0.22	0.35
Bonilla Trail Site	2.8	7	0.08	0.67	0.42	1.33	0.25	1.58
Camp Heaven	6.2	30	0.09	0.71	0.22	1.06	0.32	1.39
Camp Hummingbird	17.1	27	0.05	0.29	0.04	0.42	0.33	0.75
Research Tree	16.1	22	0.00	0.28	0.00	0.28	0.26	0.54
Three Sisters	7.7	29	0.05	1.42	0.13	1.63	0.33	1.96
Mean undisturbed + high human use	11.1	23.8	0.0	0.6	0.1	0.8	0.3	1.1
SD	6.3	8.7	0.0	0.5	0.2	0.6	0.0	0.6
Low human use								
August Creek	11.1	21	0.17	0.83	0.10	1.10	0.59	1.68
Carmanah View	12.3	3	0.00	0.00	0.00	0.00	0.00	0.00
Ford	5.2	18	0.00	0.57	0.05	0.62	0.18	0.80
High Cedar Creek	12.0	6	0.22	0.00	0.00	0.33	0.00	0.33
High Cedar Trail	11.8	6	0.55	0.17	0.00	1.00	0.33	1.33
High Logging Trail	5.9	5	0.11	1.25	0.00	1.42	0.34	1.75
High Slope Site	15.0	5	0.61	0.50	0.25	1.67	0.50	2.17
Mystic	12.5	6	0.00	0.25	0.00	0.25	0.38	0.63
Sleepy Hollow	13.5	15	0.06	0.06	0.00	0.13	0.25	0.38
Sleepy Hollow Trail	13.3	7	0.17	0.13	0.00	0.38	0.13	0.50
Stream Site	7.0	28	0.00	0.60	0.21	0.96	0.48	1.44
Walbran-August Creek	12.6	7	0.08	0.75	0.00	0.88	0.50	1.38
Wren	12.3	3	0.00	0.00	0.00	0.00	0.33	0.33
Mean undisturbed + low human use	11.1	10.0	0.2	0.4	0.0	0.7	0.3	1.0
SD	3.1	7.9	0.2	0.4	0.1	0.5	0.2	0.7
Mean all undisturbed stations	11.1	14.4	0.1	0.5	0.1	0.7	0.3	1.0
SD	4.1	10.3	0.2	0.4	0.1	0.6	0.2	0.7

Murrelet Survey Data: Carmanah-Walbran vs. Klanawa

The 14 Carmanah-Walbran stations sampled in 1999–2000 were further inland (mean 13.7 ± 4.8 [SD] km, range 7.0–21.0 km) than the 18 Klanawa stations (mean 4.7 ± 2.6 [SD] km, range

1.5–10.0 km; Mann-Whitney test, $Z = 4.45$, $P < 0.001$). Similarly, the Carmanah-Walbran stations were, on average, at higher elevations (mean 200 ± 71 [SD] m, range 120–290 m) than the Klanawa stations (mean 101 ± 91 [SD] m, range 10–330 m; Mann-Whitney test, $Z = 2.90$, $P = 0.004$). Despite these differences, we found no significant effects of distance from the sea or elevation on the relative abundance of potential predators at inland stations, whether Carmanah-Walbran and Klanawa data were tested separately or pooled ($P > 0.09$ in each test).

With the exception of the western screech-owl and northwestern crow, both rare species in our surveys, the occurrence and relative abundance of potential predators was consistently higher in the moderately disturbed Klanawa Valley than in the relatively undisturbed Carmanah-Walbran Valleys (Table 3). Potential predators were recorded at 100% of Klanawa stations and in 83% of surveys, whereas 79% of stations and 46% of surveys reported predators in Carmanah-Walbran. Significant differences in relative abundance were found for bald eagles (Mann-Whitney test, $Z = 2.51$, $P = 0.012$), Steller's jays ($Z = 4.67$, $P < 0.001$), common ravens ($Z = 2.47$, $P = 0.014$), red squirrels ($Z = 2.83$, $P = 0.005$), and all predators pooled ($Z = 5.94$, $P < 0.01$). The mean relative abundance of all predators combined was about three times higher in Klanawa than in Carmanah-Walbran.

Table 3. Occurrence (per station and per survey) and relative abundance of potential predators at inland murrelet survey stations in the relatively undisturbed Carmanah-Walbran and moderately disturbed Klanawa watersheds on southwest Vancouver Island in 1999–2000.

<i>Species</i>	<i>Occurrence per station (%)</i>		<i>Occurrence per survey (%)</i>		<i>Relative abundance (mean animals per survey \pm SD)</i>	
	<i>Carmanah-Walbran</i>	<i>Klanawa</i>	<i>Carmanah-Walbran</i>	<i>Klanawa</i>	<i>Carmanah-Walbran</i>	<i>Klanawa</i>
Bald eagle	7.1	33.3	1.3	10.8	0.01 ± 0.11	0.14 ± 0.50
Merlin	0.0	5.6	0.0	1.1	0.00 ± 0.00	0.01 ± 0.10
Western screech-owl	7.1	5.6	1.3	1.1	0.01 ± 0.11	0.01 ± 0.10
Great horned owl	0.0	5.6	0.0	1.1	0.00 ± 0.00	0.01 ± 0.10
Barred owl	0.0	5.6	0.0	1.1	0.00 ± 0.00	0.02 ± 0.21
Steller's jay	78.6	100.0	39.0	72.0	0.71 ± 1.13	1.96 ± 2.43
Northwestern crow	14.3	5.6	2.6	1.1	0.04 ± 0.25	0.01 ± 0.10
Common raven	21.4	33.3	3.9	15.1	0.04 ± 0.19	0.27 ± 0.72
Red squirrel	7.1	61.1	1.3	12.9	0.01 ± 0.11	0.15 ± 0.42
Marten	0.0	5.6	0.0	1.1	0.00 ± 0.00	0.01 ± 0.10
All predators	78.6	100.0	45.5	82.8	0.83 ± 1.19	2.62 ± 2.64
No. of stations	14	18				
No. of surveys			77	93	77	93

Point Count Data: Within Carmanah-Walbran

The only potential predators reported in point counts in 1997 were Steller's jays and common ravens (Table 4). Jays were reported more often at stations at clearcut and road edges than at stations within the interior forest (and to a lesser extent river edges). We found a significant difference in relative abundance of jays among the five habitat categories, with the lowest abundance in interior forest. Ravens were far less common in all surveys and showed no differences in relative abundance among habitat types.

Table 4. Occurrence (per station and per survey) and relative abundance of potential predators of marbled murrelets recorded during point count surveys in Carmanah-Walbran in 1997.

<i>Habitat</i>	<i>Occurrence per station (%)</i>			<i>Occurrence per survey (%)</i>			<i>Relative abundance (mean birds per survey \pm SD)</i>	
	<i>Steller's jay</i>	<i>common raven</i>	<i>no. of stations</i>	<i>Steller's jay</i>	<i>common raven</i>	<i>no. of surveys</i>	<i>Steller's jay</i>	<i>common raven</i>
Middle of clearcut	71.4	7.1	14	22.4	1.0	98	0.43 \pm 0.49	0.01 \pm 0.04
Clearcut/forest edge	100.0	0.0	13	35.1	0.0	91	0.66 \pm 0.52	0
Road/forest edge	91.7	8.3	12	42.9	1.2	84	0.79 \pm 0.86	0.01 \pm 0.04
River/forest edge	69.2	15.4	13	23.1	2.2	91	0.38 \pm 0.38	0.02 \pm 0.05
Interior forest	59.5	5.4	37	15.4	0.8	259	0.19 \pm 0.19	0.01 \pm 0.03
Kruskal-Wallis test								
χ^2 value (DF = 4)							15.96	2.61
<i>P</i>							0.003	0.625

Point Count Data: Carmanah-Walbran and Klanawa

Using the point count data from 2000 (Carmanah-Walbran and Klanawa pooled), we found significant differences in relative abundance among four habitat categories for Steller's jays and for all predators combined, but not for common ravens or red squirrels (Table 5). Jay abundance was similar in clearcut and road edges, which were both higher than at interior forest or river edges. With the Steller's jay data pooled into two habitat categories, we tested the effects of habitat within each watershed (Table 6). Jay abundance was significantly higher in the Klanawa Valley than in Carmanah-Walbran for clearcut/road edge habitats, but the reverse was true for the forest interior/river edge habitats. Within Carmanah-Walbran there was no significant difference in jay abundance between these habitat categories, but in Klanawa the clearcut/road edge category was significantly higher than the forest interior/river edge category.

Table 5. Mean relative abundance (animals per survey) of potential predators recorded at forest edge and interior point-count stations in Carmanah-Walbran and Klanawa watersheds in 2000.

<i>Habitat</i>		<i>Common raven</i>	<i>Steller's jay</i>	<i>Red squirrel</i>	<i>All predators</i>
Clearcut edge (<i>n</i> = 28 stations)	Mean \pm SD	0.08 \pm 0.17	1.06 \pm 0.67	0.07 \pm 0.14	1.21 \pm 0.69
	% occurrence	21.4	92.9	21.4	100
Road edge (<i>n</i> = 5 stations)	Mean \pm SD	0.00 \pm 0.00	1.07 \pm 0.92	0.13 \pm 0.30	1.20 \pm 0.96
	% occurrence	0.0	100.0	20.0	100
River edge (<i>n</i> = 18 stations)	Mean \pm SD	0.00 \pm 0.00	0.50 \pm 0.71	0.00 \pm 0.00	0.50 \pm 0.71
	% occurrence	0.0	50.0	0.0	50
Interior forest (<i>n</i> = 50 stations)	Mean \pm SD	0.05 \pm 0.19	0.54 \pm 0.67	0.04 \pm 0.11	0.63 \pm 0.76
	% occurrence	8.0	52.0	12.0	58
Kruskal-Wallis test	χ^2 value (DF = 3)	6.41	15.22	4.79	18.46
	<i>P</i>	0.093	0.002	0.188	< 0.001

Table 6. Mean (\pm SD) numbers of Steller's jays per survey at point count stations in edge (combined clearcut and road edges) and interior (including river edges) sites in Carmanah-Walbran and Klanawa in 2000.

<i>Habitat category</i>	<i>Carmanah-Walbran</i>	<i>Klanawa</i>	<i>Comparing watersheds Mann-Whitney test</i>
Clearcut and road edges	0.48 \pm 0.26	1.22 \pm 0.70	<i>Z</i> = 2.84, <i>P</i> = 0.005
No. of stations	7	26	
Forest interior and river edges	0.69 \pm 0.76	0.31 \pm 0.46	<i>Z</i> = 2.20, <i>P</i> = 0.028
No. of stations	39	29	
Comparing habitats within watersheds			
Mann-Whitney test	<i>Z</i> = 0.06, <i>P</i> = 0.95	<i>Z</i> = 4.77, <i>P</i> < 0.001	

Egg Predation Experiment

Loss of the chicken eggs in artificial nests was highest near the forest/clearcut edge and decreased with increasing distance from the edge (Fig. 1). This trend was apparent after 7 days and significant after 14 days ($G = 13.00$, $P = 0.025$, $DF = 4$). A strong windstorm occurred between the 7th and 14th days of the experiment, which might have caused some eggs to fall from the artificial nests. The 7-day result can be attributed to predation, but the 14-day result is best viewed as the combined effects of predation and exposure to strong winds.

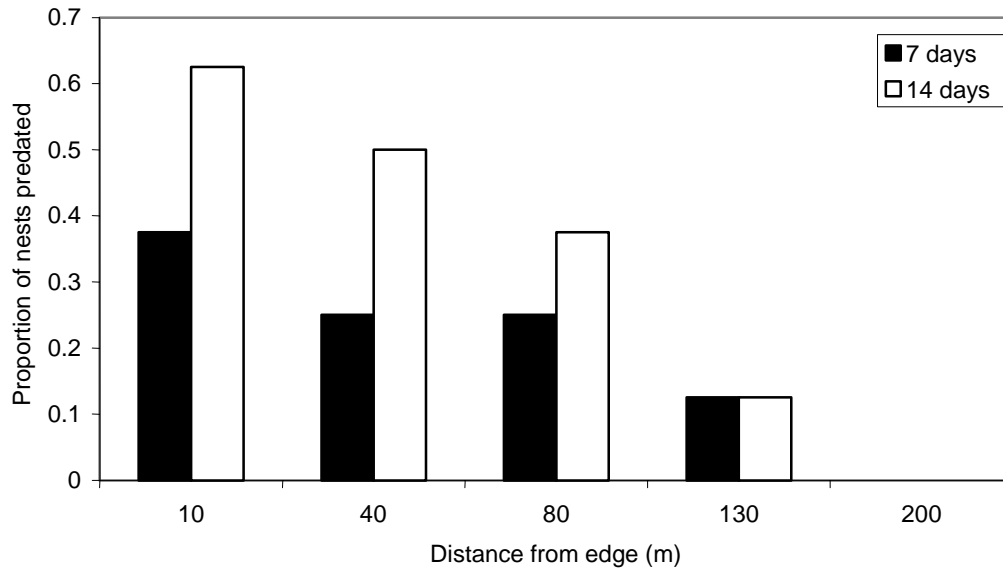


Figure 1. Predation of eggs at artificial nests at various distances into the forest interior from the clearcut edge in the Klanawa Valley after 7 and 14 days ($n = 8$ eggs at each distance, or 40 in total).

Discussion

Adequacy of the Sampling Techniques

The focus of the murrelet surveys in the Carmanah and Walbran Valleys was to detect marbled murrelets, and observations of other species were of secondary importance. Surveyors were, therefore, more likely to underestimate the percent occurrence and relative abundance of potential predators than they would in point counts dedicated to that purpose. Nevertheless, we applied the same standardized procedures at all murrelet survey stations, and the trends emerging from these data should indicate significant biological patterns. Most birds and red squirrels were detected by ear not by sight, and so predators would be equally likely to be detected at the edge of clearcuts or roads as in undisturbed forest.

Many more species of potential predators were recorded during the multi-year murrelet surveys (minimum 2 hours per survey) than in the single-year 10-minute point counts (compare Tables 1 and 3 [murrelet surveys] with Tables 4 and 5 [point counts]). Owls were more likely to be detected in the murrelet surveys, which began an hour before sunrise, than in point count surveys which began after sunrise. Many predator species, including all raptors and most owls, were rare or seldom reported with either survey method, but if they frequently preyed on murrelet adults, eggs, or chicks, even rare predators might have significant impacts on local populations. These results suggest that large multi-year samples of point counts are needed to adequately sample potential predators in these forests, and that additional surveys specifically targeted at nocturnal predators are needed.

Our sampling provided no information on arboreal rodents, other than red squirrels. Experimental work in Oregon and Washington suggests that squirrels and arboreal deer mice (*Peromyscus maniculatus* and *P. keeni*) might be important predators of murrelet eggs and chicks (Marzluff et al. 2000; Raphael et al. 2002; Bradley and Marzluff 2003). Deer mice have been reported in the old-growth forest canopy 40 m or more above the ground on southwest Vancouver Island (N. Winchester, pers. comm.). Marzluff and Restani (1999) stressed that the entire suite of predators needs to be considered when examining the effects of forest edges on predation risk. Clearly that approach would take an intensive dedicated study, and our results should be treated as preliminary, but not definitive, indicators of the likely predation risks on southwest Vancouver Island.

Distribution and Relative Abundance of Potential Predators

Potential predators of marbled murrelets were regularly encountered at most murrelet survey stations in the Carmanah-Walbran and at all stations in the Klanawa. Most of the predators reported were more likely to take eggs and chicks than adult birds. Large owls, eagles, accipiters, and falcons, which might take adults, were rare. Ravens were the most common predator likely to kill an adult murrelet. Population models indicate that predators which kill adults are likely to have a far greater impact on murrelet populations than those that take eggs or chicks, but predation causing nesting failure can contribute to population decline (Beissinger and Nur 1997; Cam et al. 2003).

Relative abundance of predators does not necessarily correlate with the risks to murrelets, because the probability of each species encountering a murrelet nest will vary relative to the predator's foraging behavior. A telemetry study in Carmanah-Walbran confirmed that Steller's jays spent most of their foraging time within 50 m of forest edges, and also showed that the jays regularly foraged in the high forest canopy in which murrelets nest (Masselink 2001). Similar detailed studies on other predators are lacking in coastal B.C.

Perhaps the most striking result to emerge from our analysis was the higher occurrence and relative abundance of predatory birds at stations on the edges of clearcuts and roads, compared with stations in undisturbed forest. This pattern applied consistently to Steller's jays in all data sets, and to common ravens in both sets of murrelet surveys but not in the point count data. The point count data were perhaps too sparse to conclusively show distributions of less common species. Owls and red squirrels were not significantly more abundant at human-made edges than in interior forest, although at the landscape level, squirrels were more common in the highly modified Klanawa Valley than in the relatively undisturbed Carmanah-Walbran. In nearby Clayoquot Sound on southwest Vancouver Island, Rodway and Regehr (2002) found that Steller's jays and northwestern crows occurred more frequently in fragmented than unfragmented forests, but red squirrels showed the opposite trend, and common ravens and bald eagles showed no significant differences in occurrence.

We recognize the need for research covering the entire suite of predators likely to affect nesting marbled murrelets, but the trends shown with corvids in our study are a concern. Jays and ravens are the most frequently documented predators at nests of marbled murrelets (Nelson 1997; Burger 2002). Predation rates at simulated marbled murrelet nests on the Olympic Peninsula, Washington correlated strongly with corvid abundance (Luginbuhl et al. 2001; Raphael et al. 2002), and in coastal forests of southeast Alaska, predation at artificial nests was correlated with densities of predators, predominantly corvids (De Santo and Willson 2001). In general, avian nest predators, especially corvids, are more likely to benefit from forest edges and fragmentation than mammalian predators (Chalfoun et al. 2002).

The results from our pilot experiment using artificial nests in the Klanawa Valley support the hypothesis of higher nest predation at the clearcut edges of old-growth forests. A larger experimental study involving a wider range of habitats and landscape types would provide a more rigorous test of the hypothesis, but other studies within the marbled murrelet's range provide some support. In montane forests on Vancouver Island, Bryant (1994) found more rapid predation of artificial nests located less than 100 m from forest edges than in the forest interior. He suggested that Steller's jays might have been a cause of this pattern. In southeast Alaska, higher nest predation was reported from forest edges bordering suburbs, where Steller's jays and northwestern crows were common, and along clearcut edges, openings and interior forest where red squirrels and jays were common (De Santo and Willson 2001).

Our survey results indicate that natural edges, such as the river/forest edges we sampled, are less likely to have increased predation risk from corvids than 'hard' edges bordering clearcuts and roads. Until there is strong contrary evidence, we support the view of the Canadian Marbled Murrelet Recovery Team (2003) that hard and natural forest edges should be treated differently, and that deleterious effects are more likely to be found at the hard edges.

Human activities in our study area were confined to logging and recreation (hiking, camping, fishing, and hunting); there were no permanent human settlements. Steller's jays and common ravens seemed to be attracted to active logging sites, camp and picnic sites, and other places where people were likely to leave food. An earlier analysis showed that northwestern crows were common along the coast (Burger et al. 2000), especially at coastal camp sites, such as at the mouth of the Carmanah and Klanawa Rivers, that are used each summer by thousands of people hiking the West Coast Trail. These trends are consistent with studies in Washington, Oregon, and southeast Alaska where human activities were associated with high corvid densities (Marzluff and Restani 1999; De Santo and Willson 2001; Gutzwiller et al. 2002) and, therefore, high predation risk for murrelets (Luginbuhl et al. 2001; Raphael et al. 2002).

We conclude that marbled murrelets nesting in watersheds on southwest Vancouver Island that are modified by clearcut logging and roads are likely to experience increased predation, due to increased numbers of jays and ravens associated with clearcut edges and roads, and to the provision of food to corvids and rodents at logging camps and recreational camp sites. Comparisons between Carmanah-Walbran and Klanawa suggest that there are both landscape-

level patterns (higher abundance of predators in the disturbed Klanawa) and patch-level patterns (higher abundance of predators at edges within Klanawa). In contrast, a telemetry study done in Desolation Sound on the southern B.C. mainland found no significant effects of edge on the success of murrelet nests (Bradley 2002); however, most of the edges considered in that study were natural (e.g., avalanche chutes) and the sample of 'hard' man-made edges was insufficient for statistical testing. In addition, most of the telemetry nests in that area were at relatively high elevations where there were fewer predators than at low valley-bottom elevations (Bradley 2002). We suggest that in low-elevation habitats, such as those sampled in our study, predation risk to murrelets is high, and forest fragmentation and edge effects contribute to reduced nesting success. Most of the murrelet nest sites and available nesting habitats in B.C. are likely to fall within such low-elevation areas, below 600 m, especially in watersheds which have experienced little timber extraction (Burger 2002).

Implications for the Management of Marbled Murrelets

Our data indicate a widespread distribution of potential predators in forests used for nesting by marbled murrelets. Steller's jays and common ravens had higher occurrence and relative abundance at stations where the forest had been disturbed by clearcuts or roads, but other predators showed no consistent effects of such disturbance. As discussed above, our study had many limitations and did not consider the entire suite of predators likely to affect murrelets. Nevertheless, there is strong evidence that jays and ravens are likely to be important predators of nesting marbled murrelets (Nelson 1997; Luginbuhl et al. 2001; Burger 2002; Raphael et al. 2002). This suggests that predation risk to murrelets and other birds is likely to be higher near forest edges bordering recent clearcuts and roads, and our pilot experiment with artificial nests supported this notion.

We therefore recommend that forest managers (a) consider the effects of fragmentation and forest edges in determining the size and location of habitats to be maintained for nesting marbled murrelets, such as Wildlife Habitat Areas (WHAs); (b) include measures of predator abundance when considering options for maintained murrelet habitat; (c) avoid having roads within maintained murrelet habitat; and (d) disallow human activities that are likely to attract corvids (e.g., camping, picnicking, boat launching) in maintained murrelet habitat. We also support expanded research in coastal B.C. to resolve the sometimes conflicting evidence on the effects of edges and fragmentation on marbled murrelets and other forest-nesting birds.

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References

- Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794–804.
- Andren, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225–255 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London.
- Batáry, P., and A. Báldi. 2004. Evidence of an edge effect on avian nest success. *Conservation Biology* **18**:389–400.
- Beissinger, S.R., and N. Nur. 1997. Appendix B: population trends of the marbled murrelet projected from demographic analysis. Pages B1–B35 in U.S. Fish and Wildlife Service. *Recovery plan for the threatened marbled murrelet (*Brachyramphus marmoratus*) in Washington, Oregon and California*. U.S. Fish and Wildlife Service, Portland, Oregon.
- Bradley, J.E., and J.M. Marzluff. 2003. Rodents as nest predators: influences on predatory behavior and consequences to nesting birds. *Auk* **120**:1180–1187.
- Bradley, R.W. 2002. Breeding ecology of radio-marked marbled murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. MSc thesis. Simon Fraser University, Burnaby, British Columbia.
- Bryant, A.A. 1994. Montane alternative silvicultural systems (MASS): pre-treatment breeding bird communities. FRDA report No. 216. Canadian Forest Service and British Columbia Ministry of Forests, Victoria, British Columbia.
- Burger, A.E. 2002. Conservation assessment of marbled murrelets in British Columbia: review of the biology, populations, habitat associations, and conservation. Technical Report Series No. 387, Canadian Wildlife Service, Delta, British Columbia. Available from <http://www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm>
- Burger, A.E. and V. Bahn. 2004. Inland habitat associations of marbled murrelets on southwest Vancouver Island, British Columbia. *Journal of Field Ornithology* **75**:53–66.
- Burger, A.E., V. Bahn and A.R.M. Tillmanns. 2000. Comparison of coastal fringe and interior forests as reserves for marbled murrelets on Vancouver Island. *Condor* **102**:915–920.
- Cam, E., L. Loughheed, R. Bradley, and F. Cooke. 2003. Demographic assessment of a marbled murrelet population from capture-recapture data. *Conservation Biology* **17**:1118–1126.

- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, M.C.E. McNall, and G.E.J. Smith. 1997. The birds of British Columbia. Vol. 3. University of British Columbia Press, Vancouver, British Columbia.
- Canadian Marbled Murrelet Recovery Team. 2003. Marbled murrelet conservation assessment 2003, Part B—Marbled Murrelet Recovery Team advisory document on conservation and management. Canadian Wildlife Service, Delta, British Columbia. Available from <http://www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm>
- Chalfoun, A.D., F.R. Thompson, and M.J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* **16**:306–318.
- De Santo, T.L., and S.K. Nelson. 1995. Comparative reproductive ecology of the Auks (family Alcidae) with emphasis on the marbled murrelet. Pages 33–47 in C. J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, editors. *Ecology and conservation of the marbled murrelet*. General Technical Report PSW-GTR-152. U.S. Forest Service, Albany, California.
- De Santo, T.L., and M.F. Willson. 2001. Predator abundance and predation of artificial nests in natural and anthropogenic coniferous forest edges in southeast Alaska. *Journal of Field Ornithology* **72**:136–149.
- Haskell, D.G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* **9**:1316–1318.
- Gutzwiller, K.J., S.K. Riffell, and S.H. Anderson. 2002. Repeated human intrusion and the potential for nest predation by gray jays. *Journal of Wildlife Management* **66**:372–380.
- Luginbuhl, J.M., J.M. Marzluff, J.E. Bradley, M.G. Raphael, and D.E. Varland. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. *Journal of Field Ornithology* **72**:556–572.
- Manley, I.A. 1999. Behaviour and habitat selection of marbled murrelets nesting on the Sunshine Coast. MSc thesis. Simon Fraser University, Burnaby, British Columbia.
- Manley, I.A., and S.K. Nelson. 1999. Habitat characteristics associated with nest success and predation at marbled murrelet tree nests (Abstract). *Pacific Seabirds* **26**:40.
- Marzluff, J.M., R.B. Boone, and G.W. Cox. 1994. Native pest bird species in the west: why have they succeeded where so many have failed. *Studies in Avian Biology* **15**:202–220.
- Marzluff, J.M., M.G. Raphael, and R. Sallabanks. 2000. Understanding the effects of forest management on avian species. *Wildlife Society Bulletin* **28**:1132–1143.
- Marzluff, J.M., and M. Restani. 1999. The effects of forest fragmentation on avian nest predation. Pages 155–169 in J.L. Rochelle, L.A. Lehmann, and J. Wisniewski, editors. *Forest fragmentation: wildlife and management implications*. Brill, Leiden.
- Masselink, M.N.M. 2001. Responses by Steller's jay to forest fragmentation on southwest Vancouver Island and potential impacts on marbled murrelets. MSc thesis. University of Victoria, Victoria, British Columbia.

- Meidinger, D., and J. Pojar, editors. 1991. Ecosystems of British Columbia. Special Report Series No. 6. British Columbia Ministry of Forests, Victoria, British Columbia.
- Nelson, S.K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). Pages 1–32 in A. Poole and F. Gill, editors. The Birds of North America, No. 276. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C.
- Nelson, S.K. and T.E. Hamer. 1995. Nest success and the effects of predation on marbled murrelets. Pages 89–97 in C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, editors. Ecology and conservation of the marbled murrelet. General Technical Report PSW-GTR-152. U.S. Forest Service, Albany, California.
- Paton, P.W.C. 1994. The effect of an edge on avian nest success: how strong is the evidence? *Conservation Biology* **8**:17–26.
- Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin and D.F. DeSante. 1993. Handbook of field methods for monitoring landbirds. General Technical Report PSW-GTR-144. U.S. Forest Service, Albany, California.
- Ralph, C.J., G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt. 1995. Overview of the ecology and conservation of the marbled murrelet in North America. Pages 3–22 in C.J. Ralph, G.L. Hunt, Jr., M.G. Raphael and J.F. Piatt, editors. Ecology and conservation of the marbled murrelet. General Technical Report PSW-GTR-152. U.S. Forest Service, Albany, California.
- Raphael, M.G., D. Evans Mack, J.M. Marzluff, and J.M. Luginbuhl. 2002. Effects of forest fragmentation on populations of the marbled murrelet. *Studies in Avian Biology* **25**:221–235.
- Resources Inventory Committee (RIC). 1997. Standardized inventory methodologies for components of British Columbia's biodiversity: marbled murrelets in marine and terrestrial habitats. Version 1.1. Publication No. 208, B.C. Resources Inventory Committee, British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia.
- Resources Inventory Committee (RIC). 2001. Inventory methods for marbled murrelets in marine and terrestrial habitats, Version 2.0. Standards for components of British Columbia's biodiversity, No. 10. British Columbia Ministry of Environment, Lands and Parks, Resources Inventory Committee, Victoria, British Columbia. Available from <http://srmwww.gov.bc.ca/risc/pubs/tebiodiv/m>
- Rodway, M.S., and H.M. Regehr. 2002. Inland activity and forest structural characteristics as indicators of marbled murrelet nesting habitat in Clayoquot Sound. Pages 57–87 in A. E. Burger and T.A. Chatwin, editors. Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. British Columbia Ministry of Water, Land and Air Protection, Victoria, British Columbia.

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