COMPARISON OF COASTAL FRINGE AND INTERIOR FORESTS AS RESERVES FOR MARBLED MURRELETS ON VANCOUVER ISLAND[1]

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Abstract. Much of the protected habitat available to the threatened Marbled Murrelet *Brachyramphus marmoratus* and other old-growth associated species in the Pacific Northwest is in narrow strips along the coast (e.g., parks and scenic fringes). Using data over two years from three watersheds on southwest Vancouver Island, we show that such shoreline strip forests represent suboptimal habitat for murrelets. Murrelet detections, including circling and subcanopy behaviors, were significantly lower at 30 coastal stations (20–250 m from the shoreline edge) than at 30 interior stations (1.5–21.0 km inland). Densities of predators were significantly higher at the coastal stations. The coastal trees were of similar mean height and diameter, but they had lower structural diversity and provided fewer and less suitable (thinner epiphyte cover on large boughs) nesting platforms than trees in the interior. When possible, reserves for Marbled Murrelets should be placed in interior and not shoreline forests.

Key words: Brachyramphus marmoratus, coastal forests, Marbled Murrelet, nesting, Vancouver Island.

Many parks and other protected areas along the coast of the Pacific Northwest consist of narrow strips of old-growth forest bordering the ocean. These strips serve as recreation areas and "scenic fringes" in areas frequented by tourists, or protect sensitive shoreline areas and fish spawning sites when clearcut logging occurs. Such strips of forest are usually included in the inventory of habitat available for the Marbled Murrelet *Brachyramphus marmoratus,* and other old-growth associated species. There is evidence from the Queen Charlotte Islands (Rodway et al. 1991), Vancouver Island (Rodway and Regehr 1999), and Washington state (Hamer 1995) that shoreline fringe forests might not provide optimal nest habitats for murrelets. In this paper we specifically address this issue by comparing murrelet detection rates, habitat measures, and densities of predators at shoreline and interior sites in three watersheds on Vancouver Island.

Marbled Murrelets are listed as threatened through most of their range in the Pacific Northwest, apart from Alaska (Ralph et al. 1995). Loss of nesting habitat through logging of old-growth forest is the greatest threat (Ralph et al. 1995, Nelson 1997), but increased predation at nests, due to edge-effects created by clear-

cut logging, is an additional problem (Nelson and Hamer 1995, Manley 1999). At sea, oil pollution, gill nets, and aquaculture pose problems for murrelets (Ralph et al. 1995). The high economic value of the forests in which murrelets nest ensures conflicts between conservation and timber extraction priorities. In both Canada and the U.S., there are procedures for protecting the murrelet's nesting habitat, but it is critically important that the protected areas meet the murrelet's nesting habitat requirements and do not have unusually high densities of predators. Our study therefore focused on the adequacy of shoreline strip forests as reserves for murrelets. Conservation efforts adequately addressing the murrelet's complex and spacious habitat requirements usually benefit other old-growth associated species.

METHODS

Our study area on southwestern Vancouver Island, British Columbia, included large tracts of coniferous old-growth forest which support one of the largest populations of Marbled Murrelets south of Alaska (Burger 1995). Coastal observation stations were paired, with one station 20 m and another 250 m from the shoreline forest edge, and each pair spaced at least 0.5 km apart along the coast. Two observers sampled murrelet activities at each pair of stations on the same morning. Interior stations were selected to represent a range of habitat types and distances from the coast. In 1998 we compared 14 coastal stations (7 pairs) with 14 interior stations (7–21 km inland) in the abutting Carmanah and Walbran watersheds. In 1999 we compared 16 coastal stations (8 pairs) with 16 interior stations (1.5–10 km inland) in the Klanawa watershed and the adjacent shoreline. Each of the 30 survey stations was sampled three times in a single season, at intervals >14 days, within the core of the breeding season (mid-May through mid-July). To test for annual variations in detections, we repeated the three surveys at the 14 interior Carmanah-Walbran stations in 1999.

To determine the presence and relative densities of Marbled Murrelets in forests, we followed the Pacific Seabird Group Inland Protocol (Ralph et al. 1994), modified for British Columbia (RIC 1997). The number of visual and auditory detections (Paton 1995) of murrelets was recorded during 2-hr surveys spanning sunrise. Some detections of murrelets (e.g., subcanopy and circling flights) were classified as "occupied behaviors" associated with nesting and near-nest behav-

ior (Paton 1995). Detections were recorded by trained and experienced observers using tape recorders, transcribed on to standard data sheets and later to spreadsheets. We also recorded the occurrence and numbers of potential predators (crows, ravens, jays, owls, eagles, falcons, accipiters, and squirrels; Nelson 1997) during the dawn surveys. We set no limits on the distance for detecting predators, but most were within 100 m; we did not use taped calls to attract them.

As an additional measure of murrelet activity, we calculated the ratio of occupied detections to all visual detections. This ratio is meant to identify stations with a high amount of occupied activity independent of the total visible activity observed, which is sometimes higher in flight corridors (Rodway and Regehr 1999). The ratio also compensates for differences in canopy openings at observation stations, which might affect the visibility and likelihood of detecting occupied behaviors. The obstruction of the visual field at observation stations was estimated in categories from 1–4 which corresponded to a projected canopy cover of 0–25%, 26–50%, 51–75%, and 76–100%, respectively.

We recorded habitat measures relevant to murrelet nesting in 30 × 30-m plots in the forest stand nearest each survey station, following the standard protocol in British Columbia (RIC 1997). Within each plot we recorded the species, diameter at breast height (dbh), and height of all trees larger than 10 cm dbh, and the number of snags >5 m tall. Tree heights were visually estimated after using a clinometer to establish the heights of 2–4 representative trees. Canopy closure (% projected canopy cover) was estimated at 4–6 random locations within the plot, then averaged. Within each tree, we recorded features important for nesting by murrelets (Hamer and Nelson 1995), including: the number of potential nest platforms (limbs >15 m above ground and >18 cm in diameter, without making judgements about suitability as nest sites); estimated epiphyte cover (0 = none; 1 = trace; 2 = 1–33% cover; 3 = 34–66%; 4 = 67–100%), epiphyte thickness (1 = sparse, 2 = intermediate, and 3 = thick mats), and mistletoe infestation (Hawksworth 1977). In this last parameter, the live crown was divided into vertical thirds, and, for each third, mistletoe was scored as: 0 = no visible infections, 1 = light infections (half or less of branches infected), or 2 = heavy infections (more than half infected). The total score was then added to give a range of scores from 0 to 6 and averaged for the whole plot.

STATISTICAL ANALYSES

Data were analyzed with SPSS 9.0. Variables not normally distributed were log-transformed, or if transformation failed to produce normality, were analyzed with nonparametric tests. To compare coastal with interior stations we used Student's t-tests (normal and transformed data) or Mann–Whitney tests (non-normal data untransformed). We used separate variances t-tests whenever Levene's test for equality of variances had a $P < 0.05$. To compare the paired coastal stations (20 m and 250 m), where each pair was sampled on the same day, we used paired t-tests (normal or transformed data) or Wilcoxon signed rank tests (non-normal data). All tests were two-tailed. We tested correlations between variables at interior stations and distance from the ocean using Pearson correlation (r) for normally distributed data and Spearman rank correlation (r_s) for non-normal data. Means are given ± SD. The level of statistical significance was $P < 0.05$.

RESULTS

COASTAL AND INTERIOR SITES COMPARED

At 14 interior stations in Carmanah-Walbran sampled three times in each year, we found no significant differences between years for total detections per survey (mean 1998: 21.1 ± 8.9, 1999: 20.6 ± 8.6; paired t-test, $t_{13} = 0.17$, $P > 0.50$), occupied detections per survey (mean 1998: 2.6 ± 2.5, 1999: 4.4 ± 3.8; $t_{13} = 1.62$, $P > 0.10$), and subcanopy detections per survey (mean 1998: 2.0 ± 2.1, 1999: 3.2 ± 3.0; $t_{13} = 1.20$, $P > 0.20$). We assumed similar lack of annual variation at other stations and pooled data from both years. Our sample was thus 30 coastal and 30 interior stations, each sampled three times in a single year. Five surveys were missed due to inclement weather and so we had a total of 88 surveys at the coast and 87 in the interior.

Detections of Marbled Murrelets per survey were higher at interior than coastal stations (Table 1). Of greatest relevance was the difference in occupied and subcanopy detections, as indicators of likely nesting activity, which were both more than five times higher in the interior than at the coast. All 87 surveys in the interior recorded murrelet detections, 49% recorded occupied detections, and 43% recorded subcanopy detections compared to 85%, 19%, and 16%, respectively in the 88 coastal surveys.

The mean canopy closure at observation stations was higher at the coast than in the interior (Table 1), which might have affected visibility and hence detection rates. We tested the effects of visibility two ways. First, using an ANOVA with canopy closure as a covariate, significant differences persisted between interior and coastal stations in total ($F_{1,57} = 25.1$, $P < 0.001$), occupied ($F_{1,57} = 8.7$, $P = 0.001$), and subcanopy detections ($F_{1,57} = 7.8$, $P = 0.001$). The variables violated assumptions used in ANOVA (they were not normally distributed and had unequal variances), but when sample sizes in groups are equal the ANOVA is robust despite these violations (Zar 1996). Second, we controlled visibility by considering the ratio of occupied to all visible detections. The differences between the interior and coast persisted (Table 1), indicating that they were not just an artifact of visibility.

Predator densities were three times higher at the coast than at interior stations (Table 1). Predators were reported in 88% of the coastal surveys but only 58% of the interior surveys. These results were mainly due to the high numbers of Northwestern Crows (*Corvus caurinus*) and Bald Eagles (*Haliaeetus leucocephalus*) at the coast. Both are primarily shoreline scavengers and seldom venture far inland, although both were seen at interior stations on rare occasions.

The comparison of vegetation attributes between coastal and interior stations yielded varying results (Table 1). We found no significant difference between the interior and coast in the mean height or diameter of trees, or tree density, but there was a higher density of larger trees (>80 cm dbh) at interior stations, which contributed to a higher mean basal area in the interior.

TABLE 1. Comparison of Marbled Murrelet activity, predator densities, and habitat characteristics at coastal vs. interior stations, and at coastal stations 20 m inland vs. 250 m inland. Means ± SD shown.

Variable	Interior	Coast	Statistic	20-m stations	250-m stations	Statistic
Measures of murrelet activity per survey						
Total detections[a]	19.89 ± 13.49	6.64 ± 6.04	$t_{58} = 6.54**$	5.12 ± 6.64	8.17 ± 5.15	$t_{14} = 3.92**$
Occupied detections	2.90 ± 4.61	0.50 ± 0.97	$Z_{32} = 2.91**$	0.51 ± 1.11	0.49 ± 0.83	$Z_{14} = 0.06$
Subcanopy detections	1.95 ± 2.92	0.38 ± 0.71	$Z_{32} = 2.91**$	0.36 ± 0.78	0.40 ± 0.66	$Z_{14} = 0.51$
Ratio of occupied to visual detections	0.23 ± 0.20	0.09 ± 0.14	$Z_{51} = 2.85**$	0.08 ± 0.13	0.10 ± 0.16	$Z_{14} = 0.47$
Relative density of predators						
Predators per survey	1.36 ± 1.23	4.18 ± 2.40	$t_{43} = 5.73**$	4.56 ± 2.72	3.80 ± 2.04	$t_{14} = 0.99$
Forest stand characteristics						
Canopy closure in plot (% tree cover)	63.71 ± 12.13	59.67 ± 13.58	$t_{57} = 1.20$	59.00 ± 14.78	60.33 ± 12.74	$t_{14} = 0.26$
Canopy closure index at observation site	1.17 ± 0.38	2.10 ± 0.71	$t_{58} = 6.34**$	2.13 ± 0.92	2.07 ± 0.46	$t_{14} = 0.24$
Mean tree height (m)	27.35 ± 5.86	28.82 ± 11.98	$t_{42} = 0.60$	28.27 ± 10.56	29.38 ± 13.61	$t_{14} = 0.64$
SD of tree height	15.10 ± 3.14	11.90 ± 4.39	$t_{53} = 3.23**$	12.32 ± 4.24	11.47 ± 4.65	$t_{14} = 0.96$
Mean diameter at breast height, dbh (cm)	55.61 ± 14.86	51.64 ± 15.74	$t_{57} = 0.99$	51.21 ± 18.31	52.07 ± 13.34	$t_{14} = 0.20$
SD of dbh	46.83 ± 14.32	37.94 ± 12.15	$t_{57} = 2.58*$	37.86 ± 13.80	38.02 ± 10.74	$t_{14} = 0.05$
Basal area all trees (m² ha⁻¹)	14.21 ± 5.39	9.38 ± 2.63	$t_{40} = 4.35**$	8.14 ± 2.47	10.62 ± 2.22	$t_{14} = 2.67*$
Density of all trees >10 cm dbh (trees ha⁻¹)	407.1 ± 149.4	364.8 ± 195.2	$t_{57} = 0.93$	308.9 ± 181.0	420.7 ± 198.7	$t_{14} = 2.59*$
Density of large trees >80 cm dbh (trees ha⁻¹)	85.44 ± 26.37	55.93 ± 19.02	$t_{57} = 4.94**$	53.33 ± 23.08	58.52 ± 14.22	$Z_{14} = 0.88$
Density of snags (snags ha⁻¹)	32.76 ± 32.06	27.04 ± 30.97	$Z_{57} = 0.64$	17.78 ± 14.43	36.30 ± 39.94	$Z_{14} = 1.69$
Tree species density (trees ha⁻¹)						
Amabilis fir Abies amabilis	109.4 ± 114.9	16.30 ± 35.94	$Z_{33} = 4.98**$	3.70 ± 9.07	28.89 ± 47.48	$Z_{14} = 2.04$
Western red-cedar Thuja plicata	58.05 ± 98.67	81.48 ± 132.7	$Z_{57} = 0.35$	49.63 ± 83.13	113.3 ± 165.6	$Z_{14} = 1.69$
Western hemlock Tsuga heterophylla	208.2 ± 100.2	119.6 ± 142.9	$t_{52} = 2.76**$	115.6 ± 151.4	123.7 ± 139.1	$Z_{14} = 0.28$
Sitka spruce Picea sitchensis	18.97 ± 36.96	17.04 ± 32.72	$Z_{57} = 0.03$	29.63 ± 42.14	4.44 ± 10.11	$Z_{14} = 2.37*$
Canopy microhabitat characteristics						
Density of potential platforms ha⁻¹	1,566 ± 681.6	722.5 ± 596.1	$t_{57} = 5.06**$	715.4 ± 598.6	729.6 ± 614.6	$t_{14} = 0.25$
Density of trees with two or more platforms (trees ha⁻¹)	75.48 ± 63.16	13.70 ± 18.15	$Z_{32} = 5.02**$	10.37 ± 10.68	17.04 ± 23.33	$Z_{14} = 0.52$
Epiphyte cover index	3.00 ± 0.59	2.83 ± 0.79	$t_{57} = 0.90$	2.72 ± 0.82	2.95 ± 0.76	$t_{14} = 0.75$
Epiphyte thickness index	1.80 ± 0.39	1.73 ± 0.41	$t_{57} = 0.71$	1.55 ± 0.39	1.90 ± 0.35	$t_{14} = 2.89*$
Epiphyte thickness index on large trees >80 cm dbh	2.51 ± 0.56	2.04 ± 0.58	$Z_{57} = 3.28**$	1.80 ± 0.60	2.27 ± 0.47	$t_{14} = 2.65*$
Mistletoe index	0.27 ± 0.25	0.35 ± 0.60	$Z_{39} = 1.26$	0.30 ± 0.67	0.41 ± 0.55	$t_{14} = 0.53$

[a] Log transformed before analysis.
* $P \leq 0.05$, ** $P < 0.01$.

The size of trees and the shape of the canopy were more variable in the interior, as indicated by significant differences in the SDs of tree height and dbh. Species composition varied somewhat between the coast and interior: we found higher densities of western hemlock (*Tsuga heterophylla*) and amabilis fir (*Abies amabilis*) in the interior than at the coast, but no differences in densities of Sitka spruce (*Picea sitchensis*) or western red-cedar (*Thuja plicata*).

The canopy microhabitat provided more potential nest sites in the interior than at the coast: both the density of potential platforms per hectare, and the density of trees with two or more potential platforms were higher inland (Table 1). Most of the measures of epiphyte cover were similar in both areas, but mean epiphyte thickness on large trees, in which murrelets would most likely nest, was higher in the interior than at the coast. Mistletoe sometimes created platforms suitable for nesting by murrelets but was relatively rare, restricted to hemlock trees, and found in similar amounts in both areas (Table 1).

COMPARISON AMONG COASTAL STATIONS

The mean frequency of all murrelet detections (log transformed) was significantly higher at the 250-m than at the 20-m stations, but occupied and subcanopy detections, and the ratio of occupied to all visual detections did not differ significantly (Table 1). Densities of predators were similar at both sets of stations. Crows and eagles were regularly seen roosting and moving about in the canopy at the 250-m stations, indicating high risk to murrelets nesting there. In general there were few significant differences in habitat measures between the two sets of stations, although tree density and basal area were lower at 20-m than 250-m stations, and Sitka spruce was more common at 20-m than 250-m. Epiphyte thickness scored slightly lower at 20-m than 250-m, probably as a result of inhibition by salt spray. Other measures of canopy microhabitat were similar at the two distances, and both had similar densities of potential platforms and trees with two or more potential platforms.

EFFECT OF DISTANCE FROM SEA AT INTERIOR STATIONS

Among the 30 interior stations we found no significant correlations with increasing distance from the sea for any of the murrelet activity measures or most of the habitat variables. Significant positive correlations with distance from sea were found for snag density (r_s = 0.73, n = 30, P < 0.001) and density of trees with two or more platforms (r_s = 0.56, n = 30, P < 0.01). Negative correlations were found for predator densities (r = −0.52, n = 30, P < 0.01) and mistletoe score (r_s = −0.38, n = 30, P < 0.05). With increasing distance from the sea the density of western red-cedar declined (r_s = −0.54, n = 30, P < 0.01), but amabilis fir increased (r_s = 0.46, n = 30, P < 0.05), and Sitka spruce and western hemlock were unaffected.

DISCUSSION

With data from two years and three watersheds we found that near-nest flight activity (occupied and subcanopy detections) of Marbled Murrelets was significantly less within 250 m of the coast than at interior stations. Although the exact relationship between detection frequencies and nest density is unknown (Paton 1995), these results suggest a significantly lower use of the coastal fringe for nesting than in the interior forests. Elsewhere on Vancouver Island, in Clayoquot Sound, Rodway and Regehr (1999) found significantly fewer occupied detections near ocean edges than farther inland. In Washington, Hamer (1995) observed no evidence of occupancy by murrelets within 800 m of the coast even though the vegetation characteristics indicated excellent habitat. Few nests have been found within 1 km of the ocean, except in parts of Alaska where there is frequently no suitable interior forest (Hamer and Nelson 1995, Manley 1999).

The low level of occupied behavior on the coast was partly due to habitat effects. We found significantly fewer of the microhabitat canopy features important to murrelets for nesting (Hamer and Nelson 1995, Nelson 1997, Manley 1999) at the coastal stations: fewer potential nest platforms, fewer trees with platforms, thinner epiphyte mats on the boughs of large trees, and less structural diversity in the canopy. A structurally diverse canopy improves access by murrelets to limbs suitable for nesting. Severe winter storms and year-round salt spray on the open Pacific coast undoubtedly inhibited epiphyte growth, blew off thick moss mats, pruned off dead limbs likely to provide platforms, and created a more uniform canopy surface. Foliage above nest platforms, providing protection from weather and reducing visibility to predators (Hamer and Nelson 1995, Nelson 1997, Manley 1999), appeared less common over platform limbs at the coast than in the interior, but we were not able to quantify this. At exposed coasts on the Queen Charlotte Islands, Rodway et al. (1991) found fewer murrelets and less suitable nesting habitat than farther inland, which they attributed to salt spray inhibiting moss growth.

A second factor associated with low murrelet activity near the coast was the high density of predators there, particularly Bald Eagles and Northwestern Crows. Both of these species are primarily shoreline scavengers and predators of marine organisms, but are likely to prey on murrelets if encountered in the forest canopy. Bald Eagles are effective predators of adult alcids at colonies (DeGrange and Nelson 1992), including those in forests (Kaiser 1989). Northwestern Crows are extremely opportunistic, and known to take eggs and chicks from alcids and forest nesting birds (Verbeek and Butler 1999). Other common nest predators, such as Steller's Jays (*Cyanocitta stelleri*), Common Ravens (*Corvus corax*), and red squirrels (*Tamiasciurus hudsonicus*) were no more common at the coast than in the interior (A. E. Burger, unpubl. data). Predators are the main cause of failure for breeding Marbled Murrelets, and were responsible for failure of 43% of 32 nests across the Pacific Northwest (Nelson and Hamer 1995), and 66% of 21 nests in British Columbia (Manley 1999). Rodway and Regehr (1999) observed high frequencies of predators at ocean edges in Clayoquot Sound, and Hamer (1995) speculated that high predator densities contributed to the lack of occupied behavior by murrelets along the Washington coast.

Marbled Murrelets are known to nest in most of the

large coniferous tree species (Nelson 1997). In our study area, Sitka spruce and western hemlock provided more potential nest sites than western red-cedar and amabilis fir (unpubl. data). We found higher densities of western hemlock and amabilis fir in the interior than at the coast, but no differences in densities of Sitka spruce or western red-cedar. Species composition therefore did not appear to be an important factor in murrelet habitat suitability.

Within the coastal strip, the occurrence and frequencies of occupied and subcanopy behaviors by murrelets, predator densities, and most habitat features were similar at the stations 20 m and 250 m from the forest edge. Epiphyte cover was thinner at the 20-m stations, but other microhabitat features were similar. The deleterious effects of the exposed shore and the high densities of eagles and crows extended at least 250 m inland. Among the 30 interior stations there was a significant increase in density of trees with two or more platforms, and a decrease in predator density, with increasing distance from the sea, suggesting that these might have been clinal effects not entirely restricted to the 250-m wide coastal strip. Murrelet detections and most other critical nest habitat features showed no correlation with distance from the sea within the interior stations, suggesting that those coastal effects did not extend beyond 1.5 km inland. Unfortunately, lack of roads or hiking trails made it impossible to sample habitats from 250 m to 1.5 km inland, so we could not test how far inland all the shoreline effects extended.

The differences between coastal and interior stations were not due to habitat fragmentation or artificial edge-effects caused by logging or road-building. All the stations, except some in the interior Klanawa Valley, were in continuous large tracts of forests (>1,000 ha) and not in isolated stands. The interior forests were therefore more suitable for murrelets, despite some fragmentation and loss of habitat.

Our coastal stations were all within Pacific Rim National Park. Much of this park is a narrow coastal strip less than 1 km wide. Elsewhere on Vancouver Island (e.g., Clayoquot Sound), the Olympic Peninsula in Washington, and in other parts of the Pacific Northwest, similar coastal strips have been protected. These strips are included in the protected habitat considered to be available for Marbled Murrelets, but our data suggest that these shoreline strips are unlikely to support viable populations of Marbled Murrelets. Furthermore, future protection of habitat, such as the implementation of the British Columbia Forest Practices Code, should consider coastal strips as suboptimal habitat. Our research shows that the shoreline effects extend at least 250-m inland, and further research is needed to establish the limits of these effects wherever murrelets might be nesting. As an interim measure, we suggest placing protected areas for murrelets >1 km inland.

LITERATURE CITED

BURGER, A. E. 1995. Marine distribution, abundance, and habitats of Marbled Murrelets in British Columbia, p. 295–312. In C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt [EDS.], Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152, Pacific Southwest Res. Sta., Forest Serv., U.S. Dept. Agriculture, Albany, CA.

DEGRANGE, A. R., AND J. W. NELSON. 1982. Bald Eagle predation on nocturnal seabirds. J. Field Ornithol. 53:407–409.

HAMER, T. E. 1995. Inland habitat associations of Marbled Murrelets in western Washington, p. 163–175. In C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt [EDS.], Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152, Pacific Southwest Res. Sta., Forest Serv., U.S. Dept. Agriculture, Albany, CA.

HAMER, T. E., AND S. K. NELSON. 1995. Characteristics of Marbled Murrelet nest trees and nesting stands, p. 69–82. In C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt [EDS.], Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152, Pacific Southwest Res. Sta., Forest Serv., U.S. Dept. Agriculture, Albany, CA.

HAWKSWORTH, F. G. 1977. The 6-class dwarf mistletoe rating system. Gen. Tech. Rep. RM-48. Rocky Mountain Res. Sta., Forest Service, U.S. Dept. Agriculture, Fort Collins, CO.

KAISER, G. W. 1989. Nightly concentration of Bald Eagles at an auklet colony. Northwestern Naturalist 70:12–13.

MANLEY, I. A. 1999. Behaviour and habitat selection of Marbled Murrelets nesting on the Sunshine Coast. M.Sc. thesis, Simon Fraser Univ., Burnaby, B.C., Canada.

NELSON, S. K. 1997. Marbled Murrelet (Brachyramphus marmoratus). In A. Poole and F. Gill [EDS.], The birds of North America, No. 276. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.

NELSON, S. K., AND T. E. HAMER. 1995. Nest success and the effects of predation on Marbled Murrelets, p. 89–97. In C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt [EDS.], Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152, Pacific Southwest Res. Sta., Forest Serv., U.S. Dept. Agriculture, Albany, CA.

PATON, P. W. C. 1995. Marbled Murrelet inland patterns of activity: defining detections and behavior, p. 113–116. In C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt [EDS.], Ecology and con-

servation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152, Pacific Southwest Res. Sta., Forest Serv., U.S. Dept. Agriculture, Albany, CA.

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, p. 3–22. *In* C. J. Ralph, G. L. Hunt Jr., M. G. Raphael, and J. F. Piatt [EDS.], Ecology and conservation of the Marbled Murrelet. Gen. Tech. Rep. PSW-GTR-152, Pacific Southwest Res. Sta., Forest Serv., U.S. Dept. Agriculture, Albany, CA.

RALPH, C. J., S. K. NELSON, M. M. SHAUGHNESSY, S. L. MILLER, AND T. E. HAMER. 1994. Methods for surveying Marbled Murrelets in forests. Pacific Seabird Group, Marbled Murrelet Technical Committee, Tech. Paper No. 1. Oregon Co-operative Wildl. Res. Unit, Oregon State Univ., Corvallis, OR.

RIC (RESOURCES INVENTORY COMMITTEE). 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, Ministry of Environment, Lands and Parks, Victoria, B.C., Canada.

RODWAY, M. S., AND H. M. REGEHR. 1999. Inland inventory: Marbled Murrelet activity and structural characteristics of old-growth forests in Clayoquot Sound, British Columbia, 1995–1997, p. 119–236. *In* T. A. Chatwin, A. E. Burger, and L. E. Jones [EDS.], Inventory of Marbled Murrelets in Clayoquot Sound, 1997. Unpublished report to B.C. Ministry of Environment, Lands and Parks, Vancouver Island Regional Office, Nanaimo, B.C., Canada.

RODWAY, M. S., J.-P. L. SAVARD, AND H. M. REGEHR. 1991. Habitat use and activity patterns of Marbled Murrelets at inland and at-sea sites in the Queen Charlotte Islands, British Columbia. Tech. Rep. Ser. No. 122. Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C., Canada.

VERBEEK, N. A. M., AND R. W. BUTLER. 1999. Northwestern Crow (*Corvus caurinus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 407. Birds of North America, Inc., Philadelphia.

ZAR, J. H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall, Upper Saddle River, NJ.

CORRELATES OF HARLEQUIN DUCK DENSITIES DURING WINTER IN PRINCE WILLIAM SOUND, ALASKA[1]

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Abstract. We evaluated relationships of Harlequin Duck (*Histrionicus histrionicus*) densities to habitat attributes, history of habitat contamination by the 1989 *Exxon Valdez* oil spill, and prey biomass density and abundance during winters 1995–1997 in Prince William Sound, Alaska. Habitat features that explained variation in duck densities included distance to streams and reefs, degree of exposure to wind and wave action, and dominant substrate type. After accounting for