Chapter 6

Characteristics of Marbled Murrelet Nest Trees and Nesting Stands

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Abstract: We summarize the characteristics of 61 tree nests and nesting stands of the Marbled Murrelet (*Brachyramphus marmoratus*) located from 1974 to 1993 in Alaska, British Columbia, Washington, Oregon, and California. Evidence of breeding 30-60 km inland was common in California, Oregon, and Washington. Nesting greater distances from the coast may have evolved to avoid nest predation by corvids and gulls which are more abundant in coastal areas. In California, Oregon, Washington, and British Columbia, murrelets nested in low elevation old-growth and mature coniferous forests, with multi-layered canopies (>2), a high composition of low elevation conifer trees ($\bar{x}$ = 91 percent) and, on the lower two-thirds of forested slopes, with moderate gradients ($\bar{x}$ = 23 percent slope). Stand canopy closure was often low ($\bar{x}$ = 50 percent), suggesting use of canopy openings for access to nest platforms. Nests in the Pacific Northwest were typically in the largest diameter old-growth trees available in a stand ($\bar{x}$ = 211 cm); many nest trees were in declining conditions and had multiple defects. It is likely that western hemlock and Sitka spruce constitute the most important nest trees, with Douglas-fir important south of British Columbia. Many processes contributed to creating the nest platforms observed. Mistletoe blooms, unusual limb deformations, decadence, and tree damage, commonly observed in old-growth and mature stands, all appear to create nest platforms. Therefore, the stand structure and the processes within a stand may be more important than tree size alone in producing nesting platforms and suitable habitat. Moss cover was also an important indicator of suitable nesting habitat.

We summarize the characteristics of 61 tree nests and nesting stands of the Marbled Murrelet (*Brachyramphus marmoratus*) located from 1974 to 1993 in Alaska, British Columbia, Washington, Oregon, and California (*table 1*). The majority of the nest site information was unpublished and obtained directly from field biologists who were conducting inland studies on the murrelet. The preponderance of unpublished nest information is due to the recent discovery of most nest sites. The only other summary was completed by Day and others (1983), based on two tree nests and five ground nests of the Marbled Murrelet.

Because of the murrelet's small body size, dense forested nesting habitat, cryptic plumage, crepuscular activity, fast flight speed, and secretive behavior near nests, its nests have been extremely difficult to locate. The first tree nest was located only in 1974 (Binford and others 1975), despite decades of searching by ornithologists in North America. Although a significant amount of nesting habitat information has been collected over the past four years, the efficiency of locating active nests is still low. Experiences gained from nest search efforts have led to the development and refinement of methodologies for locating new nests (Naslund and Hamer 1994).

Fortunately, an increased understanding of murrelet nesting ecology has allowed biologists to locate nests that have not been used for several months or, in some cases, several years. This involves searching for old nest cup depressions, worn spots or "landing pads" created on moss-covered branches by visiting adults, old fecal rings, and habitat features commonly associated with suitable nesting platforms. In addition, biologists learned that eggshells could be located in the duff and litter of nest platforms unused for a year or more.

Intensive search efforts by biologists across the Pacific Northwest have led to the discovery of 65 tree nests since 1974, with 63 (95 percent) located since 1990. Although this is still a relatively small sample size considering the large geographic area these nests represent, the sample does allow a characterization of the tree nests and nesting stands.

The two species of murrelets in the genus *Brachyramphus* (Kittlitz's and Marbled) display a complete dichotomy in their choice of nesting habitat. The Kittlitz's (*B. brevirostris*) murrelet nests up to 30 km inland on the ground on exposed rocky scree slopes, often at higher elevations. The Marbled Murrelet is unique among Alcids in selecting almost exclusively to nest on large limbs of dominant trees, which can be located long distances from the marine environment.

Long considered a subspecies of the Marbled Murrelet, the Asian race of the Marbled Murrelet (*B.m. perdix* Pallas) is distributed from the Kamchatka Peninsula south to Japan. New genetic evidence (Friesen and others 1994a) indicates the it is most likely a distinct species from the Marbled Murrelet. From the little evidence collected to date, it may be an obligate tree nesting seabird (Konyukhov and Kitaysky, this volume), with its range coinciding closely with the coastal coniferous forests of Russia and Japan (Kuzyakin 1963).

At a few sites in Alaska and Russia, at or beyond the margin of Pacific Coastal coniferous forests, the Marbled Murrelet nests on the ground. From an examination of the summer distribution of the species, approximately 3 percent of the Alaskan murrelet population may nest on the ground (Piatt and Ford 1993). These nests have been found at

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Table 1—Records of nest trees and nest stands of the Marbled Murrelet found in North America from 1974 to 1993

State/province Record no.	Location	Date found	Sources
California			
1	Big Basin Redwood State Park	7 Aug. 1974	Binford and others 1975
2	Big Basin Redwood State Park	3 Jun. 1989	S.W. Singer (pers. comm.)
3	Big Basin Redwood State Park	28 Jun. 1989	S.W. Singer (pers. comm.)
4	Big Basin Redwood State Park	5 May 1991	S.W. Singer (pers. comm.)
5	Big Basin Redwood State Park	24 May 1992	S.W. Singer (pers. comm.)
6	Jedediah Smith State Park	9 Aug. 1993	Hamer (pers. obs.)
7	Prairie Creek State Park	23 Jul. 1993	Hamer (pers. obs.)
8	Bell-Lawrence	14 Oct. 1993	Chinnici (pers. comm.)
9	Elk Head Springs	16 Sep. 1992	Chinnici (pers. comm.)
10	Shaw Creek	30 Sep. 1992	Chinnici (pers. comm.)
Oregon			
11	Boulder and Warnicke Creeks	17 Jun. 1992	Nelson (pers. obs.)
12	Cape Creek	23 May 1991	Nelson (pers. obs.)
13	Iron Mountain	30 May 1992	Nelson (pers. obs.)
14	Five Mile Flume Creek	28 Sep. 1993	Nelson (pers. obs.)
15	Five Rivers	19 May 1990	Nelson (pers. obs.)
16	Five Rivers	14 Jun. 1991	Nelson (pers. obs.)
17	Five Rivers	23 Sep. 1993	Nelson (pers. obs.)
18	Green Mountain	17 Jun. 1993	Nelson (pers. obs.)
19	Green Mountain	22 Sep. 1993	Nelson (pers. obs.)
20	Siuslaw River	13 Aug. 1991	Nelson (pers. obs.)
21	Siuslaw River	30 Aug. 1991	Nelson (pers. obs.)
22	Valley of the Giants	29 Jun. 1993	Nelson (pers. obs.)
23	Valley of the Giants	29 Jun. 1993	Nelson (pers. obs.)
24	Valley of the Giants	24 Aug. 1993	Nelson (pers. obs.)
25	Valley of the Giants	24 Aug. 1993	Nelson (pers. obs.)
26	Valley of the Giants	24 Aug. 1993	Nelson (pers. obs.)
27	Valley of the Giants	21 Sep. 1993	Nelson (pers. obs.)
28	Valley of the Giants	25 Aug. 1993	Nelson (pers. obs.)
29	Valley of the Giants	21 Sep. 1993	Nelson (pers. obs.)
30	Valley of the Giants	12 Jul. 1990	Nelson (pers. obs.)
31	Valley of the Giants	14 May 1991	Nelson (pers. obs.)
32	Valley of the Giants	14 Jul. 1992	Nelson (pers. obs.)
Washington			
33	Nemah River	7 May 1993	Ritchie (pers. comm.)
34	Lake 22 Creek	9 Jul. 1990	Hamer (pers. obs.)
35	Lake 22 Creek	2 Aug. 1990	Hamer (pers. obs.)
36	Dungeness River	10 Sep. 1990	Holtrop (pers. comm.)
37	Heart of the Hills Trail	26 Jul. 1991	Hamer (pers. obs.)
38	Jimmey Come Lately Creek	24 Jul. 1991	Holtrop (pers. comm.)

continues

Table 1—continued

State/province Record no.	Location	Date found	Sources
British Columbia			
39	August Creek, Vancouver Is.	12 Sep. 1993	Burger (pers. comm)
40	Carmanah Creek, Vancouver Is.	2 Oct. 1992	Jordan and Hughes (in press)
41	Walbran Creek, Vancouver Is.	12 Oct. 1992	Jordan and Hughes (in press)
42	Walbran Creek, Vancouver Is.	3 Aug. 1990	Manley and Kelson (in press)
43	Walbran Creek, Vancouver Is.	24 Aug. 1991	Manley and Kelson (in press)
44	Walbran Creek, Vancouver Is.	25 Aug. 1992	Jordan and Hughes (in press)
45	Caren Range	1 Aug. 1993	P. Jones (pers. comm)
46	Clayoquot River	1993	Kelson (pers. comm.)
47	Megin River	1993	Manley (pers. comm.)
Alaska			
48	Afognac Is., Alaska Peninsula	26 Jul. 1992	Naslund and others (in press)
49	Afognac Is., Alaska Peninsula	6 Aug. 1992	Naslund and others (in press)
50	Kodiak Is., Alaska Peninsula	17 Aug. 1992	Naslund and others (in press)
51	Kodiak Is., Alaska Peninsula	17 Aug. 1992	Naslund and others (in press)
52	Naked Is., Prince William Sound	13 Jun. 1991	Naslund and others (in press)
53	Naked Is., Prince William Sound	25 Jun. 1991	Naslund and others (in press)
54	Naked Is., Prince William Sound	6 Jul. 1991	Naslund and others (in press)
55	Naked Is., Prince William Sound	26 Jul. 1991	Naslund and others (in press)
56	Naked Is., Prince William Sound	1 Jul. 1991	Naslund and others (in press)
57	Naked Is., Prince William Sound	25 May 1992	Naslund and others (in press)
58	Naked Is., Prince William Sound	20 Jul. 1992	Naslund and others (in press)
59	Naked Is., Prince William Sound	5 Aug. 1992	Naslund and others (in press)
60	Naked Is., Prince William Sound	6 Aug. 1992	Naslund and others (in press)
61	Naked Is., Prince William Sound	9 Jun. 1991	Naslund and others (in press)

Augustine Island (Cook Inlet), Kodiak Island, the Barren Islands, and the Kenai Peninsula (Day and others 1983, Mendenhall 1992, Simons 1980). All of these nests were located in areas of talus where surrounding rocks formed a protected area for the nests, or in areas dominated by alder. The egg was laid on existing mat vegetation or bare soil. Whereas most of these sites were above the local tree line and had only low-lying mat vegetation, the Kenai site had a forested area on a nearby slope. An additional ground nest found on Prince of Wales Island in southeastern Alaska in 1993 was located on a platform of moss covering three intertwined roots of a western hemlock (*Tsuga heterophylla*) tree at the top of an 11-meter high cliff (Ford and Brown 1994). The nest had many of the characteristics of a tree nest when approached from down-slope, but was similar to a ground nest when approached from up slope.

Methods

We compiled information from 61 nest stands and nest trees throughout the geographic range of the Marbled Murrelet in North America using published and unpublished information. Information from three additional tree nests in Alaska were not obtained for this review. We did not include data from ground nests in this summary. We summarized tree and stand characteristics from 14 tree nests in Alaska (Naslund and others, in press), nine nests in British Columbia (Burger, pers. comm.; P. Jones, pers. comm.; Jordan and others in press; Kelson, pers. comm.; Manley, pers. comm.; Manley and Kelson, in press), six nests in Washington (Hamer, unpubl. data; Holtrop, pers. comm.; Ritchie, pers. comm.), 22 nests in Oregon (Nelson, unpubl. data), and 10 nests in California (Binford and others, 1975; Chinnici, pers. comm.; Folliard, pers. comm.; Hamer, unpubl. data; S.W. Singer, pers. comm.; Singer and others, 1991) (*table 1*).

The sample size for each nest characteristic varied because some variables were not measured at some nest sites, or the information was not available to us. A protocol that outlined a methodology for measuring the structure of nests was not available until 1993 (Hamer 1993), so some characteristics of earlier nests were not measured. Stands were delineated and stand sizes calculated generally by defining stands as a contiguous group of trees with no gaps larger than 100 m. Stand ages were derived from stand information data bases of the landowners or by aging individual trees in the stand using increment bores. Limb diameters were generally reported with the moss cover on the limb included in the measurement. Nest platform lengths were measured as the length of the nest branch until it was judged to be too narrow to support a nest (<10 cm).

We calculated the range, mean, and standard deviation for each nest and stand characteristic for each state or province. In addition, we pooled the sample of nests for what we term the "Pacific Northwest", using data from nests located in California, Oregon, Washington, and British Columbia (*tables 2* and *3*). Nests located in Alaska were treated as a separate sample (*tables 2* and *3*).

We chose to segregate the data using state or provincial boundaries because different forest types generally occur within these boundaries. Forest types in California within the murrelet's breeding range were predominately coastal redwood (*Sequoia sempervirens*). Oregon had fire regenerated stands dominated by Douglas-fir (*Pseudotsuga menziesii*), and in Washington, mixed forests of western red cedar (*Thuja plicata*), western hemlock, Douglas-fir, and Sitka spruce (*Picea sitchensis*), created by the combined forces of fire and wind, covered the majority of the landscape. British Columbia was similar to Washington, with the addition of yellow cedar (*Chamaecyparis nootkatensis*), found in stands at higher elevations. Forest types in Alaska were very distinct, with many stands dominated by mountain hemlock (*Tsuga mertensiana*) which were small in stature and diameter.

Results

Landscape Characteristics

Distance to Salt Water

A sample of 45 nests in the Pacific Northwest were located a mean distance of 16.8 km inland (*table 2*, *fig. 1*). Nests in California were found a mean distance of 13 km from salt water; the farthest inland nest in California was located 28.9 km inland (*table 2*). The farthest inland nest in Oregon was located 40 km from the sea. This coincides with a historical record of a downy young found on the ground 40 km inland on the South Fork of the Coos River in Coos County (Nelson and others 1992). In Washington, nests were located a mean distance of 16 km inland. Other information from Washington indicated nesting at stands further inland than known nest sites. A small downy chick was located by the senior author on the ground along a trail on the east shore of Baker Lake in 1991, 63 km from the ocean. Another downy chick was located 45 km inland in Helena Creek, in Snohomish County (Reed and Wood 1991). Six additional records of eggs, downy young, and fledglings found 29-55 km inland in Washington were compiled by Leschner and Cummins (1992a), and Carter and Sealy (1987b).

In British Columbia, nest trees were located a mean distance of 11.5 km from the Pacific. In addition, there was a record of a fledgling found on the ground near Hope, British Columbia, 101 km from salt water (Rodway and others 1991). This is the farthest inland distance recorded for Marbled Murrelets in North America. Nest trees in Alaska were typically located close to the coast, with a mean distance of 0.5 km (*table 2*), corresponding to the closer inland distribution of suitable nesting habitat.

Elevation

The mean elevation of nest trees from a sample of 45 murrelet nests in the Pacific Northwest was 332 m (*table 2*). In Alaska nest trees were low in elevation with a mean of 96 m and a maximum of 260 m (*table 2*).

Aspect

Nest stands in the Pacific Northwest occur on a variety of aspects. Twenty-six percent of the stands had northeast aspects, 12 percent southeast, 28 percent southwest, 12 percent northwest, and 21 percent were on flat topography with no aspect (*table 2*). In Alaska, 93 percent of the nest stands had westerly aspects (NW, W, or SW), with the majority (50 percent) facing northwest.

Slope

Nests in the Pacific Northwest were located on slopes with moderate gradients, with a mean of 23 percent. Slope gradients for nests in Alaska were higher than nests for the Pacific Northwest with a mean slope of 69 percent.

The majority of nests in the Pacific Northwest (80 percent) were located on the lower one-third or middle one-third of the slope. Nest stands in Alaska were located low in elevation, but were usually located on the top one-third of the slope, unlike nests in the southern part of the range. Nest stands in Alaska have been described as being located on gradual or moderate slopes (Naslund and others, in press).

Forest Characteristics

Age

For a sample of 16 nests in the Pacific Northwest the mean stand age was 522 years with the youngest stand age reported as 180 years old (*table 2*). The oldest stand was 1,824 years old located on the mainland coast of British Columbia, and was dated using nearby stumps from a recent clear-cut. To date, all 61 tree nests found in North America have been found in stands described as old-growth or mature forests.

Tree Size

The mean d.b.h. of trees in nest stands was not reported for many sites. Nest stands in Washington and Oregon were characterized by large diameter trees ($\bar{x}$ = 47.7 cm), a mean density of large trees (>46 cm d.b.h.) of 93.8/ha, an average

Table 2—The mean, standard deviation, range, and sample size for the forest stand characteristics of Marbled Murrelet tree nests located in North America. The Pacific Northwest data include nests located in California, Oregon, Washington, and British Columbia. For some characteristics, either no data were available for that state or province, or the sample size was too small to calculate the mean and range. Sample sizes for each variable are shown in parenthesis

Characteristics	California *n* = 10	Oregon *n* = 20	Washington *n* = 6	British Columbia *n* = 9	Pacific Northwest *n* = 45	Alaska *n* = 14
Aspect (˚)	210±122	147±63	180±121	—	166±92	267±66
	45-352	48-253	39-331	—	35-39	270-360
	(7)	(19)	(5)		(33)	(14)
Elevation (m)	286±125	379±152	348±176	321±310	332±206	96±50
	45-46	61-646	15-610	14-1097	14-1097	30-260
	(10)	(10)	(6)	(9)	(35)	(14)
Slope (pct)	18±14	41±27	21±13	3±4	23±23	69±16
	0-41	10-87	0-39	0-11	0-87	47-100
	(7)	(10)	(6)	(7)	(30)	(10)
Slope position[1]	1±0	2.1±0.9	1.3±0.5	1.3±0.7	1.5±0.8	—
	1-1	1-3	1-2	1-3	1-3	—
	(7)	(10)	(6)	(7)	(30)	
Stand size (ha)	352±432	80±49	354±401	—	206±351	31±26
	100-1100	3-149	5-990	—	3-1100	4-63
	(4)	(9)	(5)		(16)	(10)
Pct. composition low elevation trees[2]	100±0	100±0	90±9	64±29	91±19	64±14
	100-100	100-100	78-100	20-100	20-100	39-91
	(10)	(10)	(5)	(6)	(31)	(8)
Total tree density (number/ha)	235±178	120±72	136±28	297±136	182±132	575±240
	92-504	48-282	84-162	148-530	48-530	295-978
	(5)	(10)	(5)	(5)	(25)	(8)
Canopy height (m)	88±0	59±8	54±5	—	64±16	23±4
	88-88	48-75	44-59	—	38-88	16-30
	(5)	(9)	(5)		(20)	(14)
Canopy layers (number)	—	2.2±0.4	3.4±0.5	—	2.5±0.7	—
	—	2-3	3-4	—	2-4	—
		(10)	(4)		(20)	
Canopy closure (pct)	39±6	43±27	69±18	—	49±23	62±15
	25-48	12-99	36-88	—	12-99	40-85
	(7)	(8)	(5)		(21)	(12)
Distance to coast (km)	13.1±8.3	25.8±9.7	15.9±13	11.5±3.7	16.8±10.6	0.5±0.3
	4.9-28.9	1.6-40.0	4.1-34.2	3.2-17.3	1.6-40	0.1-1.2
	(10)	(10)	(6)	(9)	(35)	(14)
Distance to stream (m)	108±67	280±312	70±69	100±165	159±224	109±108
	30-215	8-1000	14-200	5-500	5-1000	2-325
	(7)	(10)	(5)	(7)	(29)	(9)
Distance to nearest opening (m)	—	67±70	65±33	—	92±131	—
	—	15-300	18-120	—	15-700	—
		(20)	(5)		(30)	
Stand age (yrs)	—	209±48	879±606	—	522±570	—
	—	180-350	450-1736	—	180-1824	—
		(10)	(3)		(16)	

[1]Slope position codes: (1) lower 1/3, (2) middle 1/3, and (3) upper 1/3.
[2]Measure of the percent of western hemlock, Douglas-fir, western red cedar, Sitka spruce, and coastal redwood in a stand.

Table 3—The mean, standard deviation, range, and sample size for platform and tree characteristics of Marbled Murrelet tree nests (n = 61) located in North America. The Pacific Northwest data include nests located in California, Oregon, Washington, and British Columbia. For some characteristics, either no data were available for that state or province, or the sample size was too small to calculate the mean and range. Calculations were rounded to the nearest cm for all measurements except nest substrate depth. Sample sizes for each variable are shown in parenthesis.

Characteristics	California *n* = 10	Oregon *n* = 22	Washington *n* = 6	British Columbia *n* = 9	Pacific Northwest *n* = 47	Alaska *n* = 14
Tree species						
Sitka spruce		1		6	7	5
Douglas-fir	4	20	3		27	
Western hemlock	1	1	2	2	6	
Western red cedar			1		1	
Alaska yellow cedar				1	1	
Coastal redwood	5				5	
Mountain hemlock						7
Tree diameter (cm)	278±136	192±47	152±45	212±84	211±91	63±18
	139-533	127-279	88-220	90-370	88-533	30-104
	(10)	(22)	(5)	(9)	(46)	(14)
Tree height (m)	73±8	67±11	57±7	58±15	66±13	23±4
	61-86	36-86	45-65	30-80	30-86	16-30
	(10)	(22)	(5)	(9)	(46)	(14)
Tree diameter at nest height (cm)	106±48	81±23	72±21	110±60	88±39	—
	70-199	36-122	40-97	50-209	36-209	—
	(5)	(15)	(5)	(5)	(30)	
Branch height (m)	47±11	51±12	37±11	33±8	45±13	13±2
	33-68	18-73	23-53	18-44	18-73	10-17
	(10)	(21)	(5)	(9)	(45)	(14)
Branch diameter at trunk (cm)	35±13	31±11	36±12	32±9	32±11	15±5
	21-61	14-56	14-49	18-43	14-61	9-27
	(8)	(19)	(5)	(9)	(41)	(12)
Branch diameter at nest (cm)	34±13	34±18	29±13	27±9	32±16	19±5
	16-61	10-81	11-46	15-38	10-81	12-28
	(10)	(20)	(4)	(7)	(41)	(11)
Branch crown position (pct)	64±13	74±12	63±15	58±11	68±14	59±12
	50-91	50-92	41-81	40-74	40-92	44-79
	(10)	(21)	(5)	(9)	(45)	(14)
Branch orientation (˚)	203±103	173±87	233±109	187±90	189±96	—
	45-360	20-360	110-342	18-341	18-360	—
	(10)	(20)	(4)	(9)	(43)	
Distance trunk to nest (cm)	47±61	101±160	26±26	134±122	89±132	62±66
	0-184	1-762	0-57	0-340	0-762	0-224
	(10)	(21)	(4)	(9)	(44)	(13)
Nest platform length (cm)	20±10	41±17	29±16	21±13	32±18	—
	8-40	12-71	10-57	12-50	8-71	—
	(10)	(21)	(5)	(6)	(42)	
Nest platform width (cm)	15±7	28±12	24±11	12±3	22±12	—
	6-23	7-51	10-39	9-19	7-51	—
	(10)	(21)	(5)	(6)	(42)	
Nest platform moss depth (cm)	2.9±2.7	5.1±2.5	2.7±0.7	4.8±1.4	4.5±2.4	3.9±1.3
	0.8-8.1	0.6-12	2.0-3.5	2.7-7.0	0.6-12	2.0-6.0
	(5)	(17)	(2)	(9)	(33)	(12)
Nest platform duff and litter depth (cm)	7.4±7.3	3.4±0.4	2.9±0.7	—	5.0±5.2	—
	2.5-20.0	3.0-3.8	2.0-3.8	—	2.0-20.0	—
	(4)	(2)	(3)		(9)	
Cover above nest (pct)	90±28	79±14	90±10	100±0	85±20	89±05
	5-100	40-100	70-100	100-100	5-100	81-95
	(10)	(18)	(5)	(2)	(35)	(8)

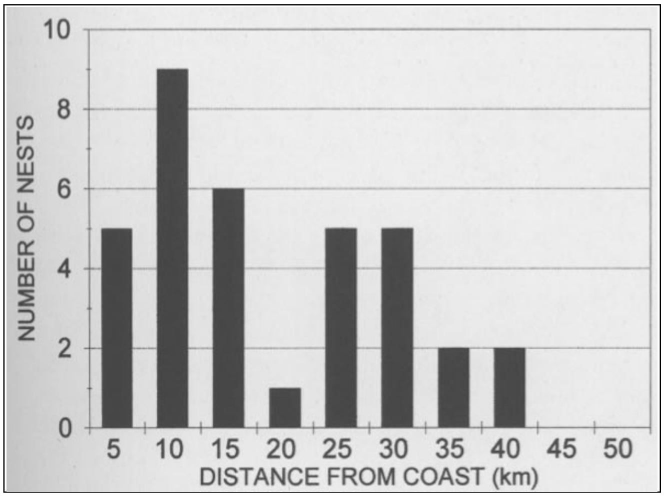

Figure 1—Distances from the Marbled Murrelet nest trees (n = 35) to the nearest salt water for nests found in the Pacific Northwest. The number of nests was listed in 5-km increments beginning with nests found 0-5 km inland.

total tree density (>10 cm d.b.h.) of 324/ha, multiple canopy layers (2-3), and the presence of snags (>10 cm d.b.h.) (mean density = 71/ha) (Nelson and others, in press). In Alaska, most nest trees were located in forests with significantly larger tree size classes (≥23 cm d.b.h.) and higher volume classes (1883-5649 m^3/ha) than other forest types (Kuletz and others, in press).

Tree Species Composition and Stem Density

Conifer species that typically grow at higher elevations in the Pacific Northwest include mountain hemlock, silver fir (*Abies amabilis*), and yellow cedar. Conifer species most abundant at lower elevations include Douglas-fir, western red cedar, Sitka spruce, western hemlock, and coastal redwood. Nest stands in the Pacific Northwest were composed primarily of low elevation conifer species ($\bar{x}$ = 91 percent) (*table 2*). In Alaska, the composition of low elevation trees was much lower, with a mean of 64 percent. The total mean tree density for nest stands in the Pacific Northwest was 182 trees/ha; total density was about three times greater in Alaska (*table 2*).

All nest trees in the Pacific Northwest were recorded in stands characterized as old-growth and mature forest. These stands were dominated by either Douglas-fir, coast redwood, western hemlock, western red cedar, or Sitka spruce. The one exception was a higher elevation nest stand found in the Caren Range of British Columbia which was dominated by old-growth mountain hemlock (60 percent) with smaller percentages of yellow cedar (20 percent) and silver fir (20 percent). In California, nest stands were dominated by coast redwood and Douglas-fir, with a component of western hemlock and Sitka spruce in some nest stands. In both central and northern California, all nest sites had a higher percentage of redwood trees than Douglas-fir. Nest stands in Oregon were dominated by Douglas-fir and western hemlock, with one site dominated by Sitka spruce. Forest types in Washington included stands dominated by western hemlock, Douglas-fir, and Sitka spruce. These stands commonly had a large component of western red cedar. Silver fir made up a smaller component of some of the nest stands in Washington.

In British Columbia, six nest stands were dominated primarily by Sitka spruce and western hemlock, with four stands also having a component of silver fir, and one stand with western red cedar. One nest stand in the Caren Range was dominated by mountain hemlock. For a sample of eight nests located in Alaska, mountain hemlock was the dominant tree species at five nests, and western hemlock was the dominant species at three nest stands (Naslund and others, in press). Sitka spruce were reported as an important component at most of these nest sites.

Canopy Characteristics

Nest stands in the Pacific Northwest had a mean canopy height of 64 m with the redwood zone included in this sample (*table 2*). The mean canopy height for stands located in Oregon, Washington, and British Columbia was 61 m. The canopy height of Alaska nest stands were lower ($\bar{x}$ = 23 m), reflecting the small stature of the trees in this geographic area.

For nest stands in the Pacific Northwest, the mean canopy closure was 49 percent, and all nest stands were reported to have 2-4 tree canopy layers where this variable was recorded (*table 2*). Canopy closures below 40 percent were reported for 40 percent of the nest stands (*fig. 2*). Mean canopy closures were especially low in California and Oregon. Canopy closures for a typical old-growth stand in Washington generally average 80 percent. Canopy closures reported from Alaska were similar to nest stands in the Pacific Northwest (*table 2*) with a mean of 62 percent.

The presence of dwarf mistletoe (*Arceuthobium*) in the nest stands or within the canopy of nest trees was not reported consistently enough to determine its importance to murrelets. Mistletoe was reported at 13 of 20 nest stands, where its occurrence was evaluated.

Stand Size

Mean nest stand size for the Pacific Northwest was 206 ha. Several nest stands were only 3, 5, and 15 ha in size. In Alaska, stands were naturally fragmented in many cases, and averaged 31 ha. Stand sizes were generally smaller in Alaska because of the naturally fragmented nature of the coastal forests in this region.

Distance to Openings

Distance of nest trees to streams for nests in the Pacific Northwest was variable, with a mean of 159 m. Nest trees were located a mean distance of 92 m from natural or man-made openings (*table 2*). A combined analysis indicated that the mean distance to an opening or stream was 123 m (n = 68, *s.d.* = 177). Sixty-six percent of the nest trees were ≤100 m from an opening (*fig. 3*).

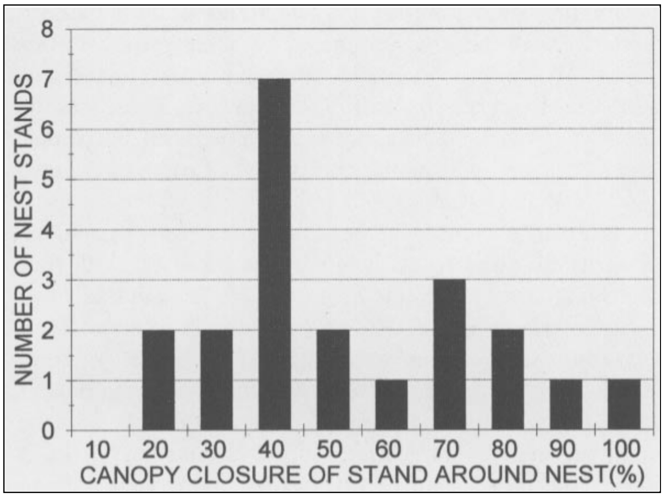

Figure 2—Canopy closure of the stand surrounding the nest tree for 34 Marbled Murrelet nests found in North America. The number of nests was listed in 10-percent increments beginning with nests with 0-10 percent canopy closure.

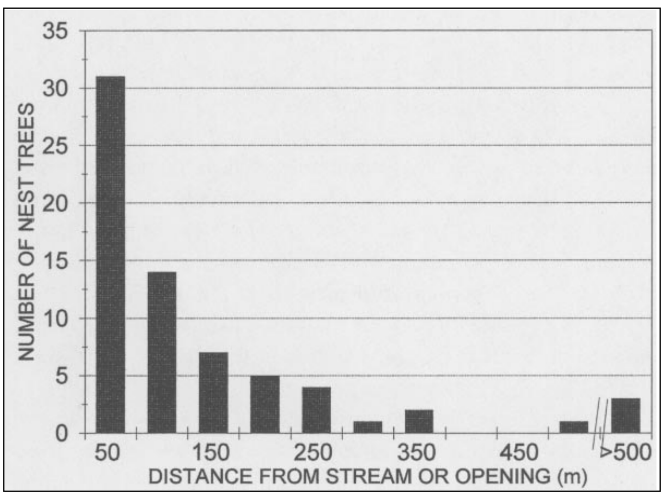

Figure 3—Distances from the Marbled Murrelet nest trees (n = 68) to the nearest stream, creek, or opening for nests found in North America. Some nests had two measurements, one to the nearest opening and one to the nearest stream.

Tree Characteristics

Nest trees used by murrelets in the Pacific Northwest included Douglas-fir (57 percent), Sitka spruce (15 percent), western hemlock (13 percent), coast redwood (11 percent), and western red cedar (2 percent) (*table 3*). In one exception, a nest in British Columbia was found in a yellow cedar (2 percent). Western hemlock was the only nest tree species reported used by Marbled Murrelets throughout their geographic range. Although Sitka spruce was only reported from Alaska, British Columbia, and Oregon, it is likely this species is also used throughout the range of the murrelet since it is common in coastal coniferous forests of Washington through California. Douglas-fir nest trees were only located in Washington, Oregon, and California. Nests in cedar trees were reported only from Washington and British Columbia, but this was probably due to a small sample size. Mountain hemlock nest trees were only reported from Alaska.

In the Pacific Northwest, the mean nest tree diameter was 211 cm, with the smallest diameter nest tree reported from Washington, which was a western hemlock 88 cm in diameter (*table 3*). Nest tree diameters were normally distributed with a maximum number of trees found between 140 and 160 cm, and 85 percent of the trees ranging between 120 and 280 cm (*fig. 4*). Nest tree diameters were much smaller in Alaska ($\bar{x}$ = 63 cm) due to the small stature of the trees in this region.

Mean nest tree heights were highest in California and Oregon where the majority of nest trees were in redwood and Douglas-fir trees which can grow to great heights. Mean tree heights were similar between Washington and British Columbia where more of the nest trees were in cedar, spruce, and hemlock. Mean tree heights in the Pacific Northwest were 66 m (*table 3*). Nest tree heights in Alaska were low, with a mean of 23 m, with one nest tree measured at 16 m.

The mean diameter of the tree trunk at nest height was 88 cm in the Pacific Northwest, with minimum trunk diameters of 36 cm and 40 cm reported for Oregon and Washington respectively. Trunk diameters at the nest height were not reported for nests in Alaska (*table 3*).

The condition of nest trees in the Pacific Northwest varied, with 64 percent recorded as alive/healthy and 36 percent as declining (n = 44). No nests were reported in snags. Nest trees with declining tops (8 percent), broken tops (37 percent) and dead tops (8 percent) were commonly reported, with only 47 percent of the nest tree tops recorded as alive/healthy. In Alaska (n = 14), 57 percent of the nest trees were reported as declining, and one nest tree was recorded as dead.

In the Pacific Northwest, mean nest branch height was 45 m (*table 3*). Mean nest branch height was highest in California and Oregon, where the mean tree height was also the highest. Mean nest branch height was lowest in Alaska (13 m), with one nest located only 10 m above the ground.

The mean diameter of nest branches measured at the tree trunk and at the nest varied little between each state or Province for the Pacific Northwest (*table 3*). Mean nest branch diameters at the nest for each state or province ranged from 27-34 cm with a mean diameter of 32 cm for the Pacific Northwest. The distribution of limb diameters at the nest in the Pacific Northwest were normally distributed, with a maximum number (22 percent) of nests located on limbs 35-40 cm in diameter (*fig. 5*). In Alaska, the smallest branch diameters at the nest were 12, 14, and 16 cm, with a mean diameter of only 19 cm. The length of the nest branches in the Pacific Northwest ranged from 1 m to 14 m, with a mean length of 5.3 m (n = 42).

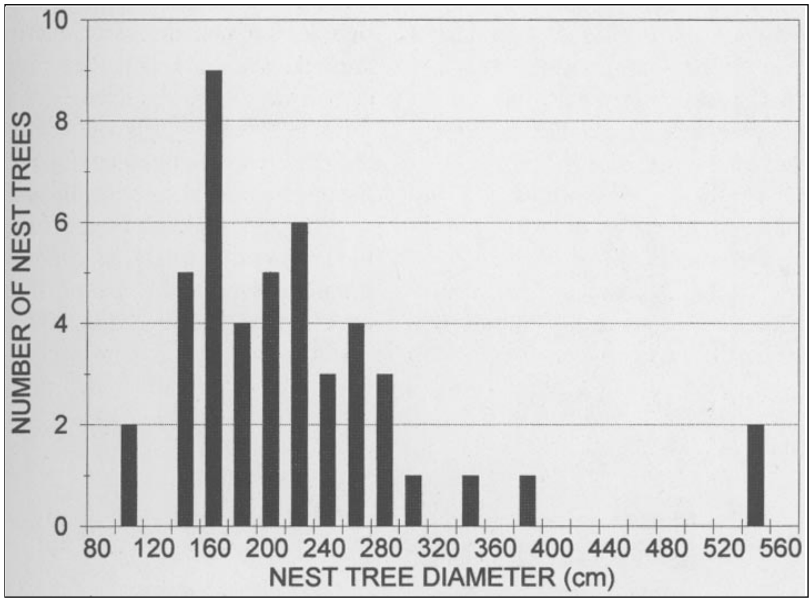

Figure 4—The diameter at breast height for 46 nest trees of the Marbled Murrelet found in California, Oregon, Washington, and British Columbia. The number of nest trees was listed in 20-cm increments beginning with trees 70-80 cm in diameter.

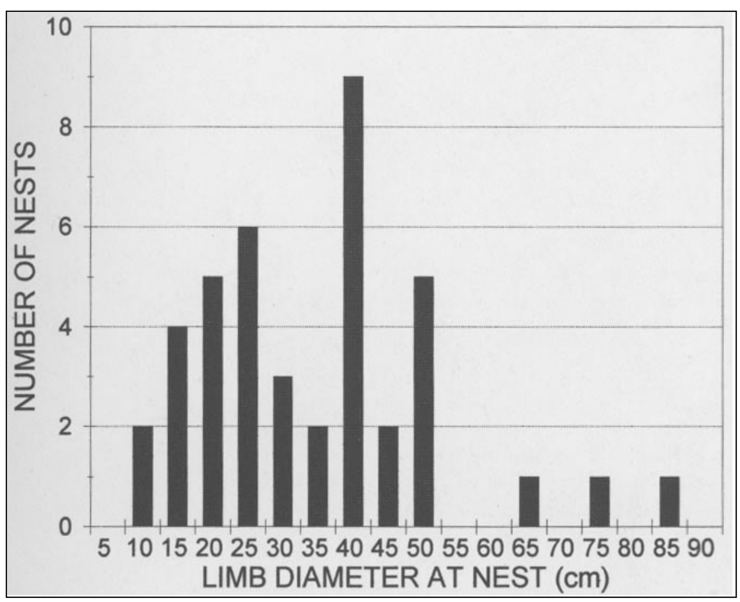

Figure 5—The diameter of the tree limbs under or next to 41 nests of the Marbled Murrelet found in California, Oregon, Washington, and British Columbia. The number of nests was listed in 5-cm increments beginning with limbs 0-5 cm in diameter.

The condition of the nest branches for nests in the Pacific Northwest varied from healthy limbs (70 percent) to those reported as declining (27 percent) or dead (3 percent) (n = 37). Nest limbs with broken ends were reported in 16 percent of the records (n = 37). In Alaska, 50 percent of the nest branches were recorded as declining, 7 percent were reported with broken ends, with 1 nest located on a dead branch (n = 14).

The position of the nest on the tree bole was calculated by dividing the nest height by the total tree height. Nests in the Pacific Northwest were located an average of 68 percent up the bole of the nest tree (*table 3*). Fifty-nine percent of the nests were located in the top one-third of the tree bole, and 87 percent of the nests were located in the top one-half of the tree. No nests were located lower than 40 percent of the total tree bole height. Nests in Alaska were also located high up the tree bole with a mean of 59 percent. Positions of the nest on the tree bole for all nests throughout the range of the Marbled Murrelet showed that the top 10 percent of the tree was not utilized to any great degree, with a maximum number of nests located 70-80 percent up the tree bole (*fig. 6*).

The majority of nest limbs in the Pacific Northwest (n = 44) were oriented toward the south or the north. Forty-four percent of the limbs faced a southerly direction ranging between 136 and 225 degrees (*table 3*). Another group of nests (26 percent) were oriented in a northerly direction ranging between 316 and 45 degrees. Nest limbs oriented toward the east or west consisted of 14 percent and 16 percent of the sample respectively.

Nest Characteristics

Nest cups were located a mean distance of 89 cm from the tree bole for nests in the Pacific Northwest (*table 3*). Here, a total of 71 percent of the nests were located within 1 m of the tree bole. This relationship was also true for nests located throughout the North American range (*fig. 7*), as 51 percent of the nests were located within 40 cm of the tree trunk.

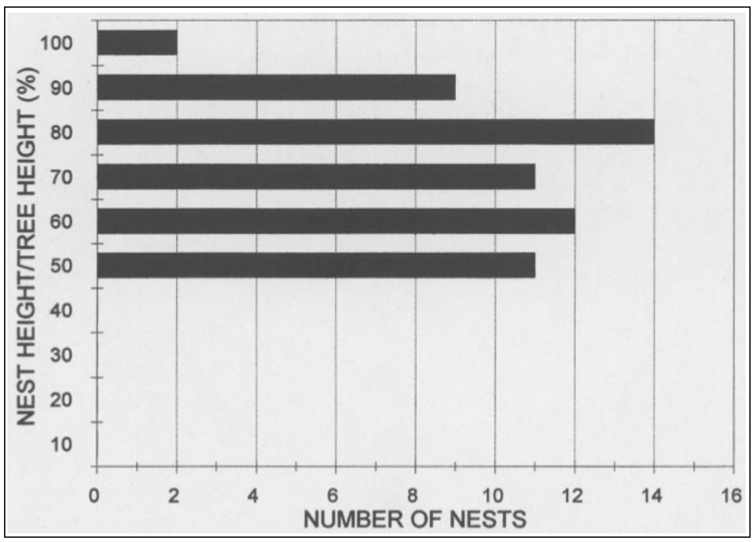

Figure 6—The relative vertical positions of Marbled Murrelet nests in relation to the heights of the tree bole for 59 tree nests found in North America.

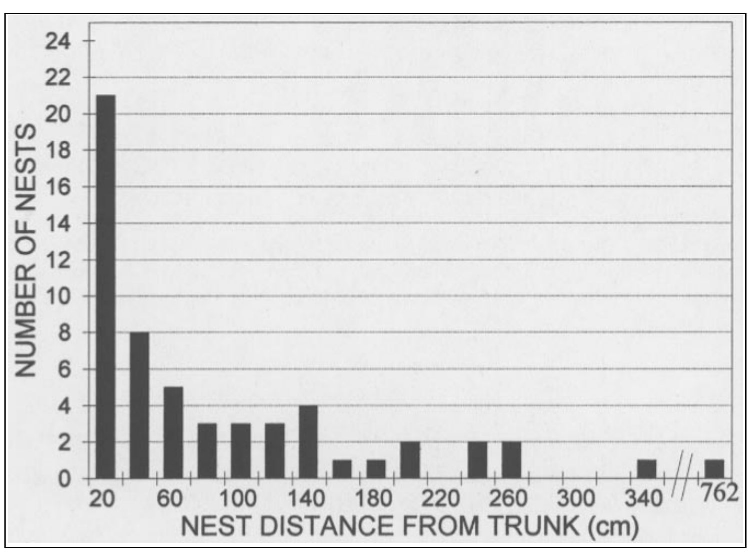

Figure 7—Nest distances from the tree trunk for 57 Marbled Murrelet nests found in North America. The number of nests was listed in 20-cm increments beginning with nests found 0-20 cm from the tree trunk

Nest platforms in the Pacific Northwest had a mean length of 32 cm and a mean width of 22 cm. The mean total platform area was 842 square cm (*table 3*). In the Pacific Northwest, moss (*Isothecium*) formed the major proportion of the substrate for 67 percent of the nests. Litter, such as bark pieces, conifer needles, small twigs, and duff, was substrate in 33 percent of the nests. For nests found throughout North America, moss formed 49 percent of the substrate, moss mixed with lichen or litter formed 30 percent of the nests, and litter 21 percent (n = 37). All nests found in Alaska had moss as a component of the nest substrate.

Mean moss depth at, or directly adjacent to, the nest cup was 4.5 cm (*table 3*). Mean litter depth was 5 cm for nests in the Pacific Northwest. Mean moss depths in Alaska were 3.9 cm. The majority (86 percent) of nests in North America (n = 52) had substrates that were >2 cm in depth with a large number of nests (n = 16) having substrate depths between 3.1 and 4.0 cm (*fig. 8*).

Nest platforms in the Pacific Northwest (n = 44) were created by large primary branches in 32 percent of the cases. In addition, 23 percent of the nests were located on tree limbs where they became larger in diameter when a main limb forked into two secondary limbs, or a secondary limb branched off a main limb. In many instances, branches were also larger in diameter where they were attached to the tree bole. Locations where a limb formed a wider area where it grew from the trunk of a tree formed 18 percent of the nest platforms. Cases of dwarf mistletoe infected limbs (witches' broom) (9 percent), large secondary limbs (7 percent), natural depressions on a large limb (7 percent), limb damage (2 percent), and an old stick nest (2 percent) were also recorded as forming platforms. Multiple overlapping branches at the point where they exited the trunk of a tree were sometimes used as a nest platform. Many of the tree limbs creating nest platforms had grooves or deformations forming natural depressions on the surfaces of the limb.

Cover directly above the nest was high in almost all cases in the Pacific Northwest, with a mean of 85 percent. Eighty-seven percent of all nests had >74 percent overhead cover. Cover above the nest platforms in Alaska was similar to that in the Pacific Northwest (*table 3*).

Discussion

Marbled Murrelets have a limit on their inland breeding distribution because of the energetic requirements of flying inland to incubate eggs and feed young. They forage at sea, carrying single prey items to the nest and feed their young several times per day during the late stages of nesting. To some extent, the inland distance information presented here is biased towards lower values, because nest search and survey efforts have been more intensive closer to the coast in all regions, where higher murrelet detection rates make locating nests an easier task. Even with the potential problems of energetic expenditure, murrelets displayed a great tolerance for using nesting stands located long distances from the ocean. Evidence of breeding was common in California, Oregon, and Washington, in areas located 30-60 km inland. Unlike many other alcids, the Marbled Murrelet forages in near-coastal shallow water environments. The use of tree limbs as a nesting substrate may have developed because older-aged forests were the only habitats that were abundant and commonly available close to the foraging grounds of this seabird. Areas of brush-free open ground or rocky talus

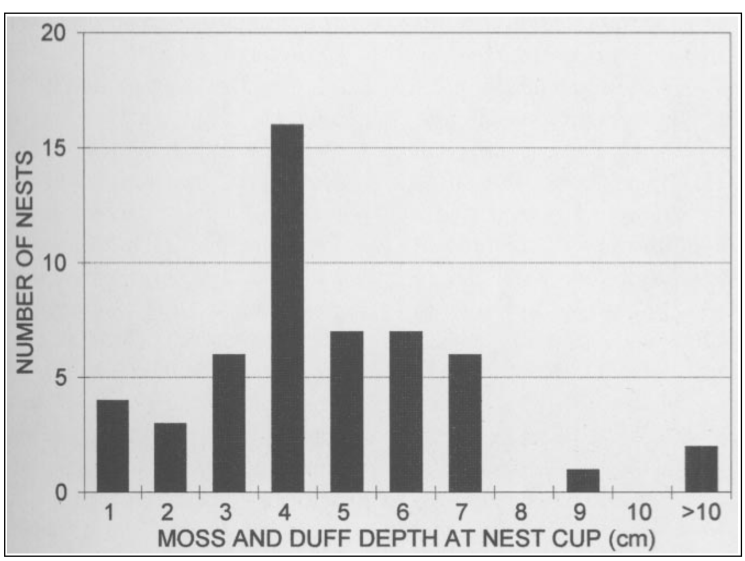

Figure 8—The depth of moss and litter under or directly adjacent to the nest cup for 52 nests of the Marbled Murrelet in North America.

slopes that are commonly used by other alcids as nesting habitat, are not commonly available along the forested coasts of the Pacific Northwest. Old-growth and mature forests also provided large nesting platforms on which to raise young. Nesting greater distances from the coast may have developed over time to avoid higher nest predation by corvids and gulls whose population numbers may be much higher in food-rich coastal areas. In addition, much of the near-coastal nesting habitat has been eliminated in the Pacific Northwest which may cause birds to nest further inland. Nest search efforts and surveys for the presence of murrelets should be conducted in areas farther inland in order to refine the abundance and distribution of this seabird away from the coast. We currently have no information to determine what proportion of the population nests in these inland areas, or any data to compare the reproductive success of far versus near-coastal nesting pairs.

In Washington, inland detection rates of Marbled Murrelets did not show declines until inland distances were >63 km from salt water (Hamer, this volume). In Oregon, most detections occurred within 40 km of the ocean (Nelson, pers. obs.). In British Columbia, murrelet detection rates in Carmanah Creek on Vancouver Island decreased with increasing distance from the ocean (Manley and others 1992). Savard and Lemon (1992) found a significant negative correlation between detection frequency and distance to saltwater on Vancouver Island in only 1 of 3 months tested during the breeding season. Inland distances for all nests in Alaska were low because rock and icefields dominate the landscape a few kilometers from the coast in most regions.

We found that all nest trees throughout the geographic range were located in stands defined by the observers as old-growth and mature stands or stands with old-growth characteristics. The youngest age reported for a nesting stand was 180 years. Marbled Murrelet occupancy of stands, and the overall abundance of the species has been related to the proportion of old-growth forest available from studies conducted in California, Washington, and Alaska (Hamer, this volume; Kuletz, in press; Miller and Ralph, this volume; Raphael and others, this volume). Carter and Erickson (1988) reported that all records of grounded downy young and fledglings (young that have fallen from a nest or unsuccessfully fledged) (n = 17) that they compiled were associated with stands of old-growth forests in California. All records of nests, eggs, eggshell fragments, and downy chicks in Washington have been associated with old-growth forests (n = 17) (Hamer, this volume; Leschner and Cummins 1992a).

Marbled Murrelets consistently nested in low elevation (<945 m) old-growth and mature forests. Tree species that are most abundant at lower elevations (<945 m) such as Douglas-fir, western hemlock, Sitka spruce, redwood, and cedar, may have a higher abundance of potential nest platforms than the higher elevation conifers such as silver fir and mountain hemlock.

Marbled Murrelets were found nesting in stands of very small size in some instances, although the reproductive success of these nests compared to stands of larger sizes was not known (but see Nelson and Hamer, this volume b). A wide range of canopy closures were reported for nest stands and around nest sites. A study conducted in Washington and Oregon compared random plots within a stand to plots surrounding the nest tree (Nelson and others, in press). They found that canopy closures were significantly lower around nest trees in Oregon compared to random plots adjacent to the nest tree, but the relationship was not significant in Washington. It is unknown how stand size and canopy closure affect nest success, but stands with lower canopy closures might have less visual screening to conceal adult visits to the nest tree (see Nelson and Hamer, this volume b). Therefore, it is possible that low canopy closures within a stand will make locating nests easier for visual predators such as corvids. In addition, smaller stands will have fewer nesting and hiding opportunities for Marbled Murrelets. They may be choosing lower canopy closures immediately around the nest to improve flight access, but select nest platforms with dense overhead cover for protection from predation, as indicated by the extremely high cover values found directly over the nest.

The majority of nests in the Pacific Northwest were located within 100 m of water, but a few nest sites were found at much longer distances (*fig. 3*). Small streams and creeks commonly bisect stands in the Pacific Northwest, creating larger openings and long travel corridors. Murrelets are often observed using these features to travel through a stand. This may be one reason nest sites were often in close proximity to streams. Many nests were also located near openings such as roads or clear-cuts, but there may be an observer bias to finding nests located in areas with better access and viewing conditions.

A variety of processes contributed to producing potential nest platforms within the forest including deformations and damage sustained by trees. This is probably why a measure of potential nest platforms, and not tree size, was the best predictor of stand occupancy by murrelets in Washington (Hamer, this volume), as larger diameter trees alone were often not responsible for the majority of available platforms within a stand. Mistletoe blooms, unusual limb deformations, decadence, and tree damage commonly observed in nest stands, all appear to create a large number of nest platforms. Therefore, the structure of a stand and the processes occurring within a stand may be more important than tree size alone in producing nesting platforms and suitable habitat for the Marbled Murrelet (see Grenier and Nelson, this volume).

It would still be desirable to know when trees, in general, begin producing potential nest platforms. In Washington, Hamer (this volume) measured potential nest platform abundance using a sample of 2,035 conifers, and found platforms were generally available when tree diameters exceeded 76 cm. The mean number of platforms/tree was found to increase rapidly with an increase in tree diameter from 50-200 cm. No increase in the mean number of platforms was evident for larger trees that ranged from 220-300 cm in diameter. These results explain why all the nest trees found in the Pacific Northwest were ≥88 cm in diameter, although mistletoe brooms on smaller trees may also provide habitat. In southcentral Alaska, the minimum d.b.h. associated with a tree having at least one platform ranged from 29-37 cm (Naslund and others, in press).

In a study completed in 1993, nest tree and stand characteristics in Washington and Oregon were compared between 15 murrelet nests and randomly located dominant trees and plots within the same nest stand (Nelson and others in press). Nest sites were similar to the forest stands in which they were located, except that a significantly higher number of potential nest platforms were recorded at nest trees, than at random trees. They also found that Marbled Murrelets selected trees at nest sites that had ≥4 potential nest platforms, and trees with ≤3 platforms were avoided. In Alaska (Naslund and others, in press), one study compared nest tree characteristics (n = 14) to a sample of random trees surrounding each nest tree, and found nest trees were larger in diameter, had more potential nest platforms, and had greater epiphyte cover. This study also concluded that Sitka spruce appeared to be the most suitable tree for nesting when compared to western hemlock and mountain hemlock, because of its high number of platforms and greater epiphyte cover. They also found that nest and landing trees tended to be larger in diameter than surrounding trees, and nest trees were more likely to contain at least one potential nest platform with moderate to heavy epiphyte cover when compared to nearby trees. Stands with high potential nest platform densities may reduce competition for nest branches and provide a high diversity of nest site choices.

Nests located high in the canopy may provide better access by adults to the nest site in dense, old-growth stands. Nesting as high in the canopy as possible may also help in avoiding predation. Although positioning the nest as high off the ground as possible would likely reduce the incidence of mammalian predators, we have also observed that the Steller's Jays (*Cyanocitta stelleri*), predators of nestlings and eggs, often forage in the lower portions of the canopy. Better horizontal and vertical cover is available in the top portions of the tree crown which may help reduce predation. Data needs to be collected on the positioning of nests within the live crown of the tree, not just the tree bole, to determine if murrelets prefer certain areas of the tree crown foliage for nesting.

Murrelets may choose to place nests near the trunk of the tree for a variety of reasons. First, overhead and horizontal cover is higher around the nest cup due to the position of the tree crown directly overhead. Second, the tree trunk itself provides a large amount of cover and visual screening and branches are typically larger in diameter near the tree bole. Also, more duff and litter, which often form the nest substrate, is trapped near the tree bole, and the percent cover of moss on the limbs of trees is higher, often forms a more complete coverage, and forms a deeper layer near the tree bole. Some conifer species typically have little or no moss available on their limbs, so that platforms created by accumulations of duff and debris are the only nest choices available for murrelets in these forest types.

Murrelets nest on large limbs. The smallest limb used at the nest cup throughout the range of the murrelet was 10 cm in diameter, which is likely the smallest diameter branch that could support a successful nest. Nests located on smaller limbs would probably have a higher likelihood of losing chicks or eggs from accidental falls, an occurrence that is well documented (Hamer and Nelson, this volume a). Nests located on limbs <16 cm diameter all had moss as a nest substrate, except in one instances where a 13 cm nest branch had litter and lichen as a substrate. Small limb diameters without a moss covering may be avoided by nesting birds because the hazards of raising eggs and young are increased without the moss to help stabilize and insulate the egg on the limb, increase the diameter of the nest limb/platform, and provide a substrate on which to create a nest cup (depression). In addition, moss and litter may help insulate eggs and chicks during cold weather and may help drain water from eggs and chicks helping thermoregulation (Naslund and others, in press). An abundance of mosses creates a multitude of nest platform choices by providing substrate on many locations throughout a single limb. In addition, the presence of dwarf mistletoe in stands can increase the number of nesting opportunities for murrelets and may be important in providing nest platforms in areas with low moss abundance and dryer conditions.

The nest site selection of the Marbled Murrelet may have evolved primarily to reduce predation. Selection of nest sites away from the coast, in dense old-growth and mature forests with multi-layered canopies, high in the forest canopy, on limbs with high overhead and horizontal cover, and near the tree bole where the tree bole itself provides a large degree of cover, may help reduce nest predation. Results from studies of murrelet habitat use to date have been derived from comparisons of stands occupied by murrelets to unoccupied stands, comparisons of stands receiving high use versus low use, or comparisons of nest trees and nest plots to random trees and plots. Although these can provide extremely useful descriptions and definitions of suitable habitat, they do not provide information on the habitat characteristics associated with successful nests. Information on the landscape and within-stand habitat characteristics that influence reproductive success is needed to fully understand murrelet nesting ecology and to model optimum habitat suitability for this species. Such studies may find that stand size analyzed in conjunction with the number of nesting and hiding opportunities within the stand (habitat quality), may greatly influence reproductive success because of predation pressures at the nest site. Habitat factors that could influence reproductive success may include stand fragmentation, stand canopy closure, and the amount of overhead and horizontal cover surrounding the nest.

Acknowledgments

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