Chapter 8

Nest Success and the Effects of Predation on Marbled Murrelets

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Abstract: We summarize available information on Marbled Murrelet (*Brachyramphus marmoratus*) productivity and sources of mortality compiled from known tree nests in North America. We found that 72 percent (23 of 32) of nests were unsuccessful. Known causes of nest failure included predation of eggs and chicks (*n* = 10), nest abandonment by adults (*n* = 4), chicks falling from nests (*n* = 3), and nestlings dying (*n* = 1). The major cause of nest failure was predation (56 percent; 10 of 18). Predators of murrelet nests included Common Ravens (*Corvus corax*) and Steller's Jays (*Cyanocitta stelleri*); predation of a nest by a Great Horned Owl (*Bubo virginianus*) was also suspected. We believe that changes in the forested habitat, such as increased amounts of edge, are affecting murrelet productivity. Successful nests were significantly further from edges ($\bar{x}$ = 155.4 versus 27.4 m) and were better concealed ($\bar{x}$ = 87.2 versus 67.5 percent cover) than unsuccessful nests. The rate of predation on Marbled Murrelet nests in this study appear higher than for many seabirds and forest birds. If these predation rates are representative of rates throughout the murrelet's range, then the impacts on murrelet nesting success will be significant. We hypothesize that because this seabird has a low reproductive rate (one egg clutch), small increases in predation will have deleterious effects on population viability. Rigorous studies, including testing the effects of various habitat features on recruitment and demography, should be developed to investigate the effects of predation on Marbled Murrelet nesting success.

Nesting success in seabirds is influenced by a variety of physical and biological factors, including food availability, habitat quality, energetics, predation, and climatic conditions (Croxall 1987, Nettleship and Birkhead 1985, Vermeer and others 1993). Because the effects of these factors can vary spatially and temporally, seabird nesting success can be highly variable among years (Birkhead and Harris 1985; Boekelheide and others 1990; De Santo and Nelson, this volume). For example, in some years, anomalous warm oceanographic conditions (El Niño) cause a decrease in prey availability, thus impacting nesting attempts and nest success (Ainley and Boekelheide 1990, Hodder and Greybill 1985, Vermeer and others 1979). In addition, disturbance to nesting habitat (e.g., habitat loss, modification) and associated cumulative impacts can affect the ability of seabirds to successfully reproduce (Evans and Nettleship 1985; Gaston 1992, Reville and others 1990).

The influence of these biological and physical factors on the nesting success of Marbled Murrelets (*Brachyramphus marmoratus*) is not fully known. In order to completely address this issue, well designed studies investigating the conditions that directly influence murrelet reproduction are needed. However, data are available on murrelet nesting success from tree nests that have been located and monitored in North America. In this paper, we summarize this information on murrelet productivity and sources of mortality. In addition, because predation was the major cause of nest failure, we discuss the implications of predation on this threatened, forest-nesting seabird.

Methods

We compiled information on nest success and failure from published and unpublished records of 65 Marbled Murrelet tree nests found in North America between 1974 and 1993. The sample size of tree nests were distributed by state and province as follows: Alaska (*n* = 18), British Columbia (*n* = 9), Washington (*n* = 6), Oregon (*n* = 22), and California (*n* = 10) (*table 1*). Success and failure of nests were determined through intensive monitoring of nesting activity, or evidence collected at the nest. The outcomes of nests were compared between regions (Alaska versus British Columbia, the Pacific Northwest and northern California). Nests were considered to fail if: (1) the chick or egg disappeared, fell out of the nest, or was abandoned; (2) the chick died; (3) unfaded eggshell fragments were found during the breeding season in nest cups without fecal rings; or (4) predation was documented. Nests were considered or assumed to be destroyed by a predator based on one or more of the following: (1) predation was observed, (2) the egg or chick disappeared prematurely between nest observations and neither were located on the ground after a thorough search of the area, and (3) evidence, such as puncture marks on eggs, or albumen or blood on eggshell fragments, was discovered and predators were aware of the nest location or seen in the immediate area. In addition to data from active nests, information on eggs, nestlings, and hatch-year birds found on the ground were compiled from published and unpublished records between 1900 and the present.

We used a Mann-Whitney U-test to compare the characteristics of nests that were successful with those of nests that failed because of predation. Variables used in the analysis were those that could have an effect on nest exposure or concealment: distance to edge, canopy cover, stand size, percent cover above the nest cup, nest height, distance of the

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Table 1—Marbled Murrelet tree nests by state or province, site, year, and outcome.

State or province Nest site/year found	Nest outcome Successful	 Failed	 Unknown	Reason for failure[1]	Predator[2]
Alaska					
Kelp Bay 1984[a]	–	1	–	Abandoned egg	–
Naked Island 1991/92[b]	–	7	3	?Predation of egg (n = 1) Abandoned egg (n = 3) Unknown/egg stage (n = 2) Unknown/chick stage (n = 1)	?Steller's Jay ?Common Raven[3] — —
Kodiak 1992[b]	–	–	2	—	—
Chugach 1992[b]	–	–	1	—	—
Afognak 1992[b]	–	–	2	—	—
Prince of Wales 1992[c]	–	–	1	—	—
SE Alaska 1993[d]	–	1	–	Predation of egg or chick	—
British Columbia					
Walbran 1990/91[e]	–	–	2	—	—
Carmanah 1992[f]	–	–	1	—	—
Walbran 1992[f]	–	–	2	—	—
Clayoquot 1993[g]	–	–	2	—	—
Carmanah 1993[g]	–	–	1	—	—
Caren 1993[h]	1	–	–	—	—
Washington					
Lake 22 1991[i]	2	–	–	—	—
Jimmycomelately 1991[i]	–	–	1	—	—
Heart of Hills 1991[i]	–	1	–	Chick fell out	—
Olympic 1991[i]	–	–	1	—	—
Nemah 1993[j]	1	–	–	—	—
Oregon					
Five Rivers 1990[k]	–	1	–	Chick fell out	—
Valley of Giants 1990[k]	–	1	–	Predation of chick	?Great Horned Owl
Five Rivers 1991[k]	1	–	–	—	—
Valley of Giants 1991[k]	–	1	–	Predation of egg	?Common Raven
Cape Creek 1991[k]	–	1	–	Predation of egg	?Common Raven
Siuslaw #1 1991[k]	1	–	–	—	—
Siuslaw #2 1991[k]	–	1	–	Predation of chick	?Steller's Jay
Boulder Warnike 1992[k]	–	1	–	?Predation of chick	?
Valley of Giants 1992[k]	–	1	–	Predation of egg	?Common Raven
Copper Iron 1992[k]	1	–	–	—	—
Valley of Giants 1993[l]	–	–	8	—	—
Green Mountain 1993[l]	–	–	2	—	—
Five Rivers 1993[l]	–	–	1	—	—
Five Mile Flume 1993[l]	–	–	1	—	—
California					
"J" Camp 1974[m]	–	1	–	Chick fell out	—
Waddell Creek 1989[n]	–	1	–	Predation of chick	Steller's Jay
Opal Creek 1989[n]	–	1	–	Predation of egg	Common Raven
Father 1991/92[o]	2	–	–	—	—
Palco 1992[p]	–	1	2	Chick died	—
Prairie Creek State Park 1993[i]	–	1	–	Unknown	—
Jedediah Smith State Park 1993[i]	–	1	–	Unknown	—

Table 1—continued

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[1] ?Predation = predation known or suspected based on available evidence.
[2] ?Predator = suspected predator; species seen in vicinity of nest.
[3] Common Raven flushed adult off one of these nests; this may have had an impact on its abandonment which occurred 2 days later.
[a] Quinlan and Hughes, 1990
[b] Naslund and others, in press
[c] Twelve Mile Arm nest; Brown, pers. comm.
[d] Unusual ground level nest located on tree roots above 11 m cliff in Log Jam Creek; Brown, pers. comm.
[e] Manley and Kelson, in press
[f] Jordan and Hughes, in press
[g] Hughes, pers. comm.
[h] P. Jones, pers. comm.
[i] Hamer, unpublished data
[j] Ritchie, pers. comm.
[k] Nelson, unpublished data; Nelson and Peck, in press
[l] Nelson, unpublished data
[m] Binford and others 1975.
[n] Singer and others 1991.
[o] Singer and others, in press.
[p] Kerns, pers. comm.

nest from the trunk, limb diameter at the nest, and nest substrate type (i.e., moss or duff). Edges were defined as unnatural openings, including, but not limited to, roads and clearcuts. Differences in the mean characteristics (ranks) were considered significant at $P < 0.05$.

Results and Discussion

Nest Success and Failure

Nesting success or failure was documented at 49 percent (32 of 65) of the nests (*table 2*). Timing of discovery (after the nesting season), limited evidence, or inadequate monitoring prevented conclusions about the outcomes at the remainder of nests. Therefore we limit our discussion to these 32 tree nests.

Seventy-two percent (23 of 32) of the nests were unsuccessful (*tables 1* and *2*). Known causes of nest failure included predation of eggs and chicks, nest abandonment by adults, chicks falling from nests, and nestlings dying (*tables 1* and *3*). Nesting success of 28 percent is lower than reported for 17 other alcid species ($\bar{x}$ = 57 percent, range = 33–86) (De Santo and Nelson, this volume), and for 11 species of sub-canopy and canopy nesting neotropical landbird migrants ($\bar{x}$ = 51 percent, range = 20–77) (Martin 1992). However, some species of seabirds (e.g., Xantus' Murrelet [*Synthliboramphus hypoleucus*]) and forest nesting neotropical migrants (e.g., Western Kingbird [*Tyrannus verticalis*]), also experienced low nesting success (33 and 20 percent, respectively) in some years (Martin 1992; Murray and others 1983). Hatching and fledging success of Marbled Murrelet nests were 67 and 45 percent, respectively. Fledging success was also lower than reported for all other alcid species ($\bar{x}$ = 78 percent, range = 66–100, n = 16) (De Santo and Nelson, this volume).

For all nests, 52 percent of the failures occurred during the egg stage, whereas in Washington, Oregon, and California most (62 percent) failed during the chick stage (*table 3*). The difference in stage of failure between the southern portion of the murrelet's range and all known nests can be explained by greater abandonment of eggs at nests in Alaska (Naslund, pers. comm.). The high incidence of abandonment in eggs in Alaska between 1991 and 1994 may have been related to limited food resources (Kuletz, pers. comm.).

Failure during the egg stage was caused by abandonment and predation. Failure during the chick stage occurred because of predation, death from a burst aorta (Palco nest in California), and falling from the nest. Chicks may fall from nests because nests are located on small platforms, or in response to unfavorable weather conditions, such as high winds, or other natural and unnatural disturbances. In Oregon, a 6-day-old chick may have fallen from its ridgetop nest tree (Five Rivers) because of gusty winds that occurred during a midday storm. Chicks are also occasionally very active on the nest, picking at nesting material, changing positions, snapping at insects, exercising their wings, and pacing on the nest limb (see Nelson and Hamer, this volume a). They could easily fall from the nest platform during these times of activity. In addition, predator activity could cause chicks to fall from the nesting platform.

In addition to failure documented at active nests, nestlings, fledglings, and eggs have been found on the ground during the breeding season at numerous sites throughout North America (*table 4*). Chicks and eggs located on the ground probably fell from nests as indicated above. However, eggs could also be carried by predators and dropped in locations distant from nest sites.

Fledglings have been discovered on the ground at varying distances from the ocean during the breeding season (up to 101 km inland). Many of these birds still retained an egg tooth and small traces of down on their head and back, indicating recent fledging. Marbled Murrelet hatch-year birds

Table 2—Summary of Marbled Murrelet nest success and failure by state and province

State/province	Nest outcome		
	Successful	Failed	Unknown
Alaska	0	9	9
British Columbia	1	0	8
Washington	3	1	2
Oregon	3	7	12
California	2	6	2
Overall total	9 (14 pct.)	23 (35 pct.)	33 (51 pct.)
Total for Washington, Oregon, and California	8 (22 pct.)	14 (39 pct.)	14 (39 pct.)

Table 3—Type and stage of Marbled Murrelet nest failure

Type of failure	Number (pct.)	Stage of failure	
		Egg	Chick
All nests			
Predation	10[1] (43)	5 (56)	4 (44)
Unknown	5[1] (22)	2 (50)	2 (50)
Abandonment	4 (17)	4 (100)	0
Chick fell out	3 (13)	–	3 (100)
Chick died	1 (4)	–	1 (100)
Total	23[2] (100)	11 (52)	10 (48)
Nests in Washington, Oregon, and California			
Predation	8 (57)	5 (62)	3 (38)
Unknown	2[1] (14)	0	1 (100)
Abandonment	0	0	0
Chick fell out	3 (21)	–	3 (100)
Chick died	1 (7)	–	1 (100)
Total	14[1] (100)	5 (38)	8 (62)

[1] One nest failed at unknown stage.
[2] Two nests failed at unknown stage.

Table 4—Marbled Murrelet chicks, eggs, and juveniles found on the ground by state and province - an indication of additional nest failure[1]

State/province	Number grounded chicks	Number whole eggs	Number grounded juveniles
Alaska	1	1	5
British Columbia	3	0	6
Washington	3	2	9
Oregon	2	1	4
California	3	0	22
Overall	12	4	46

[1] Data from Atkinson, pers. comm.; Confer, pers. comm.; Carter and Erickson 1992; Carter and Sealy 1987b; Hamer, unpublished data; Kuletz, pers. comm.; Leschner and Cummins 1992b; Mendenhall 1992; Nelson, unpublished data; Nelson and others 1992; Rodway and others 1992; S.W. Singer, pers. comm.

are believed to fly directly from inland nest sites to the ocean after fledging (Nelson and Hamer, this volume a; Quinlan and Hughes 1990). Their travel to the ocean may be unsuccessful, however, because of navigational problems or exhaustion. Unlike other alcids, hatch-year Marbled Murrelets must fly relatively long distances to reach the sea without the benefit of past flight experience, wing muscle development that comes with flight, or adult guidance. The large number of juveniles found on the ground while dispersing from nest sites raises questions about the relationship between murrelet energetics, location of the nest in relation to the ocean, and nesting success. Given that some hatch-year birds become grounded each year, and may be unable to take flight again, nest success may actually be much lower than our estimates from nest observations.

Failure because of predation

The major cause of nest failure was predation. Forty-three percent of all nests and 57 percent of nests in Washington, Oregon and California failed as a result of predation (*table 3*). Predation rates were higher (56 and 67 percent, respectively) when excluding unknown causes of failure, which could have included predation. Known predators of murrelet nests include Common Ravens (*Corvus corax*) and Steller's Jays (*Cyanocitta stelleri*) (Naslund 1993; Singer and others 1991) (*table 1*). Predation of a nest by a Great Horned Owl (*Bubo virginianus*) is also suspected. Other potential predators in forests include several species of forest owls, accipiters and American Crows (*Corvus brachyrhynchos*). No Marbled Murrelet nests are known to have been destroyed by mammalian predators, although raccoons (*Procyon lotor*), marten (*Martes americana*), fisher (*Martes pennanti*), and several species of rodents are potential predators.

Predation rates on murrelet nests appear higher than other alcids, perhaps with the exception of areas with introduced or high numbers of predators. For example, 44 percent of the eggs laid by a population of Xantus' Murrelets on Santa Barbara Island in California were taken by deer mice (*Peromyscus* spp.) during periods of egg neglect (Murray and others 1983). Rates of predation on murrelet nests also appear higher than those observed for many forest birds, with the exception of some species of sub-canopy and canopy nesting neotropical migrants (e.g., $\bar{x}$ = 42 percent, range = 18-67 percent) (Martin 1992). However, the impacts of predation on the nesting success of species that lay clutches of two or more eggs (e.g., Xantus' Murrelets, Yellow-rumped Warbler [*Dendroica coronata*]) may be less than on species that lay only one egg, such as Marbled Murrelets.

Predation on Marbled Murrelet nests has been observed or documented during both the egg and nestling stages, but most (56 percent) occurred during the egg stage (*table 3*). Predation during the egg stage is most likely to occur if an incubating adult neglects or abandons the nest. Seabirds are known to completely abandon their nests during years in which prey availability is limited (i.e., during El Niño events) (Ainley and Boekelheide 1990, Hodder and Greybill 1985, Vermeer and others 1979). In addition, seabirds may neglect their eggs for short periods to maximize foraging time and accumulate sufficient energy reserves for the lengthy incubation shifts (Boersma and Wheelwright 1979, Gaston and Powell 1989, Murray and others 1983). During this time, the eggs are subject to a variety of negative factors including predation, heat loss, and exposure to the elements.

Murrelets have been observed leaving their eggs unattended for short periods of time (2–3 hrs on several days) (Naslund 1993; Nelson and Peck, in press), and during such a time in Oregon (Cape Creek nest), an egg was taken by a predator (most likely a Common Raven). In addition, murrelets regularly left their egg unattended in the afternoon, evening, and early morning hours during a 5-day period at a nest in Alaska (Naked Island 1992), and the nest subsequently failed (Naslund and others, in press). Eggs were also abandoned when adults were flushed from the nest by a predator in California (Opal Creek) and Alaska (Naked Island) (Naslund 1993; Naslund and others, in press; Singer and others 1991). The eggs from these nests were later observed or believed to have been destroyed by a Common Raven and Steller's Jay, respectively.

In Oregon, additional egg predation was determined by finding blood and albumen on eggshell fragments. The egg disappeared from the 1991 Valley of the Giants nest after three weeks of incubation. Upon climbing the nest tree, a large eggshell fragment with blood stains was found in the nest cup. The suspected predator was a Common Raven that flew directly adjacent to the nest branch on its daily foraging forays. At the 1992 Valley of the Giants nest, eggshell fragments with blood and albumen were found at the base of a large Douglas-fir (*Pseudotsuga menziesii*) tree. An empty nest cup was subsequently discovered. The predator was most likely a Common Raven observed near the nest tree on several occasions.

In Oregon, chicks disappeared or were killed by predators at three nests during the 1991 and 1992 breeding seasons. A 3-week-old chick at the Siuslaw #2 nest was killed when its skull was pierced by a predator. Two species of corvids (Steller's Jay or Gray Jay [*Perisoreus canadensis*]) detected in the nest tree and adjacent area are the suspected predators. At the Boulder Warnicke nest, a 3-week-old chick disappeared from the nest. The predator could have been any one of the corvids that were present in the area or landed in the nest tree: Steller's Jays, Gray Jays, or Common Ravens. A 6-day-old chick disappeared at the Valley of Giants 1990 nest between 2100 and 0600 hrs on 6 August. A Great Horned Owl was heard calling from an adjacent tree (within 10 m) during this time period, and is the suspected predator.

Marbled Murrelets have limited defenses and their primary protection against predation at the nest is to avoid detection (Nelson and Hamer, this volume a; Nelson and Peck, in press). Therefore, the nestling depends on its cryptic plumage and the location of the nest for safety. If a predator discovers the nest, the chick will attempt to defend itself with aggressive behaviors as witnessed by Naslund (1993) and Singer and others (1991), when a Steller's Jay attacked a 4-day-old chick at the Waddell Creek nest in California. The chick rotated its sitting position on the nest to constantly face the predator, reared up its body and head, opened its beak, and jabbed at the predator. The chick was unable to ward off the jay and was carried away.

Nesting attempts also may fail because adults have been killed on their way to or at nest sites. In forests of southeast and southcentral Alaska, Sharp-shinned Hawks (*Accipiter striatus*) and Northern Goshawks (*Accipiter gentilis*) are known to prey on adult murrelets (Marks and Naslund 1994; Naslund, pers. comm.). In addition, Peregrine Falcons (*Falco peregrinus*) and Common Ravens have been observed chasing Marbled Murrelets just above and within the forest canopy, respectively (Hamer, unpubl. data; Hunter, pers. comm.; Suddjian, pers. comm.). A Peregrine Falcon was successful in capturing a Marbled Murrelet at one such site in central California (Suddjian, pers. comm.).

Predation of adults at the nest site also can occur. There are two known records from California and Alaska. A Common Raven flushed an adult murrelet from a nest in California (Opal Creek), and was later seen carrying what appeared to be a partial carcass (Naslund 1993, Singer and others 1991). In Alaska, an adult was killed by a Sharp-shinned Hawk seconds after it landed on a suspected nest limb (Naked Island) (Marks and Naslund 1994).

Potential for Bias

The Marbled Murrelet nests at which predation has been studied may not be an unbiased sample. The high predation rates recorded at these nests could be biased because many of the nests were located in fragmented areas and near forest edges (*table 5*) rather than in the centers of large, dense stands. Thus, there is the possibility that nest sites located by researchers are also those more easily located by predators (see below). At present we lack information to evaluate this source of potential bias.

In addition, it has been suggested that researchers studying these nests had an impact on their success (see Götmark 1992; Martin and Geupel 1993). We believe the disturbance to the nests was minimal, except at two. In southeast Alaska, researchers approached very close to an unusual murrelet nest located on tree roots near ground level (Brown, pers. comm.). The adult was flushed or disturbed on five occasions, which may have contributed to its failure (egg or newly hatched chick disappeared). The "J" Camp nest in California also failed from direct human intervention (Binford and others 1975). No human impacts are suspected at nests where the chick fell out (*n* = 1 in Oregon) or died (*n* = 1 in California), or where nests were found after they had failed (*n* = 1 each in Washington and Oregon, *n* = 2 in California). At all other nests, human impacts were also limited because: (1) some nests were monitored infrequently (*n* = 8 in Alaska and *n* = 2 in Oregon); (2) predators knew the location of the nest on day of and probably prior to discovery, and, additionally, precautions (e.g., limiting noises and number of observers near nest; see Martin and Geupel 1993) were implemented to minimize disturbance and predator attraction (*n* = 1 in Oregon, *n* = 2 in California); and (3) nests were monitored from >25 m horizontal distance from the nest and precautions (see above) were implemented (*n* = 17). For (2) and (3) above, predators were occasionally attracted to the observer's location on the ground (especially Steller's Jays), but not to the nest site, >18 m above the ground. In contrast, intensive disturbance occurred at three successful nests. In Oregon, the only nest tree that was climbed while active was successful, and in Washington, chicks at two nests fledged despite regular climbing (approximately once a day for 9–20 days) to collect nestling growth and development data.

Table 5—Characteristics of successful Marbled Murrelet tree nests compared with those that failed because of predation

State/province Site/year	Outcome[1]	Distance to edge[2] (m)	Canopy cover (pct.)	Stand size (ha)	Nest concealment (pct.)	Nest height (m)	Limb diameter (cm)	Distance from trunk (cm)	Substrate
British Columbia									
Caren 1993[a]	1	700	70	800	100	18.0	20.0	0	moss
Washington									
Lake 22 1991[b]	1	55	58	405	70	31.4	10.7	45.6	moss
Lake 22 1991[b]	1	65	74	405	95	27.7	36.5	57.0	duff
Nemah 1993[c]	1	10	65	142	80	- -[3]	- -	- -	moss
Oregon									
Valley of Giants 1990[d]	0	20	44	149	70	56.0	34.5	33.0	moss
Five Rivers 1991[d]	1	75	49	46	80	50.3	38.0	116.2	moss
Valley of Giants 1991[d]	0	28	50	149	80	50.3	41.0	17.1	duff
Cape Creek 1991[d]	0	16	65	138	95	44.2	10.0	762.0	moss
Siuslaw #1 1991[d]	1	56	60	89	85	60.3	23.3	152.0	moss
Siuslaw #2 1991[d]	0	64	52	47	80	51.5	13.0	230.0	duff
Boulder Warnicke 1992[d]	0	32	19	3	80	61.0	21.6	46.0	moss
Valley of Giants 1992[d]	0	15	66	149	70	52.0	47.0	35.0	moss
Copper Iron 1992[d]	1	300	93	542	75	49.0	34.0	1.0	moss
California									
Waddell Creek 1989[e]	0	10	40	1700	25	38.5	36.3	61.0	moss
Opal Creek 1989[e]	0	34	40	1700	40	43.7	47.7	122.0	moss
Father 1991[f]	1	69	40	1700	100	41.1	61.0	0	duff
Father 1992[f]	1	69	40	1700	100	53.2	42.0	0	duff

[1] 1 = successful, 0 = failed.
[2] Edge = Distance to nearest unnatural edge (road or clearcut).
[3] Data not available.
[a] P. Jones, pers. comm.
[b] Hamer, unpublished data.
[c] Ritchie, pers. comm.
[d] Nelson, unpublished data; Nelson and Peck, in press.
[e] Singer and others 1991.
[f] Singer and others, in press.

Habitat Characteristics and Predation of Nests

The effect of predators on avian nesting success can vary significantly with geographic location, and is dependent upon the species of predators present, accessibility of nests, type and dimension of the habitat, topography, and vegetative complexity (vertical and horizontal diversity) (Chasko and Gates 1982; Martin 1992; Marzluff and Balda 1992; Paton 1994; Reese and Ratti 1988; Yahner 1988; Yahner and others 1989). For example, alcids nesting on islands relatively free of mammalian predators, or on cliffs inaccessible to terrestrial predators, experience lower predation rates than species nesting in accessible sites and with abundant predators (Ainley and Boekelheide 1990; Hudson 1985). Because many species of birds have evolved in association with predators, the long term impacts of predation on avian nesting success are expected to be minimal in natural situations. However, rapid and unnatural changes, such as the introduction of mammalian predators (cats, goats, mice, pigs, raccoons, rats) and habitat modification, can have significant impacts on nesting success of seabirds (Bailey and Kaiser 1993; Ewins and others 1993; Gaston 1992; Murray and others 1983), and neotropical migrants (Chasko and Gates 1982; Martin 1992), respectively. In these cases, predation can be a major factor affecting avian population viability (Martin 1992).

Significant changes have occurred in the forested landscapes of the United States over the past century, including loss of late-successional forests, habitat fragmentation, and increases in the amount of edge (Hansen and others 1991; Harris 1984; Morrison 1988; Perry, this volume; Thomas and Raphael 1993). These changes have affected the abundance and distribution of many avian predators and forest nesting birds. For example, populations of corvids and

Great Horned Owls are increasing in numbers throughout the western United States, especially in response to increases in habitat fragmentation and human disturbance (Johnson 1993; Marzluff 1994; Marzluff and Balda 1992; Robbins and others 1986; Rosenberg and Raphael 1986; Yahner and Scott 1988). In contrast, numerous neotropical migrant species are declining in numbers because they are unable to adjust to fragmentation and rapidly changing habitat conditions (Hagan and Johnson 1992; Hansen and others 1991, Hejl 1992, Martin 1992, Morrison and others 1992, Rosenberg and Raphael 1986). The Marbled Murrelet was listed as a threatened species in 1992 as changes in the forested landscape appear to be negatively impacting their populations (U.S. Fish and Wildlife Service 1992).

Although the relationship between predator numbers, habitat fragmentation, and predation on Marbled Murrelet nests has not been specifically studied, we believe, based on the following data, that changes in their habitat, such as increased amounts of edge, may significantly affect their nesting success. First, evidence from murrelet nests in this study suggests that distance to edge, stand size, canopy closure, percent cover above the nest cup (nest concealment), and distance of the nest from the tree trunk may be affecting predation rates (*table 5*). In a comparison of these habitat characteristics between successful nests (n = 9) and nests that failed because of predation (n = 8, excluding Alaska), we determined that successful nests were located significantly farther from edges (U = 2.9, n = 16 trees, $P < 0.05$) (*table 5*). All successful nests were located >55 m ($\bar{x}$ = 166.3, n = 8 trees, *s.e.* = 82.3) from an edge (road or clearcut), with the exception of the Nemah nest in Washington, which was located within 10 m of an old road near the center of a 142 ha forest. In contrast, all nests that failed because of predation were located within 64 m ($\bar{x}$ = 27.4, *s.e.* = 6.0) of an edge. In a review of numerous artificial nest predation studies, Paton (1994) found evidence that predation of bird nests is higher within 50 m of edges. This result supports our hypothesis that murrelet nests near edges may be more vulnerable to predation than those located in the stand interior. In addition, nest concealment was significantly greater at successful nests ($\bar{x}$ = 87.2 percent, *s.e.* = 3.9) compared with nests that failed because of predation ($\bar{x}$ = 67.5 percent, *s.e.* = 8.2) (U = 2.3, n = 17, $P < 0.05$) (*table 5*). Nest concealment has been shown to decrease predation rates (Chasko and Gates 1982; Marzluff and Balda 1992; Martin and Roper 1988). Stand size (532.0 versus 407.4 ha, n = 11 stands) and canopy closure near nests (63.6 versus 47.0 percent, n = 16 plots) were higher and nests located closer to the trunk (46.5 versus 163.3 cm) at successful sites, but were not significantly different from nests that failed because of predation.

Second, it has been suggested that changes in forests where boundaries are contiguous with secondary succession may not create the same predation problems as those observed in static, simple forests in urban and agricultural areas that are defined by distinct boundaries (Rosenberg and Raphael 1986; Rudnicky and Hunter 1993). However, numerous studies in the eastern United States provide empirical evidence that edge effects in a forest dominated landscape (forest/clearcut edge) are similar to those in forest/urban or agricultural settings. For example, in studies of eastern neotropical migrants, predation was lower in the forest interior (>50 m from the edge) compared with edge habitat (Chasko and Gates 1982; Yahner and Scott 1988). Predation was also lower in areas with high vegetative heterogeneity and concealing cover (Chasko and Gates 1982).

Evidence from artificial nest studies in forests of the Pacific Northwest also suggests that predation of birds' nests may be affected by habitat fragmentation and forest management. On Vancouver Island, British Columbia, Bryant (1994) demonstrated that artificial ground and shrub nests located along forest/clearcut edges (within 100 m) were subject to higher predation rates than those in the forest interior (100–550 m from the edge). In the Oregon Coast Range, predation on artificial shrub nests was higher in clearcuts and shelterwood (20–30 green tress >53 cm d.b.h./ha) stands than in stands with group selection cuts (1/3 volume removed in 0.2 ha openings) and unmanaged (control) stands (Chambers, pers. comm.). Additionally, in the Oregon Cascades, Vega (1994) found that predation on ground nests was significantly greater in clearcuts compared with retention stands (12 trees/ha and 7.5 snags/ha), and predation on shrub nests was highest in retention stands compared to the other treatment types (clearcuts and mature stands). Steller's Jays, the suspected predator of the shrub nests, were more abundant in the retention stands, where they probably used the remnant trees for perching (see Wilcove 1985; Yahner and Wright 1985).

Third, despite differences in results among nest predation studies (e.g., Rudnicky and Hunter 1993 versus Yahner and Scott 1988), existing evidence strongly indicates that avian nesting success declines near edges (Paton 1994). In addition, regardless of the type of edge, fragmentation of forests often reduces structural complexity and heterogeneity of stands, and exposes remnant patches to edge effects (Hansen and others 1991; Harris 1984; Lehmkuhl and Ruggerio 1991). Because of increases in the amount of edge, productivity of interior forest species is generally impacted (Lehmkuhl and Ruggerio 1991; Reese and Ratti 1988; Yahner and others 1989), and generalist species, which benefit from the ecotone, usually increase in numbers (Yahner and Scott 1988). In addition, as vegetative complexity and canopy volume are reduced through fragmentation, bird nests (especially those located in shrubs or trees) may be more conspicuous and easier for avian predators to locate (Rudnicky and Hunter 1993; Vega 1994; Wilcove 1985; Yahner and Cypher 1987; Yahner and others 1989; Yahner and Scott 1988).

The rates of predation on Marbled Murrelet nests in this study appear higher than for many seabirds and forest birds. If the observed predation rates are representative of predation rates throughout the murrelet's range, then the impacts of predation on murrelet nesting success is significant and of concern (Wilcove 1985). Even if these high predation rates are localized to certain states or areas within states, the combination of low annual nesting success, low fecundity rates (Beissinger, this volume), and low or declining population sizes (Carter and Erickson 1992; Kelson and others, in press; Kuletz, 1994), could impact the survival and recovery of this threatened seabird.

Conclusions

Results from this study suggest that predation on murrelet nests may be relatively high compared with many alcids and forest nesting birds. Because Marbled Murrelets have no protection at nest sites other than the ability to remain hidden (Nelson and Hamer, this volume a), the availability of safe nest sites will be imperative to their survival. If logging and development (e.g., clearing land, creating patches of habitat, thinning stands) within the murrelet's range has resulted in increased numbers of predators or predation rates, and has made murrelet nests easier to locate because of increased amounts of edge and limited numbers of platforms with adequate hiding cover, then predation on murrelet nests could be significantly higher in such situations. In addition, areas heavily used by humans for recreational activities (i.e., picnic and camping grounds) can attract corvids (Marzluff and Balda 1992, Singer and others 1991) and may increase the chance of nest predation within these areas. Therefore, we hypothesize that because this seabird has low reproductive rates (one egg clutch), small increases in predation will have deleterious effects on murrelet population viability.

Rigorous studies should be developed to investigate the effects of predator numbers, predator species, predator foraging success, landscape patterns, habitat types, and forest structural characteristics on Marbled Murrelet nesting success. In implementation of these studies, hypotheses on the effects of various habitat features on fitness components (recruitment and demography) should be tested (Martin 1992, Paton 1994). At the same time, the effects of these hypotheses on coexisting species and the interacting effects these species have on one another should be evaluated (Martin 1992).

Acknowledgments

We are grateful to the biologists who kindly shared their data with us; special thanks go to Jim Atkinson, Alan Burger, Stephanie Hughes, John Hunter, Paul Jones, Kevin Jordan, John Kelson, Steve Kerns, Kathy Kuletz, Irene Manley, Ray Miller, Nancy Naslund, Bill Ritchie, Steve and Stephanie Singer, and David Suddjian for their time and generosity. We also thank Alan Burger, George Hunt, John Marzluff, Robert Peck, Steve Speich, and several anonymous reviewers for providing valuable comments on earlier drafts of this manuscript. Support for preparation of this manuscript was provided by the Oregon Department of Fish and Wildlife, USDA Forest Service, USDI Bureau of Land Management, and the U.S. Fish and Wildlife Service, U.S. Department of the Interior. This is Oregon State University Agricultural Experiment Station Technical Paper 10,540.