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EFFECTS OF FOREST FRAGMENTATION ON POPULATIONS OF THE MARBLED MURRELET

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Abstract. The Marbled Murrelet (*Brachyramphus marmoratus*) is a threatened seabird that nests on branches of large trees within older coniferous forest in coastal areas of the Pacific Northwest. Surveys suggest that murrelets often nest in continuous stands of mature, complexly structured forest but they also nest in younger forest and in stands varying in size from several to thousands of hectares. We examined how murrelet abundance and reproduction are related to the amount and pattern of nesting habitat at regional, watershed, landscape, and nest site scales. At the regional scale, abundance of murrelets, estimated from offshore surveys, was found to be correlated with amount of nesting habitat in some areas and to a lesser extent with fragmentation of that habitat. We found a similar pattern at the watershed scale. At the scale of nest sites and surrounding landscapes, fragmentation may have greater effect on likelihood of nesting and nest success. Observations of active nests from other studies indicated high failure rates (47 of 71 nests with known outcomes), mostly due to predation (33 of 47 nests). Corvids have been implicated as primary predators. Forest fragmentation can affect the abundance and distribution of corvids, and thus it is possible that fragmentation might lead to higher rates of predation on murrelet nests. Over the past 5 years we have tested this assumption in Washington using artificial nests located in stands of varying structural complexity, levels of fragmentation, and proximity to human activity. Results indicate, first, that a broad suite of predators, including at least 10 mammalian and avian species, prey on simulated eggs and chicks. Second, rates of predation are higher within 50 m of forest edge, but this relationship varies with proximity to human activity and with the structure of the adjacent regenerating forest. Predation increased with proximity to forest edges when the matrix contained human settlements and recreation areas, but not when it was dominated by regenerating forests. Abundance of some predators (e.g., Steller's Jays, *Cyanocitta stelleri*) was greater in more fragmented landscapes, but abundance of other potential predators (e.g., Gray Jays, *Perisoreus canadensis*) was greater in continuous forests, making generalizations about the effects of fragmentation difficult. Research is needed to understand how fragmentation affects both murrelet nest site selection and the risk of nest predation so that managers can provide landscapes able to support large populations of successfully breeding murrelets.

Key Words: *Brachyramphus marmoratus*; corvid; fragmentation; Marbled Murrelet; nesting habitat; nest predation; nest success.

Forest fragmentation has been implicated as an important factor affecting the status and trend of the Marbled Murrelet (*Brachyramphus marmoratus*; U.S. Fish and Wildlife Service 1997a). Forest fragmentation is the process of subdividing continuous forest patches into smaller pieces. In forests of the Pacific Northwest, timber cutting primarily drives this process. For species associated with older forest structures, fragmentation of old-growth habitat leads to a reduction in amount of that habitat as well as a change in its pattern on the landscape. The Marbled Murrelet is unique among other species considered in this volume, as it uses forest patches for nesting but not foraging. It feeds and resides on marine waters for most of the year but nests on large limbs primarily in older forest patches. Therefore, the potential effects of forest fragmentation are limited to those that might affect probability of nesting, nesting success, and survival of adults in transit to or attending nests. For this species, fragmentation will not affect foraging behavior or foraging success. In this paper, we review the potential effects of forest fragmentation on the murrelet and describe recent experimental evidence of its effects.

BIOLOGY OF THE MARBLED MURRELET

It is important to understand the biology of the Marbled Murrelet as a prelude to reviewing fragmentation effects. The Marbled Murrelet is a small seabird of the family Alcidae whose summer distribution along the Pacific coast of North America extends from the Aleutian Islands of Alaska to Santa Cruz, California. It forages primarily on small fish in the nearshore (0–5 km) marine environment. Unlike other alcids, which nest in colonies on the ground or in burrows at the marine-terrestrial interface, Marbled Murrelets nest solitarily and most often in large trees in coniferous forests, traveling up to ~100 km inland to reach suitable habitat. A small proportion of the Alaska population nests on the ground (Mendenhall 1992, Piatt and Naslund 1995). Tree-nesting Marbled Murrelets do not build a nest, but use a natural platform on which to place their single egg. Both adults share equally in incubation, exchanging once every 24 hr (Nelson and Peck 1995). A few days after hatching the chick is left alone at the nest for the duration of the 30–40 d nestling period, with adults making feeding visits, primarily at dawn and dusk (Nelson and Peck 1995, Nelson 1997). Due to population declines attributed to loss of mature and old-growth forest from logging, low nest success, and mortality at sea, this species was federally listed as threatened in Washington, Oregon, and California in 1992 (U.S. Fish and Wildlife Service 1997a) and is listed as threatened in British Columbia.

The Marbled Murrelet's unusual nesting habitat and secretive behavior during the nesting season kept it one of the least known North American birds of the latter 20th century. The first nest was not discovered on this continent until 1974 (Binford et al. 1975), and many aspects of this species' ecology, at sea and inland, are still unclear. However, in the last 10 years relatively consistent information has emerged on the association of Marbled Murrelets with older coniferous forests and on stand attributes correlated with murrelet activity and nesting. Across the range, sites with the highest likelihood of nesting murrelets have larger trees, more potential nest platforms, and/or greater moss cover on tree limbs than other sites (Grenier and Nelson 1995, Hamer 1995, Kuletz et al. 1995). Nest trees are larger on average than adjacent trees (often the largest tree within a 25–50 m radius), contain more platforms with greater cover than surrounding trees, and often have moderate to heavy epiphyte cover (Jordan and Hughes 1995, Kerns and Miller 1995, Naslund et al. 1995, Manley 1999). Nest trees are often near natural or human-created gaps in the canopy that murrelets use to access nests (Hamer and Nelson 1995, Jordan and Hughes 1995, Kerns and Miller 1995, Naslund et al. 1995, Manley 1999). Large limbs (mean diameter = 32 cm), deformities from mistletoe and other disease, damage, and moss cover create suitable nesting platforms, and these features are most often found in older forests. However, murrelet sites also have been recorded in young (60–70 yr) forests with residual old-growth trees or heavy mistletoe infestations (Nelson 1997). Suitable habitat generally occurs at <1,000 m elevation, as floristics at higher elevations lack the structural features that provide platforms. Manley (1999), however, found nests at elevations up to 1,260 m in the Bunster Range of British Columbia. Older forests at lower elevations had been heavily logged by the time of this study, but it is unknown if nests occurred at higher elevations prior to logging.

Presumably, Marbled Murrelet nesting habitat associations evolved under a regime of large expanses of old-growth conifer forests on the landscape. Wildfire was the primary disturbance agent prior to the 1800s (Agee 1993); extensive, high intensity but low frequency (150–300 yr) fires resulted in large areas of old forest (Garmen et al. 1999). Reduction in extent of old forest in the Pacific Northwest due to logging over the past 100 yr has been implicated in the decline of murrelet populations through reductions in available nesting habitat (Ralph et al. 1995). Loss of conifer forest within the inland limits of the Marbled Murrelet range has been extensive, but actual percentages based on area are difficult to extract from the literature. An estimated 30% of coastal forest remains in British Columbia (Perry 1995). As a site-specific example, 15–25% of old-growth forest in Clayoquot Sound, British Columbia, was logged during 1954–1993, most from low-elevation, large-volume western hemlock forest (Kelson et al. 1995). During the period 1982–1993, the murrelet population declined 40% in Clayoquot Sound, likely as a result of loss of nesting habitat. In western Washington and Oregon, roughly 18% of old-growth forests that occurred before logging remained by the early 1980s (Booth 1991); 5–10% of old-growth redwood forest from the early 1800s remains in California (Carter and Erickson 1992, De Angelos and De Angelos 1998).

POTENTIAL EFFECTS OF HABITAT FRAGMENTATION

Loss of coniferous forests in the Pacific Northwest may affect Marbled Murrelet nesting habitat in multiple ways, including overall decrease in the amount of habitat available and fragmentation of remaining habitat into smaller, discontinuous patches with potentially greater influence of edge phenomena. Edge effects include changes in microclimate at open edges compared with interior sites (Chen et al. 1995, 1999), changes in vegetative species, and changes in predator-prey dynamics (Kremsater and Bunnell 1999). Most studies have difficulty separating the effects of habitat loss, per se, from fragmentation, because habitat loss is a necessary consequence of fragmentation (Fahrig 1999). Fragmentation will lead to reduced area of habitat, including reduced amount of interior habitat, increased number of patches of habitat, reduced sizes of patches, increased amount of edge, and increased isolation of patches. These conditions, in turn, could affect overall population size, likelihood of nesting, survival of adults, and nesting success. These effects could differ over the short run versus the long run. For example, in the short run (say, 10 years), loss and fragmentation of habitat could cause displaced murrelets to locate in remaining patches, nest in marginally suitable habitat, or travel greater distances to locate new, disjunct sites (Divoky and Horton 1995). Although dispersal and colonization mechanisms are unknown, we speculate that if murrelets moved into remaining available habitat, nesting success in marginal or overcrowded habitat may decline over the long run, leading to smaller populations and lower nesting density. In the following sections, we review the evidence for these potential effects over a variety of geographic scales.

REVIEW OF FRAGMENTATION EFFECTS AT MULTIPLE SCALES

Regional Scale

In a review of Marbled Murrelet population changes, Ralph (1994) observed that, at a broad scale, the species' distribution on the water generally corresponded to amounts of inland old-growth forest. In California and Oregon, the marine distribution was thought to reflect remaining older forests, mostly on federal lands (reviewed by Ralph et al. 1995), with gaps in distribution on the water where older forests no longer occur. This relationship was less evident in Washington and British Columbia, but a systematic comparison of density of murrelets with density of adjacent nesting habitat has not been reported. In Alaska, breeding season concentrations generally coincided with the distribution of coastal old-growth coniferous forest (Piatt and Ford 1993). One exception was Cook Inlet, where there was an abundance of forest cover but few murrelets. The lack of correspondence in this region was explained by poor foraging conditions in Cook Inlet and a dominance of black spruce in the forest cover, which lacks the structural characteristics shared by nest trees.

To examine relationships between offshore numbers of Marbled Murrelets and amount of inland habitat in Washington and Oregon, we compared available vegetation information to published and unpublished murrelet data. As no consistent vegetation map layer was available for both states, we used different datasets but selected for similar attributes as much as possible (see Appendix for details). In Washington, we used a vegetation layer compiled from a number of sources (U.S. Fish and Wildlife Service 1997b). From this we selected late seral habitat (mixed conifer and hardwood, with >70% crown closure of conifer and >10% crown closure from trees >53 cm dbh) to represent potential Marbled Murrelet nesting habitat. At-sea data were summarized from midsummer nearshore (0–400 m) surveys conducted by the Washington Department of Fish and Wildlife in 1997 (C. Thompson, unpubl. data). For Oregon we used a Landsat-based vegetation map produced by the Western Oregon Digital Image Project (Nighbert et al., unpubl. data). We selected multi-storied stands with mean dbh >48 cm and single-storied stands with mean dbh >74 cm within the Sitka spruce zone (*Picea sitchensis*; Franklin and Dyrness 1973). At-sea data were averaged over 2-km segments from July 1996 nearshore (0–500 m) surveys (C. Strong, unpubl. data). North-south bands were established along the coast based on how the at-sea data were summarized (WA) or to represent approximately 50-km stretches of coastline (OR). Inland boundaries followed Recovery Plan (U.S. Fish and Wildlife Service 1997a) zones (80 km in WA, 56 km in OR), and we established an elevation cutoff of 1,067 m. Habitat was summarized per band as total habitat within the band; murrelet data were summarized as a relative estimate of total numbers of murrelets counted within the band.

We found no correlation between murrelet abundance and estimated amount of nesting habitat at the broad scale over the entire two-state region (Spearman correlation = 0.07, one-tailed $P = 0.391$, $N = 17$ bands; Fig. 1). As summarized in Figure 1, habitat seemed to be most abundant on the Olympic Peninsula of Washington and in southern Oregon. Murrelet abundances were greater in the far northern band of Washington and the central bands of Oregon. Because of the differences in habitat maps between the two states and the perception that relationships between at-sea distributions and inland habitat are not as evident in Washington (Ralph et al. 1995), we also computed correlations for Oregon alone. In that analysis, the correlation was very weak (Spearman correlation = 0.37, one-tailed $P = 0.132$, $N = 11$). Meyer (1999) has argued that habitat closer to shore (within about 25 km) may be more important than habitat further away. In fact, the small concentrations of murrelets off the coast of northern Oregon in 1992 were associated with state parks with old-growth stands near the coast (Strong 1995). Restricting the analysis to habitat within 25 km of shore, the correlations improved slightly (for both states, Spearman correlation = 0.38, one-tailed $P = 0.066$, $N = 17$; for Oregon alone, correlation = 0.38, $P = 0.126$, $N = 11$). We caution that this assessment was conducted at a very broad scale, using indices for habitat and at-sea abundance. Results were entirely a function of the vegetation layer used for mapping, the specific at-sea data used (dates of surveys, single vs. multi-year data, nearshore transects vs. all transects), and the north-south bands we defined. The offshore abundance of murrelets does seem to have a consistent pattern, as the at-sea distribution we depicted for Oregon

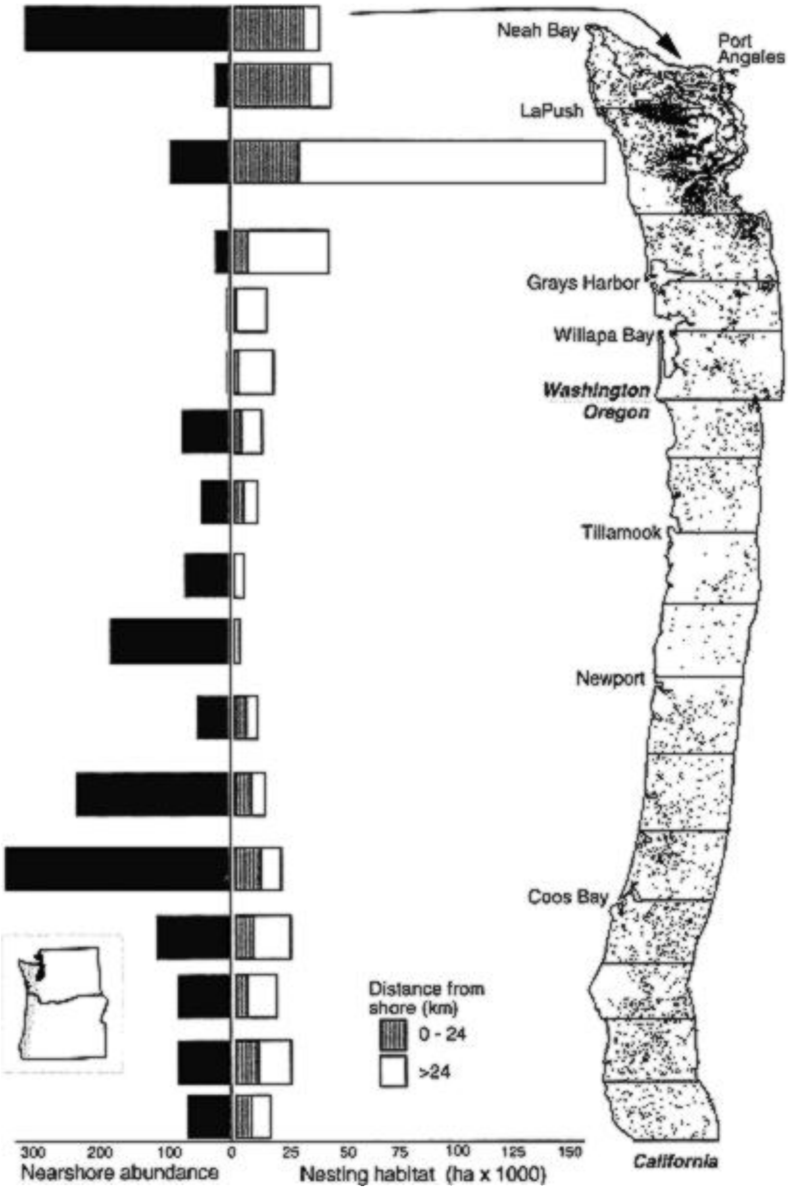

FIGURE 1. Relative abundance of Marbled Murrelets in nearshore waters within geographic bands of Oregon and Washington in relation to amount of potential nesting habitat (represented as dark polygons on map). Bars represent relative magnitudes in each zone (topmost pair of bars corresponds to northernmost habitat band). Dark bars on the habitat histogram represent habitat within 24 km of the coast; open bars represent remaining inland habitat. See text and Appendix for details and sources of data.

(based on our reanalysis of a subset of C. Strong's data) was very similar to the murrelet distribution he reported for 1992 (Strong 1995, Strong et al. 1995). More refined estimates of murrelet density and available habitat will be forthcoming from various scientists as part of an ongoing murrelet monitoring program. Specifically, it will be important to obtain consistent estimates of murrelet numbers over the whole region and to develop a more reliable estimate of the amount of nesting habitat using the same sources of data and analytical techniques across all sites.

Meyer (1999) conducted a more quantitative spatial analysis for southern Oregon and northern California. Within nine 212,000–650,000 ha subregions along the coast, greatest marine densities of murrelets were found offshore of large blocks of consolidated old-growth forest within a matrix of relatively abundant medium-sized, second-growth coniferous or hardwood forests. In subregions with few murrelets, patches of nesting habitat were relatively small, simple-shaped, and scattered. Offshore densities were higher in subregions with more continuous old growth or old growth combined with residual old-growth forest. In fact, this study found that inland habitat variables explained most of the offshore distribution in this region, with marine variables, such as type of shoreline, chlorophyll counts, and sea surface temperature, accounting for little variation (we note, however, that prey densities were not included in her analysis).

WATERSHED SCALE

Several studies have explored relationships between forest landscape patterns and murrelet activity at the watershed scale. On the Olympic Peninsula, Washington, 10 large drainages were sampled with radar for 1–3 yr to compare the numbers of murrelets flying into each drainage with the amount and configuration of habitat available (Raphael et al. 1999, 2002; see Cooper et al. 1991, Hamer et al. 1995, and Burger 1997 for details on the use of radar to sample birds). Mobile radar units were stationed within drainages where the natural topography funneled murrelets flying inland. Late-seral habitat (defined as >70% crown closure with at least 10% from trees >53 cm dbh) occurring below 1,067 m was considered potentially suitable habitat. Late-seral habitat was 1 of 10 land cover types derived from satellite imagery classification (U.S. Fish and Wildlife Service 1997b). In 2000, a year with the largest sample of drainages ($N = 10$), the maximum number of murrelets detected flying inland was highly correlated with the amount of potentially suitable habitat after accounting for drainage size (partial correlation = 0.86, $P = 0.003$; Raphael et al. 1999, 2002).

Similar results were found in Clayoquot Sound, Vancouver Island, British Columbia, from 18 watersheds sampled 3 yr with radar. Dawn and dusk radar counts were positively correlated with the size of the drainage and the amount of mature forest, with the strongest correlations between dawn counts and mature forest below 600 m (Burger 2001). In multiple regression models, 60–73% of the variation in dawn counts of murrelets among watersheds was explained by the area of mature forest at elevations <600 m, with another 8% explained by the negative effect of the combined area of logged and immature (<160 yr) forest. In a different study on Vancouver Island, which used audio-visual detections from human observers, there were significantly fewer detections (mean detections per point) in watersheds with <50% old growth compared with those with >50% (Burger 1995).

Whereas relationships between murrelet counts and overall amount of available habitat were strong across studies, relationships with the spatial configuration of habitat at this watershed scale were less revealing. For the Olympic Peninsula study, we used our map of potential nesting habitat and the program FRAGSTATS (McGarigal and Marks 1995) to define patches of potential habitat (a patch is a set of adjacent habitat pixels). We then computed a number of fragmentation metrics and tested whether radar counts of murrelets were correlated with these metrics. Radar counts were not significantly correlated with the density (number/100 ha) of late-seral patches below 1,067 m, average size of patches, or a patchiness index that described a continuum from many small patches to few large patches (Raphael et al. 2002). These results were preliminary and may have been biased somewhat by the artificial patch boundaries created by the elevation cut-off, and by the limitations of the base vegetation map.

NESTING NEIGHBORHOOD

Two studies have examined the spatial characteristics of murrelet habitat within the neighborhood of nest sites, at a landscape scale intermediate between watersheds and nest sites. Both studies found that forest-cover attributes could be useful predictors of murrelet occupancy at the neighborhood scale. Habitat features within 200-ha analysis circles ($N = 261$) were described around locations occupied and unoccupied by murrelets on the Olympic Peninsula (Raphael et al. 1995). "Occupied" locations were those where behaviors that have been associated with nesting were observed; "unoccupied" locations had no murrelet detections. Locations were screened to include only those surveyed to the Pacific Seabird Group's (PSG) protocol (Ralph et al. 1994). Within the 200-ha circular neighborhoods centered on occupied locations, there was significantly greater area in large sawtimber and old-growth forest compared with neighborhoods centered on locations with no detections. Old growth (but not large sawtimber) occurred in larger patches (mean = 18.6 ha) in "occupied" relative to "no detection" (mean = 8.5 ha) neighborhoods. A landscape pattern index, derived from a combination of variables including number of patches, Shannon's and Simpson's diversity and evenness indices, contagion, and amount of edge (computed using program

FRAGSTATS; see Raphael et al. 1995), differed significantly between occupied and unoccupied neighborhoods. Neighborhoods surrounding occupied locations had a higher landscape pattern index, indicating greater number of patches, greater variety of patch types, smaller average sizes of all patches, and greater amounts of edge. Thus, occupied neighborhoods had more intact patches of old forest but other forest classes within these neighborhoods tended to be patchier and more fragmented. The authors cautioned that the sample of survey locations was somewhat biased, weighted by one intensive study and placed at prospective timber sales.

With a similar approach in northern California and southern Oregon, Meyer (1999) used several map sources and four neighborhood sizes (50–3,217 ha circles) centered on survey stations. Stations with no detections were screened to ensure that they or the stand they were in met the PSG protocol. Analysis circles encompassing more than one station received the highest status of all stations. In general across map layers, there was more old growth, it occurred in larger patches, and was less fragmented in occupied compared with unoccupied locations. The presence of high-contrast edges (natural or clearcuts) did not deter use of a site. In the California portion of the study area, 50-ha neighborhoods were always occupied if they contained >20% old growth with >6% of that as core area (>100 m from an edge), ≥12% of the area in one large patch, a mean patch size ≥11 ha, and mean core area >3 ha.

In support of the influence of habitat fragmentation on murrelet nesting activity, a map of relatively unfragmented old-growth forest in northern California and southern Oregon from the late 1980s was predictive of the current locations of occupied sites (75% correctly predicted in the coast redwood zone of northern California; Meyer 1999). Areas highly fragmented before the late 1980s generally didn't support murrelets in the early 1990s.

NEST SITES

Murrelet nests are difficult to locate, and the sample of active nests on which to assess effects of forest fragmentation on nest fate is relatively small. Early data from small samples from several locations indicated extremely high failure rates and high rates of predation, an interpretation that has been tempered somewhat by larger sample sizes. For example, 100% of 7 nests with known outcome failed in Alaska, 3–4 of which may have been due to predation (Naslund et al. 1995). In Oregon, 6 of 9 (67%) nests failed, with 5 of the 6 failures from predation (Nelson and Peck 1995). Based on the most comprehensive compilation of nest results to date (9 nests from Alaska, 31 from British Columbia, 4 from Washington, 17 from Oregon, and 10 from California), 66% of 71 nests with known outcome have failed, and 70% of these failures were due to predation (Manley and Nelson 1999). Overall failure rates (not predation only) were similar among the states with larger sample sizes—61% in B.C., 63% in Oregon, and 70% in California—although Alaska nests had complete reproductive failure. Predation rates (% of total nests lost to predation) were more variable but increased from northern to southern latitude—33% in Alaska, 48% in B.C., 53% in Oregon, and 60% in California.

For the subsample of nests from Oregon and B.C., distance to edge (roads, clearcuts) was the most important predictor of nest fate. Successful nests were significantly further from edges ($\bar{X}$ = 141 m) than failed nests ($\bar{X}$ = 56 m, P = 0.02). Nest failure, and predation, were highest within 50 m of an edge compared with >50 m. All nests >150 m from an edge were successful or failed from reasons other than predation.

While there was a trend (P = 0.12) for successful nests in Oregon and British Columbia to occur in larger stands ($\bar{X}$ = 491 ha) compared with unsuccessful nests ($\bar{X}$ = 281 ha), the relatively limited sample of murrelet nests precludes a reliable region-wide analysis of the relationship between stand size and reproductive success. Marbled Murrelet nests and occupied sites have been found in stands ranging in size from 2–565 ha, but stand size is constrained in some geographic areas. For example, average nest stand size in Prince William Sound, Alaska, was smaller than other locations, but reflected what was available (3–63 ha; Naslund et al. 1995). Average stand size of nests in the Bunster Range in British Columbia was 224 ha (Manley 1999).

Changes in habitat configuration in forest landscapes to smaller patch sizes and more edge have been proposed as increasing nest failure by increasing the risk of Marbled Murrelet nests to predation. From observations at active nests, Common Ravens (*Corvus corax*) are known predators of Marbled Murrelet eggs and adults; Steller's Jays (*Cyanocitta stelleri*) are known predators of chicks and strongly-suspected predators of eggs (Nelson and Hamer 1995, Manley 1999). Other species implicated but not documented as nest predators include Gray Jay (*Perisoreus canadensis*), American Crow (*Corvus brachyrhynchos*), Great Horned Owl (*Bubo virginianus*), and Cooper's Hawk (*Accipiter cooperi*; Nelson 1997). Peregrine Falcon (*Falco peregrinus*), Sharp-shinned Hawk (*Accipiter striatus*), Northern Goshawk (*Accipiter gentilis*), and Red-shouldered Hawk (*Buteo lineatus*) have taken adult murrelets in forests (Marks and Naslund 1994, Singer et al. 1995, Nelson and Hamer 1995; E. Burkett, pers. comm.). It is theorized that adult murrelets' cryptic breeding plumage, limited visits to nests, and timing of visits to coincide with low light levels (dawn and dusk) evolved to minimize predation.

How these potential predators have responded to a changed forest landscape is the best indication of the extent to which the risk of predation at Marbled Murrelet nests has been elevated by forest fragmentation. For increased rates of predation to be linked to fragmentation, predators must increase in numbers or forage extensively along edges or small fragments; the diversity of predators must be highest at forest edges, small fragments, or in fragmented landscapes (Marzluff and Restani 1999); or predators must have greater foraging success along edges compared with interior habitats.

Corvid populations have increased in the western U.S. with increased urbanization, agricultural intensification, and human activity in forests and woodlands (Marzluff et al. 1994). Increases in American Crows, Common Ravens, and Western Scrub-Jays (*Aphelocoma californica*) are especially pronounced. Human refuse, bird feeders, lawns, and road kills appear to be fueling the corvid increase. Recreation sites have similar, but more local, effects in murrelet habitat, leading to large increases in ravens (S. Singer, pers. comm.) and crows (this study).

Several studies have demonstrated that Steller's Jays can be considered an edge species, and thus benefit from increased fragmentation of forest landscapes. In a study combining point counts with telemetry data in potential Marbled Murrelet nesting habitat on Vancouver Island, transects were established in forests and along three types of edges: roads, clearcuts, and rivers (Masselink 1999). The greatest number of jays was detected along clearcut edges, and numbers were higher at all edges compared with interior forest. Among sites sampled with audio-visual surveys along the central B.C. coast, Steller's Jays and American Crows were detected more frequently in sites fragmented by logging compared with unfragmented (unlogged) forest stands (Rodway and Regehr 1999).

However, it should be noted that Steller's Jay response to fragmentation is not unequivocal. In another coastal B.C. study, this species' abundance was not associated with patch size in remnant (left from logging) old-growth Douglas-fir/western hemlock forest (Schieck et al. 1995). Similarly, there were no significant correlations with landscape variables, including stand size, edge, landscape composition, and patterns in the southern Washington Cascades (Lehmkuhl et al. 1991). In Douglas-fir forest in northwestern California, only 12% of ~2,500 detections were made on edges, abundance decreased with increased proximity and length of clearcut edge, and this species was not associated with the percent of clearcut or length of edge in 1,000-ha landscape blocks (Rosenberg and Raphael 1986). These studies suggest relationships between numbers of predators and fragmentation, but further work is needed to determine whether foraging efficiency of predators is affected by fragmentation.

ARTIFICIAL NEST EXPERIMENTS

METHODS

To specifically address the effects of landscape configuration on the risk of Marbled Murrelet nests to predation and the behavior of potential predators, we conducted an artificial nest experiment for five breeding seasons on the western side of the Olympic Peninsula, Washington (Marzluff et al. 1999, unpubl. data). The study area was adjacent to a major concentration of murrelets in Washington (Varoujean and Williams 1995), and in a landscape used substantially by nesting murrelets (Harrison et al. 1999). Study stands were selected in a randomized block design to investigate the effect of forest structure (simple, complex, and very complex), proximity to human activity (<1 km and >5 km), and landscape fragmentation (stands in continuous forest versus those surrounded on at least 3 sides by 1–15 yr-old regenerating forest). Effects of fragmentation were indicated by the responses of predation and corvid nest predators to: (1) the isolation of stands by regenerating forest, (2) the distance from forest edge, and (3) the interaction of proximity to human activity with stand isolation and distance from forest edge.

Artificial nests were selected for these experiments because of the extreme difficulty in locating a sufficient sample of active nests to design a rigorous experimental study. We are aware of potential biases of using artificial nests (e.g., Major and Kendal 1996, Storaas 1988, Willebrand and Marcström 1988). However, these are minimized in our case because we (1) accurately simulated murrelet nests, eggs, and chicks, and (2) limited our presence around nests (see details below). Additionally, murrelet nests are especially easy to mimic because (1) eggs are laid in simple depressions on moss-covered branches, (2) eggs are sometimes left unattended for several hours during incubation, and (3) nestlings are left alone for much of the day after they reach three days of age (Nelson and Peck 1995, Manley 1999). We explicitly discuss any biases in our use of artificial nests elsewhere (Marzluff et al. 2001, Luginbuhl et al. 2001) and show that rates of predation at our nests are higher, but not significantly higher than those at natural nests. Here we are concerned with comparing rates of nest predation among various treatments. Such comparisons are unbiased because we used the same techniques in all tests and developed ways to assess the importance of all possible nest predators in each treatment (see below).

We climbed trees to place 923 nests in 49 stands of 80- to >200-yr-old forests. We simulated nests at typical heights and locations for murrelets: on moss-covered branches with diameter >11 cm, within the live crown, >15 m above the ground, well covered from above ($\bar{X}$ % overhead cover = 84.1%, SE = 0.39, N = 923), and close to the trunk ($\bar{X}$ distance to bole = 38.9 cm, SE = 0.84, N = 923; Hamer and Nelson 1995, Singer et al. 1995).

To minimize disturbance that might cue predators to the nest's location (i.e., damage to the bark from spurs or human scent trails left from touching the bole or limbs), we climbed trees using 11-mm static climbing rope following Perry (1978); avoided contact with the tree by climbing with ascenders and rappelling to the ground; wore latex or vinyl gloves while taking measurements and preparing the nest; and marked nest trees on the ground with white plastic flagging hung in a random direction approximately 3 m from the tree (Luginbuhl et al. 2001). The entire process of climbing, placing nests, and rappelling took approximately 90 minutes.

Nests were placed in separate trees >50 m apart and only six nests were placed in a given stand at any one time to reduce the effects of area-restricted searching practiced by Common Ravens and American Crows (Marzluff and Balda 1992), and to decrease the possibility that high nest densities may cause predators to associate our activities with food rewards (Sieving 1992, Major et al. 1994). To increase sample size per stand, we replicated experiments from three to five years per stand. No nest trees were used more than one year, but annual replication allowed us to place 18–30 nests in each stand. Each year, two artificial nests (one with an egg and one with a nestling) were placed at each of three distances from the forest edge (<50 m from the edge, approximately 100 m from the edge, and >200 m from the edge).

An important improvement we made over typical artificial nest experiments was to simulate nest contents with plastic eggs and taxidermy mounts of nestlings. We painted eggs to resemble Marbled Murrelet eggs, coated them with wax (household paraffin) to aid with predator identification (Møller 1987, Haskell 1995a), and stored them in cedar chips for >12 hr prior to placement to limit human scent. Plastic eggs were slightly larger than actual Marbled Murrelet eggs (64 mm × 44 mm vs. 59.8 mm × 37.6 mm; Nelson 1997). Nestling models were made from domestic chicken chicks preserved with borax. They were dark-colored (mostly black), approximately 10 cm long, and were placed in a posture that imitated a crouched or sleeping nestling. Although decay of mounted nestlings was limited (they appeared visually unchanged after 30 d), they emitted odor perceptible to humans. However, real Marbled Murrelet nests with a well-developed fecal ring also give off odor perceptible to humans from 2 m away (T. Hamer, pers. comm.). We used eggs and chicks because (1) they represent both life history stages of murrelets vulnerable to nest predation; (2) eggs are highly attractive to corvids (Heinrich et al. 1995) and provide visual cues to their location; and (3) chicks offer olfactory cues as well as visual ones, which may better mimic a real nest and attract scent-oriented predators (Ratti and Reese 1988, Major 1991, Whelan et al. 1994, Darveau et al. 1997). We confirmed the predatory ability of small mammals detected at chick mounts with two years of experimental research (Bradley 2000; J. Bradley and J. Marzluff, unpubl. data). Mice attacked and displaced live pigeon chicks (including those capable of vigorous defense and outweighing mice ten-fold) in captivity and in the wild. Flying squirrels attacked and killed pigeon chicks in captivity. Thus, seemingly "inappropriate" mounted chicks actually accurately indicated the importance of scent-oriented nest predators in our experiments.

The fate of each nest was monitored remotely to avoid continually advertising a nest's location. A motion-sensitive radio transmitter was placed in each model; ground crews could then determine if a nestling or egg was disturbed by checking the transmitter pulse rate (similar to a standard mortality switch). We monitored nests every other day for 30 d, the approximate incubation or brooding period of Marbled Murrelets (DeSanto and Nelson 1995). Remote monitoring allowed determination of predation date (as opposed to simply noting success or failure) while limiting the amount of human presence at the nest sites. Remote monitoring also allowed us to reclimb simulated nests immediately after predation, before other predators or heat from sunlight obscured clues to predator identity left in wax. Occasionally no evidence of predation was found on eggs or chicks despite a change in pulse rate (Luginbuhl et al. 2001). When this occurred, we reset the pulse rate and continued to monitor the nest.

We used a variety of techniques to identify potential predators. In addition to eggs, transmitters inside chicks were coated with household paraffin to record marks left by predators. We monitored 82 artificial nests using 35mm cameras attached to an active infrared motion detection system (Trailmaster® Model TM 1500, Goodson and Assoc., Inc., Lenexa, KS) as described by Hernandez et al. (1997). These cameras imprint photographs with date and time, and are equipped with auto-advance, allowing photography of subsequent predators without researchers re-visiting the nest. They provide an important way to calibrate the predator identification we based on marks in wax. Nests observed with cameras were not included in the determination of predation rate (as indicated by number of days to predation).

We used Kaplan-Meier procedures to estimate the survival rate of nest contents (Pollock et al. 1989). Survival among groups was compared with the log rank test so that all measures of survivorship were weighted equally (Lee 1980). We assumed each nest was independent in survivorship analyses. This allowed us to include covariates accounting for differences in nest microsites and set-up times in the analysis. Inclusion of covariates may better illuminate differences due to design factors (Schueck and Marzluff 1995), but use of nests as experimental units may artificially inflate our sample size (and significance levels) due to pseudoreplication (Hurlbert 1984).

The relative abundance of potential avian nest predators (corvids) was determined from surveys in study stands using a modified point count procedure. These methods are detailed in Luginbuhl et al. (2001).

RESULTS

From our experiments, rates of predation in continuous stands did not differ from rates in

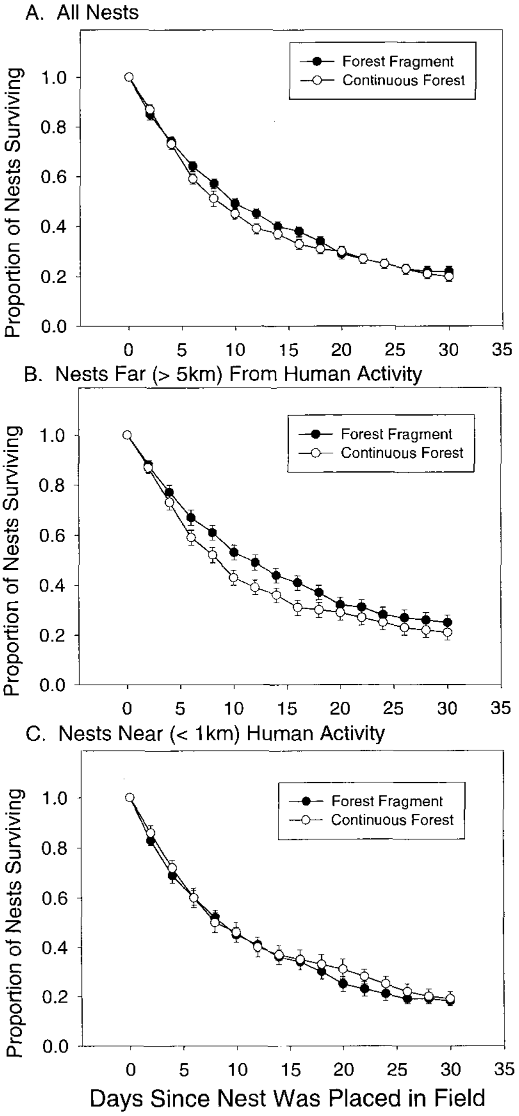

FIGURE 2. Survivorship of artificial Marbled Murrelet nests in fragmented and continuous forest, Olympic Peninsula, WA. Mean survivorship (symbols) ± 1 SE is plotted separately for (A) all forest fragments (N = 524) relative to all continuous forest (N = 399); (B) fragments (N = 249) and continuous forest (N = 179) near campgrounds and small human settlements; and (C) fragments (N = 275) and continuous forest (N = 220) far from human activity centers.

fragmented stands. Roughly 80% of nests were preyed on after 30 d, regardless of whether they were placed in forest fragments or continuous forests (Fig. 2A); the daily pattern of nest loss over the 30-d period of exposure was nearly identical in fragments and continuous forest (Fig. 2A; $\chi^2_{(1)} = 0.64$, $P = 0.42$). Proximity to human activity affected the influence of forest fragmentation on predation within a stand (interaction between proximity and fragmentation; $F_{(1,849)} = 4.7$, $P = 0.03$). Far (>5 km) from human activity, nests in fragments had slower rates of predation than nests in continuous forest (Fig. 2B; $\chi^2_{(1)} = 2.45$, $P = 0.12$). In contrast, nests in fragments near (<1 km) human activity had rates of predation similar to nests in continuous forest (Fig. 2C; $\chi^2_{(1)} = 0.25$, $P = 0.65$).

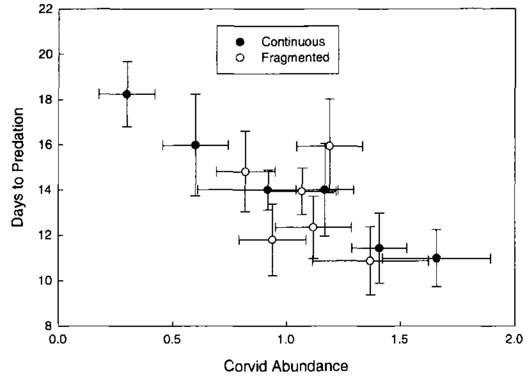

FIGURE 3. Rates of predation (mean days until a nest was depredated) in relation to mean abundance of corvids in fragmented and continuous stands in the Olympic Peninsula, WA. Values are means from 3 to 5 stands ± 1 SE. After Luginbuhl et al. (2001).

In continuous stands, predation rates (as indicated by number of days to predation) increased as abundance of corvids increased ($r = -0.98$, $N = 6$, $P = 0.001$; Fig. 3). In fragmented stands, we found no relationship between corvid abundance and rate of predation ($r = -0.35$, $N = 6$, $P = 0.500$; Fig. 3). The lack of a relation in fragmented stands may be related to edge effects (see below) that may be more important in fragmented stands, or it may reflect the narrow range (0.8–1.4 birds; Fig. 3) of predator abundance in our sample of fragmented stands.

A particular predator did not appear to account for the lack of a fragmentation effect. The effect of fragmentation was minimal regardless of whether we simulated eggs or chicks (interaction between type of mimic and fragmentation; $F_{(1,849)} = 0.66$, $P = 0.80$), despite the fact that most predation on eggs was by corvids and most predation on chicks was by mammals (Luginbuhl et al. 2001). Total corvid abundance was similar among stands varying in proximity to human activity and fragmentation (all P-values in ANOVA > 0.48, N = 113 stand years; Fig. 4). Steller's Jay abundance varied as a joint function of proximity to human activity and fragmentation (interaction: $F_{(1,108)} = 6.87$, $P = 0.01$), but this species was most abundant in

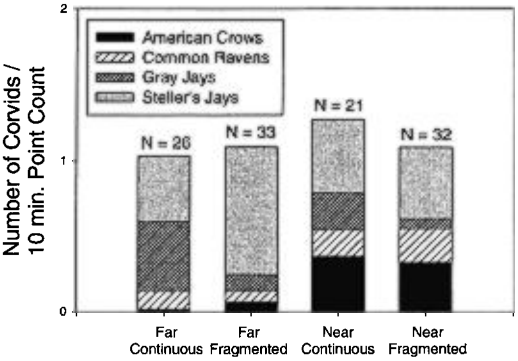

FIGURE 4. Composition of the corvid community determined by point count surveys in stands of varying contiguity and proximity to human activity centers, Olympic Peninsula, WA. Sample sizes are numbers of stands times number of years each stand was surveyed.

fragments far from human activity, which was the condition associated with the slowest (not fastest) rate of predation (Figs. 2 and 4).

The distance of a nest from the edge of the forest-matrix interface was not consistently related to the rate of nest predation. Nests within 50 m of the forest edge tended to be preyed on faster and to a greater extent than nests further into the stand's interior (Fig. 5A; $\chi^2_{(2)} = 4.75$, $P = 0.09$). This "edge effect" was consistent and strong near human activity where the edge of the forested stand abutted a campground or small settlement. There, nests within 50 m of the edge were preyed on significantly faster than nests >200 m from the edge (Fig. 5B; $\chi^2_{(2)} = 3.96$, $P = 0.05$). However, this "edge-effect" was inconsistent far from human activity where the matrix only included regenerating forest. Here, nests 100 m from the edge fared best, but rates were similar to those 50 m and 200 m from the edge (Fig. 5C; $\chi^2_{(2)} = 0.25$, $P = 0.62$).

Corvid nest predators drove the changes in nest predation in relation to distance from the forest fragment edge. In settings far from human activity the relative importance of corvid nest predation was lowest 100 m from the fragment edge (Fig. 6A), the distance associated with the lowest overall rate of predation (Fig. 5B). Likewise, fragments abutting human activity centers had the least predation 200 m from the edge (Fig. 5C), where the relative amount of corvid predation was also lowest (Fig. 6B).

Stand size did not affect predation rates. In an ongoing study in Oregon using similar methods as we report, J. Luginbuhl (unpubl. data) found no difference ($\chi^2_{(1)} = 0.23$, $P = 0.63$) in predation rates between large stands (30–60 ha) and small stands (16–28 ha). Stand shape did have a weak affect on predation rates, with higher

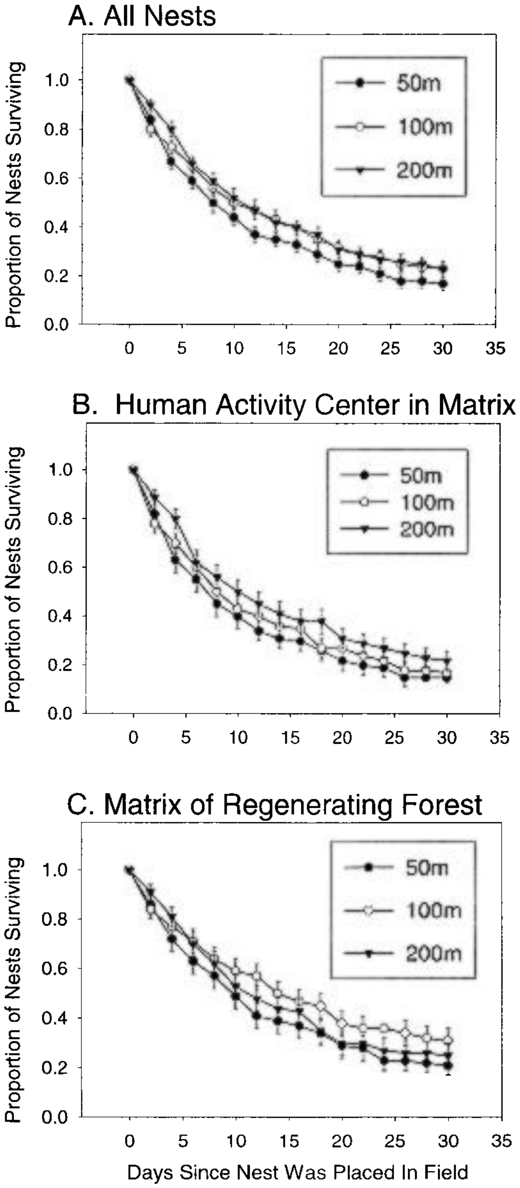

FIGURE 5. Survivorship of simulated murrelet nests at varying distances from the edge of forest fragments, Olympic Peninsula, WA. Survivorship ($\bar{X} \pm 1$ SE) at 50 m, 100 m, and 200 m is evaluated in (A) all stands regardless of proximity to human activity; (B) only in fragments surrounded by 1–15-yr-old clearcuts; and (C) only in fragments adjacent to campgrounds and small settlements. Sample sizes are 208, 204, and 206 for all fragments (A); 116, 113, and 115 for fragments surrounded by clearcuts (B); and 92, 91, and 91 for fragments adjacent to human activity (C) at 50 m, 100 m, and 200 m from the edge, respectively.

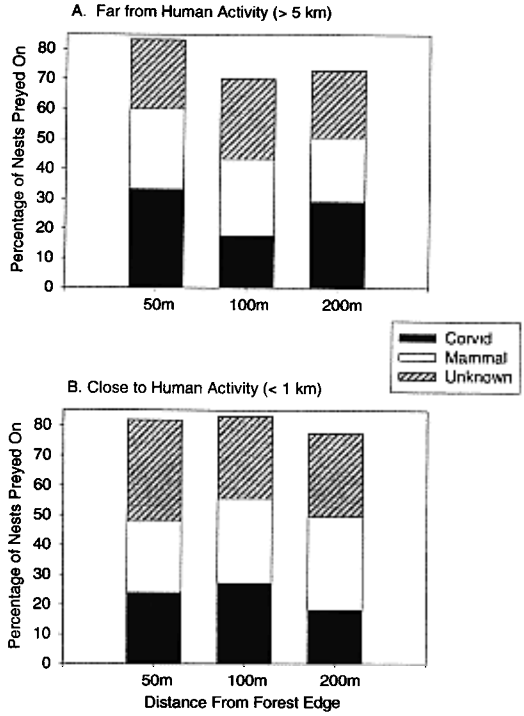

FIGURE 6. Percentage of nests at different distances from the forest edge preyed on by corvids (Gray Jays, Steller's Jays, American Crows, and Common Ravens) versus small mammals (mice, squirrels, and occasionally weasels) when the matrix is (A) far from human activity (>5 km) and (B) close to human activity (<1 km). Sample sizes are given in Fig. 4.

rates of predation in linear versus compact stands ($\chi^2_{(1)} = 3.16$, $P = 0.08$).

DISCUSSION

It is apparent that loss of older forest in the Pacific Northwest, primarily due to logging but also through other disturbance processes, has reduced the total area of suitable murrelet nesting habitat and caused remaining habitat to become more fragmented. From examining the evidence of the potential effects of habitat fragmentation on nesting habitat and populations of the Marbled Murrelet at four geographic scales, we found that it is difficult to separate the effects of fragmentation from the concomitant effect of habitat loss. Murrelet response to aspects of fragmentation generally appeared at the smaller scales investigated, including nest stands and nest stand neighborhoods, although at-sea abundances of murrelets were correlated with spatial configurations of habitat in specific locations of southern Oregon and Northern California (Meyer 1999). Marbled Murrelet nests appear particularly vulnerable to human-induced edges (e.g., roads and clearcuts) such as those studied in Oregon and British Columbia. Our work with artificial nests supported this conclusion in part, as we did find that rates of predation generally were greater within 50 m of edges, especially in stands close to human activity (recreation sites and small settlements). However, the artificial nest study also demonstrated that relationships between nest success and forest habitat likely are more complex because the composition of the nest predator assemblage is diverse and varies among locations.

The overall lack of an obvious fragmentation effect on artificial nests appears to be due to the diversity of nest predators and to our observations that other factors affecting predator abundance, such as proximity to people and refuse and forest structure, can swamp effects of fragmentation. Among corvids, the total number of individuals remained relatively constant among fragmented and continuous landscapes. This occurred despite variation in the composition of the corvid community (Fig. 4). In particular, the two species of jays showed reciprocal responses to fragmentation that likely equalized the total nest predation risk with respect to fragmentation. Steller's Jays frequented fragmented landscapes, whereas Gray Jays were most abundant in continuous landscapes (Fig. 4). Small mammals were abundant and diverse nest predators in our study area as well, and they were not confined to fragmented or continuous landscapes. This further reduced the relationship between predation and fragmentation (Marzluff and Restani 1999).

Effects of fragmentation on nesting success can vary depending on the forest structures surrounding nesting stands. In remote locations, where forests are fragmented by timber harvest and the matrix surrounding fragments is composed of regenerating forest, nest predation rates from our artificial nest experiment were not elevated, despite increases in Steller's Jay populations in such landscapes. Ongoing research in Oregon suggests that rates of predation are elevated in remote fragments surrounded by young clearcuts with berry-producing shrubs compared with fragments surrounded by clearcuts without berries or by older regenerating forest (Marzluff and Restani 1999; J. Luginbuhl et al., unpubl. data). In contrast, in locations near human settlements and recreation areas where forest fragments abut human activity centers, fragmentation is likely to increase the risk of nest predation (Fig. 5C). A diverse corvid community near human activity (Fig. 4) that feeds on human refuse, offerings at feeders, and berries in exotic plantings and early successional landscapes likely drives this effect. The relative importance of

TABLE 1. Potential Short Term and Long Term Effects of Fragmentation of Nesting Habitat on Local Population Size and Demographics of the Marbled Murrelet in the Pacific Northwest

Fragmentation effect on nesting habitat	Population size	Adult survival	Number of nests	Nest success
Reduced amount of nesting habitat	0/–[a]	0/0	0/–	–/0
Smaller patch size (reduced area of interior habitat, increased edge)	0/–	0/0	–/–	–/–[b]
Increased number of patches[c]	0/0	0/0	0/0	0/0
Increased isolation of patches	–/–	–/–	0/–	–/0

[a] Symbols to left of slash are short term effects (<10 years); symbols following slash are longer term effects (>10 years but more generally several decades). Symbols are: "–" (negative or deleterious), "0" (neutral), "+" (positive). A negative effect on any demographic parameter is assumed to cause population decline in the longer term.

[b] Effects will vary depending on suite of predators at particular sites. This often depends on the agent of fragmentation and resulting matrix. Some predators are more abundant in continuous forest, others respond to edge (see text).

[c] Effects given for number of patches per se, all else relatively equal. (In larger context of fragmentation, we assume these patches would be smaller, in addition to being more numerous.)

corvids as nest predators declined at nests greater than 200 m from edges abutting human activity (Fig. 6B).

An especially intriguing result (with management implications) is our observation that forests of simple structure are associated with the smallest corvid populations (Marzluff et al. 1999). Maintaining even-aged forests in places of human settlement should therefore be an effective management strategy to reduce regional corvid populations. The siting of recreational development in forested ecosystems also needs to be rethought. Rather than place campsites in structurally complex (aesthetically pleasing) landscapes, placement of campsites in structurally simple landscapes where predator populations are limited and where Marbled Murrelets rarely nest would reduce risk of nest predation.

Based on our review of other studies and our own work, we offer the following speculations on the potential effects of fragmentation on populations of the Marbled Murrelet. The primary effects of fragmentation are a reduction in total area of habitat, smaller average sizes of habitat patches (along with reduced area in interior habitat and increased amount of edge), increased number of patches, and increased isolation of patches. These consequences of habitat loss and fragmentation can affect population size, likelihood of nesting, survival of adults, and nesting success. As shown in Table 1, these effects differ from the short term to long term.

Reduced amount of nesting habitat potentially could result in short term displacement and crowding of nesting birds into remaining patches of habitat, although there is no direct evidence that Marbled Murrelets would respond in this way. Murrelets are thought to exhibit site fidelity (Nelson 1997); if so, birds that had been nesting in former habitat might fail to breed for several years until they either find new habitat or die. In that case, numbers of nests would decline immediately. If displaced birds move to adjacent nesting habitat, then crowding of nests will occur. In either case, population size would not be affected in the short term. However, crowding of nests could result in increased predation and lower nesting success. Assuming short term crowding, we speculate that nesting density in remaining habitat would relax to pre-harvest levels over the longer term, and population size would decrease. Changes in distribution and population declines observed at broad scales along the coast where substantial habitat has been lost (Carter and Erickson 1992, Kelson et al. 1995) support the concept that population declines are associated with loss of habitat.

Smaller patch size and its concomitant reduction in interior habitat and increased edge will result in short term and long term increases in rates of predation on nests (Manley and Nelson 1999; discussed above), although the strength of this effect will vary depending on the suite of predators occurring in the area (Andrén 1992, Nelson and Hamer 1995, Marzluff and Restani 1999). Our artificial nest results suggest that the agent of fragmentation and concomitant development of the matrix around the patches is important to the strength and significance of resultant edge effects. For example, when human settlement or recreational development fragments habitat and surrounds patches, then edge effects may be substantial. Smaller patches also may result in fewer nesting attempts overall, as some areas will no longer be considered suitable habitat and thus not be occupied by murrelets. In northern California, occupied locations contained larger patches and lower edge/area than unoccupied patches (Meyer 1999). Over the longer term these effects will lead to smaller populations if fewer fledglings are recruited into the breeding population. The effect on adult survival is less clear, as the response to fragmentation measures of species known to take adult Marbled Murrelets (see text) is not well documented (but see Rosenberg and Raphael 1986; McGarigal and McComb 1995, 1999).

Increased number of patches is not likely to affect population size or survival in the short or long term, except as an indirect consequence of related effects on patch size and total area of nesting habitat. *Increased isolation of patches* could lead to fewer nesting attempts, as potentially suitable habitat patches >5 km from other active nesting habitat are less likely to be occupied (Meyer 1999). Isolation also could lead to short and long term decrease in adult survival through increased vulnerability of murrelets to predators. Although we know of no direct evidence for this effect, we speculate that a murrelet flying over regenerating forest has greater exposure to avian predators that one flying over mature canopy, but it is also true that most flights to attend nests take place at dusk and dawn when diurnal predators are not active. If this increased risk to predation does occur, the long term result would be a reduction in number of nests and a reduction in population size.

SUMMARY

At the regional scale, we found no correlations between murrelet numbers and amount of nesting habitat at the broad scale along the entire Washington and Oregon coast; we found weak correlations if we restricted our analysis to inland habitat within 25 km of the coast. However, in southern Oregon and northern California, murrelet densities offshore were higher in subregions with more unfragmented and non-isolated old growth or old growth combined with residual old-growth forest.

At the watershed scale, we and other researchers found that numbers of murrelets flying into delineated drainages were strongly correlated with the amount of potential nesting habitat within those drainages, but that indices of fragmentation were not correlated with murrelet abundance.

At the neighborhood scale (~200-ha areas surrounding stands surveyed for murrelets), potential nesting habitat occurred in larger patches and was less fragmented at neighborhoods occupied by murrelets compared with unoccupied neighborhoods, although the entire neighborhood tended to be patchier and more fragmented due to the diversity of patches of younger forest. The presence of high-contrast edges (natural or clearcuts) did not seem to deter use of a site.

At the scale of individual nests, distance to edge was an important influence on nest fate. In Oregon and British Columbia, nest failure (primarily from predation), was highest in nests within 50 m of an edge; nests >150 m from an edge were successful or failed from reasons other than predation. Some evidence suggested that nests were more successful in larger stands (~500 ha) than smaller stands (<300 ha), but successful nests have been observed in a wide range of stand sizes.

Our artificial nest experiments showed similar rates of predation in fragmented and continuous stands; the lack of an obvious fragmentation effect appeared to be due to the diversity of nest predators, the influence of forest structures surrounding nesting stands, and proximity to human activity. Total abundance of avian predators (corvids) was similar in fragmented and continuous stands; predation rates increased with abundance of predators in continuous stands but not in fragmented stands. In remote locations far from human activity, predation rates were greater in continuous stands than in fragmented stands; predation rates were similar in fragmented and continuous stands close to human activity.

Despite the many insights that have emerged from our review of existing studies and our new work with artificial nests, a number of important research questions remain. Understanding tradeoffs between predation risk and quality of nesting habitat will require further investigation into how much simple-structured forest in a landscape is enough to reduce predator populations without reducing use of the remaining complex forest for nesting by murrelets. Additional work is certainly needed to better understand how the variety of processes interacts to affect nest site selection, survival, and reproductive success of the murrelet and how these behaviors are influenced by fragmentation of nesting habitat. In particular:

- How do the likelihood of nesting and characteristics of nest sites vary in relation to amount and type of edge?
- How does adult survival, particularly susceptibility to predation, vary with size, shape, and isolation of nesting stands?
- How does fragmentation of continuous nesting habitat affect the behavior of resident murrelets (that is, do displaced resident birds nest in adjacent stands that might be of lower quality, and can they move into stands that are occupied by other nesting murrelets)?
- What is the role and effect of mammalian predators on real nests and how do mammalian predators respond to fragmentation of murrelet nesting habitat?

Although many questions remain, we are heartened that new research is underway, much of it stimulated by requirements for monitoring population and habitat trends of this threatened species. Efforts to better define attributes of nesting habitat and to relate population trends to trends in the amount and pattern of habitat will contribute to conservation of this unique bird.

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APPENDIX

DETAILS OF HABITAT MAPPING FOR FIGURE 1

We used published reports of the characteristics of Marbled Murrelet nest stands to identify potential nesting habitat in Oregon and Washington. Given that nests have been found in smaller-diameter trees with epiphyte cover or deformities that create suitable platforms and in younger stands with remnant old-growth trees (Nelson 1997), but that remnant trees are not easily classified from satellite imagery, we accepted habitat that met the minimum dbh of known nesting stands rather than using dbh of nest trees. This may have inflated our estimates of habitat in some areas. Stands supporting tree nests in Oregon and Washington (N = 26) had a reported mean dbh of 47.7 cm (Hamer and Nelson 1995), although we were unable to discern how many trees were measured to arrive at stand diameter. Five of 9 Oregon nests were located in mature/old-growth stands, with mature trees defined as ≥46 cm dbh (Nelson and Peck 1995). In comparison, minimum nest tree size was 76 cm (N = 45) in OR and 88.5 cm (N = 6) in WA (Nelson 1997). Only potential nesting habitat was extracted from the covers described below. No spatial analyses were performed on these data.

Washington

The vegetation layer was a mosaic compiled from approximately 20 sources that identified Northern Spotted Owl (*Strix occidentalis caurina*) habitat, including satellite imagery classifications and state, federal and private agency mapping (USFWS 1997b). It included the Washington Department of Natural Resource's owl mosaic (1988–1993), the USDA Forest Service's owl habitat data from Olympic National Park, the WDNR/WDFW habitat map of the western Olympic Peninsula, harvest change data (1989 and 1991), and several private timber industry databases. This was the most up-to-date coverage for all land ownerships within the study area. Late-seral habitat was one of 10 land cover classes, and the only class that included characteristics of suitable murrelet habitat. Late seral was defined as mixed conifer/hardwood with >70% crown closure from conifers and >10% crown closure from trees >53 cm dbh. This class potentially contained some stands that would not have been included as habitat had we been able to specify tree size, composition, and structure. Resolution was 100-m pixels. We further defined suitable habitat as <1,067 m (3,500 ft) elevation. Inland extent of the marbled murrelet zone was defined as 80 km (50 mi; USFWS 1997a). Since the focus of this assessment was coastal distribution of murrelets as related to habitat, we included up to 80 km in from the outer coast, not 80 km from all salt water in WA. We separated the northern portion of the Olympic Peninsula along a watershed boundary to correspond to at-sea data around the tip of the Peninsula into the Strait of Juan de Fuca.

Oregon

The Western Oregon Digital Image Project (WODIP) vegetation layer was derived from Landsat TM imagery classification (Nighbert et al., unpubl. data) Resolution of the original data was 25 m, and was resampled to 100-m pixel size. It was comprised of 247 combinations of diameter, canopy closure, number of canopy layers, and species composition. We selected conifer and mixed conifer/hardwood, multi-storied stands with mean dbh >48 cm. We accepted all crown closures, given the range of 12–99% at OR nests (Hamer and Nelson 1995). We dropped down to the >48 cm dbh size, as opposed to including only >74 cm (the largest size class available), to capture younger, potentially suitable habitat and to keep our criteria for OR habitat similar to that used for WA. Given the fire and harvest history in portions of the Sitka spruce (*Picea sitchensis*) zone (Franklin and Dyrness 1973, Perry 1995), and the difficulty in capturing habitat within this zone (S. K. Nelson, pers. comm.), we also included single-storied stands with mean dbh >74 cm within this narrow corridor along the OR coast. These criteria may have overestimated suitable murrelet habitat in some regions. We set the inland extent of the murrelet zone at 56 km (35 mi), corresponding to the Recovery Zone (USFWS 1997a). For consistency, we applied the same elevation screen as in WA, defining habitat as ≤1,067 m, although this elevation is higher than known nest sites in Oregon.

Murrelet zones from at-sea data

Of the at-sea survey data available, we selected summer surveys from 1997 in Washington (C. Thompson unpubl. data from 1999 report). We included only nearshore transects (<500 m), as these were run more consistently. These data were summarized over variable-length transects (25–105 km), with some sections surveyed multiple times. We selected transects that, pieced together, covered the entire coastline. We used the break points between transects to establish horizontal bands along the coast. The peninsula configuration of the Washington coastline presented a different scenario than Oregon. We opted to include at-sea counts from the north side of the peninsula (the western Strait of Juan de Fuca), as these birds could potentially be accessing some of the same habitat as birds on the outer coast. At-sea densities were reported as the number of murrelets by transect length × 200-m width. For sections with multiple surveys within our temporal and spatial criteria (summer months, nearshore distances), we calculated an average density.

Of the Oregon data available (C. Strong, unpubl. data), 1996 had the more complete coverage of the coastline. For the 149 2-km stretches of shoreline surveyed in both 1996 and 1997, average nearshore densities did not differ between years ($t = 0.216$, $P = 0.829$), so we selected the 1996 data because of its greater coverage. We selected July nearshore surveys (400–600 m from shore). Densities were reported for each 2-km section, and transects were divided into three regions (north, central, south; Strong et al. 1995). We maintained regional breaks, and within regions averaged densities over 45–50 km sections. These section and region breaks established our 11 horizontal bands.