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Temporal dynamics of edge effects on nest predation risk for the marbled murrelet

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ABSTRACT

Habitat fragmentation can cause population declines greater than those expected from habitat loss alone. This can result from detrimental "edge effects", which occur when predation rates are higher at habitat edges relative to interiors. The marbled murrelet (*Brachyramphus marmoratus*) is a threatened seabird which nests in old-growth forests, a habitat that is being fragmented by ongoing harvest. There is little consensus on the magnitude of edge effects on marbled murrelets, or how they might vary by edge-type. We compared the fates of experimental murrelet nests at paired edge and interior locations at 52 sites in two regions of south-western British Columbia, Canada. Sites were chosen at "hard" edges (recent clearcuts), "soft" edges (regenerating forest), and natural edges (i.e., riparian areas). We used nest cameras to distinguish disturbances caused by known predators of real nests. Accounting for landscape-scale fragmentation, disturbances by avian predators were significantly more frequent at hard edges relative to interiors, but less frequent at soft edges. There were no edge effects at natural-edged sites. These results imply that detrimental edge effects adjacent to recent clearcuts may decline with time due to successional processes. Survey data suggest that this pattern was caused by Steller's jays (*Cyanocitta stelleri*), who were observed more often at hard edges than soft edges in one region. Where corvids are important predators, we recommend that managers maintain reserves that lessen the amount of hard edge per patch area. Harvest adjacent to reserves should proceed in stages to limit hard edge effects at any given time.

1. Introduction

Loss and fragmentation of forest habitat are major factors contributing to population declines of forest birds worldwide (Batáry and Báldi, 2004; Ferraz et al., 2007; Robinson et al., 1995; Wilcove, 1985). Forest fragmentation, defined as the "breaking apart" of continuous forest habitat into many smaller, more isolated patches (Fahrig, 1997), may lead to population declines greater than those predicted from habitat loss alone (Andrén, 1994). One of the primary drivers behind fragmentation effects are detrimental "edge effects", which occur when nest predation rates are higher at edges relative to interior areas (Andrén, 1994; Batáry and Báldi, 2004; Paton, 1994). Increased nest predation at edges may result from increased density, activity or species richness of predators at habitat edges (Chalfoun et al., 2002), or an increase in the detectability of nests at edges (Ratti and Reese, 1988). This can cause reduced reproductive success in smaller habitat fragments, which contain a higher proportion of edge area than larger habitat patches. These consequences of fragmentation are of high conservation concern, as their combined effects can influence the population growth rate at the landscape scale (Lloyd et al., 2005). Habitat managers need to know under what conditions detrimental edge effects occur, in order to

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adequately quantify the amount of productive habitat available across landscapes, and to properly assess the demographic consequences of different management strategies.

Edge effects appear to vary widely with respect to both local and regional factors (Andrén, 1994, 1995; Batáry and Báldi, 2004; Lahiti, 2001). The type of structural contrast between habitat patches and the surrounding matrix can strongly influence the strength and direction of edge effects (Andrén, 1995; Chalfoun et al., 2002; Marzluff and Restani, 1999; Rodewald and Yahner, 2001; Suarez et al., 1997). For instance, detrimental edge effects documented at high-contrast edges in landscapes fragmented by agriculture differ from those in landscapes fragmented by forestry, where edge contrast will vary depending on the stage of clearcut regeneration (Sisk and Battin, 2002). In forests that are predominantly fragmented by forestry, such as those in western North America, edge effects may therefore change with time as forests undergo succession. Thus, understanding the impacts of fragmentation effects on populations requires knowledge of how local edge effects may change over time and how the combinations of different edge-types sum at the landscape scale.

Variation in edge effects in forested ecosystems may be especially relevant for the conservation of the marbled murrelet, a seabird which nests predominately on large, mossy branches of old-growth trees (Ralph et al., 1995). Substantial harvesting of old-growth forest habitat has resulted in listing the marbled murrelet as a protected species in both Canada and in the United States south of Alaska (CMMRT, 2003; Ralph et al., 1995). These listings were based primarily on the assumption that habitat loss will reduce the population size a given area would support (Burger, 2001), but it remains uncertain how forest fragmentation per se will impact murrelet populations (Raphael et al., 2002). The issue is particularly important because nest predation appears to be a major limiting factor on marbled murrelet nesting success, particularly in the United States south of the Canadian border (Nelson and Hamer, 1995; Peery et al., 2004).

Despite clear management benefits associated with this knowledge, there is little direct evidence, and a lack of agreement, on how different edge-types affect the breeding success of the marbled murrelet (Bradley, 2002; Nelson and Hamer, 1995). This issue is relevant because murrelets appear to nest disproportionately near both natural edges such as streams and avalanche chutes, as well as anthropogenic edges such as clearcuts and regenerating forest (Baker et al., 2006; Nelson and Hamer, 1995; Zharikov et al., 2006, 2007). Developing a more comprehensive understanding of variation in predation risk among different edge-types and landscapes will improve the ability of managers to design effective murrelet reserves from remaining old growth forest, a process currently underway in coastal British Columbia.

We used artificial nests, a technique previously developed for marbled murrelets in Washington and Oregon (Luginbuhl et al., 2001; Raphael et al., 2002), to provide estimates of relative predation risk at edge and interior locations for three edge-types. This experimental approach provided sufficient power to detect differences in edge effects across edge-types that are relevant to habitat management and murrelet conservation. We supplemented these data with surveys of potential predators in the same habitats to investigate the relationship between predator densities and predation risk. If predation on murrelet nests is incidental to general movement patterns (Vigallon and Marzluff, 2005), then we would expect a direct correlation between predator abundance and artificial nest disturbance rates. However, because of complex community interactions (Werner and Peacor, 2003), the relationship between predator abundances and predation risk may differ among habitats. Our combined approach provides a comprehensive picture of variation in predation risk and allows us to assess the efficacy of using predator surveys as a management tool to predict this risk.

2. Methods

2.1. Study area

This study was carried out in two regions of coastal southwestern British Columbia, in the Nimpkish Valley on northern Vancouver Island (‘Nimpkish’; 50°12′N 126°37′W), and around Desolation Sound on the mainland coast (50°05′N, 124°40′W) (Fig. 1), from June to August in 2005 and 2004, respectively. Both regions contain large breeding populations of marbled murrelets (Bradley et al., 2004). Elevation ranges from sea level to 1500 m at Nimpkish, and to 2500 m around Desolation Sound. Climate is similar between the two regions: mean summer (April–August) temperatures are 13.4 °C and 14.8 °C, and cumulative precipitation is 300 mm and 290 mm, in Nimpkish and around Desolation Sound, respectively. Old growth forests at lower elevations are within the Coastal Western Hemlock Zone (Klinka et al., 1991), which consists of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) amabalis fir (*Abies amabilis*), douglas fir (*Pseudotsuga menziesii*), and sitka spruce (*Picea sitchensis*). Forests above 900 m are within the Mountain Hemlock Zone, which also includes mountain hemlock (*Tsuga mertensiana*) and yellow cedar (*Chamaecyparis nootkatensis*), but lacks douglas fir and sitka spruce. Shrub growth is extensive in the understory of both forest types, as well as in natural and anthropogenic gaps. Fruit producing shrubs dominate this layer, especially *Vaccinium* spp., as well as salal (*Gaultheria shallon*), and red elderberry (*Sambucus racemosa*).

2.2. Site selection

Spatial data including forest cover, watercourse locations, harvest history, topography, and road access were compiled from industrial forest cover maps in ArcView 3.3 (ESRI Inc., Redlands, CA, USA). We selected 34 sites in Nimpkish and 18 sites around Desolation Sound (Fig. 1) that were adjacent to one of three types of forest gaps, and that had sufficient amounts of old growth forest to establish interior treatments. Forests at all sites in Nimpkish were ⩾250 years old, and the mean age of sites in Desolation Sound was 289 ± 16 years. “Hard-edged” sites were located adjacent to recent clearcuts (5–11 years old), “soft-edged” sites were next to regenerating stands (17–39 years old), and “natural-edged” sites were next to large rivers or avalanche chutes (Fig. 2). Within each old growth forest patch, we defined locations as either ‘edge’ or ‘interior’. Edge habitat was defined as forest within 50 m of the edge of interest (Paton, 1994), and interior habitat was at

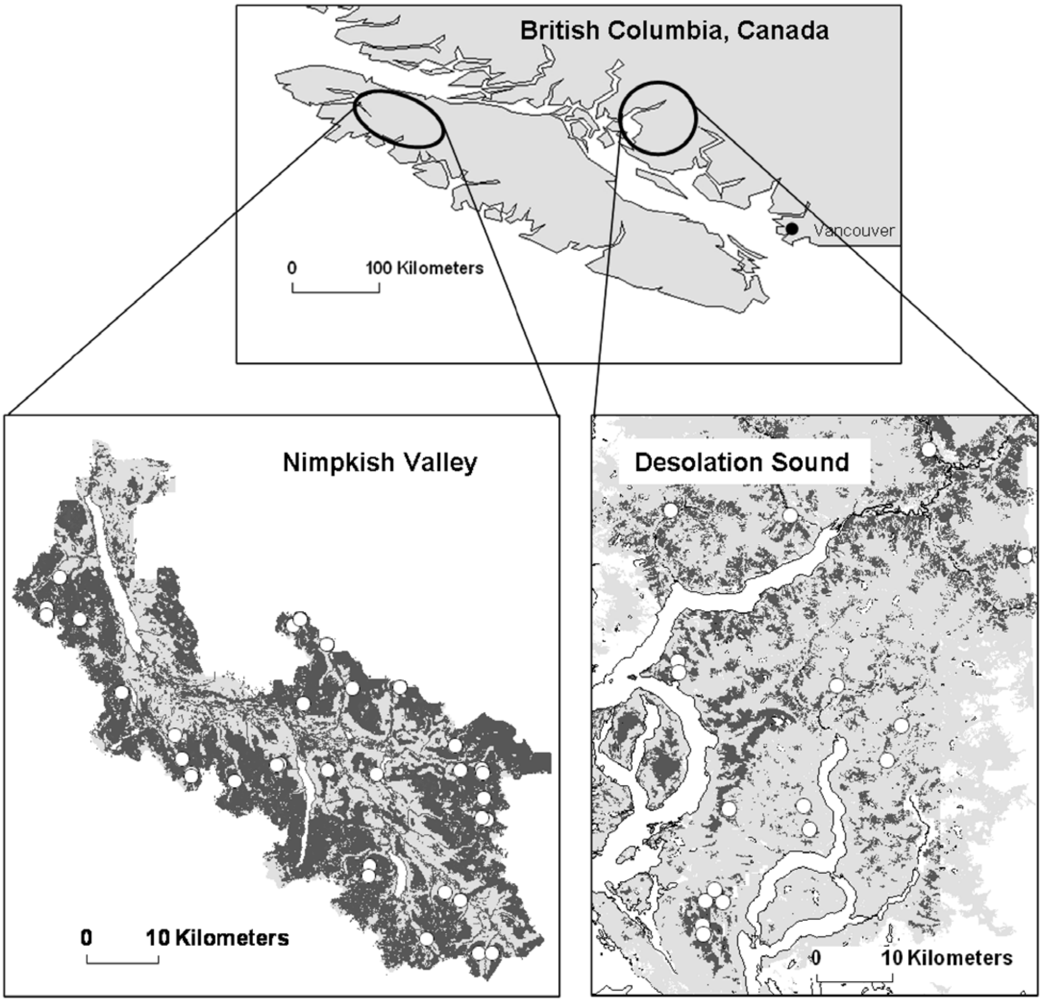

Fig. 1 – Location of the two study regions, the Nimpkish Valley, and Desolation Sound, in south-western British Columbia, Canada. Individual experimental sites are indicated by white circles. Dark shading indicates old-growth forest.

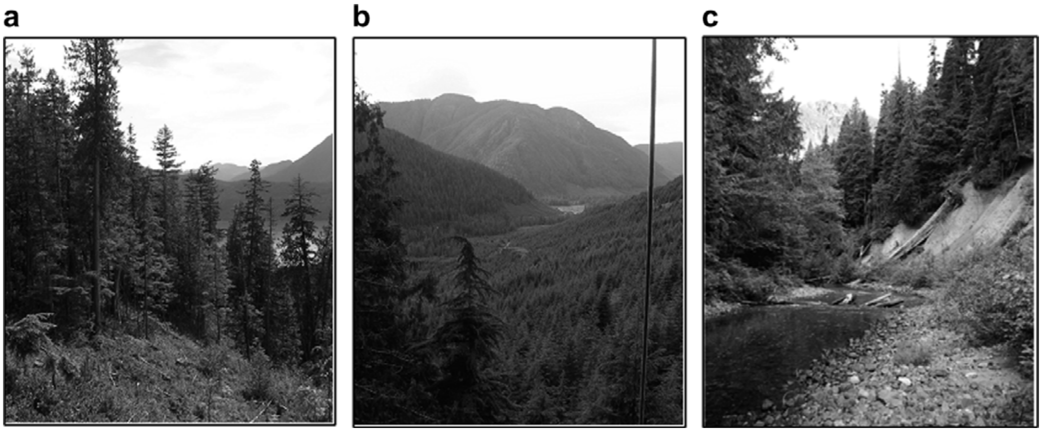

Fig. 2 – Examples of (a) hard, (b) soft, and (c) natural edges adjacent to old-growth forest patches in south-western British Columbia, Canada.

least 150 m from any other forest openings. Mean distance (±1 SD) from experimental edge was 9.5 ± 11.2 m for edge nests, and 232.5 ± 32.7 m for interior nests. An artificial egg and nestling (see below) were placed in separate trees in both edge and interior treatments, for a total of four artificial nests per site. This allowed paired comparisons between edge and interior locations at each site. Within edge and interior treatments, nests were spaced well apart from each other (73.3 ± 26.2 m) to lower the probability of non-independent discovery. We established artificial nests in platforms with characteristics similar to those of real murrelet nests (i.e., $\geqslant$15 m above the ground and $\geqslant$18 cm in diameter) (Burger and Bahn, 2004). Nest platforms were 25.8 ± 7.3 m above the ground, with diameters of 27.9 ± 21.2 cm, and had 55.4 ± 21.8% vertical cover. Nest trees were 36.0 ± 8.1 m high, had diameters at breast height of 101.3 ± 35.3 cm, and had 13.7 ± 11.2 suitable murrelet nests platforms per tree.

2.3. *Artificial nest experiment*

We estimated relative predation risk using both artificial eggs and nestlings (Luginbuhl et al., 2001; Marzluff and Neatherlin, 2006; Marzluff et al., 2000; Raphael et al., 2002). Eggs were constructed from plastic egg casings painted to mimic murrelet eggs and covered in wax to record beak and teeth marks of predators. Nestlings were created from skinned *Coturnix* quail, which were dried using 'Borax', and stuffed with cotton. The egg was designed to attract visually searching avian predators, whereas the more cryptic but smelly nestling was designed to attract olfactory-based mammalian predators. At real nests, murrelet eggs are attended by adults, but chicks are not. To minimize the presence of any human scent, all artificial nest contents were stored in bark mulch for at least 12 h before set up, and were handled with rubber gloves in the field. Each artificial nest was exposed in the field for approximately two weeks.

We manufactured weatherproof automatic nest cameras from Vivicam® 3555T digital cameras (Vivitar Corp., Oxnard, CA) and infrared sensors that detected movement of objects differing in temperature from their surroundings (Pixcontroller® Inc., Export, Pennsylvania). It took approximately 4 s to power up and initialize the cameras following motion detection, thus many nest visitors left prior to picture taking. Cameras were mounted in waterproof Pelican® cases painted "forest green" to limit their conspicuousness, and mounted on the tree trunks approximately 1.5 m directly above all 136 nests in Nimpkish. Predator photos refined our identification of marks left on eggs and aided interpretation of probable predators based on nestling remains. This information assisted identification of disturbance agents where cameras were not used (Desolation Sound), and in cases in Nimpkish where nests were disturbed, but the camera did not capture the predator. Teeth and bill impressions from avian and mammalian museum skulls provided additional assistance in identifying marks found on our artificial eggs. Identification of artificial nestling remains in Desolation Sound was helped by wax-covered "eggs" inside the nestlings which retained predator marks.

We assessed the extent to which our artificial nests sampled the same suite of predators known or thought to depredate real nests. Our cameras captured both avian predators such as Steller's jays (*Cyanocitta stelleri*) and common ravens (*Corvus corax*), which are known murrelet nest predators, as well mammalian predators such as squirrels (*Tamiasciurus* spp.), and deermice (*Peromyscus* spp.), whose role as nest predators is suspected (Bradley and Marzluff, 2003; Luginbuhl et al., 2001). Distinguishing between avian and mammalian predation is important in this study, as these two predator groups typically exhibit opposite responses to habitat fragmentation (Hannon and Cotterill, 1998). Cameras captured the majority (80%) of squirrel and mouse disturbances, but a smaller proportion (27%) of avian disturbances, probably because mammalian predators spent more time manipulating and consuming nest contents. Marks made by mammalian predators were readily distinguishable, but we were unable to distinguish avian marks on eggs to the species level (in contrast, all but one avian disturbance on nestlings was captured on camera). We therefore separated our analyses between putative avian, squirrel, and mouse disturbances.

We designed our artificial nest experiment to minimize bias associated with this method. While we acknowledge that absolute predation rates likely differ between real and artificial nests (Major and Kendal, 1996; Thompson and Burhans, 2004), we assume that any differences will be consistent across our treatments. Under this assumption, the relative differences between our treatments will reflect spatial patterns for real marbled murrelet nests. Because of low nesting densities and the high cost of finding real murrelet nests, it is not possible to obtain an adequate sample of real nests to investigate variation in edge effects at different edge-types. We therefore assert that our carefully designed artificial nest experiment is the best method available to address these questions.

2.4. *Quantification of landscape structure*

Because both the strength and direction of edge effects may vary with respect to landscape conditions (Donovan et al., 1997; Driscoll and Donovan, 2004), we quantified an index of landscape fragmentation for each experimental site to include in our statistical models describing edge effects (see below). We compiled land cover data from digital vector maps obtained from the British Columbia Ministry of Agriculture and Lands' Base Mapping and Geomatic Services (BMGS) Branch, and the industry partners Canadian Forest Products Ltd., Western Forest Products, Inc., and International Forest Products, Ltd. We converted the maps into a raster format with the cell size of 25 m^2 in ArcView 3.3. Each cell was assigned a distinct cover type, the most relevant of which was 'old-growth' forest, which was defined as forest >141 years of age (most were considerably older; i.e., 96% of Nimpkish was >250 years). We used the >141 year definition to be consistent with other studies that used this age class to assess habitat associations of marbled murrelets (Burger, 2001). Other cover types included water bodies, clearcuts, and regenerating forest. Around each nest, we sampled circular landscapes with radii of 2.3 km (1660 ha), using the Mila Grid Utilities 1.4 extension (UCL, Louvain, Belgium) in ArcView 3.3. This landscape size was used to allow comparability to a study analyzing marbled murrelet habitat selection and reproductive success around Desolation Sound (Zharikov et al., 2007), and is within the range of other landscape-scale fragmentation studies (Donovan et al., 1997; Lloyd et al., 2005). Using the program FRAGSTATS (McGarigal et al., 2002), we calculated the amount (percentage) of old-growth forest present in each landscape ('% old-growth'). Strictly speaking, this variable provides an index of habitat availability alone, not habitat fragmentation per se (i.e., it does not specifically address habitat configuration) (Fahrig, 1997). However, % old-growth was positively correlated with mean patch size ($R^2 = 0.84$, $P < 0.0001$), and negatively correlated with patch density (no. of patches/ha.; $R^2 = 0.74$, $P < 0.0001$), both of which are used commonly as indices of fragmentation per se. Consequently, we used % old-growth as an index of both site-specific habitat availability and fragmentation.

2.5. *Comparison with patterns at real nests*

For comparison with our experimental results, we applied our site definitions to identify comparably situated real marbled murrelet nest sites found around Desolation Sound (Bradley et al., 2004; Manley, 1999; Tranquilla et al., 2003; Zharikov et al., 2006). Due to limited precision in nest locations and edge boundaries, we did not attempt to classify real nests as “edge” or “interior”. Instead, we compare the effect of sites’ edge-types on nest fates between real and artificial nests.

We used the breeding success criteria of Bradley et al. (2004), who classified nests as either active (successful) or failed during the “mid-chick rearing period”, based on the presence or absence of parental visits as determined by radio telemetry data between 10 days after estimated hatching through the end of chick rearing. This proxy for nesting success was necessary because many nests were inaccessible from the ground, and direct determination of reproductive success was not possible. From the sample with known “success”, we selected real nests that were within 250 m of a hard, soft, or natural edge, and excluded any nests that had more than one edge-type within this radius. We also excluded high elevation sites >1100 m, because we did not establish any experimental nests at these elevations, and elevation is a significant predictor of nest success in real nests (Bradley, 2002). This selection process resulted in 57 real nests: 9, 5, and 43 at hard, soft and natural edges, respectively. We compared these to a subset of the artificial nests in Desolation Sound, excluding any that had more than one edge-type within a 250 m radius. This resulted in 40 artificial nests: 16, 7, and 17 at hard, soft and natural edges, respectively. Soft edges were underrepresented in this region; experimental nests were only set up at four sites.

We compared the disturbance fates of individual artificial nests to the “success” of real nests. We assumed the nest failures prior to the end of the “mid-chick rearing period” were a result of predation. Some of these failures may have been due to other causes, but nest failure is nonetheless a reasonable proxy of predation risk, which is the most common cause of nest failure for murrelets (Nelson and Hamer, 1995).

We conducted a retrospective “reverse power analysis” (Fairweather, 1991; Thomas, 1997) to determine the effect size of the study-type by edge-type interaction that was “detectable” with our sample size and a power of 0.80 (Cohen, 1988). We then explored what combinations of real and artificial disturbance patterns would produce this effect size, by stepwise exaggerations of any differences that were present between real and artificial nests at each edge-type.

2.6. *Predator surveys*

We established two parallel transects of four point-count stations with 50 m radii at 18 of our experimental nest sites in Nimpkish, and at six sites separate from our nest sites around Desolation Sound (Ralph et al., 1993). Edge transects were centred along the forest border (so that each point count station was divided equally between gap and forest habitat), and interior transects were located 150 m into the forest interior, at least 150 m from any other edge. Station centres were 150 m apart, so that distances between two adjacent detection radii were 50 m. Sampling periods at each station were 10 min in duration, during which all potential predators seen or heard were recorded. When a predator was initially observed, the distance to that predator was measured using a laser rangefinder (±1 m), or estimated if the predator was detected by sound. We quantified the habitat selection of predators within the 50 m radius edge stations by classifying their locations as ‘Gap’ (>5 m perpendicular distance from the edge into the forest opening), ‘Border’ (within 5 m on either side of the habitat edge), or ‘Forest Margin’ (>5 m from the edge into the forest interior). We did not limit our surveys to the early morning, as corvid (and squirrel) species are active throughout the day (Luginbuhl et al., 2001).

We tested for a detection bias between edges and interiors by comparing auditory to visual detections in each location. While a visual detection bias is likely between edges and interiors, there is little difference in the ability of bird calls to travel through the forest and open air at the scale of our point count stations (i.e., within 50 m) (Scoullar, 1980). We used contingency chi-square analyses to test if detection type (auditory [vocal or vocal + visual], versus visual only) was independent of edge-proximity (edge versus interior). At Desolation Sound, observation type was independent of edge-proximity ($\chi^2_1 = 0.14$, $P = 0.709$), but observation type was contingent on edge-proximity in Nimpkish ($\chi^2_1 = 3.95$, $P = 0.047$), indicating a detection bias between edges and interiors. This result was driven by a disproportionate number of visual detections at habitat edges relative to interiors. The lack of a detection bias at Desolation Sound was probably because surveys in this region were conducted in more open forests with lower mean tree heights (J. Malt, personal observation). Therefore, visibility in forest interiors was likely enhanced in this region relative to Nimpkish. Because of the detection bias found in Nimpkish, our primary inferences of predator distributions were drawn from data collected around Desolation Sound.

2.7. *Data analysis*

To analyze our artificial nest data, we ran Generalized Linear Models with nest disturbance (yes/no) as a binary dependent variable. We defined predator ‘disturbance’ of nests as any case where nest contents were visibly disturbed, including marks on eggs, and tear marks on nestlings. To provide comparable data from both regions, nests in the Nimpkish where predators were captured on camera, but lacked visible signs of disturbance on eggs or chick, were not defined as disturbed. This occurred in seven, eight, and four cases for mouse, squirrel, and avian predators, respectively. While this process resulted in the presentation of disturbance rates that were on average 26% lower in Nimpkish, it did not change the relative differences between edge-proximity or edge-type treatments for any of the predator types.

To test for edge-type and location effects on nest disturbance risk, each site was nested within edge-type and region, and we used binomial probability distributions with logit link functions using the 'Genmod' procedure in SAS® version 9.1 (SAS, 2003). Initial modelling showed no significant regional effects or regional interaction terms. We pooled data to maximize statistical power, but retained region as a term.

We tested if region, edge-proximity (edge/interior), edge-type, or nest-type (egg/nestling) predicted nest disturbance of simulated nests using four different models: disturbances by all predators combined (avian, squirrels, and mice), avian predators only, squirrels only, and mice only. We assumed that disturbances by different predator taxa were independent of each other (i.e., each model is analyzed using a separate dataset which only included disturbances caused by that predator group). Nest-type was highly significant in our initial model of all predators combined ($\chi^2_1 = 13.45$, $P < 0.001$), so we conducted subsequent analyses separately for eggs and nestlings. This was possible for avian disturbances on eggs, but there were insufficient avian disturbances on nestlings to conduct this analysis for nestlings alone. Similarly, there were too few squirrel or mice disturbances to run the full model for each nest-type, so we kept these datasets pooled. We assessed the goodness-of-fit of our model with the estimate of dispersion after fitting (deviance divided by the degrees of freedom) to determine if our data was under/overdispersed due to repeated measurements at the same site.

Independent post hoc tests were conducted for all levels of the edge-proximity by edge-type interaction of avian egg disturbances, which was the only significant interaction in all models tested. Similar generalized linear models were used to compare the fates of experimental and real nests using the Genmod procedure SAS® version 9.1 (SAS, 2003), with binomial probability distributions and logit link functions. We tested if study-type (real/experimental) or edge-type predicted nest fates (successful real nests = undisturbed artificial nests), and if the effect of edge-type was independent of study-type (study-type by edge-type interaction). For all models, we present score statistics for type 3 generalized estimating equations (significance levels for each term accounting for all other terms in the model), with non-significant interaction terms removed from the model at $\alpha = 0.10$.

We analyzed our survey data using Generalized Linear Models with nested designs (each site nested within an edge-type), Poisson distributions, and log link functions using the Genmod procedure SAS® version 9.1 (SAS, 2003). We were not able to pool data between regions because our survey design differed among regions: hard and soft-edged sites only were sampled around Desolation Sound, but all three edge-types were sampled in the Nimpkish Valley. We tested if location or edge-type predicted the total number of predators observed in each transect (from all three visits) separately for Steller's jays, gray jays, and red or Douglas squirrels.

We used a contingency χ^2 analysis to test if the type of corvid species observed (gray jays or Steller's jays) was independent of the habitat type it was observed in (Gap, Border, or Forest Margin) in Nimpkish.

3. Results

3.1. Artificial nest experiment

Sixty-five of 136 nests (40%) were discovered by predators in Nimpkish, including 47 nests (35%) that were physically disturbed. At Desolation Sound, 23 of 56 nests (35%) were disturbed. Cameras in Nimpkish documented nest disturbances by all putative nest predators present in the study area, including 4 Steller's jays, 9 gray jays (*Perisoreus canadensis*), 12 red squirrels (*Tamiasciurus hudsonicus*), 15 mice (*Peromyscus* spp.) a common raven (Fig. 3), and a sharp-shinned hawk (*Accipiter striatus*). At Desolation Sound, marks allowed us to differentiate between deermice (*Peromyscus* spp.) and squirrels (Douglas squirrels; *Tamiasciurus douglasii*, or northern flying squirrels; *Glaucomys sabrinus*), but not among avian predator species. In Nimpkish, 51% of predator disturbances were by avian species, 20% by red squirrels, 23% by mice, and 6% of nests were targeted by a combination of both avian and mammalian predators. At Desolation Sound, 57% of identifiable disturbances were caused by avian predators, 26% by squirrels, 13% by mice, and 4% by both avian and mammalian predators.

For all predators combined, disturbances of nests were higher at edges relative to interiors ($\chi^2_1 = 8.92$, $P = 0.003$; Table 1), with no significant edge-type interaction, suggesting detrimental edge effects at all three edge-types. The estimate of dispersion after fitting this model was 1.20, indicating a good fit between the predicted and observed variance of the model, and suggesting no significant spatial autocorrelation within sites. There was a significant positive correlation between % old-growth and disturbance rates ($\chi^2_1 = 3.86$, $P = 0.049$; Table 1), suggesting higher overall disturbance probability in landscapes with greater proportions of old-growth forest.

For avian predators of eggs, disturbance between edge and interior locations differed between edge-type (edge-proximity × edge-type interaction: $\chi^2_2 = 9.48$, $P = 0.009$; Figs. 4 and 5). Post-hoc testing showed detrimental edge effects at hard-edged sites (Fig. 5). In contrast, there was no significant edge effect at soft-edged sites, and soft edges had significantly less disturbance than hard edges. There were no edge effects at natural-edged sites, although disturbance rates were high overall at these sites. There was a significant positive relationship between % old-growth and avian disturbance rates ($\chi^2_1 = 4.96$, $P = 0.026$).

Squirrels disturbed eggs more often than nestlings ($\chi^2_1 = 4.76$, $P = 0.029$; Table 1), and caused detrimental edge effects at all three edge-types ($\chi^2_1 = 6.29$, $P = 0.012$; Fig. 6a and b). In contrast, mice disturbed nestlings more often than eggs ($\chi^2_1 = 8.49$, $P = 0.004$; Fig. 6c and d). Similar to squirrels, mice caused detrimental edge effects at all three edge-types, but this trend was not significant ($\chi^2_1 = 2.28$, $P = 0.131$; Table 1).

3.2. Comparison with patterns at real nests

Real nests "failed" in 33%, 40%, and 33% of cases at hard, natural, and soft-edged sites, respectively. Comparable artificial nests were disturbed in 25%, 14%, and 35% of cases at hard,

Fig. 3 – (a) A Common raven, (b) Steller's jay, (c) Gray jay, and (d) Douglas squirrel disturbing artificial eggs or nestlings, captured by motion-sensitive digital cameras in the Nimpkish Valley, British Columbia.

natural, and soft-edged sites, respectively. When comparing these patterns between real and artificial nests, the effect of edge-type on nest fate was independent of study type ($\chi^2_2 = 1.08$, $P = 0.583$). The power of this test (study-type by edge-type interaction) was 0.122, which corresponded to an effect size of 0.046. In order to have a power of 0.8 with this sample size, the effect size would have to be at least 0.151. This effect size would have occurred, for example, with four additional "failures" of real nests at hard-edged sites (7/9 versus 3/9), and three additional artificial nests disturbances at natural-edged sites (9/17 versus 6/17).

3.3. *Predator surveys*

Steller's jay detections were more probable at edges compared to interiors around Desolation Sound ($\chi^2_1 = 3.87$, $P = 0.049$; Table 2). This effect differed among edge-types however, occurring only at hard-edged sites, and not at soft-edged sites (edge-proximity × edge-type interaction: $\chi^2_1 = 4.31$, $P = 0.038$; Fig. 7). There were no significant treatment effects on Steller's jay observations in the Nimpkish Valley, nor with gray jays (Table 2).

There was a marginally significant trend towards higher detection rates of Douglas squirrels at edges relative to interiors around Desolation Sound ($\chi^2_1 = 3.55$, $P = 0.060$) (Table 2). In the Nimpkish Valley, there was a marginally significant interaction between edge-proximity and edge-type ($\chi^2_1 = 5.50$, $P = 0.064$). There were higher detection rates at edges compared to interiors at soft-edged sites, whereas interiors had higher detection rates than edges of natural-edged sites, but there was little difference between edge and interiors of hard-edged sites.

Within edge transects, Steller's jays and gray jays were distributed differently among gap, border, and forest margin locations ($\chi^2_2 = 8.52$, $P = 0.014$; Fig. 8). Steller's jays were observed at all locations at both hard and soft-edged sites, although their highest densities were observed in gaps of hard edges (Fig. 8a). In contrast, gray jays were observed infrequently, and were never observed in gaps of any kind (Fig. 8b).

4. Discussion

Understanding edge effects and differences in effects among edge-types is an essential component of effective management of wildlife populations in landscapes fragmented by industrial forestry. We have documented variation in the strength and direction of edge effects on nest disturbance risk of simulated marbled murrelet nests at different ecologically relevant edge-types. Our experiment provides information on spatial variation in potential predation risk in old-growth forests of coastal British Columbia that has hitherto been difficult to obtain for nesting marbled murrelets.

Table 1 – Treatment effects for artificial nests disturbed by avian predators, mice and squirrels around Desolation Sound and in the Nimpkish Valley, British Columbia

Effect	df	χ^2	P
All Predators (all nest-types)			
Region	1	0.15	0.696
Edge proximity	1	8.92	**0.003**
Nest-type	1	13.45	**<0.001**
Edge-type	2	7.64	**0.022**
% Old-growth	1	3.86	**0.049**
% Old-growth × Edge-type	2	5.11	0.078
Avian predators (eggs)			
Region	1	0.02	0.895
Edge proximity	1	0.05	0.832
Edge-type	2	8.02	**0.018**
Edge proximity × Edge-type	2	9.48	**0.009**
% Old-growth	1	4.96	**0.026**
Squirrels (all nest-types)			
Region	1	0.74	0.389
Edge proximity	1	6.29	**0.012**
Nest-type	1	4.76	**0.029**
Edge-type	2	3.12	0.210
% Old-growth	1	0.08	0.780
Mice (all nest-types)			
Region	1	0.08	0.777
Edge proximity	1	2.28	0.131
Nest-type	1	8.49	**0.004**
Edge-type	2	0.00	0.999
% Old-growth	1	0.50	0.481

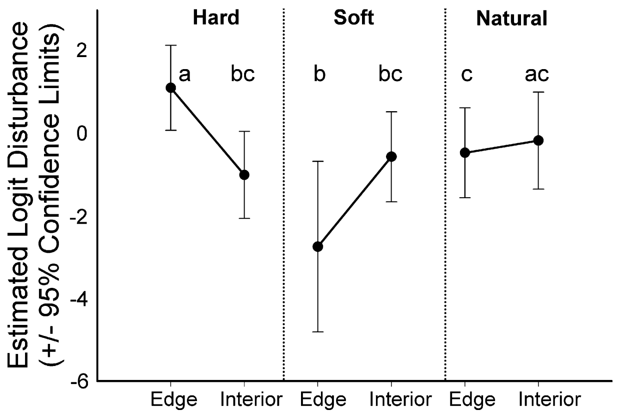

Fig. 5 – Estimated logit egg disturbance by avian predators in edge and interior habitats at hard-, soft- and natural-edged sites. Lower-case letters indicate significance of independent contrasts of the location by edge-type interaction.

4.1. *Predation risk caused by avian nest predators*

Edge effects on the disturbance probability of experimental marbled murrelet nests caused by avian predators do occur, and they appear to differ among edge-types. Avian disturbance risk on artificial eggs was considerably higher at hard edges compared to adjacent interiors, but the opposite was true at soft-edged sites. There was no significant difference in predator disturbances between edge and interior locations at natural sites. This pattern persisted when accounting for the amount of habitat fragmentation in the surrounding landscape, which can also influence variation in edge effects (Donovan et al., 1997; Driscoll and Donovan, 2004). This novel result introduces a temporal component to variation in predation risk in forests fragmented by silviculture. The relatively high predation risk at clearcut edges may decline with time, and the combined impact of anthropogenic edges on murrelet populations will depend on the relative proportions of these different edge-types across the landscape.

Why would edge effects on nest predation differ by edge-type? Nest predation rates in each of these habitats will be directly related to the abundance of predators found there, if we assume that nest predation is incidental (Vigallon and Marzluff, 2005). Nest predation would then be elevated at edges relative to interiors due to a higher density, activity, or diversity of predators found there (Chalfoun et al., 2002). Generalist nest predators may be attracted to high-contrast

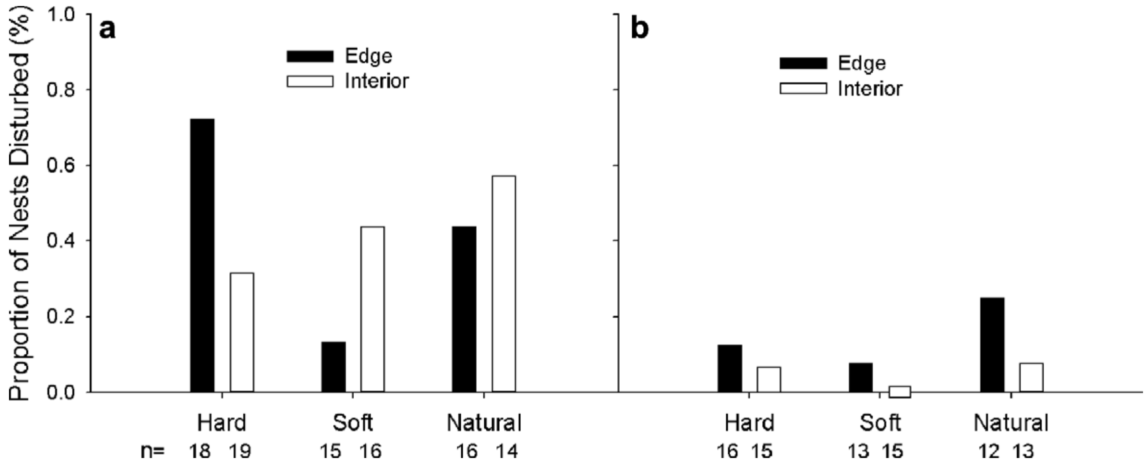

Fig. 4 – Proportion of nests disturbed by avian predators in edge and interior habitats at hard-, soft- and natural-edged sites for artificial eggs (a), and artificial nestlings (b). Data are pooled among Nimpkish Valley, and Desolation Sound, British Columbia.

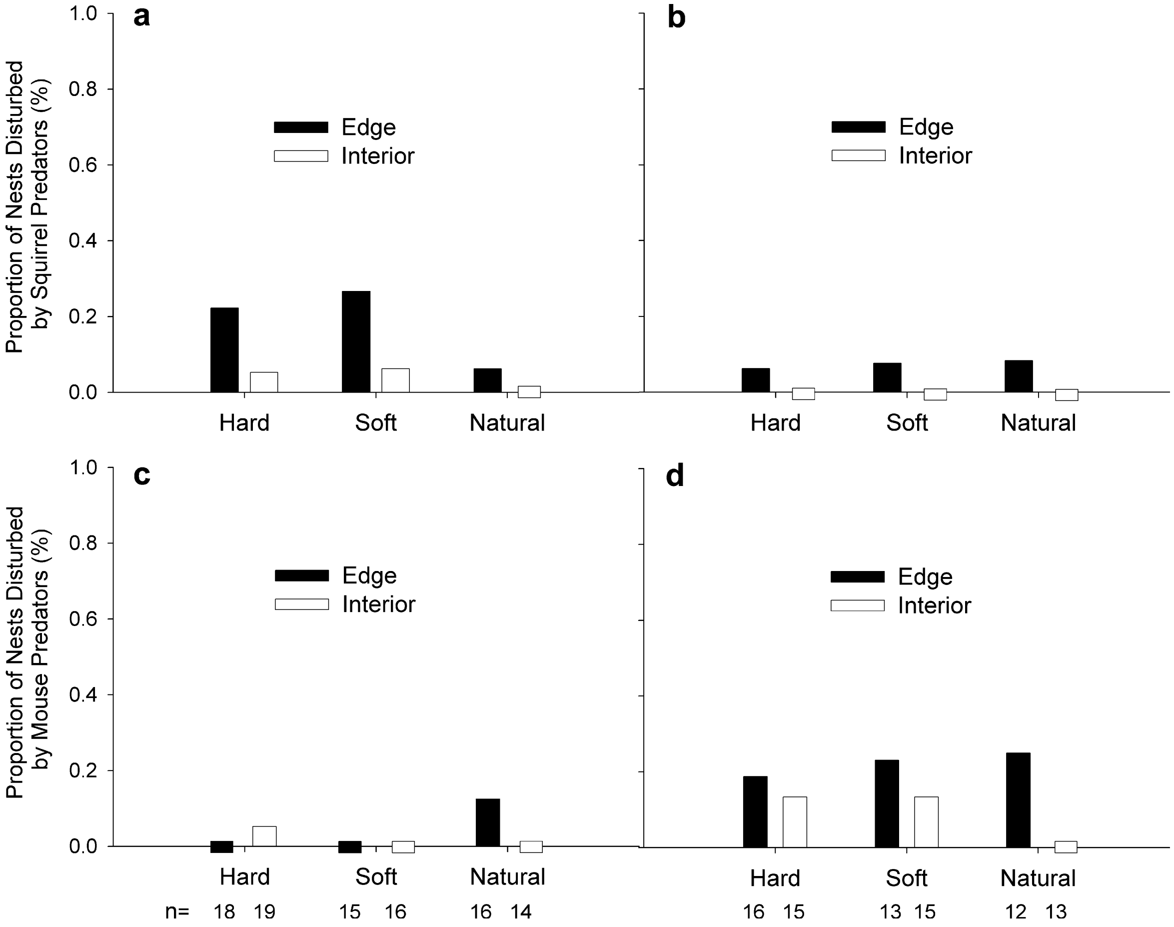

Fig. 6 – Proportion of nests disturbed by squirrels (*Tamiasciurus* spp.) (a,b) and mice (*Peromyscus* spp.) (c,d), in edge and interior habitats at hard-, soft- and natural-edged sites. Data are presented for both artificial eggs (a,c), and artificial nestlings (b,d), and pooled over Nimpkish Valley and Desolation Sound, British Columbia.

edges because these habitats provide access to different resources present in the two bordering patches (i.e., a ‘complementary resource distribution’) (Ries and Sisk, 2004). In our areas, clearcuts that have started to regenerate after the initial effects of harvesting (i.e., hard edges ~5–10 years old) often have a high-availability the berries and other resources (Vitz and Rodewald, 2006). Generalist predators may thus be attracted to the edge of forests where they can simultaneously exploit resources in clearcuts and resources in the adjacent forest, such as nesting habitat or perch sites. In contrast, older regenerating clearcuts (i.e., soft edges ~20–40 years old) have very little understory during the “competitive exclusion stage” of forest development (Franklin et al., 2002), which is characterized by canopy closure and low light levels. Thus, there are few resources available in these forest openings to attract generalist predators. Other studies have found that forests of simple structure (i.e., regenerating, even-aged stands) are associated with small corvid populations (Raphael et al., 2002). Finally, natural edges such as riparian areas may provide access to resources such as aquatic insects that are less abundant in forest interiors (Gray, 1993). However, the sizes of the natural gaps we studied are on a much smaller scale than clearcuts, and therefore natural edges are unlikely to experience as high concentrations of generalist predators relative to the interior. Additional explanations for higher nest predator activity and predation risk at high-contrast edges is that these areas are more likely to be used as travel lines (Andrén, 1995). Also, hard edges may have less nest site cover, and thus be more exposed to visually hunting predators, compared to soft or natural edges which may be more structurally diverse (Ratti and Reese, 1988).

At the landscape scale, egg disturbance by avian predators was higher with larger amounts of old-growth forest. Populations of generalist predators such as Steller’s jays are expected to increase with fragmentation and cause elevated predation risk in more fragmented landscapes (Andrén, 1992; Luginbuhl et al., 2001). In contrast, populations of forest-dependent predators such as squirrels or forest birds may actually decrease as forests are harvested (De Santo and Willson, 2001; Tewksbury et al., 1998). In Nimpkish, predator surveys indicated that landscapes in which gray jays were observed had more old-growth forest compared to those in which they were absent (Malt, 2007). Therefore, gray jays may be responsible for higher predation risk in more intact landscapes. This may also explain the higher disturbance rates observed at natural-edged sites, which had more old-growth forest in the surrounding

Table 2 – Treatment effects for predator detections around Desolation Sound and in the Nimpkish Valley, British Columbia

Effect	df	χ^2	P
Steller's jays			
Desolation sound			
Edge proximity	1	3.87	**0.049**
Edge-type	1	0.79	0.372
Edge proximity × Edge-type	1	4.31	**0.038**
Nimpkish Valley			
Edge proximity	1	0.47	0.491
Edge-type	2	2.39	0.303
Edge proximity × Edge-type	2	0.97	0.616
Gray jays[a]			
Nimpkish Valley			
Edge proximity	1	0.10	0.747
Edge-type	2	3.22	0.200
Edge proximity × Edge-type	2	0.40	0.820
Squirrels			
Desolation sound (*T. douglasii*)			
Edge proximity	1	3.55	**0.060**
Edge-type	1	0.13	0.715
Edge proximity × Edge-type	1	2.20	0.138
Nimpkish Valley (*T. hudsonicus*)			
Edge proximity	1	0.66	0.417
Edge-type	2	1.36	0.508
Edge proximity × Edge-type	2	5.50	**0.064**

[a] There were insufficient observations of gray jays to conduct this analysis in Desolation Sound.

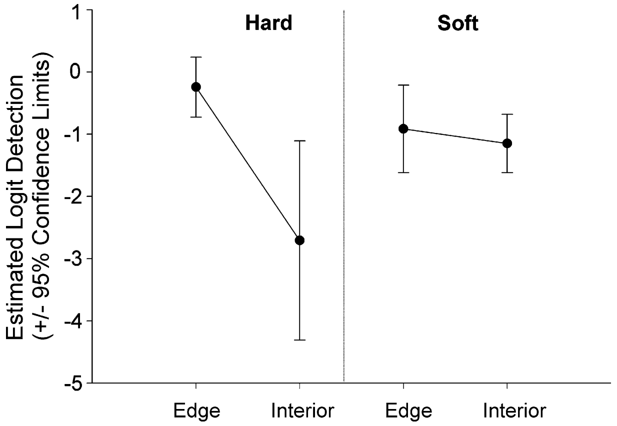

Fig. 7 – Estimated logit detection of Steller's jays at edges and interiors of hard and soft-edged sites around Desolation Sound, British Columbia.

landscapes relative to other sites (J. Malt, unpublished data). Our survey data (see below) support Steller's jays as the potential predator responsible for elevated predation risk at hard edges. Thus, it is conceivable that Steller's jays are responding to resource distributions at the patch scale, whereas gray jays are responding to habitat requirements at the landscape scale. However, while our cameras documented both species of jays disturbing our nests, we were unable to identify the majority of avian disturbances to the species level. Consequently, the relative contribution of different avian predator species in determining patch and landscape-scale disturbance risk is still relatively uncertain. Moreover, while their role as nest predators is suspected, gray jays have never been observed depredating murrelet nests (Nelson, 1997). Understanding the role of forest-dependent predators such as gray jays is essential, as management recommendations will differ widely depending on the strength of their contribution to murrelet nest predation. This will require an increased effort by researchers to definitively determine the identity of predators visiting both real and artificial nests.

4.2. *Corvid predator surveys*

Observations of corvid predators provided by our surveys were generally consistent with the distribution of avian disturbance risk on our experimental nests. At Desolation Sound, there were higher detection rates of Steller's jays at edges relative to interiors of hard-edge sites, but not at soft-edged sites. Because of this pattern, and the fact that Steller's jays consistently used clearcut gaps, we suspect that Steller's jays were responsible for variation in nest disturbance risk among the different edge-types. In contrast, gray jays may be responsible for the overall higher disturbance risk documented in less fragmented landscapes (see above). We observed Steller's jays consistently using clearcut gaps, but gray jays never left the forest edge to enter clearcuts or any other gaps in our study. Indeed, gray jays are rarely observed outside forested stands, even though they disproportionately use forest edges (Ibarzabal and Desrochers, 2004). This is consistent with the concept that generalist predators that move freely between matrix and forest habitat have more opportunity to elevate nest predation at hard edges than predators which are largely confined to forested habitats (Andrén, 1992; Marzluff and Restani, 1999). A behavioural preference for edges by Steller's jays is well supported both by survey evidence (Masselink, 2001), and resource utilization distributions obtained from radio telemetry data (Marzluff et al., 2004). Additionally, foraging observations have documented that berries make up a substantial portion of Steller's jay's diet (Masselink, 2001; Vigallon and Marzluff, 2005).

4.3. *Mammals as potential nest predators*

Because Steller's jays and other corvids are known nest predators of marbled murrelets (Hébert and Golightly, 2007; Nelson, 1997; Nelson and Hamer, 1995; Peery et al., 2004), we assume that our avian disturbance data is the most representative index of relative predation risk. However, if mammals such as squirrels or mice do prey on real murrelet nests, the combined impacts of both predator types could cause different patterns of predation risk compared to those observed from avian predators alone. The combined effects of squirrel, mice, and avian disturbance resulted in elevated predation risk at edges of all three edge-types. Thus, the addition of small mammals to the predator community could strengthen detrimental edge effects at hard sites, and cause detrimental edge effects at soft and natural sites which would not otherwise be present if avian species were the only predators. Hannon and Cotterill (1998) also found that the combination of avian and mammalian predation could cause unique patterns of predation risk.

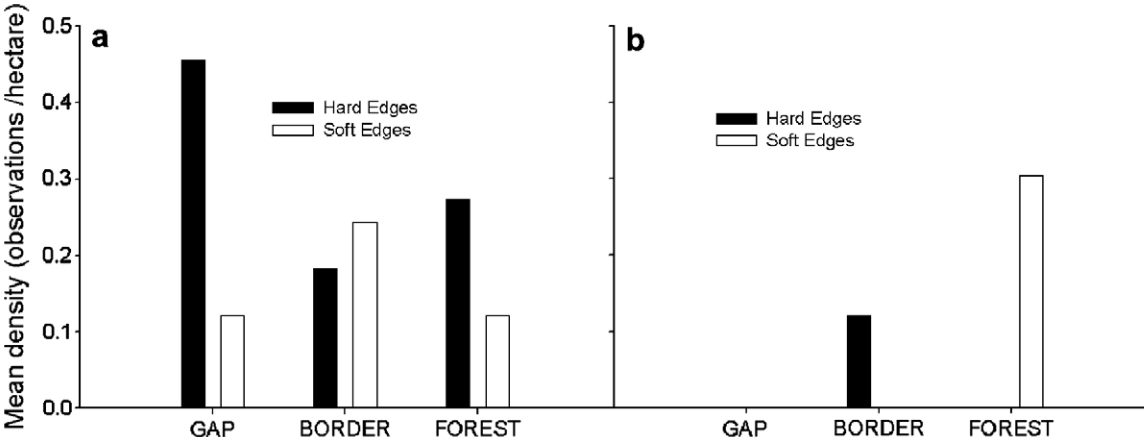

Fig. 8 – Distribution of (a) Steller's jays and (b) gray jay densities in gap, border, and forest margin habitats pooled among Desolation Sound, and the Nimpkish Valley, British Columbia.

In their study, corvid predation on small woodlots was 'compensated' by small mammal predation on large woodlots, resulting in no overall patch-size effects on nest predation. Our finding that small mammals could be responsible for detrimental edge effects are novel, as they typically cause higher predation rates in large fragments and in forest interiors (Hannon and Cotterill, 1998; Tewksbury et al., 1998). Mammalian nest disturbance at edges may be facilitated by less nest site cover (Ratti and Reese, 1988), or use of edges as travel lines (Andrén, 1995). At soft edges, both squirrel abundances and disturbance rates were high, which may be explained by high cone availability from young, regenerating trees.

These results suggest that it is pertinent not to rule out the possibility of small mammals as marbled murrelet nest predators, as their influence has the potential to change patterns of edge effects caused by avian predators. Indeed, squirrels have been shown to have the potential to drive patterns of songbird nest predation in forested landscapes of western North America (Sieving and Willson, 1998; Tewksbury et al., 1998). Also, researchers in Washington have, for the first time, documented a Douglas squirrel visiting a murrelet nest and rolling a recently abandoned egg off the nest platform (Thomas Bloxton, personal communication). In laboratory experiments, northern flying squirrels consistently attempted to prey on both eggs and nestlings, and deermice were observed forcing nestling pigeons off nest branches (Bradley and Marzluff, 2003). Given that squirrels prey on small vertebrates (O'Donoghue, 1994; Sullivan, 1991), and mice are able to kill adult passerines within nest cavities (Guillory, 1987) it is plausible that rodents could depredate a young murrelet nestling. However, they may have more difficulty flushing an adult murrelet, which is much larger than a typical passerine. If this is the case, rodent predation on murrelet eggs may be limited to periods of egg neglect. However, night-time disturbance by nocturnal predators such as mice or flying squirrels may be more likely to cause adults to flush compared to disturbance by diurnal predators such as red squirrels (Bradley and Marzluff, 2003). Nonetheless, mammalian predation of active marbled murrelet nests has yet to be observed. Thus, while mammalian predation remains a distinct possibility, avian predators likely make up a larger component of variation in nest predation risk on the marbled murrelet.

4.4. *Comparison with patterns at real nests*

The aim of this study was to provide an index of relative predation risk that could be taken into consideration when designing reserves of breeding habitat for murrelets. A review of nest success for a sample of real nests from Alaska to California found that closer distances to hard edges were associated with lower nesting success (Nelson and Hamer, 1995), which is consistent with our findings of higher predation risk at hard edges relative to interiors. In our study, patterns of nest fates between sites with different edge-types were not significantly different from those observed at real nests at sites of similar edge-types and elevation. However, the power of this test was low, and patterns would have to be highly divergent between the nest types in order for us to have a reasonable probability of yielding a significant result. Thus, these data are not sufficient for assessing potential differences in patterns between artificial and real nests, and consequently cannot be used to validate or invalidate our approach. Nonetheless, we argue (for reasons listed below) that our approach is a useful tool which provides an index of relative predation risk, in a system where these data are otherwise difficult to obtain. However, it is clear that a larger sample size of comparable real and artificial nests at different edge-types is needed for a more definitive assessment of this approach.

One main factor that may bias patterns of nest fates between real and artificial nests is artificial nests may sample a different subset of the predator community (Thompson and Burhans, 2004). We minimized this potential bias by distinguishing between predator types disturbing our nests, which allowed us to focus on confirmed predators of marbled murrelet nests. Also, one important distinction between our artificial eggs and real murrelet nests is that our nests did not contain an incubating adult (although murrelet chicks are unattended). However, video footage of a Steller's jay and a common raven depredating unattended murrelet eggs suggests that corvid predation may be more common early in the incubation period, when egg neglect is more likely (Hébert and Golightly, 2007). This supports the use of our unattended artificial eggs as realistic visual cues that are attractive to avian nest predators such as Steller's jays.

5. Management implications

Disturbance patterns by avian species, the best documented predators on marbled murrelet nests, paint a complex picture of fragmentation effects. Where generalist predators such as Steller's jays are common, they are likely to cause detrimental edge effects adjacent to recent clearcuts. As replanted forests regenerate, predation risk at these edges appears to decrease back towards, or even below interior levels (Fig. 5). Given such temporally dynamic edge effects, it is inappropriate to evaluate the potential effects of fragmentation on murrelet demographics based on a snapshot in time immediately after harvest. Long-term planning requires assessment of both the proportions and the types of edges in areas of potential nesting habitat. Evaluating the net influence of such effects on the growth rate of murrelet populations requires integrating the combined impacts of different edge-types across the entire landscape over time. Provincial habitat managers and forestry companies need to incorporate spatially explicit timber supply modelling with population modelling to accomplish this goal. This should also include consideration of other potential fragmentation effects, such as reduction in nest-site availability from microclimate edge effects (Malt, 2007), or elevated rates of tree mortality at edges (Chen et al., 1992).

This study has clear implications for the design of productive marbled murrelet reserves and associated harvesting strategies. This study predicts that new, hard edges will have the strongest negative impact on murrelet demography, consistent with current recommendations made by the Canadian Marbled Murrelet Recovery Team (CMMRT, 2003). Therefore, we recommend strategies that minimize the edge/area ratio of murrelet habitat patches, which can be achieved through the establishment of large reserves. This will minimize the local prevalence of hard edge in the short-term, and the amount of interior habitat will increase in the long-term, as these edges regenerate into less dangerous soft edges. However, in highly fragmented landscapes, larger patches of habitat may no longer be available. In these locations, areas of regenerating forest could be usefully maintained around small "cores" of existing old-growth habitat to enhance its safety for nesting murrelets. This will maintain current soft edges and minimize predation risk around existing old-growth patches. This will improve edge habitat quality relatively quickly (i.e., within 20–40 years). In the long term, such areas could be left to allow recruitment of second growth forest into old-growth murrelet habitat, producing larger old-growth patches as the buffers begin to resemble the core. If harvesting is to be done in buffer areas, it should proceed in stages, such that the amount of hard edge adjacent to any particular reserve at any given time is minimized, and the total hard edge habitat is minimized for the landscape.

These recommendations reflect our findings with the best known murrelet nest predators, and could change as we learn more about the relative contributions of other species to marbled murrelet nest failure. Patch level disturbance risk suggested that the addition of squirrels and mice to the predator community could result in edge effects on predation risk at all three edge-types. At the landscape scale, gray jays may actually increase the level of disturbance risk in intact landscapes with more old-growth forest. None of these species have been observed preying on marbled murrelet nests, but they are all suspected predators. Until better information is available, we should utilize our existing knowledge on potential edge effects caused by avian species that are known marbled murrelet nest predators. Using these guidelines to establish reserves where murrelets are known to nest will help to sustain healthy populations of murrelets. This will help to achieve the ultimate goal of maintaining sufficient high quality, low-risk habitat across the landscape to sustain murrelet populations well into the future.

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