Ecological Applications, 19(5), 2009, pp. 1274–1287

Marbled Murrelet nest predation risk in managed forest landscapes: dynamic fragmentation effects at multiple scales

JOSHUA M. MALT[1] AND DAVID B. LANK

Center for Wildlife Ecology, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6 Canada

Abstract. The effects of forest fragmentation on bird populations have been studied primarily as static phenomena. Yet when forests are allowed to regenerate, local edge contrast and landscape matrix composition change with time, and we would expect fragmentation effects to change accordingly. Describing this process is critical for the conservation of avian species sensitive to forest fragmentation, including the Marbled Murrelet (*Brachyramphus marmoratus*), a seabird threatened by ongoing harvest of old-growth forest nesting habitat. We experimentally assessed potential murrelet nest predation probability in four regions of southwestern British Columbia, Canada. We compared the fates of 448 simulated murrelet nests at paired edge and interior treatments, at sites with "hard" edges (recent clearcuts), "soft" edges (regenerating forest), and natural edges (i.e., riparian areas). Motion-sensitive digital nest cameras enabled us to focus on known predators of real nests, and patterns of nest fates did not differ between real and simulated nests. Using information-theoretic model selection (AIC) with the combined data set (116 sites), we assessed effects at patch (~13 ha), landscape (~1700 ha), and regional (~96 000 ha) scales. Nest disturbance probability at hard edges was 2.5 times that of interior sites, but soft edges had less than half the disturbance probability of interiors. There was no edge effect at natural edges. At the landscape scale, overall avian disturbance risk declined by as much as 50% with increasing amounts of regenerating forest in the surrounding matrix. These results indicate that initially negative fragmentation effects decrease as forests regenerate, at both patch and landscape scales. There was no evidence that these patterns differed between regions. Predator surveys suggested that Steller's Jays drive patterns of nest predation risk at the regional scale. Assuming that corvids are the most important predators, larger reserves of habitat will lessen negative hard-edge effects. Smaller reserves should be embedded in a protective matrix of regenerating forest to reduce predation risk at both patch and landscape scales. Our results suggest that dynamic fragmentation effects are generalizable across widespread regions and can be broadly applied to both murrelet management and the conservation of old-growth forest-breeding birds in general.

Key words: Brachyramphus marmoratus; *edge contrast; edge effects; habitat fragmentation; Marbled Murrelet; matrix composition; nest predation; old-growth forest; Steller's Jay; temporal effects.*

INTRODUCTION

Understanding the influence of forest loss and fragmentation on the demography of bird populations is a key focus of conservation ecology. Elucidating mechanisms responsible for fragmentation effects and developing adequate predictive models has proved challenging (Lahiti 2001, George and Dobkin 2002, Thompson et al. 2002, Ries et al. 2004). Our understanding of fragmentation effects on forest bird populations was formed by research conducted in eastern North America and Europe, where agriculture is the primary agent of fragmentation. In this context, avian predator populations and nest predation rates typically increase as forests are converted to agricultural land (Andrén 1992, Robinson et al. 1995, Lloyd et al. 2005), predation rates are often elevated at forest edges ("edge effects"), and smaller patches have higher rates of predation relative to larger patches (Wilcove 1985, Andrén 1994, Paton 1994). The combined effects of these processes can cause reduced reproductive success and negative population growth over broad geographical scales (Lloyd et al. 2005).

In the past decade, researchers across North America have begun to challenge this static view, promoting instead a more complex and dynamic understanding of forest fragmentation effects (Tewksbury et al. 1998, 2006, Marzluff and Restani 1999, George and Dobkin 2002, Gram et al. 2003, Wallendorf et al. 2007). For instance, when silviculture rather than agriculture is the primary agent of fragmentation, harvested areas are left to regenerate, creating dynamic landscapes where edge

Manuscript received 28 March 2008; revised 23 September 2008; accepted 23 October 2008; final version received 26 November 2008. Corresponding Editor: J. M. Marzluff.

[1] Present address: British Columbia Ministry of Environment, 10470-152 Street, Surrey, British Columbia V3R OY3 Canada. E-mail: Joshua.Malt@gov.bc.ca

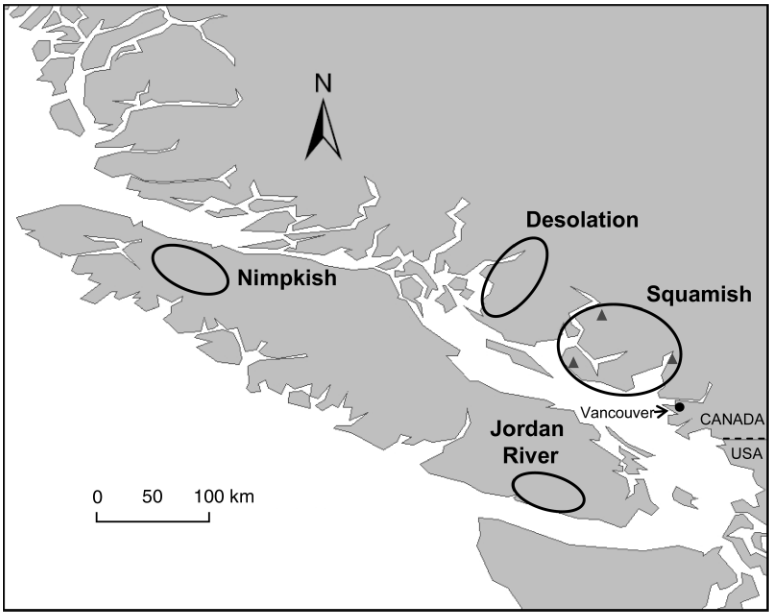

FIG. 1. Locations of the four study regions in southwestern British Columbia, Canada, where simulated Marbled Murrelet nest experiments and predator surveys were conducted (2004–2006). "Squamish" is the aggregation of three smaller study areas (denoted by solid triangles).

contrast and matrix composition change with time. Although detrimental edge effects occur at young clearcuts within a forest matrix (King et al. 1996, Flaspohler et al. 2001, Manolis et al. 2002), there is little information on how such effects change as clearcuts regenerate and edge contrast decreases (Harper et al. 2005, Lindenmayer and Fischer 2006). Moreover, virtually no attention has been paid to how temporal changes at the landscape scale influence the distribution of predation risk. Effective long-term habitat management in such forests requires detailed knowledge of how fragmentation effects change with time and impact populations at multiple scales.

The Marbled Murrelet (*Brachyramphus marmoratus*) is a threatened seabird that has the potential to be strongly influenced by forest fragmentation and edge effects. Murrelets occur along the Pacific coast of western North America, and typically nest on large, mossy branches in old-growth forests (Ralph et al. 1995, McShane et al. 2004). Because nest predation appears to be the major cause of nest failure for murrelets (Nelson and Hamer 1995, McShane et al. 2004, Peery et al. 2004), recovery efforts require information on how forest fragmentation will influence rates of nest predation in forest breeding habitat. Unfortunately, the nature and extent of these effects are unclear. Although there is evidence that murrelets prefer forest edges for easy access to nest sites (Baker et al. 2006, Zharikov et al. 2006), research investigating the effects of edges on nesting success has produced mixed results (Nelson and Hamer 1995, Bradley 2002, Zharikov et al. 2006), and putative effects of fragmentation on habitat selection and reproduction remain controversial (Burger and Page 2007, Zharikov et al. 2007*b*).

A recent study aimed at resolving these issues using simulated nests (Malt and Lank 2007*a*), adopted from Marzluff et al. (2000) and Luginbuhl et al. (2001), suggested that edge effects on nest predation risk can be temporally dynamic in western forests, and recommended the application of these results to management of Marbled Murrelet old-growth forest habitat. These results are also applicable to other forest-breeding birds, because predation by generalist nest predators such as corvids is generally opportunistic (Vigallon and Marzluff 2005). The objectives of this study are (1) to determine if dynamic effects are generalizable across broader geographic regions, (2) to incorporate effects of landscape composition on disturbance risk, and (3) to analyze effects at a regional geographic scale. We replicated the previous study in two additional regions in southwestern British Columbia, Canada, and examined effects at patch, landscape, and regional scales with the combined data set. Predator surveys were conducted to assess correspondence between predator abundance and disturbance risk.

STUDY AREA

This study was conducted in four regions of southwestern British Columbia, Canada, from June to August 2004–2006 (Fig. 1, Table 1). Research was conducted around Desolation Sound in 2004 ("Desolation"; 50°05′ N, 124°40′ W), in the Nimpkish Valley in 2005 ("Nimpkish"; 50°12′ N 126°37′ W), and near the towns of Squamish (49°45′ N, 123°10′ W) and Jordan River

TABLE 1. Comparison of the four study regions in southwestern British Columbia, Canada.

Region	Total area (ha)	Old growth (%)	Clearcuts (%)	Regenerating (%)	Mean patch size (ha)	Site elevation (m)
Nimpkish	165,145	59.0 ± 15.5	20.3 ± 12.6	8.0 ± 9.5	85.9 ± 830.2	621.7 ± 130.6
Squamish	54,830	50.5 ± 13.6	15.9 ± 8.8	11.7 ± 7.0	152.7 ± 51.5	826.5 ± 224.8
Desolation	122,173	37.0 ± 16.4	13.6 ± 7.4	14.8 ± 10.5	99.9 ± 56.9	643.2 ± 290.9
Jordan R.	41,756	47.5 ± 15.9	26.4 ± 9.2	12.8 ± 11.4	135.8 ± 66.9	462.5 ± 184.6

Notes: Values are means ± SD. All values except elevation are calculated from the average of values from 2.3-km buffers surrounding each site. Values for Squamish are the mean of the three study areas within it. Old-growth forest is >140 years old, clearcuts are 0–20 years old, and regenerating forest is 20–40 years old. Site elevation is the mean elevation of sites within each region.

(48°23′ N, 123°56′ W) in 2006. Squamish included three smaller study areas: in mountains northeast of Squamish, in the Elaho Valley, and on the Sechelt Peninsula (Fig. 1). Ecosystems at lower elevations fall within the Coastal Western Hemlock Zone, whereas forests above 900 m fall within the Mountain Hemlock Zone (Klinka et al. 1991). Mean daily temperatures and cumulative precipitation for the summer months (April–August) are 14.8°C and 290 mm for Desolation, 13.4°C and 300 mm for Nimpkish, 14.4°C and 474 mm for Squamish, and 12.3°C and 669 mm for Jordan River. All four regions are managed for industrial forestry, with ongoing old-growth and second-growth harvesting. All regions also contain breeding populations of Marbled Murrelets (Burger 2001, 2002, Bradley 2002). Average landscape characteristics of each region are given in Table 1.

METHODS

Nest experiment.—The design of our simulated nest experiment is given in Malt and Lank (2007*a*, *b*). Briefly, plastic eggs were painted to mimic murrelet eggs and covered in wax to record predator marks, and *Coturnix* quail were skinned and stuffed to mimic murrelet nestlings or an incubating adult (Raphael et al. 2002, Marzluff and Neatherlin 2006). Eggs and skins were stored in bark mulch and handled with rubber gloves to limit transfer of human scent onto simulated nests. Simulated nests were established in old-growth forests >140 years old, with suitable mossy platforms for potential Marbled Murrelet nests sites (Burger and Bahn 2004). "Hard" sites were located adjacent to recent clearcuts (5–11 years old), "Soft" sites were next to regenerating stands (17–39 years old), and "Natural" sites were next to large rivers or avalanche chutes. Within each site, we established an egg and a nestling in separate trees, in "edge" (within 50 m of the forest edge), and "interior" treatments (≥150 m from any edge), for a total of four nests per experimental site. Nests at each site were set up and retrieved as a group, so that exposure time was the same for all four nests within a site (exposure time was 13.7 ± 1.1 days, mean ± SD). We conducted edge vs. interior comparisons within sites using a nested analysis, so variation in exposure time between sites is unlikely to bias effects of edge proximity. Comparisons made between sites (edge type and landscape-scale variables) were also unlikely to be influenced by variation in exposure time, which did not vary systematically with respect to any of these variables (univariate tests; all $P > 0.10$).

We designed our experiment to minimize biases associated with this method, which can occur if simulated and natural nests sample different subsets of the predator community (Thompson and Burhans 2004). We used motion-sensitive nest cameras at 288 nests in three regions of this study (see Malt and Lank 2007*a*, *b*), which allowed us to positively identify predators disturbing our nests and calibrate marks on nests where cameras were not used, and helped to ensure that our inferences were based on disturbance patterns caused by known nest predators of Marbled Murrelet nests. Murrelet nestlings are not attended by adults; thus our simulated nestlings were realistic, and may provide olfactory cues similar to that of a real nestling with its odorous fecal ring. Although our nests with eggs did not include an incubating adult, corvid predation on Marbled Murrelets is thought to be most common during periods of egg neglect (Hébert and Golightly 2007). In some environmental conditions, murrelets may neglect their eggs relatively frequently. Hébert and Golightly (2006) observed irregular incubation patterns in 33% of their radio-marked birds ($n = 27$), for a total of 16 missed days during incubation. Therefore, our exposed eggs, which were placed on suitable Marbled Murrelet nesting platforms, may provide realistic visual cues attractive to avian predators such as Steller's Jays. Comparing depredation patterns of real and simulated nests at Desolation yielded no significant differences, although the power of this test was low ($n = 97$, but few comparable nests were at hard and soft edges; Malt and Lank 2007*a*).

The use of simulated nests is most appropriate when gathering data on the reproductive success of natural nests is difficult (Faaborg 2004, Villard and Part 2004). This is certainly the case for Marbled Murrelets, whose nests are extremely difficult and expensive to find (Binford et al. 1975, Zharikov et al. 2006). The inconsistent distribution of real nests with respect to variables of management interest, such as edge type and matrix composition, further exacerbates the difficulty of obtaining data from real nests. Consequently, we contend that our experiment is the best available method to quantify spatial variation in relative predation risk for the Marbled Murrelet, information that is essential to their effective management and conservation (Raphael et al. 2002). Nonetheless, because improperly calibrated simulated nest studies can result in biased conclusions (Thompson and Burhans 2004), we chose Desolation Sound as one of our study regions because it was possible there to compare experimental results with patterns found in real nests.

Predator surveys.—We surveyed putative Marbled Murrelet predators at 59 point-count transects in forest patches adjacent to hard, soft, and natural edges (33 of which were paired with nest experiment sites). Edge transects were centered along the forest edge to observe predators in both forest and gap habitats, and parallel interior transects were established at least 150 m from the edge. Each transect consisted of between three and six point-count stations. All predators seen or heard during a 10-minute sampling period were recorded. If a predator was observed within a 50-m radius, its distance was recorded using a laser range finder (±1 m), or estimated if it was detected by sound (±10 m). Predators detected beyond 50 m were estimated as 50–100 m, 100–200 m, or >200 m. All transects were surveyed three times, with the survey order of stations reversed each time.

Data analysis

Nest experiment.—We used generalized linear models and information-theoretic model selection to investigate the factors accounting for simulated nest disturbance at multiple scales. Disturbance (yes/no) included any case in which predators caused nest contents to be permanently altered, including beak or teeth marks on eggs, egg removal, or nestling remains that were pecked or torn apart. To allow us to pool sites with and without cameras, we did not score nests as disturbed if predators were documented by cameras, but left no physical signs of their presence (16% of cases; $n = 216$).

Analyses were run separately for avian predators, squirrels, and mice. Avian predators documented by nest cameras (Malt and Lank 2007*a*) included Steller's Jays (*Cyanocitta stelleri*) and Common Ravens (*Corvus corvax*), both known predators of Marbled Murrelet nests (Nelson and Hamer 1995, Peery et al. 2004, Hébert and Golightly 2007), and Gray Jays (*Perisoreus canadensis*), suspected predators (Nelson 1997). We did not classify small beak marks as an avian disturbance because camera images indicated that these were frequently caused by songbirds, unlikely predators of murrelet nests. Mammalian predators included red squirrels (*Tamiasciurus hudsonicus*) on Vancouver Island, Douglas squirrels (*Tamiasciurus douglasii*) and northern flying squirrels (*Glaucomys sabrinus*) on the mainland, and forest deer mice (*Peromyscus* spp.) throughout.

To calculate landscape-scale variables, we compiled 1:20 000 digital map sheets of vegetative land cover polygons (±20 m positional accuracy) from the government of British Columbia and forestry companies that operate within our study regions. We converted these maps into raster format with a cell size of 25 m^2 in ArcGIS 9.1 (ESRI, Redlands, California, USA). We sampled 1660-ha circular landscapes (2.3 km radii) around each nest, and calculated the percentage of different land cover types in each landscape using FRAGSTATS (McGarigal et al. 2002). Distinct patches were defined using the "eight-cell rule"; i.e., all eight cells surrounding the focal cell were considered part of the same patch. Land cover types included percentage clearcuts (0–20 years old), percentage regenerating forest (21–40 years old), percentage immature forest (41–140 years old), and percentage old-growth forest (>141 years old). We calculated an index of fragmentation using a principal component analysis of the variables old-growth edge density (m/ha), old-growth patch density (number of patches/ha), mean old-growth patch size (ha), and percentage old-growth core area (remaining area after removal of 50 m of edge). We also calculated the old-growth patch size in which each nest was located, a potentially important yet controversial variable for Marbled Murrelet management (CMMRT 2003, Burger and Page 2007, Zharikov et al. 2007*b*). We have constrained patch size to a maximum of 314 ha (i.e., 1 km radii), because of the potential for extremely large patches in landscapes with low levels of fragmentation and high connectivity.

We used different combinations of patch, landscape, and region variables to construct an a priori set of 28 candidate models representing different hypotheses of factors influencing variation in nest disturbance risk (see Appendix). These models were classified into three broad categories: (1) no regional effects, but independent effects at patch and landscape scales; (2) independent effects at regional, patch, and landscape scales; and (3) effects at patch and landscape scales that varied by region. Global and null models were also included. All models included nest type (egg/nestling), camera (yes/no), and elevation, all of which are known to influence predation risk or predator abundance (Bradley 2002, Malt and Lank 2007*b*), but were not directly related to the hypotheses we wished to test.

We modeled nest disturbance with generalized linear models using proc GENMOD in SAS 9.1 (SAS Institute 2003), with disturbance as a binomial response variable and a logit-link function. We specified a nested design such that sites were nested within edge types within regions. For each model, we calculated a generalized coefficient of determination (Cox and Snell 1989), adjusted for the ability to achieve a maximum value of 1 (Nagelkerke 1991). Because there was no evidence of overdispersion ($\hat{c}$ = 1.04), we did not make quasi-likelihood adjustments. We calculated Akaike's Information Criterion for small sample sizes (AIC_c) for each model, and ΔAIC_c, the difference in AIC_c between the *i*th model and the model with the lowest AIC_c (Burnham and Anderson 2002). We also calculated Akaike weights ($\acute{\omega}_i$), defined as the likelihood of each model, given the candidate set of models. Finally, we calculated the summed likelihood for selected predictor variables, by summing the Akaike weights of all models in which each variable was included across the entire set of candidate models. For the top models ($\Delta\text{AIC}_c \leq 2$), we present mean estimates ±standard errors for specified effects, converted to predicted probabilities using the following equation:

$$\pi = e^{\eta}/(1 + e^{\eta})$$

where π is the predicted probability, and η is the parameter estimate (Littell et al. 2002).

Comparison to real nests.—Using an information-theoretic approach, we assessed the support for our assumption that murrelet predators responded similarly to real and simulated nests. Under this assumption, we predicted that patterns of relative disturbance risk should be similar with respect to patch and landscape variables for these two categories of nests. To assess this prediction, we compiled a pooled data set of simulated and real nests from Desolation Sound, where both sources of nest data were available ($n = 57$ for real and $n = 55$ for simulated nests). We ran generalized linear models using combinations of our landscape metrics and edge type as predictor variables. We classified edge types of real nests according to whether there was a hard, soft, or natural edge within 250 m of the nest site (Malt and Lank 2007*a*). We were unable to compare effects of edge proximity between the two nest categories, as real nests were not distributed in a manner similar to real nests with respect to distances from edges (hence the impetus for this study). We excluded high-elevation sites (>1100 m) because we did not establish any simulated nests at these elevations. We used "nest fate" as our predicted variable, which was nest disturbance by avian predators for simulated nests, or nest failure during the "mid-chick-rearing period" for real nests (Bradley et al. 2004, Malt and Lank 2007*b*).

Using AIC_c, we compared 70 candidate models under the following hypotheses (see Appendix): (1) Neither *rates* nor *patterns* of nest fates differ between real and simulated nests; (2) absolute *rates* of nest fates differ between real and simulated nests, but *patterns* of nest fates do not; or (3) both *rates* and *patterns* of nest fates differ between real and simulated nests. Under these hypotheses, support for models in either category 1 or 2 will help to validate our approach (differences in rates will not influence the qualitative conclusions that we draw from our simulated nests), whereas support for models in category 3 will not support our use of simulated nests as indices of relative predation risk on real nests.

Predator surveys.—We modeled predator detections with generalized linear models in SAS 9.1, using a Poisson distribution and a log-link function. Our dependent variable was the mean number of detections per station for each survey transect, summed over the three surveys conducted at each site. Models were run separately for Steller's Jays and squirrels (*T. hudsonicus* and *T. douglasii* only). We also infrequently detected Gray Jays and Common Ravens, but we did not include them in our analyses due to low sample sizes. Corvid species were not pooled because of possible differences in detectability between species.

Our candidate set of 21 models was structured similarly to our nest analysis, under the three main categories of hypothesized effects listed previously (see Appendix for details).

To test for detection biases between habitat treatments, we estimated probability using observations of all birds and squirrels combined (there were insufficient detections to estimate this for corvids alone) using the program DISTANCE (Buckland et al. 2001). Probability of detection was significantly different between edges and interiors of all three edge types (edges = 0.25, 95% CI = 0.22–0.29; interiors = 0.46, 95% CI = 0.44–0.48), but was similar between sites when edges and interiors were pooled (hard sites = 0.37, 95% CI = 0.34–0.41; soft sites = 0.40, 95% CI = 0.36–0.43; natural sites = 0.40, 95% CI = 0.36–0.45). Because of this detection bias between edges and interiors, we did not include edge proximity as a predictor variable, and instead limited our assessment to edge type, region, and landscape-scale variables. We controlled for elevation effects (i.e., Bradley 2002) by including this variable in all models. There was no evidence for overdispersion in our most parameterized models ($\hat{c} = 0.76$), so we did not make quasi-likelihood adjustments.

RESULTS

Nest experiment

Pictures of potential predators.—Our nest cameras documented 132 identifiable nest discoveries by potential predators. Avian pictures included 39 Steller's Jays, 9 Gray Jays, 1 Common Raven, 1 Sharp-shinned Hawk, and 1 unidentified owl species. Mammalian pictures included 33 deermice, 17 red squirrels, 15 northern flying squirrels, and 12 Douglas squirrels.

Model selection.—There was strong support for variation in avian disturbance at the patch scale, with edge proximity, edge type, and edge proximity × edge type effects in the two top models ($\Delta\text{AIC}_c \leq 2$; summed likelihoods = 0.97, 0.97, and 0.93, respectively; Table 2). Under the top model, nests in hard edges had 2.5 times the probability of disturbance relative to nests in adjacent interiors (0.24 ± 0.05 vs. 0.10 ± 0.03; all values mean ± SE; Fig. 2a), whereas nests in soft edges were only one-third as likely to be disturbed as nests in adjacent interiors (0.08 ± 0.03 vs. 0.24 ± 0.08), and nests in natural sites showed little difference in avian disturbance risk between edges and interiors (0.19 ± 0.06 vs. 0.16 ± 0.04). Avian disturbance risk also varied at the landscape scale, with a negative effect of percentage of regenerating forest appearing in the top-ranked model ($\beta = -0.041$, CI = −0.070 to −0.012; Table 2). This predicts that avian disturbance risk for an egg at a hard-edged site would decrease by more than half (0.69

TABLE 2. Ranking of generalized linear models predicting the effects of regional-, patch-, and landscape-scale characteristics on simulated disturbance of Marbled Murrelet nests by avian predators, squirrels and mice (*Peromyscus* spp.), in four regions in southwest British Columbia, 2004–2006.

Model	R^2	n	K	LL	AIC_c	ΔAIC_c	ώ
Avian predators							
Region + edge prox. + edge type + edge prox. × edge type + % regenerating	0.36	402	14	−174.04	377.16	0.00	0.76
Squirrels							
Region + edge prox. + edge type + fragmentation	0.16	402	11	−101.93	226.54	0.00	0.58
Mice							
Region + edge prox. + edge type + edge prox. × edge type	0.17	402	12	−138.91	302.63	0.00	0.27
Region + edge prox. + edge type + patch size	0.15	402	11	−140.82	304.32	1.69	0.11
All predators							
Region + edge prox. + edge type + edge prox. × edge type + % regenerating	0.23	402	14	−229.96	489.01	0.00	0.19
Region + edge prox. + edge type + edge prox. × edge type	0.22	402	12	−232.28	489.36	0.35	0.16
Region + edge prox. + edge type + % regenerating	0.21	402	11	−233.49	489.66	0.65	0.14
Region + edge prox. + edge type + edge prox. × edge type + % old growth	0.23	402	14	−230.36	489.80	0.79	0.13
Region + edge prox. + edge type + % old growth	0.21	402	11	−233.89	490.46	1.45	0.09
Region + edge prox. + edge type + fragmentation + fragmentation × region	0.23	402	14	−230.74	490.57	1.56	0.09

Notes: Key to abbreviations: *n*, number of observations; *K*, number of parameters; LL, log likelihood; AIC_c, Akaike's information criterion corrected for small sample size; ΔAIC_c, difference between the *i*th model AIC_c and the minimum AIC_c; ώ, Akaike weight, the likelihood of each model, given the candidate set of models. Models with the lowest ΔAIC_c and the highest ώ are best supported. "Edge prox." is proximity to an edge, "% regenerating" is the percentage of forest 21–40 years old, "% old-growth" is the percentage of forest >141 years old, and "fragmentation" is an index calculated from a principal component analysis of various landscape-scale variables (see *Results: Nest experiment* for details). Only models with $\Delta AIC_c \leq 2$ are presented. All models (except null) include nest type, camera, and elevation.

± 0.13 to 0.30 ± 0.12) when the percentage of regenerating forest is increased from 1% to 40% (Fig. 3). Nests in Desolation and Jordan River are predicted to have three times the probability of disturbance compared to Nimpkish or Squamish under the top model (summed likelihood = 0.97; Fig. 4a). There was little evidence that patch- or landscape-scale effects on disturbance risk varied by region (all $\Delta AIC_c > 4$).

There was strong evidence that squirrel disturbance risk varied at the patch level, with support for models specifying edge proximity and edge type effects (summed likelihoods = 0.89; Table 2). At all three edge types, squirrel disturbance risk was, on average, three times greater at nests in edges (0.09 ± 0.02) compared to adjacent interiors (0.03 ± 0.01; Fig. 2b). Squirrel disturbance risk also varied at the landscape scale, with a positive effect of fragmentation on squirrel disturbance of nests ($\beta = 0.013$, CI = 0.005–0.021, summed likelihood = 0.83). Nests in Squamish and Desolation had 3–5 times the probability of squirrel disturbance relative to nests in Nimpkish or Jordan River under the top model (region summed likelihood = 0.99; Fig. 4b).

Mouse disturbance also varied at the patch scale, with edge proximity, edge type, and edge proximity × edge type all included in the top-ranked model (summed likelihoods = 0.88, 0.88, and 0.42, respectively; Table 2). Mouse disturbance probability was similar between nests in edges and adjacent interiors of hard edges (0.09 ± 0.03 vs. 0.12 ± 0.04) and soft edges (0.08 ± 0.03 vs. 0.07 ± 0.03), but nests in natural edges had over three times the probability of disturbance relative to interiors (0.27 ± 0.07 vs. 0.08 ± 0.04; Fig. 2c). At the landscape scale, there was a positive effect of patch size on mouse disturbance risk in the second-ranked model (summed likelihood = 0.14), although this effect had a 95% confidence interval which included zero. Mouse disturbance risk also varied by region (summed likelihood = 0.99; Table 2). Nests in Jordan River had 2–3 times the probability of mouse disturbance relative to any other region under the top model (Fig. 4c). There was little evidence that patch- or landscape-scale effects on mouse disturbance varied by region (all $\Delta AIC_c > 4$; Table 2).

All four top models predicting disturbance risk by all predators combined included effects of edge proximity, edge type, and edge proximity × edge type (summed likelihoods = 0.97, 0.97, and 0.53, respectively; Table 2). Similar to patterns of avian disturbance risk, nests in hard edges had 1.7 times the probability of disturbance relative to adjacent interiors (0.54 ± 0.05 vs. 0.31 ± 0.06; Fig. 2d), and nests in soft edges had 0.8 times the probability of disturbance relative to adjacent interiors (0.30 ± 0.08 vs. 0.40 ± 0.07). In contrast to patterns caused by avian predators alone, disturbance risk by all predators on nests in natural edges was 1.5 times that of adjacent interiors (0.52 ± 0.08 vs. 0.34 ± 0.06; Fig. 2d).

There was also support for landscape-scale effects on disturbance risk caused by all predators, with a negative effect of percentage regenerating forest ($\beta = -0.026$, CI = −0.051 to −0.002; summed likelihood = 0.32; Table 2). There was also a strong effect of region on disturbance by all predators (summed likelihood = 0.99; Table 2). The probability of disturbance by all predators in Jordan River was 2.2 times that of Nimpkish, similar to trends caused by avian predators alone (Fig. 4d). There was also a moderate level of support for a positive effect of

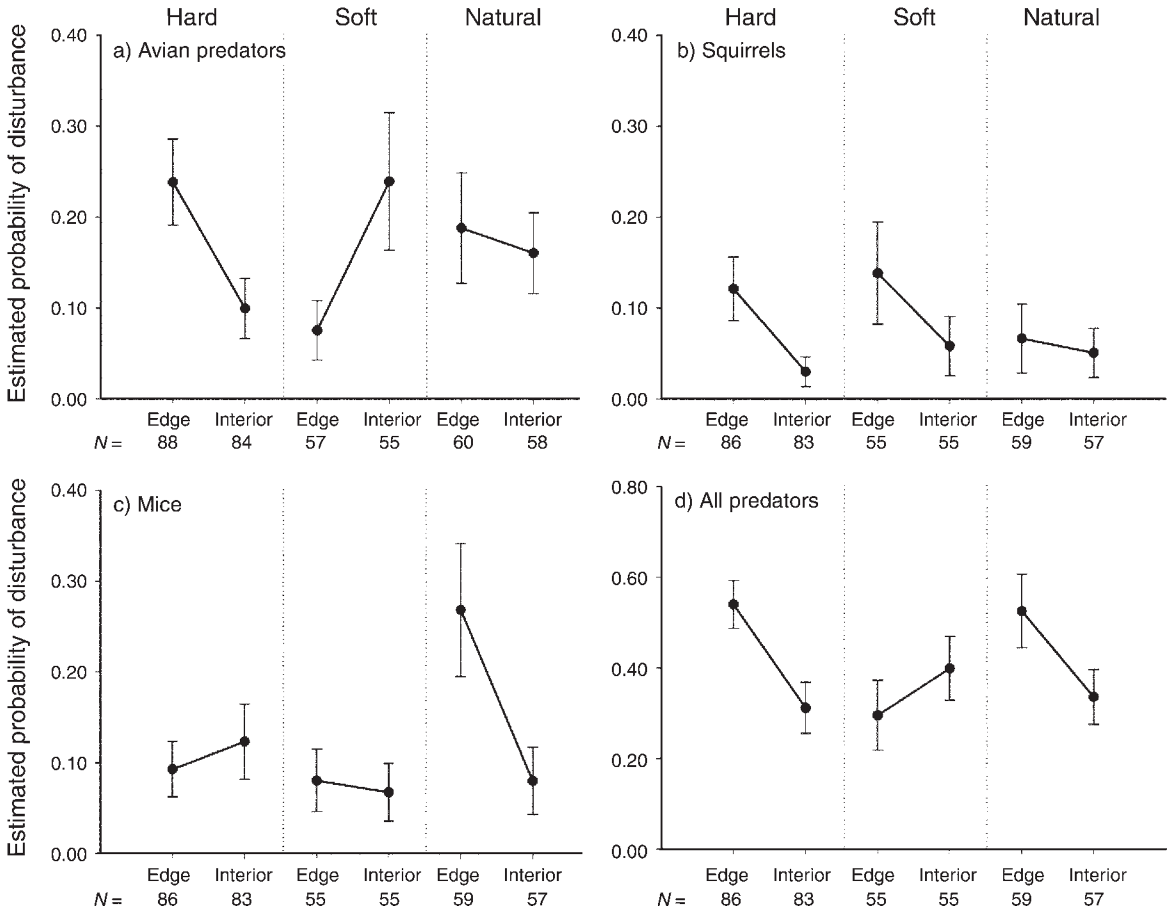

FIG. 2. Estimated probability (mean ± SE) of simulated nest disturbance by (a) avian predators, (b) squirrels, (c) mice, and (d) all predators combined, in edge and interior locations at hard-, soft-, and natural-edged sites. Sample sizes are the total number of simulated nests used to estimate disturbance probability for each treatment. These do not sum to 448 (total number of nests established) because we could not determine predator identity for all simulated nests that were disturbed.

percentage old-growth forest (summed likelihood = 0.23).

Comparison to real nests

There was strong support for differences in absolute rates of nest fates between simulated and real nests (nest category summed likelihood = 0.70), but considerably less support for differences in patterns between the two nest categories (nest category × patch size summed likelihood = 0.15; Table 3). Under the top model, there was a higher probability of nest "failure" for real nests (0.35 ± 0.07) relative to disturbance probability of simulated nests (0.18 ± 0.05). There was support for effects acting similarly on both nest categories, with a negative effect of elevation ($\beta = -0.0019$, CI = −0.0036 to −0.0003; summed likelihood = 0.94), and a positive effect of patch size ($\beta = 0.0113$, CI = 0.0031–0.0195; summed likelihood = 0.74). In contrast, the effect size for variation in patch size effects by nest category had 95% confidence intervals that included zero, suggesting that effects of patch size on nest fates did not differ between real and simulated nests.

Predator surveys

Model selection.—There was strong support for edge type effects on Steller's Jay abundance (summed likelihood = 0.55; Table 4, Fig. 5a). Steller's Jays were more abundant at hard (5.5 ± 2.2 detections/station) and soft sites (4.8 ± 2.0 detections/station) relative to natural sites (2.8 ± 1.2 detections/station) under the top-ranked edge type model. There was strong evidence that Steller's Jay abundance varied at the landscape scale, with a negative effect of the percentage of old-growth forest present in the top model ($\beta = -0.023$, CI = −0.034 to −0.012; summed likelihood = 0.71; Table 3, Fig. 6). There was also support for regional variation in Steller's Jays (summed likelihood = 0.51). Steller's Jays were detected most often in Desolation (6.7 ± 3.4 detections/station, mean ± SE) and Jordan River (4.5 ± 1.3 detections/station) compared to Nimpkish (3.2 ± 1.3 detections/station) or Squamish (3.1 ± 1.4 detections/station).

For squirrels, region and edge type effects received strong support (summed likelihoods = 1.00 and 0.83,

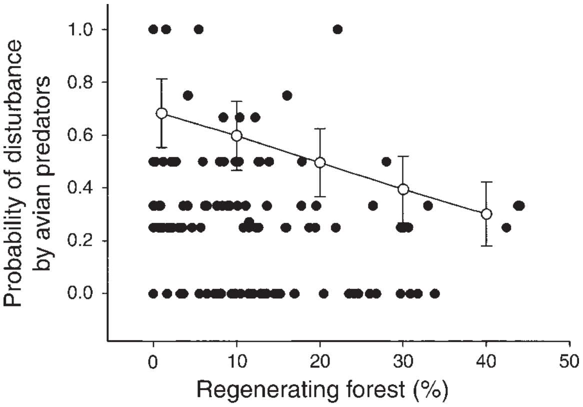

FIG. 3. The effect of regenerating forest (20–40 years old) on avian disturbance risk at the landscape scale. Solid circles are the raw data of the proportion of nests disturbed at each site. Open circles are predicted probabilities of disturbance (mean ± SE) for a nest at a hard edge, controlling for other effects in the best-supported model ($N = 402$). Sample size represents the total number of nests used to calculate the proportion of nests disturbed at each site (solid circles), and the total number of nests used to estimate disturbance probability at each level of regenerating forest percentage (open circles).

respectively; Table 4). Squirrels were more abundant at hard (2.5 ± 0.9 detections/station) and soft sites (2.5 ± 1.0 detections/station) relative to natural sites (1.7 ± 0.5 detections/station; Fig. 5b). Squirrels were also more abundant in Squamish (6.7 ± 2.4 detections/station) and Desolation (4.2 ± 1.7 detections/station) relative to Nimpkish (0.9 ± 0.3 detections/station) or Jordan River (1.0 ± 0.3 detections/station; Fig. 7b). There was also support for a negative effect of percentage old-growth forest on squirrel detections ($\beta = -0.014$, CI = –0.028 to –0.0004; summed likelihood = 0.23). Variation in fragmentation effects by region was also included in the top models (summed likelihood = 0.17 for fragmentation × region), with positive effects of fragmentation in Squamish ($\beta = 0.009$, CI = 0.0004–0.0174), but no effects of fragmentation in Desolation, Jordan River, or Nimpkish (95% confidence intervals included zero).

DISCUSSION

Variation in avian disturbance risk

Our study provides strong evidence that fragmentation effects can be temporally dynamic at multiple scales. At the patch scale, detrimental edge effects

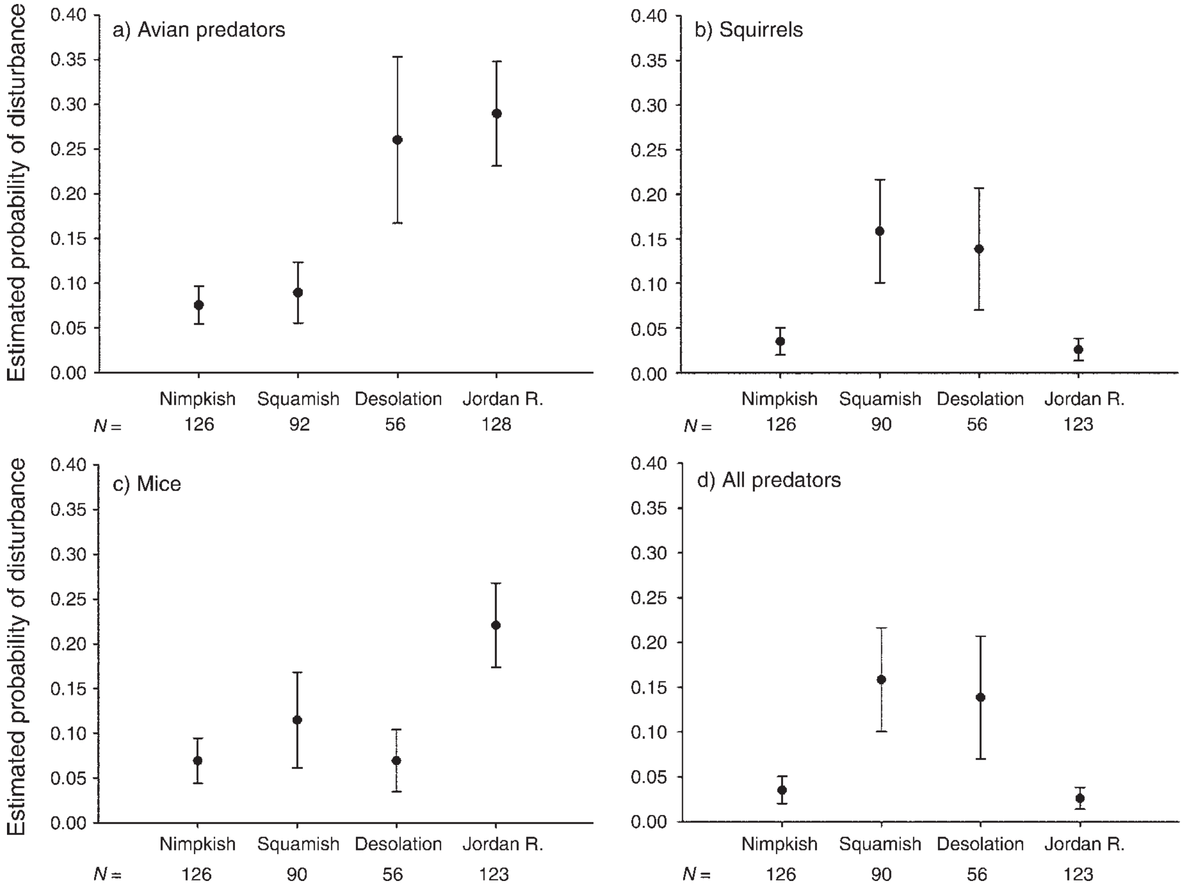

FIG. 4. Estimated probability (mean ± SE) of simulated nest disturbance by (a) avian predators, (b) squirrels, (c) mice, and (d) all predators combined, at the four study regions in southwestern British Columbia. Sample sizes are the total number of simulated nests used to estimate disturbance probability for each treatment.

TABLE 3. Ranking of generalized linear models predicting effects of nest category (real vs. simulated nests), elevation, and regional-, patch-, and landscape-scale characteristics on nest fates of real and simulated nests.

Model	R^2	n	K	LL	AIC_c	ΔAIC_c	$\acute{\omega}$
Elevation + nest category + patch size	0.15	113	4	−59.76	127.89	0.00	0.30
Elevation + patch size	0.11	113	3	−61.53	129.28	1.39	0.15

Note: Only models with $\Delta AIC_c \leq 2$ are presented. See Table 2 for key to abbreviations.

occurred at hard edges, but avian disturbance risk was decreased at soft edges. At the landscape scale, overall avian disturbance declined strongly with increased amounts of regenerating forest in the surrounding matrix. Taken together, these results suggest that negative fragmentation effects will initially occur when forests are harvested, but will decline to baseline or sub-baseline levels as clearcuts regenerate, at both patch and landscape scales. This demonstrates that fragmentation effects in regions managed for industrial forestry are more complex and dynamic than appreciated under the traditional static view of fragmentation conceived in agricultural systems (Andrén 1992, Donovan et al. 1997, Lloyd et al. 2005). To correctly evaluate the potential reproductive quality of forest habitat, managers must consider the cumulative effects of different edge types and variation in matrix composition over the long term. This will help to accurately estimate amounts of quality habitat, and to effectively assess the demographic consequences of different harvesting regimes and habitat protection plans.

Our analysis of all four regions in British Columbia corroborates our original finding of temporally dynamic edge effects for Desolation and Nimpkish (Malt and Lank 2007*b*), and adds the novel result of dynamic effects at the landscape scale. Despite strong regional differences in avian disturbance probability, there was little indication that patterns of patch- or landscape-scale effects on nest disturbance risk differed by region. This indicates that dynamic fragmentation effects can be generalized at least within southern mainland British Columbia and Vancouver Island, and probably to other areas across the Pacific Northwest. Because predation of nests by avian predators such as Steller's Jays is probably opportunistic (Vigallon and Marzluff 2005), these disturbance patterns are relevant both to Marbled Murrelets and to other bird species nesting in old-growth forests.

Our finding of decreased disturbance risk with increasing amounts of regenerating forest at the landscape scale supports the concept that the composition of the matrix is a key factor in determining landscape-scale predation risk (Rodewald and Yahner 2001, Rodewald 2003). Consequently, it may not always be appropriate to use the amount of remaining forest habitat as the sole predictor of landscape-scale predation risk (e.g., Robinson et al. 1995). Instead, assessments of predation risk should consider the importance of the landscape matrix, and how its composition will change with time as patterns of harvest and regrowth continue.

This study suggests that regenerating forest ~20–40 years old will provide relative safety from avian predators at both patch and landscape scales. Regenerating clearcuts of this age typically have simple structure and little understory vegetation, and therefore offer few supplementary resources to attract potential nest predators (Franklin et al. 2002). In contrast, resources at recent clearcuts, such as berries and insects, may supplement resources found in old-growth forest (Vitz and Rodewald 2006), thereby attracting generalist predators to these habitats (Ries and Sisk 2004). Finally, while natural disturbances such as rivers and avalanches may provide some access to insects and other resources (Gray 1993), these supplements are probably lower than those provided by the much larger clearcut areas.

TABLE 4. Ranking of generalized linear models predicting the effects of regional-, patch-, and landscape-scale characteristics on detections of potential nest predators.

Model	R^2	n	K	LL	AIC_c	ΔAIC_c	$\acute{\omega}$
Steller's Jays							
% old growth	0.17	118	3	−101.93	210.06	0.00	0.43
Region + edge type + % old growth	0.26	118	8	−96.99	211.30	1.24	0.23
Squirrels							
Region + edge type + % old growth	0.47	118	8	−71.77	160.85	0.00	0.18
Region + edge type + fragmentation + fragmentation × region	0.54	118	11	−68.23	160.96	0.11	0.17
Region	0.44	118	5	−75.22	160.98	0.13	0.17
Region + edge type + % immature	0.47	118	8	−72.24	161.80	0.95	0.11
Region + edge type + fragmentation	0.46	118	8	−72.32	161.96	1.11	0.11
Region + edge type	0.46	118	7	−73.77	162.56	1.71	0.08

Notes: Only models with $\Delta AIC_c \leq 2$ are presented. All models include elevation. See Table 2 for key to abbreviations.

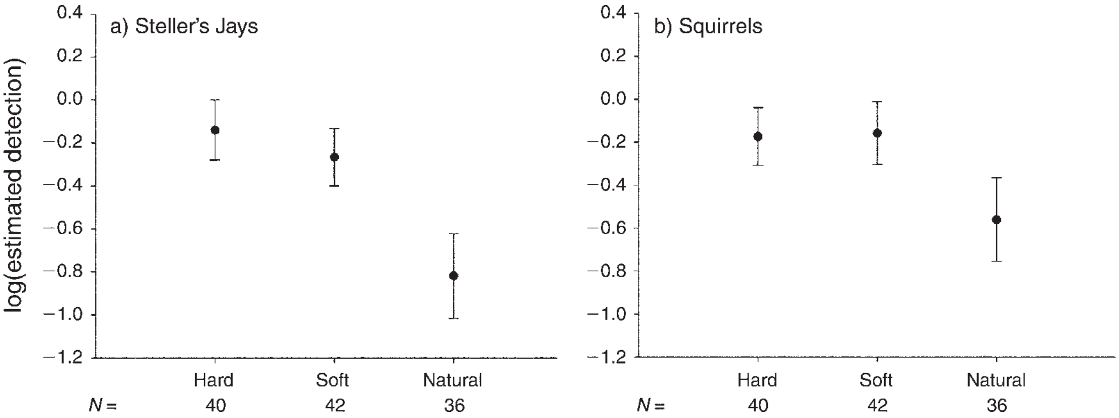

FIG. 5. Detections (mean ± SE) of potential Marbled Murrelet predators along survey transects at hard-, soft-, and natural-edged sites (edge and interiors combined): (a) Steller's Jays and (b) squirrels. Sample sizes are the total number of transects surveyed for each treatment. Prior to log transformation, values were detections per transect per station, as estimated by the best-supported model.

Reduced predation risk adjacent to regenerating forest may also apply to older forests of simple structure (i.e., 80 years of age), which similarly have been shown to have low predation risk and few avian predators (Marzluff et al. 2000).

Comparison to real nests

Although real nests "failed" more often than simulated nests were disturbed, patterns of nest fates between real and simulated nests did not differ. Real and simulated nests responded similarly to predictor variables, with increased disturbance or "failure" with increasing patch size and decreasing elevation. Elevation and patch size have been shown elsewhere to be important variables in predicting habitat selection and reproductive success for real Marbled Murrelets nests (Zharikov et al. 2006, 2007*a*). These results support our assumption that generalist predators respond similarly to both real and simulated nests, and help to validate our approach of using disturbance patterns on simulated nests as an index of relative predation risk for real Marbled Murrelet nests. The lack of support for edge type or matrix composition effects in this analysis is likely because of the relatively limited distribution of real nests with respect to these variables, resulting in low statistical power to compare patterns by nest category. This underscores the utility of simulated nest studies, which allow experimental placement of nests in treatments that have direct management significance, a task that is not possible for real nests.

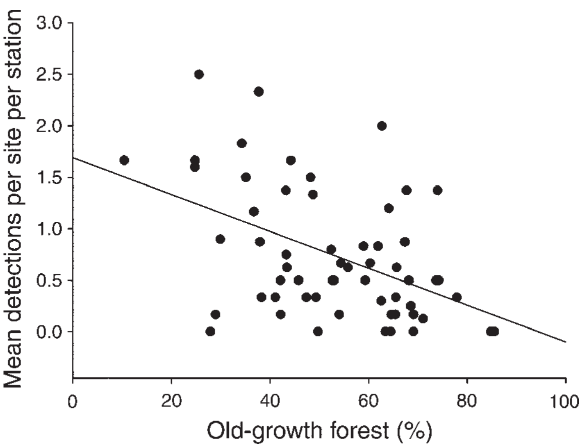

FIG. 6. The influence of the percentage of old-growth forest (>140 years old) on mean detections of Steller's Jays at survey stations in southwestern British Columbia, pooled across the four study regions ($N = 118$ transects).

Distribution of Steller's Jays

Consistent with patterns of avian nest disturbance, Steller's Jay detections were highest in Desolation and Jordan River, and lowest in Nimpkish and Squamish. The close alignment between Steller's Jay abundance and avian disturbance at the regional scale, combined with camera evidence, suggests that Steller's Jays were the dominant avian predator disturbing simulated nests. Steller's Jays may be an important cause of fragmentation effects in western forests because they are generalist predators that respond positively to landscape fragmentation, and preferentially use forest edges (Marzluff and Restani 1999, Masselink 2001, Marzluff et al. 2004, Malt 2007). Moreover, Steller's Jays were the most commonly observed predator in our surveys, and are known predators of Marbled Murrelet nests (Peery et al. 2004, Hébert and Golightly 2007).

At the landscape scale, Steller's Jay abundance increased as old-growth forest cover declined, suggesting that jay densities will increase as landscapes are harvested. This has potential negative implications for both Marbled Murrelets and forest-breeding birds in general, as increases in nest predator densities can increase nest failure and reduce population growth over broad geographic scales (Andrén 1992, Robinson et al.

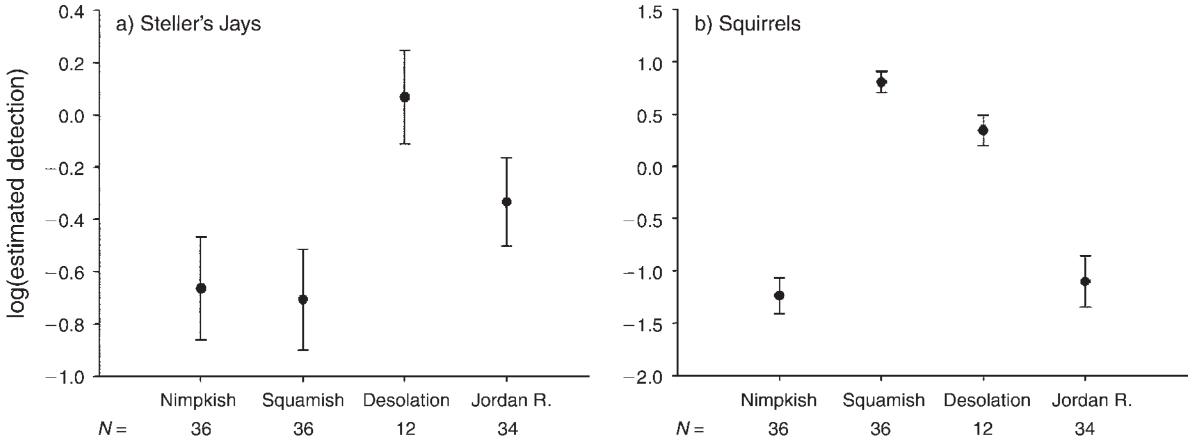

FIG. 7. Detections (mean ± SE) of potential Marbled Murrelet predators along survey transects at the four study regions: (a) Steller's Jays and (b) squirrels. Sample sizes are the total number of transects surveyed for each treatment. Prior to log transformation, values were mean detections per transect per station, as estimated by the best-supported model.

1995, Lloyd et al. 2005). Fragmented landscapes may provide a diversity of patches and edge types that provide an abundance of foraging opportunities for Steller's Jays, including an abundance of berries in young clearcuts (De Santo and Willson 2001, Masselink 2001, Marzluff et al. 2004). In line with our simulated nest results, we expected Steller's Jays to respond negatively to regenerating forest, as observed in a separate road transect study conducted in Nimpkish (Malt 2007), but our analyses did not to support such an effect. Our study may have had less power to separate this effect, as surveys were replicated over one year compared to three years in the Nimpkish study. Alternatively, jay abundance may not be reduced in landscapes with more regenerating forest because new clearcuts that attract these generalist predators are continually created, and thus remain common, irrespective of the amount of regenerating forest (J. Malt, *unpublished data*).

At the patch scale, Steller's Jays were abundant at hard-edged sites and rare at natural-edged sites, consistent with levels of avian disturbance risk observed at these sites. However, Steller's Jays were also abundant at soft-edged sites; this was unexpected, given the low level of avian disturbance risk observed at soft edges. Disturbance risk may be low near regenerating forest despite high abundance of jays because they spend relatively little time foraging there, or because nests are harder to find along this edge type (Ratti and Reese 1988).

The influence of mammalian predators

Similar to avian predators, nest disturbance by all predators was highest in Desolation and Jordan River. This indicates that at the regional scale, the addition of mammalian predators would not substantially alter patterns of predation risk caused by avian predators alone. However, while mammals are unlikely to substantially alter disturbance patterns at hard or soft sites, they have the potential to cause detrimental edge effects at natural sites that would not occur from avian predation alone. Elevated risk at natural edges appeared to be caused by mice, which disturbed nests at natural edges almost three times as often as interiors (cf. Fig. 2c).

Similar to avian patterns, there was support for a negative effect of regenerating forest on disturbance risk by all predators, suggesting that mammalian disturbance patterns will not counteract the beneficial effect of this forest type. However, there was also support for a positive effect of percentage old-growth forest, indicating that the addition of mammalian predators could result in more complex landscape effects compared to avian predators alone. A positive effect of old-growth forest may be driven by mice. In contrast, squirrel abundance was negatively related to old-growth forest at the landscape scale, suggesting that squirrels were positively affected by forest harvesting and fragmentation in this study (Koprowski 2005).

While there is some evidence that these mammals have the ability to depredate murrelet nests (see Malt and Lank 2007*a*), predation on an active Marbled Murrelet nest by mammalian predators has yet to be observed. In contrast, there are multiple observations of Steller's Jays and other corvids depredating Marbled Murrelet nests (Nelson and Hamer 1995, Nelson 1997, Peery et al. 2004, Hébert and Golightly 2007). Moreover, despite the fact that squirrels were more abundant than corvids, avian predators disturbed a larger proportion of our simulated Marbled Murrelet nests. Therefore, while the potential influence of small mammals on murrelet predation risk should not be ignored, avian predators such as Steller's Jays are probably responsible for the majority of nest predation, and therefore warrant the most attention when assessing spatial and temporal variation in predation risk for Marbled Murrelets.

Conclusions and management recommendations

Our results demonstrate that fragmentation effects in western forests managed for industrial forestry can be temporally dynamic at both patch and landscape scales. This is consistent with other research that has found differing and complex patterns in forests managed for timber harvest (Tewksbury et al. 1998, Marzluff and Restani 1999, Chalfoun et al. 2002, George and Dobkin 2002). Our findings provide helpful guidance regarding the trade-off between the size and number of reserves designed to protect breeding habitat for Marbled Murrelets and other forest-breeding birds. In British Columbia, Wildlife Habitat Areas (WHAs) are the primary mechanism used to conserve habitat for forestry-sensitive species. Where possible, we recommend the creation of larger WHAs, which will minimize the amount of habitat exposed to hard edge effects when harvesting occurs, and will also benefit other wildlife species that require large tracts of old-growth forest. When larger patches are not available, we recommend designating many smaller reserves that are embedded in a matrix of regenerating forest. The size of these reserves can then be increased over time if required, by leaving buffers to recruit into old-growth forest habitat. Maintaining a matrix of regenerating forest will have the added benefit of decreasing overall predation risk at the landscape scale.

Our findings will also help to guide the mapping of potential habitat within British Columbia and throughout the range of murrelets. A critical part of this mapping will be an assessment of habitat quality with respect to potential reproductive success. In light of our findings, we recommend that such evaluations (1) distinguish between the values of different edge types, (2) incorporate the influence of the matrix composition at the landscape scale, and (3) forecast how adjusted habitat availability will change over 20–40 year time frames. This will require incorporation of our results into spatially explicit models of murrelet habitat, and periodic updating as areas are harvested and regenerate. This assessment will help to determine if available habitat is of sufficient reproductive quality to sustain viable murrelet populations, and the amount of protection required in each region to meet population targets.

Our management recommendations are based on disturbance patterns caused by the best-known predators of Marbled Murrelets, and may require adaptation as we learn more about the contribution of other predators. While some patterns caused by mammals are divergent from those caused by avian predators alone, most of our management recommendations would still stand, should mammals prove to be important predators. Therefore, recommendations relating to these effects are likely to positively benefit the reproductive success of Marbled Murrelets even if mammals do contribute to nest failure. Acting on the best available information, including both real and simulated nests, will help to guide management strategies that promote healthy populations of forest-breeding birds over the long term.

ACKNOWLEDGMENTS

Thanks to Jeanine Bond and Michael Silvergieter for coordinating research in Squamish and Jordan River, and to all field personnel and tree climbers who aided in data collection. Data for natural nests were gathered under the direction of Fred Cooke. Thanks to the province of British Columbia, Teal Cedar Products, Northwest Squamish Forestry LP, and Elaho Logging for providing access to digital forest cover data. This research was supported by the British Columbia Forest Science Program and Forest Investment Account, B.C. Timber Sales, Western Forest Products, Canadian Forest Products, Timberwest Forest Corporation, Terminal Forest Products, International Forest Products, Island Timberlands LP, Cascadia Forest Products, Weyerhaeuser Canada, an NSERC-IPS scholarship to J. M. Malt, and an NSERC-CRD grant to D. B. Lank.

LITERATURE CITED

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73: 794–804.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

Baker, L. M., M. Z. Peery, E. E. Burkett, S. W. Singer, D. L. Suddjian, and S. R. Beissinger. 2006. Nesting habitat characteristics of the Marbled Murrelet in Central California redwood forests. Journal of Wildlife Management 70:939–946.

Binford, L. C., B. G. Elliott, and S. W. Singer. 1975. Discovery of a nest and the downy young of the Marbled Murrelet. Wilson Bulletin 87:303–440.

Bradley, R. W. 2002. Breeding ecology of radio-marked marbled murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. Thesis. Simon Fraser University, Burnaby, British Columbia, Canada.

Bradley, R. W., F. Cooke, L. W. Lougheed, and W. S. Boyd. 2004. Inferring breeding success through radiotelemetry in the marbled murrelet. Journal of Wildlife Management 68: 318–331.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York, New York, USA.

Burger, A. E. 2001. Using radar to estimate populations and assess habitat associations of marbled murrelets. Journal of Wildlife Management 65:696–715.

Burger, A. E. 2002. Conservation assessment of Marbled Murrelets in British Columbia: a review of the biology, populations, habitat associations, and conservation. Technical Report Series Number 387. Canadian Wildlife Service Pacific and Yukon Region,, British Columbia, Canada.

Burger, A. E., and V. Bahn. 2004. Inland habitat associations of Marbled Murrelets on southwest Vancouver Island, British Columbia. Journal of Field Ornithology 75:53–66.

Burger, A. E., and R. E. Page. 2007. The need for biological realism in habitat modeling: a critique of Zharikov et al. (2006). Landscape Ecology 22:1273–1281.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference. Springer, New York, New York, USA.

Chalfoun, A. D., F. R. Thompson III, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306–318.

CMMRT (Canadian Marbled Murrelet Recovery Team). 2003. Marbled murrelet conservation assessment 2003, Part B:

marbled murrelet recovery team advisory document on conservation and management. Canadian Marbled Murrelet Recovery Team Working Document Number 1. Canadian Wildlife Service, Delta, British Columbia, Canada. ⟨http://www.sfu.ca/biology/wildberg/bertram/mamurt/PartB.pdf⟩

Cox, D. R., and E. J. Snell. 1989. The analysis of binary data. Second edition. Chapman and Hall, London, UK.

De Santo, T. L., and M. F. Willson. 2001. Predator abundance and predation of artificial nests in natural and anthropogenic coniferous forest edges in southeast Alaska. Journal of Field Ornithology 72:136–149.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78:2064–2075.

Faaborg, J. 2004. Truly artificial nest studies. Conservation Biology 18:369–370.

Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield. 2001. Effects of forest edges on ovenbird demography in a managed forest landscape. Conservation Biology 15:173–183.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. Rae Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399–423.

George, T. L., and T. S. Dobkin. 2002. Introduction: habitat fragmentation and western birds. Studies in Avian Biology 25:4–7.

Gram, W. K., P. A. Porneluzi, R. L. Clawson, J. Faaborg, and S. C. Richter. 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. Conservation Biology 17:1324–1337.

Gray, L. J. 1993. Responses of insectivorous birds to emerging aquatic insects in a riparian habitat of a tallgrass prairie stream. American Midland Naturalist 129:288–300.

Harper, K. A., S. E. MacDonald, P. J. Burton, J. Chen, K. D. Brosofske, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh, and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19:768–782.

Hébert, P. N., and R. T. Golightly. 2006. Movements, nesting, and response to anthropogenic disturbance of marbled murrelets (*Brachyramphus marmoratus*) in Redwood National and State Parks, California. Department of Wildlife, Humboldt State University, Arcata, California, USA.

Hébert, P. N., and R. T. Golightly. 2007. Observations of predation by corvids at a Marbled Murrelet nest. Journal of Field Ornithology 78:221–224.

King, D. I., C. R. Griffin, and R. M. Degraaf. 1996. Effects of clearcutting on habitat use and reproductive success of the ovenbird in forested landscapes. Conservation Biology 10:1380–1386.

Klinka, K., J. Pojar, and D. V. Meidinger. 1991. Revision of biogeoclimatic units of coastal British Columbia. Northwest Science 65:32–47.

Koprowski, J. L. 2005. The responsive tree squirrels to fragmentation: a review and synthesis. Animal Conservation 2005:369–376.

Lahiti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365–374.

Lindenmayer, D. B., and J. Fischer. 2006. Landscape change and habitat fragmentation. Island Press, Washington, D.C., USA.

Littell, R. C., W. W. Stroup, and R. J. Freund. 2002. SAS for linear models. SAS Institute, Cary, North Carolina, USA.

Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source–sink dynamics. Ecological Applications 15:1504–1514.

Luginbuhl, J. M., J. M. Marzluff, J. E. Bradley, M. G. Raphael, and D. E. Varland. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. Journal of Field Ornithology 72:556–572.

Malt, J. M. 2007. The influence of habitat fragmentation on Marbled Murrelet (*Brachyramphus marmoratus*) habitat quality in southwestern British Columbia. Thesis. Simon Fraser University, Burnaby, British Columbia, Canada.

Malt, J. M., and D. B. Lank. 2007*a*. Temporal dynamics of edge effects on nest predation risk for the marbled murrelet. Biological Conservation 140:160–173.

Malt, J. M., and D. B. Lank. 2007*b*. Observing wildlife in the crowns of old-growth trees using motion-sensitive cameras. Wildlife Afield 4:43–53.

Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2002. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. Auk 119:955–970.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85:1411–1427.

Marzluff, J. M., and E. A. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. Biological Conservation 130:301–314.

Marzluff, J. M., M. G. Raphael, and R. Sallabanks. 2000. Understanding the effects of forest management on avian species. Wildlife Society Bulletin 28:1132–1143.

Marzluff, J. M., and M. Restani. 1999. The effects of forest fragmentation on avian nest predation. Pages 155–169 *in* J. L. Rochelle, L. A. Lehmann, and J. Wisniewski, editors. Forest fragmentation: wildlife and management implications. Brill Academic, Boston, Massachusetts, USA.

Masselink, N. M. 2001. Responses by Stellar's Jays to forest fragmentation on southwest Vancouver Island and potential impacts on marbled murrelets. Thesis. University of Victoria, Victoria, British Columbia, Canada.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. Fragstats: spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst, Massachusetts, USA. ⟨http://www.umass.edu/landeco/research/fragstats/fragstats.html⟩

McShane, C., et al. 2004. Evaluation report for the 5-year status review of the marbled murrelet in Washington, Oregon and California. EDAW, Seattle, Washington, USA. Prepared for the U.S. Fish and Wildlife Service, Region 1. Portland, Oregon, USA.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Nelson, K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). Number 276 *in* A. Poole and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Nelson, S. K., and T. E. Hamer. 1995. Nest success and the effects of predation on marbled murrelets. Pages 89–98 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. USDA Forest Service, Pacific Southwest Research Station, General Technical Report Number 152, Albany, California, USA.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17–26.

Peery, M. Z., S. R. Beissinger, S. H. Newman, E. B. Burkett, and T. D. Williams. 2004. Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. Conservation Biology 18:1088–1098.

Ralph, C. J., G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt. 1995. Overview of the ecology and conservation of the marbled murrelet in North America. Pages 3–22 *in* C. J. Ralph, G. L. Hunt, Jr., M. G. Raphael, and J. F. Piatt, editors. Ecology and conservation of the marbled murrelet. USDA, Forest Service, Pacific Southwest Research Station, General Technical Report Number 152, Albany, California, USA.

Raphael, M. G., D. Evans Mack, J. M. Marzluff, and J. M. Luginbuhl. 2002. Effects of forest fragmentation on populations of the Marbled Murrelet. Studies in Avian Biology 25: 221–235.

Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. Journal of Wildlife Management 52:484–491.

Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics 35:491–522.

Ries, L., and T. D. Sisk. 2004. A predictive model of edge effects. Ecology 85:2917–2926.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987–1990.

Rodewald, A. D. 2003. The importance of land uses within the landscape matrix. Wildlife Society Bulletin 31:586–592.

Rodewald, A. D., and R. H. Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanisms. Ecology 82:3493–3504.

SAS Institute. 2003. SAS 9.1, proc GENMOD. SAS Institute, Cary, North Carolina, USA.

Tewksbury, J. J., L. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. Ecology 87: 759–768.

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890–2903.

Thompson, F. R., III, and D. E. Burhans. 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. Conservation Biology 18:373–380.

Thompson, F. R., III, T. M. Donovan, R. M. Degraaf, J. Faaborg, and S. K. Robinson. 2002. A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. Studies in Avian Biology 25:332.

Vigallon, S. M., and J. Marzluff. 2005. Is nest predation by Steller's Jays (*Cyanocitta stelleri*) incidental or the result of a specialized search strategy? Auk 122:36–49.

Villard, M.-A., and T. Part. 2004. Don't put all your eggs in real nests: a sequel to Faaborg. Conservation Biology 18: 371–372.

Vitz, A. C., and A. D. Rodewald. 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. Biological Conservation 127:477–486.

Wallendorf, M. J., P. A. Porneluzi, W. K. Gram, R. L. Clawson, and J. Faaborg. 2007. Bird response to clear cutting in Missouri Ozark forests. Journal of Wildlife Management 71:1899–1905.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

Zharikov, Y., D. B. Lank, and F. Cooke. 2007*a*. Influence of landscape structure on breeding distribution and success in a threatened alcid, the marbled murrelet: model transferability and management implications. Journal of Applied Ecology 44:748–759.

Zharikov, Y., D. B. Lank, F. Huettmann, R. W. Bradley, N. Parker, P. P.-W. Yen, L. McFarlane Tranquilla, and F. Cooke. 2006. Habitat selectivity and breeding success in a forest-nesting alcid, the marbled murrelet, in two landscapes with different degrees of forest fragmentation. Landscape Ecology 21:107–120.

Zharikov, Y., D. B. Lank, F. Huettmann, and F. Cooke. 2007*b*. Interpreting habitat distribution models of an elusive species, the marbled murrelets: a response to Burger and Page. Landscape Ecology 22:1283–1289.

APPENDIX

Description of candidate model sets for predicting simulated nest disturbance, predicting predator abundance, and comparing patterns (*Ecological Archives* A019-050-A1).